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## THE INTEGRATED FUNCTIONING OF MARINE ECOSYSTEMS

*PhD thesis*

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*From the point of conception, to the moment of truth  
At the point of surrender, to the burden of proof*

*From the point of ignition, to the final drive  
The point of the journey is not to arrive*

*Anything can happen*

(Neil Peart, 1987)



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## Abstract

An ecosystem-based approach to the management of marine ecosystems is the goal of the recent European Integrated Maritime Policy, known as the Blue Book (2007), shortly followed by the new Marine Strategy Framework Directive (2008/56/EC). It is recognized that management should take into account the processes taking place within, and the interactions between ecological, social and economic systems to be effective and sustainable. Yet a quantitative knowledge about such processes and the interactions between marine ecosystems and socio-economic systems is often weak or lacking. The goal of this thesis is to explore how pressures exerted on large-scale marine ecosystems translate into state changes. The focus is on multiple pressures, and on both populations and ecosystems, i.e. on the integrated functioning of marine ecosystems. Both anthropogenic pressures, such as fishing or nutrient enrichment, and natural ones, such as climate and environmental variability, are taken into account, mainly based on the Northern Adriatic Sea case study. The Northern Adriatic Sea is a data-rich Mediterranean basin, eutrophic, heavily fished, strongly influenced by climate, and with a long history of human pressures acting on it.

Different methodologies are used in a complementary manner, such as conceptual models, ecological network analysis applied to a static trophic network model, timeseries analysis, population models, review of historical data, and meta-analysis of macroecological patterns. Case studies include species of commercial importance such as small pelagics or crabs, or charismatic predators such as sharks and skates.

Based on the study of the functioning of marine ecosystems from many different points of view, the main conclusion of this work is that an ecosystem-based approach is indeed necessary to manage marine ecosystems. The reason is that multiple interacting factors, including but not limited to external pressures, can and do influence ecosystem functioning “bottom up”, “top down”, as well as from the middle of the system.



## Riassunto

Un approccio ecosistemico alla gestione degli ecosistemi marini è l'obiettivo della recente Politica Marittima Integrata per l'Unione Europea, nota come *Blue Book* (2007), seguita a breve dalla nuova Direttiva Quadro sulla Strategia per l'Ambiente Marino (2008/56/EC). Vi si riconosce che, per esercitare una gestione efficace e sostenibile, si devono considerare i processi che si svolgono all'interno dei sistemi ecologici, sociali ed economici, e le interazioni fra tali sistemi. Tuttavia, una conoscenza quantitativa di tali processi e delle interazioni fra gli ecosistemi marini e i sistemi socio-economici è spesso scarsa, se non del tutto mancante.

Lo scopo di questa tesi è comprendere meglio come le pressioni agenti su ecosistemi marini a larga scala portino a cambiamenti di stato. Ci si è concentrati su pressioni multiple, e sia su popolazioni che ecosistemi, ovvero sul funzionamento integrato degli ecosistemi marini. Sono state considerate sia pressioni di origine antropica come pesca ed apporti di nutrienti, che naturali come la variabilità climatica ed ambientale, basandosi principalmente sul caso di studio dell'Adriatico Settentrionale. L'Adriatico Settentrionale è un bacino del Mar Mediterraneo caratterizzato da abbondanza di dati utilizzabili a scopo scientifico, ed è un ecosistema eutrofico, intensamente sfruttato dalla pesca, fortemente influenzato dal clima, ed è sottoposto a pressioni antropiche da lungo tempo.

Si sono utilizzate in maniera complementare differenti metodiche, fra cui modelli concettuali, l'analisi di reti ecologiche (*Ecological Network Analysis*) applicata ad un modello statico di rete trofica, l'analisi di serie temporali, modelli di popolazione, rassegna di dati storici, e meta-analisi di regolarità macro-ecologiche. I casi di studio includono specie di importanza commerciale come pesce azzurro o granchi, e predatori famosi come squali e razze.

La principale conclusione di questo lavoro, basata sullo studio del funzionamento degli ecosistemi marini da molti punti di vista diversi, è che un approccio ecosistemico è realmente necessario nella gestione degli ecosistemi marini. Il motivo è che il funzionamento degli ecosistemi può essere ed è effettivamente influenzato da fattori multipli interagenti fra di loro, che includono (senza essere limitati ad esse) le pressioni esterne, e che agiscono sia dal basso (cioè dai livelli gerarchici inferiori) verso l'alto, che dall'alto (cioè dai livelli gerarchici superiori) verso il basso, ed a partire dall'interno (ovvero, dalle gerarchie intermedie) del sistema.



# 1. Introduction

## 1.1 Europe, as seen through the atmosphere

When viewed from space, Europe is surrounded by the blue colour of its seas and oceans. Such a beautiful sight shows that the sea and the land are in close contact with each other, suggesting that marine ecosystems have always been important for European countries. For thousand years the seas have provided man with food without the need of sowing, farming or rearing, and the huge biodiversity of marine ecosystems is now being exploited to create new medicines, and from their bottom many resources such as oil and precious metals are being extracted. Oceans have always been sailed to travel or transport goods, and they buffer the climate of our planet, making it inhabitable. The seas and their beaches are also a source of pleasure for man, not only because of tourism, which is a valuable industry for many countries, but also because of the beautiful birds or marine mammals that one can spot along the coasts.

Indeed, a large fraction of people on Earth lives on coastal zones (Cohen et al., 1997), and their societies and economies strongly rely, directly or indirectly, on the services that marine ecosystems provide. Of course, this is a two-ways interaction. Man also exerts several pressures on marine ecosystems, such as fishing, pollution, discharges of nutrients leading to eutrophication, dredging, mining, unintentional introduction of alien species, and so on. It is not a surprise, then, that marine ecosystems and the benefits that man obtain from them can become degraded, and can be highly variable and undergo abrupt changes. Such variability, which makes the human use of ecosystem-based benefits much more complicated, is not only due to human pressures, but it is an inherent property of ecological systems, which are not static, equilibrium entities. The state of ecosystems changes with time, reflecting the inter-seasonal and inter-annual variability of the environment, or simply endogenous dynamics, such as prey-predator cycles. And one should not forget about the influence of large scale forcings on marine ecosystems such as climate change (or climatic oscillations, for those who do not believe it), and connected issues such ocean as acidification.

In light of such a complexity, the interconnection between marine ecosystems and society calls for the achievement of a good understanding of how marine ecosystems function, if man is to exploit marine ecosystems in a prosperous and sustainable way. Indeed, European marine ecosystems have been strongly impacted by man in many of the abovementioned ways, and are severely degraded (see for example Langmead et al., 2007, and Gilbert, 2010). Eutrophication due to nutrient enrichment, for

example, and connected anoxia and toxic algal blooms, have affected several ecosystems such as the Adriatic Sea, the Black Sea, the North Sea and the Baltic Sea (Artioli et al., 2008). Overfishing of marine resources has taken place in many European seas (e.g. Pauly et al., 1998; Daskalov, 2002; Christensen et al., 2003) as well as the collapse of marine top predators (Daskalov, 2002; Bearzi et al., 2004; Ferretti et al., 2008; ICCAT, 2010). Loss of coastal marine habitats due to anthropogenic pressures such as degraded water quality, destructive fishing, coastal development, and overexploitation of marine resources, is a cause of concern for many European coasts (Airoldi and Beck, 2007). Moreover, European marine ecosystems can be influenced by large scale climate variability, which seems capable of markedly and suddenly altering their structure (Conversi et al., 2010), and are vulnerable to biological invasions (Daskalov et al., 2002). The effects of different pressures can also be synergistic or influence ecosystem compartments not directly affected by the pressure, as in the case of the Black Sea where eutrophication, and the resulting degraded water quality, may have been enhanced by a trophic cascade due to the removal of top predators by fisheries (Daskalov, 2002; Daskalov et al., 2007).

## **1.2 An ecosystem-based approach to the management of marine ecosystems**

Many different pressures are acting on European marine ecosystems, and many different benefits are obtained from them, so that their sustainable management appears as a complex issue, requiring the integration of knowledge on the functioning of ecological, social and economic systems. A large body of European legislation exists concerning this topic, however this section is not meant to be a complete review, but just a short illustration of the recent legislation adopted in the European Union which is most relevant to this thesis, i.e. the Integrated Maritime Policy, also known as “Blue Book” (Commission of the European Communities, 2007), and the new Marine Strategy Framework Directive (2008/56/EC) adopted in June 2008.

The Blue Book recognizes that “the seas are Europe’s lifeblood” but “we are at a crossroads in our relationship with the oceans”. [...] “On the one hand technology and know-how allow us to extract ever more value from the sea, and more and more people flow to Europe's coasts to benefit from that value. On the other hand, the cumulated effect of all this activity is leading to conflicts of use and to the deterioration of the marine environment that everything else depends on.” European countries enjoy multiple benefits provided by the marine ecosystems surrounding them, but often such benefits are in mutual contrast with each other, or can lead to the degradation of the ecosystem state and, as a consequence, of some of the services that ecosystems provide, hence of the benefits. As an example, nutrient enrichment may lead to increased primary productivity and, as a consequence, to higher secondary production and higher revenues for pelagic fisheries targeting small zooplanktivorous fish.

Yet, nutrient enrichment could also cause eutrophication, leading to toxic algal blooms damaging tourism, to anoxia near the sea bottom causing the death of benthic fish and invertebrates, hence reducing the incomes and possibly employment within demersal fisheries.

As shown by this example, the use that man makes of marine ecosystems is characterized by contrasting issues, and the consequences of human actions impacting ecological systems may eventually reach economic and social systems, which in turn can feed back to and influence ecological systems through several pressures. The solution prospected by the Marine Strategy Framework Directive is an operational “ecosystem-based approach”, in its broadest meaning, to the management of marine ecosystems, coupling sustainable use, conservation and socio-economic issues. The goal of the Directive is to achieve a “good environmental status” for European Seas by 2020, achieving the full economic potential that society can obtain from marine ecosystem services, in a way which is sustainable and in harmony with the environment. According to the Directive, which has established European Marine Regions, Member States must develop strategies to define and then achieve a Good Environmental Status for their marine regions, through cooperation with other Member States or non-EU countries whom they share the regions with. Clear environmental targets must be set, and monitoring programmes should be established in order to assess regularly the progressions made towards such goals. Such progressions should be made by State Members by means of technically-feasible, cost-effective measures, based on prior impact assessments and cost-benefit analyses in order to evaluate their effectiveness and consequences.

It is clear that, in order to “apply an ecosystem-based approach to the management of human activities, ensuring that the collective pressure of such activities is kept within levels compatible with the achievement of good environmental status and that the capacity of marine ecosystems to respond to human-induced changes is not compromised, while enabling the sustainable use of marine goods and services by present and future generations” (2008/56/EC), it is certainly fundamental to understand how economic, social and ecological systems are interlinked. However a prerequisite is that we have a robust knowledge of how marine ecosystems function. This is not an easy task: as already mentioned marine ecosystems dynamics can be influenced both by many external forcings, e.g. anthropogenic such as fishing or natural such as climatic oscillations, and by internal factors, e.g. trophic interactions. While we have a good understanding of some of the ecological processes going on in the sea, this is not true for all of them, such as the effects of climate on marine populations. Most importantly, we have a scarce understanding of what happens when many different pressures are acting together on ecosystems, i.e. we still know little about the relative importance of, and the synergies between, fishing, climate, eutrophication, pollution, etc. Also, we know relatively little about the way that populations interact in the oceans, and how such (numerous) abiotic and biotic interactions are influenced by the above pressures. Our knowledge of the dynamics behind abrupt whole-ecosystem

reorganizations, also known as regime shifts (Scheffer and Carpenter, 2003), e.g. following the action of some anthropogenic pressure, is still limited. Indeed not enough is known about the “details”, i.e. the ecological processes, and even less is known about the overall picture, i.e. the integrated behaviour of ecosystems. Even if it may be impossible to predict with precision in a mechanistic fashion the behaviour of “complex” ecological systems such as the oceans (Bak, 1996; Ulanowicz, 2007 and 2009), if we are to make management choices concerning ecosystems based on quantitative, scientifically-sound tools, first of all we need to achieve a better understanding both of the single ecological processes acting at the system scale and, as described above, of the integrated functioning of marine ecosystems. A contribution aimed at increasing such understanding, in order to achieve an operational ecosystem-based management of the seas, is the goal of this thesis.

### **1.3 The DPSI(W)R conceptual model**

For the purpose of studying the interactions between ecosystems, society and economy, it can be useful to break down the process in several steps, by adopting the “Driving forces-Pressures-States-Impacts-Responses” causal framework (DPSIR; see Gabrielsen and Bosch, 2003). When writing about pressures, impacts, and so on (as already done previously in this introduction), such framework is being referred to.

The DPSIR framework is a conceptual model (Figure 1) representing through a causal chain or, better, a causal loop, the way that man interacts with the environment. The model starts from the main Driving forces which act on society and reflect social needs and economic demands: using an example from fisheries, such needs would be to maintain a high level of profits or of employment in that economical sector, or to satisfy the market demands for fish. Human activities, i.e. fishing in the example, are performed to satisfy the needs and the demands, resulting in Pressures on marine ecosystems, such as the removal of fish biomass, bottom destruction by dredging, etc. In a sense, driving forces “cause” pressures. Pressures lead to modifications in the environment, so that its State is affected and changes. For example, fishing pressure can lead (directly) to a decrease of the biomass of commercial fish stocks, but also (indirectly) to a higher biomass for other marine populations which are predated by the depleted commercial fish stocks and benefit from a reduced predation mortality. Also the abiotic state of marine ecosystems can be affected by fishing, e.g. dredging can resuspend bottom sediments, leading to a state of reduced water clarity and light penetration, and thus to the disappearance of macroalgae living on the sea bottom, which need light to survive. Water turbidity and the biomasses of fish stocks and other marine populations are states. As explained, fishing pressure affect such states, which change, and this leads to Impacts.

Impacts are not simply modifications of the environmental state, but need to be defined with respect of the use that man makes of the environment, i.e. impacts are the consequences, caused by changes in ecosystem quality and state, for human welfare and for the social or economic benefits that man obtain from ecosystems. Consequently, instead of DPSIR, it could be clearer to speak about DPSWR, where W stands for Welfare (Gilbert, 2010). In the fisheries example, not all state changes lead directly to impacts: a decrease of the abundance of commercial fish stocks leads to a direct impact, i.e. decreased landings, with negative economic consequences. Instead, reduced water clarity and the disappearance of macroalgae do not lead directly to impacts to human welfare. However, the disappearance of macroalgae could mean no habitat for some commercial invertebrate species, which as a consequence would disappear leading to an (economic) impact. Hence, the water clarity state change leads indirectly to an impact.

It is useful here to distinguish between “ecosystems services”, such as the provision of habitat by macroalgae, and the production of the invertebrate population which live in the macroalgae habitat, and “benefits” that man obtain from such services, such as the landed commercial invertebrate species. Impacts are defined as modifications of one or more benefits, which in turn are based upon ecosystem services. The connection between services and benefits can be direct, e.g. the connection between the production of the invertebrate population and its fishery landings, or indirect, e.g. the connection between habitat provision by macroalgae and invertebrate fisheries landings, mediated by the invertebrate population growth.

Impacts are not necessarily negative, as it can be seen from the previous fisheries example. It can happen that one marine population, which is increasing its abundance because fishing reduces the abundance of the commercial species predating on it, is a commercial species as well: then its increase will be a positive impact for fisheries. Let us consider again the example of anthropogenic nutrient enrichment. Nutrient enrichment is a pressure due to driving forces such as population increase or the need to make agricultural practices more efficient through fertilizers, and it can cause the onset of eutrophication (a state). Indeed eutrophication can lead to economically negative consequences (impacts) for tourism due to the degradation of water quality (state change), but also to economically positive consequences for fisheries targeting small pelagic fish, whose stock could increase following the greater availability of food (more primary production could mean more zooplankton, which small pelagics feed upon).

Also the conservation point of view must be considered when evaluating impacts. Let us make another example: overfishing top predators, e.g. elasmobranch fish such as sharks and skates (Gilbert, 2010, see also next chapters). The decrease of top predator populations due to fishing leads to an impact according to the above definition, since man can enjoy (i.e. benefit) simply from the existence or conservation of charismatic populations such as big sharks, i.e. this is a so-called “non-use” value

(Gilbert, 2010). Of course, biodiversity reduction can lead to other impacts than those affecting conservational and non-use values. Top predator loss can lead to trophic cascades (Paine, 1980; Polis et al., 2000), i.e. it can indirectly affect many other marine populations through prey-predator interactions which take place in the food web. Then, top predator overfishing could lead to the increase or decrease, resulting from the trophic cascade, of the biomass of commercial stocks, hence to an impact, i.e. changes to fishery landings. Two ecosystem services are affected by the fishing pressure in this example: the stability which top predators provide to the food web (directly affected), and the production of other marine populations which may increase or decrease their abundance following the trophic cascade (indirectly affected by fishing). Finally, the benefit is defined with reference to human welfare, i.e. changes to landings, and may be positive or negative.

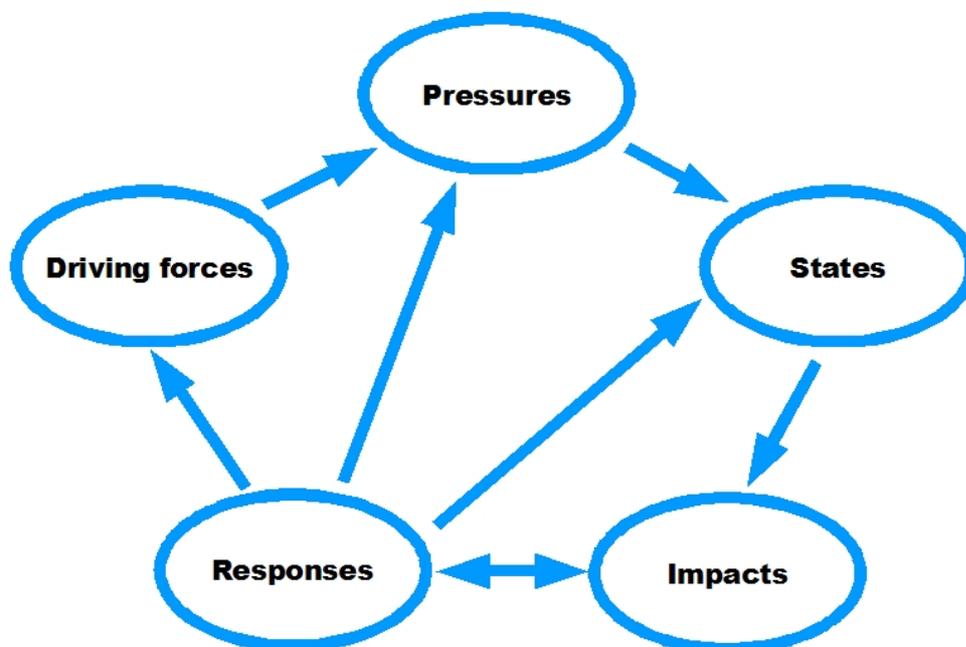


Figure 1. The DPSIR conceptual model. Driving forces in the society lead to pressures on marine ecosystems, which change ecosystem state resulting, directly or indirectly, in impacts to human welfare. Responses to such impacts, for example by policy makers, can feed back to any of the previous steps.

The last step of the DPSIR is the Responses that society or policy makers adopt in order to counteract the negative Impacts for human welfare. Such Responses may address (1) driving forces, e.g. going back to the initial fisheries example, the need to maintain a high level of employment in the fishing industry could be lowered by policies providing incentives to encourage the employment of fishermen in other economic sectors, thus leading to a decrease of the fishing effort; (2) pressures, e.g. in the fisheries example, policies to enforce fishing gears with reduced capacity of destroying the sea bottom; (3) states (not applicable to the fisheries example, but in the case of a eutrophied lake because

of anthropogenic nutrient enrichment lake, this step could be the dredging and removal of polluted sediments from the lake bottom); (4) impacts, e.g. in the fisheries example, reduced economic incomes for fishermen due to reduced landings may be compensated by government subsidies. The presence of feedbacks going from the responses to the other steps of DPSIR conceptualization (Figure 1) highlights that the management of marine ecosystems is necessarily an adaptative process, where efficient solutions must be iteratively searched for, because of the contrasting issues that policy makers must solve, of the inherent variability of ecosystem dynamics and, not least, of the incomplete empirical and theoretical knowledge we have about the functioning of marine ecosystems.

#### **1.4 Goals and perspectives of the thesis**

The work of this thesis will focus on the PSI part of the DPSIR framework, in particular on the how Pressures exerted on large-scale marine ecosystems translate into State changes. The goal is to contribute to achieve an operational ecosystem-based management of marine ecosystems, which has been called for in the Marine Strategy Framework Directive, by improving the scientific knowledge of the functioning of marine ecosystems, especially under the actions of different pressures, analyzed alone or together, and both anthropogenic and natural, such as fishing, nutrient enrichment, climate change or variability, etc. Particular attention will be paid to the integrated functioning of marine ecosystems, i.e. to emergent ecosystem characteristics or dynamics under the actions of multiple pressures. Many analyses are based upon a case-study, the Northern Adriatic Sea, an ecosystem affected by multiple pressures for which published and unpublished data were widely available, but care has also been put to provide conclusions which can be generalized to other systems.

The relationship between State changes and Impacts will be taken into account only partially, e.g. by creating conceptual models linking pressures, ecosystem services and benefits, by analysing economically-important species and providing management advices or evaluations of the exploitation levels of marine resources for the case study, or by the definition of holistic indicators of the ecosystem successional stage. This choice is justified by the belief that the understanding of the link between pressures and states is a fundamental prerequisite to achieve a real ecosystem-based approach of marine ecosystems.

The perspective taken in this thesis is a “trophic” one, i.e. the focus will be mostly on food webs, however both interactions among biota, and between biota and abiotic factors such as climate or environmental factors, will be considered. Also, a “macroscope” perspective will be adopted to look at marine ecosystems: the focus will be on large-scale systems, their integrated behaviour, and ecological processes acting on those scales. Similarly, the focus will be on macro-ecology in the case of the

definition of holistic indicators of ecosystem state through the analysis of inter-ecosystem scaling patterns. Such a macroscopic approach necessarily requires to drop some attention to biological details and to produce simple conceptual models of ecosystem functioning, in order for them to be testable. Clearly this is no excuse for the roughness which characterizes the way that this thesis deals with biological terminology, and that is due to my non-biologist background.

## 1.5 Tools: models, statistics and lessons from the past

Two main tools will be used to achieve the goals of this thesis: the construction of mathematical models (for food-webs or populations), and the analysis of “real” data, in particular statistical analysis of long-term biotic and abiotic timeseries. This is an engineering thesis, and one of the main skills of an engineer is the capability of building and validating models, which are fundamental scientific tools to achieve many tasks: they allow to make quantitative predictions, investigate management scenarios, test causalities behind correlations, learn more about complex ecosystems dynamics, e.g. by forcing one to conceptualize problems and to isolate the action of different forcing factors through simplified *in silico* experiments. Indeed all of these tasks would be impossible without models, or much more complicated and time- and resource-consuming, especially considering the time and spatial scales characterizing large-scale marine ecosystems.

On the other hand, an adequate understanding of the ecological processes driving the dynamics of marine populations or large-scale marine ecosystems is sometimes lacking, or it is not known when an ecological process is relevant to the description of ecosystem behaviour (and should be modelled), and when it is not. I believe that much about this can be learned simply by looking to data, especially historical data, and this is why statistics is widely used within this thesis. A large amount of scientific data has been collected during the last decades to address specific questions related to single trophic levels of marine ecosystems, or to be used in separate research areas such as fisheries, or plankton dynamics, or eutrophication, etc. Much about the integrated functioning of marine ecosystems could be learnt simply by putting this wide literature together, as done recently for example by Conversi et al. (2010) who, following a wide literature review and the integration of data from different trophic levels, collected for different purposes and from different ecosystems, suggest that a regime shift took place in 1987 in all of the European seas, driven by a common climate change in the Northern hemisphere.

Historical data are particularly important because they often depict ecosystems as characterized by completely different states and under the action of completely different pressures: these data are the only experiments which are available to study the response of large-scale ecosystems to pressures, since laboratory experiments are clearly impossible. Many pre-exploitation marine ecosystems used to be

radically different with respect to nowadays (Jackson et al., 2001), to a point that now it is even hard to believe that they existed, because our reference baselines have markedly shifted (Pitcher and Pauly, 1998) and we have forgotten about them. Realizing that marine ecosystems have been profoundly altered by anthropogenic impacts is a first step towards their restoration to a pristine status, which could be used to define a reference point for management purposes. But historical data are fundamental for many other reasons, for example to understand the non-linearity and hysteresis (Scheffer and Carpenter, 2003) often characterizing ecosystem dynamics: because of their own nature, such phenomena are difficult to imagine before you observe them.

Long-term timeseries are among the most important historical data, because they show continuously the time-response of ecosystems to constant or variable pressures, and are useful to build and calibrate models and to test hypotheses by means of statistics. Longer timeseries provide more statistical power, making it possible to detect the effects of weak pressures on ecosystem status, which otherwise would go unnoticed. One classical example of the importance of timeseries is the work of Pauly et al. (1998), who detected a worldwide “fishing down” of marine food webs, i.e. a reduction of the trophic level of landed species not compensated by the increase in landings that one could expect if fisheries were sustainable. Such hugely-important result came, simply, from the analysis of publicly available FAO fisheries data.

## **1.6 An overview of the following chapters**

Most of the following chapters are based upon or literally represent papers which are already published (Barausse et al., 2009, particularly Chapter 3), submitted for publication (Artioli, Y., Visentin, E., Barausse, A., Mazzoldi, C. Which future for elasmobranch in the Northern Adriatic Sea? A perspective from historical data and predictive models: Chapter 5), or in preparation, among which there are: Bartolini, F., Barausse, A., Pörtner, H.-O., Giomi, F. Climate change reduces offspring fitness in littoral spawners, Chapter 4; Barausse, A., Mazzoldi, C. When prey become predators: paradoxical effects of eutrophication on pelagic fish, Chapter 6; Barausse, A., Palmeri, L., Salcido-Guevara, L.A., Arreguin-Sanchez, F. Supply-demand scaling of consumption with biomass in food webs of aquatic ecosystems, Chapter 7 (these people, as well as other acknowledgments, are also reported at the end of each chapter). Therefore, this thesis is a paper collection and, consequently, not all of the work described here has been done by me, of course, particularly the experimental activity. However I have chosen to include the contributions of the people I have collaborated with during these months because, without them, the conclusions of this thesis would be less far-reaching or even not supported by data. After all, research is also a team work, and this thesis describes research.

The thesis is structured as follows. On Chapter 2 the Northern Adriatic Sea ecosystem, which will be the main case study in the following chapters, is described.

On Chapter 3, a description is provided of the construction and network analysis of a static food web model, built with Ecopath software, providing a snapshot of the biomass flows and stocks found in the Northern Adriatic Sea during the 1990s. The purpose is to show that the picture emerging from the ensemble of trophic flows within an ecosystem can reflect anthropogenic impacts, and can be used to learn more about ecosystem functioning.

On Chapter 4, the effects of climate on aquatic biota are considered using a long-term (1945-2010) dataset of landings, combined with statistical analyses aimed at reconstructing long-term heat wave events. An economically-important population from the lagoon of Venice (which borders the Northern Adriatic Sea) is analyzed: crabs (*Carcinus aestuarii*), with focus on thermal stress during early life stages and on how this is reflected on population dynamics (indeed the lagoon is not a marine ecosystem, but I think that the conclusions from this chapter can be easily generalized to marine systems). Landings come from the Clodia dataset, which contains precious and still-unpublished records from the fish market of Chioggia (Italy), which is located between the Northern Adriatic Sea and the Venice lagoon. The dataset will soon be online ([http://chioggia.scienze.unipd.it/Inglese/Database\\_landing.html](http://chioggia.scienze.unipd.it/Inglese/Database_landing.html)) and was kindly provided by Carlotta Mazzoldi (Dept. of Biology, University of Padova). It was also used on Chapter 5 and 6. The dataset landings come from the Northern Adriatic Sea or, as in the case of crabs, from the lagoon of Venice.

On Chapter 5, long-term timeseries for elasmobranch populations (landings from the Clodia dataset) are analyzed, together with recent fish market data, highlighting the influence on elasmobranch of both fishing and climate. Some management advices based on individual based models are provided.

On Chapter 6, using long-term data from several sources, the effect of eutrophication and size-based trophic interactions is considered on the population dynamics of economically-important pelagic fish species such as anchovy, pilchard and mackerel. A tentative explanation for the disappearance of mackerel from the Northern Adriatic Sea during the 1960s is proposed, which could possibly be generalized to other systems (e.g. the Black Sea): eutrophication triggered an autocatalytic loop, leading to the disappearance of mackerel because of the predation of small pelagic fish on mackerel eggs or larvae, or because of the competition for food between small pelagics and mackerel juveniles. Such conclusion confirms the key ecological role of small pelagic fish in Mediterranean marine ecosystems, but puts them in a different light, i.e. predators, and not only “forage” prey.

On Chapter 7, a meta-analysis of 56 mass-balanced trophic network models is presented, to investigate if the process of ecological succession is reflected in the network of trophic flows found in aquatic ecosystems, hence in ecosystem functioning. A novel inter-compartment scaling relationship linking the consumption of a network compartment to its biomass through a power law with a non-

trivial exponent is reported. The exponent of the scaling relationship is shown empirically to be related to the ecosystem successional stage and emergent properties, and is proposed as an indicator of ecosystem status and maturity.

On Chapter 8, based on the results from the previous chapters, I conclude that an ecosystem-based approach is really necessary to achieve an optimal management of marine ecosystems.



## 2. The Northern Adriatic Sea

### 2.1 Why the Northern Adriatic Sea case study?

The understanding of the functioning of large-scale marine ecosystems must necessarily be based upon real examples, and many of the following chapters will examine case studies from a Mediterranean Sea ecosystem, the Northern Adriatic Sea (Croatia, Italy, Slovenia). This choice follows from several reasons. First, there is a wide availability of biotic and abiotic information concerning the Northern Adriatic Sea, especially if compared to other Mediterranean ecosystems, which are traditionally data-poor. Therefore, this appears to be a nice case study for advancing the ecosystem-approach to the management of marine ecosystems also in the Mediterranean Sea.

Second, most of this information has been analyzed so far in traditionally-separated scientific research areas, e.g. to my knowledge, there have been no previous attempts, before the work of Conversi et al. in 2010, to find relationships between the long-term timeseries of zooplankton and small pelagic fish (feeding on plankton) collected in the basin. Also, only recently the flows of energy within the Adriatic marine food webs have been systematically described through trophic network models (see Chapter 3): consequently the work of this thesis tries to bring together, synthesize and make available to the wider scientific community a large body of literature. Sometimes such literature is grey, making this integration even more valuable, and also unpublished historical data are analyzed here, such as a part of the 1945-2010 Clodia dataset of landings from the basin (see next chapters).

Third, the Northern Adriatic Sea is close to, and has been studied from a long time at the University of Padova, for example by Umberto D'Ancona (D'Ancona, 1926), whose analysis of the Northern Adriatic fishery landings inspired the famous predator-prey model of Vito Volterra. Consequently, a large amount of information and experience is available in Padova concerning this basin, and it was also possible to start a fruitful collaboration with the Department of Biology and Chioggia Hydrobiological Station, whose well-prepared and enthusiastic people provided me with the help I needed because of my limited biological background. Moreover through the Hydrobiological Station it was also possible to interact with fishermen from Chioggia, which are a huge source of information concerning the Northern Adriatic ecosystem.

Fourth, the Northern Adriatic ecosystem is a perfect case study for the purposes of this thesis, having been under the actions of many pressures, possibly acting synergistically, for a long time, and being characterized by a peculiar and complex functioning (see Section 2.2 and Chapter 3).

Indeed, in the Mediterranean, the Northern Adriatic Sea constitutes a unique ecosystem. It is one of the most productive basins, shallow, and characterised by wide inter-seasonal and inter-annual variations in environmental parameters (e.g. temperature, salinity) and circulation, which are strongly influenced by atmospheric forcings and riverine inputs (Russo and Artegiani, 1996). Anthropogenic pressures include coastal pollution, nutrient enrichment (the eutrophication caused by the huge nutrient loads discharged by the Po River resulted, mainly in the 1980s, in anoxic conditions and fish kills; Vollenweider et al., 1992; Caddy, 2000), and commercial fishing. Indeed this basin is one of the major fishing grounds of the Mediterranean Sea, thus having a great socio-economic importance (Barausse et al., 2009). It is hard to quantify the real magnitude of the human impacts on this ecosystem, because of the presence of fishing since ancient times and of the great environmental variability, linked also to hemispheric climate oscillations (Conversi et al., 2010). Finally, additional pressures have characterized the history of this ecosystem, for example jellyfish invasions (Malej and Malej, 2004). The ecosystem, its geography and hydrography, and long-term changes in pressures, are discussed in more detail on Section 2.2.

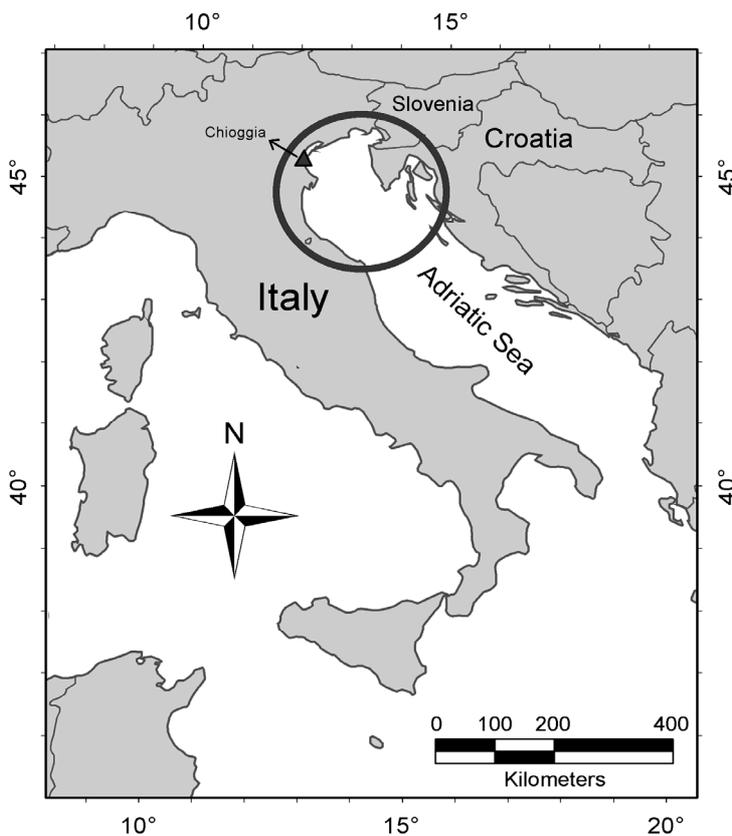


Figure 2. The Northern Adriatic Sea. The circle indicates the approximated area covered by the Northern basin within the Adriatic Sea. The triangle is the location of the fishing harbour of Chioggia.

## 2.2 A description of the Northern Adriatic Sea ecosystem

The Northern Adriatic Sea (45°40′-43°30′N, but the precise definition of its extension often varies in the literature) is a semi-enclosed basin of about 32000 km<sup>2</sup> (Figure 2). The surrounding countries, i.e. Croatia, Italy and Slovenia, are characterised by markedly different anthropogenic pressures and levels of urbanization, ranging from the strongly-inhabited Po river plain in Italy to the Slovenian forests. The basin is narrow (210 km wide at maximum) and is markedly distinct from the rest of the Adriatic because of both physical characteristics, such as its shallow depth (up to 100 m, 29 m on average), and biological ones, e.g. the Northern basin is much more productive.

