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Marine Ecology

Biotic and Abiotic Interactions

Edited by Muhammet Türkoğlu,
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MARINE ECOLOGY - BIOTIC AND ABIOTIC INTERACTIONS

Edited by **Muhammet Türkoğlu, Umur Önal**
and **Ali Ismen**

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Edited by Muhammet Türkoğlu, Umur Önal and Ali Ismen

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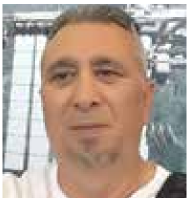
Meet the editors



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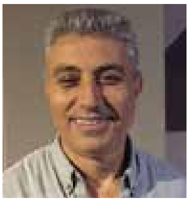

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Preface

The effects of human-induced global climate change, pollution, habitat destruction and overexploitation have taken their toll on the abundance and diversity of all organisms on earth since the beginning of industrial revolution. Particularly, the aquatic environment that covers two thirds of the earth's surface and harbours 80% of all life is being exposed to increasing levels of emissions derived from industrial activities. With a current world population of over 7 billion people, the majority of natural aquatic resources, which are one of the most important food sources on the planet, are being used to the extent that limits their capacity for regeneration. Despite ongoing attempts towards developing strategies for long-term management of aquatic resources all over the world, in many cases, efforts have met with limited success. Thus, the sustainable use of aquatic resources has become a very important reality considering a projected human population of 11 billion by the year 2100. With this reality in mind, the purpose of this book is to shed more light on the field of marine ecology by emphasizing the diversity of aquatic life on earth and its importance both as part of a balanced ecosystem and as part of critical source of food on earth.

The book covers important findings, discussions and reviews on a variety of subjects on environmental and competitive interactions of marine organisms at different trophic levels and their effects on the productivity, dynamics and structure of marine ecosystems around the world. Each chapter focuses on a specific case in the field of marine ecology. The book includes chapters on plankton ecology and productivity, fisheries ecology and fisheries management of different species, sustainable fishing practices, role of micro-algae in renewable energy production and authigenic carbonate and methane formation at deep sea. These chapters also present an opportunity to review the recent status of some important marine ecosystems and processes. We hope that researchers, academicians and students as well as experts and professionals working in the field of marine ecology will benefit from the presented, specific case studies.

As the editor and co-editors of the book, we are grateful to all authors for their contributions and the editorial staff who helped to accomplish this project.

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Section 1

Introduction to Marine Ecology

Chapter 1

Introductory Chapter: Marine Ecology—Biotic and Abiotic Interactions

Muhammet Turkoglu, Umur Onal and Ali Ismen

Additional information is available at the end of the chapter

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1. Introduction

The vastness of the oceans, the largest continuous environment on earth, has provided a safe shelter for about 20% of all living organisms until the beginning of industrial revolution. Since then, this once invincible environment has been under constant change and destruction, the results of which now are threatening all life forms on earth. With this rate of destruction, we are possibly losing our window of opportunity to protect aquatic biodiversity and learn how aquatic organisms evolved to find ways for adapting life in water. Marine Ecology, in its simplest terms the study of marine organisms and their habitats, continues to provide fundamental information to better understand the effects of global changes on eco-biology of organisms.

In many cases, marine ecology is more intricate than the relatively simple study of a specific living organism or its environment due to various intra and inter specific interactions between other organisms and due to effects of numerous factors on a particular environment. Therefore, marine ecologists rather than concentrating on a single species, organism or habitat, often find themselves simultaneously focusing on interactions between organisms and the effects of environmental factors on these organisms. During the last decades, the complex nature of these interactions is being exacerbated due to the changes induced by a variety of factors such as increased ocean temperatures, dramatic changes in weather patterns, ocean acidification, melting of glaciers, and pollution. The effects of these man-made factors are occurring in a relatively shorter time scale and in many cases are beyond the capacity of organisms to adapt to these deviations. Throughout the world, new conditions are often manifesting themselves as loss of biodiversity accompanied with other major changes such as shifts in distributions of many species toward higher latitudes and changes in timing of life cycle events.

One of the most important factors that influence life in the oceans is temperature. Temperature affects the rate biological processes proceed. In general, the metabolic rate of poikilotherms doubles with a 10°C increase in temperature. However, much less temperature differences are enough to trigger changes in weather patterns that have worldwide effects. Global mean temperatures are now 0.50°C higher than it was since 1960s [1]. A typical example of increased global temperatures is the El Niño phenomenon that occurs periodically over the Pacific Ocean and characterized by increased temperatures of surface waters. It is well established that increased water temperatures results in weakened currents and less rain in the Southern Ocean which in turn, results in dramatic changes in physicochemical and biological conditions. Fluctuation in nutrient concentrations is the most notable factor that altered circulation pattern effects. Such interruptions of nutrient fluxes have important consequences on the primary production which in turn affect fish stocks. The relationship between fluctuations in the abundance of anchovy in the Southeast Pacific Ocean [2] and the periodicity of El Niño has been established. The fluctuations in the abundance of these commercial fish stocks have important socioeconomic consequences due to enormous yields which fluctuated between 3 and 8 million tons during the last decade [3].

Another important parameter that influences life in the ocean is CO_2 levels in the atmosphere. As a result of global industrialization, CO_2 levels have increased over the last 100 years. Higher CO_2 levels in the atmosphere forces this gas into the surface waters which results in lower pH values. As a result, the mean pH value of the earth's oceans has fallen by 0.10 pH units [4]. Insignificant as it may seem, this drop corresponds roughly to 30% increase in the concentration of hydrogen ions. Organisms such as corals, bivalves, and calcareous plankton are susceptible to reduced pH levels as acidic conditions dissolve calcium carbonate. Therefore, the disruption of the calcification process may have serious consequences due to its potential to negatively affected calcareous species in the food web.

Another important factor that is becoming increasingly influential on all life on earth is the increasing rate of melting of ice in polar regions. The melting of ice causes a series of events including, sea level rise, freshening of seawater, and reduction in the speeds of major current systems in the oceans. While sea level rise will have catastrophic effects mainly for human habitation in coastal areas, freshening of seawater and its effect on currents will potentially affect all life forms due to the changes in global climate.

Although the effects of individual stressors are relatively well studied, there are limited data on compounded effects of multiple stressors [5]. Stressors such as temperature, salinity, UV, hypoxia, acidification, and pollution may be simultaneously experienced by marine organisms, especially in coastal areas. In many cases, organisms exposed to multiple stressors exhibit reduced resistance. For example, many coral reefs are simultaneously suffering from increasing temperatures, acidification, diseases, and silting [6]. Toxicity of pollutants has been shown to increase salinity or temperature stress [7]. This is particularly important because even if strict fisheries regulations become effective for a particular overexploited area in a heavily modified coastal system, expected recovery of stocks may not be possible due to increased vulnerability of early life stages to multiple stressors relative to juvenile or adult stages.

While it is relatively easier to observe the effects of altered physicochemical conditions over larger scales, the effects of pollution and over exploitation are relatively easier to observe in smaller scales. A typical example is the Black Sea which is closed basins with limited water exchange rates and relatively smaller surface areas. Between the period 1950 and 1970, the Turkish Black Sea fishery was characterized by larger predators such as tuna, swordfish, and bonito. Following a decrease in top predators as a result of increased fishing pressure, industrial fishing operations concentrated on small pelagic fish species such as anchovy and sardine. Therefore, after 1970s, there was a major shift in commercial fishing operations [8]. Due to the developments in industrial fishing methods, a steady increase was observed until late 1980s with a maximum of 600,000 tons in 1988. This increase in fish productivity was correlated with a 10-fold increase in phytoplankton biomass in the 1980s compared to that of 2–3 g m^{-2} in 1960s [8]. This dramatic increase was due to increased inputs of agricultural nitrates and phosphates into the Black Sea through rivers and the subsequent mixing of these nutrients in the water column. As a result of this enrichment, primary production was able to support—despite increased fishing pressure—high yields of small pelagic fishes for almost a decade before a major collapse observed after late 1980s. For example, in 1990, anchovy landings were only 66,000 tons, which was less than ¼ of that in 1988. This collapse in small pelagic fisheries was also experienced by other nations bordering the Black Sea and as a result, total landings dropped down to 200 thousand tons in 1991, compared to that of 900 thousand tons in 1988. It is believed that overexploitation was not the only factor for the simultaneous collapse in small pelagic fish stocks experienced throughout the Black Sea. The lobate ctenophore, *Mnemiopsis leidyi* A. Agassiz, 1865, which was reported for the first time in the Black Sea in 1982, had reached a biomass of up to 1 kg m^{-3} by the end of 1980s [9]. Its broad tolerance to a variety of physicochemical conditions, rapid growth and voracious appetite for zooplankton, fish eggs, and larvae has contributed significantly to the collapse of Black Sea fisheries. After 1990s, although reductions in concentrations of agricultural nutrients in the Black Sea and the introduction of *Beroe ovata* Mayer, 1912, the pink comb jellyfish that feeds on *M. leidyi* tipped the balance in favor of recovery of small pelagic fish stocks, we are still miles away from the point of sustainable management of fisheries in the Black Sea. Yet, even over a relatively smaller scale and with no diverse multinational management strategies that can limit the success of management programs, fisheries in the Sea of Marmara is almost an identical episode of what was experienced in the Black Sea. For example, a comparison of catch rates in 1990 and 2015 showed a 1.50- to 130-fold decrease in all reported demersal species [10] as a result of eutrophic conditions as indicated by increased periodicity and intensity of phytoplankton blooms [11–14], introduction of *M. leidyi* in early 1990s [15], continuous heavy fishing pressure and lack of effective management strategies. Recovery efforts for these two interconnected ecosystems will require a multidisciplinary approach to rebuild fishery resources. Unfortunately, decreasing fish stocks is not only an issue of semi-closed basins with highly populated areas. It is estimated that globally up to 63% of fish stocks are in need of rebuilding [16] and efforts toward rebuilding diversity will meet major challenges considering human-induced and global-scale impacts.

This book includes contributions from a variety of ecosystems around the world and presents comprehensive information on the present or recent status of a diverse group of marine organisms including primary producers, zooplanktons, shellfish, crustaceans, and fishes. The valuable information gathered from researchers all around the world will not only explain the current status of these organisms and the environment in which they thrive but it will also provide a reference for future studies to help compare how predicted or unpredicted changes will affect these organisms in coming years.

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Section 2

Marine Biogeochemistry

Chapter 2

Geo-Biological Coupling of Authigenic Carbonate Formation and Autotrophic Faunal Colonization at Deep-Sea Methane Seeps I: Geo-Biological Settings

Takeshi Naganuma

Additional information is available at the end of the chapter

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Abstract

Methane (CH_4) in sub-seafloor sediment is generated both biologically and non-biologically from organic and inorganic sources. A major part of the sub-seafloor methane is oxidized before leakage via "anaerobic oxidation of methane" (AOM) in the subsurface. The AOM-survivor methane, which is relatively minor part of the subsurface methane, leaches to the overlying water column and is eventually subject to thorough anaerobic and aerobic oxidation in the water column. The AOM with sulfate results in the generation of carbon dioxide and sulfide; the former (CO_2) is incorporated into authigenic carbonate and autotrophic biomass, and the autotrophy is energetically driven by oxidation of the latter (H_2S). These processes are typically observed at focused sites that are generally known as "methane seeps" or hydrocarbon seeps, or occasionally called as cold seeps in comparison with hydrothermal vents. Methane seeps are typically formed in passive and active continental margins, occasionally with unique features such as exposed methane hydrates, mud volcanoes, asphalt volcanoes, salt diapirs, and brine pools. Accordingly, authigenic carbonates and unique biological communities are shaped at respective methane seeps. This chapter overviews geological and biological setting for the formation of methane seeps associated with unique landscapes of carbonates and biomes.

Keywords: hydrocarbon seep, cold seep, gas hydrate, methanogenesis, chemoautotrophy, thiotrophy, methanotrophy, anaerobic oxidation of methane (AOM), sulfate–methane transition zone (SMTZ)

1. Introduction

In the view of planetary carbon cycling, the carbon-based terrestrial "life" can be seen as an intermediate between the oxidized end (carbon dioxide, CO_2) and the reduced end (methane,

CH_4), as depicted as "organics" (simplistically expressed as CH_2O) in **Figure 1**. The Earth's carbon cycling is largely driven by about 120,000 terawatts (TW) of the Solar radiation reaching the Earth's surface,[1] and about 47 TW [1] from the Earth's internal heat, which is due equally to the decay of radioactive isotopes such as uranium-238 (^{238}U), thorium-232 (^{232}Th), and potassium-40 (^{40}K) in crust and mantle [2] and to the residual heat from planetary accretion during proto-Earth formation [3].

The life is not only intermediate but also transient, and the life is otherwise dissipated, maintained by continuous supplies of oxidizing and reducing powers, simplistically represented by oxygen O and hydrogen H, respectively, after "split of water" [4]. The surface of the red planet, or red rust planet, Mars, is oxidized by Solar ultraviolet (UV) radiation due to lack of the UV-absorbing ozone layer in its thin atmosphere, resulting in the predominance (>95% v/v) of CO_2 in the Martian atmosphere [5]. The gas giant Jupiter's

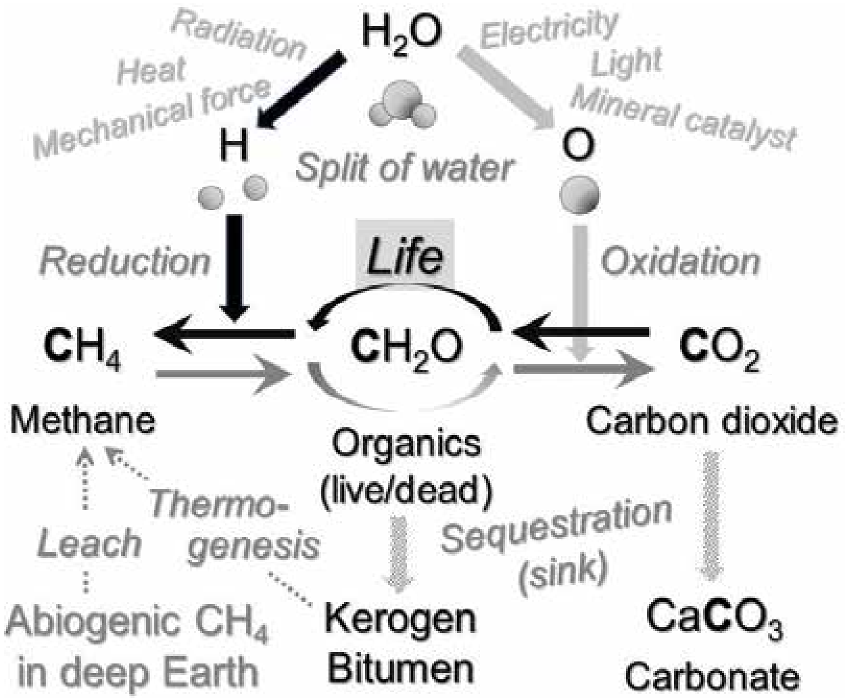

Figure 1. Schematized general view of carbon dynamics with reference to "life" and life-supporting "split of water" as the source of redox potential. Life is interpreted as the intermediate carbon compounds between the reduced end (CH_4) and oxidized end (CO_2) of the carbon cycle, and the cycle is driven by the supply of redox power from the split of water in a variety of manners.

---

[1] The canonical Solar constant (1365.4 ± 1.3 W m^{-2}) established in the 1990s or the recent Solar minimum value (1360.8 ± 0.5 W m^{-2}) [85], multiplied by the Earth's cross-sectional area (1.274×10^{14} m^2) and the Earth's albedo (0.297 ± 0.005) [86], yields about 1.2×10^{17} W (120,000 TW) of the Solar energy (light and heat) reaching the Earth's surface.

atmosphere consists of 89.8% H_2, 10.2% He, 0.3% CH_4, and others (CO_2 not detected) with some uncertainties [6]. By contrast, the Earth's atmosphere contains CO_2 (400 ppm) and CH_4 (1.7 ppm) simultaneously [7], which is regarded as a biomarker combination of a habitable planet [8]. In this context, the detection of CH_4 (mean 0.69 ppb) in the Martian atmosphere and its variability (up to 7.2 ppb) [9] was exciting enough to ignite a search-for-life on Mars. Then, the emerging problem is where and how methane is supplied on the fully oxidized Mars [10] as well as on the Earth whose surface is also oxidized by photosynthetically generated O_2. Deep-sea methane seepage is one of the methane sources to the Earth's surface, although its significance on a long time scale is yet to be fully understood.

While methane cycling occurs within the range of the global carbon cycling in atmosphere, hydrosphere (manly ocean), lithosphere (defined as crust and mantle in this chapter), and biosphere, it is also indirectly connected to the carbon sequestration or sink into lithosphere (**Figure 1**). That is, part of methane is to be sequestrated for long term, probably more than millennium long, separation from biogeochemical cycling, and such indirect sequestration occurs via the formation of authigenic carbonate at methane seeps commonly, typically, and unequivocally.

Carbonate in lithosphere represents a vast majority of the Earth's carbon pool (**Figure 2**). Most of the carbonate was precipitated in "early ocean," resulting in sequestration or removal of abundant CO_2 from "early atmosphere" that was likely similar to the modern Venus atmosphere consisting of about 8.9 MPa, or 89 bar, CO_2 (96.5% of total 9.2 MPa) [11], compared

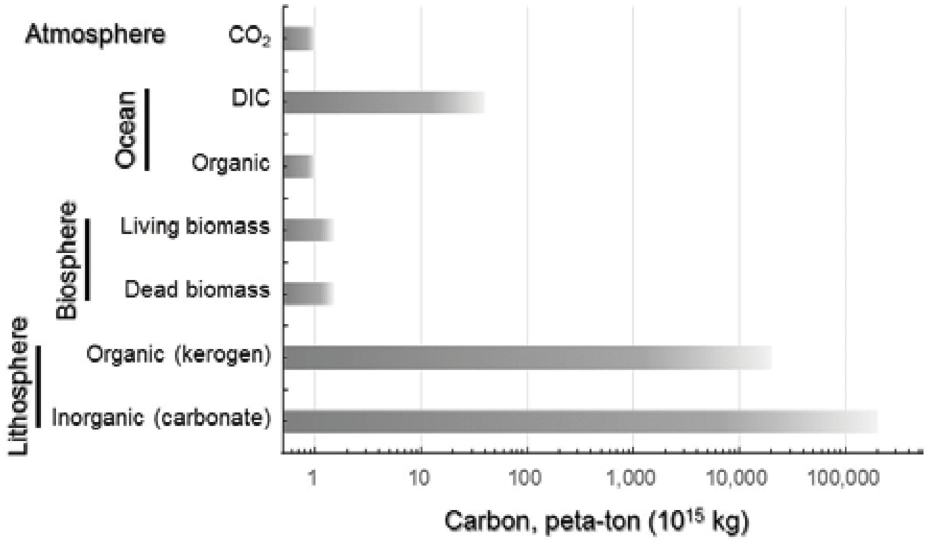

Figure 2. Global carbon pools in various forms. Most of global carbon has already been sequestrated in the lithospheric kerogen (organic) and carbonate (inorganic). Methane seeps still contribute to the sequestration via authigenic carbonate formation. Abbreviation: dissolved inorganic carbon (DIC).

with the modern Earth atmosphere of about 40 Pa CO_2 (0.04% of total 0.1 MPa) [12]. The mass sequestration of CO_2 during "early Earth" era is currently recognized as the vast estimate of sedimentary carbonate in the lithosphere. Modern carbonate formation at methane seeps corresponds only to a tiny fraction of the already-sequestrated carbonate in the past; however, it is an ongoing process, and there should be much more seeps yet to be found. That is, the more seeps are found, the more importance will be taken into account.

This chapter provides an overview of methane seeps in the deep sea that harbor and sustain unique biological communities depending not only on small amounts of photosynthetic primary production (photoautotrophy) transported from the shallow euphotic zone to the deep aphotic zone but mainly on *in situ* chemosynthetic primary production (chemoautotrophy). The latter production utilizes methane directly or exploits methane-derived biogeochemical products such as sulfide (H_2S, HS^-) via "anaerobic oxidation of methane" (AOM). As AOM produces CO_2 and bicarbonate (HCO_3^-), it facilitates the formation of authigenic carbonate, which should be connected to the colonization of chemoautotrophic organisms. The carbonate formation and faunal colonization are so connected that they often form "conglomerates" during their concomitant growths [13]. Geological and biological settings for the geo-bio connection are exemplified.

2. Geo-biological backgrounds of methane seeps

Methane seeps are also referred as cold seeps and hydrocarbon seeps. Seeping fluids are not literally cold; the fluids are geothermally warmed and often slightly warmer than ambient waters. They are called "cold" only to indicate that the seep fluids are relatively colder than the hydrothermal vent fluids that may reach >300°C. Seeping fluids sometimes contain hydrocarbons other than methane, for example, ethane, propane, and even petroleum. However, methane occupies a vast majority of the leaked hydrocarbon components, provides a material source for authigenic carbonate formation, and sustains exotic biological communities like oases in the deep sea that depend on methane and methane-derived productions. For these reasons, this chapter uses the term "methane seep" prior to others.

2.1. Origin and generation of methane

In relation to human life, methane is a colorless and odorless gas and is lighter than air. It is nontoxic but may be suffocative in confined rooms. Methane is also an important greenhouse gas but is naturally generated and emitted; its emission is not intentionally controllable by human efforts, which is different from the case of CO_2.

From a cosmological viewpoint, methane is regarded as a primordial molecule, as it occurs in the interstellar medium despite its low abundance, that is, 1–4% of carbon monoxide (CO) abundance [14]. Viewed from astrochemistry, methane was generated primordially and is still being generated foremost in interstellar molecular clouds. This astrochemical methane, in turn, can be seen as a part of original matter for the formation of proto-Solar system disk and thus of proto-Earth. Earth was formed through accretion of planetesimals [3], a large amount of methane would have been brought into the Earth during the accretion (and is still being exogenously delivered by meteorites and possibly by comets) and may still remain in Earth's interior as primordial methane and other hydrocarbons [15].

Besides the residual of primordial methane, methane is newly generated and regenerated by various processes through the carbon cycling of the Earth. Both biological (biotic, biogenic) and non-biological (abiotic, abiogenic) processes are involved in the generation of methane, also known as methanogenesis. In addition, both organic and inorganic matters serve as the starting materials for methanogenesis.

Therefore, methanogenesis pathways are roughly sorted into four categories: biotic of organic origin (fermentation), biotic of inorganic origin (CO_2 respiration), abiotic of organic origin (thermogenesis), and abiotic of inorganic origin (geothermal version of the Fischer-Tropsch process or Sabatier reaction) due to geothermalism and magmatism in crystalline rocks, as schematically outlined in **Figure 3** that employs the stable isotope signatures known as $\delta^{13}C$ and δ^2H (δD) of CH_4 as described later (adapted from [16] with δ values for atmospheric CH_4 from [17]). Generally, δ values are indicative of origins or sources, while the differences in the δ values, also known as "Δ" values, may reflect pathways/processes of methane generation/consumption or oxidation [18, 19].

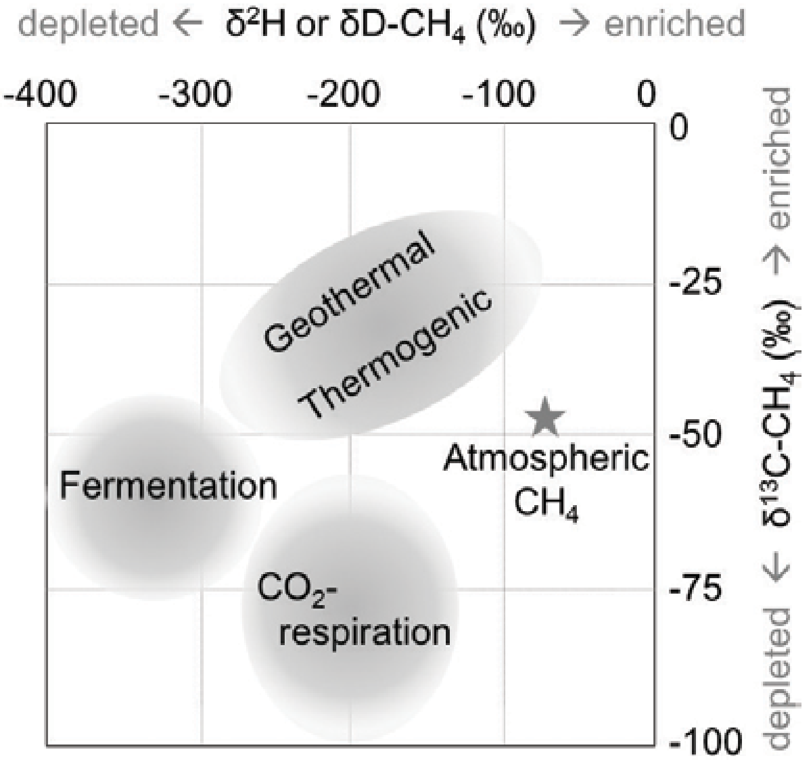

Figure 3. δ^2H (δD)-$\delta^{13}C$ diagram of methane of different origins. Biogenic methane from organic matter (by fermentation) and from inorganic CO_2 (by CO_2-respiration) is distinguishable from abiogenic methane from organic matter (by thermogenesis) and from CO_2 (by geothermal Sabatier reaction).

The origins and generation pathways, as well as consumption (oxidation) and conversion pathways, of methane stated earlier are summarized in **Figure 4**. In addition, the sources of H_2 for both biogenic and abiogenic CO_2 reduction (methanogenesis of inorganic origin) can be both organic and inorganic; the former (organic-derived H_2) can be from fermentative and/or thermogenic degradation of organic matter, while the latter could be of magmatic origin as well as "split of water." Those H_2 sources and generation mechanisms are listed in **Table 1**, including "mechanical" split-of-water along geological (lithological) faults [20], as well as briefly referred in **Figure 1**.

2.1.1. Biogenic methane of organic origin: fermentation

Methane in common originates biologically, especially microbiologically, from anaerobic degradation, or fermentation, of organic matter, during which oxygen (O) is removed

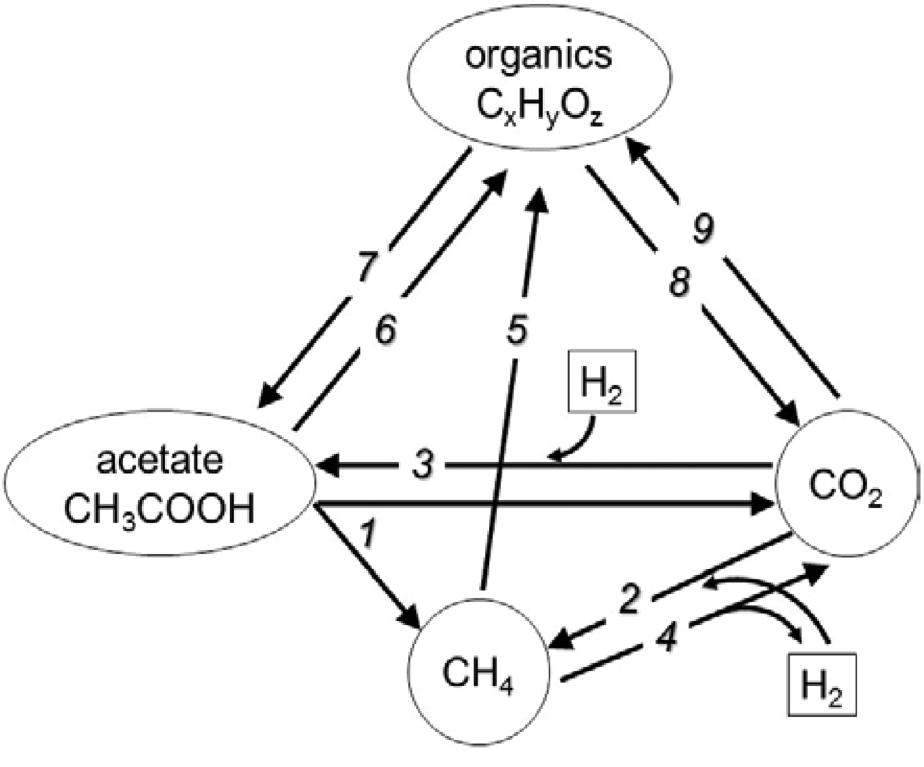

Figure 4. Schematized geochemical dynamics of methane. Origins and fates of methane are depicted with reference to key compounds (acetate and other organic matters as well as CO_2) and key paths including addition and removal of H_2. Aerobic oxidations and inputs/outputs of water are not shown. Acetate is a source of methane via syntrophic acetoclastic methanogenesis (path 1) and serves as a reductant for anaerobic sulfate reduction (as part of path 8). H_2 used for Sabatier-type methanogenesis (path 2) and autotrophic acetogenesis (path 3) is of both biotic and abiotic origins. Anaerobic oxidation of methane, or AOM, occurs via reverse methanogenesis (path 4) and with nitrate (as part of path 8). Methane and acetate are used for biosynthesis of organics (paths 5 and 6), and organics are degraded via acetate-fermentation (path 7) and anaerobic oxidations with sulfate, nitrate, Fe^{3+}, etc. (path 8). Organics may be produced via chemoautotrophy (path 9).

Biogenic	Split-of-water by light (via light reaction of photosynthesis)
	Fermentation (including syntrophic H_2 generation)
	Reverse methanogenesis ($CH_4 + H_2O \rightarrow CO_2 + H_2$)
Abiogenic	Thermogenic supply (via diagenesis of sedimentary organic matter)
	Magmatic supply (from crystalline rocks of crust and mantle)
	Lithologic split-of-water (e.g., serpentinization)
	Split-of-water by radiation
	Split-of-water by light (ultraviolet)
	Mechanical split-of-water (e.g., fault-activated H_2 generation [20])

Split-of-water ($H_2O \rightarrow H_2 + O_2$) serves as the major source of H_2 in the Earth's biosphere. Split-of-water by electricity is not included, as it mostly occurs artificially. H_2 generation via reverse methanogenesis during anaerobic oxidation of methane (AOM) is involved. Abiogenic magmatic H_2 may include primordial H_2 and H_2 from split-of-water by heat, as well as thermogenic H_2 migrated from sedimentary organic matter in diagenesis.

Table 1. Biogenic and abiogenic sources of H_2.

from organic matter (simplistically CH_2O). Fermentation is a common process and occurs in various environs. An example is enteric fermentation in gastrointestinal tracts of cellulose-digesting termites and ruminants such as cattle and sheep. It is often said that flatus of termites and ructus (belching) of cows contain methane and thus contribute to global warming, as methane is a 28–36 times more powerful greenhouse gas than CO_2 [21], and flatus of non-cellulose-digesting animals such as dog and man would contain small amounts (usually <1%) of methane, too.

Anaerobic digestion of food wastes generates methane as "biogas" [22], and anaerobic degradation of organic burials in landfills, paddy fields, and swamps also release methane as expressed in Japanese as "*sho-ki*" meaning "marsh gas." These processes and environs are mostly biological rather than geological and based on anaerobic breakdown of preexisting organic matter. In this context, methane is regarded as a by-product, an end product or an "exhaust," in contrast to our customary concept of methane as a "fuel," in such a name as biogas, from the viewpoint of human interest. In any connotation, biogenic methane produced in the past is an important component of natural gas as part of fossil fuels.

2.1.2. Biogenic methane of inorganic origin: CO_2 respiration

Biogenic methane is also produced from the inorganic carbon dioxide, CO_2, through the process that is regarded as essentially the reduction of CO_2 with H_2, that is, $CO_2 + 2H_2 \rightarrow CH_4 + H_2O$. This process can be seen as a biological version of the Fischer-Tropsch process or Sabatier reaction and is based on the biological process known as Wood-Ljungdahl pathway or reductive acetyl CoA pathway (discussed later). The "reduction of CO_2 with H_2" is also viewed as the "oxidation of H_2 with CO_2," which is biologically translated as a type of anaerobic respiration (oxidation) using CO_2 as an oxidant instead of O_2 in aerobic H_2 oxidation [23].

This view of CO_2 respiration recalls the microbiological processes of "sulfate reduction," as portrayed simplistically $SO_4^{2-} + H_2 \rightarrow HS^- + H_2O$, in the other name of "sulfate respiration"; and "nitrate reduction," $NO_3^- + H_2 \rightarrow\rightarrow\rightarrow\rightarrow N_2 + H_2O$ (again simplistic but consisting of four reductions), in the other name of "nitrate respiration" (as well as denitrification).

In both reduction and respiration views, CH_4 can be regarded as a by-product or an "exhaust," in contrast to our usual notion of methane as a "fuel," as described earlier. More important (than the reduction and respiration views) is the source of H_2 that is noted as molecular hydrogen (H_2) or a reductant (electron donor, $H^+ + e^-$). Although degrading organic matter may serve as a source of H_2 or "$H^+ + e^-$," this type of methanogenesis should be regarded as "of inorganic origin," because "inorganic origin" only points the source of carbon (CO_2), not the source of H_2 that can be organic or inorganic (**Table 1** and discussed later). For example, methane is produced by a consortium of propionate-degrading and acetogenic bacteria and methanogenic archaea. Although details are yet to be fully elucidated, propionic acid (CH_3CH_2COOH) is degraded by syntrophic propionate-degrading and acetogenic bacteria (simplistically $CH_3CH_2COOH + H_2O \rightarrow CH_3COOH + CO_2 + H_2$), and methane is produced via both "acetoclastic" ($CH_3COOH \rightarrow CH_4 + CO_2$) and "hydrogenotrophic" methanogenesis ($CO_2 + H_2 \rightarrow CH_4 + H_2O$) [24]. The former (acetoclastic methanogenesis) is taken as "of organic origin" and the latter (hydrogenotrophic methanogenesis, i.e., CO_2 respiration) is regarded as "of inorganic origin," although they comprise a one amalgamated process. Certainly, fractions of CO_2 and H_2 may truly be inorganic of primordially magmatic origin; however, not a small part of H and C atoms would have experienced "organic" phases through biogeochemical cycling, and distinction between organic and inorganic origins may only be a matter of immediate origins.

In addition, a recent experiment showed that CO (not CO_2) and H_2 are used for an energetic metabolism by symbionts of the gutless marine oligochaete worm *Olavius algarvensis* Giere, Erséus & Stuhlmacher, 1998, that inhabit non-vent, non-seep but anaerobic seagrass-degrading sediment rich in CO and H_2 [25]. This process may lead to a realistic biological version of the Fischer-Tropsch synthesis where CO rather than CO_2 plays the major role.

2.1.3. Abiogenic methane of organic origin: Thermogenesis

Methanogenesis based on anaerobic organic breakdown also occurs in abiogenic (non-biological) pathways. This process is geological rather than biological and occurs by elevated heat and pressure against the organic matter buried in deep subsurface strata. The thermal breakdown of organic burials is known as "thermogenesis," as part of geological "diagenesis," in contrast to "biogenesis" that occurs in the so-called physiological temperatures, except activities of hyperthermophilic methanogenic microorganisms (not many known species of archaea [26]) at focused geothermal sites. Formation temperatures for biogenic and thermogenic methane are generally estimated to be <50°C and 157–221°C, respectively [27], which roughly reflects formation depths, that is, shallower and deeper zones of methane generation, respectively.

During diagenetic thermogenesis of methane, carbon and hydrogen isotopes are subject to discrimination or fractionation, as occurring in biological methanogenesis, too; however, the tendency and degree of isotope fractionations are distinguishable between geological and biological methanogenesis, as described in detail in Section 3.1. Generally, thermogenic methane has more ^{13}C and ^{2}H (deuterium, D), that is, higher (enriched) $\delta^{13}C$ and δD, respectively, than biogenic methane does [28].

2.1.4. Abiogenic methane of inorganic origin: Fischer-Tropsch process or Sabatier reaction

Regardless of bio-/thermogenesis, generated methane is of organic origin. Adding to the organic origin, methanogenesis of inorganic origin occurs, too, via both biological and geological pathways to reduce carbon dioxide CO_2 with molecular hydrogen H_2 to yield methane (CH_4) and water (H_2O). The bulk reaction is essentially the same as the oxidation of H_2 with CO_2, which corresponds to anaerobic respiration using CO_2 as the oxidant (instead of aerobic respiration using O_2 as the oxidant) in a biological context. Translated into a geological context, the biological CO_2 respiration corresponds to the geothermally activated Fischer-Tropsch synthesis and Sabatier reaction [29] that are well-known processes in chemical engineering.

A similar but different pathway in terms of carbon origin ($CaCO_3$ instead of CO_2) has been assumed for abiotic methanogenesis in deeper subsurface, that is, mantle of the Earth [30, 31], though the size of methane pool in mantle has not been well estimated. In a Fischer-Tropsch or a Sabatier manner, $CaCO_3$ as well as CO_2 is reduced with H_2 to generate geothermal CH_4. In addition, serpentinization, a water-rock interaction, has been regarded as the major H_2-supplying and thus CH_4-supplying process [32]. However, as the reaction rate of serpentinization was recently revised to be slower than previously expected [33], its significance in abiotic methanogenesis has been subject to reevaluation [29, 34].

2.2. Migration and seepage of methane

A certain part of methane that originates in the subsurface will immediately migrate upward and reach the surfaces of land and seafloor by diffusion, buoyancy, compression (due to geo-pressure and subduction-driven tectonic squeeze), or geo-/hydrothermal circulations. Methane may also migrate and will be pooled for some while (in a geological sense) in the subsurface reservoirs and then eventually migrates upward and reaches the surfaces by pressurization as well as diffusion and buoyancy. Leakage of subsurface methane takes the forms of seepage, venting, eruption, and so on [35]. These forms represent processes and pathways, and this section focuses more on the latter (pathways), employing the ideas and terminologies presumed for possible methane seepage on Mars [10], despite some differences.

Subsurface methane may reach surface via “macro-seepage,” “mini-seepage,” and “micro-seepage.” The “macro” implies seeps that are visible by naked eyes, and the “mini” and “micro” are invisible by naked eyes and visible with the help of specified instruments. The distinction is just like the one between macroorganisms and microorganisms; the latter can only be seen under microscopes. Regarding their activities and fluxes, compared with hydrothermal vents that vigorously eject high flux of “focused flow,” macro-seeps are less active but efflux similarly focused flow of seep fluids via subsurface channels. Bubbles of methane gas are occasionally visible in water columns, for example, in the Eel River Basin, off northern

California [36] and Northern Gulf of Mexico [37]. By contrast, mini- and micro-seeps slowly exhale "diffuse flow" through sediment matrix pores, and the slow flows are virtually invisible and not readily detectable.

Macro-seepage is formed by subsurface channels often connected with faults. Macro-seepage is also associated with the decomposition of subsurface methane hydrates, or gas hydrates, triggered by shifts in subsurface temperature and pressure due to high-rate sedimentation, subsurface movement such as salt diapirs and mud volcanoes (described later), and so on [38]. The number of seafloor macro-seeps is unknown but may exceed the number of terrestrial macro-seeps, that is, >10,000 [39].

Mini-seepage occurs around macro-seeps, in the transition zone from focused flow centers to zero seepage surroundings. By contrast, micro-seepage is independent of macro-seepage and probably caused mainly by ongoing microbial methanogenesis in sediments. It is the least intensive, compared with the most intensive hydrothermal venting and less intensive macro-seepage. However, micro-seeps likely occur the most extensively on land and seafloor, as implied by the power law probability distributions or "size frequency distributions" [40]. The total flux of mini-seepage is unknown; however, due to their globally widespread occurrence, it is estimated that micro-seeps exhale up to 25 million tons year^{-1} of methane, which is a little more than the estimate from macro-seeps [39].

Despite the importance of invisible seeps in global methane flux, this chapter focuses on visible seeps to comprehend geo-biological landscape of methane seepage more easily. The landscape is characterized by both biological communities and authigenic carbonate rock and will lead to a concept of methane seeps not only as oases for biological communities but also as immediate sinks of leaking methane.

2.3. Anaerobic oxidation of methane (AOM)

Methane is flammable, in a day-to-day sense, in air with oxygen, and the combustion is, in a chemical sense, termed oxidation (of methane with oxygen, and reduction of oxygen with methane). Likewise, methane is oxidizable in water without oxygen but with, for example, sulfate and nitrate. This non-aerobic (non-O_2-involved) process is viewed as "anaerobic oxidation of methane" in a chemical sense, which has been often abbreviated as "AOM" in a geochemical tradition, because AOM has tremendous importance in geochemistry and also in geo-biology, as well as in resource geology and global climate change issues.

AOM was first reported in 1976 from the unusually anoxic water columns and sediments of the Cariaco Trench [41]. Methane should have been leaked from the anoxic "trench" to the overlying oxic water column and oxidized aerobically; however, it seemed that methane is already oxidized in the anoxic trench. There was a clear negative correlation between the concentrations of methane and sulfate (as well as a positive correlation between the concentrations of methane and sulfide).

Then, AOM with sulfate was postulated and formulated as thermodynamically possible as $CH_4 + SO4^{2-} + 2H^+ \rightarrow H_2S + CO_2 + 2H_2O$, $\Delta G^0 = -22.8$ kcal mole^{-1}. Geologically, the "site" or "zone" where this reaction occurs was questioned, and it is now recognized as the "sulfate-methane transition zone" (SMTZ) at relatively shallow depths in sediments (not in water column). That is, SMTZ is the zone of AOM. On the other hand, microorganisms that perform AOM, that is, co-metabolism of methane oxidation and sulfate reduction, were prefigured, but no such microbes were known at that time.

Once prefigured, microbiologists started isolating and obtaining pure cultures of the corresponding microorganisms; however, it has not yet been successful until today. In 1999, the involvement of archaea in AOM was demonstrated by $\delta^{13}C$-depletion in archaeal lipid biomarkers (due probably to $\delta^{13}C$-depeletion in the source CH_4), and, using non-culture-dependent technique (16S rRNA gene sequencing), predominance of methanogenic archaea in the Eel River Basin sediment (including the SMTZ layer) was revealed [42].

This finding led to the idea of "reverse methanogenesis" [43, 44] that convert CH_4 to CO_2 to provide reducing power [$H^+ + e^-$] to sulfate reduction. The hypothetical reverse-methanogenic archaeal phylotypes (based on 16S rRNA genes) were named "anaerobic methanotrophs" (ANME) [43]. Then, the next question was who scavenges the by-product hydrogen ($H^+ + e^-$), ANME or a partner sulfate-reducer.

Eventually in 2000, also using non-culture-dependent techniques, a microbial consortium of archaeal-bacterial symbiosis was demonstrated by microscopy coupled with microbial group-specific staining from the Hydrate Ridge sediment at a 780-m depth [45]. The AOM players were reverse-methanogenic ANME archaea and sulfate-reducing bacteria, and the consortium, or a clump of cells, is composed of archaeal cells inside and bacterial cells outside.

Other than reverse-methanogenic ANME, acetogenic and methylogenic ANMEs are also involved in the AOM processes [46]. In any case, hydrogen ($H^+ + e^-$) is released from CH_4 by ANMEs and scavenged by sulfate-reducing bacteria. In addition, other hydrogen scavengers are also involved in AOM. That is, microorganisms that utilize nitrate, nitrite, and Fe^{3+} as oxidants (electron acceptors), which are nitrate- /nitrite- /iron-reducing bacteria, are known and more will be known [47, 48].

Detailed mechanism of AOM has slowly been understood in particular reference to electron transfer [49, 50]; however, metabolic interplays between ANME and anaerobic respirers have not fully elucidated yet. For example, it is generally recognized that, in SO_4-rich marine and NO_3-rich freshwater habitats, sulfate- and nitrate-respirers play roles in AOM, respectively; however, some examples are not readily explained by the general recognition: in a freshwater wetland, AOM is associated with sulfate reduction, not nitrate reduction [51], and, also in a freshwater wetland, active AOM occurs below the nitrate-rich zone, that is, in a sulfate-poor Fe-rich zone [52].

Most of the seep methane is oxidized to CO_2, and only little reaches the sea surface to enter atmosphere. Oxidation of methane occurs aerobically in water column and anaerobically in sediments. It is estimated that anaerobic oxidation of methane (AOM) accounts for >50% reduction in the methane emission from freshwater wetland [51] and ~100% "sink" at seafloor methane seeps [53] as discussed later. Based on the stoichiometry of methane and oxygen consumptions, the advocator of the AOM hypothesis and her colleague stated that "a substantial fraction of the methane that fuels seep ecosystems is sourced from deep carbon buried kilometers under the sea floor" [54].

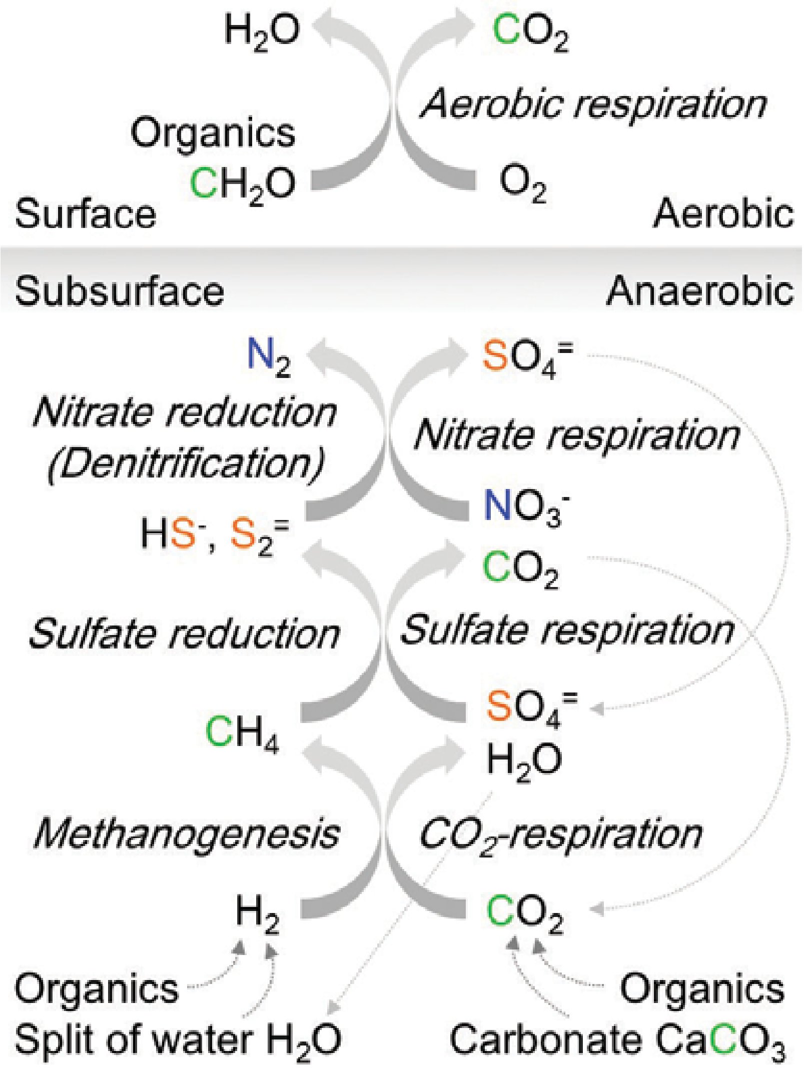

Figure 5. Chain of anaerobic respirations. Although there a battery of anaerobic respirations, only CO_2-respiration (methanogenesis), sulfate respiration (sulfate reduction), and nitrate respiration (nitrate reduction or denitrification) are shown. These respirations are connected by taking "exhaust" of a process (respiration) as "fuel" for the subsequent process.

In summary, during AOM with sulfate, carbon dioxide and sulfide are produced; the former (CO_2) is incorporated into authigenic carbonate and autotrophic biomass, and the autotrophy is energetically driven by oxidation of the latter (H_2S). By these processes, that is, AOM, carbonate authigenesis, and chemo-autotrophy, methane seepage functions as "sink" as well as "source" of methane that was once sequestrated in sub-seafloor.

2.4. Chain of anaerobic respirations

Three major biological processes at methane seeps, that is, hydrogenophilic methanogenesis (reduction of CO_2 with H_2), AOM, and chemoautotrophy, are unified together from a viewpoint of "respiration." This section explicates inter-connectivity and inter-dependency of respirations, particularly anaerobic respirations, which is hypothesized for the anoxic sub-seafloor of methane seeps.

Anaerobic respirations that provide energetic bases for chemoautotrophy and methanotrophy are not inter-dependent per se; however, they may virtually be inter-connected in anaerobic environments such as the methane seep sediments. Such inter-connections are schematically depicted as "chain" as only briefly shown in **Figure 5**, where CO_2 respiration (autotrophic hydrogenophilic methanogenesis) initiates the chain, followed by anaerobic methanotrophy (AOM) via sulfate respiration (sulfate reduction), by anaerobic thiotrophy via nitrate respiration (nitrate reduction, denitrification).[2] Chain elements are connected through the exhaust-fuel relationships, in which the exhaust from a process (respiration) is used as the fuel for the next one. Methane as the exhaust of CO_2 respiration (methanogenesis) becomes the fuel for AOM exhaling sulfide, which in turn becomes the fuel for nitrate respiration.

The chain of anaerobic respirations is still only conceptual; however, it should be useful and expandable to overview wide-ranged inter-relationships of geo-biological processes occurring in methane seeps.

3. Geo-biological settings of methane seeps

Locations of seafloor methane seeps, or sometimes methane vents, are closely tied with origins, generation processes, and migration pathways of methane, which are possible under specific conditions, set by certain geo-biological settings. If the conditions are right, the occurrence of methane seeps is expected even on extra-terrestrial planets and moons such as the red planet Mars and the Saturn's satellite Titan [10]. Conditions being right, "early Earth" and even "early Mars" would have borne methane seeps/vents that would lead to emergence of life, with dual roles of methane as "fuel and exhaust" in a recent hypothesis [55]. Then, how and where methane seeps emerge is outlined in this section.

3.1. Methane seeps in continental margins: active and passive

Not a small part of methane generated in the sub-seafloor is derived from organic degradation, in biogenic or abiogenic pathways. Therefore, continental margins that receive a large amount of organic matter from land and/or from coastal upwelling are thought to be the primary geographical setting for the formation of methane seeps. Sedimentary organic matter is subject to speedy burial due to high sedimentation rate, subject to anaerobic degradation by microorganisms to produce acetate and H_2 as well as methane, and subject to geopressure and geotherm to form diagenetic methane.

Continental margins as recipients of terrestrial source materials (organic matter) give an impression of being "passive." In fact, continental margins are largely categorized into "passive"

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[2] Oxidation of sulfide with nitrate, which is thiotrophic (thioautotrophic) biomass production based on nitrate-respiration, is seen in bacterial species belonging to the genus *Beggiatoa* Trevisan, 1842 [87]. This process was once expected for the symbiont of the hydrothermal vent tubeworm (*Riftia pachyptila* Jones, 1981) [88], but the possibility was denied later [89].

margins and "active" margins from a geological, particularly geophysical point of view. Passive margins in this context mean tectonically non-active or inactive margins, while active margins refer to the continental margins under influence of plate tectonic activities. Hence, active and passive margins denote tectonically active and inactive margins, respectively. Both margins receive inputs of terrigenous organic matter in a similar manner by river flows and erosions but to different degrees, that is, to relatively smaller and greater degrees, respectively, due to the reasons described in the following subsections.

3.1.1. Active margins

Active margins are facing plate boundaries between continental plates and oceanic plates, most of which are convergent margins (subduction zones); transform faults may also face but not so often. The rest of the plate boundaries are divergent zones (spreading axes or rifts). Rare examples of continental margin rifts are known in the Gulf of California and the Red Sea; they are only rarely seen and thus not dealt with in this chapter.

The plate-plate convergence results in subducting depressions of seafloor on the ocean side and uplift of mountain ranges on the land side, both of which run in parallel to and not too far from the coastlines. Examples are taken from the west coasts of the North and South America continents, that is, the Rocky and Andean Mountains, respectively. Rivers that flow westward (seaward) are relatively short and hosted by narrow watersheds, and therefore they transport relatively small amounts of terrigenous (allochthonous) organic matter contained in sediments to the continental margins.

In addition to the transport of allochthonous organic matter, autochthonous production (photosynthetic primary production) of organic matter occurs in light-penetrated surface waters, and certain part of the primary production is exported to underlying water column and to bottom. According to a detailed estimation, of the global primary production of 54×10^{12} kg C year^{-1}, about 4% (2.3×10^{12} kg C year^{-1}) is exported to bottom, and about 0.5 and 0.02% are buried in the margins (50–2000 m) and deep seafloor (>2000 m deep) [56], respectively, where "kilogram carbon" (kg C) equals "giga ton carbon" (Gt C) as well as "pentagram carbon" (Pg C), all indicating 10^{15} g C. Of global ocean area (about 3.5×10^{14} m^2), margins occupy only about 9%, that is, 3% by shelves (50–200 m deep) and 6% by slopes (200–2000 m deep); however, organic burial in margins (2.9×10^{11} kg C year^{-1}) is about 2.4 times greater than that in deep seafloor.

Compared with passive margins, active margins take relatively small part of the whole margin areas. However, active margins off west coasts of the North and South Americas, as well as passive margins off west coasts of Africa [57], receive the benefit of "coastal upwelling" driven by eastern boundary currents: Canary, Benguela, California, and Humboldt Currents. Coastal upwelling brings nutrients to surface water to enhance primary production, resulting in a facilitated organic transport and burial in sediments of the margins.

By contrast, active margins off eastern coasts of Eurasia continent and adjacent island arcs (archipelagos) receive less benefits from the coastal upwelling weakened by the intensified western boundary current, Kuroshio. Although they are part of the same "ring of fire" or circum-Pacific plate boundaries together with the western margins of the Americas, they are not equal counterparts in terms of upwelling benefits. Nevertheless, tectonic "squeeze" driven by subduction may equally benefit the formation of methane seeps in the active margins. An example may be the methane seep that was recently discovered in the forearc basin off Sumatra of the Sunda Arc [58].

Besides sedimentation, active margins have features of methane seepage associated with plate subduction. For example, "out-of-sequence thrusts" potentially serve as channel-forming faults for deep methane to migrate and seep more smoothly [59]. Tectonic "squeeze" (due to subduction compression) of methane-bearing strata may also facilitate the migration and seepage of methane [60, 61]. The deepest seeps of this type were found in the hadal zone of the Japan Trench at 7326-m depth in 1998 [62] and at 7336-m depth in 1999 [63], which is also the globally deepest biological community based on chemoautotrophy or methanotrophy. Topographic features include ridges, escarpments, valleys, canyons, seamounts, and so on.

3.1.2. Passive margins

Passive margins occupy greater widths and areas compared with the areas occupied by active margins. They also receive larger amounts of sediments containing terrigenous organic matter transported by the inflowing rivers from the greater watershed areas. The organic burials are eventually degraded to generate methane that will migrate by diffusion, buoyancy, or gravity depression, will be trapped by sealing strata, or will reach seafloor surface to seep. The seeps are often found at bases of escarpments and outcrops as well as in valleys and canyons.

Historically, methane seepage was first discovered in the passive margins of the Gulf of Mexico (GoM). In 1983, brine seepage associated with gutless tubeworms and mussels that resemble hydrothermal vent fauna was discovered at a 3200-m-deep base on the GoM side of the Florida Escarpment [64]. In 1984, oil seepage associated with gutless tubeworms and clams was discovered in the off-Louisiana coast of GoM [65], which was associated with subsurface methane hydrate (gas hydrate) [66]. The off-Louisiana sites have been a focus of petroleum industry and thus have been studied intensively. The "Bush Hill" (27°47.5′ N, 91°15′ W, mound crest about 540-m deep) in the Green Canyon of industrial interest is the methane seep version of the hydrothermal pilgrim sites of "Garden of Eden" and "Rose Garden" of the Galápagos Rift [67]. After the "Deepwater Horizon" drilling rig explosion near Bush Hill, ecology of the shore, water column, and benthic ecosystems have been studied extensively [16].

A unique example in the passive margin is the Cariaco Trench, or Cariaco Basin, located in the passive margin off Venezuela, which is a Dead Sea-type pull-apart basin. Because its sharply depressed topography blocks exchange with the overlying oxic water, the basin is totally anoxic in the water column from the depth of 200–300 m down to the maximum depth of about 1400 m as well as in sediments [68]. Due to the unique anoxia, a wave of studies on "anaerobic oxidation of methane" (AOM) originated from here in 1976 [41], and the Ocean Time Series Program called CARIACO (Carbon Retention in a Colored Ocean) was started in 1995 and is still ongoing.

Other examples of passive margins are found in the eastern margin of the North and South Americas, whose western margins provide examples of the active margins as stated earlier. In contrast to active margins, most of which are limitedly located along the circum-Pacific "ring of fire," passive margins occupy a vast majority of continental margins. Other than off

Americas, a number of methane seeps will be discovered in the passive margins that have been less surveyed. The passive margins off the land masses of Africa, Greenland, Svalbard, Siberia, India, Australia, China, Antarctica, and so on are under recent surveys or targeted for future surveys and exploitations [69–71].

3.2. Methane hydrates (gas hydrates)

Gas hydrates are a two-phase ice-like structure composed of crystalline water lattice (as the host molecule) and caged gas (as the guest molecule). When natural gas is trapped, they are often called "methane hydrate," focusing on the major component of natural gas and on industrial exploitability. As water ice is stable under specific temperature and pressure conditions, methane hydrates are stable only in the "gas hydrate stability zone" (GHSZ) of suitable geotherms and geopressures. The GHSZ depths in subterranean and sub-seafloor vary according to gradients of geotherms and pressures (geopressures and hydrostatic pressures). Once gradients are subject to a shift due to, for example, global warming and isostatic rebound, methane hydrates will dissociate to release methane (and other gases), possibly resulting in the formation of methane seeps [71].

Carbon storage in sub-seafloor methane hydrates is estimated to be around 500 Gt C (0.5×10^{15} kg C) at maximum [72], almost half of total atmospheric CO_2 carbon. The estimates vary by two orders of magnitude, depending on rates of sedimentation, compaction, and seepage. Seepage, however, serves as a "sink" that convert methane via oxidation to CO_2 and further to $CaCO_3$ precipitates (authigenic carbonate rocks, as described later) that sequestrate carbon back into lithosphere [73]. Therefore, microbial activities involved in methane oxidation and carbonate precipitation should be evaluated to acknowledge the roles of methane seeps as "source" and "sink" for leaching methane.

A different but similar process of methane supply from sub-seafloor is thawing of submarine permafrost, and up to 100% of thaw-released methane is subject to anaerobic oxidation in the permafrost sediments [53]. Because submarine permafrost is protected from intense cold by unfrozen bottom waters (minimum about −2°C) and subject to geotherm since the Holocene inundation, they are more susceptible to thaw and release methane than terrestrial permafrost. Therefore, the evaluation of anaerobic oxidation of methane (AOM) in submarine permafrost and associate methane seepage is an urgent matter of concern.

3.3. Mud volcanoes

Volcanoes in a general sense expel high-temperature lavas, ashes, rocks, vapor, and gases by explosively, not continuously but occasionally. While volcanoes which show that such magmatic eruptions are igneous volcanoes, mud volcanoes may be regarded as sedimentary volcanoes. Mud volcanoes exhale gas (in an eruptive manner), mud, and slurry, which are not driven by a magmatic activity and not necessarily geo-hydrothermally structured, while "asphalt volcanoes" [74] may be generated by geothermally heated supercritical water [75]. More than 600 mud volcanoes have been known on land, and several thousands are assumed on seabed although the entire picture is unclear. On land or in the sea, mud volcanoes are located in the active margins, and they are primarily driven by over-pressurization of gas-bearing fluids. The hydrocarbon components of the gas are generally of thermogenic origin, rarely of microbial origin [76], and mud volcanoes may be regarded as geothermally driven in the sense of gas formation.

Seabed mud volcanoes are often associated with a topographic feature of "pockmarks," that is, seafloor depressions as traces of eruptions or mud volcanic craters [77] as well as methane seepage (occasionally with gas babbles) and carbonates. Microbial mats are also often observed around the pockmark seeps, and some microbiological studies have been conducted, for example, at the 1-km-wide Haakon Mosby mud volcano in the Barents Sea, Arctic Ocean, where gutless tubeworms (*Oligobrachia haakonmosbiensis* Smirnov, 2000 and *Sclerolinum contortum* Smirnov, 2000) colonize in dependence most likely on endosymbiotic sulfur-oxidizing bacterial chemoautotrophy, that is, thiotrophy or thioautotrophy [78, 79].

3.4. Salt diapirs and brine pools

Buried salt deposits in ex-marine basins are compressed to form evaporites, particularly halite, that is, rock salt. The density of pure halite is about 2.16 g cm^{-3} and may not increase by further burial compression, while overlying sediments will increase in density (from initially about 2 g cm^{-3}) by continued sedimentation atop. When the density of overlying sediment reaches eventually about 2.5 g cm^{-3}, rock salt starts to rise due to gravitational instability, or Rayleigh–Taylor instability, and the salt movement is also called "salt tectonics." Rock salt is not only "light" but also "soft" enough to deform for rising, bending, and intruding fissures and faults, where movements are called salt tectonics or salt diapirism and form salt diapirs or salt domes [80].

Salt diapirs are generally impermeable and serve as "cap" and "seal" against the underlying gas/oil reservoirs and gas hydrates that may be dissociated to release free gas. Over-pressurized gas/oil may crack salt diapirs, and the cracked fractures serve as conduits for gas and oil to seep. In reverse, salt diapir may penetrate gas hydrates. For example, chemical and geological structures of water columns, seabed, and sub-seafloor of the Blake Ridge and Cape Fear diapir seeps, southeastern US Atlantic margin, have been well characterized [81]. It may also be remembered that the first discovered methane seep was one of such salt diapir seeps [64].

Salt diapirs may also fall to form pockmarks [82]. Such pockmarks are filled with brine waters to form "brine pools." It should be noted that the brine pools seen in Antarctic waters are different from the salt diapir brine pools; the Antarctic ones are formed by the sinking of brine water expelled from freezing seawater. Salt diapir brine pools are also associated with methane seepage and host chemosynthesis-based fauna [83, 84].

4. Conclusive remarks

Methane plays important roles as the most reduced C1 compound in the global carbon cycling and as the readily oxidizable intermediate in the oxic surface environment, besides its roles as a powerful greenhouse gas to global warming and a fuel to human civilization. Therefore, the processes involving generation and degradation (oxidation) of methane, whether biological or not, encompass momentous biogeochemical significance.

Methane seeps are the point sources of methane emission from subsurface to surface environments. In addition, moreover, deep-sea methane seeps serve as important "sinks" that trap the major greenhouse gases of CH_4 and CO_2 to be sequestrated in carbonate rocks. The carbonate formation in methane seeps is thus relevant to global climate issues. The geological process, that is, authigenesis of carbonates, is probably maintained or even accelerated by the actions of micro- and macroorganisms inhabiting the methane seeps and is therefore said to be "boon" of geo-biological couplings.

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Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Chapter 3

Geo-Biological Coupling of Authigenic Carbonate Formation and Autotrophic Faunal Colonization at Deep-Sea Methane Seeps II. Geo-Biological Landscapes

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Additional information is available at the end of the chapter

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Abstract

Deep-sea methane seeps are typically shaped with authigenic carbonates and unique biomes depending on methane-driven and methane-derived metabolisms. Authigenic carbonates vary in $\delta^{13}C$ values due probably to $\delta^{13}C$ variation in the carbon sources (directly carbon dioxide and bicarbonate, and ultimately methane) which is affected by the generation and degradation (oxidation) of methane at respective methane seeps. Anaerobic oxidation of methane (AOM) by specially developed microbial consortia has significant influences on the carbonate $\delta^{13}C$ variation as well as the production of carbon dioxide and hydrogen sulfide for chemoautotrophic biomass production. Authigenesis of carbonates and faunal colonization are thus connected. Authigenic carbonates also vary in Mg contents that seem correlated again to faunal colonization. Among the colonizers, mussels tend to colonize low $\delta^{13}C$ carbonates, while gutless tubeworms colonize high-Mg carbonates. The types and varieties of such geo-biological landscapes of methane seeps are overviewed in this chapter. A unique feature of a high-Mg content of the rock-tubeworm conglomerates is also discussed.

Keywords: lithotrophy, chemoautotrophy, thiotrophy, methanotrophy, stable carbon isotope, $\delta^{13}C$, isotope fractionation, $\Delta^{13}C$, calcite, dolomite, anaerobic oxidation of methane (AOM), sulfate-methane transition zone (SMTZ), *Lamellibrachia* tubeworm, *Bathymodiolus* mussel, *Calyptogena* clam

1. Introduction

Aristotle separated the world into two realms, *nature* and *living things* (originally animals), the latter having structures, processes, and functions of spontaneous formation and voluntary movements [1]. He argued the difference in the manner similar to "living organisms produce stones (e.g., calculi, shells, and other bio-mineralized materials [2]), but stones do not generate living things". However, in the view of modern science, which has an origin in the Democritean atomism that Aristotle rejected, stones may sustain, not to say generate, life as exemplified by the biological term "lithotrophy." Etymologically, the term was coined from the Greek words *líthos* and *tréphō* that correspond to English words of "stone" and "nourishment," respectively. Therefore, lithotrophy is interpreted as "stone-eating," and the corresponding organisms, that is, lithotrophs, are "stone-eaters."

Lithotrophy or stone-eating is a figurative expression and is biologically interpreted as "living on inorganic sources." For instance, human and animals feed on organic foods and thus are not lithotrophs (but organotrophs). Lithotrophs in this chapter are defined as the organisms that derive life-sustaining energy from redox processes of inorganic materials such as hydrogen sulfide and methane. It should be noted that methane in this argument is taken as semi-inorganic (and semi-organic) as discussed in the former chapter.

It should also be noted that the term "chemoautotrophy" takes the place of lithotrophy in this chapter, because chemoautotrophy (a.k.a., chemosynthesis) is more widely used in general and provides a clearer idea about energy sources in reference to light-driven photoautotrophy (a.k.a. photosynthesis). Autotrophy indicates the inorganic carbon source, that is, CO_2, for organic (biomass) production in both photoautotrophy and chemoautotrophy (Note 1). Methane, CH_4, serves as an energy source and occasionally as a carbon source via "methanotrophy," part of which is regarded as a variety of autotrophy as explained later.

