NONLINEAR DYNAMICS OF THE BLACK SEA ECOSYSTEM AND ITS RESPONSE TO ANTHROPOGENIC AND CLIMATE VARIATIONS

DOCTOR OF PHILOSOPHY

IN

MARINE BIOLOGY AND FISHERIES
MIDDLE EAST TECHNICAL UNIVERSITY
INSTITUTE OF MARINE SCIENCES

BY

EKİN AKOĞLU

MERSİN – TURKEY
JULY 2013

NONLINEAR DYNAMICS OF THE BLACK SEA ECOSYSTEM AND ITS RESPONSE TO ANTHROPOGENIC AND CLIMATE VARIATIONS

A THESIS SUBMITTED TO
INSTITUTE OF MARINE SCIENCES
OF
MIDDLE EAST TECHNICAL UNIVERSITY

BY

EKİN AKOĞLU

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY
IN
THE DEPARTMENT OF MARINE BIOLOGY AND FISHERIES

JULY 2013

Approval of
the thesis:

NONLINEAR DYNAMICS OF THE BLACK SEA ECOSYSTEM AND ITS RESPONSE TO ANTHROPOGENIC AND CLIMATE VARIATIONS

submitted by **EKİN AKOĞLU** in partial fulfilment of the requirements for the degree of **Doctor of Philosophy in the Department of Marine Biology and Fisheries, Middle East Technical University** by,

Prof. Dr. Ahmet Erkan Kıdeyş _____________________
Director, Institute of Marine Sciences

Prof. Dr. Zahit Uysal _____________________
Head of Department, **Marine Biology and Fisheries**

Assist. Prof. Dr. Barış Salihoğlu
Supervisor, **Institute of Marine Sciences** _____________________

Examining Committee Members:

Prof. Dr. Zahit Uysal _____________________
Institute of Marine Sciences, METU

Assist. Prof. Dr. Barış Salihoğlu _____________________
Institute of Marine Sciences, METU

Prof. Dr. Ahmet Erkan Kıdeyş _____________________
Institute of Marine Sciences, METU

Assist. Prof. Dr. Bettina Andrea Fach Salihoğlu _____________________
Institute of Marine Sciences, METU

Dr. Cosimo Solidoro _____________________
Istituto Nazionale di Oceanografia e di Geofisica Sperimentale

Date: *July 18, 2013*

I hereby declare that all information in this document has been obtained and presented in accordance with academic rules and ethical conduct. I also declare that, as required by these rules and conduct, I have fully cited and referenced all material and results that are not original to this work.

Name, Last name: Ekin Akoğlu

Signature:

ABSTRACT

NONLINEAR DYNAMICS OF THE BLACK SEA ECOSYSTEM AND ITS RESPONSE TO ANTHROPOGENIC AND CLIMATE VARIATIONS

AKOĞLU, Ekin

Ph. D., Institute of Marine Sciences

Supervisor: Assist. Prof. Dr. Barış SALİHOĞLU

July 2013, 126 pages

The main objectives of this research were i) to provide a quantitative understanding of the changes in the Black Sea ecosystem between 1960 – 1999, ii) to identify its food web dynamics including the infamous anchovy – *Mnemiopsis* shift in 1989, and iii) utilising this understanding to explore future progressions of the Black Sea ecosystem under predicted physical and biogeochemical changes. For this purpose, three different but complementary modelling approaches were used all of which were detailed under three distinctive chapters in this thesis manuscript; i) a steady-state modelling approach utilising Ecopath mass-balance models of the Black Sea to quantitatively analyse and differentiate its ecosystem structure and functioning under four different regimes using ecological indicators, ii) an Ecosim time-dynamic modelling approach to explore the nonlinear food web dynamics over the course of its history between 1960 - 1999 and identify the shifts that led to the transitions between its four different periods explored by the mass-balance models, and iii) an Ecopath with Ecosim (EwE) – BIMS-ECO coupled physical – biogeochemical end-to-end modelling approach to predict future changes in the Black Sea ecosystem under predicted climatological and physical conditions and explore management strategy options that are going to help the ecosystem recover to achieve its good environmental status (GES). All of the developed models were evaluated using historical time series data and results obtained from classical modelling approaches such as Virtual Population Analysis (VPA), which was carried out using data obtained from field sampling.

The mass-balance modelling results (chapter 2) showed how the Black Sea ecosystem structure started to change after the 1960s as a result of a series of trophic transformations occurred in the food web. These transformations were initiated by two main anthropogenic factors; fishing down the food web – gradually harvesting fish species in the ecosystem to the extent of extinction starting from higher trophic level species down to lower trophic level species - and nutrient enrichment that led to increasing proliferation of opportunistic organisms in the ecosystem as a consequence of the removal of predatory and competitive controls in the food web. This, in turn, caused the transfer of large quantities of energy to these trophic dead-end opportunistic groups of organisms; i.e. jellyfish and heterotrophic dinoflagellates. Concurrently, an alternative short pathway for energy transfers was formed which converted significant amounts of system production back to detritus rather than transferring up through the food web to produce fish biomass by decreasing the transfer efficiency of energy flows from the primary producers to the higher trophic levels from 9% in the 1960s to 3% in the period from 1980-1987.

The time-dynamic model results (chapter 3 and 5) delineated that a break down in the ecosystem's balance (homeostasis) *sensu* Odum (1985) happened with eutrophication, overfishing and establishment of trophic dead-end organisms. The sensitivity tests showed that interspecies competition and overfishing were the main drivers of changes within the ecosystem which were exacerbated by overpopulation of some r-selected organisms; i.e. *Noctiluca* and jellyfish species, in the food web and these were moderated by the changes in the primary production in the ecosystem. Incessant fisheries overexploitation since the beginning of 1980s that caused the anchovy stock decline continuously and lead to increasing resource competition between jellyfish and small pelagic fish brought about the anchovy stock collapse in 1989. The predation exerted by *Mnemiopsis* on small pelagic fish eggs was found to be of secondary importance compared to the resource competition. However, all these stressors acted concomitantly in eroding the structure and functioning of the ecosystem by manipulating the food web to reorganise itself by means of introduced and selectively removed organisms so that the average path length of recycled flows was shortened and the transfer efficiency of energy to higher trophic levels was further reduced to deprive the ecosystem of commercially important fish assemblages.

The coupled model forecast simulations (chapter 5) showed that a decrease in the commercial fish stocks was predicted during 2080-2099 due to fisheries exploitation. If current fishing intensity levels were kept status quo, some economically important small pelagic fish species of the Black Sea will likely disappear from the catches let alone the recovery of more valuable piscivorous fish stocks. In addition, maintaining the current exploitation levels of the fish stocks in the Black Sea was predicted to cause a further decrease in the proportion of large fish by weight in the whole fish community in the future. Fisheries were found to be the main driver in determining the future state of the stocks under changing environmental conditions. For management purposes, along with decreasing fishing mortality levels of the target stocks, monitoring and management of other fish species that were tightly coupled with the target species as a measure were found to be the most effective way of fisheries management and sustainable utilisation of fish stocks.

Keywords: Black Sea, ecosystem modelling, fisheries, food web dynamics, anthropogenic and climate variations

ÖZ

KARADENİZ EKOSİSTEMİNİN DOĞRUSAL OLMAYAN DİNAMİKLERİ VE ANTROPOJENİK VE İKLİMSEL DEĞİŞKENLERE OLAN TEPKİSİ

AKOĞLU, Ekin

Doktora, Deniz Bilimleri Enstitüsü

Tez Yöneticisi: Yrd. Doç. Dr. Barış SALİHOĞLU

Temmuz 2013, 126 sayfa

Bu doktora tezinin amacı; i) Karadeniz ekosisteminde 1960-1999 yılları arasında gerçekleşen değişimlerin kantitatif olarak açıklanması, ii) genel ve 1989 yılında gerçekleşen hamsi – *Mnemiopsis* değişimi esnasındaki besin ağı dinamiklerinin tanımlanması, ve iii) bu bulguları kullanarak Karadeniz ekosisteminin gelecekte öngörülen fiziksel ve biyojeokimyasal değişimler altında gösterebileceği değişimlerin araştırılmasıdır. Bu amaçla, tez kapsamında birbirinden farklı fakat birbirini tamamlayan üç farklı ekosistem modellemesi yaklaşım kullanılmıştır. Bu yaklaşımlar tez içerisinde; i) Karadeniz ekosisteminin geçirdiği dört farklı rejim altındaki yapısı ve işleyişinin ekolojik indikatörler aracılığı ile kantitatif olarak analizinin gerçekleştirildiği Ecopath kütle-denge modelleri kullanılarak oluşturulan sabit-hal modelleme yaklaşımı, ii) Karadeniz ekosisteminin 1960-1999 yılları arasındaki lineer olmayan besin ağı dinamiklerinin kütle-denge modelleri ile incelenmiş olan dört farklı rejim arasındaki geçişlere neden olan etkenlerinin tanımlandığı Ecosim dinamik modelleme yaklaşımı, ve iii) gelecekte öngörülen fiziksel ve biyojeokimyasal değişiklikler altında Karadeniz ekosisteminin gösterebileceği değişimleri araştıran ve ekosistemin tekrar "iyi çevresel durum" statüsüne ulaşabilmesi için gereken yönetim stratejilerinin sorgulandığı üst trofik seviye Ecopath with Ecosim (EwE) ve fiziksel – biyojeokimyasal BIMS-ECO modellerinin kullanıldığı bütünleşik modelleme yaklaşımı olmak üzere üç ayrı başlık altında incelenmiştir. Araştırmada kullanılan bütün modeller geçmiş zaman serisi verileri ve "Sanal Popülasyon Analizi" gibi klasik

modelleme yöntemleri ile elde edilmiş sonuçlar kullanılarak karşılaştırmalı olarak değerlendirilmiştir.

Kütle-denge model (bölüm 2) sonuçları Karadeniz ekosisteminin yapısının 1960'lardan sonra besin ağında gerçekleşen bir dizi trofik dönüşümler sonucunda değiştiğini ortaya koymuştur. Bu trofik değişimler; besin ağında aşağıya doğru avcılık; diğer bir değişle balıkçılığın ekosistemdeki balık popülasyonlarını yüksek trofik seviyeden başlayarak aşamalı bir şekilde alt trofik seviye balık türlerini hedef alacak şekilde ilerlemesi ve ekosistemde fırsatçı organizmaların artışına sebep olacak şekilde besin ağında gerçekleşen av-avcı ve rekabetçi mekanizmaları ortadan kaldırarak sistemdeki üretimin büyük bir kısmının trofik çıkmaz-sokak olan fırsatçı organizmalara; örn. denizanaları ve heterotrofik dinoflagellatlar, yönlenmesini sağlayan besin zenginleşmesi olmak üzere iki temel antropojenik faktör etkisinde gerçekleşmiştir. Bununla eş zamanlı olarak, sistem üretiminin önemli bir kısmının üst trofik seviyelerdeki balık popülasyonlarına ulaşamadan tekrar detritusa aktarılmasını sağlayan alternatif bir enerji transfer kısa yolu oluşmuştur. Bu kısa yol neticesinde, birincil üreticilerden üst trofik seviye organizmalara ulaşan enerji transferinin verimliliği 1960'larda % 9' dan 1980-1987 yılları arasında % 3' e kadar azalmıştır.

Dinamik model sonuçları (bölüm 3 ve 5) ise ötrofikasyon, aşırı avcılık ve trofik çıkmaz-sokak türlerin aşırı artışı ile birlikte ekosistemin dengesinde (Odum, 1985) bir kırılma gerçekleştiğini ortaya koymuştur. Model duyarlılık testleri, türler arası rekabet ve aşırı avcılığın ekosistemde gerçekleşen değişimlerin ana kaynağı olduğunu göstermiş ve bu değişimlerin *Noctiluca* ve denizanası gibi fırsatçı türlerin besin ağında aşırı artışı ile daha ciddi boyutlara ulaştığını ve tüm bu etkenlerin birincil üretimdeki değişimlerin etkisi altında seyrettiğini ortaya koymuştur. 1980'lerin başından beri aralıksız devam eden aşırı avcılık, hamsi stokunun sürekli olarak azalmasına ve buna ek olarak giderek artan ötrofik koşullar neticesinde sayıca aşırı olarak artan denizanası türleri ile hamsi popülasyonu arasındaki besin rekabetinin şiddetinin artmasına yol açmış ve nihayetinde 1989 yılında hamsi stoklarının çökmesiyle sonuçlanmıştır. *Mnemiopsis* türünün hamsi larva ve yumurtaları üzerindeki yeme baskısının bu iki tür arasındaki besin rekabetine kıyasla ikinci planda kaldığı bulunmuştur. Bununla birlikte, tüm bu stres faktörleri eş zamanlı gerçekleşerek, yabancı türlerin ekosisteme tanıtılması ve bazı balık türlerinin sistematik olarak ekosistemden çıkarılması

aracılığıyla, sistemde dolaşan resirküle madde akışının ortalama dolaşım mesafesinin ve enerji transfer verimliliğinin azalmasına neden olmuştur. Tüm bunların etkisi altında gerçekleşen besin ağı organizasyonun yeniden şekillenmesi sonucunda ekosistemdeki ekonomik açıdan değerli balık türleri önemli ölçüde azalmış ve ekosistemin doğal yapısı ve işleyişi bozulmuştur.

Bütünleşik model sonuçları (bölüm 5) 2080-2099 yılları arasında, balıkçılık baskısına bağlı olarak ticari balık stoklarında bir azalma gerçekleşebileceğini ortaya koymuştur. Günümüz balıkçılık baskısı seviyeleri gelecekte de devam ettiği koşulda, büyük pelajik balık türlerinin geri kazanılmasının mümkün olamayabileceği ve dahası günümüzde var olan bazı ekonomik balık türlerinin de ekosistemden kaybolabileceği öngörülmüştür. Buna ek olarak, balık türleri üzerindeki günümüz balıkçılık baskı seviyelerinin gelecekte de devam etmesi durumunda ekosistemdeki nispi büyük balık miktarının gelecekte daha da azalacağını göstermiştir. Balık stoklarının değişen iklim koşulları altında gelecekteki durumunu belirleyecek olan en önemli etkenin balıkçılık baskısı olduğu bulunmuştur. Bu durum göz önüne alınarak yönetimsel açıdan bakıldığında, korunması hedeflenen balık türleri üzerindeki balıkçılık ölümlerinin azaltılmasının yanı sıra, bu türler ile besin ağında bütünleşik (sıkı) ilişkiler içerisinde olan diğer türlerin izlenmesi ve stoklarının yönetimi gelecekte balık stoklarının sürdürülebilir bir şekilde kullanılabilmesinin en verimli yolu olacağı ortaya konmuştur.

Anahtar Kelimeler: Karadeniz, ekosistem modellemesi, balıkçılık, besin ağı dinamikleri, antropojenik ve iklimsel değişimler

To my wife, for her endless love and unyielding support.

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my advisor, Dr. Barış Salihoğlu, for his never-ending guidance, support, and patience during the whole course of my PhD study. Dr. Salihoğlu has been much more than just an advisor to me during this period of my life. He has also been a friend, a continuous source of inspiration and a colleague with whom I could have the chance to discuss many aspects of my research so as to prosper transferring my ideas from just being ideas to sound scientific ground. I am also indebted to Dr. Salihoğlu for providing me opportunities and support to attend meetings, workshops and conferences related to my field of research, all of which definitely contributed my development in the way to become a scientist.

I am also thankful for the contributions and comments of my thesis committee members; Dr. Ahmet Kıdeyş, Dr. Zahit Uysal, Dr. Bettina Fach Salihoğlu and Dr. Cosimo Solidoro. Their contributions to me in constituting this research as a PhD thesis are invaluable. Further, I would also like to thank Dr. Ferit Bingel, an earlier member of my thesis committee until he retired, for his insightful comments, suggestions and contributions.

I am grateful to Dr. Temel Oğuz, without whom I could not be part of and collaborate to many outstanding projects and research activities without which I would miss valuable scientific and research experience as well as opportunities to meet, discuss with and learn from many leading scientists in the field of oceanography. Dr. Oğuz’s help, tutoring and contributions to my PhD research could not be explained by plain words and without his support and guidance many valuable aspects of this PhD research would be missing.

I would like to thank Dr. Bettina Fach Salihoğlu also for providing me her expertise on, model details and results from the BIMS-ECO biogeochemical model of the Black Sea, upon which I have built the higher-trophic-level (HTL) model detailed in Chapter 5. Without her, there would be no coupled lower trophic level (LTL) – HTL modelling. I am also thankful to Dr. Heather Cannaby for running the BIMS-CIR hydrodynamic model of the Black Sea, therefore, making all the LTL and HTL modelling efforts possible.

I am indebted to Dr. Simone Libralato and Dr. Cosimo Solidoro for their great contribution, help and support. Their expertise and guidance made the first and fourth chapters of this thesis work possible.

I would like to express my gratitude to Dr. Sinan Arkın, Dr. Valeria Ibello, Çağlar Yumruktepe, Nusret Sevinç, Ceren Güraslan, Anıl Akpınar, Özge Yelekçi and Ayşe Gazihan Akoğlu for our fruitful discussions during our weekly "*Ecomodel*" meetings on various parts of this thesis research. Further, I would also like to thank Dr. Ali Cemal Gücü for sharing his valuable thoughts and comments with me in various stages of this study, especially concerning topics related to fisheries.

Last but not least, I owe my dearest wife, Ayşe Gazihan Akoğlu, a heartful of thanksgiving for her support, love and encouragement she provided and most importantly her belief in me since the very first moment we met.

Major parts of this thesis study were made possible and supported by the international projects of the Institute of Marine Sciences, Middle East Technical University, namely; Black Sea SCENE (http://www.blackseascene.net/), SESAME (Southern European Seas: Assessing and Modelling Ecosystem Changes), MEECE (Marine Ecosystem Evolution in a Changing Environment, www.meece.eu), ODEMM (Options for Delivering Ecosystem-based Marine Management, (http://www.liv.ac.uk/odemm/), PERSEUS (Policy-orientated marine Environmental Research for the Southern European Seas, http://www.perseus-net.eu/) and OPEC (Operational Ecology, http://marine-opec.eu/).

Table of Contents

List of Tables

List of Figures

1. CHAPTER: Thesis introduction

This thesis work was dedicated to explore and discover the historical and contemporary ecosystem characteristics of the Black Sea, the structure and functioning of its food web and its interactions with anthropogenic and climatological factors. The fundamental approach used to achieve the objectives was based on ecological modelling practices using three different schemes; i) a mass-balance modelling scheme, ii) a time-dynamic modelling scheme, and iii) a coupled end-to-end lower trophic level (LTL) and higher-trophic-level (HTL) modelling scheme. For this purpose, the widely adopted Ecopath with Ecosim (hereinafter EwE, Christensen, 2005) model was used in each scheme. The mass-balance modelling scheme incorporated the Black Sea ecosystem's food web structure over the second half of the 20th century using Ecopath snapshots of four discrete periods of the Black Sea between 1960-1969, 1980-1987, 1988-1994, and 1995-2000 by averaging conditions of the food web structure of the respective periods over its time frame. The time-dynamic modelling scheme took this discrete mass-balance Ecopath modelling approach onto a continuous Ecosim simulation between 1960 and 1999 and investigated the dynamics of the food web components under changing environmental and anthropogenic conditions. Finally, this time-dynamic model of the Black Sea was coupled with a detailed biogeochemical model of the Black Sea; BIMS-ECO, in order to investigate the future progressions of the ecosystem under projected future climate scenarios.

This work utilised a broad set of ecological indicators in order to bisect the Black Sea's environmental evolution (status over time) and tried to address and develop options for delivering ecosystem-based management practices which fell within the scope of the Marine Strategy Framework Directive (hereinafter MSFD, 2008/56/European Commission). MSFD is a framework that requires good environmental status (GES) to be achieved in all European Regional Seas by the year 2020 via implementing necessary management and research policies. The Black Sea is considered as one of the European regional seas due to the fact that some of its riparian countries are EU members, i.e. Bulgaria and Romania, or, like Turkey, is a candidate to become a full member. Therefore, it is of utmost benefit to Turkey to aim GES not only in the Black Sea but also in all of its national seas.

For the purpose of reaching GES, the current status of the marine ecosystems should be quantitatively documented in order to determine how far the status of any given sea ecosystem is away from reaching GES. Further, GES itself should be quantitatively identified so as to provide knowledge about what it is to aim in order to achieve GES in a given marine ecosystem. For this purpose, Cardoso et al. (2010) elaborated the eleven MSFD descriptors to provide quantitative criteria to assess the status of marine ecosystems and defined that in what condition the marine ecosystems could be considered in GES. They provided definitions to eleven descriptors made up of several indicators to delineate the GES and these descriptors were as follows:

1. Biological diversity
2. Non-indigenous species
3. Commercially exploited fish and shellfish populations
4. Food webs
5. Eutrophication
6. Sea floor integrity
7. Hydrographical conditions
8. Contaminants
9. Food safety
10. Litter
11. Energy and noise

In relation to the modelling approach adopted in this study, the analyses and the methodology used provided quantitative indicators to five of these eleven descriptors, namely i) biological diversity, ii) non-indigenous species, iii) commercially exploited fish and shellfish populations, iv) food webs and v) eutrophication. These five descriptors and the related indicators used in this thesis' study were as follows:

1. Biological diversity: This descriptor was defined in Cardoso et al. (2010) in accordance with the Convention on Biological Diversity (United Nations, 1992) as "*the variability among living organisms from all sources*

including, inter alia, [terrestrial,] marine [and other aquatic ecosystems] and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems". Three of its four attributes given in Cardoso et al. (2010) and its related indicators were of concern in this thesis study, namely; i) species state, ii) habitat/community state, and iii) ecosystem state. In this study, the indicators used related to these attributes and their explanations were summarised in Table 1.

Table 1. Indicators of biological diversity used in the study and their explanations.

Attribute	**MSFD Criteria**	**MSFD Indicators**	**Corresponding Indicators (this study)**	**Explanation**
Species state	Population size	Population biomass	Population biomass	The population biomass of any given species should be within safe biological limits so as not to drive itself to vulnerable conditions in terms of extinction.
	Population condition	Population demography	Brody growth coefficient (K) Recruitment power Instantaneous mortalities (F, M, Z)	Every population of any given species in an ecosystem should be able to self-sustain by means of its reproductive capabilities and growth performance, both of which should not be compromised by anthropogenic and/or natural stressors. Mortality levels should not exceed limits so as to cause depletion of the population in time.
		Inter- and intra-specific interactions	Mixed Trophic Impact (MTI)	Any particular species should not dominate the system so as to cause negative feedbacks to other native species. Concerning intraspecific interactions, any given cohort in a population should not dominate so as to cause negative feedback mechanisms that risk the sustainability of its population (e.g. cannibalism)
Habitat/community state	Community condition	Species composition	mean Trophic Level of community (mTLco), mean Trophic Level of catch (mTLc), Kempton's Q Index, Groups ratios	The composition of organisms in a given ecosystem should be in a state so that the proportions of the species should not adversely affect the well-being of other species or the structure and functioning of the ecosystem.
		Community biomass	mean Trophic Level of community (mTLco), Kempton's Q, Groups ratios	The community in an environment should be made up of natural proportions of the resident species so as not to dominate others adversely.
		Functional Traits	Keystoneness	Functional traits define species in terms of their ecological roles in the ecosystem, i.e. their impact on ecosystem functioning. Effects of diversity in functional traits on ecosystem processes should be evaluated (Diaz and Cabido, 2001).

Ecosystem state	Ecosystem structure	Composition and relative proportions of the ecosystem components	Community ratios	The composition and proportions of the communities that form the ecosystem should not be in negative feedback state; i.e. inhibiting each other so as to cause malfunction in the ecosystem by means of invading others' resources or habitat (e.g. Harmful Algal Blooms - HAB).
	Ecosystem processes and functions	Interactions between structural components of the ecosystem	Mixed Trophic Impact (MTI), Keystoneness	This is similar to the interspecific and intraspecific interactions on the ecosystem state.

2. Non-indigenous species (NIS): This descriptor was defined in Cardoso et al. (2010) as "*species, subspecies or lower taxa introduced outside of their natural range (past or present) and outside of their natural dispersal potential*". This category also included invasive alien species (IAS). IAS were defined as "*a subset of NIS which have spread, are spreading or have demonstrated their potential to spread elsewhere, and have an adverse effect on biological diversity, ecosystem functioning, socio-economic values and/or human health in invaded regions*" (Cardoso et al., 2010). Two of its five attributes were of concern in this thesis study as summarised in Table 2.

Table 2. Indicators of non-indigenous used in the study and their explanations.

Attribute	**MSFD Criteria**	**MSFD Indicators**	**Corresponding Indicators (this study)**	**Explanation**
# of NIS recorded in the area	Reduced risk of new invasions	Ratio between NIS and other species	Group ratios	The dominancy of NIS in a given habitat makes the ecosystem vulnerable to other invasions. Therefore, the ratio should be within safe biological limits so as not to dominate the system or other species in the ecosystem.

Environmental impact of IAS on ecosystem functioning	Absence or minimal impact of IAS adversely affecting environmental quality	Shifts in trophic nets, alteration of energy flow and organic matter cycling	Cycling indicators (Finn's Cycling Index), Finn's mean path length, proportion of flows to detritus, transfer efficiency analysis of energetic flows	The IAS should not reach to the extent that they will cause leakage in the structure and functioning in the ecosystem by means of loss of production in the food web.

3. Commercially exploited fish and shellfish populations: This descriptor applied to all living marine resources used for economical purposes (Cardoso et al., 2010). The attributes used in this thesis work and its related indicators were summarised and explained in Table 3.

Table 3. Indicators of commercial fish used in the study and their explanations.

Attribute	**MSFD Criteria**	**MSFD Indicators**	**Corresponding Indicators (this study)**	**Explanation**
Sustainability of the exploitation	High long-term yield	Fishing mortality (F), ratio of catch to biomass	Fishing mortality (F), Ratio of catch to biomass	The fisheries should not deplete the stocks. The fisheries exploitation levels (F/Z) should not approach unity in adult stocks.
Reproductive capacity	No compromise of reproductive capacity	Spawning stock biomass	Spawning stock biomass	The reproductive capacity of any given population should not be exploited to the extent that the populations cannot self-sustain themselves through their natural reproductive processes.

4. Food webs: This descriptor concerned the structure and functioning in any given marine ecosystem with respect to organic matter recycling, energy

transfers and roles of the components in the food webs Table 4.

Table 4. Indicators of food webs used in the study and their explanations.

Attribute	**MSFD Criteria**	**MSFD Indicators**	**Corresponding Indicators (this study)**	**Explanation**
Energy flows in the food web	Production or biomass ratios of components	Ratio of pelagic to demersal fish Zooplankton production required to sustain catches	Ratio of pelagic fish biomass to demersal fish biomass Ratio of piscivorous fish biomass to forage fish biomass Ratio piscivorous fish biomass to other fish biomass Primary production required (PPR) to sustain catches	The production in the food web should not be selectively exported by fisheries in exceeding levels so as to change the natural proportions of the native populations in the ecosystem to cause diversions or leakage in the flows of the food web.
	Trophic relationships securing long-term viability of components	Trophic levels (functional groups)	Trophic level decomposition (energetic flow analysis) Biomass by trophic level	The energy flows in the food web should be sufficiently distributed across all trophic levels. Trapping-down of energy in one of the trophic levels may cause loss in system's production.
Structure of food webs	Proportion of large fish maintained	Proportion of large fish by weight	Proportion of large fish by weight	This is an indicator of the fishing pressure as well as how the flows (energy, production) in the ecosystem are shared among its components. In any given ecosystem, the higher trophic levels should be sufficiently represented by predatory species.
	Abundance / distribution maintained	Charismatic indicator species	Keystoneness	These species indicate whether a food web in an ecosystem is performing well, i.e. have the diversity in the web that could be used as indicators of flows in the ecosystem. Such species are usually marine mammals and large fish species.

		Groups species targeted by fishing and their response to exploitation	Fishing in Balance Index (FiB) Mean trophic level of catch (mTLc)	Similar to biomass ratios of components, the trophic levels in a food web should not be underrepresented by means of continuous selective extraction of certain components so as to cause overpopulation in certain levels of the food web.

5. Eutrophication**:** This descriptor concerned human-introduced eutrophication and its adverse effects in terms of damage to the ecosystem structure and functioning Table 5.

Table 5. Indicators of eutrophication used in the study and their explanations.

Attribute	**MSFD Criteria**	**MSFD Indicators**	**Corresponding Indicators (this study)**	**Explanation**
Phytoplankton biomass	Increase / decrease	Opportunistic species	Ratio of opportunistic r-selected species to K-selected species	Used as a proxy for deterioration of primary production to cause adverse effects on the higher trophic level communities.

All of the above attributes and related criteria and indicators were discussed in the forthcoming chapters. The chapters 2, 3 and 5 examined the ecosystem structure and functioning with increasing level of complexity. **The second chapter was dedicated to analyse and assess the ecosystem structure and functioning of the Black Sea ecosystem utilising mass-balance snapshots of the discrete phases it had undergone in the second half of the twentieth century through a set of synthetically calculated ecological indicators of energetic flows, catches and biomasses.**

The third chapter elaborated the analyses given in the second chapter using a dynamic EwE model of the Black Sea ecosystem between 1960 and 2000, and examined the time-dynamic changes of a broader set of ecological indicators in search for different regimes prevailed during the changes the Black Sea had

undergone and the causes behind the shifts of the detected regimes as well as the dynamic evolution of the ecological indicators and what they did represent throughout the simulation period in terms of functioning of the Black Sea ecosystem.

The fourth chapter dealt with technical difficulties of coupling EwE models with biogeochemical models that were mostly written in FORTRAN and, hence, presented the FORTRAN transcription of the EwE model in order to make this powerful modelling tool ready for coupling with such models.

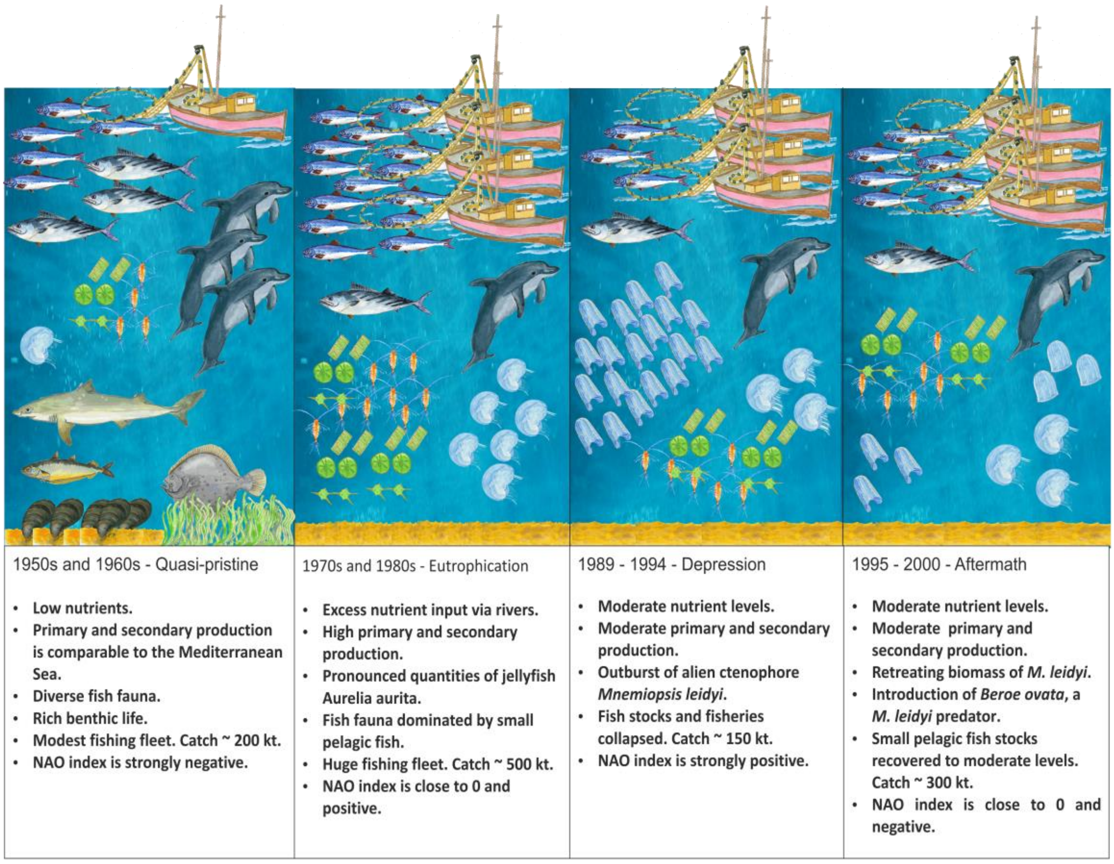
The fifth chapter expanded the time-dynamic model of the Black Sea used in the third chapter so as to include a sophisticated lower trophic level representation by coupling with a biogeochemical model of the Black Sea in order to investigate the impacts of the changes in the lower trophic level compartments under climatologic and anthropogenic drivers on the higher trophic level assemblages of the Black Sea between 1980 and 1999. This chapter also elaborated the investigation of the ecological indicators used in the previous chapters in more detail in order to describe the impacts of inclusion of a refined representation of the lower trophic level compartment on the higher trophic level organisms and aimed to explain the changes in the Black Sea from a more detailed perspective. It also aimed to answer the question of under which conditions and ecosystem-based management practices the Black Sea ecosystem could be improved towards its GES. Further, this chapter included a forecast simulation for the Intergovernmental Panel on Climate Change (IPCC) A1B carbon emission scenario in order to investigate the impacts of predicted climatologic changes between 2080 and 2099 on the Black Sea ecosystem. Finally in the sixth chapter, a summary was given in relation to the above mentioned MSFD indicators by making a detailed diagnosis of the Black Sea ecosystem structure and functioning from the perspective of its GES.

2. CHAPTER: An indicator-based evaluation of the Black Sea food web dynamics during 1960 – 2000 using mass-balance HTL models

2.1. Introduction

The Black Sea ecosystem had been through significant trophic transformations over the second half of the 20th century (Oguz and Gilbert, 2007). The history of these changes could be classified into four distinctive periods; 1) the 1960s - pre-eutrophication, 2) 1980-1987 - representing intense eutrophication, 3) 1988-1994 - the infamous *Mnemiopsis leidyi* (Agassiz, 1865) – anchovy shift, and 4) 1995-2000 - signifying the post-eutrophication phase (Figure 1). The principal reasons for these transformations have long been debated (Zaitsev, 1992; Shiganova, 1998; Kovalev and Piontkovski, 1998; Kovalev et al., 1998; Kideys et al., 2000; Oguz et al., 2003; Yunev et al., 2002, 2007; Bilio and Nierman, 2004; Oguz and Gilbert, 2007; McQuatters-Gollop et al., 2008). Whilst primarily focusing on the anchovy - *Mnemiopsis* shift in 1989 (Kideys, 2002), studies sought answers to enhance comprehension of the mechanisms underlying the observed changes (Berdnikov, 1999; Daskalov, 2002; Gucu, 2002; Daskalov et al., 2007; Oguz, 2007; Oguz et al., 2008a, b; Llope et al., 2011). The roles of trophic cascades through overfishing (Daskalov, 2002; Gucu, 2002), *Mnemiopsis leidyi* (hereafter referred to as *Mnemiopsis)* predation on anchovy eggs and larvae (Lebedeva and Shushkina, 1994; Shiganova and Bulgakova, 2000; Kideys, 2002) and the combination of bottom-up and top-down controls (Bilio and Nierman, 2004; Oguz, 2007; Oguz et al., 2008a, b) were all suggested as significant factors catalysing these changes.

