

**MODELING THE IMPACT OF FISH AND FISHERIES ON MARINE
BIOGEOCHEMISTRY: A CASE STUDY IN THE SARGASSO SEA**

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IN

**THE DEPARTMENT OF OCEANOGRAPHY
MIDDLE EAST TECHNICAL UNIVERSITY
INSTITUTE OF MARINE SCIENCES**

BY

DENİZ DİŞA

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**A THESIS SUBMITTED TO
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**IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
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Deniz DİŞA

ABSTRACT

MODELING THE IMPACT OF FISH AND FISHERIES ON MARINE BIOGEOCHEMISTRY: A CASE STUDY IN THE SARGASSO SEA

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The ocean has a crucial role in global carbon cycle. Marine ecosystems are responsible for storing the carbon within the ocean body by means of uptaking atmospheric carbon into the ocean, transforming it into organic carbon through photosynthesis and transporting to the profound depths of the ocean. Playing a significant role in the marine food webs, grazing on plankton and providing nutrient to ecosystem by its metabolic activities, fish is thought to have a considerable impact on carbon export. For this reason, having regard to its increasing trend especially after 1950s, fishing is expected to impact carbon cycle directly by changing the fish biomasses. However, how fish impacts the biogeochemistry of marine ecosystems is not known clearly and to be assessed quantitatively.

In this regard, this study aims to analyze the impact of fish and fisheries on marine biogeochemical processes by setting up an end-to-end model that simulates lower and higher tropic levels of marine ecosystems simultaneously. For this purpose, a biogeochemical model, which simulates lower tropic level dynamics (e.g. carbon export, nutrient cycles) and an ecosystem model, which simulates fisheries exploitation and higher tropic level dynamics (e.g. food web) were online and two-way coupled. Simulating the ecosystem from one end to the other with a holistic

approach, the coupled model provided a more realistic representation of the ecosystem. It served as a tool for the analysis of fishing impacts on marine biogeochemical dynamics.

Coupled model resolved the inefficiencies of biogeochemical model, which was because of being “closed” by zooplankton. Results pointed out 56% decrease in the mesozooplankton biomass due to higher trophic level predation. Simulations estimated an approximately 24% increase in the carbon export compared to the biogeochemical model simulations, which had no fish compartment. This increase was due to the change in the plankton compositions and enhanced outflows to detritus. The changes in the lower trophic level dynamics were statistically more consistent with the empirical data.

Moreover, results obtained by applying different fishing intensities indicated that changes in fisheries exploitation levels directly influence the marine nutrient cycles and hence, the carbon export. Depending on the target and the intensity of fisheries, considerable changes in the biogeochemical responses obtained. For example, in the scenario where new potential target mesopelagics harvested in addition to the current fisheries revealed 12% decrease in the carbon export. The same scenario also indicated 11-15% changes in the remineralization flows.

As a result of this study, unlike the models that do not represent the fish explicitly, how marine biogeochemical processes are impacted by the activity of fish assemblages and fisheries exploitation was delineated.

Keywords: Fisheries, Biogeochemistry, Ecosystem Modeling, Carbon Export, End-To-End Modeling

ÖZ

BALIK VE BALIKÇILIĞIN DENİZ BİYOJEOKİMYASI ÜZERİNDEKİ ETKİSİNİN MODELLEME YÖNTEMİYLE İNCELENMESİ: SARGASSO DENİZİNDEN BİR ÖRNEK ÇALIŞMA

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Okyanuslar küresel karbon döngüsü üzerinde önemli bir role sahiptir. Denizel ekosistemler, atmosferden deniz ekosistemi içerisine alınan karbonun fotosentez yolu ile organik maddeye dönüştürülerek okyanusun derin bölgelerine taşınımına ve bu yolla atmosferik karbonun okyanus içerisinde depolanmasına olanak sağlamaktadır. Denizel besin ađı içerisinde yer alan balıkların, planktonlar üzerinden beslenmesi ve metabolik aktiviteleriyle ekosisteme besin sağlamaları sebebiyle karbon taşınımını büyük oranda etkilediđi düşünülmektedir. Bu sebeple özellikle 1950'lerden sonra hızlı bir artış gösteren ve denizel ekosistemler üzerinde gözle görülür deđişimlere sebep olan balıkçılıđın, balık biyokütlelerini deđiştirme yoluyla karbon döngüsünü doğrudan etkilemesi beklense de balıkların denizel ekosistemlerin biyojeokimyası üzerindeki etkisi halen tam olarak ortaya konamamıştır.

Bu çalışmada, balıkçılıkla deđişen balık stoklarının deniz ekosisteminin biyojeokimyası üzerindeki etkisinin öngörülmesini sağlamak amacıyla deniz ekosisteminin alt ve üst trofik seviyelerinin bir arada ve etkileşimli olarak modellenmesi gerçekleştirilmiştir. Bu amaçla, deniz ekosisteminin besin döngüleri, karbon taşınımı, alt trofik seviye canlılarının yaşamsal aktiviteleri gibi unsurlarını simule eden tek boyutlu bir biyojeokimyasal model ile besin ađı, balıkçılık, üst trofik seviye canlıların dinamikleri gibi unsurları simule eden bir denizel ekosistem modeli birleştirilmiştir. Oluşturulan bütünleşik (end-to-end) model deniz ekosistemini en alt seviyeden en üst seviyeye kadar temsil etmesi sebebiyle ekosistemi daha gerçekçi bir

şekilde ele alan bütüncül bir yaklaşım sunmaktadır. Model, balıkçılık baskısının besintuzu döngüsü başta olmak üzere alt trofik seviyelere kadar olan etkisinin analizine imkan sunmaktadır.

Bütünleşik model, biyojeokimsiyal modelin ekosistemi zooplankton seviyesine kadar temsil etmesinden kaynaklanan yetersizliklerin ortadan kalmasını sağlamıştır. Elde edilen sonuçlar üst trofik seviye canlıların beslenme baskısı sebebiyle mezozooplankton biyokütlesinde %56'lık bir azalmayı işaret etmektedir. Ayrıca, bütünleşik model tahminleri, balığı dahil etmeyen biyojeokimyasal modele oranla %24 daha fazla karbon taşınımı göstermektedir. Bu artış, plankton kompozisyonlarındaki değişim ve detritusa giden akışlardaki artışla açıklanabilmektedir. Modellerin birleştirilmesiyle alt trofik seviye dinamiklerinde gerçekleşen değişimler istatistiksel olarak verilere daha başarılı bir şekilde uymaktadır.

Farklı balıkçılık senaryolarının test edilmesiyle elde edilen sonuçlar, değişen balıkçılık baskısının besintuzu döngülerini doğrudan etkilediğini göstermektedir. Bu çalışmanın sonucunda, bu zamana kadar balığın etkisini dahil etmeden geliştirilen biyojeokimyasal modellerden farklı olarak, balıkların denizel ekosistemlerin biyojeokimyası üzerindeki önemli rolü ortaya konmuştur.

Ek olarak, farklı balıkçılık senaryolarının uygulandığı analiz sonuçları balıkçılık baskısının denizel besin döngülerini ve karbon taşınımını doğrudan etkilediğini göstermektedir. Balıkçılığın hedeflediği türlere ve şiddetine göre biyojeokimyasal süreçlerdeki değişimler farklılık göstermektedir. Örneğin, halihazırdaki balıkçılığa ek olarak balıkçılığın potansiyel yeni hedefi olan mezopelajik türlerin avcılığının da eklendiği senaryo karbon taşınımında %12 azalış göstermiştir. Aynı senaryo, remineralizasyon akışlarında %11-15 oranlarında değişimleri ortaya koymaktadır.

Bu çalışmanın bir sonucu olarak, balığı doğrudan dahil etmeyen modellerin aksine, biyojeokimyasal süreçlerin balıkçılık aktiviteleri ve balık kompozisyonlarından nasıl etkilendiği açıklanmıştır.

Anahtar Kelimeler: Balıkçılık, Biyojeokimya, Ekosistem Modellemesi, Karbon Taşınımı, Sondan Sona Modelleme

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1. INTRODUCTION

In recent decades, scientists have started to study the complex interaction of biological, geological and chemical processes through, which materials and energy are exchanged and reused on the Earth. These interrelated processes, known as biogeochemical cycles, operate on timescales ranging from microseconds to eons and spatial scales ranging from the unicellular organism to the entire atmosphere-ocean system. The ocean plays a critical role in the global biogeochemical cycles of a variety of biologically active elements and chemical compounds (e.g. carbon, nitrogen, phosphorus, silicon etc.), which are keys for the regulation of climate, marine biology and chemistry (Sarmiento et al., 2010). The way nutrients cycle can constrain rates of biological processes and influence the structure of the ecosystems.

Human activities such as fossil-fuel combustion, rising atmospheric carbon dioxide, excess nutrient release, agriculture, climate change and pollution have a growing influence on ocean chemistry, both regionally and globally. Major trends observed include a shift in the acid-base chemistry of seawater, reduced subsurface oxygen levels, rising coastal nitrogen levels, and widespread increase in mercury and persistent organic pollutants. Anthropogenic impacts on inorganic carbon, nutrients, and dissolved oxygen are linked and affect biological productivity. Furthermore, they are projected to increase in the future, impacting ocean biota and marine resources negatively (Doney, 2010). Thus, marine biogeochemical dynamics is increasingly linked to the state of ecosystem health, sustainability and climate.

Detecting the temporal trends in ocean biogeochemistry and more definitive assessments of the resulting implications for ocean life and marine resources are the key scientific challenges emerging today (Doney, 2010). To understand the mechanism of how carbon and nutrients (e.g. nitrogen and phosphorus) cycle, underlying processes need to be better clarified.

The biogeochemical state of the sea denotes the cycling and transformations within the ocean, which are governed by biological dynamics, and fluxes across the ocean boundaries with the land, atmosphere, and sea floor (Scott Doney, 2003).

The main external material source terms to the ocean are the river inputs and atmospheric deposition of dust aerosols, and precipitation. On the other side, the main sink terms are the losses to the seafloor through the burial of the small fraction of sinking particulate matter that is not utilized either in the water column or in surface sediments. Ocean upwelling and mixing bring CO₂ and nutrient rich waters from subsurface to the surface and enhances subsurface O₂ levels via ventilation.

Since phytoplankton convert CO₂ and nutrients into particulate organic matter via photosynthesis and release O₂ in the ocean surface, they hold a crucial biogeochemical role. The temperature, light, and limiting nutrients (e.g. nitrogen, phosphorus, iron, and silicon) determine the rate of primary production. Grazing on the phytoplankton and linking primary producers to the rest of the food web, zooplankton have a considerable control over CO₂ and nutrient cycling. Similarly, proceeding upward through the marine food web, all of the organisms encountered (e.g. fish, marine mammals, and marine birds) have a place connected to the marine biogeochemistry. However, there is not enough scientific knowledge about relationship between marine biogeochemistry and higher trophic level organisms, especially the fish assemblages.

1.1.Global Fishing Trends and Impacts on Marine Biogeochemistry

The World's marine fisheries resources are under enormous pressure of fisheries (Pauly et al., 2002). Increases in fishing pressure, especially after the 1950s, caused rapid and widespread population declines of several target and non-target fish species (Worm et al., 2009). The direct consequences of the population declines on the ecosystem such as shifts in biodiversity, change in species dominance and higher variability in fish recruitment (Cury et al., 2008), are a matter of concern. It also has indirect impacts on organisms resulting from the propagation of the direct impacts through the food web. For instance, evolutionary characteristics of populations may be changed due to selectively removal of the larger, fast-growing individuals by fishing. This may lead to irreversible changes in the marine gene pool (Pauly et al., 2002).

Another fishing related change in the marine ecosystems is the simplification of the food webs. The number and the length of the pathways linking fish to the primary producers are reduced as a result of the changes in fish recruitments. Within more diversified food webs, predators can compensate the fluctuation in prey abundances by switching between preys (Pauly et al., 2002). However, in the case of simplified food webs, fluctuations in prey abundances are cascaded to predators.

Playing a significant role in the marine food webs, fish is expected to impact marine biogeochemistry. Being comprised of vital elements (i.e. carbon, nitrogen and phosphorus) and storing them within their body cells, fish form a potential source of nutrient. Mortality of fish contributes to detrital matter, which in turn provide nutrient to ecosystem through remineralization. It also influences nutrient flows through ingestion and release by respiration, excretion, defecation. Moreover, being a predator of plankton, it has a control over plankton biomasses. Changes in food web structure alter zooplankton levels and thus phytoplankton compositions. This affects lower trophic level processes such as primary production and remineralization.

Yet, the role of fishes in the marine biogeochemistry is poorly known and often neglected (Davison et al., 2013). The impacts of fish and fisheries on marine biogeochemistry need to be assessed quantitatively. Therefore, the principal aim of this study is to analyze the impacts of fish and fisheries on marine biogeochemical processes as well the ecosystem by setting up a model that simulates feedback between lower and higher trophic levels of marine ecosystems. In order to assess the direct and indirect effects of fishing on marine ecosystem dynamics, an adequate end-to-end model (whole-of-system model, i.e. models that incorporate dynamics from physics to top predators), which represents the key linkages among ecosystem components from the bottom to the top of the food web can be utilised (Travers et al., 2007). Hence, the first objective of this thesis study is to develop such a tool to investigate the direct and indirect impacts of fish on marine biogeochemical processes. In this way, it is aimed to understand how fishing related changes in food web structure influence marine nutrient cycles, transport of material through food web and lower trophic level dynamics (e.g. primary production).

Until recently, different parts of marine ecosystems have been modeled independently with a research focus on selected components. For instance, several biogeochemical models were developed in order to assess the carbon fluxes in the ocean and to understand plankton dynamics. On the other hand, models developed for fisheries usually focused on economically valuable single species or small groups of species without involving other components of the ecosystem that are coupled with the food web and the effects of abiotic factors (Travers et al., 2007).

From this aspect, end-to-end (E2E) ecosystem modelling approaches differ from earlier models by attempting to represent the entire ecological system (including human components and abiotic environment). E2E models integrate physical and biological processes at different scales; and allows dynamic two-way coupling between ecosystem components. The term coupling is used for the integration of physical models of the abiotic environment, biogeochemical models describing nutrient and plankton dynamics, and models representing higher trophic levels (i.e. fishes, marine birds, mammals and fishery). They implement feedback between ecosystem components. With increased interest in the concept of end-to-end models, the gap between climate modeling and fisheries modeling is closing (Akoglu et al., 2015; Kearney et al., 2012a).

Representing the effects of human activities on living organisms within ocean, ranging from the lowest trophic levels (phytoplankton and zooplankton) to the highest trophic levels (fish, birds and mammals), end-to-end models are expected to provide valuable tools for assessing the effects of fishing on ecosystem dynamics (Travers et al., 2007). With this perspective, in this study, a one-dimensional biogeochemical model involving carbon export and nutrient cycles was online and two-way coupled to a food web model simulating higher trophic level dynamics as well as fisheries exploitation.

1.2. Carbon Export and the Role of Fish

One of the main “services” that the marine ecosystem provides is the carbon export. The ocean has a crucial role in global carbon cycle through storage, transport, and transformation of carbon components. More specifically, marine ecosystems capture

large quantities of inorganic carbon from the atmosphere into the ocean, convert it into organic carbon through photosynthesis and transport to the ocean floor. This process is known as the biological carbon pump (BCP). About 70% of the CO₂ concentration difference over the top 1000 m of the ocean is maintained by biological carbon pump (Davison et al., 2013).

Three factors contribute to the biological pump: the sinking of organic particles through the water column (passive transport), advection and diffusion of dissolved organic matter and the transport of organic material by the vertical migration of animals.

Fish are thought to have a considerable impact on carbon export from the surface to the bottom of the ocean. They contribute to both active and passive transport of carbon through the ocean. They are a source of carbon and impact the carbon balances by their metabolic activities such as excretion and respiration. Considering the role of fish in carbon cycle and having regard to increasing trend of fisheries especially after 1950s, fishing is expected to impact carbon cycle directly through changes in the population structures of the fish communities. Therefore, the second objective of the study is to provide explanations to how carbon export from the surface to the bottom of the ocean is influenced by fish by using the end-to-end model.

1.3. Fishing down the marine food webs: Newly target Mesopelagics

The mean trophic level (TL) of fish landed can indicate the exploitation level of the underlying ecosystems. Within a food web, an organism occupies a niche depending on its size, the anatomy of its mouth and its feeding preferences. TL is a descriptor of this niche, expressing how many steps away an organism is located from the base of marine food webs. Base of the food web including phytoplanktonic and benthic algae and detritus has a TL equal to 1. TL of an organism is calculated from the TLs of its preys. Closer the position to the base of the food web an organism, the lower TL it gets.

Large fishes with higher TL are usually more valuable than smaller fishes with lower TL. Thus, increased landings of fishes with lower TL usually imply a reduction of the abundance of the higher TL species. This shows a shift of mean TL towards lower values and this process is known as ‘fishing down the marine food web’ (Pauly et al., 1998; Pauly et al., 2005).

As a result of depletion of fish stocks with higher TLs, mesopelagic fish community has attracted attention as a potentially harvestable resource (St. John et al., 2016), globally. While a small proportion of mesopelagic fish is considered as suitable for human consumption, they are mainly fished to produce fishmeal for aquaculture and production of nutraceuticals. Mesopelagic fisheries targeting nutraceutical-rich species to meet these demands are a new and emerging concept, convergent with the theme of *BlueGrowth*, which is a long term EU strategy to support sustainable growth in the marine and maritime sectors as a whole.

Mesopelagic fish lives in the twilight zone, at a depth range of 200-1000 meters. Lanternfish (myctophids) dominates this fish community. The global biomass of mesopelagic fish is thought to be high (e.g. 10 billion tones according to the recent estimations (St. John et al., 2016)). However, this estimate is uncertain since mesopelagic fishes remain one of the least investigated components of the open-ocean ecosystem (Irigoiien et al., 2014).