Circulation is primarily driven by air-sea interactions and freshwater discharge (Artegianni et al., 1997). A mean water temperature for the 1990s of about 14.5 °C was calculated based on the Medatlas database (MEDAR group, 2002; the basin was divided into layers of one meter depth and the mean temperature was weighted by water volumes), however extreme seasonal variations for the Mediterranean sea of about 12 °C offshore and 22 °C near the coast are observed (Russo and Artegianni, 1996), as well as large decadal oscillations (Kamburska and Fonda Umani, 2009). The combined effects of freshwater input, wind and seasonal heat budgets contribute to further complexity leading to changing stratification of the water column and extension of the Po river plume (Fonda Umani, 1996). Rivers exert a strong influence on the system, affecting circulation, leading to a very short residence time (less than 3.3 months on average, Artioli et al., 2008), influencing the biological dynamics of low-medium trophic levels (Santojanni et al., 2006) and causing eutrophication and related phenomena of anoxia (Artioli et al., 2008; Caddy, 2000; Degobbi et al., 2000; Justic et al., 1987) through the high nutrient loads discharged, particularly by the Po river with its enormous but varying freshwater input (about 50 km<sup>3</sup> y<sup>-1</sup>), which represents half of the total runoff into the Northern Adriatic Sea (Raicich, 1994). The Po freshwater inflow, summed up to that of the other rivers from Northern Italy, is about 20% of the river runoff into the whole Mediterranean Sea (Russo and Artegianni, 1996). Riverine nutrient inputs were (Artioli et al., 2008) 351000 t y<sup>-1</sup> of total nitrogen (TN) and 12000 t y<sup>-1</sup> of total phosphorus (TP) during the 1990s; during the 1975-1985 peak eutrophication period, they were 243000 t y<sup>-1</sup> of TN and 21000 t y<sup>-1</sup> of TP. The ecosystem appears to be P-limited (Artioli et al., 2008).

Spatial heterogeneities are marked, too. The main freshwater inputs are on the western coast, where slopes are gentler and muddy-sandy and coastal lagoons are found, such as those of Venice and near the Po river delta. Instead the eastern coasts are steeper, rocky and reach greater depths. In addition, temperature and salinity patterns are different (Russo and Artegianni, 1996). Consequently the two sides of the Northern Adriatic generally present different habitats for marine species. The phytoplankton standing crop and its high but variable productivity (592 mg C m<sup>2</sup> d<sup>-1</sup>, estimated during the 1990s, Giordani et al., 1999) decrease eastward (Fonda Umani, 1996; Figure 3) due to the large

influence of nutrient discharges coming from the western rivers. However, nutrient release from sediments could be important in the system (Artioli et al., 2008). Wind-driven upwelling events are observed on both coasts and mesoscale eddies contribute to spread offshore the Po river discharge (Russo and Artegiani, 1996). Recently, primary productivity appears decreasing (Mozetic et al., 2010).

The planktonic productivity sustains an equally high production of fish and invertebrates that are heavily exploited by industrial and artisanal fleets: landings increased after 1945 and reached a maximum around mid-1980s (Clodia dataset, not shown), reaching in the 1990s more than  $100000 \text{ t y}^{-1}$  (Chapter 3) consisting mainly of zooplanktivorous pelagic fish and invertebrates. Discard rates can also be high (Chapter 3). The Northern Adriatic Sea makes up to 25–30% of Italian marine landings (e.g. ISTAT 1998, 2000a,b, 2002) and it is possibly the most fished of the Mediterranean basins. During 1990–2005 on average 6.8–8.6% of landings from the Mediterranean Sea came from the Northern Adriatic Sea, which represents only 1.3% of its surface (recalculated from FAO (2007) GFCM dataset; Black Sea and Azov Sea were excluded).

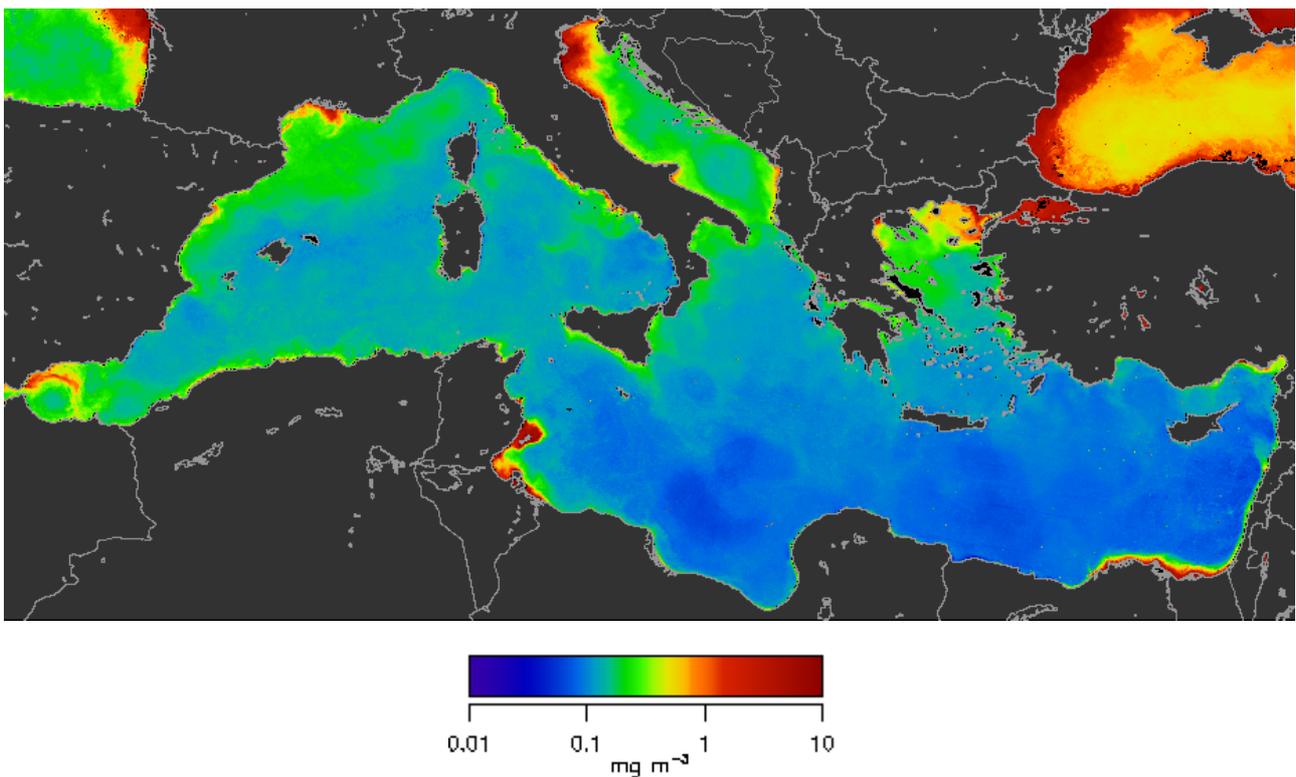


Figure 3. Satellite-based estimates of Chlorophyll-*a* concentration in the Mediterranean marine waters. Data refers to June 1998 and was downloaded on 16/11/2010 from the Ocean Colour Portal ([http://oceancolour.jrc.ec.europa.eu/data\\_portal/oc\\_portal/main.php](http://oceancolour.jrc.ec.europa.eu/data_portal/oc_portal/main.php)) of the Institute for Environment and Sustainability, European Commission - Joint Research Centre. The high productivity of the Northern Adriatic Sea compared to other Mediterranean waters, including the Central Adriatic, can be clearly seen. The Po river plume is easily distinguishable, as well as the eastward- and southward-decreasing productivity gradient that it produces.

### 3. The portrait of an ecosystem

#### 3.1 A trophic network model of the Northern Adriatic Sea

The task of understanding how pressures translate into state changes for marine ecosystems can be achieved through multiple practical tools, including but not limited to the review of historical data, timeseries analysis, statistical and deterministic models, integrated ecosystem assessment (Kenny et al., 2009; Gilbert, 2010), and so on. However, these tools must necessarily be based upon some conceptual model that we have for the functioning of marine ecosystems, which is then a prerequisite for making operational the ecosystem-based approach to the management of marine ecosystems.

Conceptual models indeed reflect the scientific knowledge or, better, ignorance concerning the topic, therefore they are necessarily biased or incomplete. For this reason, it is important to root robustly our conceptualization of the functioning of a system on sound empirical data. Assuming that a clear conceptualization is lacking for a case study, what better approach to conceptualization than taking a photograph of the ecosystem?

Indeed, trophic network models may be defined as “snapshots” of the energy (or mass, or nutrients, depending on the chosen currency for the medium) flowing, or stocked into biotic or abiotic matter, in a given ecosystem in a particular moment in time. The terms “photograph” and “snapshot” have been used because such models are not simulations but static descriptions of a particular state of the ecosystem in a particular period. More precisely, a trophic network model is a flow network representing a set of ecological flows within the ecosystem, such as predation (i.e. the flows within the food web, notice that “trophic” is derived from the Greek word for “food”), but also respiration, excretion and egestion, flows to and from detritus, exports and imports from the system, etc. The nodes of the network, among which predatory flows are exchanged, represent the populations or trophic or functional groups within the ecosystem.

Trophic network models are gaining a great popularity in the scientific community and more and more of them are being constructed (Ulanowicz, 2004; Christensen and Walters, 2004; Christensen et al., 2005) for purposes ranging from answering theoretical ecology questions, analyzing ecosystem functioning and emerging properties, or evaluating the ecosystem “health” status (Baird and Ulanowicz, 1989, Baird et al., 1991; Heymans et al., 2004) through the so-called “ecological network analysis” (e.g. Baird et al., 1991; Ulanowicz, 1986; Ulanowicz and Puccia, 1990). Such static models are also commonly used as a basis to create time and space simulations of the biomass trajectories of the

populations found in the food webs of aquatic ecosystems (see Christensen et al., 2005), to evaluate the effects of different pressures or to test fishing management scenarios, and in general to practically implement the “ecosystem approach to fisheries” (Garcia et al., 2003).

In the case of the Northern Adriatic Sea, a clear conceptual model of the food web functioning was lacking. Hence, following the abovementioned considerations, a quantitative model of the trophic network of the Northern Adriatic Sea marine ecosystem during the 1990s was constructed, with the goal of analysing its trophic structure and functioning, identifying the key trophic groups and assessing the anthropogenic impacts on the ecosystem using the Ecopath (see section 3.2) modelling protocol. An intensive and time-consuming activity of data gathering was set up, based both on literature and newly-collected field data, to create a high quality model which could be robustly used for management applications. Yet, trophic network models are particularly data demanding, not only if compared to the effective availability of information. Therefore, in order to highlight the forced limitation of the following analysis, in the title of this chapter the word “portrait” was put instead of “photograph”.

### 3.2 The Ecopath modelling approach

The static trophic network model was constructed using Ecopath software (Polovina, 1984, Christensen and Walters, 2004, Christensen et al., 2005), version 5.1.0.205. The ecosystem is described in terms of standing stocks and fluxes connecting the compartments, called “groups”, each group representing living organisms or non-living, bioavailable matter called “detritus”. The trophic network is assumed to be mass-balanced over the modelled time frame, and consequently fluxes in and out from each compartment must be equal, so that the modelled currency (matter or energy) is conserved. For each group, two budgets can be written (Christensen et al., 2005):

$$B_i \cdot (P/B)_i = \sum_{j=1}^N B_j \cdot (Q/B)_j \cdot DC_{ji} + Y_i + (P/B)_i \cdot B_i \cdot (1 - EE_i) + E_i + Ex_i + BA_i \quad (1)$$

$$Q_i = P_i + R_i + GS_i \cdot Q_i \quad (2)$$

where  $N$  is the number of groups in the model,  $B$  is the group biomass,  $P/B$  is the production rate for the group equal to total mortality  $Z$  under steady state assumption,  $Q/B$  is the consumption rate,  $DC_{ji}$  is the diet matrix, representing the fraction of prey  $i$  in the diet of predator  $j$  (so that

$\sum_{j=1}^N B_j \cdot (Q/B)_j \cdot DC_{ij}$  is the production preyed by other groups),  $E$  is the net emigration,  $Ex$  is the net export,  $BA$  is the biomass accumulation (a zero accumulation term means a steady state situation, as it is often assumed for Ecopath models),  $Y$  represents the fisheries catches,  $EE$  is called the ecotrophic efficiency i.e. the fraction of production which is used in the system,  $R$  is the respiration,  $GS$  is the fraction of unassimilated consumption because of egestion and excretion. The quantity  $(1 - EE) \cdot P/B$  is the “other mortality”  $M_o$  unexplained by the model (e.g. due to illness and old age).

For each group  $DC$ ,  $Y$ ,  $GS$  and also  $E$ ,  $Ex$  and  $BA$  (if any) must be specified, as well as at least three out of four of  $B$ ,  $P/B$ ,  $Q/B$  and  $EE$ . The unspecified parameters are then calculated by solving the resulting linear system. Usually  $EE$  is left as an unknown because it is difficult to estimate. Respiration is calculated by difference but it can be specified to estimate another unknown parameter.

### 3.3 Time frame, input data and model structure

The model represents the Northern Adriatic Sea during the last decade of the 20<sup>th</sup> century. More specifically, data was obtained (where possible) for the years 1996-1998. Biomasses are expressed as  $t\ km^{-2}$  (wet weight) and fluxes as  $t\ km^{-2}\ y^{-1}$  (wet weight).

Two previous Ecopath models have been published for this area, but one covers only a small portion ( $14000\ km^2$ ) with a high degree of group aggregation (Zucchetta et al., 2003), whilst the other one considers the Northern and Central Adriatic as a whole, although they are markedly different (Coll et al., 2007). The imaginary line linking the Croatian island of Pago to the Italian city of Ancona is chosen as the southern boundary of the model. Coastal lagoons and the Po river delta are not included.

The model comprises 34 groups, focusing on the upper trophic levels and on commercial species. There are 14 fish groups, 11 invertebrate and 2 other top predator groups (dolphins and birds), in addition to 4 plankton groups, 2 detritus groups and 1 benthic primary producer group. Data for the balanced model is reported on Table 1 and 2. Only a few ecotrophic efficiencies were guessed to estimate highly uncertain input data.

A description of the groups of the model (input data, assumptions, species included) is provided in the following sections, along with information on data sources and data treatments for landings and discard. Also, balancing criteria and main changes in initial input data are discussed. Numerical input data for the initial unbalanced model, as well as data sources, are summarized in Annex I.

Table 1. Input data for the balanced model and calculated indices. Inputs in italics have been calculated by Ecopath. There is no biomass accumulation or net migration for any group.  $F$  is the fishing mortality,  $M_2$  the predation mortality,  $M_0$  the other, unexplained mortality.  $F / Z$  represents the exploitation rate.

Group name	B (t km <sup>-2</sup> )	P / B (y <sup>-1</sup> )	Q / B (y <sup>-1</sup> )	EE	P / Q	R / B	Trophic level	Omnivory index	F	M <sub>2</sub>	M <sub>0</sub>	F / Z
1. Dolphins	0.0063	0.054	14	<i>0.278</i>	0.004	11.146	4.3	0.079	0.015	0	0.039	0.28
2. Seabirds	0.0106	4.61	69.34	<i>0</i>	0.066	63.657	3.71	1.43	0	0	4.61	-
3. Sharks	0.056	0.4	3.077	<i>0.894</i>	0.13	2.215	3.92	0.32	0.243	0.114	0.043	0.61
4. Rays	0.012	0.724	4.137	<i>0.87</i>	0.175	2.792	4.06	0.297	0.394	0.235	0.094	0.54
5. European hake	0.052	1.18	4.12	<i>0.936</i>	0.286	2.322	4.19	0.102	0.678	0.427	0.075	0.57
6. Zoobenthivorous fish - hard bottom	0.19	1.9	6.408	<i>1</i>	0.296	2.586	3.43	0.162	0.098	1.802	0	0.052
7. Zoobenthivorous fish - soft bottom	0.84	1.18	6.306	<i>1</i>	0.187	3.234	3.65	0.174	0.404	0.775	0.001	0.34
8. Mackerel	0.998	0.62	6.506	<i>0.265</i>	0.095	4.91	3.79	0.235	0.039	0.125	0.456	0.063
9. Horse mackerel	0.96	0.57	5.941	<i>0.593</i>	0.096	4.48	3.82	0.272	0.118	0.219	0.232	0.21
10. Other small pelagics	0.329	1.889	8.294	<i>0.851</i>	0.228	3.917	3.23	0.012	0.312	1.294	0.282	0.17
11. Anchovies	7.118	1.1	12.44	<i>0.909</i>	0.088	7.608	3.2	0.015	0.128	0.872	0.1	0.12
12. Sardines	4.71	0.87	8.709	<i>0.949</i>	0.1	5.226	3.12	0.102	0.329	0.497	0.044	0.38
13. Nectobenthic zooplanktivorous fish	0.4	1.18	6.442	<i>0.989</i>	0.183	3.974	3.4	0.126	0.372	0.796	0.013	0.32
14. Omnivorous fish	0.114	1.624	15.04	<i>0.996</i>	0.108	8.152	2.44	0.489	0.715	0.903	0.006	0.44
15. Benthic piscivorous fish	0.2	0.85	3.304	<i>0.972</i>	0.257	1.958	4.3	0.098	0.59	0.237	0.024	0.69
16. Flatfishes	0.14	1.3	6.975	<i>0.923</i>	0.186	3.583	3.48	0.132	0.726	0.474	0.1	0.56
17. Squids	0.05	3.506	26.967	<i>0.974</i>	0.13	14.023	4.25	0.098	1.101	2.316	0.089	0.31
18. Benthic cephalopods	0.1	3.3	6.6	<i>0.992</i>	0.5	2.409	3.87	0.264	1.883	1.39	0.027	0.57
19. Crustacea 1	5.384	2.894	17.785	<i>0.957</i>	0.163	5.998	2.67	0.467	0.084	2.686	0.124	0.029
20. Crustacea 2	1.01	7.908	51.181	<i>0.997</i>	0.155	29.198	2.31	0.244	0	7.885	0.023	-
21. Mantis shrimp	0.08	1.5	4.56	<i>0.896</i>	0.329	1.692	3.46	0.102	1.292	0.052	0.156	0.86
22. Non commercial bivalves	24.9	1.415	6.35	<i>0.511</i>	0.223	0.808	2.29	0.223	0.002	0.721	0.692	0.0014
23. Commercial bivalves	<i>0.895</i>	1.415	6.35	0.9	0.223	0.808	2.29	0.223	0.669	0.605	0.142	0.47
24. Gastropods	<i>7.839</i>	1.735	9.716	0.9	0.179	2.151	2.28	0.255	0.041	1.52	0.174	0.024
25. Filter feeding invertebrates	7.652	0.761	3.804	<i>0.952</i>	0.2	1.331	2.5	0.251	0.043	0.682	0.036	0.057
26. Echinoderms	8.847	0.803	2.514	<i>0.428</i>	0.319	0.58	2.44	0.324	0.093	0.251	0.459	0.12
27. Polychaetes	26.989	1.644	14.27	<i>0.667</i>	0.115	4.777	2.16	0.145	0.001	1.096	0.548	0.00061
28. Jellyfish	1.02	14.813	44.439	<i>0.15</i>	0.333	20.738	3.01	0.285	0	2.222	12.591	-
29. Zooplankton	3.279	65	185	<i>0.917</i>	0.351	75.045	2.21	0.174	0	59.623	5.377	-
30. Pelagic bacteria	4.014	136	758	<i>0.413</i>	0.179	440.08	2	0	0	56.171	79.829	-
31. Macroalgae and phanerogams	<i>42.486</i>	1.699	-	0.2	-	-	1	0	0.023	0.316	1.359	0.014
32. Phytoplankton	13.2	175	-	<i>0.402</i>	-	-	1	0	0	70.337	104.663	-
33. Discard	0.058	-	-	<i>0.953</i>	-	-	1	0	-	-	-	-
34. Detritus	361.93	-	-	<i>0.999</i>	-	-	1	0.359	-	-	-	-



## 3.4 Description of the groups

### 3.4.1 Detritus groups

There are two detritus groups, representing the abiotic bioavailable pools in the ecosystem. Detritus corresponds to dead particulate organic matter in the water column, adsorbed to sediments or in the interstitial water. Detritus biomass was calculated as the sum of particulate organic matter in water and surface sediments, subtracting biomass of pelagic bacteria and phytoplankton. Consequently it comprises the biomass of sediment bacteria. Discard group represents dead or damaged organisms discarded into the sea by fisheries.

### 3.4.2 Lower part of the trophic network: primary producers and plankton

Microbial loop (Azam et al., 1983) is often poorly considered by Ecopath modellers, due to difficulties in parameter estimates (Christensen et al., 2005) and a fishery oriented approach. However, given the recognized importance of microbial loop in planktonic energy pathways of the Northern Adriatic Sea (e.g. Fonda Umani and Beran, 2003), pelagic bacteria, phytoplankton and zooplankton (micro and meso) were included in separated groups and, since there was not enough data to construct a HNAN (heterotrophic nanoflagellates) group, zooplankton diet was consequently corrected to simulate the not negligible HNAN's bacterivory (Fonda Umani et al., 2003). A group of jellyfish was included, since the Northern Adriatic has been characterized by intense outbreaks of species like *Pelagia noctiluca* and *Aurelia aurita*, whose causes are still unclear (Benovic and Lucic, 2001; Malej, 2001). In addition, jellyfish are recognized to have a potentially important trophic role (Regner, 1996). Given that reliable data about 1990s was lacking, a low biomass value from a 1984 survey was used in order to avoid overestimation of their predation on zooplankton.

Besides phytoplankton, primary producers in the model comprise a group of macroalgae and phanerogams. The real extent of the vegetated bottom in the Northern Adriatic Sea is highly uncertain and thus a low ecotrophic efficiency was given as input (Christensen et al., 2005, p. 56) instead of biomass.

### 3.4.3 Invertebrates

Invertebrates were mainly sorted according to taxonomy (e.g. echinoderms, polychaetes) and data availability. The "Crustacea 1" group represents macro-crustaceans, including some commercial species like Norway lobster, while "Crustacea 2" group comprises amphipods, isopods and benthic copepods. Two commercially important groups were included (mantis shrimp and commercial bivalves) and cephalopods were split into groups characterised by different habitats (benthic cephalopods and squids). Filter feeding invertebrates is a heterogeneous group including benthic

organisms like poriferans, bryozoans, cnidarians, ascidians and sipunculids, for which not enough data was found to construct separated groups.

#### 3.4.4 Fishes and top predators

The construction of fish groups followed a step-wise procedure, starting from the species list for the Adriatic (Riedl, 1991; Relini, 2006) and expert knowledge. A cluster analysis on diet composition based on the Bray Curtis index was applied in order to aggregate fish species into groups, except for flatfish, ray and shark groups, which were defined taxonomically. In some cases, results from cluster analysis were modified, changing the functional groups for some species on the basis of their commercial status and / or ecological habitat (Annex I).

Biomasses were taken from Medits trawl surveys (Bertrand et al., 2002) referred to the Northern Adriatic Sea, stock assessment (Cingolani et al., 2004a, 2004b; Santojanni et al., 2003; Santojanni et al., 2005), acoustic surveys (Azzali et al., 2002) and, for hard substrates, visual census (Orlando Bonaca and Lipej, 2005; Mazzoldi, unpublished data). Concerning pelagic species, acoustic surveys were used as initial inputs because stock assessments cover both the Central and the Northern Adriatic Sea, and stock assessment values defined the lower confidence interval during balancing.

Medits trawl surveys employ a bottom trawl net and take place every year at daytime during summer. They can underestimate the biomass of pelagic species or of species which are mainly caught during night like *Squilla mantis*, which lives in burrows during the day. Also migrating fishes (especially diadromous) could be underestimated, given the presence of lagoons and of the Po river delta.

In general, trawl surveys underestimate benthic and demersal biomasses, with estimates down to 50% (Sparre and Venema, 1998) or even much more (Fiorentini et al., 1999) of the real biomass. Moreover, the Medits data used, if unpublished, did not include the Croatian and Slovenian waters of the modelled area, which have higher densities for many demersal species. Thus, Medits biomasses (corrected where possible using the efficiencies in Fiorentini et al., 1999) were compared to the biomasses required to sustain the catches in the basin in order to have total or fishing mortalities ( $F$ ) in agreement with published values for the Northern Adriatic Sea, or at least with similar or close ecosystems. The required biomasses were thus back-calculated (e.g. as  $B = Y / F$ ) and they were, in some cases, more than ten times higher than Medits estimates. Such results are in agreement with what Sanchez and Olaso (2004) found by comparing trawl surveys and stock assessment for the Cantabrian Sea. Hence, to calculate fishing mortalities (see below), biomass data for demersal groups was increased accordingly. It was assumed that the biomass of species for which published mortalities were not available was underestimated in the same proportion of ecologically similar species or species from the same group. In some cases (e.g. rays) the biomass was simply increased of 100% following Sparre and

Venema (1998), thus fishing mortalities can be overestimated. The uncorrected biomass values are left as initial inputs (Annex I) to stress these assumptions but during balancing they were changed upwards.

For each species, diets and other parameters like Von Bertalanffy's  $k$ , asymptotic length, total weight, length-weight conversion parameters, etc., were derived from literature. Published, quantitative (for diets) data referred specifically to the study area and the modelled period was given the preference. When data was lacking, values for similar species, qualitative data and expert knowledge (for diets) were used. When information about the Northern Adriatic Sea was absent, data for similar or close ecosystems was chosen. If no information was available on the main preys of piscivorous species, the percentage of preyed fish was sorted among all the fish species with mean length lower than the one of the predator (the bigger ones eat the smaller ones in the ocean), proportionally to their biomass. Then results were corrected by resorting to personal knowledge about feeding habits of that species. A similar procedure was employed to calculate the percentage of predation on macro-crustaceans specifically made upon mantis shrimp.

Production rates (i.e. total mortalities) were taken from published values for the Northern Adriatic Sea or calculated as the sum of fishing and natural mortality ( $Z = F + M$ ). Fishing mortalities were taken from literature (e.g. stock assessment) or calculated as  $F = Y / B$ . Natural mortalities (i.e. the sum of predation mortality  $M_2$  and "other" mortality  $M_0$  due to illness and old age) were taken from published values for the ecosystem or from empirical equations (e.g. Pauly, 1980; Brey, 1999). In few cases,  $P/B$  was calculated by roughly using the gross efficiency value ( $GE = P / Q$ ) of similar species or taken from the middle of the 0.1-0.3 acceptable range (Christensen et al., 2005). Individual consumption rates were mainly calculated using empirical equations (e.g. eq. 17 and eq. 19 in Christensen et al., 2005).

Finally, the diet for every single fish group was calculated as the average of the diets of the species composing it, each weighted on the product of the species biomass and consumption rate, while production and consumption rates were calculated as the average values for the composing species weighted on their biomass.

A group of seabirds partially feeding on discard and a dolphin group were included in the model.

### **3.5 Fisheries and catch data**

The fishing activities in the modelled area were represented using six fleets sorted by gear and nationality: five Italian fleets (hydraulic dredges, mid-water trawlers, bottom trawlers, beam trawlers, other fisheries including artisanal fisheries) and one aggregated Croatian-Slovenian fleet. The major

focus was on Italian fleets because they are responsible of the larger catches and more data is available. Landing and discard data is reported in Table 3. Italian commercial landings were taken from the Italian Institute of Statistics (ISTAT 1998, 2000a, 2000b) for Veneto, Friuli Venezia Giulia and Emilia Romagna regions, and combined with unpublished data from the Chioggia fish market, which is the major one in the Northern Adriatic Sea, and sorted among fleets following the procedure on Section 3.5.1. Landings for Croatia and Slovenia come from FAO-GFCM statistics (FAO, 2007) and, based on fishing harbour and effort distribution, only one third of Croatian catches was assumed to occur inside the modelled area. Unreported landings for all fisheries were estimated to be 40% of official landings for both Italian and Croatian-Slovenian fleets, based on estimates obtained from employees of fish markets.

The discard was estimated using direct measures made during 16 cruises on mid-water trawl, bottom-trawl and beam-trawl commercial fishing boats from Chioggia, the biggest Northern Adriatic fishing harbour, from autumn 2006 to summer 2007 (Duci, 2007). Discard quantities were extrapolated to 1996-1998, corrected to account for effective mortality rates and integrated with other sources (see Section 3.5.2).

#### 3.5.1 Sorting of landings among fleets

Italian landings were sorted among fleets using the percentages of landings pertaining to different gears reported for 2004 by Osservatorio Socio Economico della Pesca dell'Alto Adriatico (2005). Those percentages were corrected according to Visentin (2007) for sharks and rays and by considering the relative variation of fishing effort from 2004 to 1996-1998 taken from the IREPA onlus database ([www.irepa.org](http://www.irepa.org)). The uncorrected percentage of landings of species  $j$  coming from fleet  $i$  were corrected first by multiplying the landings from the different fleets for species  $j$  by the proper 1996-1998/2004 effort ratios (i.e. for the proper fleets), and then by forcing them to sum to the total landings of species  $j$  for 1996-1998 while keeping their new relative abundance. It must be noted that this last correction could be biased by the assumption of constant catchability. Finally, the percentages were corrected by resorting to expert knowledge.

#### 3.5.2 Discard and by-catch

Some preliminary measures of the effective mortality rates of discarded organisms were performed in laboratory. Field mortality rates were guessed to be higher than in the laboratory and were corrected consequently: assumed mortality rate ranges from 25% to 100% for invertebrates and is 100% for fishes.

The measured discard by gear  $i$  for species/group  $j$  was multiplied by the proper mortality rate and then expressed as percentage (averaged over the different seasons) of the commercial landings by

gear  $i$ . The result was then extrapolated to the whole fleet  $i$  and referred to 1996-1998 by multiplying that percentage by the 1996-1998 total commercial landings by fleet  $i$ . When data was available, a last correction was performed by multiplying the resulting amount of discard by fleet  $i$  for species  $j$  by the relative biomass variation from 2006 to 1996-1998 of species/group  $j$ , and then dividing it by the sum of the relative biomass variations from 2006 to 1996-1998, weighted on their respective 2006 landings from fleet  $i$ , of the groups making up the commercial landings for fleet  $i$ . This was made to take into account that discard was not measured in 1996-1998 but in 2006-2007. Note that corrections are based on 2006 data since 2007 data was not available. Again, results could be biased by changes in catchability for the considered fleet. The relative biomass variations were computed from unpublished Medits trawl surveys data, acoustic surveys (e.g. Azzali et al., 2002), stock assessment (Cingolani et al., 2004a and 2004b) and catch per unit effort data (computed from several sources, e.g. ISTAT landings and IREPA fishing effort, unpublished sources, etc.). 2006 landings for groups/species  $j$  from fleet  $i$  were calculated in the same way as the 1996-1998 ones above, using effort and landings data for year 2006 instead of 1996-1998 taken from FAO, ISTAT, Chioggia market and IREPA (also for landings) data.

Table 3. Landings and discard, sorted by fisheries: one Slovenian-Croatian fleet and five Italian fleets divided by gear: hydraulic dredge, mid-water trawling (“volante”), bottom trawling (“coccia”), beam trawling (“rapido”), other fisheries.

Group Name	Landings (t km <sup>-2</sup> y <sup>-1</sup> )						Sum
	Hydraulic dredges	Other and artisanal fisheries	Beam trawling	Bottom trawling	Mid water trawling	SLO-CRO fisheries	
Sharks		0.00164	0.00296	0.00165	0.00419	0.00319	0.0136
Rays		0.000263	0.00129	0.000941	0.000232	0.002	0.00473
European hake		0.000108		0.0192	0.00106	0.0149	0.0353
Zoobenthivorous fish - hard bottom		0.00551	0.00054	0.0032	0.000146	0.00677	0.0162
Zoobenthivorous fish - soft bottom		0.0691	0.0108	0.0833	0.00292	0.00114	0.167
Mackerel		0.00447		0.00594	0.0158	0.0117	0.0379
Horse mackerel		0.00399		0.0053	0.0141	0.00471	0.0281
Other small pelagics		0.000125		0.000422	0.0174	0.00344	0.0214
Anchovies		0.00487		0.0165	0.679	0.0102	0.711
Sardines		0.00538		0.0182	0.751	0.224	0.999
Nectobenthic zooplanktivorous fish		0.0115		0.0249	0.0202	0.0163	0.0729
Omnivorous fish		0.0598		0.00492	0.0101	0.00492	0.0797
Benthic piscivorous fish		0.00207	0.000668	0.00782	0.000182	0.0082	0.0189
Flatfishes		0.00526	0.0316	0.0146		0.00231	0.0538
Squids		0.00375		0.0319	0.00198	0.00648	0.0441
Benthic cephalopods		0.0957	0.0112	0.0548	0.0032	0.0126	0.178
Crustacea 1		0.0234	0.00734	0.0277	0.000644	0.00895	0.0680
Mantis shrimp		0.0239	0.0295	0.0411	0.00115		0.0957
Commercial bivalves	0.241		0.249	0.0622		0.000577	0.553
Gastropods	0.000539	0.0141	0.000362			0.000531	0.0155
Filter feeding invertebrates						0.0000852	0.0000852
Sum	0.242	0.335	0.345	0.425	1.523	0.343	3.213

Group Name	Discard (t km <sup>-2</sup> y <sup>-1</sup> )						Sum
	Hydraulic dredges	Other and artisanal fisheries	Beam trawling	Bottom trawling	Mid water trawling	SLO CRO fisheries	
Dolphins		0.0000134		0.00000168	0.00000168	0.0000774	0.0000942
Zoobenthivorous fish - hard bottom		0.000789		0.00159		0.000064	0.00244
Zoobenthivorous fish - soft bottom	0.0000061	0.052300	0.016700	0.0989	0.000077	0.0045	0.172
Mackerel		0.00016		0.000208	0.000721	0.0000453	0.00113
Horse mackerel		0.0222	0.0000408	0.0415	0.0192	0.00266	0.0856
Other small pelagics		0.00573		0.0000833	0.0719	0.00369	0.0814
Anchovies		0.0595	0.0000391	0.117	0.0171	0.00614	0.200
Sardines		0.164	0.000108	0.322	0.047	0.0169	0.550
Nectobenthic zooplanktivorous fish		0.0219	0.0105	0.0398	0.00154	0.002	0.0757
Omnivorous fish		0.00056		0.00113		0.0000454	0.00174
Benthic piscivorous fish		0.0311	0.00429	0.061		0.00259	0.0990
Flatfishes		0.00837	0.0342	0.00407		0.00121	0.0479
Squids		0.0035	0.000183	0.00696	0.0000368	0.000288	0.0110
Benthic cephalopods		0.0027	0.00393	0.00396		0.00028	0.0109
Crustacea 1	0.0135	0.0648	0.27	0.0262	0.0000263	0.0094	0.384
Crustacea 2		0.00000549	0.00000183		0.00000266	0.000000192	0.00000523
Mantis shrimp		0.002	0.00229	0.00317		0.000198	0.00766
Non commercial bivalves	0.0045	0.00958	0.0435	0.000442		0.00142	0.0594
Commercial bivalves	0.0142	0.00975	0.016	0.00545		0.000936	0.0463
Gastropods	0.00498	0.0514	0.23	0.0146	0.000000919	0.0077	0.309
Filter feeding invertebrates	0.000017	0.0925	0.0608	0.163	0.000343	0.00845	0.325
Echinoderms	0.000937	0.173	0.442	0.182	0.0000991	0.0209	0.819
Polychaetes	0.0000107	0.0024	0.0118	0.00043		0.000378	0.0150
Jellyfish		0.000018		0.0000357	0.00000328	0.00000161	0.0000586
Macroalgae and phanerogams		0.152	0.812	0.00337	0.00000271	0.0249	0.992
Sum	0.0382	0.930	1.958	1.097	0.158	0.115	4.297
Commercial/Discard ratio	6.33	0.36	0.18	0.39	9.64	2.99	0.75

Other sources were also used to integrate the data, including Giovanardi and Andaloro (1997), Pranovi et al. (2001), Morello et al. (2005) and Santojanni et al. (2005). Since there was not precise quantitative data available for dolphins, their by-catch was back-calculated as the product of fishing mortality and biomass  $Y = F \cdot B$ , with  $F = 0.015 \text{ y}^{-1}$  from Fortuna (2006). The by-catch was sorted among different gears following qualitative considerations (Bearzi and Fortuna, 2006; Bearzi, 2002), accounting for the potential hostility of fishermen towards dolphins depredating them (Bearzi et al., 2004) and weighting the higher density of dolphins in the Croatian area. Consequently Slovenian-Croatian by-catch was calculated as the product of fishing mortality and absolute dolphin biomass in Croatia and then divided by the model total surface, and the same was for the Italian catch.