Authigenic formation of *líthos* (stones and rocks) at methane seeps is associated with the generation of inorganic sources that feed living organisms via chemoautotrophic and methanotrophic metabolisms. In addition, their metabolisms in turn facilitate the formation of authigenic carbonates. These rock-forming (geological) and biomass-producing (biological) processes are interwoven, and they literally, more than metaphorically, interweave to form "conglomerates" of rocks and organisms [3].

Authigenic carbonates and associated unique faunas thus represent the typical landscape of methane seeps. Methane seeps are formed by various settings as reviewed in the former chapter, and a variety of carbonates and faunas (and rock-fauna conglomerates) are formed, accordingly. This chapter provides an overview of the types of authigenic carbonates and faunas based on chemoautotrophy and methanotrophy. Profiles of a stable carbon isotope signature ($\delta^{13}C$) of authigenic carbonates and faunal tissues are summarized. In addition, high-magnesium (Mg) contents of the conglomerate carbonates, which are potentially associated with certain geo-biological processes, will be discussed.

2. Backgrounds for landscapes of deep-sea methane seeps

Landscapes of deep-sea methane seeps are characterized by unique and exotic biological communities based on microbial chemo(thio)autotrophic and methanotrophic biomass production, not on photosynthesis (photo-autotrophy), in the dark. Representatives of the methane seep biota are mussels, clams, and gutless tubeworms (**Figure 1**). The landscapes are also featured

Figure 1. Landscape of a methane seep at 1100 m depth, off Hatsushima Island, Sagami Bay, Central Japan. The *Bathymodiolus* Kenk and Wilson, 1985 mussels and *Lamellibrachia* Webb, 1969 tubeworms colonize the authigenic carbonate rocks. The *Calyptogena* Dall, 1891 clams are half-buried in the sediment to move around carbonate rocks to exploit available sulfide. Photo by JAMSTEC.

by occurrences of authigenic carbonate rocks that take forms of seafloor pavements, cementations, and slabs buried in sediments (**Figure 1**). The biological processes (biomass production, production and consumption of methane, etc.) and carbonate-forming processes are interrelated in rather a complex manner, and the interrelationships and the involved processes will be outlined from a geochemical point of view, with particular respect to stable carbon isotopes.

In addition to abiogenic carbonates, some organisms such as mollusks and foraminiferas produce carbonate as protective shells through the process of biomineralization. Biomineralized carbonates, particularly dolomite, are also produced by microorganisms as exemplified by *Desulfovibrio brasiliensis* Warthmann et al., 2005 [5], for dolomite formation or dolomitization [4–6] and *Bacillus subtilus* (Ehrenberg, 1835) John, 1872, possessing the *etfa* gene (involved in energetic electron transfer) for $CaCO_3$ deposition [7], although it is uncertain whether they are actually involved in carbonate formation in methane seeps. Carbonate formation in methane seeps is likely facilitated by the conversion of CH_4 to HCO_3^-, that is, oxidation of methane, which is mediated by microorganisms. Oxidation of methane is done both aerobically and anaerobically, and anaerobic oxidation of methane (AOM) coupled with sulfate reduction (sulfate respiration) produces sulfide, HS^-, that supports chemo(thio)autotrophic biomass production in the dark.

2.1. Stable carbon isotope deviation ($\delta^{13}C$) and fractionation ($\Delta^{13}C$)

Methane, CH_4, is often geochemically characterized by the ratio of stable isotopes of $^{13}C/^{12}C$ and $^{2}H/^{1}H$ or D/H (D stands for deuterium). The ratios are generally expressed as deviations (depletion or enrichment; δ) from the reference standard ratios such as the Vienna Pee Dee Belemnite (VPDB) with the $^{13}C/^{12}C$ ratio of 0.0112372 for $\delta^{13}C$, and the Vienna Standard Mean Ocean Water (VSMOW) with the $^{2}H/^{1}H$ (D/H) ratio of 0.00015576 for $\delta^{2}H$ (δD) as well as the $^{18}O/^{16}O$ ratio of 0.00200520 for $\delta^{18}O$. The unit of ‰ (per mil) instead of % (percent) is generally used for these deviations. For example, if a $^{13}C/^{12}C$ ratio of 0.0101135 is determined for biogenic methane, its $\delta^{13}C$ is −100‰, as calculated as (0.0101135/0.0112372 − 1) × 1000.

These deviation parameters ($\delta^{13}C$, δ^2H (δD) and $\delta^{18}O$) are regarded as the indicative of dynamics (origins, sources, processes, pathways, sinks, changes, etc.) of methane and carbonates as shown in **Figure 3** of the former chapter, with careful cautions for interpretations required. For example, methane that has high $\delta^{13}C$ and δ^2H values (enriched in ^{13}C and ^2H) is generally regarded as abiotic origins (geothermal and thermogenic sources); however, the "enriched" methane may also be interpreted as "leftover" or residual of methane oxidation that removes lighter isotopes (^1H and ^{12}C) faster and leaves heavier isotopes (^2H and ^{13}C) behind, or isotope fractionation (discrimination), resulting in the isotopically "enriched" (heavy) residual methane, as discussed later.

The product of methane oxidation (carbon dioxide, CO_2) and the derived carbonate rock ($CaCO_3$) contain no hydrogen isotopes but stable oxygen isotopes, ^{16}O and ^{18}O, of geochemical interest. The deviation (depletion or enrichment) parameter $\delta^{18}O$ of carbonates is indicative of oxygen dynamics (origins, sources, processes, pathways, sinks, etc.) but is more readily influenced by temperature, fluid inclusion, diagenesis, and so on, than $\delta^{13}C$ [8]. Therefore, this chapter deals mainly with $\delta^{13}C$ that may serve as a "signature" of carbon dynamics as

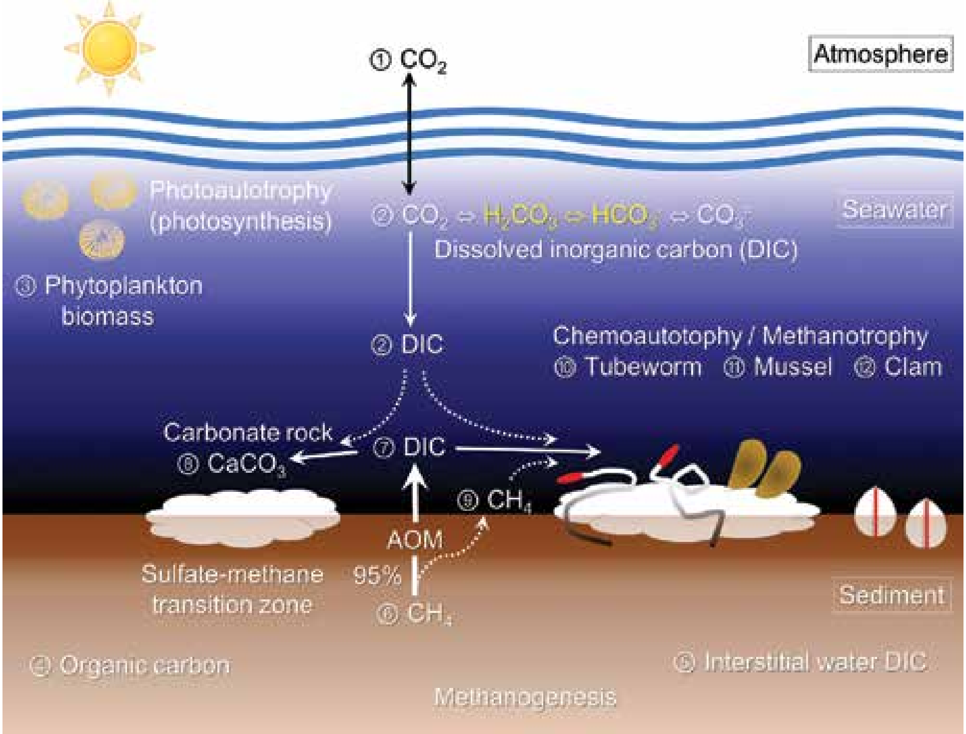

Figure 2. An illustrated general view of carbon dynamics with reference to the processes occurring at a methane seep. Numbers in circles from 1 to 12 correspond to the numbers in **Tables 2** and **3**.

	Carbon species	Form	δ^{13}C (‰)	Reference
1	CO_2	Gas (atmospheric)	-8.00	[9]
2	DIC	ca. 90% HCO_3^-	0.00	[9]; Bjerrum plot [13] Figure 1.1.2, p.5
3	Organic C	Phytoplankton biomass	-22.0	[9]
4	Organic C	Sedimentary	-27.0 to -22.0	In general [9]
			-30.0 to -22.0	Methane seeps [23, 24, 26, 144]
			-80.0 to -47.0	Brine seep at Florida Escarpment [27, 28]
5	CO_2	Interstitial water	-50.0 to -5.00 (DIC)	[25, 40, 145]
			-38.0 to +11.0 (DIC)	[26]
			-21.0 to +1.00 (CO_2)	[26]
			-27.5 (CO_2)	[33]
6	CH_4	Sedimentary	-100.0 to -40	In general [32]
			-101.3 to -27.2	[23, 26, 31, 33]
7	post-AOM CO_2	CH_4-derived (oxidized)	Not found	
8	$CaCO_3$	Authigenic carbonate	-60.0 to +26.0	[50, 56]
9	post-AOM CH_4	Residual (unoxidized)	Possibly -27.2	Eel River Basin [33]
10	Tubeworm	Soft tissue	-55.0 to -18.0	[23, 31, 41–48]
	(*Lamellibrachia*)	Tube (chitin + protein)	-28.1 to -19.9	[24, 41–44]
11	Mussel	Soft tissue	-76.0 to -36.4	[27, 31, 49, 146, 147]
	(*Bathymodiolus*)	Shell ($CaCO_3$)	-6.80 to -2.60	[27, 147]
12	Clam	Soft tissue	-69.2 to -32.5	[23, 43, 44, 146]
	(*Calyptogena*)	Shell ($CaCO_3$)	-2.00 to +0.35	[23, 43, 144, 148, 149]

Table 1. Stable carbon isotope ratio deviation, δ^{13}C (‰), of different carbon species and forms involved in the carbon dynamics associated with methane seepage.

depicted in **Figure 2** and summarized in **Table 1**, and fractionation parameters (Δ^{13}C) in the processes and pathways of carbon dynamics (focusing on methane dynamics) is also discussed later and summarized in **Table 2**.

2.1.1. *δ^{13}C values before and after methanogenesis*

Taking atmospheric CO_2 as the starting material of methanogenesis, its δ^{13}C value is currently estimated at about −8‰ (**Table 1**) [9] with an estimate of a decrease rate of 0.05–0.06‰ year^{-1} [10], possibly due to the input of lighter carbon (^{12}C) into atmosphere by artificial fossil fuel combustion, that is, the so-called "Suess effect" [11]. Air-to-seawater transport prefers lighter $^{12}CO_2$ to heavier $^{13}CO_2$ and thus decreases its δ^{13}C by 2‰ (Δ^{13}C of −2‰, **Table 2**) [12]. Part of

Process	Carbon isotope fractionation process	$\Delta^{13}C$ (‰)	Reference
1 → 2	Air-to-sea transfer of CO_2	−2.00	[12]
2 → 1	(Sea-to-air transfer of CO_2)	(−10.0)	[12]
2	Hydration of CO_2 (^{13}C-enrichment in HCO_3^-)	+8.00	[14]
2 → 3	HCO_3^- to CO_2 by carbonic anhydrase	+10.0	[15]
2 → 3	Photoautotrophy (photosynthesis in seawater)	−29.0 to −11.0	[16–19]
3 → 4	Diagenesis (shallow burial)	−4.00 to −5.00	[22, 150]
	Diagenesis (deep burial)	few	[150]
4 → 5	Anaerobic oxidation (organic C to CO_2)	Not found	
4 → 6	Methanogenesis (organic C to CH_4)	−61.5 to −31.1	Peatland [29]
		−83.0 to −72.0	From methanol [30]
6 → 7	AOM	−29.00	With nitrate (not sulfate) [36]
7 → 8	Carbonate authigenesis (from CO_2 or DIC)	Almost 0	In general [9]
		+0.08, +19.44	Certain seep cases [28]
7 → 10	Chemoautotrophy	−33.0 to −24.0	Calvin-Benson cycle [151]
		−11.0 to −10.0	Reductive TCA cycle [152, 153]
	Biomineralization (shell formation)	A few; +10.0	To DIC; to food [154]

Table 2. Stable carbon isotope fractionation, $\Delta^{13}C$ (‰), during geo-biological processes of carbon dynamics associated with methane seepage.

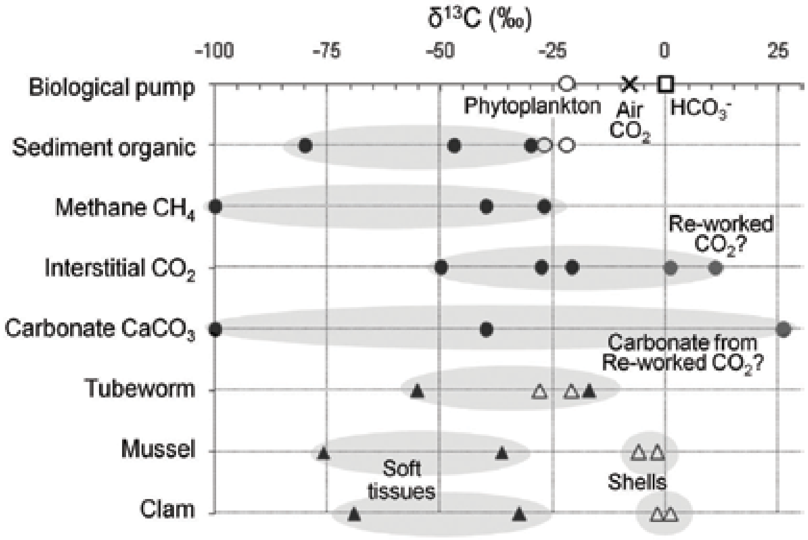

Figure 3. A schematized view of $\delta^{13}C$ variability from atmospheric CO_2 to authigenic carbonate and autotrophic fauna. The $\delta^{13}C$ values are taken from **Table 2**.

CO_2 in seawater will be hydrated toward a chemical equilibrium of CO_2-H_2CO_3-HCO_3^--CO_3^{2-} (virtually CO_2-HCO_3^--CO_3^{2-}), and these are collectively termed "dissolved inorganic carbon" (ΣDIC or simply "DIC"). Among DIC, HCO_3^- is the predominant ion form at seawater pH of 8.00 [13]. Fractionation between ^{12}C and ^{13}C also occurs during hydration of CO_2 into HCO_3^-, back-conversion (by carbonic anhydrase) from HCO_3^- to photosynthetically available CO_2, and photosynthesis mainly by phytoplankton that assimilate CO_2 via C3 pathway (Calvin-Benson cycle, **Table 2**) [14–19]. After all fractionations together, $\delta^{13}C$ of eventually (photosynthetically) produced biomass is generally taken as −22.0‰ [9].

About 0.50% of the photosynthetically produced organic matter is buried in the sediment [20], where the process is often termed as "biological pump" shown in **Figure 3** [21]. The $\delta^{13}C$ values of the "biologically pumped" sedimentary organic matter decreases from −22.0‰ in shallow (fresh) to −27.0‰ in deep (old) layers, due to diagenetic fractionation [22]. Almost the same $\delta^{13}C$ values, −22.0 to −30.0‰, of sedimentary organic matter from methane seepstwere reported [23–26]. However, very depleted $\delta^{13}C$ values, as low as −47.0 to −80.0‰, of sedimentary organic matter were also reported from the methane seep at the base of Florida Escarpment in the Gulf of Mexico [27, 28], which may be associated with "brine" seepage from very old organics or organics of non-photosynthetic origins.

Strong fractionation occurs during methanogenesis, for example, as strong as $\Delta^{13}C$ of >−60.0‰ in a Finnish peatland [29] and >80‰ from methanol in the laboratory [30]. Therefore, methane generated from sedimentary organic matter often shows depleted $\delta^{13}C$ values, as low as −40.0 to −100‰ [26, 31–33]. Care should be taken to such cases that even biogenic methane may be enriched (having high $\delta^{13}C$ values) due to microbial oxidation as described subsequently and thus mistakenly regarded as abiogenic (thermogenic) methane [34].

2.1.2. *$\delta^{13}C$ values after anaerobic oxidation of methane*

In methane oxidation, heavier methane ($^{13}CH_4$) is less preferably oxidized, and therefore $\delta^{13}C$ of the resultant CO_2 is depleted by 5.00 to 30.0‰, that is, $\Delta^{13}C$ of $CH_4 \rightarrow CO_2$ is generally −5.00 to −30.0‰ [34]. A decrease in $\delta^{13}C$, or $\Delta^{13}C$, during aerobic microbial methane oxidation is reported to be −15.0 to −30.0‰ [35]. AOM with nitrate (not sulfate) is reported to result in $\Delta^{13}C$ of about −30.0‰ [36]. Although $\Delta^{13}C$ of "AOM with sulfate" has not been determined, it would not be too far from these fractionation values.

Theoretically, $\delta^{13}C$ values of the resultant DIC forms (CO_2, HCO_3^-, and CO_3^{2-}) after AOM are depleted and actually determined to be −41.0‰ for DIC (virtually HCO_3^-) in interstitial water, compared with $\delta^{13}C$ −24.0‰ of sedimentary organic matter [25]. It should be remembered that $\Delta^{13}C$ of $CO_2 \rightarrow HCO_3^-$ is about +8.00‰ [14] (**Table 2**), leading to a generally accepted idea and the fact that $\delta^{13}C$ of DIC in non-seep, non-vent seawater is −2.00‰ or roughly 0‰. Returning to seep-methane-derived DIC, $\delta^{13}C$ −41.0‰ of DIC would possibly correspond to $\delta^{13}C$ −49.0‰ of CO_2. However, such a theoretical view is often challenged by reality. An example of sequential $\delta^{13}C$ values from sedimentary organic matter (−22.0%) and biogenic methane (−68.0‰) to CO_2 (−20.0‰ to +1.00‰) and DIC (−38.0 to +11.0‰) [26] is tough to be elucidated.

Common name	**Functional name**	**Autotrophy**	**Δ^{13}C from DIC (‰)**	**Reference**
Calvin-Benson cycle	C3; Reductive pentose phosphate cycle	Photo (O/A), Chemo, Methanol	−33.0 to −24.0	[151]
Hatch-Slack pathway	C4 carbon fixation	Photo (O)	−16.0 to −10.0	[151]
CAM pathway	Crassulacean acid metabolism pathway	Photo (O)	−20.0 to −10.0	[151]
Reverse Krebs cycle	Reverse tricarboxylic acid (rTCA) cycle	Photo (A), Chemo	−11.4, −10.0	[152, 153]
Wood-Ljungdahl pathway	Reductive acetyl CoA pathway	Chemo (Methanogenesis)	−36.0	[152]
3-Hydroxypropionate pathway		Photo (A), Chemo	−14.0 + 3	[155, 156]
3-Hydroxypropionate/4-hydroxybutyrate cycle		Chemo	+2.50	[157]
Dicarboxylate/4-hydroxybutyrate cycle		Chemo	Not found	

Photo, oxygenic (O), and anoxygenic (A) photosynthesis or photoautotrophy; Chemo, chemoautotrophy; and, Methano, methanotrophy.

Table 3. Pathways and fractionation factors, Δ^{13}C (‰), of autotrophic CO_2 assimilation.

2.1.3. δ^{13}C values of authigenic carbonates and autotrophic faunas

Generally, fractionation in δ^{13}C, that is, Δ^{13}C, from DIC to carbonates is regarded to be zero [9]. Therefore, authigenic carbonates in methane seeps should have depleted δ^{13}C values, as authigenesis starts with oxidation of depleted methane and proceeds with the resultant depleted CO_2, as typically shown by the δ^{13}C values of around −50‰ in the matrices, nodules, and cements of authigenic seep carbonates [37–39]. However, again, theories are challenged by unexpectedly high δ^{13}C values (**Figure 3**), for example, as high as +16 and +24‰ in carbonates of the Eel River Basin seeps [37, 40]. The involvement of ordinary (non-seep, non-vent) DIC and "leftover" DIC that had not been incorporated into earlier carbonate authigenesis (therefore enriched), as well as "re-worked" DIC that had been generated from leftover (enriched) CH_4, is imaginable.

The seep methane and derived CO_2 after AOM will also be incorporated into faunal biomass via thioautotrophic or methanotrophic biomass production by symbiotic bacteria, respectively. As the source methane and CO_2 are depleted in δ^{13}C, the biomass δ^{13}C should be depleted accordingly. The observed δ^{13}C values in soft tissue of the gutless tubeworms are within the range from −55.0 to −18.0‰ [23, 31, 41–48]. The δ^{13}C values of tubeworm soft tissue are relatively higher (enriched) compared with those in the soft tissue of mussels and clams inhabiting the same seeps (**Table 1**; **Figure 3**) [46, 47, 49, 50], which may be related to the possible dual CO_2-fixation pathways (C3 pathway and rTCA cycle, **Table 3**) in seep tubeworms as predicted for the endosymbiont of the vent tubeworm *Riftia pachyptila* Jones, 1981, by metaproteomics [51]. Hard tissues such as shells of mussels and clams show generally higher δ^{13}C values than those in soft tissues, some of which are close to that of ordinary DIC (**Table 1**; **Figure 3**).

3. Authigenic carbonate rocks

Authigenic carbonates have recently been recognized as an important "carbon sink" in the global carbon cycling next to marine carbonates and organic matters [52], and the authigenesis occurs mainly at methane seeps via anaerobic oxidation of methane (AOM). In other words, methane seeps are often accompanied by authigenic carbonate rocks, that is, carbonate rocks that are formed in situ (autochthonously) in the seabed of methane seeps. The process generates structurally and compositionally multi-staged carbonates that are explained by not simply geochemical but biogeochemical or even microbial involvements [53]. The process may be accelerated due possibly to microbial involvements, as shown by "fresh" ages of authigenic carbonates, as fresh as 195 years old to almost zero for the carbonates exposed on the shelf slope of the Gulf of Mexico [126]; otherwise, from 53,400 to 1700 years old (53.4–1.70 kiloyears ago, ka) in the Gulf of Mexico, 45.5–3.00 ka in the Cong Fan, and 1.60–1.10 ka in the Black Sea [54], as well as 6.40–0.80 ka in the Hydrate Ridge [55].

A simplified mechanism of carbonate rock formation, or authigenesis, is as follows: methane is oxidized (mainly anaerobically with sulfate in the sediment) to generate DIC (CO_2-HCO_3^--CO_3^{2-}), which will react with Ca^{2+} and Mg^{2+} to precipitate $Ca(Mg)CO_3$. The precipitates will grow into aggregates and conglomerates of visible sizes. The real processes are not that simple [56], and they often take the forms of slabs in the sediment and pavements on the sediment, as well as half-buried aggregates with wide-ranged $\delta^{13}C$ values. Modes of carbonate occurrence are regarded as affected not only by microorganisms but also by carbonate-dwelling macro-fauna such as tubeworms and mussels [57].

Gutless tubeworms are occasionally incorporated in aggregates (**Figure 1**), as they require physically hard substrates for settlement and chemically aerobic-anaerobic boundaries, at which carbonates are exactly deposited though anaerobic oxidation of methane (AOM) with sulfate. Sulfide, an AOM byproduct, is aerobically oxidized by symbiotic bacteria (of the host tubeworms) with O_2 to obtain metabolic energy for thioautotrophic chemosynthesis; the symbionts are localized inside of the host cells and are termed "endosymbionts." The gutless tubeworms, therefore, colonize the hard substrates that lay in the zone where sulfide and O_2 coexist, that is, exactly the zone of carbonate deposition, almost overlapping the sulfate–methane transition zone (SMTZ).

Mussels that harbor thioautotrophic and/or methanotrophic symbiotic bacteria are epibenthic and colonize the carbonate rocks that extrude the sediment for settlement (**Figure 1**). By contrast, clams depending on bacterial thioautotrophy are semi-endobenthic and live half-buried in the sediment between and around carbonate rocks (**Figure 1**).

Types of authigenic carbonate rocks are generally grouped into calcites (as well as aragonites) and dolomites. Calcite is further divided into high- and low-Mg calcite according to their Mg contents. Interrelations between carbonate rock types and seep faunal types, that is, between calcites-dolomites and mussels-clams-tubeworms, are hypothesized as discussed later.

Extreme ^{13}C depletion is seen in the authigenic carbonates, when they are formed from depleted DIC (CO_2-HCO_3^--CO_3^{2-}) via AOM against biogenic-depleted methane having $\delta^{13}C$ values as low as −125‰ [58]. On the other hand, enriched DIC is derived from oxidation (probably aerobic oxidation after AOM) of residual ^{13}C-enriched methane and yields ^{13}C-enriched carbonates accordingly. Therefore, the $\delta^{13}C$ ranges of authigenic carbonates are relatively greater than those of seep mussels, clams, tubeworms, and so on.

3.1. Authigenic calcite and aragonite

Among the carbonates, calcite/aragonite and dolomite are often seen in the methane seep environs. Calcite and aragonite are the carbonate polymorphs used in many marine organisms (mollusks, brachiopods, foraminiferans, corals, etc.); they have the same chemical formula ($CaCO_3$) but are different in crystal structures [59]. Aragonite is about 1.50 times as soluble (unstable) as calcite in seawater. Calcite that has lower contents of impurity magnesium, Mg, is more stable than high-Mg calcite. Therefore, the stability order on the deep seafloor is generally low-Mg calcite, high-Mg calcite, and aragonite.

Despite the stability next to low-Mg calcite, high-Mg calcite is often seen in the methane seep environs, with occasional association with tubeworm settlement. By contrast, low-Mg calcite is associated with mussel colonization. The formation and occurrence of less stable high-Mg calcite has not yet been fully elucidated. It may be associated with the attachment and growth of colonies of tubeworms and will probably provide a platform to investigate mineral-animal (and bacteria) interaction from a geo-biological point of view.

3.2. Authigenic dolomites

Dolomite, $CaMg(CO_3)_2$ in an ideal chemical formula, is formed by replacing calcium ions of calcite with magnesium ions. Or, high-Mg calcite may be regarded as an intermediate form of dolomitization. Once there was a paradox about dolomitization at low temperatures, that is, at physiological temperatures, it was solved by the laboratory experiment using sulfur-reducing (sulfate-respiring) bacteria [4–6].

Authigenic dolomite in methane seeps has rarely been studied, and an example from the naturally exhumed fossil seep in Greece showed depleted $\delta^{13}C$ values as low (light, depleted) as −8.00 to −29.0‰, maybe indicative of dolomite formation at the AOM zone in the sediment [60]. Authigenic dolomite in drill-cores from the oil fields in the Santa Barbara Basin, off California, showed $\delta^{13}C$ values of −16.0 to +9.00‰; lighter values are also indicative of dolomite formation in the relatively shallower zone of AOM with sulfate reduction, while heavier values may come from the relatively deeper zone of methanogenesis [61].

4. Autotrophic faunas: Tubeworms, mussels, and clams

Methane seeps and hydrothermal vents, as well as organic falls such as whale carcasses, are located not too far from each other, particularly along the Pan-Pacific "Ring of Fire." Similarities in taxonomic structures and energetic metabolisms (including chemoautotrophy and methanotrophy) between seep and vent fauna have been studied. While the importance of the β-diversity, that is, site-specific diversity, among the seeps and vents worldwide has been pointed out [62], faunal assemblages in the semi-enclosed Guaymas Basin in the Gulf of California (six seeps and four vents without topo-/geographic barriers) share species compositions [63]. In the same but a greater way, the ring-of-fire-type array of seeps and back-arc basin vents in the active margins (convergent margins) contribute to biogeographic connectivity of vent and seep faunas but does not support the "stepping stone" hypothesis by whale carcasses [64].

The gutless tubeworms that represent the exotic seep/vent faunas had already been known (but only sporadically sampled) since the beginning of the twentieth century, before the massive colonies were discovered in association with deep-sea volcanism at the Galápagos Rift in 1977 [65]. It took 4 years to propose that the gutless tubeworms (polychaetes) depend for their nutrition on sulfide−/sulfur-oxidizing chemoautotrophic (thiotrophic or thioautotrophic) biomass production by endosymbiotic bacteria in their specialized sac-like tissue, trophosome [66]. The trophosome is a natural "culture vessel" of, for example, not-yet-cultured thiotrophic gamma-proteobacterial *Candidatus* Endoriftia persephone in the case of the giant vent tubeworm *R. pachyptila* Jones, 1981 [67], and has still been enthusiastically investigated from not only biological but also biomedical and biotechnological points of view [68].

It also took 3–4 years after the first discovery of methane seeps in the Gulf of Mexico [69] for scientists to reveal that seep mussels depend not on thiotrophic but on methanotrophic endosymbionts in gills [70, 71]. In 1987, methanotrophic symbiosis was also found in a non-vent, non-seep gutless tubeworm (*Siboglinum poseidoni* Flügel and Langhof, 1983 from polychaetes) from the sediment of the central Skagerrak strait [72, 73] and some other vent/seep mussel species, but not for clams [74]. While many bivalve and gastropod mollusks have chemo−/methanotrophic symbionts [75], this chapter focuses on bivalve mussels (*Bathymodiolus* Kenk and Wilson, 1985) and clams (*Calyptogena* Dall, 1891) from seep (and vent) habitats.

Symbiosis with more than one symbiotic species in one host, which is dual or multiple symbiosis, is known for gutless tubeworms; an example is the vent-dwelling tubeworm that hosts multiple thiotrophic species as endosymbionts [76]. In addition, dual symbiosis with both thio- and methanotrophic endosymbionts has been known for the seep mussels (*Bathymodiolus* spp.) in, for example, the Gulf of Mexico [77] and off-Congo passive margins [78], as well as other invertebrates (mostly gutless oligochaetes) dwelling non-vent, non-seep habitats (Note 2).

In addition to thiotrophy and methanotrophy, in 2011, hydrogenotrophy (chemoautotrophy based on hydrogen oxidation) appeared as the third way of a vent mussel (and possibly for seep mussels) [79].

4.1. Thiotrophy and methanotrophy

Photosynthesis and chemoautotrophy differ in energetic processes but share the CO_2-fixing pathways, for example, the best-known Calvin-Benson cycle (reductive pentose phosphate cycle). Currently, eight autotrophic CO_2-fixing pathways, including Calvin-Benson cycle, are known for life even in the dark chemoautotrophy (**Table 3**) [80]. Dual pathways are widely known in chemoautotrophy-based macro-organisms, such as siboglinid (formerly known as vestimentiferan and pogonophoran) tubeworms, of hydrothermal vents and methane seeps [48].

In addition to a variety of CO_2-fixation pathways, a battery of energetic pathways with diverse reductants and oxidants (electron donors and acceptors) is also known for chemoautotrophy [81, 82]. The most representative one in the methane seeps is the oxidation of sulfide. If chemoautotrophy is based on sulfide oxidation, it is correspondingly termed "thiotrophy" or "thioautotrophy." While aerobic oxidation of sulfide is most common, anaerobic oxidation of sulfide with nitrate, $HS^- + NO_3^- \rightarrow HSO_4^- + N_2$ (Note 3), (nitrate reduction, nitrate respiration, or denitrification), is possible, although its occurrence in methane seeps is not necessarily evident.

Both aerobic and anaerobic oxidation of H_2 can also provide an energetic basis for chemoautotrophy. Aerobic oxidation of H_2 with O_2 has recently been recognized as widespread among the hydrothermal vent chemoautotrophy [79, 83]. H_2 is also oxidized anaerobically with CO_2, which corresponds to the autotrophic CO_2 respiration, or autotrophic hydrogenotrophic methanogenesis, and represented by the thermophilic species of *Methanothermobacter thermoflexus* (Kotelnikova et al. 1994) Boone 2002 and *M. thermautotrophicus* (Zeikus and Wolfe 1972) Wasserfallen et al. 2000. However, in a non-thermophilic environment such as artificial anaerobic digesters, non-autotrophic CO_2 respirers dominate the microflora [84], which gives an implication for considering CO_2 respirers in the "cold" methane seeps.

Methanotrophy, feeding methane as "food" or "fuel," may be placed between autotrophy and heterotrophy, because methane can be placed between inorganic and organic matter [85]. For most methanotrophs, methane serves as the dual sources for metabolic energy (catabolism, dissimilation) and biomass production (anabolism, assimilation). In this context, if methane is taken as half-organic and half-inorganic, methanotrophs are accordingly regarded as half-autotrophs and half-heterotrophs. However, the "type X" (or type Ib) methanotrophs and Verrucomicrobia-related methanotrophs are known to possess the CO_2-fixing enzyme, RuBisCO, and assimilate CO_2 via the Calvin-Benson cycle [86], and they are probably more widespread than previously presumed [87, 88].

Anaerobic oxidation of methane (AOM) is also a form of methanotrophy that is conducted by more than one microbial species, that is, archaeal-bacterial consortia, as described earlier. Both archaeal methanogens and bacterial sulfate-respirers (sulfate-reducing bacteria) are reported to assimilate CH_4-derived (CH_4-oxidized) CO_2 autotrophically via the Calvin-Benson cycle [89].

4.2. Tubeworms

The gutless tubeworms, or siboglinid veriforms, represent the most enigmatic and intriguing organisms of the seep fauna in terms of body plan, morphology, life cycle, metabolisms, endosymbioses, and so on [90]. The first specimen of the gutless tubeworms was dredge-sampled in 1900 during the Siboga Expedition (1899–1900) from 462 m deep, off Selayar Island, Flores Sea, Indonesia [91], where methane seepage is presumed to occur in the active margin [92], and was later described as the new species *S. weberi* Caullery, 1944 [93], with proposals of the new genus *Siboglinum* Caullery, 1914, and the new family Siboglinidae [94] (Note 4).

Thereafter, siboglinid worms, typically >10-mm long and <1-mm wide, were collected sporadically from various oceanographic sites. Due to their unique and enigmatic body plan with

Year	Species	Genus	Family	Order	Class	Phylum
Current	236 accepted [158]	32 accepted [158]	Siboglinidae [94]	(Sabellida) [159]	(Polychaeta) [160])	(Annelida) [158])
2015	*Lamellibrachia sagami* Kobayashi, Miura and Kojima, 2015 [96]					
1997			Siboglinidae [94, 161, 162]			
1985	*Escarpia spicata Jones, 1985,* *Escarpia laminata* Jones, 1985 [104]	*Escarpia* [104]				Vestimentifera
1981	*Riftia pachyptila* Jones, 1981 [163]	*Riftia* [163]				Pogonophora
1975	*Lamellibrachia luymesi* van der Land and Nørrevang, *1975* [103]					
1969				Vestimentifera		
1964	*Lamellibrachia barhami* Webb, 1969 [164]	*Lamellibrachia* [164]	Lamellibrachiidae			
1944	*Siboglinum weberi* Caullery, 1944 [93]					Pogonophora
1937				Pogonophora		
1933			Sabellidae			
1914		*Siboglinum* [94]	Siboglinidae [94]			

Other marine gutless worms (mostly belonging to the subclass Oligochaeta, class Clitellata) are not listed. Only accepted highest taxa, that is, accepted parents, as well as representative species and genera, are listed with accepted references. Current supra-taxa are also listed but in parentheses. Currently (as of May 2018), the family Siboglinidae is the highest taxon (parent) of all the vent/seep gutless tubeworms.

Table 4. Taxonomic changes in positions and statuses of "gutless tubeworms" (mostly belonging to the class Polychaeta) that inhabit hydrothermal vents and methane seeps.

no mouth, no anus, and no digestive tract, their way of living was interpreted to depend on dissolved organic matter absorbed from somewhere of body surface including the anterior "beard"; they were often called "beard worms." The interpretation was based on the common belief that animals are heterotrophic. The heterotrophic animal view is still correct even now in a strict sense (that siboglinid worms depend eventually on organic matter produced by symbiotic bacteria), but the less-defined phrase "autotrophic animal" was advocated for siboglinid worms in a broad sense [66].

The gutless siboglinid worms often host a single thiotrophic endosymbiont species. A non-vent, non-seep gutless tubeworm (*S. poseidoni* Flügel and Langhof, 1983) harbors a methanotrophic symbiont [72, 73] probably of one species. However, gutless tubeworms may occasionally possess a single but probably methanotrophic endosymbiont, or thiotrophic but multiple endosymbionts. For example, the sediment-dwelling *Oligobrachia mashikoi* Imajima, 1973, hosts a symbiont that bears the genes of methanotroph-related 16S rRNA and CO_2-fixing enzyme RuBisCO, suggesting the possible involvement of a CO_2-fixing methanotroph, that is, "type X" or type Ib methanotroph [95]. Another sediment-dwelling worm (*S. poseidoni*) also has a methanotrophic endosymbiont [73]. Regarding multiple symbioses, some individuals of *Lamellibrachia* sp., currently described as *Lamellibrachia sagami* Kobayashi et al. [96], from the off-Hatsushima seep, Sagami Bay, central Japan, were reported to have four distinct thiotroph-like symbionts in their trophosome tissue [97–100], and *L. anaximandri* Southward, Andersen and Hourdez, 2011, despite vent-dwelling, also hosts multiple thiotrophic species as endosymbionts [76].

Due to their unique and enigmatic body plan, their taxonomic position and status have been confused and subject to not a few, not minor changes (**Table 4**), and still investigated by modern phylogenetic and phylogenomic approaches [101, 102]. As to their physiology, the "giant tubeworm" or *R. pachyptila* that inhabits hydrothermal vents is probably the most popular, well known, and well studied. The methane seep counterparts would be *L. luymesi* van der Land and Nørrevang [103] and *Escarpia laminata* Jones, 1985, inhabiting the base of Florida escarpment in the Gulf of Mexico [104], which are known to have extreme longevities as long as possibly >300 years [105–107].

The giant tubeworm *R. pachyptila* grows quickly to >2 m high as far as the worm can uptake sulfide emitted from the vents (**Figure 4A**). By contrast, the seep tubeworm *L. luymesi* may also grow over 2 m long (not high) only slowly over >200-year longevity [108], as well as *E. laminata* may grow over 300 years [107]. Individual worms of the colonies of *Lamellibrachia* Webb 1969 often look "trimmed" within the limits of seeped methane/sulfide (**Figure 4B**). Not only trimmed, their bodies are often twisted to crawl on seafloor and even buried in the sediment. It has been pointed out that the posterior extension, or "root," of *Lamellibrachia* worms functions to "sip" sulfide from the sulfate–methane transition zone (SMTZ) in the sediment [109] as well as to "dump" sulfate and protons (H^+) to SMTZ [110]. Sulfate dumped into or below SMTZ will facilitate anaerobic oxidation of methane (AOM) with sulfate, and sulfide will be regenerated from the dumped sulfate and protons via AOM.

A whole process including symbiotic thiotrophy (aerobic oxidation of sulfide) and AOM in sediment may be viewed as an "extended symbiosis" that circulates the regeneration of sulfide and sulfate as if it functions as a "coffee percolator" (Note 5). The H_2S/SO_4^{2-} percolator is driven by methane supplies, eventually leading to the generation of CO_2-HCO_3^--CO_3^{2-} from methane and thus to authigenesis of carbonates. The *Lamellibrachia* worms are often associated with carbonates and even incorporated in carbonates occasionally to form conglomerates as discussed later (**Figure 5**).

The tubeworm soft tissue that contains an amount of endosymbiotic thiotrophic bacteria is relatively higher (more enriched) in $\delta^{13}C$ than soft tissues of mussels and clams of the same

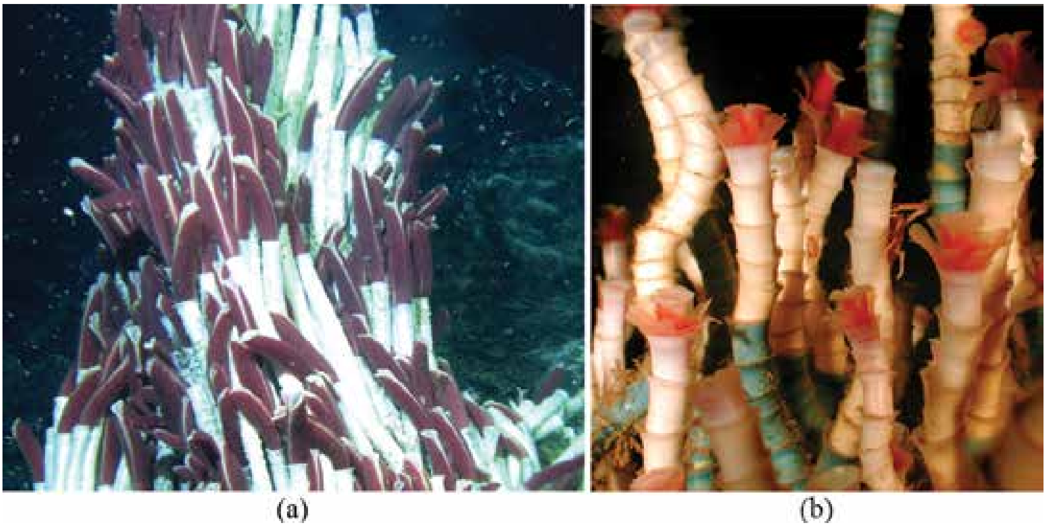

Figure 4. The gutless tubeworms of a hydrothermal vent and a methane seep. (A) *Riftia pachyptila* Jones, 1981, inhabiting a vent site of the East Pacific rise at 2500 m depth [167]. (B) *Lamellibrachia luymesi* van der Land and Nørrevang [103], from a methane seep at 550 m depth in the Gulf of Mexico. The blue-stained tube indicates approximately 14 months of growth [168]. Photograph by Charles R. Fisher.

Figure 5. The seep tubeworm *Lamellibrachia sagami* Kobayashi et al. [96], being embedded in authigenic carbonate formed in the off-Hatsushima methane seep at 1100 m depth, Sagami Bay, Central Japan. The width of the photograph corresponds to 7 cm. Photograph by the author.

seep (**Figure 3**) [46]. Tubes of the worms show intermediate $\delta^{13}C$ values compared with those of soft tissues, with a weak tendency of $\delta^{13}C$ becoming heavier toward the posterior end of the tubes [104]. This may be associated with the phenomenon that lower (more depleted) $\delta^{13}C$ values are seen in the tubeworm-associated high-Mg carbonates than those colonized by *Bathymodiolus* mussels [39, 50, 57, 111].

4.3. Mussels

The mussels belonging to the genus *Bathymodiolus* Kenk and Wilson, 1985, represent the vent and seep fauna as well and harbor endosymbiotic bacteria eventually in their gills. While juveniles of vent mussels host epi-symbionts almost everywhere on their surfaces, endosymbiotic colonization becomes restricted to gill tissue during the mussel growth [112], and even adults are subject to continued bacterial colonization attacks throughout their lifetimes [113]. Although the process was observed with vent *Bathymodiolus* mussels, it may similarly occur to the seep *Bathymodiolus* mussels, as it is known for the shallow-water tropical lucinid clam *Ctena orbiculata* (Montagu, 1808) cited as its synonym *Codakia orbiculata* (Montagu, 1808) [114].

Their endosymbionts are thiotrophs or methanotrophs or both. The vent mussel *B. thermophilus* Kenk and Wilson, 1985, in the East Pacific Rise has only thiotrophic symbionts [66, 115], while the seep mussel *B. childressii* Gustafson, Turner Lutz and Vrijenhoek, 1998, in the Gulf of Mexico hosts only methanotrophic symbionts [70]. A vent *Bathymodiolus* species in a western Pacific harbors a CO_2-fixing methanotroph, that is, "type X" or type Ib methanotroph [116].

Dual symbiosis, in which a single host harbors both thiotrophic and methanotrophic bacteria, has been described for seep mussels from the Gulf of Mexico (*B. brooksii* Gustafson, Turner, Lutz and Vrijenhoek, 1998) [71], off Congo passive margins [78] and other seep mussels, as well as vent mussels. A vent *Bathymodiolus* mussel is known to harbor hydrogen-oxidizing autotrophic bacteria [79], which process is now regarded as probably more widely and ubiquitously distributed in deep-sea environments [83].

The small mytilid mussel, *Idas* sp., inhabiting carbonate crusts at the off-Nile fan seep harbors six endosymbionts probably of thiotrophs, methanotrophs, and previously unrecognized roles [117]. Similarly, *B. heckerae* Turner, Gustafson, Lutz and Vrijenhoek, 1998, inhabiting the "asphalt" seep in the Gulf of Mexico [118, 119] harbors multiple endosymbiotic bacterial species, one of which belongs probably to the genus *Cycloclasticus* Dyksterhouse, Gray, Herwig, Lara and Staley, 1995 [120]. The symbiotic *Cycloclasticus* appeared to degrade and derive carbon and energy from short-chain alkanes such as ethane and butane [121], despite lack of genes responsible for the degradation of polyaromatic hydrocarbons that are seen in other *Cycloclasticus* species [122].

Overall, it can be said that the seep mussels possess high plasticity and flexibility in harboring and depending on a variety of endosymbionts and their energetic metabolisms: from single via dual to multiple symbioses with thiotrophs and methanotrophs via hydrogenotrophs to asphalt-degrading heterotrophs. This symbiotic plasticity may facilitate evolution and ubiquity of these mussel species [123–125].

The *Bathymodiolus*, as well as *Idas*, mussels attach and settle on hard substrates such as basalts in hydrothermal vents and carbonates in methane seeps, like tubeworms do. However,

	Modern carbonate in the off-Hatsushima methane seep, Sagami Bay		**Miocene carbonate (17.2–14.4 Ma), Hayama Group, Miura Peninsula**	
	With tubeworms	Without tubeworms	With fossil tubes	Without fossil tubes
$\delta^{13}C$	−28.0 to −27.0‰	−34.0 to −33.0‰	Not determined	
$CaCO_3$ (%)	34.0–43.0	52.0–86.0	39.0–40.0	66.0–67.0
$MgCO_3$ (%)	12.0–15.0	<0.10	14.0–15.0	<0.10
FeO_2 (%)	4.00–6.00	5.00–15.0	4.00–5.00	28.0–29.0
SiO_2 (%)	28.0–31.0	<0.10–37.0	28.0–29.0	<0.10
AlO_2 (%)	9.00–10.0	<0.10–12.0	9.00–10.0	<0.10

Table 5. Comparison of $\delta^{13}C$ values (‰) and compositions of selected chemical species (weight-to-weight %) in modern and Miocene carbonates with reference to the presence/absence of living tubeworms or fossil worm tubes [3, 100, 165, 166].

Bathymodiolus mussels tend to colonize ^{13}C-enriched carbonates, compared with tubeworm association with ^{13}C-depleted high-Mg carbonates [39, 50, 57, 111].

4.4. Clams

The "giant white clams" or the vesicomyid clams belonging to the genes *Calyptogena* Dall, 1891, also represent the fauna of both hydrothermal vents and methane seeps. They are mostly dependent on endosymbiotic bacterial thiotrophs for their nutrition, not on methanotrophs [74]. However, a thyasirid clam, *Axinulus hadalis* Okutani et al. [126], living within (but a few meters deeper from) the deepest methane seep community [127], was reported to have dual endosymbionts, which were speculated to be thio- and hydrogenotrophs, that is, sulfur- and hydrogen-oxidizing chemoautotrophs, respectively [128].

The *Calyptogena* clams are semi-endobenthic and live half-buried in the sediment between and around carbonate rocks. Therefore, the clams are not associated with carbonate rocks for living, although they occur in close vicinities. This may be confirmed by the difference in $\delta^{13}C$ values of the clam shells and carbonate rocks, which would reflect different carbon sources despite their habitat vicinities [129].

5. Conglomerates of carbonates and tubeworms

Authigenic carbonates "grow" in the zone anaerobic oxidation of methane (AOM) and sulfate–methane transition zone (SMTZ) in the sediment of methane seeps, as shown by low $\delta^{13}C$ values. Similarly, the gutless tubeworms such as *Lamellibrachia* species grow toward posterior rather than anterior to "percolate" (exploit and regenerate) sulfide in the horizon of AOM zone overlapped with SMTZ, also as indicated by the tendency of lower $\delta^{13}C$ toward the posterior end of the tube [24]. Sipping of sulfide and dumping of sulfate at the root (posterior end) of the tubeworms may change the local pH and thus affect the conditions for favored formation calcite to aragonite [57, 130]. These growths of authigenic carbonates and autotrophic tubeworms occur concomitantly near the posterior of worm tubes [130] and often intercalate each other to form mineral-animal "conglomerates" (**Figure 5**). Although detailed observation suggested that a nodular high-Mg calcite is formed before tubeworm settlement [130], the coupling of high-Mg calcite and tubeworm colonization has not been elucidated.

The conglomerates of calcite and *L. sagami* in the off-Hatsushima methane seep, Sagami Bay, central Japan, were studied with reference to $\delta^{13}C$ and Mg contents and were compared with those from the past authigenic carbonate formed in the Miocene, 17.2–14.4 million years ago (Ma), from the Hayama Group, Miura Peninsula, central Japan. The two sites, that is, modern and past methane seeps, are only <50.0 km distant, and the data from the modern and past carbonates revealed that the high content (~15.0%) presence of Mg in relatively high $\delta^{13}C$ (<30.0‰ against >30.0‰) calcite is closely associated with conglomeration with tubeworms in both modern and fossil specimens (**Table 5**) [3, 100, 131].

6. Conclusive remarks

Authigenic carbonates and autotrophic faunas provide unique and typical landscapes of methane seeps (**Figures 1** and **2**). The carbonates and faunas are formed and maintained not independently but interactively via microbial activities of methanogenesis, anaerobic (and aerobic) oxidation of methane, anaerobic respirations such as sulfate reduction, and carbonate (particularly dolomite) formation. During these microbial processes, the stable carbon isotope ratios ($\delta^{13}C$ values) do shift with respective ranges of isotopic fractionation ($\Delta^{13}C$, **Tables 2** and **3**). Not only microorganisms but also macro-fauna may contribute to form and shape authigenic carbonate rocks. In the case of rock-tubeworm conglomerates, tubeworms actively recycle sulfide and sulfate in sediment, resulting in the acceleration of "growth" of the conglomerates.

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Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Notes

(Note 1) In the strict sense, chemolithoautotrophy should be used instead of lithotrophy or chemoautotrophy; however, the term is only used by experts in rather a narrow area of microbiology and sounds too technical for non-expert audience.

(Note 2) Endosymbiosis is widespread in non-vent, non-seep organisms [123]. Chemoautotrophic bacterial endosymbiosis was characterized with the gutless oligochaetes *Inanidrilus leukodermatus* (Giere, 1979) from 5-m-deep sediment in a Bermuda inlet [135] and *Olavius crassitunicatus* Finogenova, 1986, from 270- to 359-mdeep sediment in the Peruvian passive margin [136], as well as a marine nematode *Astomonema* sp. from coral reef sediments in the Bahamas [137]. Multiple endosymbiosis of the gutless oligochaete *Olavius algarvensis* Giere, Erséus and Stuhlmacher, 1998, was subject to genetically and biochemically dissected by metaproteomics [138] that revealed unusual pathways, for example, use CO and H_2 for energetic metabolism [139]. Animal-bacterial chemo−/methanotrophic symbioses have recently been recognized as more widespread and ubiquitous in anaerobic sediments, besides vents, seeps, and organic falls, than previously presumed [140]. A microbiome of an individual of the gutless oligochaete *I. exumae* Erséus, 2003, differs markedly from those of other 22 individuals [141], which also demonstrates the symbiotic plasticity that may facilitate the adaption and evolution of this group of the gutless tubeworms.

(Note 3) Anaerobic oxidation of sulfide with nitrate, which is anaerobic thiotrophy (thioautotrophy) based on nitrate-respiration, is seen in bacterial species belonging to the genus *Beggiatoa* Trevisan, 1842 [132]. This energetic metabolism was once expected for the endosymbiont of the hydrothermal vent tubeworm (*R. pachyptila* Jones, 1981) [133], but the possibility was denied later [134].

(Note 4) Maurice Jules Gaston Corneille Caullery (1868–1958), a French zoologist, studied the first specimen of the "beard worm" and proposed the new family Siboglinidae and new genus *Siboglinum* Caullery, 1914, presumably named after the Dutch "Siboga" Expedition (1899–1900), during which the specimen was dredge-sampled. "Siboga" was the name of the vessel, which originally was a 50-m-long gunboat owned by the government of the Dutch East Indies [142]. Caullery described the new family Siboglinidae in 1914 based on the simultaneously proposed new genus *Siboglinum*. The type species of the genus, *S. weberi* Caullery 1944, was described subsequently 30 years later, in 1944. It is reasonably considered that the specific epithet "*weberi*" was named after the leader of the "Siboga" expedition, Max Carl Wilhelm Weber, a German-Dutch zoologist.

(Note 5) The sulfide/sulfate "percolator" in the seep system can be viewed as "extended symbiosis" between gutless host tubeworms, thiotrophic endosymbionts, and sulfate-consuming AOM microbial consortia. In these relationships, biologically true symbiosis is postulated only between host worms and internal thiotrophs, and the involvement of external AOM consortia is regarded as "extended". By contrast, true endosymbiosis of a host worm and two bacterial symbionts, that is, dual symbiosis of sulfur-oxidizing and sulfate-reducing bacteria is seen in the gutless oligochaete worm *Olavius algarvensis* Giere, Erséus and Stuhlmacher, 1998, and *Olavius crassitunicatus* Finogenova, 1986, that host multiple (more than dual) endosymbionts [136, 143].

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Section 3

Plankton Ecology and Diversity

Chapter 4

Plankton Ecology and Productivity in Jamaican Waters with New and Unique Applications

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Additional information is available at the end of the chapter

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Abstract

Unique applications of plankton ecology and productivity in Jamaican waters are presented. While traditional indices were inadequate descriptors of mangrove lagoon water quality, planktonic indices (total Chlorophyll *a*, zooplankton groups and species) were more reliable. Phytoplankton biomass was used to indicate a longitudinal gradient along the Hellshire Coastline, identifying non-point sources of enrichment, and movement of water masses in the absence of expensive Eulerian current meters. Along that same coast, mean primary production, determined by ^{14}C techniques, confirmed a gradient from the eutrophic Kingston Harbour (21.1 g C m^{-2}year^{-1}) to the oligotrophic control site (0.52 g C m^{-2} year^{-1}). Maximum inshore station values (36.75–18.39 g C m^{-2} year^{-1}) were more than 20 times greater than offshore and exceeded Harbour values, confirming non-point sources and localized mechanisms as important inshore sources of eutrophication. The novel use of Ecopath with Ecosim (EwE) software to model trophic flows within planktonic communities was done in two bays. For Discovery Bay, on Jamaica's north coast, the model indicated a developing ecosystem with open mineral cycles and poor nutrient conservation while in Foul and Folly Bays on the southeastern coast the model indicated greater resilience and ability to recover from perturbations. These applications have facilitated informed management decisions for sustainable use in Jamaican coastal ecosystems.

Keywords: Jamaica, mangrove lagoons, plankton, production, Ecopath, non-point sources, Kingston Harbour

1. Introduction

Jamaica is an archipelagic state with territorial waters approximately 24 times its land mass. Consequently, the range of water masses and associated water qualities include eutrophic bays and harbours, mangrove lagoons, pristine and mesotrophic bays as well as oligotrophic offshore waters. These have provided a vast and varied expanse for plankton ecology research. Plankton research in Jamaican waters has traditionally used species composition and abundances to characterize the different water masses, indicate eutrophication levels and distribution as well as to indicate the trophic status of areas and their ability to support fisheries.

Kingston Harbour, the seventh deepest natural Harbour in the world, borders Jamaica's capital city, Kingston and is distinctive for the inflow of 21 identifiable gullies and streams [1] that carry storm water, partially treated sewage, agriculture run off and now large quantities of solid waste. Kingston Harbour is the most extensively studied bay in Jamaica and consequently the plankton have been used to characterize the Harbour as eutrophic [2–6] as well as indicate the influence of these waters on the south coast shelf [4, 7]. Kingston Harbour waters have been tracked using planktonic indices as leaving the Harbour and flowing south west towards the Hellshire coastline. Relative abundance of *Lucifer faxoni* and *Penilia avirostris* [4] have been used as indicators of Kingston Harbour waters in areas of the south-east shelf of Jamaica.

Early research [8] sought to indicate distinct assemblages of zooplankton that characterize offshore (oceanic), shelf and Kingston Harbour waters along with associated "indicator species". More recent studies have also compared oceanic, shelf and Kingston Harbour waters using zooplankton abundances as well as community composition [9]. However, novel uses of zooplankton to indicate water quality have involved exploring the use of these indices in mangrove lagoons threatened by anthropogenic stress.

The new and unique uses of plankton as indicators around Jamaica involve their use in characterizing the eutrophication status of mangrove lagoons, their use to assess coastal dynamics and water movement as well as the use of plankton productivity in the characterization and understanding of ecological functions and trophodynamic flows in different water masses.

2. Plankton as indicators in mangrove lagoons

Mangroves are a diverse species of tropical woody trees found primarily in Tropical and Sub-tropical intertidal (wetland) environments. They are estimated to cover a global area of between 137,760 and 152,000 km^2 [10]. Mangroves provide a suite of regulating, supporting and provisioning ecosystem services [10] including shoreline protection, carbon sequestration and storage, water quality enhancement and promoting high biodiversity by providing food and shelter for fish, marine invertebrates, and birds. Mangrove forests are threatened globally by deforestation due to coastal development, mariculture (primarily shrimp farming), timber harvest, water diversion and over-exploitation. Jamaica's wetland area has been estimated at ~17,700 with 9731 ha being mangrove dominated forests [11]. Mangroves are reported to be found along 290 km or 29% of Jamaica's coastline and covering approximately 97 km^2 [12]. Unfortunately, many areas of Jamaica's mangroves are threatened by eutrophication which if left undetected and unchecked, also leads to reduction and loss of this vital ecosystem and the services it provides.

Water quality monitoring of mangrove waters is particularly problematic because natural conditions in mangrove lagoons often yield unexpected or confounding values for indices commonly used in coastal water quality monitoring. Traditional coastal water quality indices used extensively in Jamaica's coastal waters include: nutrients, water clarity (light penetration), biochemical oxygen demand (BOD), bacterial content as well as the planktonic communities, especially the phytoplankton [13]. Mangrove lagoons have natural low light conditions, high turbidity, high detritus, and often low salinity associated with land runoff. The existing indices would therefore identify all mangrove lagoons as polluted, relative to the non-mangrove areas of the bay [14]. Also, there is the danger of not indicating eutrophic conditions in mangroves because they are "masked" or modified by the natural physiographic conditions. For example, while high phytoplankton biomass is a reliable index of eutrophication, mangals may have low phytoplankton biomass because of the inhibitory effects of the phenolic materials (tannins) in the water [15]. Several studies have attempted to identify appropriate water quality indicators for use in Jamaica's mangrove lagoons [14, 16–18]. These have explored using planktonic communities instead of traditional water quality indices, or mangrove root communities as water quality indices for mangrove lagoons.

2.1. The methods used

The methods used to investigate planktonic communities as effective water quality indices in mangrove lagoons required sites with mangroves experiencing different levels of nutrients and in relatively close proximity. Sampling was done at six contrasting mangrove areas in the south-east coastal areas of Jamaica which ranged from eutrophic, disturbed lagoons in Kingston Harbour and Hunts Bay to pristine mangrove areas in Wreck Bay (**Figure 1**).

All the lagoons, however, share the characteristics of low light penetration because of tannin coloured waters, fluctuating salinities, high turbidity, and high detritus with associated microbial activity. Sampling was usually conducted for 1 year or to represent the wet and dry seasons and parameters included physicochemical: depth (±0.08 m), temperature (±0.10°C), dissolved oxygen (DO) (±0.2 mg l^{-1}), Salinity (±0.2‰), pH (±0.2 units) and Reduction/Oxidation potential- REDOX (±20 mV), phytoplankton biomass (Chlorophyll *a*), zooplankton abundance and species composition as well as species composition and abundance of mangrove foot fouling communities. The suite of physicochemical variables was read in situ using Hydrolab® or YSI® Mulit-parameter data loggers. For phytoplankton biomass water samples were collected in replicate at all stations using a horizontal Niskin sampler (3.5 l). Samples were filtered through a fractionating tower of nitex screening 20 μm, Whatman GFD glass fibre filters 2.7 μm and Whatman GFF glass fibre filters 0.7 μm at approximately 15 mmHg pressure [19]. Chlorophyll *a* extraction was conducted at room temperature in the dark for 24 h using 6 ml of 90% acetone [20] and was read using a Turner Designs TD700 Version 1.8 laboratory fluorometer.

Zooplankton samples were collected using a range of standard plankton nets including 64, 100, 135 or 200 μm. Replicate (n = 2) oblique or vertical hauls (depending on station depth) were done at each station as close to the mangrove roots as was possible. Animals were always

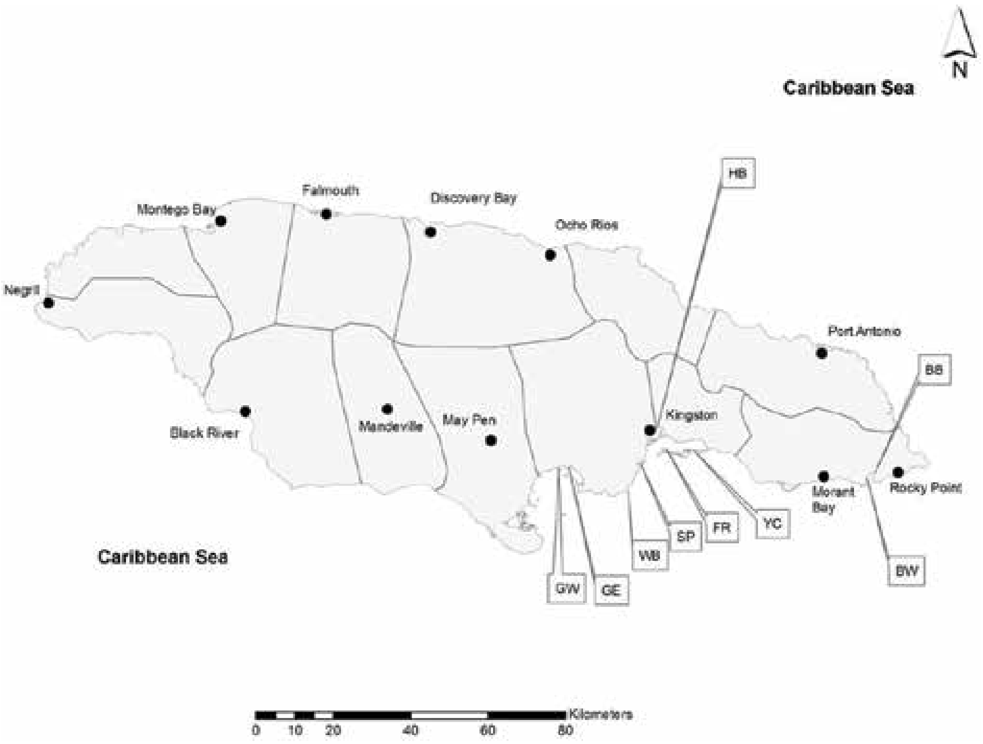

Figure 1. Map of Jamaica showing the mangrove areas sampled on the south-east coast of the island. BB – Bowden Bridge; BW – Bowden West; YC – Yacht Club; FR – Fort Rocky lagoon; HB – Hunts Bay; SP – Great Salt Pond; WB – Wreck Bay; GE – Galleon East; GW – Galleon West.

preserved immediately in the field after collection using 10% formalin. Samples were enumerated and identified for all taxa present using binocular microscopes (mag. ×10–×40) and with the aid of zooplankton guides [21–26]. In most studies, in addition to species lists, community analysis tests were employed which used species composition to investigate station affinities and identify possible associations. These included Jaccard Community Coefficient (JCC), Percentage Similarity Coefficient (PSC), and Principal Components Analysis (PCA). Cluster analysis diagrams/dendrograms were used [18] for to display station linkages using the PSC and JCC values. Mangrove root fouling communities were examined in the range of lagoons using both natural and artificial substrates (settlement panels) placed in the same area as the mangrove roots. Species composition and biomass of these root fouling communities were analysed contemporaneously with other parameters.

2.2. Findings and significance

2.2.1. Physicochemical parameters

Plankton is sensitive to many environmental influences such as salinity, temperature, dissolved oxygen levels, turbidity, and other factors [2, 13, 15, 27]. It was expected that these influences would be significantly different between mangrove lagoons due different levels of anthropogenic stress in each area. Hunts Bay (in Kingston Harbour) is a known eutrophic site while Wreck Bay is pristine [28, 29]. Consequently, the ideal water quality indices were expected to indicate a range of conditions (with Wreck Bay mangal as the pristine extreme and Hunts Bay mangal as the eutrophic extreme).

Most physicochemical parameters used in these mangrove water quality studies showed significant differences between stations, with the exception of particulate organic matter (POM). However, the distribution of these parameters between lagoons did not show the expected pattern. Furthermore, the lack of significant difference in POM values between stations was not expected since this parameter is often an important indicator in water quality analyses [30, 31]. POM is usually suspended matter of organic and inorganic origins. Usually the mixing of fresh water with sea water involves a marked change in pH and increases the level of dissolved salts, which promote the coagulation of fine particulate matter [30]. With the diverse sources and the shallow nature of mangrove lagoons, high POM may be a constant feature; irrespective of the eutrophication levels being experienced in the lagoons. Thus, POM may not be an adequate descriptor of the eutrophic status in mangrove lagoons.

When examining the physicochemical variables used across studies, depth at the station should be considered because of the influence of this variable on mixing and therefore on several physicochemical parameters (e.g. dissolved oxygen (DO), temperature, salinity). The studies showed that shallow and more exposed stations (e.g. Hunts Bay – HB) would consistently have extreme and episodic values for variables like temperature and salinity [18]. While other mangrove areas like the Great Salt Pond (GSP) which was also shallow did not have high temperatures because of the constant shading provided by mangrove trees. Temperature, therefore, is not an adequate descriptor of eutrophication status.

