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Effects of Climate Changes on the Mediterranean Nektonic communities, and consequences on commercial fisheries

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Introduction

According to the most recent estimates by the Intergovernmental Panel on Climate Change [1], the mean annual temperature on the Earth surface is expected to raise between 1.4 and 5.7°C by 2100. This will intuitively have major consequences, both direct and indirect, on the structure and functioning of terrestrial as well as aquatic ecosystems.

Global change becomes therefore a subject of primary importance in ecology. Empirical as well as theoretical evidence indeed shows that climate change constitutes one of the major forcings acting on ecosystems worldwide [2–5].

In particular, the present features of marine ecosystems, such as hydrodynamics, productivity and water acidity are predicted to undergo substantial modifications as a consequence of changes in the meteo-climatic drivers [6]. Specifically, these changes may determine potential impacts on the distribution and abundance of nektonic populations, as a consequence even of little temperature variations [7].

In more detail, climate change can influence individuals, populations and communities through the physiological and behavioural responses to environmental modifications [8]. Most marine organisms, in facts, being ectothermic (that is, depending on external conditions for the regulation of body temperature), show the tendency to distribute in proximity of areas characterised by thermal conditions that are optimal for a given species [7]. As a consequence, it is reasonable to expect shifts in the distributional ranges of marine populations, following the possible variations in the thermal regime of waters due to climate change. Moreover, even if temperature variations had no direct significant consequences over a given population, the same population could find itself facing competition with new species that, because of the same variations, could invade its habitat [9].

In addition, changes in distributional ranges and interactions among previously separated populations can determine profound reconfigurations of the communities living in a given area. These reconfigurations would necessarily impact, either in a positive or in a negative way depending on the specific cases, fishing activities both at the commercial and the recreational levels [7].

In this context, the number of studies intended to understand and predict the effects of the temperature raise on the structure and functionality of marine ecosystems is rapidly growing.

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According to the last IPCC projections, in the Mediterranean the mean temperature raise due to climate change will be higher than the global average [1]. Therefore, modifications in the biological communities driven by climatic factors are particularly likely to happen. As a matter of fact, such a phenomenon has already been detected and seems to be taking place at a constantly increasing rate [10, 11]. What theory suggested to be reasonably expectable is presently happening, in the form of thermophilic species, historically occupying the southern parts of the basin, expanding their ranges northward and coming to interact with autochthonous populations. In addition to this process, called meridionalisation, tropical species are also becoming ever more present in the basin, producing what is known as the tropicalisation of the Mediterranean Sea [12].

In this context, the northern Adriatic Sea represents an interesting case study. It constitutes the northernmost part of the Mediterranean Sea, excluding the Black Sea [13], and it is characterised on its western coast by sandy beaches interspersed with river deltas and lagoons, while the eastern side is mainly rocky [14]. It is a shallow basin, with a mean depth of just 33 m, entirely extending over a continental shelf area. The seafloor presents a gentle slope toward the centre, where the maximum depth doesn't exceed 75 m [14].

The geographic positioning of the area determines a sub-Atlantic climate, due to the influence of the cold winds blowing primarily from the north-east (like the one locally known as *bora*), to the considerable discharge of cold water from many relatively short rivers originating in the nearby Alps, and to the scarce if not negligible influence of the main Mediterranean currents [15]. The peculiar climatic conditions determine an attenuation of the Mediterranean characteristics in the biological communities, not only in terms of a reduction of the occurrence of the most thermophilic elements, but also with the presence of microthermic elements, which can be regarded as glacial relicts [16, 17].

The circulation of water masses is mainly cyclonic, with an inbound current flowing along the eastern coast in a NW direction, introducing relatively warm waters with a high salinity. The sudden drop in temperatures taking place during winter, on the other hand, determines a denser and colder water mass which flows southwards following the western shores [18]. Seasonal differences in temperature produce a vertical stratification during the summer period, while during winter the water column undergoes a thorough mixing [14]. This phenomenon deeply affects the transport within the basin [19, 20], influencing the dynamics of suspended and dissolved nutrients and supporting primary production. Therefore, during the warm season the nutrient content of the superficial water layer decreases because of the uptake by the phytoplankton, while the deep layer is enriched; conversely during winter the nutrient concentrations are more homogenous, reaching high levels along the coast as well as in the open sea [19, 21, 22]. More generally, the nutrient load introduced with runoff (mainly from the river Po) and the scarce depth which forbids dilution, combined to the hydrodynamic features cause the waters of the northern Adriatic to be particularly rich [23], sustaining a dense biological community, as well as one of the most developed fisheries in the Mediterranean [24], employing about 1800 vessels in 2010, totalling a GT of 22900 tons and directly employing 3800 people [25].

In this context, in accordance to the trend highlighted for the whole Mediterranean, thermophilic alien species are being recorded with an increasing trend also in this area, ranging from top predators (*Coryphaena hyppurus*, *Pomatomus saltatrix*, *Sphyraena viridensis*), to small pelagic fish (*Sardinella aurita*), to planktonic and benthic invertebrates [11, 26–30].

In synthesis, in the northern Adriatic basin the peculiarities in the geoclimatic context and the consequent adaptations in the biological communities, together with the extensively developed fishery all concur to make the area potentially highly vulnerable to the effects of climate change, thus rendering it an invaluable case study to investigate such impacts on the biological community and on the related human activities.

All this considered, this thesis will try to investigate the possible effects of climate change on the Mediterranean nektonic communities, by focusing on the northern Adriatic sea case study. The work will articulate in two main phases:

1. A thorough characterisation of the vulnerability of the northern Adriatic ecosystem to climate modifications. This phase can be further subdivided as follows:
    a. An analysis of the biological communities of the area, with the aims of justifying the existence of a lacuna, sensu Marcello [16], and evaluating the opportunity to define it as a Boreal enclosure, with regards to the presence of organisms typically associated with Boreal climate. Special emphasis will be put on the role of this lacuna/enclosure as an 'early proxy' for impacts of climate change, by assessing the presence of signs of change at the population/community level.

   b. A study of the present situation of the northern Adriatic fisheries, both in the open Sea and in the Venice Lagoon, with a focus on shifts in the time series of landings possibly tied to climate-related dynamics, to assess the vulnerability of the renewable resources exploitation, and of the nektonic communities themselves, to Climate Change.

2. The development of a dynamic food-web model of the northern Adriatic ecosystem. The model will explicitly account for the effects of temperature on the system components, and consider the potential of invasion by thermophilic alien species already signalled in the area or whose arrival is likely. The goal in this phase will be both studying the potential of the model itself, and analysing future scenarios related to Sea Surface Temperature raise projections, to gain knowledge about the dynamics driving the system and to provide some hints about the direction towards which it may evolve, setting the base to discuss effective management options.

Chapter 2

Venetian lacuna or Boreal enclosure?

The Northern Adriatic biogoegraphic peculiarities in the context of climate changes

Abstract

Along the Italian coasts of the Northern Adriatic Sea, there is a well delimited portion that historically has been described in terms of 'Venetian lacuna', due to the subatlantic climatic conditions which resulted in a lack of Mediterranean plant species. Since this makes the area a candidate to highlight early signs of change related to climate modifications, a wide spectrum analysis, considering both plant and animal communities in marine and terrestrial environments, was carried out to confirm the presence of the lacuna and assess the opportunity to define it as a 'Boreal enclosure', and to investigate the possibility to describe the influence of the lacuna/enclosure at the community level to highlight possible trends of variation. This performed by revising the available literature about the lacuna, analysing the temporal variations in terrestrial plants and marine communities and reconstructing the winter SST isotherm trend in the Northern Adriatic. Results highlighted the presence of boreal affinity species (both plants and animals) in the terrestrial as well as in the marine environment. The time series analysis showed the presence of clear signs of change in the marine ecosystem at the community level with a decrease of cold affinity species (and a consequent increase of warm affinity ones), and at the population level with a shift towards colder months in their life-cycles. In the terrestrial environment, conversely, the temporal analysis of plant communities showed no clear trend of variation, apart from a significant increase in non-indigenous species. The study confirmed the existence of a Northern Adriatic Boreal enclosure, highlighting its role in the detection of early signs of climate change, and pointed out the vulnerability of this semi-enclosed area, claiming for the definition of proper management objectives and strategies.

2.1 Introduction

The Italian coasts of the of the Northern Adriatic Sea, in the segment delimited by the estuaries of the Adige and Tagliamento rivers, show climate-related adaptations in the biological communities which make them strongly atypical within the Mediterranean context.

As far back as 1913, Béguinot [1] had reported about an 'Italo-Adriatic lacuna' which Marcello [2] later described more precisely as the 'Venetian biogeographic lacuna'. In synthesis, both the authors noted that many typically Mediterranean plant species found on Istrian and Dalmatian coasts, and, on the Italian side of the Adriatic, from Emilia-Romagna southwards, were missing from venetian coasts. All this was explained in relation with the climate of the Northern Adriatic shores, which presents subatlantic features rather than Mediterranean ones, due to the exposition of the basin to cold north-easterly winds, while it is protected from the influence of warm, south-westerly ones. Furthermore, the area is located close to one of the most windy and rainy sector of the Alps, the sea basin is quite shallow on average, with a mean depth of only 34 m, and it is excluded from the main Mediterranean water circulation (Figure 2.1).

All these morphological and climatic features have been supposed to produce a lack of Mediterranean species, favouring, on the other hand, the presence of boreal taxa (species and subspecies typical of the middle-European Atlantic coasts), which in many cases can be considered as endemic within the Mediterranean context [3].

Within this framework, the aims of this chapter are:

- to revise the available literature about the taxonomic specificity of the Venetian area, justifying the existence of a lacuna, also in compartments other than vegetation, and evaluating the opportunity to define it as a Boreal enclosure;
- to investigate the opportunity to describe the influence of the lacuna/enclosure at a community level, through the analysis of the plant communities of shores and dunes in different sites across Europe;
- to assess the presence of 'early signs' of changes at the population/community level, due to possible effects of climate modifications.