The pre-eutrophication phase of the 1960s characterised a healthy mesotrophic ecosystem with primary production values between 100-200 mgC m^{-2} y^{-1} (Oguz et al., 2012). Relatively rich biological diversity of the 1960s' Black Sea comprised fishes from large demersal fish species such as turbot (*Psetta maeotica,* Pallas, 1814), Black Sea striped mullet (*Mullus barbatus ponticus*, Essipov, 1927), spiny dogfish (*Squalus acanthias*, Linnaeus, 1758), and Black Sea whiting (*Merlangius merlangus euxinus,* Nordmann, 1840) to piscivorous pelagic fish; Atlantic bonito (*Sarda sarda*; Bloch, 1973), bluefish (*Pomatomus saltator*; Linnaeus, 1776), and Atlantic mackerel (*Scomber scombrus*; Linnaeus, 1758) as well as small pelagic fish; predominantly the Black Sea anchovy (*Engraulis encrasicolus ponticus*; Alexandrov, 1927), Black Sea horse mackerel (*Trachurus mediterraneaus ponticus*; Aleev, 1956), and Black Sea sprat (*Sprattus sprattus phalaericus*; Risso, 1827). Three cetacean species; the Black Sea common dolphin (*Delphinus delphis spp. ponticus*; Barabash-Nikiforov, 1935), the Black Sea bottlenose dolphin (*Tursiops truncatus spp. ponticus;* Barabasch, 1940), and the Black Sea harbour porpoise (*Phocoena phocoena spp. relicta*; Abel, 1905) constituted the top predators of the system. During the subsequent two decades, the stocks of both pelagic piscivorous fishes and marine mammals had been overexploited and further, primary and secondary pelagic production increased excessively due to nutrient enrichment from the rivers discharging mainly into the northwestern shelf of the Black Sea. The small pelagic fish species and the moon jelly; *Aurelia aurita* (Linnaeus, 1758), thus became dominant in the ecosystem. The benthic flora and fauna deteriorated to a great extent due to the frequent hypoxia events on the shelf waters (Zaitsev, 1992; Zaitsev and Mamaev, 1997; Mee, 2006). Simultaneously, the Turkish fishing fleet developed enormously in size and technology (Gucu, 2002) and the fisheries yield attained 700 kt, a significant proportion (~500 kt) of which consisted of anchovy. In 1989, the non-indigenous comb jelly species *Mnemiopsis leidyi* (Agassiz, 1865), which was introduced to the Black Sea ecosystem in the early 1980s via the ballast waters of shipping vessels, flourished both in abundance and biomass. This same year also coincided with the collapse of the total Turkish fisheries yield from an average of 700 kt during the early 1980s to only 150 kt in 1989 (Oguz, 2007). Subsequently, the Turkish fishery yield recovered to about 300 ± 100 kt whereas it remained at very low levels throughout the rest of the Black Sea (Oguz et al., 2012). During this recuperation period, blooms of *Mnemiopsis* were suppressed naturally due to the appearance of another non-indigenous gelatinous species; *Beroe ovata* (Mayer, 1912), an inherent *Mnemiopsis* predator. By the end of the 1990s, the Black Sea ecosystem as a whole was characterised by moderate primary (200-400 mgC m^{-2} y^{-1}, Oguz et al. (2012)) and secondary productivity (Mee, 2006; McQuatters-Gallop, 2008) although the ecosystem of the northwestern shelf and western coastal waters were still far from recovery and rehabilitation (Oguz and Velikova, 2010).



1950s and 1960s - Quasi-pristine	1970s and 1980s - Eutrophication	1989 - 1994 - Depression	1995 - 2000 - Aftermath
• Low nutrients. • Primary and secondary production is comparable to the Mediterranean Sea. • Diverse fish fauna. • Rich benthic life. • Modest fishing fleet. Catch ~ 200 kt. • NAO index is strongly negative.	• Excess nutrient input via rivers. • High primary and secondary production. • Pronounced quantities of jellyfish Aurelia aurita. • Fish fauna dominated by small pelagic fish. • Huge fishing fleet. Catch ~ 500 kt. • NAO index is close to 0 and positive.	• Moderate nutrient levels. • Moderate primary and secondary production. • Outburst of alien ctenophore *Mnemiopsis leidyi*. • Fish stocks and fisheries collapsed. Catch ~ 150 kt. • NAO index is strongly positive.	• Moderate nutrient levels. • Moderate primary and secondary production. • Retreating biomass of *M. leidyi*. • Introduction of *Beroe ovata*, a *M. leidyi* predator. • Small pelagic fish stocks recovered to moderate levels. Catch ~ 300 kt. • NAO index is close to 0 and negative.

Figure 1. The schematic illustration of the four periods in the Black Sea. The figure was depicted based on the classifications in the published literature and inspired from an earlier work (Fig. 10) in Langmead et al. (2007).

In order to investigate the aforementioned changes and the underlying mechanisms, the various aspects of the functioning of the Black Sea lower trophic food web were studied in terms of aggregated biogeochemical models (e.g. Oguz and Salihoglu, 2000; Oguz et al., 2001, 2008b; Oguz and Merico, 2006; Lancelot et al., 2002; Gregoire and Lacroix, 2003; Gregoire and Friedrich, 2004; Gregoire et al., 2004, 2008; Gregoire and Soetaert, 2010; Tsiaras et al., 2008; Staneva et al., 2010; He et al., 2012). Further, mass-balance models of different complexities were also invoked by Gucu (2002), Daskalov (2002), and Orek (2000). Gucu (2002) focused on the second half of the 1980s when examining the role of increased fishing pressure on the collapse of anchovy stocks, whereas Daskalov (2002) adopted a broader time frame starting from the pre-eutrophication period and pointed out that trophic cascade initiated by overfishing played a leading role on the ecosystem changes. However, both of these studies lacked the quantification and insight of ecosystem characteristics of the Black Sea during these changes. **In this chapter of thesis work, we expanded upon these previous works by using a set of indicators which quantify the condition of the ecosystem for the systematic analysis of each defined ecosystem period and providing understanding of the interactions between the food web components that led to the aforementioned changes in the Black Sea.** Our approach was taken from the point of the "ecosystem health" which will ultimately form reference points for the evaluation of the transformations of the Black Sea's ecosystem structure and functioning over recent decades based on quantitative ecosystem metrics. Here, ecosystem health was used to define the potential of an ecosystem to sustain its structure and functioning over time under stress (Shaeffer et al., 1988; Costanza, 1992; Haskell et al., 1992; Costanza and Mageau, 1999). The methodology adopted to assess ecosystem health was to apply ecological network analysis (Ulanowicz, 1986) on the mass-balance snapshots of the ecosystem and utilise its derived ecological indicators of four quasi-persistent, i.e. characterised by distinctive prevailing conditions, ecosystem states as described above. Such techniques, although using in-situ data with a limited set of indicators that are applicable to many regions, are currently being applied to many other seas within the scope of the Indiseas project (www.indiseas.org). The Indiseas project aims to determine a set of reliable ecological indicators to be applied globally regardless of the ecosystem characteristics under investigation with the target of establishing a baseline for comparative studies of contrasting marine ecosystems. **In this thesis chapter, the static mass-balance trophodynamic models of the Black Sea with the implementation of ecological indicators were used for the analysis of food web dynamics from 1960 to 2000. This chapter may be considered as the first example of employing ecological indicators for the analyses and evaluation of historical food web changes in this particularly much exploited and biologically diverse ecosystem.** A better understanding of the roles played by ecosystem drivers and key species is vital for future ecosystem management of the Black Sea in the face of continuous anthropogenic pressures and climatic change.

2.2. Materials and Methods

The static mass-balance modelling of the food web was implemented by developing an Ecopath (Christensen et al., 2005) food web model for each ecosystem period (Figure 1). The Ecopath models of the Black Sea were built to represent the general food web structure of the inner Black Sea basin, avoiding the extremely variable conditions of the Northwestern Shelf (NWS). The model covered an area of 150 000 km^2 where fisheries operated intensively (Oguz *et al.*, 2008a) in the vicinity of the exclusive economic zones (EEZs) of the six riparian countries. The geographical representation of the model did not include depths greater than 150 m in the open Black Sea where anoxia prevails.

2.2.1. The Model Setup

Four mass-balance Ecopath models were set up to represent the four distinctive periods of the Black Sea ecosystem as described in the previous section. Ecopath comprises a series of linear equations that define a mass-balance state of the food web in the form of functional groups (each representing a species or groups of species) linked by trophic interactions. The functional groups are regulated by gains (consumption, immigration) and losses (mortality, emigration), and are linked to each other by predator-prey relationships. Fisheries extract biomass from the targeted and by-catch groups. Each linear equation describes flows of mass into and out of discrete biomass pools of the form

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

where for each functional group i, B stands for biomass, $(P/B)_i$ stands for the production to biomass ratio, $(Q/B)_j$ stands for the consumption to biomass ratio 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 migration rate, *BA* is the biomass accumulation rate, and *EE* is the proportion of the production utilised in the system (Christensen et al., 2005). *EE* must be less than or equal to unity under the assumption of mass-balance conservation. *E* and *BA* values were assumed to be zero for all groups. Typically, three of *B*, *(P/B)*, *(Q/B)* or *(P/Q)* and *EE* parameters and diet composition are defined as input for each functional group and the values of remaining parameters are estimated by the Ecopath mass-balance algorithm. Ecopath software computes mass-balance by solving the system of equations for the unknown parameters of all groups. A balanced model, however, might not be obtained at the first parameterisation, thus it may require iterative adjusments to the input values (usually the diet composition) following the guidelines given by Christensen et al. (2005).

The model set-up in this investigation presented a simplified representation of the pelagic food web structure using ten functional groups (Table 6); five of which were the guilds of ecologically similar species, namely dolphins, pelagic piscivorous fish, demersal fish, small pelagic fish, zooplankton and phytoplankton, whilst the other three groups were individual species; the comb jelly *Mnemiopsis*, the moon jelly *Aurelia aurita* (hereafter referred to as *Aurelia*) and the heterotrophic dinoflagellate *Noctiluca scintillans* (Ehrenberg, 1834) (hereafter referred to as *Noctiluca*). These organisms were represented by exclusive groups since they played specific roles (r-selected behaviour; Pianka, 1970) in ecosystem functioning and were important indicators of ecosystem changes during the specified periods. Since the aim of this chapter was to investigate the changes in ecosystem structure of the Black Sea and not the interactions amongst different types of fisheries, fisheries were collectively represented although the Black Sea industrial fisheries included mainly three gears; trawling, gill-netting and seining. Thus, a single fleet was considered in the model, and fisheries yields by species were pooled to ensure correctly aggregated catches for each functional group. For each modelled state of the Black Sea, an average annual catch value was calculated from the data for the period investigated. The average value was then divided by the total area of the fishing grounds (150 000 km^2; Oguz et al., 2008a) to obtain the yield per unit of fishing area.

Table 6. Trophic groups and main species included in the model setup.

Groups	**Main Species**
Dolphins	Black Sea common dolphin Black Sea bottlenose dolphin Black Sea harbour porpoise
Pelagic Piscivorous Fish	Bluefish Atlantic bonito Atlantic mackerel
Demersal Fish	Black Sea whiting Black Sea turbot Black Sea striped mullet
Small Pelagic Fish	Black Sea anchovy Black Sea sprat Black Sea horse mackerel
Aurelia	*Aurelia aurita*
Mnemiopsis	*Mnemiopsis leidyi*
Noctiluca	*Noctiluca scintillans*
Zooplankton	Mesozooplankton Microzooplankton
Phytoplankton	Diatoms Dinoflagellates
Detritus	POM + Detritus

Each given ecosystem state was described by key parameters and input data for each functional group such as biomass per unit area, rates of production and consumption, diet composition, and fishery losses. The units were in gC m^{-2} $year^{-1}$ for quantities and $year^{-1}$ for rates. Models that include jellyfish organisms are prone to bias considering that the significant portion of the wet weight of these organisms are of water. Hence, in such cases, carbon weight is the preferred currency (Pauly et al., 2009). Because our model set-up included gelatinuous organisms as important components of the food web, carbon weight was used as the model currency. Considering that the catch statistics and in-situ data available in the literature were in tons and grams wet weight per square meter respectively, the values were converted into grams carbon per square meter using conversion factors specific to the concerning group as listed in Table 7.

Table 7. Multipliers used to convert biomass and catch values from grams wet weight into grams carbon.

Group	**Conversion Multiplier (grams wet weight to grams carbon)**	**Reference**
Phytoplankton	0.1	O'Reilly and Dow (2006)
Zooplankton	0.08	Dow, O'Reilly and Green (2006), Weslawski and Legezynska (1998)
Noctiluca	0.08	Dow, O'Reilly and Green (2006)
Aurelia	0.002	Oguz et al. (2001)
Mnemiopsis	0.001	Oguz et al. (2001)
Fish groups	0.11	Oguz et al. (2008a)

On the basis of data availability, the biomass values for dolphins and pelagic piscivorous fish were used as input parameters for the 1960s model set-up; whereas, for the remaining three model set-ups the estimated *EE* values for these two species groups were used as input due to the lack of biomass estimates for these organisms in the literature corresponding to the respective model periods. The *EE* parameters for all of the remaining groups were calculated by the model in all model set-ups. The fraction of the consumption which is not assilimated was set to the Ecopath's default value 0.2 for all groups. The fisheries yields and other input values used for the parameterisation of the four Ecopath models were summarised in Table 8. The input data were derived from the literature and previously published mass-balance modelling studies concerning the Black Sea and used with slight rounding modifications. However, the input *P/B* and *Q/B* parameters for *Mnemiopsis* were not taken from elsewhere but assumed to be identical to *Aurelia*'s. Further, since the input parameters inherited from previously published models composed of more functional groups (e.g. microzooplankton and mesozooplankton in Daskalov (2002)) compared to the model set-up used in this study (e.g. zooplankton), the weighted average values of the input parameters for such groups were computed and used in the four mass-balance models.

Table 8. Input parameters of functional groups in four model periods. Catch values were obtained from Prodanov et al. (1997) and complemented from Shlyakhov and Daskalov (2008). P/B and Q/B values were from Daskalov (2002). Biomass estimations of groups in period 1960-1969 were from Daskalov (2002). Biomass estimates for the latter periods for fish groups were from Shlyakhov and Daskalov (2008) and for lower trophic level groups were from Shiganova et al. (2008) except phytoplankton group, of which biomass values were from Nesterova et al. (2008). Estimated EE values of dolphins and pelagic piscivorous fish in period 1960-1969 were used in the models of the latter periods as inputs. "Est." stands for "Estimated" and denotes parameters computed by the Ecopath mass-balance algorithm. P1, P2, P3 and P4 denote model periods of 1960-1969, 1980-1987, 1988-1994 and 1995-2000 respectively.

Groups	**Biomass (gC m^{-2} year^{-1})**				**Production/Biomass (year^{-1})**				**Consumption/Biomass (year^{-1})**				**Ecotrophic efficiency**				**Catch (gC m^{-2} year^{-1})**			
	P1	P2	P3	P4	P 1	P2	P3	P4	P1	P2	P3	P4	P1	P2	P3	P4	P1	P2	P3	P4
Dolphins	0.010	Est.			0.350				19.000				Est.	0.286			0.001			
Pelagic piscivorous fish	0.020	Est.			0.550				5.000				Est.	0.995			0.010	0.026	0.016	0.006
Demersal fish	0.050	0.329	0.121	0.086	0.630				1.500				Est.				-	0.021	0.024	0.016
Small pelagic fish	0.200	1.457	0.538	0.553	1.500				11.000				Est.				0.020	0.410	0.170	0.245
Aurelia	0.030	0.480	0.112	0.128	11.000				29.200				Est.				-			
Mnemiopsis	-	-	0.821	0.176	-	-	11.000		-	-	29.200		Est.				-			
Zooplankton	0.660	0.903	0.540	1.207	44.000				345.000				Est.				-			
Noctiluca	0.090	1.060	0.736	0.500	7.300				36.200				Est.				-			
Phytoplankton	0.880	1.950	1.950	1.194	291.000				N.A.				Est.				-			

The diet composition matrix that incorporated the relative proportions of predation on each group followed those from previous studies by Gucu (2002) and Daskalov (2002) except for some specific adjustments (Table 9). The diets of small pelagic fish and demersal fish were taken from Gucu (2002) and used without modifications. The model of Gucu (2002) only included one jellyfish group by pooling all the jellyfish species (*Aurelia*, *Mnemiopsis* and *Pleurobrachia pileus*) in the Black Sea. Although the model set-up used in our study included distinctive groups for *Aurelia* and *Mnemiopsis* and completely exluded *Pleurobrachia*, their diets were assumed to be identical and therefore the diet composition given in Gucu (2002) for the jellyfish group was used intact and the same for these two groups. The diet of zooplankton group was taken from Gucu (2002) (50% phytoplankton and 50% detritus), however, modified to include 60% phytoplankton and 40% detritus assuming that zooplankton had more preference to graze on phytoplankton than detritus. The diet of piscivorous fish was also inherited from Gucu (2002) (50% small pelagic fish, 10% demersal fish and 40% import) but modified to include 60% small pleagic fish and 40% import by excluding the demersal fish group in their diet. The ommision of demersal fish from the diet was done considering that the habitat distributions of these two groups were quite distinct and therefore piscivorous fish group was inclined to have more consumption on the small pelagic fish group. The diet of dolphins was taken from Daskalov (2002) (96% small pleagic fish, 3.5% demersal fish and 0.5% piscivorous fish), however, modified to include 90% small pelagic fish, 9.5% demersal fish and 0.5% piscivorous fish in order to obtain mass-balance. The diet items of *Noctiluca* were constructed following Oguz et al. (2001), who included its grazing on phytoplankton, zooplankton and detritus. The relative proportions of the items in the diet of *Noctiluca* were determined following the study of Umani et al. (2004).

Table 9. Diet composition matrix used in all model periods (compiled mainly from Gucu (2002) and Daskalov (2002)). The details were explained in the text.

Group/Species	**Dolphins**	**Pelagic piscivorous fish**	**Demersal Fish**	**Small pelagic fish**	***Aurelia***	***Mnemiopsis***	**Zooplankton**	***Noctiluca***
Dolphins								
Pelagic piscivorous fish	0.05							
Demersal fish	0.095		0.1					
Small pelagic fish	0.9	0.60	0.35					
Aurelia								
Mnemiopsis								
Zooplankton			0.2	1.00	0.5	0.5		0.15
Noctiluca								
Phytoplankton					0.10	0.10	0.60	0.60
Detritus			0.35		0.40	0.40	0.40	0.25
Import		0.4						

2.2.2. Ecological Indicators

The four ecosystem periods were examined by utilising several indicators provided by the Ecopath model package using the final mass-balance biomass and flow estimates. **Mixed Trophic Impact** (MTI) analysis was performed to analyse the relative direct and indirect effects of variations within a group's biomass on the biomass of the other groups (Ulanowicz and Puccia, 1990). The direct impact of any one group upon another, related to predation or fishing, might cascade to other groups through any order of indirect interaction. MTI enables to quantify all possible direct and indirect interactions between two groups. By defining MTI (m_{ij}) as the product of all the impacts that group i has on group j, it is calculated as

$$m_{ij} = \prod_{i=1}^{n} (d_{ji} - f_{ij}) \tag{2}$$

where d_{ji} denotes the positive effects that i has on j and is calculated by means of the fraction of prey i in the diet of the predator j and f_{ij} signifies the negative effects that j has on i, calculated through the fraction of total consumption of prey i used by predator j (Libralato et al., 2006). Mixed trophic impact values scale between -1 (strong negative impact) and 1 (strong positive impact) and are relative measures of the interactions between two groups. Negative values indicate an inhibiting and positive values indicate a promoting effect between two corresponding groups.

Furthermore, **keystone** functional groups were determined for each model period. Keystone groups are groups or species with relatively low biomass values despite having an important functional role in their ecosystems (Power et al, 1996). The keystone value of each group is calculated as

$$KS_i = \log[\varepsilon_i(1 - p_i)] \tag{3}$$

where KS_i is the keystoneness of group i, and p_i is the ratio of the biomass of group i (B_i) to the sum of the biomass values of all groups and is calculated as

$$p_i = \frac{B_i}{\sum B_i} \tag{4}$$

following Libralato et al. (2006).

The **transfer efficiency** (TE) is an index for the measure of efficiency with which energy is transferred between adjacent trophic levels. It is calculated as the ratio of production of a trophic level to the production of the preceding trophic level (Lalli and Parsons, 1993). Thus, the primary producers and detritus groups are conventionally attributed to TL I, the herbivorous fraction of flows and biomasses to TL II, first order carnivorous flows and biomasses to TL III and second order carnivorous flows and biomasses to TL IV. This classification allowed us to distinguish biomasses and flows along the primary producer-based and the detritus-based food chains. Here, transfer efficiencies were calculated by disaggregating functional groups' biomasses and flows at each integer trophic level (TL), and then aggregating the results by integer TLs as defined by Lindeman (1942).

Additionally, some commonly used ecosystem indices and synthetic ecological indicators were also employed in assessing the ecological status of the Black Sea ecosystem for the four model periods (Table 10). These indicators were chosen because they could easily be calculated by using simple mathematical algorithms. They can be derived with the utilisation of basic network theory and are readily integrated into a number of ecological network and mass-balance analyses packages such as Ecopath.

Table 10. Ecosystem indices and synthetic ecological indicators used to assess the ecological status of the Black Sea ecosystem in the four model states

Indicator	**Definition**	**Units**
Total System Throughput (TST):	The sum of all flows within the ecosystem (Odum, 1971).	gC m^{-2} $year^{-1}$
Total Primary Production / Total Respiration (TPP / TR):	Ratio of total primary production in the system to the sum of all respiratory flows (Odum, 1971). In mature ecosystems, this ratio is close to unity (Tomczak et al., 2009).	-
Net System Production:	It equals to primary production minus respiratory flows in the system. In mature ecosystems, this difference is expected to be close to zero (Christensen, 1995).	gC m^{-2} $year^{-1}$
Total Primary Production / Total Biomass:	This ratio is expected to be low in mature ecosystems and high in developmental stages (Christensen, 1995).	-
Mean Trophic Level of the Catch (mTLc):	As fishing pressure increase, the mean trophic level of the catch is expected to decrease (Pauly et al., 1998).	-
System Omnivory Index (SOI):	Average omnivory index (food spectrum) of all consumers weighted by each consumer's consumption (Christensen et al., 2005). The higher the SOI is, the more web-like the ecosystem's food chain is.	-
Finn's Cycling Index (FCI):	A measure of TST recycled in the ecosystem. This value is expected to be high in mature ecosystems (Finn, 1976).	-
Finn's Mean Path Length:	The average number of steps along which the system production flows through the ecosystem. In mature ecosystems this value is expected to be high (Finn, 1976).	-
Primary Production Required (PPR):	This is the amount of primary production required to sustain the given amount of catches within the ecosystem (Odum, 1971).	-
Ratio of jellyfish biomass to the sum of all zooplankton biomass	This ratio indicates the importance/dominance of jellyfish in the whole zooplankton community. It is expected to increase with fishing (Shannon et al., 2009).	-

2.3. Results

2.3.1. Model Outputs

The mass-balance models calculated the ecotrophic efficiency values of all groups in the first period (Table 11). In the latter periods, due to the lack of stock assessment studies for dolphins and pelagic piscivorous fish, the ecotrophic efficiency values calculated in the first period were used for these two groups as input parameters and their biomass values were computed by the mass-balance algorithm (Table 11).

For all the other functional groups, ecotrophic efficiency values were calculated by the model for periods two, three and four. Further, respiratory flows for all functional groups were calculated from energetic balance of the sources and sinks in each functional compartment (Table 11) as the model product and were in compliance with the energy budget of each state variable described in the model which assumed that the consumption of a group was the sum of production, respiration, and unassimilated food. The increases in respiratory flows of zooplankton and gelatinous organisms as well as small pelagic fish from the first period to the second and third periods were remarkable. The decrease in estimated biomass levels of piscivorous fish from the first period to the latter periods was also pronounced and found to be in correspondence with the explanations provided by others (Gucu, 2002; Oguz, 2007).

The primary production values calculated by the model were 256, 567, 567 and 347.5 mg C m^{-2} d^{-1} for the four periods respectively. The primary production values were found to be marginally overestimated for the first period (100-200 mgC m^{-2} d^{-1}) and underestimated for the second and third periods (600-800 mgC m^{-2} d^{-1} for 1975-1990) and in the last period primary production matched the literature averages (200-400 mgC m^{-2} d^{-1}) (Oguz et al., 2012, Yunev et al. 2002).

Table 11. Basic output parameters calculated by the Ecopath for the four modelled periods. P1, P2, P3 and P4 denote model periods of 1960-1969, 1980-1987, 1988-1994 and 1995-2000 respectively.

Parameter / Group	**Ecotrophic Efficiency**				**Biomass (gC m^{-2}y^{-1})**				**Respiration (gC m^{-2}y^{-1})**			
	P1	**P2**	**P3**	**P4**	**P1**	**P2**	**P3**	**P4**	**P1**	**P2**	**P3**	**P4**
Dolphins	0.296				-	0.01	0.01	0.01	0.15	0.15	0.15	0.15
Piscivorous fish	0.995				-	0.05	0.03	0.01	0.07	0.17	0.11	0.05
Demersal fish	0.811	0.427	0.791	0.862	-				0.03	0.19	0.07	0.05
Small pelagic fish	0.924	0.413	0.618	0.603	-				1.46	10.64	3.93	4.04
Aurelia	0				-				0.37	5.93	1.38	1.58
Mnemiopsis	0				-				-	-	10.15	2.18
Zooplankton	0.108	0.727	0.992	0.25	-				153.1	209.50	125.30	280.0
Noctiluca	0				-				1.949	22.96	15.94	10.83
Phytoplankton	0.541	0.372	0.230	0.753	-				-			
Detritus	0.483	0.306	0.183	0.783	-				-			

2.3.2. Mixed Trophic Impact

The MTI analysis was performed separately for fishery and interspecies competition among gelatinous organisms and small pelagic fish, and predation impact of the opportunistic species *Noctiluca* on zooplankton and phytoplankton groups (Figure 2). According to the analysis, fisheries incurred positive mixed trophic impacts on demersal (0.489) and small pelagic fish (0.308) groups, whereas it sustained negative impacts on dolphins (-0.650) and pelagic piscivorous fish (-0.645) groups for the period 1960-1969. The positive impacts on small pelagic and demersal fish groups were realised due to the positive indirect impacts of fisheries on these groups (i.e. the exploitation of their predators; dolphins and pelagic piscivorous fish) exceeded the direct negative impacts due to harvesting. Conversely, in the model period 1980-1987, the fisheries impacts on all fish groups as well as dolphins were negative (-0.954 for dolphins, -0.865 for piscivorous fish, -0.029 for demersal fish and -0.058 for small pelagic fish) due to the increasing exploitation rates exerted by fisheries on all target groups. The fisheries impact on small pelagic fish groups turned to positive (0.120) for 1988-1994 because of the collapse of the small pelagic fishery and its respective stocks, generating a shift in the fishery hence realising the relatively more intensive targeting of demersal and pelagic piscivorous fish groups. The fisheries impacts were calculated as negative for small pelagic fish (-0.055) and positive for demersal fish (0.036) during 1995-2000 due to the recovery of the small pelagic fishery which realised some release of fishing pressure on the demersal fish species along with more intensive targeting of small pelagic fish. As expected, the fishery exerted negative impacts on all other targeted groups in all four time periods other than those denoted above.

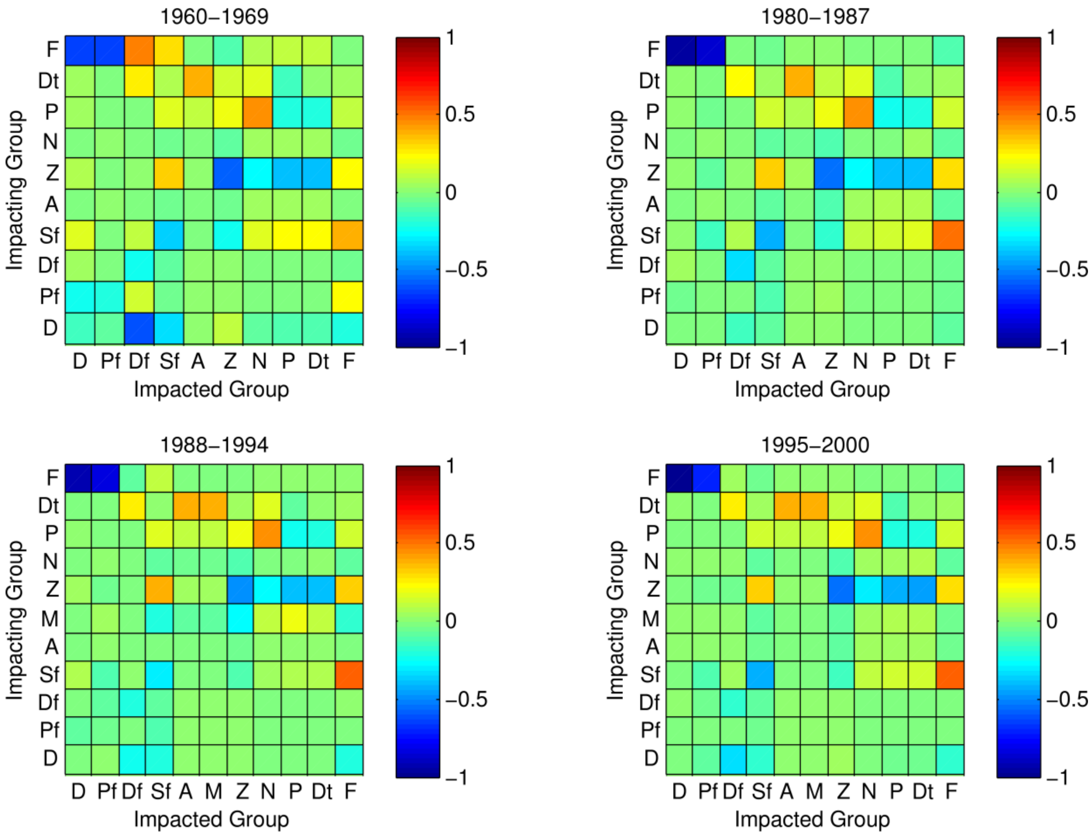


Figure 2. Mixed trophic impact relationships between functional groups in the four model periods. Abbreviations: F (Fisheries), Dt (Detritus), P (Phytoplankton), N (*Noctiluca*), Z (Zooplankton), M (*Mnemiopsis*), A (*Aurelia*), Sf (Small pelagic fish), Df (Demersal fish), Pf (Pelagic piscivorous fish), D (Dolphins).

Because the gelatinous species *Aurelia* displayed a preference for zooplankton consumption, its MTI on small pelagic fish group was negative (-0.0477 for 1960-1969 and -0.0856 for 1980-1987). After the outburst of *Mnemiopsis*, *Aurelia*'s impact remained negative but its MTI values diminished by nearly half to -0.0285 and -0.0473 during 1988-1995 and 1995-2000, respectively. On the contrary, *Mnemiopsis* maintained a stronger negative impact on the small pelagic fish groups (-0.209 and -0.0650) during the last two periods.

Direct predation of the heterotrophic dinoflagellate *Noctiluca* exerted a negative mixed trophic impact on zooplankton group (-0.0673 in 1960-1969, -0.122 in 1980-1988, -0.116 in 1989-1994 and -0.107 in 1995-2000) in all periods. A notable significant change occurred between the first and the second time periods due to increasing *Noctiluca* biomass in accordance with the degradation of the food web. On the other hand, *Noctiluca*'s mixed trophic impact on phytoplankton group was positive and equal to 0.0517 in 1960-1969; because *Noctiluca*'s direct negative impact on phytoplankton (predation) was outcompeted by its indirect positive impact, which was the consumption of the main predator of phytoplankton, i.e. zooplankton. In the model period 1988-1995, the impact of *Noctiluca* on phytoplankton was calculated negative (-0.0197) due to *Noctiluca*'s increasing biomass concentration in the ecosystem. For the last period (1995-2000), the impact of *Noctiluca* on phytoplankton was calculated positive and was equal to 0.059 due to its diminishing biomass values. In the model period of 1980-1987, *Noctiluca* demonstrated a slightly negative impact on the phytoplankton group.

2.3.3. Keystoneness

The keystoneness index (KS) of the functional groups showed relevant differences in the four time periods (Figure 3). In all periods, with the exception of 1960-1969, zooplankton group had the highest KS values. In 1960-1969, the dolphins group acquired the highest KS value of -0.143, and was followed by comparable KS values of zooplankton (-0,404), small pelagic fish (-0.428), phytoplankton (-0.532) and piscivorous fish (-0,561) demonstrating the dolphins' top-down control on the lower trophic levels. Considering that food webs are under the tension of either top-down / bottom-up or wasp-waist controls in terms of trophic relationships, predator keystone species could be interpreted as exerting top-down control on their food web. Similarly, when producers are the most keystone groups, it could be inferred that their primary or secondary production shapes the food web by transferring the resources from the bottom to the top of the food web. The same period displayed much smaller KS values (around -1) for the heterotrophic dinoflagellate *Noctiluca* and jellyfish *Aurelia*, along with the demersal fish group because of their marginal dominance during the first period. However, the keystoneness indices of *Aurelia* and *Noctiluca* increased slightly to -0.772 and -0.881 respectively closely following the KS value of small pelagic fish (-0.623) in 1980-1987 in contrast to a major reduction in the dolphins' keystone level to -0.75 as well as similar reductions in the KS values of the piscivorous and demersal fish groups (-0.913, -1.028 respectively). This decline suggested a decrease in the top-down predatory control mechanism on the intermediate trophic level species. In the third period, 1988-1994, *Mnemiopsis* was the second most keystone species after zooplankton with a KS index value of -0.46. It was followed by the dolphins and phytoplankton groups with index values of -0.491 and -0.498 respectively. The KS values of small pelagic fish, pelagic piscivorous fish, *Noctiluca*, and *Aurelia* were calculated as -0.767, -0.824, -0.857 and -1.255 in this period respectively. During the last period, 1995-2000, dolphins, phytoplankton, and small pelagic fish groups followed the zooplankton group in terms of keystoneness with KS indices of -0.414, -0.433 and -0.659 respectively. The keystoneness of *Mnemiopsis* decreased to -0.839 following the small pelagic fish. *Noctiluca* followed *Mnemiopsis* with a keystone index value of -0.896. *Aurelia*, demersal fish, and piscivorous fish groups were the last three groups with KS index values of -0.971, -1.203 and -1.262 respectively.