Dissolved oxygen (DO) behaved in a similar manner to temperature and was thus equally unreliable with only the high variability in DO values about the mean (episodic variability) at polluted stations being a consistent indicator. The eutrophic Hunts Bay (HB) had a high oxygen concentration (averaging >7 mg l^{-1}) but also with the greatest fluctuation about the mean. Poor water quality was expected at this station [13, 32, 33]; with constant blooms of sometimes toxic phytoplankton species. Ranston and Webber [32] further reported a rapid decline in DO from super-saturation at the surface to almost anoxic conditions at depth. Dissolved oxygen in natural waters varies with temperature, salinity, turbulence, the photosynthetic activity of algae and plants, and atmospheric pressure. The solubility of oxygen decreases as temperature and salinity increase. Significant variations in DO can occur over 24-h periods, in response to variation in temperature and biological activity (i.e. photosynthesis and respiration). Biological respiration, including that related to decomposition, reduces DO concentrations [34]. Increases in DO relate to phytoplankton concentrations as algal blooms in eutrophic waters can cause DO concentrations to raise dramatically. According to Gordina et al. [35], oxygen super-saturation is indicative of a degree of eutrophication and Borsuk et al. [36] suggested that oxygen depletion in estuarine bottom waters resulted from chemical and biological oxygen consumption associated with the decomposition of organic matter in the sediments and water column. This makes dissolved oxygen (DO) values in coastal systems difficult to explain as both extremes in DO (very high or very low values) may be indicative of deteriorating water quality. Hence, the diurnal fluctuation in this parameter has been suggested to be a better index than the absolute value.

Reduction/Oxidation Potential (REDOX) characterizes the oxidation state of natural waters. Oxygen, iron, and sulphur, as well as some organic processes can affect REDOX. Anaerobic respiration and the resultant increase in hydrogen sulphide are usually associated with a sharp decrease in REDOX and is evidence of reducing conditions [34]. REDOX values ranged between 250 and 300 mV for the mangrove stations sampled across the studies and while the variation between stations was statistically significant the overall similarity of the relatively low REDOX values [18] suggested that high reducing conditions are a constant feature of all these mangrove lagoons. More pristine bays like Discovery Bay on Jamaica's north coast have been reported to have REDOX values in excess of 500 mV [37]. Not all studies analysed nutrients across stations, however, where sampled Nitrates and Phosphates varied significantly between stations but with no consistent spatial pattern [14].

2.2.2. Biological variables

The biological variables that have been used to assess mangrove water quality in Jamaica include zooplankton species composition, frequency of occurrence, zooplankton community coefficients, total abundances and totals of numerically important sub-groups (e.g. Calanoids, harpactocoids, larvae), Chlorophyll *a* (phytoplankton biomass) and number of zooplankton "indicator species" m^{-3}. In some studies sessile root fouling organisms (epibiota) were analysed for their value in indicating ecosystem health, however, these were deemed unreliable for water quality. According to Hoilett and Webber [14] epibiota on the roots of the red mangrove which hang into the lagoon or are found on artificial substrates show interesting trends but the natural physiographic conditions (substrate type, degree of exposure, presence of rivers etc.) associated with each lagoon must be taken into consideration before conclusions can be made relating eutrophication to epibiota distribution. They indicated, however, that there is some value in the use of sessile fauna of individual taxonomic groups and Todd and Webber [16] also found *Phallusia nigra* (a solitary black ascidian) to be a useful indicator of varying eutrophication in the Kingston Harbour mangroves being found in high concentrations at the more disturbed sites like Buccaneer Swamp. However, the absence of *P. nigra* is not in itself an indicator of pristine conditions as the species does not occur in the eutrophic Hunts Bay.

Total phytoplankton biomass most consistently showed the expected eutrophication gradient [14, 18] across mangrove lagoons. According to Campbell et al. [18] Chlorophyll *a* was the most reliable planktonic index distinguishing stations as oligotrophic (0.21–0.55 mg m^{-3}) mesotrophic (0.57–2.55 mg m^{-3}) eutrophic (3.00–6.55 mg m^{-3}) and extremely eutrophic (>31.17 mg m^{-3}). However phytoplankton size fractions (which are extensively used in coastal water qualities) may be unreliable as the effect of low light negates the effect of high nutrients that would make the larger fractions, ≥ 20 μ in diameter, dominate. Hence, eutrophic mangrove lagoons have been shown to have greater proportions of the picoplankton fraction (0.2–2 μ diameter) than expected [14, 18].

Principal Components Analysis (PCA) used by Campbell et al. [18] showed harpacticoids and the animal *Dioithona oculata* (a cyclopoid) were major components for all stations as well as the larval plankton. *Acartia tonsa* (a calanoid) was identified by Hoilett and Webber [14] as consistently occurring across mangrove areas and varying along an eutrophication gradient. Mean total numbers of zooplankton varied significantly between stations. Campbell et al. [18], for example, showed total values ranging between 789 animals m^{-3} at pristine Wreck Bay (WB) to 114,970 animals m^{-3} at eutrophic Hunts Bay (HB). HB also had maximum fluctuations about the mean. The group Larvae followed a similar pattern of distribution to the total numbers. The zooplankton in mangrove lagoons has been consistently found to be dominated by copepods and larvae [14, 18]. However, harpacticoid copepods and individual species like *A. tonsa* and *D. oculata* show greatest potential as indicators of eutrophication in mangrove lagoons.

Taxonomic richness (number of species) varied significantly across mangrove areas for most studies but did not seem to follow the expected eutrophication trend. For example, Fort Rocky lagoon (FRL) in the Port Royal mangroves which would be considered mesotrophic, had highest taxonomic richness [14, 18]; while Wreck Bay, a pristine mangrove area had consistently low richness. High diversity or high richness in zooplankton communities is usually a reliable index of pristine conditions [37]. However, the similarities in taxonomic composition between studies and across different lagoons, seem to suggest that mangrove lagoons have a 'basal group' of commonly occurring zooplankton species, where individual species or sub-groups (like larvae and harpacticoids) may only be used as indicators if they vary in relative abundance according to the levels of eutrophication of each lagoon. The entire group Harpacticoida, though sometimes small in total numbers, occurred with great frequency throughout the sampling period at all mangrove lagoons.

Some zooplankton species may also be useful as indicators of the influence of mangrove waters on other systems. For example, *D. oculata* is known to form swarms in water <30 cm deep among the prop roots of red mangroves (*Rhizophora mangle*) [38] and these swarms persist and remain with the mangrove water [39]. Another important species in this regard could be *A. tonsa* which was reported by Dunbar and Webber [5] to be one of the 'hardier' euryhaline species which dominated the eutrophic Hunts Bay and so has the potential to be indicative of the eutrophic conditions associated with the mangrove lagoons. However, *A. tonsa* may be indicative of eutrophic bays in general and not necessarily eutrophic mangrove areas [40, 41].

Total zooplankton abundances in mangrove lagoons can be extremely high reaching 10^5 individuals m^{-3} [42]. This was comparable to values found in some mangrove lagoons in Jamaica. However the values did not follow the eutrophication gradient. Total abundance of zooplankton in the eutrophic Hunts Bay was found to be as high as 563,339 animals m^{-3} [18]. However, Francis et al. [33] found values of 16,499 animals m^{-3} in Hunts Bay and Hoilett and Webber [14] reported means in excess of 1,000,000 animals m^{-3} found in the immediate area of the *R. mangle* roots at Wreck Bay. The latter being the most pristine mangrove site examined during the study. Hunts Bay receives nutrient rich water as well as high levels of pollution from several gullies [32] and areas of the mangroves have also been disturbed by "dredge and fill" activities occurring in the Bay. This disturbance of the sediments will also lead to significant enrichment of the water column. The pristine mangrove areas of Wreck Bay (WB) by contrast have no consistent enrichment sources and the sediments are made of coarse calcareous material. Total zooplankton abundances therefore were not shown to be reliable as indicators of eutrophication in mangrove lagoons.

Mangroves are tightly bound to the coastal environments in which they occur [43, 44]. They are influenced by physical and chemical conditions and can, also help to create them. As a result, changes to the system can have cascading long-term effects. Monitoring of these changes must be efficiently and accurately done and elements of the phytoplankton and zooplankton communities are here shown to be reliable indices for such monitoring exercises. The use of planktonic indices (e.g. Chlorophyll *a*, zooplankton groups like harpacticoids and larvae as well as individual species) have here been shown to be more reliable indicators of mangrove lagoon water quality than many physicochemical variables and the sessile root community. Furthermore, species like *D. oculata* and *A. tonsa* can be used to indicators of penetration of mangrove waters to other parts of the coast.

3. Phytoplankton and coastal dynamics

3.1. Phytoplankton biomass along the Hellshire coast

Coastal circulation, in tropical waters, has been attributed to astronomical tides, river discharge and meteorological forces of which wind is most important [45]. The strength and significance of each are dependent on a wide range of topographic, hydraulic and meteorological controls [46]. Gravitational circulation can also be a major contribution to the dynamics of an estuary at sub-tidal scales; however this is not usually evident in small, shallow, well mixed bays with weak freshwater inflows. This study seeks to use the phytoplankton biomass and distribution as a descriptor in the coastal dynamics of the Hellshire Coastline. The distribution and influence of Eutrophic Kingston Harbour waters has been of interest in Jamaica as the Hellshire Coastline has tremendous potential for tourism development. Understanding the sources of water to this area is critical to managing the resource.

The Hellshire coastline (**Figure 2**) is located to the southwest of Kingston Jamaica and covers approximately 27 km, of which the eastern portion (15 km). It has six major bays each with white sand beaches and coral reefs associated with the seaward edge of the bay [4]. To the north-east of the Hellshire coast is the Kingston Harbour which is highly eutrophic and believed to be a potential source of degradation to the Hellshire area.

Sherwin and Deeming [47] reported that flow from Kingston Harbour is initially to the south and then west towards the Hellshire coastline. Water is advected through this area along a path of least resistance and should experience oceanic dilution with increasing distance from the harbour. This knowledge, along with the observation of deterioration of coral reef and seagrass bed communities along the Hellshire Coastline, led to postulating that the influence

Figure 2. South-east coast of Jamaica showing Kingston Harbour and the Hellshire Coast.

of eutrophication from the Kingston Harbour was the source of high nutrient waters which flowed along the Hellshire coastline.

The bays investigated along Hellshire were Half Moon Bay (HMB), Two Sister's Bay (TS), Sandhills Bay (SH), Engine Head Bay (EH) and Wreck Bay (WB), which are in order of increasing distance from the Kingston Harbour as illustrated in **Figure 3**. The overall purpose is to indicate whether the bays are primarily influenced by the Eutrophic Kingston Harbour via or indicate whether there are other sources and conditions that influence in the phytoplankton distribution and hence water quality along the coastline.

3.1.1. The methods used

Thirteen stations were investigated over the study period November 1999 to January 2001. Station positions were selected based on the location of the shoreline irregularities in order to investigate the longshore current and so trace water masses throughout the area. Six stations were located outside of the reef system, approximately 2 km from the shoreline (within the continental shelf), which were termed 'nearshore stations'. A second set of seven stations were located within the embayments, between the shoreline and the reef system, which were termed 'inshore stations' (**Figure 3**). Nutrient loads exiting the Kingston Harbour are restricted to the upper 7 m of the water column [4, 7, 48–50] hence samples were collected in surface layers only. These stations were included to allow for a more accurate assessment of the phytoplankton biomass distribution between bays and the potential retention time of each bay.

Sampling occasions were selected based on the tidal phase, i.e. rising tide and falling tide. This was thought to represent extremes of circulation within the region as high tide would account for a fast turn over time or retention time and low tide accounting for longer retention time. Tidal cycle data were obtained from the Port Royal Tide Gauge and the Port Royal Jamaica Tide Charts.

At each station, surface water samples were collected within the first meter of the water column for all inshore ad nearshore stations and the phytoplankton biomass determined as Chlorophyll a using fluorometry, as previously described in this chapter.

3.1.2. Findings and significance

It was expected that with improved water quality or increased distance from the eutrophic influence of the Kingston Harbour, phytoplankton total biomass would gradually decrease [42]. It was also expected that with increased distance from the Kingston Harbour, a decrease in netplankton biomass and an associated increase in picoplankton would also be observed. This would be a result of netplankton being able to proliferate in nutrient rich area, whereas picoplankton would dominate in nutrient poor area due to their surface area to body ratio. It was also expected that total biomass should decline with distance from nutrient source. This trend would also be expected as stations change from inshore/bay towards the nearshore and offshore areas.

Analysis of 112 whole water samples revealed that, as expected, mean phytoplankton biomass showed a gradual decrease with increased distance from the eutrophic source (Kingston Harbour) and at nearshore stations (**Figure 4**). This supports the theory of dilution of Harbour waters by oceanic with increased distance from the harbour. The biomass at inshore stations, however, fluctuated with distance from Kingston Harbour, with a few stations found further along the coastline having a higher biomass than stations found closer to the harbour (**Figure 5**). This suggests that stations such as Engine Head Bay and Wreck Bay are atypical of expected trends even when weak trends exist.

Figure 3. Hellshire Coast showing nearshore (2 km from shore) and inshore (within the bay) phytoplankton sampling stations.

To properly analyse the variations in phytoplankton biomass collections had to be separated based on tidal cycle as it was found that the phytoplankton biomass during a rising tide varied significantly from those collected during a falling tide (ANOVA $p < 0.001$;

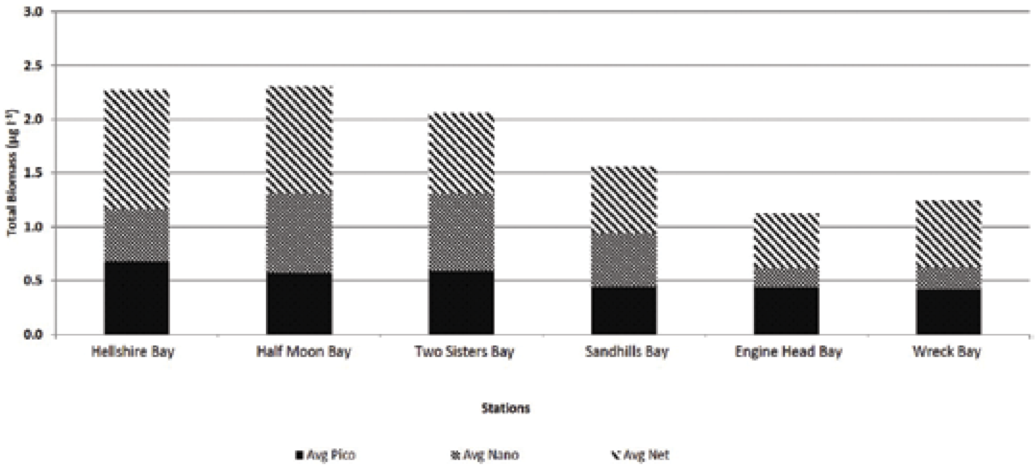

Figure 4. Mean total phytoplankton biomass (µg l^{-1}) for all samples for nearshore surface stations along the Hellshire Coastline, St. Catherine.

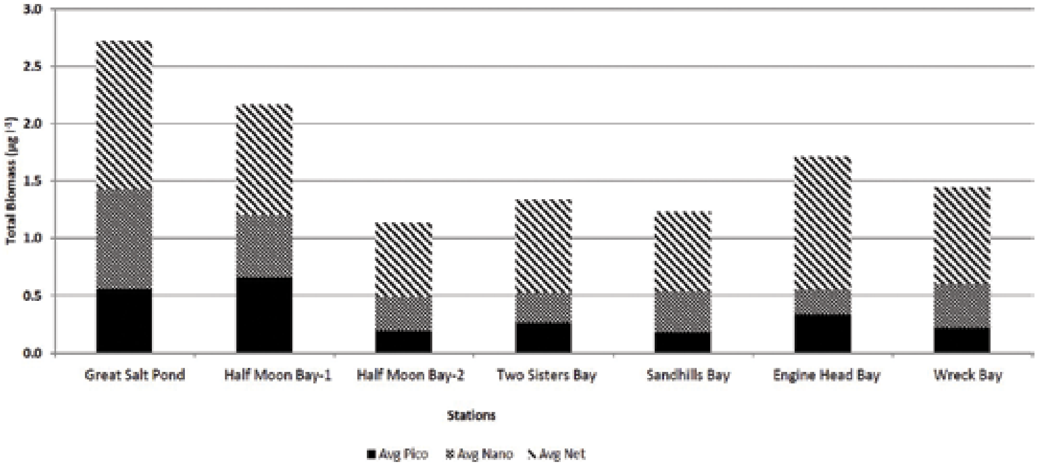

Figure 5. Mean total phytoplankton biomass (µg l^{-1}) for all samples for inshore stations along the Hellshire Coastline, St. Catherine.

df = 110). Average total biomass for nearshore surface stations collected during a rising tide showed the expected decrease along the coastline with increased distance from the Harbour (**Figure 6**).

In the case of the inshore stations the three stations closer to the Harbour showed a general decrease in biomass from the Great Salt Pond station to the Two Sister's Bay station followed by an increase from the Sandhills Bay to Wreck Bay stations (**Figure 7**). When nearshore stations were compared to the inshore stations it was found that moving from the Kingston Harbour towards Sandhills Bay the nearshore stations were generally higher than that of the

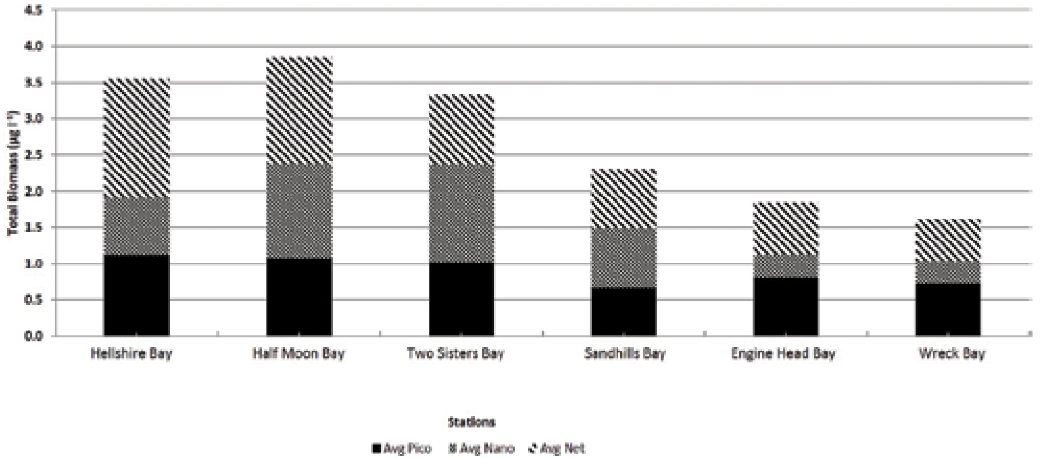

Figure 6. Total phytoplankton biomass (µg l^{-1}) for nearshore surface stations during rising tide events along the Hellshire Coastline, St. Catherine.

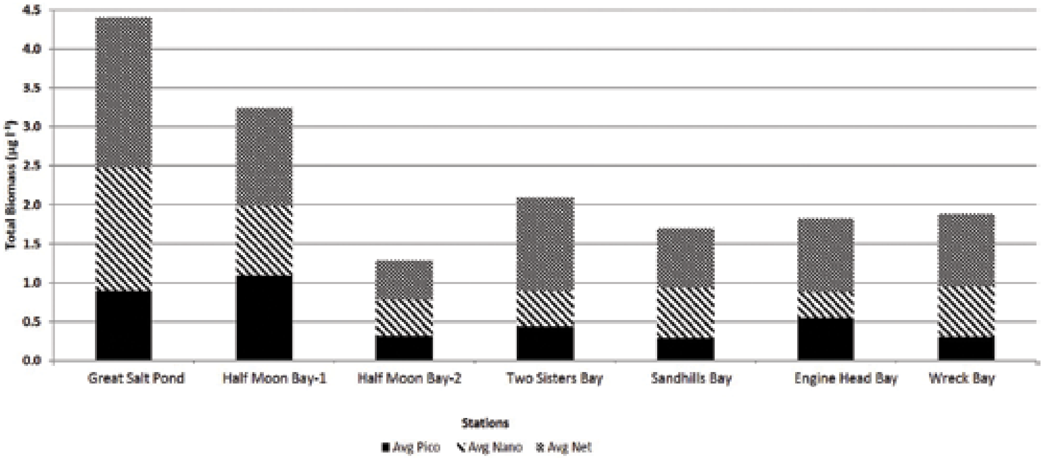

Figure 7. Total phytoplankton biomass (µg l^{-1}) for inshore station during rising tide events along the Hellshire Coastline, St. Catherine.

inshore station with the exception of Engine Head Bay and Wreck Bay where the biomass were slightly higher in the inshore areas. This pattern was even more evident when sampling occasions were analysed independent of each other. The variation in phytoplankton total biomasses was found to be significantly different between inshore and nearshore stations by way of ANOVA ($p < 0.001$; $df = 74$).

A gradual decrease in total biomass with increased distance from the Kingston Harbour was observed, although this pattern was not consistent. In some instances it was found that stations further away from the harbour on occasion had a higher biomass than that of the stations found closer to the harbour. Data indicate that the Two Sister's nearshore station had a higher biomass than that of the Half Moon Bay Station which is closer to the Kingston Harbour, followed by the Wreck Bay, which is located the furthest away from the harbour.

Further Analysis of variance tests showed the falling tide event to be significantly different from the data collected during the rising tide events. The general pattern in phytoplankton distribution was completely different from that of trends observed on the rising tide occasions. The nearshore stations showed a no significant difference between the total biomass of the surface stations (**Figure 8**). Total biomass for these stations seemed to be constant in moving from Half Moon Bay to Sandhills with a reduction in biomass found at the Engine Bay Station, followed by an increase at Wreck Bay which was greater than Half Moon Bay, Two Sisters Bay and Sandhills but less than Hellshire Bay.

At the inshore stations (**Figure 9**), values demonstrated an initially decrease in total biomass moving southwest along the coastline towards Sandhills followed by an exponential increase for the rest of the coastline. Wreck Bay had the highest biomass of all the stations. Statistically, inshore stations were significantly different from the nearshore stations ($p < 0.001$).

Interestingly **Figures 6–9** illustrated that during both rising tide and falling tide occasions, the biomass observed at Wreck Bay was not the lowest along the Hellshire Coastline as would be expected. In fact, during the falling tide event the biomass at Wreck Bay was the highest biomass collected on that occasion.

When percentage biomass was plotted for each station based on biomass it was seen that this trend was observed at some stations but not all. During the rising tide events it was seen that in some instances netplankton biomass decreased for some locations when inshore biomass were compared with nearshore biomass (**Figures 6** and **7**). This was evident for the stations associated with Two Sisters Bay, Sandhills Bay, Engine Head Bay and Wreck Bay when

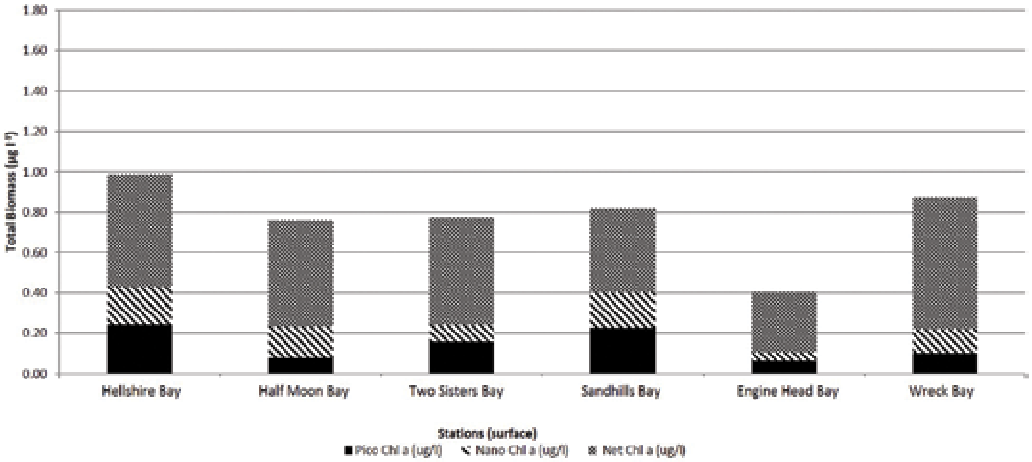

Figure 8. Total biomass (µg l^{-1}) for nearshore surface station during falling tide events along the Hellshire Coastline, St. Catherine.

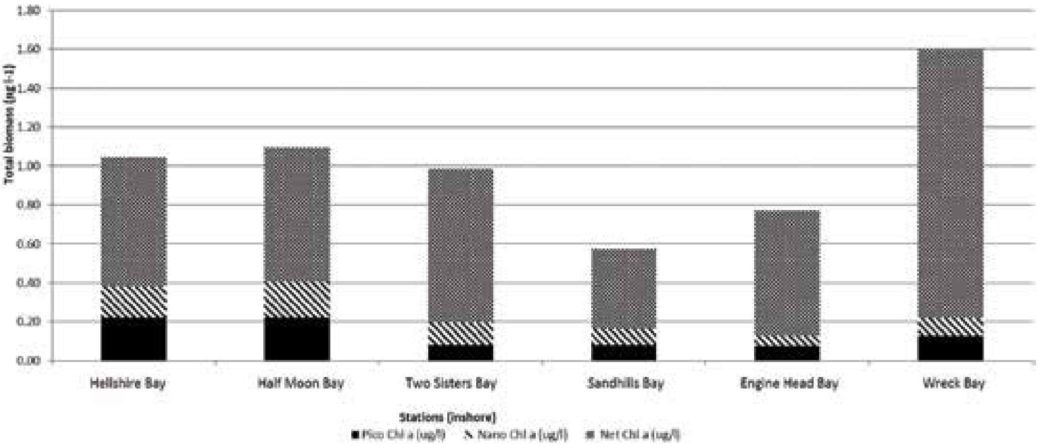

Figure 9. Total biomass (µg l^{-1}) for inshore stations during falling tide event along the Hellshire Coastline, St. Catherine.

inshore stations were compared with nearshore stations, with a corresponding increase in picoplankton. Similar trend was observed for the percentage of netplankton during a falling tide where increases were observed when inshore stations were compared with nearshore. However, this was not observed for the picoplankton size class and there was no consistent pattern as percentage composition fluctuated along the coastline.

Phytoplankton distribution fluctuates along the Hellshire coastline with bay stations differing significantly from nearshore stations. In some instances it has been seen that regardless of tidal regime phytoplankton biomass at some down-coast stations was greater than up-coast (close to Kingston Harbour) stations with variables being observed especially at Wreck Bay, which is the furthest bay from the Kingston Harbour. This observed variability may be accounted for based on localized activity and retention due to circulation patterns in the inshore waters of some bays, especially Wreck Bay. Phytoplankton biomass was therefore successfully used to identify the existence of non-point sources of enrichment along Hellshire and proved to be a useful tool in coastal assessment that could inform management practices in an area. Therefore, in the absence of difficult to track Lagrangian devices or expensive Eulerian current meters, the phytoplankton have been used to indicate the influence of eutrophic waters on down-current well mixed bays on the south coast of Jamaica.

4. Primary productivity

4.1. Phytoplankton production along the Hellshire Coast South-east Jamaica

There has been a paucity of plankton productivity studies in Jamaican waters for both phytoplankton and zooplankton and direct production assessment of phytoplankton have only been conducted along the Hellshire area, south coast of Jamaica.

Phytoplankton are important components of any marine ecosystem as they are responsible for significant portions of the primary production in that environment. Three principal properties; species composition, biomass and production, have been commonly used in the assessment of the phytoplankton community [51]. Tropical oceanic waters are typically high diversity, low biomass and low production environments while Caribbean coastal and inshore waters are characterized by lower diversity (few species dominating and proliferating) resulting in relatively higher biomass and productivity values [52]. This high biomass and production in nearshore waters is often induced by sudden enrichment from land run off from point and non-point sources [53]. These considerations are important in understanding the ecosystem whether this understanding is needed for water quality analysis, conservation, development, ecosystem energetics or fisheries management. The Hellshire coast of the southeastern Jamaica (**Figure 2**) with a eutrophic Kingston Harbour to the north [13] and an oligotrophic Caribbean Sea to the south provided an ideal setting to evaluate the expected gradient of impact from a point source of land based run off on the primary production of a multiple use coastal area.

4.1.1. The methods used

Six litre samples of water were taken from a standard depth equivalent to 20–40% of surface illumination at three inshore stations (Hellshire Bay, Half Moon Bay, and Wreck Bay) three offshore stations equidistant from the Kingston Harbour and a control far removed from both Harbour and Hellshire influences [50]. These stations were selected on the basis of their estimated productivity since they all enjoy no light limitation. The samples were kept in a cool dark place while being transported to the laboratory where 250 mL portions from each of the seven stations were preserved for identification and enumeration, one litre replicates were filtered for chlorophyll a biomass determination and triplicate 300 ml portions were placed into BOD bottles. Four milliliter aliquots were removed from each filled BOD bottle to allow for the addition of the radioactive material. One milliliter of Sodium Bicarbonate solution containing 20 micro curies of radioactive carbon ^{14}C was added to each BOD bottle using a 5 ml hypodermic syringe [54]. One milliliter of 3(3,4-dichlorophenyl1)-1,1-dimethylurea (DCMU), a photosynthesis inhibitor was added to one of each triplicate [19, 55]. The sealed bottles were incubated for 4 h in the sea at various depths which simulated 20–40% of surface illumination at their original stations [56]. This was done to ensure that the algal cells remained at light intensities similar to their natural habitat.

Determination of Primary production by ^{14}C technique was carried out as described by Steemann Nielsen [57], modified for scintillation counting by Wolfe and Schelske [58], and as reported by Parsons et al. [54]. The scintillation count was carried out on a Beckman liquid scintillation system counter (model no LS 100). Size fractionating was conducted by filtering 250 mL of the incubated sample through nucleopre filters of three pore sizes (20, 2 and 0.2 μm). Components less than 0.2 μm in size were treated by the acid bubbling method before the addition of the scintillation fluid [59, 60].

4.1.2. Findings and significance

The mean primary production for the sampling period was greatest at the Kingston Harbour (21.1 g C m^{-2} $year^{-1}$) and lowest at the oligotrophic control site (0.52 g C m^{-2} $year^{-1}$) confirming the expected difference eutrophic and oligotrophic primary production. Although these values are not high when compared globally [61] the comparisons between the values recorded at different areas of the Hellshire coast are important.

Primary production values and size distribution at offshore stations (2.63–0.88 g C m^{-2} $year^{-1}$) were lower with increasing distance from the Harbour and indicated an exponential decline in production with distance from the Harbour point source. This is expected based on the volume, consistency and significance of the point source as reported in similar studies [61]. Values at inshore stations (36.75–18.39 g C m^{-2} $year^{-1}$) were more than 10 times greater than offshore stations at the same distance from the Harbour, with primary production values at one station (Hellshire Bay) exceeding that at the eutrophic Kingston Harbour and other turbid and enriched estuaries [62, 63]. Inshore waters are therefore much more productive than offshore waters and on occasion demonstrated higher productivity than eutrophic waters without significant point source inputs.

At all seven stations the nanoplankton fraction (2–20 μ diameter cells) dominated production, especially at the Harbour and inshore stations. Production in the picoplankton (0.2–2 μ diameter cells) and netoplankton fractions (greater than 20 μ diameter cells) together contributed 40–50% of the primary production indicating some, but not great diversity in the composition responsible for the primary production throughout the area.

Mean assimilation numbers, which are an indication of the efficiency of the biomass in primary production, were found to be similar at the offshore stations and the control station (17–19 g C g Chl^{-1} h^{-1}). At all offshore stations picoplankton and nanoplankton assimilation were marginally higher than netplankton assimilation which indicates a homogenous system with no differential efficiency with marginal dominance in efficiency by the nanoplankton at the control station. Assimilation numbers at the inshore stations (45–70 g C g Chl^{-1} h^{-1}) were significantly greater (2–3 times greater) than those recorded at offshore stations and surprisingly even higher than the Harbour and three time greater than assimilation values reported by Glover in cultures in 1980. Phytoplankton at inshore stations influenced by non-point sources of enrichment are therefore significantly more efficient at primary production than the phytoplankton influenced by the enrichment from the known point source at the Harbour.

Within the inshore stations the picoplankton fraction (0.2–2.0 μm diameters cells) dominated the assimilation with highest values, not at stations close to the Harbour. This size fraction dominates where nutrient enrichment is low but consistent either from the non-point sources or by retention and regeneration mechanisms to facilitate proliferation [64, 65]. These results indicate that the non-point sources and the mechanisms operating at the inshore stations bays are significant sources of primary production to the Hellshire coast, a feature which is not uncommon where ground water percolates into the coastal waters [66].

4.1.3. An extreme rainfall event

Primary production values associated with the extreme rainfall event were variable at the offshore stations but only significantly higher at the offshore station furthest from the Harbour. Production at the Harbour declined from 21.1 to 8.76 g C m^{-2} $year^{-1}$ while values increased dramatically, ten times higher than values over the normal period, to 11.39 g C m^{-2} $year^{-1}$ at the station furthest from the Harbour. The reduced primary production at the Harbour even in the presence of increased point source enrichment may be the result of reduced light climate and reduced salinity [67] as silt laden fresh waters engulfed the entire coast. The increased production at great distance from the point source demonstrates the influence of the point source in flushing and providing significant enrichment but with reduced siltation to an offshore body of water resulting in algal proliferation. The occurrence of the extreme rainfall event resulted in marked changes in the size fractionated primary production pattern at offshore stations. The nanoplankton fraction which normally represented 50–60% of the production year round was as high as 90% after the rainfall event. The effect of this event on the phytoplankton production along the Hellshire coast was the result of exploitation of the changed condition by one genus *Protoperidinium* sp. which dominated the samples observed confirming the work of Zeeman [68], Webber et al. [49] and Adolf et al. [69].

The point source of the Kingston Harbour is an important contributor to the primary production of the Hellshire coast and under extreme rainfall events becomes the overwhelming feature determining the quantity, efficiency and location of primary production. The non-point sources along the Hellshire coast are also important but become significant localized impacts limited to inshore waters with significance determined by persistence of non-point release and nearshore mechanisms which facilitate retention and regeneration of especially picoplankton cells.

5. Modelling trophic flows through the plankton using Ecopath

While several studies have been done on these individual ecosystems, few, if any, have attempted to link or compare the areas, in terms of energy flow (as is possible using Ecopath). Ecopath was first developed to estimate the standing stock and production budget of a coral reef ecosystem in the Hawaiian Islands [70, 71]. It was further modified for use in any kind of aquatic ecosystem [72] and requires the input of at least four basic parameters as well as the diet composition for each consumer group. These parameters included: biomass; production/biomass ratio; consumption/biomass ratio and ecotrophic efficiency. Once these inputs of the basic parameters and diet compositions are completed, a mass-balanced trophic model of the ecosystem was produced by balancing the model, that is, modifying the entries until input = output for each consumer group.

One of the most important applications of this software is its ability to apply a selection of Odum's twenty four attributes of ecosystem maturity [73] to the mass-balanced model [72, 74] in order to facilitate a description of the stage of an ecosystem's stage of development. This can be a very important tool to be used for effective management of the fisheries in these areas. The economies of a large number of countries are dependent on, or partially dependent on, the fisheries of these countries. If any attempts are to be made to effectively manage these fisheries, the systems which support these fisheries must be understood.

5.1. The methods used

A fairly novel use was made of the software when Ecopath 5.1 and Ecopath with Ecosim (EwE) were used to model the trophic flows within the plankton communities in Discovery Bay, on Jamaica's north coast [75] and Foul and Folly Bays located in the Morant Wetlands on the extreme eastern end of the island [76], respectively. Ecopath with Ecosim is usually used to model trophic flows through fish and other macrofauna, with the plankton being used as an input or source of food.

Discovery Bay was considered to be a fairly pristine bay, with mean zooplankton abundances between 1077 ± 91 and 3794 ± 87 animals m^{-3} and phytoplankton biomass between 0.4 and 0.8 mg $m^{-3.}$ Foul and Folly Bays were found to be even more pristine with mean total zooplankton abundances ranging from 282 ± 56 to 3459 ± 752 animals m^{-3} and phytoplankton biomass between 0.14 ± 0.04 and 0.34 ± 0.2 mg m^{-3} [76].

5.2. Findings and significance

The Ecopath model for Discovery Bay indicated that "it was clear that this was still a developing ecosystem with open mineral cycles and poor nutrient conservation" [75]. Furthermore, the bay "would not be particularly resistant to perturbations. It would therefore be unable to easily recover from significant stresses (eutrophication; increased fishing efforts etc.) imposed on the ecosystem" [75]. This was thought to be indicative of the need for management strategies to control the use of the bay.

On the other hand, the Ecopath model of Foul and Folly Bays (Morant wetlands) indicated greater resilience in these bays than in Discovery Bay. They would therefore be better able to recover from stresses such as eutrophication [76]. The assessment of the plankton further identified the presence of high abundance of larvae, which when coupled with fast flowing currents through the bays, provides evidence that this area could be an "important source of larvae to other areas of Jamaica's south coast" [76]. Therefore, a strong recommendation for the area's protection could be made.

6. Overall conclusion

The new and unique uses of plankton ecology and productivity around Jamaica has been wide and varied with some interesting examples are demonstrated in this chapter. The specialized zooplankton communities which allow water quality characterization in mangrove lagoons, the description of coastal dynamics and the identification of point and non-point sources which result in spatial variation in primary production and the modelling of coastal trophodynamic flows to influence conservation and fisheries management are all unique and important. Through plankton ecology and production Jamaica's coastal ecosystem has benefited significantly from the improved understanding, meticulous monitoring, enhanced descriptions and innovative applications. This has facilitated informed management decisions for the sustained use of coastal ecosystems around Jamaica which can be extrapolated to other small islands and archipelagic states.

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Chapter 5

Ecology of Planktonic Atlantic Cod (*Gadus morhua*)

Stig Skreslet

Additional information is available at the end of the chapter

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Abstract

Atlantic cod larvae surviving the first weeks after hatching settle next years juvenile recruitment on Georges Bank (USA). It probably supports Hjort's critical period hypothesis that effects of climate on marine biological productivity control early-life history processes and recruitment in fish populations. Climate also regulates local ultraviolet sea surface radiation, which may potentially kill microbes pathogenic to planktonic cod eggs. Survival capacities of cod larvae depend on maternal effects on egg qualities attained during oogenesis, influenced by variable food sources for female cod. Actual survival of first-feeding cod larvae requires proper abundance of preferred prey, copepod nauplii, produced by fertile females. Temporal and spatial mismatch between cod larvae and prey is normal, extensive and lethal, counteracted by opportunistic behavior that optimizes encounters. In spawning habitats of Northeast Arctic cod, the abundance of *Calanus finmarchicus* nauplii possibly results from coastal biological productivity in the previous year, which may explain time lags in positive correlations between vernal river discharge and NEA cod recruitment. Extensive meltwater storage for year-round hydroelectric production probably limits food web productivity, survival of NEA cod larvae and stock recruitment. Global climate change and stock management interact ecologically with other anthropogenic influences concerning sustainability of Atlantic cod population systems.

Keywords: Norwegian Sea, Barents Sea, Gulf of St. Lawrence, Lofoten Islands, North Atlantic Current, Norwegian Coastal Current, Arctic Mediterranean Ecosystem, hydrological cycle, NAO, AO, UVR

1. Introduction

Like many other bony fish, Atlantic cod (*Gadus morhua*) emerges from its egg as a very tiny larva that spends its first juvenile life span in planktonic communities. The species inhabits the North Atlantic, from the eastern coasts of the United States of America and Canada to the Baltic and Barents Seas in Northwestern Europe. The species segregates into population systems ranging from local units inshore to extensive units that occupy wide continental shelf systems.

Atlantic cod is a socio-economic commodity traded in international markets for nearly a millennium, which created wealth that built nations and financed wars [1]. Harbors and communities for landing, processing and marketing cod products expanded when cod migrated in abundance for annual reproduction in known spawning grounds. Migrations failed in other periods, leaving starving families, bankrupt companies and weak local and national economies. Despite being subject to intensive scientific investigations from fisheries biologists for more than a century, the ecological causes for fluctuations in the economy of cod fisheries are still an ecological enigma.

About 150 years ago, a pioneer in Norwegian marine science, Georg Ossian Sars, was the first to observe fish to spawn pelagic eggs. He reported that fertilized eggs of cod spawning at the Lofoten Islands in Northern Norway (**Figure 1**) were buoyant, accumulating just beneath the sea surface in calm weather. He studied the embryonal development and kept eggs in aquaria until the hatching of cod larvae. By doing that, he developed criteria for identification of different stages in the morphological development of juvenile cod. He organized marine research expeditions in Arctic waters and found that adult cod spawning at Lofoten spent their summers in the northern Barents Sea, which established its status as one population. Sars understood the life history of Atlantic cod and discovered the population structure and migratory nature of Northeast Arctic Cod (NEA cod), which became his legacy as founder of international fisheries biology.

Today, bilateral research and management organized by Russia and Norway have succeeded in maintaining NEA cod at a sustainable level. Comprehensive research develops understanding of how the population interacts with other species in different habitats within its population system. Several planktivorous fish fall prey in habitats for somatic growth of juvenile and

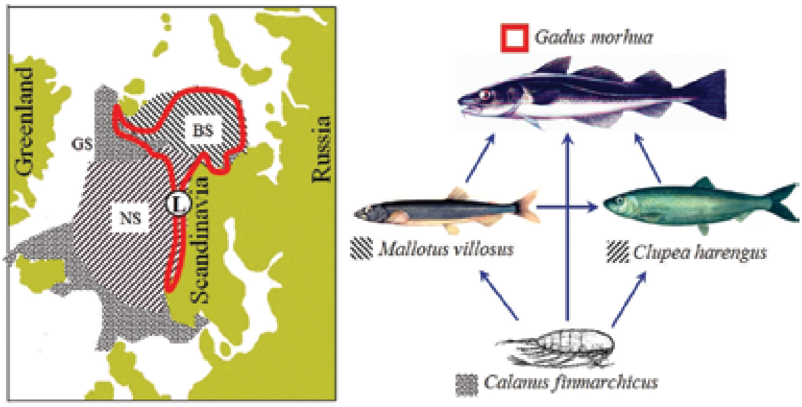

Figure 1. Main geographic distribution of NEA cod (*G. morhua*), Barents Sea capelin (*Mallotus villosus*), Norwegian spring spawning herring (*Clupea harengus*) and *C. finmarchicus* in the Norwegian, Greenland and Barents Seas (NS, GS and BS, respectively). (**L**) Main spawning habitat of NEA cod in the Lofoten archipelago. (Arrows) Directions of trophic energy flow.

adult cod in the Barents Sea (**Figure 1**). A single planktonic copepod species (*Calanus finmarchicus*) is the preferred prey of NEA cod larvae, and it produces much of the biomass that directly and indirectly fuels the entire food web of NEA cod. Sars did not know this, and he could not explain how an abundance of cod migrated to Lofoten in some years and were missing in others. Decades later, his successor as leader of the Norwegian fisheries science, Johan Hjort, concluded at the end of his service that fluctuations in the yield from fisheries in general were possibly due to environmental variability in population systems of fish [2, 3]. He suggested a concept of trophic causality in marine food webs, where primary production of phytoplankton was subject to interannual fluctuations, which regulated the reproduction and growth of zooplankton being food for juvenile fish. Hjort even hypothesized that the first encounter between larva and its prey was a critical period when starvation and mortality regulated the proportion of larvae that would live until the age of recruitment to the exploited stock.

For scientists who joined Hjort's paradigm, *C. finmarchicus* stood out as a key to understanding survival of fish larvae in the North Atlantic, being the most abundant metazoan species in Arcto-boreal waters [4]. Therefore, the scene for scientific testing of Hjort's critical period hypothesis has frequently been habitats that feature a short planktonic food chain, established by Atlantic cod and *C. finmarchicus* that reproduce in concert.

Unfortunately, Hjort left fisheries science after World War I. His interdisciplinary research group in fisheries ecology dissolved when the Norwegian government would no longer finance the operation of a seagoing research vessel, but his legacy survived. For more than a century, his critical period concept was a beacon for the international community of fish population ecologists and fisheries biologists, but they now question its general validity [5]. The current understanding is that interannual variability in recruitment of NEA cod can result from many sources acting throughout pre-recruit life, one of the most important being cannibalism from older year-classes [6]. Some even concluded 'the quest for solving the Recruitment Problem has been called off' [7]. However, maybe Hjort and modern fellow scientists did not study the same population system, meaning that its state has changed along the course of a century and that Hjort was correct in his time. Ecological conditions ruling then may still work but overshadowed by man-made variables in modern times.

2. Geographic distribution, genetic variability and early ontogeny

Atlantic cod belongs to the family of Gadidae, a circumpolar taxon on the northern hemisphere. It is also true for the genus of *Gadus* that contains several species. Mackie and Richie [8] suggested that *G. morhua* has evolved into two closely related subspecies, the Pacific cod *G. morhua macrocephalus* and the Atlantic cod *G. morhua morhua*. In this paper, information referring to cod and *G. morhua* addresses only Atlantic cod.

Atlantic cod establishes populations on the continental shelves on both sides of the North Atlantic. It occurs from North Carolina to the Labrador Sea on the eastern shelf of North America and occurs periodically in southern Greenland depending on sea temperatures. In European waters, it exists from the Bay of Biscay to the Svalbard archipelago at N80° and from Iceland at W20° to Novaya Zemlya at E50°. It may live for considerably more than 20 years and grow into large size, exceeding 55 kg and a total length >1.8 m, which is not common today due to extensive commercial exploitation.

Atlantic cod displays a variety of ecotypes adapted to particular environmental conditions. Some are stationary in coastal waters, and others migrate to spawn at a distance from where they forage and grow between spawning seasons. Cod wintering in Newfoundland bays at subzero temperatures produces antifreeze glycoproteins that prevent formation of ice crystals in their plasma [9]. The plasticity of physiological and biochemical processes that allow short-term adaptation in cod are not known, but epigenetic changes caused by methylation of DNA seems to be a promising field of research.

New genomic research on Atlantic cod revealed that two distinct ecotypes of homozygotes occur [10, 11]. One is an original ecotype that adjusts rapid changes in swim-bladder volume resulting from vertical migration close to the surface. The other has evolved from the original, having the same genome except for some inverted DNA regions. The inverted genome changes the swim-bladder function and causes cod to forage and migrate in deep water. The two ecotypes occur on both sides of the Atlantic.

In Europe, the original genome dominates from the British waters to the Baltic and White Seas, which includes Norwegian Coastal (NC) cod [11]. The inverted genome occurs in NEA cod that forage and grow in Barents Sea habitats, except when adults migrate to spawn in March-April along the Norwegian shelf even as far south as below N62°. NEA cod are homozygous for the genomic inversions, while NC cod are homozygous for the ancestral non-inverted genome. Experimental crossing of the two homozygotes produces heterozygotes. Such heterozygous cod are common in coastal waters north of Lofoten and less common at the southern spawning habitats of NEA cod. It is rare in the White Sea and the Skagerrak coast of southern Norway [11]. In the theory, mating by two heterozygous cod in Norwegian waters may result in heterozygous offspring as well as homozygous siblings being either NEA cod or original NC cod, but scientific evidence remains unobserved in nature.

No information exists about differences in the early ontogeny from fertilization to hatching of eggs in the three ecotypes. Variability in ontogeny probably rather depends on environmental effects during ripening of eggs in female ovaries and ambient temperature on embryonic development before eggs hatch. In general, embryonic ontogeny lasts for a couple of weeks, being inversely related with temperature, in Northern Norway typically lasting about 3 weeks at 3°C [12].

Cod larvae emerging from the egg carry a yolk sac that supports further development of organs necessary for subsequent intake and digestion of prey. At this stage, the larva has no functional jaw but an opening to the mouth cavity that allows it to drink seawater, which causes passive accumulation of small microalga (1–4 μm) in the gut. However, cod larvae may actively filter larger microalgae (6–10 μm) at rates 500–7000 times the drinking rate, facilitated by flagella on the visceral arches [13]. The larger algae may constitute nearly 40% of the gut content in larvae 7 days old but decreases in older larvae requiring animal protein to grow.

Marine microalgae accumulate orthophosphate (PO_4-P) from seawater and store intracellular polyphosphate [14], which may be imperative for somatic development and survival of cod larvae. They use phosphate for synthesis of adenosine triphosphate (ATP) that transfer energy to all intracellular life processes, and for bio-syntheses building skeletal calcium phosphate (aragonite), phospholipids in every cellular membrane and nucleotides building DNA and RNA in all cells. Thus, feeding on phytoplankton seems essential to develop organs and morphological capacities necessary to hunt and digest prey. NEA cod larva is about 4.5–5.1 mm long when the yolk sac is empty [15], and they need animal protein to grow. Van der Meeren and Næss [16] observed that cod larvae reared in mesocosms stayed alive feeding unselectively on protozoans but increased their specific growth rate from 2.8 to 21.7% when changing to their preferred prey, the nauplius of copepods.

3. Coastal ecotypes distinguished by egg retention in northern Norway

Based on numerical modeling, Myksvoll et al. [17] identified three categories of spawning strategies of Atlantic cod in Norwegian waters. The categories represent oceanic cod, migratory coastal cod and fjord cod. Oceanic cod is equivalent to NEA cod spawning in habitats from where the eggs drift offshore into the Norwegian Coastal Current (NCC). It runs northwards outside the official Norwegian coastal baseline that encloses all islands and headlands along the coast, transporting the progeny of NEA cod to nursery habitats in the Barents Sea. Coastal cod spawn among islands inside the baseline but outside fjords. Their eggs are temporarily retained by eddies and backwaters between shallow archipelagos, which causes the eggs from several spawning habitats to hatch within the region of a common population system. Fjord cod spawn at the head of fjords, and the retention of eggs supposedly lasts long enough to cause hatching within the fjords.

An empirical study in 20 Norwegian fjords south of the Lofoten Islands as far as to the eastern North Sea demonstrated retention of cod eggs particularly in fjords with shallow sills [18]. In a large fjord at about N70°, and with no sill that separated it from the Barents Sea, cod eggs spawned in March-April did not accumulate at the fjord's head. Most were probably buoyant in high-salinity surface water (≥33 psu) advected by predominant wind drift to hatching habitats outside the fjord [12]. Retention of locally spawned eggs only appeared to occur in a small side fjord with shallow sill, after the vernal freshwater discharge had started in May. Coastal cod in the main fjord grow faster than cod in the side fjord, but both mature at the same age, while earlier than NEA cod [19]. The two stocks perhaps fit the distinction between coastal and fjord cod suggested by Myksvoll [17].

Fevolden and Pogson [20] concluded that genetic heterogeneity exists among resident populations of cod in different fjords. Thus, the gene flow among fjord populations throughout Northern Norway may be considerably lower than previously believed. However, Myksvoll et al. [21] observed that parts of the eggs spawned by fjord cod left the local fjord at rates that depended on local estuarine circulation and winds during the main spawning season (March-April). Few eggs and larvae seem to drift from one fjord to another, but the rates are possibly sufficient to establish genetic connectivity that makes neighboring fjords unite into metapopulations ('population of populations').

4. Plankton ecology of cod spawning habitats in fjords

Every fjord in Norway is probably a spawning habitat for Atlantic cod. The typical fjord is an estuarine system where freshwater is discharged to the fjord's head, its inner part. The discharge may occur naturally as vernal meltwater from rivers in May–July or from hydroelectric power plants governed to produce in other seasons. Discharged freshwater mixes with seawater imported from the open sea, which produces brackish surface water that contains far more seawater than freshwater when it leaves a fjord. The brackish outflow causes a salter compensation current to flow in opposite direction underneath, which tends to retain cod eggs by transporting them toward the head. However, retention depends on how buoyant eggs spawned during runoff are and the amount of freshwater discharged.

Most Norwegian cod spawn their eggs before the maximum vernal freshwater run-off season in May–June. Cod eggs sink in brackish fjord water (salinity <30 psu), and all are buoyant at 34 psu which is classified as coastal water [22]. Thus, the eggs do not ascend into a brackish surface current flowing out of a fjord. Physical modeling support that they normally attain neutral buoyancy in more saline coastal water advected by the compensation current, which retains the eggs at the fjord's head [21]. However, a proportion of cod eggs spawned in years with exceptionally low discharge or in locations that receive little freshwater from small drainage areas may be subject to seaward transport by wind-driven surface advection. Heavier eggs may remain neutrally buoyant at larger depths and stay retained by inward advection, and their proportion varies with the salinity gradient between the surface outflow and the compensation current.

Little information exists on the first feeding and growth of fjord cod larvae into metamorphosis and subsequent recruitment to fjord stocks. However, the estuarine biota of fjords differs from habitats for first-feeding larvae in Lofoten, which is evident in one of the regions modeled by Myksvoll et al. [17]. There, a permanent fjord stock of Atlantic cod recruited juveniles <1 year old every autumn or winter [23]. The habitat is a typical fjord characterized by a 156 m deep basin separated from a deeper fjord system by its 60 m deep sill. Today, its two rivers receive regulated freshwater outflow from hydroelectric production. In its previous natural state, the vernal meltwater discharge generated strong estuarine circulation that started in May and reached maximum in June [24]. A characteristic spring bloom of diatoms, dinoflagellates, euglenophytes and about 6-μm-long nannoflagellates develop in April [25]. The production of diatoms decreased in May, while the production of other phytoplankton proceeded. Nannoflagellates dominated in a year with moderate freshwater supply, and euglenophytes dominated when the discharge was stronger. The dominating nannoflagellate species probably originated from freshwater habitats [25] and possibly continued to grow in the fjord's oligohaline surface water. Euglenophytes are large flagellates about 50 μm long that may also live in freshwater. They may be both phototrophic and phagotrophic that feed on bacteria and small flagellates. Thus, the brackish water biota of Norwegian fjords forms food webs that in general deviate from what occurs in the euhaline habitats (>30 psu) of cod larvae in Lofoten.

Fjord stocks of *C. finmarchicus* in juvenile ontogenetic stages (nauplii and immature copeodids) tend to be abundant during moderate freshwater discharge in May-June and practically absent when the discharge was strong [26]. However, Bucklin et al. [27] observed that *Calanus* in fjords often consists of three species, *C. finmarchicus*, *C. glacialis* and *C. helgolandicus*. They are difficult to distinguish by morphological characters, and it is probable that copepods previously identified as *C. finmarchicus* in Norwegian fjords may be a mixture of these. In any circumstance, if estuarine circulation retains cod larvae in fjords, it seems that they would have richer diets of microalgae and nauplii and a better scope for survival in years with reduced estuarine circulation.

5. The population system of Northeast Arctic cod

NEA cod is one of the most thoroughly studied fish stocks worldwide [6], which covers all levels of its life history and all parts of its geographically extensive and ecologically complex population system. Commercial fishing has occasionally caught adult NEA cod in Spitsbergen waters at about N80°, and their spawning occurs in Norwegian coastal waters from about N60° to about N70° at the entrance of the Barents Sea. Adult cod >6 years old repeat annual upstream spawning migrations in Atlantic water flowing northwards along the continental shelf break, termed the Norwegian Atlantic Current (NAC). They return to the banks of the Barents Sea to forage between each spawning and mainly occupy western habitats influenced by warm Atlantic water. Immature cod mainly occupy the colder eastern parts, north of the Russian coast. While adults prefer temperatures >1°C, the juveniles tolerate −1.8°C in the northern Barents Sea [28].

Eighty years of research have tried to settle whether NEA cod and a variety of local stocks in Norwegian coastal waters effectively make up one large population or >1 non-interbreeding groups [29]. Important steps made lately [10, 11] indicate that some interbreeding may occur, possibly mainly in Lofoten where most NEA cod spawn. The Lofoten fishery lands mostly NEA cod, but it traditionally starts with the arrival of NC cod that assumedly migrate from banks on the continental shelf. Some of the NC cod possibly pass by, destined to spawn in habitats on the mainland coast. Other NC cod spawn in concert with NEA cod in Lofoten, which opens for some interbreeding. However, it has been suggested that the mating of cod involves lekking, starting when females ready to spawn seek aggregations of males that compete for female attention. Male courting involves dancing, fin postures and noisy muscular drumming on their swim bladders [30]. NC cod and NEA cod possibly have different courtship displays that discourage mating. However, ripe NEA cod and NC cod may occur simultaneously in close spawning habitats and even be caught in the same catch at spawning grounds off the Lofoten Islands [29]. This suggests that some interbreeding between NEA and coastal cod may occur, at least by chance in seawater where gametes from both kinds of cod are mixed. If both parents may be homozygous, one with original genome and one with the inverted NEA cod genome, the offspring will be heterozygous.

Normally, the massive immigration of NEA cod from the Barents Sea is likely to outnumber NC cod in Lofoten. That may not be true in years when NEA cod failed to migrate into some of the traditional spawning habitats in Lofoten, while NC cod perhaps occurred in normal abundance. Thus, some scientific results reported on cod eggs and larvae from Lofoten may not strictly represent NEA cod. In any circumstance, cod larvae of either kind probably do not behave very differently to local environmental conditions in a common habitat and represent Atlantic cod in general.

In the main spawning habitat of NEA cod in the Lofoten archipelago, Wiborg [15] observed that larvae <6 mm long had stomachs containing mainly copepod eggs and nauplii of *C. finmarchicus* and *Metridia* spp. *C. finmarchicus* that was most abundant in Lofoten is widely distributed in the North Atlantic [4]. During copulation with males, the females of *C. finmarchicus* store semen in their spermatecs, i.e., small organs keeping spermatozoa alive for fertilization of eggs on later occasions. The females are batch spawners, meaning that they produce eggs repeatedly in numbers and at frequencies that depend on the amount of feasible food. Their diet is mainly autotrophic microalgae and to some extent ciliates and other heterotrophic microorganisms. The females produce their first egg batches during the phytoplankton spring bloom, which in boreal habitats lasts for about 1 month, starting after spring equinox at 20–21 March. NEA cod in Lofoten has by then started their spawning season that peaks in the late March or early April, and the abundance of their first-feeding larvae culminate during a period from the late April to the middle of May [31].

The eggs of *C. finmarchicus* hatch in 1 or a few days depending on ambient seawater temperature. The emerging nauplius stage one (NI) molts into a succession of stages (NII–NVI) before the individual grows through six copepodid stages (CI–CVI), the last being sexually mature adults. The mouth of cod larvae ≤6 mm can possibly handle any nauplius stage and even *C. finmarchicus* CI [15]. Thus, an understanding of how reproduction success correlates with recruitment to an exploited cod stock depends on variables that regulate the abundance of proper food.

Wiborg [15] supposed that adult *Pseudocalanus* spp. and *C. finmarchicus* CII were appropriate prey for >6 mm cod larvae. Lynch et al. [32] used data from Georges Bank to develop a conceptual model for larval cod feeding on stage-structured prey populations. The model suggested that *C. finmarchicus* alone was not a sufficient prey for 6 mm and larger cod larvae. They needed a supplement of *Pseudocalanus* spp. for their survival and growth. However, Lynch et al. [32] had no information on prey smaller than *C. finmarchicus* CI and could not address dietary requirements for smaller cod larvae.

As they grow, new generations of NEA cod larvae drift northwards from the spawning habitats. Their habitat is now the NCC where the sea surface temperature may be about 10°C during summer [33]. Cod larvae grown at this temperature in experimental culture metamorphose into juveniles at a total length of <35 mm [34]. Metamorphosis is gradual, starting with changes related to swimming performance [35]. At 20 mm length, the spine displays a complete set of visible vertebrae, and a full set of functional fins have developed. At 35 mm length, the upper jaw is nearly as long as the lower, and the stomach digests the exoskeleton of copepods, which combined make the juvenile successfully feed on *C. finmarchicus* CIII–CV. However, its typical external morphology of older cod showing an upper jaw longer than the lower appears only when the juvenile cod is about 65 mm long.

NEA juveniles that enter the southwestern Barents Sea in August-September 5 months after spawning have total lengths 5.5–8 cm long, their size being directly proportional with sea temperatures ranging from 4.8 to 6.3°C [36]. They are then nektonic, forming schools foraging on zooplankton in depths down to about 100 m. They still feed on *C. finmarchicus* that gradually molt into stage CV copepodids that enter diapause, which means that they no longer perform diurnal vertical migration (DVM). They sink toward the bottom, which possibly stimulates both carnivorous zooplankton and juvenile cod to enter hyper-benthic habitats of the Barents Sea.

In terms of fisheries science, the abundance of juveniles of the year is termed 0-group fish until the end of the calendar year [6], when the generation becomes 1-group fish. Every year in August-September, Norwegian and Russian scientists survey the abundance of juvenile fish in the Barents Sea, using advanced acoustic instruments and trawls. They also monitor older fish and their predators and prey, which paint a comprehensive picture of the Barents Sea as a large habitat system for commercial fish stocks.

The Barents Sea is often described as an ecosystem [37, 38], which is not strictly true according to the theory of systems ecology [39]. A true ecosystem should conserve biogenic energy that flows through the system's complete food web, at least containing populations that are the most influential producers of biomass. The Barents Sea is different, being extremely open regarding exchange of biomass with the Norwegian Sea.

Only parts of the population system of NEA cod occupy the Barents Sea. Most of its spawning habitats occur along half of Norway's coastline (**Figure 1**). They overlap the population systems of *C. finmarchicus* and the Norwegian spring spawning herring (*Clupea harengus*), both having population systems that occupy the Norwegian Sea. NEA cod also overlaps with parts of the population system of Barents Sea capelin (*Mallotus villosus*) that extends farther north. Both herring and capelin migrate to spawn eggs deposited in benthic habitats along the Norwegian coast. Their meroplanktonic larvae feed on *C. finmarchicus* nauplii and copepodids while transported by the NCC. 0-group juveniles of herring and capelin compete for planktonic food in the Barents Sea, and older than 0-group juvenile herring are predators on capelin larvae.

0-group herring and capelin are essential for chick survival in colonies of cliff-breeding seabirds along the Norwegian coast. The adult seabirds do not compete with their offspring, some foraging rather on juveniles of cod and other Gadidae that spawn along the Norwegian coast. A number of seals and whales prey on Atlantic gadoids and compete with human exploitation, which combined accounts for most of the mortality in NEA cod after recruitment to the exploited stock.

When herring start to mature sexually, they leave the Barents Sea for their first spawning along the Norwegian coast. After each annual spawning, adult herring migrate to the western Norwegian Sea to feed during summer, mainly on *Calanus hyperboreus*, a copepod that reproduces in the Greenland Sea [40]. It may have a multiannual life cycle in high-Arctic water, which possibly maintains a pan-Arctic population system. Another copepod, *Calanus glacialis*, has a circumpolar distribution associated with polar sea ice and the Arctic continental shelves of Eurasia and North America. The polar production of *C. glacialis* is important to the growth of capelin, which establishes a major food chain for NEA cod.

Many benthic invertebrates that fall prey to cod in the Barents Sea reproduce by meroplanktonic larvae. The deep-sea prawn *Pandalus borealis* is an important demersal food source for NEA cod and widely distributed in the Barents Sea. Its larvae may live in pelagic habitats for 2–3 months before they settle as epibenthic juveniles. The species occurs along the entire coast of Norway, and some of the recruitment of juveniles to the Barents Sea stock is due to dispersal of larvae by advection of Atlantic water from reproduction habitats in Norwegian coastal waters [41].

NEA cod is a very opportunistic predator in the Barents Sea. It is omnivorous on every stage in its life history. The animal diet of juveniles changes gradually from mesozooplankton (0.2–2 cm) like copepods to macrozooplankton (>2 cm) like decapods, and to planktivorous fish. They eventually turn to predation on a variety of epibenthic invertebrates and demersal fish living at or on the bottom. It is also cannibalistic, a behavior it expresses even as a larva [34]. 1-group NEA cod is a major predator on 0-group cod when there is little capelin in the Barents Sea, and cannibalism on older cod increases with increasing size of the cod spawning stock [6]. Cannibalism is an investment in the ecological resilience of the population, because it shortcuts and increases the trophic flow of biomass to the spawning stock, which buffers effects of predation and fishing on adult cod.

The versatile trophic roles of NEA cod couple its population to an interspecific multitude of population systems that differ in geographic extension, which makes the Barents Sea a very complex habitat system. It interacts with the Norwegian Sea and other large systems situated between the Eurasian and North American continents. Drainage of freshwater from continental watersheds forces the haline circulation of the Arctic seas (**Figure 2**), which shapes the hydrology of the Arctic Mediterranean Ecosystem (AME). The river systems are habitats

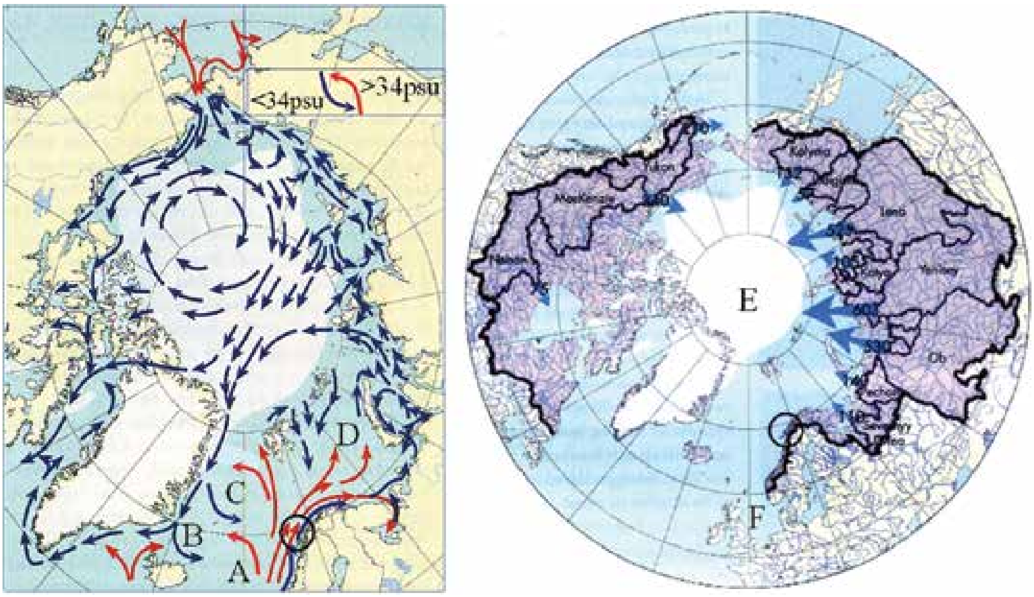

Figure 2. Polar projections of the Arctic Mediterranean Ecosystem, showing catchment areas for drainage of freshwater (right) and main circulation of sea surface water (left) distinguished by salinity (psu). (A) Norwegian Sea. (B) Icelandic Sea. (C) Greenland Sea. (D) Barents Sea. (E) Polar Sea. (F) North Sea. (Circle) Vestfjord, Lofoten Archipelago and offshore habitats of planktonic Northeast Arctic cod (*G. morhua*) (modified from imr.no (left) and caff.is (right)).

for diadromous fish that live parts of their life cycle in brackish and marine habitats. Several of them fall prey to Atlantic cod and other marine species within the AME. All are subject to ecological changes caused by hemispheric climate variability that causes bottom-up forcing of food webs based on the ecosystem's plankton production [42].