Furthermore, harvesting of mesopelagic fish community could have potential impacts. They contribute to transferring production from plankton to larger predatory fish and to marine mammals and seabirds (Smith et al., 2011). Mesopelagics serve as a food source for higher trophic level organisms such as marine mammals, sharks and tunas (Brophy et al., 2009; Potier et al., 2007). Thus, they impact the biodiversity. Mesopelagics also have an integral role in carbon sequestration (St. John et al., 2016). They contribute to the export of organic carbon from the surface of the ocean, where it is produced, to depth. They also impact the carbon balances by their metabolic activities (e.g. respiration, excretion etc.)

Harvesting of mesopelagic species is not at an industrial scale yet. Before newly target mesopelagics are overexploited, the function of the mesopelagic community in the marine food web and biogeochemical processes needs to be assessed. Thus, the

third objective of this study is to understand the function of mesopelagic fish within biogeochemical processes.

A variety of models exist that integrate upper trophic level dynamics with environmental forcing of marine ecosystems (Fulton et al., 2011; Plagányi, 2007; Travers et al., 2007). Some examples couple biogeochemical–physical models to species-focused individual based or bioenergetics models, such as the SEAPODYM model for tuna (Lehodey et al., 2008) and the NEMURO.FISH model for herring and saury (Megrey et al., 2007). These models are suitable for the analysis of the environmental impacts on the target fish species. However, they do not involve the rest of the organisms in the food web such as the preys, predators and competitors of the target fish species. There are other models, such as Ecopath with Ecosim (Christensen and Walters, 2004), OSMOSE (Shin and Cury, 2001) and ATLANTIS (Fulton et al., 2004) involving various functional groups. In these models, functional groups can respond to the change in environmental variations. However, two way feedback down to the level of primary production or biogeochemistry is not possible (Kearney et al., 2012b).

However, online and two-way coupled model provided by this study can address these shortcomings with a holistic approach. It integrates detailed biogeochemistry of the marine ecosystems with entire food web from nutrients to the mammals and with the fisheries exploitation. Based on its novel structure, the end-to-end model provided is believed to improve our capacity to understand the contribution of fishing effects on observed and future changes.

1.4.Study Area

Although the coupled model scheme proposed in this work is quite generic, for this study Sargasso Sea is selected as study area. The model is parameterized in accordance with the dynamics of the Sargasso Sea. Furthermore, data obtained from Bermuda Atlantic Time Series Study (BATS) station in the Sargasso Sea is used for validation. There exist two main reasons, which make the Sargasso Sea favorable for this study. Firstly, a detailed 1D biogeochemical model developed for this region is available in Middle East Technical University Institute of Marine Science (METU

IMS). Secondly, extensive data provided at BATS enables the investigation of model performance through comparison of results with provided observational data.

Nevertheless, the model can be made applicable to different marine ecosystems through reparameterization.

1.4.1. Location

The Sargasso Sea is an open ocean area located in the North Atlantic Subtropical Gyre bounded by clockwise flows of major ocean currents. The name comes from the pelagic macro-alga *Sargassum* that is ubiquitous in this gyre and surrounding waters (Michaels, 1996). Western and northern boundaries of the Sargasso Sea are formed by the Gulf Stream and the North Atlantic Drift while eastern boundary is formed by the Canary Current. The North Equatorial Current and the Antilles Current form the southern boundary (Figure 1). However, the boundaries of the Sargasso sea is not precise. They vary with the encircling currents (Laffoley et al., 2011).

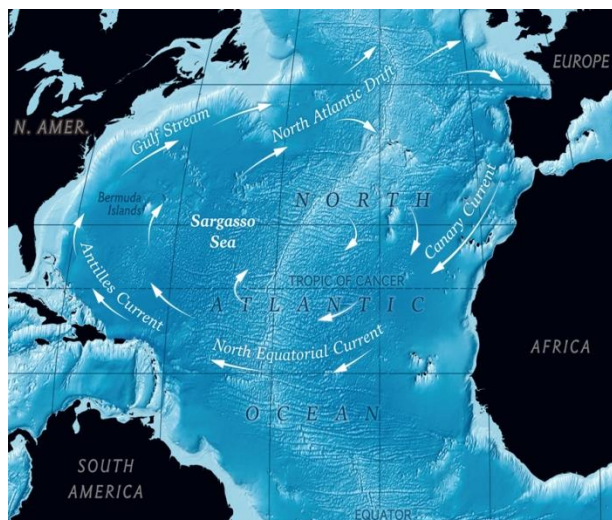


Figure 1 Location of North Atlantic Ocean, Sargasso Sea and Bermuda Islands

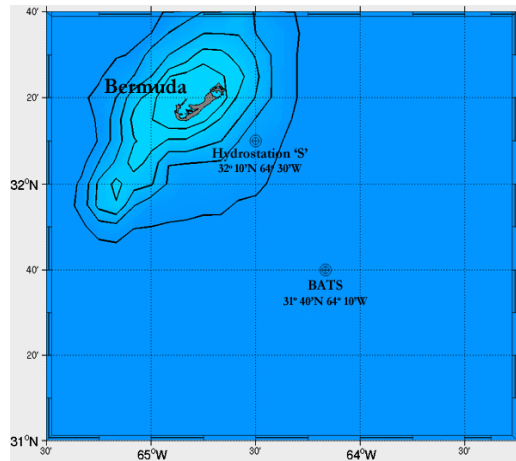


Figure 2 Location of Bermuda Atlantic Time Series Station

The hydrographic and biogeochemical data have been collected at the Bermuda Atlantic Time-Series Study (BATS) site within the Sargasso Sea since 1988. Bermuda lies in the northwest corner of the Sargasso Sea and BATS is situated near the Bermuda Islands, at 31° 40' N and 64° 10' W (Figure 2). It samples the ocean on a biweekly-to-monthly basis and measures the hydrographic, biological and chemical parameters throughout the water column within the Sargasso Sea. BATS provide information for: Chlorophyll-a, nutrients (nitrate, phosphate, silicate), temperature, salinity, primary production, zooplankton biomass and sediment trap (carbon export).

Data procured at BATS aims at highlighting the importance of biological diversity in understanding biological and chemical cycles and resolving the major seasonal and decadal patterns together with interannual variability.

1.4.2. Physical Settings

The BATS region of the Sargasso Sea is characterized by weak geostrophic recirculation of the Gulf Stream with a net flow of less than 5 cm s⁻¹ towards the southwest (Siegel and Deuser, 1997). There are meso-scale eddies throughout this region including cold core rings and smaller cyclonic and anticyclonic eddies (McGillicuddy, 1998; Siegel et al., 1999) (Figure 3). Instantaneous flow rates caused

by these eddies are typically $20\text{-}50\text{ cm s}^{-1}$ in the near-surface waters (Siegel and Deuser, 1997).

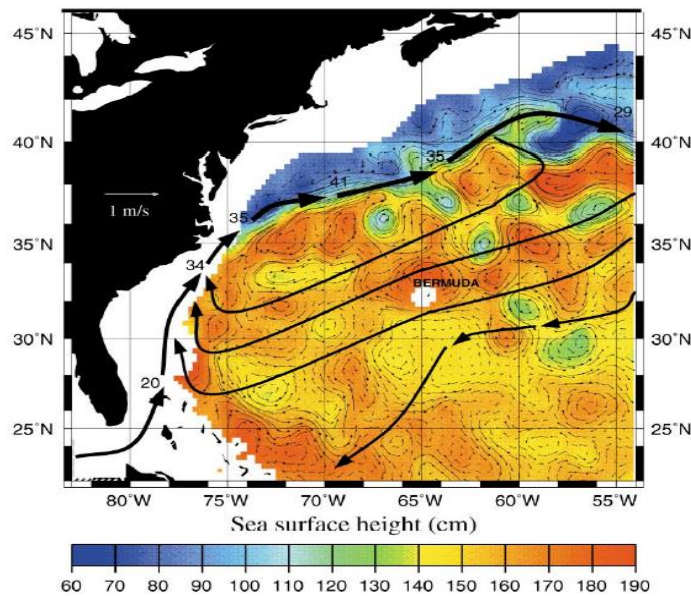


Figure 3 Eddy characteristics and circulation around BATS region

The cold water rings have a cyclonic circulation and can persist for years (Cornillon et al., 1986). In contrast, warm core rings have an anticyclonic circulation that transports the Sargasso Sea water westwards where they eventually join the Gulf Stream. In addition to these rings, there are smaller mode water eddies/lenses of uniform water density that form in midwater and rotate in an anticyclonic direction beneath the surface. These features are collectively referred to as mesoscale eddies and have diameters ranging from 10 to 100 km. The different types of eddies create localized upwelling and downwelling and impact the upper layers of the Sargasso Sea by mixing surface and deeper waters. This affects nutrients, heat and salinity, which together create localized areas of high productivity (Benitez-Nelson and McGillicuddy Jr, 2008; Glover et al., 2002; Volk and Hoffert, 1985) or low productivity (Mouriño-Carballido and McGillicuddy, 2006).

The centre of the gyre is also characterized by a net Ekman downwelling (McClain and Firestone, 1993) with rates of 4 cm day^{-1} near BATS.

Between 31°N latitude and the Gulf Stream there is a region of mode-water (subtropical mode water or 18°C mode water) formation (Talley and McCartney, 1982). This mode-water is created each winter when convective mixing forms deep

mixed layers at a temperature of approximately 18°C (Michaels, 1996). Later it sinks and spreads southward. This region is also associated with nutrient enrichment of the surface layer (Talley and Raymer; Woods and Barkmann, 1986; Worthington, 1976). Between 25°N to 31°N there exist a transition region. From 25°N to the south, a relatively oligotrophic subtropical convergence zone takes place. Here, nutrient-rich mode water underlies the permanently stratified euphotic zone for most of the year (C. Malone et al., 1993; Halliwell Jr et al., 1991; Siegel et al., 1990).

In summers, Bermuda region is under the influence of a large high-pressure system, the Bermuda-Azores high. In the fall and winter, this high pressure system weakens and the storm fronts that move over North America on approximately weekly intervals begin to extend down to Bermuda and further south. The strong winds and cold, dry air associated with these fronts cool and homogenize the surface waters and progressively deepen the mixed layer. North of Bermuda, mixed layers of 400 m occur nearly every year at a temperature near 18°C. On the south of Bermuda, mixed layers rarely extend below the nominal depth of the euphotic zone, i.e. 100-150 m. The mixed-layer depths near Bermuda show a large amount of interannual variability over most of this range, since the island is at the transition between these two regions and it very sensitive to the interannual variations in atmospheric forcing (Michaels, 1996).

BATS station is in an area of strong meridional gradients in seasonality, which influences the biogeochemistry. The weak mixing to the south of Bermuda leads to a permanently stratified water column that has all of the characteristics of an oligotrophic ecosystem throughout the year (Christensen and Walters, 2004).

In the Subtropical Convergence Zone (STCZ) warm and cold water masses meet and create distinct temperature fronts in the upper 150 m of the ocean in the fall to spring seasons (Katz, 1969; Weller, 1991). Two or three bands of these fronts form each year and they are a dynamic seasonal feature of the Sargasso Sea. Water converges from both sides into these fronts causing strong frontal jets or eastward counter currents to form. Because of this convergence, Sargassum weed accumulates at the surface of the fronts forming large rafts of weed, and other organisms also accumulate there. Thus, the fronts are likely important feeding areas for predatory pelagic fishes and migratory marine mammals in the Sargasso Sea. As the surface

waters of the STCZ get warmer in the late spring and summer the frontal zones move further north (Laffoley et al., 2011).

To the north of Bermuda, the deep winter mixed layers result in blooms of larger phytoplankton including diatoms and coccolithophores and a complex transition to oligotrophy in the summer (Siegel et al., 1990). Both of these seasonal patterns can occur at the BATS site depending on the intensity of winter mixing.

1.4.3. Biochemistry

The Sargasso Sea is seasonally oligotrophic. The dominant feature is the spring bloom. Nutrient input coming from winter mixing drives the spring bloom (Dugdale et al., 1961; Ryther and Menzel, 1960). More than half of the total annual new production takes its source from the new production during the spring bloom (Michaels et al., 1994; Doney et al., 1996; Siegel et al., 1999). In this period, eukaryotic pico- and nano-phytoplankton and *Synechococcus* are the dominant phytoplankton groups (DuRand et al., 2001). Diatoms are typically a small component of the phytoplankton biomass in the Sargasso Sea (Lomas and Bates, 2004) and have rarely been found to bloom at the Bermuda Atlantic Time-series Study (BATS), (Steinberg et al., 2001). However higher diatom populations have been observed in summer-time cyclonic and mode-water eddies in this region (McGillicuddy et al., 2007; Sweeney et al., 2003).

In the northern Sargasso Sea, winter convection due to the mixing during strong storm events and eddy activity cause entrainment of additional macronutrients as a nutrient source (Lomas and Bates, 2004). Particularly mesoscale eddies are substantial sources of macronutrients fueling primary production in surface. Nitrogen fixation is another source of DIN to surface waters of the Sargasso Sea (Hood et al., 2001). In the southern Sargasso Sea, on the other hand, winter temperatures do not consistently cool enough to result in overturn. There is little eddy kinetic energy. Thus, water column is stratified. Surface DIN and DIP levels are nearly undetectable throughout the year (Salihoglu et al., 2008). When there is no vertical mixing, nitrogen fixation and atmospheric deposition of DIN are larger sources of DIN to surface waters (Hansell et al., 2004; Hastings et al., 2003). Dissolved organic forms

of N and P (DON and DOP, respectively) are typically at least 90% of the total N and P pools (Cavender-Bares et al., 2001). Although the average carbon to nitrogen to phosphorus ratio (C:N:P) of organic particulate matter is close to the Redfield ratio, selected regions, depths, and seasons vary considerably (Hebel and Karl, 2001). The composition and structure of the food webs could be linked to this local and temporal variation in the elemental composition of particles (Salihoglu et al., 2008). Si is predominantly used by one group of phytoplankton, diatoms, to create silica shell. Model simulating nutrient cycling in the North Atlantic (Lima and Doney, 2004), relates the temporal variability in diatom blooms at BATS to the variations in Si abundance. Mode water eddies mix up particularly high Si (Bibby and Moore, 2011) and cause higher diatom abundances than the absence of eddy activity (Krause and Nelson, 2010).

Sargasso system is highly sensitive to nutrient inputs, which are in turn intimately tied to climate variability and anthropogenic impacts. These factors increasingly influence macronutrient cycling and phytoplankton growth in this region (Lomas et al., 2013).

1.4.4. Productivity and Carbon Sequestration

Although the Sargasso Sea is described as oligotrophic with low macronutrient concentrations, it has a high net annual primary production rate per unit area, which is comparable to the levels found in some of the most productive regions in the global ocean (Lomas et al., 2013). Several factors contribute to this. Sargasso Sea is located in the sub-tropics and has a deep euphotic layer. Primary production is higher than the plankton respiration in the euphotic zone in sub-tropical regions. Integrated annual net primary production over the entire area of the Sargasso Sea is estimated to be some three times higher than in the Bering Sea (Lomas et al., 2013; Steinberg et al., 2001), conventionally referred as one of the World's most productive seas. Secondly, most of the production in the Sargasso Sea is recycled by bacteria (Carlson et al., 1996; Steinberg et al., 2001). Strong eddy characteristics of the region also contribute to the high primary production. As a result of this high primary productivity, the Sargasso Sea plays a key role in the global ocean

sequestration of carbon (Laffoley et al., 2011). In the Sargasso Sea the overall contribution of biological and physical processes to carbon sequestration is approximately equal, but the processes vary seasonally and geographically (Laffoley et al., 2011). Food webstructure and phytoplankton community distribution are important determinants of variability in carbon production and export from the euphotic zone (Salihoglu et al., 2008). The annual carbon cycle in the Sargasso Sea is simply a release of carbon dioxide from the sea surface to the atmosphere in the summer and absorption of carbon dioxide by the ocean during the winter. The overall winter absorption is greater than the summer release because of winter cooling and surface mixing in the northern Sargasso Sea resulting in a strong net sink into the ocean in the winter. The net sink of carbon dioxide in the Sargasso Sea represents ca 7% of the global net biological carbon pump (Lomas and Moran, 2011) and 18 – 58% of the annual North Atlantic carbon sink estimated over the period 1992 – 2006 (Ullman et al., 2009).

2. MATERIAL and METHODS

In this chapter, lower trophic level (LTL) and higher trophic level (HTL) models, which are coupled into an end-to-end model and methods followed in the coupling process are explained.

2.1. Biogeochemical Model: North Atlantic Generic Ecosystem Model

NAGEM is a one-dimensional multi-component lower trophic level ecosystem model that includes detailed algal physiology and nutrient cycles. It was originally designed for the Sargasso Sea to delineate the underlying mechanisms of the time-varying fluxes of carbon in this region (Salihoglu et al., 2008). Later, it was further improved to understand the functioning and magnitude of the biological carbon pump (Yumruktepe, 2016 submitted).

Five phytoplankton algal groups (AG) included as state variables in this model are i) low-light adapted *Prochlorococcus*, ii) high-light adapted *Prochlorococcus*, iii)

Synechococcus, iv) autotrophic eukaryotes and v) large diatoms. They represent the dominant autotrophic biomass in the Sargasso Sea. Algal groups dissociate mainly depending on their sizes. Their dependencies on light and nutrient compositions differ as well (Table 1).

Table 1 Size, pigment and nutrient characteristics of algal groups

Algal Group (AG)	Size (μm)	Pigments	Nutrients
Low Light Adapted <i>Prochlorococcus</i>	~ 0.7	chl <i>a</i> , chl <i>b</i> , PPC	NH ₄ , PO ₄
High Light Adapted <i>Prochlorococcus</i>	~ 0.7	chl <i>a</i> , chl <i>b</i> , PPC	NH ₄ , PO ₄
<i>Synechococcus</i>	~ 1	chl <i>a</i> , PE, PPC	NH ₄ , PO ₄ , NO ₃ ,
Autotrophic Eukaryotes	~ 2.5	chl <i>a</i> , chl <i>c</i> , PSC, PPC	NH ₄ , PO ₄ , NO ₃
Diatom	~ 20	chl <i>a</i> , chl <i>c</i> , PSC, PPC	NH ₄ , PO ₄ , NO ₃ , Si

The chlorophyll a equations are linked to cellular carbon, nitrogen, and phosphorus state equations by variable cellular carbon to chlorophyll a, nitrogen to chlorophyll a, and phosphorus to chlorophyll a ratios (Salihoglu et al., 2008).