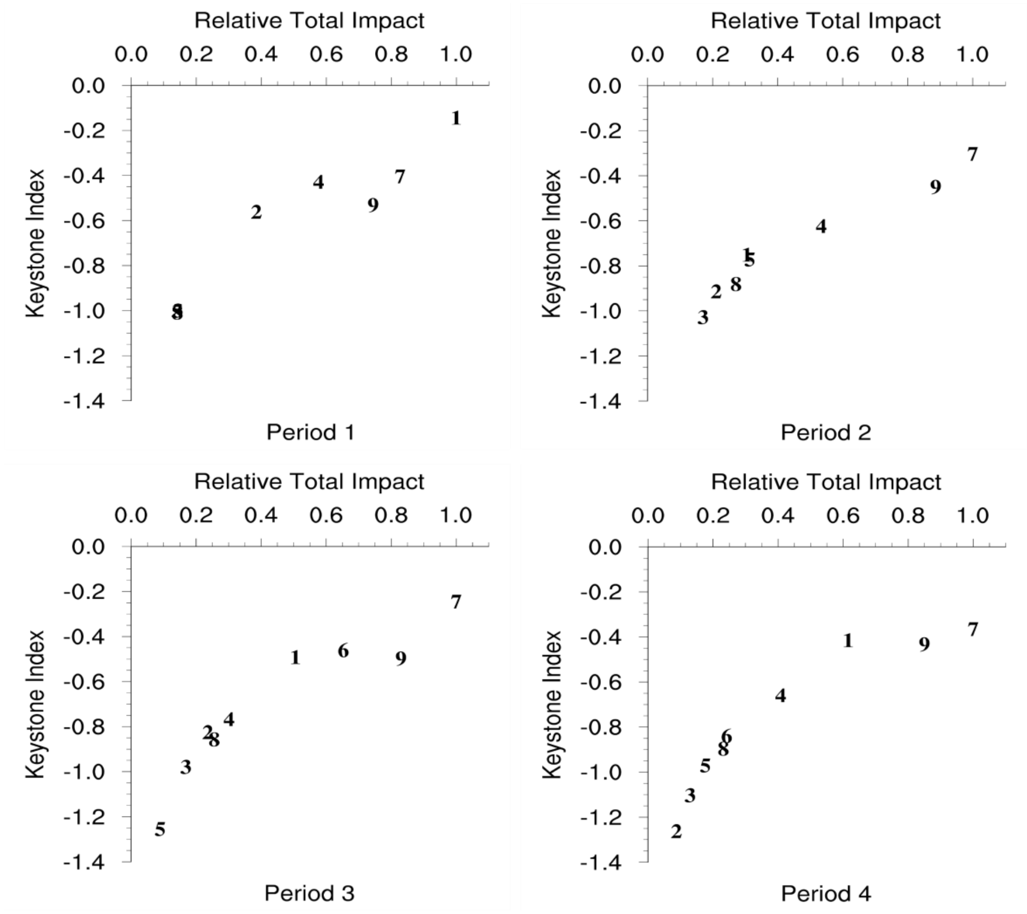


Figure 3. Keystoneness and relative total impact of functional groups on the structuring of the Black Sea food web in four model periods. 1) Dolphins, 2) Piscivorous fish, 3) Demersal fish, 4) Small pelagic fish, 5) *Aurelia*, 6) *Mnemiopsis*, 7) Zooplankton, 8) *Noctiluca*, 9) Phytoplankton.

2.3.4. Trophic flows and transfer efficiency

The overall transfer efficiency from the producer and detritus compartments (TL I) to TL II increased from 1.4% in 1960-1969 to 8.2% in 1980-1987 and 10.6% in 1988-1994 but decreased to 3% in the last model period (Table 12). However, the transfer efficiency from TL II to TL III decreased from 8.9% in 1960-1969 to 3.2% in 1980-1987 and 2.2% in 1988-1994 because TL III comprised both the small pelagic fish and a given portion of flows attributed to jellies, where the latter constituted a larger share of the biomass during these periods. Finally, as jelly biomasses declined to moderate values, the transfer efficiency from TL II to TL III increased slightly to 3.8% in period 1995-2000. The transfer efficiencies of all flows from TL III to TL IV were calculated as 6.3%, 7.3%, 8.7% and 7.4% in the four modelled periods, respectively. Considering the transfer efficiencies from TL IV to TL V, a rough estimate of 0.5% was calculated for each period; however this estimate was biased by the relatively low dolphin biomass due to the lack of reliable observational data.

Table 12. Transfer efficiency of flows across trophic levels in the four modelled periods.

Source \ Trophic level	1960-1969				1980-1987				1989-1994				1995-2000			
	II	**III**	**IV**	**V**	**II**	**III**	**IV**	**V**	**II**	**III**	**IV**	**V**	**II**	**III**	**IV**	**V**
Producer	1.4	9.0	6.3	0.5	8.2	3.2	7.3	0.5	10.8	2.2	8.7	0.5	3.0	3.8	7.4	0.5
Detritus	1.4	8.9	6.3	0.5	8.3	3.2	7.3	0.5	10.3	2.2	8.7	0.5	3.0	3.8	7.4	0.5
All flows	1.4	8.9	6.3	0.5	8.2	3.2	7.3	0.5	10.6	2.2	8.7	0.5	3.0	3.8	7.4	0.5

2.3.5. Summary statistics and synthetic indicators

The results of the analyses of the synthetic indicators and the statistical parameters (

Table **13**) calculated for the four model periods were summarised in this section. Total System Throughput (TST) increased from 681.733 gC m^{-2} y^{-1} in the period 1960-1969 up to 1,405.977 gC m^{-2} y^{-1} in 1980-1987 with increasing productive capacity of the ecosystem due to eutrophication. In the periods 1988-1994 and 1995-2000, TST values were calculated as 1,316.583 gC m^{-2} y^{-1} and 1,020.347 gC m^{-2} y^{-1} respectively.

Table 13. Summary statistics of the four mass-balance models of the Black Sea ecosystem for their respective periods.

Parameter/Period	**1960-1969**	**1980-1987**	**1988-1994**	**1995-2000**	**Units**
Summary Statistics					
Sum of all consumption	234	381	247	450	gC m^{-2} y^{-1}
Sum of all exports	99	318	411	49	gC m^{-2} y^{-1}
Sum of all respiratory flows	157	250	157	299	gC m^{-2} y^{-1}
Sum of all flows into detritus	191	458	502	223	gC m^{-2} y^{-1}
Total system throughput	682	1,406	1,317	1,021	gC m^{-2} y^{-1}
Sum of all production	286	623	608	408	gC m^{-2} y^{-1}
Mean trophic level of the catch	3.36	3.07	3.1	3.0	-
Gross efficiency (catch/net p.p.)	0.000	0.001	0.000	0.001	-
Calculated total net primary production	256	567	567	347	gC m^{-2} y^{-1}
Total primary production / total respiration	1.63	2.27	3.61	1.16	-
Net system production	99	318	410	49	gC m^{-2} y^{-1}
Total primary production / total biomass	1320	91	117	90	$year^{-1}$
Total biomass / total throughput	0.003	0.004	0.004	0.004	$year^{-1}$
Total biomass (excluding detritus)	1.94	6.24	4.86	3.87	gC m^{-2}
Primary Production Required / Total PP (PPR/TotPP)	6.87	52.82	25.84	28.93	%
Network Flow Indices					
System Omnivory Index	0.072	0.122	0.115	0.116	-
Finn's Cycling Index	9.40	4.61	2.76	15.01	**(% of TST)**
Finn's mean path length	2.662	2.477	2.320	2.936	-

Net system production increased from 98.934 gC m^{-2} y^{-1} in 1960-1969 to 317.918 gC m^{-2} y^{-1} in period 1980-1987. In the periods 1988-1994 and 1995-2000, net system production was calculated as 410.443 gC m^{-2} y^{-1} and 48.563 gC m^{-2} y^{-1} respectively. The ratio of total primary production to the sum of all respiratory flows in the system was calculated as 1.63 in 1960-1969. In period 1980-1987, this ratio increased to 2.274. It further increased to 3.614 in 1988-1995. In the last period of 1995-2000, this ratio decreased to 1.162.

The mean trophic level of catches (mTLc) decreased from 3.36 in 1960-1969 to 3.07 in period 1980-1987. mTLc values were calculated as 3.10 and 3.03 in the periods 1988-1994 and 1995-2000 respectively. Furthermore, the catches by trophic levels showed that different trophic levels dominated the fisheries catches in particular periods (Table 14). In period 1960-1969, TL III and TL IV constituted 64% and 35% of the entire fisheries yield in the system respectively. In 1980-1987, the percentage of TL IV organisms in fisheries catches decreased to 7.8% whereas TL III species constituted 90% of the yield. In 1988-1995, the catch composition comprised 82% of TL III groups and 12.6% of TL IV groups. In the last period 1995-2000, the percentage of TL IV organisms in the catches decreased to 4.5% whereas TL III organisms increased to 92%. Similarly, the biomass distribution by trophic levels in the system reflected the dominance of different trophic level species in the four model periods (Table 15). The ecosystem was dominated by TL IV and TL III organisms which represented 64.5% and 35% of all biomasses respectively in period 1960-1969 illustrating the dominance of higher-trophic-level groups within the ecosystem. In period 1980-1987, TL III organisms constituted over 90% of the total biomass within the ecosystem whereas TL IV organisms decreased to 7.7%. This was the result of the removal of top predatory species from the ecosystem by fisheries. The percentage of TL IV organisms in the total living biomass increased to 12.5% when TL III organisms decreased to 83% in period 1988-1995. This was a direct consequence of the collapse of small pelagic fish stocks, which in turn, reflected as an increase in the relative biomass proportion of higher-trophic-level species in the community. In the last period (1995-2000), the proportion of TL IV organisms decreased to 5% and TL III organisms increased to 92% due to the recovery of the small pelagic fish stocks.

Table 14. Catches by trophic levels in four modelled periods of the Black Sea.

Trophic Level	1960-1969	1980-1987	1988-1994	1995-2000
V	0.00004	0.00004	0.00004	0.00004
IV	0.0109	0.0355	0.0266	0.0133
III	0.02	0.415	0.175	0.249
II	0	0.00824	0.00937	0.00614
I	0	0	0	0

Table 15. Living biomass by trophic levels in four modelled periods of the Black Sea.

Trophic Level	1960-1969	1980-1987	1988-1994	1995-2000
V	0.0004	0.0004	0.0004	0.0004
IV	0.0487	0.187	0.0878	0.0558
III	0.24	1.929	1.142	0.8
II	0.771	2.172	1.679	1.817
I	0.88	1.95	1.95	1.194

Finn’s Cycling Index (FCI) decreased from 9.4% in 1960-1969 to 4.61% in 1980-1987. It further decreased down to 2.76% in 1988-1994. This indicated that energy turnover in the food web decreased from 1960-1969 to periods 1980-1987 and 1988-1994. The FCI increased to 15.01% in period 1995-2000 due to a slight ecosystem-wide recovery, i.e. improving transfer efficiency rates of trophic flows through the food web and reduction in the proportion of the short-circuited energy flows, in response to the reduced eutrophication and the introduction of *Mnemiopsis*-predator *Beroe*. This impact was also reflected in the Finn’s mean path length which was calculated as 2.662, 2.477, 2.320 in periods 1960-1969, 1980-1987, and 1988-1994 respectively, showing a shortening in the average distance of a unit of energy travelled within the food web as the system degraded (i.e. short-circuiting of energy flows) in periods 1980-1987 and 1988-1994. A subsequent increase in Finn’s mean path length to 2.936 in 1995-2000 agreed with the slight recovery observed in ecosystem conditions.

The biomass ratios of *Aurelia*, *Mnemiopsis* and *Noctiluca*, which could be considered as r-strategist species, to the community biomass in general and plankton biomass in particular, increased from 0.0435 in 1960-1969 to 0.347 and 0.633 in periods 1980-1987 and 1988-1994 respectively. This reflected the increased perturbations, i.e. stress conditions *sensu* Odum (1985), which prevailed in the Black Sea ecosystem during these latter periods.

2.4. Discussions and conclusions

2.4.1. Considerations specific to the methodology

The chapter of the thesis considerably utilised parameterisations of previous mass-balance modelling studies in the Black Sea with minor modifications and followed a similar modelling scheme, however, it elaborated these former contributions by focusing on the ecosystem functioning itself through energetic flows and prey-predator interactions with the help of synthetically produced trophic indicators. Further, it included important functional groups such as dolphins and *Mnemiopsis*, which were not considered in the previous studies utilising Ecopath models. These aspects of this chapter differed from the similar earlier studies and up till now this had been a deficiency in the literature shadowing the understanding of the trophic characteristics of the changes the Black Sea ecosystem had undergone in the second half of the 20th century.

The simplicity of the model scheme, i.e. the inclusion of a limited number of functional groups, was designed purposefully in order not to overcomplicate the models to cause increasing source of uncertainty in the model outputs due to the increased number of parameters required to set up the models. However, the modelling scheme was capable of adequately representing the general structure of the Black Sea food web so as to derive interpretations from ecological indicators calculated utilising the food web's functional properties. It was more of a concern for this chapter to examine the characteristics of the food web over the model periods by focusing on traits of organisms rather than dealing with specific species dynamics within the ecosystem.

In this chapter of the thesis, it was assumed that the *EE* values calculated by the mass-balance model set-up in the first period of the Black Sea for dolphins and pelagic piscivorous fish groups would approximately remain unchanged in the latter model periods. This assumption might have significantly impacted the calculated values of indicators such as keystoneness for these groups. Therefore, this situation should be noted when evaluating the results of the keystoneness analysis. However, considering the complete absence of stock assessment studies for these two functional groups, this assumption was inevitable. Further, the exploitation levels of pelagic piscivorous fish should have remained approximately stable over the years if the high fisheries demand on these fishes was acknowledged (Gucu, 2002; Oguz, 2007; Oguz et al., 2008b), hence leading to high *EE* estimates used in the mass-balance models. Pelagic piscivorous fish in the Black Sea have always been under exceeding levels of exploitation and their predators have been limited in the system. Hence, it could be assumed that *EE* values for this functional group might have fluctuated around the same mean value over the four modelled periods. On the other hand, dolphins had been exploited intensively in the Black Sea until the ban of its fisheries in 1966 in USSR, Bulgaria and Romania and finally in 1983 in Turkey. Therefore, a decreasing EE value was most likely to be expected for dolphins group over the four modelled periods. In this aspect, it could be stated that mass-balance model set-ups in this chapter led to relatively higher estimates of natural mortality values for this group. However, by-catch has been a significant mortality source for dolphins even after the dolphin fisheries ban in the Black Sea (2000-3000 individuals per year, Ozturk et al., 1999), which might have compensated the release of fishing pressure on this group after the fishing bans so as to cause high “natural” mortality levels.

2.4.2. Interpretation of model results

This chapter of the thesis provided an assessment of the Black Sea ecosystem structure and functioning using the ecological indicator approach pioneered by Odum (1969, 1985) and elaborated upon by many others (Ulanowicz and Puccia, 1990; Christensen, 1995; Costanza and Mageau, 1999; Ulanowicz, 2004; Shannon et al., 2009; Gaichas et al., 2009). A similar approach was previously implemented in the Black Sea by Christensen and Caddy (1993) with limited scope that compared the *pre-*

Mnemiopsis (early 1980s) and post-*Mnemiopsis* (early 1990s) eras and examined the likely impacts of introduction of *Beroe ovata* on the *Mnemiopsis* population. This chapter's work expanded upon this in terms of complexity of analysis and time periods of the ecosystem examined. It differed from those of Gucu (2002) and Daskalov (2002) because of the interpretation of model products since the mass-balance modelling in this chapter comprised the entire food web and its quantitative analysis through the use of ecological indicators to assess the ecosystem status prevailed in the Black Sea during the last few decades.

Evidence of top-down control in the first period (1960-69) was demonstrated by the highest KS value belonging to dolphins group in the food web. One interesting outcome of the analysis was the lack of recovery of dolphins even though the dolphin fishery was banned after 1966 in USSR, Bulgaria, Romania and 1983 in Turkey (Birkun, 2008). This was clearly supported by the MTI and transfer efficiency (TE) analyses. In MTI analysis, the continuous increase in the negative impact of fisheries on dolphins even after the fishing ban suggested that excessive harvesting of small pelagic fish did not leave sufficient food resources for dolphins to promote their population growth, hence, consolidated the indirect negative impact of fisheries on dolphins. TE analysis further quantified increasing resource supply to TL II in accordance with intensive eutrophication, but this did not propagate further up in the food web due to the short-circuiting of energy flows by the gelatinous population which dominated the food web. This short-circuiting and the decrease in energy transfer efficiency to higher trophic levels were also signified by the decrease in Finn's Cycling and Finn's Mean Path Length indicators starting from the first period. Further basis for the severity of this short-circuiting effect was provided by the KS value of *Mnemiopsis* in 1988-1994, which suggested *Mnemiopsis* as being the second most significant keystone species after the zooplankton group.

The impact of intensive eutrophication was also reflected in the TST values of the ecosystem which increased almost two-fold between the first and second model periods. This reversal in the food web from a top-down controlled state to become more influenced by bottom-up controls was demonstrated by the highest keystone values calculated for zooplankton and phytoplankton groups in the latter three model periods. Fisheries also played an important role in this reorganisation as depicted by the decrease in the mean trophic level of catch (mTLc) and the mean trophic level of community (mTLco) indices due to selective extraction of particular fish groups from the ecosystem so that top-down control on the food web abated. This “fishing down the food web” (Pauly et al., 1998) impact has been continuing in the Black Sea since the 1960s.

In accordance with the notion defined by Odum (1985), the stability of the Black Sea ecosystem had been regressed from many aspects. The net system production, an indicator expected to be close to zero in mature ecosystems, increased roughly three-fold from the first period to the latter two periods. Similarly, the TPP/TR ratio increased by about four-fold from a close-to-unity value (typical for healthy ecosystems) in the first time period to the subsequent time periods also suggesting this deterioration (growing instability) in the ecosystem. The biomass ratio of the sum of opportunistic species *Mnemiopsis*, *Aurelia*, and *Noctiluca* with respect to the total zooplankton increased by more than an order of magnitude from the first period to period 1988-1994. These species had no natural predators within the Black Sea ecosystem. Hence, the accumulated energy in their respective TLs of these organisms was not transferred upwards in the trophic chain but was circuited back to detritus by means of natural mortality. This leakage in the food web reduced the TE of flows through the trophic chain up to TL III (Figure 4).

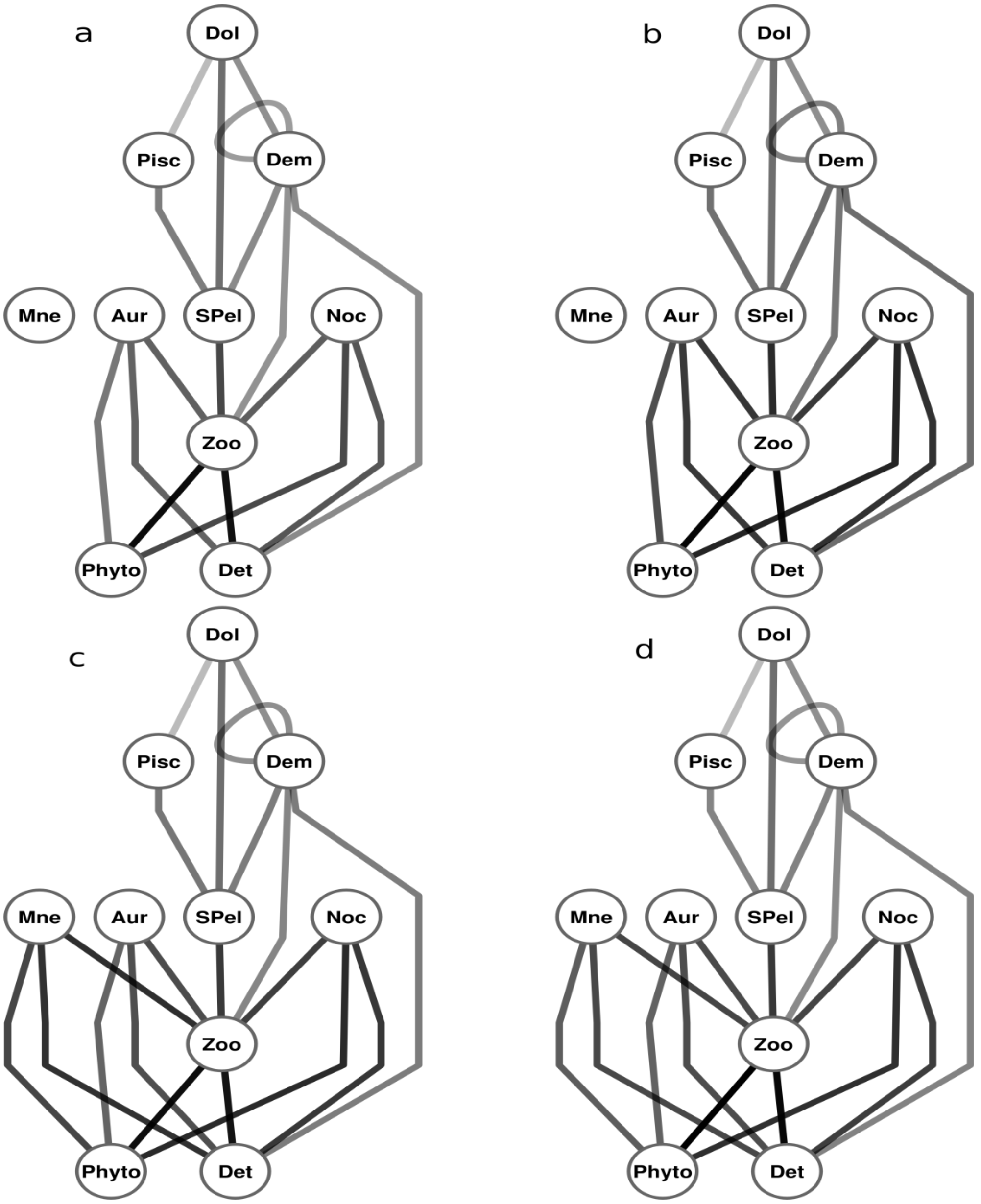


Figure 4**.** Trophic flows between the model compartments in periods a) 1960-1969, b) 1980-1987, c) 1988-1994 and d) 1995-2000. The opacity of the lines is proportional to the magnitude of flows and normalised across different periods between 0-255. Special attention should be paid to the consolidation of flows within the lower trophic level compartment along with the increase in flows in period 1980-1987, and proliferation of alien comb jelly *Mnemiopsis* in period 1988-1994. The path length of the flows cycled within the system from period 1960-1969 to other periods decreased as the flows trapped down to the lower trophic level compartments of the food web. Introduction of the alien comb jelly further forked lower trophic level flows in three new pathways. Abbreviations: Dol (Dolphins), Pisc (Pelagic piscivorous fish), Dem

(Demersal fish), SPel (Small pelagic fish), Aur (*Aurelia*), Mne (*Mnemiopsis*), Noc (*Noctiluca*), Zoo (Zooplankton), Phyto (Phytoplankton), Det (Detritus).

In conclusion, contrary to Gucu (2002) and Daskalov (2002) who suggested overfishing as the prime cause of the collapse of small pelagic fish stocks in 1989, according to the analyses in this chapter I conclude that this collapse was most probably related to more than one single cause. Indeed, overexploitation by fisheries was severe and evident in the various system indices, such as i) the decrease in the mean trophic level catches from 3.34 in 1960-1969 down to 3.07 in 1980-1987, ii) the increase in primary production required to support catches from 6.87 % in 1960-1969 to 52.82 % in period 1980-1987, and iii) the increase in proportion of opportunistic species within the plankton community. Further, the impact of increased competition between gelatinous organisms and small pelagic fish for resources as calculated in the MTI analysis with increasing negative impact index values between these groups in period three and four provided an additional strong explanation for the collapse. The negative impact of trophic competition between *Aurelia* and small pelagic fish in 1980-1987 was demonstrated by the MTI analysis. This trophic competition was further exacerbated by the proliferation of *Mnemiopsis* as shown by the strong negative impact between *Mnemiopsis* and small pelagic fish in period 1988-1994. Based on what was demonstrated by the ecological indicators and statistical properties of the Black Sea ecosystem examined in this chapter, I propose that the synergistic effects of "*resource competition*" with jellyfish and "*overexploitation*" by fisheries were the most likely causes to lead such a collapse in the small pelagic fish stocks in 1989.

Using the Black Sea ecosystem as a case study, this chapter of the thesis validated that the structure and functioning of a marine ecosystem can be examined coherently through a carefully selected set of ecological indicators even by utilising a simple mass-balance model such as Ecopath. Moreover, if complemented by a time-dynamic Ecosim model of the Black Sea of similar or a more detailed food web complexity (chapters 3 and 5), and further supplemented by the application of network analyses to obtain dynamically varying ecological indicators used in this chapter, the findings of this section may be regarded as a simplistic but quantitative assessment of the Black Sea's food web structure and functioning over the last few decades in order to provide a baseline towards establishing the goal of "integrated ecosystem assessment" (Levin et al. 2009) for the region.

3. CHAPTER: Modelling regime shifts of the Black Sea food web dynamics using a complex food web representation

3.1. Introduction

For more than a decade, regime shifts; i.e. persistent changes in the ecosystems' organisation, structure and functioning (Kinzig et al., 2006), have been a special focus in marine research in link with the impacts of anthropogenic forcing on climate and ecosystems (Steele, 1998, 2004). Recent studies have been increasingly focused on regime-shift phenomena along with the recent advances in ecological and statistical modelling tools that enabled both diagnostic and prognostic analyses under different environmental scenarios and anthropogenic impacts (e.g. Reid et al., 2001; Beaugrand, 2004; Daskalov et al., 2003, 2007; Möllmann et al., 2008, 2009; Llope et al., 2011). Ecosystem models have recently emerged as important tools to develop Ecosystem-Based Management (EBM) strategies to address community-scale ecological questions (e.g. Fulton et al., 2005; Plaganyi, 2007) under changing regimes as well as investigating historical progressions of ecosystems. Lower trophic level models have long been used in this respect for the investigation of the consequences of intrinsic and extrinsic pressures on marine ecosystems (e.g. Oguz et al., 2001; Salihoglu, 2009; Salihoglu et al., 2011). During recent decades, together with the advancement of higher trophic level models focusing on fish, end-to-end ecosystem models, which represent the ecosystem from biogeochemical processes up to top predators, that would provide a holistic understanding of the changes in marine ecosystems with respect to climatic and anthropogenic impacts started to develop (Fulton, 2010).

Ecopath with Ecosim has emerged as one of the most widely acclaimed higher trophic level model and has been applied to a great range of marine and freshwater ecosystems for more than two decades. Specifically in the last decade, with the recognition of the usefulness of such end-to-end holistic modelling approaches, Ecopath and Ecosim models have been used to investigate regime shifts and/or system reorganisations in marine ecosystems, with or without coupling with lower trophic level and hydrodynamic models, using indicator-based assessment methods which inspected the ecosystem in question through a set of ecological indicators (Fulton et al., 2005; Coll et al., 2006, 2009). This indicator-based ecosystem assessment was pioneered by Odum (1969), who formed the basis of the approach known today as “the ecosystem theory”. In his pioneering work entitled “*The Strategy of Ecosystem Development*”, Odum quantified many aspects of ecosystem development through various statistical parameters and indicators of ecosystems and put forward their expected behaviours under changing ecological conditions so as to determine its properties of structure, i.e. the organisation of organisms across the food web, and functioning, i.e. properties of energetic flows transferred through various trophic levels from grazing and detritus-based food chains. Only after quantifying these attributes and properties, it could have been possible to deduce whether a given ecosystem was under stress, e.g. exposed to anthropogenic pressure like overfishing, or balancing itself and its processes (*ecological homeostasis*, Odum (1985)). This pioneering work was further elaborated by many ecologists over the course of time (Odum, 1985; Shaeffer et al., 1988; Christensen, 1995; Rapport et al., 1992, 1998; Costanza and Mageau, 1999; Shannon et al., 2009; Shin et al., 2010b, c) and applied to a number of ecosystems, either marine or terrestrial, across the world (Christensen and Cury, 2005; Cury and Christensen, 2005; Shin et al., 2005). Furthermore, it was developed to include indicators and parameters derived synthetically from “ecological network theory” (Ulanowicz, 1986). Such studies on fishery and ecosystem related indicators have been presented by Coll et al. (2005, 2006) and Fulton et al. (2005) showing usefulness of such trophodynamic indicators in ecosystems analysis. Similar tools to investigate changes in the food web structure under different pressures were recently used by Cury et al. (2005), Guénette et al. (2006) and Travers et al. (2010). Further, Fulton et al. (2005) demonstrated the effectiveness of ecological indicators as the most reliable tools to investigate the ecosystem impacts of fishing by providing the characterisation of ecosystem state and indicating the causality of the changes it had undergone. All these studies proved the effectiveness of using ecological indicators in assessing ecosystem changes over a long period of time and investigating their likely/unlikely consequences. **In this aspect, this chapter of this thesis work was dedicated to investigating the presence of different regimes in the food web dynamics and ecosystem properties of the Black Sea in a holistic approach using synthetically obtained time series of ecosystem indicators so as to support the**

findings of indicator-based mass-balance model analysis in the previous chapter. This chapter further investigated the presence of significant changes in the Black Sea ecosystem in the second half of the 20th century that could be attributed as different persistent regimes.

3.2. Materials and Methods

The mass-balance Ecopath model of the Black Sea detailed in section 2.2.1 was further developed by disaggregating the functional groups of small pelagic fish, pelagic piscivorous fish and demersal fish, which were aggregated guilds of multiple species, into individual species components. Further, new state variables were introduced; i.e. two new jellyfish species and another detritus compartment; particulate organic matter (POM). The model was extended to include twenty-two functional groups, which comprised twelve fish groups; Black Sea anchovy (*Engraulis encrasicolus ponticus*; Alexandrov, 1927), Black Sea sprat (*Sprattus sprattus phalaericus*; Risso, 1827), Black Sea horse mackerel (*Trachurus mediterraneaus ponticus*; Aleev, 1956), Atlantic bonito (*Sarda sarda*; Bloch, 1973), bluefish (*Pomatomus saltator*; Linnaeus, 1776), Atlantic mackerel (*Scomber scombrus*; Linnaeus, 1758), turbot (*Psetta maeotica*, Pallas, 1814), Black Sea whiting (*Merlangius merlangus euxinus*, Nordmann, 1840), spiny dogfish (*Squalus acanthias*, Linnaeus, 1758) and Black Sea striped mullet (*Mullus barbatus ponticus*, Essipov, 1927), four jellyfish; *Mnemiopsis leidyi* (Agassiz, 1865), *Aurelia aurita* (Linnaeus, 1758), *Pleurobrachia spp.* and *Beroe ovata* (Mayer, 1912); two detritus groups; one sediment and one representing particulate organic matter (POM); one phytoplankton and one zooplankton group due to lack of time series data for functional sub-groups; one heterotrophic dinoflagellate *Noctiluca scintillans* (Ehrenberg, 1834) and one dolphins group to represent the Black Sea marine mammals, which were mainly composed of Black Sea common dolphin (*Delphinus delphis spp. ponticus*; Barabash-Nikiforov, 1935), Black Sea bottlenose dolphin (*Tursiops truncatus spp. ponticus;* Barabasch, 1940) and Black Sea harbour porpoise (*Phocoena phocoena spp. relicta*; Abel, 1905) (Table 16, Figure 5). Anchovy was defined as a multi-compartment group and was represented with two subgroups; one for `eggs and larvae`, and the other for `adult` life stages. The compartments were linked to each other by means of von Bertalanffy growth function (VBGF). Three fishing types were identified; trawlers, purse seiners and gill-netters to represent the fishery impact on the ecosystem.

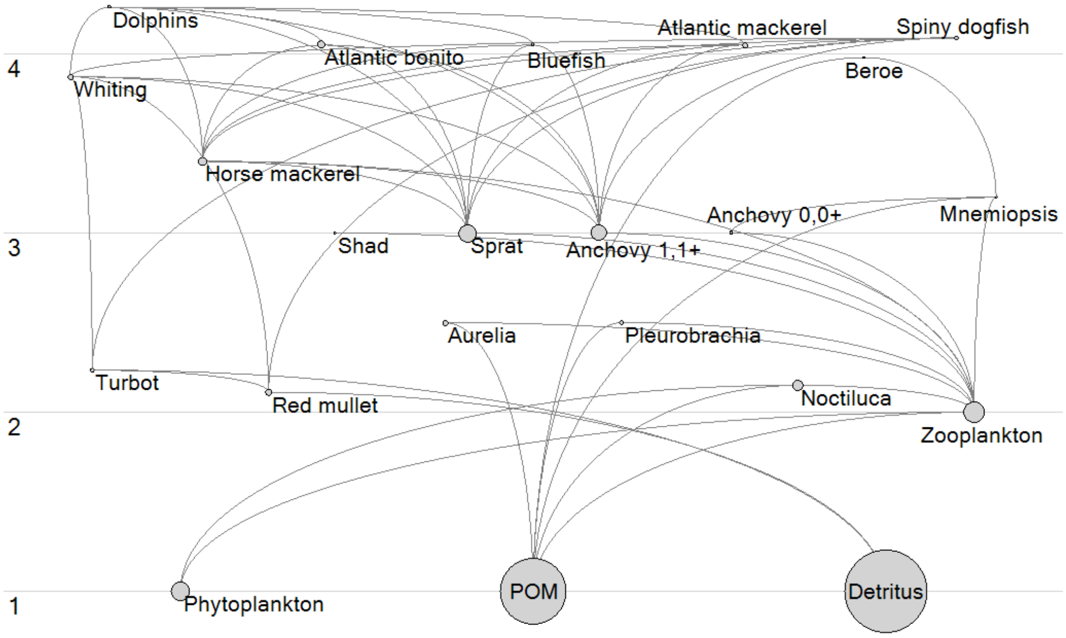


Figure 5. Schematic view of the Black Sea time-dynamic Ecopath with Ecosim model. Horizontal straight lines which are numbered with integers on the y-axis denote trophic levels. Arches show flows between groups. Nodes are the state variables and proportional to the biomass of groups in 1960.

The model currency was chosen as gC m^{-2} y^{-1} based on the reasons detailed in section 2.2.1. The in-situ biomass data and catch statistics, which were used to fit the model, were available in wet weight and converted to the model currency using the specified wet-weight to grams carbon conversion multipliers given in Table 7.

The mass-balance model was setup and balanced for the quasi-pristine conditions of the early 1960s based on the mass-balance model of the first period in Chapter 2. For this purpose, the P/B and Q/B values of aggregated groups in the simplified mass-balance models of Chapter 2 were used for the individual species forming the corresponding group in this chapter's model, which included representations at the individual species level. For instance, the P/B and Q/B values of small pelagic fish group in the Ecopath model of the first period in chapter 2 were used for the species which formed the small pelagic fish group; i.e. horse mackerel, shad, sprat, and anchovy in this chapter's model. Similarly, the pelagic piscivorous fish; Atlantic bonito, bluefish and Atlantic mackerel, and demersal fish; turbot, whiting, red mullet and spiny dogfish, were parameterised using the same approach. The input biomass and catch values of the fish species were obtained from Prodanov et al., (1997). For the fish species with no biomass estimates for the initial year, an EE value of 0.9 was assumed.

Concerning groups/species other than fish and dolphins, data from Shiganova (2008) were used for input biomass values except for the phytoplankton group. For phytoplankton, input biomass value was taken from Nesterova (2008). Although *Mnemiopsis* and *Beroe* species were not present in the ecosystem conditions of 1960s and introduced in late 1980s and 1990s respectively, these two species were included in the model set-up of 1960s because it was not possible to introduce these two groups into the ecosystem at their specific year of introduction unless included in the initial model set-up. Therefore, their input biomass values were set to unrealistically low values in order to prevent them interacting within the food web with other components of the model until their year of introduction.

All of the basic input parameters (Table 16) were then perturbed within 20 % coefficient of variation using a Monte-Carlo style parameter search routine in EwE in order to obtain the best fitting combination of initial conditions to the time series used to fit the model.