6. Variable female fecundity and egg mortality in NEA cod

The number of spawning NEA cod has varied much since World War II (**Figure 3**). Naval warfare prevented trawl fishing in the Barents Sea during 1940–1945, and shortage of fuel reduced traditional coastal fishing with hand-line, longline and gillnets. The reduced exploitation of NEA cod allowed the spawning stock biomass (SSB) to recover from prewar fishing mortality. After the war, technological development resulting from warfare gave rise to considerable modernizing of the international fishing fleet that commenced fishing for Atlantic cod in the Barents Sea and on banks along the Norwegian coast.

Post-war SSB declined to about 20% in 1958, not only because of legal landings of fish. International competition in the fishing industry, inadequate reporting of catches and landings, as well as weak public management bodies, opened for fishing with illegal trawls and unreported discarding of dead or dying juvenile fish. Increased public awareness about illegal practices, jurisdictional improvements and increased research on resources started about 1970. The political process gradually improved the national and international fisheries management, which to some extent explains how the NEA cod SSB recovered during the last decade. However, it may also result from global warming. Advection of warmer water by the Norwegian Atlantic Current (NAC) and the NCC has increased the area of benthic foraging habitats of NEA cod, which promotes the growth of adult cod and their production of eggs.

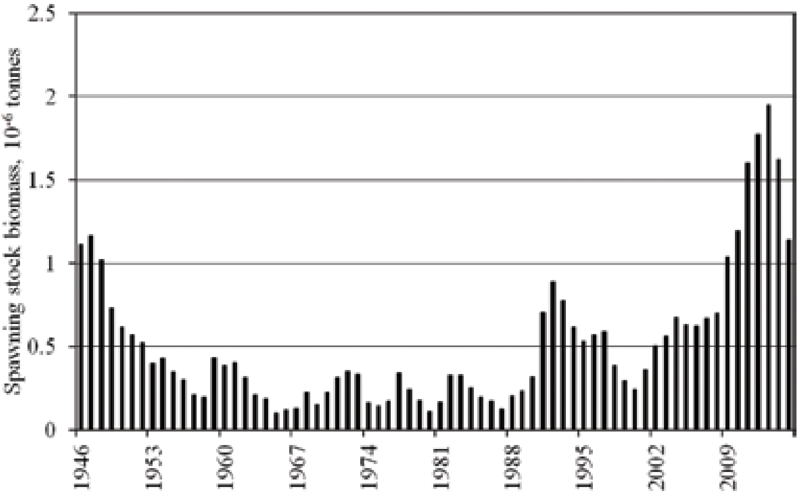

Figure 3. NEA cod (*G. morhua*) spawning stock biomass (tonnes) during 1946-2015 (data from ICES Arctic Fisheries Working Group 2015).

Atlantic cod is very fecund and iteroparous, spawning many eggs usually every year throughout its life, which perhaps could last >30 years before the introduction of industrial fishing. Then, some first-spawning NEA cod could be as old as 14 years, while they today mature at an age of 6–9 years. Cod in Icelandic waters, and the Irish and North Seas spawn at an earlier age and smaller size but have higher size-specific fecundity [43].

Old NEA cod tend to have more eggs than younger fish at the same size [44], but the egg production varies with amount and quality of food available between each spawning season. The amount of fat stored in the female liver during gonad development influences the quality of the eggs in terms of size and yolk content. Old cod grown large emerge in the spawning habitats earlier than smaller fish, and their larger eggs have maternal qualities that increase the potential for survival of their eggs and larvae. However, low sea temperatures may delay zooplankton reproduction and cause temporal mismatch between first-feeding cod larvae and their prey [45].

About 90% of the NEA cod eggs die before hatching [46], but little knowledge exists about egg predation by carnivorous zooplankton, planktivorous fish and seabirds. During peak spawning by NEA cod in Lofoten, an abundance of their eggs may float just underneath the sea surface film when there is no wind but disperse in the upper mixed layer when there is wind stress and turbulence. In any circumstance, predation on the enormous amount of eggs normally spawned by NEA cod in Lofoten may not be of major importance to the mortality of eggs and larvae and recruitment to the population.

Canadian scientists expressed concern that ultraviolet radiation (UVR) might harm survival in eggs of cod and *C. finmarchicus* in the Gulf of St. Lawrence. Laboratory experiments confirmed that exposure to UVR was harmful to both [47], but modeling suggests that events of UVR mortality in Lofoten have only minor direct influence on the overall mortality of cod eggs and larvae [48]. The modeling experiment applied hydrographical time series and UVR doses calculated from satellite data, ozone measurements, meteorological data and in situ diffuse extinction coefficients. Only when thin ozone layer and slack winds coincide with meager phytoplankton stocks would UVR induce mortality harmful to cod eggs and larvae in Lofoten.

Contrary to being detrimental, UVR in Lofoten possibly initiates ecological processes that protect eggs of cod and *C. finmarchicus*. In August-September of 1973–2000, 0-group abundance of NEA cod was positively correlated with average 11-day maximum doses of UVR in two periods earlier in the same year, one around 1 April (**Figure 4**) and one around 1 May. The first coincided with the spawning period of cod and the other when most larvae have normally hatched. Skreslet et al. [49] suggested that ultraviolet radiation (UVR) probably counteracted mortality caused by harmful marine bacteria. The rationale for the assumption was that bacteria frequently infest fertilized cod eggs incubated in cultures with natural seawater [50]. Infestation may start 2 hours after fertilization and cause eggs overgrown by various coccoid, rod-shaped, vibrioid and filamentous bacteria many days before hatching. To prevent mortality in cultures of marine fish eggs and larvae, the aquaculture industry now usually sterilizes seawater by UVR and ozone.

In Lofoten, large amounts of ovarian fluids from females and semen from males mix and probably provide a rich growth medium for bacteria naturally occurring in seawater. UVR

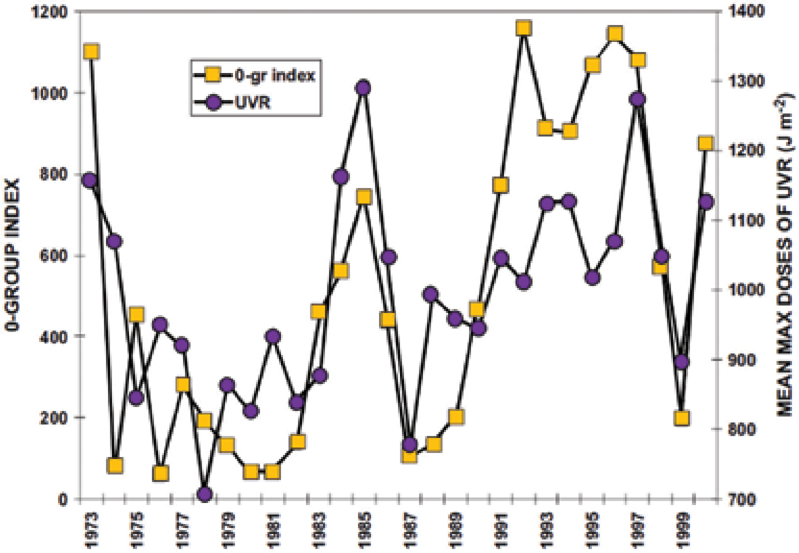

Figure 4. Interannual variation in 0-group abundance of NEA cod (*G. morhua*) in the Barents Sea during August-September and average maximum doses of UVR in Lofoten during April of the same year ($p = 0.01$) (modified from Ref. [49]).

may directly kill bacteria growing on cod eggs accumulating underneath the sea surface film during calm weather, but the eggs then risk detrimental effects of UVR exposure [47]. When there is wind, the eggs disperse in the upper mixed layer and escape lethal UVR because of its high extinction coefficient in coastal seawater. However, the eggs may experience brief doses as they circulate near the surface. Thus, the important effect of UVR may not be the duration of exposure but the dose that eggs are exposed to when close to the surface. The intensity of UVR in Lofoten depends on ozone layer thickness and local conditions regarding cloud cover and albedo caused by snow cover on the alpine landscape.

There is a possibility that high UVR doses do not effectively kill bacteria on large numbers of infested cod eggs, but rather disinfect the circulating seawater itself, killing germs that are potentially infectious. Another and more intriguing explanation is an indirect ecological relationship with cod eggs, caused by viruses that turn virulent by UVR and reproduce by lysis of bacteria [51].

7. Mortality and survival strategy of cod larvae

Fisheries biologists calculate the abundance of NEA cod that enter the exploited stock each year, by virtual population analysis (VPA) made on commercial catches. They are still juveniles, being 3-group cod in their third year after hatching. An early VPA [52] attempted to establish a theoretical relationship between the number of NEA cod eggs spawned per year and the subsequent abundance of recruits. Recruitment tended to decrease when the stock fecundity was $>10^{15}$ eggs, and the best recruitments in 1942–1968 occurred when the fecundity was lower (**Figure 5A**). Extremely low recruitment usually followed years with very low egg production, except for 1 year that resulted in the strongest recruitment of all. Details from the study show that the recruitment declined as the fecundity increased from 1942 to 1945 (**Figure 5B**). The recruitment increased after the war ended, even while fishing reduced the spawning stock biomass. The relationship may indicate that larvae were subject to density-dependent mortality, meaning that the number of larvae hatched from a large number of eggs exceeded the habitat's carrying capacity for production of prey.

Wiborg [15] reported a plankton sample taken in Lofoten in April 1930. It contained an extraordinary abundance of cod larvae dead before capture. Their body had decayed and only heads remained, indicating death at sea from starvation, probably showing a rare evidence of density-dependent mortality. Offspring from very fecund oviparous fish must in general tolerate extremely high rates of mortality depending on density-dependent regulatory mechanisms. Most of this mortality occurs during a critical pelagic larval stage, concentrated during a relatively short period in early development [53].

Not before 1977, did the US Northeast Fisheries Center organize MARMAP, an investigation that came forward with results that support Hjort's critical period concept. After 11 years of extensive data acquisition on the Georges Bank Morse [54] observed that their scientific production index of ≤6 mm long Atlantic cod larvae correlated positively with the abundance of age 1 recruits next year (**Figure 6**). Newly hatched cod larvae were slightly longer than 4 mm, which means that the establishment of cod year-class strength during 1997–1987 occurred during the first weeks of life after hatching.

The genome of cod larvae has evolved some strategic capacities that optimize their ability to locate, observe and attack prey. The yolk-sac larva is rather passive in the first days after hatching. At 5°C, it may each minute make about five short bursts of swimming at a speed of 5 cm min^{-1} [55].

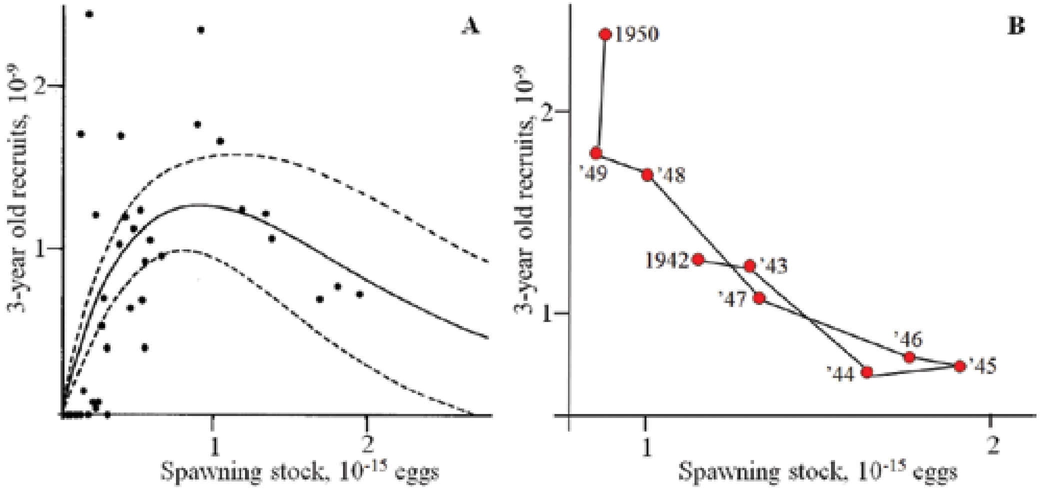

Figure 5. Ricker stock and recruitment equation fitted to data for NEA cod (*G. morhua*) (1942–1968). Number of 3-year-old recruits of NEA cod plotted against total stock fecundity. (A) Stock-recruitment curve with 95% confidence limits. (B) Details from 1942 to 1950 (extracted from Garrod and Jones [52] and presented by permission of the authors).

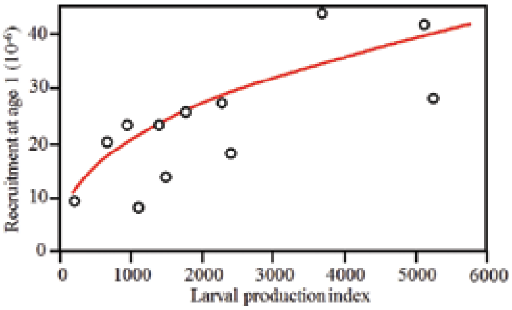

Figure 6. Production index of ≤6 mm Atlantic cod larvae (*G. morhua*) on Georges Bank 1977–1987 related to subsequent recruitment at age 1 (redrawn from Ref. [54]).

The swimming activity culminated 6 days after hatching, 1–2 days before the yolk reserves were exhausted. Two to three weeks after hatching the larva had developed a saltatory search pattern. Starved larvae swam in bursts for 0.2 seconds, stopping to reposition for 0.8 seconds by using their pectoral fins, while larvae having fed on nauplii lowered both duration and frequency of their burst swimming [56]. At encounters with prey, the larva stopped and positioned itself while curling its tail for the swift attack and when successful sucking the prey into its mouth cavity. The larvae accepted nauplii 120–360 μm long but selected 200 μm when prey densities >50 l^{-1}. In a natural environment with few copepod nauplii, the cod larvae may forage on small prey like tintinnids and oligotrich ciliates but then experience slow growth and lower survival rates [16].

Swarming is a normal survival behavior in zooplankton [57] but also provides options for predators. The abundance of cod larvae and nauplii of *C. finmarchicus* in Lofoten may correlate positively when the sea is calm (**Figure 7**). The cod larvae probably navigate successfully in marginal gradients of prey in the periphery of swarms or patches. The capacity results from bilateral vision, which makes it statistically probable that the next sighting of prey occurs in the direction of higher prey abundance. When the larva succeeds to see prey at both sides after each attack, it is likely to remain in a position with optimal prey density for some time.

Newly hatched nauplii in stage NI have slow locomotion in the viscous medium of cold seawater. They are small and hardly sink according to Stokes' law. Every ecdysis into a higher stage of development increases the locomotion and capacity to swarm. Onset of turbulence probably dissolves patches where nauplii and cod larvae occur together [58] but offer other options. Wind mixing forces micro-turbulence that moves nauplii toward cod larvae in ways that increases the rate of encounters between cod larvae and their prey. Microturbulence at winds stronger than 4 m s^{-1} even exceeds contact rates obtained by swimming [59].

Strong and steady wind causes small and neutrally buoyant particles to disperse, while particles with other properties may be subject to sorting by Langmuir circulation that generates vortices aligned with the wind [60]. Every vortice rotates opposite of the next, which causes bands of upwelling separated by bands where surface water sinks and causes accumulation of foam and floating debris (**Figure 8**). NEA cod eggs are positively buoyant in the upper mixed layer in Lofoten and possibly accumulate at the surface below the flotsam. Negatively phototactic organisms perhaps accumulate in up-welling bands during daytime. During a period of

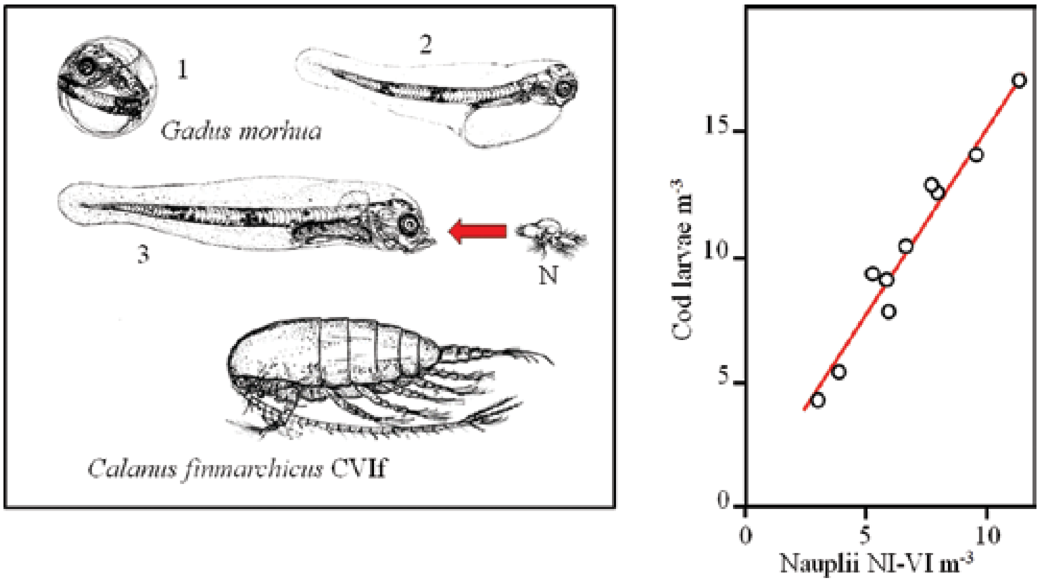

Figure 7. Planktonic Atlantic cod (*G. morhua*): fully developed embryo (1), newly hatched larva with yolk sac (2) and larva with fully developed digestive system (3). Female (CVIf) and nauplius (N) of *C. finmarchicus* (left). (Right) Correlation ($p = 0.01$) between abundance of cod larvae (total length >4.8 mm) and nauplius I–VI of *C. finmarchicus* in Lofoten (graph redrawn from Ref. [58]).

moderate gale (15 m s^{-1}) decreasing to fresh breeze (9 m s^{-1}) during sampling at noon, abundance of cod larvae in Lofoten correlated positively with the abundance of female *C. finmarchicus* [58]. The copepod was possibly foraging on phytoplankton and producing eggs, while cod larvae foraged on nauplii. The micro-turbulence was possibly optimal in a kind of 'bottle neck' between two vortices where upwelling occurred (**Figure 8**), allowing cod larvae

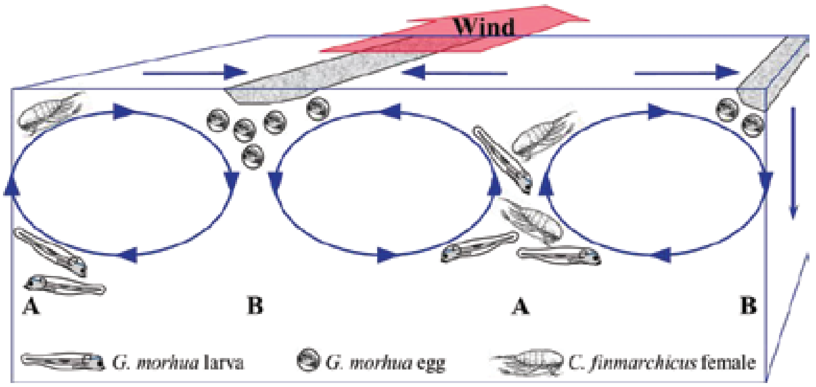

Figure 8. Langmuir circulation according to Ref. [60] showing how NEA cod larvae (*G. morhua*) possibly correlate positively with female *C. finmarchicus* during strong wind at noon in Lofoten, supposedly due to (A) up-welling and negative phototaxis [58]. Buoyant eggs of NEA cod possibly accumulate under stripes of flotsam floating on the surface where down-welling occurs (B). Nauplii of *C. finmarchicus* and microalgae (not shown) disperse in the mixed layer.

to change tactics from stalking to ambush on prey. However, in calming weather, patches with cod larvae possibly contain spawning females of *C. finmarchicus* producing eggs developing into feasible prey for resumed stalking.

8. History of variable NEA cod recruitment

The number of NEA cod that enter fisheries as 3-year old juveniles (3-group cod) varied from 1946 to 2015, showing a shift in abundance after 1973 (**Figure 9**). For the next 42 years, there were only four year-classes with more than 1 billion 3-group recruits. During the 28 preceding years, 14 year-classes were stronger than 1 billion. Seven were stronger than 1.5 billion, which has not happened after 1973. Taking the entire period, there seems to be an inverse relationship between recruitment and SSB (**Figure 3**). However, the increase in SSB since 1990 seems to have improved and stabilized the recruitment at a level that on average has exceeded 0.5 billion 3-group cod, compared with the previous period when recruitment was very weak in many years during 1968–1992. Before, a series of years with mostly strong recruitment occurred in 1956–1967, despite the SSB was in general low in the period 1953–1964. Three extremely strong year-classes, exceeding 2 billion 3-gr cod, were recruited to the fisheries in 1951–1953 (**Figure 9**), following reproduction by comparatively strong SSB in 1948-50 (**Figure 5**).

Increase in stock fecundity of NEA cod in 1942-45 (**Figure 5**) caused comparably low stock recruitment in the first post-war years (**Figure 9**), possibly resulting from density-dependent mortality. It indicates that the abundance of cod larvae exceeded the carrying capacity of their habitats, i.e., the production of copepod nauplii. By 1948, the spawning stock fecundity had decreased to ~10^{-15} eggs (**Figure 5**) which reduced density-dependent mortality and possibly allowed the >2 × 10^9 recruits of 3-gr cod in 1951–1953 (**Figure 9**). The SSB and the spawning

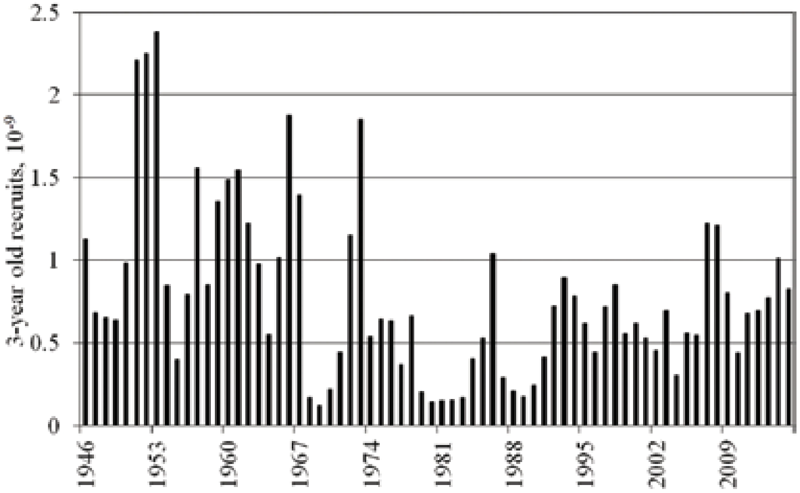

Figure 9. Abundance of 3-group Northeast Arctic cod (*G. morhua*) in the Barents Sea (1946–2015) (data from ICES Arctic Fisheries Working Group 2015).

stock fecundity continued to decrease (**Figures 3** and **5**) but still resulted in strong recruitment until 1967 and the last year-class that exceeded 1.5 billion 3-group cod in 1973 (**Figure 9**). In all following years, no comparable recruitment has occurred.

The causal relationships behind differences between NEA cod recruitment in 1946–1973 and 1974–2015 (**Figure 9**) are obscure and certainly complex. They call for an approach based on multiple variables [61], including variability in natural processes, socio-economic relationships regarding exploitation and other anthropogenic influences. It is possible that the historic maximum in SSB at the end of the period (**Figure 3**) results from a combination of successful management of the NEA cod stock and global climate change.

9. Plankton links cod recruitment to global climate?

Klyashtorin and Lyubushin [62] drew attention to how many fish populations vary with the annual global temperature anomaly (global dT) which is based on air temperature at the surface of the planet. Global dT is characterized by a sinusoidal 60-year cycle that is in phase with sea temperature in the Barents Sea observed in the Kola meridian. Recruitment to the NEA cod stock lagged about a decade after both global dT and Barents Sea temperatures. Global dT was also in phase with annual North Atlantic Oscillation (NAO) from the 1930s to the early 2000s. NAO represents the difference in barometric pressure between the Azores and Iceland. The index is positive when the difference is higher than the average and negative when lower.

The abundance of *C. finmarchicus* immigrating to a fjord habitat near Lofoten during September-October correlated positively with average NAO in March-July (**Figure 10**), resulting from variable precipitation in Norwegian alpine landscapes [42]. It forces meltwater discharge from rivers to the NCC on the mid-Norwegian shelf during May-August. The discharge initiates vertical turbulence in the frontal jet current that marks the transition between NCC and offshore shelf waters (**Figure 11**). Inorganic nutrients brought to the euphotic zone generate primary production that makes female *C. finmarchicus* ripen batches of eggs repeatedly in June-August. The species spawns vigorously during June-July in the marginally stratified frontal zone of the NCC [63]. The abundance of nauplii correlates negatively with salinity along the NCC jet [49, 64], resulting from freshwater discharge stimulating biological production. The new generation drifts northwards, some of it into the Vestfjord during autumn [65] when freshwater outflow decreases and the NCC obtains a landward vector due to decreased stability [66].

The outer part of Vestfjord is wide and has a sill about 200 m deep between the mainland and the Lofoten Islands (**Figure 11**). A series of >600 m deep basins inside the sill serve as the wintering habitat for a large wintering stock of *C. finmarchicus*. The copepods mature and mate after midwinter, and the females produce nauplii while transported by a seaward current running along the south shores of Lofoten [67, 68]. NEA cod traditionally spawn at 5–6°C in a gradient between this current and warmer water underneath.

The reported abundance of *C. finmarchicus* wintering in a side fjord (**Figure 10**) did not correlate significantly with 0-group NEA cod [49]. Observations in 1997–1998 revealed that *Calanus helgolandicus* and *Calanus glacialis* contaminated the sampled time series. Although

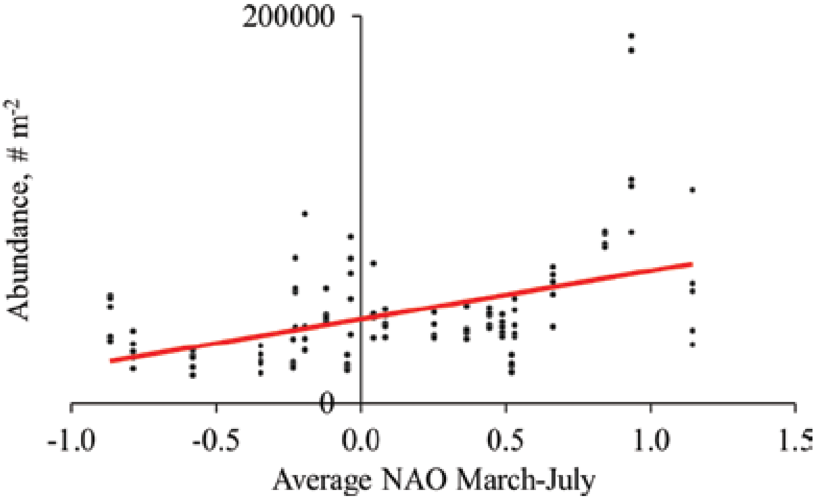

Figure 10. Abundance of *C. finmarchicus* during October as the function of North Atlantic Oscillation (NAO) in March-July of the same year, sampled 1983–2005 in 382 m deep fjord basin storing Atlantic water advected from the Norwegian Sea [42].

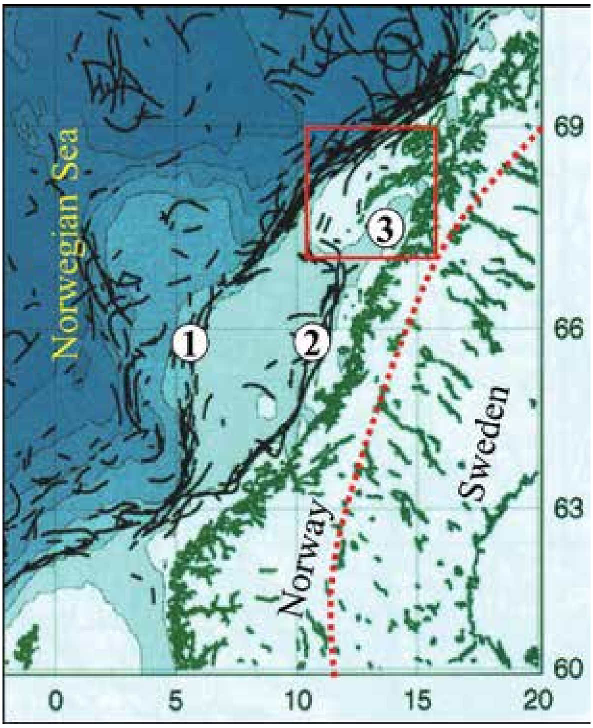

Figure 11. Norwegian Sea shelf break jet (1) and NCC jet (2) as indicated by Argo drifter tracks showing surface velocities >40 cm s^{-1} (from Ref. [64]). (3) Vestfjord wintering habitat for *C. finmarchicus*. (Rectangle) Habitat for joint reproduction of NEA cod and *C. finmarchicus* in April. (Stippling) Watershed between Norway and Sweden. (Right margin scale) Latitude. (Bottom margin scale) Longitude.

C. finmarchicus may usually dominate over other *Calanus* spp. in the time series, genomic work on *Calanus* spp. in Norway shows that *C. glacialis* in fjords may be more abundant than previously experienced [27]. The interannual variability in abundance of *C. glacialis* and *C. helgolandicus* is unknown. At present practical considerations and costs of genomic work prevent samples of *C. finmarchicus* to be cleaned from contamination by other *Calanus* spp. Thus, proportionality between abundance of *C. finmarchicus* in Vestfjord and survival rate of NEA cod larvae in Lofoten remains a missing part in the complete ecological puzzle about climate variability and stock recruitment.

10. The role of freshwater discharge in marine fish reproduction

Helland-Hansen and Nansen [69] were among Johan Hjort's contemporary colleagues in oceanography and the first to discuss whether interannual differences in marine fish recruitment resulted from climate variability and freshwater discharge. They observed that 1-year-old sprat (*Sprattus sprattus*) and herring (*C. harengus*) were abundant 1 and 2 years after rainy years, respectively. The interesting proposal did not materialize in comprehensive empirical research, not before the International Geosphere-Biosphere Program in Canada (1964–1974) addressed effects of St. Lawrence River discharge on marine ecology in the Gulf of St. Lawrence.

A paper by Sutcliffe [70] initiated a series of publications that documented landings of fish and shellfish from the Gulf of St. Lawrence to vary with freshwater discharge, most correlations being positive while some negative. For a period after 1949, a modeled survival index for NEA cod correlated positively with natural meltwater discharge from rivers along the Norwegian coastline [71]. The correlation was highest with run-off from Møre (**Figure 12**), a region south of the mid-Norwegian shelf (cf. **Figure 11**). It broke down after 1960, possibly because increasing fishing

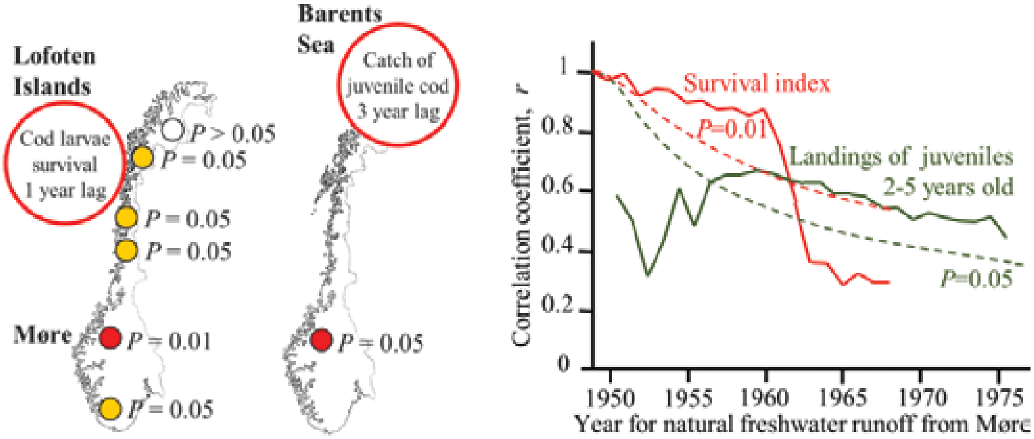

Figure 12. Maps of Norway showing positions (dots) of locations for 30 days of maximum freshwater discharge correlating positively with survival of NEA cod larvae (*G. morhua*) 1 year later and Norwegian landings of juvenile NEA cod 2–5 years old from the southern Barents Sea 3 years later. Graph shows stepwise calculation of correlation coefficients with population variables from the NEA cod stock as the function of freshwater discharge at Møre. (Stippled curves) Critical values for p (redrawn from [71, 72]).

efforts decreased the stock fecundity below 10^{15} eggs (**Figure 5**). It is possible that decreasing SSB (**Figure 3**) eventually obliterated density-dependent mortality of cod larvae as a forcing factor in the causal relationship between larval prey abundance and recruitment to the exploited stock.

Positive correlation observed between natural vernal discharge and landings of juvenile NEA cod to ports on the Norwegian Barents Sea coast [72] existed until 1975 (**Figure 12**). Occasional recruitment stronger than 1.5 billion 3-group cod occurred until 1973 (**Figure 9**), which has never happened again. After 1975, river flow used in the correlation had regulated flow due to hydroelectric production, which obstructed options for continued testing of correlations.

Time lags in the Canadian and Norwegian correlations with freshwater discharge indicate causal relationships occurring on extensive spatial and temporal scales, exemplified by Steven [73]. He summarized research on plankton ecology in the Canadian IBP, stating that entrainment in the St. Lawrence Estuary fed inorganic nutrients into a geostrophic brackish plume flowing along the southern coast. It stimulated primary production >100 mgC m^{-2} h^{-1} from April to July over several hundreds of km downstream, which resulted in zooplankton production with biomass maxima 600–700 km away. Estimated time for particles to drift from the estuary to the Cabot Strait where the Gulf meets the open Atlantic was 80–90 days.

The phenology in plankton development along the Norwegian coast probably shows similar scales in time and space. Freshwater outflow from any section of the coast probably stimulates primary production in the marginal frontal zone of NCC and reproduction of *C. finmarchicus* during summer [49]. Increased shear stress between NCC water and the underlying salter layer results in lateral advection of a thin layer transporting coastal plankton offshore into the Norwegian Sea [74, 75]. Helland Hansen and Nansen [69] suggested that the seaward vector changes to landward advection during autumn, later confirmed by physical modeling [66]. Thus, *C. finmarchicus* that starts ontogeny in coastal habitats may continue growing in the Norwegian Sea and return to complete the life cycle in Norwegian coastal waters farther north.

During autumn, advection of Atlantic water by the NAC transports zooplankton from the deep Norwegian Sea to the shallow Barents Sea, to be foraged by pelagic 0-group cod. Few cod larvae from Lofoten are transported into the Norwegian Sea [76], which may be different for fractions hatched in coastal habitats farther south in Norway. The fate may not be detrimental to this fraction, considering that they may benefit from rich zooplankton production in the central Norwegian Sea [77].

11. Conceptual model for reproduction ecology of NEA cod

More than one hundred years of information from research on Atlantic cod make it possible to suggest a conceptual model for the reproduction and recruitment ecology of NEA cod (**Figure 13**). Ecological premises for successful first feeding of NEA cod occur in Year 0, 1 year in advance of the actual spawning. Then, a spring generation of *C. finmarchicus* produced in the North Sea [78], and in Norwegian fjords [75, 79], migrates onto the mid-Norwegian shelf in early summer. Their food source is planktonic primary production that occurs along the NCC jet (**Figure 11**). It continues through summer like a chemostat process, depending on

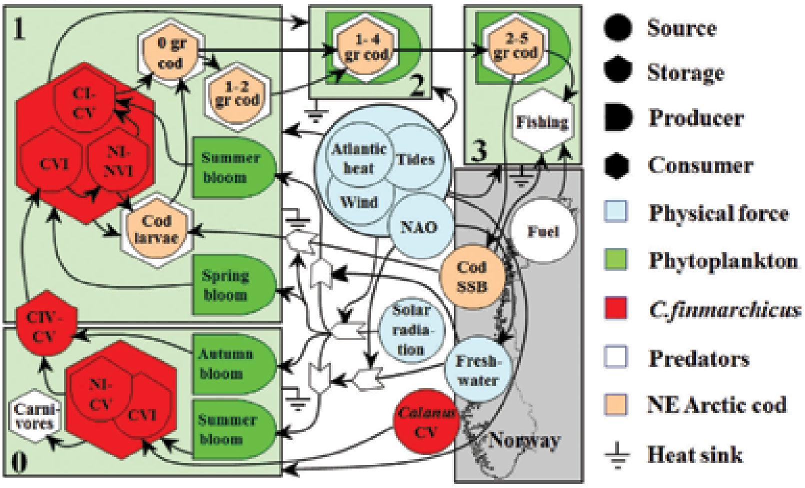

Figure 13. Transfer of trophic energy within and between population systems of *C. finmarchicus* and NEA cod (*G. morhua*) as influenced by sources of forcing (circles). (Year 0) Primary production on the mid-Norwegian shelf and growth of summer generation reproduced by source generation of *C. finmarchicus* imported from the North Sea. (Year 1) Spawning of NEA cod in Lofoten during spring bloom in April and reproduction of *C. finmarchicus* having wintered in the Vestfjord, followed by export of plankton community from the Norwegian to the Barents Sea and cannibalism on 0-gr cod. (Years 2–3) Growth of juvenile NEA cod, predation by older juveniles and recruitment to exploited stock three years after initial forcing by vernal freshwater discharge. (Cod SSB) Spawning stock of cod >6 years old. (NI–NVI) Nauplii. (CI–CVI) copepodids (Figure modified from [65, 74, 85]) (symbols: adopted from Odum [39]).

the strength and duration of vernal freshwater discharge from rivers. NAO and precipitation over Norway in March-July regulate freshwater drainage from alpine landscapes in May–August, which initiates extensive eddy formation and fluxes of inorganic nutrients to the euphotic zone of the NCC frontal system. *C. finmarchicus* reproduces in this habitat increasingly with declining surface salinity, but the progeny does not remain in the NCC summer habitat [49]. The new generation is probably subject to flushing onto the mid-Norwegian shelf where it grows into copepodid stages CIV–CV [80], before being transported by advection into the Vestfjord for overwintering (**Figure 11**).

During Year 1 in the Vestfjord and its numerous branches (**Figure 13**), the spring bloom in April occurs as a batch culture, assimilating nutrients made available by vertical convection to depths of 150–200 m by the end of winter. Within a couple of weeks, microalgae consume nutrients accumulated in the euphotic zone. Female *C. finmarchicus* (CVI) forage on the biomass and produce eggs and nauplii (NI–NVI) that promote survival and growth of cod larvae as they are transported by the NCC along the narrow shelf to the north of Lofoten [76]. They forage on the summer production of plankton that results when plumes of brackish water from fjords export phytoplankton and zooplankton that continue reproduction on the shelf [81]. During this period, the cod larvae metamorphose into 0-group juveniles that continue feeding on zooplankton. Some suffer cannibalism from older juveniles when other prey is lacking [6]. Cannibalism varies in the following years, finally adjusting the number of cod recruiting as 3-group juveniles to fisheries statistics. However, fast-growing 2-group as well as slow-growing 4–5 group cod may recruit simultaneously in real fisheries.

Figure 13 is a very simplified presentation of what happens in nature. Tidal and wind mixing of seawater forces turbulent diffusion of heat and inorganic nutrients, which directly or indirectly regulate growth and biological productivity in a multitude of organisms from microbes to fish. The spectrum of solar radiation ranges from infrared (IR) to photosynthetic active radiation (PAR) and UVR, all being coupled to recruitment of NEA cod in various ways.

Compared with coastal and fjord cod, the NEA cod population system is particular in terms of large spatial and temporal life history scales. Its genomic constitution is not compatible with vertical migration near sea surface because of restricted swim-bladder functions [11]. It is possibly the cause for juveniles to leave epipelagic habitats after completion of full metamorphosis at a size of ~6 cm, and later in life preferably migrate horizontally within an extensive mesopelagic habitat.

Successful reproduction and recruitment to exploited cod stocks depend on the fate of the individual under influence of many ecological variables. The combination of modern fishing and management of Atlantic cod is a major anthropogenic variable that regulates spawning stocks. Out-fished stocks produce few eggs with little chance of causing stock recovery, which is evident in North American waters where populations show few signs of recovery. Adequate management of NEA cod made it recover from overfishing before 1990 to reaching a historic maximum after 2010 (**Figure 3**). Inadequate management may explain decline in stocks of NC cod, which at present is enigmatic, and require increased scientific attention to recover and improve stocks. However, it may be futile if unfortunate anthropogenic manipulation of climate and habitat systems remains unchecked.

12. Assessment of anthropogenic production of hydropower

Seasonal variability in run-off from land is typical of coastal regions, interacting with many marine habitats and population systems globally. Marine systems in the northern hemisphere respond seasonally to accumulation of snow on land during winter, followed by snow-thaw during spring and early summer. The quest for electric energy has caused construction of large power plants of great socio-economic importance. The production of electricity occurs the year-round which causes freshwater discharge to increase during winter, at the expense of natural vernal outflow from rivers. In Norway for the period 1969-73, the average peak flood in May was reduced to 52% in the most developed region, while the average reduction for all regions was 16% [82].

Human regulation of freshwater flow on the marine environment gives very enigmatic effects, and there is little empirical evidence available for solving the problem. However, the understanding of processes involved is sufficient for building and testing of numerical models. Myksvoll et al. [83] modeled a fjord system subject to regulated discharge from a hydroelectric plant. They observed that larger proportions of fertilized eggs drifted out of the fjord than during natural winter discharge, suggesting that decreased retention of eggs in regulated fjords may impair recruitment of juveniles. Taking into account that the national capacity for storage of freshwater in reservoirs increased from 11% in 1972 to 21.2% in 2009, the observed decline in populations of coastal and fjord cod along the Norwegian coast may be a result.

After completion of the Canadian IBP in the Gulf of St. Lawrence, Steven [73] stated 'It seems safe to conclude that the force of the river flow, which depends on the amount of fresh water discharged, determines the amount of nutrients brought to the surface and carried seawards into the Gulf and this in turn determines the size of the annual crops of phytoplankton and zooplankton, on which depend survival and growth of the young stages of fish and other animals at higher trophic levels.' He and other oceanographers [84, 85] argued on scientific evidence that hydroelectric production with seasonal regulation of river flow may reduce biological production and ecological carrying capacity for commercial exploitation of marine resources.

Concern about effects of regulated river flow raised discussions in dedicated scientific meetings with international participants [86, 87]. Both these meetings and a committee established by the Government of Canada [88] concluded that the concern was relevant, but the scientific knowledge was insufficient to reach conclusions. A review by Drinkwater and Frank [89] concluded that decline in some coastal fisheries with an overall negative impact on the biota is generally associated with reductions in freshwater flow. However, none of these assessments took into full account the complexity and scales of time and space of ecological processes involved in reproduction and growth of marine resources.

13. Trophodynamic framework of the Arctic Mediterranean Ecosystem

The fluxes of energy and biomass in true marine ecosystems occur within food webs of basin-scale prototypes large enough to conserve energy produced by the system's primary production. Bucklin et al. [90] proposed that *C. finmarchicus* has established a population system contained in the Northeast Atlantic, genetically different from two other populations, one south of Iceland and one in the western North Atlantic. It circulates anticlockwise in the Norwegian Sea, between the coasts of Norway, East Greenland and northern Iceland. However, it also occupies fjords and coastal waters in Norway and parts of the North Sea [78] and exports biomass into the Barents and Polar Seas by advection of Atlantic water (**Figure 2**). *C. hyperboreus* and *C. glacialis* have population systems associated with less-saline polar water (<34 psu). Carnivorous macrozooplankton and planktivorous fish including herring, capelin and 0-group Atlantic cod that feed on *Calanus* spp. disperse assimilated biomass over extensive time and space scales within the Arctic Mediterranean Ecosystem (**Figure 1**), by a food web that even includes diadromous populations. With 90% reduction of energy by entropy on each trophic level, <1% of the annual marine primary production would remain as biomass on trophic levels higher than *Calanus* spp. Thus, the Arctic Mediterranean Ecosystem seems to be the prototype of a closed ecosystem that circulates and conserves most of the biogenic energy fluxes within its food web. Hemispheric climate variability as indicated by tropospheric NAO and stratospheric Arctic Oscillation [42] seems to force bottom-up control of biological production from primary production to the trophic levels of Atlantic cod (**Figure 13**). Roles of seabirds, seals, whales and human fisheries exert top-down control, which also NEA cod older than 0-group do by being cannibalistic. Understanding the intricacies of marine ecosystem control requires methods that are now at hand.

Sophisticated and very promising modeling that couples geophysical and hydro-chemical parameters in the Norwegian Sea computes production of microalgae and reproduction and growth of *C. finmarchicus* in neritic and oceanic habitats [80, 81, 91]. However, model results based on average seasonal run-off from unregulated rivers in 1931–1960 [91] do obviously not represent interannual variability in plankton production in Norwegian shelf waters today.

Comprehensive hydroelectric development in Norway started decades before World War II and escalated during post-war decades [82] until most large rivers were regulated by the end of the previous century. Hydrological data that summarize discharge from undeveloped as well as regulated catchment areas are in general unavailable and hard to get for scientific purposes. Thus, the full potential for the scientific use of existing high-quality geophysical and ecological models depends on future cooperation between national water resource authorities, academic institutions and managers of marine resources.

Progress in marine ecological science aimed at understanding how complex basin-scale marine ecosystems respond on extensive time scales to global climate variability requires conceptual closing of gaps between plankton ecology and fisheries research [92]. Interdisciplinary nesting of geophysical and plankton production models with multispecies population models under development by fisheries biologists would pay adequate tribute to pioneering scientific generalists like Johan Hjort and his contemporary oceanographers.

14. Conclusions on planktonic forcing of Atlantic cod recruitment

Empirical US research on Georges Bank cod in 1977–1987 observed positive correlation between abundance of cod larvae and recruitment to the stock of juvenile Atlantic cod in the following year. Larvae growing from 4 mm length to 6 mm in a couple of weeks had evidently finished the critical period of first feeding, which supports Johan Hjort's classical critical period concept in fisheries science.

Seasonal river flow from eastern Canada correlated with landings of fish from the Gulf of St. Lawrence. Similarly, interannual variability in natural meltwater discharge from Norway correlated positively with abundance of recruits to the NEA cod stock for decades after World War II. Time lags suggested that river flow initiated geophysical forcing of planktonic primary and secondary production in mid-Norwegian shelf waters during summer, on spatial and temporal scales similar to production forced by St. Lawrence River flow. This probably explains trophic coupling of produced copepod biomass to food chains of first-feeding larvae of NEA cod 1 year later.

In the spawning habitats of NEA cod, stock fecundity and effects of UVR on pathological microbes probably control hatching success and abundance of first-feeding cod larvae. Abundance of preferred prey and changes in ambient physical processes influence patchiness, prey gradients and encounters with prey, which make cod larvae shift between tactics for stalking and ambush. Successful foraging on phytoplankton and copepod nauplii during the first weeks after hatching promotes growth to a size >6 mm which probably makes cod larvae escape the critical period of extreme mortality. Mortality at lower rates occurs during the following months of meroplanktonic growth until the end of metamorphosis at a size of ~6 cm. By then, advection of coastal water has transported the 0-group to their juvenile habitat in the Barents Sea.

Extensive industrial fishing of Atlantic cod and modern stock management regulations in our times exert strong influence on spawning stock size and fecundity, which influences egg production and abundance of first-feeding cod larvae. The density of their prey results from local stock abundance of reproducing female copepods emerging from their overwintering habitats. Their abundance results from biological productivity in the previous summer and climate forcing exerted by a range of energy sources, including effects of natural and regulated freshwater outflow.

The population system of NEA cod and the marine food web of the Arctic Mediterranean Ecosystem are no longer pristine. It was in the times of Johan Hjort, before World War I, when fishing for cod relied on artisan methods and climate maintained a natural hydrological cycle. The population system was probably close to pristine for some years after World War II when NEA cod had recovered after prewar trawling efforts. River flow to the mid-Norwegian shelf was mostly natural, which probably caused its planktonic production to be richer and support recruitment of many year-classes of NEA cod stronger than 10^9 juveniles until 1973. After that, reduced recruitment coincided with technological development in fisheries and production of hydroelectric energy.

Johan Hjort's critical period concept is still valid but can probably only predict recruitment to pristine fish stocks. It may not be useful in extensively regulated modern management of highly industrialized fisheries, but is still a relevant theory in general ichthyoplankton science.

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Chapter 6

Encounters in the Zooplankton: Implications for Pelagic Ecosystem Dynamics

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Additional information is available at the end of the chapter

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Abstract

Many important phenomena in the plankton are driven by encounters among individuals. These encounters are mediated by the relative motion of zooplankters, either through the swimming ability of organisms, the small-scale hydrodynamic turbulence, or both. Through selected case studies, in this chapter, we illustrate how encounter rates influence the predator-prey interactions and reproduction, two of the major processes regulating the zooplankton population dynamics. Estimations on the encounter rates among zooplankters were made on the basis of the Gerritsen-Strickler and Rothschild-Osborn models, which consider non-turbulent and turbulent conditions, respectively. In a first case, we show how the predatory impact of siphonophores is over the fish larvae, in the southern Gulf of Mexico. In the absence of water turbulence, a predator encounters 38–40 prey in a day at surface waters, but under the influence of the wind, encounters can increase between 1.2 and 3.3 times depending on the wind velocity and prey speed. In a second case, we examined the encounters between a copepod predator and a cladoceran prey, the dominant groups in the meromictic lagoon of Clipperton atoll. Here, a predator can encounter a high number of prey (until 441) in a day, due to the high density of prey. Turbulence conditions enhance encounter rates, but even if encounters are high, it does not mean that a predator can ingest a high number of prey. In a third case, we analyzed the mate encounters of the holoplanktonic mollusk *Firoloida desmarestia* from the southern Gulf of Mexico, throughout an annual cycle. Results indicated that May is the high reproductive season, a period where a female can encounter 17 males in a day, under turbulent conditions. As *F. desmarestia* is a low abundant species, the role of wind-induced turbulence proved to be highly important in increasing encounters between mates. These case studies illustrate the importance of encounters among zooplankters in the growth and maintenance of populations in the plankton. Future field and experimental studies are needed to achieve a better understanding of the pelagic ecosystem dynamics.

Keywords: body length, mate encounters, population dynamics, predator-prey interaction, spatial overlap, swimming speed, wind-induced turbulence

1. Introduction

In aquatic ecosystems, biological interactions among different trophic levels or within reproductive populations are ultimately done at the individual level. As all living forms, zooplankters are confronted to the problem of capturing prey, avoiding predation, and finding mates [1, 2]. These processes are mediated by individual encounter rates, which in turn are governed by the morphology, behavior, and ecology of planktonic organisms. Thus, the global properties of zooplankton populations and of pelagic food webs are partially shaped at the individual level [1].

From the perspective of a small plankter, the marine pelagic environment is too vast. Zooplankton feed on suspended particulate organic matter, whose concentration is perhaps 10^{-2}–10^{-5} mg C cm^{-3}, approximately few rice grains in a cubic meter [3]. Zooplankters should therefore solve the problem of finding food in a three-dimensional highly diluted environment [1].

Encounter rates are strongly related to how an organism moves through the water [2]. Zooplankters have developed a wide variety of forms (ranging from protozoa to large siphonophores) and behavioral strategies for finding food or mates [4, 5]. Species exhibit different swimming behaviors which are closely related to their foraging strategies and life styles [6]. For instance, active predators have more probabilities to find prey than slow-moving predators, but at the same time, they could be exposed to a major risk of predation [2]. Hence, swimming and predation strategies of organisms might represent a balance between the need to capture a prey and the risk of being eaten.

The study of the relative motion on the encounter rates has shed considerable light on the understanding of plankton ecosystem dynamics [7]. Besides the swimming behavior of organisms, encounter rates are influenced by small-scale water turbulence [8–10]. When the wind blows, the energy transferred by the wind stress propagates downward into the aquatic systems and generates mixing and turbulence [11] that affect the spatial structure of zooplankton. Turbulence has its greatest effect on encounters of small individuals with low motility, and may influence plankton populations with either favorable or detrimental consequences [12, 13]. Moderate levels of turbulence may increase the encounters between mates or predators and prey, but higher turbulent velocities may reduce ingestion rates of predators [13, 14]. Owing to the growing interest in understanding the dynamics of plankton populations and pelagic food webs, scientists have developed theoretical models to estimate the encounters among zooplankters and to quantify the effect of the turbulence [15, 16]. Through the analysis of selected cases studies, in this chapter, we illustrate how encounter rates may influence pelagic trophic interactions and reproduction of plankton populations.

2. Encounter models

Based on the problem of aircraft encounters of the Swiss Air Force, Gerritsen and Strickler [15] developed a study addressing the encounter probabilities of random moving objects in a three-dimensional space. The authors transferred the problem to the pelagic environment and deduced a mathematical model describing the encounters between potential predators and prey. The assumptions of the model were: (i) plankters are considered dimensionless points in the space, (ii) plankters are randomly distributed, (iii) plankters move in a random direction, (iv) plankters swim at a constant speed, and (v) predators have a constant encounter radius (*R*) in all directions. The formulation of the model is:

$$C_{GS} = \frac{\pi R^2 N}{6} \frac{(x+y)^3 - |x-y|^3}{xy} \tag{1}$$

where C_{GS} = encounter rate by a single predator in a second (prey s^{-1} predator^{-1});

R = the encounter radius (m) of predators;

N = number of prey per m^3;

x = prey velocity (m s^{-1}); and

y = predator velocity (m s^{-1}).

Later, Rothschild and Osborn [16] considered the influence of the wind blowing at surface waters over the encounter rates. They introduced the effect of turbulent velocity by modifying the equation of Gerritsen and Strickler [15] as follows:

$$x \text{ is replaced by } \sqrt{x^2 + w^2} \tag{2}$$

$$y \text{ is replaced by } \sqrt{y^2 + w^2} \tag{3}$$

The term w represents the water turbulent velocity and can be estimated as the root-mean-square of the turbulent kinetic energy (k). The calculation of the terms k and w is fully explained in the Appendix of Lemus-Santana et al. [17].

The Gerritsen and Strickler (hereinafter referred as the GS model) and the Rothschild and Osborn (hereinafter referred as the RO model) models have been widely cited by marine researches because they generalize predator-prey scenarios under non-turbulent (GS model) and turbulent (RO model) conditions in the pelagic environment. Their use was also extended in the estimations of mate encounters. The basic components related to these models are: (i) the speed at which an organism (predator, mate) moves relative to its encounter partner (prey, mate), (ii) the population density of the encounter partner (prey or mate), (iii) the perception distance of the predator or mate, and (iv) the turbulent velocity in the surrounding environment.

2.1. Predation strategies and swimming in the zooplankton

Swimming modes and velocity of zooplankters are highly variable and intimately related to their feeding strategy. Plankton predators display two basic feeding modes: the "ambush" and the "cruising" strategies. In the "ambush" or "sit-and-wait" strategy, predators remain motionless most of the time and only capture their prey while they are stationary, e.g., siphonophores, some medusae, cydippid ctenophores, and chaetognaths. In the "cruising" strategy, predators swim almost continuously and capture their prey while swimming, e.g., many scyphozoan medusae, some lobate ctenophores, and some herbivorous copepods and fish larvae [6, 9, 18, 19].

Zooplankton morphologies are highly variable. They include unicellular and multicellular forms, individual and colonial animals, and invertebrate and vertebrate species. Owing to the high variety in morphologies and sizes, swimming speeds are frequently related to their body length per unit time, usually a second (BL s^{-1}).

Copepods, the most abundant animals in the zooplankton, display variable swimming and feeding ways. Adults exhibit two main modes of locomotion: slow swimming and jumping. Slow swimming is a forward gliding-like motion, interrupted by jumps or brief sinking periods; jumping is a fast forward motion of the body resulted from the stroke of appendages [19]. Swimming velocity is about 1–5 BL s^{-1}, or until 350 BL s^{-1} in the case of escape responses [19, 20]. Copepods can be herbivorous or carnivorous. Filter-feeding (herbivorous) species use their appendages to generate feeding currents to capture phytoplankton cells. Carnivorous species can be either ambush or cruising predators, and detect their prey by chemical or hydromechanical signals [21].

Chaetognaths are voracious predators in the zooplankton community. Some species display neutral buoyancy, while others are slightly denser than the seawater. These differences are reflected in the swimming and predation strategies used by chaetognaths: species with neutral buoyancy tend to be ambush predators, whereas those with negative buoyancy will be active predators, displaying short bursts of swimming alternated with passive sinking [19].

Fish larvae swim by undulating their body. The long, slim clupeid larvae show a rhythmic swimming pattern alternating with resting periods; in the laterally flattened anguilliform larvae, swimming motion is due to undulations of the whole body with the wave amplitude increasing toward the tail [19]. Cruising speeds vary depending on the species and the fluid flow, and most frequently, they range between 1 and 3 BL s^{-1}, although escape responses may be as high as 20 BL s^{-1} [19, 22].

Medusae display a varied array of morphologies and swimming styles. Swimming speed and acceleration in these animals are related to the bell streamlining and velar aperture ratio [23]. Basically, medusa species can be grouped in "prolate" and "oblate" forms. The oblate species display more flattened bells than the prolate ones. Usually, prolate medusae are ambush predators; they spent most of the time motionless with the tentacles extended waiting for swimming prey. In contrast, oblate medusae are cruising predators and swim most of the time [23]. Swimming velocities of small species (10–120 mm bell size) are 1–2 BL s^{-1} [19].

2.2. Perception distance

The perception distance refers how far a zooplankter can sense another. In the vast pelagic environment, remote detection is essential for zooplankters to detect and capture prey, sense and escape from predators, or find mates [10]. While some species use their visual ability to perceive another organism, other non-visual species use chemical or mechanical signals [10, 24].

For visual predators, the distance at which a species can perceive its prey is a function of the size and motion of the prey, the contrast between the prey and the background, as well as the light intensity and turbidity level in the surrounding water [25]. Fish larvae and heteropod mollusks are among the most important visual predators within the zooplankton. In fish larvae, visual system is the best developed sensory organ and plays an important role in the survival and feeding of larvae [22]. Most feeding activities of fish larvae occur during the day, and visual perception range increases with larval growth [26]. First feeding larvae perceive their prey within distances less than about 0.5–1 body lengths, whereas in large larvae (10–30 mm), the perception distance increases to 10–16 body lengths [26, 27]. Heteropod mollusks have also well-developed eyes, and their visual acuity increases with their developmental stage [28]. Some species are able to move the eyes in scanning movements allowing a wide field of view to detect their prey in the surrounding environment [29]. *In situ* observations of Hamner et al. [30] showed that a heteropod species initiate the attack behavior when the prey is at a distance of up to 60 cm.

A zooplankter moving through the water generates a micro-scale mechanical disturbance in the surrounding fluid that can be detected by another organism, either prey, predators, or mates. This singularity is called rheotactic ability and has been observed in a variety of planktonic organisms [31]. Rheotactic ability is well developed in many copepod species, but rotifers, chaetognaths, ciliates, and ctenophores also display this sensorial ability. In copepods, the first antennae are covered by an array of sensorial setae highly sensitive to fluid motion [31].

Chemical signals in the ocean are used for many zooplankters for the recognition of mates and food particles. For instance, organic matter released by sinking particles may provide chemical cues used for bacterioplankton to locate food resources; copepods can detect dissolved organic matter in the ocean and are able to test whether algal cells should be ingested or discarded due to chemo-sensorial organs near the mouth [10]. Chemical cues are effective means in the recognition of potential mates in the aquatic environment. Due to their chemosensorial abilities, zooplankters can distinguish conspecifics from other species and can recognize males from females. Some chemical signals are rapidly dissipated into the water by diffusion and turbulence, but other energetically costly molecules have solved this problem [32]. Thus, in some copepod species, males are able to find stationary females located up to 20 mm away following the pheromones released by them [33].

3. Case studies

3.1. Ambush predator vs. motile prey: siphonophores as predators of fish larvae

Siphonophores are pelagic cnidarians that exhibit a complex development. These gelatinous organisms are widely distributed in the oceans and represent a significant portion of the zooplankton biomass [34]. Siphonophores are colonial animals with variable forms. The colony consists of a few basic types of zooids attached along a central stem [5]. As all colonial organisms, zooids have highly specialized functions: the pneumatophores used for buoyancy, the nectophores to propel the colony, the gastrozooids for digestive processes, the gonozooids for reproduction, and the bracts with a protective function [35].

These animals are among the most voracious predators in the plankton food webs. They prey on a wide variety of small animals such as copepods, polychaetes, mollusks, mysids, sergestids, and fish larvae, among others [36]. Observations of siphonophores in their natural environment revealed that the feeding behavior consisted of two phases: a fishing phase when the tentacles are spread to wait for a prey and a swimming phase when the tentacles are retracted and they began to swim to another place to relax their tentacles [36]. The fishing position of a siphonophore depends on its floatation and its ability to extent its stem. Some species capture their prey by extending a long-line posture, with the tentacles hanging down from the floating stem. The sit-and-wait (ambush) strategy to capture prey items demands little energy and mostly depends on the swimming speed of prey to increase the encounter rates [35]. Generally, each gastrozooid in the colony has its own tentacle, which captures and processes prey independently [5]. Thus, as the number and length of tentacles increase, the predatory impact of a siphonophore will also increase proportionally to the area of the curtain of fishing tentacles [5].

The effect of siphonophores and other gelatinous zooplankters on fish larvae populations is of particular relevance due to the importance of ichthyoplankton to fisheries. Even when fish larvae constitute only a small fraction on the diet of gelatinous and soft-bodied zooplankters, in some cases predation on fish larvae can significantly reduce the abundance of a cohort, affecting the recruitment of juveniles to adult population [37, 38]. In an attempt to understand the predatory impact of siphonophores on fish larvae in the southern Gulf of Mexico, Sanvicente-Añorve et al. [39] estimated and compared the predator-prey encounters in relation to the wind-induced turbulence during two contrasting wind periods.

The study of Sanvicente-Añorve et al. [39] was carried out in the southern gulf (**Figure 1**) during two months: April (wind speed 5.25 m s^{-1}) and October (6.5 m s^{-1}) of 2001. A total of 149 zooplankton samples were collected in six vertical strata of the water column (0–10, 10–20, 20–30, 40–60, 60–80, and 80–100 m) using a multiple opening-closing net equipped with 75-cm diameter and 500-μm mesh size. The direction and speed of winds at 10 m above the sea surface were measured with an anemometer. In the laboratory, fish larvae and siphonophores were separated from samples, and their biomass was measured as displacement volume (ml, 100 m^{-3}). Fish larvae were also counted, and number of individuals was standardized to 100 m^3 of water.

Encounter rates between siphonophores (predators) and fish larvae (prey) were calculated under non-turbulent (GS model) and turbulent (RO model) conditions. As the predators do not move while feeding (ambush strategy), their speed was taken to be zero, and their encounter radius was taken as 10 cm, because more than 80% of the siphonophores biomass was constituted of small calycophorans. Since most larvae were in the 3–5.5 mm body length interval, and assuming that they can swim at 1–2 BL s^{-1}, the authors considered the extreme fish larvae velocities: 0.003 (1 BL s^{-1}, 3 mm body length) and 0.011 m s^{-1} (2 BL s^{-1}, 5.5 mm

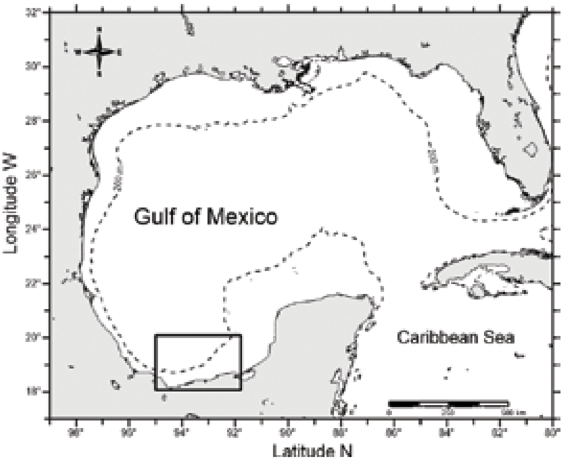

Figure 1. Location of the study area in the southern Gulf of Mexico.

body length). With volumetric units, a Spearman's rank correlation was also performed to examine the kind of relationship (negative, positive, random) issued between predators and prey at each vertical stratum in order to go deeply in the knowledge of their ecological relationship [40].