Cell quota approach is used to estimate the algal growth and nutrient uptake. Each algal group has separate cellular carbon, nitrogen and phosphorus compartments. Growth limitation is governed by the least available nutrient or energy source (N, P, Si or light).

Zooplankton are divided into two groups depending on their sizes and preys. Microzooplankton represent organisms with a size of less than 200 μm such as phagotrophic protists, and small animals that pass through a 200 μm mesh net. They graze on *Prochlorococcus*'s, *Synechococcus* and autotrophic eukaryotes. Mesozooplankton represent a size range in between 200 μm and 2000 μm , which corresponds mostly to copepods. Mesozooplankton grazes on large phytoplankton (i.e. diatom) and microzooplankton.

There are two detritus groups in the model, slow and fast sinking detritus. Each group has unique sinking and remineralization rates. Slow sinking detritus is smaller in size and highly coupled with the planktonic interactions. It receives input from losses due to non-grazing mortality and unassimilated grazed fraction. Zooplankton mortality is the other input to the slow sinking detritus group. It is easily recycled, suspended or sinking slowly. Fast sinking detritus is formed by aggregation of slow

sinking detritus. It represents the detrital pool of more refractory material. It is assumed to sink faster than the slow sinking detritus.

Remineralization of small and large detritus provides sources for dissolved organic nitrogen (DON) and dissolved organic phosphorus (DOP) pools. Since carbon is not limiting, there is no dissolved organic carbon (DOC) compartment in the model. Dissolution of silicate in the detritus compartment provides a source for silicate, while remineralizations of DON and DOP pools provide sources for NH_4 and PO_4 . Nitrification process is involved in the model as a flow from NH_4 to NO_3 with a constant rate. Biogeochemical model implicitly represents the bacterial activity through remineralization and nitrification processes. Additionally, atmospheric deposition of nitrate and nitrogen fixation are inputs to model. Conceptual diagram of the biogeochemical model is given in Figure 4.

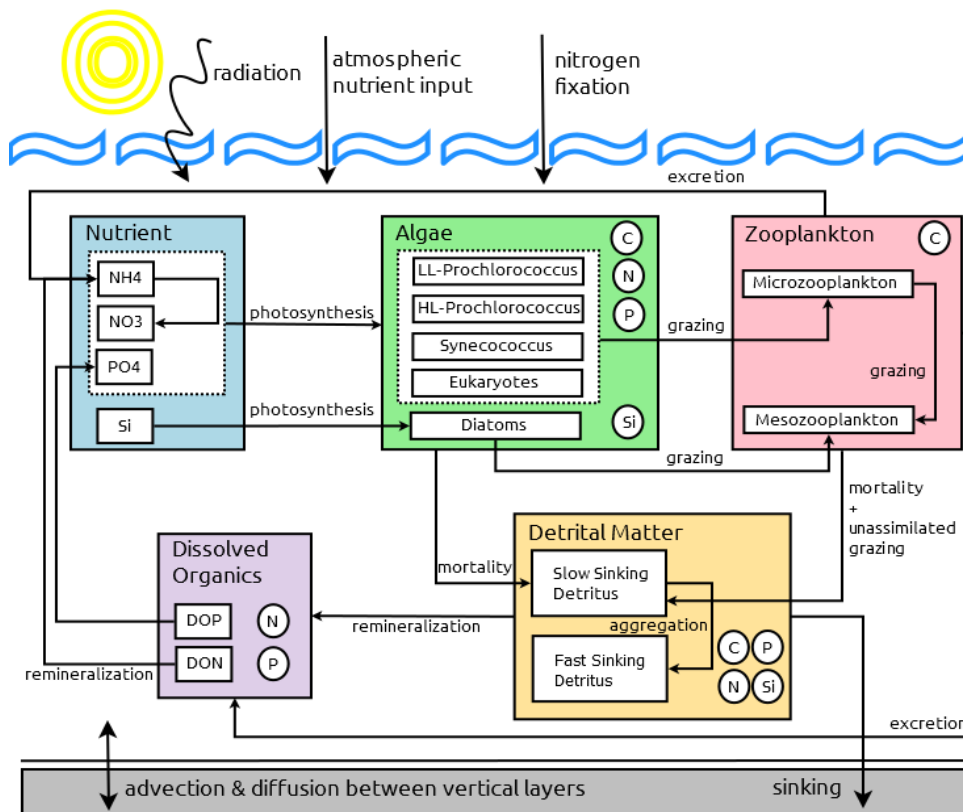


Figure 4 Conceptual diagram of the biogeochemical model (Yumruktepe, 2016 submitted)

NAGEM simulates the water column from surface to the 3000 m depth. It has 3000 vertical layers and each one is 1m. Advection and diffusion between vertical layers are provided as forcing from physical environment.

State equations of the model are listed below.

2.1.1. State Equations

Phytoplankton State Equations:

$$\frac{\partial AG_i}{\partial t} + w \frac{\partial AG_i}{\partial z} - \frac{\partial}{\partial z} K_z \frac{\partial AG_i}{\partial z} = [\min(\mu_{ll_i}, \mu_{nul_i})] AG_i - m_i AG_i - I_{AG_i} Z_{s+l}$$

Terms on the left side represent the changes in each algal group that are produced by local time (t) variations, vertical (z), advection (w), and vertical diffusive flux (K_z), respectively. The right side represents the biological processes including light-limited and nutrient-limited growth, natural mortality, and losses due to microzooplankton and mesozooplankton grazing, respectively.

Zooplankton State Equations:

$$\frac{\partial Z_s}{\partial t} = \sum_{i=1}^4 \lambda^* I_{AG_i} Z_s - I_{Z_s} Z_l - e_s Z_s - m_{z_s} Z_s$$

$$\frac{\partial Z_l}{\partial t} = \lambda^* I_{AG_5} Z_l + \lambda^* I_{Z_s} Z_l - e_l Z_l - m_{z_l} Z_l$$

The terms on the right side of zooplankton state equations are assimilated fraction of ingested phytoplankton biomass, grazing on microzooplankton by mesozooplankton, excretion, and mortality, respectively.

Nutrient State Equations:

$$\frac{\partial NH_4^+}{\partial t} = \sum_{i=1}^5 (-\rho_{NH_4^+}) - nitr + 0.5e_s Z_s \left(\frac{N}{C}\right)_{Z_s} + 0.5e_l Z_l \left(\frac{N}{C}\right)_{Z_l} + c_a DON$$

The biological processes involved in the ammonium state equation are uptake by each algal group, nitrification, excretion by microzooplankton, excretion by mesozooplankton, and remineralization of DON. The particulate carbon pools of each zooplankton group are converted to a nitrogen equivalent using a nitrogen to carbon ratio for each group to estimate the amount of nitrogen in the excretion.

$$\frac{\partial \text{NO}_3^-}{\partial t} = - \sum_{i=3}^5 \rho_{\text{NO}_3^- i} + \text{nitr} + \delta(z)(\text{FN} + \text{Nfix})$$

The first term on the right hand side of the nitrate state equation is nitrate uptake by each phytoplankton algal group. Second term corresponds to the nitrification, which transfers ammonium to nitrate at a constant rate. The last term is the atmospheric deposition of nitrate and nitrogen fixation.

$$\frac{\partial \text{PO}_4^{3-}}{\partial t} = - \sum_{i=1}^5 \rho_{\text{PO}_4^{3-} i} + c_p \text{DOP}$$

The only biological loss term for phosphate is uptake by each phytoplankton algal group, biological gain term is remineralization of DOP.

$$\frac{\partial \text{Si}}{\partial t} = -\rho_{\text{Si}_5} + c_{\text{Si}} \text{De}_l \text{Si}$$

The loss term for silicate is uptake by algal group 5 (i.e. diatoms). The gain term is dissolution of large detritus.

Dissolved Organic Matter (DOM) State Equations:

$$\frac{\partial \text{DON}}{\partial t} = 0.5e_s Z_s \left(\frac{\text{N}}{\text{C}} \right)_{Z_s} + 0.5e_l Z_l \left(\frac{\text{N}}{\text{C}} \right)_{Z_l} + c_{\text{DON}} \text{De}_s + c_{\text{DON}} \text{De}_l - c_a \text{DON}$$

$$\frac{\partial \text{DOP}}{\partial t} = e_s Z_s \left(\frac{\text{P}}{\text{C}} \right)_{Z_s} + e_l Z_l \left(\frac{\text{P}}{\text{C}} \right)_{Z_l} + c_{\text{DON}} \text{De}_s + c_{\text{DON}} \text{De}_l - c_a \text{DOP}$$

The biological processes represented in DON state equation are excretion by microzooplankton, excretion by mesozooplankton, remineralization of small detrital nitrogen, remineralization of large detrital nitrogen, and remineralization of DON, respectively. The particulate carbon pools of each zooplankton group are converted to a nitrogen equivalent using nitrogen to carbon ratio for each group to estimate the amount of nitrogen in the excretion.

The DON and DOP equations are very similar to each other, the only difference being that half of the zooplankton excretion joins the DON pool, whereas all the excreted phosphorus enters the DOP pool. The other half of the zooplankton excretion directly joins the ammonium.

Detritus State Equations:

$$\begin{aligned} \frac{\partial \text{De}_s}{\partial t} + (w + sc_{\text{des}}) \frac{\partial \text{De}_s}{\partial z} - \frac{\partial}{\partial z} K_z \frac{\partial \text{De}_s}{\partial z} = & \sum_{i=1}^5 [m_i P_i] + \sum_{i=1}^4 (1 - \lambda^*) I_{P_i} Z_s \\ & + m_{Z_s} Z_s + (1 - \lambda^*) (I_{P_5} + I_{Z_s}) Z_l \\ & + m_{Z_l} Z_l - c_c \text{De}_s - \text{aggDe}_s \end{aligned}$$

Three terms on the left side represent physical processes. It is assumed that slow sinking detritus sinks at a constant rate (sc_{des}). The right side of slow sinking detritus state equation represents the biological processes including the death and unassimilated grazed fraction of algal groups, mortality of microzooplankton, unassimilated fraction of microzooplankton biomass that are grazed by mesozooplankton, mortality of mesozooplankton, remineralization of slow sinking detritus and aggregation of slow sinking detritus into fast sinking detritus, respectively.

$$\frac{\partial \text{De}_l}{\partial t} + (w + sc_{\text{del}}) \frac{\partial \text{De}_l}{\partial z} - \frac{\partial}{\partial z} K_z \frac{\partial \text{De}_l}{\partial z} = \text{aggDe}_s - c_c \text{De}_l$$

Left hand side of the fast sinking detritus state equation is similar to the slow sinking detritus state equation. The only source term is at the right hand side is the

aggregation of slow sinking detritus into fast sinking detritus and the only sink term is the remineralization of fast sinking detritus.

2.2. Food Web Model: Ecopath with Ecosim-FORTRAN

Ecopath with Ecosim (EwE) is an ecological modelling software package designed for straightforward construction, parameterization and analysis of dynamic trophic models (Christensen and Walters, 2004; Christensen et al., 2005). EwE is freely available and widely used all over the world mainly for estimating biomass and food consumption of the elements (species or groups of species) of an aquatic ecosystem. It allows dynamic representation of complex interactions within a food web.

EwE has three main components: **Ecopath** – a static, mass-balanced snapshot of the system; **Ecosim** – a time dynamic simulation module; and **Ecospace** – a spatial and temporal dynamic module.

EwE is written for the Microsoft.NET framework. Although EwE has the capability of serving as a platform, which supports the ecosystem approach, it is limited with the software's ability to integrate with other models written in FORTRAN language. Thus, aiming at enabling setting-up integrated end-to-end (E2E) modelling schemes; EwE was later recoded in FORTRAN (Akoglu et al., 2015). In this study, FORTRAN version of the EwE (hereinafter called EwE-F) is used for coupling.

EwE-F includes only Ecopath (Ecopath-F) and Ecosim (Ecosim-F) modules. These modules are explained below.

2.2.1. Ecopath

The Ecopath module produces a snapshot of the ecosystem at steady state. Based on satisfying two master equations explained below, it provides mass and energy balances of each group within the food web. Mass balance is ensured by calculation of source and sink terms. Prey-predator relationships within the food web and fisheries impact are taken into account.

First Equation:

$$B_i \times \left(\frac{P}{B}\right)_i - \sum_{j=1}^n B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ji} - B_i \times \left(\frac{P}{B}\right)_i \times (1 - EE_i) - Y_i - E_i - BA_i = 0$$

Production
Predation Mortality
Other Mortality

Fisheries Mortality
 Net Emigration
 Biomass Accumulation

where, for each functional group i , B stands for biomass, (P/B) stands for the production rate per unit of biomass, (Q/B) stands for the consumption rate per unit of biomass of predator j , DC_{ji} is the fraction of prey i in the average diet of predator j , Y is the landings, E is net emigration rate, and BA is the biomass accumulation rate (Christensen et al., 2005). EE is the ecotrophic efficiency representing the proportion of mortality of a group that is not attributable to predators or fishing activities.

First equation indicates the conservation of mass. For each group, difference between mass in and out is equal to change in mass. That is, produced amount is either lost by mortality (predation, fishery or other mortalities such as mortality due to old age, diseases, etc.) or lost by net emigration to out of the system (if this term is negative, then there is mass gain into the system) or accumulated as biomass.

Second Equation:

Consumption = production + respiration + unassimilated food

This equation is based on the principle of conservation of energy within a group. Energy balance is ensured within each group.

As input, Ecopath requires at least three of the following four input parameters included in the first equation: biomass, production/biomass ratio (or total mortality), consumption/biomass ratio, and ecotrophic efficiency for each of the functional groups. Here, the ecotrophic efficiency corresponds to the proportion of the

production that is used in the system. Ecopath sets up a series of linear equations to solve for unknown values establishing mass-balance. If all four basic parameters are available, biomass accumulation or net migration can be estimated for that group.

2.2.2. Ecosim

Ecosim provides a dynamic simulation capability at the ecosystem level. It inherits mass balanced representation of the system from Ecopath and uses it as initial condition. Based on the differential equation given below Ecosim provides time dynamic simulation.

Differential Equation:

$$\frac{dB_i}{dt} = \gamma_i \cdot \sum_{j=1}^n Q_{ji} - \sum_{j=1}^n Q_{ij} + I_i - (M_i + F_i + e_i) \cdot B_i$$

where dB_i/dt is the rate of change of biomass (B) of group i over time t , γ is the growth efficiency of group i , $\sum Q_{ji}$ is the sum of the consumptions of group i over all of its preys, $\sum Q_{ij}$ is the sum of the predation on group i by all of its predators, I is the immigration, M is the non-predation mortality, F is the fisheries mortality and e is the emigration rate of group i (Walters et al., 1997).

Ecosim can be operated under the influence of forcing functions such as fishing mortalities and/or efforts or changes in primary productivity.

2.3. Coupled Scheme

Coupled scheme of the models was designed in a way that lower trophic part of the ecosystem (up to zooplankton) was represented by the biogeochemical model and higher trophic part of the ecosystem (starting from fish) was represented by the food web model. For this purpose, state variables that already existed in the biogeochemical model were removed from the food web model. Later, new linkages

were established between food web and biogeochemical models. For each time step and for each depth, both of the models give feedback to each other. By this way, an online and two-way coupled model scheme was set up.

Harmonization steps are explained in two steps.

Step 1. Removal of LTL groups from the food web model

By (Vasconcellos, 2004), six Ecopath models were constructed representing oceanic ecosystems of the North, Central and South Atlantic for the 1950s and the late 1990s (1997-1998). Ecopath parameterization of North Atlantic ecosystem for the late 1990s is used as a base for the food web model. In the model, there exist 37 groups. 31 of them are regarded as HTL groups (i.e. fish, birds and mammals) while the rest (i.e. bacteria, plankton and detritus) are regarded as LTL groups (Figure 5).

Input parameters of the North Atlantic model for the late 1990s.

	B (kg·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE	Landings (kg·km ⁻²)
Baleen whales	24.634	0.020	4.394		0.000
Toothed whales	51.144	0.020	6.689		0.000
Beaked whales	0.536	0.020	8.806		0.000
Seabirds	0.204	0.078	72.779		0.000
Pelagic sharks		0.390	10.000	0.9	1.731
Yellowfin	0.015	1.050	15.530		0.005
Bluefin	2.030	0.500	4.000		0.731
Skipjack	0.463	1.350	19.610		0.162
Albacore	0.000	0.800	9.600		0.000
Bigeye	26.944	0.750	17.160		9.430
Swordfish	0.059	0.700	4.000		0.030
Billfishes	0.051	0.404	4.690		0.010
Large planktivorous fish		0.112	1.800	0.1	0.006
Large epipelagic fish	2.204	0.690	8.938		0.661
Medium epipelagic fish		1.080	7.671	0.9	15.909
Small epipelagic fish		2.053	12.549	0.9	0.017
Large mesopelagic fish		0.150	3.550	0.9	0.000
Small mesopelagic fish	1724.369	1.983	18.250		0.000
Small bathypelagic fish		1.040	3.650	0.9	0.000
Medium bathypelagic fish		0.190	0.290	0.9	0.000
Large bathypelagic fish		0.270	0.490	0.9	0.662
Small bathydemersal fish slope	45.054	0.345	0.628		21.619
Large bathydemersal slope	53.246	0.175	0.318		10.519
Small bathydemersal abyss	121.430	0.378	0.687		0.000
Large bathydemersal abyss	189.631	0.209	0.380		0.000
Small squids		4.600	36.500	0.9	0.163
Large squids		4.600	36.500	0.9	0.000
Benthic cephalopods		1.150	2.300	0.9	0.000
Meiobenthos	1234.000	2.250	22.650		0.000
Macrobenthos	545.000	1.000	9.850		0.000
Megabenthos	493.000	1.100	6.700		0.000
Heterotrophic bacteria	28167.000	18.450	25.000		0.000
Small zooplankton shalow	118184.639	17.300	57.700		0.000
Large zooplankton shalow	7377.317	8.700	29.000		0.000
Small zooplankton deep	46164.009	17.300	57.700		0.000
Large zooplankton deep	1392.264	8.700	29.000		0.000
Phytoplankton	13500.000	259.274			0.000
Detritus					0.000

31 HTL groups

7 LTL groups

Figure 5 List of organisms and parameters used in the Ecopath model constructed by Vasconcellos et al., (2004)

Since in the coupled model LTL dynamics are represented by the biogeochemical model in a detailed way, six LTL groups were removed from the Ecopath model. Instead, LTL groups and their ecological parameters inherited from biogeochemical model were entered to the Ecopath.