## 3.6 Model balancing

To detect any internal inconsistency, input data was compared with a broad set of criteria summarized in this section. Given that the initial data yielded an unbalanced model not satisfying those constraints (e.g. mass balance), the inputs were varied using a search and try procedure until a physically, physiologically and ecologically sound model was obtained (Table 1 and 2). The balancing procedure followed a top down approach (top predator compartments were balanced first) and more uncertain data (e.g. diets and biomasses) was varied first within assumed uncertainty ranges. A manual adjustment was preferred to automatic routines (e.g. Kavanagh et al., 2004), since the balancing procedure itself can give a better understanding of the structure of the network (e.g. which parameters the balancing is sensitive to, which groups are constraining the ecosystem by their consumption).

The balancing of the model is achieved when all ecotrophic efficiencies are lower than one and all respirations are positive, otherwise mass is not conserved and the model is not physically making sense. Also, the balanced model should make physiological sense, i.e. gross efficiency ratios ( $GE = P / Q$ ) must be acceptable ( $GE$  varies among about 0.1 and 0.3 with some exceptions, Christensen et al., 2005, p. 49) and  $R / B$  ratios must be higher for smaller organisms and within literature ranges (e.g. 50–100 year<sup>-1</sup> for copepods, Christensen et al., 2005, p. 51). In addition to the above criteria, tests resembling a calibration were applied to the outputs calculated by Ecopath, e.g. comparing fractional trophic levels with literature values based on stable isotopes analysis (Dame and Christian, 2008), checking if the partition of total mortality among different sources for a group is acceptable (e.g. fishing mortalities in agreement with stock assessments, natural mortalities in agreement with empirical relationships), checking if ecotrophic efficiencies have reasonable values (e.g. Opitz, 1993, suggests  $EE < 0.7$  for phytoplankton; values are commonly higher for intensively preyed or fished groups, which do not die of old age, Christensen et al., 2005). The main changes made to initial inputs during balancing are described in the next section.

### 3.6.1 Main changes to input data during balancing

Biomasses of pelagic groups derived from acoustic surveys were changed to the lower value of their confidence range ( $\pm 20\text{-}30\%$ , Azzali et al., 2002), yielding estimates of biomass and fishing mortalities more in agreement with stock assessment and literature (Cingolani 2004a, 2004b; Sinovic, 2001a). Also, with those high biomasses, the predation exerted by mackerels and horse mackerels appeared far too high and could have been balanced only by an unrealistic increase in the biomass or production of their preys. The final results are a compromise, so some fishing mortalities appear still low. Differences between acoustic surveys and VPA estimates could be due, to some extent, also to real geographic differences as stock assessment includes larger, less productive areas.

Biomasses of demersal species derived from Medits surveys were increased as described on Section 3.4.4, while trying to keep the relative biomass proportion among demersal groups. Mantis shrimp biomass was strongly underestimated because of its night-time activity. For the other groups, the increases were from 1.8 to 9 times the original biomass values, except for flatfish (18 times) and benthic piscivorous fishes (47 times). For the former, the cause could be the behaviour of some flatfish living during part of the year in the lagoons, near the coast and in the Po delta (Tortonese, 1975). For the latter, the reason could be the higher density of benthic piscivorous fish in the Croatian area, not covered by surveys, and to the rocky habitats preferred by some of the species, that hence are less easily detected by the bottom trawl. Finally, some landing statistics are aggregated and could contain landings for species not included in the surveys and, also, biomass for some species included in the model could not be achieved from the surveys. Hence, again, the initial input biomasses can be underestimated absolutely and with respect to catches.

Total mortalities for exploited groups were changed both to achieve balancing and to try to yield realistic natural mortalities (e.g. previously taken from literature or calculated following Pauly (1980) and Brey (1999) for single fish species, and then weighted on their biomasses to yield the natural mortality of the whole group). Changes were minor except for a 25% increase of flatfish total mortality and a 114% increase in the fishing mortality of Zoobenthivorous fish – hard bottom, the latter possibly explained by a FAO statistics underestimation of the landings in the rocky Croatian area.

The most adjusted diets were, in general, those of groups with high predation impact (e.g. mackerels, horse mackerels, benthic piscivorous fishes). Since the ecotrophic efficiency of sardines was about 1.2 during the balancing and that of anchovies was about 0.7 and they have similar trophic roles, the predation of mackerels, horse mackerels and squids was directed on the latter, which were particularly abundant in the modelled period, until balancing was achieved.

Parameters for planktonic groups were slightly changed within confidence intervals to balance the detritus box. However it cannot be excluded that the needed flows to detritus are brought by external inputs, like the Po river inflow, that are not considered in the model. Zooplankton production was lowered since it was probably underestimated and with the goal of obtaining a more realistic  $R / B$  ratio.

The ecotrophic efficiency of macroalgae and phanerogams was increased to 0.2 because the initial value would have implied a disproportionately high biomass. Invertebrate parameters underwent minor changes compared to fish, stressing the lower predatory and fishing constraints imposed on those groups, which generally have lower ecotrophic efficiencies.

### 3.7 Analyses performed

Indices based on flows and biomasses, or both, were given by Ecopath or calculated. Analyzed flows include primary production, total productions, consumptions, respirations, catches, etc. and the total system throughput (TST), calculated as the sum of all the flows in the modelled network (Ulanowicz, 1986). Total primary production:total biomass ratio and the gross efficiency of fishery (catches:total primary production ratio) were calculated to analyze respectively the productive and developmental stage of the ecosystem, and exploitation. Finn's cycling index (FCI, Finn, 1976) represents the percentage of flows recycled in the food web. The percentage of recycling after the removal of detritus groups is called predatory cycling index (PCI, Christensen et al., 2005). Finn's mean path length, representing the mean number of nodes that energy inflow into the ecosystem passes through before exiting the network, was calculated as an indicator of ecosystem maturity (Christensen et al., 2005).

The trophic level for a group  $j$  is calculated from its diet as the weighted average of the trophic levels of its preys (Christensen et al., 2005):

$$TL_j = 1 + \sum_{i=1}^N DC_{ij} TL_i \quad (3)$$

assigning TL one to primary producers and detritus. The trophic specialization of a predator  $j$  was analysed using the omnivory index (Christensen et al., 2005):

$$OI_j = \sum_{i=1}^N (TL_i - (TL_j - 1))^2 \cdot DC_{ij} \quad (4)$$

The system omnivory index was calculated as the average of the OI of the predator groups, weighted on the logarithm of their absolute consumption, to analyse if the network is chain-like or web-like (Christensen, 1995; Christensen et al., 2005).

In addition, the food web was aggregated into discrete trophic levels sensu Lindeman (1942) using the trophic aggregation routine of Ecopath (Christensen et al., 2005). In the resulting linear food chain (the Lindeman spine), the efficiency of energy transfers (TE) among two contiguous trophic levels was calculated according to Christensen et al. (2005) as the fraction of the flows leaving the lower trophic level that are preyed upon at the next higher trophic level or exported (i.e. harvested). The global transfer efficiency of the spine was calculated as the geometric mean of transfer efficiencies for TL 2-4. The flows originating from detritus were also computed separately from those originating from primary producers.

Mixed trophic impact (MTI) routine (Ulanowicz and Puccia, 1990) was applied to evaluate the propagation of predation and fishing effects throughout the food web. The net direct impact of a group  $j$  on another group  $i$  is written as the difference of the positive impact that  $j$  has on  $i$  (i.e.  $DC_{ji}$ ) and the

negative impact that  $j$  has on  $i$  (i.e. the fraction  $f_{ji}$  of predation mortality of  $i$  that is due to  $j$ ), i.e.  $MTI_{ji} = DC_{ji} - f_{ji}$ . Fisheries are treated as predators. Following from additional assumptions, for each couple of groups / fleets the sum  $m_{ji}$  of direct and indirect impacts that one has on the other can be derived, to identify trophic cascade-like situations and non-intuitive indirect effects. MTI can also work as a sensitivity analysis to discover which groups would be mostly influenced by a change of biomass of a given group.

The “keystoneness” index (KS, Libralato et al., 2006) identifying keystones, i.e. groups having a disproportionately high overall effect on the other groups of the system with respect to their biomass, was calculated as  $KS_j = \log[\varepsilon_j(1 - p_j)]$ .  $p_j$  is the fraction of the living biomass in the system comprised by group  $j$  and  $\varepsilon_j$  is the overall impact of group  $j$  on the other living groups in the food web (but not on itself), i.e.  $\varepsilon_j = \sqrt{\sum_{i \neq j} m_{ji}^2}$ , where the sum is on all the groups (excluding detritus) and not on fleets. The terms  $\varepsilon_j$  were also analysed separately to identify the overall most impacting groups on the other living groups of the network.

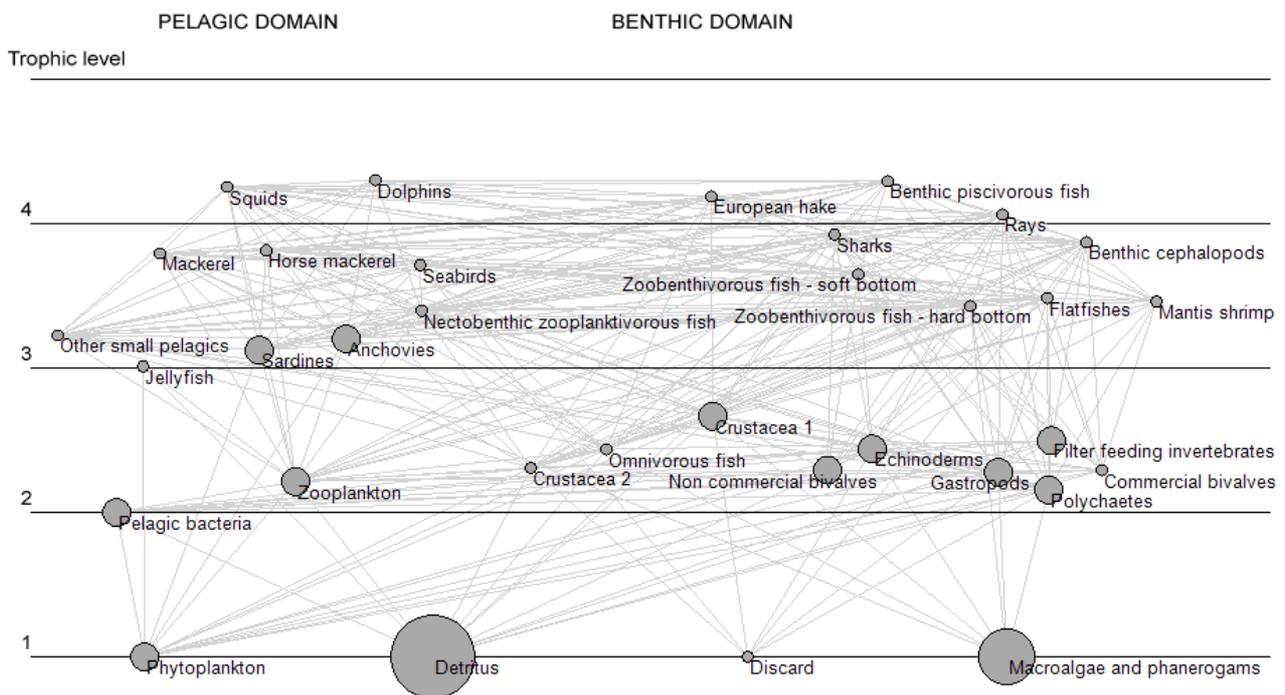


Figure 4. Northern Adriatic Sea food web. Trophic connections between groups are shown, while circles are proportional to the order of magnitude of their biomass. Figure created with Ecopath 6 ([www.ecopath.org](http://www.ecopath.org)).

The primary production required (PPR) to sustain the catches of a group was calculated according to Christensen et al. (2005, pp. 65-67) as equivalent flows from both primary producers and detritus, to evaluate the sustainability of fisheries (Pauly and Christensen, 1995).

Information-theory indicators have been calculated. Ascendency (Ulanowicz, 1986) is the product of total system throughput and network average mutual information, and it should have the propensity to increase with maturity. The upper theoretical bound to ascendency is named development capacity, and the difference between it and ascendency, named overhead, represents the strength in reserve of the ecosystem to respond to perturbations. Internal flow overhead (also called redundancy) has been identified as an indicator of stability and resilience (Ulanowicz, 1986, 2004; Heymans et al., 2007).

### 3.8 Network analysis results

The pedigree index (Christensen et al., 2005) of the model is 0.561 ( $N = 32$ , measure of fit = 3.71) ranging within the highest values reported in the literature (from 0.164 to 0.676, Coll et al., 2007).

#### 3.8.1 Trophic network structure and flow analyses

##### *Trophic levels*

Trophic levels in the system range from 1.0 to 4.3 (Table 1 and Figure 4). The top predators (dolphins, benthic piscivorous fish, squid, European hake and rays) are assigned to  $TL > 4.0$ . All other fish groups (except omnivorous fish), birds, benthic cephalopods, mantis shrimps and jellyfish are placed in  $TL > 3.0$ .

The analysis of the variance of diets through the omnivory index reveals that the more specialised groups (i.e. preying on a narrow range of trophic levels) are pelagics such as zooplanktivorous fishes and squids, and predators such as dolphins, European hake and benthic piscivorous fish. Among invertebrates, different degrees of omnivory are found, ranging from specialised feeders such as polychaetes (mainly detritivorous) to echinoderms, whose high OI reflects the heterogeneity of the species composing the group. The most omnivorous groups are Crustacea 1 (macro-crustaceans) and omnivorous fishes.

##### *Ecotrophic efficiencies*

*EE* values range from 0 for seabirds, to 1 for zoobenthivorous fish living on hard and on soft bottom. *EE* values are close to one for most fish groups (Table 1), as they are caught or preyed before

dying of old age, with the exception of mackerels and horse mackerels, which are abundant and scarcely preyed or exploited. Elasmobranchii present *EE* slightly lower than fish average, indicating that they are apex predators, not much preyed within the ecosystem.

Some benthos and plankton groups have markedly lower *EE*'s: non commercial bivalves, echinoderms, polychaetes, jellyfish, pelagic bacteria and phytoplankton.

### *Lindeman spine and efficiency of energy transfers*

The aggregation of flows into discrete trophic levels highlights the importance of TL 2 in the ecosystem. About 40% of the total system throughput of the model is flowing out from it and it contains 41% of the living biomass of the ecosystem (Figure 5). Also, flows to detritus mainly originate from TL 1 and 2.

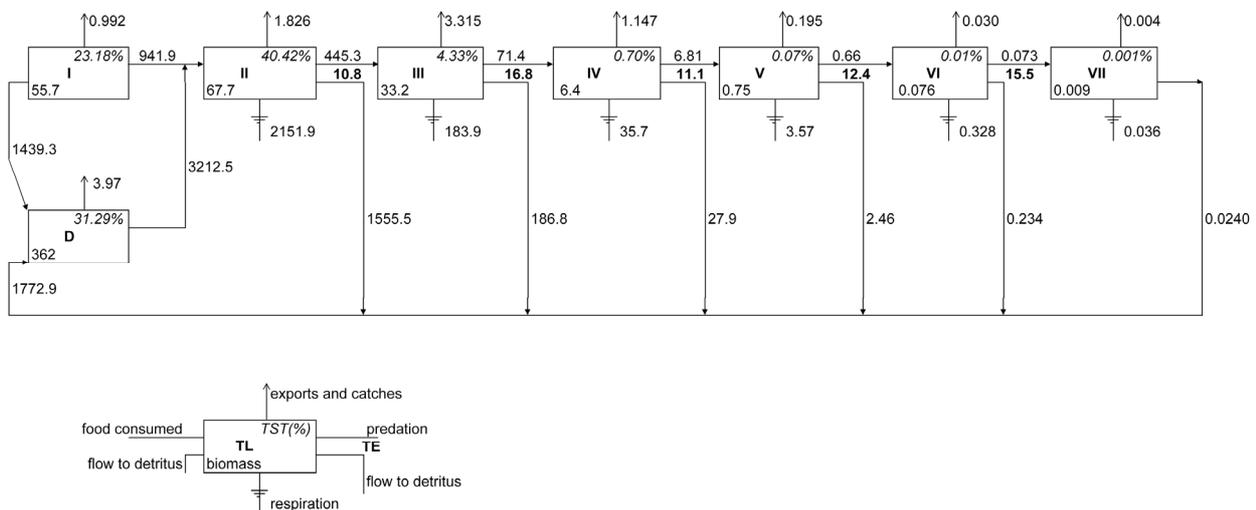


Figure 5. Lindeman spine aggregation of flows and biomasses in the ecosystem. D represents detritus. TST(%) represents the percentage of TST flowing through the trophic level. Trophic levels higher than TL 7 are not considered because of their negligible overall contribution.

The transfer efficiency of energy from TL 2 is lower than the mean value for the ecosystem (Table 4) because flows from TL 2 are mainly respiration and backflows to detritus.

If the flows originating from primary producers and detritus are considered separately, the inefficiency of energy transmission from TL 2 is found only in the detritus chain (TE = 8.8), while in the grazing chain the transfer efficiency from TL 2 is about the double (TE = 17.4).

Globally, the ecosystem has a transfer efficiency of 12.6%, close to the 10% value usually found in marine ecosystems (Pauly and Christensen, 1995). The primary producer-based chain is more efficient than the detritus-based one (Table 4). Flows based on detritus are 66% of the total. The exports (i.e. catches) are mainly concentrated on TL 2 and 3, and the high transfer efficiency from TL 3

underlines the exploitation of that trophic level (Figure 5). From TL 4 upwards transfer efficiencies are increasing, both for primary producer-based and detritus-based energy chains (Table 4).

Table 4. Transfer efficiencies among discrete trophic levels, in the energy chains based on primary production, detritus and both.

Energy source \ from TL	II	III	IV	V	VI	VII	VIII	IX	X
Primary producers	17.4	12.7	10.2	12.6	15.3	16.5	17.1		
Detritus	8.8	19.1	11.5	12.3	15.5	16.6	17.0		
All flows	10.8	16.8	11.1	12.4	15.5	16.6	17.0	18.0	22.9
Transfer efficiencies (calculated as geometric mean for TL II-IV)									
From primary producers:	13.1%								
From detritus:	12.4%								
Total:	12.6%								

#### *Analysis of biomasses, flows and catches*

Biomasses are concentrated in the lower trophic levels (Figure 5), particularly in the benthic compartment (benthos, macroalgae and phanerogams), in the plankton groups and in sardines and anchovies (Table 1).

The total system throughput is mainly composed of consumption (45%), flows to detritus (31%) and respiratory flows (23%), while the sum of exports and catches represents only 0.11% (Table 5) of TST. The production (Figure 6a) is dominated by the pelagic compartment, plankton in particular, followed very far by benthic invertebrates and macroalgae and phanerogams. Among fish, the pelagic production is about 5.6 times the demersal one. Consumption, too, is dominated by the pelagic groups (Figure 6b), but zooplanktivorous fishes are more important, with sardines and anchovies making together 2.8% of the whole consumption flows. Landings reflects the network structure (Figure 5 and 7, Table 3) since they are dominated by species at low trophic levels, e.g. bivalves, sardines and anchovies. The mean trophic level of the catch is 2.71, lower than the value (3.07) reported by Coll et al. (2007) for Northern and Central Adriatic Sea, and the mean trophic level of commercial landings is 3.11 (Table 5).

The ratio landing / discard is 0.75 on the average, widely varying (Table 3) from about 10 in the efficient mid-water trawl fleet to 0.2 in the beam trawl fleet. Discard makes up 57% of the total catches.

#### *Flow-based and biomass-based indicators*

System statistics are reported in Table 5. The total primary production:total biomass (excluding detritus groups) ratio is comparable to productive ecosystems like the Northern Benguela during 1990s (which yielded  $16.2 \text{ y}^{-1}$ , Heymans et al., 2004) and thus seems quite high, reflecting the eutrophicated state of the ecosystem. However this indicator could depend on the choice of the groups included in the model.

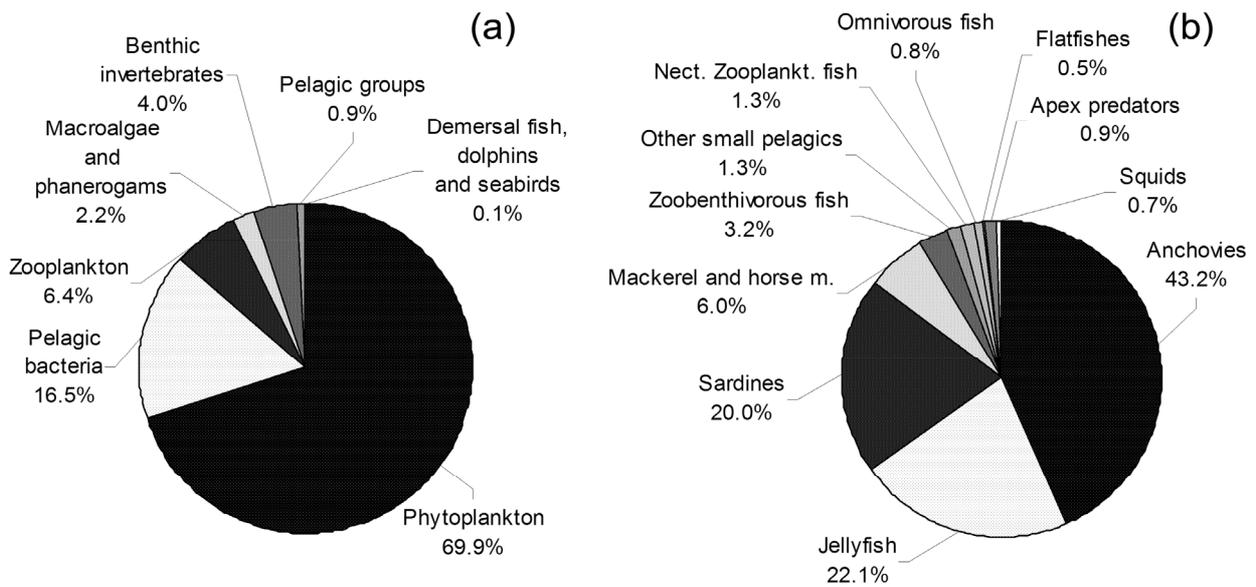


Figure 6. (a) Total production in the ecosystem. Pelagic groups include anchovies, sardines, other small pelagics, mackerels, horse mackerels, squids and jellyfish. (b) Consumption flows excluding benthos and plankton. Apex predators include sharks, rays, benthic piscivorous fish, hakes, dolphins and seabirds.

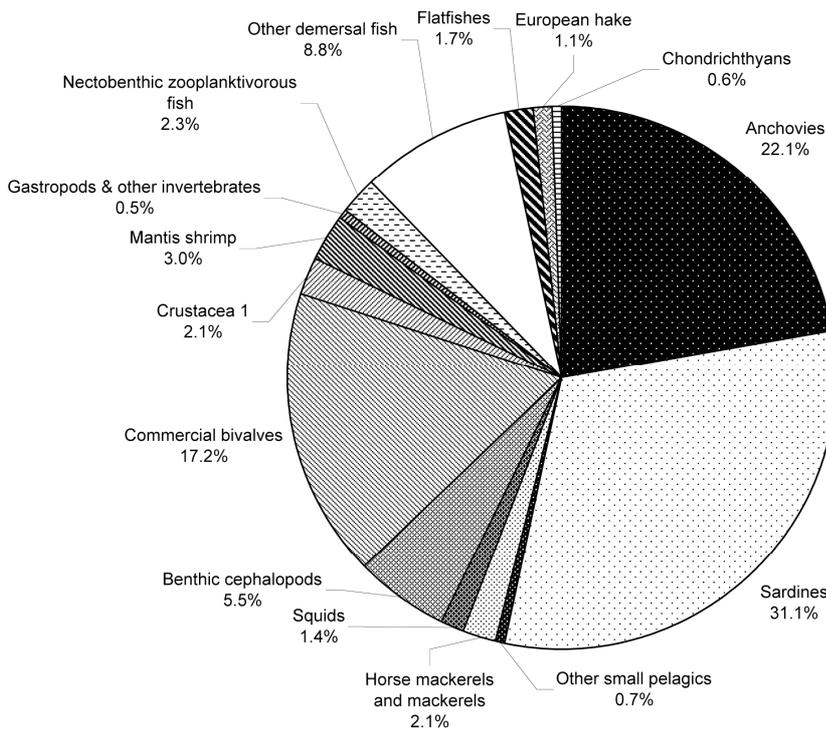


Figure 7. Representation of landings. They are dominated by low trophic level groups like small pelagics and bivalves.

Table 5. Main system statistics. See Christensen et al. (2005) for details.

Sum of all consumption	4 679.012	t km <sup>-2</sup> year <sup>-1</sup>				
Sum of all exports	11.477	t km <sup>-2</sup> year <sup>-1</sup>				
Sum of all respiratory flows	2 375.427	t km <sup>-2</sup> year <sup>-1</sup>				
Sum of all flows into detritus	3 216.658	t km <sup>-2</sup> year <sup>-1</sup>				
Total system throughput	10 283	t km <sup>-2</sup> year <sup>-1</sup>				
Sum of all production	3 303	t km <sup>-2</sup> year <sup>-1</sup>				
Mean trophic level of the catch	2.71					
Mean trophic level of the landings	3.11					
Mean trophic level of the discards	2.41					
Gross efficiency of fishery (catch / total primary production)	0.003152					
Calculated total primary production	2 382.184	t km <sup>-2</sup> year <sup>-1</sup>				
Total primary production / total respiration	1.003					
Net system production (total p.p. - total respiration)	6.757	t km <sup>-2</sup> year <sup>-1</sup>				
Total primary production / total biomass (excluding detritus)	14.536	year <sup>-1</sup>				
Total biomass / total throughput	0.016	year				
Total biomass (excluding detritus)	163.88	t km <sup>-2</sup>				
Total catches	7.509	t km <sup>-2</sup> year <sup>-1</sup>				
Connectance Index	0.348					
System Omnivory Index	0.216					
Throughput cycled (excluding detritus)	43.71	t km <sup>-2</sup> year <sup>-1</sup>				
Predatory cycling index	1.14	% of throughput without detritus				
Throughput cycled (including detritus)	2 554.06	t km <sup>-2</sup> year <sup>-1</sup>				
Finn's cycling index	24.85	% of total throughput				
Finn's mean path length	4.306					
Finn's straight-through path length	1.597	without detritus				
Finn's straight-through path length	3.236	with detritus				
PPR to sustain catches, total	314.83	t km <sup>-2</sup> year <sup>-1</sup>				
PPR to sustain catches, total	5.62%	% of detritus and p.p. production				
PPR to sustain catches, coming from p.p.	86.65	t km <sup>-2</sup> year <sup>-1</sup>				
PPR to sustain catches, coming from detritus	228.18	t km <sup>-2</sup> year <sup>-1</sup>				
source / currency	Ascendency (flowbits)	Ascendency (%)	Overhead (flowbits)	Overhead (%)	Capacity (flowbits)	Capacity (%)
Import	5.8	0	0.3	0	6.2	0
Internal flow	7 073.2	17.6	24 262.8	60.4	31 336.1	78
Export	30.8	0.1	107	0.3	151	0.4
Respiration	2 818.7	7	5 878.9	14.6	8 697.6	21.6
Total	9 928.6	24.7	30 249	75.3	40 190.8	100

The total primary production:total respiration ratio is about one. However, excluding the high bacterial flows which overshadow all other energy transfers (i.e. deleting the bacterial group, transforming the feeding on bacteria into imports and forcing an export of phytoplankton equivalent to its former bacterial consumption) a ratio of 3.912 is found. The system omnivory index is markedly reduced in the bacteria-free network (from 0.216 to 0.171) and the moderately low value, compared for example to a broad range of 55 ecosystems (oceanic, tropical, shelves, upwelling, estuaries, etc.) described on Chapter 7, suggests a linear more than web-like network.

### *Cycle analysis*

The percentage of recycled ecosystem flows is much lower if cycles through detritus are excluded from the computation ( $PCI \ll FCI$ , Table 5), decreasing from 24.85% to 1.14% of total system throughput. Ecosystem flows are thus based on intense detritus recycling. Excluding bacteria, results radically change, as FCI becomes 7.43% of TST and PCI becomes 2.10% of TST. The change of FCI shows that much of the recycling in the ecosystem is driven by the microbial loop, even if it remains constrained to low trophic levels as bacteria are incompletely preyed ( $EE = 0.413$ ).

### 3.8.2 Mixed trophic impact and related indicators

MTI graphical representation (Figure 8) highlights that pelagic fish groups are very sensitive to zooplankton and, in a lower degree, to phytoplankton. An increase of these groups would positively impact anchovies, sardines, other small pelagics, mackerels, horse mackerels and nectobenthic zooplanktivorous fish, both directly and indirectly, and hence fisheries. Unlike other plankton groups, pelagic bacteria are markedly impacting only low trophic levels (i.e. detritus, phytoplankton, etc.). Phytoplankton influences also some benthic groups and the role of benthic primary producers is comparatively marginal in the system. Anchovies impact positively their predators, dolphins, European hakes and squids, while negatively, through competition, themselves and sardines. Crustacea 1 (macrocrustaceans) strongly impact both low trophic level benthos and high trophic level demersal fishes. Detritus appears to impact mostly benthos and demersal fish (flatfishes, omnivorous fish and, less markedly, elasmobranchii and zoobenthivorous fish) which would benefit from an increase of its biomass.

Some top down control is exerted by squids on mackerels and horse mackerels, by mackerels and horse mackerels on squids, anchovies and few other fish groups, by zoobenthivorous fish living on soft bottom on some fishes, especially demersal. However in general predators are not impacting other fish or invertebrate groups (Figure 8).

In the modelled period, commercial fleets would have benefited from an increase of zooplankton and phytoplankton. The pelagic production, favouring pelagic fish, sustains fisheries (Figure 8). Commercial fleet show some impacts on specific groups, i.e. beam trawling on flatfish, bottom trawling on benthic piscivorous fish and mantis shrimp, or Slovenian-Croatian fleet on dolphins, however in general impacts appear small (Figure 8).

The keystone index presents the highest values for zooplankton and macrocrustaceans, (Figure 9), confirming the MTI results. Other groups with a fundamental trophic position are mainly the pelagic ones: phytoplankton, pelagic bacteria, anchovies, mackerels and horse mackerels, squids.

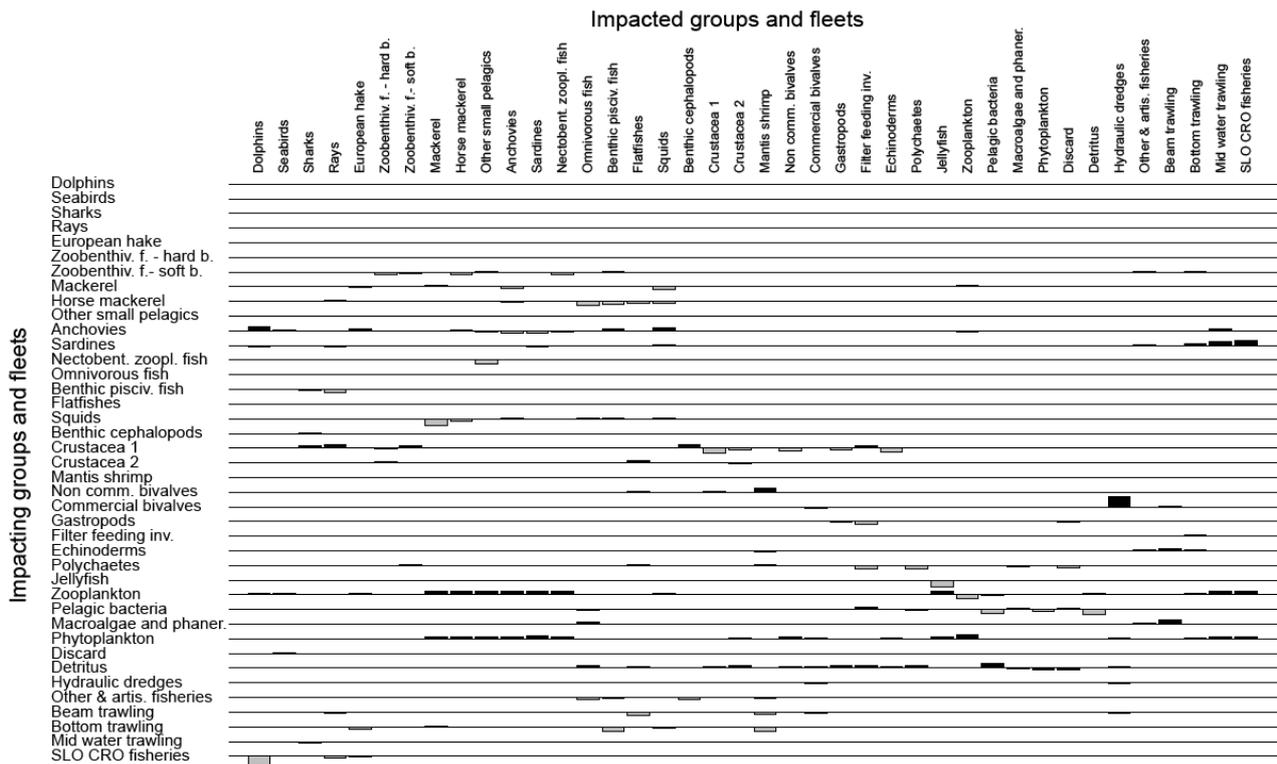


Figure 8. Mixed trophic impact graphical representation. A rectangle up means a positive impact (sum of direct and indirect impacts) of one group on another, a rectangle down means a negative impact. The absence of top down control by apex predators is clear (no rectangles can be seen on the corresponding rows).

The classification, by the use of  $\varepsilon$  terms (Figure 10), of the groups and fleets which are overall the most impacting on the living groups of the Northern Adriatic Sea is in line with previous findings. The ecosystem is dominated by the medium-low trophic levels: planktonic groups, pelagic fishes and squids, which are r-selected and resilient organisms, and detritus. Crustacea 1 are confirmed as one of the most impacting groups. Some fleets appear to be particularly impacting: bottom trawling, beam trawling and other-artisanal fisheries, underlining the role of man as predator in the ecosystem. The high overall impact of Croatian-Slovenian fleet is related to its high negative impact on dolphins. Most top predators and fish groups are not able to influence the network (especially if compared to medium-low trophic levels), having low values of overall impact on the ecosystem.

### 3.8.3 Ascendency and information theory indicators

Information theory indicators are reported in Table 5. Ascendency expressed as percentage of development capacity stays nearly constant (23.7%) when excluding bacteria from the network, while the several contributions to ascendency and overheads show more marked changes (e.g. redundancy becomes 51.1%, overhead on imports becomes 3.8%). The comparison of percent ascendency to published values taken from 55 ecosystems of several kinds, described on Chapter 7, shows that it is

among the lowest, while percent redundancy ranks from medium to high (without and with bacteria, respectively), suggesting that the Northern Adriatic Sea is at an immature (*sensu* Odum, 1969) yet resilient stage.