Results of this study showed that in the absence of water turbulence (GS model), vertical profiles of encounter rates depend on the velocity and density of prey. Under these conditions, a siphonophore can encounter 10–11 small fish larvae (3 mm) in a day, and 38–40 large (5.5 mm) larvae at surface waters (**Figure 2A**). Encounter values were the highest at the third level (20–30 depth) due to a high prey density. Considering the influence of the wind (RO model) at surface waters, a siphonophore can encounter 27–34 small fish larvae in a day, and 47–50 larger ones (**Figure 2B**). These results indicate that turbulence can increase the encounters between 1.2 and 3.3 times depending on the wind velocity and prey speed, at the surface. These values are on the same order of magnitude found by other authors. Analyzing the gut content of a siphonophore species, Purcell [41] estimated that the predation rate of *Rhizophysa eysenhardti* could be 9 fish larvae day^{-1} siphonophore^{-1} in their natural environment. Also, Purcell and Kremer [42] observed from laboratory experiments that *Sphaeronectes gracilis* consume 14–37 copepods day^{-1} siphonophore^{-1} at prey densities of 5–20 individuals per liter. The time required to digest the consumed prey varies between 2 and 17 hours, depending on the size of prey [36].

Spearman's correlations between predators and prey revealed random relationships in the 0–10 m layer in April, and in the 0–20 m layer in October, whereas positive patterns were found deeper in the water column. The authors argued that turbulent energy can disrupt plankton patches and induce a random distribution in the zooplankton, whereas a positive relationship may be the result by a high level of spatial overlap among siphonophores, fish larvae, and copepods; these small crustaceans provide enough food for both kinds of organisms, which results in a limited predation on fish larvae by siphonophores.

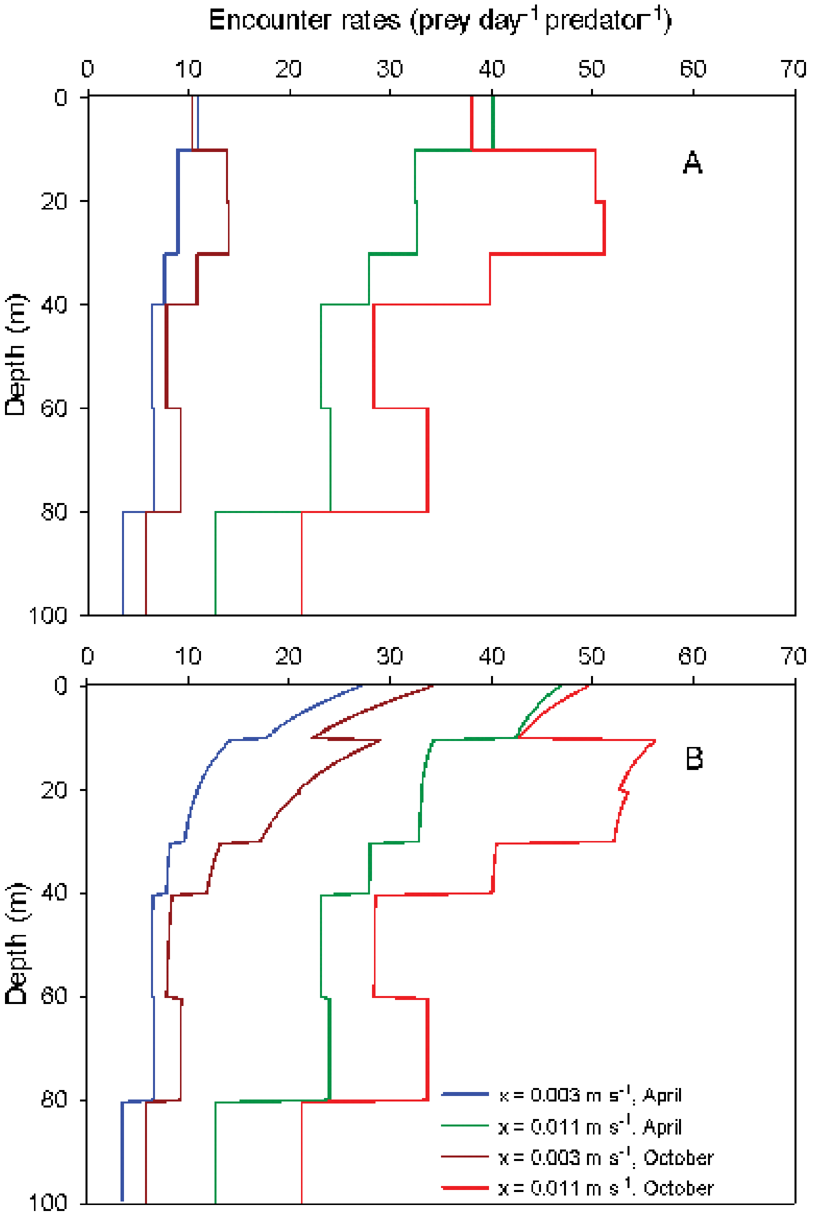

Figure 2. Encounter rates between siphonophores and fish larvae under non-turbulent (A) and turbulent (B) conditions in the southern Gulf of Mexico.

3.2. Cruising predator vs. motile prey: copepods as predators of cladocerans

Copepods and cladocerans are among the major groups of freshwater zooplankton. Copepods generally comprise the major portion of zooplankton biota. Most freshwater species are free-living, while others have adopted parasitic or commensalistic lifestyles [43]. In consequence, feeding strategies varied from small-particle feeding to predation and parasitism [44]. Although they are herbivorous in the earlier stages, mature stages of free-living forms usually are voracious predators [45]. Cyclopoids and calanoids are the most common groups of freshwater copepods.

Most cladoceran species are small (0.2–6 mm) animals that have a distinct head and a trunk and appendages enclosed in a bivalved carapace. Cladocerans usually reproduce by cyclical parthenogenesis, although sexual reproduction is also possible. Most species are filter-feeding, and phytoplankton is their primary source of food [46].

Copepods and cladocerans can move independently of the surrounding flow in low turbulent environments. Cyclopoid copepods swim alternating an active hop and a passive sink phase, whereas calanoids spent a majority of their time floating through the water, propelled by vigorous vibration of their feeding appendages [47]. Swimming of planktonic cladocerans generally consists of sinking and refloating (hop-and-sink behavior); however, swimming behavior is variable depending on species. Movement is principally achieved by the action of their antennae, the main form of propulsion [48].

In the eastern tropical Pacific, Clipperton arises as the most isolated atoll in the world (**Figure 3**). Clipperton is among the few atolls in the world in which the lagoon is completely closed [49]. Maps of Clipperton atoll from the beginning of the nineteenth century showed two small inlets communicating the lagoon with the sea; however, between 1840 and 1849, the two inlets were closed due to natural conditions [50]. Since then, meromictic conditions have been gradually developed due to a positive balance between precipitation and evaporation rates [49]. Before the closure of Clipperton, the biota of the lagoon was similar to the surrounding sea region; in the 1960s, two euryhaline fishes (*Caranx lugubris* and *Kuhlia mugil*) were the only conspicuous fauna in the lagoon [50, 51]. Currently, the lagoon exhibits a strong pycnocline that separates two distinct ecosystems: the bottom layer dominated by bacteria in a detritus food chain, and the upper layer dominated by brackish zooplankton in a short grazing food chain [52, 53]. In the absence of planktivorous fishes, the mesoplankton biota in the upper layer is dominated by the cyclopoid copepod *Acanthocyclops robustus* and by the cladoceran *Latonopsis australis* [54]. While the copepod preys on the cladoceran, the latter is a filter-feeding species [54, 55]. Thus, the seasonal dynamics of these species in the lagoon depend on their predator-prey relationship. In an effort to understand the ecosystem dynamics in the upper layer of the lagoon, Sanvicente-Añorve et al. [56] estimated the predator-prey encounter rates and examined the role of wind-induced turbulence for extreme wind conditions.

This study [56] came from an expedition to the atoll in April 2015. Hydrological conditions in the lagoon and encounters rates were assessed by examining *in situ* and previous records in the lagoon, as well as wind speed data from a NOAA buoy located near the atoll. The predator-prey (copepod-cladoceran) encounter rates were estimated on the basis of the GS and RO models. Extreme wind conditions in the area (1.5 and 8 m s^{-1}) were used to calculate turbulent velocities in the lagoon. The speed of both animals was taken between 1 and 2 BL s^{-1}, taking 1.2 mm body length for the copepod, and 0.7 mm for the

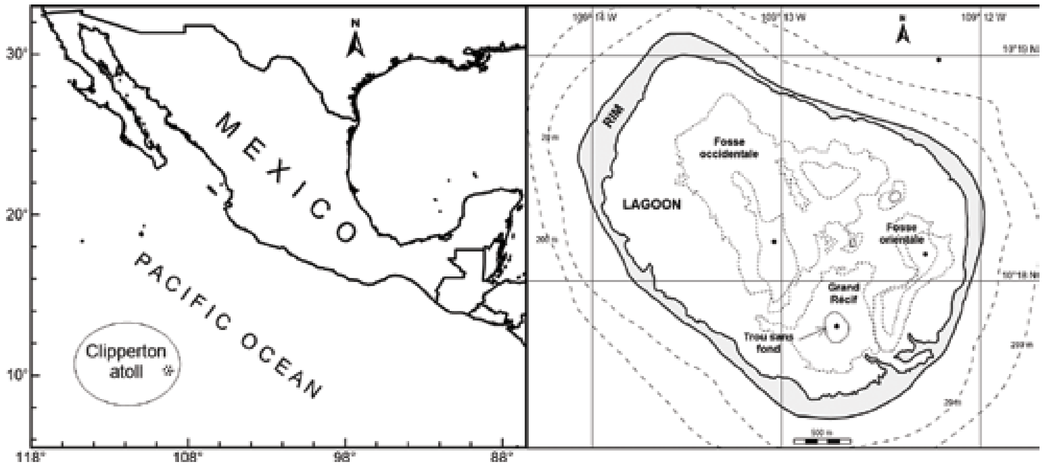

Figure 3. Clipperton atoll, eastern Tropical Pacific.

cladoceran [19, 57]. The perception distance of the predator was taken a little more than a half of its length, that is, 0.7 mm, because cyclopoid copepods do not seek the prey, most probably they detect motile prey around them [58, 59]. Mean population density of the cladoceran prey was taken to be 1241 ind m^{-3} [60].

Results of this study showed that, for the lowest animals' speed (1 BL s^{-1}) and no effect of the wind (GS model), the encounter rate was 220.5 prey day^{-1} $predator^{-1}$ in the water column; encounters doubled for 2 BL s^{-1} animals' speed. By contrast, considering the effect of the wind (RO model) and 2 BL s^{-1} in animals' speed, encounter rates increased to 1018.7 prey day^{-1} $predator^{-1}$ for the lowest wind velocity (1.5 m s^{-1}), and to 2845.7 prey day^{-1} $predator^{-1}$ for the highest wind velocity (8.0 m s^{-1}), at surface waters (**Figure 4**). Predator-prey (copepod-cladoceran) encounters in the eutrophic lagoon of Clipperton are higher than those found for other kind of organisms in oligo- and mesotrophic marine regions. Thus, off California, the encounters between a siphonophore predator and its copepod prey were between 8.1 and 15.4 prey day^{-1} $predator^{-1}$ for a copepod density of 250 ind m^{-3} [42]; in the southern Gulf of Mexico, the encounters between siphonophores and fish larvae were estimated between 34.1 and 49.6 prey day^{-1} $predator^{-1}$ for a fish larvae density of 1.27 ind m^{-3}.

Differences in encounter rate values between Clipperton lagoon and marine areas are due to two main causes: first, the fetch (distance over which the wind blows without an obstacle) in Clipperton lagoon is too small (3.8 km) compared to large marine areas (hundreds of kilometers), and second, a higher density of zooplankters in Clipperton related to marine areas. Therefore, even in the absence of wind-induced turbulence, encounters between predators and prey are high. However, high encounters do not necessarily mean high ingestion rates. If prey are highly abundant and predators are satiated, the remaining prey will survive to reproduce into the water. Given the absence of planktivorous fishes in Clipperton lagoon, it seems that the population dynamics of both the copepod *A. robustus*

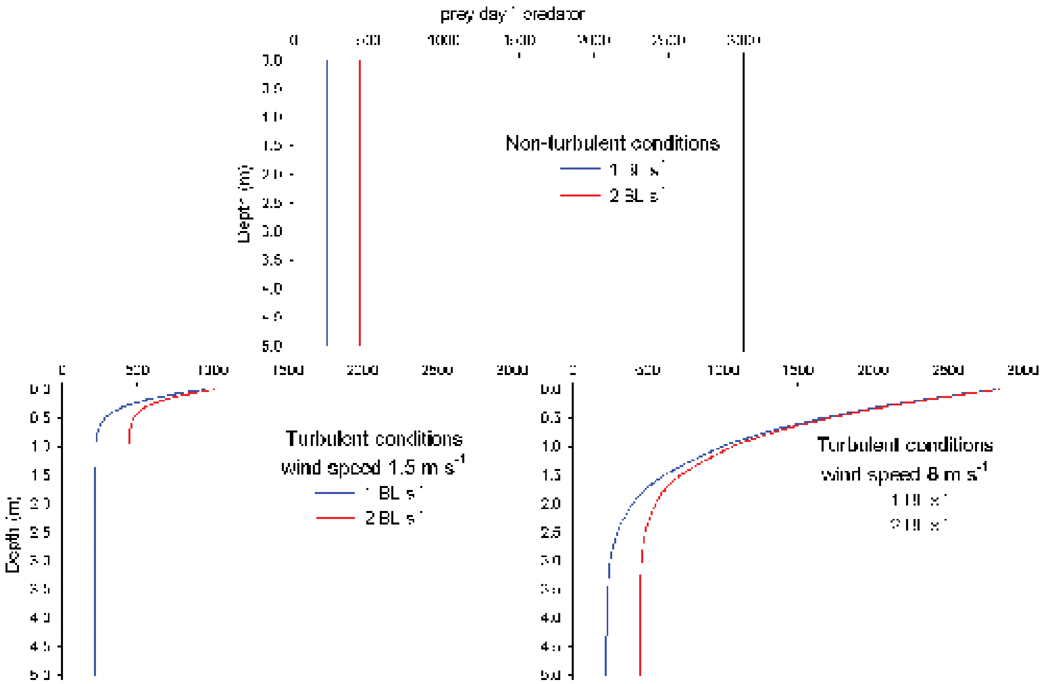

Figure 4. Encounter rates between copepod predators and cladoceran prey in Clipperton atoll under non-turbulent and turbulent conditions.

and the cladoceran *L. australis* may follow a Lotka-Volterra pattern. Estimations on encounter values should be supported with further field or experimental studies analyzing the gut content of species to achieve a better understanding of the mutual control of their population dynamics.

3.3. Mate encounters in the holoplanktonic mollusk *Firoloida desmarestia*

The mollusk *Firoloida desmarestia* (Heteropoda, Gastropoda) is a low abundant holoplanktonic species mainly distributed in tropical and subtropical oceanic waters [61]. This small, shell-less mollusk has a transparent cylindrical body of up 40 mm, a proboscis, a rounded swimming fin toward the anterior part of the body, and a dorsal visceral mass posterior to the ventral fin [62–64]. Due to the weight of the dorsal visceral mass, *F. desmarestia* swims with the fin directed upward in the water column [64, 65]. As all heteropods, *F. desmarestia* swims by rapid undulations of its fin, and sometimes, flexion of the trunk and tail is used to accelerate swimming when hunting its prey or escaping from predators [65]. This species is carnivorous and visually locates its prey. It has well-developed eyes with a narrow, strip-like retina that allows image formation through scanning movements of the eyes [29]. *Firoloida desmarestia* mainly eats gelatinous zooplankton, and among its major predators are fishes, other heteropod species, medusa, and siphonophores [64].

Firoloida desmarestia is a sexually dimorphic species. Males have a sucker on the edge of swimming fin, a big penis, a large tentacle aside each eye, and a tail filament; females lack the sucker and tail, but have a permanent string of eggs at the end of the body [64, 66].

In the southern Gulf of Mexico, the species reproduces throughout the year and is more abundant in the upper layer [17]. In a first attempt to understand the population dynamics of the species, Lemus-Santana et al. [17] analyzed its seasonal abundance, sex ratio, size structure, spatial overlap between males and females, as well as the encounter rates between mates under turbulent (RO model) and non-turbulent (GS model) conditions. Zooplankton samples of this study were taken in neritic waters of the southern Gulf of Mexico (**Figure 1**) over 28 oceanographic stations using a multiple opening-closing net equipped with 75-cm diameter and 505-μm mesh size nets at five levels of the water column (0–6, 6–12, 12–18, 45–55, and 95–105 m) and during four months (February, May, August, and November of 1995).

The estimations of the mating encounter rates were made in the 18 m upper layer, where adults were more abundant. Results of this analysis were expressed as the number of males encountered by a single female in a sphere of 40 cm diameter (33.5 L volume) and during one day. The calculation of the turbulent velocity was made for different wind speeds: 5, 3.8, 3.1, and 6.1 m s^{-1}, which represents wind conditions in February, May, August, and November, respectively. The velocity of *F. desmarestia* individuals was taken to be 2 BL s^{-1}, with 20 mm mean body length for females and 15 mm for males. The encounter radius was assumed to be 20 cm due to visual abilities of heteropods [30].

This study showed that adults were mainly found in the upper 0–18 m water layer, whereas young individuals mostly occurred in the 45–105 m water layer. Vertical distribution of males and females indicated that both sexes overlapped more than a half, suggesting a non-reproductive barrier due to differential vertical distribution of both males and females. Analysis of the size class structure indicated that the species reproduces long-year, with a high reproductive peak in May, and a low reproductive season from August to February.

From August to February (the low reproductive season) and under non-turbulent conditions, mate encounters were lower than 1.5 males day^{-1} $female^{-1}$; in May, encounters were as high as 10 males day^{-1} $female^{-1}$, at the 12–18 m layer (**Figure 5A**). Under turbulent conditions, mate encounters during the low reproductive season were as high as 4.9 males day^{-1} $female^{-1}$; in May, the high reproductive season, encounters reached their maximum value (17.2 males day^{-1} $female^{-1}$) at the 12–18 m water layer due to a high population density and turbulence degree (**Figure 5B**). Thus, turbulent conditions increase the encounters between 4.1 (August) and 6.3 (November) times at surface waters.

For low abundant populations, the chance of random encounters between mates is very low. In this case, wind-induced turbulence has high importance in increasing encounters between mates. This is especially important for *F. desmarestia* and other heteropod populations, in which the low number of individuals limits the encounters of mates. In spite of the low density of the *F. desmarestia* population in the southern Gulf of Mexico, it seems that the mate encounters are

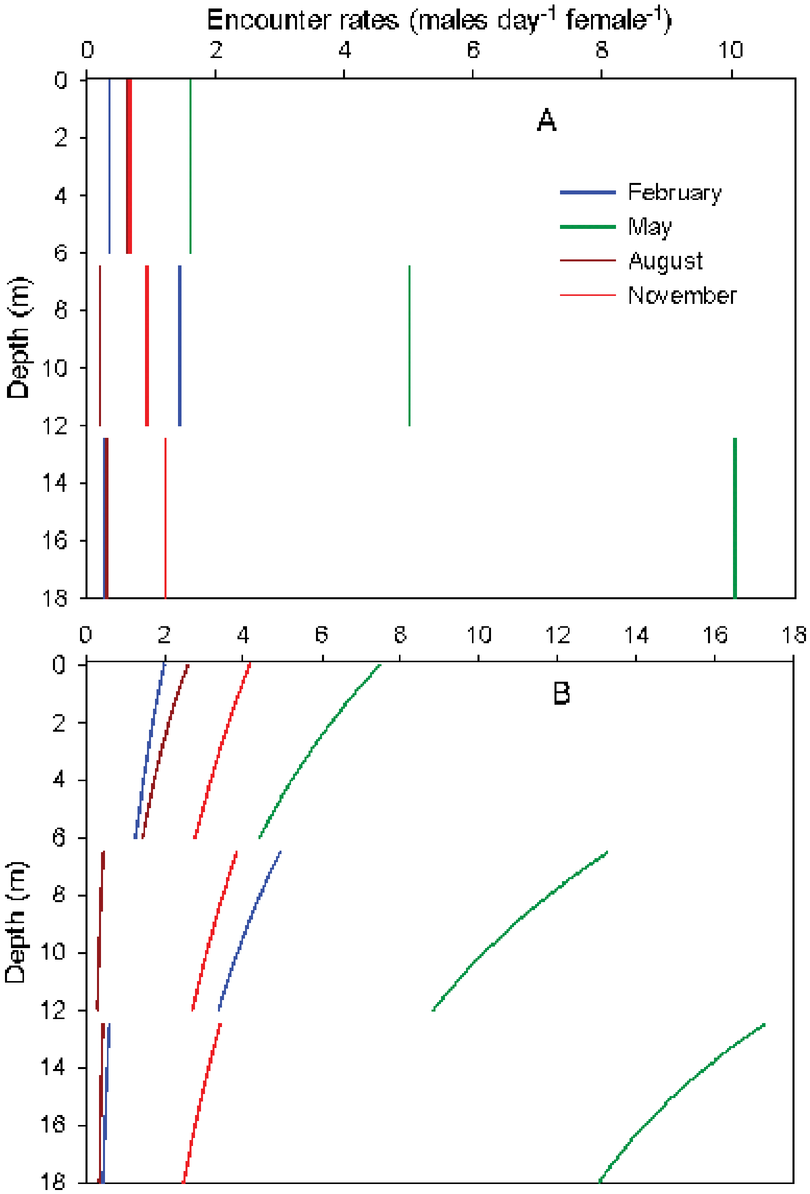

Figure 5. Encounter rates between *Firoloida desmarestia* mates under non-turbulent (A) and turbulent (B) conditions in the southern Gulf of Mexico.

enough to maintain the population throughout the year. Besides the influence of turbulence conditions, Lemus-Santana et al. [17] proposed that limited mate encounters may be compensated by some adaptive strategies of the species: (i) the presence of a seminal receptacle in females suggesting that only one successful reproductive encounter is required to be fertilized, (ii) the presence of well-developed eyes with scanning movements allowing to perceive surrounding organisms, including mates, and (iii) the existence of an exocrine gland in females associated with the state of the reproductive system, probably acting as a male attractor.

4. Conclusions

Growth of zooplankton populations highly depends on food resources and successful reproductive processes. The case studies examined here show how encounters among zooplankters influence the pelagic food webs and species reproduction, and how wind-induced turbulence enhances the encounters among zooplankters.

In oligo- and mesotrophic marine environments, where the fetch is on the order of hundreds of kilometers, the influence of micro-turbulent conditions can enhance encounters as high as 6.2 times, at surface waters. In contrast, in small eutrophic aquatic bodies, encounters are high even in the absence of wind-induced turbulence, due to a high density of zooplankters.

Many zooplankton species display low abundant densities. Therefore, the probability of sexual encounters in the pelagic environment is very low, especially for species swimming at low speeds. Under these conditions, wind-induced turbulence has high importance in increasing sexual encounters between mates, and perhaps may be one of the major causes maintaining the population growth rates.

Estimations on the predator-prey encounter rates can help to make inferences on plankton trophodynamics. Once encountered, ingestion of prey depends on the ability of predator to catch the prey, on the satiation level of predators and on the relative velocity between predators and prey. If prey is highly abundant, probably the predator would be unable to consume all prey and most of them will survive. Also, even when wind-induced turbulence enhances encounter rates, a relatively high velocity between predators and prey would make the encounters unsuccessful because the capture of prey would be more difficult. Further field and experimental studies need to be done to achieve a better understanding on plankton food webs.

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Section 4

Fisheries Ecology and Management

Marine Fisheries in Nigeria: A Review

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Additional information is available at the end of the chapter

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Abstract

Fisheries production especially from marine is important for the socio-economic development of Nigerians and its contribution to the nation's economic growth through the Gross Domestic Product (GDP). Nigeria is blessed with enough marine fisheries resources that could enhance increased fish production. Yet, fish supply from domestic production is far below the fish demand of her citizens. This chapter is therefore focused on marine fisheries in Nigeria. We adopted a desk review approach. This chapter is divided into different sections such as the Nigerian fisheries sector, marine fisheries resources in Nigeria, status of marine fisheries production in Nigeria, marine fisheries regulations, and constraints to optimal marine fisheries production in Nigeria. We concluded that the contribution of aquaculture to marine fisheries production has been low, compared to the marine capture fisheries production. Also, we noted that despite the availability of regulations, non-compliance by fisher folks has not helped to optimize marine fisheries production. We therefore recommended that the culture of marine fishes should be intensified. Marine waters should also be protected against destruction and pollution as a result of human activities. Available marine fisheries regulations should be enforced and violators of the regulations should be punished as stipulated in the regulations.

Keywords: marine fisheries, fisheries regulations, fisheries resources, optimal fisheries production, sea fisheries decree

1. Introduction

Nigeria is a maritime state where 9 of the 36 federal states have a coastline in the Atlantic Ocean. The coastal federal states of Nigeria are Ogun, Lagos, Ondo, Edo, Delta, Bayelsa, Rivers, Akwa Ibom, and Cross Rivers States, found in the southern part of the country. The importance of the fisheries sector to individuals and the economy of many developed and

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developing countries cannot be overemphasized. It is notable that fish provides more than 60.0% of the world's supply of protein, especially in developing countries [1]. Its importance could be felt directly and indirectly among rural and urban residents in Nigeria. In Nigeria, fisheries, particularly an important subsector, contributes about 3.00–5.00% to the agriculture share of the Gross Domestic Product (GDP). Fish are an important protein source in the diet of Nigerians. Protein from fish is highly digestible and of high nutritional value and consists of complete arrays of amino acids, vitamins, and minerals [2]. Apart from its high quality, fish is a cheaper source of protein compared to other animal protein sources such as beef, pork, chicken, and goat meats [3].

The fisheries subsector of the Nigerian agriculture is an essential tool for rural development through its provision of income, high-quality protein, and socioeconomic development of fishing communities in Nigeria [4]. The relevance of the fisheries sector to the Nigeria economy and benefits derived by Nigerians from fish and other fish products led to the high consumption and hence the increased demand for fisheries products. In order to meet up with increasing demand for fisheries products, Nigerian federal governments have tremendously implemented a series of projects targeted at increasing the local supply of fish [5]. Thanks to some of the projects like second and third phases of Fadama, although some improvements were recorded in terms of output level of fish, the gap between the demand for and supply of fish keeps increasing as a result of the use of traditional fishing methods, as is the artisanal fishery, which has the major source of protein from fish relied on, despite the increasing growth rate of the Nigerian population. Government's effort on the fisheries sector is however directed to the popularization and adoption of aquaculture, which is currently the fastest food industry globally at the neglect of the artisanal fishery.

This has led to the government's resolve to augment fish supply with importation of frozen fish and other fish products. Several reports have indicated that several millions of the Nigerian currency is being expended on fish importation [6]. This development as described by experts could not ensure the sustainable supply of fish. It is in fact regarded as a mere waste of the national resources that could have been directed to the development of the fisheries sector. Despite the neglect of the artisanal fishery, it provides the largest proportion of domestic fish supply in Nigeria [7]. Artisanal fishery in Nigeria is from two main sources that are the marine and inland fresh water capture fisheries with up to sixty percent of the artisanal fishery coming from marine water bodies. It is the belief of this chapter that if as much attention paid to the aquaculture of inland fisheries could be given to the marine aquaculture fishery, the domestic fish production in Nigeria has the potential to outstrip the fish demand in the country.

The rest of this chapter is divided into five sections, which are on (1) describing the fisheries sector in Nigeria, (2) examining the marine fisheries resources in Nigeria, (3) the status of marine fisheries production in Nigeria, (4) the marine fisheries regulations in Nigeria, and (5) the constraints to optimal marine fisheries production in Nigeria. Based on our discussion, recommendations were made on means to increase local fish supply in Nigeria through the marine fisheries.

2. The Nigerian fisheries sector

The fisheries sector is crucial to the Nigerian economy for contributing about 5.40% of the nation's Gross Domestic Product (GDP) [8, 9]. It is noted that fishery is an important economic sector in terms of employment, food security, enterprise development, and foreign exchange earnings and also important in terms of the livelihoods of many rural people and nutrition. The importance of the fishery sector is such that it is the most common and cheapest animal protein source to mankind especially among the poor dwellers in Nigeria [10]. Nigerians have been regarded to have a huge appetite for fish with an annual demand of 1.50 million metric ton [10]. This figure has since been on the increase such that [11] projected the fish demand as 2.055 million metric ton in 2015.

Based on sources, the fish supply to meet the increasing fish demands by Nigerians is from two major groups, which are the domestic production of fish and importation of fish. Importation has served as a major supply of fish in Nigeria providing more than half (56.0%) of fish supply [12]. Fish importation refers to the supply of fish to Nigeria from foreign countries in order to augment the locally produced fish in the country. According to Agbo [13], Nigeria spent over ₦125 billion per annum on importation of 1.90 million metric ton of fish in 2015. According to FMARD [14], Nigeria spent ₦97 billion on fish in 2010 alone in spite of all the endowed marine resources, rivers, lakes, and creeks of the nation. Based on the study of Vaughan et al. [15] on analysis of major food imports obtained from the National Bureau of Statistics, fish was the second major food commodities with highest import bills in the period 2006–2010 with an annual average of ₦113.63 billion. The relevant figures indicated that the value of fish imports keeps increasing and this has been attributed to the increasing growth rate of the Nigerian population, while domestic fish production only increases at decreasing rates. Olaoye et al. [7] reported that the quantity of fish imported rose from 557,884 tons to 739, 666 tons between 2000 and 2007 with foreign exchange value on importation being $241,065.54 million and $594,373.69 million in 2000 and 2007, respectively. With these figures, Nigeria has been considered as the largest importer of fish in developing world [7, 16–19].

Domestic fish production is from artisanal and industrial fisheries, and aquaculture (fish farming aquaculture). Artisanal fishery refers to the harvesting or capturing of fishes from natural water bodies such as rivers, streams, lakes, and ponds by small scale fisher folks using both traditional and modern fishing gears [20]. According to Olaoye et al. [21], stakeholders in artisanal fishery include local fishermen and women who fish either on part-time or full-time basis employing all sorts of gears and techniques, which may be destructive, cheap, and locally sourced. It is usually operated at subsistence level (although, some are for commercial purposes) in rural areas. It is a nonindustrial fishery that covers the activities of small-scale canoes operating in the coastal areas, creeks, lagoons, inshore water, and the inland rivers [22–24]. Artisanal fishing involves the use of crude fishing tools and implements, little or no credit and lack of infrastructural facilities, and lack of skills [25, 26]. Due to its operation at subsistence level, it is known as the small-scale fisheries and traditionally occupies the most important component of domestic fish production, contributing up to 90% [27–30]. In buttressing their point, [31] noted that artisanal fisheries employ 18 times more fishermen than the industrial fisheries while supporting the welfare of over 100 million persons globally.

The industrial fisheries are a higher and mechanized level of fish production, which depends on the use of trawling vessels for fishing and shrimping in the territorial and offshore waters [23]. It refers to the industrial fishing in inshore and offshore water of the seas. The marine resources in these waters include demersal, pelagic, and shellfish resources, mainly shrimps, prawns, and crabs, that exist in commercial quantities. This sector is purely industrial and highly capital intensive requiring over N100 million for a one-boat operation [32]. The area of operation is at least 5 nautical miles. Its status is high capital outlay and advanced technology application; about N50.0bn is invested by the private sector in fishing vessels and onshore processing and handling facilities [23].

Aquaculture, to which fish farming belongs, is the commercial rearing of fish in conditions where all basic means of production can be controlled within their respective limitations and from which producers aim to obtain optimal economic results [18]. Scholars [33, 34] also defined aquaculture as the rearing of aquatic organisms under controlled or semicontrolled environments for the social and economic benefits of mankind and livestock. The aquatic organisms that could be reared include fish, insects, bivalves and pearls, mollusks, crustaceans, and aquatic plants, while the controlled environments include ponds, cages, pens, and raceways [18]. Based on the above definitions, fish farming that involves the rearing of fish species under human controlled environments for the economic and social benefits of mankind is a subset of aquaculture [4]. World Bank Group [35] viewed fish culture, also known as fish farming, as an efficient animal protein production system providing essential nutrition for over 1 billion people. It was further submitted that fish farming provides important services such as supporting nutritional well-being, source of feedstock for industries, contributing to rural development, increasing export opportunities, and enhancing more effective administration of natural resources and conservation of biological diversity [36, 37].

One merit of fish farming and aquaculture generally is that it allows overexploited species to be raised in the hatchery and then restock into the natural waters [21]. According to Ejiola and Yinka [38], aquaculture is the least exploited fishery subsector with the vast brackish water fishing grounds almost unexploited. One of the reasons is its neglect as a result of the expensive nature of aquaculture to most poor households. Aquaculture is currently the fastest growing livestock production sector in Nigeria and worldwide [4]. The contribution of the Nigerian aquaculture production has been increasing since 1995 with the contribution of 0.07% to world aquaculture production and 0.42% of world aquaculture production in 2014 [39]. The above classification into capture (fishing) and culture fisheries (aquaculture) is based on the culture/management system.

The next classification of fisheries is based on the type of environment or habitat where fish are reared or captured. This is classified broadly into brackish water, fresh water, and seawater/marine water fisheries. Fresh water refers to water without salt or marine origin, such as generally found in lakes, rivers, canals, dams, reservoirs, paddy fields, and swamps; marine water refers to inshore and open waters and inland seas in which salinity generally exceeds 20%, while brackish water refers to mixed sea water and fresh water and salinity varies with the tide [40]. Examples of brackish water environments are estuaries, mangroves, and mouth of rivers, where sea water enters during high tide. Since this chapter is only concerned with marine fisheries, brackish water and fresh water fisheries shall be neglected, while attention is being concentrated on marine fisheries in the context of industrial, artisanal, and culture fisheries.

2.1. Marine industrial fisheries

This can be grouped into offshore tuna fishery, coastal demersal fish fishery, and coastal shrimp fishery. Tuna is mainly found in the off-shore tuna fishery and forms part of the large Gulf of Guinea stocks. Off-shore resources are located between the country's territorial limit (30 nautical miles) and the exclusive economic zone (EEZ) (200 nautical miles). Nigeria is yet to actively participate in the exploration of the offshore tuna resources due to technical constraints [1]. In the coastal demersal fish fishery, the trawling industry is well developed and organized under the Nigerian Trawler Owners' Association (NITOA). There are 40 trawling companies in Nigeria. Most of the companies are owned by Nigerians. Those Nigerian companies have fleet sizes of less than four while larger companies, with fleet sizes of four or more are owned in partnership with foreign investors [1]. The shrimping industry in Nigeria is operated on the continental shelf from 5 nautical miles with vessels licensed in accordance with the provisions of fisheries law and regulations.

2.2. Marine artisanal fisheries

This can be categorized into coastal canoe fishery, brackish water or estuarine canoe fishery, and artisanal pelagic fish bong shad and Sardinella fishery. The coastal canoe fishery is operated within the 5 nautical miles nontrawling zone, but due to motorization and targeted stocks, some operators may venture farther into the sea. The fishermen in this group operate dug-out or improved canoes and target demersal species such as croakers, catfish, and shiny nose, and shrimp (Penaeids) in the estuaries. The artisanal pelagic fish bond and Sardinella fishery are low-technology, labor-intensive fisheries using canoes 6 to 13 m long either paddled or motorized. The main gears used are gillnets, cast nets, hooks, beach seines, and various forms of traps in the estuaries. The fishermen target small pelagic, *Sardinella* spp. and *Ethmalosa* spp.

3. Marine fisheries resources in Nigeria

Fisheries resources are fishery products or output that comes from fishing and aquaculture [41]. Fishing resources consist of products from open water bodies like rivers, lakes, reservoirs or dams, and oceans, while aquaculture resources include fishery products from enclosed environments such as ponds, tanks, dams, and reservoirs. Nigeria is blessed with a land area of 923,768 km^2, an 853 km coastline, and a 200 nautical miles exclusive economic zone (EEZ). In addition, the country is endowed with marine waters of 30 nautical miles [43]. Within the EEZ, Nigeria has exclusive rights to the exploration and exploitation of the fishes and other natural resources [42]. Artisanal fishing was supported in the brackish and coastal waters of Nigeria industrial fishing could only be operated outside the 5 nautical miles restriction of the 1992 Sea Fisheries Act. According to Onyema [44], nine of the 36 federal states in Nigeria have a coastline with the Atlantic Ocean.

At the marine artisanal level, fisheries resources include fish belonging to Sciaenid community including croakers and bonga, shad, catfish, sardines, soles, shiny-nose, etc., *Polydactylus* spp. (polynemidae), as well as members of the Sphyraenidae, Lutjanidae, Elopidae, Serranidae, and Carangidae families. Sharks, sail/saw fishes, as well as penaeids, palaemonids, and carid shrimps are also caught by small-scale fishermen. The Nigerian industrial coastal fishing activities consist of trawling for demersal finfish, shell fish, and penaeid shrimps. There are about 104 marine fish species belonging to 50 families in Nigeria [45]. According to FAO [1], the species composition is dominated by croakers (*Pseudotolithus* spp.), grunts (*Brachydeuterus* spp.), various soles, catfish (Arius spp.), and shrimps (*Penaeus* spp.).

The finfish species are heterogeneous and belong to suprathermocline and subthermocline communities. The major target families/species of the suprathermocline community (i.e., sciaenids) include:

a. *Sciaenidae* (Croakers): *Pseudotolithus typus* (Bleeker, 1863), *Pseudotolithus senegalensis* (Valenciennes, 1833), *Pseudotolithus elongatus* (Bowdich, 1825), *Pseudotolithus senegalensis* (Cuvier, 1830), *Brachydeuterus auritus* (Valenciennes, 1832), *Selene setapinnis* (Mitchill, 1815)

b. *Ariidae* (Catfish): *Carlarius heudelotii* (Valenciennes, 1840), *Arius gigas* (Boulenger, 1911), *Arius latiscutatus* (Günther, 1864), *Arius parkii* (Günther, 1864)

c. *Haemulidae* (Grunters): *Pomadasys jubelini* (Cuvier, 1830), *Pomadasys suillus* (Valenciennes, 1833), *Pomadasys incisus* (Bowdich, 1825), *Pomadasys perotaei* (Cuvier, 1830)

d. *Cynoglossidae* (Tongue Sole): *Cynoglossus senegalensis* (Kaup, 1858), *Cynoglossus canariensis* (Steindachner, 1882), *Cynoglossus monodi* (Chabanaud, 1949) and *Cynoglossus browni* (Chabanaud, 1949)

e. *Polynemidae* (Threadfins): *Polydactylus quadrifilis* (Cuvier, 1829), *Galeoides decadactylus* (Bloch, 1795)

f. *Carangidae* (Jackfish): *Caranx hippos* (Linnaeus, 1766), *Caranx crysos* (Mitchill, 1815), *Caranx latus* Agassiz, 1831, *Caranx lugubris* (Poey, 1860)

g. *Sphyraenidae* (Barracudas): *Sphyraena barracuda, Sphyraena afra, Sphyraena guachancho*

h. *Clupeidae: Sardinella* spp.

The sparid community comprises mainly the following major families and species:

a. Lutjanidae (Red snappers): *Lutjanus goreensis* (Valenciennes, 1830), *Lutjanus fulgens* (Valenciennes, 1830), *Lutjanus agennes* (Bleeker, 1863) and *Lutjanus dentatus* (Duméril, 1861)

b. Serranidae (Groupers): *Epinephelus aeneus* (Geoffroy Saint-Hilaire, 1817)

c. Sparidae: *Dentex canariensis* (Steindachner, 1881), *Dentex angolensis* (Poll & Maul, 1953), *Dentex congoensis* (Poll, 1954)

d. Breams: *Pagrus* spp., *Pagellus bellottii* (Steindachner, 1882) *and Pagus* spp.

Fishery resources in the inshore shrimp industry include the following in order of importance:

a. White prawn (*Penaeus notialis*) (Pérez Farfante, 1967)

b. Brown or Guinea shrimp (*Holthuispenaeopsis atlantica*) (Balss, 1914)

c. Rose or red deep-water shrimp (*Parapenaus longirostris*) (Lucas, 1846)

d. Stripped or tiger shrimp (*Penaeus monodon*) (Fabricius, 1978)

e. Palaemonidae-Estuarine prawn from Decapoda (*Nematopalaemon hastatus*) (Aurivillius, 1898)

4. Status of marine fisheries production in Nigeria

The world fish production has drastically been affected by the marine fisheries production globally and in Nigeria. According to the FAO's [46] report, total fish production in the world was only 19.3 million tons in 1950, which increased tremendously to 163 million tons in 2009. Throughout history, marine fishing has always been the largest contributor to global fish production. As at 2009, marine capture fisheries contributed about half (49%) of the world fish production, in comparison with mariculture (21%), fresh water aquaculture (23%) and inland capture fishery (6%) [47]. The highest marine fisheries production was 87.7 million tons in 1996, while the global recorded production was 79.5 million tons in 2009. This implies that although the global fish production has increased, marine fisheries contribution to total fish production has been on the decrease since 1996.

Rabo et al. [41] reported the total fish caught by African fishers to be 6.30 million metric tons and that 3.80 million tons (about 60 percent) was from the marine waters with Nigeria being among the top African countries in terms of total fish catch. They contributed further that Nigeria's 2005 fish catch was 579,500 metric tons live weight and less than half of the catch was from inland waters. This illustrates that the Nigerian fish production has been dominated by marine fisheries (fishing and aquaculture).

A more recent report of the FAO [39] noted that the total world fisheries production has been on the increase from 145.9 million tons in 2009 to 167.2 million tons in 2014. It was also reported that marine fisheries contributed 101.1 million tons, which is about 69.3% of the total world fish production in 2009 [39]. The total marine fisheries in 2010 declined to 100.0 million tons (67.5%) out of the 148.2 million tons of world fish production the same year. The total marine fisheries production also increased to 105.8 million tons in 2011, but its contribution to total world fisheries production was only 68.0%. In 2012, marine fisheries decreased to 104.1 million tons contributing only about 66.0%, while total marine fisheries increased to 106.5 million tons in 2013 contributing 65.3% to world fisheries production. In 2013, the fisheries production increased to 167.2 million tons with marine fisheries contributing 108.2 million tons (64.7%). A closer look at the report of FAO [39] indicated that inland water aquaculture contributed more than inland water fisheries, while marine fisheries contributed more than marine aquaculture.

5. Marine fisheries regulations in Nigeria

A number of policies, decrees, and acts have been put in place by successive Nigerian governments as a way of regulating the stocks of marine fisheries resources in the country. These regulations include the Sea Fisheries Act of 1971, the Sea Fisheries (Licensing) Regulations of 1971, the Sea Fisheries (Fishing) Regulations of 1972, the Exclusive Economic Zone Decree of 1978, the Sea Fisheries Decree of 1992, and the 1995 Sea Fisheries Regulations. Each of them is discussed below.

5.1. The Sea Fisheries Act of 1971

Although conscious efforts at developing the nation's fisheries could be said to have started in 1941, there was no real national fisheries policy in place. During this period, there were some programs aimed at increased fish production through input supply at subsidized rates, technology transfer, and revolving loan schemes among fishermen [48]. The first national policy was put in place by the federal government with the advice of the Federal Department of Fisheries when the Sea Fisheries Decree was promulgated under the Decree No 31 of 1971 to control and regulate coastal fisheries. The Sea Fisheries Act is an act to make provisions for the control, regulation, and protection of sea fisheries in the territorial waters of Nigeria [49]. The act has 14 sections with Section 1 being on licensing of motor fishing boats; application for a license, grounds for issue of a license, and renewal of a license were detailed in Sections 2–4. Sections 5 and 6 were on appeals and returns, respectively, while Section 7 was on the enforcement of the Act. Section 8 prohibited the use of any explosive substance, or any noxious or poisonous matter that could destroy fish within the territorial waters of Nigeria. Offenses against the act and penalties for such offenses were detailed in Section 9, while any fishing boat and apparatus used in contradiction to this act shall be forfeited according to the government, as contained in Section 10. Section 11 provided the Minister of Agriculture the power to make regulations for furthering the interests of sea fishing industry in Nigeria and for giving effect to the provisions of this act. The interpretation of the contents of the act were explicitly stated in Section 12, whereas Section 13 repealed the 1961 Sea Fisheries (Lagos) Act, the 1965 Sea Fisheries Law, the 1967 Sea Fisheries (Motor Fishing Boats Licensing) Regulations, and the 1969 Sea Fisheries (Licensing) Regulations.

5.2. The 1971 Sea Fisheries (Licensing) Regulations

These contain six regulations and two schedules on the licensing of motor fishing boats. Application form for a license or renewal of a license to operate or to navigate a motor fishing boat within the territorial waters of Nigeria and the particulars that must be stated in such application as contained in Form A of Schedule I are prescribed in these regulations [43]. Form B of Schedule I prescribes the form of license to operate or navigate a motor fishing boat, while Schedule II contains the fees for licenses. It was, however, indicated that nothing in these regulations shall be applied to motorized and nonmotorized fishing canoes.

5.3. The 1972 Sea Fisheries (Fishing) Regulations

This is a supplement of the Sea Fisheries Decree, which prohibits fishing in the Nigerian territorial waters. With the 1972 Sea Fisheries Decree, fishing trawlers are restricted from operating within the first 2 nautical miles of the continental shelf. The essence of this was to ensure that industrial vessels are not competing with local artisanal canoe fishers. It was the outcome of artisanal fishers' complaints that industrial fishing trawlers were destroying their fishing nets [50]. Etim et al. [51] noted that the regulation assigns exclusive right to the artisanal canoe fisheries to exploit the inshore area in order to reduce the conflicts between the industrial and artisanal sectors.

The provided regulations are that:

i. No fishing vessels (except canoes) shall fish within the first 2 nautical miles of the waters of the Nigerian Continental Shelf. This is the 'nontrawling zone.'

ii. Trawlers fishing in the inshore waters should use a mesh size of not less than 3.00 inches (76.0 mm) toward the cod-end and trawlers shrimping shall not use a mesh size less than 44.0 mm toward the cod-end. The minimum size of fish to be caught was also fixed at 3.00 cm.

iii. All catch should be landed at port, and that no part of it may be exported away from Nigeria at sea.

iv. Any part of the catch for export shall be exported in the usual manner and subject to any foreign exchange regulations for the exportation of such commodities from Nigeria.

v. No shrimp trawling is permitted in the inshore water of the Lagos-West fishing grounds.

vi. Penalties involving fines, imprisonment, or both are provided for those contravening the regulations [43].

5.4. The 1978 Exclusive Economic Zone Decree

The Exclusive Economic Zone Decree Act was promulgated by the Federal Government of Nigeria in 1978 in line with the provisions of the UN Convention on the Law of the Sea [50]. The Act empowers Nigeria to extend her territorial waters by 200 nautical miles seaward from the coast of Nigeria [52]. With this Act, the natural resources of the exclusive economic zone within the Federal Republic of Nigeria can be exploited under the Nigerian regulations. It also contains the penalties (fines, imprisonment, or both) for contravening the provisions of this act.

5.5. The 1992 Sea Fisheries Decree

The 1971 Sea Fisheries Act was repealed and replaced by the 1992 Sea Fisheries Decree in order to continuously promote the sustainability of the inshore fisheries and the fisheries of the EEZ in the country [52]. It was promulgated under the Decree No 71 of 1992 Laws of the Federation of Nigeria and contains 17 sections. The provisions of this decree were on the licensing of motor fishing boats, penalties for unlicensed motor fishing boats enjoying the rights of licensed boats, powers and duties of licensing officers, and the penalty for violating the provisions of this decree. Section 1 of the decree provided that only dully registered and licensed motor fishing boats and reefer vessels are allowed to be navigated within the territorial waters of the country [53]. The 1992 Sea Fisheries Decree also extended the restriction placed on industrial vessels from competing with local fishers to 5 nautical miles. Although the decree was silent on fish sizes that could be captured, it mandated the Nigerian Institute for Oceanography and Marine Research (NIOMR), Lagos, to publish the minimum total length of different species that could be caught during each year [50].

5.6. Sea Fisheries Regulations of 1995

The 1995 Sea Fisheries Regulations originated from the Sea Fisheries Decree No 71 of 1992 and contains in addition to the provisions of the Sea Fisheries Decree 1992 Fish Inspection and Quality Assurance as the main text concerning the control of fishery products [52].

6. Constraints to optimal marine fisheries production in Nigeria

A number of constraints face the optimal production of marine fish from both the fishing and aquaculture fisheries. These constraints are as a result of threats to the marine fisheries resources and could be grouped into natural and human factors.

6.1. Natural factors

The natural factors affecting the marine fisheries resources include salinity, wind speed and direction, ocean currents, nutrient availability, carbon dioxide concentration in the ocean, strength of upwelling, rain and snow, as well as the interaction among these different factors [54, 55]. The consumption of small fish by large predator fish, mammals, and seabirds also constitutes a serious threat to certain fish species [56, 57].

In Nigeria, excessive pressure is put on inshore fishes because of Nigeria's relatively narrow continental shelf, which extends for about 15 km in the western area and ranges from 60 to 80 km in the eastern area [58]. This limits the trawlable area to 3.20 km^2 (27.9%) out of the 11.5 km^2, which Nigeria is blessed with [59, 60]. Lastly, the low-lying nature of the Nigerian coast makes it susceptible to storm surges, coastal erosion, and inundation of the coastal mangrove and wetlands, which destroy rare and fragile habitats for marine fish breeding and nursery [61].

6.2. Human factors

The human factors that constitute threats to fishery resources are categorized and discussed under three broad headings: overfishing, environmental activities, and climate change.

6.2.1. Problems of overfishing

Globally, and in Nigeria, overfishing is the primary human activity, which poses as threat to marine fishery resources. Overfishing occurs when so many fish are taken from a fish population such that the stock capacity to produce maximum sustainable yield on a continuous basis is diminished [62]. In Nigeria, overfishing is caused by several interrelated factors such as increase in population, ghost fishing, and problems associated with the creation of EEZ, and inadequate data, and high interest rates on loan.

6.2.1.1. Increase in population

Nigeria, which is currently the seventh largest country in terms of human population, has been projected to be the third largest country by year 2050 [63]. Although the domestic fish production has increased based on different programs of the Federal Government, this increase is at a slower pace when compared with the nation's growth rate, and hence, the increasing human population puts more pressure on the marine fishery resources. The FAO predicts that by 2030 an additional 37.0 million tons of fish per year will be needed to maintain current levels of fish consumption for an expanding world population [64]. This gap continues to grow on a daily basis as the world population increases.

6.2.1.2. Ghost fishing

According to FAO [39], ghost fishing is caused by abandoned, lost, or otherwise discarded fishing gear. Lost nets and those intentionally abandoned in the sea by fishermen continue to catch fish and nonfish species [65]. Although ghost fishing is under 1.00% of landed catches [66], according to a recent FAO and United Nations Environmental Program reports, the problem is likely to escalate due to the increased scale of fishing operations, introduction of highly durable fishing gear made of long-lasting synthetic materials, and lack of serious concern shown by the international community to address the problem [67].

6.2.1.3. Problems associated with the creation of EEZ

The creation of the EEZ also set into motion its own dynamic system leading to compliance and enforcement problems. The majority of coastal states, especially developing states, cannot afford the sophisticated patrol vessels or satellite vessel monitoring systems (VMS) required for monitoring and surveillance of the vast and turbulent waters of the EEZ with less risk. The inability of coastal states to effectively monitor and enforce conservation measures in their EEZ encourages fishing in the area by unauthorized persons including foreign fishing vessels, thus exacerbating the depletion and collapse of marine fish stocks [68].

6.2.1.4. Inadequate data and high interest rate on loan

The above problems are further compounded by the lack of relevant data and information on fishing vessels, catch landings, and fish stock biomass, especially in developing countries including Nigeria. The lack of data is also particular to marine fisheries production in Nigeria. For instance, while the inland aquaculture of finfish was put at 313.2 thousand tons, that of marine/coastal aquaculture of finfish and other aquatic animals and plants was either unavailable or considered as negligible [39]. High interest rates on investment loans have prevented prospective investors in the marine fisheries industry from taking loans from commercial, merchant, development, and even microfinance banks [21]. This thereby limits the marine fishery production in Nigeria.

6.2.2. Environmental factors

Environmental factors affecting the availability, adequacy, and affordability of fish demands of Nigerians as a result of the deplorable state of the marine fisheries resources include pollution of aquatic environments and destruction of habitat.

6.2.2.1. Pollution of aquatic environments

Pollution of the aquatic environments is a major threat to marine fish populations all over the world. Dumping of toxic waste in the sea and emptying of ballast water from ships into the sea are other human activities polluting the aquatic environment. The problem of invasion of exotic fish species is linked to ballast water from ships. In Nigeria, the sources of pollution of the aquatic environment are industrial waste, raw/untreated domestic sewage, run-off of fertilizers and pesticides, sand mining, construction of canals, and oil spills [69, 70]. Excluding unreported cases, more than 1.07 million barrels of oil were spilled in Nigeria from 1960 to 1997 [71–73]. The millions of tons of polythene bags and other types of nonbiodegradable debris that have been washed by rain water into the aquatic environment constitute new threats to marine fisheries.

6.2.2.2. Habitat destruction

Habitat loss and environmental degradation of coastal zones, wetlands, deltas, and mangrove areas due to developmental activities and growth in aquaculture constitute the main reasons for the collapse of marine fish species that spawn in freshwaters [74]. Habitat loss also occurs in the high seas through deep-sea fishing activities [75]. This situation is particular in Nigeria since the discovery of oil in the 1970s and consequent neglect of the agriculture by the government and citizens that fuelled rural-urban migration in the country. This has also led to increased population growth especially in urban cities and hence contributed to intense urbanization [76], especially along the coastal areas. The establishment of new coastal settlements, such as Victoria Garden City in Lagos and Eagle Island in Port Harcourt, led to the reclaiming of lagoons and filling of mangrove swamps and estuaries for building of social infrastructures and industrial estates [77].

6.2.3. Climate change

The most fundamental impact of climate change on fish is through increase in global temperature. The 2007 report of the Intergovernmental Panel on Climate Change (IPCC) reveals that global average surface temperatures over the last 100 years have increased by 0.74 ± 0.18°C, while the rate of warming over the last 50 years is almost double that of the last 100 years (0.13 ± 0.03°C vs. 0.07 ± 0.02°C per decade) [78]. Global warming is responsible for the unprecedented warming of the oceans [79]. Ocean warming globally affects marine fishery resources in many ways such as the destruction of coral reef ecosystems [80].

7. Conclusion

Marine fisheries have been found to contribute significantly to the global fisheries production as well as to Nigeria when compared with inland freshwater fisheries. However, while production earned from inland fisheries has regularly been increasing, marine fisheries production has been fluctuated with increase at some time and with decrease at other times. Review of literatures also indicated that contribution of aquaculture to marine fisheries production has been low when compared to the marine fishing production. Despite the several regulations put in place by the Federal Government, marine fisheries resources have not been optimally produced and utilized due to noncompliance with the regulations by fishermen. The current trend in marine fisheries resources and production could then be regarded as deplorable and this has been blamed on both natural and human factors. It is recommended that the aquaculture of marine fishes should be intensified. Marine waters should also be protected against destruction and pollution as a result of human activities. Available marine fisheries regulations should be enforced and violators of the regulations should be punished as stipulated in the regulations, while some of the provisions of the regulations such as mesh size, fish size, etc. should be modified to allow for optimal marine fish production in Nigeria.

Conflict of interest

The authors hereby declare that there is no conflict of interest in this chapter preparation.

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Marine Stock Enhancement in India: Current Status and Future Prospects

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Additional information is available at the end of the chapter

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Abstract

India is a 12 mega-diversity nation known for its biodiversity richness. The geographic territory of India is an integral part of Central Indian Ocean Region consisting of three distinct marine ecosystem zones such as the Arabian Sea, Bay of Bengal and Indian Ocean. India is endowed with an exclusive economic zone of 2.02 million km2, coastline of over 8000 km and a variety of coastal ecosystems. The estimated number of marine fish species known from India constitutes 2443 species distributed in 230 families. According to the IUCN extant (2014), 50 species are threatened (6 of them critically endangered, 7 endangered and 37 vulnerable), while 45 are near-threatened. Marine fish diversity is in ever-increasing danger with depletion of resources. Overdependence on fish has led to overfishing resulting in the dwindling of diversity and abundance of stocks. Central Marine Fisheries Research Institute has initiated marine stock assessment practices in India and its present report in 2016 recorded a total of 709 species which is lower than 730 species recorded in 2015 in the landings showing an alarming situation on the exploited marine fishery resources of India. This situation demands restorative measures such as restocking, stock enhancement and sea ranching.

Keywords: depletion of fish resource, restorative measures, Central Indian Ocean

1. Introduction

Biodiversity is under threat worldwide, so a major issue of the twenty-first century [1]. Fish contribute more than one-half of the total number (54,711) of vertebrate species recorded so far [2]. The descriptions of 33,059 species of fish are known from all over the world [3]. India is one among 12 mega-diversity countries because of its biodiversity richness. The Central

Indian Ocean Region includes Indian Territory along with other countries such as Bangladesh, Indonesia, Maldives, Malaysia, Myanmar, Thailand and Sri Lanka.

The Central Indian Ocean Marine Region consists of the Arabian Sea, Bay of Bengal and a large area of the Indian Ocean south of India and Sri Lanka. Arabian Sea and Bay of Bengal bounding west and east coasts of the Indian peninsula merge with the Indian Ocean at the peninsula's southern most extremity. India having vast marine resources in the form of coastline (over 8000 km), exclusive economic zone (EEZ, 2.02 million km^2) and various ecosystems of coastal area including estuary, coral reefs, marshes, mangroves, lagoons, rocky and sandy areas [4]. The Andaman and Nicobar Islands, Gulf of Mannar, Gulf of Kachchh and Lakshadweep also fall within the marine waters of EEZ of India.

Conservation of fish is important because of their functional significance and vital role in communities of aquatic ecosystem [5]. In terms of diversity of species, the fish surpass all other groups of animals [6]. The marine fish diversity of India is in ever-increasing danger with depletion of living resources despite the acknowledged notion that it is crucially important for the survival of humanity. Furthermore, fish may be considered as appropriate indicators of aquatic biodiversity, since their rich diversity is reflective of a wide range of environmental conditions [7]. Fish diversity is also reported to be a major element in the health assessments of some estuaries [8]. The lack of a sustainable management regime will further accelerate the rate of resource decline. As a result, 31% of global fish stocks are classified as overfished and a further 58% as fully exploited, with no ability to produce greater harvests. The accelerated rate of species extinction and endangerment is a matter of great concern because of species in the wild, being an ingredient of the web of life, has a role to play in the normal working of the ecosystem. The need to preserve biodiversity and sustainably to manage fishery resources is too urgent to be ignored due to depletion of major resources and dwindling catches. The consequences of loss of species from the web of marine life are widespread, affecting the whole ecosystem or micro-ecosystem of which the lost species was a component [9]. Extinction of a species affects other species and can accelerate the extinction of more species through a chain reaction. Most of these concerns have not been translated into a practical reality. Increasing population density, industrial growth and socio-economic development will give rise to a variety of activities, the collective impact of which will multiply the pressures on the coastal zone and its resources.

2. Indian marine fish diversity

Every region of the sea is a repository of biodiversity which acts as a home for a wide variety of life. Among various living organisms, fish are most diverse vertebrate occupying various habitats of different types of ecosystem. A healthy habitat requires the variability among species for maintaining the ecosystem's flexibility. The taxonomists have a leading role not only in realizing species diversity but also in protecting its potential by recognizing diversity in the ecosystem and documenting it. The number of fish species reported from fresh and marine waters of India is 3231, which constitutes 9.70% of fish known from the world [3]. Gopi and Mishra [10] reported 2443 marine fish of India which is 75.6% of total fish species so far reported from India. The estimated number of Indian marine fish species is classified into 230 families, where 12 families are having more than 40 species and other families in order of decreasing number of species are: Gobiidae (190), Pomacentridae (92), Labridae (85), Serranidae (85), Carangidae (66), Blenniidae (65), Apogonidae (63), Chaetodontidae (48), Lutjanidae (45), Sciaenidae (43), Syngnathidae (42) and Myctophidae (41). Nine families of Indian marine fish are monotypic; 7 families have 2 species in 1 or 2 genera; 35 families have 20 or more species and 12 of which have over 40 species. A total of 96 families are represented by only 1 genus each. The order Perciformes is the most species-rich group of Indian marine fish having a total of 1367 species accounting for 56.0% of the total marine fish species. The other orders such as Scorpaeniformes, Anguilliformes and Tetraodontiformes each contribute 4.30% of the total Indian marine fish species reported.

A survey of the literature showed that the scientific database of Indian marine fish fauna is scanty and efforts should be made to complete it. However, the Zoological Survey of India has initiated efforts to collect the literature of Indian marine fish and published the state fauna series in order to describe the fish fauna of marine and estuarine waters of Lakshadweep [11], West Bengal [12, 13], Gujarat [14], Puducherry [15], Andhra Pradesh [16], Odisha [17], Tamil Nadu [18], Maharashtra [19], Andaman and Nicobar Islands [20] and Karnataka [21]. Besides, Talwar and Kacker [22] carried out work on 'commercial sea fishes of India' and described a total of 548 species of commercially important Indian marine fish of 89 families.

Knowledge of fish diversity of the particular region is considered to be essential not only for their rational management but also for the conservational strategies for the ichthyo-fauna of that region.

Fish and fisheries today form an important element in the economy of India like many nations. But, some of our own actions such as overfishing of marine waters that upset the integrity of the environment pose serious threats to marine ichthyo-fauna and stocks of fish. The studies are considered to be essential to determine the status of marine fish whether they are threatened or not in order to prevent them from their possible extinction. The efforts on ecosystem restorative measures are needed for restoration of marine ecosystems to check the diminishing population of marine fish.

3. Causes of fish depletion

3.1. Overfishing

Fish are immensely important to human beings as they have long been a staple food item, but overfishing because of overdependence on fish has led in the dwindling of their many species. Fishing through dynamiting and poisoning, which are the worst forms of reckless exploitation that bring about the mass mortality of fish and inflict considerable collateral damage. Such activities have been considered to be detrimental to lush coral reefs in mega biodiversity regions of the Indo-Pacific [6]. Increasing demand for fish and advancement in technology have drastically enhanced the exploitation of ocean resources and led to serious pressures on marine fish. Lack of management or mismanagement has led the loss of fisheries sustainability.

Several fish species and stocks have already collapsed, while many others will meet the same fate in the future. When some species are removed, this can lead to loss of other species, shifts in relative abundance and reduced resilience [23, 24].

3.2. Habitat alteration

Anthropogenic activities are considered to be the major cause of habitat alteration caused by depletion in marine fish diversity. The sea has long been used as an ultimate dumping ground for all kinds of pollutants including solid, liquid, organic and inorganic wastes; in which some are biodegradable, others are not. Marine life is affected by pollutants directly or indirectly which change the whole ecosystems including genetic resources that may cause mass mortalities of fish and other organisms. More devastating are the hidden changes in many species including changes in the genetic composition of marine organisms by directly acting on the DNA to bring about gene mutations (change at a single locus) or chromosomal aberrations (changes of chromosomes at many loci), and by way of environmental modifications which impose selective pressure on genotypes [25]. Discharge of essential nutrients to marine ecosystems can cause eutrophication resulting in algal blooms, oxygen deficits and changes in species composition.

Chemicals pollute the sea, which enter from land, air and rivers. These pollutants may be natural or artificial from industries, agriculture, etc. The chemical pollutants may act on fish directly or by changing the environment indirectly. These chemicals enter into the food chain and affect the organisms in time and space from the source. Those chemicals which are not metabolized may accumulate in the tissues of various organs of the body and affect the organism through biological magnification. Food chains of marine organisms are long, and the members of the upper trophic level of the food chain are affected by the maximum concentration of non-degradable chemical poison, because the carnivores of upper trophic level acquire the chemicals from the eaten prey containing chemicals. So, the top members such as carnivores of food pyramid receive quite significant quantities of the chemical as food chain prolonged. The poison of chemical contamination by biological magnification was found to be in the bodies of oceanic fish like tuna and swordfish. Mustafa and Zofair [26] reported the problem of biological magnification of DDT in carp which led to the proteolysis and interference in pathways of protein biosynthesis.

A number of workers such as Shomura and Godfrey [27], Shomura and Yoshida [28] and Norse [29] reported the accumulation of non-biodegradable solid wastes such as glass, plastic and metal containers in the bed of sea for decades, which change the marine habitats and cause mortality of animal's entanglement and ingestion. Recently, CMFRI [30] reported the occurrence of macroplastics of 5.00 cm and 3.00 cm lengths in the gut of *Coryphaena hippurus* (Linnaeus, 1758) and *Euthynnus affinis* (Cantor, 1849), respectively, collected from different regions of India Sea.

3.3. Oil pollution

Oil spills are considered to be a major cause of marine pollution. Leakage from tankers during transportation of crude oil, a collision of tankers, rigs operation, pipeline leaks and washing of tankers are major sources of oil spills. Oil spills destroy the fish habitats and alter the ecological conditions of seawater which led to the mass mortality of fish and other organisms. It is estimated that 252–336 million gallons of oil spilt into the Persian Gulf during Gulf War [31]. Adverse environmental change, especially in spawning habitats, decreases the stock strength of the coastal fish.

Recently, the oil spill was recorded because of the collision of two cargo ships (MT BW Malpe and MT Dawn Kanchipuram) on January 28, 2017 at Kamarajar Port, Ennore. For damage control, it is estimated that 65 tonnes of slick was removed from out of the spillage. The damage of sedentary organisms due to oil pollution near the high toxic level (HTL) at Kasimedu was recorded on a survey conducted between Pazhaverkad and Kovalam coasts of India, but the organisms of the lethal toxic level (LTL) were healthy and unaffected.

3.4. Fly ash deposition

The studies on the impact of the effluents from burning coal of Tuticorin Thermal Power Station was carried out for 6 months during July–December, 2017, which indicated that fly ash and hot water discharges are more adversely affected compared to chemical effluents released from thermal power station.

3.5. Public sewage

The impact and analysis of untreated municipal or public sewage discharge to the coastal sites of Tuticorin indicated more deterioration condition of the marine water as compared to other sites. Similarly, maximum number (13 × 106) of total plate count of marine sediment was recorded from the fisheries harbor site at Visakhapatnam than the sites where public sewage is disposed.