Ecopath model of the coupled scheme has 31 HTL groups (i.e. fish, birds and mammals). Although they have lower TL, benthic organisms, which are crucial for ecosystem functioning are kept in the HTL groups since biogeochemical model does not include them. The remaining eleven (two zooplankton, five algal groups, two detritus, DOP and PO₄) comes from NAGEM and stands for LTL groups (Figure 6).

Input parameters of the North Atlantic model for the late 1990s.

	B (kg·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE	Landings (kg·km ⁻²)
Baleen whales	24.634	0.020	4.394		0.000
Toothed whales	51.144	0.020	6.689		0.000
Beaked whales	0.536	0.020	8.806		0.000
Seabirds	0.204	0.078	72.779		0.000
Pelagic sharks		0.390	10.000	0.9	1.731
Yellowfin	0.015	1.050	15.530		0.005
Bluefin	2.030	0.500	4.000		0.731
Skipjack	0.463	1.350	19.610		0.162
Albacore	0.000	0.800	9.600		0.000
Bigeye	26.944	0.750	17.160		9.430
Swordfish	0.059	0.700	4.000		0.030
Billfishes	0.051	0.404	4.690		0.010
Large planktivorous fish		0.112	1.800	0.1	0.006
Large epipelagic fish	2.204	0.690	8.938		0.661
Medium epipelagic fish		1.080	7.671	0.9	15.909
Small epipelagic fish		2.053	12.549	0.9	0.017
Large mesopelagic fish		0.150	3.550	0.9	0.000
Small mesopelagic fish	1724.369	1.983	18.250		0.000
Small bathypelagic fish		1.040	3.650	0.9	0.000
Medium bathypelagic fish		0.190	0.290	0.9	0.000
Large bathypelagic fish		0.270	0.490	0.9	0.662
Small bathydemersal fish slope	45.054	0.345	0.628		21.619
Large bathydemersal slope	53.246	0.175	0.318		10.519
Small bathydemersal abyss	121.430	0.378	0.687		0.000
Large bathydemersal abyss	189.631	0.209	0.380		0.000
Small squids		4.600	36.500	0.9	0.163
Large squids		4.600	36.500	0.9	0.000
Benthic cephalopods		1.150	2.300	0.9	0.000
Meiobenthos	1234.000	2.250	22.650		0.000
Macrobenthos	545.000	1.000	9.850		0.000
Megabenthos	493.000	1.100	6.700		0.000
Mesozooplankton	0.015	182.000	365.000		0.000
Microzooplankton	0.022	182.000	365.000		0.000
LL prochlorococcus	0.005	34.500	34.500		0.000
HL prochlorococcus	0.017	91.300	91.300		0.000
Synechococcus	0.030	128.000	128.000		0.000
A. Eukaryotes	0.092	91.300	91.300		0.000
Diatom	0.120	27.400	27.400		0.000
PO ₄	1.164	259.2744			0.000
DOP	0.529				0.000
Fast Sinking Detritus	0.011				0.000
Slow Sinking Detritus	0.182				0.000

HTL groups
from food web
model

LTL groups
from
biogeochemical
model

Figure 6 List of organisms and parameters used in the Ecopath part of the coupled model

Standalone NAGEM was run for 4 years after 10 years spinning up. Ecopath parameters of LTL groups were derived from the last year's outcome of this run. The depth integrated time averaged values of the state variables were entered to Ecopath as biomass input. For plankton, total mortalities were entered as production/biomass ratios. For algal groups, total mortality corresponds to the sum of natural mortality and grazing by zooplankton while for zooplankton there is one mortality term. Consumption/biomass ratio is the third input entered. For algal groups, nutrient (PO_4) uptakes were calculated to reflect consumption whilst the grazing is the consumption term for zooplankton.

Diet composition was also revised. Small zooplankton shallow and small zooplankton deep groups were consolidated and obtained values were entered to diet matrix as microzooplankton diet composition input. Similarly, for diet composition of mesozooplankton, large zooplankton shallow and large zooplankton deep groups were consolidated. In the model provided by (Vasconcellos, 2004), while most of the HTL groups predated on zooplankton, there also existed some fish groups (e.g. large planktivorous fish, small epipelagic fish and medium epipelagic fish) predated on phytoplankton. In the coupled Ecopath model, HTL predation on phytoplankton was equally distributed to diatoms and autotrophic eukaryotes.

Since bacterial activity was implicitly involved in the biogeochemical model, heterotrophic bacteria were removed from the system.

HTL groups and plankton were introduced to Ecopath as consumers while the rest was introduced as detritus.

The final input parameters for the Ecopath model are given in Table 2.

Table 2 Input parameters of the Ecopath part of the coupled model

Group Name	Biomass	Production / Biomass	Consumption / Biomass	Ecotrophic Efficiency	Unassimil. / Consumption
Baleen whales	2.20E-04	2.28E-06	5.02E-04		2.00E-01
Toothed whales	4.57E-04	2.28E-06	7.64E-04		2.00E-01
Beaked whales	4.79E-06	2.28E-06	1.01E-03		2.00E-01
Seabirds	1.83E-06	8.96E-06	8.31E-03		2.00E-01
Pelagic sharks		4.45E-05	1.14E-03	9.00E-01	2.00E-01
Yellowfin	1.35E-07	1.20E-04	1.77E-03		2.00E-01
Bluefin	1.81E-05	5.71E-05	4.57E-04		2.00E-01
Skipjack	4.14E-06	1.54E-04	2.24E-03		2.00E-01
Albacore	1.59E-09	9.13E-05	1.10E-03		2.00E-01
Bigeye	2.41E-04	8.56E-05	1.96E-03		2.00E-01
Swordfish	5.29E-07	7.99E-05	4.57E-04		2.00E-01
Billfishes	4.52E-07	4.61E-05	5.35E-04		2.00E-01
Large Plank. fish		1.28E-05	2.06E-04	1.00E-01	2.00E-01
Lg. Epi. fish		7.88E-05	1.02E-03	9.00E-01	2.00E-01
Md. Epi. fish		1.23E-04	8.76E-04	9.00E-01	2.00E-01
Sm. Epi. fish		2.34E-04	1.43E-03	9.00E-01	2.00E-01
Lg. Meso fish		1.71E-05	4.05E-04	9.00E-01	2.00E-01
Sm. Meso fish	1.54E-02	2.26E-04	2.08E-03		2.00E-01
Sm. Bathyp. fish		1.19E-04	4.17E-04	9.00E-01	2.00E-01
Md. Bathyp. fish		2.17E-05	3.31E-05	9.00E-01	2.00E-01
Lg. Bathyp. fish		3.08E-05	5.59E-05	9.00E-01	2.00E-01
Sm. Bathyd. slp		3.94E-05	7.17E-05	9.00E-01	2.00E-01
Lg. Bathyd. slp	4.76E-04	1.99E-05	3.63E-05		2.00E-01
Sm. Bathyd. Abs	1.09E-03	4.31E-05	7.84E-05		2.00E-01
Lg. Bathyd. Abs	1.70E-03	2.39E-05	4.34E-05		2.00E-01
Sm Squids		5.25E-04	4.17E-03	9.00E-01	2.00E-01
Lg Squids		5.25E-04	4.17E-03	9.00E-01	2.00E-01
Benth. ceph.		1.31E-04	2.63E-04	9.00E-01	2.00E-01
Meiobenthos	1.10E-02	2.57E-04	2.59E-03		2.00E-01
Macrobenthos	4.87E-03	1.14E-04	1.12E-03		2.00E-01
Megabenthos	4.41E-03	1.26E-04	7.65E-04		2.00E-01
Large Zoop.	1.50E-02	2.08E-02	4.17E-02		3.00E-01
Small Zoop.	2.20E-02	2.08E-02	4.17E-02		3.00E-01
LL Prochloro	5.10E-03	3.93E-03	3.93E-03		0.00E+00
HL Prochloro	1.66E-02	1.04E-02	1.04E-02		0.00E+00
Syenoco	3.00E-02	1.46E-02	1.46E-02		0.00E+00
Aut. Eukaryotes	9.21E-02	1.04E-02	1.04E-02		0.00E+00
Diatom	1.20E-01	3.13E-03	3.13E-03		0.00E+00
PO ₄	1.16E+00	2.59E+02			
DOP	5.29E-01				
Large Detritus	1.12E-02				
Small Detritus	1.82E-01				

Step 2. Setting up Linkages

Mass balanced output of the Ecopath-F constituted the initial conditions for the Ecosim-F. Ecosim-F was integrated into the biogeochemical model as a module. Given the Ecopath-F results as inputs to the coupled model, at each time step, Ecosim-F was called for HTL group as a box model and depth integrated flows affecting LTL dynamics were calculated.

Biogeochemical and fisheries models can be coupled into an end-to-end model with respect to the main processes linking lower and higher trophic levels of the ecosystem (Figure 7). The main linking process is predation, which affects the growth of predators and the mortality of the prey. Additionally, HTL mortality, excretion and egestion transfer material back to LTL. These transferred materials contribute to the detritus, nutrient pools and bacterial pool of LTL models (Cury et al., 2008).

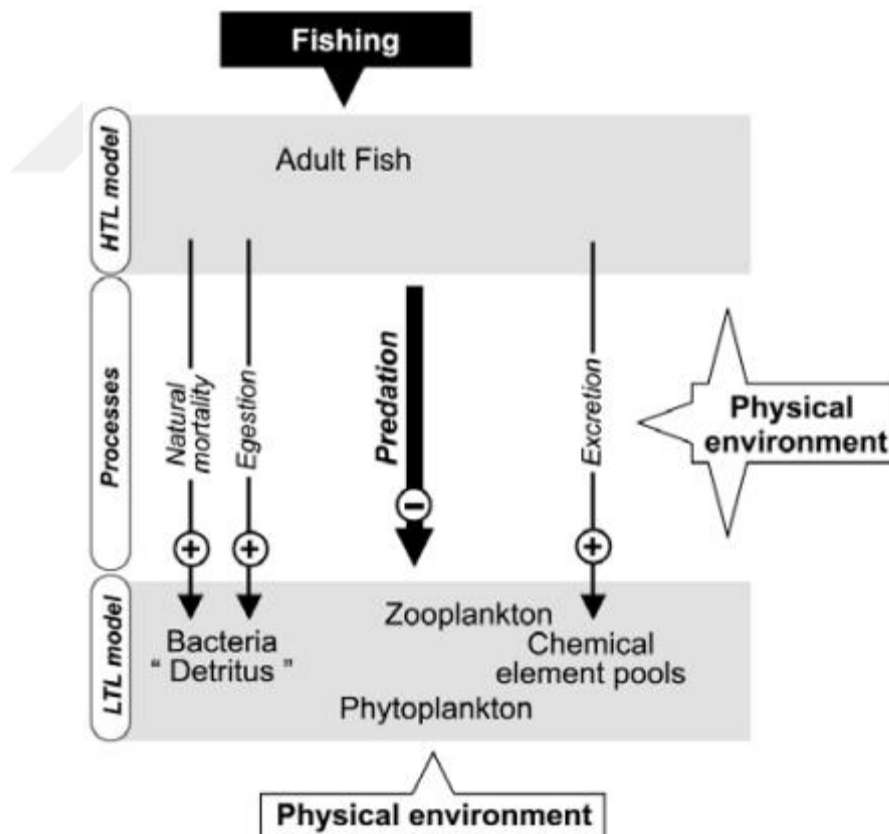


Figure 7 The process of coupling a LTL model with a HTL model, from from Shin et al. (2010)

In this study, there are 5 processes linking HTL and LTL models. They are the predation of HTL groups on LTL groups, excess nutrient exudated from HTL groups depending on the cellular nutrient ratios, excretion of HTL groups, mortality of HTL groups and unassimilated part of the food consumption by HTL groups.

Predation:

HTL groups are predating on zooplankton, diatom and autotrophic eukaryotes. Thus, HTL predation was added to their state equations as sink terms.

$$\frac{\partial Z_s}{\partial t} = \sum_{i=1}^4 \lambda^* I_{AG_i} Z_s - I_{Z_s} Z_l - e_s Z_s - m_{z_s} Z_s - \sum_{j=1}^{31} \mathbf{Pred} Z_{s_j}$$

$$\frac{\partial Z_l}{\partial t} = \lambda^* I_{AG_5} Z_l + \lambda^* I_{Z_s} Z_l - e_l Z_l - m_{z_l} Z_l - \sum_{j=1}^{31} \mathbf{Pred} Z_{l_j}$$

$$\frac{\partial AG_i}{\partial t} + w \frac{\partial AG_i}{\partial z} - \frac{\partial}{\partial z} K_z \frac{\partial AG_i}{\partial z} = [\min(\mu_{ll_i}, \mu_{nul_i})] AG_i - m_i AG_i - I_{AG_i} Z_{s+l} - \sum_{j=1}^{31} \sum_{l=1}^5 \mathbf{Pred} AG_{ij}$$

Excess amount of cellular nutrients and excretion:

Fish has a cellular nutrient (C:N:P) ratio around 88.5:16:1 (Sterner and George, 2000). Depending on this ratio, excess amount of cellular nitrogen and phosphorus are assumed to be released to DOP and DON pools at each time step. Additional source for DON and DOP pools are the excretion of HTL groups. Thus, state equations of DON and DOP were modified accordingly.

$$\frac{\partial \text{DON}}{\partial t} = 0.5e_s Z_s \left(\frac{\text{N}}{\text{C}}\right)_{Z_s} + 0.5e_l Z_l \left(\frac{\text{N}}{\text{C}}\right)_{Z_l} + c_{\text{DON}} \text{De}_s + c_{\text{DON}} \text{De}_l - c_a \text{DON} + \sum_{j=1}^{31} \text{ExcN}_j + \sum_{j=1}^{31} \text{ExuN}_j$$

$$\frac{\partial \text{DOP}}{\partial t} = e_s Z_s \left(\frac{\text{P}}{\text{C}}\right)_{Z_s} + e_l Z_l \left(\frac{\text{P}}{\text{C}}\right)_{Z_l} + c_{\text{DON}} \text{De}_s + c_{\text{DON}} \text{De}_l - c_a \text{DOP} + \sum_{j=1}^{31} \text{ExcP}_j + \sum_{j=1}^{31} \text{ExuP}_j$$

Mortality and unassimilated part of the food consumption:

Similar to the plankton, when HTL groups die, they go to slow sinking detritus. Unassimilated fraction of food consumption of HTL groups goes to slow sinking detritus compartment as well.

$$\begin{aligned} \frac{\partial \text{De}_s}{\partial t} + (w + sc_{\text{des}}) \frac{\partial \text{De}_s}{\partial z} - \frac{\partial}{\partial z} K_z \frac{\partial \text{De}_s}{\partial z} = & \sum_{i=1}^5 [m_i \text{P}_i] + \sum_{i=1}^4 (1 - \lambda^*) I_{\text{P}_i} Z_s \\ & + m_{Z_s} Z_s + (1 - \lambda^*) (I_{\text{P}_5} + I_{Z_s}) Z_l \\ & + m_{Z_l} Z_l - c_c \text{De}_s - \text{aggDe}_s \\ & + \sum_{j=1}^{31} \text{M}_j + \sum_{j=1}^{31} \text{Unass}_j \end{aligned}$$

After 10 years spinning up, LTL part of the coupled end-to-end model ran for the years 1996-1999 in line with the HTL part of the model, which was parameterized for late 1990s.

In the coupled scheme, Ecosim is dimensionless and runs as a box model. For this reason, depth integrated HTL calculations needed to be distributed to the water column in order to be linked with one dimensional biogeochemical model. Considering that organisms mainly live within the upper 250 meters of the oligotrophic Sargasso Sea and fish is capable of travelling 250 meters in one hour (Davison et al., 2013), at each time step (i.e. one hour), HTL calculations were equally distributed to the first 250 meters of the water column.

2.4. Numerical Integration

Originally, EwE-F uses 4th Order Runge-Kutta method to solve ordinary differential equations, whilst NAGEM equations are solved with Crank-Nicolson method. Crank-Nicolson method can be written as an implicit Runge-Kutta method. While, explicit Runge-Kutta methods have small absolute stability region, implicit Runge-Kutta methods have the form stable over a wide range of time steps, sometimes unconditionally. This issue is especially important in the solution of partial differential equations. For this reason, in the coupled model, all of the state equations are solved with Crank-Nicolson method.

2.5. Scenarios

In order to understand how biogeochemistry of the ecosystem is impacted by the fisheries, various scenarios were tested. The coupled model was run under three scenarios and the results are compared.

Scenario 1: Constant Fisheries (Reference Scenario)

Ecopath's mass balance routine provides initial fishing mortality (F) estimates according to the catch amounts entered in the model. In this scenario, during four years of time dynamic simulations, coupled model used these initial F estimates invariably for the whole simulation period assuming that fishing activities did not change throughout the simulation period. Hence, there were no time series of fishing effort or mortality.

Scenario 2: No Fisheries

One of the important analysis to be conducted is how the ecosystem would be if there was no fishing. For this purpose, fishing parameters entered to Ecopath were set to nil and no time series data were used in the coupled model. This scenario implies that there was not any fishing fleet operating in the model domain.

Scenario 3: Fishing Newly Target Species, Mesopelagics

In the human's search for "new resources", recent observations have identified a large unexploited biomass of mesopelagic fish living in the deep ocean. Although they are not currently exploited, mesopelagics have attracted attention as a potentially harvestable resource (St. John et al., 2016). Exploitation of this community is a potential problem in terms of the consequences for the ecosystem. For this reason, in order to assess the role of this community in the food web and on the biogeochemistry, an exploitation scenario is applied in which mesopelagic communities are harvested.

Landing values under different scenarios are given in Table 3.