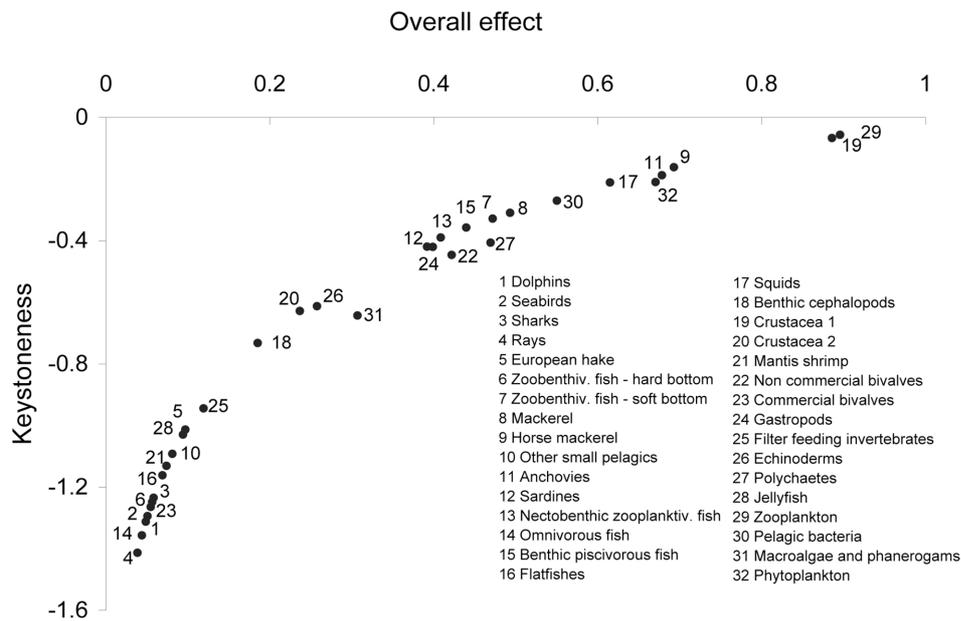


Figure 9. Keystoneness index *sensu* Libralato et al. (2006). The rank of zooplankton (first) highlights its key ecological role. Instead top predators have low keystone and overall effect.

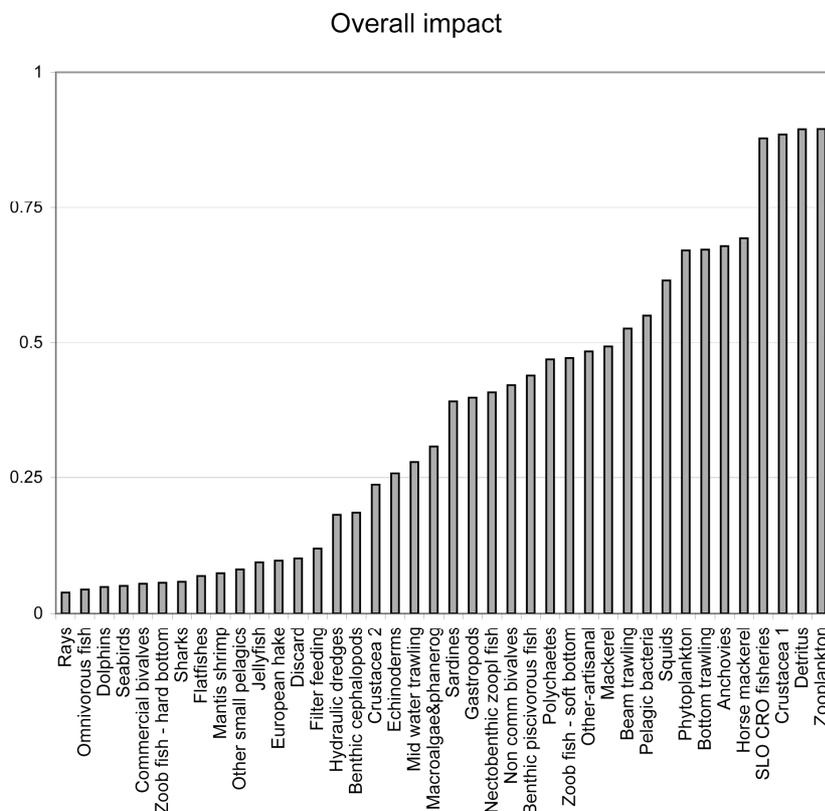


Figure 10. Groups and fleets ranked by their overall impact on the other living groups of the ecosystem. The Northern Adriatic Sea appears to be dominated by r-selected species.

## 3.9 Discussion

### 3.9.1 Trophic network structure and flow analyses

The trophic levels for the groups are in agreement with existing literature (Stergiou and Karpouzi, 2002; Pinnegar et al., 2003; Coll et al., 2007). The lower TL of seabirds compared to other piscivorous groups (i.e. dolphins, European hake, benthic piscivorous fish) is in relation to their high consumption of discard.

*EE* values allow some considerations on resource exploitation. Anchovies and other small pelagic fish (i.e. sprats) present lower *EE* than other fish. The cause is to be found in the abundance and inter-annual variability of the pelagic fish biomass in the Northern Adriatic Sea (Azzali et al., 2002). For example anchovies in 1996-1998 were much more abundant than sardines, which is a species with a similar trophic role and also heavily fished, and hence they were not as intensely exploited, while sardine exploitation rate (Table 1) is close to the 0.4 threshold which should not be exceeded (Cingolani et al., 2004a).

*EE* for elasmobranchii appear quite high, given the low predation that they undergo. This result must be put in relation to heavy fishing exploitation ( $F / Z > 50\%$ , Table 1, see also Chapter 5) combined with their low productivity. In fact, the environmental status of these groups is even more worrying than the one appearing from the model, because in the Northern Adriatic Sea a huge fraction of landed sharks and rays have not reached sexual maturity (Visentin, 2007; Chapter 5).

Low *EE* for some benthic groups are due to their high and only partially preyed biomass. Jellyfish display a very low *EE* because they are almost not preyed in the system, and thus their production, based on zooplankton, is simply “wasted back” to detritus, unlike their intensely-preyed trophic niche competitors (small pelagics). Other planktonic groups with low *EE* are phytoplankton and pelagic bacteria. For both, only 40% of the production is used in the ecosystem. For the former, the very intense blooms characterizing micro-algae in the Northern Adriatic Sea (Degobbis et al., 2000) could be the cause: most of the production dies and is transformed into detritus without being grazed. Zooplankton causes about half of the predation mortality of bacteria and 40% of the predation mortality of phytoplankton, but on the contrary it has a high *EE*. Thus, zooplankton appears as a key, bottleneck group, controlling the energy transfer from the largely unexploited production of bacteria (hence, indirectly, detritus), phytoplankton and detritus, to the above trophic levels, which are intensely consuming it (e.g. anchovies and sardines are responsible of 64% of its predation mortality, see also Chapter 6). The low transfer efficiency from TL 2 to TL 3 in the detritus chain (Table 4) highlights the bottleneck role of zooplankton in that chain. Indeed zooplankton is the main predator of pelagic bacteria, which belong mainly to the detritus chain due to their diet. Bacteria flows dominate TL 2, being about 73% of its throughput and, consequently, the main cause of the detritus chain inefficiency

from TL 2 is that the bacterial production is incompletely preyed ( $EE = 0.41$ ), e.g. by zooplankton, and thus not transmitted to TL 3. The lower transfer efficiency for the detritus chain from TL 2 could be due also to the low  $P / Q$  ratio for bacteria, given the intrinsic uncertainty in plankton estimates. However similar low  $GE$  values are found in the literature (Arias-Gonzalez et al., 1997), bacterial growth efficiency, defined as  $P / (P + R)$ , is acceptable (Del Giorgio and Cole, 1998) and the slight changes to bacterial parameters made during balancing did not affect the results. The higher transfer efficiency from TL 2 in the primary producer-based chain (Table 4) is related to the intense predation by zooplankton on phytoplankton (40% of phytoplankton predation mortality), and the complete consumption of zooplankton production ( $EE = 0.92$ ) by TL 3.

Similarly to zooplankton, another group with intermediate trophic position in the network and high  $EE$  is Crustacea 1. Given the high predation they undergo and their high absolute consumption upon different trophic levels (high OI), macro-crustaceans represent another fundamental trophic group in the ecosystem.

The Lindeman spine highlights that low trophic level groups are quantitatively dominating both flows and biomasses in the Northern Adriatic Sea. Flows are mainly based on detritus, showing the importance of microbial loop, as bacteria consume about 80% of detritus production. Therefore, the microbial loop appears to be comparable to grazing. Unlike stated by Odum (1969), detritus predominance does not appear as a sign of ecosystem maturity, since the Northern Adriatic Sea seems to be at a developmental stage (see below). Rather it is probably linked to the shallowness of the basin and the intense circulation favoring sediment resuspension and water column-benthic compartment interactions, the exogenous loads of organic matter by the Po river, the largely unused phytoplankton production flowing into detritus, the high benthic biomass composed of many detritus feeders, and sediment resuspension due to bottom fishing activities (Turner et al., 1999). Also, the cycle analysis shows that a big part of the detritus-based cycling matter is constrained to the bottom of the food-web, as it is flowing through the incompletely-preyed bacteria.

The increase of transfer efficiencies in the upper trophic levels is unexpected (Lalli and Parsons, 1997) but it has been found also for the Northern and Central Adriatic Sea by Coll et al. (2007). The cause could be the impact of fisheries upon higher trophic levels, as hypothesized by Libralato et al. (2005), given that a higher proportion of catch or predation results in higher transfer efficiencies.

The analyses of biomass and flows highlighted the importance of the pelagic compartment, with respect to the demersal one, in line with what found in the Northern and Central Adriatic Sea (Coll et al., 2007) and other Mediterranean areas (Coll et al., 2006). Considering the catches, fishing is concentrated on the low trophic levels, as indicated also by the gross efficiency of fishery (catch:total primary production ratio), which is higher than the weighted global average (Christensen et al., 2005, p.

58) and that of the Northern and Central Adriatic Sea together (Coll et al., 2007), even if values are probably not directly comparable given the high quantity of discard in this ecosystem.

Discard estimates are huge and higher than those reported for the Northern and Central Adriatic (Coll et al., 2007), e.g. 3.8 times higher for invertebrates. Despite differences in literature sources and assumptions in the calculations shown in this study, the higher discard rate likely reflects differences in discard practices and the higher impacts that fishing gear can have on the northern part of the basin, because of its shallowness and of the high benthic and pelagic biomass sustained. Note that fishing impacts are largely underestimated by the model because, for example, habitat destruction by trawling is not accounted for.

The total primary production:total biomass ratio found here is clearly higher than  $8.82 \text{ y}^{-1}$  found by Coll et al. (2007) for the Northern and Central Adriatic Sea pooled together, also if differences in the structure of models are accounted for, and if B and P/B of phytoplankton are reduced to the lower pre-balancing values. This ratio reflects the more intense productivity of the Northern basin, highly influenced by the Po river plume, and also indicates that the sustained biomass per unit of primary production is lower in the Northern Adriatic Sea. The total primary production:total respiration ratio is close to one, i.e. the “optimum” that an ecosystem should approach in development (Odum, 1969). However, the cause is simply to be found in the very high bacterial flows in the ecosystem, which overshadow all other energy transfers. If these flows are excluded, the ratio becomes significantly higher than the value reported by Coll et al. (2007) for the Central and Northern Adriatic Sea, again indicating the Northern Adriatic as a more productive and immature ecosystem.

### 3.9.2 Mixed trophic impact and related indicators

MTI and related analyses highlighted that the main groups influencing the Northern Adriatic food web are in the low trophic levels (detritus, phytoplankton and zooplankton), markedly affecting fish groups and invertebrates. This strongly suggests that the ecosystem is bottom up controlled. Phytoplankton, despite its abundance, appears to be a key resource, whose increase can positively influence the fished, medium-high trophic levels, in agreement with the higher TE of the grazing chain suggesting higher efficiency (i.e. optimization) with respect to the detritus chain. The scarcer impact of macroalgae and phanerogams on the network could be linked to the decrease of their biomass with respect to the beginning of the century because of several anthropogenic impacts (Airoldi and Beck, 2007; Munda, 1993), stressing again the key role of pelagic production in the ecosystem. The bottleneck role of zooplankton is corroborated by the lower influence that phytoplankton has on the system (if compared to zooplankton) and by the scarce impact of bacteria, which zooplankton is the main predator of, on the upper trophic levels.

Benthic and demersal compartments would highly benefit from a detritus increase and, since the high un-preyed production of phytoplankton flows back to detritus, pelagic primary production appears to sustain those compartments too. Indeed, an increase in phytoplankton would favor both fisheries targeting pelagic species and fleets targeting benthic or demersal species. The contradictory role of anthropogenic eutrophication is clear, since it is also linked to positive impacts by sustaining the heavy fishing as suggested by Marasovic et al. (1988).

Anchovies and Crustacea 1, too, exert strong influence on the trophic network. The latter group preys on a large variability of species, resulting in a variety of both direct and indirect impacts. Anchovies, by far the most abundant pelagic group, exert a negative impact on their competitors for zooplankton (sardines, other small pelagics) and on zooplankton, and a positive effect on many predators (e.g. mackerels, horse mackerels, squid, hake, benthic piscivorous) suggesting a mild wasp-waist control. The importance of these pelagic fish for the ecosystem is in agreement with the results of other models (Coll et al., 2006, 2007).

With the exception of small pelagic fish, other fish groups do not seem to impact at all their preys, suggesting that the upper trophic levels are too much depleted to be able to play a part in the ecosystem. In the past, before intensive fishing started, apex predators like sharks, rays and dolphins were much more abundant (Jukic-Peladic et al., 2001; Bearzi et al., 2004; Granzotto et al., 2006; Fortibuoni et al., 2010; Chapter 5) and presumably exerted stronger effects on the food-web: as already mentioned it was the Northern Adriatic Sea landings during 1910-1924 that inspired the Volterra predator-prey model (D'Ancona, 1926). Now not even fisheries, with some exceptions, seem to impact the fish groups (Figure 8). These results suggest that the Northern Adriatic Sea is in a fishing state, meaning that it has been so long and intensely fished that it is in a depressed state and the depleted higher trophic levels are not reactive even to fishing, as hypothesized also by Zucchetto et al. (2003). There is no contradiction with the failure to detect recent negative trends in Northern and Central Adriatic demersal resources (Manfrin et al., 1998), which could indicate that we are observing an already depleted situation, yet stable and resilient (as shown by medium-high redundancy), and sustained by the energy of eutrophication, by refugium zones like the Croatian rocky archipelago and by the disappearance of top predators, now scarcely impacting, whose past predation could have been unbearable for many species during the 1990s.

This model shows that now the ecosystem is dominated by small, fast-growing and resilient organisms like plankton, small pelagic fish and squids, which are better fit to survive under a high fishing pressure and bottom anoxic conditions (Caddy and Rodhouse, 1998; Caddy, 2000), and capable of rapidly increasing their number in response to the released control from apex predators. Excessive exploitation and eutrophication are good explanations of their predominance, which is a symptom of

anthropogenic stress (Odum, 1985; Caddy, 2000). For example, in coastal ecosystems, explosions of microbial populations appear to follow a collapse by overfishing (Jackson et al., 2001).

### **3.10 The portrait of a stressed ecosystem - conclusions**

From the constructed model, a comprehensive portrait of the Northern Adriatic ecosystem functioning emerges, and a quite consistent (robust?) one, despite the knowledge gaps that emerge as well, such as incomplete information on fish and invertebrate diets, benthic and demersal biomasses, unreported catches and mortalities of fish and benthos.

The analyses show that the trophic structure of the Northern Adriatic Sea is dominated by the low trophic levels, which comprise most of the flows and biomasses. The production of these levels is not completely exploited within the network, as benthos is not completely preyed and zooplankton is acting as a bottleneck, limiting the energy from the low trophic levels effectively reaching the upper food-web. The importance of the microbial loop energetic pathway, comparable to grazing with respect to the magnitude of flows involved (66% of the trophic network flows originate from detritus, which is mainly consumed by bacteria), is an emergent property of the model. The ecosystem appears to be highly productive, mainly in the pelagic compartment, in line with its eutrophicated status, and bottom up controlled. The pelagic primary productivity, due to the flow of the un-preyed phytoplankton production to detritus, sustains both the pelagic and the benthic-demersal compartments and, consequently, high fishery landings and impressive discard quantities.

With few exceptions, the Northern Adriatic top predators appear depleted, un-reactive to fishing and unable to impact not only other fish groups, but even the remaining of the network, unlike the first half of the 20<sup>th</sup> century. Hence overexploitation, at least partially, could be responsible for what seems to be a lack of top down control in the ecosystem (see also Chapter 5; however, further investigations about the past strength of top down control in the system are needed to confirm this hypothesis entirely). In addition eutrophication, with its negative effects on demersal fauna (Breitburg, 2002), even synergistic with fisheries (e.g. bottom gears can enhance benthic hypoxia by sediment resuspension, Caddy, 2000), could have markedly affected trophic pathways and ecosystem structure (Breitburg, 2002; de Leiva Moreno et al., 2000). For example, the very low ascendancy suggests that the Northern Adriatic Sea is at a stressed and immature stage sensu Odum (1969, 1985). The predominance of r-selected populations, which have a great influence on the ecosystem, further supports the role of fishery and eutrophication in shaping the Northern Adriatic communities. These organisms are, too, indicators of anthropogenic stress (Odum, 1985; Caddy, 2000). However, characteristics of the Northern Adriatic Sea such as its natural variability and productivity may also contribute in favoring r-

selected organisms. Thus it cannot be excluded *a priori* that the stress and immaturity are of natural origin, like for example in upwelling ecosystems, which share many characteristics with ecosystems subjected to cultural eutrophication and overexploitation (Caddy, 2000).

The Northern Adriatic Sea has been fished since ancient times, so that the shifting baseline syndrome (Pauly, 1995) does not seem to be simple to overcome, and even pre-industrial fishing and pre-anthropogenic eutrophication reference points are scarce or missing for many species. Indeed, the comparison of the model results with few existing historical data suggests that the low maturity and stressed state of the Northern Adriatic Sea are not only due to natural characteristics, but mainly to anthropogenic pressures, however this is not a proof. To understand, at least with respect to the beginning of the 20<sup>th</sup> century, if we are actually observing an already collapsed or “fished down” ecosystem, the analysis of more historical records is strongly needed. Such analysis will be the goal of some of the next chapters.

### **3.11 Acknowledgments**

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## 4. The effects of climate change on the population dynamics of a littoral spawner

The current trend of climate change and the projections of its future impacts clearly indicate that we require a deeper understanding of its effects both at species and community level (IPCC, 2007). This is particularly relevant for aquatic ecosystems where field studies have documented variation in abundance, composition, population dynamics and reproductive timing and location occurring over the past few decades (e.g. Hughes, 2000; Parmesan and Yohe, 2003; Edwards and Richardson, 2004; Durance and Ormerod, 2007; Hsieh et al., 2009). To date, only few studies have been able to explain patterns of climate-dependent ecological trends through empirical, laboratory-based demonstrations of species vulnerability to thermal stress (Helmuth et al., 2006a; Pörtner and Knust, 2007; Farrell et al., 2008). In these works, conceptual and predictive models on the effect of climate changes on adult ectotherms were built, however to disentangle the whole species tolerance the focus should be on those life stages which constitute the “weakest links”. An adult-based model can underestimate the effect of climate change because mature stages display a wider thermal niche with respect to embryos, larvae and spawners (Pörtner and Farrell, 2008). Adults of intertidal species, for example, can cope with extreme thermal fluctuations and regularly experience body temperatures which largely exceed the thresholds predicted by climatic based models both at large and local scales (e.g. Helmuth et al., 2006b; Helmuth, 2009). On the other hand, many studies have pointed out that early life stages of marine organisms are particularly vulnerable to climatic fluctuations and environmental extremes (e.g. Przeslawski et al., 2005; Hammond and Hofmann, 2010; but see Hamdoun and Epel, 2007).

In this chapter, the findings of laboratory experiments characterizing the thermal sensitivity of embryos in a highly adaptable and tolerant ectotherm (the crab *Carcinus aestuarii*) are integrated with the analysis of long-term landing (from the Clodia dataset) and climatic timeseries over a 65 year period. The goal is to predict how the effects of climate change on offspring fitness translate into population dynamics. The abovementioned experimental work was not performed by me and is not reported here, because its detailed description would be beyond the goals of this thesis. A full description can be found in Bartolini, F., Barausse, A., Pörtner, H.-O., Giomi, F. Climate change reduces offspring fitness in littoral spawners (in preparation). The main conclusions of the laboratory findings are that crab embryos, especially early stages, are highly vulnerable when exposed to thermal stress conditions (e.g. heat waves, which climate change is expected to exacerbate, Meehl and Tebaldi, 2004). It is worth mentioning that adults of *Carcinus aestuarii* are extreme eurytherm species which easily tolerate, through

adjustments of circulatory and ventilatory physiology, large and acute fluctuations of temperature (Giomi and Pörtner, submitted). *C. aestuarii* embryos, although sharing the same thermal niche of the adults, are markedly sensitive to deviations from the thermal optimum. Thus, climate regime can directly affect the fitness of highly resistant species during their vulnerable ontogenetic phases. Therefore, the physiological mechanisms highlighted in laboratory experiments provided an empirical base to investigate the causes behind the long-term population dynamics of a littoral spawner (i.e. crabs) subjected to climate fluctuations as well as to thermal regime shifts.

## 4.1 Materials and methods

### 4.1.1 Temperature and climatic data

No long-term continuous water temperature timeseries over the period covered by landings were available, therefore water temperature was computed based on air temperature. There are two long-term air temperature timeseries in the Venice lagoon, one from the meteorological station of Istituto Cavanis (Istituto Veneto di Scienze, Lettere ed Arti, 2010) covering 1900-2009 (henceforth “Cavanis” timeseries) and another from the station “Osservatorio Bioclimatologico dell'Ospedale al Mare del Lido di Venezia” (De Biasio et al., 2009; Città di Venezia - Istituzione Centro Previsioni e Segnalazioni Maree, 2010) covering 1940-2002 (henceforth “Lido” timeseries). Both timeseries are incomplete over 1940-2009: years 1952 and 1954-1958 and other 74 days are missing from Cavanis; Lido records stop in 2002, and contain 31 additional missing days. Cavanis data were chosen because they are more representative of meteorological conditions over the lagoon (the Lido station is close to the sea; De Biasio et al., 2009), but Lido data provided similar results (not shown).

Only daily maximum and minimum temperature was available at Cavanis for the whole period of the long-term study. Missing measurements were filled by converting data from Lido and, after 2002, from the Marco Polo airport (33 values, taken from <http://www.wunderground.com>) through a least-square linear regression with the Cavanis data available during 1940-1961 (to fill the 1952 and 1954-1958 missing values) or during the decade that the missing data belongs to (to minimize the issue of changing relationships over time, De Biasio et al., 2009). Regressions were made separately for maxima and minima and were highly significant ( $r^2$  ranging from 0.94 to 1.00).

The resultant daily extreme air temperatures were converted into water temperatures using a logistic function, calibrated on 1992-2010 air-water temperature measurements from the Chioggia Hydrobiological station ([http://chioggia.scienze.unipd.it/Inglese/Parameters\\_Lagoon.html](http://chioggia.scienze.unipd.it/Inglese/Parameters_Lagoon.html)). A visual scatterplot inspection confirmed that the air-water temperature relationship was non-linear (Chapra, 1997), and S-shaped as it can be for example in streams (Mohseni and Stefan, 1999). The calibration

gave a satisfactory fit ( $r^2 = 0.91$ ,  $RMSE = 2.06^\circ\text{C}$ ;  $T_{\text{water}} = 28.7 / (1 + 7.975 \cdot e^{-0.1355 \cdot T_{\text{air}}}) + 1.261$ , temperatures in  $^\circ\text{C}$ ), given that water temperature is not influenced only by air temperature (Chapra, 1997). Moreover, the timeseries length should compensate for the approximation made using the conversion, if no systematic errors are present, by increasing the statistical power of the analyses.

The number of heat wave events per year was calculated from the Cavanis air temperature, following two definitions (Meehl and Tebaldi, 2004): the first (henceforth “worst 3-day heat wave”) identifies only the most acute annual event, defined as the warmest temperature that the minima never went below for three consecutive days, i.e. the annual 3-day period with the lowest relief from heat. The other definition (henceforth “threshold heat wave”) allows to identify multiple heat waves per year as well as their duration, based on two temperature thresholds: T1 is defined as the 97.5<sup>th</sup> percentile of maximum temperatures over 1940-2009, and T2 as the 81<sup>st</sup> percentile. A threshold heat wave is the longest period of consecutive days satisfying three conditions: (1) the daily maximum temperatures must exceed T1 for at least three days, (2) the average, over the whole period, of daily maximum temperatures must exceed T1, (3) the daily maximum temperature must exceed T2 every day of the period. This definition can actually lead to the identification of distinct heat waves but without days between them (e.g. in this case  $T1 = 31.2^\circ\text{C}$  and  $T2 = 26.0^\circ\text{C}$ , so that for example the sequence of daily maximum temperatures 32.0, 32.0, 32.0, 27.0, 34.0, 34.0, 34.0 ( $^\circ\text{C}$ ) represent two consecutive waves lasting three and four days): in such case, consecutive heat waves were considered as a single event.

#### 4.1.2 Landings data

Ripe female crab (“mazzanette” in the local dialect) landings from the fish market of Chioggia were available in wet weight kilograms during 1945-2010. This particular landing category was chosen as a population proxy instead of the “crab” market category because: 1 - ripe crabs are clearly recognizable since they display a pronounced yellowish abdomen, ensuring that all ripe *Carcinus aestuarii* were recorded in this category at the fish market and no other species was included. This made the landings very reliable despite the long period covered, unlike the “crab” category whose composition probably changed through the decades; 2 - ripe crab landings can provide an estimate of the yearly reproductive potential of the population.

Ripe crab landings (which are also called “spawner crab landings” in this chapter) were assumed to be proportional to ripe crab biomass and hence to the crab population biomass. The assumption of proportionality between ripe crab biomass and population biomass seems acceptable given the short lifespan, 3-4 years, of this species (Baeta et al., 2005). The assumed proportionality between landings and biomass could be biased by several factors (Pauly et al., 1998), such as changes over time in discarding practices, underreporting, market demands or fishing effort. However, discarding does not occur given the commercial value of ripe crabs, which however is not so high to hypothesize significant

underreporting, and market demands did not change (personnel of the Chioggia fish market, pers. comm.) due also to the artisanal nature of the fishery.

Fishing effort for ripe crabs could be considered roughly constant over time, given the traditional nature of the fishery, especially in the last 30-40 years (personnel of the Chioggia fish market, pers. comm.; Libralato et al., 2004), so that landings could be a proxy for biomass. However, fishing effort in general increased in the lagoon after 1945, and during the last 10 years artisanal fishing effort decreased (Libralato et al., 2004; Fortibuoni et al., 2009), therefore it was cautelatively considered that crab fishing effort could be not constant in the analyses done.

Despite its limitations, the abovementioned “crab” market category (1980-2010) was used as a relative measure of total population biomass with respect to the ripe individuals.

#### 4.1.3 Timeseries elaborations

The presence of temporal trends in timeseries was tested using the non parametric Mann-Kendall test and, if significant, slopes were computed using Sen’s robust estimator (Gilbert, 1987). To investigate the effects of warming or heat waves on population biomass levels, ripe crab landings were compared to indices of thermal stress based on temperature. Long-term relationships were investigated through bivariate correlations or multiple linear regression (Legendre and Legendre, 1998). Cross-wavelet analysis was used to test if short-term landing oscillations were related to heat waves. An in-depth description of this complex analysis can be found in Torrence and Compo (1998) and Grinsted et al. (2004). Wavelet analysis yields a representation of a timeseries in a time frequency space, identifying the time-periods when that timeseries is characterized by oscillations of a given frequency. Cross wavelet analysis highlights the time-periods when two timeseries have common high power for a given frequency, and the corresponding phase relationship between them. Cross wavelet analysis was performed using the MATLAB® code provided by A. Grinsted (<http://www.pol.ac.uk/home/research/waveletcoherence/>). The Morlet wavelet was used and significance levels were determined against red noise (first order autoregressive process). Non-normally distributed timeseries were percentile transformed (Grinsted et al., 2004).

## **4.2 Results**

### 4.2.1 Temperature and climatic data

Annual maximum air temperature did not display long-term trends over 1940-2009 (Mann-Kendall  $Z = -1.01$ ,  $p = 0.31$ ), even if the highest maxima were in the 1940s (Figure 11a); annual minima increased with time (Mann-Kendall  $Z = 2.19$ ,  $p = 0.03$ , Sen’s slope =  $0.03\text{ }^{\circ}\text{C y}^{-1}$ ; trends tested without

filling Cavanis missing data, but doing it did not affect trends), suggesting a warming trend in the ecosystem. Strikingly, the examination of extreme events during 1940-2009 revealed an unstable and changing ecosystem. For example the temperature of the annual worst 3-day heat wave showed no overall trend (Mann-Kendall  $Z = 0.87$ ,  $p = 0.38$ ) but oscillated abruptly, increasing from 1991 (Figure 11b). The annual number of days with water temperature always exceeding 18°C, which laboratory experiments showed to be a threshold that crab early life stages are sensitive to, was also examined. The timeseries displayed again no trend (Mann-Kendall  $Z = -0.56$ ,  $p = 0.57$ ) but higher values were found until the mid-1960s and from the mid-1980s (Figure 11b). Threshold heat waves at Cavanis showed a surprising distribution, confirmed also by Lido data (Figure 11c): in the beginning heat waves were much more frequent (at least one wave per year during 1941-1954) and longer, with a striking 90-day event in 1950. A period with few and shorter waves followed until the mid-1980s, when extreme events became more frequent and longer. Both timeseries displayed negative trends (heat wave days, Cavanis: Mann-Kendall  $Z = -1.89$ ,  $p = 0.06$ ; Lido: Mann-Kendall  $Z = -2.55$ ,  $p = 0.01$ ). Interestingly, the Lido timeseries showed no waves during 1964-1991 with the exception of 1985 and 1988: both years came two years before the two lowest landings of ripe crabs (Figure 11d), suggesting a negative effect, delayed in time, of acute thermal stress on crabs.

#### 4.2.2 Landings

Landings over 1945-2010 showed no long-term trend (Mann-Kendall  $Z = -0.43$ ,  $p = 0.67$ ; Figure 11d), but were higher from the mid-1960s to the mid-1990s. This landing trajectory could reflect similar patterns of increased nutrient inputs to the lagoon after World War II, and, possibly, of fishing effort variations (see Materials and Methods). However the pattern is opposite to those of heat wave duration and the number of days with water temperature exceeding a physiologically-relevant temperature threshold, indicating that thermal stress, either due to extreme meteorological conditions or thermal regime shifts, could have played a role in the long-term population dynamics of crabs. Landings also showed marked inter-annual variations, especially from the 1980s to the mid-1990s. A possible explanation is represented by the dystrophic crises which impacted the lagoon at the end of the 1980s, affecting benthic communities (Libralato et al., 2004), but the influence of the concurrent increase of heat waves after a long period of calm (Figure 11c) cannot be excluded.

Cross-correlation analysis (Legendre and Legendre, 1998) between landings of crabs and ripe crabs revealed a strong relationship between population level and ripe crab biomass at 1-year lag (Spearman  $r_s = 0.67$ ,  $p = 0.00004$ ). The relationship was weaker with no lag ( $r_s = 0.53$ ,  $p = 0.002$ ), and even weaker with longer lags, suggesting that most recruits enter the population one year after spawning. Then, in the same or (mostly) in the next year, they reach sexual maturity and thus contribute to ripe crab landings (Klein Breteler, 1976; Baeta et al., 2005), so that the relationship between ripe

crabs landed on one year and those landed one or two years later represents the effects of past spawning biomass (and, also, the survival of individuals for more than one year).

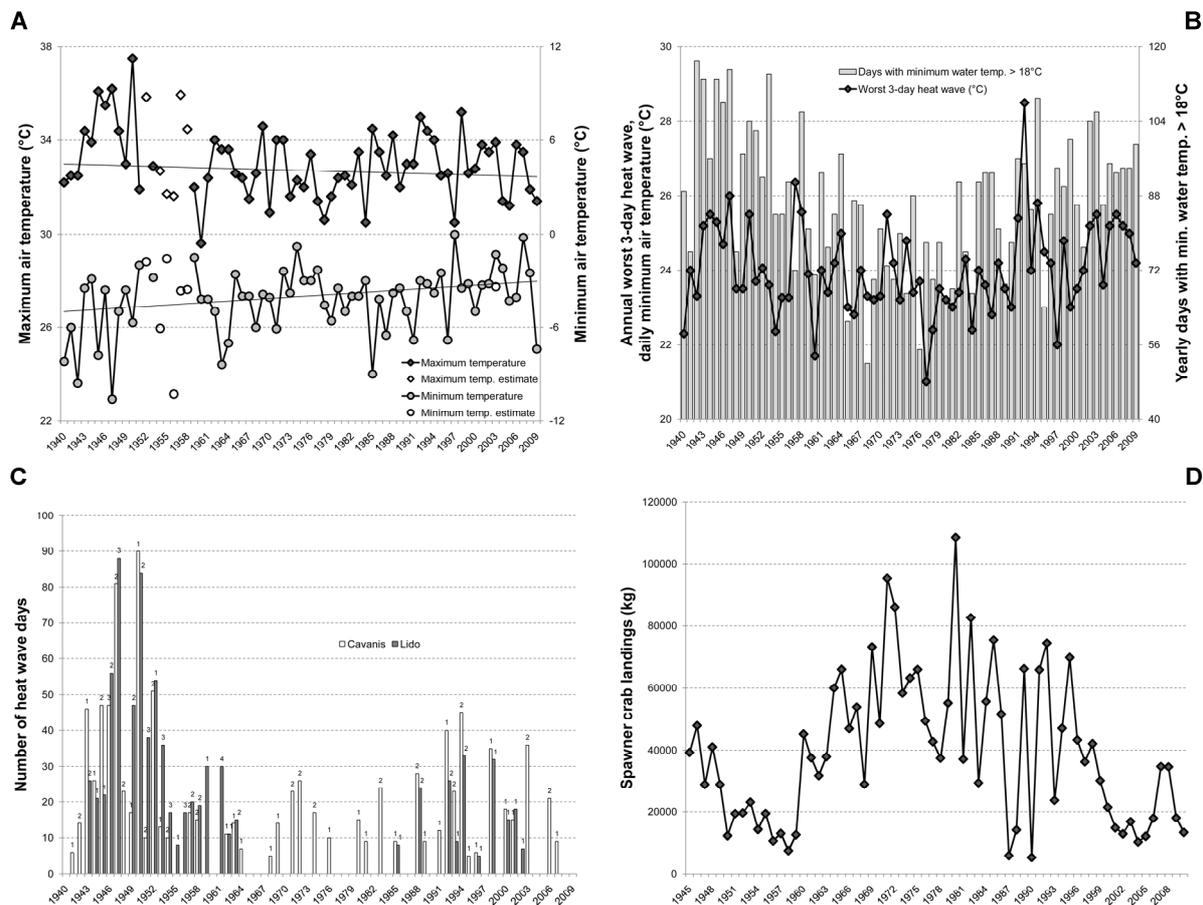


Figure 11. Climatic and landing timeseries from the Venice lagoon: (A) Annual minimum (filled circles) and maximum (filled diamonds) air temperature (°C) measured at the Cavanis station. Daily missing values were filled based on other temperature timeseries from the lagoon, and empty symbols represent such estimates in the case that they represent yearly extremes. Lines indicate time trends. Maximum air temperature did not show clear long-term trends but was highest in the 1940s, while minimum temperature increased over time, about  $+0.03\text{ }^{\circ}\text{C y}^{-1}$ . (B) Annual worst 3-day heat waves (filled diamonds) according to Meehl and Tebaldi (2004), and the number of yearly days with minimum water temperature always exceeding  $18^{\circ}\text{C}$  (columns). Neither of the timeseries displayed trends but in both of them the extreme events seem to increase after the mid-1980s. (C) Number of annual heat wave days calculated according to the threshold definition in Meehl and Tebaldi (2004) from daily maximum air temperature during 1940-2009, at Cavanis (missing data filled) and Lido (2003-2009 missing). Data labels above the rectangles in the chart indicate the number of heat waves per year. Both timeseries display more frequent and longer heat waves until about mid-1960s, and then fewer and shorter heat waves until about the mid-1980s, when extreme events increase again similarly to Figure 11b. During 1964-1991 no heat waves took place at Lido, excluding the 1985 and 1988 events which come exactly two years before the two lowest values of ripe crab landings over 1945-2010 (Figure 11d). (D) Landings of "Mazzanette" ripe crabs (kg wet weight) from the fish market of Chioggia. Although no clear trend is present, marked inter-annual oscillations can be appreciated especially during the 1980s and mid-1990s, as well as an overall pattern with the highest values in the middle of the timeseries, opposite to the pattern of climatic timeseries in Figure 11a-c.