Table 16. Basic input parameters of state variables in the Black Sea time-dynamic model. “Est.” denotes the estimated parameters by the Ecopath mass-balance algorithm.

Group name	**Biomass in habitat area (gC/m²)**	**Production / biomass (/year)**	**Consumption / biomass (/year)**	**Ecotrophic efficiency**	**Catch (gC/m²)**
Dolphins	0.012	0.436	5.773	Est.	0.001
Atlantic bonito	Est.	0.504	5.290	0.695	0.012
Bluefish	Est.	0.505	4.359	0.980	0.000
Atlantic mackerel	0.035	0.512	5.385	Est.	0.006
Whiting	Est.	0.705	2.131	0.996	0.000
Turbot	Est.	0.614	1.637	0.755	0.001
Red mullet	Est.	0.653	2.111	0.828	0.001
Spiny dogfish	Est.	0.552	1.904	0.431	0.000
Horse mackerel	0.065	2.739	9.164	Est.	0.013
Shad	Est.	2.284	9.601	0.983	0.001
Sprat	0.258	2.888	13.011		0.003
Anchovy 1,1+	0.260	2.977	9.780	Est.	0.015
Anchovy 0,0+	0.013	23.033	69.638	Est.	-
Aurelia	0.037	12.393	34.514	Est.	-
Beroe	0.000	9.636	27.555	Est.	-
Mnemiopsis	0.000	8.631	34.514	Est.	-
Pleurobrachia	0.024	7.300	37.183	Est.	-
Noctiluca	0.085	8.770	38.395	Est.	-
Zooplankton	0.390	43.810	268.707	Est.	-
Phytoplankton	0.335	291.000	-	Est.	-
POM	20.000	-	-	0.413	-
Detritus	80.000	-	-	0.000	-

The diet composition matrix of the model (Table 17) was largely based on data available by stomach content analysis and compiled from FishBase (Froese and Pauly, 2011) and references therein.

Table 17. Relative diet proportions of the state variables.

Prey \ predator	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**1**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
Dolphins																			
Atlantic bonito	0.05																		
Bluefish	0.05																		
Atlantic mackerel	0.05																		
Whiting	0.05					0.1		0.5											
Turbot					0.05	0.1		0.1											
Red mullet					0.1	0.1	0.1	0.1											
Spiny dogfish																			
Horse mackerel	0.15	0.1	0.1	0.1				0.1											
Shad																			
Sprat	0.3	0.3	0.3	0.3	0.35			0.1	0.2										
Anchovy 1,1+	0.35	0.4	0.4	0.4	0.5			0.1	0.2										
Anchovy 0,0+																0.1			
Aurelia																			
Beroe																			
Mnemiopsis															0.9				
Pleurobrachia																			
Noctiluca																			
Zooplankton						0.1			0.6	1	1	1	1	0.5		0.8	0.5	0.15	
Phytoplankton																		0.6	0.9
POM														0.5	0.1	0.1	0.5	0.25	0.1
Detritus						0.6	0.9												
Import		0.2	0.2	0.2															

Concerning lower trophic level groups, the biomass estimations from in-situ sampling data were used to fit their simulated biomass values. For the zooplankton group, the data were obtained from Shiganova (2008) and for the phytoplankton group the data obtained from Nesterova (2008) were used. However, the zooplankton groups that had no natural predators in the ecosystem, i.e. *Aurelia*, *Pleurobrachia*, *Noctiluca*, *Mnemiopsis* (until 1997) and *Beroe*, were forced with biomass estimates obtained from in-situ samplings. The primary productivity of the phytoplankton group was forced using calculations from Oguz et al. (2012).

The dynamic model of the Black Sea was run starting from the year 1960 until the end of the year 1999. The fish groups were forced with time series of fishing mortality estimates obtained from conventional models (e.g. Virtual Population Analysis (VPA)). The time series of catch data and VPA biomass estimations of fish groups used to fit the model and the time series of fishing mortality values used to force the fish groups were taken from Prodanov et al. (1997) for the years (1960-1992) and complemented from Shlyakhov (2008) for the years 1993-1999. However, time series of catch and VPA biomass estimations had occasional gaps and these were left missing. Concerning fishing mortalities, the missing values at the start/end of the time series were complemented by continuing the first/last fishing mortality value until the beginning/end year of the simulation. For groups that completely lacked fishing mortality estimates, hence, biomass estimations, the fishing mortality values were estimated so as to achieve better fits for the simulated catches to the statistical catch data. However, the fishing mortalities for these groups were not changed year-to-year but kept constant throughout the simulation period.

In the dynamic module of Ecopath with Ecosim, the mass-balance system of linear equations of Ecopath detailed in the previous chapter was transferred to the time-dynamic domain in the form of a differential equation:

$$\frac{dB_i}{dt} = \left(\frac{P}{Q}\right)_i * \sum_{i=1}^{k} Q_{ji} - \sum_{j=1}^{k} Q_{ij} + I_i - (M_i + F_i + e_i) * B_i \tag{5}$$

where dB_i/d_t is the rate of change of biomass *(B)* of group *i* over time *t*, *(P/Q)* is the gross efficiency, $\Sigma\ Q_{ji}$ is the sum of the consumptions of group *i*, $\Sigma\ Q_{ij}$ is the sum of the predation on group *i*, *I* is the immigration (incoming migration), *M* is the non-predation mortality, *F* is the fisheries mortality and *e* is the emigration rate (outgoing migration) of group *i* (Walters et al., 1997). This system of differential equations was numerically integrated over time under the influence of forcing functions and initial condition settings for the state variables.

3.2.1. Model Assessment

First, model skill assessments were carried out by evaluating the degree of fit of simulated biomass and catch values with the VPA estimates of fish biomass, catch statistics of fish groups and in-situ measurements of unforced lower trophic level groups. The model was calibrated by tuning vulnerability (half-saturation) settings of the functional groups as well as Monte-Carlo style parameter searching for the mass-balance Ecopath model. For biomass and catch estimates simulated by the EwE model, the goodness of fit measure was the weighted sum of squared deviations (SS, Mood et al., 1974) of log biomasses/catches from the log predicted biomasses and/or catches and Akaike Information Criterion (AIC; Akaike, 1974). For LTL groups, i.e. zooplankton and phytoplankton biomass, the same measure of goodness of fit was calculated against the in-situ time-series data from which biomass predictions were obtained.

Similar to section 2.2.2, Ecological Network Analysis (ENA, Ulanowicz, 1986, 2004) was applied to the outputs of the dynamic Ecosim model in order to derive synthetic indicators and system metrics of the ecosystem. Fluctuations of synthetic indicators and system metrics over the simulation time of the dynamic model were analysed using the annual biomass, catch and flow estimates. Afterwards, a sequential algorithm based on the Student’s t-test (Student, 1908) for the detection of regime shifts (Sequential T-test Analysis for the detection of Regime Shifts (STARS) analysis, Rodionov, 2004) was applied to the indicators. This analysis is based on sequential data processing in which the number of samples is not fixed and come in sequence. For each new sample appended to the end of the data series, a t-test is applied to determine whether a regime shift was present (Rodionov, 2004). Due to the presence of significant autocorrelation in the time series of the synthetic indicators, pre-whitening (Rodionov, 2006) was applied to the synthetic time series before applying regime shift detection algorithm.

The ENA indicators in addition to those used in the evaluation of mass-balance models were summarised in Table 18. Such synthetic indicators were valuable to assess the ecosystem status and responses in different conditions as detailed in Odum (1969) and discussed as ecosystem and fishery indicators in Christensen et al. (1995) and Shannon et al. (2009).

Table 18**.** Ecosystem indices and synthetic ecological indicators used to assess the ecological status of the Black Sea ecosystem with the Ecosim model.

Indicator	**Explanation**
Ratios	
Piscivorous fish to other fish ratio	Expected to decrease with increased exploitation.
Ratio of predatory fish biomass to forage fish biomass	This ratio is an indicator of the “fishing down the food web” effect as a result of harvesting top predatory fish species. It is expected to decrease with fishing (Shannon et al., 2009).
Ratio of demersal fish to pelagic fish	This ratio is an indicator of the “fishing down the food web” effect as a result of harvesting top predatory fish species. It is expected to decrease with fishing. (Shannon et al., 2009).
Ecosystem metrics	
Biomass	Total biomass of living groups in the ecosystem.
Catch	Total fisheries catches.
Kempton's Biodiversity Index (Q)	Increase in this index indicates an increase in biomass of high trophic level (TL >= III) organisms (Kempton and Taylor, 1976). A decrease would indicate a degraded state (Shannon et al., 2009).
Fishing in balance index (FiB)	FiB = 0 when a decrease/increase in TL is matched by a corresponding respective increase/decrease in catch. Increasing FiB may indicate the geographic expansion of the fishery or that it is now covering previously underexploited stocks. Decreasing FiB may indicate a collapsed ecosystem or geographic contraction of the fisheries (Shannon et al., 2009).

3.3. Results

3.3.1. Evaluation of Hindcast Model Results

The sum of squared deviations (SS) for 38 time series and AIC score for 76 data points were calculated as 470 and 576 respectively. Considering the gaps in time series for most demersal species; i.e. whiting, turbot and spiny dogfish, and certain fish species; bonito, bluefish and red mullet, did not have stock estimates but only catch statistics, the SS and AIC values indicated that the model had a good fit and medium uncertainty (Figure 6 and Figure 7).

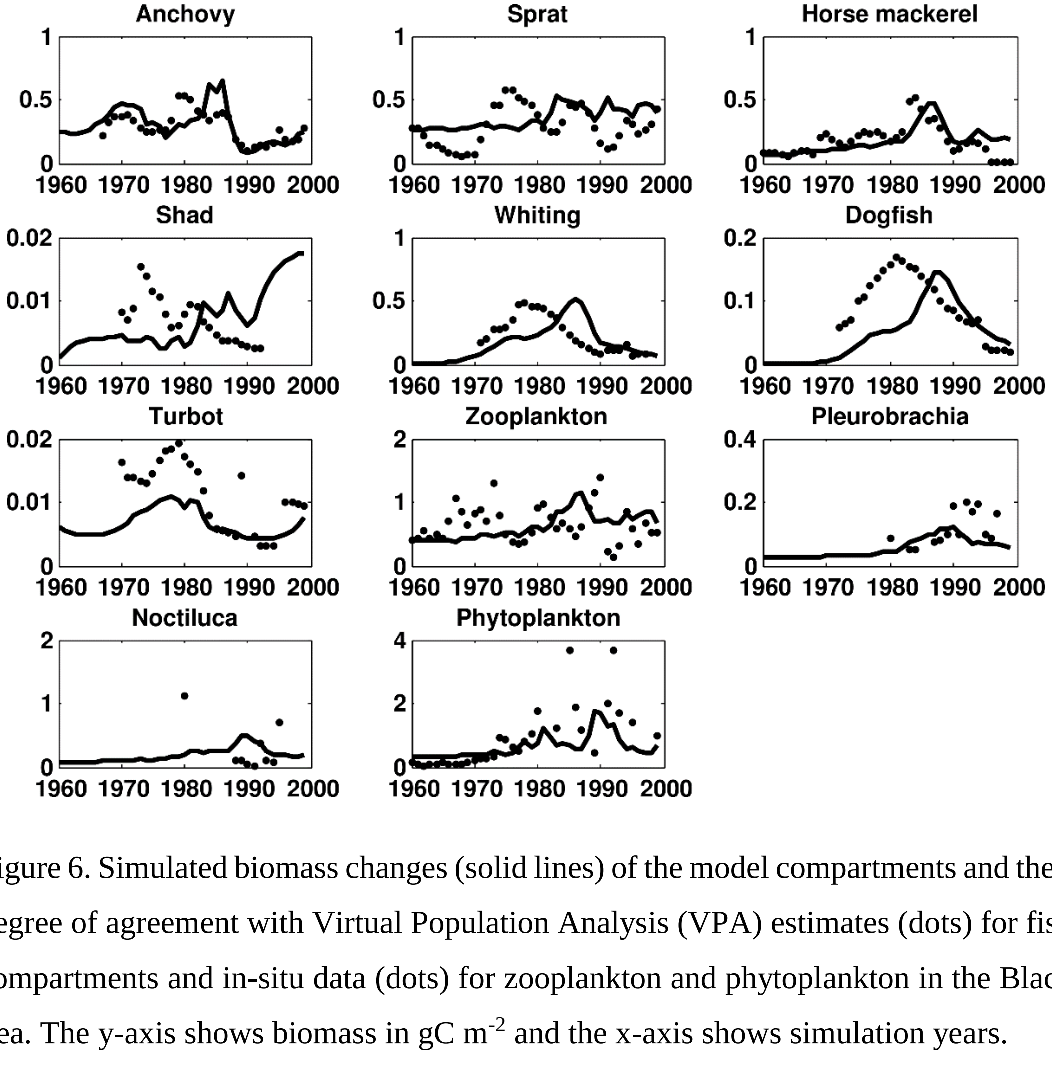


Figure 6. Simulated biomass changes (solid lines) of the model compartments and their degree of agreement with Virtual Population Analysis (VPA) estimates (dots) for fish compartments and in-situ data (dots) for zooplankton and phytoplankton in the Black Sea. The y-axis shows biomass in gC m^{-2} and the x-axis shows simulation years.

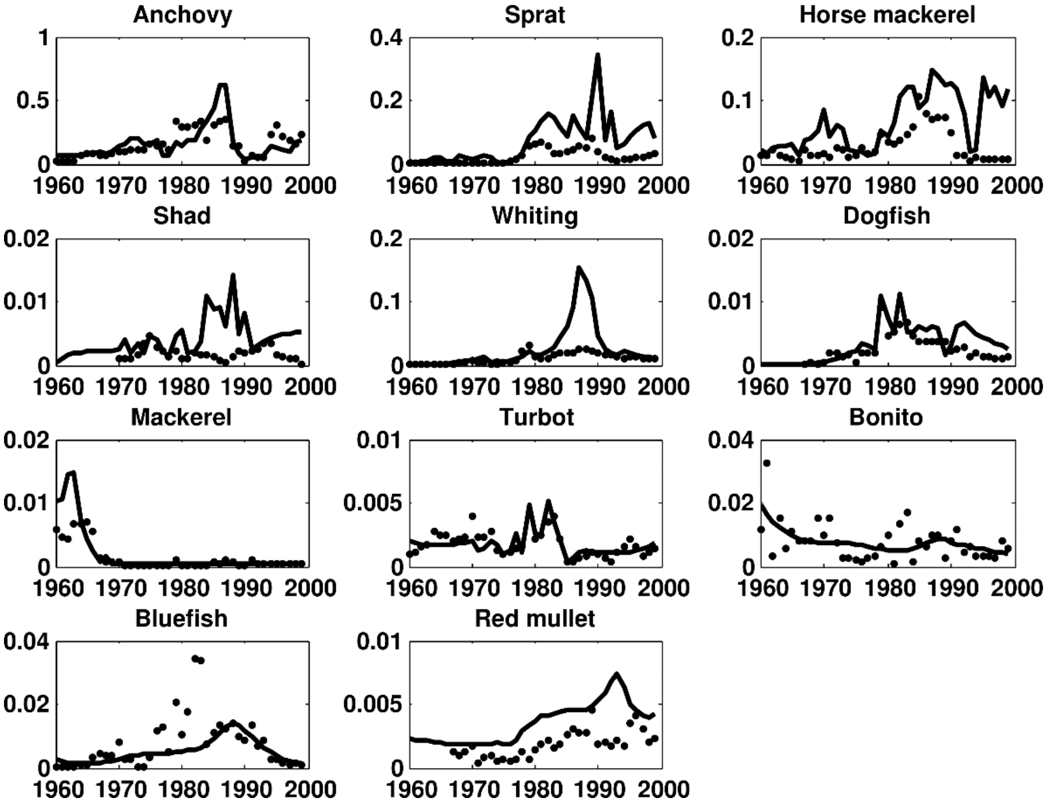


Figure 7. Simulated yield changes (solid lines) of the model compartments and their degree of agreement with statistical catch data (dots) in the Black Sea. The y-axis shows biomass in gC m^{-2} and the x-axis shows simulation years.

3.3.2. Assessment of Indicators and Ratios

The system throughput (TST) values indicated the presence of four different regimes separated by three significant shifts in 1977, 1988 and 1993 respectively. The period 1960 – 1976 was characterised as a relatively low-capacity flow regime with a mean value of 301 gC m^{-2} y^{-1}. The shift in 1977 corresponded to the beginning of the intense eutrophication period after the onset of eutrophication in the Black Sea during early 1970s and the mean value of TST in this period increased to 629 gC m^{-2} y^{-1}. A third shift occurred in 1988 and the mean value of TST was calculated as 1098 gC m^{-2} y^{-1} during 1988-1992 (Figure 8). One last shift occurred in 1993 and the mean throughput decreased to 593 gC m^{-2} y^{-1} during its corresponding regime. Considering the system's primary production, there were three regimes realised with two significant shifts in 1978 and 1994. Further, the timing of these shifts almost matched the shifts in TST occurred in 1977 and 1993 with a one year delay (Figure 8). The mean values of primary production for these three regimes were calculated as125.7 mgC m^{-2} d^{-1}, 494.0 mgC m^{-2} d^{-1} and 315.3 mgC m^{-2} d^{-1} respectively. These estimates were quite close to the predictions given by Yunev et al. (2002) as; ~150 mgC m^{-2} d^{-1} before 1970s, ~600 mgC m^{-2} d^{-1} between 1980 and 1990, and ~300 mgC m^{-2} d^{-1} after 1990. This showed that the fluctuations in the system's primary production, which was a consequence of changes in eutrophication, were the driving factor for the detected regimes in the TST as well.

The STARS analysis of ascendency of the system indicated that two successive regimes prevailed with mean values of 24.2% and 26.4% (Figure 8) separated with a shift in 1976; which closely matched the onset of intense eutrophication. However, considering the system overhead; i.e. resilience, four regimes were detected with shifts in 1971, 1977 and 1994. The first three regimes were characterised by gradually decreasing mean values of 45.2%, 42.5%, 36% respectively. During the last regime began in 1994, the overhead value of the system increased slightly to 38.5% (Figure 8).

The recycling in the system (FCI) showed decreasing trends in the detected first three regimes. The first regime change in the mean value of FCI occurred in 1968. During 1960-1967, the mean value of FCI was calculated as 5.29. Afterwards until 1976, the mean FCI decreased to 3.89. In the third period starting with 1976, the mean value of FCI further decreased and was calculated as 1.46. Finally, a last regime shift occurred in 1994 and thereafter the mean value of FCI increased up to 2.32. This showed that along with the increase in the system's flow capacity, the cycling of energy decreased significantly until 1994. This was in accordance with the increasing populations of trophic dead-end species such as jellyfish and *Noctiluca* (Figure 8), all of which diverted significant proportions of recycled matter back to detritus during those corresponding years. With the decrease in the energetic capacity of the system with alleviating eutrophic conditions starting with the collapse of the USSR in 1991 (Shiganova et al., 2008), the recycling of energy in the system increased (Figure 8) via the limitation exerted on these opportunistic groups by constrained system production. A similar pattern which supported this situation was detected by the STARS analysis in the mean path length indicator (Figure 8) with detected regime shifts in 1968, 1977, 1988 and 1996. During the first four regimes, the mean path length travelled by a unit of energy continuously decreased from a mean value of 2.60 in the first regime down to mean values of 2.50, 2.37 and 2.32 in the latter three. In the last regime starting from 1996, the mean value of the mean path length indicator increased up to 2.37. These two indicators suggested that along with the development of the ecosystem by means of energetic capacity, the recycled energy in the system through the food web was confined to lower trophic level compartments. To an extent, this matched the regimes detected in the proportion of flows to the detritus compartment (Figure 8). The shifts in the proportion of flows to detritus occurred in 1973, 1983 and 1999 respectively and the mean values of this indicator were calculated for the four regimes were 0.12, 0.14, 0.12 and 0.13 respectively. This delineated that the increasing eutrophic conditions led to increased amounts of flows diverted back to detritus within the food web.

Considering ecosystem's biomass, four regimes were detected with shifts in 1973, 1981 and 1993 respectively. Until the third shift, the mean values of biomass increased continuously and were calculated as 1.74 gC m^{-2}, 2.76 gC m^{-2} and 4.49 gC m^{-2} in the first three regimes. In the last regime starting with 1993, the mean value of biomass decreased down to 3.05 gC m^{-2}. These three regimes could be characterised as i) a low-biomass regime until 1972 without over-enrichment in the ecosystem, ii) (1973-1980) a medium-biomass regime started with the onset of eutrophication, iii) a high-biomass regime between 1981 and 1992 under intensive eutrophic conditions, and iv) (1993-2000) again a medium-biomass regime with alleviating eutrophic conditions. This interpretation was similar to the one delineated by Oguz et al. (2008b), however, considering only the size of the anchovy stock. Considering catches (Figure 8), three regimes were detected by the STARS analysis with shifts in 1979 and 1991. In the first period corresponding to 1960-1978, the mean value of catches was calculated as 0.19 gC m^{-2} y^{-1}. This was succeeded by another regime (1979-1990) with a higher mean value of 0.58 gC m^{-2} y^{-1}. The third period of 1991-1999 was characterised with a mean value of catches as 0.34 gC m^{-2} y^{-1}. The coincidence in timing of the third regime shift with the collapse of the anchovy stocks as well as the outburst of alien ctenophore *Mnemiopsis leidyi* was found noteworthy. Another indicator with respect to catches, the mean trophic level of the catch, showed significant changes in 1971, 1987 and 1998 (Figure 8). The mean trophic level of catch was calculated as 3.24 in the first period and decreased to 3.18 for the period 1972-

1986. In 1987, mTLc increased to a mean value of 3.23 until a last decrease down to 3.16 occurred in 1998. The increase in mTLc in 1987 was related to the decreasing proportion of small pelagic fish in the catches as they moved close to their stocks' collapse in 1989. A similar perspective was also observed in Kempton's Q index (Figure 8). The first three of the four detected regimes matched almost exactly with those detected for the mTLc indicator with marginal shifts in the onsets of the regimes. The three shifts in Kempton's Q indicator which realised four regimes occurred in 1979, 1988 and 1997 respectively. The mean values of Kempton's Q were calculated as 1.26, 0.71, 1.41 and 1.82 respectively during these four regimes detected by STARS analysis. The decrease in the mean value of this indicator from the first regime to the second was an indicator of the decrease in the proportion of HTL species, notably predatory fish and marine mammals, in the ecosystem and overdevelopment of LTL fish and organisms as a result of increased productive capacity of the ecosystem due to increasing eutrophic conditions. The increase in the Kempton's Q in 1988 was due to the collapse of the small pelagic fish stocks, most notably anchovy, which resulted in an increase in the relative proportions of higher trophic level fish groups in the ecosystem. The last shift in 1997 was found to be related to the settlement of another alien ctenophore *Beroe*, which had a higher TL (> III) because it only predated on *Mnemiopsis* (TL = III), in the Black Sea.

Two regimes were detected in the Fishing in Balance index (Figure 8). First regime (1960-1982) was characterised with a mean value of FiB quite close to 0 although with an increasing trend starting with the onset of 1970s. The first shift in the mean value of FiB occurred in 1983 and lasted until 1991. During this second regime, the mean value of FiB index was equal to 0.022, indicating both an expansion in fisheries and catch in accordance with the description of Gucu (2002). In 1991, a second shift in the mean value of FiB occurred along with the collapse of small pelagic fisheries, and starting from 1991 until the end of the simulation, the mean value of FiB index was calculated as 0.005. Contrary to FiB, the mean value of the relative Primary Production Required (%PPR) to support catches (Figure 8) constantly decreased until 1994 and realised three regimes with shifts in 1967 and 1977. The mean values of %PPR in these three regimes were calculated as 51.6%, 31.8% and 12.9% respectively. This decrease was due to the disproportional increase in system's primary production compared to the increase in the catches. In 1994, a final regime shift detected by the

STARS algorithm and the mean %PPR increased to 19% along with recuperating fisheries.

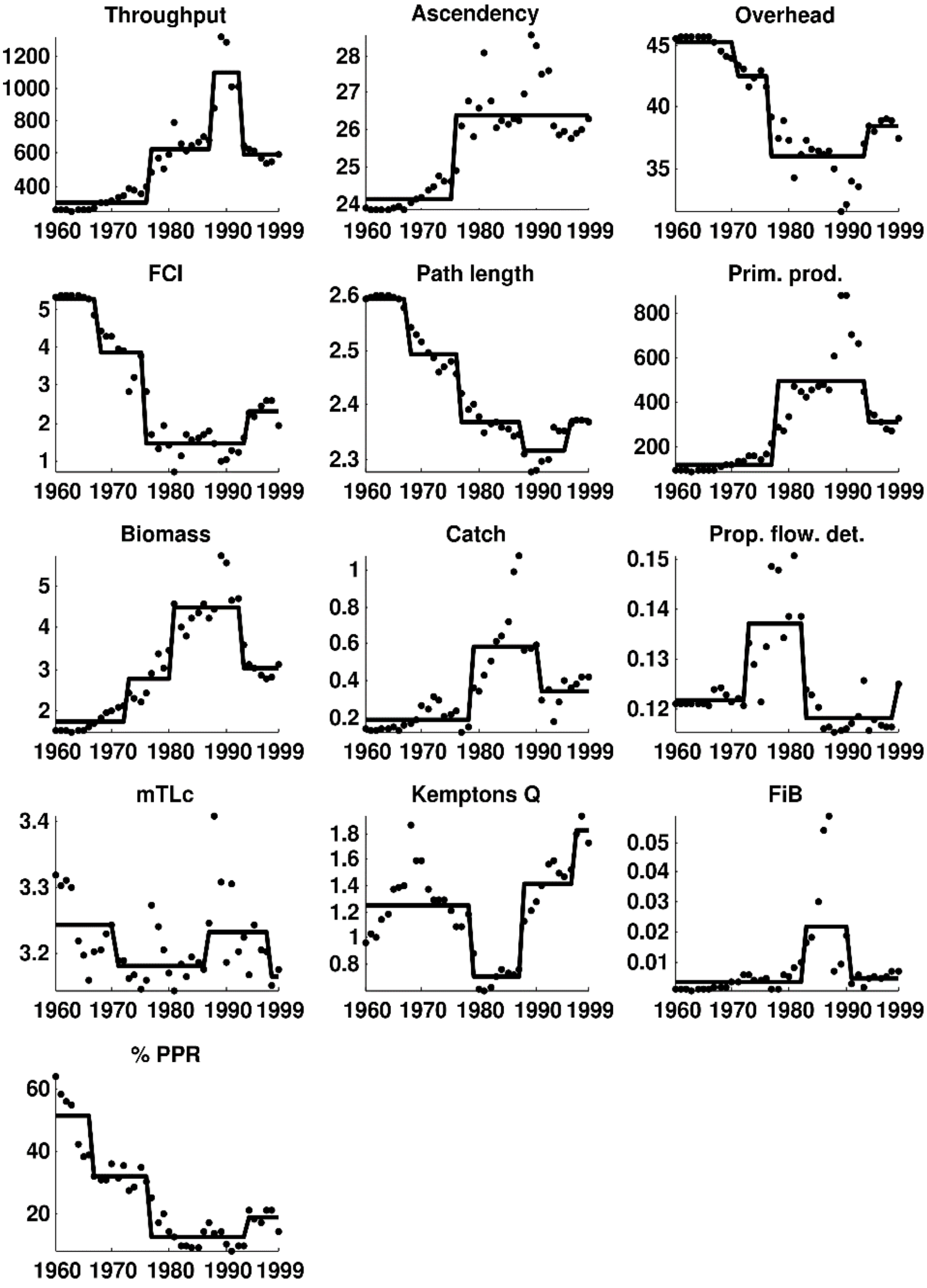


Figure 8. The time-dynamic changes in the indicators (dots) and the regimes detected (lines) by the STARS algorithm. Abbreviations are as follows: TST (Total System Throughput), FCI (Finn's Cycling Index), %PPR (relative Primary Production Required to support catches), mTLc (mean trophic level of catch), and FiB (Fishing in Balance). The TST, primary production, catch, and biomass properties are in gC m^{-2}

y^{-1}. FCI is percent of TST. Ascendency, overhead and %PPR are in percentages. Other indicators are unitless. The x-axis denotes simulation years.

Considering ratios, although some inverse trends occurred during specific years when catastrophic events like anchovy-*Mnemiopsis* shift occurred, the proportion of large fish by weight in the ecosystem decreased after 1965 realising the decrease in the mean trophic level of the catches observed throughout the simulation (Figure 9).

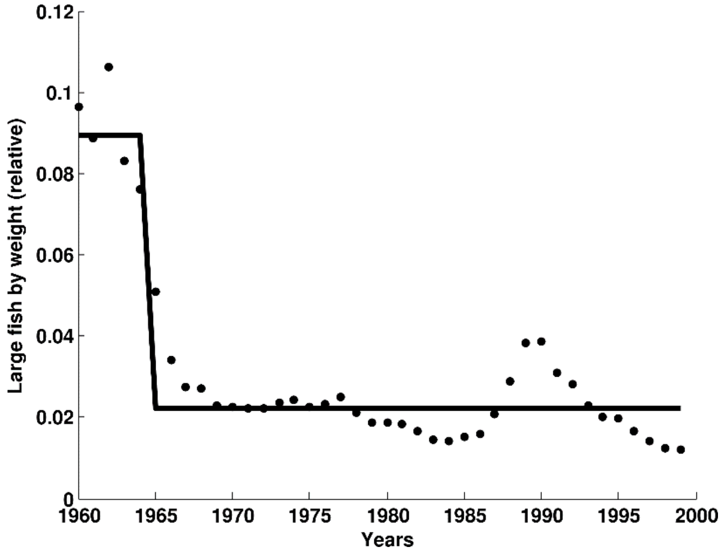


Figure 9. Large fish by weight simulated by the time-dynamic model. Dots represent the model simulation and line represents the regimes detected by the STARS analysis.

Considering ratios of fish groups (Figure 10), the consequences of fisheries exploitation were also found to be evident. The ratio of piscivorous fish to forage and other fish in the Black Sea had declined with time. The STARS algorithm detected two regimes in these two ratios both of which separated by a shift in 1965. Further, the ratio of demersal fish to pelagic fish increased during 1971 and decreased again in the 1994 showing the impact of fisheries exploitation on the ecosystem.

The ratio of opportunistic zooplankton (jellyfish and heterotrophic dinoflagellates) to total zooplankton biomass increased in the early 1970s reaching up to 55% of the whole zooplankton community in 1980s. This finding was also justified by the in-situ observations (Shiganova et al., 2008). After 1994, this ratio decreased to an extent so as to decrease the dominance of opportunistic zooplankton in the zooplankton community.

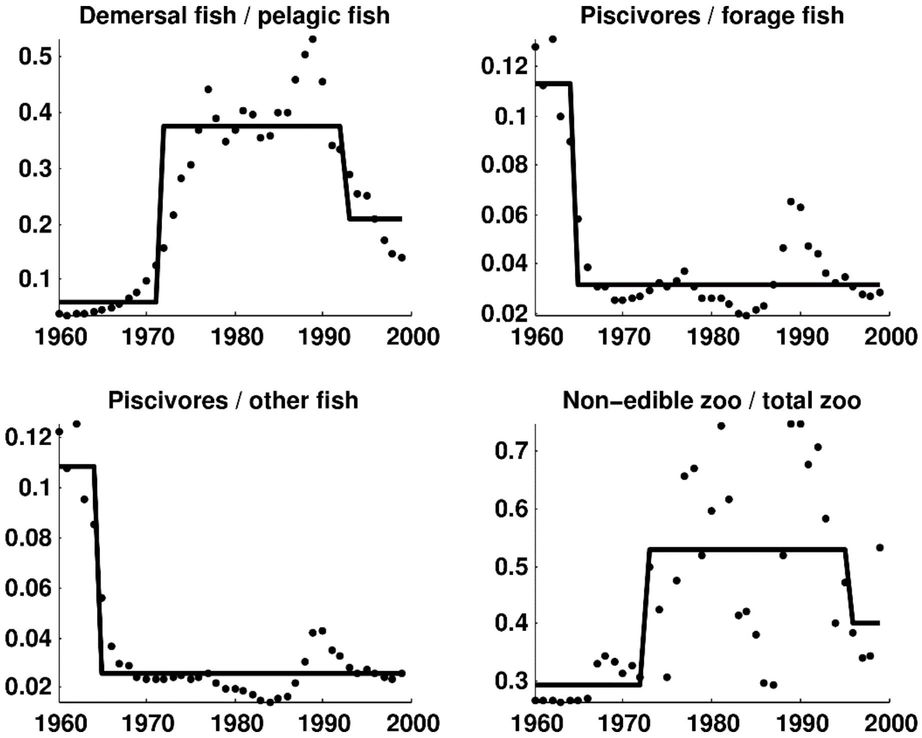


Figure 10. The time-dynamic changes in the ratios (dots) and the regimes detected (lines) by the STARS algorithm. The x-axis denotes simulation years.

The increasing enrichment in the Black Sea ecosystem was also delineated by the biomass ratio of heterotrophic dinoflagellate *Noctiluca* to the sum of the biomasses of *Noctiluca* and phytoplankton (Figure 11). Although there were significant fluctuations, there was a general increasing trend in the ratio in accordance with the increase in the primary production and total system throughput of the ecosystem (Figure 8).

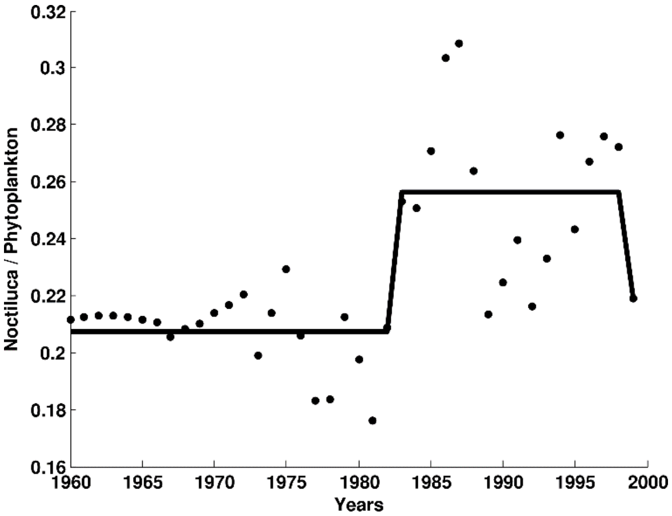


Figure 11. The ratio of heterotrophic dinoflagellate *Noctiluca* biomass to the sum of *Noctiluca* and phytoplankton biomass. Dots represent the model simulation and line represents the regimes detected by the STARS analysis.

3.4. Discussions and conclusions

The analysis of dynamic indicators showed parallel trends with the results inferred from the indicators of mass-balance models. First and foremost, increased enrichment in the ecosystem starting from early 1970s led to increased throughput values in the system (Figure 8) so as to increase the system's ascendency and decrease the system's overhead, i.e. resilience, to perturbations (Figure 8). In other words, bottom-up enrichment increased the energetic capacity of the Black Sea ecosystem enormously as evident in the increase in primary production (Figure 8). This resulted in overpopulation of opportunistic species, i.e. jellyfish and heterotrophic dinoflagellates, which had limited predators in the system, hence, diverting this excessive energy back to detritus compartment before reaching to higher trophic level organisms. This characteristic of the Black Sea was also shown by the mass-balance modelling study in chapter 2 and in agreement with the results provided by Caddy and Christensen (1993). Further, this was also supported by the increased proportion of flows to the detritus compartment (Figure 8) as well as the continuous decrease in Finn's cycling index (Figure 8) and the mean path length of a unit of energy travelled in the system (Figure 8). This showed that intensive LTL cycling of energy in the food web due to over-proliferation of opportunistic organisms deprived the HTL groups, i.e. fish, of significant resources from system's production, which otherwise would be shared across the upper trophic levels of the food web to support their biomass development. Further, the increasing proportion of opportunistic zooplankton in the total zooplankton community was a reason of this situation (Figure 10).