2.6. Validation

2.6.1. Data

Data provided in BATS Station serves as a great opportunity for the validation of the coupled model. Primary production, chlorophyll-a concentration, carbon export and zooplankton biomass data was extracted from BATS database for the modeling period of 1996-1999. For these years, all available data at BATS are compared with the corresponding model estimates.

BATS database holds zooplankton biomass data in terms of the mesh size. Measurements with mesh sizes less than 200 μm were considered as microzooplankton as in the biogeochemical model and compared with depth integrated model estimates of microzooplankton biomasses. Similarly, measurements with mesh sizes more than 200 μm were considered as mesozooplankton and compared with depth integrated model estimates of mesozooplankton biomasses.

For the validation of HTL part of the model, catch data in Food and Agriculture Organization (FAO) database was used. Catch estimates of the model were compared with the FAO statistics. (Vasconcellos, 2004) gives the list of species for each functional group considered in calculation of the landing input for Ecopath. North

Atlantic catches for the years 1996-1999 were extracted from FAO statistics for the same species and consolidated with respect to the functional groups.

Table 3 Fisheries targets and intensities of three scenarios.

Group name	Scenarios		
	Constant Fisheries	No Fisheries	Mesopelagic Fisheries
Baleen whales	0.00E+00	0.00E+00	0.00E+00
Toothed whales	0.00E+00	0.00E+00	0.00E+00
Beaked whales	0.00E+00	0.00E+00	0.00E+00
Seabirds	0.00E+00	0.00E+00	0.00E+00
Pelagic sharks	1.77E-09	0.00E+00	1.77E-09
Yellowfin	5.41E-12	0.00E+00	5.41E-12
Bluefin	7.46E-10	0.00E+00	7.46E-10
Skipjack	1.66E-10	0.00E+00	1.66E-10
Albacore	9.07E-14	0.00E+00	9.07E-14
Bigeye	9.63E-09	0.00E+00	9.63E-09
Swordfish	3.02E-11	0.00E+00	3.02E-11
Billfishes	1.03E-11	0.00E+00	1.03E-11
Lg. Plank. fish	6.36E-12	0.00E+00	6.36E-12
Lg. Epi. fish	6.75E-10	0.00E+00	6.75E-10
Md. Epi. fish	1.62E-08	0.00E+00	1.62E-08
Sm. Epi. fish	1.76E-11	0.00E+00	1.76E-11
Lg. Meso fish	0.00E+00	0.00E+00	1.64E-08
Sm. Meso fish	0.00E+00	0.00E+00	1.64E-08
Sm. Bathyp. fish	0.00E+00	0.00E+00	0.00E+00
Md. Bathyp.fish	0.00E+00	0.00E+00	0.00E+00
Lg. Bathyp. fish	6.75E-10	0.00E+00	6.75E-10
Sm. Bathyd. slp	1.64E-08	0.00E+00	1.64E-08
Lg. Bathyd. slp	5.70E-09	0.00E+00	5.70E-09
Sm. Bathyd. abs	0.00E+00	0.00E+00	0.00E+00
Lg. Bathyd. abs	0.00E+00	0.00E+00	0.00E+00
Sm Squids	1.66E-10	0.00E+00	1.66E-10
Lg Squids	0.00E+00	0.00E+00	0.00E+00
Benth. ceph.	0.00E+00	0.00E+00	0.00E+00
Meiobenthos	0.00E+00	0.00E+00	0.00E+00
Macrobenthos	0.00E+00	0.00E+00	0.00E+00
Megabenthos	0.00E+00	0.00E+00	0.00E+00

2.6.2. Method

Lower Trophic Level Reparameterization:

After the models were coupled, some reparameterization work needs to be conducted. In the original biogeochemical model, mortality term of the zooplankton stands for the sum of predation mortality and natural mortalities such as mortality due to old age, diseases, etc. Thus, since in the couple scheme, mortality of zooplankton due to predation is represented explicitly by the dynamics HTL groups, mortality parameters of zooplankton need to be adjusted.

In the original biogeochemical model, mortality terms of the zooplankton were set to 0.5 $\mu\text{m C/L/day}$. In the coupled model, they need to be equal to natural mortality excluding predation. Since it has not been possible to measure non-predation fraction of the natural mortality of zooplankton, model fit statistics was used for setting these terms. Starting from the initial values, mortality terms were decreased step-wise and a variety of model fit statistics were calculated (Reckhow et al., 1990).

Calculated statistics are the followings:

Note that for the following equations O_i stands for the i^{th} observation, P_i for the i^{th} prediction, n for number of observations, \overline{O} for the mean of observations and \overline{P} for the mean of the predictions.

1. RMSE —the root mean squared error

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^n (P_i - O_i)^2}{n}}$$

The root mean squared error measures the size of the discrepancies between predicted and observed values. Values close to zero indicate a close match.

2. RI—the reliability index

$$RI = \exp \sqrt{\frac{1}{n} \sum_{i=1}^n \left(\log \frac{O_i}{P_i} \right)^2}$$

The reliability index gives the average factor by which model predictions differ from observations. RI should be close to 1. A reliability index of 2 indicates that on the average the model predicts the observations within a multiplicative factor of two (Stow et al., 2003).

3. MEF—the modeling efficiency

$$MEF = \frac{\left(\sum_{i=1}^n (O_i - \bar{O})^2 - \sum_{i=1}^n (P_i - O_i)^2 \right)}{\sum_{i=1}^n (O_i - \bar{O})^2}$$

The modeling efficiency measures how well a model predicts relative to the average of the observations. A value near one indicates a close match between observations and model predictions. If MEF is zero, then model predictions for individual observations are as good as average of the observations. If it is even less than zero, then the observation average would be a better predictor than the model results.

Model fit statistics were calculated for each trial of natural zooplankton mortality in the coupled model. The values offering higher model performance were set as the natural mortality terms.

2.7. Ecosystem Indicators

The ecosystem response to the change in the fisheries intensity can be evaluated by several indicators. In this study, firstly Q-90 Statistics is used in order to understand how fisheries influence ecosystem diversity. Secondly, PPR% (percent primary production required index) is calculated to examine the primary production needed to generate the fish biomass that is captured by fisheries.

2.7.1. The biodiversity index: Q-90 Statistics

Q-90 statistics describes the slope of the cumulative species abundance curve between the 10th and 90th percentiles (Figure 8).

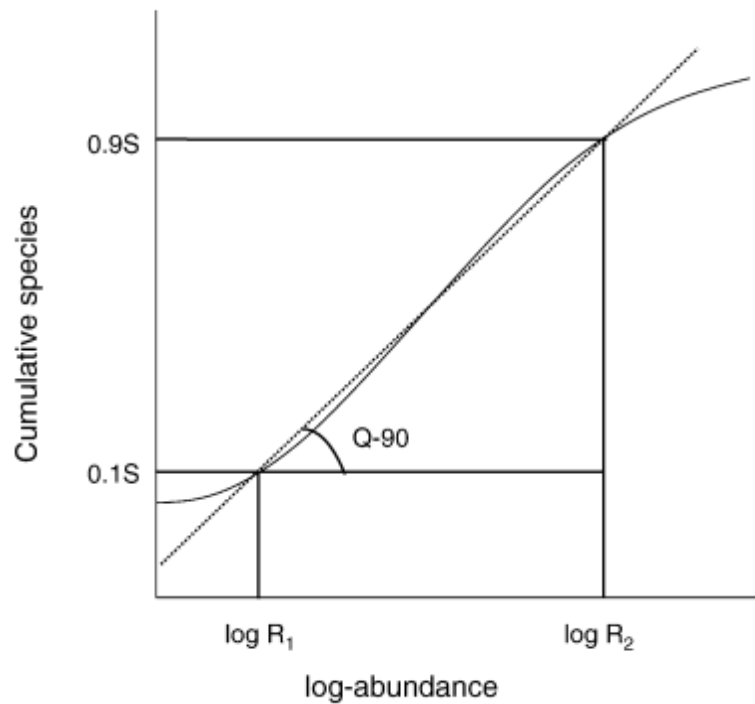


Figure 8 Illustration of Q-90 statistics from (Ainsworth, 2004)

The Q-90 statistic is defined as:

$$Q-90 = \frac{0.8S}{\log(R_2/R_1)}$$

where S is the total number of functional groups in the model; R1 and R2 are the representative biomass values of the 10th and 90th percentiles in the cumulative abundance distribution.

The 10th and 90th percentiles are determined by:

$$\sum_1^{R_1-1} n_R < 0.1S \leq \sum_1^{R_1} n_R$$

$$\sum_1^{R_2-1} n_R < 0.9S \leq \sum_1^{R_2} n_R$$

where n_R is the total number of functional groups with abundance R .

2.7.2. Percent Primary Production Required Index: PPR%

The ecological cost of harvesting depends on the trophic levels of the harvested fish. The higher the trophic level, the higher the ecological cost is (Oguz et al., 2012). This cost can be explained in terms of primary production required.

PPR is calculated by:

$$PPR = \sum_{i=1}^m \left[Y_i \cdot \left(\frac{1}{TE} \right)^{TL_i-1} \right]$$

where TE is transfer efficiency, Y_i is the catch for the species i , and TL_i is the trophic level of the species i .

Normalization of PPR by primary production (PP) gives the percent primary production required (%PPR) index (Pauly and Christensen, 1995).

$$\%PPR = \frac{1}{9} \cdot \frac{PPR}{(PP \cdot 100)}$$

3. RESULTS

3.1. Coupled Model Results

Results of the coupled model differed considerably from the biogeochemical model where there was no interaction with the HTL. Predation of HTL organisms altered the LTL food web dynamics. Although the difference between the modelled outputs of AG1-AG5 and microzooplankton were low, higher differences occurred for mesozooplankton. Coupling of fish strongly influenced DOM dynamics and detritus levels.

Additional inflows due to mortality and unassimilated food of the HTL groups caused a significant increase (i.e. 19%) in the slow sinking detritus. Furthermore, change in the biomass and composition of the plankton due to the HTL predation increased the flows from plankton to the slow sinking detritus. Following this increase, flows from detritus to DOM increased considerably (i.e. 34% and 16% from detritus to DOP and DON, respectively) because the concentration of slow sinking detritus compartment increased. Moreover, additional inflows due to the respiration and excess nutrients exudated by the HTL groups increased DON and DOP levels.

After the integration of HTL groups, the mean biomass of slow sinking detritus increased from 200 $\mu\text{m C/day}$ to 238 $\mu\text{m C/day}$ (Figure 9). In parallel to the slow sinking detritus, the mean biomass of fast sinking detritus increased from 12.15 $\mu\text{m C/day}$ to 14.37 $\mu\text{m C/day}$ since the aggregation of slow sinking detritus constituted the source of fast sinking detritus. DON and DOP levels increased from 1204 $\mu\text{m N/day}$ to 1303 $\mu\text{m N/day}$ and from 35.74 $\mu\text{m N/day}$ to 51.32 $\mu\text{m C/day}$, respectively.

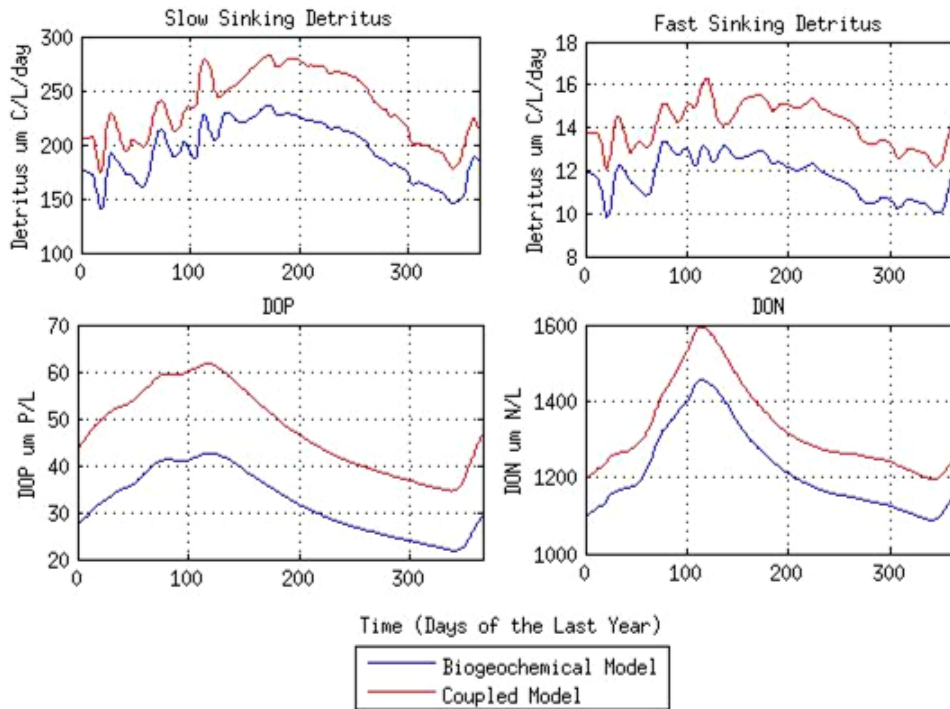


Figure 9 Comparison of coupled model and biogeochemical model for DOM pools and detritus

Change in the nutrient levels influenced algal groups. The mean biomass of LL adapted *Prochlorococcus* slightly changed from 8.74 $\mu\text{m C/day}$ to 8.48 $\mu\text{m C/day}$, while the mean biomass of HL adapted *Prochlorococcus* changed from 44.66 $\mu\text{m C/day}$ to 39.45 $\mu\text{m C/day}$. The biomass of *Synechococcus* slightly increased from 31.27 $\mu\text{m C/day}$ to 31.72 $\mu\text{m C/day}$ on the average and autotrophic eukaryotes' biomass increased 39.01 $\mu\text{m C/day}$ to 44.63 $\mu\text{m C/day}$. Coupled model estimated the mean biomass of diatom 46.8 $\mu\text{m C/day}$ while biogeochemical model estimated 44.94. Zooplankton biomasses lowly changed in response to the change in the algal group biomasses. The mean microzooplankton biomass remained much the same with a change from 17.66 $\mu\text{m C/day}$ to 17.69 $\mu\text{m C/day}$. Mesozooplankton showed the higher change from 5.12 $\mu\text{m C/day}$ to 8.34 $\mu\text{m C/day}$.

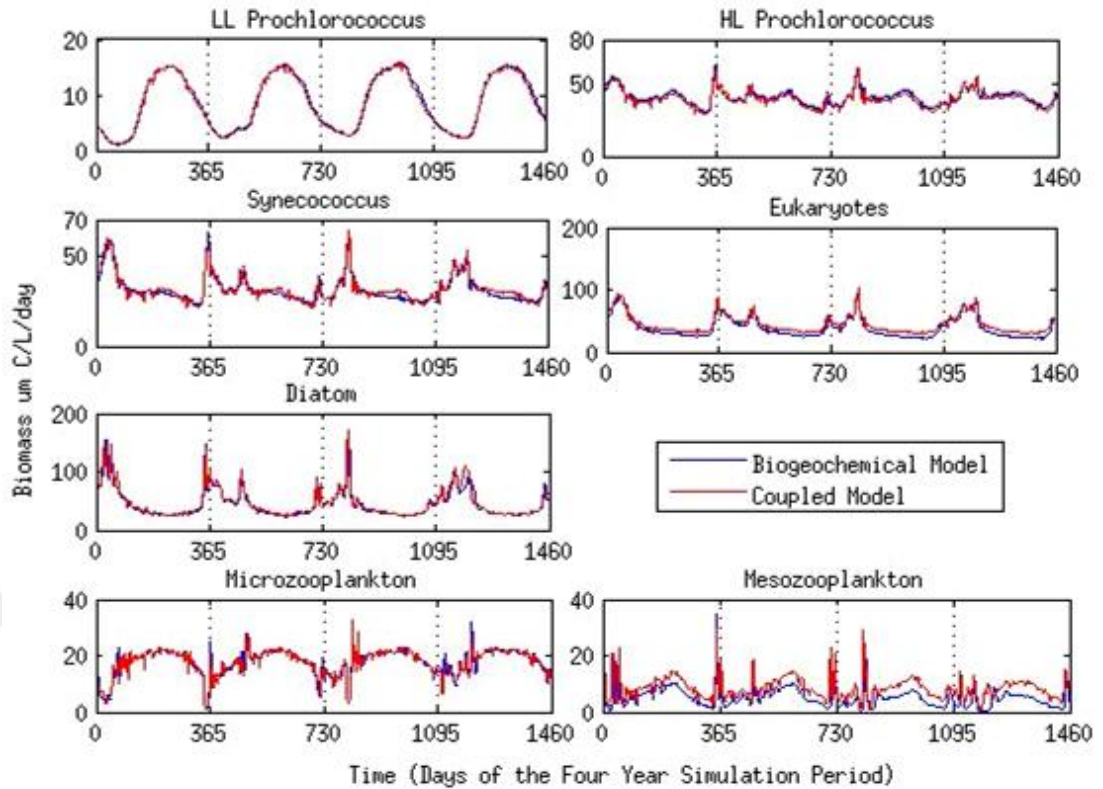


Figure 10 Comparison of final coupled model and standalone biogeochemical model for LTL organisms

Coupled model phytoplankton estimations showed similarity with the other studies. (Casey et al., 2013) presents *Prochlorococcus*, *Syneococcus* and autotrophic algae biomass for the years 2005-2011 (See Figure 11). Although our model covered the years 1996-1999, algal groups' biomass estimates were parallel with their results in magnitude, vertical abundance and seasonal distribution patterns (Figure 11).