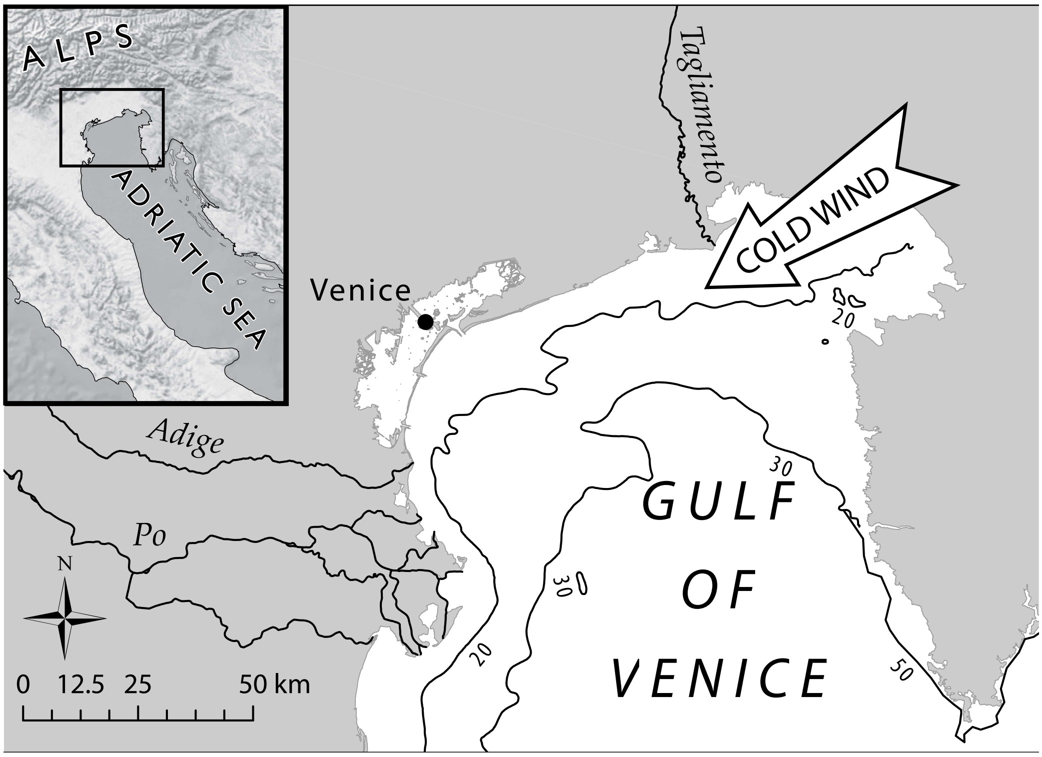

Figure 2.1: Study area

2.1.1 Peculiarities of the Venetian lacuna

The first description of the Venetian lacuna was based on floristic studies of the Northern Adriatic shores. Béguinot [4] and later Marcello [2] described a gradual reduction of thermophilic plant species starting from the Gargano area, on the Ionian Sea coast, northwards. This reduction culminated in the coast segment delimited by the mouths of the Adige and Tagliamento rivers (respectively on S and N, Figure 2.1), where Mediterranean species could be found only occasionally. Specifically, the authors listed two groups of Mediterranean species which could be recorded respectively South and North of the lacuna, but not inside it (Table 2.1).

This lack of Mediterranean vegetation 'made room' for other species, better suited to the peculiar climatic conditions of the area. As an example, among the species listed as typical of Venetian shores by Marcello [2], several have a cold/boreal affinity (see supplementary table S.2.1, on page 33).

Concurrently, Pignatti [5] sketched the same phenomenon at a community level. Apart from the fixed zonation which was the one typically found in sandy coastal systems worldwide [6, 7], according to the author,

Table 2.1: Mediterranean plant species found South of the Venetian lacuna, (Group 1), and North of it (Group 2) (according to Béguinot [4] and Marcello [2]).

Group 1	Group 2
Cerastium granulatum	*Laurus nobilis*
Malcolmia confusa	*Spartium junceum*
Helianthemum apenninum	*Colutea arborescens*
Asterolinon linum-stellatum	*Rhamnus alaternus*
Valerianella puberula	*Pistacia terebinthus*
Melilotus sulcata	*Cotinus coggygria*
	Dictamnus albus
	Phillyrea latifolia
	Vitex agnus-castus

Northern Adriatic plant communities were characterised by a noteworthy species composition, where besides some thermophilic species (*Quercus ilex, Rubia peregrina, Osyris alba,* etc.), many species with cold and temperate affinity were found. This singular phytogeographic blend was later recognised and reinforced by several authors [8–13]. A rough list, including the plant species mentioned by different authors is reported in Table S.2.1.

Similarities among Atlantic and Northern Adriatic coastal communities can be recognised also in other compartments, apart from vegetation. The terrestrial gastropods *Cepaea nemoralis* and *Fruticicola fruticum*, indicators of cool, moist climate, are found close to the sea in the venetian area like on the Atlantic coasts, while in the rest of Italy they show a more inland distribution [3]. Similarly, *Cernuella virgata*, another gastropod, shows a dunal distribution in the area of interest, while on the rest of the Adriatic coast it is found on marly substrates; *Euparypha pisana* is found with the typically Atlantic phenotype *testudinea* on the venetian shores, where it shows a life-cycle comparable to that of its Atlantic conspecifics [3]. In analysing the distribution of terrestrial gastropods, Sacchi noted that it seems to follow closely the limits defined by the winter Sea Surface Temperature isotherms (as measured in 1961, Figure 2.2), with boreal affinity species limited inside the 7°C isotherm, whereas typically Mediterranean species, as *Eobania vermiculata*, aren't found farther north than the 8°C limit, and more thermophilic species are recorded only south of the 9°C curve (Figure 2.2).

Several insect species with a Northern-Europe distribution were found on the venetian coasts, where they are considered glacial relicts (Table S.2.1): for some of these species, in the Adriatic area, an inverted life-cycle has been described in comparison with the Atlantic populations [14], suggesting an adaptation to local environmental conditions that might be close to the southern distributional limit.

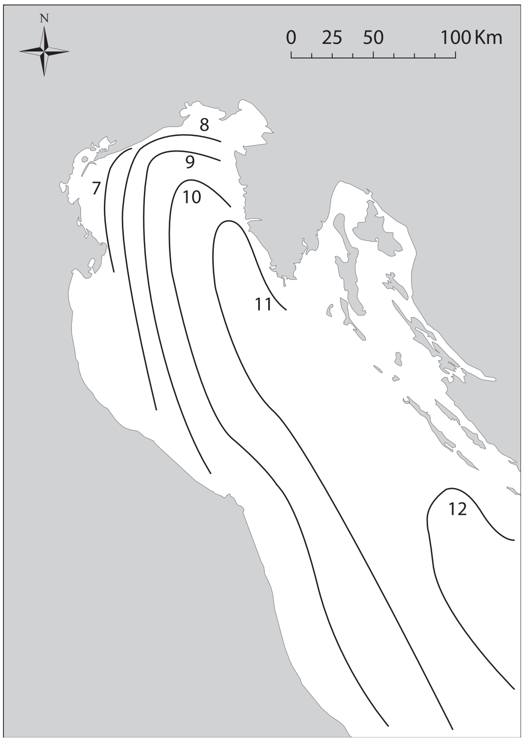

Figure 2.2: 1961 Winter sea surface isotherms in the Northern Adriatic Sea (from Sacchi [3], redrawn).

Concerning marine species, the brown alga *Fucus virsoides* is notably the only Mediterranean example of the genus Fucus, and its distribution matches exactly the limits of the Venetian lacuna. The species, which is very close to *F. spiralis* from the Northern Atlantic shores [15], shows boreal affinity and can be considered a glacial relict [16]. Several boreal affinity invertebrates are described in the Northern Adriatic, such as mysid and amphipod crustaceans [14], and the brown shrimp *Crangon crangon* [17]. The gastropod *Littorina saxatilis*, which is widely diffused in the Northern Atlantic and North Sea, in the Mediterranean context is only present in the Venetian area, being substituted in the rest of the basin by *Littorina neritoides* [14, 18].

Among vertebrates, the Northern Adriatic hosts large populations of two boreal fish species: European flounder *Platichtys flesus* and sprat *Sprattus sprattus* [19]. Both species, which are common in the Northern Atlantic and North Sea, in the Mediterranean limit their presence to the northern parts of the basin (latitudes above 40°N), such as the Gulf of Lion, the Adriatic Sea, the Aegean Sea and the Black Sea [19]. As revealed by recent genetic analyses [20, 21], these populations are almost completely isolated (both among themselves and with the Atlantic ones), confirming the hypothesis that the two species constitute real glacial relicts, trapped in the southern edge of their distributional range. All this can induce modifications in the life cycles, as described for sprats, which in the Adriatic area spawn during the winter season, while Atlantic populations spawn during summer [22].

Overall, it is evident that the Northern Adriatic ecosystem is populated by many different boreal species, allowing to define it as a 'Boreal enclosure' rather than a lacuna based on the lack of Mediterranean species. A list of the species characterising this enclosure is reported in Table S.2.1.

2.2 Materials and Methods

2.2.1 Shore-dunes plant communities comparison across Europe

Worldwide, sand dune systems are characterised by a variety of habitats occupied by distinctive plant communities which are organised along a zonation, following a sea-inland environmental gradient, with the most pioneering annual communities on the beach and the woods in the inland sheltered zone. Plant communities of beaches, embryo-dunes and mobile dunes are usually described as azonal [9, 23], as their presence seems to be linked to unfavourable non-climatic ecological features such as stress-factors or severe soil conditions [24]. These communities indeed are characterised by a very narrow specific composition, with species strictly adapted to the severe environmental features [7], but usually showing a broad distribution on a global scale [25, 26]. For this reason, they present a similar structure and a comparable specific composition, even in different climatic zones [27], with vicariance described mostly at the subspecies level. On the contrary, the communities of the sheltered zones (fixed dune systems) are delineated by specific and coenological features which are more related to local conditions such as climate, morphology, lithology and history [8, 28]. At present, while many research works have concentrated on the more structured plant communities of the sheltered zone, none investigated the phytogeographical features of beach and foredune habitat types in the Northern Adriatic coasts.

In order to explore plant communities composition in relation to the climatic affinity, communities recorded on the Northern Adriatic coasts have been contrasted with several sites distributed across Europe. The attention was focused on azonal communities of beaches, embryo-dunes and mobile dunes, also considering the microprairie habitat, which occupies an intermediate position (transition or semi-fixed dunes) along the coastal zonation.

For the meta-analysis, a database containing phytosociological vegetation samples was built. An extensive review, covering geographic and climatic variability at the European scale, allowed the collection of 1818 vegetation surveys (see supplementary table S.2.2, on page 34). Within each habitat type, only samples with comparable plot size were selected using the standardised procedure proposed by Haveman and Janssen [29].

Although communities could be named differently, they were grouped according to the authors' structural and ecological description and their position along the zonation (Table 2.2).

Table 2.2: Plant community types used for the meta-analysis.

Position	Plant community description	Main diagnostic species
Upper beach	Annual, nitrophilous community of the strandline zone of the beach	*Cakile maritima*
Foredunes	Pioneer, perennial community of the low embryonic shifting dunes, dominated by dune forming plants	*Elymus farctus*
Mobile dunes (white dunes)	Perennial herb community of stabilized mobile dunes dominated by rhizomatous species	*Ammophila arenaria*
Transition dunes and/or semi-fixed dunes (grey dunes)	Perennial community of the inland side of mobile dunes, dominated by chamaephytic species, lichens and mosses	Abundant carpets of lichens and mosses

To summarise the floristic characteristics of each community type in terms of climatic affinity, chorological spectra representing the frequency of the species of a given chorological type in each community were analysed. The distribution range of the species was mainly according to Pignatti [30] and Tutin *et al.* [31, 32], although in some cases additional sources were used.