Indeed the autocorrelation of the ripe crab timeseries, which was strongest with lags of 1-3 years, and the partial autocorrelation function (Legendre and Legendre, 1998) confirmed this

conclusion (results not shown), moreover suggesting that most crabs live up to three years (see also Baeta et al., 2005). Consequently (1) I took the 2-year lagged ripe crab landings as a predictor of the effects of spawning biomass (and of the inter-annual survival of individuals) on the population in multiple regression analysis (neglecting the few recruits that become mature the same year that they enter the population (Klein Breteler, 1976; Baeta et al., 2005), or two years later; landings and 2-year lagged landings correlated well: Pearson  $r = 0.41$ ,  $p = 0.001$ ); (2) I cross-correlated landings and temperature timeseries with a 2-year lag, to simulate the effect of thermal stress on crab early life stages, as indicated by laboratory experiments.

Table 6. Correlations of ripe crab landings (1945-2010) with thermal stress indices based on water temperature (0- and 2-year lagged). Spearman  $r_s$  is reported, with the corresponding  $p$  value in parentheses.  $T_{\min}$  and  $T_{\max}$  are daily minimum and maximum temperatures.  $18^\circ\text{C}$  is a threshold affecting the early life stages of *C. aestuarii*. Strongest correlations are found with lagged minimum temperature-based indices.

	Lag (years)	
	0	2
Annual maximum temperature	-0.05 (0.71)	-0.19 (0.13)
Annual days with $T_{\min} > 18^\circ\text{C}$	-0.34 (0.005)	-0.38 (0.002)
Annual days with $T_{\max} > 18^\circ\text{C}$	-0.29 (0.02)	-0.18 (0.15)
Annual mean daily $T_{\min}$	-0.47 (0.00008)	-0.46 (0.00009)
Annual mean daily $T_{\max}$	-0.23 (0.06)	-0.27 (0.03)

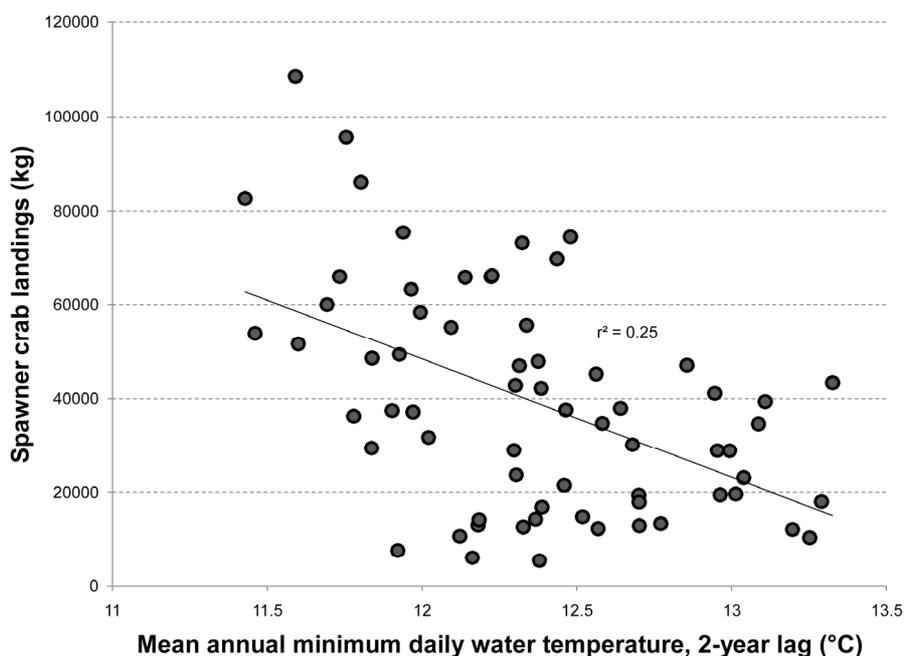


Figure 12. Relationship between ripe crab landings (1945-2010) and mean annual minimum daily water temperature, with a 2-year lag. The strong relationship ( $r = -0.50$ ,  $p = 0.00002$ , the line is a least-square fit) between the two timeseries suggest that the lack of relief from thermal stress exerts a marked influence on crab early life stages (as indicated by the lag) and therefore on population dynamics.

#### 4.2.3 Relationship between thermal regime and landings

Landings over 1945-2010 negatively correlated with several thermal stress indices (Table 6; Figure 12). The strongest correlations were detected with a lag of two years (non-lagged correlations are reported on Table 6 for comparison), suggesting that thermal stress affects crab early life stages and (with a consequent delay) the population, and with minimum water temperatures.

Landings were predicted through multiple linear regression using as predictor the most correlated lagged stress index from Table 6 (i.e. the 2-year lagged annual mean daily minimum temperature; using the 2-year lagged annual number of days with minimum temperature  $> 18^{\circ}\text{C}$  yielded similar results, not shown), and the 2-year lagged landings. The latter predictor not only simulated that more ripe crabs mean a higher population two years later, but eliminated the potential issue that it could be difficult to distinguish the effect of thermal stress on landings from those of fishing effort variations / anthropogenic nutrient enrichment, whose time patterns are similar. It can be reasonably assumed that eutrophication severity and fishing effort had changed slowly over time, particularly over the 2-3 years time scale characterizing population variations due to spawning or thermal stress. Then, predicting landings from the landings two years before already takes into account that fishing effort was high or low, and the lagoon eutrophic or not. Therefore, the correlation with lagged landings represents also these several other factors.

The multiple regression showed population levels to be predicted by a combination of the spawning population and thermal stress two years before (Table 7). The standardized regression coefficients, representing the relative weight of the predictors, indicated that the lagged effect of thermal stress on crab landings was comparable to or higher than that of the 2-year lagged landings, which is noteworthy since, as discussed, lagged landings roughly weigh spawning biomass, inter-annual population survival, and levels of fishing effort-eutrophication. Therefore thermal stress on early life stages seemed to be as important for the population as the sum of these other factors. In the regression, landings were slightly overestimated in the initial and final years of the timeseries, and not all extreme oscillations were well simulated (Figure 13).

Actually these oscillations appeared to be related to acute climatic events: cross-wavelet analysis highlighted that landings and the 2-year lagged temperature of the annual worst 3-day heat wave were characterized by high common power during about mid-1980s – mid-1990s, with anti-phase short-term oscillations (Figure 14). Indeed isolated peaks like the one in the figure could be spurious, but another heat wave definition, and a different temperature timeseries (Lido), suggested similarly that extreme heat waves affected crab early life stages and population in that period (see Results and Figure 11).

Table 7. Prediction of ripe crab landings (kg) from 2-year lagged landings (kg) and 2-year lagged annual mean daily minimum water temperature (°C), through multiple linear regression.  $\beta$  is the standardized regression coefficient corresponding to the predictor on the left column, and B is the regression coefficient. Predictors were only slightly multicollinear (variance inflation factor = 1.25; O'Brien, 2007) and the regression was highly significant ( $R^2 = 0.30$ , adjusted  $R^2 = 0.28$ ,  $F_{(2,61)} = 13.3$ ,  $p = 0.00002$ ).

Predictors	$\beta$	Std. Err. of $\beta$	B	Std. Err. of B	t(61)	p value
Intercept (kg)			288611.6	77783.8	3.71	0.0004
2-year lagged spawner crab landings (kg)	0.23	0.12	0.231911	0.121219	1.91	0.06
2-year lagged annual mean daily minimum water temperature (°C)	-0.41	0.12	-20950.5	6109.5	-3.43	0.001

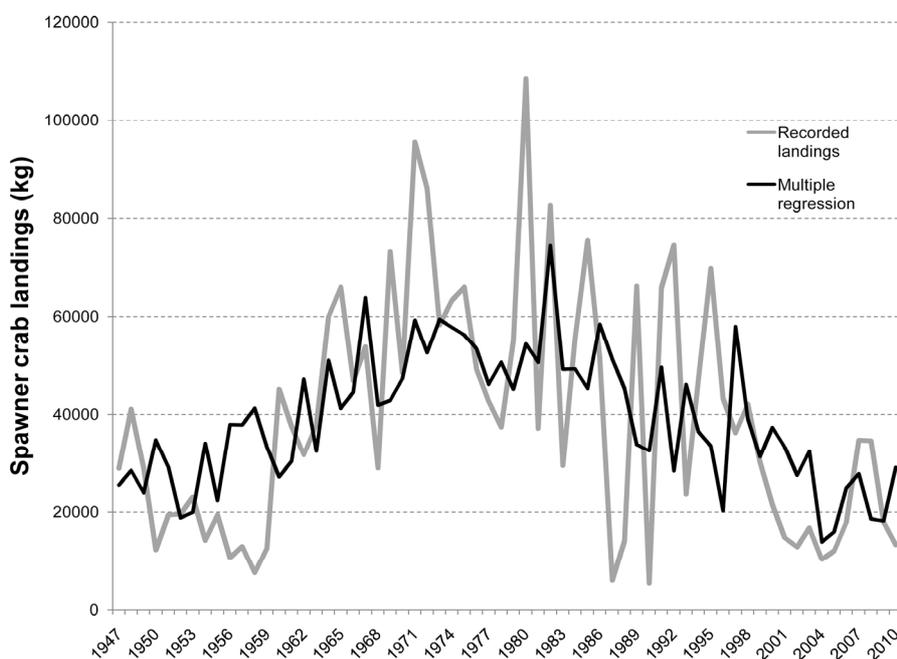


Figure 13. Ripe crab landings (kg), as recorded at the fish market (grey line) and predicted by multiple linear regression (black line). The simulated values reproduced quite well the observed landings, with the exception of some abrupt oscillations.

### 4.3 Discussion

Temperature data highlighted that environmental conditions over the Venice lagoon, particularly extreme events, underwent remarkable changes in the past, so that the ecosystem appears as a perfect case study for testing climate change effects on biota. Correlations emerged between crab landings and lagged temperature-based indices of thermal stress, both for long-term trends and sudden abrupt variations, suggesting that climatic conditions impacted early life stages of crabs and, consequently, markedly affected population biomass, with a strength at least comparable to the effects of spawning biomass.

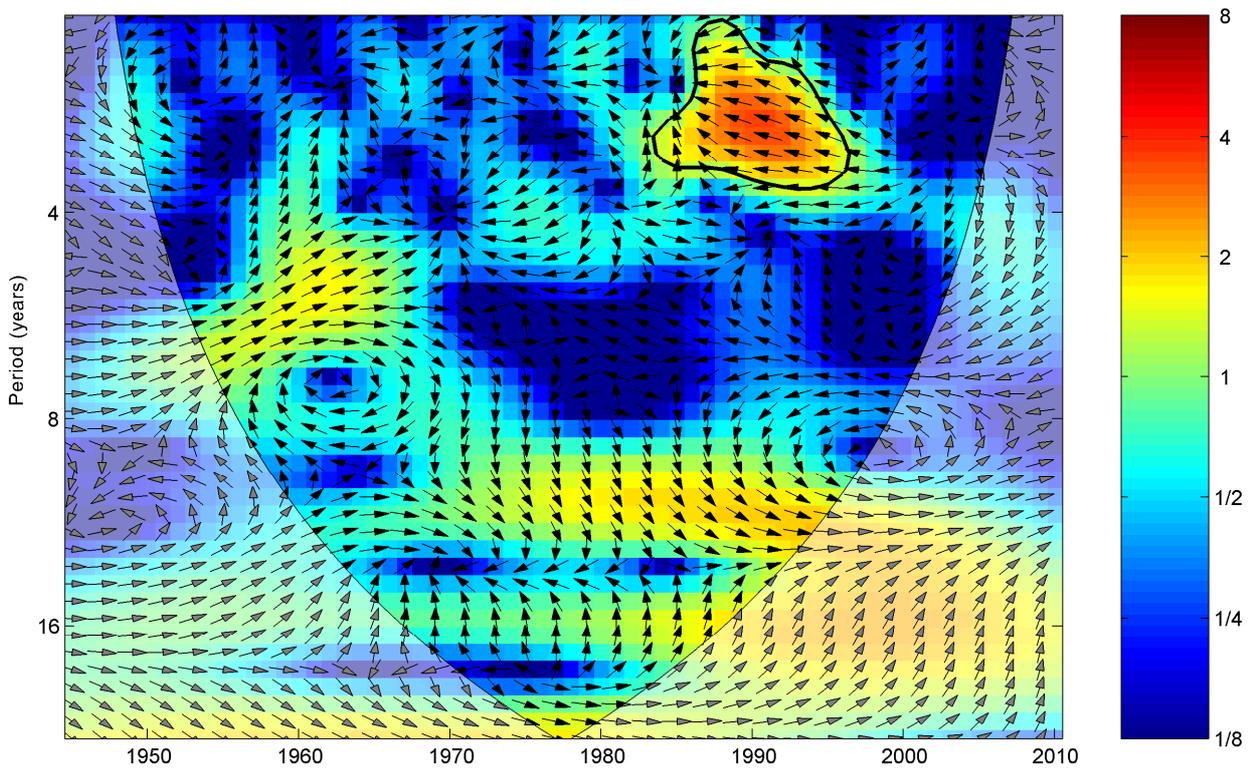


Figure 14. Cross wavelet transform of the ripe crab landings and the annual worst 3-day heat wave (2-year lagged) timeseries. The paler area is the cone of influence, where biases due to edge effects are found, and the thick contour indicates areas with 5% significance level. Arrows indicate the timeseries relative phase (pointing left: anti-phase; right: in-phase; down: crab landings leading lagged heat waves by  $90^\circ$ ).

Results highlighted stronger relationships of crabs landing with minimum temperatures than with maxima. Indeed, daily maxima are reached only for short periods, while daily minima represent the temperature that is exceeded the whole day, i.e. they measure the lack of relief from thermal stress. Maximum temperatures are commonly used to investigate the effects of acute thermal stress on aquatic biota (Pörtner and Knust, 2007), but here it is suggested that in some cases minima could be more appropriate. As in any observational study, the correlations identified could be spurious, but they are supported by different statistical methodologies and thermal stress definitions, are based upon physiological processes and thresholds shown to be relevant by sound laboratory experiments, and the strongest correlations are found with a biologically-sound 2-year lag. Indeed there are many alternative explanations for changes in landings on the long-term (fishing effort variations and eutrophication) and on the short-term (dystrophic crises, even if the genus *Carcinus* is very resistant to anoxia, Crothers, 1968). However all of these different explanations are not mutually exclusive. Given that the trajectories of fish and invertebrate landings in the lagoon resemble that of crabs (Libralato et al., 2004), it is also possible that climate (quite neglected, so far) acted on the lagoon ecosystem synergistically with fishing and nutrient enrichment.

## 4.4 Conclusions

The sensitivity of physiological processes to thermal stress that was evidenced in laboratory experiments (not reported here) provided an empirical base to investigate the causes behind the long-term dynamics of a littoral spawner population subjected to climate fluctuations and thermal regime shifts. In general it is not trivial to demonstrate that physiological responses caused by environmental change are directly related to variations of population abundance. However, by integrating experimental work with historical data analysis, here it is provided strong evidence that a process at the individual level, the thermal stress during the ontogenesis of eurythermy, is also relevant at the population level. The relative influence of temperature and spawning biomass on recruitment was evaluated quantitatively, concluding that the two factors are at least comparable. Finding a mere correlation between environmental variability and recruitment success was not the goal here: the analyses made followed from sound experimental work which, by unambiguously identifying physiological processes involving only very specific life stages, led to the formulation of a clear *a priori* hypothesis to be tested at the population scale.

The finding that thermal stress can cause dramatic changes in the abundance of aquatic populations and drive their long-term dynamics, as in the case of *C. aestuarii*, underlines the importance of considering climate in the management of commercially important species: for example environmental change could overshadow the effect of biomass removal due to fishing and even be synergistic with it in unpredictable ways. Moreover, ecosystem populations are linked through prey-predator interactions, and marked climate-driven changes in the abundance of one population could cascade across the food-webs and affect other populations in potentially important ways (e.g. Pace et al., 1999). These conclusions become critical when put in a global change perspective, because the current trend of increasing temperature and extreme events such as heat waves (Meehl and Tebaldi, 2004) is expected to exacerbate the way that climate was shown here to influence littoral spawners.

## 4.5 Acknowledgments

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## 5. The loss of top predators

The management of fisheries in eutrophic ecosystems, such as the Black Sea or the Northern Adriatic Sea in the Mediterranean Sea, was characterized in the past mainly by a bottom up approach. Until recently, the degradation of environmental conditions in the Black Sea was linked to the effects of anthropogenic eutrophication (Daskalov, 2002). In the Northern Adriatic Sea, much attention within fisheries science has been paid to low trophic levels such as small pelagic fish stocks, which were favoured by the increase of primary productivity and are influenced by climate (e.g. Marasovic et al., 1988; Grbec et al., 2002; Cingolani et al., 2004a and 2004b; Santojanni et al., 2003 and 2006). Actually, there is evidence based on historical records or scientific surveys that upper trophic levels of the Northern Adriatic food web have been depleted by fisheries (see Discussion on Chapter 3 and D'Ancona, 1926, Jukic-Peladic et al., 2001, Bearzi et al., 2004, Granzotto et al., 2006, Fortibuoni et al., 2010), but the ecological, social and economic consequences of the loss of top predators are ignored.

Recently, it has been shown that trophic cascades can also impact large-scale marine ecosystems (Frank et al., 2005), and much of the changes which took place in the Black Sea in the last decades have been attributed to overfishing (Daskalov, 2002; Daskalov et al., 2007). Therefore, it seems important to investigate closely the long-term changes of predators in the Northern Adriatic Sea as well. Hence, in this chapter: (1) evidence is provided for a striking decline of elasmobranch predators in the Northern Adriatic Sea during the last century, and possible causes such as climate and fishing are examined, using an integrated approach: analysis of historical records (Past), recent fish market samplings (Present), and modelling (Future). These different methodologies provide consistent results, making the conclusions particularly robust; (2) since overexploitation indeed seems the most plausible cause of the elasmobranch decline, some management solutions are proposed.

### 5.1 Which future for elasmobranch in the Northern Adriatic Sea? A perspective from historical data and predictive models

Life history characteristics such as large size, slow growth rate, late maturity and low fecundity resulting in low reproductive rates make elasmobranchs more sensitive to exploitation than bony fish (Bonfil, 1994; Camhi et al., 1998; Smith et al., 1998; Walker and Hislop, 1998; Dulvy et al., 2000; Stevens et al., 2000; Dulvy and Reynolds, 2002; Field et al., 2009). Moreover, they are often the top predators in an area and therefore show low abundances relative to other fish groups (Bonfil, 1994).

These attributes make elasmobranchs scantily resilient to fishing mortality, inclined to rapid stock depletion and unable to quickly rebound to population reduction (Smith et al., 1998; Stevens et al., 2000; Musick, 2005; Myers and Worm, 2005; Dulvy et al., 2008).

Elasmobranchs are exploited worldwide, either as the target of specific fisheries or, more often, as the bycatch of fisheries targeting other more abundant or valuable resources (Bonfil, 1994; Walker, 1998; Stevens et al., 2000). As bycatch, elasmobranchs are not subject to economic extinction prior to get close to local extinction (Camhi et al., 1998; Casey and Myers, 1998; Musick et al., 2000; Dulvy et al., 2003; Musick, 2005). Landings are often unreported or aggregated in multispecies categories, making the detection of species-specific trends in landings extremely difficult (Bonfil, 1994; Walker, 1998; Dulvy et al., 2000; Myers and Worm, 2005). Even if one category remains stable over time, its multispecies composition may mask the decrease in one or more species, compensated by an increase in others. Sensitivity to exploitation, due to life history characteristics, is species specific, with larger, slower-growing species more vulnerable than smaller, faster growing ones (Smith et al., 1998; Walker and Hislop, 1998). A shift from large to smaller species, as a consequence of competitive release, was documented in a skate community in the Western Seas area of the north-east Atlantic, while the change went unremarked in the skate landing record as skate were registered as a single category (Dulvy et al., 2000).

Even if data on elasmobranch landing and stock status are often poor or non-existent (Bonfil, 1994; Polidoro et al., 2008), the emerging picture shows a dramatic decline in or collapse of several elasmobranch populations, and of large predatory species in particular (i.e. Bonfil, 1994; Stevens et al., 2000; Baum et al., 2003; Ellis et al., 2005; Myers and Worms, 2005; Musick, 2005; Dulvy et al., 2008; Ferretti et al., 2008). In the last review of the IUCN Red List, almost 20% of the evaluated species of sharks and their relatives ( $N = 1046$ ) are considered at higher risk of extinction, while for more than 40% evaluation data are deficient (Polidoro et al., 2008). Some species are already considered locally extinct (Brander, 1981; Casey and Myers, 1998; Dulvy et al., 2003). Since most elasmobranchs are top predators, the decline or disappearance of their populations may influence marine communities through direct and indirect trophic interactions (Jennings and Kaiser, 1998; Stevens et al., 2000; Baum et al., 2003; Field et al., 2009), with the ecosystem responding to elasmobranch removal in a variable and unpredictable way (Stevens et al., 2000).

Worldwide, elasmobranch fisheries have increased in response to growing demand, in particular for highly valuable parts, such as shark fins; the accessibility of new areas (i.e. open ocean, deep sea bottom); and the utilization of highly-technically-equipped fishing boats (Walker, 1998, 2005; Baum et al., 2003; Clarke et al., 2007; Polidoro et al., 2008). This, together with a decline in several elasmobranch stocks, has led to a call for an improvement in international action for the management of sharks and related species to ensure sustainable elasmobranch fisheries (FAO, 2000; Walker, 2005).

Fishery data are considered “a vital component of the fishery management process” (Morgan and Burgess, 2005), and analyses of historical time series may highlight decreases in populations that could otherwise have gone unnoticed (Casey and Myers, 1998). Official landing data have several limitations, among which are the aggregation of data in multispecies categories, underestimation of the catch due to the unregistered discard of undersized elasmobranch and to unreported catch, and, in many cases, no estimation of fishing effort (Bonfil, 1994; Morgan and Burgess, 2005). However, official data can constitute an invaluable aid in highlighting population trends, supporting the data collected with research trawls, in most cases necessarily performed on small spatial and temporal scales.

This chapter aims to describe the status of elasmobranch fishery in the Northern Adriatic Sea using data from the fish market of Chioggia, home of the major fishing fleet of the area. First, trends in one of the longest time series of landing statistics (1945-2008) are analysed; second, landing fluctuations in relation to climate indices, river flow rate and water temperature are analysed; third, the current elasmobranch landing composition is assessed in terms of species, sex-ratio, size-frequency distribution and, for males, stage (mature vs immature); and, fourth, for two species, on the basis of the collected data, a demographic model to predict population trends under different management scenarios is developed.

## 5.2 Materials and methods

### 5.2.1 Fishery landing data

Official landing data from Chioggia’s fishery fleet were obtained from the Chioggia fish market. Data (in kilograms live weight) were available yearly from 1945 to 2008, and monthly from 2005 to 2008. Species were aggregated in broad categories varying between years. From 1945 to 1996 elasmobranchs were reported grouped into three main categories: “Asià” (*Mustelus* spp., *Squalus* spp., and other four shark species), “Razze” (*Raja* spp.) and “Gattucci” (*Scyliorhinus* spp.); while from 1997 elasmobranchs were recorded in eight categories, according to the genus (Table 8). *Alopias vulpinus* was occasionally reported separately also before 1997. In addition, the *Myliobatis aquila* (“Colombi”) catch was occasionally reported, with negligible quantity, and, at times, a category of sharks without skin (“Cani spellati”) was recorded. *M. aquila* was added to *Raja* spp. data, while “Cani spellati” to the “Asià” or “Cani palombi” category, depending on the period.

The Chioggia fleet is the major fishery of the Northern Adriatic Sea (Granzotto et al., 2006) and, in 2007, comprised ca. 389 fishing boats, mainly fishing the northern part of the Adriatic, even if a few boats trawl further afield. The fishing vessels are equipped with one or more types of fishing gear: hydraulic dredges, mid-water trawlers, otter trawlers and beam trawlers and/or with artisanal fishing

equipment such as traps, gill nets, etc. (data from the Chioggia Coast Guard). No long-term data on variation in fleet composition and the fishing equipment employed are available. As a consequence, catch per unit of effort was not calculated. Fishing capacity was available only for the period 1997-2008, expressed as number of boats, fleet tonnage (GRT) and fleet power (Hp). Since results of trends in time of landing data corrected for any measure of fishing capacity were not different from those of uncorrected data (results not shown), for uniformity with data referring to landing before 1997 only the results for landings uncorrected for fishing capacity are reported.

Using fish market statistics, the 2007 landings were attributed to the different fishing equipment employed, to estimate the contribution of fishing gear to the catch of each category.

Table 8. Categories of elasmobranchs registered at the Chioggia fish market during the two periods: 1945-1996 and 1996-2008

Species	Categories 1945-1996	Categories 1997-2008
<i>Alopias vulpinus</i>	“Asia”	“Cani volpe”
<i>Galeorhinus galeus</i>	“Asia”	“Cani canesca”
<i>Lamna nasus</i>	“Asia”	“Cani smeriglio”
<i>Myliobatis aquila</i>	“Razze”	“Razze”
<i>Mustelus</i> spp.	“Asia”	“Cani palombo”
<i>Prionace glauca</i>	“Asia”	“Cani verdesca”
<i>Raja</i> spp.	“Razze”	“Razze”
<i>Scyliorhinus</i> spp.	“Gattucci”	“Cani gattuccio”
<i>Squalus</i> spp.	“Asia”	“Cani spinarolo”

### 5.2.2 Environmental data

Landings were compared to environmental variables over the long-term: annual mean of sea water temperature (°C) measured at 2 m depth at Trieste (Stravisi, 2009) from 1945-2008; annual mean discharge of the Po river ( $\text{m}^3 \text{s}^{-1}$ ) measured at Pontelagoscuro (Ferrara) from 1937-2008 (data retrieved in June 2009 from the Global River Discharge Database, <http://www.sage.wisc.edu/riverdata/>; Tartari et al., 1991; ARPA Idrometeo Emilia Romagna, pers. comm.); and climate variability using the North Atlantic Oscillation index (NAOi, annual mean) and the winter (December to February) Western Mediterranean Oscillation Index (WeMOi), 1937-2008. Years before 1945 were included only in time-lag analyses.

NAOi is the normalized pressure difference between Gibraltar and SW Iceland (Jones et al., 1997; data retrieved in June 2009 from <http://www.cru.uea.ac.uk/cru/data/nao.htm> and [http://www.cru.uea.ac.uk/~timo/projpages/nao\\_update.htm](http://www.cru.uea.ac.uk/~timo/projpages/nao_update.htm)). In the Northern Adriatic Sea, NAOi positively correlates with surface temperature (Supic et al., 2004). WeMOi (Martin-Vide and Lopez-

Bustins, 2006; data from 2001 to 2008 provided by J.A. Lopez-Bustins) is the difference in the standardized values between surface atmospheric pressure in San Fernando (Spain) and Padua (Italy, 35 km from Chioggia). Although the relationship between this index and the properties of the Northern Adriatic Sea has not been analyzed yet, during winters characterized by a strongly positive WeMOi there is a deep low pressure over the Gulf of Genoa, hence mild and wet winter weather over northern Italy, which might lead to warmer and less salty water in the Northern Adriatic Sea. In a negative phase of the WeMOi, Northern Italy is under the influence of the winter anticyclone of Central Europe, leading to dry and cold conditions over the Northern Adriatic Sea, that is, colder and saltier water (J.A. Lopez-Bustins, pers. comm.).

### 5.2.3 Fish market surveys

From October 2006 to July 2007 the fish market was visited weekly or twice a week, to estimate catch composition, assess sex, measure individual sizes, and estimate the percentage of sexually mature males. A total of 79 assessments were undertaken either at the night- or the day-selling auctions, when fish are sold in the wholesale fish market. All landed elasmobranchs were identified. All individuals of each species or, in a few surveys, when the time allowed by the fish market operators was not enough to sample all landed elasmobranchs, a random subsample of individuals, were sexed and/or measured. Sex was attributed based on the presence of claspers in the pelvic fins in males.

Measurements, taken with a meter to the nearest mm, included: for sharks: total length (TL, from the tip of the snout to the end of the caudal fin), standard length (SL, from the tip of the mouth to the beginning of the caudal fin), and, for males, length of the claspers (CL, from the posterior edge of the cloaca to the tip of the clasper, Conrath, 2005); for skates: TL (from the tip of the rostrum to the end of the tail), disk width (DW, distance between the tips of the widest portion of pectoral fins), and, for males, CL (as above). Sexual maturity in males was attributed on the basis of the length of claspers relative to the pelvic fins: a male was considered sexually mature if the claspers were rigid, due to calcification, and at least 1.5 cm longer than the pelvic fins (Lucifora et al., 2002; Conrath, 2005; Demirhan et al., 2005; Sulikowski et al., 2006; Barone et al., 2007; Capapé et al., 2008; Saïdi et al., 2008). This method of assessing sexual maturity, not supported by the analysis of testes and ductus deferens, could attribute the status of “mature” to individuals actually “maturing” (Conrath, 2005; Capapé et al., 2008; Saïdi et al., 2008), consequently over-estimating the number of mature males, however it was the only feasible way given that the fish arrive at the market eviscerated. Similarly, since individuals were eviscerated, it was not possible to attribute sexual maturity to females.

#### 5.2.4 Data analyses

All data are reported as mean  $\pm$  standard deviation. Parametric or non-parametric tests were applied according to data distribution and test assumptions. When appropriate, data were log-transformed.

The non-parametric Mann-Kendall test (Gilbert, 1987) was employed to detect temporal trends in the annual landing data categories and, if statistically significant, slopes were computed with Sen's robust estimator (Gilbert, 1987). Given the inconsistency in aggregating species into categories, a first analysis was performed on the whole data set, applying the broad categories used up to 1996 to the more recent data, while a second analysis was employed for the data from 1997 to 2008, using eight categories. Because of strong biases (see Section 5.3), data from the "Asià" category from 1986 to 1993 were excluded from the trend analysis. Similarly, data from 1986 to 1993 were excluded also in the analyses of total elasmobranch landings. Substituting missing data with a linear interpolation from 1985 to 1994 did not change results. Trends were analysed separately before 1986 and after 1993.

To analyse periodicities in annual (1945-2008) and monthly landing time series, a spectral analysis based on Fast Fourier Transform (FFT) was carried out (Bloomfield, 2000). Total elasmobranch and "Asià" were analysed only until 1985. As a pre-treatment, each time series was linearly detrended and, if necessary, padded with zeros (Bloomfield, 2000). Only oscillation periods up to a quarter of the length of the time series were considered (Legendre and Legendre, 1998). Trawling is banned during August giving us data for the month not comparable with those of the other months. Therefore, monthly data was analysed after substituting the average of the July and September landings, for each year, with that of August.

Time trends in environmental variables were tested with the non-parametric Mann-Kendall test. Correlations from 1945-2008 among environmental variables and between environmental variables and the three main categories of annual landings were estimated with the non-parametric Spearman rank correlation coefficient  $r_s$  (Legendre and Legendre, 1998), since some time series were not normally distributed even after transformations. Landings for "Asià" sharks from 1986 to 1993 were considered missing data. Bonferroni correction for multiple testing was applied (Legendre and Legendre, 1998), leading to significance levels  $\alpha = 0.05 / 6 = 0.008$  and  $\alpha = 0.05 / 12 = 0.004$  for correlations among environmental variables, and between landings and environmental variables respectively. The correlation between the moving averages of landings, and environmental variables that showed the strongest correlations from the previous analyses, was also calculated (Legendre and Legendre, 1998) to highlight possible correspondences between their long-term trends. The window of the moving average was chosen as the integer period closest to the period of the strongest fluctuating component of each time series, as identified by the FFT analyses.

Finally, a delayed effect of environmental variables on fish biomasses was tested with Spearman correlation coefficients using the three main annual landing categories (1945-2008) and forward-lagged environmental variables. Lags ranged from one to six years in order to find a compromise between the number of tests made and the slow growth of elasmobranch. The Bonferroni correction was conservatively applied leading to a significance level  $\alpha = 0.05 / 6 = 0.008$ .

Results of correlations between environmental variables and landings were also calculated excluding the last 15 years for skates and the last 22 years for *Scyliorbinus* spp., since these categories showed a marked final decrease in landings (see Section 5.3). If correlations disappeared, the results were considered spurious being driven only by the marked landing trends.

TL and SL highly correlated in shark species (all  $r > 0.95$ ,  $p < 0.0001$ ), while DW highly correlated with TL in skates (all  $r > 0.93$ ,  $p < 0.0001$ ). TL was therefore used in the analyses. Analyses were performed only for species presenting a sample size of measured individuals  $> 100$ . Descriptive data only are reported for the other species. Similarly, tests of differences were not applied if within a group the sample size was  $< 15$ . For each species, differences from an expected sex-ratio of 1:1 were checked with the Chi-square test, and differences in size between sexes were analysed with the Mann-Whitney U-test or t-test

Since no significant differences were found between left and right claspers (for all the species,  $p > 0.135$ ) and their length highly correlated (for all the species,  $r > 0.98$ ,  $p < 0.0001$ ), the average of the left and right claspers was calculated and used in the analyses. To check the attribution of sexual maturity to males based only on clasper characteristics, an ANCOVA analysis of covariance was applied to CL with maturity as grouping variable and male size (TL) as covariate, with the expectation that the achievement of sexual maturity implied a change in CL relative to male size (Conrath, 2005; Sulikowski et al., 2006; Saïdi et al., 2008). Moreover, size differences between immature and mature males were tested with the Mann-Whitney U-test or t-test. The percentage of mature individuals was computed for 3 cm intervals of TL, and a logistic ogive was fitted to the data to estimate the size at which 50% of individuals ( $TL_{50}$ ) were sexually mature (Conrath, 2005).

### 5.2.5 Demographic models

To simulate present and future trends of elasmobranch populations, an Individual-Based Model (IBM) was set up. Such models have been widely used to study fish population dynamics (e.g. van Winkle et al., 1993; Rose et al., 1999; Hall et al., 2006; Russo et al., 2009) and have the advantage over classical population dynamics models in considering the uniqueness and variability of individuals (Grimm, 1999). The model was written in MATLAB® (v7.02).

Due to data availability, the IBM was set up only for two species, a viviparous species (*M. mustelus*) and an oviparous one (*S. canicula*). The model is a 0D model aimed to reproduce, with a

monthly timestep, the basic life-cycle of any single individual (growth-reproduction-death). All parameters and the main assumption are listed in Table 9. Given that males are able to inseminate more than one female each month, it was assumed that in the system there will be always enough males to guarantee the fecundation of females, then only females were considered in the models.

Growth was simulated with the Von Bertalanffy growth function. Reproduction was considered only for individuals longer than the species' length at maturity. It was assumed that *M. mustelus* females had equal probability of being fecundated each month of the mating season (May-June, Saïdi et al., 2008). Once fecundated, a female gave birth to a random number of juveniles: this number was extracted from a normal distribution with a fixed standard deviation (0.7, corresponding to a maximum range of  $\pm 2$  individuals) and the average varying with the length ( $juv = 0.256 \cdot TL - 23.48$  from Saïdi et al., 2008). The birth occurred after 9-11 months (with equal probability, Saïdi et al., 2008; Smale and Compagno, 1997). During the year, a female of *S. canicula* laid a random number of eggs each month with a mean that was linearly dependent on its size (Capapé, 1977) and on the probability of finding females bearing eggs in that particular month (Capapé et al., 2008), and a standard deviation of 0.7 ( $= \pm 2$  eggs). The eggs hatched after 5-11 months (mean incubation period of 8.5 months) and were predated with a rate of  $2.99 \text{ y}^{-1}$  (Frisk et al., 2004). Sex ratio of juveniles was 1:1.