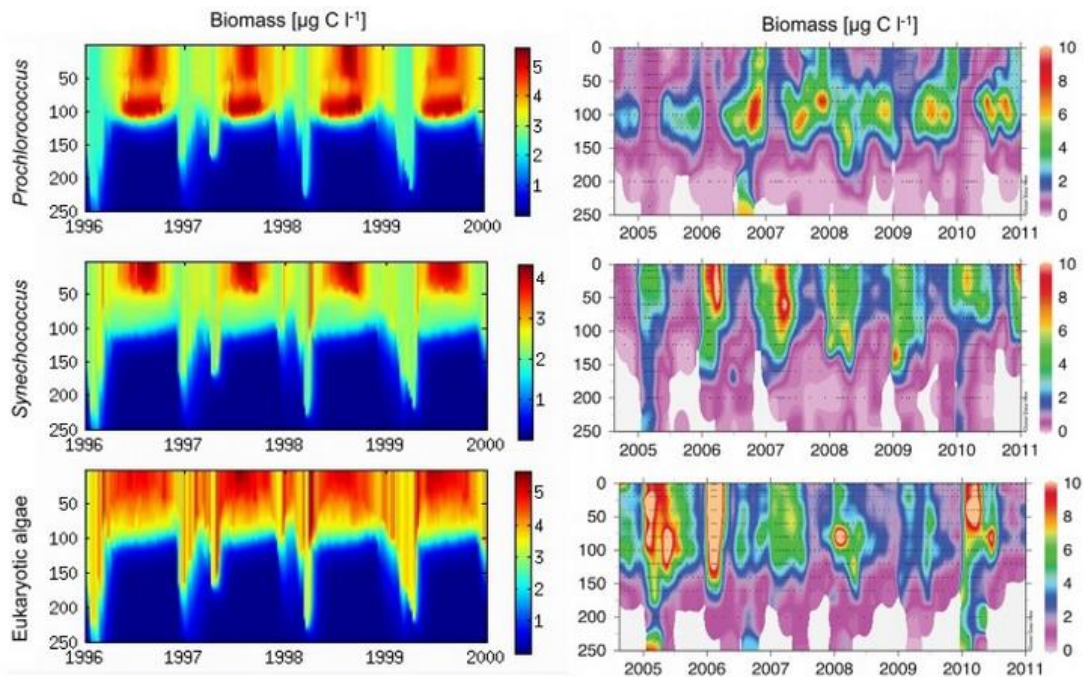


Figure 11 Comparison of our modelled algal group biomass (Left) with estimates given in (Casey et al., 2013) (Right)

Coupling with HTL impacted the flows between the compartments. HTL outflows and increased flows from plankton increased the DOM and detritus pools. Although fish predation was added on zooplankton, average zooplankton biomass increased due to increased phytoplankton level. Total grazing flow from phytoplankton to zooplankton and total mortality from phytoplankton to zooplankton increased. Despite this, since nutrient uptakes of AG's increased, total AG biomass was higher after coupling. In this sense, flows from detritus to DOM and DOM to nutrients slightly increased.

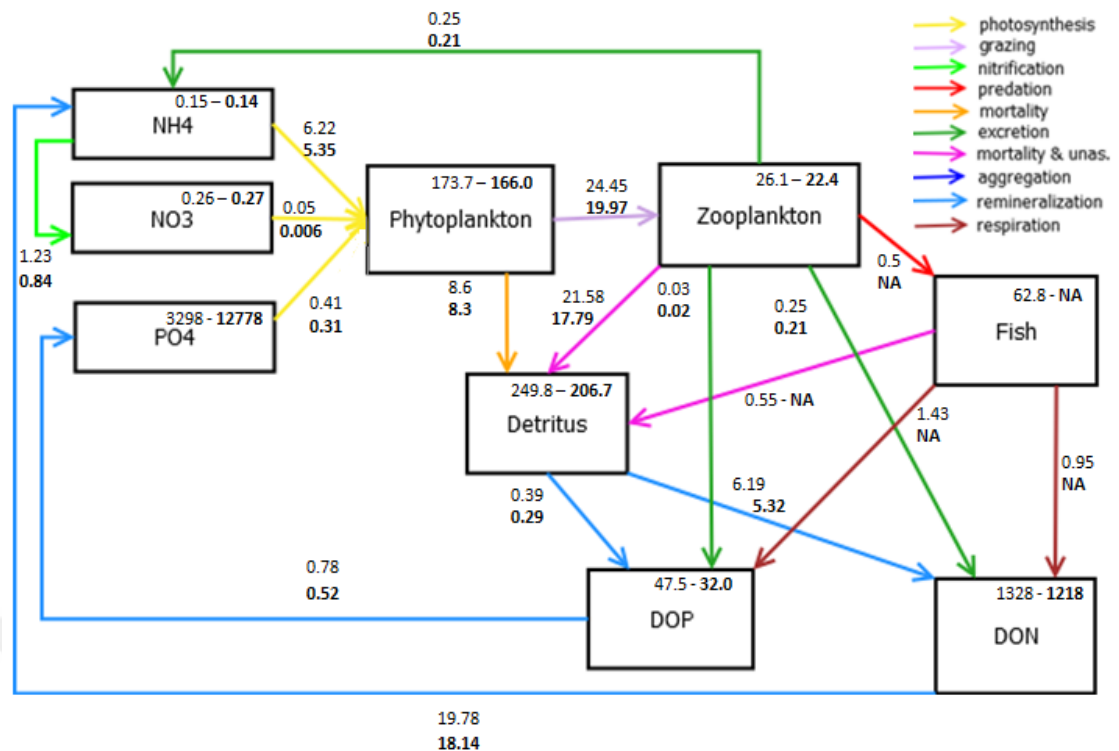


Figure 12 Comparison of final coupled model and biogeochemical model considering flows between model compartments. The bold numbers indicate the time average depth-integrated flows estimated by the biogeochemical model, while the others show the time average depth-integrated flows estimated by the coupled model.

3.2. Comparison with Data

Zooplankton

Integration of HTL caused an increase in mesozooplankton biomass. Fish has a direct control on zooplankton acting as a predator and indirect control by providing nutrients to the system, by this way influence phytoplankton and in turn affect zooplankton. In our case of Sargasso Sea, zooplankton biomass increased due to changed plankton compositions. Coupled model zooplankton estimation was coherent with the BATS data. Although fish predation was explicitly involved in the coupled model, since zooplankton biomass increased, their mortality terms were not decreased further in order to fit the BATS data.

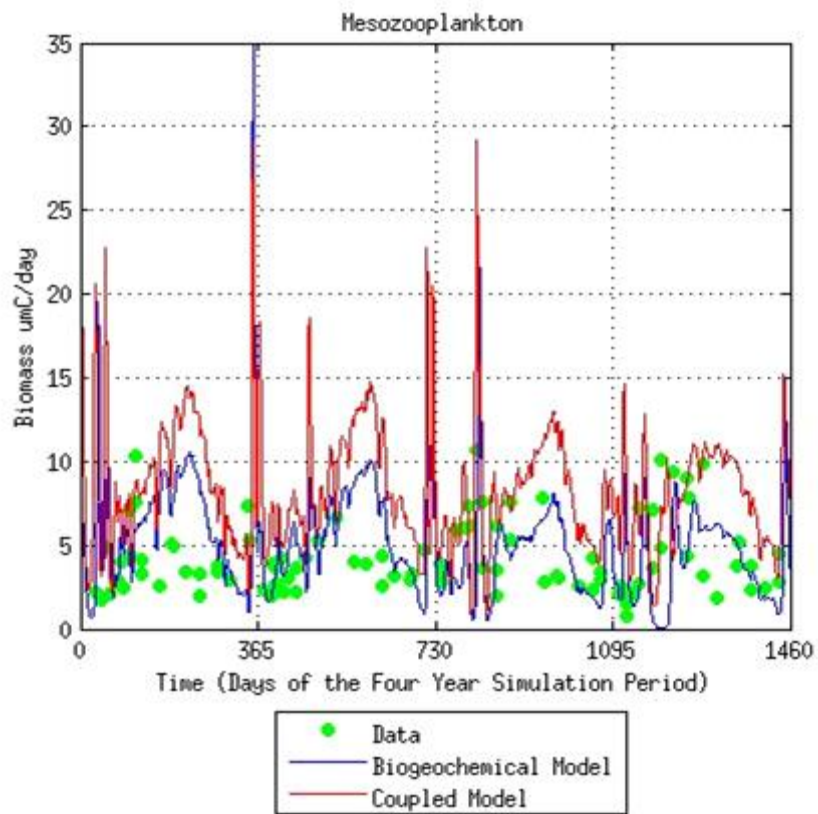


Figure 13 Comparison of coupled model, biogeochemical model and BATS data for mesozooplankton

Coupled model did not differ from the biogeochemical model in representing microzooplankton.

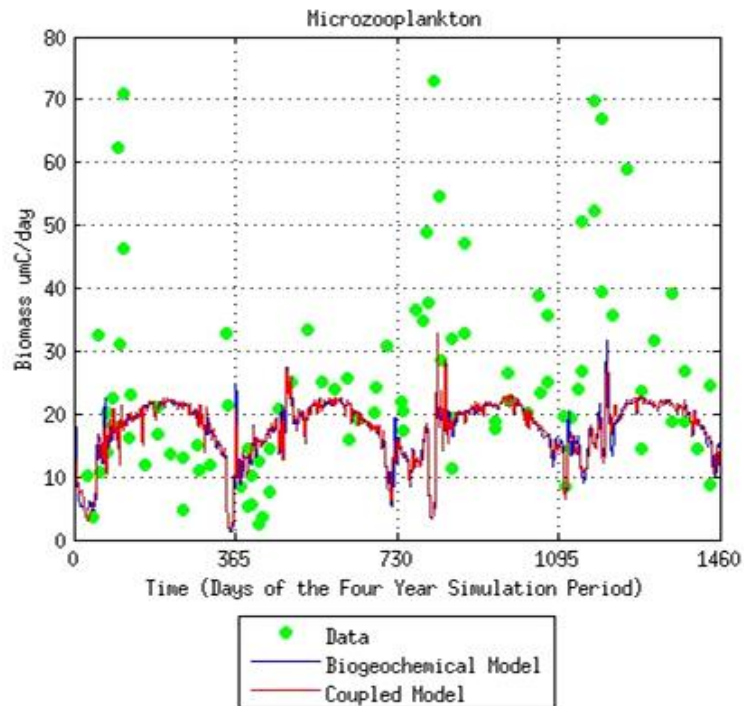


Figure 14 Comparison of the coupled model, biogeochemical model and BATS data for microzooplankton

Chlorophyll-a Concentration

Coupled model estimated lower Chl-a concentration than the biogeochemical model. Change in the algal groups' composition impacted the Chl-a distribution throughout the year. Integration of HTL slightly improved the model performance in representing Chl-a (Table 4).

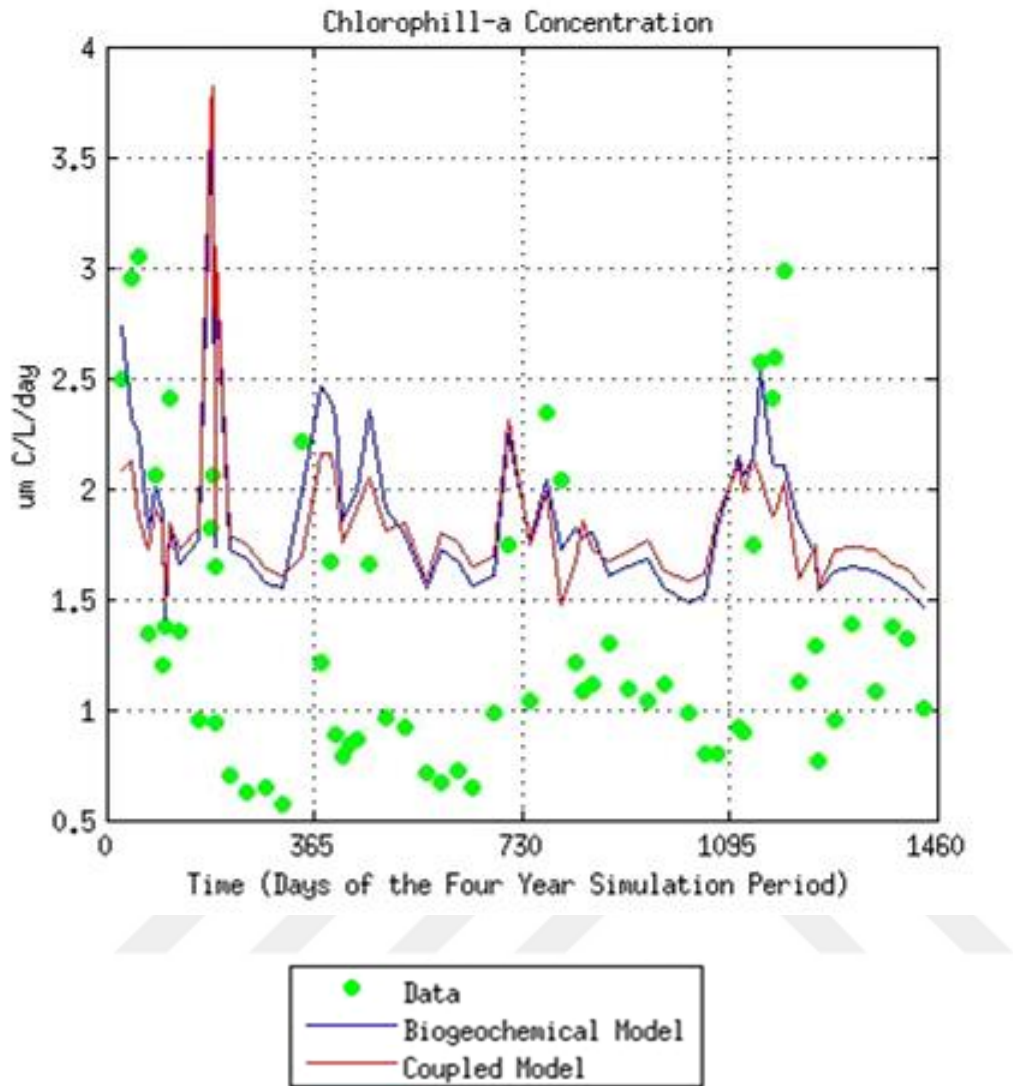


Figure 15 Comparison of coupled model (red line), biogeochemical model (blue line) and BATS data (green dots) for Chl-a levels.

After linking with HTL, Chl-a estimations decreased from 1.92 $\mu\text{m C/day/L}$ (i.e. the mean of the biogeochemical model) to 1.88 $\mu\text{m C/day/L}$ (i.e. the mean of the coupled model) on average.

Primary Production

Coupled model estimation for primary production were 15% higher than the biogeochemical model. The change in the primary production showed a better fit with the data as suggested by the model skill statistics (Part 3.4., Skill Assessment).

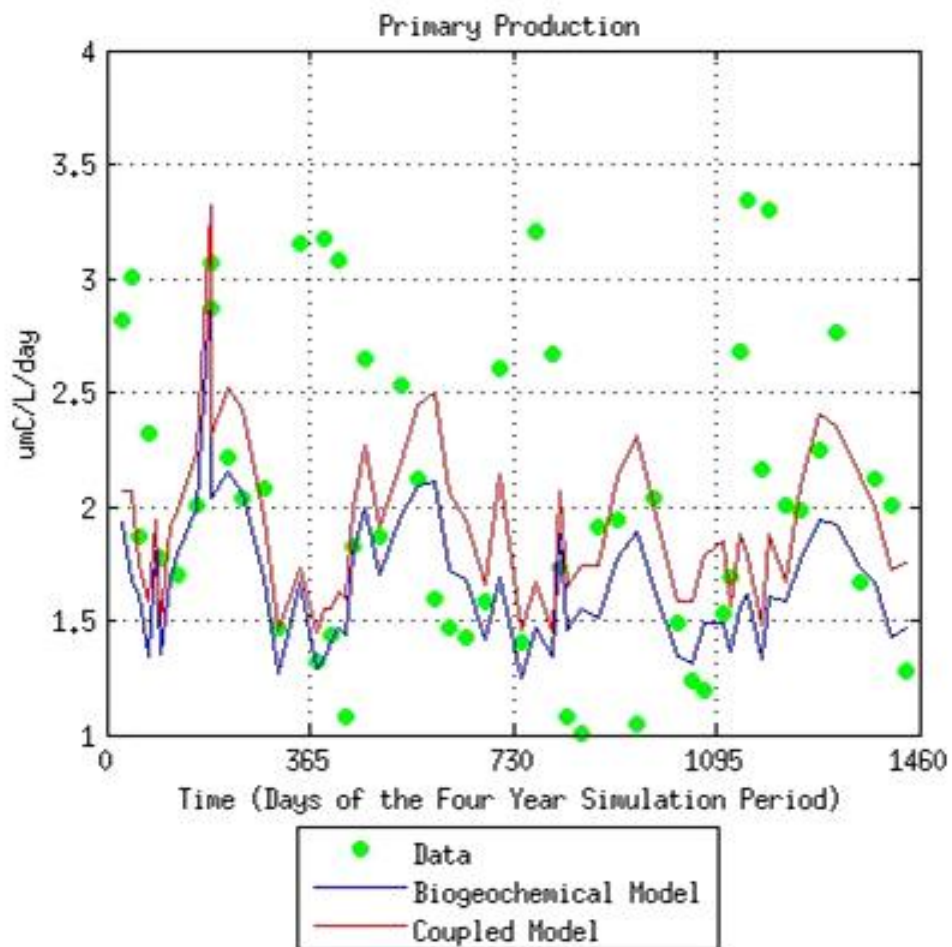


Figure 16 Comparison of coupled model (red line), biogeochemical model (dark blue line) and BATS data

Biogeochemical model estimated primary production $1.68 \mu\text{m C/day/L}$ on the average while the coupled model's mean estimation was $1.94 \mu\text{m C/day/L}$.

Carbon Export

Carbon export was calculated for each meter depth separately. Sediment trap data is available at BATS for depths 150 m, 200 m and 300 m. Following the common practice in the literature and to show the export from the euphotic zone, the export at 300 m was analyzed (Figure 17). Coupled model output showed a notable increase in the carbon export compared to the biogeochemical model.