Community similarity across different European coastal areas has been tested through PCA, using the software package SYNTAX 2000 [33], applying UPGMA and a similarity ratio coefficient. Since they constitute a confounding factor in the community characterisation, non-indigenous species (NIS) have been excluded from this analysis.

2.2.2 Temporal variations in biological communities

Terrestrial plant communities

To analyse vegetation changes through the time, several methods are usually adopted, such as repeated relevés, permanent plots [34] and field experiments, but the most frequent indirect approach for monitoring temporal dynamics involves the use of chronosequences and associated space-for-time substitution [35, 36]. The method provides an appealing alternative to long-term studies and, despite some limitations [37], it received support from different studies, indicating a close correspondence between synchronic and diachronic data [36, 38].

Temporal dynamics in sand dunes habitats along the Venetian coast have been analysed using a diachronic spatial approach [39], by comparing vegetation data collected with the same protocol in different periods. The analysis focused on the same four habitats considered at the European scale (Table 2.2).

Up-to-date and past phytosociological surveys regarding the Northern Adriatic area allowed the identification of four chronosequences which started in the '50s of the past century and ended in 2011. Each chronosequence was composed by 4 time spans: 58 surveys for 1959 [5], 15 surveys for 1980 [11], 47 surveys for 2000 (3 in Poldini *et al.* [40] and 44 unpublished) and 41 surveys for 2011 (unpublished data). In the case of the *Tortula ruraliformis* community, no data in the '80s were available. All recent surveys were recorded by using the Braun-Blanquet seven-degree scale of abundance and dominance [41], adopting the same method used by past authors. Surveys were recorded at the same localities specified by past authors, although not exactly in the same plots, due to the lack of precise information. The numbers of plots per temporal stage were not equal because of insufficient historical data, particularly for the '80s. However, since this work was conducted retrospectively on historical data collected at different times, they were retained to avoid the loss of precision due to the lack of intermediate observations. Chorological spectra representing the frequency of the species of a given distribution type in each habitat in each time span were analysed.

Pignatti [30] was used as reference to define the species distributional ranges; in this case, also NIS were taken into consideration. The significance of differences along the chronosequences was assessed through independent groups paired $t-$tests, on data previously angular transformed [42].

Marine communities

The only data source to reconstruct time series of marine communities is often represented by landing records of fishing activities [43]. Even if potentially affected by various bias, this kind of data is recognised to be useful to study the temporal variations of marine assemblages, particularly in relation to the nekton component [44]. The time series of landings (1947–2011) was reconstructed by using the annual data from the most important fish market in the Northern Adriatic, located in Chioggia.

In order to analyse the marine community composition in terms of climatic affinity, each species was characterised on the basis of the thermal range of its distributional data according to Pranovi *et al.* [45]. Coordinates of punctual observations of individuals belonging to the species of interest in the northern hemisphere were retrieved from the Global Biodiversity Information Facility website (`data.gbif.org`), and medians and interquartile ranges of latitudinal distributions were computed. Arbitrary latitudinal thresholds of 30°N and 45°N were set, corresponding to the southern and northern limits of the Mediterranean Sea (excluding the northernmost parts of Adriatic and Black Seas), thus defining three 'climatic zones': 'cold' (above 45°N), 'temperate' (between 30°N and 45°N) and 'warm' (below 30°N). Climatic affinity was attributed to a given species depending on the climatic zone in which the median of its latitudinal observations was comprised. If the interquartile range of a species wasn't wholly comprised in the same zone as its median, an intermediate affinity was attributed, and if its range covered all the three zones, the species was classified as 'ubiquitous' [45].

Landings of species belonging to different affinity groups were analysed by dividing the time series into three periods, 1945–1977 (corresponding to the expansion of the fishery in terms of fishing capacity), 1978–1999 (the intermediate phase), and 2000–2010 (corresponding to the phase possibly more affected by climate changes). A comparison in terms of relative catch composition between the three periods was carried out. In addition, the absolute variation during the three periods for each climatic affinity group was analysed in terms of median and interquartile range.

In order to assess possible temporal variations at the population-life cycle level, the monthly time series of brown shrimp (*Crangon crangon*), flounder (*Platichthys flesus*), and sprat (*Sprattus sprattus*) landings have been further analysed by applying a Seasonal Decomposition Analysis, to obtain seasonal, trend and irregular components [46]. Also in this case, time series were split in three periods. The comparison among them allowed to highlight possible variations in the seasonal dynamics.

2.2.3 Winter sea surface isotherm trend analysis

According to the evidence reported by Sacchi [3], the boundaries of the lacuna along the coastline seemed to match those of the 7°C winter sea surface isotherm, recorded in 1961 (Figure 2.2). In order to assess the presence of variations in the thermal regime of the studied area, the evolution of the spatial pattern of the Winter SST has been analysed. Georeferenced satellite SST data (AVHRR, available from 1982 to 2006, and MODIS, available since 2002) were retrieved from the NASA Earth observations database (`http://neo.sci.gsfc.nasa.gov/`), and used to reconstruct raster maps of the Winter period (defined as the monthly average SST recorded in January, February and March) in the years 1982, 1990, 2000 and 2010. From these maps, isotherm curves were extracted using QGIS 1.8.0, to be compared to the 1961 situation reported by Sacchi [3].

2.3 Results

2.3.1 Shore-dunes plant communities comparison across Europe

Results of the phytosociological surveys review at the European scale, about the fore– and fixed dunes communities, are reported in Figure 2.3. In general, the analysis allowed to discriminate two or three main clusters, with the Mediterranean and Northern chorological types, and subordinately the Western type, playing a major role in defining the groups (in each analysed community the three chorotypes explained more than 80% of variance).

With reference to the Northern Adriatic area (NAD), a clear declining trend in the similarity with the other Mediterranean sites could be noted moving along the sea-inland gradient, from the *Cakile maritima* community landward, although the Mediterranean chorotype relative contribution remained almost stable across the different communities (23 – 27%) (Figure 2.3*a*). The NAD Cakile plant community grouped with the other Mediterranean areas, given the high percentage of both Western (29%) and Mediterranean species (36%); on the contrary, communities from North-

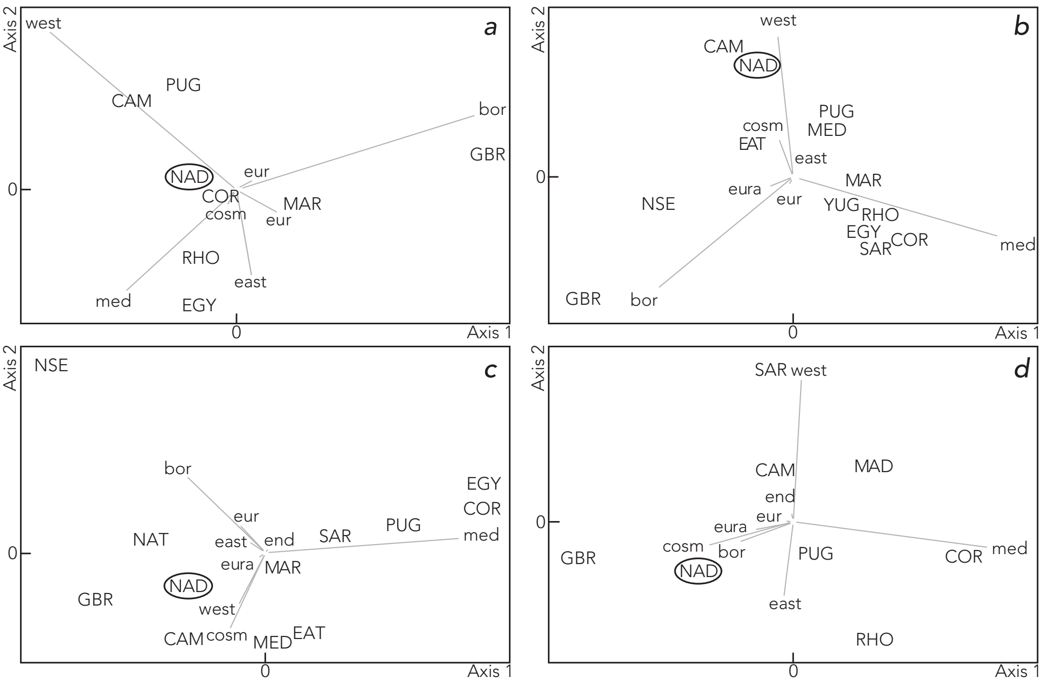

Figure 2.3: PCA for coastal plant communities — *a*) *Cakile maritima* community (variance explained by axis 1 and 2: 80.98%), *b*) *Elymus farctus* community (variance explained by axis 1 and 2: 90.42%), *c*) *Ammophila arenaria* community (variance explained by axis 1 and 2: 83.98%), *d*) *Tortula ruralis* community (variance explained by axis 1 and 2: 93.09%).

ern Europe (GBR) were strongly characterised by species of boreal affinity (39%) (Figure 2.3*a*).

In the embryonic shifting dunes, the NAD *Elymus farctus* community displayed a high Western component (31%), and an almost equal contribute from Mediterranean species (38%) (Figure 2.3*b*). This is much lower, however, than the one shown by other strictly Mediterranean communities, which ranged from 53% to 71%. In the NAD *Ammophila arenaria* community, the Western component decreased (15%), and the community enriched in in Boreal (5%), Eurasian (5%) and European (3%) species (with a temperate climate affinity), and Eastern species (18%) (Figure 2.3*c*). Finally, on the transitional dunes, the *Tortula ruraliformis* community showed a complex and diverse structure where beside the Mediterranean component (31%) many other types, such as Eastern (17%), Western (8%), Boreal (7%), Eurasian (7%), European (2%), and Endemic (5%) gained in importance (Figure 2.3*d*). The boreal elements, which were completely absent within the strictly Mediterranean communities, notably contributed to delineate the higher affinity with boreal sites than with the Mediterranean ones.

2.3.2 Temporal variations in biological communities

Terrestrial plant communities

From the above reported analyses, Mediterranean, Western and Boreal elements proved to be the most important in characterising the affinity among sites across Europe. Focusing on these types, the time-framed (1950 – 2011) comparison highlighted no clear trends of change (Figure 2.4). The temporal variations were gradual and, if present, significant differences have been detected mostly in the comparison between the two extremes of the chronosequence (1950s and 2011). The *Cakile maritima* community showed a gradual increase in Mediterranean species ($t-$test 1950s–2011, $p < 0.001$). The same temporal trend was observed for the proportion of both Western and Boreal species (1950s–2011, n.s.). Conversely, in the *Elymus farctus* and in the *Ammophila arenaria* communities, Mediterranean species significantly decreased through the chronosequence (1950s–2011, $p < 0.01$, for both communities), whereas species with Western or Boreal affinity remained substantially stable. Given its more complex structure in terms of ground cover and species diversity, the *Tortula ruraliformis* community revealed major variations in time. Western species showed a significant increase in their proportion (1950s–2000s and 2000s–2011 comparison, $p < 0.001$), whereas all other groups either thermophilic (Mediterranean: $p < 0.001$ for both time-spans) or with cold affinity (Boreal: $p < 0.001$ for both time-spans; orophilous: $p < 0.001$ for both time-spans) decreased.