Second, fisheries played a structuring role on the ecosystem of the Black Sea. The decreasing mTLc suggested that a "fishing down the food web" (Pauly et al., 1998) effect had been realised in the ecosystem. This effect was also supported by the decreasing ratio of piscivorous organisms (predatory fish and marine mammals) to forage and other fish assemblages (Figure 10). By the end of 1960s, many of the higher trophic level fish species had already been overexploited leading to the shift in 1965 detected by the STARS analysis, which was in accordance with the analysis of Oguz (2007). This thinning-out (Petersen, 1903) of the Black Sea ecosystem's fish community was also reflected by the decreasing Kempton's Q index from 1960s to the end of 1970s. Kempton's Q, which indicates the proportion of organisms in the ecosystem with a trophic level equal to or higher than III, decreased significantly by the end of 1970s (Figure 8).

The relative primary production required to support catches (%PPR) decreased through the simulation period until its shift in 1994. However, at a first glance, the %PPR would have been expected to increase in accordance with the increases detected in the "Catch" and "FiB" indicators of the system when catches started to increase significantly. Considering this decrease in the mean value of %PPR, it could be concluded that the disproportionate increase in the system's primary productivity capacity far exceeded the increase in the catches. If the absolute PPR value was considered (Figure 12), it was shown that the value of PPR increased in accordance with the increasing catches. With the overexploitation of higher trophic level fish species by the end of 1960s and with the onset of overenrichment as well as the expansion of fishing fleet, the catches started to increase, however, the mean trophic level of the catch was significantly lower compared to 1960s (as evident in the shift in mTLc in 1967) because it consisted of mostly lower trophic level fish species like small pelagic fish. Therefore, the %PPR decreased continuously until 1994 due to the disproportionate increase in system's primary production compared to the increase in catches. In 1994, with the alleviating eutrophic conditions, a decreasing shift in the mean value of %PPR occurred. After this year, the fisheries and the fish stocks recovered; however, the catch did not reach to those levels of 1980s and the primary productivity of the system was considerably constrained compared to the 1980s, hence, an increase in the %PPR and a regime shift for this indicator were detected.

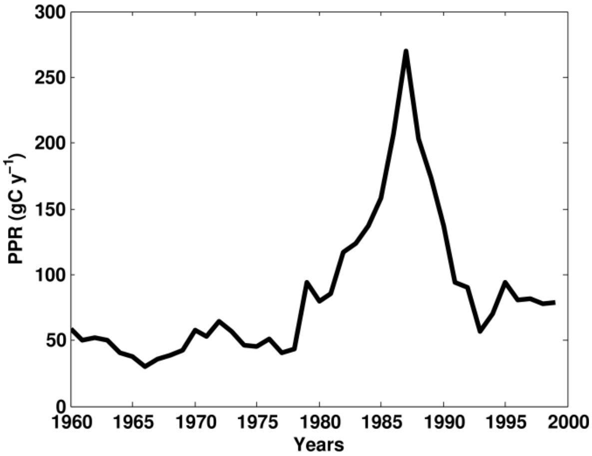


Figure 12. Primary Production Required (PPR) to sustain fisheries catches.

Considering the final status of the Black Sea ecosystem in the end of the simulation period in 1999, it could be inferred that the ecosystem conditions in the Black Sea was more degraded compared to the 1960s, however, in a better situation than that observed during the 1970s and 1980s considering the above discussed changes in the synthetic indicators and ratios. The most important factors that drove these changes over time was the eutrophication and fisheries exploitation. As detected in the primary production, the ecosystem experienced two shifts in 1978 and 1994. The shift in 1978 was due to the onset of intensive eutrophication and the latter was due to the alleviating eutrophic conditions and pollution in the Black Sea. The consequences of this alleviation were evident in the shift observed in the non-edible zooplankton to total zooplankton ratio towards the end of 1990s, which led to decrease in the proportion of these opportunistic organisms among the total zooplankton community. The timing of this shift in the zooplankton assemblage was also supported by Shiganova et al. (2008) depending on in-situ sampling data and regarded as “a sign of ecosystem rehabilitation at the zooplankton community level”.

4. CHAPTER: Translation of Ecopath with Ecosim into FORTRAN 95/2003 language for coupling

4.1. Introduction

Since the very first steps taken by the founding father of ecology (Haeckel, 1866), ecosystem research has developed to become a challenging field of science with the increasing understanding of the nonlinear interactions between the components that make up an ecosystem. This had first led to the development of primitive "ecosystem" models in the form of simple mathematical functions to represent prey-predator relationships (Lotka, 1920; Volterra, 1926). Later with the advancement in the computing technology during the second half of the 20th century, these mathematical representations of individuals in the ecosystem started to be used to build up mathematical models to represent multi-species interactions by coupling these equations with one another. For a couple of decades, such models of biogeochemistry and lower and higher trophic levels have been used in the marine environment with a certain degree of success. Though useful for understanding fundamental interactions, these representations of the ecosystems were short on explaining the holistic picture in the marine environments they represented. This led to the necessity for building integrated descriptions of food webs by coupling these models with one another in order to form a complete ecosystem representation from the microbiological and primary production processes up to fish assemblages and marine mammals through schemes called End-to-End (E2E) models (Rose et al., 2010; Salihoglu et al., 2013). This has been proven to be a challenging task (Fulton, 2010).

Hydrodynamic and biogeochemical models, which have been developed for more than a couple of decades, have been used together to assess the interactions between the biological and physical processes in the marine environment on the level of lower trophic level processes. Parallel to these efforts, various comprehensive models focusing on higher trophic level processes have been developed such as Ecopath (Polovina, 1984; Christensen and Pauly, 1992), Ecosim (Walters et al., 1997; 2000), OSMOSE (Shin et al., 2004) and ATLANTIS (Fulton et al., 2011). Among these tools, Ecopath with Ecosim (Christensen et al., 2005) was the most adopted tool in marine ecosystems as an end-to-end model. However, though its success, EwE is considered to be short on representing the nutrient cycle and lower trophic level dynamics such as primary and secondary productions and focused on the representation of life processes of fish species and other HTL organisms with annual and multiannual development cycles. In the recent years, this shortcoming of EwE has been tried to be remedied by utilising simple offline (Libralato and Solidoro, 2009) and complicated online (Beecham et al., in prep.) linking methodologies with existing models to a limited extent. However, these efforts has yet to be successful to the degree that they could be recognised and widely adopted by ecosystem modellers because until now these efforts either utilised only offline coupling and/or incorporated complicated programming tricks far more sophisticated than the modelling itself. This was the consequence of the fact that biogeochemical and hydrodynamic models were mostly written FORTRAN whereas EwE was prescribed in Visual Basic.

Considering above mentioned complications, in this chapter of the thesis, the first version of Ecopath with Ecosim translated into the FORTRAN language was presented in the endeavour of providing a useful tool for directly incorporating EwE as a module in existing biogeochemical models. Therefore, in this chapter, the methodology used for the translation was explained and evidence of the reliability of the code was provided by means of comparisons between standard EwE 6 version and the EwE-FORTRAN using the Generic 37 model scenario, which is distributed by the EwE 6 package, as a comparative test case. Further, the FORTRAN version of the model explained in the subsequent sections was also used for offline and one-way coupling with BIMS-ECO model for the analyses and testes detailed in Chapter 5. **By providing such a tool, it was believed that it will be useful in expanding the application of the software either for coupling and/or analyses by the interested scientific community, which have been hampered by the lack of a FORTRAN version of the model until now.**

4.2. Materials and Methods

The calculations in the Ecosim dynamic model were classified under four main groups; i) nutrient calculations, ii) prey-predator calculations, iii) derivative function calculations, and iv) integrator calculations, all of which were summarised in the subsequent subsections.

4.2.1. Nutrient calculations

Ecosim dynamic model starts with initial state calculations for setting up the initial conditions of state variables and parameters using basic input parameters of Ecopath. As a first step, the total and free base nutrient concentrations, which are going to drive the production of every state variable, are calculated as

$$N_{biomass} = \sum_{i}^{n} B_i^E \tag{6}$$

where $N_{biomass}$ is the biomass available in the system for the nutrient budget, *i* is the group number, *n* equals to the number of state variables and B_i^E is the Ecopath biomass estimate of group i. Then total nutrient concentration (N_{total}) is calculated as

$$N_{total} = \frac{N_{biomass}}{\left(1 - N_{BaseFreeProp}\right)} \tag{7}$$

where $N_{BaseFreeProp}$ is the base proportion of free nutrients, which equals to a value close to unity. Hence, free nutrient concentration (N_{free}) is estimated as

$$N_{free} = N_{total} - N_{biomass} \tag{8}$$

and free base nutrient concentration ($N_{FreeBase}$) equals

$$N_{FreeBase} = \left((\frac{P}{B})_i^{max} - 1 \right) \times N_{free} \tag{9}$$

and minimum nutrient concentration available in the system (N_{min}) is calculated as

$$N_{min} = 0.00101 * N_{free} \tag{10}$$

The above-calculated parameters are used in calculating the production of primary producers in the model and detailed in subsection “4.2.3”.

4.2.2. Prey – predator calculations

In Ecosim, the interaction between a prey *i* and predator *j* is determined according to the foraging arena theory (Christensen et al., 2005). According to this, the biomass of prey *i* is divided into two components; i) a vulnerable portion available to the predator *j*, and ii) an invulnerable portion which is not accessible by the predator *j* (Walters et al., 1997). The assumption behind this is that at a given time the whole biomass of prey is not available to all of its predators due to geographical/spatial implications (such as prey that is being hidden or far from the predator’s reach). The conceptual diagram of this theory was shown in Figure 13.

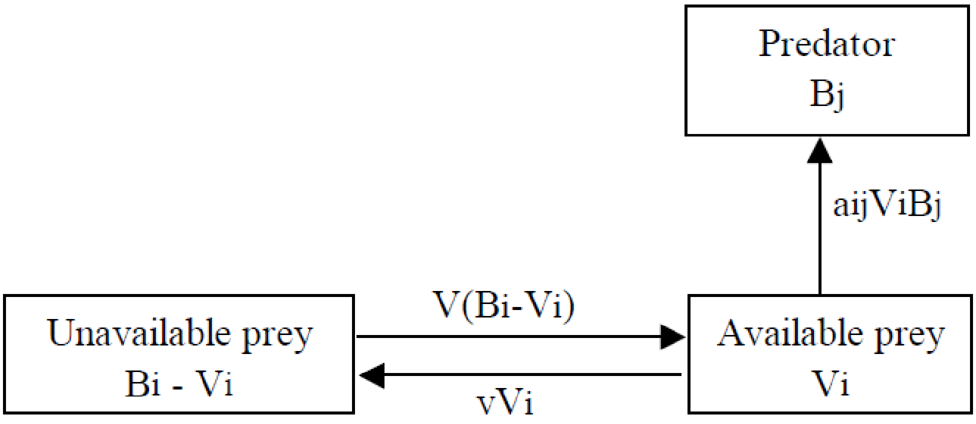


Figure 13. Flow between vulnerable ($\boldsymbol{V_i}$) and invulnerable prey biomass ($\boldsymbol{B_i - V_i}$) in Ecosim. $\boldsymbol{v}$ is the exchange rate between vulnerable and invulnerable compartments. $\boldsymbol{a_{ij}}$ is the search rate of the predator *j* for prey *i* (from Christensen et al., 2005).

The second step in Ecosim before the time-dynamic simulation is the calculation of base consumption to biomass rates $\left(\left(\frac{Q}{B}\right)_j^{base}\right)$ of state variables and is computed as

$$\left(\frac{Q}{B}\right)_j^{base} = \frac{\sum_i^n Q_{ji}^E}{B_j} \tag{11}$$

where $\sum_i^n Q_{ji}^E$ is the Ecopath consumption of the predator *j* summed over all of its preys and B_j is the biomass of the predator *j*. If *j* is a split group, then B_j is the abundance of group *j* in its corresponding subgroup. Utilising this value, the main $\left(Q_i^{main}\right)$ and risk time (consumption rate of the group when there are predators around) consumptions of predator *j* $\left(Q_i^{risk}\right)$ are calculated as

$$Q_j^{main} = (1 - R_t) \times \left(\frac{Q}{B}\right)_j^{base} \tag{12}$$

$$Q_j^{risk} = R_t \times \left(\frac{Q}{B}\right)_j^{base} \times \left(\frac{M2_j}{B_j^E + M0_j}\right) \tag{13}$$

where R_t is the predation effect on feeding time, $M2_j$ and $M0_j$ is the predation and natural mortality of predator *j* respectively, and B_j^E is the Ecopath biomass of predator *j*. Subsequently, vulnerability rates (v_{ji}) between predator *j* and- prey *i* is calculated for all prey-predator pairs using the user-entered vulnerability multipliers (x_{ji}) as

$$v_{ji} = x_{ji} * \left(\frac{Q_{ji}^E}{B_i^E}\right). \tag{14}$$

where Q_{ji}^E is the Ecopath consumption of prey *i* by predator *j*, and B_i^E is the Ecopath biomass of prey *i*. Using this value, predator search rate of predator *j* for prey *i* (A_{ji}) is computed as

$$A_{ji} = \frac{\left(\frac{Q_j^{max}}{Q_j^{max}{}_{-1}}\right) \times 2 \times Q_{ji}^E \times v_{ji}}{B_i^E \times B_j \times v_{ji} - Q_{ji}^E \times B_j}. \tag{15}$$

where Q_j^{max} is the maximum relative consumption of predator *j* and B_j is the biomass of predator *j* at time 0. The relative prey switching parameter $(T_j^{RelaSwitch})$ of predator *j* for prey *i* at each simulation time step is calculated considering the base prey switching parameter $(T_j^{BaseTimeSwitch})$ of predator *j*, which is calculated using Ecopath values, as

$$T_j^{BaseTimeSwitch} = \frac{A_{ji} \times (B_i^E)^{SP_j}}{\sum_i^n (A_{ji} \times (B_i^E)^{SP_j})} \tag{16}$$

$$T_j^{RelaSwitch} = \frac{\dfrac{A_{ji} \times (B_i(t))^{SP_j}}{\sum_i^n (A_{ji} \times (B_i(t))^{SP_j})}}{T_j^{BaseTimeSwitch}} \tag{17}$$

where SP_j is the user-entered switching power parameter of predator *j* in the Group Info tab of Ecosim and $B_i(t)$ is the biomass of prey *i* at simulation time *t*. From this, vulnerable pool of biomass of prey *i* (V_i) is calculated as

$$V_i = \left(x_{ji} - 1\right) * \left(\frac{Q_j}{2 * v_{ji}}\right). \tag{18}$$

where Q_j is the consumption of predator *j* in its corresponding foraging arena and calculated by multiplying the Ecopath consumption of predator *j* of prey *i* with the feeding time, which is a relative indicator of time spent by predator *j* for seeking prey *i*. Hence, feeding time ranges between 0 and 1 and depends on the concentration of the predators of *j* present in the system at time step *t*.

4.2.3. Derivative Function Calculations

The state equation of a variable *i* is

$$\frac{di}{dt} = f(B_i) + I_i - \sum_{j}^{n} Q_{ji}(t) - M0_i - F_{i,} - E_i \tag{19}$$

where $f(B_i)$ is production as a function of biomass, I_i is emigration, Q_{ji} is consumption of *i* by predator *j*, $M0_i$ is natural mortality, F_i is the fishing mortality and E_i is the emigration. If *i* is a primary producer, $f(B_i)$ equals to

$$f(B_i) = \frac{R_i^{max} * N_{free}}{N_{free} + N_{FreeBase}} * \frac{\left(\frac{P}{B}\right)_i^E * R_i^{max}}{1 + B_i(t) * \left((\frac{\left(\frac{P}{B}\right)_i^E * R_i^{max}}{\left(\frac{P}{B}\right)_i^E - 1}) / B_i^E \right)} * F(t) * B_i(t) \tag{20}$$

where $\left(\frac{P}{B}\right)_i^E$ is the Ecopath production to biomass ratio, B_i^E is the Ecopath biomass of producer, $B_i(t)$ is the biomass of producer at time *t*, R_i^{max} is maximum relative production to biomass ratio, $N_{free}$is total amount of free nutrients and $N_{FreeBase}$ is the free base nutrient concentration.

For consumer groups the state equation becomes in the form of

$$\frac{di}{dt} = g_i^{max} * \sum_{i}^{n} Q_{ij}(t) + I_i - \sum_{j}^{n} Q_{ji}(t) - M0_i - F_{i,} - E_i \tag{21}$$

where g_i^{max} is the maximum growth efficiency of group i, $Q_{ij}(t)$ is the consumption of group *i* on group *j* at simulation time *t*, Q_{ji} is the consumption of group *I* by its predator *j*, and the rest of the parameters are identical to those of the state equation for primary producers. g_i^{max} is estimated as

$$g_i^{max} = \left(\frac{P}{Q}\right)_i^E \tag{22}$$

where $\left(\frac{P}{Q}\right)_i^E$ is the Ecopath production to consumption ratio of group i. The consumption of predator *j* on prey *i* (Q_{ji}) is calculated as

$$Q_{ji} = \sum_i^n A_j^{eff} * \frac{V_i}{0.5 * \left(1 + H_j * A_j^{eff} * V_i\right) + 0.5 * \left(\frac{Q_j^{max}}{Q_j^{max} - 1}\right)} * B_j(t) \tag{23}$$

where A_j^{eff} is the effective search rate of predator *j* and H_j is the handling time of the predator. H_j is calculated as

$$H_j = \frac{B_j}{Q_j^{max} * B_j^E * \left(\frac{Q}{B}\right)_j^E} \tag{24}$$

where B_j is the biomass of predator *j* at time 0, B_j^E is the Ecopath calculated biomass of predator *j*. $\left(\frac{Q}{B}\right)_j^E$ is the Ecopath consumption to biomass ratio of predator *j*. And A_j^{eff} is calculated as

$$A_j^{eff} = \frac{\left(\frac{Q_j^{max}}{Q_j^{max} - 1}\right) * Q_{ji}}{V_i * B_j} * F_j^{time} * T_j^{relaswitch} \tag{25}$$

where F_j^{time} is the feeding time of predator *j*, which is equal to unity at simulation time 0. And (V_i) is the final vulnerable biomass of prey *i* and is equal to

$$V_i = \frac{V_{ji}^{eff}}{v_{ji} + V_{ji}^{eff} + \left(\frac{A_j^{eff} * B_j(t)}{0.5 * \left(1 + H_j * A_j^{eff} * V_i^*\right) + 0.5 * \left(\frac{Q_j^{max}}{Q_j^{max} - 1}\right)}\right)} * B_i(t) \tag{26}$$

where (V_i^*) is the initial vulnerable biomass estimate of prey *i* and equals to

$$V_i^* = \frac{V_{ji}^{eff}}{v_{ij} + V_{ji}^{eff} + \left(\frac{A_j^{eff} * B_j(t)}{\frac{Q_j^{max}}{Q_j^{max} - 1}} \right)} * B_i(t) \tag{27}$$

where (V_{ji}^{eff}) is the effective vulnerability rate and calculated as

$$V_{ji}^{eff} = v_{ji} * F_i^{time} \tag{28}$$

4.2.4. Integrator Calculations

A 4th-order Runge-Kutta numerical integration technique (Press et al., 1992) is used to solve the system of linear equations (Eqns. 19 and 21) along with successive over-relaxation (Barrett et al., 1994) for the detritus groups and the state variables that have fast turnover rates. At the end of each time step, the feeding times for predators are updated taking into account the new biomasses. Firstly, consumption to biomass rates are calculated at the end of the time steps using estimated biomasses. Following, new risk rates ($RiskRate_j$)are calculated for each predator j as

$$RiskRate_j = \frac{M2_j}{B_j} + M0_j \tag{29}$$

then optimum consumption (Q_j^{opt}) is calculated for the predator using the risk rate as

$$Q_j^{opt} = Q_j^{main} + \frac{Q_j^{risk}}{RiskRate_j} \tag{30}$$

Lastly, new feeding times (F_j^{time}) are calculated as

$$F_j^{time} = 0.1 + 0.9 * F_j^{time} * \left(1 - F_j^{timeAdjusted} + \frac{F_j^{timeAdjusted} * Q_j^{opt}}{\left(\frac{Q}{B}\right)_j^t} \right) \tag{31}$$

where $F_j^{timeAdjusted}$ is the user-entered feeding time adjustment rate in the Group Info tab of Ecosim.

4.2.5. The Skill Assessment of EwE-FORTRAN

The skill of the FORTRAN transcribed version of Ecopath with Ecosim (EwE-FORTRAN) was tested with the sample hypothetical model named “Generic 37”, which is distributed with the Ecopath with Ecosim 6 model package. The “Generic 37” model was run both with EwE 6 and EwE-FORTRAN programs and the results of the simulated biomasses of state variables were compared.

4.3. Results and Discussions

The residuals of the state variables calculated from the comparison of the simulations of Generic 37 model with EwE 6 and EwE-FORTRAN models justified that the FORTRAN version of the model had skill to reproduce the results of the EwE 6 for the Generic 37 model scenario (Figure 14). The residuals ranged between the orders of 10^{-6} and 10^{-4}, and the maximum error was found to be on the order of 10^{-4} for groups feeding on detritus (groups 6, 8, 16, 17, 24, 27, 29, 31) and the detritus group (group 37). This suggested that detritus dynamics might not have been correctly formulated in the FORTRAN version of the model and should be further refined. However, the magnitude of the misfits concluded that EwE-FORTRAN was capable of being used in coupling with biogeochemical models as detailed in chapter 5 without introducing significant sources of error to the resulting model scheme.

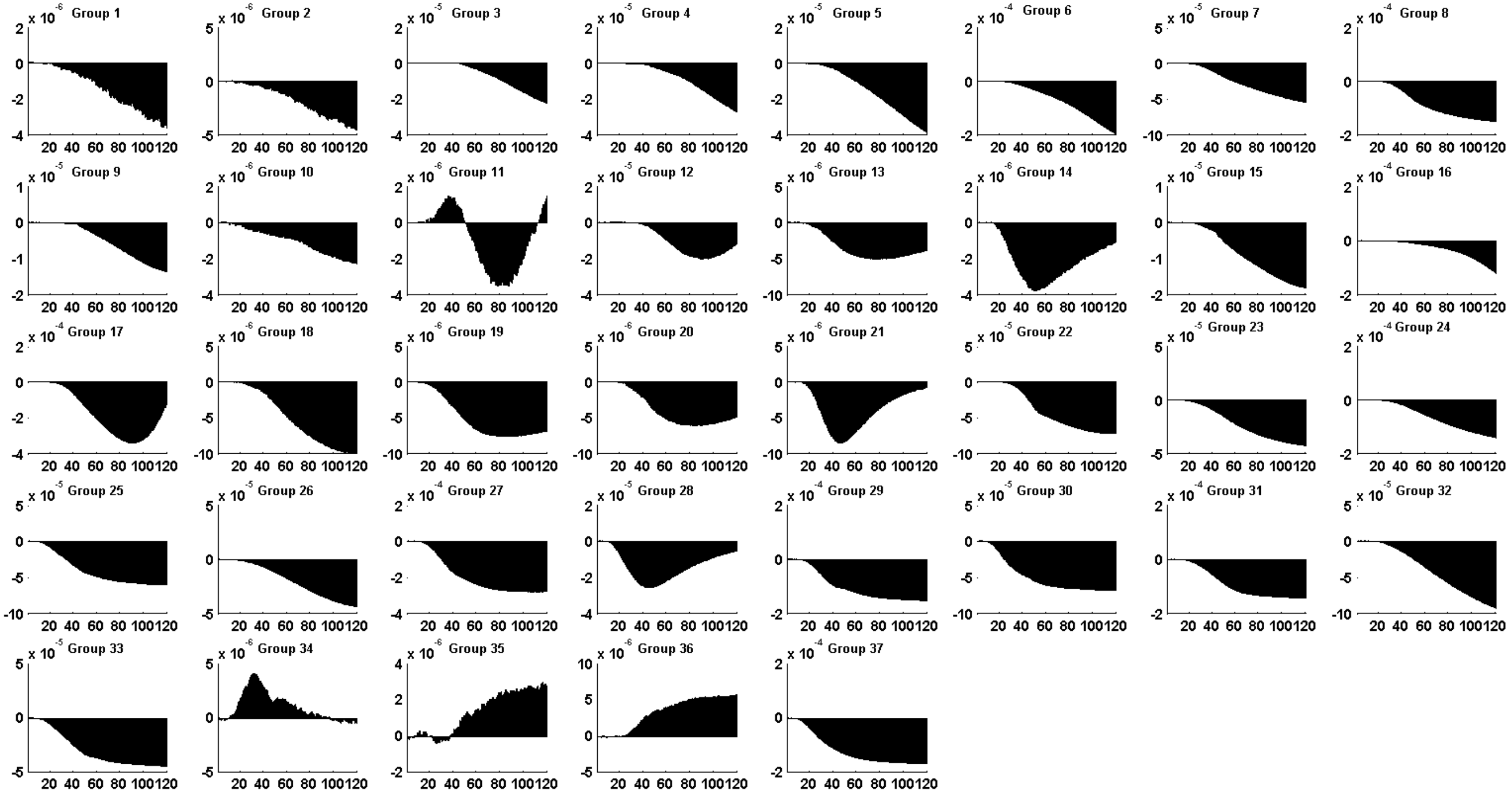


Figure 14. The residuals of the simulated biomasses of the state variables showing the degree of misfit between EwE 6 and EwE-FORTRAN model simulation outputs for the Generic 37 model.

5. CHAPTER: Scenarios on future ecosystem functioning under changing climatological and fisheries conditions

5.1. Introduction

For more than a decade, end-to-end models have increased the understanding of ecosystems at a broader scale including the feedbacks and interactions between coupled physical, chemical and biological systems (Fulton, 2010; Shin et al., 2010a; Rose et al., 2010; Travers et al., 2007). These models were considered as integrated ecosystem models that included ecosystem components from primary producers up to top predatory organisms and their interactions with the abiotic environment (Fulton, 2010). With such models, not only were the impacts of anthropogenic activities such as fishing and pollution examined, but long-term effects of climate variability and its consequences on the ecosystem scale could have also been investigated.

Ecopath with Ecosim model could be regarded as an end-to-end representation of the marine ecosystem from primary producers to top predators such as fish, marine mammals and even sea birds. Because the primary motivation in developing the EwE model focused on fisheries, the life history of fish groups was formulated in detail, whereas, the lower trophic level groups with relatively higher rate of turnover remained weakly prescribed. Further, concerning the complicated biogeochemical processes that take part in a given system's primary and secondary productivity processes under the strong influence of physical drivers such as mixing, temperature, and light, the lower trophic level representation of EwE could be considered as rather simplistic (see section 4.2.1). It did not incorporate these processes explicitly, however, implicit representations of their effects on the biogeochemical processes such as the production capacity of primary producers were represented through implementation of forcing and mediation functions. Therefore, for the sake of better representation of these aforementioned processes and their impacts, the EwE model was required to be coupled with advanced biogeochemical models which functioned in conjunction with hydrodynamic models.

In chapters 2 and 3, the changes in the Black Sea ecosystem were investigated through a set of indicators using steady-state (Ecopath) and dynamic (Ecosim) ecosystem models. Such modelling schemes were effective in capturing the impacts of the changes in the food web structure and functioning through implicit (eutrophication) and explicit (fishing) representation of anthropogenic pressures. However, the dynamics of biogeochemical processes and their impacts on the production capacity of the system as well as the influence of the physical environmental parameters were required to be included in terms of more sophisticated representations in order to put forward the impacts of climate scale variability on the ecosystem. Therefore, in this chapter, the Black Sea dynamic EwE HTL model was coupled to the physical (BIMS-CIR) and biogeochemical LTL (BIMS-ECO) models of the Black Sea in order to investigate such interactions and feedbacks and their consequences on the ecosystem both historically and prognostically so as to explore likely progressions of the ecosystem state and functioning of the Black Sea under historical and predicted climate and fishing scenarios for the future. **Hence, the main objectives of this chapter were; i) to evaluate and understand the impact of the short-term climate and physical variability and the introduction of invasive species on the Black Sea ecosystem using a hindcast scenario, and ii) to investigate the potential implications of climate change on the ecosystem's structure by the end of the 21st century.**

5.2. Materials and Methods

The Black Sea EwE and BIMS-ECO lower trophic level (LTL) models were coupled to form an end-to-end representation of the Black Sea ecosystem in zero-dimensional space. The HTL model was modified in terms of lower trophic level groups; i.e. groups other than fish, to match the structure of the BIMS-ECO model. The EwE model of the Black Sea was run one-way and offline coupled with BIMS-ECO model. The lower trophic level variables; i.e. phytoplankton, zooplankton, *Noctiluca*, *Aurelia* and *M. leidyi* were forced with the simulated biomasses by the BIMS-ECO model. The higher trophic level groups; i.e. fish species and dolphins, which were not included in the BIMS-ECO model, were simulated by the EwE Black

Sea model. The resulting scheme of the one-way offline coupled model was shown in Figure 15.

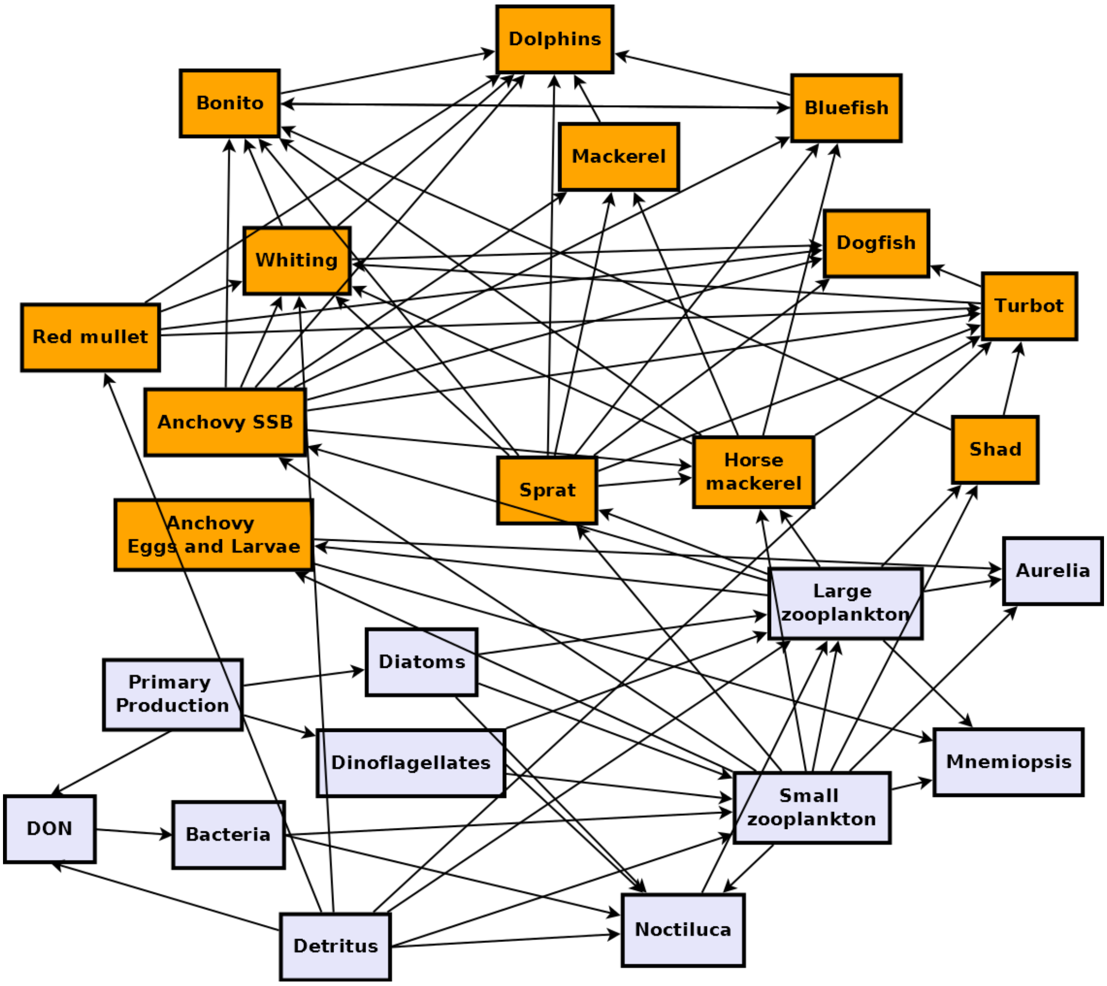


Figure 15. Coupled Black Sea model scheme. Light-grey boxes represent BIMS-ECO model compartments and orange boxes represent EwE Black Sea model compartments. Arrows indicate flows in terms of prey-predator interactions.

5.2.1. The Hydrodynamic and LTL Biogeochemical Model

The hydrodynamic model was a modified version of the sigma coordinate, free surface Princeton Ocean Model (POM; Blumberg and Mellor, 1987). The model domain incorporated the entire Black Sea (41°S - 46°N, 28°E - 41.5°E) excluding the Azov Sea. It consisted of a 0.1^{o} x 0.0625^{o} resolution Arakawa C-type of horizontal grid and a 26-level vertical grid. The sigma levels were compressed at the surface and bottom boundary layers. The maximum depth of the model domain was 2200 m. Considering that the Black Sea is a semi-enclosed sea, the lateral boundary conditions were no-slip and zero-heat, and salt fluxes were prescribed everywhere in the whole domain except the Bosphorus and Kerch straits as well as the mouths of the eight largest rivers draining into the Black Sea (Danube, Dniester, Dnieper, Inguri, Rioni, Yesilirmak, Kizilirmak, and Sakarya). At the mouths of the rivers and straits, boundary conditions of temperature and salinity were prescribed as inflow conditions. Diffusive heat and salt fluxes were set to nil in the straits outflow points (Cannaby et al., 2012).

The biogeochemical ecosystem model used in this study was the BIMS-ECO model based on the 1D model by Oguz et al. (2001). The model had 12 state variables that included two phytoplankton groups, small and large phytoplankton representing flagellates and diatoms respectively, micro- (< 0.2 mm, Zs) and mesozooplankton (> 0.2-2 mm, Zl), bacterioplankton (B), labile pelagic detritus (D), DON, nitrate (N), ammonium (A), as well as the opportunistic heterotrophic dinoflagellate *Noctiluca scintillans* (Zn) and the gelatinous carnivores *Aurelia aurita* (Za) and *Mnemiopsis leidyi* (Zm) (Figure 16).