Table 9. Parameters used in the Individual Based Model.

	<i>Mustelus mustelus</i>	<i>Scyliorhinus canicula</i>
VBGF parameters	$L_{\infty} = 205 \text{ cm}^a$	$L_{\infty} = 56.8 \text{ cm}^d$
	$K = 0.06 \text{ y}^{-1}^a$	$K = 0.23 \text{ y}^{-1}^e$
	$t_0 = -3.55 \text{ y}^a$	$t_0 = -0.85 \text{ y}$
Length at maturity	$L_m = 117 \text{ cm}^b$	$L_m = 44 \text{ cm}^{a,f}$
Natural mortality rate	$M = 0.05 \text{ y}^{-1}^c$	$M_{\infty} = 0.23 \text{ y}^{-1}{}^g$ (the value has been raised at 0.27)
Fishing mortality rate	$F = 0.05 \text{ y}^{-1}$ , distributed monthly on the basis of observed data	$F = 0.39 \text{ y}^{-1}$ , distributed monthly on the basis of observed data
Mating/laying season	May-June <sup>b</sup> , with equal probability each month	During all the year <sup>f</sup>
Fecundity	4-18 embryos per year depending on size <sup>b</sup> , sex ratio 1:1	38-115 eggs per year, depending on size, not uniformly distributed in time <sup>f</sup> , sex ratio 1:1. Predation rate on eggs = $2.99 \text{ y}^{-1}{}^h$

<sup>a</sup> Froese and Pauly, 2010; <sup>b</sup> Saïdi et al., 2008; <sup>c</sup> Serena et al., 2004; <sup>d</sup> Zupanovic, 1961; <sup>e</sup> Rodriquez-Cabello, 2005; <sup>g</sup> Frisk et al., 2001; <sup>f</sup> Capape' et al., 2008; <sup>h</sup> Frisk et al., 2004

For both species, any individual could die any month due to natural mortality (disease, predation, senescence) and/or fishery. Natural mortality rate for *M. mustelus* was assumed equal to  $0.05 \text{ y}^{-1}$  (Serena et al., 2004) and to be constant, given that predation on juveniles is not higher than the one

on adults because of the large size at birth (34-42 cm, Saïdi et al., 2008). In contrast, predation on the juveniles of *S. canicula* is considerable and hence the mortality rate was assumed as a function of length (Gulland, 1987; Lorenzen, 2000):

$$M(L) = M_{\infty} \left( \frac{L_{\infty}}{L} \right)^c \quad (5)$$

where  $M$  is the mortality rate at length  $L$ , and  $M_{\infty}$  is the mortality rate estimated for the Von Bertalanffy maximum length  $L_{\infty}$ . In a first stage, the allometric exponent  $c$  was set to 1 (Lorenzen 2000) and  $M_{\infty}$  to 0.23 (Frisk et al., 2001).

When an individual reached the maximum observed length, it died. Due to the size range, *M. mustelus* is fished from birth, while *S. canicula* is fished only if it is longer than 380 mm, as observed in this study. The annual fishing mortality rate,  $F$ , was estimated via a best fitting of the model results to the landings from 1998-2008 (when *Mustelus* spp. were grouped in a separate category from other sharks; it is assumed that the proportion of species within categories did not change consistently in the considered period), assuming that landing trends reflect abundance trends (see Section 5.2 and 5.4). The monthly distribution of observed landings was applied to modulate  $F$  to reflect monthly variability in landings.

The mortality of small discarded *S. canicula* was discounted, given their high survival rate (Revell et al., 2005). The annual mortality rate was modulated based on the average monthly data of observed landings.

The annual mortality rates were converted into a monthly probability,  $p$ , of death using the following equation:  $p = \frac{2R}{24 + R}$ , where  $R$  is the generic mortality rate.

To simulate the population dynamics of both species, the IBM was executed for all of the individuals of the initial population (arbitrarily set equal to 500 individuals for both species) and all the offspring for 50 years. The size-spectrum of the initial *M. mustelus* population was derived from fish market surveys (under the assumption that landings size-spectrum is similar to the population one) and that of *S. canicula* from Abella and Serena (2005) (given that all the smaller juveniles are not represented in the landings size-spectrum). Due to the stochasticity of the model, this procedure was repeated 20 times in order to represent a statistically consistent trend of the population.

Finally, the model was used to forecast two simple scenarios, thus assessing the potential impact of two different fishery management strategies:

- minimum catch size: in this scenario it is assumed that any individual caught before maturity would be discarded and survive, hence the probability of being fished was evaluated by the model for mature individuals only;

- day-off: in this scenario the fishing effort is recalculated assuming that fishermen work only 4 days per week instead of 5. This does not imply a reduction of 20% in the annual fishing rate because the fishery is closed during August and the 4-days policy is already in force during September, so the 20% reduction was applied monthly only when necessary.

### 5.3 Results

#### 5.3.1 Fishery landing data

Between 1945 and 2008, the total official landings of elasmobranchs in the Chioggia fish market declined significantly (Mann-Kendall  $Z = -6.90$ ,  $p < 0.0001$ , Sen's slope =  $-1\,755.9\text{ kg y}^{-1}$ ), with the catch in each of the last five years representing a reduction of 85.6% compared to the 1940s (Figure 15). The post-1993 decline ( $Z = -3.91$ ,  $p < 0.0001$ , Sen's slope =  $-2\,742.5\text{ kg y}^{-1}$ ) is much stronger than before 1986 ( $Z = -3.17$ ,  $p = 0.0015$ , Sen's slope =  $-1\,122.5\text{ kg y}^{-1}$ ).

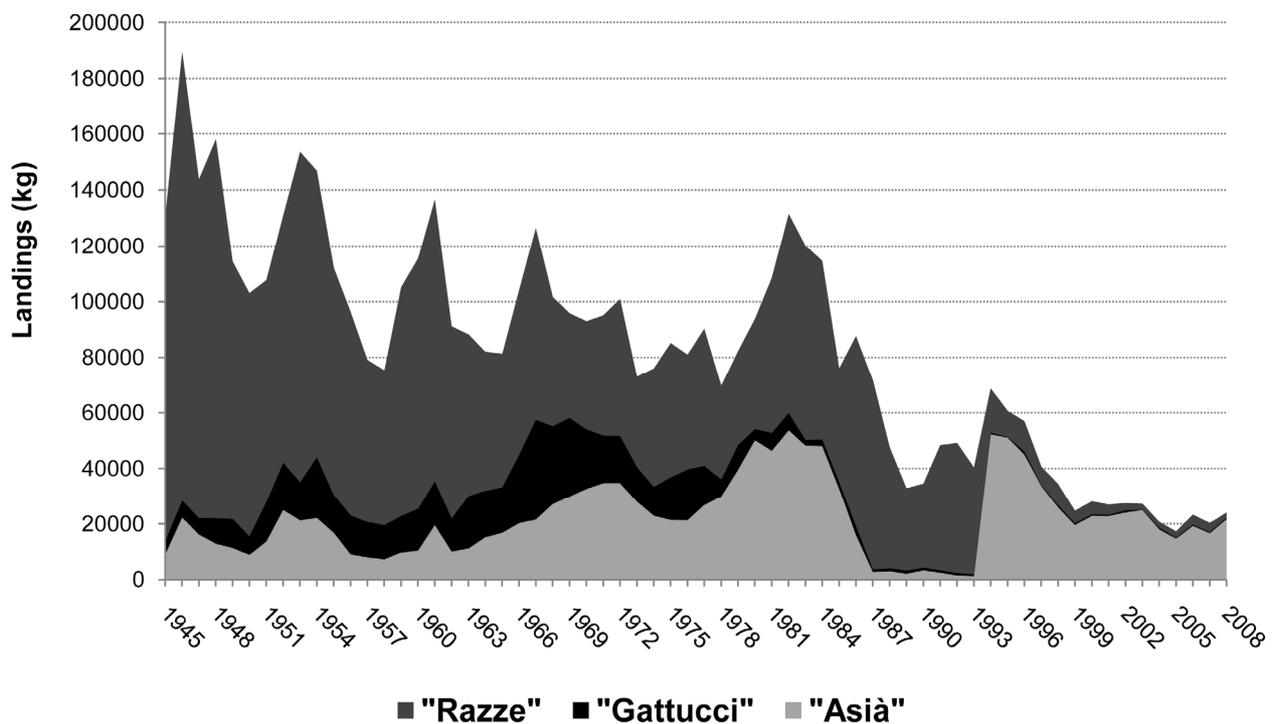


Figure 15. Yearly landing data of elasmobranch from 1945 to 2008 at Chioggia's fish market. Landing is grouped in three categories: "Razze" (*Raja* spp.), "Gattucci" (*Scyliorhinus* spp.), "Asià" (*Mustelus* spp., *Squalus* spp., *Alopias vulpinus*, *Galeorhinus galeus*, *Lamna nasus*, *Prionace glauca*). "Razze" and "Gattucci" showed a marked decrease in landing, while "Asià" showed a positive trend before 1986 and negative after 1993. From 1986 to 1993 the quantities of landing of "Asià", close to zero, were biased due to unreported landing.

Considering the three broad categories (“Asià”, “Gattucci” and “Razze”), the skates showed the most dramatic reduction ( $Z = -8.44$ ,  $p < 0.0001$ , Sen’s slope =  $-1\,584.6\text{ kg y}^{-1}$ ), representing only 2.1% of the average 1940s catch in each of the last five years. Since 1994, landings have been particularly low. *Scyliorhinus* spp. showed a similar reduction ( $Z = -6.50$ ,  $p < 0.0001$ , Sen’s slope =  $-268.4\text{ kg y}^{-1}$ ), representing 6.2% of the average 1940s landing. The category “Asià”, including all the other sharks, showed a weak but significant increase in landing ( $Z = 3.68$ ,  $p < 0.001$ , Sen’s slope =  $303.2\text{ kg y}^{-1}$ ). From 1986 to 1993 the category “Asià” showed an abrupt decrease in landing, falling close to 0 (Figure 15). This is related to a law introduced in those years compelling the analysis of mercury concentration in shark meat that could not exceed 0.7 ppm. In 1992 the law was changed, requiring the analysis of mercury concentrations only on large sharks and raising the acceptable threshold to 1 ppm. As a consequence, from 1986 to 1993 sharks were, for the most part, sold illegally, while after 1993 they were again registered in the fish market statistics (Lanfredi C. and Mazzoldi C., interviews with fishermen, unpublished). “Asià” landings increased before 1986 ( $Z = 5.23$ ,  $p < 0.0001$ , Sen’s slope =  $847.3\text{ kg y}^{-1}$ ) and then strongly declined after 1993 ( $Z = -3.51$ ,  $p < 0.001$ , Sen’s slope =  $-1\,947.9\text{ kg y}^{-1}$ ).

In general, landing composition changed strikingly from a predominance of skates in the 1940s (85.31%), to a predominance of “Asià” between 2004 and 2008 (85.34%). *Scyliorhinus* spp. represented 4.95% of the 1940s catch, and represents 2.15% today (Figure 15).

All three categories exhibited periodic peaks in landings over the period 1945-2008 (Figure 15). Spectral analysis reveals that skate landings showed a strong periodicity of about 7 years, which became less regular and pronounced after 1969 and then disappeared after 1994. *Scyliorhinus* spp. showed a 13.5 year and a less pronounced 8.3 year periodicity, but after 1977 landings declined markedly and the oscillations disappeared. From 1945-1985, the composite group of “Asià” sharks showed a main periodic component of period 9 years and a less pronounced one of 7 years.

Considering the data from 1997 to 2008, the *Mustelus* spp. category represented, on average, 69.7% of the total landing, *Squalus* spp. 13.4%, *Scyliorhinus* spp. 1.9%, skates and rays 14.6%, while all other elasmobranchs together made up less than 0.5%. From 1997 to 2008, *Squalus* spp. showed a significant decline ( $Z = -2.61$ ,  $p = 0.0092$ , Sen’s slope =  $-173.2\text{ kg y}^{-1}$ ), while *Mustelus* spp. exhibited a negative, if not quite significant, trend ( $Z = -1.65$ ,  $p = 0.1$ ).

FFT analysis of monthly landings from 2005 to 2008 (Figure 16) highlighted a 12-month periodicity for *Squalus* spp. (which also displayed a weaker 6-month periodicity), *Mustelus* spp. and *Scyliorhinus* spp. Records of *Prionace glauca* and *Alopias vulpinus* were too scanty to allow for analysis. *Raja* spp. landings showed a 12 month-period oscillation conspicuous in a main landing peak from April to July. *Mustelus* spp. was mainly landed from April to November, while *Scyliorhinus* spp. and *Squalus* spp. were generally fished from October to July.

Most elasmobranchs are landed as bycatch (89.1 ± 9.9 %, range: 78.4 – 100 %): *Mustelus* spp., *Scyliorhinus* spp. and skates as the bycatch of otter and beam trawling, and *Squalus* spp. and *A. vulpinus* of mid-water trawling. Instead the artisanal fishery, periodically targeting elasmobranchs, contributes little to the total catch (Figure 17).

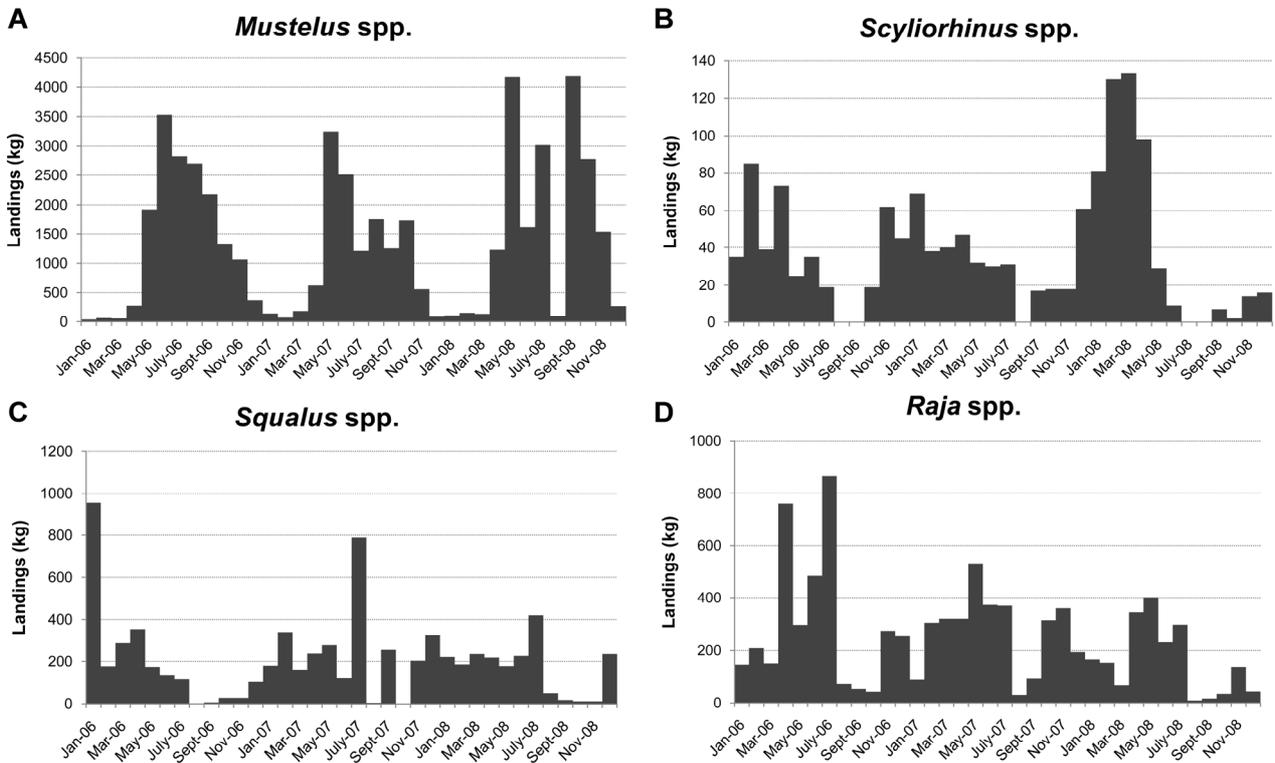


Figure 16. Monthly landing (2006-2008) of (A): *Mustelus* spp.; (B) *Scyliorhinus* spp.; (C) *Squalus* spp.; (D) *Raja* spp. All groups showed seasonal variations in landing.

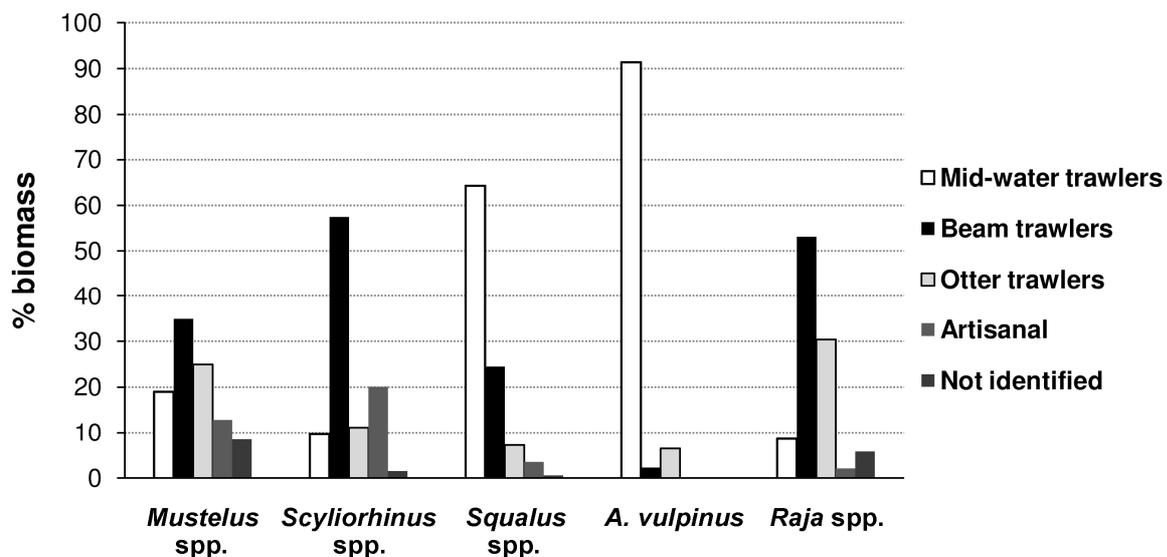


Figure 17. Biomass percentages of the different elasmobranch species caught with different fishing gears (data from 2007). All species were mainly caught as bycatch of either mid-water or bottom trawlers.

### 5.3.2 Environmental data and relationship with elasmobranch landings

From 1945 to 2008, water temperature increased ( $Z = 3.22$ ,  $p = 0.0013$ , Sen's slope =  $0.0119^{\circ}\text{C y}^{-1}$ ) and WeMOi decreased ( $Z = -2.51$ ,  $p = 0.012$ , Sen's slope =  $-0.0109 \text{ y}^{-1}$ ). Po River inflow ( $Z = 0.90$ ,  $p = 0.37$ ) and NAOi ( $Z = -1.69$ ,  $p = 0.091$ ) did not show clear trends. Environmental variables were not correlated (Annex II, Table A2.1).

All correlations between water temperature and landings were disregarded as they were not significant excluding from the analyses the last few years. At zero time lag, skate landings showed a clear positive relationship with WeMOi ( $r_s = 0.38$ ,  $p = 0.0019$ ; the correlation was significant for long-term trends also, i.e. 7-year moving average for skates, and 5-year for WeMOi:  $r_s = 0.73$ ,  $p < 0.0001$ , Figure 18a) and there was a close-to-significant positive correlation with NAOi ( $r_s = 0.34$ ,  $p = 0.0064$ ; also considering long-term trends, i.e. 4-year moving average for NAOi, skates as above:  $r_s = 0.49$ ,  $p < 0.0001$ , Figure 18b). “Asià” and *Scyliorhinus* spp. sharks did not correlate with any variables. All the zero time-lag correlation coefficients are reported in the Table A2.1 (Annex II). Forward-lagged Po discharge, NAOi and WeMOi did not correlate with any landing category (not shown), with three exceptions: Po River discharge at 1-year lag with “Asià” sharks ( $r_s = 0.40$ ,  $p = 0.002$ ), WeMOi at 1-year lag with skates ( $r_s = 0.33$ ,  $p = 0.008$ , possibly a spurious consequence of the stronger correlation of skates and WeMOi at zero time lag and of autocorrelation), and WeMOi at a 5-year lag with “Asià” sharks ( $r_s = -0.37$ ,  $p = 0.005$ ).

### 5.3.3 Fish market surveys

A total of 2770 individuals were sampled at the fish market, 2339 sharks and 431 skates, belonging to 13 species, with *M. mustelus* as the most abundant species (Table 10). In all the species with enough data available (*M. mustelus*, *M. punctulatus*, *S. acanthias*, *R. asterias*, and *R. clavata*) immature males were significantly smaller than mature ones (in all the species,  $p < 0.0001$ ) and clasper lengths were significantly larger in mature males than in immature ones, taking into account male size (in all the species  $P < 0.036$ , Annex II, Table A2.2). Minimum size at maturity and  $TL_{50}$  are reported in Table 11 in comparison with published data. No estimates were made for  $TL_{50}$  of *M. punctulatus* and *S. canicula* due to the low number of mature males and, in the latter species, the high size overlap between mature and immature males. Sex-ratio significantly differed from an expected 1:1 in *M. mustelus* (M:F = 1.25:1,  $\chi^2_1 = 21.31$ ,  $p < 0.0001$ ), *S. canicula* (M:F = 0.54:1,  $\chi^2_1 = 14.88$ ,  $p = 0.0001$ ), *S. acanthias* (M:F = 1.36:1,  $\chi^2_1 = 5.49$ ,  $p = 0.019$ ) and *R. clavata* (M:F = 0.59:1,  $\chi^2_1 = 10.07$ ,  $p = 0.001$ ). Males were slightly but significantly larger than females in *M. mustelus* ( $t_{826} = 2.83$ ,  $p = 0.005$ ) and *R. asterias* ( $t_{215} = 3.46$ ,  $p = 0.001$ ), however size ranges widely overlapped between sexes. In all the other species, the sex-ratio did not differ from 1:1 (for all the species,  $p > 0.347$ ), and sexes did not differ in size (for all the species,  $p > 0.075$ ).

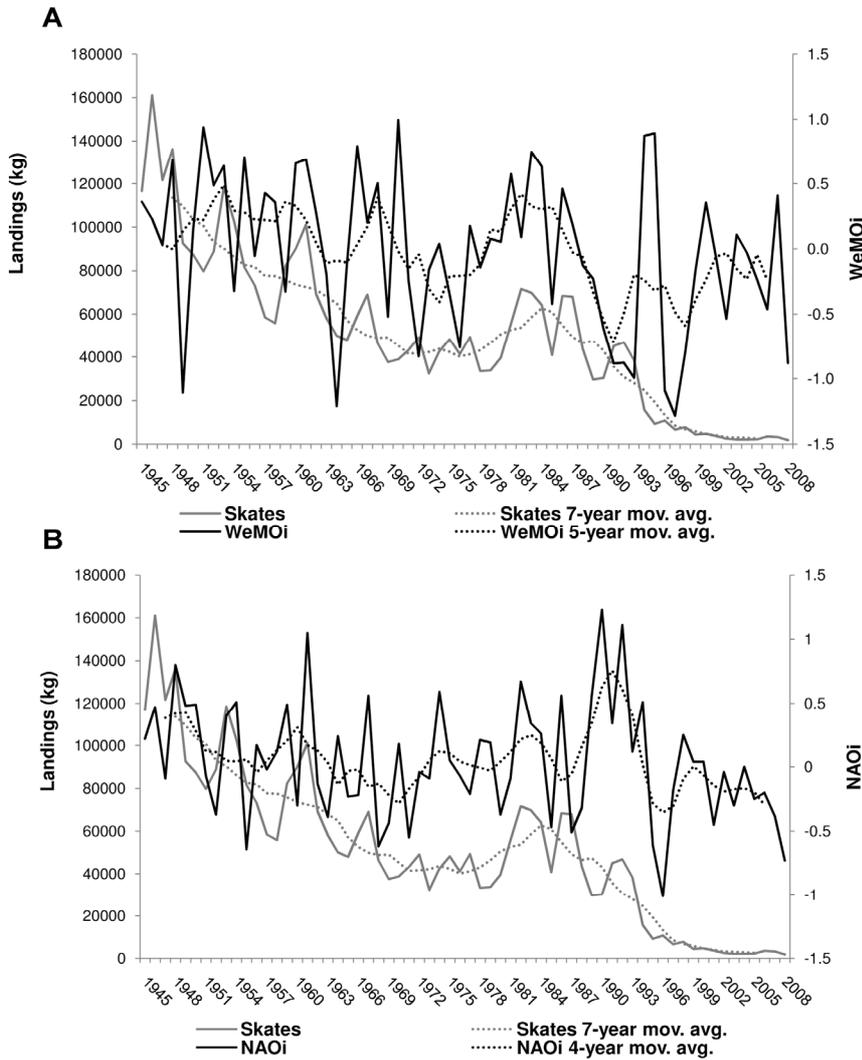


Figure 18. Landings time series of skates and environmental variables (A: WeMOi, B: NAOi). WeMOi: winter Western Mediterranean Oscillation Index; NAOi: annual mean of the North Atlantic Oscillation Index. Data are reported as annual value and moving average (mov. avg.).

Very few individuals of the remaining species were recorded at the fish market. While specimens of *S. stellaris* were found throughout the sampling period, all *M. asterias* samples were found on the same sampling day in October, the five specimens of *A. vulpinus* were noted in June and July, and most of the samples of *R. miraletus* in March. The fifteen samples of *M. aquila* were found between May and July and sexual maturity was attributed to only one immature male.

Table 10: Fish market samples. Number (N) and size (TL) of males and females for each species, their relative percentage in the whole sample and the percentage of immature males in the samples are reported. In parentheses the number of the subsample of measured specimens is reported. For species with less than three specimens, individual sizes are directly reported.

Species	Males		Females		N total	%	%
	TL (mm)	N	TL (mm)	N			
<i>Alopias vulpinus</i> (Bonaterre, 1788)	1700 / 1820	2	1444.7 ± 81.6	3	5	0.18	100
<i>Galeorhinus galeus</i> (Linnaeus, 1758)	642	1		0	1	0.04	100
<i>Mustelus asterias</i> (Cloquet, 1821)	770 / 790	2	770 / 780	4	6	0.22	0
<i>Mustelus mustelus</i> (Linnaeus, 1758)	780.5 ± 219.5	942 (467)	744.0 ± 248.5	752 (361)	1694	61.15	62.4
<i>Mustelus punctulatus</i> (Risso, 1826)	653.4 ± 154.5	110 (63)	594.3 ± 92.7	101 (61)	211	7.62	83.6
<i>Scyliorhinus canicula</i> (Linnaeus, 1758)	430.4 ± 32.6	59 (45)	432.2 ± 44.5	109 (99)	168	6.06	86.7
<i>Scyliorhinus stellaris</i> (Linnaeus, 1758)	743.0 ± 101.6	8	618.1 ± 165.0	9 (8)	17	0.61	25.0
<i>Squalus acanthias</i> (Linnaeus, 1758)	632.1 ± 89.7	136 (95)	640.5 ± 158.4	100 (56)	236	8.52	47.8
<i>Squalus blainville</i> (Risso, 1826)		0	980	1	1	0.04	-
<i>Raja asterias</i> (Delaroche, 1809)	509.7 ± 129.7	120 (108)	451.7 ± 110.1	124 (109)	224	8.81	57.5
<i>Raja clavata</i> (Linnaeus, 1758)	630.4 ± 149.8	56 (46)	668.9 ± 174.7	95 (68)	151	5.45	33.9
<i>Raja miraletus</i> (Linnaeus, 1758)	387.5 ± 49.4	10	404.1 ± 70.0	11 (7)	21	0.76	30.0
<i>Myliobatis aquila</i> (Linnaeus, 1758)		4 (0)		11 (0)	15	0.54	-

Table 11: Estimated male minimum size at maturity (TL min.) and size at which 50% of males are sexually mature (TL<sub>50</sub>) in the present study and in literature. For a better comparison, in parentheses, with reference, the study area is reported.

Species	Present study		Literature data		Reference
	TL min. (mm)	TL <sub>50</sub>	TL min. (mm)	TL <sub>50</sub>	
<i>M. mustelus</i>	665	830	880	971	Saïdi et al., 2008 (Southern Mediterranean)
<i>M. punctulatus</i>	757	-	760	814	Saïdi et al., 2009 (Southern Mediterranean)
<i>S. canicula</i>	410	-	430/340*	-	Capapè et al., 2008 (North-western Mediterranean); * Zupanovic, 1961 (Adriatic)
<i>S. acanthias</i>	555	566	670	820	Avsar, 2001 (Black Sea)
<i>R. asterias</i>	420	576	450	517/505*	Barone et al., 2007; *Romanelli et al., 2007 (North-western Mediterranean)
<i>R. clavata</i>	480	619	470	593	Krstulović Šifner et al., 2009 (Northern and Central Adriatic Sea)

#### 5.3.4 Demographic models

A good fit between model and observed data was obtained for the *M. mustelus* population, setting the fishing mortality at 0.23 which is in line with published estimates (e.g. Barausse et al., 2009; Chapter 3).  $M_{\infty}$  was increased to 0.27 to obtain a good fit for *S. canicula* without imposing an extremely high  $F$  value. The increase of 17% in the parameter is reasonable given the uncertainty related to the empirical relationship suggested by Frisk et al. (2001) and to the VBGF growth rate (Rodriguez and Cabello, 2005). In such a way  $F$  could be fixed to the reliable value of 0.39 and the ratio  $F/Z=0.6$ , in line with the estimate in Chapter 3 and Barausse et al. (2009) and lower than the estimate provided by other authors for the same species (Sanchez and Olaso, 2004).

The model emphasizes the declining trend of the *M. mustelus* population, forecasting a reduction of 80% over the next 50 years. The collapse of the *S. canicula* population would be even more dramatic with the population potentially plummeting to less than 10% of its current level in 50 years, almost reaching local extinction (Figure 19a,b). Oscillations with a period of approximately 8 years are evident in the *S. canicula* population: the amplitude is decreasing with time (i.e. with total population) and is lower for the catchable population. Such oscillations could be a computational artifact, but they can also be seen in the fish market landings, so that they could reflect real population cycles.

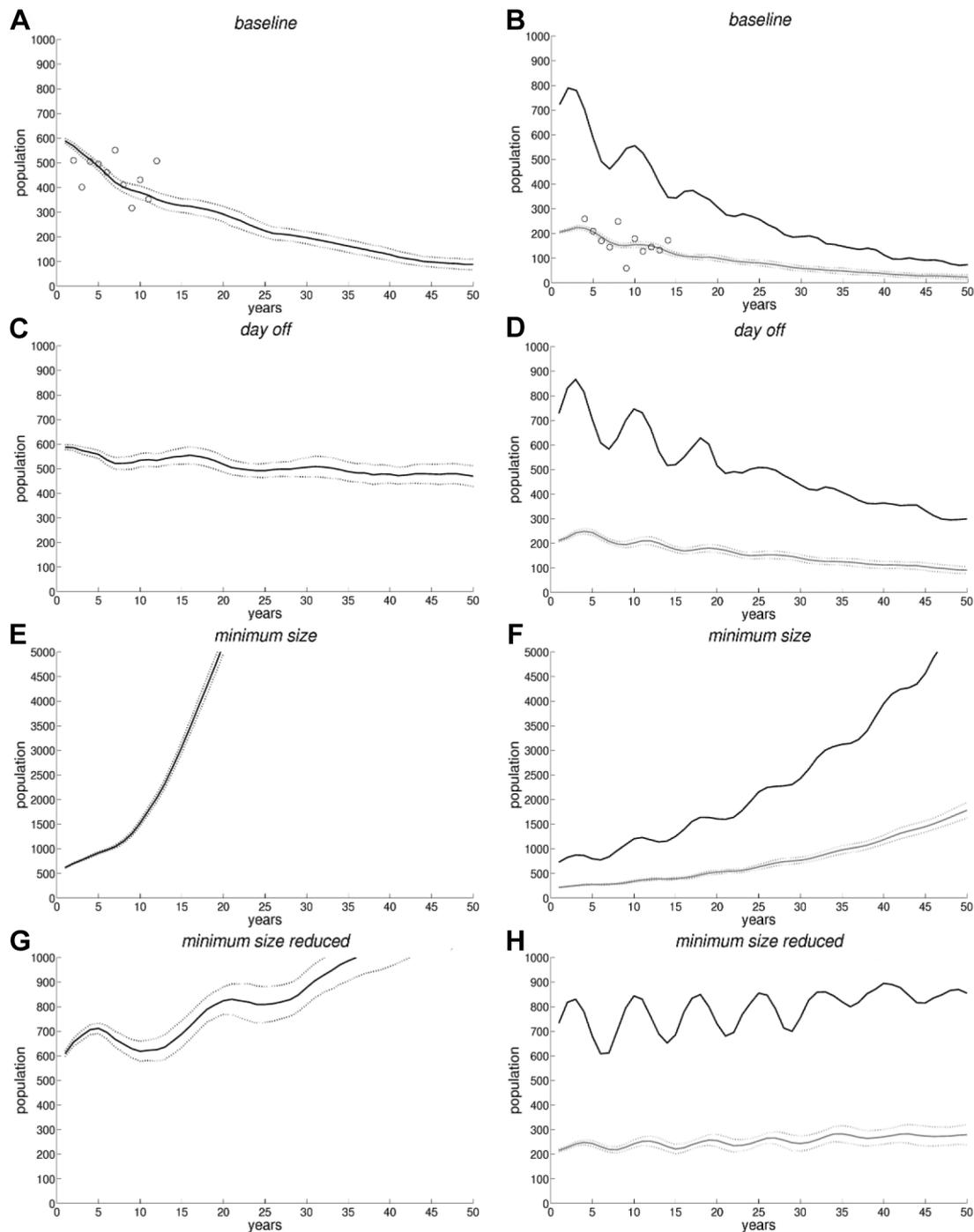


Figure 19. Future projections of populations of *M. mustelus* (left) and *S. canicula* (right) as forecast by the model. A and B no management (or baseline) scenarios, C and D day-off scenario, E and F minimum-size catch scenario with threshold at length at maturity, G and H minimum-size catch scenario with threshold defined to obtain the same reduction in landings as in the day-off scenario. Solid blacklines are total population, solid grey lines are population of *S. canicula* over 380 mm (i.e. catchable population under current regulations). Dotted lines are the 95% interval of confidence; black dots represent landings as observed in the Chioggia fish market from 1998 to 2008 and are rescaled for comparison (*M. mustelus* x0.025, *S. canicula* x0.33).

The day-off scenario shows that stopping the fishery one day a week would stabilize the population of *M. mustelus* (Figure 19c) and significantly slow the decline of *S. canicula* (Figure 19d). In

turn, preventing the catch (or equivalently imposing the discard) of immature individuals would allow a significant increase in both populations (Figure 19e,f).

A rigorous comparison of the two strategies should be based on an equivalent reduction in landings (and hence revenue for fishermen), in term of either abundance or biomass. The two scenarios that were assumed are considerably different from the fishermen's point of view: the minimum size scenario for *M. mustelus* implies a decrease of 90% in the elasmobranch individuals landed (and 56% of the biomass fished, calculating the weight with the classical allometric function, Froese and Pauly, 2010) versus an effective decrease of 15% assumed by the day-off scenario, while for *S. canicula* minimum-size assumes a decrease of approximately 60% in landings (in term of both abundance and biomass) versus 19% in the day-off scenario. A new minimum size threshold was therefore set for each species, defined as the length that produces the same reduction of biomass landed assumed in the day-off scenario. This length is 705 mm for *M. mustelus*, and 415 mm for *S. canicula*. In both cases, populations show an increase, even if remarkably smaller than in the original minimum-size scenario (Figure 19g,h).