A common increasing trend across the four communities has been detected for the non-indigenous species group. The trend was less clear in the *Cakile maritima* community, in which alien species fluctuated around an average value, whereas in the other three communities the pattern was definite, with the most significant increases in the *Tortula ruraliformis* community ($p < 0.001$ for both time-spans).

Marine communities

The time series of landings was divided in three periods: 1947–1977, 1978–1999 and 2000–2011. In general, data showed that the nekton assemblage is dominated by Cold and Temperate affinity species, accounting for more than 65% through the entire time series, even if a slight increase in the proportion of Temperate/Warm species has been recorded (Figure 2.5*a*). The temporal trends detected in the time series can be there-

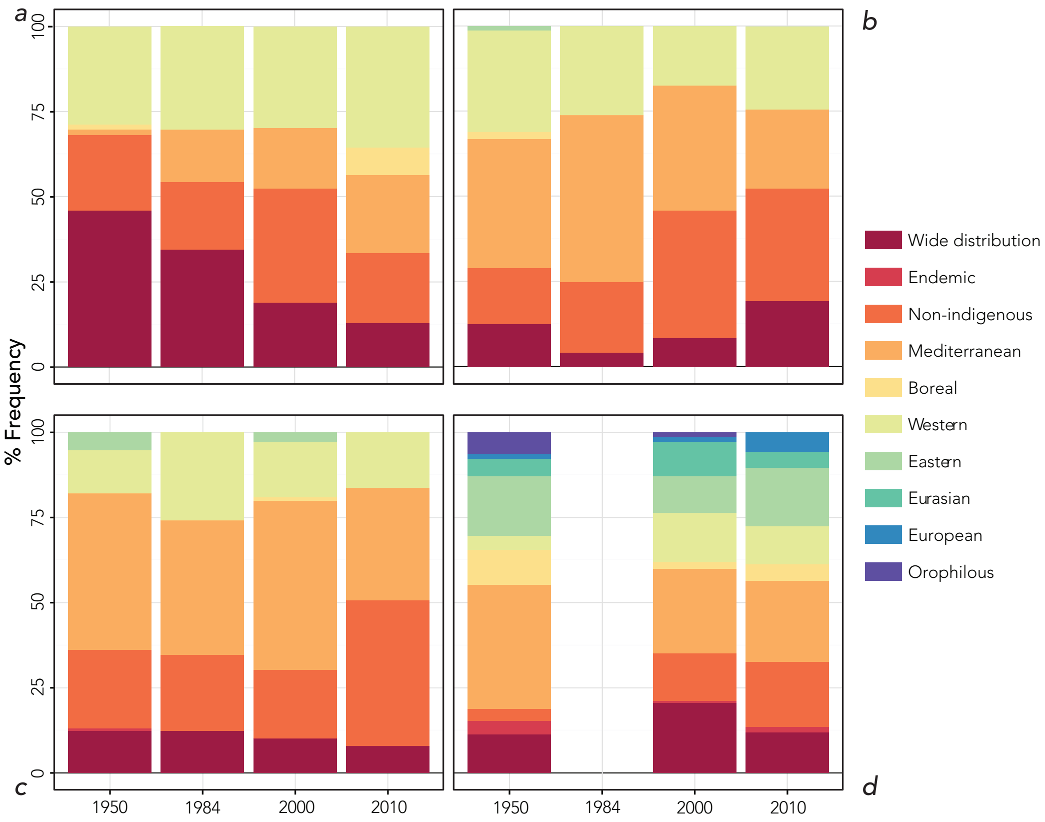

Figure 2.4: Temporal variations in the frequency of the geographic elements in the coastal plant communities — *a) Cakile maritima* community; *b) Elymus farctus* community; *c) Ammophila arenaria* community; *d) Tortula ruraliformis* community.

fore ascribed to variations of Cold and Temperate species (Figure 2.5*b*).

Both groups, indeed, showed a significant (Kruscal-Wallis test, $p < 0.01$) variation among different periods, specifically an increase between the first and the second period, and a decrease in the third (Figure 2.6*a*/*b*). On the other side, Warm species, which were historically very rare in the basin, underwent a substantial increase in the most recent period (Figure 2.6*c*).

In order to assess possible variations at the population level in terms of life cycles, the attention was focused on three cold affinity nektonic species, performing the analysis on the same three time periods as above.

- The brown shrimp (*Crangon crangon*): in the first period the monthly landings trend showed a minimum in May and a maximum in October, with a secondary peak in January (Figure 2.7). In the second period, the mean landings decreased significantly, particularly in the

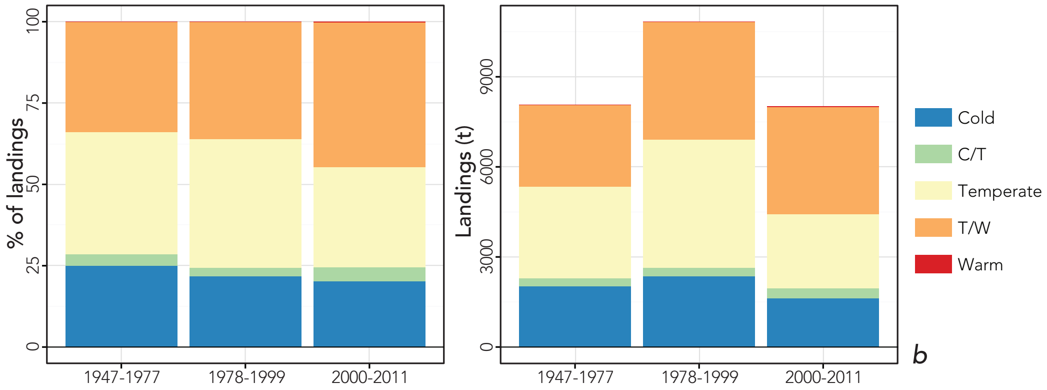

Figure 2.5: Landings composition in terms of climatic affinity groups in the analysed periods; (*a*) relative composition, (*b*) absolute values.

warmer months, and the maximum abundance was registered in January, while the October peak becomes less significant. In the third period considerable landings were achieved only in winter, while for the rest of the year catches were negligible. On the other hand, the phase of low catches extended in this case from April to November. The seasonal decomposition of the monthly time series of landings confirmed these observations, showing both a change in the pattern and shift in the landings seasonality in the three analysed periods (Figure 2.8). Moreover, by analysing the Seasonal component/Remainder range ratio, an increase of the seasonal component importance during the series has been recorded (Table 2.3).

- The flounder (*Platichthys flesus*): in the first period, the monthly trend showed a maximum in December, followed by a minimum in January/February and a secondary peak in May (Figure 2.9). In the following periods the spring peak disappeared and landings in the

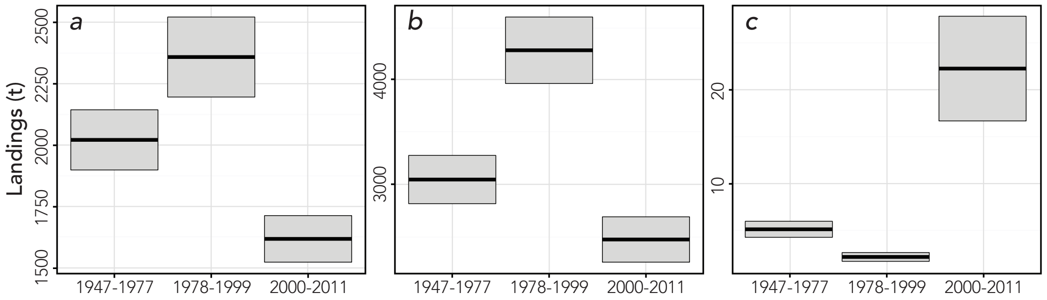

Figure 2.6: Temporal variations of the three main climatic affinity groups (*a* — Cold, *b* — Temperate, *c* — Warm) in the analysed periods; mean ± s.e.

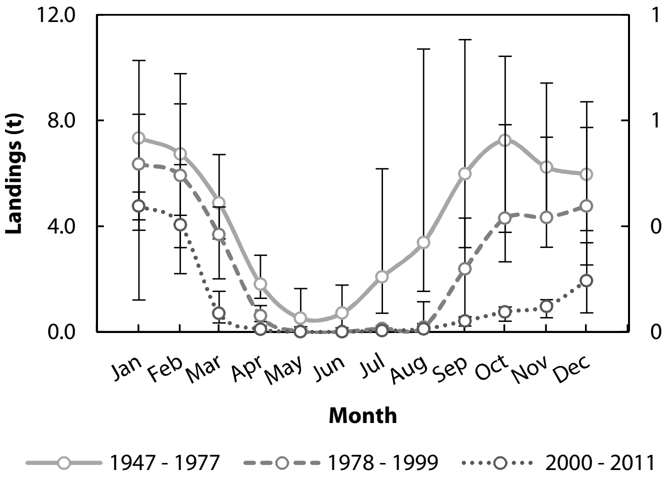

Figure 2.7: *Crangon crangon* monthly landings; medians and interquartile ranges in the periods 1947–1977 (left scale), 1978–1999 and 2000–2011 (right scale).

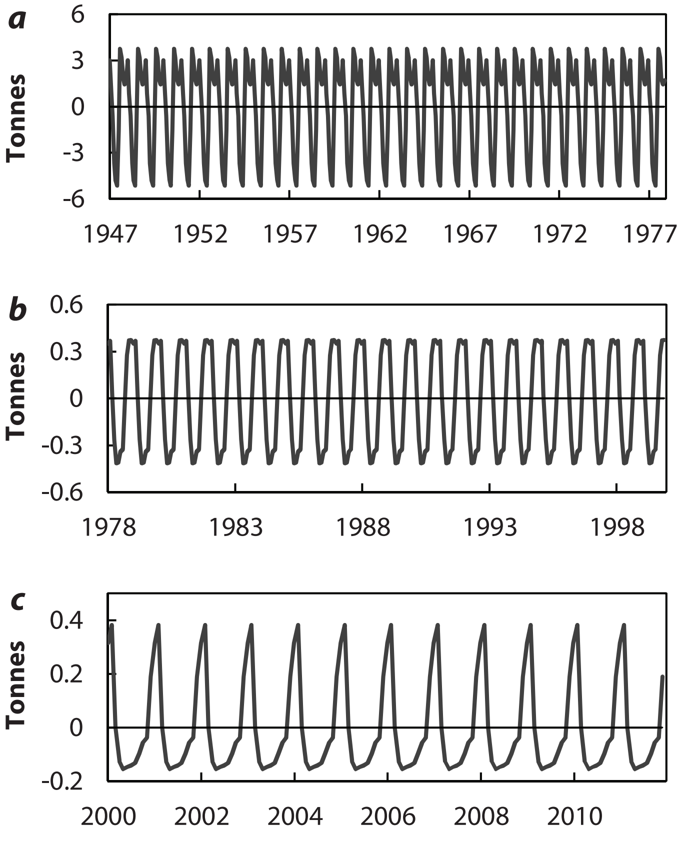

Figure 2.8: Seasonal decomposition of the time series of landings for *Crangon crangon*. Seasonal component in the periods 1947–1977 (*a*), 1978–1999 (*b*) and 2000–2011 (*c*).

warmer months became significantly lower, while towards the end of the year they started to grow, peaking in December. However, while in the second period the winter maximum was comparable to that of the first one, in recent years it became significantly lower.
Seasonal decomposition confirmed observations, highlighting a change in the pattern and a shift among the three periods (Figure 2.10). As in the case of the brown shrimp, the seasonal component became more important in more recent years (Table 2.3).