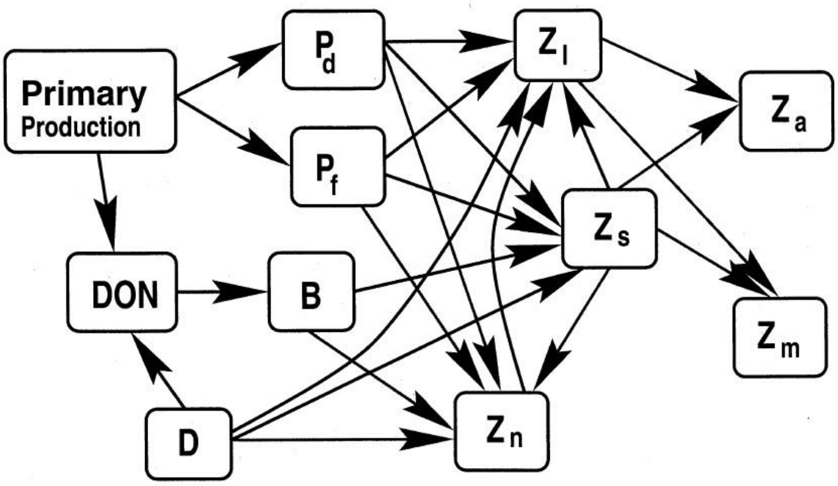


Figure 16. BIMS-ECO lower trophic level model structure (from Oguz et al., 2001).

M. leidyi was introduced into the model, however, forced to be dormant until the start of 1988. In the current version of BIMS-ECO used in this study, the impact of the introduction of *Beroe ovata* into the Black Sea in 1990 was prescribed as an additional grazing term on *M. leidyi* (Cannaby et al., 2012).

5.2.2. HTL Model

The Ecosim dynamic model was run from 1980 until the end of 1999 for hindcast validation, up until the most recent date at which adequate fisheries biology data were available. . The fish groups were forced with time series of fishing mortality estimates obtained from conventional models (e.g. Virtual Population Analysis (VPA)). The time series of catch data and VPA biomass estimations of fish groups that were used to fit the model and the time series of fishing mortality values that were used to force the fish groups were taken from Prodanov et al. (1997) for the years 1980-1992 and complemented from Shlyakhov (2008) for the years 1993-1999. However, time series of catch and VPA biomass estimations had occasional gaps and these were left missing. Concerning fishing mortalities, the missing values at the start/end of the time series were complemented by continuing the first/last fishing mortality value until the beginning/end year of the simulation. For groups that completely lacked fishing mortality estimates, hence, biomass estimations, the fishing mortality values were estimated so as to achieve better fits for the simulated catches to the statistical catch data. Because no catch or stranding statistics were available for marine mammals in the Black Sea, the fishing mortality for this group was set to an estimated fixed value of 0.5 between 1960-1966 (until the start of the fishing ban on Black Sea marine mammals in USSR, Bulgaria and Romania), 0.3 during 1967-1982 (until the start of the fishing ban on Black Sea marine mammals in Turkey) and 0.001 onwards in order to represent the significant effect of by-catches due to fishery operations. The jellyfish compartments were forced with biomass values simulated by BIMS-ECO model since they did not have natural predators within the system prior to the introduction of *B. ovata* in 1992 (Konsulov and Kamburska, 1998). The primary producers were forced with time series of nonlinear production estimates and zooplankton groups were forced with biomass estimations by the BIMS-ECO model during the simulation period. The time series of catch data and stock assessments of other models such as VPA were used as a measure for the model fitting. The model was calibrated utilising vulnerability (half-saturation) settings of the functional groups as well as Monte-Carlo style parameter search routine for the mass-balance Ecopath model. For biomass and catch estimates simulated by the EwE model, the goodness of fit measures were the weighted sum of squared deviations (SS, Mood *et al.*, 1974) of log biomasses/catches from the log predicted biomasses and/or catches and Akaike Information Criterion (AIC; Akaike, 1974). For phytoplankton groups, the same measure of goodness of fit was calculated against the *in-situ* time series data from which biomass predictions were calculated. There were 36 time series consisting of in-situ catch and biomass measurements and statistical catch data which were used to fit the model (for more details see section 3.2).

5.2.3. Scenarios

One hindcast scenario entitled Present Day (PD) was used by means of the BIMS-CIR hydrodynamic model. The PD scenario was run for 20 years from 1980 until the end of 1999. Surface forcing was prescribed using 6-hourly fields of wind stress, fresh water fluxes (evaporation, convective precipitation and large-scale precipitation), and radiation fields (surface shortwave radiation, surface long-wave radiation, evaporative heat flux, and convective heat flux). The PD scenario was forced with the data extracted from Institut Pierre Simon Laplace (IPSL) Climate Model 4 (CM4) Ocean Atmosphere Global Circulation Model (OA-GCM) (Marti et al., 2006). Further, one climate forced simulation (A1B) was run from 2080 until the end of 2099. For this simulation, the model setup, initial conditions and river inputs were identical to the end of the control simulation. The A1B scenario was evaluated and compared against PD scenario on the basis of fractional change in the multiannual simulated model outputs of the state variables. For any given state variable *i*, the fractional change (*fc*) was calculated as

$$fc_i = \frac{B_{i_{A1B}}}{B_{i_{PD}}} - 1 \qquad (32)$$

where $B_{i_{A1B}}$ and $B_{i_{PD}}$ were the average biomass of *i* over the whole simulation periods of A1B and PD respectively. In order to test any given fractional change of state variable i was statistically significant, a Kruskal-Wallis non-parametric 1-way ANOVA test (Kruskal and Wallis, 1952) was applied to the model simulated time series biomass values of the state variables.

The progressions in the fish community structure under 50% increased and decreased fishing mortality levels for all fish groups were investigated in section 5.3.5 using the present day (PD) scenario. Furthermore, the sensitivity of the Black Sea ecosystem to various fishing and primary productivity conditions was also explored by means of six different scenarios focusing on the anchovy-*Mnemiopsis* shift using the PD simulation in order to investigate the underlying causalities of the incident (Table 19).

Table 19. Fishing scenarios used to explore the causalities of anchovy-*Mnemiopsis* shift under different combinations of changing fishing mortality levels on the anchovy stocks and alternating primary production and food web conditions.

Scenario	**Explanation**
Scen. 1	F_{msy} (Fishing mortality (F) required to obtain Maximum Sustainable Yield (MSY)) value forced on anchovy stocks
Scen. 2	F_{msy} value forced on anchovy stocks in combination with invariant primary production equal to the year of 1980 throughout the simulation period
Scen. 3	F_{msy} value forced on anchovy stocks along with no *Mnemiopsis* and *Beroe* introduction to the food web

Scen. 4	F_{msy} value forced on anchovy stocks along with invariant primary production equal to the year of 1980 throughout the simulation period and no *Mnemiopsis* and *Beroe* introduction to the food web
Scen. 5	Status quo (PD) fishing mortality values applied on anchovy stock along with no *Mnemiopsis* and *Beroe* introduction to the food web
Scen. 6	Status quo (PD) fishing mortality values applied on anchovy stock along with invariant primary production equal to the year of 1980 throughout the simulation period

5.3. Results

5.3.1. Evaluation of Hindcast Model Results

The sum of squared deviations (SS) for 36 time series and AIC score for 72 data points were calculated as 164 and 475 respectively. Considering that the time series had gaps for most demersal species; i.e. whiting, turbot, and spiny dogfish; and some fish species such as bonito, bluefish, Atlantic mackerel, and red mullet did not have any stock estimates but only catch statistics, the SS and AIC values could be evaluated as the model had a good fit and medium uncertainty (Figure 17 and Figure 18).

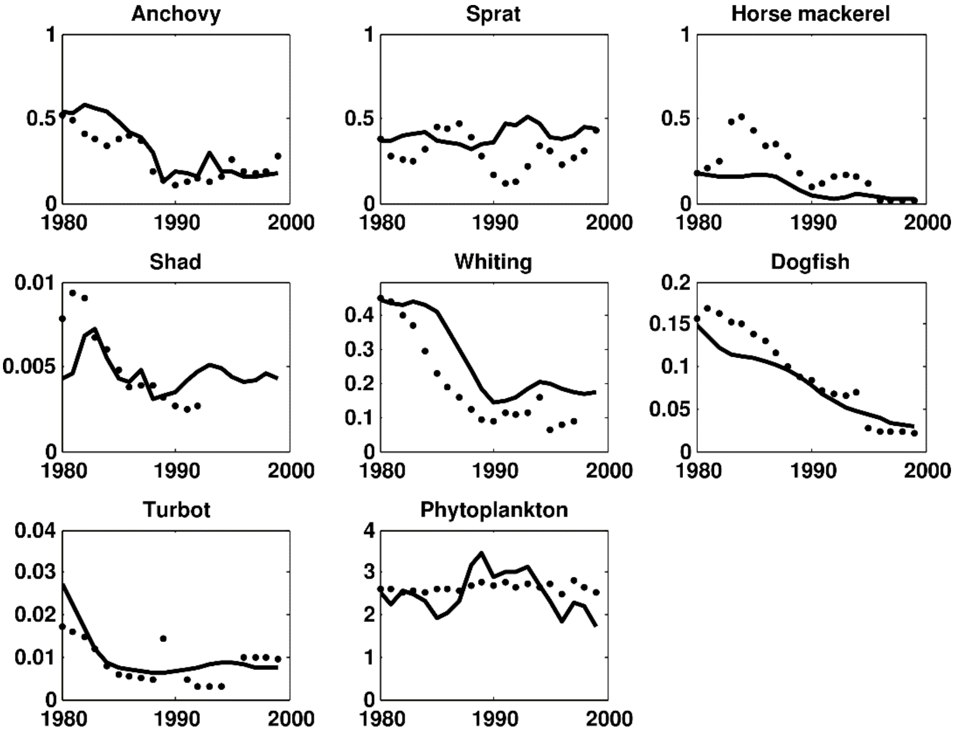


Figure 17. PD run: Simulated biomass changes (solid lines) of the model compartments and their degree of agreement with Virtual Population Analysis (VPA) estimates (dots) for fish compartments. The y-axis shows biomass in gC m^{-2} and the x-axis shows simulation years.

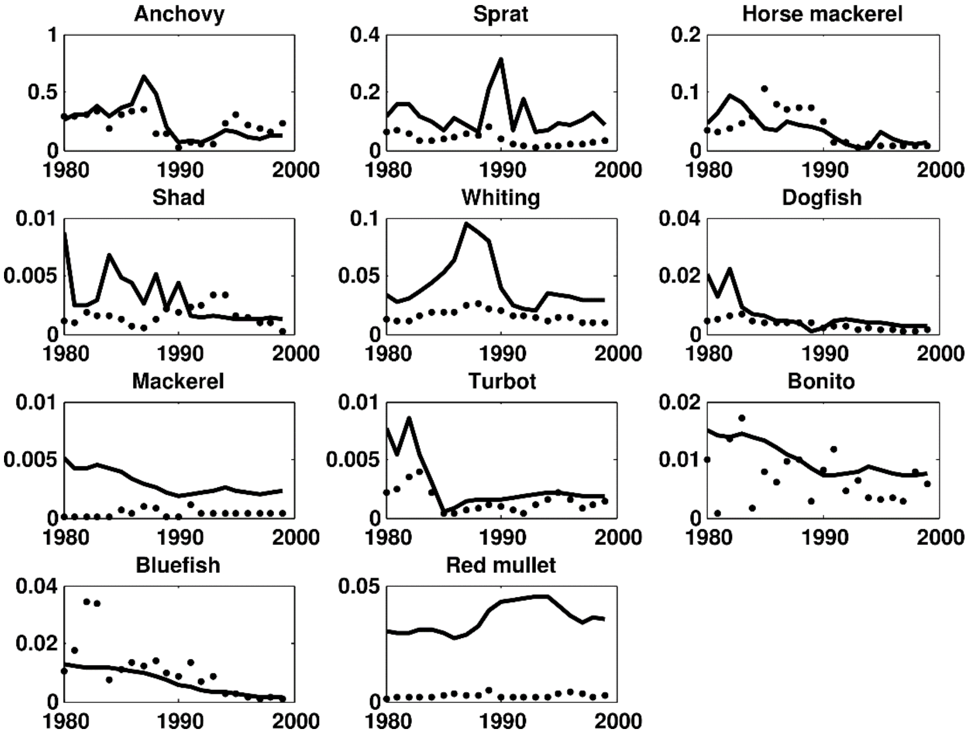


Figure 18. PD run: Simulated yield changes (solid lines) of the model compartments and their degree of agreement with statistical catch data (dots) in the Black Sea. The y-axis shows biomass in gC m^{-2} and the x-axis shows simulation years.

5.3.2. Changes in LTL

The annual mean depth-integrated basin-averaged primary production in the A1B scenario was simulated to increase significantly compared to the PD scenario according to the Kruskal-Wallis test ($p < 0.05$) and calculated to be 5% higher (mean 206 mgC m^{-2} d^{-1}) than the PD scenario reflecting the impact of changed circulation patterns in the A1B scenario due to the basin-wide 3 ºC temperature increase (Figure 19).

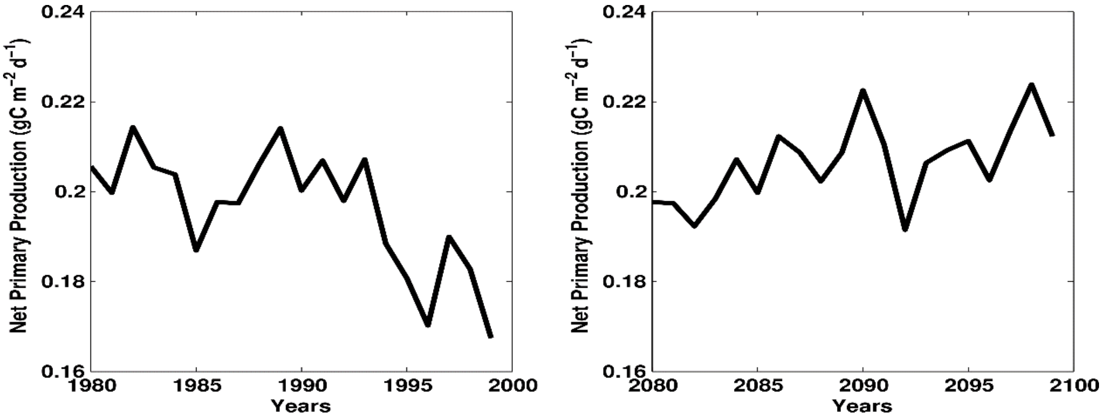


Figure 19. Annual mean time series of depth-integrated and basin-averaged net primary production of PD (left) and A1B (right) scenarios in the Black Sea (from Cannaby et al., 2012).

Considering the annual mean depth-integrated basin-averaged phytoplankton biomass values, the PD and A1B scenarios differed significantly ($p < 0.0001$) according to the Kruskal-Wallis test (Figure 20) and an increase in the phytoplankton biomass was simulated. However, zooplankton biomass did not show significant difference ($p = 0.28$) between PD and A1B scenarios according to the Kruskal-Wallis test (Figure 21). In the PD simulation, the zooplankton biomass was simulated to decrease significantly with the appearance of *Mnemiopsis* in the year of 1988 (Cannaby et al., 2012).

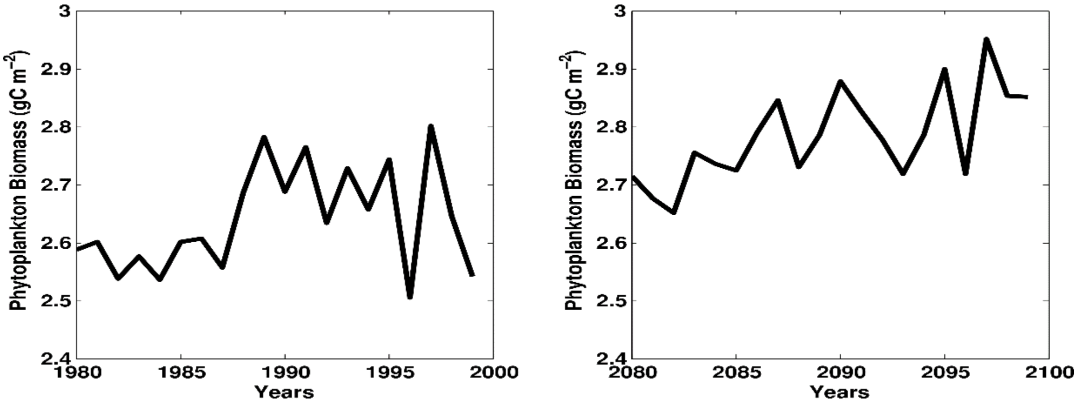


Figure 20. Annual mean time series of depth-integrated and basin-averaged phytoplankton biomass of PD (left) and A1B (right) scenarios in the Black Sea (from Cannaby et al., 2012).

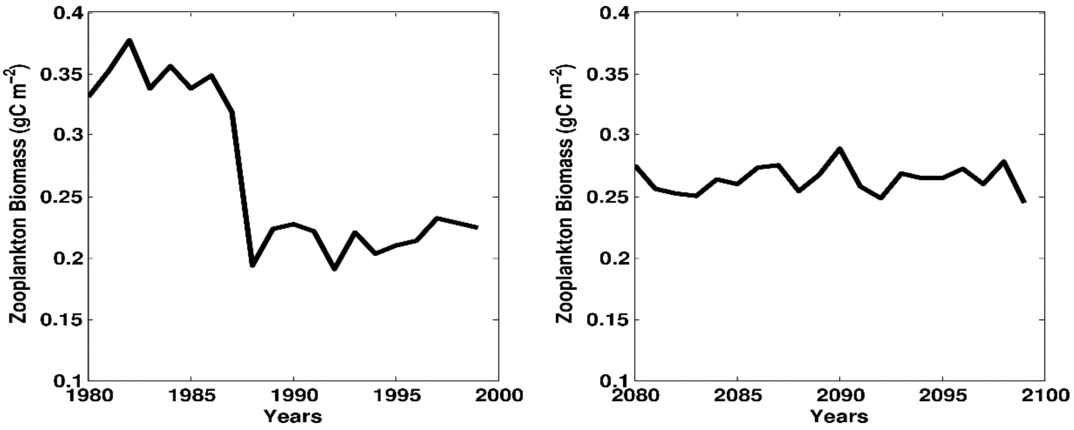


Figure 21. Annual mean time series of depth-integrated and basin-averaged zooplankton biomass of PD (left) and A1B (right) scenarios in the Black Sea (from Cannaby et al., 2012).

Concerning the biomass variations of *Aurelia*, although a significant difference was observed considering the minimum and maximum values, the 20-year biomass fluctuations did not show significant difference between PD and A1B scenarios according to the Kruskal-Wallis test (p = 0.3) (Figure 22).

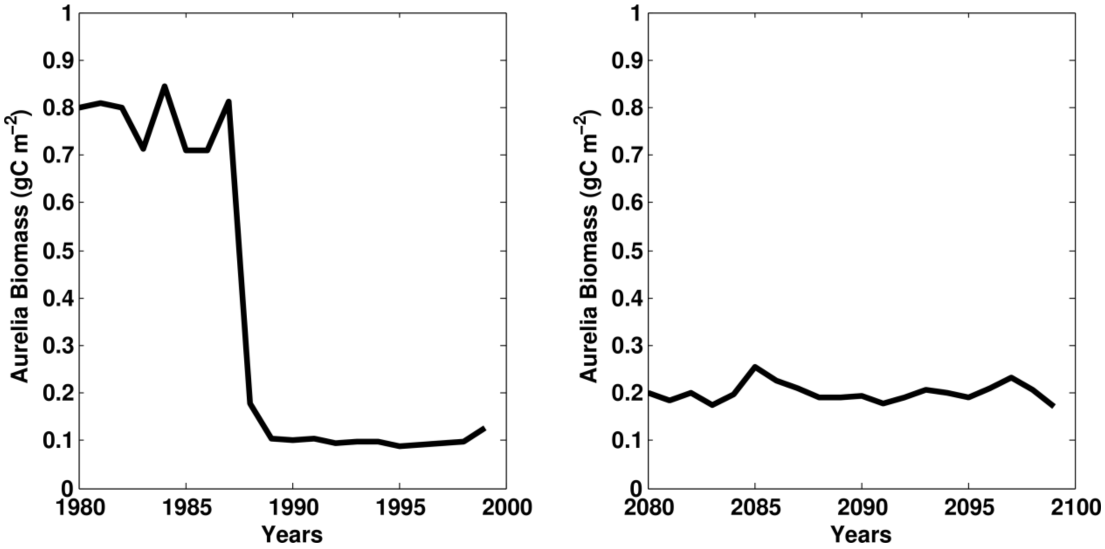


Figure 22. Annual mean time series of depth-integrated and basin-averaged *Aurelia* biomass of PD (left) and A1B (right) scenarios in the Black Sea (from Cannaby et al., 2012).

Contrary to *Aurelia*'s, the biomass of *Mnemiopsis*, however, showed significant difference between PD and A1B scenarios according to the Kruskal-Wallis test (p = 0.001) (Figure 23).

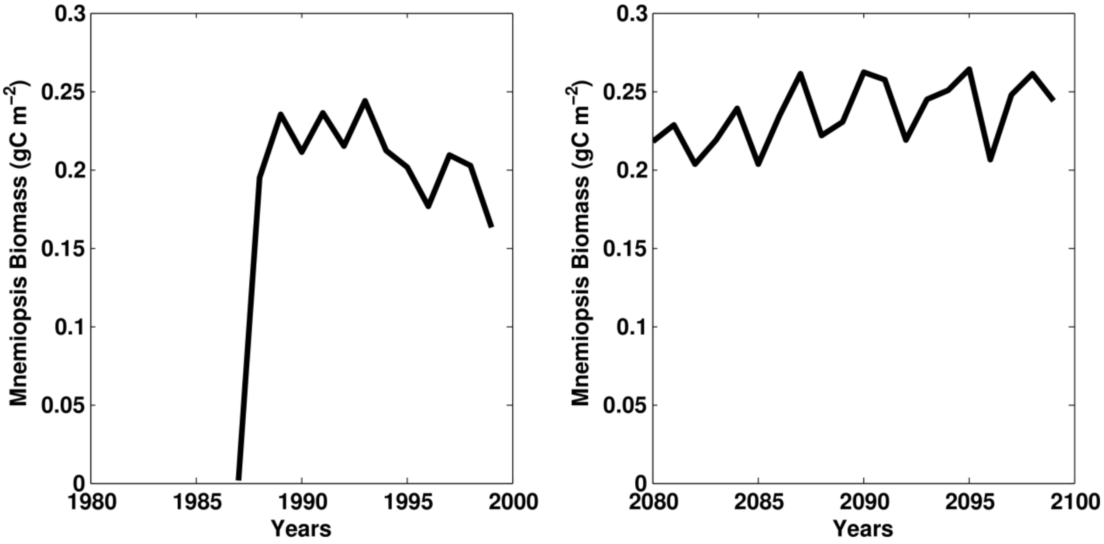


Figure 23. Annual mean time series of depth-integrated and basin-averaged *Mnemiopsis* biomass of PD (left) and A1B (right) scenarios in the Black Sea (from Cannaby et al., 2012).

5.3.3. Changes in HTL

Although a decrease in the total fish biomass was simulated between Present Day (PD) and Forecast (A1B) scenario runs, this decrease was not found significant (p ~= 0.4) according to the Kruskal-Wallis test (Figure 24). However, examining the results on the level of species/groups, the results showed that significant changes occurred within all individual populations except dolphins, bonito, mackerel, whiting, and turbot (Figure 25). Excluding red mullet, shad, and sprat, all of the remaining fish and dolphin populations were simulated to decrease in A1B scenario relative to the PD scenario. The anchovy spawning stock biomass was simulated to decrease down to a mean of 0.12 gC m^{-2} y^{-1} (162 kt) during the A1B scenario and sprat (0.56 gC m^{-2} y^{-1}, ~760 kt) was the most dominant small pelagic fish species in the ecosystem. Other notable fish groups in the ecosystem were simulated to be shad, and red mullet with mean biomass values of 0.06 gC m^{-2} y^{-1} (86.4 kt), 0.43 gC m^{-2} y^{-1} (581.6 kt), respectively. Apart from these groups, all other groups were simulated at significantly lower average biomass values compared to the PD scenario and could be considered as vulnerable species by means of sustainability of their stocks. This decrease simulated in the fish stocks was related to the assumption that high contemporary fisheries exploitation rates will continue in the Black Sea ecosystem in the A1B simulation. This resulted in the decrease of biomass values of many fish assemblages although an increase in the basin-wide primary productivity was predicted by the biogeochemical model. The increasing biomass levels of shad and sprat were found to be related to the reduced competitive strength of anchovy for resources, hence, favouring these species with more food available in the ecosystem. Under this circumstance, their development and growth were supported by the indirect positive impact of fisheries, i.e. selectively removing anchovy, the dominant competitor of the two, from the ecosystem. Similarly, such a competitive advantage enhancing the growth of red mullet was experienced along with the decreasing biomass values of whiting and spiny dogfish due to fisheries exploitation. However, considering that whiting and spiny dogfish groups significantly fed on other demersal fish species (see Table 17), it could be stated that their exploitation also decreased the predation pressure on its rivals, i.e. red mullet, hence supporting its increased establishment within the demersal fish compartment.

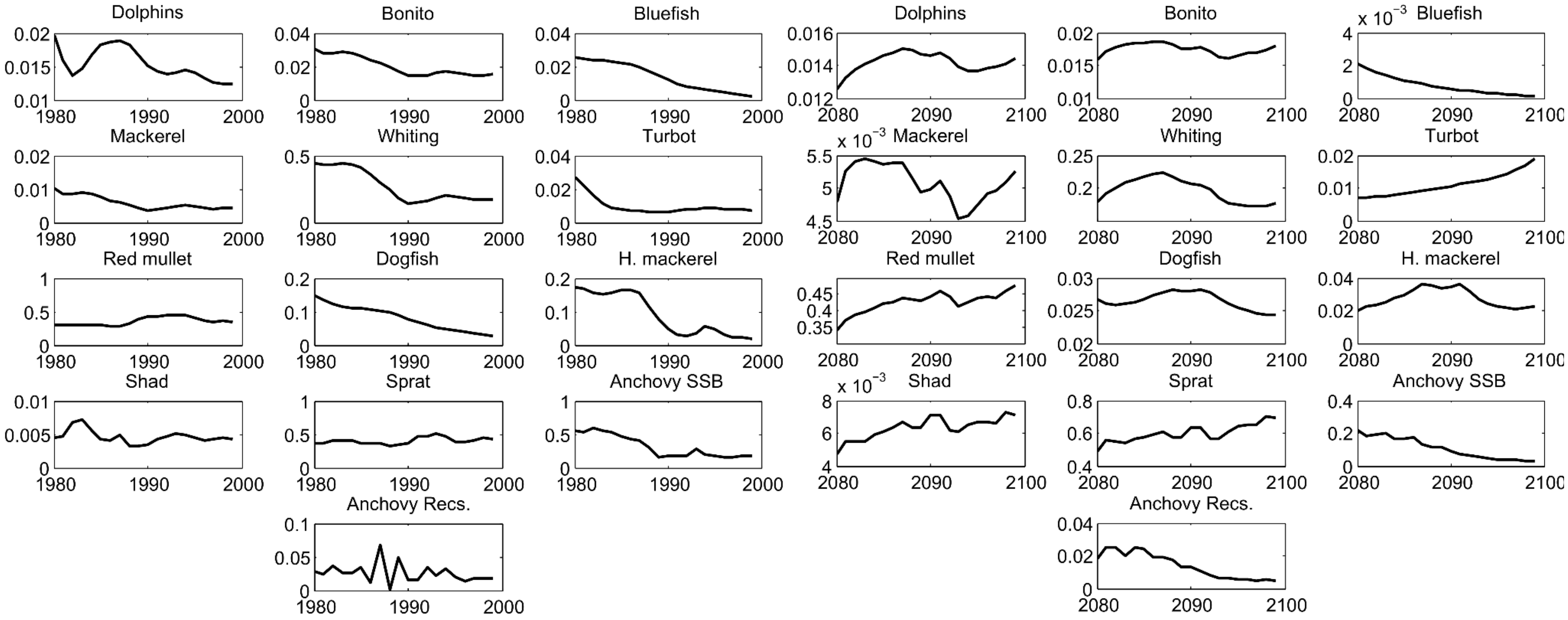


Figure 24. Biomass distributions of fish and dolphins groups in PD (left) and A1B (right) simulations. The y-axis shows biomass in gC m^{-2} and the x-axis shows simulation years.

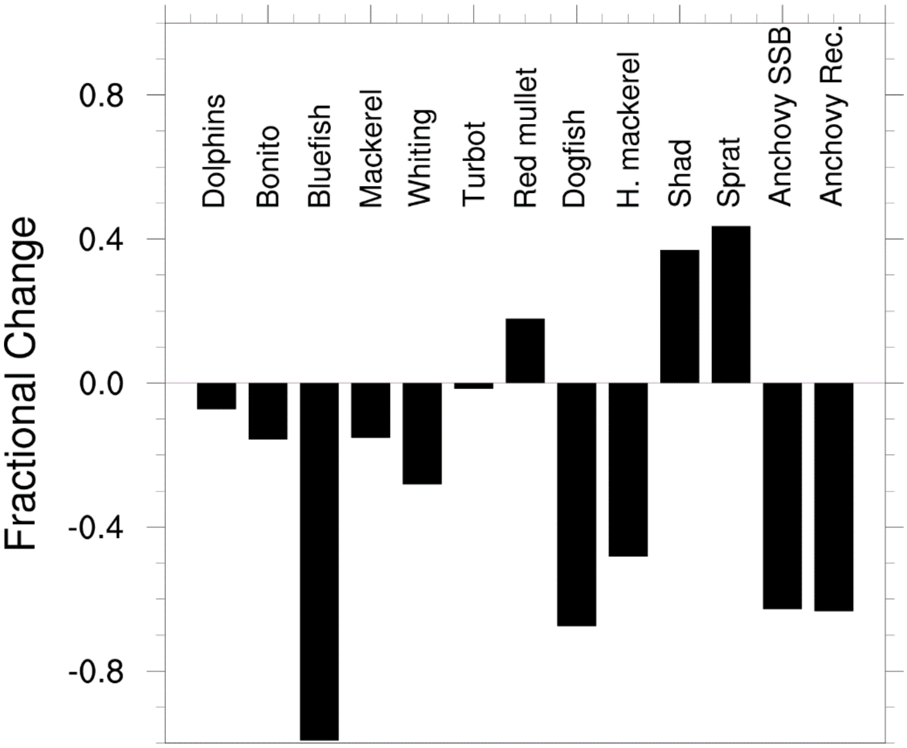


Figure 25. Fractional change predicted for fish and dolphin groups in A1B (2080-2099) scenario relative to the PD (1980-1999) scenario.

5.3.4. Assessment of Indicators and Ratios

Considering the system's throughput (TST), it decreased from a mean value of 436 gC m^{-2} y^{-1} in the early 1980s to a mean value of 353 gC m^{-2} y^{-1} in 1988 and remained around this value after the anchovy-*Mnemiopsis* shift in the 1989-1990 until the end of the PD scenario. The mean value of TST showed a marginal but significant increase up to 371 gC m^{-2} y^{-1} with the onset of the A1B scenario due to the simulated increase in the system's primary productivity (Figure 26).

The system's ascendency showed a significant shift in 1988 from 12.0% to a mean value of 11.2% and afterwards, contrary to TST, no significant shift in the mean value of this indicator was detected between PD and A1B scenarios (Figure 26). In 1988, the overhead (resilience) of the Black Sea ecosystem increased from a mean value of 65.8% to 68.5% as a result of the decrease in the system's ascendency. This indicated that almost coinciding with the anchovy-*Mnemiopsis* shift, the Black Sea ecosystem, afterwards, transitioned into a new state which could be characterised by improved ecosystem conditions compared to the 1980s.

In the PD simulation, the relative primary production required to sustain catches (%PPR) showed one significant shift in 1989 from an average value of 82% to 36% along with the collapse of the anchovy fishery. %PPR fluctuated around this lower mean value throughout the rest of PD and entire A1B simulations (Figure 26). In accordance with %PPR, the STARS algorithm identified one significant shift in the annual mean value of the catches in the PD scenario. Catches showed a significant decrease in 1990 from a mean value of 0.68 gC m^{-2} y^{-1} to 0.32 gC m^{-2} y^{-1} coinciding with the collapse of anchovy stocks and the proliferation of *Mnemiopsis* in late 1980s. The mean value of catch did not show any significant shift from its 1990s values and remained at a lower level in the A1B scenario compared to 1980s simulated by the PD scenario (Figure 26).

The STARS analysis detected a significant change in the mean value of the system's primary production, which was simulated by the BIMS-ECO model, in 1995 from 203 gC m^{-2} y^{-1} down to 165 gC m^{-2} y^{-1} (Figure 26) along with alleviating eutrophic conditions with the onset of 1990s. With the start of the A1B simulation, in accordance with the increased primary productivity simulated by the BIMS-ECO model (Figure 19), the primary production showed a significant increase to a mean value of 215 gC m^{-2} y^{-1} in 2083, which further increased up to a mean value of 241 gC m^{-2} y^{-1} by the end of 2090s with the continuous increase of primary productivity in the system (Figure 19).

The FiB index indicated a contraction in fisheries by means of quantity as a consequence of decreasing fish stocks in the ecosystem (Figure 26). However, after its shift in 1990 from a mean value of 0.013 to -0.006, the mean value of FiB index did not show a significant change between PD and A1B scenarios. On the other hand, the mTLc of the fleet changed significantly in the years 1990 and 2094 (Figure 26). The first significant change in mTLc from a mean value of 3.12 to 3.06 in 1990 was a consequence of the infamous anchovy-*Mnemiopsis* shift incident. The second shift occurred by the end of the A1B scenario and mTLc decreased down to a value of 3.04. The reason behind this decrease was the continuous decrease in the stocks of many higher trophic level fish and dolphin groups in the A1B scenario along with the increasing dominancy of particular lower trophic level demersal fish species, i.e. red mullet, instead of its relatively higher trophic level demersal counterparts, i.e. whiting and spiny dogfish. This resulted in the increasing dominancy of lower trophic level fish species in the catches not only by means of the absence of higher trophic level piscivorous fishes but also with the absence of higher trophic level demersal fish assemblages. This compositional change in catch was also reflected by the changes in Kempton's Q indicator (Figure 26). The first shift in this indicator occurred in 1992 from a mean value of 0.76 to 1.024 after the anchovy-*Mnemiopsis* shift, which resulted as an increase in the relative proportion of the organisms of and above trophic level III in the ecosystem with the collapse of the anchovy stock. Kempton's Q further increased to 1.43 in 2080 with the changing conditions of the A1B scenario compared to PD but this time by means of successful establishment of a high trophic level (TL > III) jellyfish predator *Beroe ovata*. This latter increase was further intensified by the continuous decrease of anchovy, the dominant fish in the ecosystem, stock in the Black Sea by its continued intensive selective extraction during the A1B scenario, which, to an extent, outcompeted the decrease in the higher tropic level fish species in the ecosystem.