## 5.4 Discussion

### 5.4.1 Fishery data

The results from Section 5.3, related to one of the largest Mediterranean fisheries, highlighted a dramatic decline, of almost 86%, in elasmobranch landings. This negative trend is even stronger over the last fifteen years. An alarming reduction emerged for skates and *Scyliorhinus* spp., whose landings decreased 47 and 16 times respectively, while the multi-genera group of “Asià” showed a weak increase. This group, too, shows a clear landing decrease since 1994. These data reflect the worldwide picture emerging for elasmobranch fishery (Bonfil, 1994; Dulvy et al., 2008). Although quantitative comparisons of trends are not feasible, due to differences in data availability and collection, time range, etc., decreases of similar magnitudes have been reported in different geographical areas: the Northeast and Northwest Atlantic (Dulvy et al., 2000; Stevens et al., 2000; Baum et al., 2003; Musick, 2005), Australia (Punt and Walker, 1998; Robbins et al., 2006), southern Brazil (Amorin et al., 1998), Gulf of Mexico (Baum and Myers, 2004), northern South China Sea (Cheung and Pitcher, 2008), the Mediterranean Sea (Ferretti et al., 2008). In the Adriatic Sea, a consistent reduction in the relative abundance of Hypotremata, and especially *Raja clavata*, has been highlighted (Jukic-Peladic et al., 2001; Krstulović Šifner et al., 2009; Fortibuoni et al., 2010).

Although statistics from the fish market are undoubtedly biased by unreported catches, as highlighted by the lack of data relative to “Asià” in the period 1986-1993, there is no reason to hypothesize that the unreported portion of the catch changed considerably in the last few years. The

decrease in landings likely reflects a real population decrease for several reasons. Elasmobranchs represent mainly bycatch, as highlighted by the data on the amounts of sharks and rays caught with different fishing gear, and market demand did not substantially change (C. Mazzoldi, interviews with fish market employees, unpublished). The high fishing pressure exerted in a small, landlocked area, such as the Northern Adriatic Sea, makes it unlikely that such a decrease in landings could be attributed to marked changes in fishing grounds, as suggested for other Mediterranean zones (Abella and Serena, 2005). However, some changes towards a greater exploitation of southern fishing grounds by largest fishing boat cannot be excluded. Moreover, landing decrease cannot be the result of a decrease in fishing effort. Indeed, even if no long-term effort time series are currently available, it can reasonably be assumed that fishing effort in the last few years is at least comparable to, if not much higher than, the effort during the 1940s and 1950s. The data reported here provide novel information on the past levels of elasmobranch populations in the basin, if compared for example to scientific surveys. Systematic scientific trawl surveys only started in the Adriatic during the 1980s or 1990s (Vrgoc et al., 2004) and do not allow to appreciate the full extent of the elasmobranch decrease (e.g. see Fig. 4 in Coll et al., 2009) which emerges by landing data before those decades. In addition, landings timeseries are continuous, allowing to investigate the causes of the observed trends, e.g. to test the influence of the environmental variability (see below). Older surveys, for instance the Hvar expedition (1948-1949), give only pinpoint estimates that, in addition, may be hardly comparable with results from modern trawl surveys (Jukic Peladic et al., 2001).

Climate change is expected to influence fisheries, with effects that can vary depending from species characteristics (Klyashtorin, 2001; Brown et al., 2010). In a global scenario of climate changes, a large decrease in fish populations could be ascribed to either climate change or exploitation. Regarding elasmobranch populations in the Northern Adriatic, the question is: is the observed decline the consequence of environmental change or of exploitation? Correlations of landings with environmental variables indicate that the environment influences elasmobranchs, in particular skates. However, the findings from this study show that the environment alone cannot account for the extent of the landing decrease, especially the marked decline of the last few years. WeMOi increased in the nineties while skate landings decreased, despite their positive correlation. NAOi does not show a definite trend and the skate decline from ca. 1984 coincided with an initial NAOi increase. The most probable explanation for the decrease in elasmobranch landings seems to be a marked population decline due to overfishing, a conclusion supported also by other results, such as the high fraction of immature individuals found in landings and the outputs of demographic models (see discussion below).

Of course, other anthropogenic pressures besides fishing impacted the Northern Adriatic Sea during the last decades and might influence elasmobranch abundances, but the characteristics of the decline of elasmobranchs, i.e. a marked, long-term and multi-species decrease, suggest that the cause

must be a pressure exerted on the whole basin and over many decades. Indeed a decrease in elasmobranch was highlighted also before the 1950s by naturalists' descriptions (Fortibuoni et al., 2010). Eutrophication and anoxic phenomena appear unable to explain the elasmobranch decline. Eutrophication peaked from the mid-1970s to the mid-1980s (Artioli et al., 2008), e.g. well after the decline of skates had started, and before the decline of "Asià" sharks, so that there seems to be no temporal match between eutrophication and changes in elasmobranch abundance. Similarly, anoxic phenomena connected to eutrophication do not appear to be a good explanation for the long-term decline of elasmobranch populations, as they were mainly concentrated in the 1970s and 1980s, and moreover they rarely affected wide areas of the basin (Degobbi, 1989; Degobbi et al., 2000).

In addition to long-term trends, strong oscillations in landings for all categories were identified. Given their regularity and marked amplitude, it is unlikely that such fluctuations can be related to variations in fishing effort or market demands. Fishery has been demonstrated to magnify fluctuations in bony fish abundances (Beddington and May, 1977; Hsieh et al., 2006), and fishery-induced truncation of the age structure of populations causes unstable population dynamics, reducing the capacity to buffer environmental events (Hsieh et al., 2006; Anderson et al., 2008). These findings, however, relate to Teleost fish which have higher fecundity and, in general a lower age at maturity than elasmobranchs, characters that correlate (respectively) positively and negatively with the coefficient of variation in larval abundance (Hsieh et al., 2006). The results of this study show the opposite. Indeed from 1990 fluctuations in skate landing moved out of phase with WeMOi and then disappeared, while landings dropped, suggesting that strong fishing pressure reduced population abundances to such low levels as to interfere with or to mask processes of natural fluctuation, breaking down their relationship with climate oscillations.

Explanations for the periodicities of elasmobranch may include population cycles and strong year-classes causing population outbursts, or fluctuations in the abundance of their prey (or of other organisms, whose effect is propagated through the food-web, e.g. zooplankton in the middle Adriatic fluctuates with a 5.5 to 7.3 year period, Baranovic et al., 1993, and small pelagic fish present a 3 - 5 year periodicity in landings, Azzali et al., 2002). However such hypotheses are not fully convincing and they can explain only some the periodicities (e.g. the 8-year second-order periodicity observed in *Scyliorhinus* spp., as evidenced by the IBM, see below). But elasmobranch landing peaks are relatively abrupt and generally in phase for all the three categories, suggesting a different, perhaps common mechanism. At 0-year lag, environmental variables correlated not only with long-term trends, but also coincided with instantaneous, short-term oscillations of landings (WeMOi and NAOi with skates). Given the slow growth and long life span of elasmobranchs, a non-lagged response of elasmobranch to changes in environmental variables appears to be explainable by migration from the area covered by Chioggia's fleet rather than as the result of strong year classes. Such migration could be a direct response to the

disappearance of favorable environmental conditions or a response to changes in prey abundance caused by changes in environmental conditions. Annual skate landings are related to WeMOi and NAOi, which however do not correlate, so they probably affect migration differently: skates could prefer warmer water year-round (positive correlation with NAOi) and particularly in winter (positive correlation with WeMOi). Such conditions could be favorable for living, spawning and/or for their prey.

Migrations seem to take place seasonally, as reported in other studies for the thornback rays, *R. clavata* (Hunter et al., 2006). Indeed a 12-month (and 6-month for *Squalus* spp.) periodicity of monthly landings was found. Such 12-month oscillations cannot be the result of seasonal variations in the fleet's activity, since different categories, all landed mainly as bycatch, alternate throughout the year, nor of seasonal differences of catchability among categories, because the fishing grounds of Chioggia's fleet cover almost the whole northern Adriatic and, again, these species are mainly bycatch.

Monthly data suggests that skates migrate during winter. Since it is during winter that waters near Chioggia are markedly cooler than those southwards and eastwards (Russo and Artegiani, 1996), this result mirrors the hypothesized preference of skates for warmer waters and their dislike of cold winters (low WeMOi). Monthly data indicates that *Mustelus* spp. is likely to frequent Northern Adriatic waters during warmer months, while *Scyliorhinus* spp. is abundantly caught during winter months. Given the wide variation in water temperature in the Northern Adriatic compared with the deeper waters of the rest of the Mediterranean (Russo and Artegiani, 1996), the observed seasonality of these two species can be related to their geographical distribution, with *Scyliorhinus* spp. distributed at higher latitudes than *M. mustelus* (Froese and Pauly, 2010).

The grouping of several species in broad categories in the fishery statistics eliminates the possibility of reconstructing the decline or increase of a single species. In particular, the "Asià" category, including several species belonging to different families, is poorly informative, given that the group composition might have changed. And indeed this category exhibits the least definite trend. In contrast, the "Razze" and "Gattucci" categories include fewer species, and thus the more marked relationship of skates with environmental variables likely reflect biological and ecological characteristics common to all the species included in the category. At present, from the surveys at the fish market, "Razze" contains only three species (*R. asterias*, *R. clavata* and *R. miraletus*), while "Gattucci" only two (*S. canicula* and *S. stellaris*) and given the dramatic reduction in landing, population declines are substantial regardless of the species included. Fish market sampling revealed a current composition of landed elasmobranch highly dominated by just one species, the smooth-hound *M. mustelus*, with all the others modestly contributing to the sample. An increase in the catch of *M. mustelus*, at least relative to other species, was found in the Adriatic by Jukic-Peladic et al. (2001) also. *G. galeus*, *M. asterias*, *S. stellaris*, *S. blainville* and *R. miraletus* were particularly rare at the Chioggia fish market. The low number of *M. aquila*

could be related to the extremely low commercial value of the species, while that of *A. vulpinus* could reflect the decline of the thresher shark population in the Mediterranean, as recently noted by Ferretti et al. (2008). The lack of data on landing composition in the past does not permit a detailed analysis, however some conclusions can be drawn. Several other species are or were reported to occur in the Northern Adriatic Sea (D'Ancona, 1926; Serena, 2005; Froese and Pauly, 2010). Although the sampling of this study can not be considered exhaustive, given the limited number of visits to the fish market, fishery selectivity and possibly landing preferences for some species, the species *Dipturus batis*, *Rostroraja alba* or *Raja montagui*, whose disappearance from the Adriatic was suggested by Jukic-Peladic et al. (2001), were never recorded. *R. alba* and *D. batis* attain large maximum sizes (Froese and Pauly, 2010), a character considered an indicator of vulnerability (Dulvy et al., 2000). However current and published data show that a decrease in landings does not involve only the largest species, but also species characterized by smaller maximum and sexual maturity sizes, such as *S. canicula* (Jukic-Peladic et al., 2001; Capapé et al., 2008) and the three recorded species of *Raja* (Demirhan et al., 2005; Ungaro, 2004; Barone et al., 2007; Krstulović Šifner et al., 2009). Examples of sustainable harvest of elasmobranch do exist, in different geographical areas (Walker, 1998; Gertseva, 2009), and in other Mediterranean areas, such as the Northern Tyrrhenian-Ligurian Sea, where the same species overexploited in the Adriatic, *S. canicula*, *R. asterias* and *R. clavata*, appear to be sustainably harvested (Abella and Serena, 2005). Low fishing pressure and the harvest of low proportion of populations are the pre-requisite of a sustainable harvest (Walker, 1998; Abella and Serena, 2005). In the Northern Adriatic Sea, the long-term extremely high fishing pressure exerted in a small area and the absence of limitation in elasmobranch catches likely make this fishery unsustainable at these levels.

A further indication of a non-sustainable harvest of elasmobranch in the Northern Adriatic Sea comes from the assessment of the percentage of sexually-mature males during the surveys at the fish market. Even if, as in other fishing areas (e.g. Carbonell et al., 2003), small-sized individuals are usually discarded at sea, in the surveys of this study immature males represented from 30% to more than 80%, of the sample for all the analysed species. The minimum size of mature males and  $TL_{50}$  estimated in this study were, in general, different from published data on these species in the Mediterranean. For *M. mustelus*, *S. acanthias* and *S. canicula* (only minimum size was estimated) the estimates of this study were smaller than those reported in literature, while the reverse applied to skates. For *M. punctulatus* (only minimum size was estimated) measures were similar. Differences in size at maturity can be related to geographical variations (Ellis and Shackley, 1997; Stenberg, 2005; Capapé et al., 2008; Saïdi et al., 2008). However, the attribution of sexual maturity in this study was based only on clasper characteristics (length relative to pelvic fin and rigidity) and, even if claspers were at least 15 mm longer than pelvic fins (Demirhan et al., 2005), maturing males may have been included in the mature category, consequently decreasing the minimum size and  $TL_{50}$  (Conrath, 2005; Capapé et al., 2008; Saïdi et al.,

2008), and overestimating the number of mature males. Moreover, as females reach sexual maturity at a larger size than males in most of the species (Ellis and Shackley, 1997; Cortés, 2000; Demirhan et al., 2005; Barone et al., 2007; Saïdi et al., 2008; Saïdi et al., 2009), and males and females did not differ in size in the samples of this study for most of the species, an even larger percentage of immature females is expected. The removal of such a high percentage of individuals before their contribution to the maintenance of the population is expected to drive the population to collapse (Myers and Worm, 2005).

In three of the analysed species, *M. mustelus*, *S. canicula* and *R. clavata*, sex-ratio differed significantly from the expected 1:1. As sexes differed in size only in *M. mustelus* and even in that species the difference was really slight, this data suggests a different catchability of males and females, possibly related to spatial sexual segregation (Rodríguez-Cabello et al., 2007). This factor needs to be further investigated, given that a different yield may unbalance sex-ratio and consequently negatively affect populations.

#### 5.4.2 Demographic models

The demographic model was able to reliably reproduce recent annual population trends, as depicted by landing data, of both *M. mustelus* and *S. canicula*. This was possible despite the highly simplified model, not accounting for example for spatial ecology or resource availability, because fishing (the only external forcing considered in the model) is the most important factor influencing long-term population trends, as the analysis on historical data evidenced. A further proof of the validity of the model is its ability to reproduce oscillations in the *S. canicula* population with a period equal to the second order period of *Scyliorbinus* spp. landings. This also corroborates the previously made hypotheses on the causes of first order periodicities in elasmobranch populations: the model considered the major population dynamics and was able to reproduce only the second order oscillations, hence the first order period has to be explained by another mechanism, such as migration.

As the model is able to reproduce population trends it allows us to qualitatively compare different management scenarios to assess their ability to revert or at least slow down the decline of elasmobranchs population. The results of the management scenarios of the models lead to a clear conclusion: imposition of a minimum catch size is by far a more efficient strategy to reverse the depletion trend of these stocks than fishery effort reduction. The results of the third scenario (the modified minimum-catch size strategy) indicated that any strategy that protects juveniles, even if just partially, is more effective than an analogous reduction of fishing effort on the whole size spectra.

The outcome of the model could be generalized to any similar situation: indeed, even if the model has been implemented and calibrated with local data, no environmental data are directly included in the model. Hence the results could be qualitatively extended to other areas where elasmobranchs are in decline due to strong overfishing and the proportion of immature individuals landed is high.

## 5.5 Past, present and future of elasmobranch in the Northern Adriatic Sea

All of the different methodologies that were used in this study provide consistent indications on the status of elasmobranchs in the Northern Adriatic Sea. The long-term data show unequivocally an extraordinary decline in elasmobranch fishery, likely reflecting a similar decline in population abundances, whose ecological and socio-economical consequences are unexplored in the ecosystem. The most probable cause of such decline appears to be overfishing. The heavy harvest of immature individuals, highlighted by fish market surveys, forecasts a bleak future for elasmobranch in the Northern Adriatic Sea. A probable extinction for *M. mustelus* and *S. canicula* emerged from the models, if no specific management approaches are applied. A decline in extinction risk “as fishing becomes more selective for older age classes” has been predicted for sharks by Myers and Worm (2005). As high survival rates of discarded elasmobranch are reported for several species (Revill et al., 2005; Mandelman and Farrington, 2007; Enever et al., 2009), a management approach that includes minimum size thresholds based on the actual size at maturity of the different species appears promising and applicable in different areas, as highlighted by the results of the models shown here. Furthermore, the models suggest that any strategy aiming to protect juveniles, including the establishment of permanent or seasonal closures of areas functioning as nursery or reproductive grounds (Hunter et al., 2006; Rodríguez-Cabello et al., 2007), could be effective. As highlighted at different levels (Clark et al., 2003; McIlgorm et al., 2010), the results of this study too stressed the need for management strategies to take long- as well as short-term variations in environmental conditions into precautionary consideration, given the emerging relationship between landings, at least of skates, and climate indices.

## 5.6 Acknowledgments

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## 6. When prey become predators: paradoxical effects of eutrophication on pelagic fish

An ecosystem approach to fisheries (Garcia et al., 2003) and, in general, an ecosystem-based approach to the management of marine ecosystems require new conceptual models about the functioning of marine food webs. Commercially important marine populations should not be considered in isolation, and their management should take into account not only fishing pressure, but also trophic interactions and other pressures exerted on the ecosystem. The goal of this chapter is to show that this different perspective can lead to key insights on the functioning of marine ecosystems, simply through the construction of new conceptual models. The pelagic food web of the Northern Adriatic Sea is conceptualized and then analyzed by means of long-term timeseries (e.g. landings from the Clodia dataset) to provide an explanation for the (still unsolved) disappearance of mackerel from the ecosystem during the 1960s.

### 6.1 Long-term changes in the pelagic food web of the Northern Adriatic Sea

Landings of pelagic fish from the Chioggia fish market (Figure 20) show that, during the 1960s, mackerel (mainly *Scomber scombrus*) landings strongly decreased and remained low for the following decades. Approximately at the same time, the landings of small pelagic fish such as anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) increased, possibly following the increasing eutrophication of the ecosystem (e.g. Marasovic et al., 1988), as well as the increasing commercial exploitation. In the late 1980s, small pelagic fish stocks collapsed and, about two years later (i.e. 1989, anchovy collapsed in 1987, see for example Cingolani et al., 2004b) mackerel landings increased slightly, but without reaching the previous high levels. Similar trends can also be observed in the landings of Croatian fisheries (Sinovcic, 2001b; Grbec et al., 2002), so that they cannot be due only to variations in fishing effort. These trends are also found in recent fishery-independent biomass estimates (Azzali et al., 2002; Fig. 7 in Coll et al., 2009): therefore landing data roughly represent biomass trends. And, most importantly (see below), since mackerel and other small pelagics are usually caught with the same fishing gears, Figure 20 can be used to quantify the relative variations (i.e. with respect to each other) of the biomasses of pelagic fish species.

The relative trends of pelagic fish are paradoxical, because mackerel predated on anchovy and sardine (Froese and Pauly, 2010; Carlotta Mazzoldi, pers. comm.; moreover mackerel is bigger than

sardine, and in the sea usually the big eat the small) so that one could expect that their trends are similar: since increasing eutrophication led to an increase of the biomass of small pelagic fish, i.e. the prey of mackerel, it should have led to more favourable conditions for this medium-sized pelagic predator (Marasovic et al., 1988). Of course, mackerel could have declined due to other factors than prey availability, but fishing cannot be the cause of such an abrupt decrease, and some authors proposed that the disappearance of mackerel from the ecosystem was caused by changes in environmental conditions (e.g. salinity; Orel et al., 1986; Grbec et al. 2002), but “the absence of mackerel during the last few decades is [...] not fully understood” (Grbec et al., 2002). A different explanation is proposed here, but I would like to stress that it is not mutually exclusive of the hypothesis that mackerels were negatively affected by environmental change (Grbec et al., 2002). Here the purpose is simply to show the power and the insights provided by an ecosystem approach, and the importance of conceptual models.

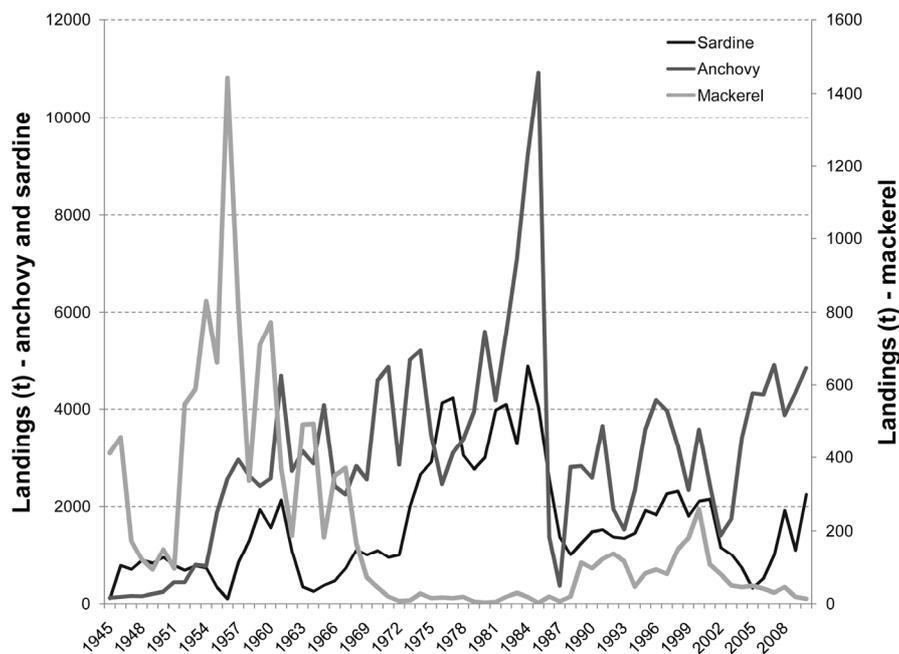


Figure 20. Landings (1945-2010) for mackerel (light grey line), anchovy (dark grey line) and sardine (black line) from the Clodia dataset. When small pelagic fish increased, their predator (mackerel) paradoxically decreased.

## 6.2 A conceptual model of size-based trophic interactions in the Adriatic pelagic food web

The conceptual model proposed here is inspired by the theoretical framework found in Walters and Kitchell (2001), as well as by the work of Ulanowicz (1997 and 2009) on autocatalysis. Small pelagic fish are zooplanktivorous (Froese and Pauly, 2010), and are sometimes known to eat fish eggs.

Therefore, they can potentially control the abundance of their own pelagic predators, by competing for zooplankton with the juveniles of the predator (which often eat zooplankton, as in the case of mackerel, Froese and Pauly, 2010) or by eating the eggs of the predator (but the theory works also if this latter process does not take place). However predators, such as mackerel, eat small pelagics, controlling their abundance and protecting their own juveniles: this process is called “cultivation” (Walters and Kitchell, 2001). Here it is proposed that, before the 1960s, mackerels were abundant so that they were able to exert top down control on small pelagic fish, protecting their own juveniles, and that during the 1960s the situation changed, and small pelagics were able to reduce mackerels to very low biomass levels through competition or predation on juvenile stages. But what caused the shift from a mackerel-dominated system to a zooplanktivorous-dominated one?

Eutrophication increased after World War II in the Northern Adriatic Sea, peaking in the 1970s and 1980s (e.g. Sangiorgi and Donders, 2004; Artioli et al., 2008), because of anthropogenic nutrient enrichment. Here it is proposed that, in the 1960s, increasing primary production due to anthropogenic nutrient loads favoured the faster-growing, smaller zooplanktivorous fish with respect to mackerel, triggering a self-reinforcing feedback which disrupted the cultivation control: more small pelagics eating zooplankton and mackerel eggs meant less mackerel, hence lower predation on anchovy and sardine and thus more zooplanktivorous fish. In this conceptual model, this increase of primary productivity is proposed to be the factor that started the decline of mackerel: small pelagic fish can exploit in a more advantageous manner a state of increasing primary production (because also the secondary production increases, i.e. zooplankton, which they feed upon), because they are smaller and hence they grow faster. This conceptual model works because it takes into account size (not only concerning the growth process, but also in the case of trophic interactions, which are size-based: for example, the preys can eat the juvenile stages of their predator). The disappearance of mackerel, just when its prey (anchovy and sardine, and zooplankton in the case of juveniles; zooplankton presumably increased following increased eutrophication) became more abundant due to eutrophication, is only apparently paradoxical, and here it is suggested that small pelagics proliferated in the ecosystem at the same time also because of this autocatalytic feedback (Ulanowicz, 2009) releasing them from top down control.

Indeed, some evidence supports this conceptual model, first of all the negative correlation between the biomasses of mackerel and small pelagics: mackerel disappeared when small pelagics increased, and it increased after their collapse with a biologically-reasonable (Sinovicic, 2001b) lag of two years (Figure 20). Moreover, small pelagics eat fish eggs in the Northern Adriatic Sea (Legovini, 2009), indeed in very low quantities, but small pelagics are very abundant, so that their predation on eggs could be very high for mackerel anyway. Following the collapse of small pelagics in 1987, the abundance of copepods increased in the Gulf of Trieste (Conversi et al., 2010) suggesting (1) that small pelagics were able to exert top down control on copepods (so, if they controlled zooplankton

abundance, why not the number of the eggs of other fish?) and (2) that small pelagics can be potential competitors for zooplankton with mackerel juveniles.

Indeed, this conceptual model is only tentative and the analysis of other data could be useful to test it more deeply (e.g. an analysis of the habitat use overlap between mackerel juveniles and small pelagics, Walters and Kitchell, 2001), even if I think that the proposed hypothesis is difficult to confirm or disprove, as in most large-scale observational studies.

However, the conceptual model is interesting because it puts both small pelagic fish and eutrophication in a different light. Small pelagics can also be important predators, not only “forage” preys. Anthropogenic nutrient enrichment is thought to structure large marine ecosystems from bottom up, by means of the propagation through the food webs of eutrophication effects such as increased primary production, intense algae blooms or hypoxia. While the consequences of eutrophication for demersal resources are hard to forecast, because for instance more productivity can be counterbalanced by anoxic episodes negatively affecting bottom fauna, pelagic fisheries are generally considered to benefit from nutrient enrichment: the increased planktonic production fuels the grazing food chain, ultimately leading to higher pelagic fish biomass (e.g. Marasovic, 1988). The hypothesis reported here suggests that this view is incomplete, because pelagic fishes respond differently to the onset of eutrophication, and losers and winners depend essentially on trophic interactions among them, and on population characteristics related to body size.

Moreover, the conceptual model highlights the importance of a size-based, integrated approach to the management of fisheries, and suggest that bottom up effects such as those of eutrophication can actually lead to counterintuitive top down dynamics within marine ecosystems.

### **6.3 Acknowledgments**

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## 7. An indicator of the successional stage of aquatic ecosystems

### 7.1 A phenomenological network perspective on macroecology

The sustainable management of marine ecosystems is characterized by multiple spatial and temporal scales of action, reflecting those scales characterizing the many ecological processes relevant for a given ecosystem service, and which often markedly differ among them. As already mentioned man obtains multiple benefits from marine ecosystems and exerts multiple pressures on them, so that multiple scales are even more probable. Finally, the spatial-temporal scales of human action (e.g. those of stakeholders, legislation, etc.) may not completely match those of ecological processes, generating problematic scale mismatches (Gilbert, 2010): for example, measures developed by countries for achieving a sustainable management of their own fisheries can have limited effects, if commercial stocks migrate in and out of their Exclusive Economical Zone and can be fished by vessels from other countries in an unregulated manner. Or, the lifetime of political institutions can be too short compared to the time needed to see the results of particular management measures: since such institutions are often driven by short-term electoral payoffs, management results which can only appear in the long-term will often not be implemented. A tragic example is the flood at the beginning of November 2010 which affected wide areas of North-Eastern Italy, some of which have been under water for days, including Padova. After a big flood in 1966, it was clear that new protective hydraulic management measures were necessary, but they were never done as the political payoff of regional institutions (lasting only few years) was lacking.

As Simon Levin put it, “the problem of pattern and scale is the central problem in ecology, unifying population biology and ecosystems science, and marrying basic and applied ecology” (Levin, 1992). In the previous chapters the focus has shifted across different scales and approaches, including reductionistic analyses and integrated and holistic views. The main objects of study were the ecosystem functioning at the population or ecosystem scale. This chapter “zooms out” to an even greater extent by considering macroecological scales.

Macroecology (Brown, 1995) is a scientific research area dealing with ecological regularities, such as the relationship between organism abundance and body size (the so-called size spectra), on large spatial scales, e.g. ecosystems or, in the case of this chapter, several large aquatic ecosystems worldwide. Indeed, the approaches to the study of marine ecosystems outlined in the previous chapters have led to useful insights. However, the goal of this chapter it to show that, by dropping even more

details, different but very general, and equally useful insights on integrated ecosystem functioning can be achieved. A metaphor which could apply here is that of medicine: indeed, very sophisticated medical tests can be performed to diagnose the causes of a disease in a patient, yet body temperature measurement will always be used, as far as it can be foreseen. Despite its roughness and inability to identify the causes of an illness, it is a quick and effective way to determine its intensity.

Such metaphor is also appropriate when considering that the goal of this chapter is to propose and test an indicator of the whole-ecosystem status and maturity. To do this, it is assumed in a phenomenological fashion that the trophic flows of energy and matter within ecosystems reflect the ecological successional status of the system itself (Ulanowicz, 1997; Ulanowicz, 2009). High temperature is not necessarily the cause of illness in a sick person, but generally it is the symptom, and here similarly the configuration of flows is taken to bear the scars of the pressures, both natural and anthropogenic, which acted or are still acting on the ecosystem. Hence, if ecological processes acting on different scales lead to emergent regularities in ecosystems, such regularities can potentially be used for practical purposes such as the definition of ecosystem indicators.

A meta-analysis of trophic network models was set up by collecting data from a large number (56) of Ecopath models, which was a quite natural choice given the familiarity with the modelling approach of the software (Chapter 3). A novel regularity was identified in all models in the form of a power law, linking consumption with biomass in the network compartments, and whose exponent is proposed as a large-scale indicator of the ecological succession stage of the ecosystem. Indeed it was tempting to write about an indicator of the integrity or health of the ecosystem, to use some common ecological terminology, hence hinting at the effect of anthropogenic pressures. However, as shown on Chapter 3, it is difficult to determine if a stressed ecosystem status was caused by natural or anthropogenic pressures without a deep knowledge of the system functioning and history, which is certainly not the scale for a meta-analysis based on a large number of models.

## 7.2 Allometries in model ecosystems

Allometric scaling relationships, i.e. functions of the form  $y \propto x^a$  with  $a \neq 1$ , provide a formidable way to reduce the complexity of ecological systems and, potentially, are of great help for modelers. For example many quantities, often difficult to measure, can be expressed as a function of body size (Peters, 1983; Schmidt-Nielsen, 1984; Brown et al., 2004; Marquet et al., 2005; Woodward et al., 2005; White et al., 2007). Also, allometric relationships are scale-invariant, i.e. their functional form is unaffected by a scale change  $x \rightarrow c \cdot x$  which yields  $y \propto c^a \cdot x^a$ . Consequently, scaling relationships

involving several orders of magnitude make one wonder whether a common principle could be acting across different and seemingly unrelated scales.

More and more ecological patterns are found to be scale-invariant (Peters, 1983; Schmidt-Nielsen, 1984; Garlaschelli et al., 2003; Brose et al., 2004; Brown et al., 2004; Marquet et al., 2005; Woodward et al., 2005; Dunne, 2006; White et al., 2007) yet, perhaps surprisingly, things are different for food webs, i.e. the network representation of “who eats whom” in ecosystems. It is often difficult to obtain accurate food web data and to disentangle invariant patterns from local environmental variability (Brown and Gillooly, 2003; Dunne, 2006) and, as a result, few scaling relationships or even regularities have been observed in food webs and in binary food web models (Milo et al., 2002; Garlaschelli et al., 2003; Brose et al., 2004; Brown et al., 2004; Woodward et al., 2005; Dunne, 2006), whose properties have also been argued to be scale dependent (Dunne, 2006). Moreover, in the case of trophic flow networks, where the flows, such as predatory interactions among compartments representing species or functional groups, imports and exports are quantified, scientific research has focused on the analysis of the peculiarities of single or few ecosystems, and not (with few exceptions) on the search of general inter-ecosystem patterns. To date, however, the increasing number of publications describing trophic flow network models (Ulanowicz, 2004; Christensen et al., 2005) constitutes a standardized dataset large enough to look for scale-invariant properties. A large database of 56 mass-balanced trophic flow networks models of aquatic ecosystems was analyzed, with flows and biomasses expressed as wet weight, by far the most common currency in the literature. This chapter reports the existence of a remarkably regular and (to my knowledge) novel pattern, found in a wide range of different aquatic ecosystems from all over the world, linking the food consumption of a food web compartment, e.g. a population or a taxonomic or functional group, to its biomass through a power law. Ecological theory and statistical analyses are exploited to show that both individual processes, such as the scaling of metabolic rates with individual body mass, and emerging ecosystem dynamics, such as trophic structure and ecological succession, can offer hints about the origin of the scaling.

## **7.3 Materials and methods**

### 7.3.1 The model database

The analyzed database comprises 56 mass-balanced, flow network models of aquatic food webs from different worldwide locations (Figure 21; see Table A3.1 in Annex III) built with Ecopath software (Christensen et al., 2005; see also Chapter 3), whose compartments represent single species populations, organisms grouped according to taxonomy, functional role or other criteria, or dead

organic material (detritus). Only models covering one or more years (so that biomass and consumption represented annual or inter-annual means) and with wet weight currency were collected, to avoid biases due to currency or seasonality. However, the consumption-biomass scaling (the investigated regularity, described below) was observed also in carbon, energy and seasonal networks (Table A3.2 in Annex III). Models were chosen according to the quality of input data, to the number of compartments (29 per model on average) and with the goal of covering a wide range of ecosystems, including continental shelves (16 models), upwelling marine ecosystems (14), oceanic ecosystems (4), mangrove ecosystems (2), coral reefs (3), rivers (3), lakes (10), bays (2), continental shelf - coastal lagoon systems (2). In addition to Ecopath models, 8 NETWRK models (Ulanowicz, 2004; Table A3.2) were analyzed to check for the influence of different balancing algorithms.

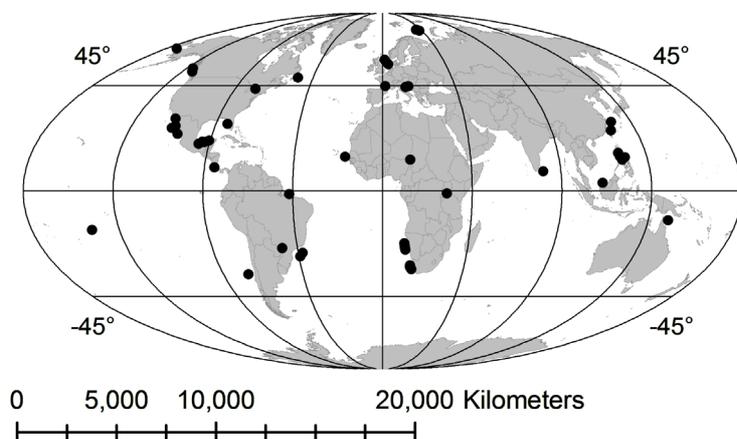


Figure 21. Locations of the 56 analyzed ecosystems (Mollweide projection, central meridian 0°), as indicated by the circles.

### 7.3.2 The importance of the mass-balance approach

In an Ecopath network, for each compartment, two mass balances are written (Equation 1 and 2 from Chapter 3). Since the estimates of flows and biomasses in most models are uncertain, especially when referred to large spatial scales, such balances guarantee the mutual compatibility of data providing a further quality check, and allow the estimation of poorly known flows or biomasses (Ulanowicz, 2004; Christensen et al., 2005). In networks where steady-state conditions are not met, a biomass accumulation term (Christensen et al., 2005) can be included in Equation 1. However, mostly steady-state models were chosen (so that the consumption of a compartment is also its through-flow), and the others had few and generally negligible accumulation terms. Consumption was analyzed instead of respiration (i.e. metabolism) in the scaling relationship (see Equation 6 below) since the latter is generally poorly characterized and computed by difference from Equation 2 in Ecopath models (Christensen et al., 2005).