- The sprat (*Sprattus sprattus*): in the period 1947–77, the monthly trend showed a maximum in November and a second peak in March, while the lowest values were recorded in August (Figure 2.11). During the second period, while these two maximums were maintained, a consistent drop in landings was registered, which is more evident in the central months of the year. During the third phase the trend remained quite similar, except for the November peak which was missing, so that landings were even more concentrated in the colder months.
  The seasonal decomposition confirmed these observations (Figure 2.12), and like in the previous two cases, the seasonal component became more important in the more recent period (Table 2.3).

Table 2.3: Seasonal component/Remainder range ratio for the seasonal decomposition of the time series of landings for the three species considered (for details see section 2.2.2).

	1st period	2nd period	3rd period
Brown Shrimp	0.15	0.48	0.58
Flounder	0.19	0.44	0.62
Sprat	0.12	0.16	0.52

2.3.3 Winter sea surface isotherm trend

In order to assess the presence of thermal regime modifications in the recent time, the attention has been focused on the Winter sea surface 7°C isotherm, which according to Sacchi [3] delimited the extent of the lacuna in the terrestrial ecosystem. Results highlighted the complete absence of this isotherm in all the considered years during last decades (Figure 2.13).

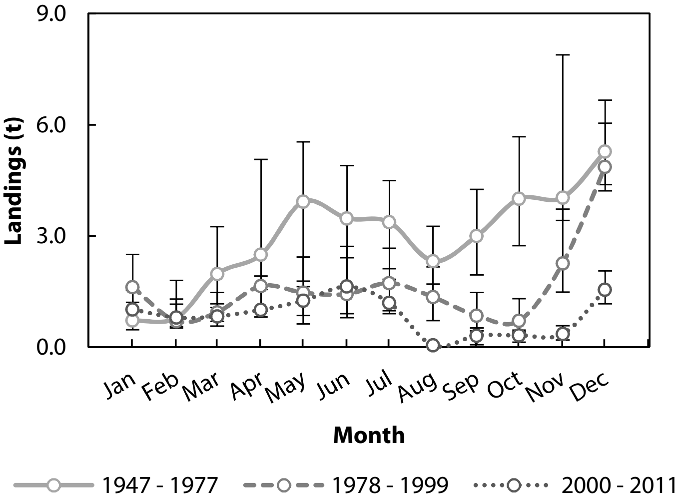

Figure 2.9: *Platichtys flesus* monthly landings in the analysed periods; medians and interquartile ranges.

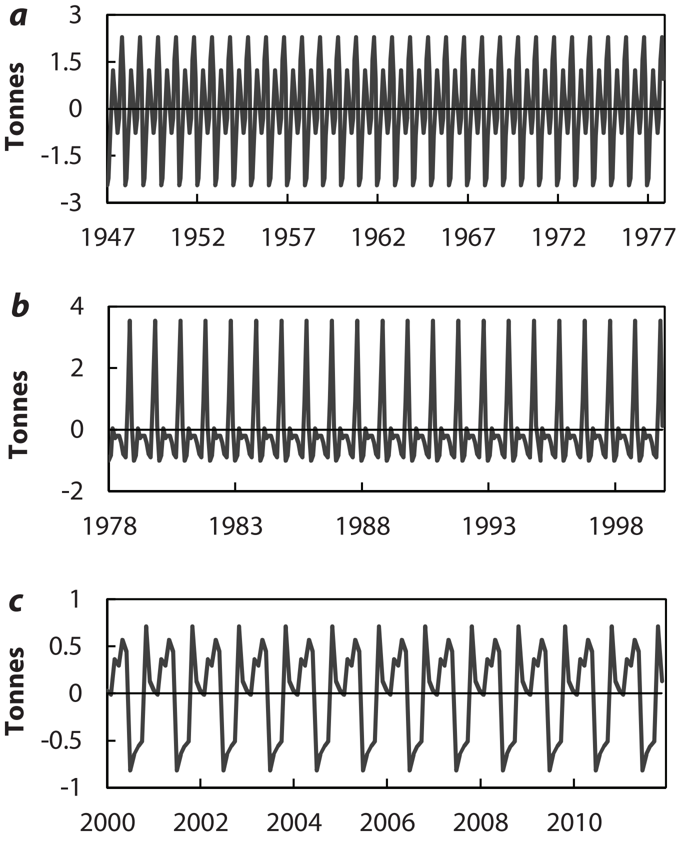

Figure 2.10: Seasonal decomposition of the time series of landings for *Platichtys flesus*. Seasonal component in the periods 1947–1977 (*a*), 1978–1999 (*b*) and 2000–2011 (*c*).

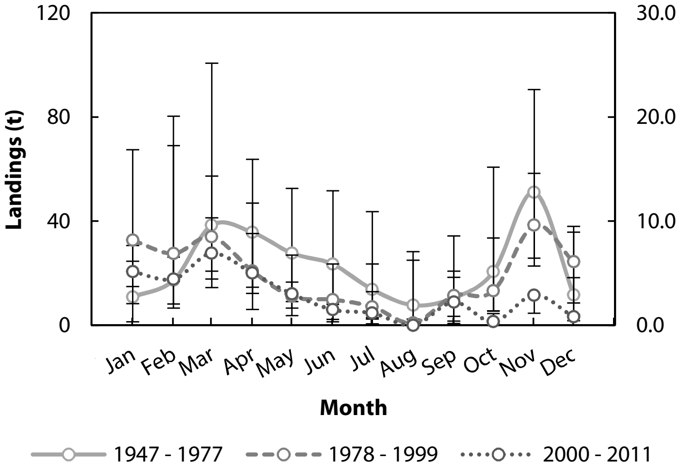

Figure 2.11: *Sprattus sprattus* monthly landings; medians and interquartile ranges in the periods 1947–1977 (left scale), 1978–1999 and 2000–2011 (right scale).

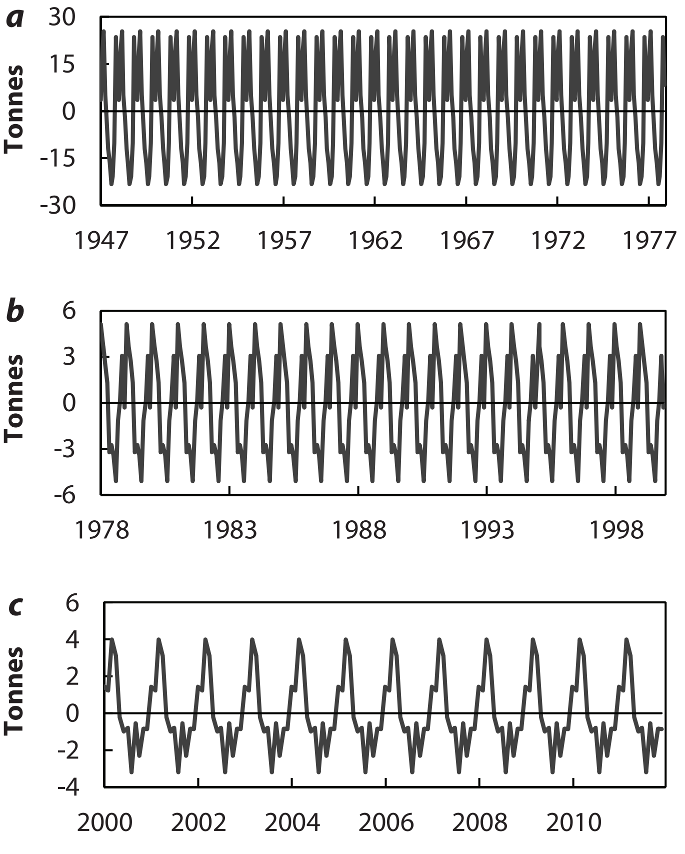

Figure 2.12: Seasonal decomposition of the time series of landings for *Sprattus sprattus*. Seasonal component in the periods 1947–1977 (*a*), 1978–1999 (*b*) and 2000–2011 (*c*).

Data collected showed a high interdecadal variability, with 1990 and 2000 presenting an almost complete absence of thermal gradient and a SST higher than 11°C; while years 1982 and 2010 showed a more articulated pattern. Considering the SST in February (the coldest month of the year), a 7°C isotherm could be drawn close to Venetian coasts only in 1982 and 2010, delineating a pattern more similar to that described by Sacchi [3] for the 1961 conditions.

2.4 Discussion

Since the beginning of the last century, the analysis of plant communities suggested some peculiarities of the Northern Adriatic area, with particular reference to the West coast. All this was formalised by Béguinot [4] and later by Marcello [2], focusing on the reduction in terms of presence of typical Mediterranean species and describing the so called 'Venetian biogeographic lacuna'. Moving from these bases and including other compartments besides terrestrial vegetation (both invertebrate and vertebrate species ad marine ecosystems), allows to verify that this lacuna is filled up by species with an Atlantic/boreal affinity. This suggests the presence of a sort of 'boreal enclosure', in which the climatic peculiarities, described by Marcello [2] as negatively affecting Mediterranean species, become a positive driver for the presence of cold affinity species.

A review of available literature confirmed the presence in the area, both in terrestrial and marine environments, of many species typically distributed on the Atlantic coasts of Northern Europe, some of which can be considered endemic for the Mediterranean basin, and of species that, in reason of phenological adaptations to local conditions, differentiate from other Italian populations, both in terrestrial and marine environments.