Considering the cycling properties of the ecosystem, the mean path length travelled by a unit of energy increased from 4.96 to 6.23 in 1988 along with the catastrophic disturbance of the system in 1989 by means of anchovy-*Mnemiopsis* shift and further decreased down to 5.85 with the onset of the A1B scenario in 2080. This showed that with the onset of 1990s along with alleviating eutrophic conditions, the system transitioned into a more healthy state but with the onset of A1B scenario, the increased primary productivity reverted this improvement backwards to some extent. However, the FCI decreased from 3.05 to 1.93 in 1988 contrastingly (Figure 26). This showed that the catastrophic shift of the 1989-1990 decreased the material cycling along with *Mnemiopsis*'s overpopulation in the food web and this situation continued with episodic blooms of Mnemiopsis in early 1990s and after the proliferation of *Beroe ovata* in the ecosystem in 1997. The FCI showed a significant change in 2080 and increased to 2.32 due to "relatively" decreasing dominancy of jellyfish and other opportunistic organisms in the system moderated by the decrease in the system's primary productivity compared to the intensive eutrophic conditions of the 1980s. In conjunction with these changes, the mean value of the proportion of flows to detritus, after its first decrease in 1988 from 0.21 to 0.20, decreased further to 0.2 in 1997 until its rise in 2091 to a mean value of 0.20 (Figure 26). This latest increase in the mean value of the proportion of flows to detritus indicated that such a continuous increase in the primary productivity of the system, i.e. nutrient enrichment, as simulated by the BIMS-ECO model for the A1B scenario, had the possibility to revert the improved conditions of the Black Sea food web obtained during the 1990s back to its undesired state experienced during 1980s.

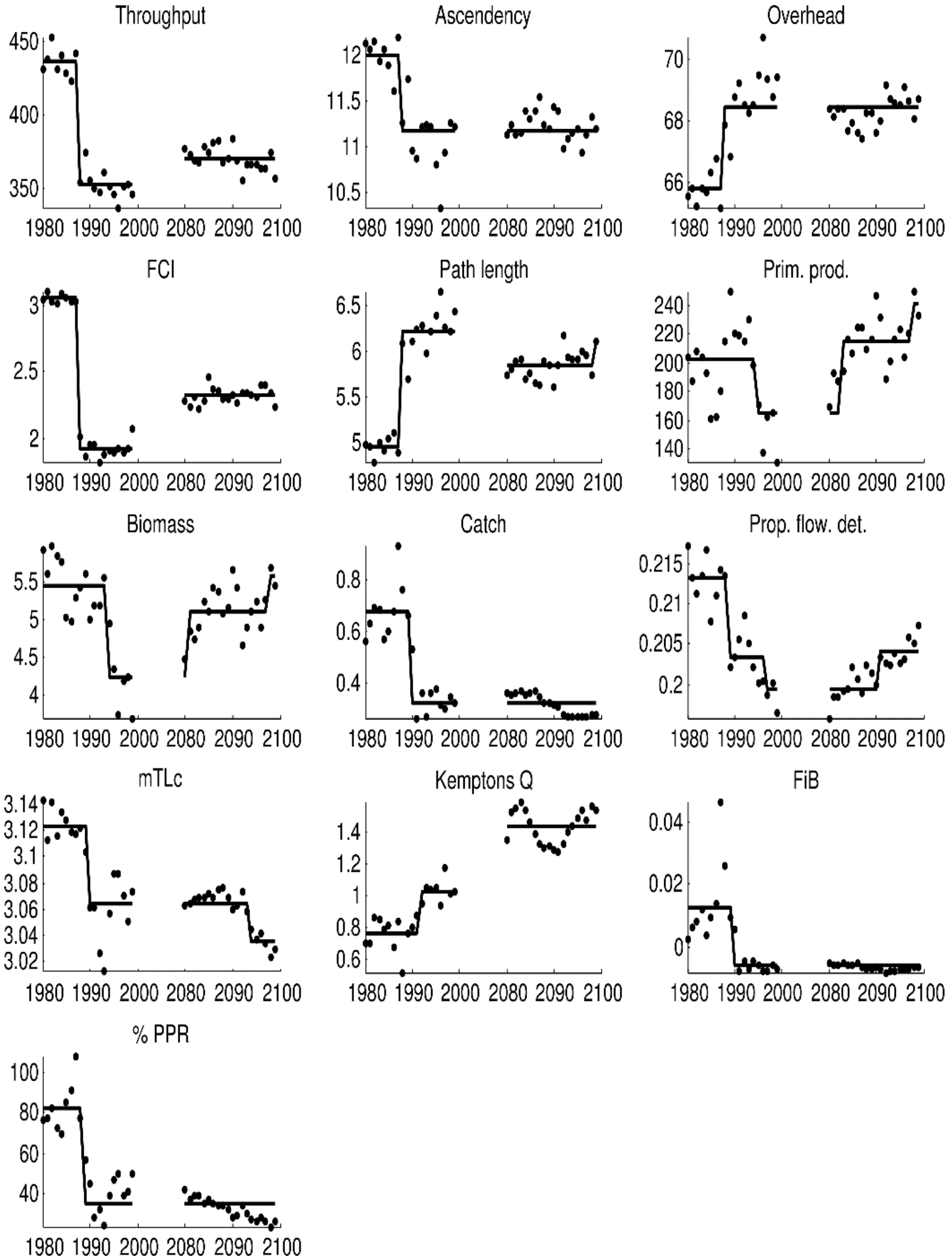


Figure 26. The time-dynamic changes in the indicators (dots) and the regimes detected (lines) by the STARS algorithm. Abbreviations are as follows: TST (Total System Throughput), FCI (Finn's Cycling Index), %PPR (relative Primary Production Required to support catches), mTLc (mean trophic level of catch), and FiB (Fishing in Balance). The TST, primary production, catch, and biomass values are in gC m^{-2} y^{-1}. FCI is percent of TST. Ascendency, overhead and %PPR are in percentages. Other indicators are unitless. The x-axis denotes simulation years.

Considering ratios, the fisheries exploitation caused the relative proportions of fish assemblages change significantly (Figure 27). The ratio of piscivores including marine mammals to forage fish and to other fish showed a significant decrease in 1991 and 1990 respectively and these two ratios proceeded with even decreased mean values with the onset of the A1B scenario in 2080.

Considering demersal fish, the STARS algorithm detected four regimes in the ratio of demersal to pelagic fish which were realised in 1988, 1997 and 2087. The first shift in 1988, which almost coincided the anchovy-*Mnemiopsis* shift, increased the mean value of the ratio of demersal fish populations to pelagic fish from 0.70 to 0.93 along with the collapse of the small pelagic fish populations. In 1997, the mean value of this ratio decreased to 0.80 with recovering interactions in the food web of the Black Sea ecosystem. However, in 2087 in the A1B scenario, the ratio increased to 0.90. This concluded that under status quo exploitation levels of the fishery, the severity of the impact of fisheries on the ecosystem will be exacerbated in A1B scenario.

The ratio of opportunistic zooplankton (jellyfish and heterotrophic dinoflagellates) to total zooplankton biomass decreased to low levels after 1995 along with the alleviating eutrophic conditions after the anchovy-*Mnemiopsis* shift in 1989-1990. However, an increase in the mean value of this ratio was detected at the end of the A1B scenario in 2097 by the STARS analysis due to increasingly dominating role of opportunistic zooplankton along with the intensifying productive (eutrophic) conditions by the end of the A1B scenario as indicated by the shift (increase) in the mean value of system's primary production in 2098 (Figure 26).

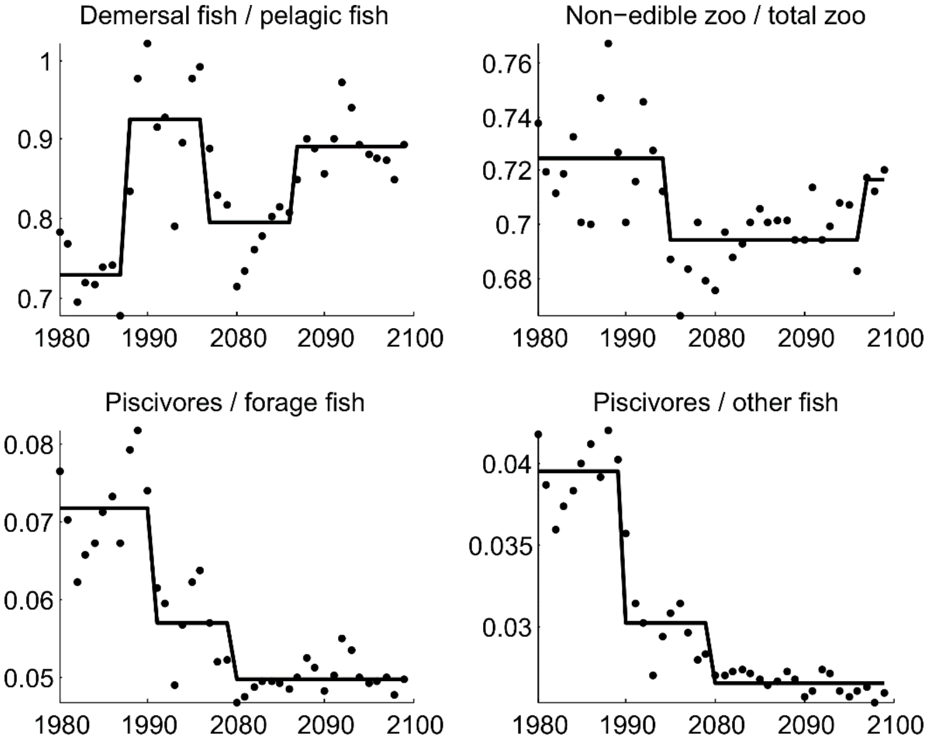


Figure 27. The time-dynamic changes in the ratios (dots) and the regimes detected (lines) by the STARS algorithm. The x-axis denotes the simulation years.

5.3.5. Sensitivity of results to changes in fishing mortality

The simulated biomass values under three scenarios with three different fishing mortality (F) rates, (F status quo, F with 50% increase and F with 50% decrease) were shown in Figure 28. In the scenario with 50% less fishing mortality for all fish species, the biomass of all fish species showed a significant increase with respect to the scenario in which F values equalled to the status quo rates, and a 50% increase in fishing mortality rates of the fish species resulted in a more moderate decrease in simulated biomass values of the fish community within the Black Sea ecosystem.

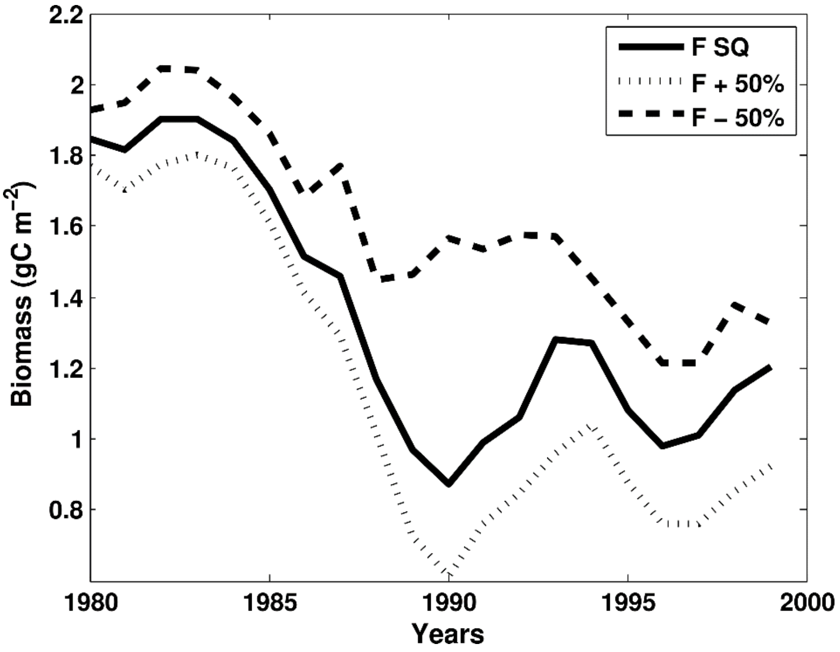


Figure 28. Simulated changes in all fish biomass under current (F), 50% increased (F + 50%) and 50% decreased (F – 50%) fishing mortality values for the PD scenario.

From a statistical perspective, the simulated changes in all fish biomass with a 50% increase in fishing mortality values of each fish species relative to PD scenario was not significant (p = 0.05) whereas the simulation with a %50 decrease in fishing mortality values of each fish species were found to be significantly different (p = 0.01) relative to PD scenario (Table 20) in the Kruskal-Wallis test.

Table 20. Statistics of change in fish biomass under fishing mortality increase (+50%) and decrease (-50%) relative to PD.

	Change range at 50% increase in fishing mortality (F) relative to PD	Change range at 50% decrease in fishing mortality (F) relative to PD
	All fish biomass (fractional change)	All fish biomass (fractional change)
Mean	-0.16	0.233
Range:	0.615 – 1.80	1.21 – 2.05

Percentile 25; Percentile 75	-0.241, -0.065	0.085, 0.241
Test Kruskal-Wallis (p-value)	0.0453	0.0094

The relative proportions of large fish by weight to the total fish biomass for the three simulations with different fishing mortality levels were shown in Figure 29. In all three scenarios, the changes in the large fish biomass were found to be significantly different ($p < 0.0001$). This underlined the importance of fisheries management for sustaining the relative proportions of fish stocks within a given ecosystem.

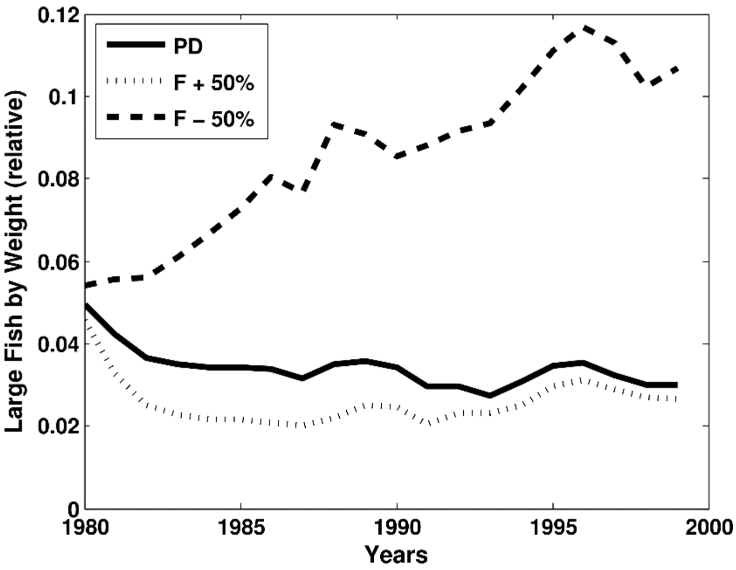


Figure 29. Large fish by weight in Present Day (PD) scenario for three different fishing mortality regimes.

5.3.6. Experiments of Anchovy Stocks Collapse

The reasons behind the anchovy stock's collapse were investigated under six different scenario settings detailed in Table 19. All of the applied scenarios except scenarios 3 and 4 simulated a decrease in the anchovy stock biomass in 1989-1990 and a trailing decrease in the stock after 1993 (Figure 30). The trailing decrease was due to the basin-wide decrease in primary production simulated by the biogeochemical model, which was removed in constant primary productivity conditions in scenarios 2 and 4. The slight decrease in 1989-1990 observed in scenarios 3 and 4 was related to the decrease in the forced zooplankton biomass values in that particular year. Considering these, the decrease in 1989-1990 was related to a combination of the impacts of fishing and over-proliferation of alien species *Mnemiopsis*, which in turn caused a reduction in the zooplankton biomass in 1988-1989. Both of the scenarios with F_{msy} values applied on the anchovy stocks and with F_{msy} values and an invariant primary production equal to that in 1980 applied simulated the anchovy stocks collapse in 1989-1990, whereas, scenario 2 did not experience a trailing decrease after 1995. This showed that the trailing decrease was solely related to the simulated decrease in the basin-wide primary production by the BIMS-ECO model. Scenario 3 with F_{msy} values applied and the invasion of alien ctenophores removed, the first collapse of the anchovy stock in 1989-1990 vanished. Scenario 4, where F_{msy}, an invariant primary production equal to that in 1980 applied and the invasive ctenophores were removed from the ecosystem, showed fluctuations, however, the simulated time series of the anchovy biomass was stable to prevent any sort of sharp decrease considering the criterion whether a simulated decrease/increase fell within the one standard deviation distance of the simulated time series biomass data. Further, removal of *Mnemiopsis* predation on anchovy eggs and larvae but keeping the *Mnemiopsis*' predation pressure on zooplankton in the system by means of forced zooplankton biomass values (scenarios 3 and 4) still caused a slight decline in 1988-1989 in the anchovy stocks. However, the opposite was not found to be true.

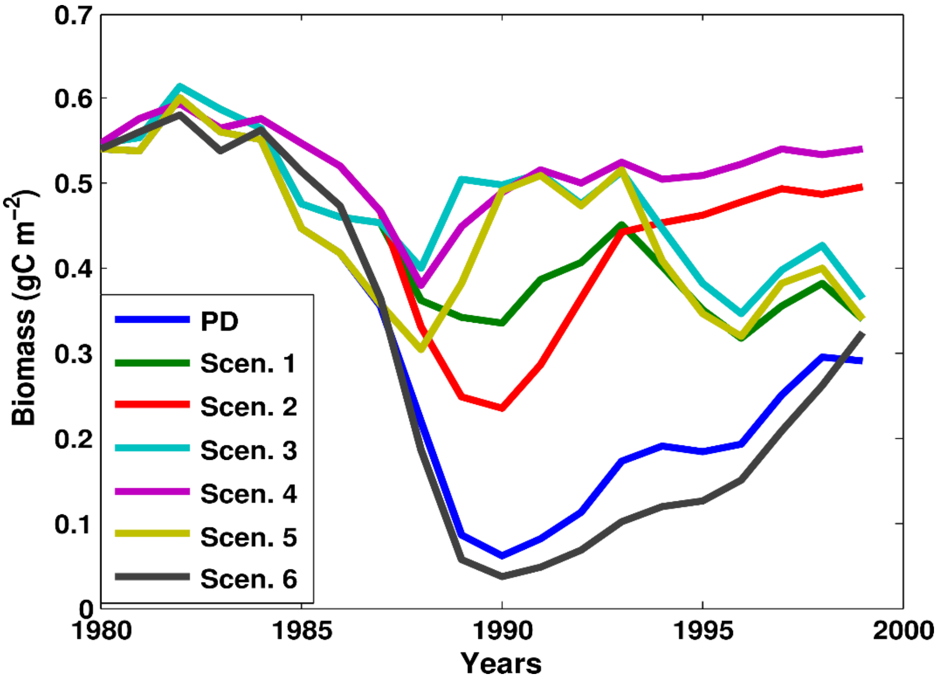


Figure 30**.** The simulated anchovy stock biomass progressions in PD; Scen. 1: F_{msy} = 0.41; Scen. 2: F_{msy} = 0.41 and constant primary production (~293.6 mgC m^{-2} day^{-1}); Scen. 3: F_{msy} = 0.41 along with no *Mnemiopsis* and *Beroe* introduction; and Scen. 4: F_{msy} = 0.41, constant primary production (~293.6 mgC m^{-2} day^{-1}) along with no *Mnemiopsis* and *Beroe* introduction, Scen. 5: PD ecosystem conditions but with no *Mnemiopsis* and *Beroe* introduction, and Scen 6: PD ecosystem conditions with constant primary production (~293.6 mgC m^{-2} day^{-1}).

In line with the simulated biomass predictions, the simulated catches showed similar behaviour. The only scenarios in which such a collapse was not observed were Scen. 3 and 4. Considering these, in a condition of invariant and constant primary production equal to the initial conditions of the model and where no alien invasions/introductions occurred, the maximum sustainable yield for the anchovy stock was calculated to be able to reach ~300 000 kt with an exploitation rate (F/Z) of 0.14 (F = 0.41). However, in 2000s, the conditions were quite different than that of the 1990s. Considering the changes in primary production capacity (the decrease) of the Black Sea ecosystem and the current stock progressions where invasive species were present, sensitivity analysis of the Present Day model concluded that an MSY of ~200 kt with an exploitation rate of 0.11, which equalled F_{msy} to 0.33, was possible (Figure

31) and will likely prevent catastrophic events like anchovy-*Mnemiopsis* shift in the future under such circumstances where various environmental and trophic episodic phenomena may occur.

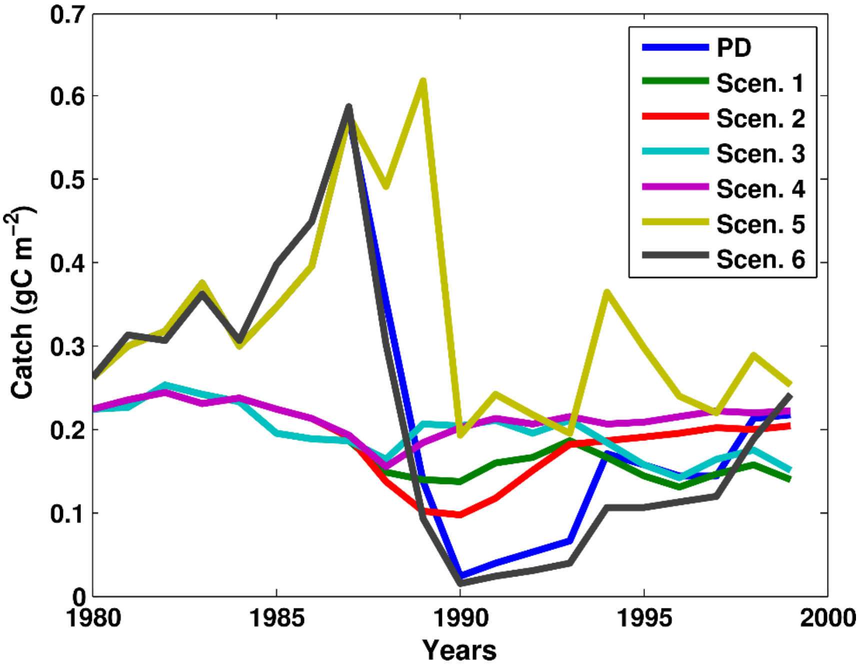


Figure 31. The simulated anchovy stock catch progressions in PD; Scen. 1: $F_{msy} = 0.41$; Scen. 2: $F_{msy} = 0.41$ and constant primary production (~293.6 mgC m^{-2} day^{-1}); Scen. 3: $F_{msy} = 0.41$ along with no *Mnemiopsis* and *Beroe* introduction; and Scen. 4: $F_{msy} =$ 0.41, constant primary production (~293.6 mgC m^{-2} day^{-1}) along with no *Mnemiopsis* and *Beroe* introduction, Scen. 5: PD ecosystem conditions but with no *Mnemiopsis* and *Beroe* introduction, and Scen 6: PD ecosystem conditions with constant primary production (~293.6 mgC m^{-2} day^{-1}).

5.4. Discussions and conclusions

In this section, the reasons behind the collapse of small pelagic fish stocks, in general, and anchovy-*Mnemiopsis* shift, in particular, occurred in 1989 were discussed and this was followed by the explanations of relative changes between the PD and A1B scenarios by means of the regime shifts in the synthetic indicators and ratios detected by the STARS analysis. Finally, the management option for the fisheries on anchovy stocks provided in the previous section was revisited considering the multi-species interactions in the ecosystem.

The BIMS-ECO biogeochemical model simulated a decrease in the zooplankton biomass with the appearance of the *Mnemiopsis* in the Black Sea ecosystem. This was reflected as an increase in the phytoplankton biomass with the onset of 1990s. This impact of decreased secondary production resources after/during the anchovy-*Mnemiopsis* shift was observed in the decreasing biomass of forage fish groups. According to Prodanov et al. (1997) and Daskalov (1998), heavy overfishing could have led to this decline of the small pelagic fish stocks. Oguz et al. (2008b) also underlined the competitive interference between *Mnemiopsis* and small pelagic fish. As a contribution, I also related this decrease to changes in average primary productivity of the 1990s. As indicated by the sensitivity experiments in section 5.3.5, it could be concluded that the anchovy-*Mnemiopsis* shift occurred in 1989 was due to the synergistic impacts of overfishing and resource competition with *Mnemiopsis*. However, the impacts of both of these factors were mediated by the changes in the primary productivity of the system. The predation of *Mnemiopsis* on anchovy eggs and larvae was found to be negligible compared to trophic competition between anchovy and *Mnemiopsis*. Finally, the experiments delineated that it could not be due to only one single factor; i.e. overfishing (Daskalov, 2002; Gucu 2002; Llope, 2011) or trophic competition and/or *Mnemiopsis* predation on anchovy eggs and larvae (Kideys, 2002).

The A1B simulation, along with the predicted basin-wide significant ($p < 0.0001$) increase in the primary production compared to the PD scenario due to changes in circulation patterns, would have led an increase in the fish stocks, however, under the assumption that the contemporary exploitation levels of fish species continued, this inhibited the likely positive impact of such a productivity change.

The catch indicator showed significant changes between PD and A1B scenarios according to the STARS analysis. This was a result of the continuation of the unmanaged exploitation of the fish assemblages during the A1B scenario as shown by the decreasing mTLc values throughout the simulation. This was also shown with the three different regimes detected in the primary production indicator by the STARS analysis between PD and A1B scenarios. The simulated increase in Kempton’s Q index were not due to the recovery of the piscivorous fish stocks but rather due to the simulated decrease in the forage fish biomass values for the A1B scenario, which in turn, resulted in relatively increased proportions of the piscivorous fish both in the fish community and the catches. Although a similar situation realised by the fishery concerning lower trophic level fish species, i.e. small pelagic fish and most demersal fish species, the decreases in the mTLc in A1B scenario indicated that the decreases in the stocks of certain fish species in these assemblages were compensated by their peers in their respective functional group of organisms (e.g. decrease in anchovy stocks led to greater establishment of shad and sprat among the small pelagics; the decrease in turbot and whiting led to greater establishment of red mullet among the demersals). Considering the fractional change calculated for fish and marine mammal groups, all of the populations except red mullet, shad and sprat were simulated to decrease (Figure 25).

Compared to the period after 1990s in the PD scenario, in A1B scenario the proportion of flows to detritus was simulated to increase in 2091 along with the increased primary productivity of the system. This underlined the fact that, in such circumstances that will lead to increased productivity in the Black Sea, hence, eutrophication, will likely reverse the rehabilitating structure of the ecosystem realised by the onset of 1990s, leading to stress in the functioning of the food web and deteriorate its integrity as it was the case during 1980s. Contrastingly, the FCI increased with the onset of A1B simulation indicating better material cycling in the food web. This indicated that the jellyfish populations will not have pronounced effects in the ecosystem conditions predicted for the A1B scenario although enrichment of the system was possible to some degree. However, towards the end of the A1B simulation, the ratio of non-edible zooplankton to total zooplankton increased (Figure 27). This indicated the tendency of the Black Sea ecosystem to return back to undesirable food web conditions under predicted productivity increases. The decrease in the mean path length indicator occurred with the onset of A1B scenario further supported this interpretation.

Considering the multispecies interactions and an ecosystem-based approach to the management of fish resources of the Black Sea, the calculated MSY value for anchovy (see section 5.3.6) should be revisited. In order to obtain long-term consistent yield from the anchovy stocks, a value of 200 kt at an exploitation rate of 0.11 was found to be feasible. However, this exploitation intensity could only be succeeded in a single-species, i.e. anchovy, dominant Black Sea ecosystem. With this exploitation regime, recovery of the already depleted stocks of mackerel, bonito and bluefish would not be possible. Further, the extinction of the Black Sea marine mammals was highly expected by 2080 according to the simulation results of the A1B scenario (Figure 24, Figure 27, and Figure 29). The sensitivity analyses carried out using the PD run put forward that for the recovery of the Black Sea piscivorous fish and mammal stocks by 2080; strict management measures should be reinforced on the fishing fleet of the Black Sea. First and foremost, **only looking from the ecosystem perspective**, the fisheries for mackerel, bonito, and bluefish should end up in a complete halt. But this perspective was found to be detrimental by means of socio-economic impacts on fisheries. Therefore, a compromise should be made and in order to prevent such a catastrophic effect, the fisheries of these species could be either subsided financially or compensated by means of other value-added marketing of other profitable fish products. However, only by minimising the fishing mortality for these groups proved to be not sufficient for the recovery. Further considering the piscivorous fish and mammals, the exploitation rate of forage fish groups should be rearranged sparingly to ensure providing a consistent feeding stock for their recovery. Hence, the sensitivity experiments indicated that anchovy catch should not exceed ~200 kt considering all these implications. A value close to this estimation was also given by Oguz et al. (2012).

In conclusion, the environmental conditions in the Black Sea simulated by the A1B scenario will not be favourable from many aspects including the fishery as put forward by means of indicators, ratios and fishing experiments. Further, continued increase in system’s primary productivity by means of nutrient enrichment proved to have a deteriorating impact on the functioning of the food web as shown by the analysis of cycling indicators, i.e. FCI, proportional flows to detritus and mean path length. This situation was found to bring about the possibility of reinstating the Black Sea ecosystem back to its undesired conditions of 1980s. Under such an ecosystem state, the regulation of fisheries as an activity could be focused on single species, i.e. anchovy, so as to maximise the yield and the profit. However, in such circumstances, fisheries of other target groups were simulated to disappear in the Black Sea and, further, anchovy was predicted to be replaced by sprat under continuous exploitation.

Therefore, it was proposed to decrease the exploitation levels of the forage fish stocks and completely halt the fisheries on piscivorous organisms for the sake of the Black Sea ecosystem as well as its sustainability of economic goods and services in the long term. The economic loss that would be created with such an action should also be compensated by means of marketing strategies so as to alleviate the drawbacks by introducing value-added capture production of other fisheries. This will increase the prices of the capture fishes in the market marginally but compensate the socioeconomic loss during the fisheries moratorium period for these target species.

6. CHAPTER: Thesis conclusions

6.1. Dynamics of the Black Sea Ecosystem

Considering the indicator-based analyses of ecological characteristics of the Black Sea carried out in this thesis work, it was shown that the dynamics of the Black Sea ecosystem during the second half of the 20th century were driven by two significant factors; i) fisheries, and ii) eutrophication. The remaining processes of changes were initiated by these two most significant factors as a series of a chain reaction.

First, during 1960s, the predatory species in the ecosystem were overexploited by the fisheries as indicated by the decreasing mTLc and Kempton's Q and increasing PPR values. This was followed by the development of forage fish groups after the release of predatory pressure on their stocks to dominate the system. Second, starting with eutrophic conditions, the community size of small pelagic fish grew and opportunistic species like jellyfish and *Noctiluca* became abundant. The resulting ecosystem structure was dominated by forage fish in the higher trophic level and opportunistic plankton species in the lower trophic level as shown by increasing keystone values of these groups in 1980s. After the collapse of small pelagic fish stocks in 1989, the eutrophic conditions started to alleviate and small pelagic fish stocks started to recover. This new ecosystem structure of 1990s was characterised by a medium stock level as shown by the biomass and catch indicators.

The sensitivity experiments using PD simulation showed that the most significant factor for the anchovy stock collapse was fisheries and it was followed by resource competition between small pelagic fish and opportunistic jellyfish species. The outburst of *Mnemiopsis* contributed adversely to the ever-present resource competition between small pelagic fish and jellyfish by outcompeting all the other groups' grazing on zooplankton with its high consumption to biomass ratio. The levels of primary production were also influent on the progression of the anchovy stocks but only due to the fact that it was one of the determining factors of available zooplankton in the ecosystem. Further, considering the presence of voracious predators like jellyfish, the deterministic factor of the resource availability to the forage fish species was the grazing intensity on zooplankton by these opportunistic plankton. However, none of these factors was found to be sufficient enough to cause such a catastrophic anchovy-*Mnemiopsis* alone.

Future simulations of the Black Sea ecosystem (A1B) showed that, under contemporary fishing exploitation levels, most significant fish species were likely to experience significant decreases in their stocks. These species were found to be anchovy, predatory species, and certain demersal fish species. In such circumstance, due to released predation and resource competition pressures, species like sprat, shad and red mullet will likely substitute these species in their respective environments and develop their populations. Further, examining the indicators related to the energy flows in the A1B scenario, it was shown that increased primary production in the Black Sea bore the possibility to deteriorate the food web structure and functioning and cause increasing dominancy of opportunistic organisms so as to reinstate undesirable conditions of eutrophication across the food web. Under such situation, management of fish stocks and their exploitation levels were found to be the most effective tool to prevent catastrophic events in the ecosystem. However, sustainable management of fish stocks could only be possible when considered together with their peers' stock dynamics rather than only evaluating the stock progressions of economically important species in isolation from the ecosystem-wide impacts of anthropogenic and climatologic stressors as well as the nonlinear interactions in the food web with other lower and higher trophic level organisms.

6.2. The MSFD Perspective

Biological diversity (MSFD-D1, Table 21) of the Black Sea ecosystem had experienced significant transformations since 1960s. The population biomasses of top predatory species, i.e. dolphins, bluefish, bonito and mackerel, diminished to the extent that their structuring role in the ecosystem almost vanished as put forward by the keystoneness analysis (section 2.3.3). Further, the proportion of higher trophic level organisms in the ecosystem decreased in time with the onset of 1970s due to continued overexploitation of their stocks, which in turn, released the top-down control (section

2.3.3) exerted by these predatory species and this was followed by the resource enrichment (section 2.3.5) in the Black Sea so that the development of lower trophic level fish species, i.e. anchovy and sprat, and other gelatinous predators were promoted (see Table 14 and Table 15). The decrease in the Kempton's Q indicator starting from 1960s also reflected this shift in the dynamic simulations (sections 3.3.2 and 5.3.4). All these changes brought the top predatory species almost to the brink of extinction in the Black Sea (e.g. Atlantic mackerel) so that they could not self-sustain their populations' growth any longer. Future simulations put forward that these organisms were likely to disappear completely from the Black Sea ecosystem if contemporary fishing exploitation levels on these species prevailed in the future (section 5.3.3) and the overexploitation of their food resources continued.

Concerning non-indigenous species (MSFD-D2, Table 21) in the Black Sea, after 1988, *Mnemiopsis* became the most dominant zooplankton in the ecosystem until mid-1990s. This was proven by the increasing keystoneness value of this organism (section 2.3.3). Further, the feedbacks of this dominancy were quantified by the MTI analysis (section 2.3), especially by the strong negative impact of *Mnemiopsis* against small pelagic fish and trophic zooplankton. This was due to the changes in the energy cycling through the food web, which was brought to the ecosystem along with the increasing dominating role of gelatinous organisms in the 1970s and 1980s (section 2.3.4). The transfer efficiency of energy from primary producers to higher trophic level groups was clogged by these gelatinous zooplankton and because they had no natural predators in the ecosystem, the energy restrained by these organisms were "*short-circuited*" back to detritus without contributing to the production of higher trophic level organisms at and above trophic level III.

Commercial fish stocks (MSFD-D3, Table 21) were also negatively impacted by all these changes. Their continuously high fishing mortalities caused a decline in their stocks' biomass along with the above mentioned transformations in the energy cycling through the food web. Even the stocks of anchovy, the inexhaustible fish with respect to fisheries in the ecosystem, continuously declined with the onset of 1980s until its collapse in 1989 as simulated by the hindcast simulation of the time-dynamic model (section 3.3.1) and to some extent, by the dynamic simulation of the coupled model in section 5.3.1. This decrease was evident in the spawning stock biomass of anchovy and also in the weakening recruitment power of the younger stages to the adult stock (Figure 24).

The food web structure and functioning (MSFD-D4, Table 21) of the Black Sea ecosystem had also experienced significant transformations. Concerning PPR, the required primary production to sustain catches had increased continuously until the collapse in 1989 (Figure 12). This structure was also supported by the decreasing ratio of predatory fish to other fish and demersal fish to pelagic fish since the beginning of the simulation period in 1960. Further, the trophic level decomposition of catches (Table 14) and community biomass (Table 15) explicitly delineated the occurrence of this shift with increasing ratio of lower trophic level fish and organisms in the catches and in the community biomass respectively. Time-dynamic model results also supported this hypothesis with the continuously decreasing large fish by weight simulated from the beginning of 1960s (Figure 9). However, the most significant change in the food web dynamics was the "*short-circuiting*" of flows back to detritus by gelatinous organisms, hence, leaving the higher trophic level organisms up in the food web deprived of the significant part of the system's production which could have been used for the growth of their populations. This short-circuiting was realized by *Aurelia* and *Noctiluca* in the 1970s and 1980s until the outburst of *Mnemiopsis*. Afterwards in the early 1990s, this short-circuiting was realised predominantly by *Mnemiopsis* until the eutrophic conditions started to alleviate in the mid-1990s and finally *Beroe ovata* arrived and settled in the ecosystem.