### 7.3.3 The consumption-biomass (CB) scaling

The hypothesis to be tested is that the consumption  $Q_{in}$  (i.e., ingestion) of a trophic network compartment representing consumers can be adequately described by a power law function of the compartment biomass  $B$ :

$$Q_{in} = a \cdot B^{SDB} \quad (6)$$

where the choice of the exponent name ( $SDB$ , i.e. Supply Demand Balance) will become clear later, and the choice of a power law function followed from an analogy with the well-known individual scaling of metabolism with body size (such choice was also justified *a posteriori*, see below). Equation 6 represents the consumption-biomass (CB) inter-compartment scaling relationship. Notice that it represents an inter-compartment or inter-species scaling, not an intra-species scaling as in the case of the way that consumption and biomass are related in the famous Lotka-Volterra equations.

### 7.3.4 Statistical analyses

For each network Equation 6 was linearized with a  $\log_{10}$  transformation and fitted to data employing all but detritus and autotroph compartments. Sometimes  $\log_{10} B - \log_{10} Q_{in}$  plots were skewed (e.g. because of more disaggregated medium-high trophic level compartments, characterized by lower consumption) and contained outliers (i.e. compartments deviating from the linear trend), so that proper, robust statistical tools were used (but at the price of some statistical power). The strength of the linearized Equation 6 was evaluated using Pearson's correlation coefficient  $\rho$  (two-tailed t-student test,  $H_0: \rho = 0$ ; Legendre and Legendre, 1998) and non-parametric Kendall's  $\tau$  rank correlation coefficient (two-tailed test, with large-sample approximation, Helsel and Hirsch (1992), for  $N > 10$ ,  $H_0: \tau = 0$ ; Legendre and Legendre, 1998). To overcome the effects of outliers,  $SDB$  was calculated from log-transformed data using Kendall-Theil robust estimator (Helsel and Hirsch, 1992), i.e. the median of the slopes of the lines connecting all the possible couples of points, and the intercept was estimated as  $\log_{10} a = \text{median}(\log_{10} Q_{in}) - SDB \cdot \text{median}(\log_{10} B)$ . In allometric relationships, ordinary least squares regression on log-transformed data is usually employed, but here its assumptions (Legendre and Legendre, 1998) are not met because both  $B$  and  $Q_{in}$  are affected by error (Christensen et al., 2005). Other common methods for fitting bivariate slopes (Legendre and Legendre, 1998) were not applicable since information about the data was lacking (e.g. error variances) and because of sensitivity to outliers. Actually, it was recognized that outliers could also be a valuable source of information, because the exceptions which did not follow the CB scaling could highlight, by contrast, possible generating processes of such scaling. Consequently, outliers of the linearized Equation 6, where each point  $(\log_{10} B, \log_{10} Q_{in})$  represents a compartment, were visually inspected and then systematically identified through both the Stahel-Donoho robust multivariate outlyingness measure and a skewness-adjusted generalization of it (Hubert and Van der Veeken, 2008).

Finally, partly following the theoretical framework and hypotheses developed in Bendoricchio and Palmeri (2005) and since the computed *SDB* exponents were found (see Section 7.4) to have similar values, but still displayed some variability across ecosystems, the possible reasons were explored by comparing *SDB* to food web indicators and ecosystem attributes coming from ecological network analysis (some have already been described on Chapter 3, but for ease of consultation they are all listed and described in the Section A3.3 of Annex III, alternatively see Ulanowicz, 1986; Baird et al., 1991; Christensen et al., 2005) through non-parametric Spearman's  $r_s$  rank correlation coefficient (Legendre and Legendre, 1998).

## 7.4 Results

The consumption of a trophic network compartment was found to be well described, across compartments, by Equation 6, i.e. by a power law function of its biomass (Figure 22 and A3.4 in Annex III; Table A3.5 in Annex III). Equation 6 provides a good and, generally, highly statistically significant description of the data for each ecosystem (log-transformed Equation 6, mean  $R^2 = 0.77$  for the 56 networks), over four orders of magnitude on the average, eight at most (Table A3.5). The CB inter-compartment scaling relationship holds for several kind of aquatic ecosystems, ranging from rivers, lakes and transitional waters to coastal basins and open oceans, regardless of differences in salinity, depth, covered surface, temperature, latitude, total ecosystem biomass and primary production (Table A3.1), and despite the variedly aggregated networks (compartments represent single species populations or taxonomic or functional groups), with different numbers of compartments (Table A3.5).

The calculated *SDB* were usually close to but greater than 1 (thus justifying the choice of a non linear model), with a narrow range of variability (mean *SDB*  $1.11 \pm 0.15$  s. d.; Table A3.5). The number  $N$  of network compartments negatively correlated with *SDB* (Spearman's  $r_s = -0.48$ ,  $p = 0.00019$ ,  $n = 56$ ), but the relationship disappeared after excluding from the analysis the networks with  $N < 18$  ( $r_s = -0.21$ ,  $p = 0.18$ ,  $n = 42$ ) or more. Thus highly aggregated, hence possibly biased networks, showed higher exponents values. Remarkably, 95% confidence intervals of *SDB* did not contain 1 in only 5 networks (Table A3.5), all displaying *SDB*  $> 1$  and with low  $N$  or, possibly, poor data quality in the case of a reconstructed historical food web for Laguna de Bay. Isometric scaling (*SDB* = 1) can trivially explain the abovementioned insensitivity of the scaling with respect to aggregation (with the exception of models with very few compartments), because when aggregating two compartments  $i$  and  $j$ , Equation 6 reads  $Q_{in,i+j} = a \cdot B_i^{SDB} + a \cdot B_j^{SDB} \cong a \cdot (B_i + B_j)^{SDB}$ .

Several statistically significant correlations emerged between *SDB* and food web indicators and ecosystem attributes (significance level  $\alpha = 0.05$ ; Table 12; Figure 23). All of these correlations but two would be discarded applying Bonferroni correction for multiple testing (Table 12; Legendre and Legendre, 1998), but the consistency of their meaning (discussed in Section 7.5) support their ecological soundness. Also, it is reassuring that correlations were detected between *SDB* and flow-biomass or flow-flow ratios, which are fitter for inter-ecosystem comparison (Baird et al., 1991), and not with absolute flows or biomasses (Table 12 and A3.6 in Annex III).

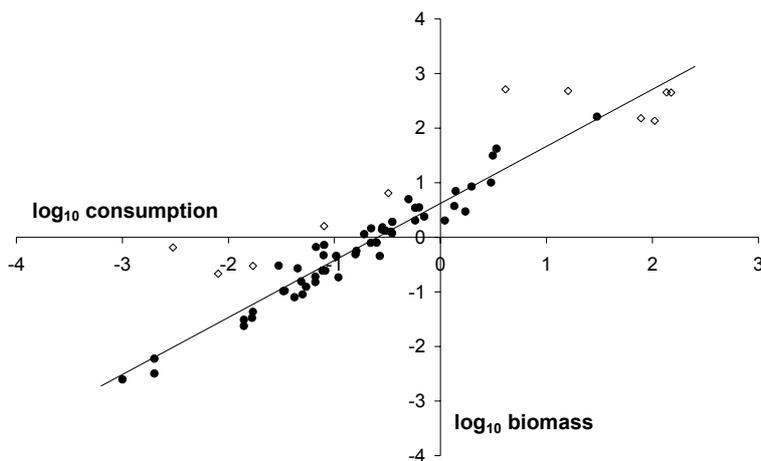


Figure 22. The CB scaling relationship in the North Sea food web during 1991 (Mackinson and Daskalov, 2007). The line represents the power law ( $\log_{10}Q_{in} = 1.04 \cdot \log_{10}B + 0.62$ ;  $Q_{in}$  is consumption,  $B$  is biomass) fitted to the 62 consumer compartments (full circles and empty diamonds, the latter representing outliers according to the Stahel-Donoho method, see Hubert and Van der Veecken, 2008). If outliers, i.e. sea-mammals, birds and middle-low trophic level organisms, are not considered,  $R^2$  changes from 0.88 to 0.95.

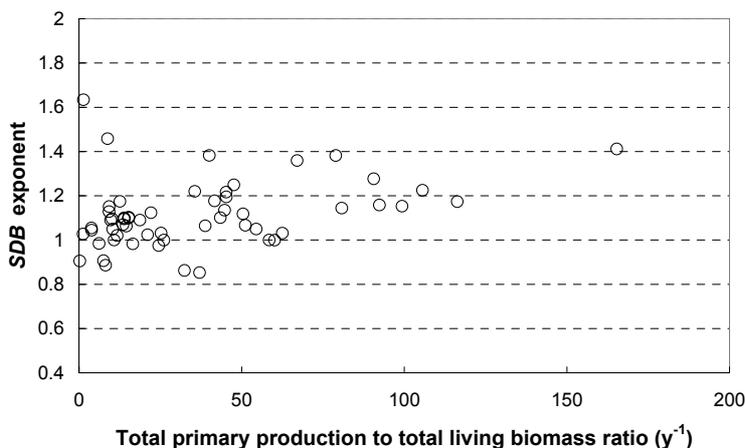


Figure 23. The relationship between the *SDB* exponent and the total primary production to total living biomass ratio ( $y^{-1}$ ). The exponent and the ratio are positively correlated (Spearman's  $r_s = 0.38$ ,  $p = 0.00377$ ,  $n = 56$ ).

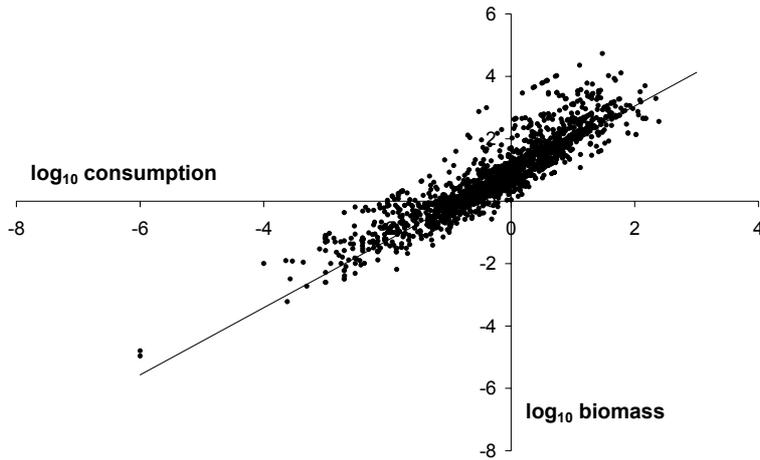


Figure 24. The relationship between consumption and biomass for all the 1599 consumer compartments from the 56 aquatic trophic flow networks. Data is well approximated ( $R^2=0.82$ ) by a common power law and lies in a remarkably narrow window on the plot, despite striking ecological differences among ecosystems. Kendall-Theil robust fit yields  $\log_{10}Q_{in} = 1.08 \cdot \log_{10}B + 0.90$ , where  $Q_{in}$  is consumption,  $B$  is biomass.

Table 12. Correlations between *SDB* and selected food-web indicators or ecosystem attributes (described in the Section A3.3 – Annex III). If not specified, indicators are dimensionless. The superscripts highlight statistically significant correlations at the following  $\alpha$  levels: \* stands for a p-value < 0.05, and \*\* stands for a p-value < 0.00385 (i.e.  $\alpha = 0.05 / 13$ , according to the Bonferroni correction for multiple testing). In some ecosystems there were no fisheries, so that for the catch-based “Gross efficiency of fishery” indicator the number  $n$  of valid cases is 46.

Correlation between <i>SDB</i> and:	Spearman $r_s$	p-value	$n$
Total primary production / Total living biomass** ( $y^{-1}$ )	0.38	0.00377	56
Total primary production / Total respiration	0.20	0.135	56
Total respiration / Total living biomass* ( $y^{-1}$ )	0.27	0.0413	56
Total living biomass / Total system throughput** ( $y$ )	-0.39	0.00279	56
Gross efficiency of fishery (Fishery catches / Total primary production)	0.22	0.151	46
Finn's cycling index*	-0.28	0.0337	56
Finn's mean path length*	-0.30	0.0245	56
Finn's straight-through path length*	-0.27	0.0470	56
System omnivory index	-0.17	0.215	56
Ascendency / Development capacity	0.16	0.241	56
Internal ascendency / Internal capacity	0.02	0.857	56
Internal overhead / Development capacity	-0.17	0.213	56
Internal capacity / Development capacity*	-0.29	0.0319	56

The superimposed scatterplot of the 1599 consumer compartments of the 56 food webs (Figure 24) reveals that the relationship between biomass and consumption is well approximated by Equation 6 not only locally, but also across worldwide distributed, remarkably different ecosystems (Table A3.1). Also, Figure 24 shows that points deviating from the scaling are more spread upwards. To clarify this issue, for each ecosystem compartments which were statistical outliers of the log-transformed Equation 6 were identified (Section 7.3.4). About 85% of the outliers were above the fitting line and, also, the scaling did not apply equally well to all organisms (even if outliers decreased considerably when accounting for data skewness; Table A3.5 and A3.7 in Annex III). Plankton, microbenthic fauna, seabirds and mammals represented a relatively large fraction of outlier compartments when compared to fish and invertebrates, despite the fact that these latter categories included most model compartments and that their data were expected to be affected by not-negligible errors as well (Christensen et al., 2005).

## 7.5 Supply-demand scaling of consumption with biomass in food webs of aquatic ecosystems

### 7.5.1 The meaning of the CB scaling

The way Equation 6 relates food intake with mass resembles the well-known scaling of individual metabolic rate with body mass (Peters, 1983; Schmidt-Nielsen, 1984; Brown et al., 2004), re-stated for populations or aggregations of them. The good agreement of Equation 6 with data indicates that, at the ecosystem scale, the consumption for a compartment (e.g. a population) is a function mainly of its biomass, just like metabolism is chiefly determined by body mass for individual organisms. Instead taxonomy and other distinctive characteristics of the compartment organisms such as mean size, size distribution, numerical abundance, physiological traits, behavior, life history or habitat (e.g. benthic versus pelagic) do not modify substantially the overall energetic budget of the food web compartment, at least in the case of the fish and macro-invertebrate communities that the Ecopath models focus upon (notice however that extrapolations to include planktonic communities, or big predators, should be done very carefully, as Ecopath models are, in general, fishery-oriented and contain few compartments describing very small or very big organisms). This result seems independent of the currency of the models, since the CB scaling was found also in carbon and energy flow networks (Table A3.2).

Yet, some differences with individual metabolic scaling should be noted. Here  $Q_{in}$  represents consumption, i.e. ingested flows, not basal metabolic rate (even if, for individuals, also active metabolic

rate and ingestion follow a power law of body mass, Peters, 1983). Furthermore, in the case of individuals, bigger organisms are characterized by a proportionally slower metabolism, while *SDB* takes a narrow range of values usually close to or slightly greater than 1, so that the average consumption per unit biomass of a compartment in fish and macro-invertebrate communities is roughly constant irrespective of which and how many organisms it represents, or that the compartments with higher overall biomass consume proportionally (slightly) more.

### 7.5.2 Possible causes of the CB scaling

To ascertain what causes such a strong and widespread inter-compartment scaling pattern, in this section the reason why some particular compartments do not seem to fit into Equation 6 is examined, as it could clarify by contrast why all the other compartments do in the most diverse aquatic ecosystems of the planet. For plankton and microbenthic fauna, the deviations from the scaling could be explained by the higher uncertainty in estimating biomass or consumption on large spatial and temporal scales (models are averaged over one or more years) or, for the latter category, deviations could be an artifact due to data skewness (see results with different outlier detection methods on Table A3.7; this could be the case for mammals as well).

However, one could also observe that the CB scaling is common to the most different consumers of an ecosystem, but that outliers not fitting into the scaling belong mainly to high or low trophic levels, i.e. generally the least connected from a trophic perspective, since they are at the “bottom” or on the “top” of the food web. Trophic interactions are among the main processes shaping energy flows and biomass distribution in ecosystems (Christensen et al., 2005), where everything is connected to everything else but with varying degrees, so it is straightforward to speculate that organisms only loosely connected to the rest of the ecosystem by means of such interactions would stand out and not follow the overall scaling. This could be the case for birds and mammals, which often are apex predators (i.e. their mortality is not directly affected by the other compartments) and spend part of their life feeding outside water, so they are partially decoupled from the ecosystem dynamics. Microbenthic fauna and plankton are sensitive to non-trophic factors (e.g. water temperature) and strongly coupled to food sources influenced by forcings external to the ecosystem, e.g. they feed on primary producers whose growth depends on light and nutrients, or on detritus resulting from algae exudates or sediment resuspension. Instead, the weight of interplaying trophic constraints should be higher in the middle of the food web, where outlier compartments are less frequent.

Of course, these considerations provide interesting clues about the causes of the CB scaling, but indeed no explanations. As an alternative starting point, it is argued that the ubiquity and strength of the CB scaling call for one, or more, common generating mechanisms, which must be really efficient yet simple. Also the little variability of the estimated *SDB* exponents, all close to 1, points towards the

action of a common factor. Indeed one of the simplest attributes of all organisms, which is strongly related to many other quantities and processes of ecological interest, is body mass. A derivation of the CB scaling from the scalings of individual consumption and population abundance with body mass is now discussed, showing that, even if not fully convincing, again it provides hints about the existence of scaling outliers.

Individual metabolic rate  $q$  scales interspecifically with body mass  $m$  as  $q \propto m^b$ , where  $b$  is about 0.6-0.8 and usually higher for fish and ectotherms (Peters, 1983; Schmidt-Nielsen, 1984; Brown et al., 2004; Glazier, 2005). Based on few analogous existing relationships (Peters, 1983), it is assumed that individual ingestion  $I \propto m^d$  with  $b \leq d < 1$ , i.e. ingestion is proportional to the field metabolic rate of free living, growing and reproducing organisms, which generally exhibits a scaling exponent between those of basal and maximum metabolic rates (Peters, 1983; Savage et al., 2004; Glazier, 2005). The number  $N$  of organisms of a species scales, often not strongly (Marquet et al., 2005; White et al., 2007), with species average body mass as  $N \propto m^L$  when measured for different species belonging to the same location or region.  $L$  is usually close to -1 in aquatic ecosystems, spanning from -0.6 to -1.6 (see Marquet et al., 2005, White et al., 2007, and references therein).

Equation 6 can be re-written as  $Q_{in} \propto N \cdot m^d \propto B^{SDB} = (N \cdot m)^{SDB}$ , i.e.  $m^{d+L} \propto m^{(1+L) \cdot SDB}$ . Being  $d$  roughly close to 1, the approximation that the average  $I$  in a compartment equals the  $d$ -power of the average body mass  $m$  of the individuals of the compartment was used (Savage, 2004), consequently neglecting the distribution of individual body masses. Thus the CB scaling follows from individual scalings if  $SDB = (d + L)/(1 + L)$ . If  $d \rightarrow 1^-$ , which could be a rough approximation for field metabolism (see discussion above), then  $SDB \rightarrow 1$ , a value that most computed exponents are statistically indistinguishable from. However this derivation would not yield the observed  $SDB$  values in the common case of  $L = -1$  and when  $L = -d$ , i.e. when the energetic equivalence rule is locally valid (White et al., 2007; actually the energetic equivalence rule is usually referred to metabolic rate, and not to ingestion as it is done here, but this approximation should be acceptable because  $b$  and  $d$  are similar). Moreover,  $d$  needs to be very close to 1 (which is probably not realistic) to achieve the measured  $SDB$  values (e.g. even if  $d = 0.95$ ,  $L = -0.75$  yields  $SDB=0.8$  which is within 95% confidence intervals of the calculated  $SDB$  for just eighteen networks, Table A3.5). Consequently, this derivation is not persuasive, however it highlights that important causes of deviation from the CB scaling could be the effects of temperature and thermoregulation on individual metabolism, which have not been considered here. For birds and mammals, high individual energetic requirements due to endothermy (Peters, 1983; Schmidt-Nielsen, 1984; Brown et al., 2004) could cause the upwards deviations from the scaling (Table A3.7). Also the environmental temperature that they experience outside water, which affects metabolism and consumption (Peters, 1983; Brown et al., 2004; Christensen et al., 2005) and is clearly different from the

temperature of the water that most aquatic food web organisms live in, as well as the different  $d$ 's characterizing endotherms (Glazier, 2005), could be possibly linked to their outlier status.

Actually, when trying to derive the CB scaling from such body mass scalings, one could make an additional simplification, based on the fact that the analyzed models are mostly fishery oriented. For this reason most organisms in a model, even those belonging to different compartments, have similar size (e.g. fish and macro-invertebrates), hence they have similar individual ingestion  $I$  since  $m$  is roughly constant (assuming that the factor of proportionality between  $I$  and  $m^d$  is inter-specifically constant). Since  $Q_{in} = N \cdot I$  and  $B = N \cdot m$ , if it is assumed that only  $N$  varies substantially with respect to the other terms,  $Q_{in}$  and  $B$  change proportionally to each other when  $N$  varies, so that  $Q_{in} / B$  will be roughly constant (it would scale with  $m^{d-1}$  but  $m$  is roughly constant) and  $SDB = 1$ . Outliers would be expected to be those compartments characterized by body sizes markedly different from the rest of the network compartments, i.e. the largest and smallest species (highest and lowest trophic levels), as it was found. Therefore, the scaling of consumption with biomass is due to the fraction of the variance of the numerical abundance  $N$  which is not correlated to the mean organism size  $m$  (because it is assumed that  $m$  is constant and  $N$  varies). This is surprising because *a priori* one could expect body size to play an important role in the really tight scaling of consumption with biomass: indeed, in fish communities, body size can be considered to be constant as a first approximation, but it is not really constant and it plays a key role in several ecological processes (e.g. Chapter 6). If this explanation was true, then the CB scaling would follow from one simplifying assumption often found in Ecopath models (i.e. that most organisms in the model have similar body sizes) and should be considered valid only for compartments containing organisms with similar sizes, e.g. in food web models of fish communities. However, this final explanation is characterized by some weakness as well, because it does not elucidate why the SDB exponents appear to be slightly but systematically higher than one.

Finally, I notice that in Ecopath models  $Q_{in}$  can be estimated as the product of two factors,  $(Q_{in}/B) \cdot B$  (e.g. Chapter 3), and consequently the scaling could be, at least partly, trivially caused by the way that the models are constructed (lack of statistical independence between  $Q_{in}$  and  $B$ ). However many models were included in the analysis, so that a large number of different methods was used to estimate  $Q_{in}$ ,  $B$  or  $Q_{in}/B$ , guaranteeing that flows and biomasses are not systematically biased by some unknown factor and that (at least in some models) they are representative of the real “field” values, which is what really matters for the purpose of the analysis. In addition, some non-Ecopath models were also analyzed (Table A3.2) to further clarify the point of systematic biases due to model construction: reassuringly, the scaling was detected in those models as well.

### 7.5.3 Supply-demand balance in ecosystems

So far, the focus of the discussion was on the regularity of the CB scaling, seeking explanations starting from simple and general processes, but further insights can be achieved by looking at how small differences among the estimated exponents reflect the different environmental and trophic conditions of the ecosystems. The statistically significant correlations that *SDB* displayed with food web indicators and ecosystem attributes seem to indicate that the exponent is inversely related to ecosystem maturity (Odum, 1969). *SDB* positively correlated with the primary production-total living biomass (i.e. excluding detritus) ratio and the Schrödinger ratio (total respiration-total living biomass ratio) which are expected to be higher in early-successional ecosystems, while it negatively correlated with the fraction of flows recycled in the ecosystem (Finn's cycling index), the mean chain length weighted on flows, considering cycles (Finn's mean path length) but also neglecting them (Finn's straight-through path length), the living biomass per unit of biomass flow in the network and the fraction of development capacity due to inter-compartmental flows (which is positively correlated with the degree of cycling, Section A3.3), which are usually higher in more complex, near-climax communities (Section A3.3).

Following an economic analogy, also interestingly advocated in metabolite transportation networks to explain the scaling of metabolic rate with body mass (Banavar et al., 2002), one could say that the variability of the exponent reflects the balance of supplies and demands in the food web (Bendoricchio and Palmeri, 2005) during the ecosystem succession (Odum, 1969), hence the acronym *SDB*. Immature ecosystems are characterized by high relative supplies (as exemplified for example by ecosystems attributes such as high primary production per unit of living biomass) and low demands (e.g. a short, linear food web) but with time, in the absence of intense disturbances, supplies are allocated to meet demands, such as higher stored biomass and cycling, so that *SDB* decreases. Demands can be thought as costs, since loops are redundant and biomass needs energy to be maintained, that ecosystems must bear to achieve a better exploitation of resources. Cycles provide independence from external inputs, while a high biomass per unit of energy flow can be sustained only if organisms are efficient and niche-specialized. It is worth stressing that this supply-demand interpretation is a phenomenological, and not mechanistic one: I am simply reporting that, in systems characterized by a developmental stage (sensu Odum, 1969), the scaling exponent seems to be higher. It is not clear how or if the exponent values are causally related to such developmental state, i.e. to biomass-specific system productivity, cycling, etc., but this does not affect the empirical evidence that the exponent reflects (i.e. it is correlated to) “supplies” and “demands” at the ecosystem level.

According to the abovementioned framework, it is not expected (nor observed) that *SDB* will lower indefinitely, since too efficient and specialized ecosystem configurations would be vulnerable to external disturbances (Ulanowicz, 1986; Ulanowicz, 1997) and thus unstable. Consequently, not only *SDB* time-variations may be used to monitor the ecosystem successional stage, but an “optimum” value

may exist. Notice that several statistically significant correlations were detected between *SDB* and indicators expressed as ratios, which indeed are fitter to provide a measure of supplies and demands which is relative and can encompass separate tendencies of ecological succession such as resilience versus efficiency (Ulanowicz, 1997).

As an ecosystem indicator should be, *SDB* is appealingly simple, easily understandable by policy-makers due to the economic analogy, and weights equally (being a slope on a bilogarithmic diagram) high trophic level compartments, whose biomass is scarce but whose conservation can be of utmost importance, and low trophic level compartments, which can overshadow all other organisms in holistic ecosystem indicators based on trophic flows, e.g. primary production-total respiration ratio, total system throughput, and fishery catches (Christensen et al., 2005). Unlike many other ecosystem indicators, confidence intervals can be computed for *SDB*, although wide ones (Table A3.5). Wide confidence intervals are not unexpected, because uncertainty must inherently be high when trying to synthesize the status of an ecosystem into a single number. The uncertainty of the *SDB* estimates could partly be reduced by excluding outlier compartments from the calculations, should they deviate from the CB scaling due to ecologically meaningful reasons, but the often not-negligible errors affecting flow and biomass estimates in trophic flow network models (Christensen et al., 2005) cannot be eliminated. Consequently, in the conclusion of the chapter, the results presented here are discussed in relation to the issue of data quality.

## 7.6 Conclusions

Indeed, overall limitations of this analysis must be recognized due to the quality of the data. Trophic flow network models are affected by uncertainty and constructed upon assumptions and approximations to deal with missing information, and both network balancing, and subjective modeller's choices such as how many compartments should be included in the model and to which degree of taxonomic aggregation, can potentially bias flows, biomasses and holistic network properties (Baird et al., 1991; Ulanowicz, 2004; Christensen et al., 2005). Nevertheless the data that was analyzed is among the best available up to date for trophic flow networks on large spatial scales, and it is also argued that the great amount of data and the many different ways that they were originally collected should ensure that real patterns emerge, eliminating most of the potential biases.

And, indeed, despite the variety of ecosystems, the many criteria for model construction and balancing and the different degree of aggregation of the food webs, a common, widespread scaling was identified, moreover a quite tight one and with a remarkably constant exponent. Some explanations and speculations about the origin of such scaling (which to my knowledge was never reported before), the

systematic deviations from it and the observed *SDB* values were provided, taking inspiration from different yet simple ideas: individual-level processes such as the scaling of metabolic rate with individual body mass, population-level processes such as the variability of population abundance and its relationship with body mass, and ecosystem-level constraints such as the food web position of a compartment or the balance of resource supplies and demands in the trophic network.

Clearly these hypotheses are tentative and leave open questions about the origins of the scaling, but they are not mutually exclusive. Of course, the energetic budget of a food web compartment is the sum of the individual metabolic requirements of the organisms belonging to it. Yet, it is also the position of that compartment in the food web, as it was speculated, and the effect of the whole-ecosystem dynamics emerging from the interactions of many organisms, as demonstrated by trophic cascades (Frank et al., 2005), i.e. ecosystem structure and functioning, that can affect both the abundance of the organisms of the compartment and the food available to them and, hence, the biomass and consumption of the compartment. Here it was showed that the way that these two quantities scale together is clearer from a systems perspective, i.e. when looking at the large-scale functioning of the ecosystem as a supply-demand-like process. In particular, as shown by the correlations, the *SDB* exponent appears to be quantitatively related to the balance of supplies and demands in the whole network, i.e. to the overall trophic functioning of the ecosystem. Therefore *SDB* appears to be a good candidate for the role of indicator of the successional stage of aquatic ecosystems.

The supply-demand-like system behaviour leads to a straightforward analogy between the functioning of food webs and other flow networks, such as economic markets and metabolite transportation networks. In particular, a supply-demand mechanism has been advocated as an explanation for the power-law individual metabolic scaling based on the analysis of optimal metabolite transportation networks (Banavar et al., 2002). Intriguingly, from the results reported here a supply-demand relationship emerges too, again for a transportation network (the food web), and again leading to a power law scaling of energy (i.e. flows) with mass.

As a final remark, it may not appear surprising that the consumption of a food web compartment scales across compartments with its biomass: after all, the same holds true intraspecifically (flows are proportional to biomass in the Lotka Volterra equations), and consumption is mainly a function of biomass also for individual organisms. However these considerations only entail that a relationship should exist for compartments, but do not define which kind of relationship it should be. Moreover, here it is also showed that extrapolating from individuals to the particular relationship which is reported for compartments is not straightforward.

Furthermore, in food webs, consumption is known to be linked to strikingly many factors other than biomass, such as temperature (Peters, 1983; Brown et al., 2004; Christensen et al., 2005), encounter rates and functional responses (e.g. search rates, prey abundance and availability, satiation,

prey handling time and predation risk tradeoffs; Christensen et al., 2005; Begon et al., 2006), food competition (Christensen et al., 2005; Begon et al., 2006) and, in the case of fish, morphometrics, diet and asymptotic weight (Christensen et al., 2005), just to name a few. So, the fact that biomass alone can yield a good first estimate of the consumption of a compartment, an approximation holding even worldwide to some degree (Figure 24), implies that trophic flow network models could be constructed with relatively fewer data than it is now realized. For example, timeseries of catch per unit effort (Christensen et al., 2005) or other proxies for biomass, that could be used to reconstruct historical trophic flow network models, are often available. Recent suggestions that the holistic properties of trophic flow networks are insensitive to parametrization errors (Kones et al., 2008), are encouraging about the potential usefulness of the findings reported here to infer about the trophic flows and the functioning of ecosystems of the past.

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## 8. How do marine ecosystems function? - Conclusions

In this thesis, I explored the way that pressures translate into state changes in large-scale marine ecosystems, and how ecosystem functioning is consequently affected. The focus of this work was on the Northern Adriatic Sea, a perfect case study for the abovementioned purposes, being a complex ecosystem under the influence of several anthropogenic pressures and environmental forcings.

Many different approaches were used to gain insights on the integrated functioning of marine ecosystems. Ecological network analysis was applied to a static model of the Northern Adriatic food web, highlighting key characteristics of the trophic flows, as well as possible signatures on the food web of the effects of fishing and eutrophication. The study of the effects of climate on a crab population of the Venice lagoon, bordering the Adriatic Sea, showed that it is possible to scale from physiological processes relevant at the laboratory scale to the dynamics of populations, and also that thermal stress on early life stages due to climate can strongly influence the abundance of aquatic populations. The investigation of the effects of fishing and climate on elasmobranch populations, through a combination of historical data analysis, fish market sampling and modelling, evidenced that these predators are overfished in the Adriatic Sea but that proper management actions can reverse their long-term decline, whose ecosystem consequences are unexplored. A conceptual model of the Northern Adriatic pelagic food web, based on the concepts of autocatalysis and size-based interactions, suggested that nutrient enrichment, which is a bottom up pressure, triggered top down dynamics within medium trophic levels, strongly altering the abundance of pelagic fish. A meta-analysis of 56 food web models showed that aquatic trophic networks display regularities reflecting their successional stage, which can be influenced for example by anthropogenic pressures or environmental forcings, and that such regularities could be used to construct an indicator of the state of the ecosystem.

Different spatial scales were taken into account in the analyses, ranging from populations to ecosystems and macroecological scales involving worldwide ecosystems. Also temporal scales varied: short-term as well as long-term variations of populations were considered.

Indeed some of the findings related to the Northern Adriatic Sea may be difficult to extrapolate to other marine ecosystems. Clearly, the material configuration of an ecosystem depends also on chance and on its unique history (Ulanowicz, 2009) as well as on the particular local environmental characteristics and anthropogenic pressures. However, I feel that the work of this thesis conveys also a general message. Although many different perspectives were taken, many different methodologies were used and many different scales were analyzed, it was clear that all the many different factors taken into account (human pressures, environmental forcings, dynamics within the system) could strongly

influence ecosystem functioning. Nutrient enrichment and fishing were identified as key anthropogenic pressures in the Northern Adriatic Sea, climate was shown to affect marine (and lagoon) populations in several ways (migrations, impact on early life stages), size-based trophic interactions (possibly) led to unexpected and strong top down dynamics, and indeed the way that consumption scaled with biomass in aquatic food webs appeared to be related to the ecosystem successional stage.

An important message is that, in general, the effects of pressures on marine ecosystems cannot be analyzed in isolation, because they were shown to interact with each other in synergistic and unpredictable ways. For example, the trophic flow network of the Northern Adriatic Sea was probably shaped both by eutrophication and fishing, and skates seemed to be influenced both by climate and exploitation. Moreover, one should also take into account the dynamics which can originate within ecosystems, e.g. through trophic interactions. For example, it was hypothesized that the Adriatic pelagic fish communities were strongly influenced by an autocatalytic feedback loop triggered by the onset of eutrophication: thus the management of fisheries resources in the Northern Adriatic Sea seems to be closely linked to the issue of eutrophication.

Therefore, after a practical examination of ecosystem functioning from several points of view, I conclude that, indeed, it is true that to manage ecosystems in the best possible way, the focus must be at the ecosystem scale and not on single pressures or on ecosystem compartments separately. The “ecosystem approach” concept may look complex, and indeed it is, but from a practical point of view, as shown by this thesis, an ecosystem-based approach to management is clearly justified and necessary to manage marine ecosystems.

Of course, an ecosystem approach does not mean that every forcing, every pressure and every process should be taken into account, e.g. modelled or monitored. Based on the work of this thesis, I conclude that there are two complementary key methodologies (at least) to identify the most important factors influencing ecosystem functioning, in order to achieve an operational ecosystem-based management. On one hand, data analysis is a key part of the ecosystem approach, both to isolate the effects of single pressures on single ecosystem compartments (e.g. laboratory data) or to understand more about emergent ecosystem dynamics (e.g. historical data). In particular, this thesis shows that the study of the past can teach us many things about ecosystems and the integrated way they function. On the other hand, one cannot make laboratory experiments for large-scale marine ecosystems and historical data are limited, therefore modelling is a key part of the ecosystem approach. Modelling was used only partially in this thesis, but simply because there were so many data to analyze and which could provide important insights on ecosystem functioning. Indeed the construction and validation of mathematical models of the functioning of ecosystems is one of the key ways to integrate ecological information, in order to provide predictions about the future and to produce useful and quantitative

management advices concerning marine ecosystems. This is why I think that the importance of ecological modelling will keep on growing in the near future.



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*The point of departure is not to return*

*Anything can happen*

(Neil Peart, 1987)

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