It is worthy to note that this boreal affinity can reflect also at level of the entire community. Extending the analysis to plant communities composing the whole sea-inland zonation (from the beach to the transitional dunes), at an European scale, makes it possible to detect a clear pattern, with an increase of boreal affinity of the NAD site, moving landwards. An augmented complexity in the community structure (from the simple *Cakile maritima* to the well-structured *Tortula ruraliformis* community), implies a shift from a Mediterranean to a North Atlantic similarity. The *Tortula ruraliformis* community (Tortulo-Scabiosetum), recorded on the stabilized dunes, and described by Pignatti [5] as endemic of the Northern Adriatic

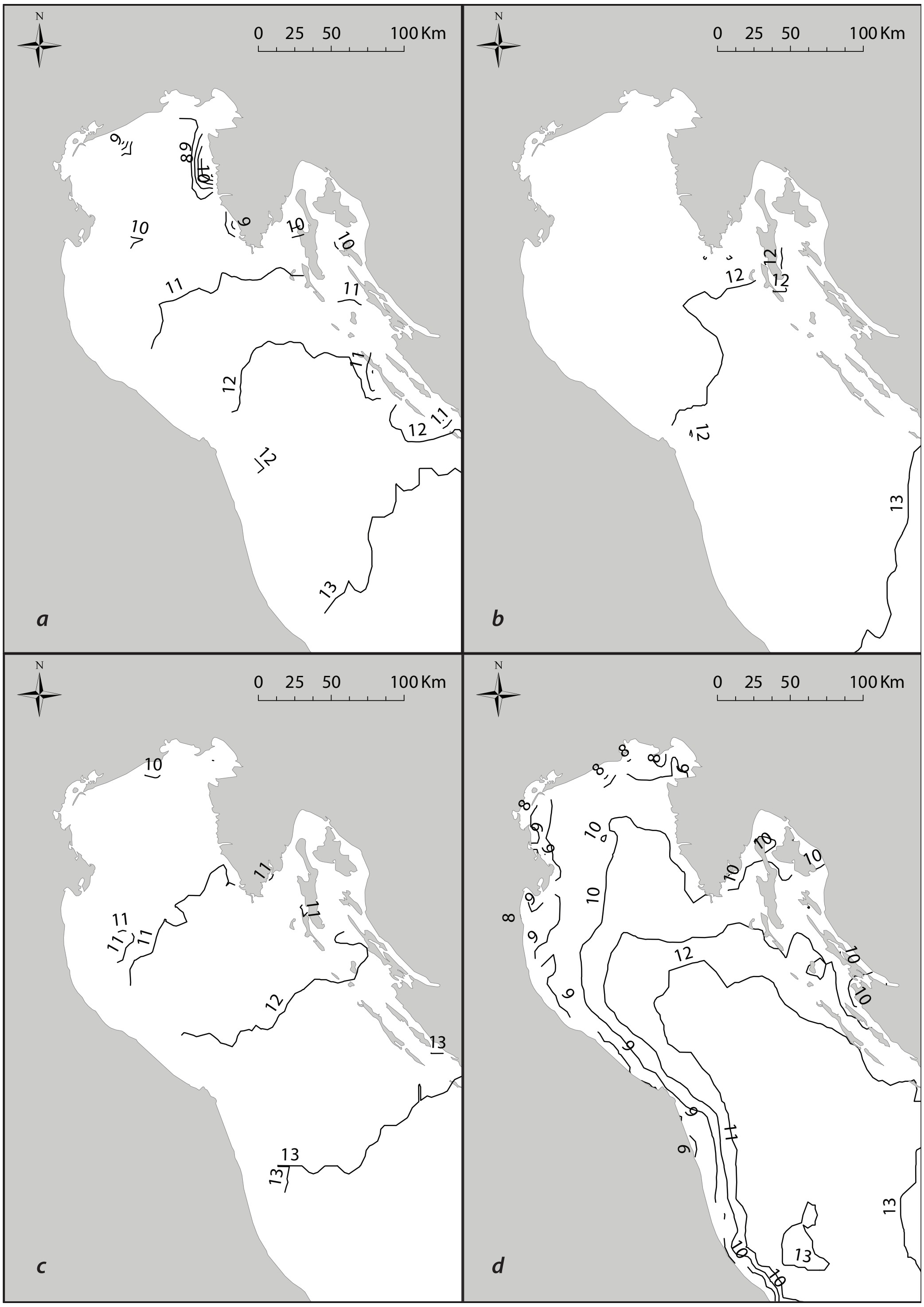

Figure 2.13: Winter sea surface isotherms recorded in the Northern Adriatic Sea in 1982 (*a*), 1990 (*b*), 2000 (*c*) and 2010 (*d*); elaborated from AVHRR and MODIS satellite data.

area, is structurally close to the Atlantic Tortulo-Phleetum, sharing with it many species, such as *Tortula ruraliformis*, *Phleum arenarium*, *Hypochaeris radicata* and *Silene otites*. The only difference is related to edaphic conditions, since the near-absence of acidophilic species in the Tortulo-Scabiosetum, and the abundance of calciphilous ones, can be explained in terms of different sand composition, being usually low in calcium in the Atlantic beaches, whereas it is rich in this element in the Adriatic area [5, 47].

A similar situation can be described for the marine environment, where the nekton assemblage has been found to be composed for about 25% by species with cold or cold/temperate affinity.

These results are in complete agreement with the description of the Adriatic basin as a 'biodiversity hotspot' [48], highlighting, however, peculiarities of the North-Western area.

Results of the time-series analysis highlight different temporal trends, depending on the considered environment. At the terrestrial plant community level, analysed for climatic affinity groups, the main differences have been recorded in the comparison between the extremes of the time series, with no clear patterns and a significant increase only in terms of NIS. On the contrary, the nekton assemblage showed important variations in composition with a significant decrease of the cold affinity group and an increase of the warm and temperate/warm species. All this could be related to the different factors/drivers acting in the two environments, as well as to the ecological features of species and communities.

In particular, plant communities have been proven to be able to keep occupying a site long after environmental conditions become unfavourable, as a consequence of the life-history characteristics of the resident species [49]. To describe the time lag in response of populations to changes in climate conditions, Gorham [50] coined the term 'biological inertia'. Inertia of resident plant communities can thus mask both deterioration in the ecosystem conditions and unstable behaviour resulting from environmental stressors. Time lag in the initial response means that after a perturbation communities head for a process of 'relaxation' (sensu Tilman *et al.* [51]), a passing through a sort of transition state, before it will be evident the change in structural characteristics, such as species composition [52].

Within this context, the recorded spreading of NIS can be an early sign of change, becoming a quite important element to be considered. Climate variations, indeed, have been described to directly influence the likelihood of the alien species naturalisation, namely their ability to form free-living, self-sustaining and persisting populations in the wild [53, 54]. Resident species can become increasingly less adapted to the local environment, whereas newcomers might be better adapted and more competitive under the new climatic conditions, opening the so-called ’invasion window’ [55, 56]. This could be the case of *Ambrosia psilostachya*, one of the most invasive NIS on the Adriatic coast [57]. Wan *et al.* [58], examining responses of *A. psilostachya* to experimental warming and clipping, reported that warming affected ragweed stems and resulted in a significant increase in the aboveground biomass. Although no difference in pollen production per stem was recorded in the laboratory, the total pollen production was expected to increase because of the higher number of stems. All this combined with a recorded significant increase in the pollen diameter, would finally result in an augmented competitive power in comparison with native species. In the marine environment, changes have been detected both at the assemblage and population level. In this case, one possible confusing factor (source of bias) could be related to the fact that patterns are reconstructed by using landings data, which can be partially affected by changes in fishing activities. Previous studies carried out in the same area (the Venice lagoon), however, demonstrated the reliability of this kind of data in describing changes related to climate variations, in particular temperature regime [45].

Despite the nekton assemblage being dominated by cold/temperate species, the increase of the warm affinity group confirms the northward shifts of thermophilic species recently described in the Adriatic Sea [59–61]. Moving from the community to the population level offers the opportunity to analyse not only variations in terms of abundance, but also changes in the seasonal cycle of boreal affinity species. A common pattern among the three species has been detected, with a clear shift towards the winter season/coldest months. This, like the inverted reproductive season for the sprat (winter instead of summer, as in the Atlantic basin) [22], can be an adaptation to the mutating climatic conditions. In relation to the exposure to global changes, some areas and habitats where the distributional range shifts are physically constrained, *e.g.* semi-enclosed basins and polar areas, can be particularly critical. It is the case of the Adriatic Sea which, being a semi-enclosed basin of an inland sea, would become a sort of *cul-de-sac* for endemic species, which simply cannot migrate further [62].

Results confirm that, due to its geographic peculiarities, such as exposure to NE winds and low influence of warm ones from SW, the closeness to the Alps (in a highly rainy and windy sector), the presence of many rivers and the shallowness of the sea, the Northern Adriatic area can be defined as a ’boreal enclosure’, representing a sort of *refugium* for cold species. All this suggests the role of the Northern Adriatic as a hotspot for biodiversity, but also highlights its vulnerability to climate changes. In facts, since the Mediterranean surface waters are expected to warm by an average of 3.1°C by the end of the 21st century [63], deep changes in the ecosystem structure and functioning can be expected [64, 65].

On the other hand, it must be considered that there are many factors, other than climate, which can play an important role in affecting species distribution and dynamics over time. Within this context, the Northern Adriatic Sea summarises many of the critical elements of a 'typical' coastal area, such as heavy exploitation level of renewable resources, presence of aquaculture activities, high seaside touristic pressure, and extended seaport activities. Being quite impossible to discriminate between the effects of each driver (climatic, anthropogenic, etc.) on the ecosystem structure and functioning, the implementation of an integrated approach realising in an adaptive management strategy is required. Within this context, the management objectives should necessarily focus on one side on the implementation of long-term monitoring programs, on the other on maintaining the self-sustaining ecological processes in order to increase the system resilience, which is recognised to play a crucial role to cope with climate changes [66, 67].

Table S. 2.1: Boreal affinity species recorded in the Venetian coastal area.