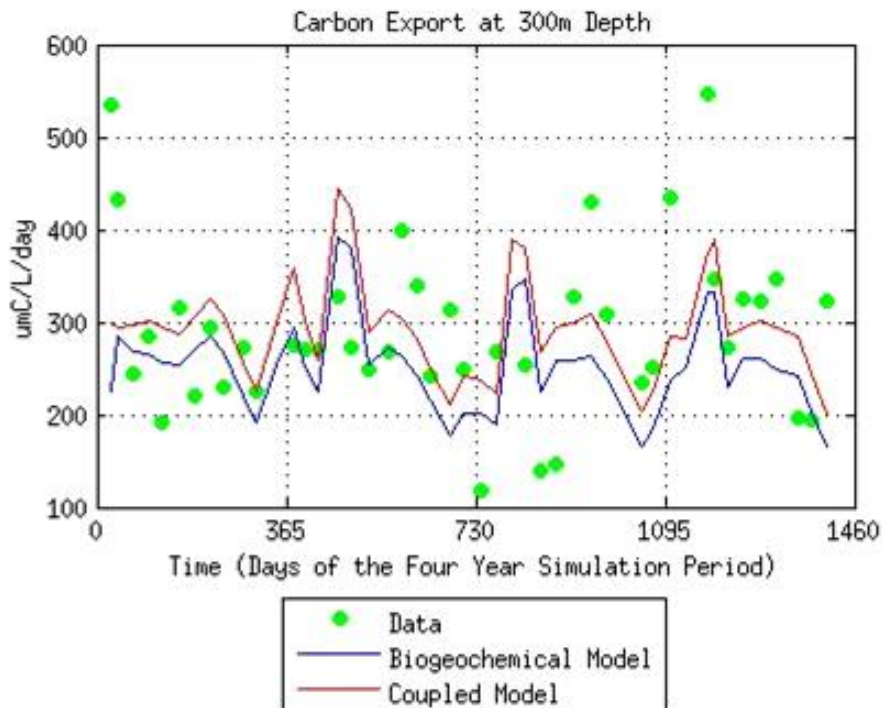


Figure 17 Comparison of coupled model (red line), biogeochemical model (dark blue line) and BATS data (green dots) for carbon export.

Addition of HTL groups increased exported carbon levels 16% from 252 $\mu\text{m C/day}$ up to 293 $\mu\text{m C/day}$. Coupled model fitted to the BATS data better than the biogeochemical model as suggested by the model skill statistics in Part 3.4. (Skill Assessment).

3.3. Skill Assessment

Model skill analysis clarified comparative performances of the models. RMSE, RI and MEF calculated for the coupled model and the biogeochemical model as explained in Part 2.6.2. Results showed that coupling with HTL improved the biogeochemical model in representing carbon export and primary production (Table 4). The performance of the coupled model did not differ from the biogeochemical model for microzooplankton and nutrients (i.e. NO_3 , PO_4 and Si) estimations. Biogeochemical model provided better estimations for mesozooplankton than the coupled model.

Table 4 Model fit statistics for zooplankton, carbon export, PP, Chl-a and nutrients.

	Microzooplankton		Mesozooplankton		Cexp		PP	
	Coupled	NAGEM	Coupled	NAGEM	Coupled	NAGEM	Coupled	NAGEM
RMSE	22.42	22.36	5.06	3.38	133.62	147.88	0.27	0.28
RI	1.43	1.42	1.46	1.61	1.17	1.19	1.89	1.75
MEF	-0.29	-0.28	-4.31	-1.37	0.05	-0.16	0.23	0.18

	CHL-a		NO ₃		PO ₄		Si	
	Coupled	NAGEM	Coupled	NAGEM	Coupled	NAGEM	Coupled	NAGEM
RMSE	0.12	0.11	3.4	3.26	0.12	0.1	1.52	1.32
RI	3.75	1.59	1.21	1.2	1.23	1.19	1.23	1.1
MEF	-0.39	-0.14	0.77	0.79	0.94	0.96	0.94	0.96

RMSE of carbon export decreased about 10% after integration of HTL and RI became closer to 1. Microzooplankton, total primary production, chlorophyll a concentration and nutrients (i.e. NO₃, PO₄ and Si) results of the two models were similar. For primary production, coupled model provided MEF closer to 1 and error (i.e. RMSE) lower than the biogeochemical model. This means that coupled model's predictions for primary production fitted better to the BATS data.

3.4. Scenario Results

No Fishing:

For each scenario tested, carbon exported at 300 m and material recycling was analyzed. No fishing scenario enabled to analyze how the system would be functioning especially at lower trophic levels if fishing pressure was removed for all species. Carbon export and the material flows between the compartments were changed considerably when currently harvested species were kept in the system.

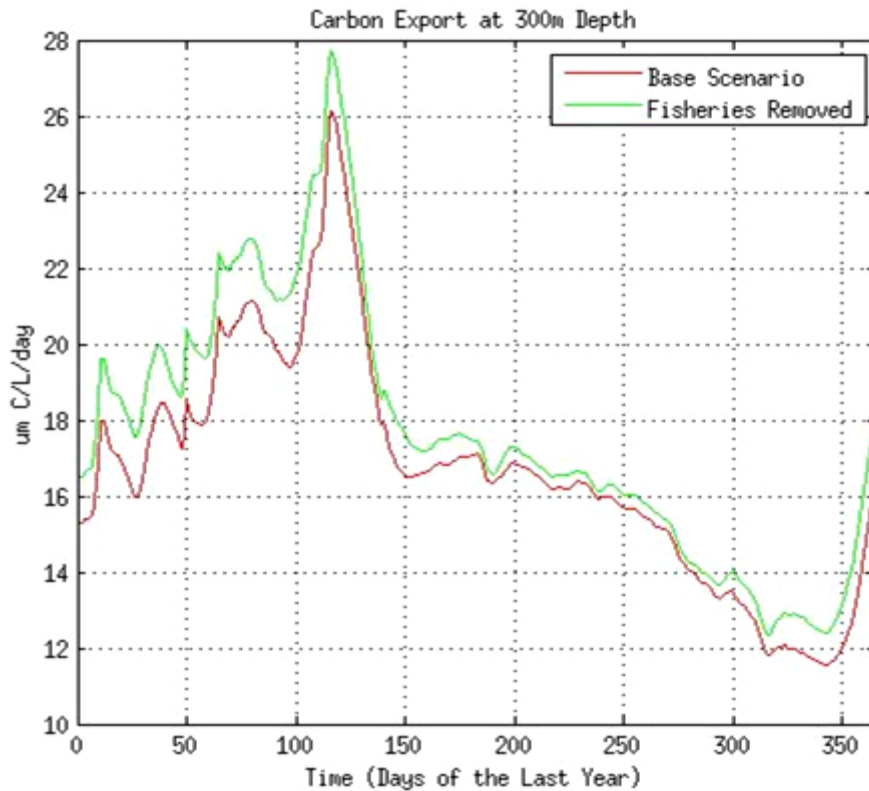


Figure 18 Change in the carbon export when fisheries was removed (with respect to the reference scenario)

Carbon export at 300 m increased from 16.67 C/L/day to 17.61 C/L/day. This result was in parallel to the decrease in the detritus level. Total fish stock increased 49% with respect to the reference scenario. Increase in the fish biomass was followed by increasing flows from fish to detritus, DOP and DON compartments by 51%, 59% and 58% respectively. Higher fish biomass resulted in higher grazing pressure over zooplankton. Despite this, zooplankton biomass increased due to increased. Outflows from zooplankton compartment and grazing pressure on phytoplankton increased. Higher DOP pool provided higher remineralization and thus higher PO_4 . DON pool and thus remineralization from DON remained almost the same. Changed algal group composition influenced nutrient uptake dynamics. Nitrification increased slightly.

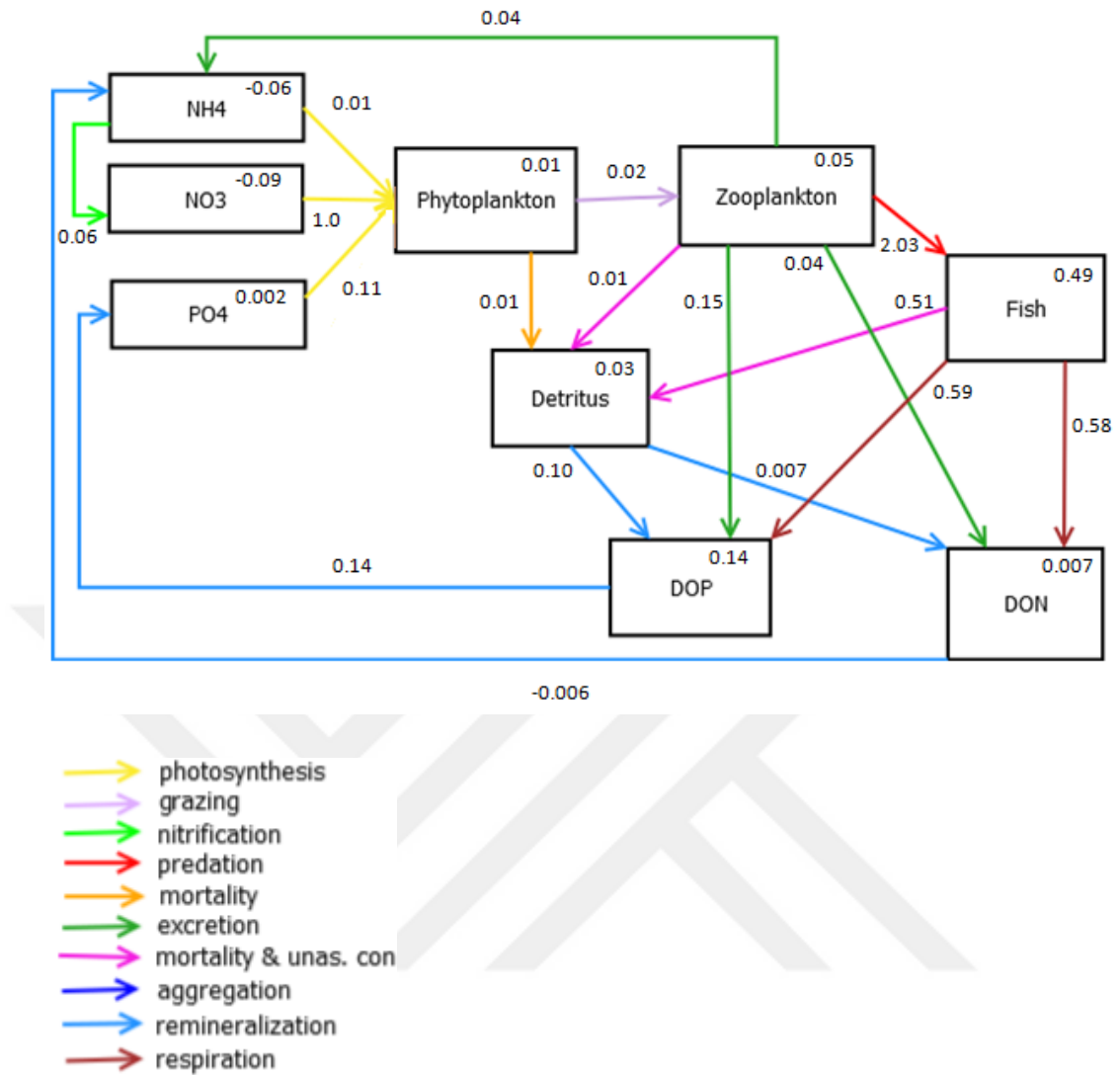


Figure 19 Change in the flows when fisheries was removed). Numbers show the change in percent with respect to the reference scenario.

Fishing Newly Target Species, Mesopelagics:

Harvesting of mesopelagics with a fishing mortality rate 0.1/year in addition to current fisheries caused a decrease in the carbon export. Decrease in the fish biomass and change in the food web structure impacted LTL dynamics. Zooplankton and phytoplankton compositions altered. DOM, detritus and nutrient levels changed in response to the food web structure.

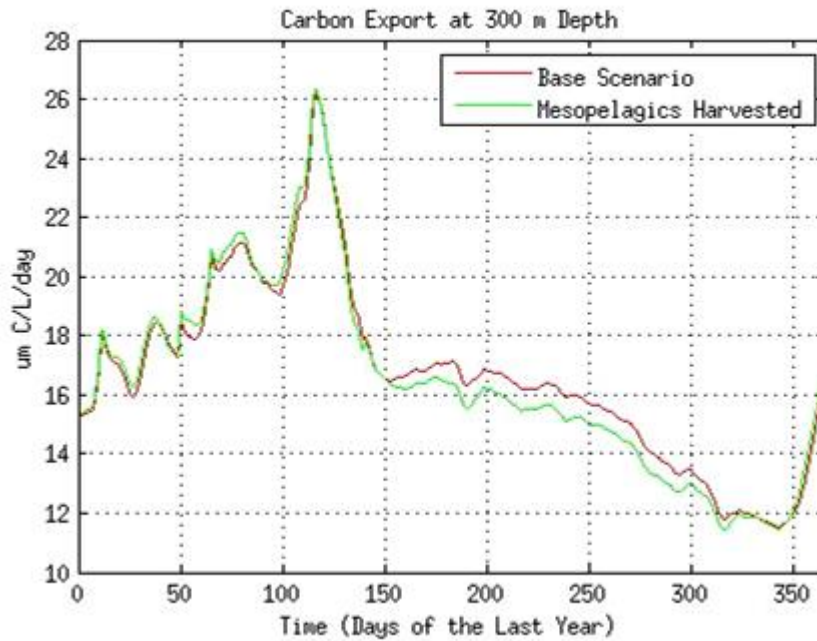


Figure 20 Change in the carbon export when mesopelagics were harvested (with respect to the reference scenario)

Carbon export at 300 m depth did not differ from the reference scenario. Although mesopelagic harvesting decreased mesopelagic stocks, its cascading impact caused fluctuations in the food web. Complex prey-predator relationships within the food web increased the biomass of some fish species while the biomass of the others decreased. As a result, harvesting mesopelagics increased the overall fish biomass. Flows from fish to detritus and DOM increased in parallel. Microzooplankton biomass increased while mesozooplankton biomass decreased. Total zooplankton slightly increased. Phytoplankton biomass and mortality flow of phytoplankton did not differ significantly. Detritus compartment became less nitrogen rich, while phosphorus content increased. Thus, bulk remineralization from detritus to DON and DON to nutrients decreased while remineralization from detritus to DOP and DOP to PO_4 decreased.

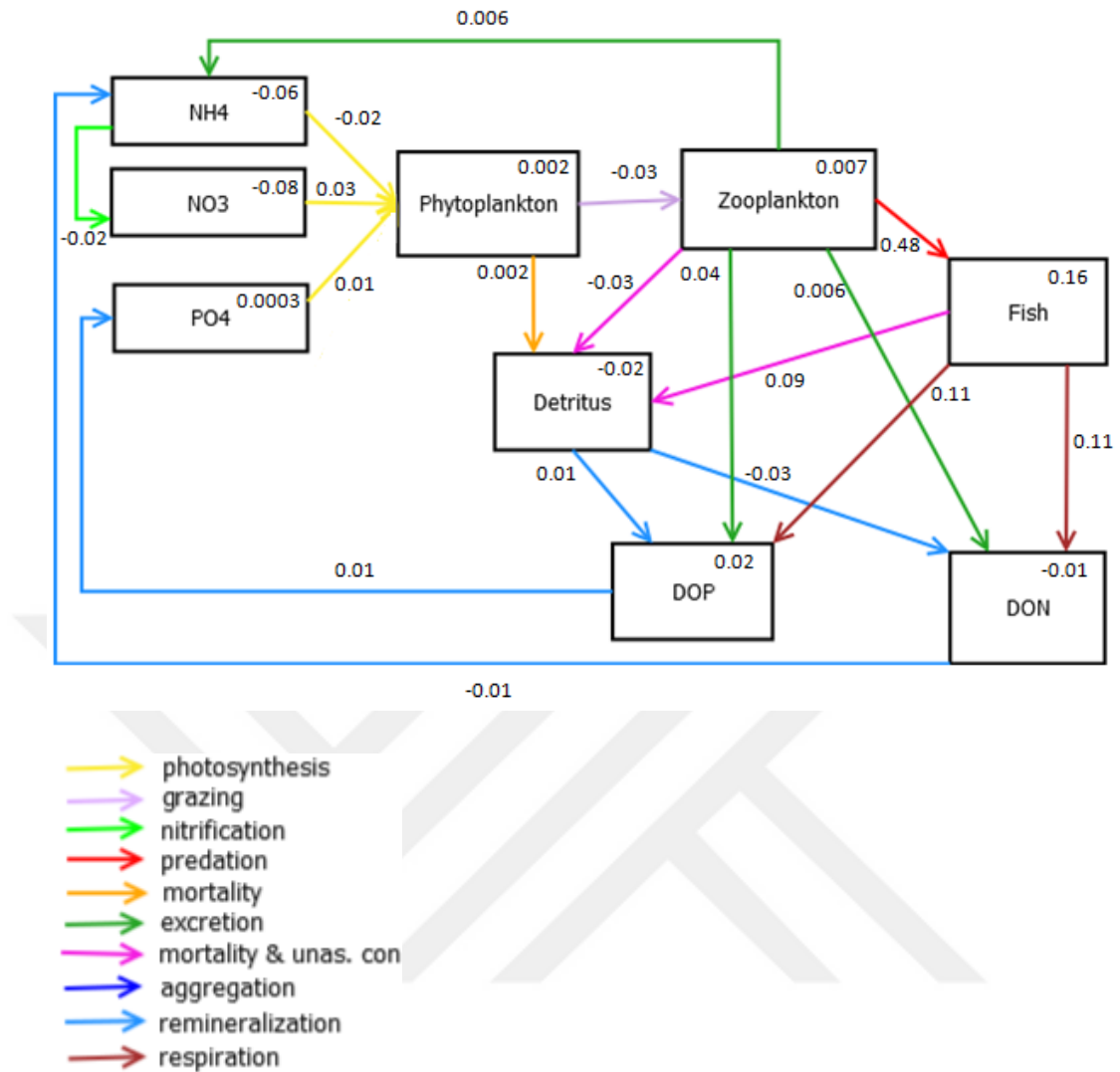


Figure 21 Change in the annual averaged flows when mesopelagics were harvested (with respect to the reference scenario)

3.5. Ecosystem Indicators

3.5.1. Biodiversity

Q-90 index was calculated for each scenario to analyze how the ecosystem biodiversity was influenced under each scenario. The higher the Q-90 value is, the more biodiversity the ecosystem has. If there was no fishing, biodiversity would be higher than the current situation (i.e. reference scenario). On the contrary, fishing mesopelagics caused a decline in the biodiversity (Table 5).