3.6. Climate change

Burning of fuels, industrialization, urbanization, etc. are major sources of different harmful gases such as CO_2, CH_4, NO and CFCs which led to the production of the greenhouse effect. The heating of earth's surface resulting into melting of ice in glaciers and poles are expected to further raise the sea level in the range of 21–71 cm by the year 2070. This could mean that many fisheries dependent on upwelling will suffer or cease to exist. The marine fish whose genotypes can withstand the changing environment and new selection pressures will survive as a genetic core for new directions in evolution. At worst, effects could include loss of critical coastal habitats, alterations in oceanic circulation patterns and loss of many existing fisheries. The study of impact of climate change on the vulnerability of Indian marine fish was carried out under the NICRA project, and criteria were developed for exposure, sensitivity and adaptive capacity of Indian species to enable assessment of the vulnerability of fish species.

Criteria were formulated as:

$$\text{Vulnerability} = (\text{Exposure} + \text{Sensitivity}) - \text{Adaptive capacity} \tag{1}$$

Vulnerability assessments have been carried out at different centers as per the developed criteria. This also allows for predictive evaluation based on 40-year catch data. For this, 40-year data on fishery biology and environmental parameters of Indian coast were analyzed.

In India, some institutions at the national or state level are devoted to the study of the propagation of some food fish species, based on their biology and reproductive potential. Hence, government support and active participation of financial institutions may be essential to provide an initial thrust to new ventures. In this framework, the Central Marine Fisheries Research Institute (CMFRI) is the pioneering institution, which has initiated marine aquaculture research and has been developing appropriate marine aquaculture technologies in India [32–38]. Indian marine fisheries data collection is a quite systematic statistically renounced activity in India by CMFRI by the research institutes of the Indian Council of Agricultural Research (ICAR) since 1950s. Monitoring and assessment of the exploited marine fishery resources of India are one of the important mandates of CMFRI. For sustainable fisheries, stock assessment data are considered to be essential and important as a reference for the management of exploited resources. The Indian Institute, CMFRI has been gathering the data by establishing the National Marine Living Resources Data Centre (NMLRDC) regarding the landings of different species of marine fish and their biology. The center has already collected information of the exploited marine fish species and other resources to create a strong data base.

Among the Asian countries, India ranks second in culture and third in capture fisheries production and is one of the leading nations in marine products export. The marine fish landings in India were approximate at 3.63 million tonnes during the year 2016 which is 6.60% more than the previous year. Rajiv Gandhi Centre for Aquaculture (RGCA) in India has been undertaking natural stock enhancement activities including, breeding of Asian sea bass: cage culture of Asian sea bass; fattening of rock lobsters; breeding and culture of mud crabs; Artemia production; breeding and culture of groupers and culture of Tilapia [39]. But, unfortunately, this phenomenal growth also brought in imbalances in the exploitation across the regions and among the resources. The present situation demands for the development of suitable scientific strategies on the basis of available database of marine resources of region and country wise for the management and exploitation of fishery resources.

4. Marine fish and their conservation categories

Various methods have been developed for the conservation assessment of fish. The major classification system used internationally for assessing the status of the threat to each species is that adopted and developed by the World Conservation Union or International Union for the Conservation of Nature and Natural Resources (IUCN). The IUCN [40] Red list is a catalog of taxa that are facing the risk of extinction or the threat in their wild habitats. The fish species restricted to limited geographic area and facing anthropogenic threats because of alteration in their habitats are considered to be more liable for becoming threatened species.

The uses of Red data list are to develop awareness about the importance of threatened biodiversity, identification of endangered species, providing a global index of the decline of biodiversity and defining conservation priorities at the local level and guiding conservation action. Following different categories of threat status were addressed:

i. **Extinct (EX)**: Extinct taxon is the condition of the species where all the individuals died without suspicion.

ii. **Extinct in the wild (EW)**: Extinct in the wild taxon is the condition of the species where exhaustive surveys failed to record an individual species in habitats and known to survive in captivity or under culture system.

iii. **Critically endangered (CR)**: Critically endangered taxon is species, which is facing great risk of extinction near future in wild.

iv. **Endangered (EN)**: A taxon is endangered whose numbers are so small that the species is at the extreme risk in wild for extinction.

v. **Vulnerable (VU)**: Vulnerable taxon is the species, which is facing a high risk in the wild in some time future for its extinction, but is not endangered or critically endangered.

vi. **Near threatened (NT)**: Near threatened taxon is the species which does not satisfy the criteria of endangered or critically endangered or vulnerable category, but may enter in the category of threatened in near future.

vii. **Least concern (LC)**: Least concern taxon is the abundant and widespread species which does not satisfy the criteria of threatened or vulnerable or endangered and critically endangered categories.

viii. **Data deficient (DD)**: Data deficient taxon is the species whose information on abundance and distribution is considered to be inadequate for its assessment for extinction risk, but its biology may be well known.

ix. **Not evaluated (NE)**: A taxon is Not Evaluated when it has not yet been evaluated against the criteria.

The conservation categorizations of the marine fish of India were assessed by Gopi and Mishra [10] and they put forwarded that 50 species of marine fish are threatened, 6 of them critically endangered, 7 endangered and 37 vulnerable of the 50 threatened fish species, most of them (40 species) are cartilaginous (elasmobranchs-sharks, skates and rays) and the remaining 10 species are teleost fish. In addition, more than 45 species are near threatened.

Marine conservation is a subject that focuses on issues which attempt to save from massive economic disaster. A common resolve for biodiversity protection and sustainable management of fishery resources must exceed geographical boundaries of nations, and there should be the willingness for cost sharing in both *in-situ* and *ex-situ* methods of conservation. For each species or population facing genetic risk, the most appropriate conservation methods are *in-situ* or *ex-situ* methods.

In-situ conservation strategy is focused on ecosystem preservation from extensive pollution; sedimentation and alienation for possible species management for maintaining a viable fish population size, especially for normal breeding, recruitment and genetic diversity. *In-situ* conservation of marine organisms is carried out by declaring the appropriate and suitable natural conservation areas such as marine protected areas (MPAs) by designating as National Parks or Wild Life Sanctuaries or Biosphere Reserves in order to safeguard the depleted, threatened, rare or endangered species. Presently there are 31 MPAs in India covering a total area of 627.2 km^2 [41], out of which 4 National marine parks, 3 marine sanctuaries and 4 biosphere reserves are considered to be very important to protect Indian marine ecosystems with their resources [42] (**Table 1**).

Ex-situ conservation strategy is made outside the natural habitat in the form of live collections, gametes or DNA fragments. It can be categorized into two major types including Gene banks are useful for keeping broodstocks of different species and varieties in ponds, tanks and aquaria. Germplasm storage involves cryopreservation, mainly of gametes and embryos. These sources should admit the genetic resources of wild marine fish in addition to their original interest in the management of species. National Bureau of Fish Genetic Resource (NBFGR) is the prime institute of India carrying out fish sperm cryopreservation for long-term gene banking, and has developed the facilities for 27 species so far [43]. Cryopreserved sperm can be effectively utilized in order to overcome the milt-related problems of those fish

S. no	Name of marine protected area	Established/created	Total area	Parts of India
Marine national parks				
1.	Gulf of Kachchh National Marine park	1980	400 km^2	Gujarat
2.	Gulf of Mannar National Marine park	1986	623 ha	Tamil Nadu
3.	Mahatma Gandhi Marine National Park	1983	281.50 km^2	Andaman and Nicobar Islands
4.	Rani Jhansi Marine National Park	1996	256.14 km^2	Andaman
Marine sanctuaries				
5.	Bhitarkanika Gahirmatha Sanctuary	1997	1435 km^2	Odisha
6.	Malvan Marine Sanctuary	1987	29.12 km^2	Maharashtra
7.	Gulf of Kachchh Marine Sanctuary	1980	295.03 km^2	Gujarat
Biosphere reserves				
8.	Sunderbans	1989	9630 km^2	West Bengal
9.	Gulf of Mannar	1989	10,500 km^2	Tamil Nadu
10.	Great Nicobar	1989	885 km^2	Andaman and Nicobar Islands
11.	Kachchh	2008	12,454 km^2	Gujarat

Table 1. Marine protected areas of India.

where inadequate milt is produced or because of lack of synchronization in the maturity of two sexes being an issue for induced breeding in several cultivable fish species. An innovative approach for fish conservation was adopted by the NBFGR by declaring a State Fish for each of the states in India in the year 2006 [43]. As a result, 16 states of the country became partners with NBFGR in compliance with this concept for conservation and enhancement of their selected State Fish.

5. Marine fish management

The marine fisheries management must be based on population subdivisions into smaller biological units or stocks. Stock-specific fisheries management includes the identification of discrete stocks, their growth, recruitment and mortality, etc. which is carried out on large scale to ensure the sustainability of a population, while maximizing its harvest. Information on morphological, physiological, and behavioral variability, parasite distributions, otolith elemental composition provide insights into a stock structure. Fish stocks are changing because of natural and anthropogenic activities. Therefore, conservation of fish stocks is, needless to say, of principal magnitude for appropriate management purpose through the implementation of different stocking strategies.

6. Marine stock enhancement

Marine stock enhancement (MSE) is an integral component of fisheries management involving the release of cultured organisms to enhance or restore the depleting marine fish stock. A large number of countries are investigating the major potential for releasing cultured juveniles to boost up the marine fisheries. In this direction, the First International Symposium on Stock Enhancement and Sea Ranching (ISSESR) was organized in Norway in the year 1997 [44] and the second ISSESR in Japan in 2002 [45]. The Third ISSESR, hosted by NOAA in the United States in September 2006, proposed seven significant themes and also supported the development of restocking, stock enhancement and sea ranching policies for possible sustainable fisheries management. These events were considered to be instrumental in the development of the emerging discipline. Apart from these, other milestones including scientific conferences and reviews have also helped in the advancement of the science regarding releasing a wide range of valuable coastal species [46–57]. Stock enhancement program must be integrated along with a fishery management that involves habitat protection and release of juveniles with appropriate control of fishing effort [58].

6.1. Restoration of depleted stock

Restoration of severely depleted stock due to overfishing or any other perilous consequences can be achieved by releasing the cultured juveniles into the natural habitats for its rational exploitation in future.

It is to reconstruct conservation hatcheries for the implementation of possible conservation strategies to lend a hand to restore endangered or threatened species in wild.

Restocking includes the endeavors to replace the existing, self-recruiting stocks, with stocks having more desirable traits such as higher growth rate, reduced the tendency to stunt, etc. Restocking can thrive more where there is evidence that recruitment limitation cannot be overcome effectively by other fisheries administration tools and limiting factors are implicit. The large-scale restocking is carried out to enhance the depleted stocks of commercially important species to improve catches which may deeply affect the genetic reliability of a population. Ryman et al. [59] have elaborated two kinds of potential genetic concerns associated with this method, that is, introgression, whereby the genetic characteristics of natural populations are compromised by way of loss of adapted genes through interbreeding, displacement or eradication of the entire population due to the introduction of disease(s) and homogenization of a genetically differentiated population as a result of flooding with common exogenous gene pools.

6.2. Stock enhancement

The release of cultured juveniles into wild population(s) to augment the natural supply of juveniles and optimize harvests by overcoming recruitment limitation.

The term 'stock enhancement' is often used to describe most forms of stocking with an ultimate goal of enhancement practice to increase stock size of the species which occurred naturally to optimize its harvest or increase catch rates. Both stock enhancement and restocking are likely to be effective for some coastal invertebrate fisheries, because the shallow inshore distribution and sedentary behavior of the species involved can create self-replenishing populations on a relatively small spatial scale [56]. Stock enhancement and restocking are potential measures that could either reduce the time needed to rebuild certain capture fisheries to a more productive level or increase the productivity of some 'healthy' fisheries [57]. An important issue that has immense resource prospect viability via a stock enhancement and sea ranching is ignored. Stock enhancements are separated into two types: (1) The enhancement of existing wild stock for open-access fishery of the fish species which may or may not be self recruiting is called wild fishery, which is carried out in those inland water bodies that are not having property rights for this. In general, the recapture rate of stocked fish is low and repeated enhancement is not always necessary to maintain the fishery. (2) Culture-based fisheries includes stocking of small water bodies undertaken on a regular base and the activity is the only means of satisfying the fishery in the form of stock enhancement practices. In the last 10 years, marine stock enhancement has begun to be treated scientifically [58] and strides are now being on the way in gaining a scientific understanding of the stock-replenishment potential afford by hatchery releases [60]. Restocking and stock enhancement must be positioned within a fishery management scheme to facilitate which integrates releases with appropriate control of fishing effort and habitat protection [57].

6.3. Sea ranching

The release of cultured juveniles into unenclosed marine and estuarine environments for harvest at a larger size in 'put, grow and take' operations.

Sea ranching is also an alternative way to increase productivity from fisheries habitats, wherein animals are released for harvest at a larger size. Sea ranching or artificial recruitment of aquatic organisms is carried out into their natural habitat for stock improvement or enhancing the production and its conservation. The sea ranching technique involves the development of brood stocks, its breeding and larval rearing, nursery rearing and release of seed at suitable sites and monitoring of the released and natural stocks. The history of sea ranching is very old [61] and is said to have been originated in the USA as early as 1870. Afterwards, many maritime countries such as Japan, Norway and Iceland have launched successful ranching programs for marine stock enhancement. A total of 33 developing countries have reported marine stocking activities involving 59 species [55]. With the development of technologies of controlled breeding, seed production and nursery rearing, the programs of sea ranching of marine prawn, pearl oyster and clams were started in India in the mid-1980s. Ranching is advantageously carried out in bays, lagoons, shallow water bodies and in the protected ecosystems.

The global efforts on marine stock enhancement have begun scientifically in the recent years [58]. In India, natural stock enhancement activities have been undertaking by Rajiv Gandhi Centre for Aquaculture (RGCA), which has already ranched the Asian Sea bass, *Lates calcarifer* (Bloch, 1790) and the Mud Crab *Scylla serrata* (Forskal, 1775) at Pazhayaar estuary in Tamil Nadu. The other program of MPEDA-RGCA for sea ranching of 1000 juveniles of the marine finfish, Cobia was the first of its kind in India. The ranching program with tagging of fish before its release was initiated to carry out the research studies to know the type of trophic dependence in the Indian estuarine marine food web [62]. Our knowledge of trophodynamics of marine and estuarine fish is considered to be important and essential in order to sustain the marine stock enhancement.

Stock enhancement of penaeid prawns along the Kerala coast of India was considered to be not successful because of heavy mortality of hatchery-grown post larvae on their release to the sea. Moreover, they were neither acclimatized to the sea water nor acquired skills of predator avoidance. The efforts are intended to revive depleted marine snail species *such as Turbinella pyrum* (Linnaeus, 1767) (sacred chank), *Babylonia spirata* (Linnaeus, 1758) (whelk), *Volegalea cochlidium*_(Linnaeus, 1758) (spindle shells), *Chicoreus ramosus* (Linnaeus, 1758) (murex) and *Chicoreus virgineus* (Roding, 1798) along the coast of Tamil Nadu in India. A total of 10,000 juveniles and 0.50 million larvae of the different species of snails were sea ranched in the Gulf of Mannar in the year 2010. Natural stocks of all of the species of snails are exploited for their meat, shells and opercula.

7. Future prospects

International and regional cooperation is vital in a global drive for the conservation of marine fish resources, where sea resources contribute substantially to their economy. Since conservation and sustainable management demand limitations on exploitation, a mechanism of financial and technical support which can guarantee continued income through alternate sources will be needed. It should be realized that sustainability can be more productive in the long run than over-exploitation which exhausts the resource, leaving people out of work.

Marine diversity is yet to find its deserved place in the teaching and training curricula with respect to the research in the genetic diversity of fish stocks. It is strongly recommended that educational programs should be developed or reoriented to offer a prominent place to the conservation of marine resources. These educational efforts will be deeply facilitated by promoting the development of more interactive multimedia software and the production of standard books on the topic; training and expertise typically need to be built up in the relevant disciplines, such as environmental law, fisheries management and ecological economics. For example, a training course on 'Stock Assessment of Tropical Fishes' was conducted at ICAR-CMFRI. The training Course was jointly organized by the ICAR-CMFRI and Bay of Bengal Programme Inter-Governmental Organization (BOBP-IGO), Chennai during November 23–December 6, 2016.

Public awareness about marine biodiversity conservation, particularly its genetic aspect, is too low or non-existent. The fishing community continues to think about breed-release (restocking) as a way of enhancing depleted stocks, and release of alien or genetically modified species as a solution to declining catches without a concern about the genetic implications of doing so. Public knowledge should be promoted by outreach programs in simple language that it may reach and understood by all.

Accountable stock enhancement requires new information on rearing techniques, release strategies, monitoring and evaluation of hatchery-release effects (genetic and ecological) on wild stocks to produce possible disease defense in stocks. For the long-term enhancement strategy and making stocking economically successful harvest, rights are needed to be made.

Proper research involving improvements in seed quality shows unexploited potential to increase survival for future improvement in the efficiency of enhancement. Conditioning fish stocks prior to release will play a major role from the acclimation research on behavioral, physiological, developmental, ecological, environmental and feeding deficits in newly stocked organisms. Both short- and long-term attention is needed in field assessments of the effects of conditioning.

Powerful molecular tools (genetic tags and genetic fingerprinting) must be used which may aid in the genetic management of stocked populations for monitoring wild and hatchery stocks. For example, population genetic structure of Indian anchovy, *Stolephorus indicus* (Van Hasselt, 1823) studied using mitochondrial DNA markers, microsatellite marker development in *Eleutheronema tetradactylum* (Shaw, 1804) using next-generation sequencing technology, population genetic structure of *Lutjanus argentimaculatus* (Forsskal, 1775) using microsatellite markers, molecular taxonomic studies on *Protapesgallus_*(Gmelin, 1791)*, Scomber indicus* (Abdussamad, Sandhya and Arun, 2016) from the Indian coast.

Advancement needs to be made for selecting release sites, release microhabitat and the magnitude of stocking; density-dependence and carrying capacity are key considerations.

Adaptive management or better-improved methods for evaluating stocking effectiveness, species interactions and environmental influences are key to understand the uncertainties about stocking success in a realistic and objective manner in light of the specific objectives of a stocking program. Mitogenomic approach to study environmental adaptation and their response to fluctuations in environmental conditions were studied in Indian oil sardine, *Sardinella longiceps* (Valenciennes, 1847) using whole mitogenome scans [30]. The evidence was recorded for diversifying selection on ATP6, CO1, CO2, CO3, Cyt b, ND1, ND2, ND4 and ND5 parts of OXPHOS genes, which involved in metabolic divergence for critical adaptation in the structuring of sub-population of Indian oil sardine [30].

Interactions of hatchery and wild stocks should be expected and the effectiveness of increasing production with hatchery releases needs to be tested on a large scale for the enhancement of total production.

For the success in the management of stocked populations effectively, there must be improvements in stocking programs considering institutional arrangements involving all stakeholders, the social and legal framework to integrate stocking plans with harvest regulations, cost-recovery and fisheries management plans to make out the role of government for the possible achievements.

8. Major challenges

Significant programmatic funding and also the agency(ies) are absolutely essential for a reliable stocking program for the production and release of an enormous quantity of seed.

Such programs, however, require cooperation from hatchery operators to supply disease-free seed and from fishers to protect the stocked animals until they reach a substantial size in natural waters before harvesting.

Cage culture or aquaculture has made possible the large-scale production of commercial finfish all over the world and considered as the most competent and cost-effective mode of fish cultivation. Marine fish farming in cage has great potential to increase the fish production to compensate the drop in marine fish production. The Indian bays of coastline such as Larson Bay, Andaman and Nicobar, Lakshadweep, Gulf of Mannar, Ratnagiri, Goa, Karwar, Palk Bay, etc. are considered to be ideal sites for cage farming. The Indian institute, CMFRI has already developed and demonstrated the technology for cage farming for marine fish such as cobia, snappers, rabbit fish, sea bass and groupers at selected places along the coastline of India.

India being rich in marine biodiversity, there are opportunities for providing financial benefits to the coastal communities and the profit made should encourage the community to conserve the reckless deteriorating biodiversity. With the growing importance of ecosystem services, there is going to be a lot of importance given to biodiversity conservation and biotechnological interventions. Regarding an association including biodiversity communities, biotechnologists and conservationists will alter the operating environment of the sector from exclusively fishery dependent activities to 'earning from biodiversity conservation'. As the population growth continues, demand for food is going to place even greater pressure on fish populations. In India, aquaculture ranks first in providing food and the marine fishery industry is in a phase of rapid growth and thus ranks second after aquaculture. Clearly, we cannot rely, in the future, only on aquaculture or wild-caught seafood of marine fisheries to satisfy the ever-increasing demand. Fishery management agencies worldwide are struggling with the paradox of trying to conserve fish stocks while also meeting an increasing demand for seafood which may fill the gap in supply. Exacerbating this situation leads to stock depletions that they can no longer support fishing. The steadily increasing demand, owing to population growth and human health recommendations to increase seafood in the diet, is placing enormous harvest pressure on wild fish stocks. The alarming consequence of such high demand for seafood is that two-thirds of the world's coastal fisheries are now fully exploited, overexploited or depleted and need to be rebuilt [45].

The widespread human onslaught on aquatic habitats has added a sense of urgency to investigate the possible link between habitat destruction and the breakup of gene pools, reorganization of genetic variability and loss of sustainability in fish populations. Caution is needed in establishing links between the status of fish populations and genetic diversity as determined by molecular tools. Fish have been subjected to so much exploitation pressure and environmental modification that it is necessary to monitor at least the target wild populations for genetic changes. The development of molecular techniques has made it possible to decipher the genetic constitution of a species by chemical tools and has revolutionized our ability to understand the genetic impact of human actions. A genetic variability in marine fish has an adaptive value; hence it is vital for species conservation, long-term survival and the sustainability of fishery in diverse microhabitats. Fish with adaptable genotypes perpetuate and recruit to their population and ensure that a range of genotypes exists probably be competent of thriving in whatsoever environmental conditions prevail. As new technologies are developing, advances are made in stocking technologies too, which may be helpful to replenish recruitment-limited and depleted stocks. Although stocking marine organisms has been practiced for well over a century, there is still lack of knowledge needed to guide the effective use of hatchery releases. Faced with depleted stocks and the expanding gap in seafood supply, there are remaining many essential suspicions about how to use stocking technology fruitfully. Subsequently, there are few good reports of the clearly successful application of hatchery releases to augment marine fisheries. MSE should be targeted at local populations having limited recruitment, high commercial level and over fishing pressures, for example, the demersal fish such as *Nemipterus japonicus* (Bloch, 1791) and *Pampus argenteus* (Euphrasen, 1788), as they are found to be less adaptive to climatic variability and do not migrate over large areas, and also have good recapture efficiencies. However, it cannot be expected for practice of highly migratory pelagic fish [63] such as *Trichiurus lepturus* (Linnaeus, 1758), *Harpadon nehereus* (Hamilton, 1822), *Sardinella longiceps* (Valenciennes, 1847) and *Rastrelliger kanagurta* (Cuvier, 1816) which are continuous spawners and possess the high potential to adapt to climatic changes. Bhathal and Pauly [64] pointed out that there is a scarcity of information on the fish fauna of the Indian coastal zones, and their seasonal occurrences in bays and estuaries. The magnitude of the genetic impacts of stock enhancement programs should depend on the size of the populations and its genetic diversity, stocking intensity, released progenies and gene flow among populations. Monitoring and assessment on stocking impacts in terms of population sizes and genetic diversity are also very crucial [65]. The development of breeding technologies is necessary to diminish genetic risks. Bell et al. [57] emphasized on the key elements of the approach which require rigorous research including responsible methods for reducing the cost of producing fit juveniles, optimizing survival of animals released in the wild and minimizing the effects of releases on conspecifics and other species in the ecosystem remain.

It is a matter of immense pleasure that CMFRI is one of the institutions in India and also there is no other research organization better suited for leading India's marine fishing sector to greater heights. The role of CMFRI is to provide scientific sustain and suggestions to the governments and do authentic checks while undertaking the journey. Establishment of state wise National Marine Fisheries Data Centre for the collection of detail information regarding the health of stock, Management Advisories and Marine Stewardship for certification are considered to be important initiatives of CMFRI for proper management of marine fisheries.

Managing the fisheries stock alone will not go ahead to sustainability. Instead, there is a requirement of an urgent call to think upon of the services provided by the entire ecosystem and expand appropriate management interventions. Hence, Ecosystem Approach to Fisheries Management (EAFM) aims at development and management of fisheries, while considering the health of the entire ecosystem. At present, CMFRI present a good example of the integration of Satellite Remote Sensing (SRS) used for establishment of 'e-infrastructure' in the marine fisheries sector. Application of GIS rooted inferences allows better decisions to be made on factors such as closed areas, stock abundance, stock enhancement, marine reserve locations, fishing effort distribution, behavior and fishing mortality rates. The book 'Marine Fisheries and Mariculture in India' is an effort to strengthen the present status of marine fishing and mariculture (marine aquaculture) in India.

This review contributes to a better understanding of what needs to be done and will hopefully serve as a catalyst for further work on the enhancement of marine fisheries. The marine aquaculture scenario of India is vast, as there is great scope for developing farming of shrimps, pearl oysters, mussels, crabs, lobsters, sea bass, sea cucumber and mullets. Although about 1.20 million ha is suitable for land-based saline aquaculture in India, currently only 13.0% is utilized.

Proper techniques should be used; especially in regard to co-management of stock enhancement and sea ranching is needed. But, it is not easy to evaluate an appropriate stocking level in the present scenario. Stock enhancement and sea ranching are being recast in the new millennium as more useful fishery-management tools than yet before. Marine fisheries scenario reveals that progress in fisheries evaluation methods appropriate to enhancements provides the means for its practical implementation and emphasizes the need for taking an integrated analysis of the role of enhancements within fisheries management systems; through a stakeholder participatory and scientifically learned and accountable planning progression. But, it is convinced that a shortage of funds and lack of expertise and the absence of an effective international mechanism of financial support will hamper conservation in India. An establishment of possible links/network, in addition to the attending technical cooperation and economic support, will be helpful in influencing, motivating and decision-making. It is the quickest possible way of stimulating marine conservation by the development of comprehensive management programs, which aim to defend the environment and safeguard their ecological acquaintances.

Fish and their diversity are often used as ecological indicators for assessing the health of the habitat, enabling to better understand the significance of their natural heritage and the sustainable livelihood. Consistent views have been expressed by Risser [66], who explained biodiversity's direct relationship with ecosystem processes and with the response of the ecosystem to disturbances. The richer the diversity of life, the greater is the ecosystem's strength and resilience, which allow it to maintain its equilibrium in ecosystem. Realization of the global scale of environmental impacts of economic activities accounts for the unprecedented prominence of the paradigm of sustainable development throughout the world. Preservation of ecosystem integrity and resilience and protection of biodiversity is key to achieve the sustainability of wealth in India. The connectivity of oceans makes marine conservation an issue of global concern. There are, however, great disparities between the industrialized and developing countries in their conservation efforts.

9. Conclusion

The marine fish fauna of India stays face to face several threats such as uncontrolled fishing, habitat degradation, sea pollution, etc., because of which presently 50 species are in threatened and 45 near threatened category of IUCN extant. So, marine fisheries need management and conservation measures to maintain sustainable use of marine biodiversity in future. Stock enhancement program must be integrated along with a fishery management that involves habitat protection and release of juveniles with appropriate control of fishing effort.

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The Natural Ecology and Stock Enhancement of the Edible Jellyfish (*Rhopilema esculentum* Kishinouye, 1891) in the Liaodong Bay, Bohai Sea, China

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Additional information is available at the end of the chapter

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Abstract

Among the edible jellyfish species, *Rhopilema esculentum* Kishinouye, 1891, is one of the most abundant jellyfish species consumed. Therefore, this jellyfish species is an important fisheries source in China. The jellyfish fisheries in China show annually considerable fluctuations and have a very short season. In the chapter, we firstly try to review the natural ecology of *R. esculentum*, which includes the distribution and migration, growth model, and survival rate in the Liaodong Bay (LDB) based on the results of our field studies for more than 20 years. Secondly, we focus on reviewing the jellyfish fishery and population dynamic in the LDB. Thirdly, we emphasize the themes, including the survey methods, catch prediction, enhancement assessment, and fishery management, based on our survey results from 2005 to 2010. Finally, we present our field and experiment results of resource restoration. The high commercial value of *R. esculentum* enhancement in the LDB has made this a very successful enterprise.

Keywords: *Rhopilema esculentum*, distribution, population dynamic, jellyfish fishery, enhancement and releasing

1. Introduction

Several species of scyphozoan jellyfish with mild stings are considered to be edible jellyfish. They are also used for medicinal purposes, such as treatment of high blood pressure, bronchitis, and a multitude of other diseases. They have been caught commercially and exploited along the coasts of Indian, Northwest Pacific, and Western Central Pacific Oceans by several countries, such as Thailand, Indonesia, Malaysia, the Philippines, Japan, South Korea, and China for over a thousand years [1–5]. Among the edible species, *Rhopilema esculentum* Kishinouye, 1891, is the most abundant and important species in the Asian jellyfish fishery. In particular, large edible jellyfish aggregates around the river mouth, and *R. esculentum* in the order Rhizostomae, are considered to be delicacy food in Chinese cooking. The Chinese have commercially exploited the jellyfish along the coasts of China for over a thousand years, and the jellyfish industry has become a commercial fishery. For these reasons, *R. esculentum* was selected as the species to be cultured and released for commercial harvest [1, 6, 7].

Despite its importance as a commodity, scientific studies in Southeast Asia have lagged behind the rapid development of exploitation [5]. But, in China, scientists paid more attention to the biology and fishery of edible jellyfish; a series of research projects have been carried out over 20 years for the purpose of commercial development. The research results on *R. esculentum* from the author's team only cover life cycle, experimental ecology, natural ecology, and stock enhancement, including distribution and locomotion, stock structure, growth model, feeding habit, and catch prediction [8–18].

In addition, the technology of artificial breeding, pond culture, and stock enhancement in nature was further developed along the coastal waters of northern China [6, 7, 19, 20]. In China, the Liaodong Bay (LDB) of Bohai Sea is one of the most important jellyfish fishing grounds, and the jellyfish fisheries in the Bay is characterized by considerable fluctuations in the catch, varying from about 400 tons to 290,000 tons, and including a short fishing season. The earliest enhancement experiment was put in practice in 1984 for the purpose of stabilizing and increasing catches. From 1984 to 2004, the tentative stock enhancement has been conducted for 11 times [6, 7, 19–21], and from 2005 to 2010, the large-scale stock enhancement of jellyfish (*R. esculentum*) was carried out for the first time in LDB where 157–365 million juvenile jellyfish (bell diameter of >1.00 cm) per year were released.

In this chapter, the natural ecology of *R. esculentum* in the LDB, based on our field and experiment study for more than 20 years, is reviewed. In the meantime, the large-scale release of cultured jellyfish, fishery forecast, and jellyfish fisheries management is presented.

2. Life cycle and environmental adaptation of *R. esculentum*

Researches on the life cycle of *R. esculentum* have been conducted since the 1970s [11] (**Figure 1**). The medusae are dioecious. Fully, developed oocytes are released into open seawater and fertilization and embryogenesis occur subsequently. Cleavage of the zygote is total and equal. A hollow blastula is formed 5–6 h after fertilization at 21.0–23.0°C. Gastrulation occurs by invagination. A total of 7–8 h after fertilization, actively swimming planula larvae appear in experimental conditions. Most of the planula larvae metamorphose into scyphistomae with four tentacles in 3–4 days and scyphistomae eventually occur with 16 tentacles in 15–20 days. During the course and after full growth, the scyphistomae continuously form podocysts. It is a way of asexual reproduction. Two months later, strobilation occurs at

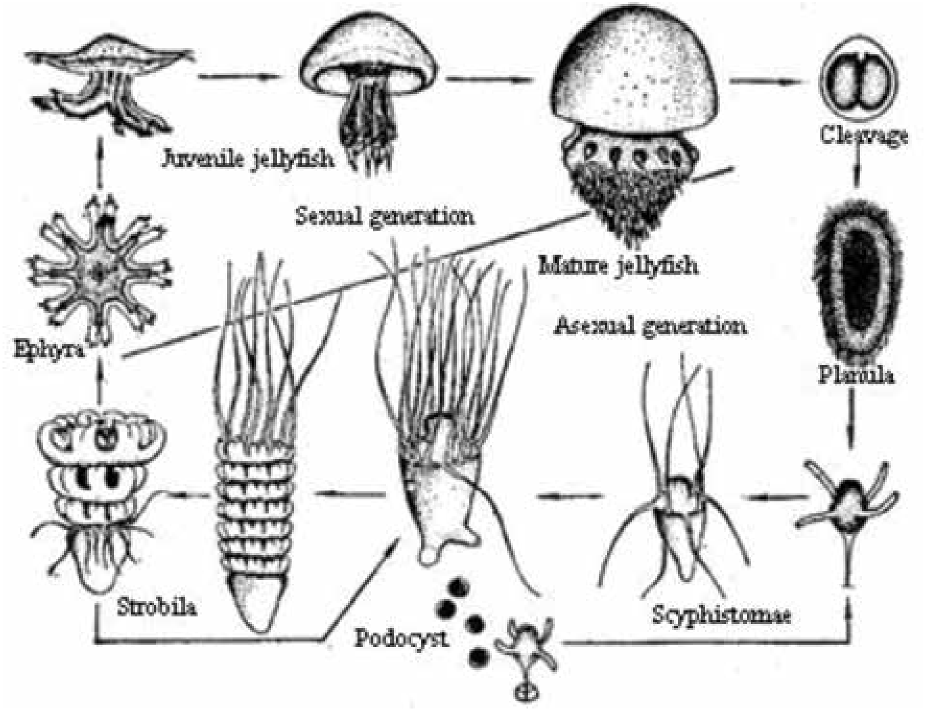

Figure 1. Life cycle of *Rhopilema esculentum* Kishinouye, 1891 [11].

18.0–20.0°C. Generally, a strobila produces 6–10 ephyra larvae. The ephyra larvae reach to about 20.0 mm in diameter in about 15 days in the laboratory and may attain 50.0 mm in diameter within 30 days. In the LDB, ephyra larvae grow into mature jellyfish 250–450 mm in diameter in 2–3 months.

The life cycle of *R. esculentum* is similar to those of *Nemopilema nomurai* Kishinouye, 1922, and *Rhopilema hispidum* (Vanhöffen, 1888). The ephyra larvae of *N. nomurai, R. esculentum,* and *R. hispidum* are differentiated by different shapes of lappet, rhopalar cleft, gastric cirrum, and nematocyst battery [12, 22].

The asexual reproduction methods, strobilation regulation, and mechanism of artificial control have been demonstrated. On the basis of life history in previous periods, the feeding habits (i.e. prey taxonomic group, size), feeding rate, and growth rate of medusae and scyphistomae were examined. In the meantime, effects of physical factors (i.e. temperature, salinity, light, food, pollution, fish activity) on different development stages of jellyfish *R. esculentum* were studied [8–10, 13, 14, 17, 18, 23]. The main conclusions are as follows: Suitable weak light can stimulate planula metamorphosis, while dark conditions promote podocyst excystment, and the survival rate of polyps decreases with increasing light intensity. The podocysts do not excyst below 10.0°C and the excystment rate increases between 15.0 and 30.0°C. Increasing temperature from 2.00–10.0°C to 22.0°C in winter induces strobilation in 2 weeks. A scyphistoma produces 7–8 ephyra larvae, on average. The optimal growth temperature for ephyra larvae is 24.0°C, with a favorable range of 16.0–28.0°C. No podocysts are produced when salinity is less than 6 psu; the optimum salinity range for podocyst generation is from 20.0 to 22.0 psu. Planula larvae of *R. esculentum* are the most favorable food for its early scyphistomae, while trochophores (trochophore larvae) of shellfish (*Crassostrea gigas* Thunberg, 1793) and blastula larvae of sea urchins (*Hemicentrotus pulcherrimus* A. Agassiz, 1864) are food supplements for early scyphistomae. Fully developed scyphistomae, ephyra larvae, and young medusae can be fed with *Artemia* spp. nauplii and zooplankton.

3. Natural ecological habit of *R. esculentum*

3.1. Distribution of *R. esculentum* in China

R. esculentum is a common large jellyfish, which is the warm-water estuarine species in China, and this species can provide adaptation to a wide range of water temperatures and salinity. The main habitat of this species in China was from the Yalu River estuary in the north to the area of Beibu Gulf in the south. In addition, *R. esculentum* is also found in the Western Japan, Southern Korean peninsula, and Russia Far East. The habitats of juvenile *R. esculentum* are estuarine regions, where they grow and reproduce. Because of the temperature variations based on the differences in various geographical locations, the breeding season and the moving route of *R. esculentum* in different marine ecosystems are not the same. In coastal areas extending from the South to the North of China, there are many geographical *R. esculentum* populations, such as Eastern Guangdong, Southern Fujian, Eastern Fujian, Southern Zhejiang, Hangzhou Bay, Haizhou Bay, Laizhou Bay, Bohai Bay, and Liaodong Bay populations [7].

3.2. Distribution and locomotion of *R. esculentum* in the Liaodong Bay

The northern part of the LDB is covered by ice blocks in winter and a high proportion of polyps over winter and they carry out strobilation in the next spring. With regard to juvenile and young medusae liberated by strobilation near their native environments, there are large amounts of researches in the LDB, including on the stock structure, growth model, geographic, and seasonal distribution and population dynamics carried out by Li et al. [15, 16], Liu et al. [24], and Dong et al. [7]. More information on distribution, migration, growth, and optimum fishing season of the jellyfish species should be obtained in order to select releasing sites and establish an adequate catch prediction model before the fishing season.

Horizontal distribution and habitat depth of the *R. esculentum* population in the LDB is related to their ecological characteristics. Juveniles of *R. esculentum* tolerate salinity values of 10–20 psu; adult jellyfish tolerate salinity values of 12–35 psu; and their optimal salinity value is 23–28 psu [10, 23]. *R. esculentum* have a sensitive sensation which can move vertically across different layers of water. This species often floats above the water during the calm dawn and evenings or cloudy days, whereas they inhabit in the bottom or near the bottom during the night and day with wind, storm, and rapids. This vertical movement behavior of jellyfish based on its sensitive sensation in the phylogeny is of great significance for maintaining the survival of population and relative stability of habitat.

Due to being a planktonic species, the moving ability of *R. esculentum* is weak; hence, the wind, wind direction, currents, and tides can affect the distribution of jellyfish. As a relatively independent stock, *R. esculentum* of the LDB mainly shows a distribution in the waters, both sides of 5-m isobaths, and its amount accounts for more than 90.0% of the total resources in the LDB. Juveniles of *R. esculentum* all occur near the estuarine regions in early and mid-June. *R. esculentum* mainly appears in the 5-m isobaths near the estuaries of Shuangtaizi, Daling, Xiaoling, and Liao Rivers (**Figure 2**). Areas of dense jellyfish distribute in different estuaries and coastal waters in different years. Compared to late June, the jellyfish uniformly distribute in early July in the estuarine waters, which still mainly concentrate in the 5-m isobaths. More jellyfish are also found in the 5–10-m isobaths during the year.

In mid- and late July, distribution of jellyfish *R. esculentum* is still concentrated within the 10-m isobath. But its abundance in the 5–10-m isobaths tends to spread slightly toward deeper waters or other layers where less jellyfish are found. In different years, the center fisheries' jellyfish zone extends from the Liao River to the Daling and Xiaoling River and even to inshore of Jinzhou.

When compared, ecological characteristics and migration patterns of two important large jellyfish species *R. esculentum* and *N. nomurai* inhabited in the LDB are different from each other. Dong et al. [7, 22] showed that the salinity range of 20.0–27.5 psu is the most appropriate

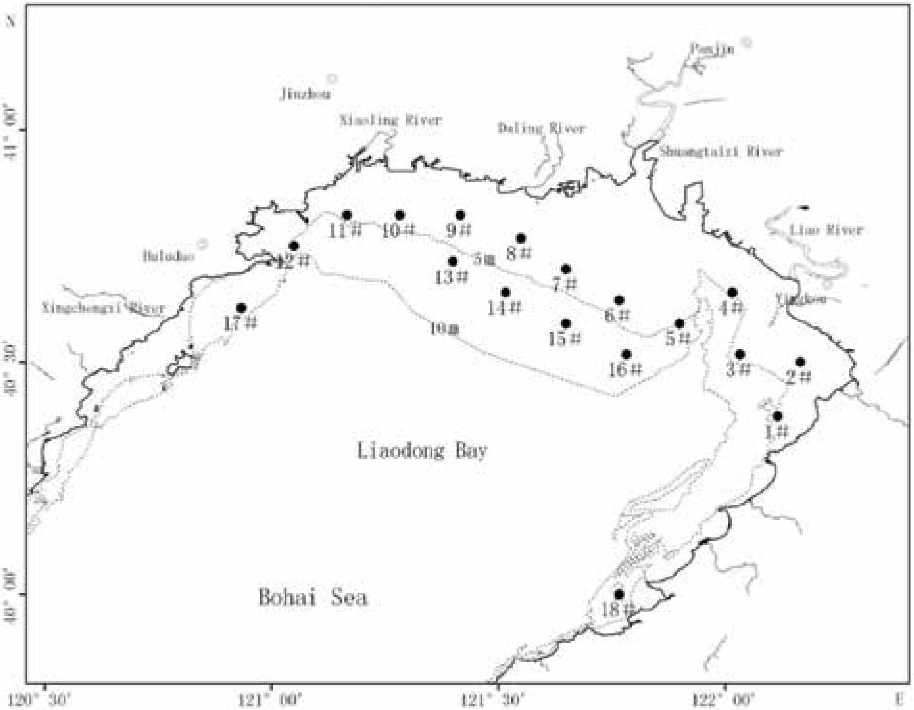

Figure 2. Survey sites of *Rhopilema esculentum* Kishinouye, 1891 in the Liaodong Bay during 2005–2010.

for *N. nomurai* podocyst reproduction, survival and somatic growth of polyps, and asexual production of podocysts. The optimum salinity range is in the range of 20.0–22.0 psu for podocyst generation of *R. esculentum* and 14.0–20.0 psu for survival of planula larvae [18, 23]. Juveniles of both species all are found in the estuary and shallow coastal areas, where there are low-salinity and high-temperature values (T 20.4–24.4°C and S 24.7–31.6 psu). But as the season progresses, *N. nomurai* becomes bigger and more mature and this restricted distribution expands to the whole LDB or advances to the southern Liaodong peninsula [25]. However, jellyfish *R. esculentum* inhabit the coastal waters of the 5–10-m isobaths of the LDB throughout [7, 26].

3.3. Growth model of *R. esculentum*

The growth model of the jellyfish *R. esculentum* is very important in order to predict the best fishing season. Since the jellyfish shrink after the first 10 days (10 d) of September without asymptotic values, it is impossible to show the growth pattern of jellyfish by means of regular asymptotic growth equation [15]. Its growth pattern may be described with a polynomial expression as a function of time, as follows:

$$L_t = 0.2198 + 0.4146\,t + 0.2203\,t^2 + 0.03824\,t^3 - 0.002249\,t^4. \tag{1}$$

L_t designates the arc length of the jellyfish swimming bell; t is time in 5-d units, beginning on June 20 (t_0) when the strobilae of jellyfish release ephyra larvae in the field. The correlation is significant according to the F test statistic ($F = 4126 > F_{0.005}(1, 9) = 13.61$).

4. Stock enhancement history of *R. esculentum*

4.1. Experimental release of cultured jellyfish

The tentative stock enhancement efforts were conducted 11 times between 1984 and 2004 by Liaoning Ocean and Fisheries Science Research Institute with the aim of stabilization and increase of the jellyfish fisheries. During 1984–1986, 2.00×10^5, 5.0×10^5, and 2.10×10^5 ephyra larvae (bell diameter of 5.00–15.0 mm) were released into the northern Yellow Sea from June to July each year. The recapture rate was estimated to be 1.20–2.50%.

The numbers from 4.60×10^6 to 1.73×10^7 of ephyra larvae (bell diameter of 5–10 mm) were released in the Dayang River estuary on the northern Yellow Sea during 1988–1993. The annual recapture rate ranged from 0.07 to 1.02%.

In 2002, 1.20×10^6 juveniles (bell diameter of 20 mm) were released into Jinpu Bay, the northern Yellow Sea, where the recapture rate was estimated to be 1.20%.

In 2004, 5.30×10^6 juveniles were released to the coastal waters near to the Dayang River estuary, the northern Yellow Sea. The jellyfish catch was 79.0 tons throughout the jellyfish fishing season with each individual averaging 7.00 kg wet weight. The recapture rate was about 0.20%.

Year	Released time (day/month)	Released size BD (mm)	Released amount (10^8 ind.)
2005	25–30, May; 16–25, June	≥10.0	1.57
2006	12–20, June	≥10.0	2.58
2007	16–25, June	≥10.0	2.50
2008	16–25, June	≥10.0	3.00
2009	01–07, June	≥10.0	3.18
2010	01–07, June	≥10.0	3.65

BD: bell diameter.

Table 1. Releasing records of ***Rhopilema esculentum*** Kishinouye, 1891, in Liaodong Bay during 2005–2010.

4.2. Large-scale release of jellyfish culture

Based on the life history, the technology of artificial breeding was researched and developed. We concluded that abundant juvenile jellyfish can be obtained in a very short time by adjusting the physical factors (light, temperature, salinity, and food) in jellyfish culture. During 2005–2010, yearly, over 500 million juvenile jellyfish produced by polyps in the previous year were raised to more than 20 breeding centers. The total volume of artificial breeding tanks for juveniles was about 30,000–40,000 m^3 in Liaoning Province. Steady and high-efficiency production capability of juvenile jellyfish establishes the foundation for large-scale stock enhancement of jellyfish.

During 2005–2010, the large-scale release and enhancement of *R. esculentum* were conducted by the Ocean and Fisheries Bureau of Liaoning Province in the LDB of the Bohai Sea, where 157–365 million juvenile jellyfish (bell diameter of >1 cm) were yearly released. In breeding centers, juveniles which will be released were transferred into plastic bags with oxygen-saturated sea water and were released into natural waters of 3–5-m depth. Young *R. esculentum* jellyfish individuals were released into the northern coastal areas of the LDB near Huludao, Jinzhou, Panjin, Yingkou, and Wafangdian cities. The Jellyfish individuals were all released during 01 June–25 June (for Jinzhou in 25–30 May, 2005), when their bell diameters were 1 cm, similar to those in nature. The released juveniles immediately mixed with the natural jellyfish comprising a mixed stock (**Figure 2**; **Table 1**).

5. Population dynamic survey and output forecast

5.1. Survey of released jellyfish

Mixed jellyfish stock monitoring was undertaken in late May, from early to mid-June, late June, from early to mid-July, and from mid- to late July between 2005 and 2010 in order to determine the survival, growth, and recapture rates of the released jellyfish. Eighteen survey sites within the 10-m isobaths were established in the juvenile jellyfish habitat of the LDB. The sites from 1 to 11 were within the 5-m isobaths, and the others at 5–10-m isobaths. As jellyfish grew, drift nets of different mesh size were used: dense mesh net (60 m length × 8 m height, 1 cm mesh size); middle mesh net (60 m length × 7 m length, 3 cm mesh size); and giant jellyfish net (60 m length × 8 m length, 10 cm mesh size) (**Figure 2**).

5.2. Various sources of mortality

The numbers of released jellyfish decreased due to various mortalities over time. It is very important to estimate how to reduce mortality during the whole developmental process from the beginning of release to the end of fishing season. It is helpful for managers to decide on appropriate measures to improve the efficiency of enhancement. Four different causes of mortality are listed in **Table 2**: (i) Handling mortality (M_1): In the period when the jellyfish were transferred into plastic bags full in oxygen, transported, and released in the natural waters, handling mortality occurred; (ii) Abrupt mortality (M_2): It occurred during 2–3 days after the cultured juvenile jellyfish were released into the sea, resulting from the sudden change of physical conditions and preys and so on; (iii) Natural mortality (M): It is caused by a combination of factors, including predation, competition, disease, and changes in environmental conditions during 40–50 days from the end of June to the beginning of fishing season; And (iv) Unlawful fishing mortality (F): Jellyfish death was caused by fishing with various kinds of nets before the fishing season opened. According to the various mortality experiments of 2005 and 2006, various mortalities were estimated by Ye et al. [1] and Dong et al. [7]. The average handling mortality was estimated as 6.00%, the abrupt mortality was 79.0%, and the average natural mortality was 55.0% of the jellyfish surviving after release. But the percentage of this unlawful fishing mortality is very difficult to estimate.

5.3. Catch forecast

The basic method of catch forecast is to survey the relative abundance with high-efficiency fishing drift nets in late June and early July. Eighteen sites were established in the main jellyfish fishing areas. The relative abundance is the average number of jellyfish caught on 1 net

t	number	BD (cm)	Mortality
t_0	N_0	1.0	↓ M_1: Handling mortality.
t_1	N_1	1.0	↓ M_2: Abrupt mortality.
t_2	$R_1 = N_2 + R_0$	3.0	↓ F: Unlawful fishing mortality.
t_3	R_2	16.0 to 49.4	↓ M: Natural mortality
t_4	$Y=Y_1 + Y_2$		

N_0 = released number; N_1 and N_2= number of released jellyfish surviving at different stages; R_0 = natural jellyfish stock; R_1 = mixed stock composed of released jellyfish and natural jellyfish; Y = total yield caught in fishing season; Y_1 and Y_2 = catch of natural jellyfish and released jellyfish; BD = bell diameter; t_0 = releasing time; and t_4 = fishing season.

Table 2. Mortality characters of the jellyfish ***Rhopilema esculentum*** Kishinouye, 1891, in the Liaodong Bay.

in 1 3-h catch. The catch forecast is obtained based on the model of relative abundance and fishing effort. The original forecasting equation was reported by Li et al. [16]:

$$Y = -17{,}963 + 98.2x_1 + 4.6x_2. \tag{2}$$

where Y = the forecasting output; x_1 = relative abundance; and x_2 = fishing effort. This relationship is significant (R = 0.97; standard deviation S = 2898; F = 31.57 > F (4, 2) $_{0.005}$ = 26.28).

From 2005 to 2010, the number of fishing vessels has been constant and had little effect on catch. The forecast catch was based on the relative resource only briefly [7]:

$$Y = -8580 + 1019.6\ (9.97 + 0.424x). \tag{3}$$

where Y = the forecasting output; x = relative abundance; and statistical test results were significantly correlated at 0.05 level (R = 0.85).

6. Jellyfish fisheries and management

6.1. Fishing ground and fishing methods

In **Figure 2**, the survey areas show the main fishing ground of about 5000 km^2, and it is located in the northern part of 40°30′N with 5–10-m depth. The actual fishing areas are smaller than the real area, and there are about 10,000 fishing boats in the narrow area in blooming year. At the jellyfish fishing season, there are two fishing boats per square km. In the years of low yield or no-releasing jellyfish year, fewer fishing vessels engaged in fishing production.

The fishery is characterized by large fluctuations of the annual catch and a short fishing season that has lasted only 2–3 days in recent years. From 2005 to 2010, edible jellyfish enhancement was carried out in the LDB, and the government participated in the management of jellyfish resources. The production of jellyfish in the LDB was maintained at the level of 15.7–91.0 thousand tons, and the output value was 173–546 million Yuan. In the years without releasing jellyfish, 2010–2017, the output of jellyfish in LDB dropped to less than 2000 tons (**Table 3**).

The jellyfish fishing grounds where great numbers of edible jellyfish occur are characterized by having a large tidal range, shallow depth, semi-enclosed waters, fresh water inflow through river systems, low salinity, and abundant foods. Fishing gear used includes various trawls, set nets, drift nets, push nets, and hand nets. The most efficient drift nets that were set at a depth of 2–10 m are placed across the current flow with a system of floats and sinkers. The length of each net is 30–50 m, with height of 8–12 m. A vessel loads 10–30 nets, which depends on the power of the vessel. The optimal jellyfish fishing period is 10–20 August. Because fishermen were eager for jellyfish fishing, and the fishing season generally advances at the end of July to early August.

	Year	Output (10^3 ton)	Number of fishing boats	Price (Yuan/kg)	Value (10^6 Yuan)
Releasing jellyfish year	2005	91.0	10000*	6	546
	2006	30.9	10,367	7	216
	2007	33.6	11,469	7	235
	2008	17.5	10,427	10.8	186
	2009	23.5	9461	10	235
	2010	15.7	6156	11	173
No releasing jellyfish year	2011	1.0	2061	16.6	17
	2012	1.3	2020	15.3	19
	2013	0.5	636	10	5
	2014	0.4	737	10.5	4
	2015	0.6	649	6.7	4
	2016	0.5	714	6.8	3.4
	2017	0.08	531	5.6	4.4

Table 3. Edible jellyfish (***Rhopilema esculentum*** Kishinouye, 1891) fishery in the Liaodong Bay from 2005 to 2017.

7. Evaluation of releasing effect

From 2005 to 2010, a total of 1.648 billion jellyfish were released by proliferating in the LDB. The average recapture rate of releasing is 1.77%, and 25.24 million jellyfish were recaptured. The individual weight was ca. 1.50–2.50 kg and recapture output was 48,500 tons which accounted for 22.86%of total edible jellyfish harvest during 2005 and 2010. Higher economic benefits were created, as much as 334.37 million Yuan (**Table 4**).

Year	Recapture amount (10^4ind.)	Recapture rate (%)	Recapture output* (10^4 t ind.)	Recapture value (10^4 Yuan)
2005	502	3.20	1.25	7500
2006	807	3.13	1.60	7200
2007	527	2.11	0.32	3000
2008	306	1.02	0.28	2267
2009	214	0.67	1.08	10,000
2010	168	0.46	0.32	3470
Total	2524	1.77	4.85	33,437

*Output counted as unprocessed fresh jellyfish.

Table 4. Evaluation on releasing effect of ***Rhopilema esculentum*** Kishinouye, 1891, in the Liaodong Bay during 2005–2010.

8. Habitat protection area in Liaodong Bay

According to the survey data for the jellyfish over the years, the concentrated distribution area of juvenile *R. esculentum* was within the 5-m isobaths of Shuangtaizi, Liao, Daling, and Xiaoling estuary.

Jellyfish were distributed in the 10-m isobaths in the northern part of the LDB; hence, the water area in the 10-m isobaths may be the habitat of jellyfish which can be delimited as the habitat protection area. In the protection areas, juvenile *R. esculentum* appeared more frequently from the Shuangtaizi to Daling estuaries. Therefore, it is speculated that the concentrated distribution area of *R. esculentum* polyps was from the Shuangtaizi to the Daling estuaries. The pink color area in **Figure 3** between Shuangtaizi and Daling estuaries was marked as the core area of jellyfish habitat protection area. The light blue water in the 5-m isobaths was designated as the buffer zone for the jellyfish habitat protection area. The water within the 5–10-m isobaths (gray) was delimited as the experimental area for the jellyfish habitat protection area.

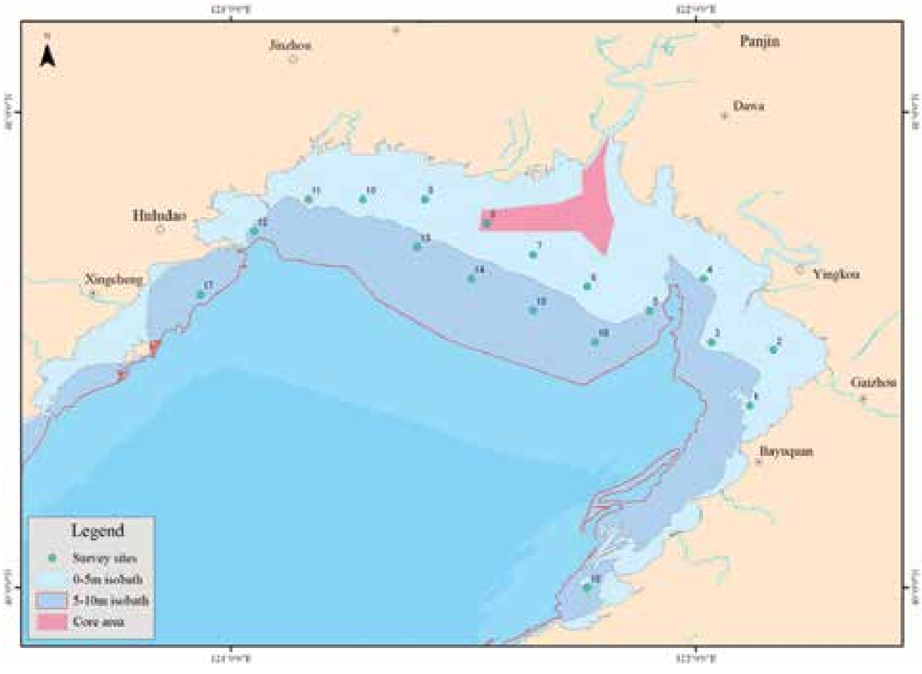

Figure 3. The habitat protection area of *Rhopilema esculentum* Kishinouye, 1891, polyp in the Liaodong Bay.

9. Discussion on the reasons for the decline of quantity

9.1. Effect of marine engineering and trawl net

In recent years, the marine engineering construction and trawl net caused damage for habitat of *R. esculentum* polyp. In LDB coastal waters, the fisherman catch crabs, conch, fish, benthic shellfish, and other economic categories using the trawl, dredge net, and pump, which can damage the habitat of *R. esculentum* polyp. Moreover, many human activities such as the port expansion, waterway dredging, and reclamation could occupy the habitat of *R. esculentum* polyp. The floating mud caused by these human activities may also cause the death of polyp in natural sea water, which reduces the number of jellyfish polyp in the natural sea water, affecting the production of jellyfish in the coming year in the LDB.

9.2. Effect of runoff on the resources of jellyfish in LDB estuary

Ye et al. [1], Jiang et al. [26], and Dong et al. [7] have used the variable runoff, the occurrences of wind and temperature, and the relative abundance to study the effects of these factors on the number of jellyfish in the LDB. The results showed that runoff was the most important factor that affected the number of jellyfish in the LDB.

9.3. Effect of the first catching time for jellyfish

The most juvenile *R. esculentum* individuals appeared in mid- and late June in the LDB. The time of sexual maturity for medusa is late August and early September in the LDB. Hence, according to the growth of jellyfish, the August and early September is the appropriate first catching time of jellyfish. In recent years, the first catching time of jellyfish was in late July for 9 consecutive years. Basing on the gonads' dissection, the jellyfish gonads were not yet fully mature in late July. Moreover, jellyfish are dioecious, and there is the mutual induction process between ovulation and fertilization. Studies by Dong et al. [27] have proved that the interactions among mature individuals in jellyfish were very important for ovulation and fertilization. Therefore, in late July, the proportion of sexual reproduction may be low in nature water. The premature catching time of jellyfish could reduce the jellyfish fishing yields and economic benefits, and affect the number of jellyfish polyps, thereby affecting the number of jellyfish in the next year.

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Overview on Mediterranean Shark's Fisheries: Impact on the Biodiversity

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Additional information is available at the end of the chapter

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Abstract

Bibliographic analysis shows that the Mediterranean Sea is a hot spot for cartilaginous species biodiversity, including sharks, rays, and chimaeras; 49 sharks and 36 rays were recorded in this region. However, they are by far the most endangered group of marine fish in the Mediterranean Sea. The IUCN Red List shows clearly the vulnerability of elasmobranchs and the lack of data; 39 species (53% of 73 assessed species) are critically endangered, endangered, or vulnerable. The biological characteristics of elasmobranchs (low fecundity, late maturity, and slow growth) make them more vulnerable to fishing pressure than most teleost fish. Overfishing, the wide use of nonselective fishing practices, and habitat degradation are leading to dramatic declines of these species in the Mediterranean Sea. In general, elasmobranchs are not targeted but are caught incidentally. In many fisheries, they are, however, often landed and marketed. A decline in cartilaginous fish species landings has been observed while fishing effort has generally increased. Better understanding of the composition of incidental and targeted catches of sharks by commercial fisheries are fundamentally important for the conservation of these populations. Moreover, problems encountered by elasmobranchs in the area are highlighted, and conservation measures are suggested.

Keywords: elasmobranchs, Mediterranean Sea, bycatch, biodiversity, fisheries

1. Introduction

The Mediterranean is known to be an important habitat for cartilaginous fish and is thought to encompass unique breeding grounds for species such as the white shark *Carcharodon carcharias* (Linnaeus, 1758) and the thornback ray *Raja clavata* Linnaeus, 1758. Forty-nine sharks and thirty-six rays were recorded in this region.

Elasmobranchs represent about 1 percent of the total fish landings. These landings decrease from about 26,000 tons in 1984 to about 14,000 in 2015 (official statistic FAO).

Going back in the history, it has been demonstrated that sharks in the Mediterranean Sea have declined by more than 97 percent in number and "catch weight" over the last 200 years. They risk extinction if current fishing pressure continues [1]. The last 200 years have seen a dramatic decline of large predatory sharks in the Mediterranean Sea. This loss of top predators could hold serious implications for the entire marine ecosystem, greatly affecting food webs throughout this region.

There is evidence that the elasmobranchs of the Mediterranean are declining in abundance, diversity, and range due to the intense fishing activity primarily in response to the rapidly increasing demand for shark fins, meat, and cartilage. However, this direct fishing mortality is not the only impact on elasmobranch populations. There are fishing impacts on habitats through disturbance of biotic communities and substrates. Shipping and underwater exploration, construction, mining, and electrical installation and aquaculture offshore in cages also affect habitats, and increasing ambient sound, light, electromagnetic fields, and chemical contamination stimulate the sensory systems of these fishes.

Cartilaginous species, including sharks, rays, and chimaeras, are by far the most endangered group of marine fish in the Mediterranean Sea; among 73 assessed species in the Mediterranean, the Red List status of Chondrichthyans shows that 39 (53% of all) are critically endangered, endangered, or vulnerable [2]. The biological characteristics of elasmobranches (low fecundity, late maturity, slow growth) make them more vulnerable to fishing pressure than most teleost fish. Overfishing, the wide use of nonselective fishing practices, and habitat degradation are leading to dramatic declines of these species in the Mediterranean Sea. In general, elasmobranchs are not targeted but are caught incidentally. In many fisheries they are, however, often landed and marketed. Better understanding of the composition of incidental and targeted catches of sharks by commercial fisheries is fundamentally important for conservation of these populations.

In this chapter, we try to provide an overview on the bycatch of sharks in the Mediterranean, their impact on biodiversity, and some recommendations for the conservation of this group of fish. We refer when necessary to the Gulf of Gabès (Tunisia). The Gulf of Gabès is in fact a "marine biodiversity hot spot" of significant regional importance and the most important fishery area of the Tunisian fishing fleet. The Gulf is the preferred habitat for many iconic Mediterranean vertebrate species—a wintering and foraging area for the loggerhead turtle (*Caretta caretta* (Linnaeus, 1758)), a nursery for several elasmobranch species, and a suitable habitat to many other fish species such as groupers and tunas. Cetaceans, especially bottlenose dolphin (*Tursiops truncatus* (Montagu, 1821)), are encountered there.

2. Status of elasmobranches in the Mediterranean Sea

2.1. Mediterranean elasmobranch fauna

Cartilaginous fishes belong to the Chondrichthyes class comprising sharks, batoids (skates, stingrays, guitarfishes, and sawfishes), and chimaeroid fishes and including about 1200 living species [3]. The chimaeras fall in the subclass of Holocephali and the sharks and rays in the subclass of Elasmobranchii. For chimaeroid, two species occur in the Mediterranean, the common rabbitfish *Chimaera monstrosa* Linnaeus, 1758, and the large-eyed rabbitfish *Hydrolagus mirabilis* (Collett, 1904). The latter species is widespread; it is probably relatively common in the Northeast Atlantic and less common in the western and southern Atlantic [4]. In 2013, a large female was recorded in the eastern Mediterranean Sea for the first time by Hassan [5]. We deal in this review with this latter subclass, generally named elasmobranchs comprising sharks (Squalii and Pleurotremata) and rays (Batoidea and Hypotremata).

According to [6], 86 species of elasmobranchs thought to occur in the Mediterranean Sea. This number comprises 49 species of sharks from 17 families and 37 batoid species from 9 families.

Recently captures of the spinetail devil rays *Mobula japanica* (Müller and Henle, 1841) were reported from the northern coast of Tunisia (central Mediterranean) [7, 8] from Algerian coasts [9] and from Turkey [10]. Comparison with the partial mitogenome of *M. japanica* suggests sister-cryptic species complex and two different taxonomic units. However, the limited divergence within the species (>99.9% genetic identity) may be the result of a geographically and numerically restricted population of *Mobula mobular* (Bonnaterre, 1788) within the Mediterranean Sea [11]. Another genetic study combined genetic and morphological data challenges the notion that *M. mobular* and *M. japanica* are two separate species. However, additional and population-level sampling, combined with genetic analysis and morphological examination, are necessary before any conclusions can be drawn about the species status of *M. japanica* [12]. According to its status, *M. japonica* is not considered in this work.

2.2. Spatial distribution of elasmobranchs in the Mediterranean Sea

Historically, the diversity of Chondrichthyans was greatest in the western Mediterranean Sea, particularly in the coastal waters of North African countries (**Figure 1**). Diversity is slightly lower in the northwest Mediterranean countries [2]. This spatial distribution is also shown in works of [13, 14].

Within the Mediterranean, the distribution of elasmobranch fishes is not homogenous [15]. Some areas are considered critical habitat for elasmobranchs. However, a big lack of knowledge on critical habitats for this group was noted in the Mediterranean. For example, the Tunisian waters provide a nursery area for the white shark *C. carcharias* (center of Tunisia), for the sandbar shark *Carcharhinus plumbeus* (Nardo, 1827) [16, 17] (Gulf of Gabès, south of Tunisia), and for the blackchin guitarfish *Glaucostegus cemiculus* (Geoffroy Saint-Hilaire, 1817) [17].