	Phyla/Classes	Relevant species	Notes	Source
Terrestrial plants	Bryopsida	*Tortula ruralis*	Plant species of cold/boreal affinity	[2, 4, 5, 8-11, 13]
	Equisetopsida	*Equisetum ramosissimum*		
	Pinopsida	*Juniperus communis ssp. communis*		
	Magnoliopsida	*Anthericum ramosum* *Berberis vulgaris* *Brachypodium rupestre* *Calamagrostis epigejos* *Crategus monogyna* *Cornus sanguinea* *Erica carnea* *Frangula alnus* *Gentiana pneumonanthe* *Hippophae rhamnoides* *Parnassia palustris* *Phleum arenarium* *Polygonatum odoratum* *Quercus robur* *Silene otites* *Stachys recta* *Stipa pennata* *Teucrium montanum* *Viburnum lantana*		
Terrestrial animals	Gastropods	*Cepaea nemoralis* *Fruticicola fruticum*	Cool climate indicators	[3]
		Cernuella virgata	Found on dunes like on Atlantic coasts. On Mediterranean littorals it is replaced by *C. maritima*	[3]
		Euparypha pisana	*Testudinea* phenotype has Atlantic diffusion. The life-cycle is analogous to that of Atlantic populations	[3]
	Insects	*Scatella ciliata* *Philotelma defecta* *Hydrellia discors* *Psilopa pulicaria* *Paracoenia fumosa* * *Medetera mixta* *Medetera chrysotymiformis* *Helcomyza ustulata* * *Caenia spp.* * *Neolomnophora virgo* *	Some (*) show an inversion of the seasonal cycle	[14, 68]
		Canace nasica	Widespread on Northern Atlantic shores, it is found on Venetian ones probably as a glacial relict.	[14]
Marine organisms	Algae	*Fucus virsoides*	Endemic. All other representatives of the Fucus genus have a boreal, cold water distribution.	[15]
	Crustaceans	*Ploenexes bicuspis* *Ampelisca sarsi* *Corophium insidiosum* *Orchomenes humilis*	*O. humilis* is found all over the Mediterranean, but in the north-Adriatic it lives at the same depths it inhabits in Atlantic waters	[14, 18]
		Crangon crangon	In the Mediterranean Sea, the presence is limited to the northern parts of the basin, such as in the Gulf of Lion, Adriatic Sea and Black Sea.	[17]
	Gastropods	*Littorina saxatilis*	Widespread on Northern Atlantic shores, it is found on Venetian ones probably as a glacial relict.	[14]
	Fish	*Pomatoschistus minutus*	Widespread on Northern Atlantic shores, in the Mediterranean it is found mainly in the Northern Adriatic. The Mediterranean population belongs to a different subspecies (*P. minutus elongatus*) than the Atlantic one (*P. minutus minutus*)	[19]
		Platichthys flesus	In the Mediterranean Sea, the presence is limited to the northern parts of the basin (latitudes above 40°N), such as in the Gulf of Lion, Adriatic Sea, Aegean Sea and Black Sea. Recent genetic analyses referred it as a boreal relict.	[19, 20]
		Sprattus sprattus sprattus	In the Mediterranean Sea, the presence is limited to the northern parts of the basin (latitudes above 40°N), such as in the Gulf of Lion, Adriatic Sea, Aegean Sea and Black Sea. Recent genetic analyses referred it as a boreal relict. In Adriatic waters it shows an inverted reproductive cycle.	[19, 21, 22]

Table S. 2.2: List of the phytosociological surveys used in the meta-analysis of the shore-dunes plant communities across Europe (*Unp.* = Unpublished data).

	Association	Survey Area	Number of surveys	Area code	Source
Cakile maritima	Honkenio – Cakiletum	Great Britain	39	GBR	[69]
	Salsolo – Cakiletum	North Adriatic	43	NAD	Unp.
	Salsolo – Cakiletum aegyptiacae	Camargue – France	10	CAM	[70]
	Salsolo – Cakiletum aegyptiacae	Corfu Island – Greece	15	COR	[71]
	Salsolo – Cakiletum aegyptiacae	Marche region – Italy	12	MAR	[72]
	Salsolo – Cakiletum aegyptiacae	Rhodes Island – Greece	12	RHO	[73]
	Salsolo – Cakiletum aegyptiacae	Taranto (Puglia) – Italy	18	PUG	[74]
	Senecioni joppensis – Cakiletum aegyptiacae	Mediterranean coasts of Egypt	15	EGY	[75]
Elymus farctus	Agropyretum boreoatlanticum	Great Britain	51	GBR	[69]
	Agropyretum mediterraneum	Mediterranean	50	MED	[28]
	Cypero – Agropyretum	Sardinia – Italy	6	SAR	[76]
	Echinophoro – Agropyretum	Camargue – France	11	CAM	[70]
	Echinophoro – Agropyretum	Taranto (Puglia) – Italy	15	PUG	[74]
	Elymo – Agropyretum	North Sea	121	NSE	[28]
	Eryngio – Agropyretum	Rhodes Island – Greece	15	RHO	[73]
	Euphorbio – Agropyretum	Eastern Atlantic	433	EAT	[28]
	Sileno succulentae – Agropyretum	Mediterranean coasts of Egypt	5	EGY	[75]
	Sporobolo – Agropyretum	North Adriatic	29	NAD	Unp.
	Sporobolo – Agropyretum	Corfu Island – Greece	25	COR	[71]
	Sporobolo – Agropyretum	Former Yugoslavia	8	YUG	[77]
	Sporobolo – Agropyretum	Marche region – Italy	13	MAR	[72]
Ammophila arenaria	Echinophoro – Ammophiletum	Camargue – France	13	CAM	[70]
	Echinophoro – Ammophiletum	Corfu Island – Greece	6	COR	[71]
	Echinophoro – Ammophiletum	Marche region – Italy	3	MAR	[72]
	Echinophoro – Ammophiletum	Mediterranean	40	MED	[28]
	Echinophoro – Ammophiletum	North Adriatic	53	NAD	Unp.
	Echinophoro – Ammophiletum	Sardinia – Italy	8	SAR	[76]
	Echinophoro – Ammophiletum	Taranto (Puglia) – Italy	25	PUG	[74]
	Elymo – Ammophiletum	North Sea	223	NSE	[11]
	Elymo – Ammophiletum	Great Britain	28	GBR	[69]
	Euphorbio – Ammophiletum	North Atlantic	238	NAT	[28]
	Otantho – Ammophiletum	Eastern Atlantic	100	EAT	[28]
	Sileno – Ammophiletum	Mediterranean coasts of Egypt	6	EGY	[75]
Tortula ruralis	Armerio pungentis – Thymelaeetum tarton.	Maddalena – Italy	10	MAD	[78]
	Astragalo – Festucetum arenariae	Great Britain	36	GBR	[69]
	Malcolmio – Helichrisetum stoechadis	Camargue – France	16	CAM	[70]
	Crucianelletum maritimae	Corfu Island – Greece	6	COR	[71]
	Scabiosetum argenteum	Taranto (Puglia) – Italy	6	PUG	[74]
	Scrophulario – Crucianelletum maritimae	Sardinia – Italy	4	SAR	[76]
	Thimion capitati	Rhodes island – Greece	5	RHO	[73]
	Tortulo – Scabiosetum	Noth Adriatic	46	NAD	Unp.

Chapter 3

Vulnerability of Artisanal Fisheries to Climate Changes in the Venice Lagoon

Abstract

Within the context of global warming, the western coast of the northern Adriatic Sea can be regarded as an extremely vulnerable area. Owing to the local geographic features, this area has been described as the Venetian lacuna, where Mediterranean Sea climatic conditions are replaced by Atlantic Ocean ones, supporting the presence of glacial relicts, such as sprat *Sprattus sprattus*, flounder *Platichthys flesus* and brown shrimp *Crangon crangon*. Nektonic assemblage therefore represents a good candidate in terms of an early proxy for thermal regime alterations. It represents a dynamic component of the lagoon ecosystem, changing in space and time, actively moving through the entire system, and dynamically exchanging with the open sea. Here, the first signals of the change have been already detected, such as the presence of alien thermophilic species. Within this context, since the beginning of the century, sampling of the nektonic assemblage has been carried out, integrating them with landings data from the fish market. Vulnerabilities to thermal regime changes have been tested by (1) categorising species according to the mean distribution area in terms of latitudinal range (over 45°, $30^\circ - 45^\circ$ and below 30°), and (2) analysing both spatial and temporal variations within fishing grounds. Results indicated a high potential vulnerability of the artisanal fishery to climate change, as the commercial catch is entirely composed of species from cold ($> 45^\circ$N) and temperate (between 45° and 30°N) latitudes. At present no alien thermophilic species have been recorded within the lagoon, which is possibly a sign of good resilience of the assemblage. Finally, abundance of species from cold latitudes has decreased during the past decade. All of this has been discussed in the context of the mean annual temperature trend.

3.1 Introduction

Climate change is one of the major drivers affecting structure and function of both terrestrial and marine ecosystems, and effects are expected to grow in the near future [1–5]. Mediated mainly by modifications in thermal regimes, ocean currents and coastal upwelling, several changes in marine ecosystems have been described already, such as shifting in geographic distributions towards higher latitudes [6–8], increasing extinction rates [9, 10] and reorganization of local communities in relation to substitutions of native species by exotic thermophilic ones [11, 12]. Even if the real effects of these changes on a global scale are currently under discussion, on a local scale they are producing significant change in terms of structure and function of marine ecosystems [5]

Among other human activities, global changes are expected to directly affect fisheries worldwide [10, 13]. Changes both in productivity and distribution areas, decreasing of target species abundance, species replacement, direct effects of warming on growth, survival, migratory behaviour and reproductive rates of many species are expected to greatly affect marine resources and their exploitation, with social and economic costs for human populations [14].

In relation to the exposure to global changes, some areas and habitats, such as semi-enclosed basins and polar areas, where the range shifts are physically constrained, could be more vulnerable than others. For the Mediterranean Sea basin, the potential vulnerability exists where this inland sea acts as a *cul-de-sac* for endemic species as highlighted by Ben Rais Lasram *et al.* [8]. Within this context, the western part of the northern Adriatic Sea shares similar geography. This area, together with the Gulf of Lion, represents one of the coldest zones of the Mediterranean Sea basin, and has been described as the Venetian lacuna. This is defined as an interruption of the Mediterranean Sea ecosystem due to the presence of Atlantic climate conditions. Its terrestrial composition was first described by Marcello [15], noting the absence of typical Mediterranean plants. Successively, an effect on marine environment was recognised, namely to intertidal assemblages [16], and the geographical limit of the lacuna was found to coincide with the winter season isotherm of 7°C.

The Venice Lagoon, located in the middle of the lacuna, could be especially vulnerable in this context, being a semi-enclosed area, inside two other basins with the same peculiar features (Adriatic and Mediterranean Seas). Owing to the millenary coexistence, local populations are strongly linked with the lagoon environment, with fishing activities deeply rooted in local traditions. At present, the exploitation of marine renewable resources occurs as two different activities: an artisanal fishery [17, 18] and recent mechanical clam harvesting, developed about three decades ago after the introduction of Manila clam *Ruditapes philippinarum* in the lagoon in 1983 [19].

Being multigear and multitarget, the artisanal fishery in the lagoon can be defined as a small-scale fishery according to the current European Commission classification (*i.e.* fishery performed by boats $<$ 12 m overall length equipped with passive gear) [20]. Conversely, the clam harvest, being a single-target activity carried out with mechanized gear that disturbs the ecosystem [21], can be defined as a semi-industrial fishing activity. During recent decades, the interaction between the two activities presented a source of conflicts, with negative direct impacts of the mechanical harvesting on the artisanal fishery [22, 23]. For the above reasons, the vulnerability of the artisanal fishery in the Venice Lagoon represents an interesting issue to be analysed in terms of relevance for its social, economic and ecological implications [24, 25].

The aims of this chapter are: to offer a description of the present situation of the artisanal fishery in the Venice Lagoon; to analyse landings time series for detecting modifications (*e.g.* regime shifts), potentially related to climate changes; to assess the potential vulnerability of the renewable resources exploitation to climate changes in the Venice Lagoon.