Table 5 Q-90 index of the ecosystem in different scenarios

Scenario	Q-90 Index
Reference Scenario	5.51
No Fishing	7.09
Mesopelagics Fished	4.13

3.5.2. Primary Production Required to Sustain Fisheries

PPR% showed the fraction of primary production, which is required to sustain the fish that is captured by fisheries. The scenario in which mesopelagics were harvested exhibited the highest PPR% values of 0.19. Since the biomass of mesopelagics is high, harvesting them, even with a relatively low fishing mortality rate (i.e. 0.1/year), considerably increased the total primary production required to sustain fisheries. PPR% for the reference scenario was calculated to be almost zero. This result was ascribed to low fish existence in the area.

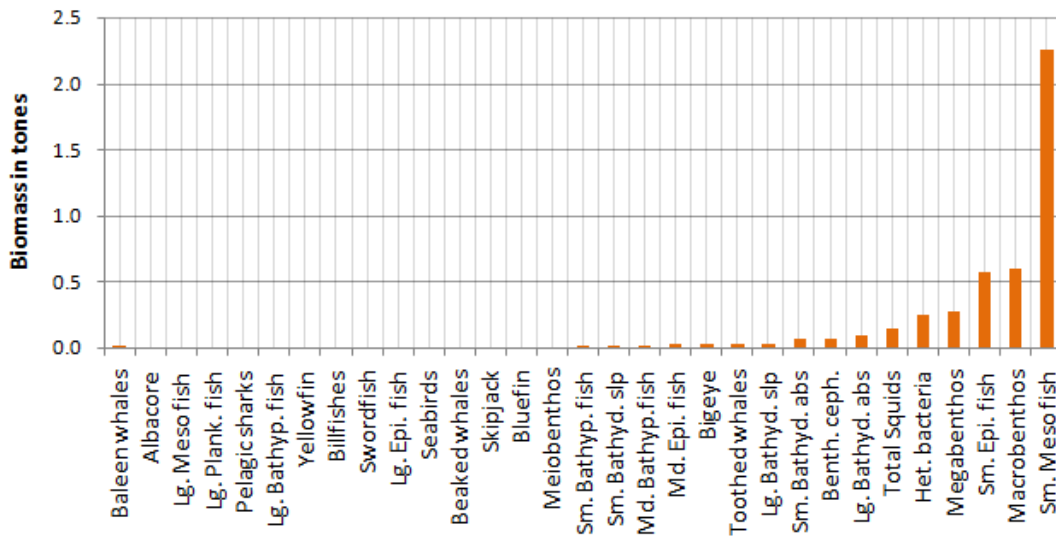


Figure 22 Biomass of fish species in North Atlantic

4. DISCUSSION

The online two-way coupled end-to-end model, which was developed in this study is unique in terms of representing the dynamics of marine biogeochemistry, fisheries and the entire food web in an integrated way. Different from the previous studies, in this study a detailed LTL forcing drove the functioning of the HTL organisms and an explicitly represented nonlinear HTL dynamics acted on the LTL dynamics. Thus, this study contributed to the efforts that have been put forward (Akoglu et al., 2015; Kearney et al., 2012a) in furtherance of simulating the marine ecosystems from a holistic perspective.

The main advantage of integrated ecosystem simulations is the ability of analyzing how the components of an ecosystem interact with each other. In this study we carried out several analyses in order to delineate the interactions between fish, fisheries and biogeochemistry.

The first objective of the study was understanding how fishing related changes in the food web structure influence marine nutrient cycles, transport of material through food web and lower trophic level dynamics.

Studies carried out for fresh water ecosystems showed the important role of fish in nutrient cycling in aquatic ecosystems. In their study where (McIntyre et al., 2008) investigated how fish can create biogeochemical hot spots in streams, they concluded that fish excretion could meet more than 75% of ecosystem demand for dissolved inorganic N and fish distributions could influence local N availability. The results obtained from our study indicated that fish has an influencing role on nutrients also in marine systems. In our case study of Sargasso Sea, metabolic activities (e.g. respiration, excretion, excess cellular nutrients) and mortality of fish created a total of 3 $\mu\text{m C/day}$ inflows to DOM and detritus pools, which corresponded up to 0.03% of the total detritus and DOM pools. This low fraction is ascribed to the scarce fish abundance in Sargasso Sea.

Fish can directly control plankton by acting as a predator. With the settings of this study, explicit inclusion of fish into the model directly increased mesozooplankton biomass. Increased zooplankton levels indicated that nutrient supply sourcing from

mortality and metabolic activities of fish impacted zooplankton biomass positively despite the predatory effect of fish.

The analyses delineated that explicit representation of fish increased the detritus fish, which eventually influenced DOM pools positively. Increase in the DOM pools increased the remineralization process. However, depending on the targets and the intensity of fisheries, change in the plankton structure may suppress the increase in the remineralization. This is mainly because fisheries could change the composition of LTL organisms (i.e. zooplankton and phytoplankton). In nature, fisheries exploit fish and change HTL community composition. Exploited species may disappear or significantly diminish while the other species may become more abundant depending on prey-predator relationships. Such a change in HTL community composition, in turn, impact LTL dynamics due to changed grazing on zooplankton and detrital flows from fish. LTL composition directly influences the magnitude and the content of the flow from plankton compartments to DOM and detritus compartments. By this way, changed flows from LTL groups may impact the remineralization negatively, which may suppress the increase in remineralization, which was because of increased detritus as a result of additional respiration, excretion and exudation flows from fish. (Beaugrand et al., 2010) states that community body size largely determines the types and strengths of the flows of energy and materials in ecosystems and affects both ecological networks and the way ecosystems are structured and function. Their results indicated that the biological carbon pump could be reduced because organic carbon would reside longer in surface waters where it would be processed through smaller-sized zooplankton (i.e. microzooplankton) and dissipated through more complex food webs and additionally because the total biomass of copepods (i.e. mesozooplankton) may decrease. Similarly, our study showed that since phytoplankton had different nutrient uptake rates and different cellular nutrient ratios, nutrient levels in the environment and in the detritus content changed depending on fisheries. When mesopelagics were harvested, phytoplankton composition changed, which eventually changed the nutrient content of detritus (Figure 21), and in turn, influenced the bulk remineralization from detritus to DOP and DON oppositely. Remineralization from detritus to relevant DOM pool depended on the nutrient concentration (i.e. C:N:P ratios) of the detritus. P/N ratio of

detritus increased resulting in higher remineralization from detritus to DOP and lower remineralization from detritus to DON.

It should be noted that Sargasso Sea is an oligotrophic system and even in this system nutrient cycles and carbon export give an ample response to removal of fisheries. A system in which fish is more abundant compared to the Sargasso Sea (Figure 23) would cause higher change in the flows.

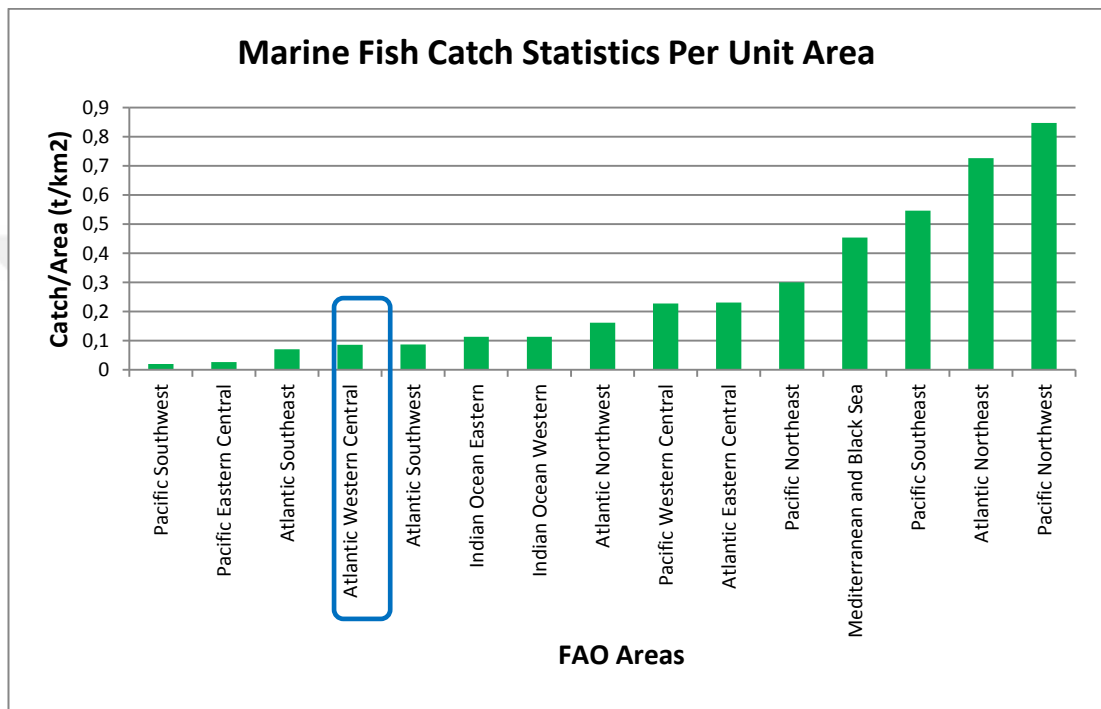


Figure 23 Marine fish catches per unit area for FAO regions. According to FAO fishing areas Sargasso Sea corresponds to the area so called “Atlantic Western Central”.

Our results related to the marine biodiversity indicated that increasing fisheries decreased the biodiversity while closure of fisheries increased the biodiversity. This underlined the important link between fisheries and marine biodiversity. In this sense, target and the intensity of the fisheries are determinant. This link was also emphasized by other studies. (Agardy, 2000) denoted that marine biodiversity is being lost at an alarming rate as genetically unique marine populations are extirpated. Fisheries with higher intensity can also cause simplification of the food web reducing the number of pathways linking primary producers to top predators (Pauly et al., 2002).

(Daewel et al., 2014) reviewed different modeling approaches with respect to their ability to adequately simulate zooplankton mortality, which is necessary for modeling the energy transfer from LTL to fish. They stated that the lack of a dynamical link between LTL and HTL has important implications for the simulated zooplankton dynamics. In our study, predation mortality of zooplankton was included in the model. By this way, impacts of fish predation on zooplankton dynamics were represented explicitly.

Most of the NPZ models are “closed” by using for zooplankton mortality term, which usually does not differentiate different sources of mortality. Zooplankton mortality term is difficult to define and usually not parameterized empirically. (Edwards and Yool, 2000) pointed out that the steady state solution of models could be very sensitive to the choice of the functional form of the closure term. Additionally, the models in which zooplankton is a closure, spatial and temporal dynamics of predator are not included. Thus, seasonal dynamics in zooplankton predation mortality could not be revealed.

To solve the closure term problem and allow the energy transfer from lower to higher trophic levels to be more realistically simulated (i.e. allowing E2E ecosystem representation (modeling)), they proposed coupling HTL modeling tools to biogeochemical models. Several studies (Neuheimer et al., 2009; Ohman and Hsieh, 2008; Travers et al., 2007) highlighted the importance of taking the spatial-temporal differences in predator abundance into consideration while estimating ecosystem functionalities. In our study the integration of the models addressed the most fundamental issue of these complications arising due to the incompetency of the closure terms, i.e. inexistence of explicit zooplankton predators. According to the conservation of mass principle, an entity coming to the zooplankton compartment could either leave the compartment as an outflow (i.e. outflow to detritus, to DOM pools or to the nutrients) or accumulate in the zooplankton compartment. Since it was the closure term in the biogeochemical model, it was not possible to transfer the entity to the higher trophic level organisms. Adding HTL organisms on top of the zooplankton compartment resolved this problem. Since zooplankton was explicitly linked to its predators in the coupled model, accumulated biomass in those compartments were either transferred to the HTL part of the model via fish consumption to form the fish biomass or lost to detrital groups via natural mortality.

Contrary to this, in the biogeochemical model, the sinks of zooplankton only ended up in detritus.

Secondly, this study aimed to provide explanations to how carbon export from the surface to the bottom of the ocean is influenced by fish by using the developed end-to-end model.

This study showed that when fish was explicitly involved in the model, carbon exported from surface to the depths of the Sargasso Sea increased. Carbon export was calculated as a function of the detritus compartment. Therefore, direct and indirect impacts of fish on detritus compartment affected the carbon export. Fish and fisheries could influence detritus (and thus carbon export) by two means. First, fish may enrich the detritus with its mortality term and with the release of excess cellular nutrients. Second, fish may change the plankton compositions due to its predation pressure on plankton and due to additional nutrients provided to algal groups by metabolic activities of fish. Elevated nutrient levels increase algal growth and primary production, which increases zooplankton biomass and positively impact flows from plankton compartments to detritus compartment.

In our case study of Sargasso Sea, coupling with HTL increased the carbon export (Figure 16). This showed that enrichment of detritus due to HTL dynamics positively impacted the carbon export. Coupled model results provided statistically better fit with BATS data.

Scenario analyses revealed the strong coupling between carbon export and fisheries. Different fisheries scenarios presented different carbon export estimates. Removal of fisheries increased carbon export since currently harvested fish stocks were left in the system and this created higher flows from HTL compartment to detritus. On the contrary, exploitation of mesopelagic fish decreased carbon export since total detritus decreased as a result of low inflows to the detritus compartments. The change in the carbon export due to fisheries depends on the target and the intensity of the fisheries.

Final objective of this thesis work was understanding the function of mesopelagic fish within biogeochemical processes.

Studies about the active transport of carbon by mesopelagic fishes showed that carbon export by fishes can be as much as 28% of the total flux, and can exceed 20

mg C m²d⁻¹ (Hidaka et al., 2001). (Davison et al., 2013) estimated the carbon exported by actively moving mesopelagics as 15–17% (22-24 mg C m² d⁻¹) of the total carbon exported at North East Pacific (144 mg C m² d⁻¹).

Our study examined how mesopelagics impact passively transported carbon by their metabolic activities (e.g. respiration, excretion etc.), by their predation impact on plankton and by transferring material through the food web. Active transport of the material by fish was not included in the model structure considering that the focus of this study was understanding the link between fish and nutrient cycling in terms of metabolic activities and grazing/predation of fish. According to our results, harvesting mesopelagic with a fishing mortality rate of 0.1/year decreased passive carbon export by 2%. It also impacted LTL dynamics (i.e. nutrient cycling, carbon export). In our study area, harvesting of mesopelagics resulted in an increase in the total fish biomass due to complex prey-predator relationships within the food web. Fluctuations in biomass of HTL groups decreased the carbon export.

Results of the coupled model revealed changes in the nutrient cycling (i.e. remineralization, nitrification etc.) at varying levels. Removal of mesopelagics increased zooplankton and phytoplankton levels. Overall change in plankton and HTL organisms (i.e. both mesopelagics and other fish) decreased the detritus level, which as a result impacted the flows from detritus to DOM pools and from DOM pools to nutrients.

Current estimates of global mesopelagic fish biomass (i.e. 10 billion tons (St. John et al., 2016) highlights the importance of mesopelagic fish communities within the marine ecosystem. This less known but highly influential community (in terms of linking upper and deeper parts of the ocean and linking different groups of the food web) holds the potential of changing global marine ecosystem dynamics significantly as indicated by the results of our study.

By using the developed model that simulated lower and higher tropic levels of marine ecosystems simultaneously, we carried out several analyses in order to achieve our principal aim, which was to analyze the impacts of fish and fisheries on marine biogeochemical processes as well as the ecosystem.

Although the coupled model developed in this study was set up for the Sargasso Sea, the model has a generic structure. The modelling scheme could easily be applied to other ecosystems after required reparameterization and restructuring. The model enables the analysis of issues related to marine biogeochemistry, food web, fisheries and their interrelated dynamics. Questions arising from the nonlinear and sophisticated characteristics of the marine ecosystem could be addressed to the developed integrated model.

The model structure is suitable for further improvements. For instance, the carbon export estimated by the developed model is only through the passive transport. However, active transport plays an important role in carbon export through the water column. Ignoring the actively transported material may lead to underestimation of the potential consequences of changing fisheries exploitation strategies. For this reason, although it was not involved in the scope of this master thesis study, in the near future directions of this study, active transport of material by vertically migrating of organisms (e.g. fish and zooplankton) will be examined.

Additionally, bacterial dynamics could be incorporated in the model explicitly as a compartment. This will enable more competent analysis of bacterial activities and their interaction with fish and fisheries. (Azam, 1998) stated that behavioural and metabolic responses of bacteria to the complex structure of the organic matter field influence ocean carbon fluxes in all major pathways such as microbial loop, sinking, grazing food chain, carbon storage, and carbon fixation. It was also pointed out that in earlier studies (Williams, 1998) diminished fish production was related to the dominant microbial loop while in another study (POMEROY and DEIBEL, 1986) the richness of the fishery was ascribed to uncoupling of bacteria from primary production during the spring bloom. Rather than representing bacterial activity implicitly using constant remineralization rates, functioning of bacteria and their dynamic responses to the spatio-temporal changes in the environmental conditions could be involved in the model. Impacts of bacteria on seasonal variability of marine biogeochemistry could be examined. By this way, relationship between bacterial activities and other living organisms (e.g. plankton, fish) and nutrient dynamics could be revealed.

This study demonstrates the functioning of marine ecosystems from a holistic approach. It is novel in terms of representing marine biogeochemistry, entire food web and fisheries in an integrated way and allowing dynamic multi-way interactions between them. It also provided an efficient tool and essential way of thinking that might be used for development and implementation of policies and regulations to conserve marine ecosystems. Human activities cause great changes in the ocean. Some of the changes are reversible while some are not, causing a shift in the state of the marine ecosystems. Climate change, ocean acidification, exploitation of fish stocks are some examples that we have encountered until now. In the future of the ocean, cascading impacts of the current problems and potentially new ones could cause more irreversible changes. Thus, before it becomes too late we need to bring the environmental problems into our focus first to define and then to solve them by implementation of conservative measures. In this sense, our study contributed to the understanding of the relationships between fish assemblages and marine biogeochemistry from the perspective of the functioning of the entire food web under fisheries exploitation, and paved a few steps towards development of effective conservation strategies for the marine environment in the light of its novel findings.

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