2.3. Elasmobranch landings

Elasmobranch species are exploited mainly for their fins and meat. They are sometimes targeted by commercial fisheries, while in majority of the cases, they are incidentally caught as bycatch. In the Mediterranean Sea, elasmobranch fish catches represent only 1.15 percent of the total landings (Statistic FAO 1980–2015). A decline in cartilaginous species landings has been observed while fishing effort has generally increased. According FAO statistics of elasmobranchs, the catches show a decreasing trend: 26000 tons in 1983–1984 and 14,000 in 2015 (**Figure 2**).

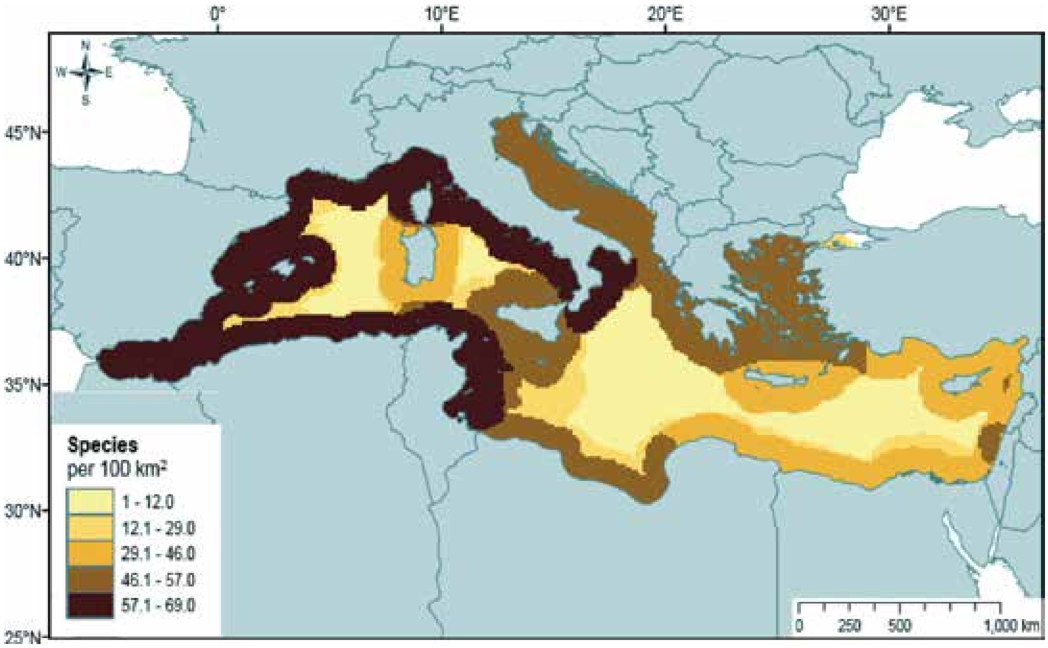

Figure 1. Historical species richness of Chondrichthyans within the Mediterranean Sea [2].

The increase of production noted after 2008 is not really related to augmentation of catch but to the contribution of new countries to the FAO official statistic such as Libya. The contribution of African countries is becoming noticeable; in fact, they contributed by more than 70% of elasmobranch production of the area during the last 7 years (**Figure 2**).

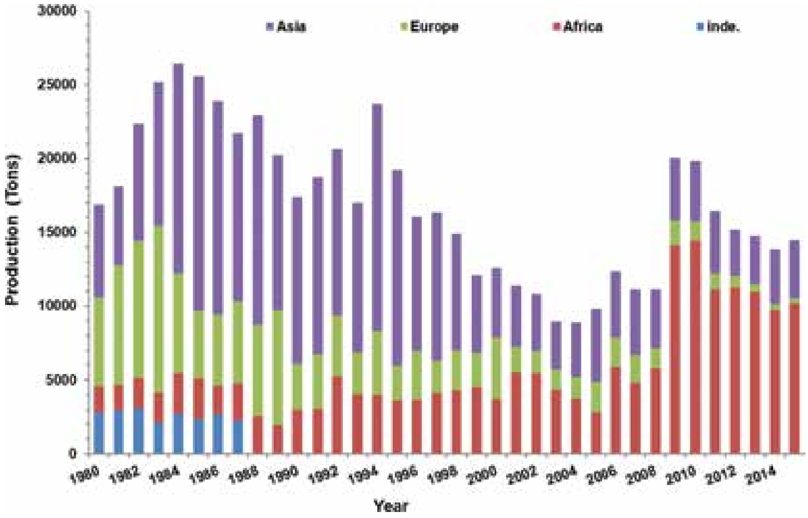

Figure 2. Mediterranean elasmobranch production according to FAO statistics from 1980 to 2015.

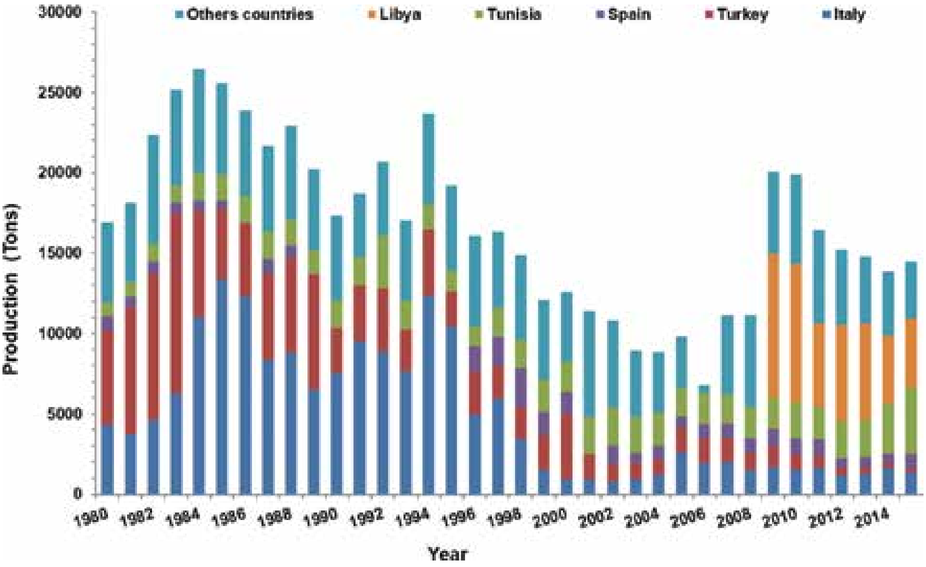

Figure 3. Contribution of some countries in the Mediterranean elasmobranch production according to FAO statistics from 1980 to 2015.

During the last 7 years, the major elasmobranch-fishing countries within the Mediterranean are Libya and Tunisia; in fact they contributed by more than 70% of production (**Figure 3**). Italy and Turkey known to be the major elasmobranch-fishing countries within the Mediterranean, between 1980 and 2008, register a dramatic decrease in catch. Tunisian landings did not show

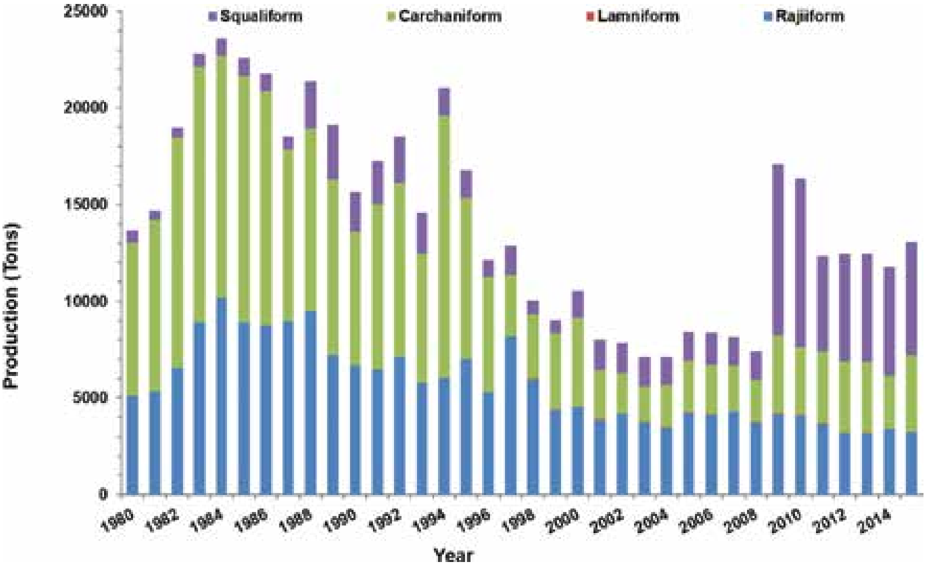

Figure 4. Landing evolution of some elasmobranch groups in the Mediterranean between 1980 and 2015.

any notable variations from 1980 to 2015. Those from Libya appear for the first time in FAO statistics and seem to be important (**Figure 3**).

It should be noted that the Mediterranean landings of Carcharhiniformes, the most represented group among the elasmobranchs and the most commercially fished, recorded notable decrease (**Figure 4**).

3. Elasmobranch fisheries

Effects of fishing on marine megafauna are widespread and diverse, primarily due to overexploitation and bycatch [18, 19]. The capture of threatened vertebrates in fisheries is an increasingly prominent international issue [20]. There are particular concerns on elasmobranchs as they are particularly vulnerable to fishing mortality because of their life histories including slow growth, late maturity, and low fecundity rates [21, 22]. Elasmobranchs are less able to sustain their populations under fishing pressures that are sufficient to sustain target teleost and invertebrate species [23]. According to [22], a decline in elasmobranch populations has been observed throughout the world and was particularly marked in the Indo-Pacific and Mediterranean Sea. The loss of some shark and batoid populations from aquatic ecosystems has socioeconomic and ecological consequences [24, 25].

The Mediterranean is considered a biodiversity hot spot for elasmobranchs [6, 22], being at the same time the area in the world with the highest proportion of threatened species because of unregulated fishing [2]. Besides fishery activities, Mediterranean elasmobranch populations are affected by pollution and habitat degradation resulting in drastic population declines [1]. In this area, some species are commercially targeted, but the majority are taken incidentally.

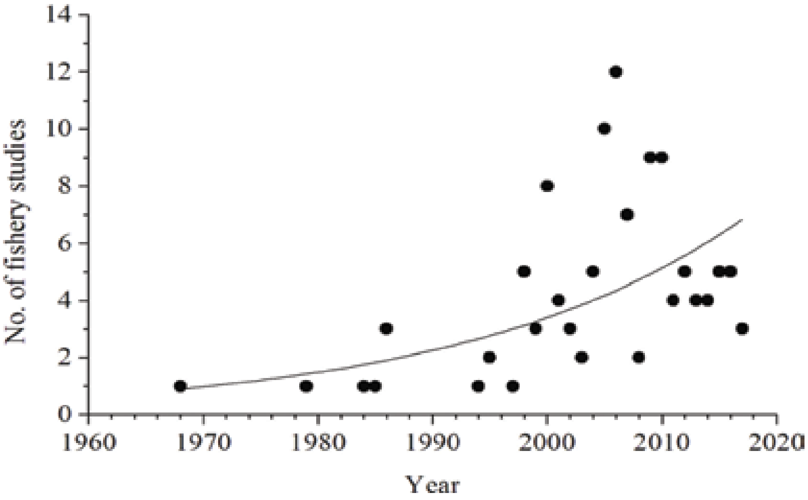

Figure 5. Temporal distribution of the number of published papers dealing with elasmobranch captures in the region in the Mediterranean Sea.

Mediterranean elasmobranch species are mainly coastal occurring within the range of fisheries, potentially producing high bycatch mortality [6].

The historically low economic value of elasmobranch products compared to bony fishes has resulted in a lower priority for research and conservation of these species in the Mediterranean Sea. The chronology of appearance of publications related to elasmobranch captures in the Mediterranean Sea shows an increased concern in recent year (**Figure 5**).

Given the socioeconomic and ecological consequences of declining shark and ray populations, there is an imperative to address declines by implementing effective conservation management.

3.1. Fisheries targeting elasmobranchs

In the Mediterranean Sea, few fisheries are targeting elasmobranchs; this fish group is mainly landed as bycatch [6, 26]. Elasmobranch species were targeted due to the decline of bony fish stocks and the increase in shark domestic consumption. The elasmobranch species were targeted mainly using specific gillnets and longline.

3.1.1. Gillnets

Fisheries targeting sharks in the Mediterranean Sea are generally seasonal and local [27–29]. These fisheries operate on the basis of the seasonal abundance of elasmobranch species. Furthermore, in some coastal communities, sharks represent a subsistence fishery between more profitable fishing seasons for teleosts, mollusks, and crustaceans [29]. These fisheries are very heterogeneous because the targeted species, the type of vessels, and the gears used vary locally and seasonally. Few studies have been undertaken to assess the biological characteristics and impact of these fisheries.

Smooth-hound sharks (*Mustelus* sp.) are targeted by specific gillnets in the north Adriatic Sea during spring [27] and in restricted area along the Mediterranean Turkish coasts [28]. In Tunisia, the fishery of smooth-hounds began in the mid-1980s using special gillnets called "Gattatia" from February to June along the Gulf of Gabès coasts (**Figure 6**). This gillnet has a stretched mesh size of 120–160 mm [29]. In recent years, sandbar sharks and the blackchin guitarfishes have become the object of directed artisanal fisheries using a special gillnet (stretched mesh size of 240–340 mm) locally known as "kallabia." Sandbar sharks are targeted through April–June and, moreover, the guitarfishes during summer months [29]. In addition, *Carcharhinus* sp. and guitarfishes have become the object of directed artisanal fisheries along the Libyan coasts using gillnets [30, 31]. During the fishery season, gillnets are left in place and inspected daily.

3.1.2. Longlines

The longline targeting sharks is known mainly in Tunisia and Libya. Decline in catches of swordfish in the area has shifted the pelagic longline to target elasmobranchs. The sandbar sharks are fished through July–October [32]. During 2007/2008 the catch rates of *C. plumbeus* in pelagic longline were 15.22 invidious/1000 hooks [32]. On the other hand, *Carcharhinus* sp.

Figure 6. Elasmobranch species landed by specific gill nets in the Gulf of Gabès.

and guitarfishes are seasonally fished along Libyan coasts using bottom and pelagic longlines [30, 31]. Unfortunately, there is no data on species composition and catch rates about Libyan shark fisheries.

Although, these gears are considered selective, they bring several other nontarget species: *Scyliorhinus canicula* (Linnaeus, 1758); *Squalus acanthias* Linnaeus, 1758; *Scyliorhinus stellaris* (Linnaeus, 1758); *Myliobatis Aquila* (Linnaeus, 1758); *Pteromylaeus bovinus* (Geoffroy Saint-Hilaire, 1817); *Galeus melastomus* (Rafinesque, 1810); *Centrophorus granulosus* (Bloch & Schneider, 1801); *Raja radula* Delaroche, 1809; *Raja miraletus* Linnaeus, 1758; *Carcharhinus* sp.; *Dasyatis* sp.; etc. [27, 29–32]. Among sharks, *Mustelus* genus is the most targeted species throughout the whole Mediterranean Sea [27, 29–32]. Indeed, this genus is present in the entire Mediterranean Sea, while the other species such as guitarfishes and sandbar sharks are more abundant in Tunisia and Libya [30, 31, 33].

3.2. Incidental capture

Research on elasmobranch bycatches has focused mainly on industrial fisheries [34]. However, recently, it appears that small-scale fisheries are also an important source of mortality for marine vertebrates [35, 36]. In fact, all cartilaginous fishes are caught accidentally in most fishing gear in the Mediterranean [37].

3.2.1. Small-scale fisheries

Small-scale fisheries, including artisanal and traditional fisheries, comprise over 80% of the Mediterranean fleets [38]. In the Mediterranean Sea, small-scale fisheries represented essentially by set nets and bottom longline are included in various métiers that are characterized by different fishing grounds, seasons, and target species.

The small-scale fisheries capture mainly elasmobranch species inhabiting the continental shelf [38–42]. In general, species composition and importance varied regionally. In the Gulf of Gabès, trammel net captures were dominated by the smooth-hound sharks; however, stingrays and skates were the most captured species in Balearic Islands, Corsica, and Aegean Sea [38–42].

Bottom longline targeting teleost fishes caught incidentally several demersal elasmobranch species [43–45]. In the Aegean Sea, skates (*R. radula*, *R. clavata*, and *R. miraletus*) represent 6 to 19% of the total catch. These rates vary with the hook size [43, 44]. In Adriatic Sea, bottom longline capture *Raja* sp., *G. melastomus*, and *Mustelus mustelus* (Linnaeus, 1758) [45]. Along the Lebanese coasts, small-scale fisheries capture incidentally more batoids than sharks: *Rhinobatos rhinobatos* (Linnaeus, 1758); *Torpedo marmorata* Risso, 1810; *R. miraletus*; *G. cemiculus*; and *C. granulosus* are the most fished species. [46]. Furthermore, small-scale fisheries affect mainly small species or newborns and juveniles of large species [42]. Among captured elasmobranch, discards and retained species varied also regionally based on its economic value [38–44].

The Mediterranean elasmobranch species are mainly coastal and benthic (80%), which make them vulnerable to fishing activities concentrated mainly on the coasts [6]. Considering the importance of small-scale fleet in the Mediterranean Sea, they represent a significant source of mortality for early-life stages of elasmobranch species. These fisheries operate mainly in nursery areas and coincide with the parturition period of most species. Because of the overlap of small-scale fisheries with critical area worldwide, they may be among the greatest current threats to nontargeted megafauna [35, 47].

3.2.2. Industrial fisheries

All cartilaginous fishes are caught accidentally in most industrial fishing gear in the Mediterranean [37]. It seems that trawlers, pelagic longlines, and purse seine constitute the most important threat to elasmobranch species.

3.2.2.1. Trawlers

Although trawlers represent about 10% of the Mediterranean fleet, they contribute by approximately 50% of the landed catch, which emphasize their importance. This technique generates several problems: juvenile catches, important discards, and negative impact on the environment [48]. In the Mediterranean, discards constitute over 40 percent of the catch [49].

For this fishing gear, very often the information concerns a listing of species without an estimate of catch rates by fishing effort. Recently, preliminary information on this issue was reported in the Aegean Sea [50], in the Gulf of Gabès [51], and in Turkish coasts [52].

All elasmobranch species are caught by trawlers; 62 species are listed in trawl fisheries in Greece, 62 species in Catalonia and 74 in Italian waters, 31 species in the Gulf of Gabès, and 20 species in Iskenderun bay [51–53]. However, demersal species, particularly *Etmopterus spinax* (Linnaeus, 1758), *G. melastomus*, *S. canicula*, *Mustelus* sp., and Rajidae are most caught [50, 54–56].

The proportion of elasmobranch in catch varied locally. In the Alboran Sea, elasmobranch species represent 4.91 to 8.24 percent by weight of total catches [56]. In Iskenderun bay and the Gulf of Gabès, elasmobranchs represent 23% and 5.4%, respectively [51, 52].

Among rays, it is noted that *R. clavata*, *R. radula*, and *R. miraletus* are the species most commonly caught in the Mediterranean trawling [53, 57]. This technique generates occasional catch of pelagic sharks as *Alopias vulpinus* (Bonnaterre, 1788); *Prionace glauca* (Linnaeus, 1758); *Isurus oxyrinchus* Rafinesque, 1810; *C. carcharias*; and rarely *Cetorhinus maximus* (Gunnerus, 1765).

3.2.2.2. Longlines

Generally, two types of longlines are used in the Mediterranean: bottom and surface longlines.

The surface longline targets, according to the hook size and immersion depth, swordfish (*Xiphias gladius* Linnaeus, 1758), albacore (*Thunnus alalunga* Bonnaterre, 1788), and tuna. This gear captures accidentally at least 12 species of sharks [58–62]. The most affected species are *P. glauca* and *I. oxyrinchus*. The catch rate of sharks was highest in the Alboran Sea followed by the Adriatic Sea [60–62].

Bottom longline catches especially batoids; in the Aegean Sea, the Rajidae (*R. radula, R. clavata*, and *R. miraletus*) represent 6 to 19 percent of the total catch. These rates vary with the hook size [42]. In the Gulf of Gabès, bottom longline targeting groupers captures incidentally the most abundant species such as *Mustelus* sp. and *Rhinobatos* sp. [31].

3.3. Impact of fisheries

Despite their sensible life-history characteristics, Mediterranean shark captures have historically received less attention than bony fish. Unfortunately, the overexploitation added to biological characteristics of the group has led many species to be threatened or disappeared from many areas [31].

Scarce data exist to quantify the historical level of elasmobranch exploitation in the Mediterranean, as the long-term sources of information to assess shark removals are very rare in this region [63]. The decline of elasmobranch species in the Mediterranean was recognized by IUCN [2] and also confirmed by fishers [64], while the rate of reduction in the different sectors of the Mediterranean is unclear by species. The decline importance varies locally in relation to fisheries importance (**Figure 7**).

Spatiotemporal analyses of large shark abundances in the Mediterranean Sea show that population status spatially ranges from overexploited to locally depleted and local extinction [1]. The case was also reported for *Squatina squatina* (Linnaeus, 1758) [65]. Recent analysis of the frequency of occurrence of smooth-hounds in fishery catch data showed that the species have declined by 80–90% since the beginning of last century to almost disappear in a large part of their original distributional range during the 1980s and 1990s [66]. Bibliographic data gathered in scientific bottom trawl surveys carried out off the southern coasts of Sicily from 1994 to 2009 and between a depth of 10 and 800 m indicated an

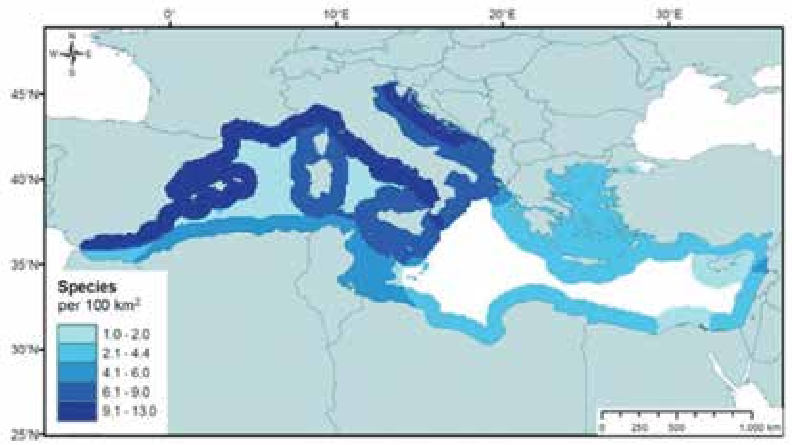

Figure 7. Extinct and possibly extinct species in the Mediterranean Sea, showing that local extinctions have been most prevalent in the NW Mediterranean Sea [2].

important decline in abundance of the most captured species [67]. Analysis of Italian annual landing for elasmobranchs between 1997 and 2004 decreased 77% compared with the previous years (1959–1982). This decrease may be attributed to overharvesting that occurred during the 1980s and 1990s in Italian seas [68]. Several species (*Rhinobatos* sp., *Carcharhinus* sp., *Mustelus* sp., etc.) previously considered as common along the Mediterranean Sea were absent on MEDITS trawling surveys between 1994 and 1999 and currently appear to be disappeared from the north coasts [53].

In the frame of ACCOBAMS-GFCM Project on mitigating interactions between endangered marine species and fishing, developed with the collaboration of the RAC/SPA and a substantial financial support from the MAVA foundation, results of a pilot action on mitigating bycatch and depredation of elasmobranchs, sea turtles, and cetaceans in surface and bottom longline fisheries operating in the Gulf of Gabes (2016–2017) indicate a significant decline in catch rates of the most targeted species mainly *C. plumbeus* comparatively to summer 2007/2008. In addition, there is a shift for other species habitually considered as unwanted such as *Dasyatis* sp.

This decline can be attributed to a number of factors, mainly the intense fishing activity throughout the coastal and pelagic waters of the basin, such as the Gulf of Lions [69], the Tyrrhenian Sea [63], and the Adriatic Sea [70]. Moreover, the lack of biological information and appropriate fishery databases limits the assessment and management plan of elasmobranchs in this area [36].

Today, it is thought that economically viable and biologically sustainable yields can be taken from some of the relatively more productive species, such as *Mustelus*, under careful management [36]. However, in the Mediterranean Sea, bycatch and direct fisheries are unregulated, unmonitored, and unreported to national or international management agencies.

4. Compilation of conservation and mitigation measures for elasmobranch bycatch

Given this situation, several conservation measures for these fish are taken or suggested at the national, regional, and international levels. We review some of them.

4.1. General measures

- The shark fin trade

The trade in shark fins consists of cutting and keeping the fins of the shark and throwing the mutilated living part back into the sea. This is a cruel and wasteful practice since only 2 to 5% of the shark is exploited. Although the actual extent of shark fin trade in the Mediterranean is unknown, this practice is now a major global problem.

According to GFCM regulations (REC.CM-GFCM, 36/2012/3), the removal of fins and their purchase and sale are prohibited. Similarly, the butchering of specimens onboard the vessel and prior landing is prohibited.

- Marine protected areas

Marine protected areas (MPAs) are recognized as effective tools for protecting the marine environment and as an approach that takes into account the ecosystem as a whole. Today, most of these protected areas occur in coastal waters in the north of the region, highlighting the importance of identifying MPAs along the southern and eastern coasts, as well as on the high seas.

- International conventions

Several conventions relating to the conservation and management of ichthyofauna in the Mediterranean Sea have been ratified by all Mediterranean countries.

4.2. Mitigation of incidental catches of elasmobranchs by longline

In the light of the experiences of several longline fisheries, the following recommendations should be noted:

- Plunge hooks deeper and the day.

The main species of pelagic sharks, as well as stingrays (*Dasyatis* sp.), are generally taken in surface waters, and shark activity is generally nocturnal.

- Avoid attracting sharks and rays.

In particular, avoid dumping garbage, viscera, and unmarketable fish into a fishing area if you do not want to attract scavengers like most elasmobranchs.

- Reduce the time of setting, to avoid that elasmobranchs are attracted in large numbers by captured prey.

- Avoid certain types of bait that may be more attractive than others; several observations made by professionals have shown that sharks are more attracted to squid than to fish. To avoid catching stingrays and sharks mackerel or horse mackerel should be used instead of sardines.

On the other hand, the development of artificial baits could be an important contributor to the reduction of catches of sharks and rays.

- Reduce the mortality caused by fishing operations.

Most of the elasmobranchs caught by longlines are alive at the time of longline recovery; it is advisable to be able to release them immediately by avoiding, if possible, any bruising. In general, the use of monofilament snoods, which sharks can more easily cut, is preferable than any other type of braided synthetic fiber or steel [57].

- Move elasmobranchs away from baited hooks.

Pretreatment of baits with some synthetically produced substances may keep Carcharinids away without affecting other fish.

- Small magnets of steel alloy, neodymium, and boron would be able to keep small sharks or skates away from baited hooks.
- Guidelines for Recreational Fishing for Sharks and Rays in the Mediterranean Prepared by RAC/SPA for recreational fishermen as a contribution to the Action Plan for the Conservation of Cartilaginous Fish in the Mediterranean Sea aim, among other things, to reduce the potentially harmful impacts of recreational fishing activities on the Mediterranean shark and ray populations by advocating release. This Code of Conduct recommends the use of circular hooks; J-hooks are more likely to be swallowed than circular hooks. Barbed hooks are difficult to remove and can cause damage to internal organs. Circular hooks generally cling to the jaw and are easier to catch for quick release.

In order to evaluate the efficiency of some measures to reduce bycatch in the Gulf of Gabes (Tunisia), we evaluated the effect of hook shape (circle hook) and bait nature during experimental trips (23 fishing sets) conducted during summer 2016.

The nature of the bait and the shape of the hook may have impact on CPUE of the sandbar shark and other endangered shark listed in appendix II of the SPA/BD Protocol.

The CPUE of sandbar shark varies from 6.73 (individual/1000 hooks) with mackerel or other teleost used as bait to 17.94 when using elasmobranch bait. The use of circular hooks increased shark caches and specimens size while allowing more easy release of captured shark.

We focus mainly on endangered species in appendix 2 of the protocol concerning specially protected areas and biological diversity in the Mediterranean because this list was adopted by the GFCM in the Recommendation GFCM/36/2012/3 on fishery management measures for conservation of sharks and rays in the GFCM area.

In fact, GFCM parties shall ensure a high protection from fishing activities to elasmobranch species listed in Annex II of the SPA/BD protocol of the Barcelona Convention (list of endangered or threatened species) that must be released unharmed and alive to the extent possible.

Specimens of sharks' species listed in Annex II of the SPA/BD Protocol cannot be retained on board, transshipped, landed, transferred, stored, sold, or displayed or offered for sale.

5. Conclusion

About 86 species of elasmobranchs are thought to occur in the Mediterranean Sea (49 species of sharks and 37 batoids). The distribution of elasmobranch fishes is not homogenous. Concentration of rays and sharks occurred in coastal waters of the western basin and the central Mediterranean, especially in the waters of Tunisia and Libya.

Some areas are considered as critical habitats for elasmobranchs such as the Gulf of Gabès (Tunisia).

Elasmobranchs are incidentally caught as bycatch, but sometimes they are directly targeted by commercial and recreational fisheries in some areas. Catches represent a mean of 1.1 percent of the total landings during the last 35 years. The catches show a decreasing trend from 1983 (about 26,000 tons) to 2015 (about 14,000 tons). The major elasmobranch-fishing countries within the Mediterranean are Libya and Tunisia for the last 7 years.

Small-scale fisheries, represented essentially by set nets and bottom longline, engender capture of several demersal species, with variable abundance among areas. All cartilaginous fishes are caught accidentally in most industrial fishing gear in the Mediterranean. It seems that trawlers, pelagic longlines, and purse seine constitute the most important threat to elasmobranch species.

Protection is currently granted to chondrichthyan fish species under various regional and international conventions where generally few species are considered. Few countries have developed their own legislation.

Taking action to collect reliable statistics on landings and bycatch of elasmobranchs should be a priority for shark's conservation. Thanks are given to the GFCM which started a program to collect data on bycatch in the Mediterranean Sea.

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Chapter 11

An Update on Reproduction in Ghost Shrimps (Decapoda: Axiidea) and Mud Lobsters (Decapoda: Gebiidea)

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Additional information is available at the end of the chapter

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Abstract

In this report, I review the taxonomic history, body adaptations, ecology, and reproduction of the infraorders Axiidea (ghost shrimps) and Gebiidea (mud lobsters). Known until recently as the "Thalassinidea," modern classification divided Axiidea into six families and Gebiidea into five. Ghost shrimps are characterized by having the first and second pereiopod chelate and a soft and delicate body, whereas mud lobsters possess the first pereiopod chelate or subchelate and second pereiopod subchelate or simple with a hard and heavily calcified body. Among the main body adaptations of these organisms are distinguished: (i) carapace laterally compressed, (ii) pleon longer than the cephalothorax in ghost shrimps but usually shorter in mud lobsters, and (iii) anterior feet thrown directly forward. Current accounting of axiideans and gebiideans reaches around 781 and 240 extant species, respectively, with major number of species in Callianassidae and Upogebiidae within of each clade. Male reproductive system involves paired testes linked to the vas deferens that open in gonopores on the ventral coxal segment of the fifth pereiopod. In females, the reproductive system is composed of paired and colored ovaries, one ovary shorter than another, and a pair of short and translucent oviducts linking each ovary to the gonopore, this latter located on the ventral coxal of the third pereiopod. When present in males, the first pleopod is sexually dimorphic. Most ghost shrimps show distinct sexual dimorphism in body size and the major cheliped which become them in a promising group for growth studies. Hypertrophied chelipeds in males are often used to defend galleries against invasion from other shrimps from the same or opposite sex or during the intense male-to-male competition for sexual partners. Knowledge about sexual systems of these species remains limited; however, available information suggests that hermaphroditism might be commonly present in axiideans and gebiideans. Regarding mating systems, all species of ghost shrimp and mud lobster with solitary habits and remarkable sexual dimorphism in the major cheliped are expected to be polygamous. Finally, considerable variability among Axiidea and Gebiidea species in fecundity and egg size may indicate important differences in the reproductive strategy and may also reflect a latitudinal trend as observed in other decapods.

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Keywords: Thalassinidea, taxonomy, ecology, sexual systems, mating systems, sexual dimorphism

1. Taxonomic origin of Thalassinidea

The term "Thalassinoides" is introduced for the first time into subsection Macrura (reptant) by the zoologist Latreille [1], including in it the genera *Gebia* Leach, 1816; *Thalassina* Latreille, 1806; *Callianassa* Leach, 1814; and *Axius* Leach, 1815. Next, this term is Latinized as Thalassinidea Latreille, 1831, incorporating it to the suborder Pleocyemata Burkenroad, 1963. Dana [2] divided Thalassinidea into Eubranchiata (species with thoracic branchiae) and Anomobranchiata (species with abdominal branchial appendages), classifying the taxa Gebidae; Callianassidae Dana, 1852; and Thalassinidea Latreille, 1831, into Eubranchiata and *Callianidea* H. Milne Edwards, 1837, and *Isaea* H. Milne Edwards, 1830, into Anomobranchiata. The famous zoologist de Saint Laurent [3] elevated the genus *Upogebia* Leach, 1814 (e.g., Callianassidae) to family rank, and she reorganized the families Callianassidae; Callianideidae Kossmann, 1880; and Axiidae Huxley, 1879, into superfamily Axioidea [4]. In another work published in the same year, she divided Reptantia into 10 groups that in her opinion were caused by the process called "radiation Triassique" [5]. In her work, she stated that infraorder Thalassinidea was the only group of Reptantia impossible to define precisely and so introduced the term (French) "Thalassinacea." De Saint Laurent [5] argued that in "Thalassinacea," relationship between the epistome and the carapace varied notably from one family to another, also the number of chelate pereopods (sometimes one and sometimes two); an appendix interna was not always present. From these observations, she proposed the separation of "Thalassinacea" into infraorders Axiidea and Gebiidea, thus transferring the families Axiidae and Callianassidae for the former infraorder and Laomediidae; Upogebiidae Borradaile, 1903; and Thalassinidea for the latter infraorder [5].

The first cladistic analysis of Thalassinidea was conducted by Poore [6]. He found the group to be monophyletic and divided into three superfamilies (Callianassoidea, Axioidea, Thalassinidea). A subsequent phylogenetic study using molecular data divided Thalassinidea into two major clades [7]. The first clade composed of the families Strahlaxiidae Poore, 1994, and Callianassidae and the second clade of Laomediidae Borradaile, 1903, Upogebiidae, and Thalassinidea (see also [8] sperm data; [9] molecular data). Sakai [10] compared the gastric mill in species of the Thalassinidea and found the group "diphyletic." From his information, he proposed the division of Thalassinidea into superorder Callianassoidea composed of five families (Axiidae; Callianassidae; Callianideidae; Ctenochelidae Manning and Felder, 1991; Gourretiidae Sakai, 1999) and Thalassinidea composed of three families (Laomediidae, Upogebiidae, Thalassinidea). In the former group, all species are characterized by the presence of a propyloric ossicle simple, whereas in the latter group by having a propyloric ossicle triangularly protruded downward [6]. Lastly, Robles et al. [11] undertook a molecular phylogeny of the thalassinideans and discovered the same two groups proposed by de Saint Laurent [4, 5] and other researchers [12–14].

Taxon
Class Malacostraca
Subclass Phyllocarida
Subclass Hoplocarida
Subclass Eumalacostraca
Superorder Syncarida Packard, 1885
Superorder Peracarida Calman, 1904
Superorder Eucarida Calman, 1904
Order Euphausiacea Dana, 1852
Order Decapoda Latreille, 1802
Suborder Dendrobranchiata Spence Bate, 1888
Suborder Pleocyemata Burkenroad, 1963
Infraorder Achelata Scholtz and Richter, 1995
Infraorder Anomura MacLeay, 1838
Infraorder Astacidea Latreille, 1802
Infraorder Axiidea de Saint Laurent, 1979
Family Axiidae Huxley, 1879
Family Callianassidae Dana, 1852
Family Callianideidae Kossmann, 1880
Family Gourretiidae Sakai, 1999
Family Micheleidae Sakai, 1992
Family Strahlaxiidae Poore, 1994
Infraorder Brachyura Latreille, 1802
Infraorder Caridea Dana, 1852
Infraorder Gebiidea de Saint Laurent, 1979
Family Axianassidae Schmitt, 1924
Family Kuwaitupogebiidae Sakai, Türkay and Al Aidaroos, 2015
Family Laomediidae Borradaile, 1903
Family Thalassinidea Latreille, 1831
Family Upogebiidae Borradaile, 1903
Infraorder Glypheidea Van Straelen, 1925
Infraorder Polychelida Scholtz and Richter, 1995
Infraorder Procarididea Felgenhauer and Abele, 1983
Infraorder Stenopodidea Spence Bate, 1888

Table 1. Families of Axiidea and Gebiidea within the classification of the arthropod superclass Multicrustacea based on Dworschak et al. [15], updated by worms [22].

Currently, it is reasonably assumed by researchers that Axiidea and Gebiidea represent two distinctly separate infraorders of decapods whose main evolutionary characteristic is the fossorial lifestyle [15]. Members of Axiidea (casually known as ghost shrimps) are characterized by having the first and second pereiopod chelate and a soft and delicate body, whereas all Gebiidea (casually known as mud lobsters) possess the first pereiopod chelate or subchelate and second pereiopod subchelate or simple with a hard and heavily calcified body [15, 16]. Recent discovery of new species has added a series of new families within Axiidea and Gebiidea [17, 18]. Considering this information, modern classification of both groups divided Axiidea into six families and Gebiidea into five (**Table 1**). Nevertheless, taxonomy of old name Thalassinidea follows being very controversial among carcinologists from the "American school" and opinions of Sakai, particularly in what concerns to the correct use of the names Axiidea and Gebiidea versus Callianassidea and Thalassinidea [19, 20].

2. A body adapted for a fossorial lifestyle

In order to understand and define what is meant by ghost shrimp and mud lobster, the general morphological components of the infraorders Axiidea and Gebiidea need to be examined.

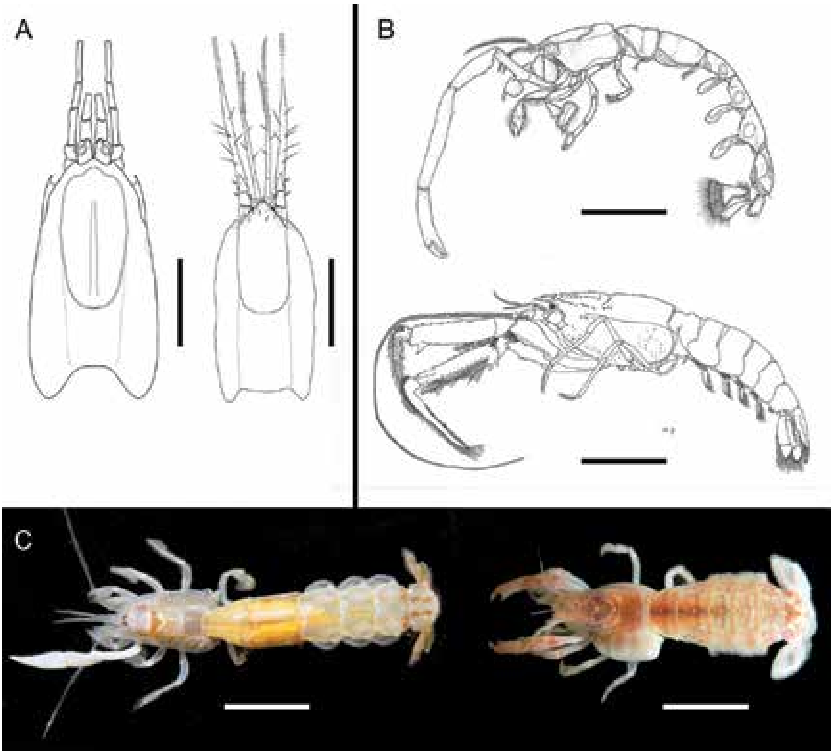

Figure 1. Main morphological adaptations in Axiidea and Gebiidea. (A) Carapace of *Neocallichirus grandimana* (left panel) and *Axianassa linda* (right panel), dorsal view; (B) male specimen of *Callichirus seilacheri* (top panel) and *Naushonia macginitiei* (Glassel, 1938) (down panel), lateral view; (C) male specimen of *Lepidophthalmus siriboia* (left panel) and *Upogebia omissa* (right panel), dorsal view. (a,B) left and right panel, scale bar = 1 cm, 0.5 cm, respectively; (B) top and down panels, scale bar = 1 cm, 0.5 cm, respectively.

The carapace in most of these species (except in laomediids of the genus *Naushonia*) is laterally compressed and can be strongly ornamented (**Figure 1A**, left and right panel), with spines and tubercles as in Thalassinidea and Upogebiidae (Gebiidea) or unornamented as in Callianassidae and Callianideidae (Axiidea) [15, 16]. The pleon is longer than the cephalothorax in most ghost shrimps (**Figure 1B**, top panel) but usually shorter in mud lobsters (**Figure 1B**, down panel), and anterior feet are thrown directly forward in all members of these clades [15, 16] (**Figure 1C**, left and right panel).

3. Diversity and ecological importance

Inhabiting most oceans and seas of the world, ghost shrimps (Axiidea) and mud lobsters (Gebiidea) exhibit a greatest diversity with about 423 and 192 extant species, respectively [21]. According to information available in database World Register Marine Species, for Axiidea and Gebiidea, those values have increased in about 85% and 25%, respectively, during the last decade [22]. In terms of extant species, family Callianassidae exhibits the greatest diversity within infraorder Axiidea whereas Upogebiidae within Gebiidea (**Table 2**).

Both axiideans and gebiideans are known for constructing burrows of different shapes and depths [23–27] (**Figure 2A**) and for playing an important role in shaping the community structure in intertidal and shallow water of marine habitats [28–31]. Bioperturbation produced by these organisms, i.e., the activity of water and sediment expulsion from the galleries, contributes to the suspension of organic matter, nitrogen fixation, and the increases of food availability among the trophic levels [32–34] (**Figure 2B**). Members of Axiidea and Gebiidea can be found inhabiting as sponge symbionts, living between coarse coral rubble or even associated to hydrocarbon seeps

Taxon	Number of genera	Extant species
Infraorder Axiidea		
Family Axiidae	63	205
Family Callianassidae	67	495
Family Callianideidae	6	18
Family Gourretiidae	9	20
Family Micheleidae	4	33
Family Strahlaxiidae	3	10
Infraorder Gebiidea		
Family Axianassidae	2	15
Family Kuwaitupogebiidae	1	1
Family Laomediidae	4	21
Family Thalassinidea	1	11
Family Upogebiidae	13	192

Table 2. Number of genera and species for each family of Axiidea and Gebiidea based on database of worms [22].

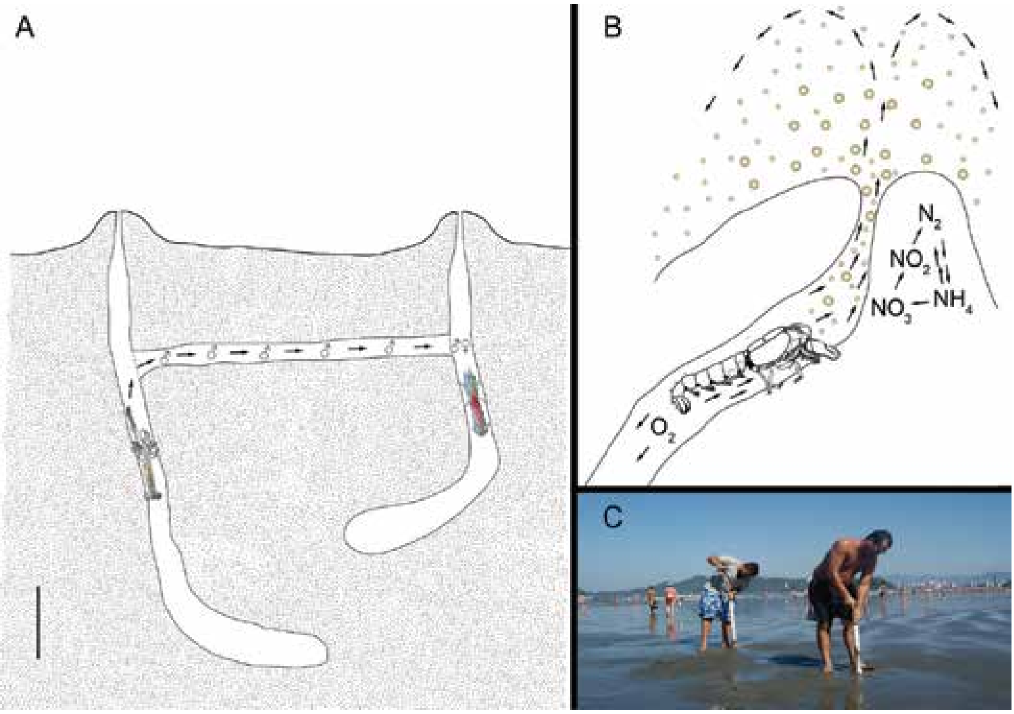

Figure 2. (A) Burrow morphology and copulatory behaviour in Callichirus seilacheri (Callianassidae), scale bar = 20 cm; (B) model of bioperturbation activity in Axianassa linda (Axianassidae); (C) fishermen harvesting Callichirus major (Callianassidae) at São Paulo State, Brazil.

and hydrothermal vents in deep water [35–38]. Some species of ghost shrimps are considered ecosystem engineers because of their capacity to modify, maintain, and/or create habitats for other marine invertebrates [39–40]. Also, several ghost shrimps and mud lobsters are used as a bait for recreational fishing and human consumption [41–45] (**Figure 2C**).

Dworschak et al. [15] stated that most ghost shrimps and mud lobster species are characterized by solitary habits; however, such assumption lacks empirical support from the available literature. With the exception of larval period [46–49], axiideans and gebiideans spend their lifetime within of gallery [15], which makes it difficult to capture and study them. As a result, the knowledge about population dynamics and reproduction of these species is restricted to about 6.00% of already described species, being most of these studies realized in species of the families Callianassidae and Upogebiidae [40, 50–56].

4. Reproductive biology

4.1. Gonopores and primary sexual characters

The location of the male and female sexual openings in Axiidea and Gebiidea is similar to described universally for the reptant decapods [57]. Males possess prominent gonopores on the ventral coxal segment of the fifth pereiopod, whereas females have oval gonopores on the ventral coxal segment of the third pereiopod [40, 58, 59] (**Figure 3A**).

Information about internal anatomy of the reproductive system is virtually nonexistent in most species of ghost shrimps and mud lobsters. Scarce information published point out that male reproductive system involves paired testes dorsally to the hepatopancreas and the intestine and is located between first and second abdominal somites, whose connection with genital openings (gonopores) is produced through a pair of translucent or whitish vas deferens [60] (**Figure 3B**). Secreting epithelium of the vas deferens is responsible for forming the gelatinous spermatophoric mass [61], as observed in other decapods [62]. Female sexual system is composed of paired orange or dark red ovaries (depending upon developmental stage), one ovary shorter than another, both visible through pleonal region and a pair of short and translucent oviducts linking the ovary to gonopore [59, 60] (**Figure 3C**). Seminal receptacle or spermathecae have not been described for any Axiidea and Gebiidea, despite attempts to find them [63]. Laboratory observations show that females of callianassid shrimps are not able to store sperm [64], as reported in most brachyuran crabs [65].

4.2. Secondary sexual characters

Males of most ghost shrimps and mud lobsters can be identified by the absence/presence and morphology of the first pleopod. The first pleopod is absent in most males of Axianassidae, Laomediidae, Strahlaxiidae, and Upogebiidae and in numerous Callianassidae [15, 16, 66, 67]. When present, the male first pleopod is uniramous and can be unsegmented as in *Thalassina* [68], bisegmented as in *Callichirus* [58], or composed of four articles as in *Ctenocheles* [69]. Male first pleopod in some species as *Callianidea mariamartae* Hernáez and Vargas, 2013, and *Marcusiaxius lemoscastroi* Rodrigues and de Carvalho, 1972, is morphologically similar to gonopods of Brachyura [70, 71], showing a tiny size and function totally unknown [15]. First pleopod plays an important role during the mating behavior of caridean shrimps [72] and brachyuran crabs [65]; however, their function is not clearly defined in Axiidea and Gebiidea.

Female first pleopod is present in all females of Axiidea and Gebiidea [15]. It is uniramous and consists of one article in Axianassidae, two articles in most families, or three articles in Callianassidae, with the distal part sometimes appearing as a shovel (Callianassidae) or flagellum (Laomediidae, Callianideidae) [58, 59, 66, 73]. Depending upon species, sometimes the first two pairs or all female pleopods are used for carrying the eggs during the incubation of embryos [55, 74–76]. Females use pleopods 3–5 to generate strong water currents during the spawning and so help the larvae release from the burrow [76].

Ghost shrimps constitute a promising group for growth studies because many of them show marked differences between relative growth of chelipeds of males and females during post-puberty phase. In Callianideidae and Callianassidae, for instance, males show a positive allometric growth of the major cheliped in relation to body size, whereas this morphometric relationship is isometric in females of both families [40, 77]. According to Rodrigues and Höld [78], hypertrophied chelipeds in males of ghost shrimps are often used to defend galleries against invasion from other shrimps from the same or opposite sex. Also, Felder and Lovett [51] suggest that antagonistic interactions among males of callianassid shrimps might cause

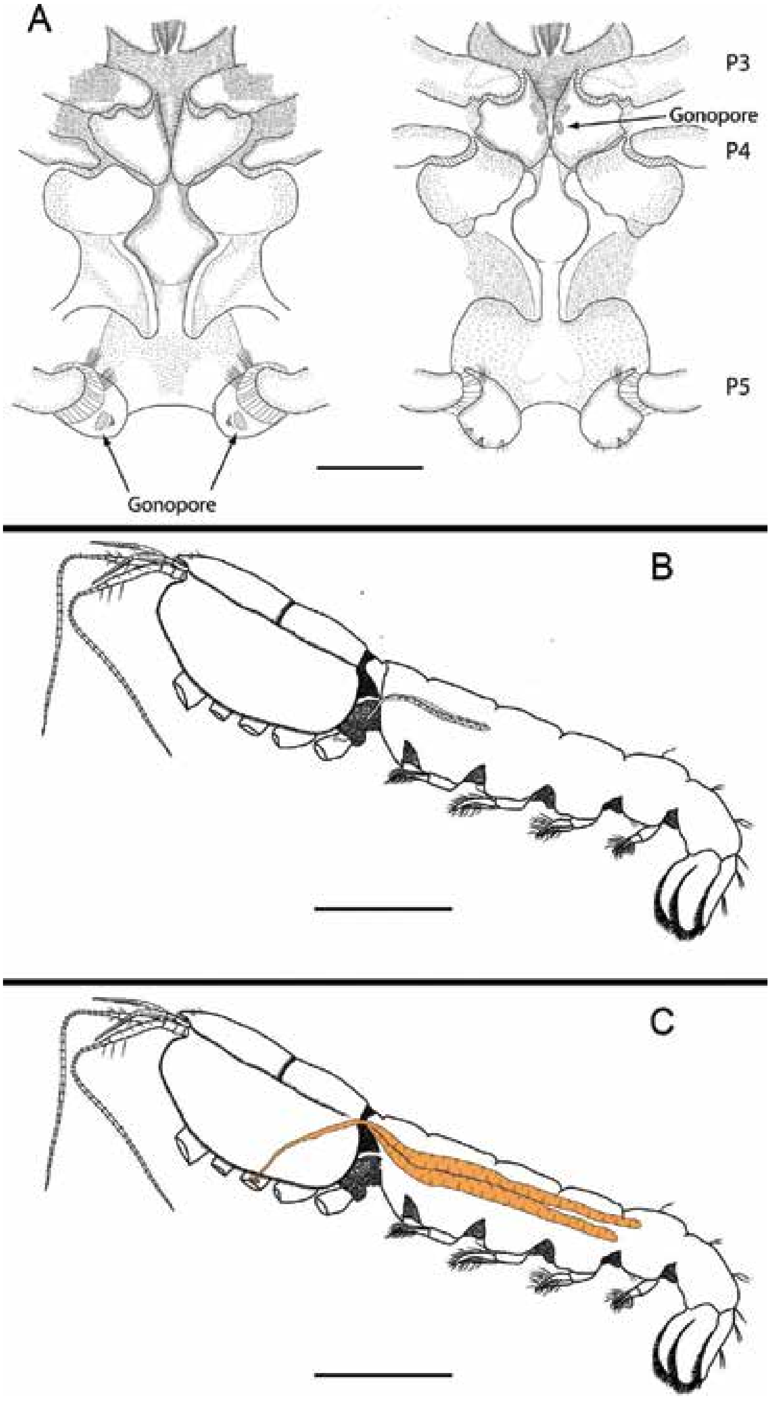

Figure 3. Schematic representation of the external genitalia and reproductive system in males (A, left panel, B) and females (A, right panel, C) of ghost shrimps and mud lobster. A–C scale bar = 5 mm.

a high mortality of adult males, thus creating a bias toward females in these populations. Consequently, development of extremely larger chelipeds in callianassid species not only includes morphometric changes during sexual maturity but also can provide some advantages to males, a competition for sexual partners, as were widely documented in several species of Caridea Dana, 1852 [72].

4.3. Sexual systems

Sexual system varies considerably in Decapoda. Most caridean shrimps and brachyuran crabs are gonochoric, that is, all individuals in the population exhibit separate sexes throughout their lifetime [65, 72]. Other species are sequential hermaphrodites in which the individual changes sex at some point in the life history [79–84]. If the initial sex is male, the condition is known as protandry; the converse situation is protogyny [85]. Finally, several species have been reported as simultaneous hermaphrodites sensu Ghiselin [86], that is, an organism has both male and female sexual organs at the same time [72, 87, 88].

While the sexual system of most groups of Decapoda is well known such as Caridea [72], Astacidea [89], Anomura [90], and Brachyura [65] for most axiideans and gebiideans, the distribution of the sexes among individuals is not clear. This is because many researchers have omitted to report explicitly the sexual system of their focus species, wrongly accepting that most ghost shrimps and mud lobsters are gonochoric. Secondly, because in ghost shrimp and mud lobster studies, the sex ratio as a function of size is rarely reported, which is crucial to determine any sex changing through the ontogeny of one species [91].

Several studies conducted in Axiidea and Gebiidea species have reported morphological evidences that aim for a sexual system more complex than simply the existence of separate sexes during the lifetime of these species. For instance, in the intertidal mud lobster *Upogebia major* (De Haan, 1841) (Upogebiidae) and in the ghost shrimp *Callichirus major* (Say, 1818) (Callianassidae), male has the gonad divided in a posterior ovarian section and an anterior testicular section [92, 61] (**Table 3**). In both species, ovarian section produces functional oocytes. In other species of ghost shrimps and mud lobsters have been reported specimens with male and female gonopores which have been classified as intersexed (**Table 3**). To summarize, for 21 species of Axiidea and 12 of Gebiidea, explicit information—or strong indirect evidence—on their sexual system was available. Of these, 26 species are gonochoristic (i.e., all individuals in the population exhibit separate sexes throughout their lifetime); 2 males are hermaphrodites, and 10 species present intersexed specimens (**Table 3**). Considering this information and given that reproductive biology has been studied in only a small proportion of the 781 ghost shrimps and 240 mud lobsters, it can be concluded that hermaphroditism might not be unusual in these organisms.

4.4. Mating systems

Overall, monogamous decapods usually live in heterosexual pairs as a form to ensure the mating and optimize the survival [93]. In most monogamous species, disproportionate sexual dimorphism

Taxon	**Sexual system**	**Intersex**	**Reference**
Axiidea			
Callianassidae			
Biffarius filholi (A. Milne-Edwards, 1878)	Gc		[54]
Callianassa aqabaensis Dworschak, 2003		I (M,F)	[116]
Callianassa subterranea (Montagu, 1808)	Gc		[117]
Callichirus garthi (Retamal, 1975)	Gc	I (F)	[40]
Callichirus islagrande (Schmitt, 1935)	Gc		[63]
Callichirus major (Say, 1818)	H (M)	I (F)	[100]
Callichirus seilacheri (Bott, 1955)	Gc	I (F)	P. Hernáez unpublished data
Lepidophthalmus bocourti (A. Milne-Edwards, 1870)	Gc		P. Hernáez unpublished data
Lepidophthalmus louisianensis (Schmitt, 1935)	Gc		[51]
Lepidophthalmus sinuensis Lemaitre and Rodrigues, 1991	Gc		[118]
Lepidophthalmus siriboia Felder and Rodrigues, 1993	Gc		[56]
Neocallichirus maryae Karasawa, 2004	Gc		P. Hernáez unpublished data
Neocallichirus nickellae Manning, 1993	Gc		P. Hernáez unpublished data
Neotrypaea californiensis (Dana, 1854)	Gc		[119]
Neotrypaea tabogensis (Sakai, 2005)	Gc		P. Hernáez unpublished data
Nihonotrypaea harmandi (Bouvier, 1901)	Gc		[120]
Nihonotrypaea japonica (Ortmann, 1891)	Gc		[53]
Nihonotrypaea petalura (Stimpson, 1860)	Gc		[120]
Sergio mirim (Rodrigues, 1966)	Gc		[121]
Sergio trilobata (Biffar, 1970)	Gc		[122]
Callianideidae			
Callianidea mariamartae Hernáez and Vargas, 2013	Gc		[70]
Gebiidea			
Axianassidae			
Axianassa australis Rodrigues and Shimizu, 1992	Gc		P. Hernáez unpublished data
Upogebiidae			
Austinogebia edulis (Ngoc-Ho & Chan, 1992)		I (M)	[123]
Austinogebia spinifrons (Haswell, 1882)		I (F)	[124]
Paragebicula edentata (Lin, Ngoc-Ho & Chan, 2001)		I (M)	[125]
Upogebia dawsoni Williams, 1986	Gc		[126]
Upogebia deltaura (Leach, 1816)		I (M)	[50]

Taxon	Sexual system	Intersex	Reference
Upogebia major (De Haan, 1841)	H (M)		[92]
Upogebia omissa Gomes Corrêa, 1968	Gc		P. Hernáez unpublished data
Upogebia pusilla (Petagna, 1792)	Gc		[127]
Upogebia stellata (Montagu, 1808)	Gc	I ()	[128]
Upogebia thistlei Williams, 1986	Gc	I (M)	[129]
Upogebia vasquezi Ngoc-Ho, 1989	Gc		[130]

Table 3. Probable sexual system and the presence of specimens intersexed in 21 ghost shrimps and 12 mud lobsters. Empty spaces are left where no information is available; (Gc) = gonochoristic, (H) = hermaphroditic, (I) = intersex, (M) = male, and (F) = female.

of chelipeds is not observed because sexual selection is weak given that monogamy evolved from fidelity between heterosexual pairs [94]. On the contrary, in polygamous species there is no fidelity among individuals of the opposite sex, wherefore agonistic encounters are common between adult males during the search for receptive females [72, 95]. In these species, males invest heavily in structures, such as chelipeds, that are used as armament against other potential competitors [96, 97]. Considering this information, all species of ghost shrimp and mud lobster with solitary habits and remarkable sexual dimorphism in the major cheliped are expected to be polygamous.

In the intertidal ghost shrimp *Callichirus seilacheri* (Bott, 1955), the burrow is individually inhabited by one male or a female (**Figure 2A**), and adult male develops hypertrophied chelipeds which is a potential evidence of intense male-to-male competition for sexual partners and therefore an indirect evidence of polygamy [98]. In a study conducted in *Callichirus islagrande* (Schmitt, 1935), an intertidal species in that males possess highly developed chelipeds [59], the egg mass of females is fertilized by multiple males which denotes polyandry [63]. In both species, the authors assume that mating occurs when the male digs a straight and almost horizontal connection from its gallery to other nearby galleries in search of a receptive female (**Figure 2A**), such as one that is observed in *Upogebia noronhensis* Fausto-Filho, 1969 [98]. Unfortunately, information about mating system in Axiidea and Gebiidea is virtually nonexistent. Further studies including behavioral experiments between male and female specimens should be carried out to investigate a possible mating system in these species.

4.5. Sexual dimorphism in body size

In general, females of ghost shrimps attain, in average, a larger body size than males such as *Biffarius filholi* (A. Milne-Edwards, 1878) [99], *C. major* [100], and *Lepidophthalmus siriboia* Felder and Rodrigues, 1993 [56]. Females usually invest more energy into somatic growth than males when their reproductive success depends on reaching a larger body size [101]. In decapods, such evolutionary trend is explained by the fact that fecundity in females increases with body size [74, 102–105]. Supporting this assumption, fecundity in species of callianassids increase with the female size, resulting in greater production of eggs in larger females [54, 74, 75].

4.6. Egg number and egg size

The considerable variability among Axiidea and Gebiidea species in view of fecundity and egg size (**Table 4**) may indicate important differences in the reproductive strategy and may also reflect a latitudinal trend, as was observed in other decapods [106–110]. In *C. seilacheri,* for instance, females produce the highest number of eggs compared to those axiideans and gebiideans where data are available. However, this ghost shrimp and mud lobsters are the largest species among those listed in **Table 4**, and it is assumed that the area available for egg attachment increases with female size [102, 111]. When compared to a similar-sized species *Upogebia deltaura* (Leach, 1816) (18.9 mm CL, 5304 eggs) [50], fecundity in *C. seilacheri* is still substantially higher (18.6 mm CL, 9612 eggs). Moreover, this species produces considerably larger eggs (0.884 mm) than *U. deltaura* (0.558 mm). It is speculated that these differences in egg numbers in similar-sized species are related to the elasticity of the abdomen, which provides more space for egg attachment.

Egg size is one of the most variable parameters in decapods and offers valuable information on a species' reproductive strategy. It is a useful indicator of the duration of embryogenesis and larval size at hatching [112]. Moreover, several studies on ghost shrimps and mud lobsters showed a clear relation between egg size and type of larval development [113–115]. Such information, however, is restricted to just a few species of both clades.

Taxon	**Carapace length (mm)**	**Number of eggs**	**Egg length (mm)**	**Reference**
Infraorder Axiidea				
Family Callianassidae				
Biffarius filholi	5.5–14.9	1985	0.68	[54]
Callichirus garthi	18.6–23.2	17,450	0.88	[40]
Callichirus kraussi (Stebbing, 1900)	n.a.	122	1.52	[113]
Callichirus major (Brazil)	10.3–15.0	4564	0.79^{a}	[75]
Callichirus seilacheri	12.2–17.2	2387	0.71	P. Hernáez unpublished data
Lepidophthalmus louisianensis	n.a.	598	n.a.	[47]
Lepidophthalmus sinuensis	7.0–16.8	251	1.22	[118]
Pestarella tyrrhena (Petagna, 1792)	5.2–10.4^{b}	270	1.18	[131]
Infraorder Gebiidea				
Family Upogebiidae				
Upogebia affinis (Say, 1818)	n.a.	10,000	n.a.	[132]
Upogebia deltaura	16.6–18.9	4757	0.56	[50]
Upogebia pusilla	14.7–16.6	n.a.	n.a.	[127]

n.a., information not available. Letter in superscript indicates information obtained from further estimation

Table 4. Carapace length of ovigerous females and number and length of eggs in some ghost shrimp and mud lobster species.

5. Conclusion

An updated classification of the infraorders Axiidea (ghost shrimps) and Gebiidea (mud lobsters) divide each of these clades into six families and five families, respectively. However, controversial taxonomic history of these infraorders is far from over due to recent discovery of new taxa. Diagnostic features of these organisms mainly include (i) carapace laterally compressed, (ii) pleon longer than the cephalothorax in Axiidea but usually shorter in Gebiidea, and (iii) anterior feet thrown directly forward. A recent count estimates the diversity of Axiidea and Gebiidea in about 781 and 240 extant species, respectively. In general, information about reproduction of these organisms is virtually nonexistent. Scarce reports about external and internal genital apparatus show that male possesses gonopores on the ventral coxal segment of the fifth pereiopod whereas females on the ventral coxal segment of the third pereiopod. Males of most ghost shrimps and mud lobsters can be identified by the absence/presence and morphology of the first pleopod and sexual dimorphism in the major cheliped during post-puberty phase. According to available information, gonochorism is the sexual system most common within Axiidea and Gebiidea. However, two cases of hermaphroditism and several cases of intersexuality have been also reported in ghost shrimps and mud lobsters that would be indicating the need of further studies about this topic in these organisms. Regarding mating system, all species of ghost shrimp and mud lobster with solitary habits and remarkable sexual dimorphism in the major cheliped are expected to be polygamous. Lastly, considerable variability among Axiidea and Gebiidea species in fecundity and egg size seems to indicate important differences in the reproductive strategy of these decapods.

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Section 5

Biotechnology

The Role of Microalgae in Renewable Energy Production: Challenges and Opportunities

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Additional information is available at the end of the chapter

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Abstract

Microalgae are one of the most effective sources of renewable energy production. It can grow at high rates and capable of producing oil along the year. Microalgae biomass was first suggested as a feedstock for biofuel production and received early attention for commercial application. Microalgae are expected to be a vital raw material for amino acids, vitamins and productions of valuable byproducts. The cultivation of microalgae is known to be the most gainful business in the biotechnological industry. It is a waste less, environmentally pure, energy and resource saving route. Biodiesel production from algal lipid is non-toxic and highly biodegradable. Conversion of biomass to biofuel can be achieved by different methods which are broadly classified into: thermal, chemical and biochemical methods, in addition to the large number of different agents for decomposing and hydrolysing. We can obtain the low-cost energy production from the wastewater treatment by using microalgae. Finally, biodiesel production by microalgae in Egypt is not practical at the economical level. In order to improve biodiesel fuel quality, the alga must be subjected to genetic engineering for up-regulation of fatty acid biosynthesis and/or by down-regulation of β-oxidation. Economically, the algal biomass must be processed for bio-refinery to maximize its utilization for different applications.

Keywords: microalgae, cultivation, biomass production, conversion, challenges and opportunities

1. Introduction

Recently, algae have become the latest feasible source being targeted for biofuel production since they exhibit several attractive features [1]. Microalgae are capable of producing oil all year long. Oil productivity of microalgae is greater compared to conventional crops [2].