Eutrophication (MSFD-D5, Table 21) had also significant impact on the ecosystem and could be regarded as the primary reason of the increased settlement of the opportunistic, i.e. *Noctiluca scintillans* and/or r-selected (gelatinous species) organisms in the ecosystem. This settlement led to the changes in the functioning of the food web, hence, limiting the carrying capacity of the Black Sea ecosystem. The negative impact of these changes were reflected in the decreasing overhead, i.e. resilience, values of the ecosystem (Figure 8). In conjunction with other anthropogenic (overfishing) and climatological (Oguz et al., 2008b) pressures, the Black Sea ecosystem became famous for its rises and falls (Kideys, 2002) and was started to be considered as a natural laboratory to investigate the impacts of synergistic effects of concurrent alien introduction, overfishing, climatological changes and eutrophication on the structure and functioning of a marine ecosystem.

Table 21. Summary of MSFD Descriptors

Descriptor	**Indicator**	**Condition by 2000s**	**Projected condition in 2080-2099**
Biological Diversity	Kempton's Q	Decreased due to the decrease in the relative proportion of higher trophic level organisms.	Expected to increase due to the significant decrease in the anchovy fish biomass rather than the recovery of higher trophic level species.
	Community Ratios	Decrease in the relative proportion of piscivorous fish in the fish community. Increase in the relative proportion of demersal species.	Expected to decrease (concerning predatory fish) and increase (concerning demersal fish) (Figure 27)
	mTLco	The community biomass of fish species was composed of lower trophic level forage fish groups.	Expected to increase due to the decreasing biomass of small pelagic fish rather than the recovery of higher trophic level species.
Non-indigenous species	Keystoneness	Introduced species played a structuring role in the food web.	Increased establishment expected due to the predicted increase in system's primary production.
	MTI	Increase in the negative MTI of introduced species.	Expected to increase marginally due to their increase in numbers in accordance with the increasing primary production values.
	Transfer Efficiency	Decrease in the transfer efficiency of flows.	Expected to decrease marginally.

	Proportional. flows to detritus	Increase in the flows diverted to detritus due to proliferation of introduced species which had no significant predators in the ecosystem.	Expected to increase if the primary productivity of the system continues to increase.
	FCI	Reduced cycling due to overdevelopment of introduced species which diverted flows back to detritus.	May decrease if the primary productivity of the system continues to increase.
Commercial fish	mTLc	Decreased significantly.	Expected to further decrease due to unmanaged fisheries exploitation.
	Catch %PPR	Increased due to the increased harvesting of fish species.	Expected to fluctuate around 2000s' values.
Food web	FCI	Decreased recycling in the food web due to the confinement of energetic flows in the lower trophic level compartment.	May further decrease if the primary productivity of the system continues to increase.
	Transfer efficiency	The energy transfer efficiency from primary producers to those of TL III and above decreased significantly.	Expected to fluctuate around contemporary levels.
	Proportional flows to detritus	Proportional flows to detritus increased with increasing numbers of trophic dead-end species such as *Aurelia*, *Mnemiopsis*, *Noctiluca* and *Beroe*.	Expected to increase by 2100 if enrichment of the ecosystem continues.
Eutrophication	Opportunistic species	Their numbers increased along with intense eutrophication. Mainly jellyfish and *Noctiluca*.	Expected to increase marginally due to increased primary production projected for 2080-2099.

References

Akaike, H., 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19 (6), 716–723.

Barrett, R., Berry, M., Chan, T. F., Demmel, J., Donato, J., Dongarra, J., Eijkhout, V., Pozo, R., Romine, C., and van der Vorst, H, 1994. Templates for the Solution of Linear Systems: Building Blocks for Iterative Methods, 2nd ed. Philadelphia, PA: SIAM, 107 pp.

Beaugrand, G., 2004. The North Sea regime shift: Evidence, causes, mechanisms and consequences. Progress in Oceanography, 60 (2–4), 245-262.

Berdnikov, S. V., Selyutin, V. V., Vasilchenko, V. V., Caddy, J. F., 1999. Trophodynamic model of the Black and Azov Sea pelagic ecosystem: consequences of the comb jelly, *Mnemiopsis leidyi*, invasion. Fisheries Research, 42, 261-289.

Bilio, M., and Niermann, U., 2004. Is the comb jelly really to blame for it all? *Mnemiopsis leidyi* and the ecological concerns about the Caspian Sea. Marine Ecology Progress Series 269, 173 – 183.

Birkun, A., 2008. The state of Cetacean populations. In: Oguz, T. (ed.), State of the Environment of the Black Sea (2001 - 2006/7), Publications of the Commission on the Protection of the Black Sea Against Pollution (BSC) 2008-3, Istanbul, Turkey, pp. 365-396.

Blumberg, A. F., and Mellor, G. L., 1987. A description of a three dimensional coastal ocean model. In: Heaps, N. (ed.), Three dimensional coastal ocean models, A.G.U., Washington. pp. 1-16.

Cannaby, H., Fach, B. A., Akoglu, E., Salihoglu, B., 2012. Synthesis report for Climate Simulations, Marine Ecosystem Evolution in a Changing Environment (MEECE) Black Sea Regional Report D3.4, 51 pp.

Cardoso, A. C., Cochrane, S., Doerner, H., Ferreira, J. G., Galgani, F., Hagebro, C., Hanke, G., Hoepffner, N., Keizer, P. D., Law, R., Olenin, S., Piet, G. J., Rice, J., Rogers, S. I., Swartenbroux, F., Tasker, M., van de Bund, W., 2010. Scientific Support to the European Commission on the Marine Strategy Framework Directive – Management Group Report, Luxembourg: Office for Official Publications of the European Communities, 57 pp.

Christensen V., and Cury P., 2005. Application of ecological indicators for assessing health of marine ecosystems. In: Jorgensen, S. E., Costanza. R., Xu, F. L., (eds.) Handbook of ecological indicators for assessment of ecosystem health. Boca Raton, FL, USA: CRC Press, pp. 193–212.

Christensen, V., 1995. Ecosystem maturity – towards quantification. Ecological Modelling, 77, 3-32.

Christensen, V., and Caddy, J. F., 1993. Reflections on the pelagic food pelagic food web structure in the Black Sea. In: Second Technical Consultation on Stock Assessment in the Black Sea, Ankara, Turkey, 15-19 February. FAO Fisheries Report, 495, pp. 84-101.

Christensen, V., and Pauly, D. 1992. Ecopath II - a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling, 61(3-4), 169-185.

Christensen, V., Walters, C. J., Pauly, D., 2005. Ecopath with Ecosim: A User's Guide, Fisheries Centre, University of British Columbia, Vancouver, Canada, 154 pp.

Coll, M., Palomera, I., Tudela, S., Sarda, F., 2005. Trophic flows, ecosystem structure and fishing impact in the South Catalan Sea, Northwestern Mediterranean. J. Mar. Syst. 59, 63–96.

Coll, M., Santojanni, A., Palomares, I., Arneri, E., 2009. Food-web changes in the Adriatic Sea over the last three decades. Mar Ecol Prog Ser, 381, 17–37.

Coll, M., Shannon, L. J., Moloney, C. L., Palomera, I., Tudela, S., 2006. Comparing trophic flows and fishing impacts of a NW Mediterranean ecosystem with coastal upwelling systems by means of standardized models and indicators, Ecological Modelling, 198 (1–2), 53-70.

Costanza, R., 1992. Toward an operational definition of ecosystem health. In: Costanza, R., Norton, B. G., Haskell, B. D. (eds.), Ecosystem Health: New Goals for Environmental Management, Island Press, pp. 239–256.

Costanza, R., and Mageau, M., 1999. What is a healthy ecosystem? Aquatic Ecology, 33, 105-115.

Cury, P., and Christensen, V., 2005. Quantitative ecosystem indicators for fisheries management. ICES Journal of Marine Science, 62: 307-310.

Cury, P., Shannon, L., Roux, J., Daskalov, G., Jarre, A., Moloney, C., Pauly D. 2005. Trophodynamic indicators for an ecosystem approach to fisheries. ICES Journal of Marine Science, 62, 430-442.

Daskalov G. M., 1998. Pêcheries et changement environmental à long-term en mer Noire. PhD thesis. Centre d'océanologie de Marseille, Univ. Aix-Marseille II (in French).

Daskalov, G. M., 2002. Overfishing drives a trophic cascade in the Black Sea. Marine Ecology Progress Series, 225, 53-63.

Daskalov, G. M., 2003. Long-term changes in fish abundance and environmental indices in the Black Sea. Marine Ecology Progress Series, 255, 259-270.

Daskalov, G., Prodanov, K., Zengin, M., 2007. The Black Sea fisheries and ecosystem change: discriminating between natural variability and human-related effects. In: Proceedings of the Fourth World Fishery Congress, AFS Book, 1946 pp.

Diaz, S., and Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. TRENDS in Ecology & Evolution, Vol. 16, No.11.

Dow, D. D., O’Reilly, J. E., Green, J. R., 2006. Microzooplankton. In: Link, J. S., Griswold, C. A., Methratta, E. T., Gunnard, J. (Eds.), 2006. Documentation for the Energy Modelling and Analysis eXercise (EMAX). US Dep. Commer., Northeast Fish. Sci. Cent. Ref. Doc. 06-15; 166 p.

Finn, J. T., 1976. Measures of ecosystem structure and function derived from analysis of flows. J. Theor. Biol., 56, 363-380.

Froese, R. and Pauly, D. (eds.) 2011. FishBase. World Wide Web electronic publication. www.fishbase.org, version (08/2011).

Fulton, E. A., 2010. Approaches to end-to-end ecosystem models. Journal of Marine Systems, 81, 171–183.

Fulton, E. A., Anthony, A. D. M., Punt, A. E., 2005. Which ecological indicators can robustly detect effects of fishing? ICES Journal of Marine Science, 62, 540-551.

Fulton, E.A., Link, J., Kaplan, I.C., Johnson, P., Savina-Rolland, M., Ainsworth, C., Horne, P., Gorton, R., Gamble, R.J., Smith, T., Smith D., 2011. Lessons in modelling and management of marine ecosystems: The Atlantis experience. Fish and Fisheries, 2:171-188.

Gaichas, S., Skaret, G., Falk-Petersen, J., Link, J. S., Overholtz, W., Megrey, B. A., Gjøster, H., Stockhausen, W. T., Dommasnes, A., Friedland, K. D., Aydin, K. Y., 2009. A comparison of community and trophic structure in five marine ecosystems based on energy budgets and system metrics. Progress in Oceanography, 81, 47–62.

Grégoire, M., and Friedrich, J., 2004. Nitrogen budget of the northwestern Black Sea shelf inferred from modelling studies and in situ benthic measurements Mar. Ecol. Prog. Ser. 270, 15-39.

Gregoire, M., and Lacroix, G., 2003. Exchange processes and nitrogen cycling on the shelf and continental slope of the Black Sea basin. Global Biogeochemical Cycles, 17(2), 1073.

Gregoire, M., and Soetaert, K., 2010. Carbon, nitrogen, oxygen and sulphide budgets in the Black Sea: A biogeochemical model of the whole water column coupling the oxic and anoxic parts, 221(19), 2287-2301.

Gregoire, M., Raick, C., Soetaert, K., 2008. Numerical modelling of the central Black Sea ecosystem functioning during the eutrophication phase. Progress in Oceanography, 76, 286-333.

Gregoire, M., Soetaert, K., Nezlin, N., Kostianoy, A., 2004. Modelling the nitrogen cycling and plankton productivity in the Black Sea using a three-dimensional interdisciplinary model. Journal of Geophysical Research, 109, C05007.

Gucu, A. C., 2002. Can overfishing be responsible for the successful establishment of *Mnemiopsis leidyi* in the Black Sea? Estuarine, Coastal and Shelf Science, 54, 439-451.

Guénette, S., Heymans, S. J. J., Christensen, V., Trites, A. W., 2006. Ecosystem models show combined effects of fishing, predation, competition, and ocean productivity on Steller sea lions (*Eumetopias jubatus*) in Alaska. Canadian Journal of Fisheries and Aquatic Sciences, 63, 2495-2517.

Haeckel, E., 1866. Generelle Morphologie der Organismen. Allgemeine Grundzige der organischen Formen- Wissenschaft, mechanisch begriindet durch die von Charles Darwin reformirte Descendenz-Theorie. 2 vols. Reimer, Berlin.

Haskell, B. D., Norton, B. G., Costanza, R., 1992. What is ecosystem health and why should we worry about it? In: Costanza, R., Norton, B. G., Haskell, B. D. (eds.), Ecosystem Health: New Goals for Environmental Management, Island Press, pp. 3–19.

He, Y., Stanev, E. V., Yakushev, E., Staneva, J., 2012. Black Sea biogeochemistry: Response to decadal atmospheric variability during 1960–2000 inferred from numerical modelling, Marine Environmental Research, 77, 90-102.

Kempton, R. A., and Taylor, L. R., 1976. Models and statistics for species diversity. Nature, 262, pp. 818–820.

Kideys, A. E., Kovalev, A. V., Shulman, G., Gordina, A. and Bingel, F., 2000. A review of zooplankton investigations of the Black Sea over the last decade. Journal of Marine Systems, 24(2000), 355-371.

Kideys, E. A., 2002. Fall and rise of the Black Sea Ecosystem. Science 297, 1482-1483.

Kinzig, A. P., Ryan, P., Etienne, M., Allison, H., Elmqvist, T., Walker, B. H.,

2006. Resilience and regime shifts: assessing cascading effects. Ecology and Society 11(1), 20.

Konsulov, A. S., and Kamburska, L. T., 1998. Ecological determination of the new Ctenophora *Beroe ovata* invasion in the Black Sea. Proceedings of the Institute of Oceanology, Varna, 2, pp. 195–198.

Kovalev, A. V., and Piontkovski, S. A., 1998. Interannual changes in the biomass of the Black Sea gelatinous zooplankton. Journal of Plankton Research, 20(7), 1377-1385.

Kovalev, A., Niermann, U., Melnikov, V., Belokopitov, V., Uysal, Z., Kideys, A. E., Unsal, M., Altukhov, D., 1998. Long-term changes in the Black Sea Zooplankton: The role of natural and anthropogenic factors. In: Ivanov L. I., and Oguz, T. (eds.), Ecosystem Modelling as a Management Tool for the Black Sea. 2. Environmental Security - Vol. 47, NATO Science Series, pp. 221-234.

Kruskal, W. H., and Wallis, W. A., 1952. Use of ranks in one-criterion variance analysis. Journal of the American Statistical Association, 47 (260), 583–621.

Lalli, C. M., and Parsons, T. R., 1993. Biological oceanography: an introduction. Pergamon Press, Oxford, 296 pp.

Lancelot, C., Stanevab, J., van Eeckhout, D., Beckers, J. M., Stanev, E., 2002. Modelling the Danube-influenced North-western Continental Shelf of the Black Sea. II: Ecosystem Response to Changes in Nutrient Delivery by the Danube River after its Damming in 1972. Estuarine, Coastal and Shelf Science, 54(3), 473-499.

Langmead, O., McQuatters-Gollop, A., Mee, L. D. (Eds.). 2007. European Lifestyles and Marine Ecosystems: Exploring challenges for managing Europe’s seas. 43pp. University of Plymouth Marine Institute, Plymouth, UK.

Lebedeva, L. P., and Shushkina, E. A., 1994. Modelling the effect of *Mnemiopsis* on the Black Sea plankton community. Oceanology, Vol. 34(I), 72-80.

Levin, P. S., Fogarty, M. J., Murawski, S. A., Fluharty, D., 2009. Integrated Ecosystem Assessments: Developing the Scientific Basis for Ecosystem-Based

Management of the Ocean. PLoS Biol 7(1): e1000014.

Libralato, S., Christensen, V., Pauly, D., 2006. A method for identifying keystone species in food web models. Ecological Modelling, 195, 153-171.

Libralato, S., Solidoro, C., 2009. Bridging biogeochemical and food web models for an End-to-End representation of marine ecosystem dynamics: The Venice lagoon case study, Ecological Modelling 220: 2960–2971.

Lindeman, R. L., 1942. The trophodynamic aspect of ecology. Ecology, 23, 399-418.

Llope, M., Daskalov, G. M., Rouyer, T. A., Mihneva, V., Chan, K., Grishin, A. N., Stenseth, N. C., 2011. Overfishing of top predators eroded the resilience of the Black Sea system regardless of the climate and anthropogenic conditions. Global Change Biology, 17, 1251–1265.

Lotka, A. J., 1920. Analytical Note on Certain Rhythmic Relations in Organic Systems. Proc. Natl. Acad. Sci. 6, 410–415.

Marti, O., Braconnot, P., Bellier, J. R. B., Bony, S., Brockmann, P., Cadule, P., Caubel, A., Denvil, S., Dufresne, J. L., Fairhead, L., Filiberti, M. A., Foujols, M. A., Fichefet, T., Friedlingstein, P., Gosse, H., Grandpeix, J. Y., Hourdin, F., Krinner, G., Levy, C., Madec, G., Musat, I., Noblet, N. D., Polcher, J., Talandier, C., 2006. The new IPSL climate system model: IPSL-CM4, Note du Pole de Modelisation, 26.

McQuatters-Gollop A., Mee, L. D., Raitsos, D. E., Shapiro, G. I., 2008. Nonlinearities, regime shifts and recovery: the recent influence of climate on Black Sea chlorophyll. Journal of Marine Systems, 74, 649–658.

Mee, L. D., 2006. Reviving dead zones. Scientific American 295, 54-61.

Möllmann, C., Diekmann, R., Muller-Karulis, B., Kornilovs, G., Plikshs, M., Axe, P., 2009. Reorganisation of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. Global Change Biology, 15, 1377-1393.

Möllmann, C., Muller-Karulis, B., Kornilovs, G., and St. John, M. A., 2008.

Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a simple ecosystem. ICES Journal of Marine Science, 65, 302–310.

Mood, A. M., Graybill, F. A., Boes, D. C., 1974. Introduction to the Theory of Statistics (3rd Edition). McGraw-Hill, 480 pp.

Nesterova, D., Moncheva, S., Mikaelyan, A., Vershinin, A., Akatov, V., Boicenco, L., Aktan, Y., Sahin, F., Gvarishvili, T., 2008. The state of phytoplankton. In: Oguz, T. (ed.), State of the Environment of the Black Sea (2001 - 2006/7), Publications of the Commission on the Protection of the Black Sea Against Pollution (BSC) 2008-3, Istanbul, Turkey, pp 173-200.

O'Reilly, J. E., Dow, D. D., 2006. Phytoplankton and primary production. In: Link, J. S., Griswold, C. A., Methratta, E. T., Gunnard, J. (Eds.), 2006. Documentation for the Energy Modelling and Analysis eXercise (EMAX). US Dep. Commer., Northeast Fish. Sci. Cent. Ref. Doc. 06-15; 166 p.

Odum, E. P., 1969. The strategy of ecosystem development. Science, 104, 262-270.

Odum, E. P., 1971. Fundamentals of Ecology. Saunders, Philadelphia, 574 pp.

Odum, E. P., 1985. Trends expected in stressed ecosystems, BioScience 35, 419– 422

Oguz, T., 2007. Nonlinear response of Black Sea pelagic fish stocks to over-exploitation. Marine Ecology Progress Series, 345, 211-228.

Oguz, T., Akoglu, E., Salihoglu, B., 2012. Current state of overfishing and its regional differences in the Black Sea. Ocean and Coastal Management, 58, 47-56.

Oguz, T., and Gilbert, D., 2007. Abrupt transitions of the top-down controlled Black Sea pelagic ecosystem during 1960-2000: Evidence for regime-shifts under strong fishery exploitation and nutrient enrichment modulated by climate-induced variations. Deep-Sea Research, 54(I), 220-242.

Oguz, T., and Merico, A., 2006. Factors controlling the summer *Emiliania* *huxleyi* bloom in the Black Sea: a modelling study. J. Marine Systems, 59, 173-188.

Oguz, T., and Salihoglu, B., 2000. Simulation of eddy-driven phytoplankton production in the Black Sea. Geophysical Research Letters, 27(14), 2125-2128.

Oguz, T., and Velikova, V., 2010. Abrupt transition of the northwestern Black Sea shelf ecosystem from a eutrophic to an alternative pristine state. Mar. Ecol. Prog. Ser. 405, 231-242.

Oguz, T., Cokacar, T., Malanotte-Rizzoli, P., Ducklow, H. W., 2003. Climatic warming and accompanying changes in the ecological regime of the Black Sea during 1990s. Global Biogeochem. Cycles, 17(3), 1088.

Oguz, T., Ducklow, H. W., Purcell, J. E., Malanotte-Rizzoli, P., 2001. Modelling the response of top-down control exerted by gelatinous carnivores on the Black Sea pelagic food-web. Journal of Geophysical Research, 106(C3), 4543-4564.

Oguz, T., Fach, B., Salihoglu, B., 2008a. Invasion dynamics of the alien ctenophore *Mnemiopsis leidyi* and its impact on anchovy collapse in the Black Sea. Journal of Plankton Research, 34(II), 1385-1397.

Oguz, T., Fach, B., Salihoglu, B., 2008b. A coupled plankton-anchovy population dynamics model assessing nonlinear controls of anchovy and gelatinous biomass in the Black Sea. Mar Ecol Prog Ser, 369, 229-256.

Orek, H., 2000. An application of mass balance Ecopath model to the trophic structure in the Black Sea after anchovy collapse. M. S. in Marine Science, Middle East Technical University, 119 pp.

Ozturk, B., Ozturk, A. A., Dede, A., 1999. Cetacean By-catch in the Western Coast of the Turkish Black Sea in 1993-1997. In Evans, P. G. H., Cruz, J., Raga, J. A., (Eds.). Proc. 13th Annual Conf. European Cetacean Society, Valencia, Spain.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F., 1998. Fishing down marine food webs. Science, 279, 860-863.

Pauly, D., Graham, W., Libralato, S., Morissette, L., Palomares Deng, M. L., 2009. Jellyfish in ecosystems, online databases and ecosystem models. Hydrobiologia, 616, 67–85.

Petersen, C. G. J., 1903. What Is Overfishing?. Journal of the Marine Biological Association, 6, 587-594.

Pianka, E. R., 1970. On r and K selection. American Naturalist 104(940), 592–597.

Plaganyi, E. E., 2007. Models for an ecosystem approach to fisheries. FAO Fisheries Technical Paper. No. 477. Rome, FAO, 108 pp.

Polovina, J. J., 1984. An overview of the ECOPATH model. Fishbyte, 2(2), 5-7.

Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., Daily, G., Castilla, J. C., Lubchenco, J., Paine, R. T., 1996. Challenges in the quest for keystones. Bioscience, 46(8), 609-620.

Press, W. H., Flannery, B. P., Teukolsky, S. A., and Vetterling, W. T., 1992. "Runge-Kutta Method" and "Adaptive Step Size Control for Runge-Kutta." §16.1 and 16.2 in Numerical Recipes in FORTRAN: The Art of Scientific Computing, 2nd ed. Cambridge, England, Cambridge University Press, pp. 704-716.

Prodanov, K., Mikhaylov, K., Daskalov, G., Maxim, K. and others, 1997. Environmental management of fish resources in the Black Sea and their rational exploitation. GFCM Stud. Rev., 68, 178 pp.

Rapport, D. J. 1992. Evolution of indicators of ecosystem health. In: McKenzie, D. H., Hyatt, D. E., McDonald, V. J. (Eds.), Ecological Indicators. Proceedings of the International Symposium on Ecological Indicators, Fort Lauderdale, Florida, Elsevier Science, London, vol. 1, pp. 121-134., vol. 1:.

Rapport, D., Costanza, R., Epstein, P. R., Gaudet, C., Levins, R. 1998. Ecosystem Health. Malden, MA, Blackwell Science.

Reid, P. C., Borges, M., Svendsen, E., 2001. A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. Fisheries Research, 50, pp. 163–171.

Rodionov, S. N., 2004. A sequential algorithm for testing climate regime shifts. Geophysical Research Letters, 31, L09204.

Rodionov, S. N., 2006. The use of prewhitening in climate regime shift detection, Geophysical Research Letters, 31, L12707.

Rose, K. A., Allen, J. I., Artioli, Y., Barange, M., Blackford, J., Carlotti, F., Cropp, R., Daewel, U., Edwards, K., Flynn, K., Hill, S. L., HilleRisLambers, R., Huse, G., Mackinson, S., Megrey, B., Moll, A., Rivkin, R., Salihoglu, B., Schrum, C., Shannon, L., Shin, Y. –J., Smith, S. L., Smith, C., Solidoro, C., St. John, M., Zhou, M., 2010. End-To-End Models for the Analysis of Marine Ecosystems: Challenges, Issues, and Next Steps, Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 2, 115-130.

Salihoglu, B., 2009. Effects of ENSO on the Cold Tongue and the Warm Pool ecosystems in the equatorial Pacific Ocean: a modelling study. Journal of Marine Systems, doi:10.1016/j.jmarsys.2008.12.004.

Salihoglu, B., Fach, B. A., Oguz, T., 2011. Control mechanisms on the ctenophore *Mnemiopsis leidyi* population dynamics: A modelling study. Journal of Marine Systems, doi:10.1016/j.jmarsys.2011.03.001.

Salihoglu, B., Neuer, S., Painting, S., Murtugudde, R., Hofmann, E. E., Steele, J. H., Hood, R. R., Legendre, L., Lomas, M. W., Wiggert, J. D., Ito, S., Lachkar, Z., Hunt Jr., G. L., Drinkwater, K. F., and Sabine, C. L., 2013. Bridging marine ecosystem and biogeochemistry research: Lessons and recommendations from comparative studies, J. Mar. Syst., 109, 161–175.

Schaeffer, D. J., Henricks, E. E., Kerster, H. W., 1988. Ecosystem health: 1. Measuring ecosystem health, Environ. Manage. 12, 445–455.

Shannon, L. J., Coll, M., Neira, S. 2009. Exploring the dynamics of ecological indicators using food web models fitted to time series of abundance and catch data. Ecological Indicators, 9, 1078–1095.

Shiganova, T. A., 1998. Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. Fish.

Oceanogr., 7(3/4), 305-310.

Shiganova, T. A., and Bulgakova, Y. V., 2000. Effects of gelatinous plankton on Black Sea and Sea of Azov fish and their food resources. ICES Journal of Marine Science, 57, 641-648.

Shiganova, T. A., Musaeva, E., Arashkevich, E., Kamburska, L., Stefanova, K., Mihneva, M., Polishchuk, L., Timofte, F., Ustun, F., Oguz, T., 2008. The state of zooplankton. In: Oguz, T. (ed.), State of the Environment of the Black Sea (2001 - 2006/7), Publications of the Commission on the Protection of the Black Sea Against Pollution (BSC) 2008-3, Istanbul, Turkey, pp. 201-246.

Shin, Y. –J., Travers, M., Maury, O., 2010a. Coupling low and high trophic levels models: Towards a pathways-orientated approach for end-to-end models. Progress in Oceanography 84, 105–112.

Shin, Y.-J., Bundy, A., Shannon, L. J., Simier, M., Coll, M., Fulton, E. A., Link, J. S., Jouffre, D., Ojaveer, H., Mackinson, S., Heymans, J. J., and Raid, T., 2010b. Can simple be useful and reliable? Using ecological indicators to represent and compare the states of marine ecosystems. ICES Journal of Marine Science, 67, 717-731.

Shin, Y.-J., Shannon L. J., Cury, P. M., 2004. Simulations of fishing effects on the southern Benguela fish community using an individual based model: learning from a comparison with ECOSIM. In: Ecosystem Approaches to Fisheries in the Southern Benguela. Shannon, L. J., Cochrane, K. L. and S. C. Pillar (Eds.). African Journal of marine Science 26: 95-114.

Shin, Y.-J., Shannon, L. J., Bundy, A., Coll, M., Aydin, K., Bez, N., Blanchard, J. L., Borges, M. F., Diallo, I., Diaz, E., Heymans, J. J., Hill, L., Johannesen, E., Jouffre, D., Kifani, S., Labrosse, P., Link, J. S., Mackinson, S., Masski, H., Möllmann, C., Neira, S., Ojaveer, H., Ould Mohammed Abdallahi, K., Perry, I., Thiao, D., Yemane, D., Cury, P. M., 2010c. Using indicators for evaluating, comparing and communicating the ecological status of exploited marine ecosystems. Part 2: Setting the scene. ICES Journal of Marine Science, 67, 692-716.

Shin, Y-J., Rochet, M-J., Jennings, S., Field, J. G., Gislason, H. 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. ICES Journal of Marine Science, 62, 384–396.

Shlyakhov, V. A., and Daskalov, G. M., 2008. The state of marine living resources. In: Oguz, T. (ed.), State of the Environment of the Black Sea (2001 - 2006/7), Publications of the Commission on the Protection of the Black Sea Against Pollution (BSC) 2008-3, Istanbul, Turkey, pp. 321-364.

Staneva, J., Kourafalou, V., Tsiaras, K., 2010. Seasonal and Interannual Variability of the North-Western Black Sea Ecosystem, TERR. ATMOS. OCEAN. SCI., 21(1).

Steele, J. H., 1998. From carbon flux to regime shift. Fisheries Oceanography, 7(3/4), 176-181.

Steele, J. H., 2004. Regime shifts in the ocean: reconciling observations and theory. Progress in Oceanography 60, 135–141.

Student, 1908. The probable error of a mean. Biometrika, Vol. 6(1), 1-25.

Tomczak, M. T., Müller-Karulis, B., Leili Jarv, Kotta, J., Martin, G., Minde, A., Pollumae, A., Razinkovas, A., Strake, S., Bucas, M., Blenckner, T., 2009. Analysis of trophic networks and carbon flows in South Eastern Baltic coastal ecosystems. Progress in Oceanography, 81(1-4), 111-131.

Travers, M., Shin, Y. –J., Jennings, S., Cury, P., 2007. Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. Progress in Oceanography, 75, 751–770.

Travers, M., Watermeyer, K., Shannon, L. J., Shin, Y. J., 2010. Changes in food web structure under scenarios of overfishing in the southern Benguela: Comparison of the Ecosim and OSMOSE modelling approaches. Journal of Marine Systems, 79:101-111. DOI: 10.1016/j.jmarsys.2009.07.005.

Tsiaras, K., Kourafalou, V. H., Davidov, A., Staneva, J. 2008. A three-dimensional coupled model of the western Black Sea plankton dynamics: Seasonal variability and comparison to SeaWiFs data. J. Geophys. Res., 113, C07007.

Ulanowicz, R. E., 1986. Growth and development: ecosystem phenomenology. Springer Verlag, New York, 203 pp.

Ulanowicz, R. E., 2004. Quantitative methods for ecological network analysis. Computational Biology and Chemistry, 28(5-6), 321-339.

Ulanowicz, R. E., and Puccia, C. J., 1990. Mixed trophic impacts in ecosystems. Coenoses, 5(1), 7-16.

Umani, S. F., Beran, A., Parloto, S., Virgilio, D., Zollet, T., de Olazabal, A., Lazzarini, B., Cabrini, M., 2004. *Noctiluca scintillans* Macartney in the Northern Adriatic Sea: long-term dynamics, relationships with temperature and eutrophication, and role in the food web. J. Plankton Res., 26(5), 545-561.

United Nations, 1992. Convention on Biological Diversity (CBD), Rio de Janeiro, 28 pp.

Volterra, V., 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi, Mem. Acad. Lincei, 2, 31–113.

Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries, 7(2), 139-172.

Walters, C., Pauly, D., Christensen, V., and Kitchell, J. F. 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. Ecosystems, 3(1):70-83.

Weslawski, J. M., Legeżyńska, J., 1998. Glaciers caused zooplankton mortality? Journal of Plankton Research 20(7), 1233-1240.

Yunev, O. A., Carstensen, J., Moncheva, S., Khaliulin, A., Ærtebjerg, G., Nixon, S., 2007. Nutrient and phytoplankton trends on the western Black Sea shelf in response to cultural eutrophication and climate changes. Estuarine, Coastal and Shelf Science, 74, 63-76.

Yunev, O. A., Vedernikov, V. I., Basturk, O., Yilmaz, A., Kideys, A. E., Moncheva, S., Konovalov, S. K., 2002. Long-term variations of surface chlorophyll-a and primary production in the open Black Sea. Mar Ecol Prog Ser, 230, 11–28.

Zaitsev, YU. P., 1992. Recent changes in the trophic structure of the Black Sea. Fisheries Oceanography, 1(II), 180-189.

Zaitsev, YU. P., Mamaev, V., 1997. Biological Diversity in the Black Sea: A Study of Change and Decline. United Nations Publications, New York, 208 pp.

CURRICULUM VITAE

PERSONAL INFORMATION

Surname, Name: Akoğlu, Ekin

Nationality: Turkish

Date and Place of Birth: 09 February 1982, Çanakkale

Marital Status: Married

Phone: +90 324 521 24 06

Fax: +90 324 521 23 27

Email: ekin@ims.metu.edu.tr

EDUCATION

Degree	**Institution**	**Year of Graduation**
PhD	METU, Institute of Marine Sciences	2013
MS	METU, Institute of Marine Sciences	2008
BS	Istanbul University, Faculty of Fisheries	2004
High School	İçel Anadolu High School, Mersin	2000

WORK EXPERIENCE

Year	**Place**	**Enrolment**
Feb, 2013 – Present	METU, Inst. of Marine Sciences	Project assistant
Dec, 2008 – Feb, 2013	METU, Inst. of Marine Sciences	Research assistant
Oct, 2007 – July, 2008	METU, Inst. of Marine Sciences	Project assistant
Oct, 2005 – Jan, 2007	METU, Inst. of Marine Sciences	Project assistant

FOREIGN LANGUAGES

C2 English, A2 German, A1 Italian

PUBLICATIONS

1. Oguz, T., **Akoglu, E.** and Salihoglu, B., 2012. Current state of overfishing and its regional differences in the Black Sea. Ocean and Coastal Management, 58(2012): 47 – 56.

2. Breen, P., Robinson, L. A., Rogers, S. I., Knights, A. M., Piet, G., Churilova, T., Margonski, P., Papadopoulou, N., **Akoglu, E.**, Eriksson, A., Finenko, Z., Fleming-Lehtinen, V., Galil, B., Goodsir, F., Goren, M., Kryvenko, O., Leppanen, J. M., Markantonatou, V., Moncheva, S., Oguz, T., Paltriguera, L., Stefanova, K., Timofte, F., Thomsen, F., 2012. An environmental assessment of risk in achieving good environmental status to support regional prioritisation of management in Europe. Marine Policy, 36(5): 1033 – 1043.

3. Celebi B., Gucu A.C., Ok M., Sakinan S., **Akoglu E.**, 2006. Hydrographic indications to understand the absence of *Posidonia oceanica* in the Levant Sea (Eastern Mediterranean). Biol. Mar. Medit., 13(4): 34 – 38.

HOBBIES

Playing the Guitar, Music Theory, Computer Technologies