The oil content of microalgae which ranged from 20 to 50% is more than other competitors; microalgae yield 15–300 times more oil for biodiesel production than traditional crops on an area basis. Creation of biodiesel from algal lipid is non-toxic and greatly biodegradable. Microalgae can propagate at great rates which can be 50 times more than that of the fastest growing terrestrial crop [3]. They can complete their growth cycle in few days by photosynthesis process that converts sun energy into chemical energy. They have higher photon conversion efficiency; it is about 3–8% against 0.5% for terrestrial plants. Microalgae do not vie for land with food crops [4]. They grow in fresh water, seawater, wastewater or non-arable lands, and can be grown almost anywhere [5]. Therefore, they have minimal environmental effect such as deforestation. So, microalgae are an alternative fuel feedstock that could avoid fuel versus food conflict [6]. Comparing with other renewable energy sources such as solar, geothermal, wind, tidal energy, etc., algae are more controlled and stable for production of energy compared to land-based biomass, algaculture has the potential to produce larger amounts of biofuel with no use of good water or fertile land [1].

Microalgal biomass was first suggested as a feedstock for biofuel production in the 1960s [7] and received early attention from the US National Renewable Energy Laboratory (NREL) in the 1980s. This interest resurged based on their potential for cultivation near coal, petroleum and natural gas power plants. In the last few years, many research and commercial applications of microalgae have gained more interest. Recently, renewable energy source is organic matter derived from microalgal biomass [8]. Newly, high value microalgae and products are commercially cultivated in both closed photobioreactors (PBRs) and open raceway ponds although over 90% of current production is from open raceways. Of course, PBRs have several advantages over open ponds as a cultivation system. However, an open pond is considerably cheaper. Microalgae, which are using in cultivation, is microscopic single cell and have a possible to produce large amounts of lipids (40–50% w/w oil) suitable for biodiesel production. Using sunlight, carbon dioxide and nutrients alone, algae can create and accumulate large amounts of neutral lipids, carbohydrates and other valuable co-products [9]. Studies show that algae could yield up to 10,000 gal/acre (about 94,000 l/ha) of biofuel per year, while corn would only yield 60 gal/acre (about 560 l/ha) annually and potential algae-derived biodiesel yields range from 5000 to 100,000 l/ha/a. Microalgae can also produce up to 60% of their biomass in the form of oil or carbohydrates, from which biofuel and many other industrially important products can be obtained, In addition to, potential use of algae for CO_2 sequestration process. The emissions of CO_2 from industrial unit are the primary nutrient for growing microalgae. This provides the opportunity for the algae to turn pollutants into lipids [10]. Research and scientific studies carried out at several universities and research institutes around the world regarding the benefits and potentials of algaculture have proven that algae can provide future global energy needs in a sustainable and cost-effective way. Many researchers considered biodiesel produced from microalgae as the third-generation biofuels. Microalgae can be a sustainable renewable energy source for biodiesel to overcome the limitations of first- and second-generation biofuels. Biodiesel production using microalgae is attractive in a number of respects and is the most obvious choice. Conversion of biomass to biofuel can be achieved by different methods which are broadly classified into: thermal, chemical and biochemical methods [11].

Biotechnology-based conversion processes can be used to ferment the biomass carbohydrate content into sugars that can then be further processed. As one example, the fermentation path to lactic acid shows promise as a route to biodegradable plastics. Biomass can be fermented to provide ethanol and biogas [12]. Unconventional is to employment thermochemical conversion processes, that use gasification or pyrolysis of biomass to yield a hydrogen-rich synthesis gas that used in a widespread range of chemical processes. Therefore, a bio-refinery is a facility that contributes biomass conversion processes and tools to produce fuels and chemicals from biomass. Concept of bio-refinery is equivalent to the petroleum refinery, which harvests numerous fuels [13].

2. Energy

Energy is essence of life. Broadly, it is defined as the ability to do work or the ability to cause alteration, such as manufacturing molecules or moving substances. Potential energy can be believed of as kept energy. Chemical energy, in the bonds among atoms in a molecule, is a form of potential energy. Kinetic energy can be believed of as free energy, and is commonly linked with motion. Heat (dynamic motion of molecules) and movement of large objects (such as ourselves) are formulae of kinetic energy.

There are many forms of energy, including: chemical, electrical, gravitational, mechanical, nuclear, radiant and thermal energy. The official SI unit for energy is the joule (J); energy can also be measured in calories or British thermal units (Btu) [14]. In physics, energy is a property of objects which can be transferred to other objects or converted into different forms [15]. The "ability of a system to perform work" is a common description, but it is misleading because energy is not necessarily available to do work [16].

Public energy forms include the potential energy stored by an object's position in a force field (gravitational, electric or magnetic), the kinetic energy of a moving object, the chemical energy free out when a fuel burns, the elastic energy stored by stretching solid objects, the radiant energy approved by light and the thermal energy with an object's temperature. Entirely of the many forms of energy are exchangeable to other types of energy. In physics, there is a widespread law of conservation of energy which states that energy can be neither produced nor be damaged; however, it can alterated from one shape to another. Energy conversion includes creating electric energy from heat energy by way of a steam turbine, or by lifting against gravity which led to mechanical work on the object and accumulations gravitational potential energy in the object. If the object falls to the ground, gravity does mechanical work on the object which converts the potential energy in the gravitational field to the kinetic energy liberated as heat on impact with the ground. Living organisms want available energy to stay alive, such as the energy humans get from food. Civilization gets the energy it needs from energy resources such as fossil fuels, nuclear fuel or renewable energy such as solar energy which comes from the sun and required for survival all living organisms (**Figure 1**).

The procedures of Earth's climate and ecosystem are driven by the radiant energy Earth receives from the sun and the geothermal energy contained within the earth.

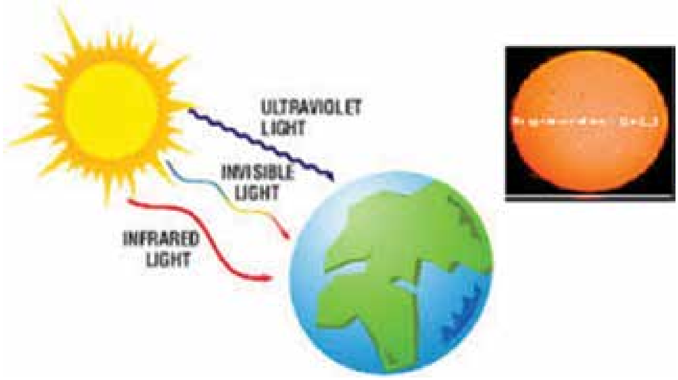


Figure 1. The Sun is the source of energy on the Earth.

2.1. History of energy

The term energy comes since the Ancient Greek: energeia "activity" [17] which perhaps seems for the first time in the work of Aristotle in the 4th century BC. In reverse to the recent definition, energeia was a qualitative philosophical theory, broad sufficient to include ideas such as gladness and pleasure.

In 1807, Thomas Young was possibly the first to use the term "energy" instead of vis viva or living force, in its recent common sense [18]. Gustave-Gaspard Coriolis termed "kinetic energy" in 1829 in its recent common sense, and in 1853, William Rankine created the word "potential energy". The law of energy conservation was also first recommended in the early 19th century, and put on to any isolated system. It was discussed for some years whether heat was a physical substance, dubbed the caloric, or simply a physical quantity, such as momentum.

In 1845, James Prescott Joule open the theory of energy conservation, formalized largely by William Thomson (Lord Kelvin) as the field of thermodynamics. Thermodynamics assisted the quick advance of clarifications of chemical processes by Rudolf Clausius, Josiah Willard Gibbs and Walther Nernst. It moreover led to a mathematical construction of the concept of entropy by Clausius and to the starter of radiant energy laws by Jožef Stefan. The energy conservation is a consequence of the fact that the laws of physics do not change over time, according to Noether's theorem [19].

2.2. Forms of energy

The whole energy of a system can be divided in different ways. For instance, classical mechanics differentiates between kinetic energy, which is decided by an object's motion through space, and potential energy, that is a function of the site of an object inside a field (**Figure 2**). It may be too suitable to discriminate gravitational energy, thermal energy, numerous kinds of nuclear-powered energy (which use capacities from the nuclear force and weak force), electric energy (from the electric field) and magnetic energy (from the magnetic field) between others. Several of these taxonomies overlap; for example, thermal energy ordinarily involves partly of kinetic and partly of potential energy (**Figure 3**).

Figure 2. Energy is converted into the same amount of energy in other forms, mostly light energy and thermal energy.

Potential energies are frequently measured as positive or negative depending on whether they are greater or less than the energy of a specified base state or configuration such as two interacting bodies being infinitely far apart. Some example of different kind of energy with description is shown in **Table 1** and **Figure 4**.

2.3. Types of energy

Energy is the power we use for transportation, for heat and light in our homes and for the manufacture of all kinds of products. There are two sources of energy: renewable and nonrenewable energy [20] **Figure 5**.

2.3.1. Nonrenewable sources of energy

We use the most types of energy which originates from fossil fuels, for instance, natural gas, coal and petroleum. Uranium is considered as nonrenewable source, but it is not a fossil fuel. It is changed to a fuel and undergoes the nuclear power plants. As soon as these normal

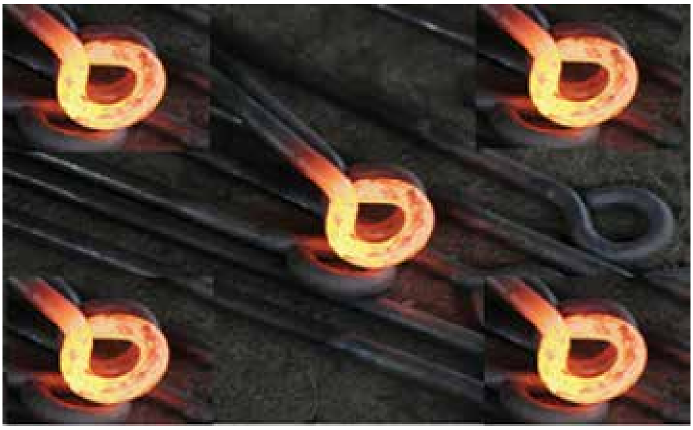
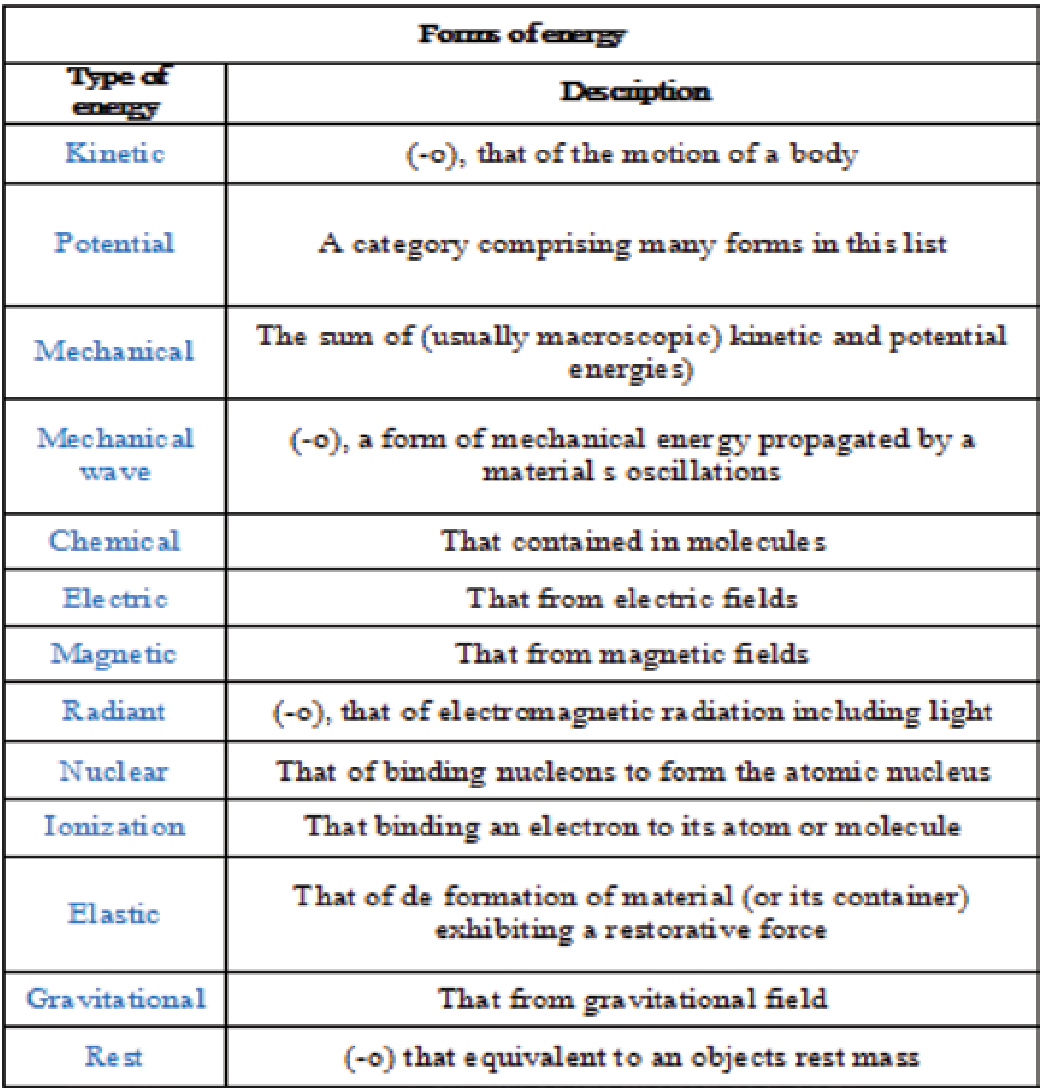


Figure 3. Thermal energy is energy of microscopy constituents of matter, which may include both kinetic and potential energy.



Forms of energy

Type of energy	Description
Kinetic	(-o), that of the motion of a body
Potential	A category comprising many forms in this list
Mechanical	The sum of (usually macroscopic) kinetic and potential energies)
Mechanical wave	(-o), a form of mechanical energy propagated by a material s oscillations
Chemical	That contained in molecules
Electric	That from electric fields
Magnetic	That from magnetic fields
Radiant	(-o), that of electromagnetic radiation including light
Nuclear	That of binding nucleons to form the atomic nucleus
Ionization	That binding an electron to its atom or molecule
Elastic	That of de formation of material (or its container) exhibiting a restorative force
Gravitational	That from gravitational field
Rest	(-o) that equivalent to an objects rest mass

Table 1. Some examples of different kinds of energy.

resources are used up, they are gone forever. The process of meeting these fuels can be dangerous to the biomes from which they originate. Fossil fuels are set through a process named burning for create energy. Burning liberates pollution, such as sulfur dioxide and carbon monoxide which can result in acid rain and global warming.

2.3.2. Renewable sources of energy

Renewable energy resources can be used over and over again. Renewable resources contain wind, geothermal energy, solar energy, hydropower and biomass. That resource generates much less pollution, both in gathering and production, than nonrenewable sources.

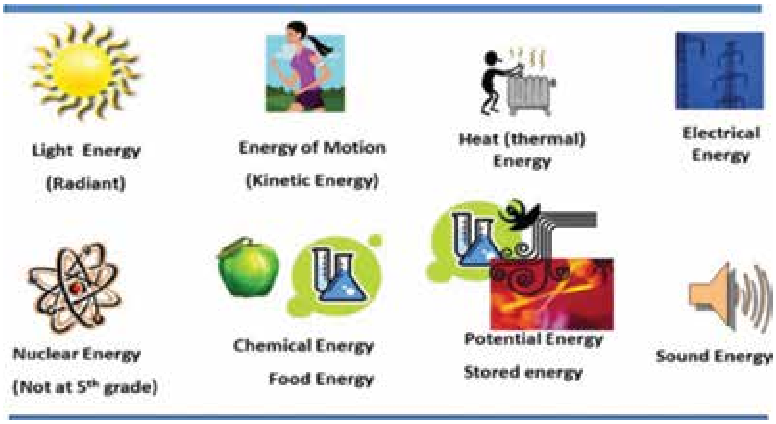


Figure 4. Forms of energy.

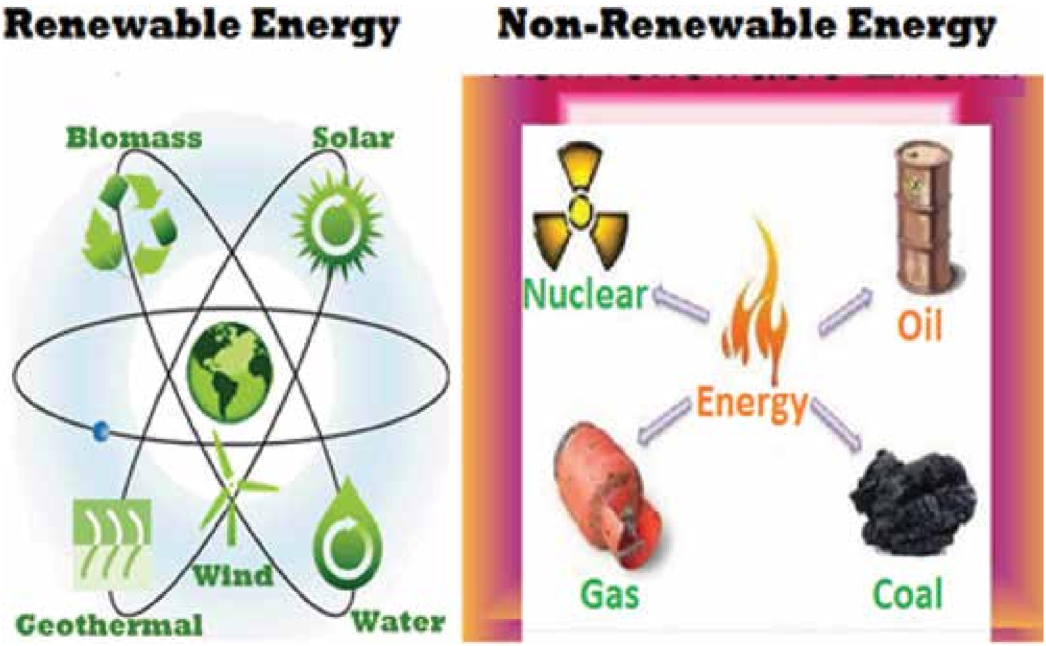


Figure 5. Types of energy.

- The sun produces the solar energy. Some people use solar panels on their homes to convert sunlight into electricity.
- Wind turbines generate electricity. Turbines look like giant windmills
- Earth's crust produces the geothermal energy. Engineers extract steam or very hot water from the Earth's crust and use the steam to generate electricity.
- Dams and rivers generate hydropower. When water flows through a dam it activates a turbine, which runs an electric generator. Biomass includes natural products such as wood, manure, corn and algal biomass of living organisms which used as energy source.

3. Biomass production

Biomass, a renewable energy source, is organic matter resulting from living, or newly living organisms. It can be used as a source of energy and it most ultimately pointed to plant-based materials which are not used for feed, and are specially named lignocellulosic biomass. Biomass can either be used in a straight line throughout burning to create heat such as forest residues and municipal solid waste, or indirectly after converting it to various types of biofuel. Conversion of biomass to biofuel can be summarized by different methods which are generally classified into: thermal, chemical and biochemical methods [11].

3.1. Biomass sources

Biomass is considered the simply source of fuel for domestic use in several developing countries even today. Biomass is entire biologically created matter based in hydrogen, carbon and oxygen. The assessed biomass yield in the world is 104.9 petagrams (104.9×10^{15} g–about 105 billion metric tons) of carbon/year, approximately half on land and half in the ocean [21].

Even today, wood remains the largest biomass energy source [22]; examples include forest residues (such as dead trees). Wood energy is derived by using lignocellulosic biomass (second-generation biofuels) as fuel. Depending on the biomass source, biofuels are divided generally into two main groups. First-generation biofuels are resulting from origin such as corn starch and sugarcane. Sugars existing in the biomass are fermented to yield bioethanol, which can be used immediately in a fuel to yield electricity or act as a flavor to gasoline [23]. Second-generation biofuels use non-food-based biomass sources, for instance, municipal waste and agriculture. These biofuels are often composed of lignocellulosic biomass, which is not edible and is a low-charge waste for several industries. Although being the favored substitute, except the second-generation biofuel neither yields an inexpensive production nor achieved by technological issues. These issues appear essentially due to chemical slowness and building inflexibility of lignocellulosic biomass [24].

Energy derived from biomass is projected to be the largest non-hydroelectric renewable resource of electricity in the US between 2000 and 2020 by Energy Information Administration [25]. There is research involving algae as non-food source can be yielded at rates of 5:10 times those of other kinds of land-based agriculture, for example, soy and corn. As soon as gathered, it can be fermented to yield biofuels, for example, ethanol and methane, in addition to hydrogen and biodiesel [26].

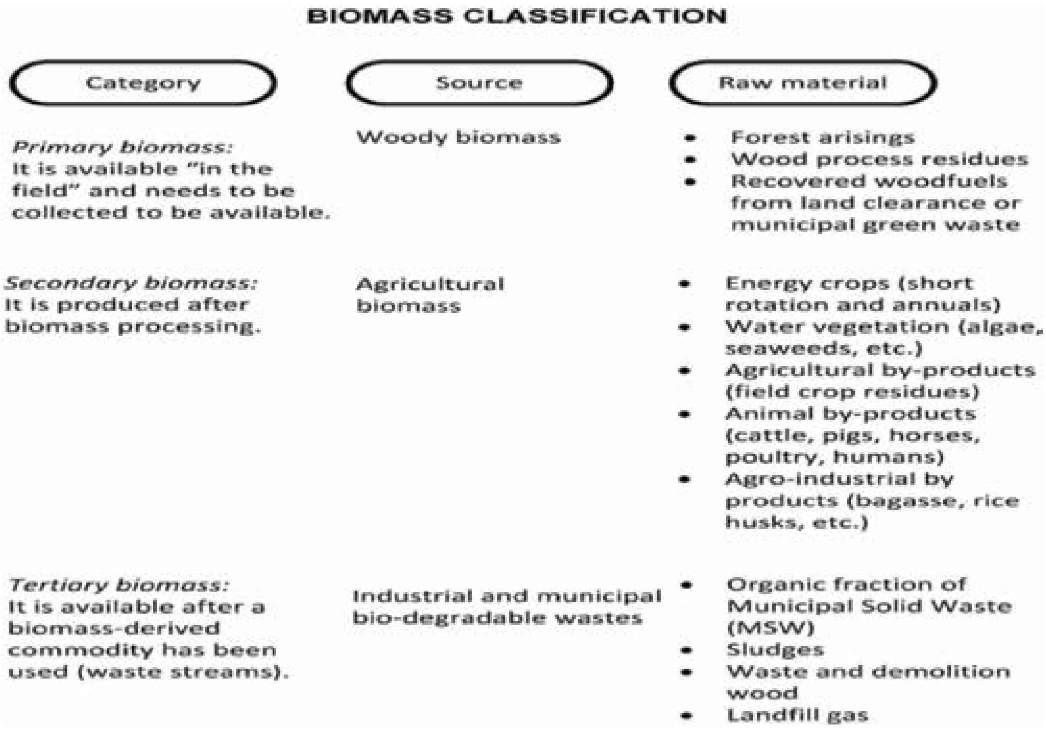
3.2. Biomass types

Researchers characterize the various types of biomass in different ways but one simple method is to define four main types, namely woody plants, herbaceous, plants/grasses, aquatic plants and manures.

Resources of biomass include primary, secondary and tertiary. The first one (primary biomass resources) consisted directly by photosynthesis process and are income directly from the land. They contain permanent short-rotation woody crops and herbaceous crops, the seeds of oil crops and remains produced from the collecting of forest trees and agricultural crops. Secondary biomass resources result from the processing of primary biomass resources such as agricultural by-product (field crop residues) and water vegetation (algae, seaweeds, etc.). Tertiary biomass resources are post-consumer residue streams including animal fats and greases, used vegetable oils, packaging wastes and construction and demolition debris [27] as shown in **Table 2**. Algae used as third generation of biofuels production. This generation of biofuels is advanced and is based on biological. Many species of algae naturally produce low levels of long-chain fatty acids, when they are stressed, this algae species can be screened and/or modified to increase the production yields of long-chain fatty acids.

3.3. Algae

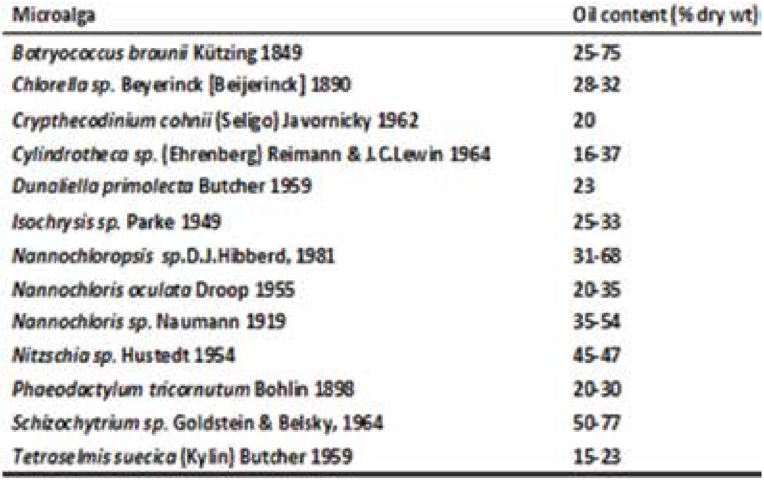
Microalgae are prokaryotic or eukaryotic photosynthetic organisms. Indeed, they can grow quickly in fresh or salt water due to their unicellular or simple multi-cellular building structure. Because of their simple cellular structure, they are very capable converters of solar energy. Microalgae are oxygen-producing microorganisms containing chlorophyll "a", mostly autotrophs, using atmospheric CO_2 as primary carbon source [28]. As the cells of microalgae grow in aqueous suspension, they have efficient access of water, CO_2 and other nutrients [29]. Microalgae are one of the oldest living organisms in our planet and have more than 300,000 species. Several species of them have oil content up to 80% of their dry body weight. **Table 3** shows oil contents of different microalgal species [30].



BIOMASS CLASSIFICATION

Category	Source	Raw material
Primary biomass: It is available "in the field" and needs to be collected to be available.	Woody biomass	• Forest arisings • Wood process residues • Recovered woodfuels from land clearance or municipal green waste
Secondary biomass: It is produced after biomass processing.	Agricultural biomass	• Energy crops (short rotation and annuals) • Water vegetation (algae, seaweeds, etc.) • Agricultural by-products (field crop residues) • Animal by-products (cattle, pigs, horses, poultry, humans) • Agro-industrial by products (bagasse, rice husks, etc.)
Tertiary biomass: It is available after a biomass-derived commodity has been used (waste streams).	Industrial and municipal bio-degradable wastes	• Organic fraction of Municipal Solid Waste (MSW) • Sludges • Waste and demolition wood • Landfill gas

Table 2. Biomass classification.



Microalga	Oil content (% dry wt)
Botryococcus braunii Kützing 1849	25-75
Chlorella sp. Beyerinck [Beijerinck] 1890	28-32
Crypthecodinium cohnii (Seligo) Javornicky 1962	20
Cylindrotheca sp. (Ehrenberg) Reimann & J.C.Lewin 1964	16-37
Dunaliella primolecta Butcher 1959	23
Isochrysis sp. Parke 1949	25-33
Nannochloropsis sp.D.J.Hibberd, 1981	31-68
Nannochloris oculata Droop 1955	20-35
Nannochloris sp. Naumann 1919	35-54
Nitzschia sp. Hustedt 1954	45-47
Phaeodactylum tricornutum Bohlin 1898	20-30
Schizochytrium sp. Goldstein & Belsky, 1964	50-77
Tetraselmis suecica (Kylin) Butcher 1959	15-23

Table 3. Oil content of different microalgal species.

Microalgae can grow in wastewater, thus giving it the ability to address treatment, utilization and disposal concerns [9]. Also, it can be grown in arid and semi-arid regions with poor soil quality, with a per hectare yield estimated to be many times greater than that of even tropical oil seeds [9].

3.4. Advantages of using algae as renewable energy source

Microalgae can be considered as a sustainable energy source of next generation biofuels [31]. Microalgae are able to create oil along the year. Microalgae produce oil is more compared to conventional crops. Microalgae oil content is in the range of 20 to 50% which is better than other challengers. Microalgae yield 15–300 times greater oil for biodiesel production than traditional crops. Biodiesel yield from algal lipid is distinguished with a high biodegradable and non-toxic. Microalgae can cultivate in high amounts arrived to 50 times greater than that of switchgrass, which is the more growing terrestrial crop. Microalgae can complete the whole growth cycle in limited days by way of photosynthesis process that alters sun energy into chemical energy. They grow in fresh water, seawater, wastewater or non-arable lands [5]. Therefore, they have minimal environmental effect such as deforestation. So, microalgae are an alternative fuel feedstock that could avoid fuel versus food conflict [6]. The cultivation of microalgae needs less water than other energy oil crops. **Table 4** shows comparison of different sources of biodiesel [32].

Production of biodiesel from microalgae can fix CO_2. Roughly 1 kg of algae biodiesel fixes 1.83 kg of CO_2. Microalgae cultivation has a higher CO_2 mitigation rate between 50.1 ± 6.5% on cloudy days and 82.3 ± 12.5% on sunny days for different algal species [33]. Microalgae cultivation can use phosphorus and nitrogen as nutrients from wastewater resources. Therefore, microalgae can provide the additional advantage for wastewater bioremediation. Furthermore, microalgal biodiesel can decrease the liberation of NO_x. Microalgae yield significant by-products for instance H_2, ethanol, biopolymers, carbohydrates, proteins, beautifying products, animal feed, enricher, biomass remains, etc. [34]. Improvement of microalgae does not need stimulant for growth. The warming value of microalgal biodiesel is greater than that of the other terrestrial plants. The great heating value of biodiesel resulting from soybean or rapeseed is 37 MJ/kg, while biodiesel resulting from algae is 41 MJ/kg [35].

3.5. Algal biomass

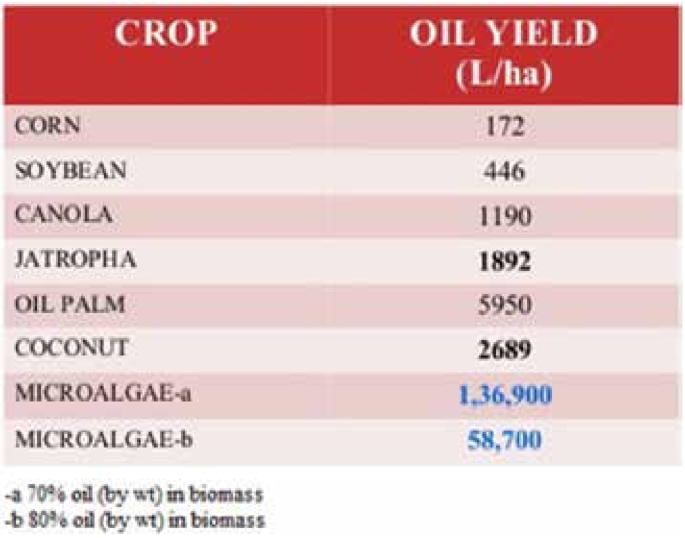
Algal biomass is a renewable resource that has the potential to supply a limited portion of international energy needs [36].

3.5.1. Selecting algae species

Preference toward microalgae is due largely to its less complex structure, fast growth rate and high-oil content (for some species) This characteristics of the strain should be taken into consideration. There are greater than 100,000 types of algae, with varying ratios of three main types of molecule: protein, oils and carbohydrates. Types of algae great in carbohydrates in addition to oils create starches that can be liberated then fermented into ethanol; the residual proteins can be converted into animal grains [1]. Research into algae for the mass-production of oil is mainly focused on microalgae organisms capable of photosynthesis that are less than 0.4 mm in diameter, including the diatoms and cyanobacteria; as opposed to macroalgae.

3.5.2. Isolation

In the end of eighteenth century, Robert Koch was one of the first scientists focused on the isolation of microorganisms in pure culture, followed by Sergei Winogradsky who initiate the field of microbiology and he was responsible for the first isolation of microorganism. Unialgal



CROP	OIL YIELD (L/ha)
CORN	172
SOYBEAN	446
CANOLA	1190
JATROPHA	1892
OIL PALM	5950
COCONUT	2689
MICROALGAE-a	1,36,900
MICROALGAE-b	58,700

-a 70% oil (by wt) in biomass
-b 80% oil (by wt) in biomass

Table 4. Comparison of different sources of bio diesel.

culture means it contains only one kind of alga, usually a clonal population, or cultures may be "axenic," meaning that they contain only one alga. There are four main techniques for obtaining unialgal isolates: spraying, streaking, serial dilution and single-cell isolations [37].

Spraying and streaking are useful for single-celled, colonial or filamentous algae that will grow on an agar surface; cultures of some flagellates may also be founded by these methods. A lot of flagellates, and in addition to other forms of algae, must be separated by single-organism isolations or serial-dilution procedures. Spraying procedure, a stream of air is utilized to diffuse algal cells from a mixture onto the surface of a petri plate having solidified medium with agar for growth.

Single-cell/filament/colony separation: the first stage in this process is to prepare a count of "micropipettes" (very fine-tipped) from glass Pasteur pipettes. Hold a pipette in both hands; the tip end is caught with a forceps so that the glass near the tip is within the flame of a Bunsen burner (gas flame). The pipette is held in the flame only until the glass becomes marginally soft. This is determined by testing for flexibility by moving the tip with the forceps. Then the pipette is removed from the flame and pulled out straight or at an angle so that there is a bend.

You can differ the diameter of the fine pulled tip by altering the speed of pulling. You would need a fine diameter tip if you are trying to separate very small algae, but a bigger diameter tip is necessary for large cells.

Addition of antibiotics to the growth medium is necessary to prevent growth of cyanobacteria and other bacteria, while addition of germanium dioxide will inhibit diatoms growth. Treatment of culture, isolated algae, by an extensive washing procedure via one or more antibiotics is called axenic culture. Resistant stages such as zygotes or akinetes can be treated with bleach to kill epiphytes, and then planted on agar for germination.

3.5.3. Cultivation

Two basic alternatives for microalgae cultivation exist and their relative merits are the basis of ongoing debate.

3.5.3.1. System used in cultivation

Microalgae cultivation using sunlight energy can be carried out in open ponds, covered ponds or closed photobioreactors, based on tubular, flat plate or other designs [38]. Algae houses are utilizing numerous variance methods to grow the algae, involving covered ponds, open ponds, bioreactors and raceways. Algae grow normally in brackish, fresh or salt water centered on the algae species. An algal biofuels house must assess the cost and accessibility of water at the site of the production capacity. Water evaporation is the main problem, may be depending on the climate or whether of the system that used for growth of the algae open or closed. **Table 5** presents a short comparison of open pond systems and closed photobioreactors. Each system has benefits and drawbacks with respect to optimal growth conditions.

Figure 6 shows fixation of carbone dioxide in photobioreactors, utilizing microalgae to convert carbon dioxide and solar energy into algal biomass through photosynthesis process. The microalgae transferred to isolated photobioreactor for hydrogen creation, where the algae will transform solar energy into hydrogen gas using a biophotolytic procedure under sulfur deficiency.

Parameter	Open pond	Photobioreactor
Building	Very simple	More complicated—varies by design
Charge	Inexpensive to construct, operate	More expensive construction, operation
Growth rates (g/m2-day)	Low: 10–25	Movable: 1–500
Water losses	High	Low
Biomass concentration	Low: 0.1–0.2 g/L	High: 2–8 g/L
Temperature control	Difficult	Easily controlled
Species control	Difficult	Simple
Contamination	Great risk	Low risk
Light utilization	Poor	Very high
CO_2 liberation to atmosphere	Great	Almost none
Area requirements	Large	Small
Depth/diameter of water	0.3 m	0.1 m
Surface: volume ratio (m^2/m^3)	~6	60–400

Table 5. Advantages and disadvantages of open pond and closed systems which are used for algal growth.

After the hydrogen yields stage, the algal biomass will be gathered and used for various purposes: the algae can be utilized immediately as a food for human or as animal feed or in aquaculture. After nutrient control, algal biomass can hold big quantities of important biomolecules,

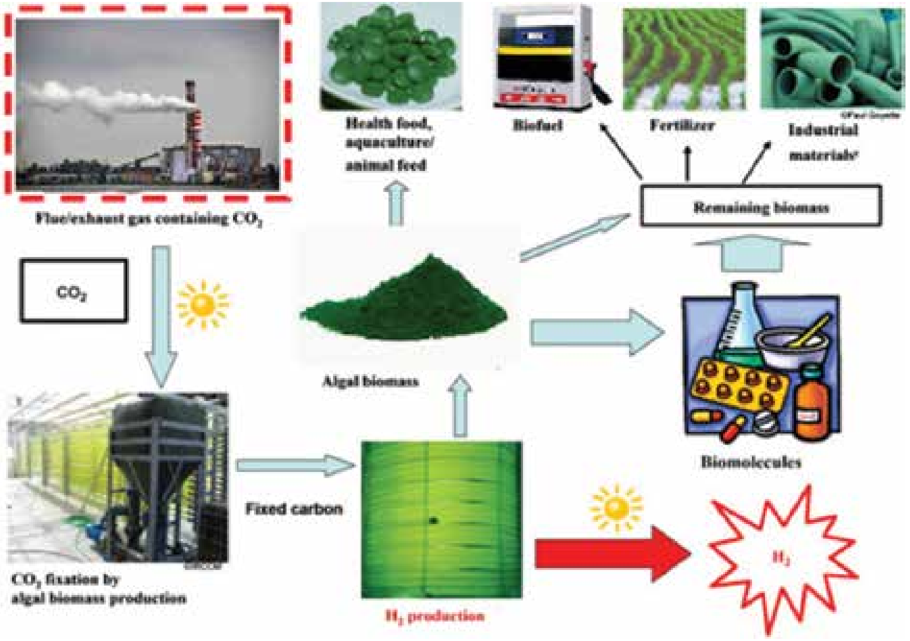


Figure 6. Fixation of carbone dioxide in photobioreactors, utilizing microalgae to convert carbon dioxide and solar energy into algal biomass through photosynthesis process.

which will be removed for industrial trade. However, these substances generally contain few percent of the biomass, leaving the common of the fixed carbone dioxide in the residual biomass. The remaining algal biomass from different method steps can be utilized either as a fertilizer for agriculture in which case the fixed carbon will be retained for some years, or for storing of the fixed carbone dioxide by industrial uses like manufacture of plastics. Remaining biomass can also be utilized as an energy transporter by removal of biodiesel through the direct conversion of the biomass to other energy transporters by biological or thermochemical procedures [39].

3.5.3.1.1. Photobioreactors

Photobioreactors, the closed systems are much more expensive than ponds. Indeed, most companies pursuing algae as a source of biofuel are pumping nutrient-laden water through plastic tubes (called "bioreactors") that are exposed to sunlight (and so-called photobioreactor or PBR). PBR can have different sizes and shapes: plastic bags, flat panels, tubes, fermenter like and others, as shown in **Figure 7**. Vertical tubes are the most popular system due to their relatively easy maintenance, high surface to volume ratio and low cost [40]. Between the advantages of utilizing photobioreactors are resistance to infection with uninhabited algae types and the possibility of simply controlling different factors, including temperature, light intensity and pH. The PBR can be located outdoors or indoors using artificial light or sunlight or a mixture of both. A recent study showed that different wavelengths may have a significant influence on biomass and lipid productivity, as well as on the lipid profile [41]. Recent researches aimed at improving the efficiency of photobioreactors [42] and have shown that the key to greater yields of up to 100 g dry mass m^{-2} h^{-1} is a pronounced heightening of algal flux tolerance.

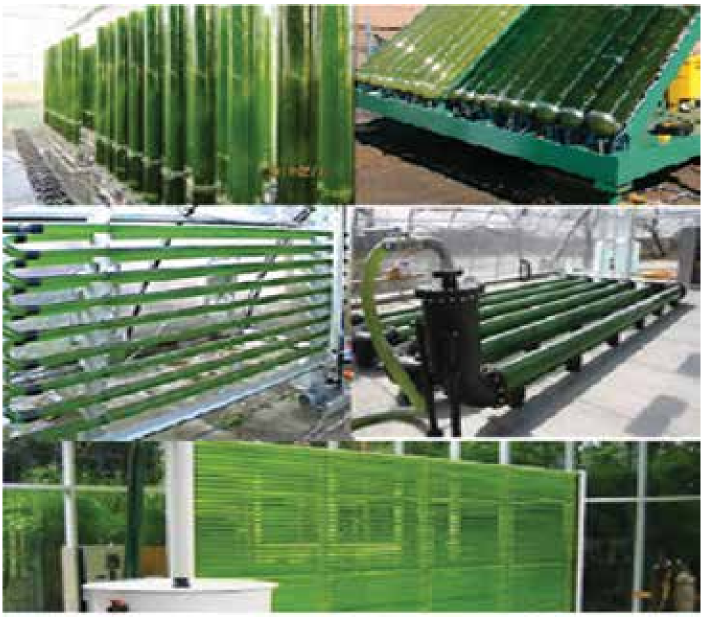


Figure 7. Different shapes of closed system.

http://dx.doi.org/10.5772/intechopen.73573

3.5.3.1.2. Open ponds

Open ponds can be considered a cheap and easy to build, as extended as the area is relatively flat. Cultivation can be prepared immediately above the soil and some simple surface covering for reducing water loss due to seepage, and the other enhancements can be prepared to increase solar energy capture, and reduce the contamination process. The most common types are raceway (**Figure 8**), circular, inclined and unmixed. Open-pond systems for the most part have been given up for the cultivation of algae with high-oil content [43]. Open systems using a monoculture are vulnerable to viral infection. However, such open ponds also suffer from various limitations, including more rapid (than closed systems) biological invasions by other algae, algae grazers, fungi, amoeba, etc., and temperature limitations in colder or hot humid climates and water decrease by evaporation process. It became a main problem, limiting its latter problem is offered. Wastewaters and marine waters can be used as environment and considered a good match for this system due to the water sustainability issues that would prevent large open-pond cultivation from using potable water and the cost of this operation is relatively low. Therefore, this system is able to generate the biomass with a good price [44]. In general, open ponds constitute the cheapest method of producing algae in large quantities [45].

3.5.4. Requirements for cultivation

3.5.4.1. Nutrients

Nutrients such as phosphorus (P), potassium (K) and nitrogen (N) are vital for microalgae growth and are necessary quantities of fertilizer. Iron and silica, in addition to many trace elements, which considered essential marine nutrients, the lack of one can limit the growth of microorganism. A suitable nutrient source for algae is from the sewage wastewater treatment, agricultural, flood plain run-off, all presently major pollutants. However, this wastewater cannot feed algae immediately, but the first process through anaerobic digestion by bacteria. If wastewater is not processed before it reaches the algae, it will possibly kill much of the desired algae strain. Anaerobic digestion of wastewater produces a mixture of methane, carbon dioxide and organic fertilizer. Since the organic fertilizer that comes out of a digester is liquid, and approximately suitable for algae growth, it must first be cleaned and sterilized [1].

Figure 8. Open system (raceway pond).

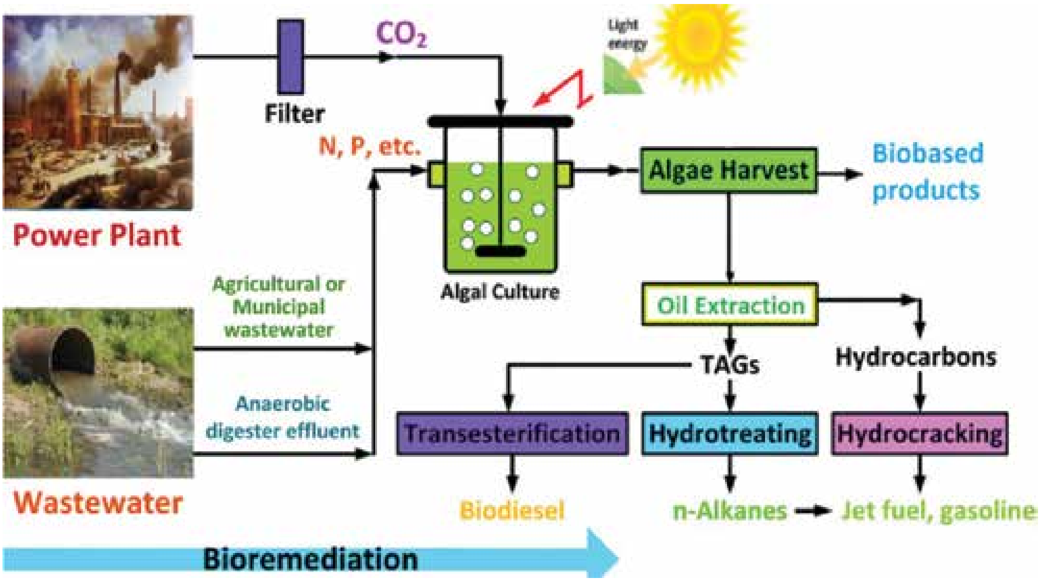


Figure 9. Using of CO_2 (industrial produced) in enrichment of algal biomass production.

3.5.4.2. CO_2 enrichment

One method to increase productivity is to increase the concentration of carbon dioxide [44, 46]. Indeed, the enzyme responsible for CO_2 fixation (ribulose-1,5-bisphosphate carboxylase oxygenase), has a little affinity for CO_2 and also functions as an oxidase of 1,5-bisphosphate, act with oxygen. So, oxygen is a competitive inhibitor with CO_2 and subsequently the atmospheric concentration of CO_2 is amount lower than that of oxygen, which can has a major effect. Assessment of this problem has been achieved by the improvement of carbon concentration mechanisms, where the cell locally induces the CO_2 concentration around the Rubisco enzyme to confirm its function in CO_2 fixation [47]. So this mechanism is common between the algae and demonstrates the benefits of increasing of the CO_2 concentration in mass cultures. Actually, dispersing CO_2 into the culture medium is known to raise its cellular density and two different methods are often reported, the use of CO_2 to adjust pH and CO_2 enrichment as a way to moderate flue gas [48]. Of course any feedstock used in large-scale production will play an important role on the price and CO_2 is not an exception. Thus, this type production should optimally be coupled to a bioremediation process, as shown in **Figure 9**.

4. Production of energy from algal biomass

4.1. Harvesting of algal biomass

In common logic, production of biodiesel from microalgae is actual like to the production of first-generation biodiesel. The biomass created is then cropped. The lipids are removed and then treated via transesterification into fatty acid methyl ester, generally named biodiesel. Though, dissimilar oil seed plants, cropping microalgal cells can demonstrate to be relatively challenging. The small cells moving in water cannot be accessed as simply as microscopic organism, and subsequently oil extraction becomes more complex than the traditional process used for oil seeds in development centuries. Many standard techniques have been evaluated for use in mass algal cultivation and their limitations are reviewed in detail elsewhere [49]. Thus, harvesting can be done at once or divided into different steps, each one varying depending upon the desired final total solids concentration. Of course, selection of crop process will differ according to the critical use of the biomass. Nutraceutical yields may need physical procedures for cropping, thus preventing chemical contamination and sustaining the product's natural features. In this situation, the high value of the product will contribute in the high cost and energy power of the method.

Harvesting methods are one of the major problem in developing a possible biodiesel from microalgae production process is how to successfully harvest the biomass in a cost-effective way [50]. A variety of approaches are possibly available, including flocculation, centrifugation, filtration, sedimentation and mat creation, a number of recent studies provide some hope for the near-term development of a cost-effective harvesting technology.

4.1.1. Centrifugation

Centrifugation has been the technique of choice in small scale studies since it is extremely effective and capable of harvesting all species. However, it has been said that this technique is also energy severe for request to what is fundamentally a little value yields anywhere there is a need to preserve as high net energy ratio as possible. This is indeed real if great levels of removal are required [51].

4.1.2. Flocculation

Flocculation is a procedure used to eliminate algae and other suspended particles from water during its treatment to harvest potable water. In this method, we added external compound that causes flocs to suspended algae. Actually, floc creation is a physico-chemical procedure and the resulting particle size is a function of mixing speed [52]. Because of the negative charge of microalgae cell wall, they tend to remain distributed in solution. Flocculation factor can neutralize this charge, yield the cells to cumulative and settle which facilitates the harvest procedure. Chemical flocculation procedures and the factors that can be used in microalgal cultures have been methodically examined [53]. A desirable flocculant should be inexpensive, non-toxic, recyclable and efficient at low concentrations. Different chemical flocculants can be applied, alum or alkali are traditionally used, but cannot be considered for application in harvesting microalgae for biofuels production because, in addition to cost attentions, their toxic nature precludes further use of the algal biomass. This process might be adapted to make a cost-effective harvesting technology for biofuels production from microalgae if the correct compound could be found. Some algal strains have a natural ability to auto-flocculate under some specific conditions, while others can be flocculated by the addition of a bacterial culture [54].

4.1.3. Filtration

Filtration can be right actual method of crop if the species is large abundant or propagates in filaments. Yet, again this proposes that the favorite species be sustained as closely similar monoculture. Most microalgae are also minor to be successfully collected this way, since their small size and extracellular material quickly clog on filters that have been tested.

4.1.4. Sedimentation/flotation

Several microalgal types have the odd properties of either floating or depositing in the non-existence of adequate mixing. While this propriety might be utilized as advantage in a minimum at first dewatering process, as soon as again the applicability of this process would need a full level of species control through crop growing. Furthermore, these properties lead to low cropping cost, may too negatively impact mixing requests hence it could be highly difficult to sustain these strains as consistently dispersed cells through cultivation.

4.1.5. Biofilm formation

Microalgal types that willingly consist of biofilms have been low focused for biofuels yield hence it is clearly hard to conserve them as a homogenous suspension in the crop growing medium. Though, many modern studies, with two diverse systems, have revealed that this type of growth way can propose the ease and the simple of mechanical harvesting, resulting slurries with a dry weight content of 9–16%. In some event, microalgal were developed or grown on a rotating drum, that was else an open-pond system and simple harvesting process was done by simply unspooling and scratching the cotton fiber that was used [55]. In alternative method, the algae were grown on a regular surface which was drip-watered. In the last growth phase, the algae were improved by simple mechanical scratching [56]. Most harvesting process was greatly simplified in addition to succeeded high rates of biomass production at suitable light conversion efficiencies.

4.2. Technologies for converting biomass into liquid fuels

Scientific hard work has shown that it is possible to produce a variety of liquid biofuels from cellulosic biomass (next generation' feedstock); however its cost is not competitive with petro fuels, even with recent price hikes. Multiple steps are required for conversion into a liquid fuel. Recent studies have indicated that 6:10% of energy in biomass is utilized in feedstock preparation [57]. The two primary conversion pathways are thermochemical and biochemical process, as shown in **Figure 10**.

4.2.1. Thermochemical conversion

These technologies typically use high temperatures and pressure to depolymerize lignocelluloses into small molecular weight organic and inorganic compounds which can be transformed into hydrocarbons, alcohols, aromatics and other organics [57].

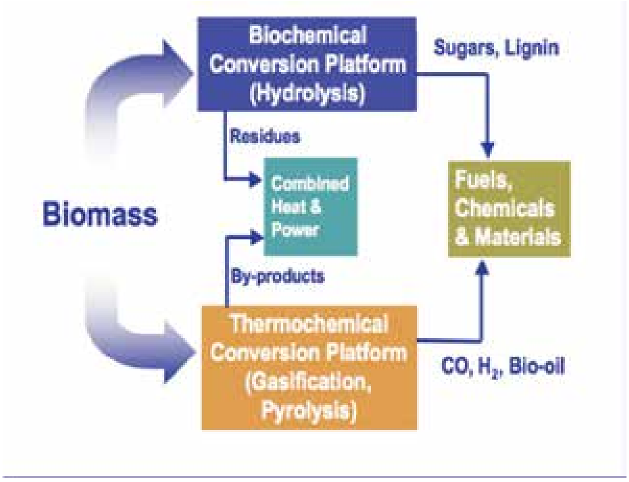


Figure 10. Methods of biomass conversion.

4.2.1.1. Gasification

The two major thermochemical pathways for converting biomass to gaseous and liquid fuels are gasification and pyrolysis. Gasification is the thermochemical partial oxidation of hydrocarbons in the biomass at high temperature (800–1000°C) to a combustible gas mixture (typically containing H_2, CH_4, CO_2 and C_2H_4) [58] (**Figure 11**).

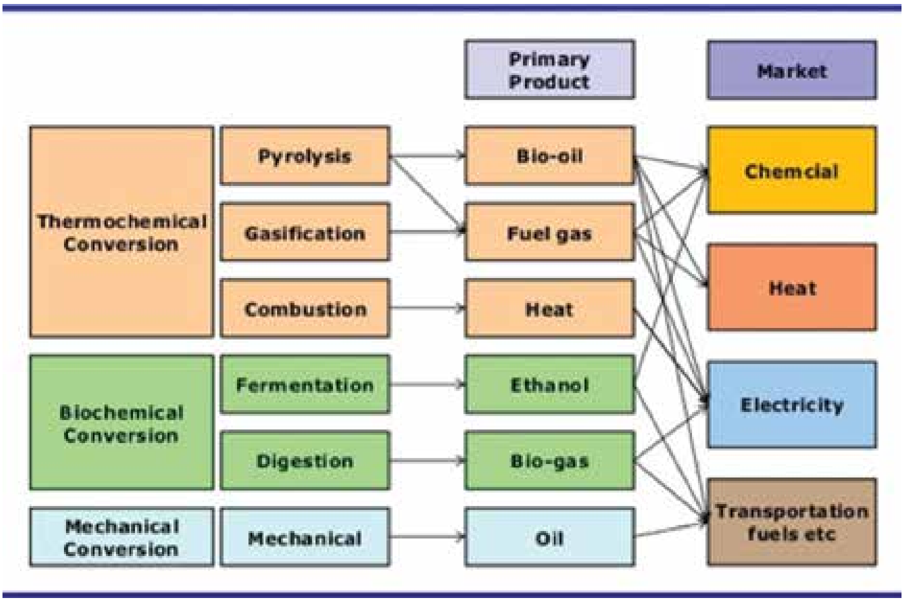


Figure 11. Biomass conversion processes and product.

In gasification procedure, the biomass is thermally decayed at great temperature in O_2 hungry environment to avoid the explosive gas from combustion. This synthesis gas (a mixture of CO_2, CO, CH_4 and H_2) is transformed to a liquid fuel such as synthetic diesel using Fischer-Tropsch technology.

4.2.1.2. Pyrolysis

Pyrolysis method depends on using high temperature in the non-existence of O_2 to transform the biomass into bio-oil. Pyrolysis can be classified as fast, conventional or flash according to the heating rate, particle size, operating condition of temperature and solid seat time. For instance, if bio-oil yield is to be maximized fast, this is required that biomass is heated to 500°C for around 10 second. Pyrolysis temperatures are approximately 475C, where gasification is ready at temperatures fluctuating from 600 to 1100°C.

4.2.2. Biochemical conversion

This process is described as enzymatic hydrolysis in addition to microbial digestion. It includes decomposition of the biomass into hemicellulose, cellulose and lignin and transforming the hemicellulose and cellulose into fermentable sugars, subsequently the use of yeast and specific bacteria to transform the sugar to ethanol. This method needs a pre-treatment stage (steam, ammonia and acid) to decomposition of the biomass into fluid slurry. Use of acid to destroy lignocellulosic fibers can be used also to destroy much of the hemicellulose sugar earlier then can be fermented into ethanol, causing low incomes [59]. Nowadays there are researcher variations and combinations of thermochemical and biochemical pathways for converting biomass into useful energy products.

4.2.2.1. Anaerobic digestion

The natural process is called anaerobic digestion and is the micro-biological conversion of organic matter to CH_4 in the deficiency of O_2. The biochemical transformation of biomass is finished throughout alcoholic fermentation to yield liquid fuels, while fermentation with anaerobic digestion produce biogas (H_2, NH_4, CO_2 and CH_4) generally by four stages that includes hydrolysis, acidogensis, acetogensis and methanogensis). The decomposition is caused by natural bacterial action in different stages and occurs in a variety of natural anaerobic environments including water sediment, waterlogged soils, natural hot springs, ocean thermal vents and the stomachs of various animals.

4.2.2.2. Fermentation and hydrolysis

Some methods permit biomass to be converted into gaseous fuel, for instance, CH_4 or H_2 [60]. One genetic-modified procedure uses bacteria and algae to yield H_2 immediately instead of the usual biotic energy carriers. The second way uses agricultural remains in fermentation for produce biogas. This method is documented and used for waste treatment in a wide range. Lastly, high temperature in gasification supplies a crude gas for the production of hydrogen by a second reaction step. Also in biogas, there is also the opportunity of using the compact by-product as a biofuel. Traditional fermentation plants producing biogas are in routine use, ranging from farms to large municipal plants.

4.2.2.3. Transesterification

Transesterification is a chemical combination of bio-oil with an alcohol (methanol or ethanol) [61]. The resulting biodiesel is an alkyl ester of fatty acid, which contains an alcohol group attached to a single hydrocarbon chain comparable in length to that of diesel (C10H22–C15H32). The transesterification method means biodiesel production [62] in which glycerin is extracted from the fat or vegetable oil [63]. Plants late two products are methyl esters and glycerin that is used in soaps and other products. Transesterification of triglycerides can be improved by using catalysts which are divided in to alkali, acid and enzyme. Alkali-catalyzed transesterification is the best and faster than acid-catalyzed transesterification, so it used commercially [64, 65].

4.3. Challenges and opportunities

Challenges for production of biofuel from microalgae are summarized in these points: (1) microalgae require a large amount of nutrients and CO_2.(2) Low lipid yield high growth or in reverse a high lipid yield with low growth rate.(3)High cost of closed systems and difficult of maintenance of open pond cultivation. (4) Presence of several numbers of steps and high cost methods involved in the oil production in addition an imbalance in an energy cost. (5) Small market-high value co-products. (6) Presence of few commercial cultivating farms, so there is a lack of data on large-scale of cultivation [66].

Opportunities are brief in these topics: (1) heterotrophic and mixotrophic cultivation. (2) Using of super strain and applied of genetic modification. Use of wastewater in algal cultivation and practical biorefineries [66].

4.4. Current status of energy production from algal biomass in Egypt

Egypt depends on a mixture of energy resources; a lot of them are produced from fossil fuel with proportion approximately 98% and depends on other renewable energy sources to cover its needs with percent about 2%. The electricity sector exhausts around 30% from its yield of fossil fuels while industrial needing in Egypt exhausts around 40% from its production. Egypt yield large quantity of fossil fuel represented in natural gas and oil, however, Egypt exhaust the energy severely according to US Energy Information administration, the exhaustion rates of crude oil in Egypt through 2000–2011 are in permanent increasing above the production rates **Figure 12**, but the production rates of natural gas are sufficient or go above its consumption which leads to spread some of its production out of the country [67].

The energy catastrophe in Egypt is liberated from the gap between the accessible energy sources and the exhaustion levels, as the natural gas can not only enough to the growing request of energy in the continuous individuals rise.

So there are two methods to solve the problem of energy in Egypt and succeed the sustainable development which becomes the alarm worldwide:

First: Rationalization of current consumption of energy and improving the efficiency of its use: Industrial Modernization Centre made a study aiming to decrease the energy exhaustion to 20% in 2022 dispersed on several sectors as: 9.4% in industrial division, 5.4% in

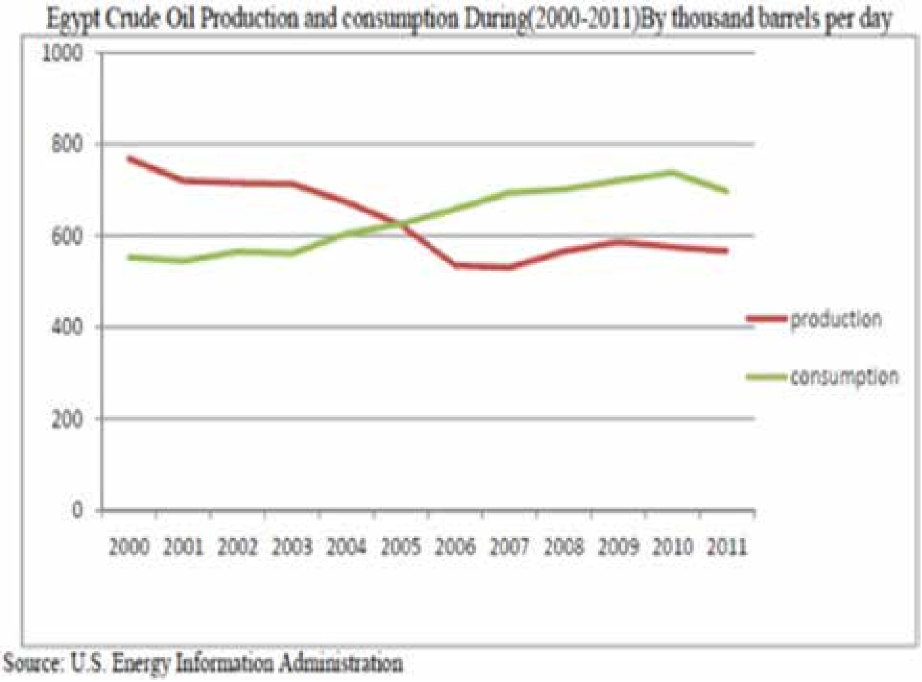


Figure 12. Represent the production and consumption of oil in Egypt during the period (2000–2011).

transportation section, 3% in trade and housing section, 0.45% in governmental and public building, 0.05% in irrigation and agricultural section as well as 2.5% in the natural gas yield.

Second: depending on renewable energy resources: Egypt has a several renewable sources such as solar, wind power and biomass. For this reasons, nowadays, the Egyptian government encourages renewable energy including biomass energy. And there are many attempts for the creation of biofuel from algal biomass. Some researchers in Faculty of Agriculture, Cairo University; Faculty of Science, Alexandria University; Agriculture Research Center; Institute of Petroleum Research and National Research Centre started in production of biodiesel on laboratory scale. Also, there are some projects on production of biodiesel from microalgae in selected Mediterranean Countries" Med-algae project (http://www.med-algae.eu) was done during 2013–2014. It is a new technology project which can contribute to the goals of the European Union (EU) strategy on "Climate change and energy. The project supported by the programme European Neighborhood and Partnership Instrument (ENPI) - Mediterranean Sea Basin Joint Operational Programme. The group consist of 12 organizations: research organizations, academic institutions, energy agencies, private organizations from 6 countries: Italy, Cyprus, Malta, Greece, Lebanon and Egypt represented by the Faculty of Science, Alexandria University and National Research Centre. Final conclusion of the project refers to biodiesel production by *Nannochloropsis* sp. is not practical at the economical level if the alga is employed for just biodiesel production. In order to enhance biodiesel fuel quality, the alga must be subjected to genetic engineering for up-regulation of fatty acid biosynthesis and/or by down-regulation of β-oxidation. However, supplementation of biodiesel with other short-chain fatty acid esters may be a good choice. Economically, the algal biomass must be processed for bio-refinery to maximize its utilization for different applications [68].

5. Conclusion

Microalgae are one of the most effective sources of renewable energy production. Microalgae are contain up to 50:70% protein, 30% lipids, over 40% glycerol, up to 14% carotene and a fairly high concentration of vitamins B1, B2, B3, B6, B12, E, K, D, etc., compared with other plants or animals. Algal industry techniques is integrated process to CO_2 capture, contribute to solve global warming problem and produce valuable byproducts such as lipids (oils), carbohydrates, proteins and various feedstocks that can be converted into biofuels and other useful materials. Microalgae are probable to be an essential raw material for amino acid, vitamin and yields of valuable by-products. The production of microalgae is known to be the more gainful business in the biotechnological process. It is a waste less and environmentally safe. Microalgae are capable of producing oil all year long. Oil productivity of microalgae is greater compared to conventional crops. The oil content of microalgae is in the range of 20–50% which is greater than other competitors. Biodiesel production from algal lipid is non-toxic and highly biodegradable. Microalgae can grow at high rates which can be 50 times more than that of switchgrass, which is the fastest growing terrestrial crop. Microalgae have higher photon conversion efficiency; it is approximately 3–8% against 0.5% for terrestrial plants. Microalgae are an alternative fuel feedstock that could avoid fuel versus food conflict and it can be cultivated in wastewater as a source of nutrients. The costs of algal cultivation and harvest for biofuel production are covered by the wastewater treatment function.

Recommendations

Wide transfer of the algae industry techniques to achieve the greatest benefit from the process of algal cultivation (opened and closed photobioreactor) to produce the economic and required valuable materials (biofuel).

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During the last decades, aquatic resources have been severely depleted due to human-induced factors such as overexploitation and pollution and more recently due to deviations in the physicochemical parameters of oceans, dramatic changes in weather patterns and melting of glaciers. The effects of these man-made factors are occurring in a relatively shorter time scale and, in many cases, are beyond the capacity of organisms to adapt to these deviations. The majority of natural aquatic resources, which are one of the most important food sources on the planet, are being used to the extent that limits their capacity for regeneration. Despite ongoing attempts towards developing strategies for long-term management of aquatic resources all over the world, efforts have met with limited success.

Thus, the sustainable use of aquatic resources has become a very important reality considering a projected human population of 11 billion by the year 2100. With this reality in mind, the purpose of this book is to shed more light on the field of marine ecology by emphasizing the diversity of aquatic life on earth and its importance both as part of a balanced ecosystem and as part of critical source of food on earth.

The book covers important findings, discussions and reviews on a variety of subjects on environmental and competitive interactions of marine organisms at different trophic levels and their effects on the productivity, dynamics and structure of marine ecosystems around the world. Each chapter focuses on a specific case in the field of marine ecology and was written by researchers with years of experience in their respective fields.

We hope that academicians, researchers and students as well as experts and professionals working in the field of marine ecology will benefit from these contributions. We also hope that this book will inspire more studies to help better understand the marine environment and develop strategies to better protect this crucial element of life on earth.

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