3.2 Materials and methods

3.2.1 Sampling activities

Sampling was conducted over two periods from 2001 to 2003 and 2009 to 2010. Fyke nets were deployed and the catches were examined monthly (mean $\pm$ s.e. $=$ 22.2 $\pm$ 2.4 traps per month) when fishermen emptied them. Four sampling areas, located in the three main basins, ensured data represented the primary lagoon fishing grounds (Figure 3.1). Collected specimens were classified and counted, and for each taxon the total wet mass was recorded directly onboard (only cases of dubious attribution were transferred to the laboratory as samples).

Fishermen visited the traps relative to the expected catch amount (which varied seasonally), thus optimising their effort. Because of this, the

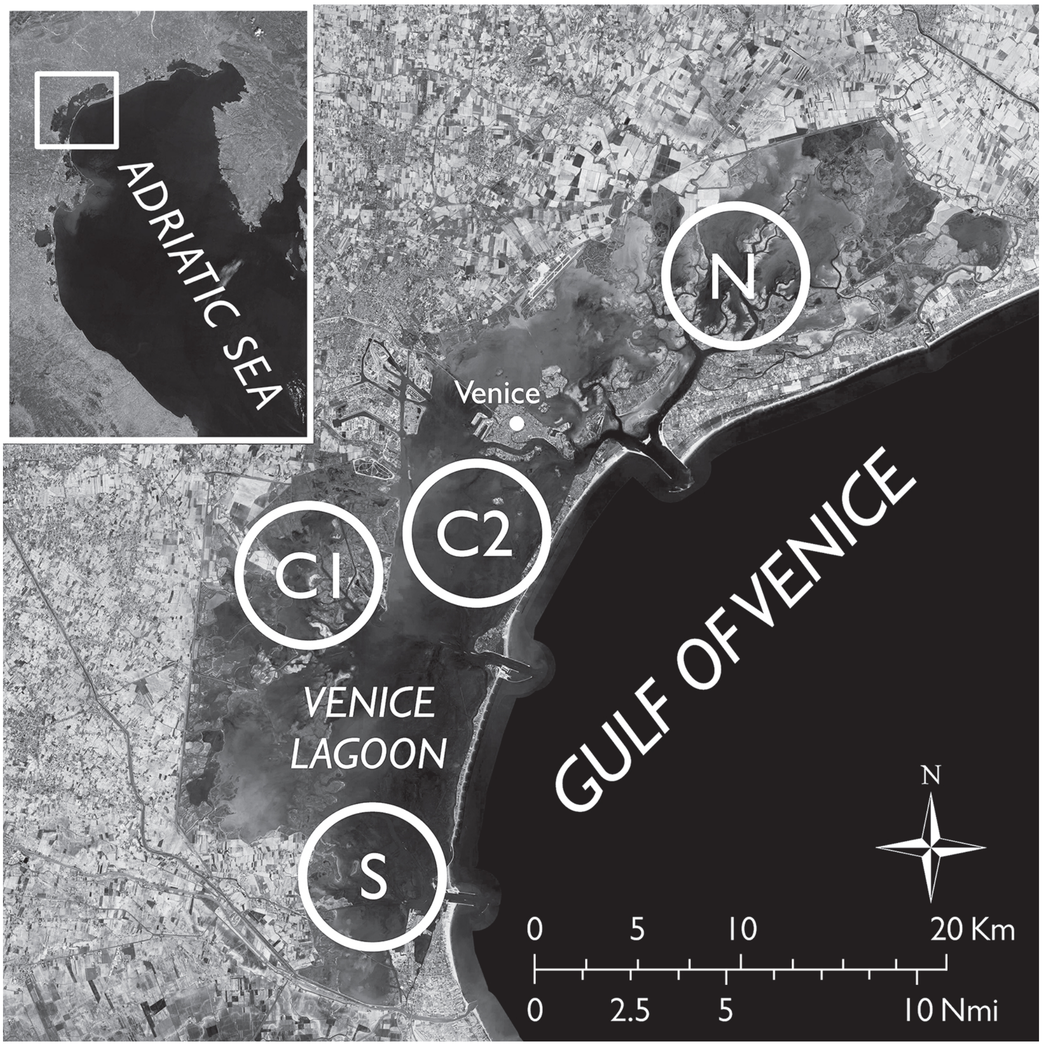

Figure 3.1: Sampling areas in Venice Lagoon (N, northern basin; C1 and C2, central basin; S, southern basin).

amount of catch observed during sampling may have represented the outcome of one or more days' fishing depending on the time of year. Therefore, in order to obtain homogenous data, a standardisation in terms of catch (g) per trap per day was performed, taking into the account the number of days since the previous visit by the fishermen. Once the composition of the catches was characterised, the complete time series of landings for targeted species, from 1945 to 2011, was reconstructed with data from the fish market of Chioggia, which represents the most important market in the area. As interests were to analyse the global trend of each exploited species, no correction was applied given that species were simultaneously targeted by different fishing gears in the lagoon and at sea.

3.2.2 Data analysis

Species were grouped as target (species targeted by the fishing activity), incidental (species of commercial interest but not representing the main target) and discard (species with no commercial value). A further classification was carried out according to ecological guilds [26, 27], *i.e.* estuarine (all the life cycle in the lagoon), marine migrant (regularly migrating between lagoon and sea environment), marine stragglers (occasionally present in the lagoon, preferring marine salinity areas), anadromous and catadromous species (regularly migrating between freshwater and marine areas and vice versa, passing through the lagoon) and finally freshwater species (typical of freshwater environment and occasionally recorded in the brackish waters).

In order to assess the thermal affinity of each sampled species, distributional data for the Northern hemisphere were obtained from the online database of the Ocean Biogeographic Information System (OBIS; `www.iobis.org`) within the Global Biodiversity Information Facility (GBIF; `http://data.gbif.org/`). Arbitrary latitudinal thresholds were set at 30° N (southern limit of the Mediterranean Sea basin) and 45°N (northern limit of the basin, excluding the northernmost parts of the Adriatic and Black Seas), defining a northern cold zone (> 45°N), a central temperate zone (between 45° and 30°N; typical of the Mediterranean Sea) and a southern warm zone (< 30°N). The main latitudinal ranges for the species were estimated by means of the median and interquartile range of the latitudinal component of the distributional data. Finally, the thermal affinity for each taxon was attributed based on whether its median fell in the cold, temperate or warm zone. In cases where the interquartile range was not fully included in the same zone as the median, an intermediate thermal affinity was attributed. Globally, six groups were defined: cold, cold-temperate (CT), temperate, temperate-warm (TW), warm and ubiquitous species. This classification was applied both for analysing the field samples catch composition, and for studying temporal trends in the reconstructed time series of landings. Differences among categories were analysed by using the Mann-Whitney $U-$test.

The time series (1970–2011) of the water temperature (annual mean) for the Venice Lagoon and the winter North Atlantic Oscillation (NAO) have been reconstructed with respective values collected from local databases (see also `www.istitutoveneto.it`) and on the U.S. National Oceanographic and Atmospheric Administration (NOAA) climate prediction centre website (`www.cpc.ncep.noaa.gov`). The presence of regime shifts in the time series has been detected by applying the sequential $t-$test analysis of regime shift (STARS) developed by Rodionov [28, 29], based on a sequential $t-$test analysis. Temporal trends have been analysed by plotting annual landings for each target species against both water temperature and NAO. The same procedure was applied to landing data aggregated on the basis of the species thermal affinity.

Statistical significance of correlations was tested through the application of generalised additive models (GAM) [30]. GAM represents a semi-parametric regression technique for exploring relationships between response and predictor variables, having greater flexibility for drawing out the long-term non-linear trends than chain or linear modelling methods. Some predictors can be modelled non-parametrically, using a smoothing function, in addition to linear and polynomial terms, allowing the response shape to be fully determined by the data.

The following additive formulation was used: $Y = a + s_1(V_1) + \cdots - s_n(V_n) + \varepsilon$, where a is the intercept, s the thin plate smoothing spline function [31], $V \ldots V_n$ the predictors and ε the random error. Model fitting and testing were carried out using the MGCV package [32], in R 2.13 (R Core Development team; `www.r-project.org`).

3.3 Results

3.3.1 Field sampling activity

The complete list of sampled species is given in Table 3.1. In terms of biomass contribution, target species (11 taxa) accounted for c. 80% of total catches, incidental catches (11 taxa) for 19% and discarded species (33 taxa) for c. 2% (Figure 3.2*a*). For the ecological guilds (Figure 3.2*b*), the observed pattern is related to the exploitation of a typical nektonic assemblage in a transitional water area. Estuarine and marine migrant species were well represented in the catches (18 and 21 species), accounting for 43 and 18% in biomass, and 12 species belonging to the marine stragglers category ($<$ 1% of total biomass). Finally, a moderate contribution to total catches came from the catadromous species group (37%), comprising only two species,

Table 3.1: Sampled species

Scientific name	Common name	Ecological guild	Fishery category	Climatic affinity
Alosa fallax	Twaite shad	Anadromous	Discard	Cold
Anguilla anguilla	European eel	Catadromous	Target	Cold
Aphanius fasciatus	Mediterranean killifish	Estuarine	Discard	Temperate
Atherina boyeri	Sand smelt	Estuarine	Target	Temperate
Belone belone	Garfish	Marine migrant	Discard	Cold/Temperate
Boops boops	Bogue	Marine straggler	Discard	Temperate/Warm
Carcinus aestuarii	green crab	Estuarine	Target	Temperate
Chelidonichthys lucerna	Tub gurnard	Marine migrant	Discard	Ubiquitous
Chelon labrosus	Thicklip gray mullet	Marine migrant	Incidental	Cold/Temperate
Conger conger	Conger eel	Marine straggler	Discard	Cold
Crangon crangon	Brown shrimp	Marine migrant	Target	Cold
Dicentrarchus labrax	European seabass	Marine migrant	Incidental	Cold
Diplodus annularis	Annular seabream	Marine migrant	Discard	Temperate
Diplodus puntazzo	Sharpsnout seabream	Marine straggler	Discard	Temperate
Diplodus sargus	White seabream	Marine straggler	Discard	Temperate
Diplodus vulgaris	Two-banded seabream	Marine straggler	Discard	Temperate
Engraulis encrasicolous	European anchovy	Marine migrant	Discard	Temperate/Warm
Gambusia holbrooki	Eastern mosquitofish	Estuarine	Discard	Temperate
Gobius cobitis	Giant goby	Marine straggler	Incidental	Temperate
Gobius niger	Black goby	Estuarine	Incidental	Cold
Gobius paganellus	Rock goby	Estuarine	Incidental	Cold
Hippocampus guttulatus	Long-snouted seahorse	Estuarine	Discard	Ubiquitous
Hippocampus hippocampus	Short-snouted seahorse	Estuarine	Discard	Cold/Temperate
Knipowitschia panizzae	Adriatic dwarf goby	Estuarine	Discard	Temperate
Lithognathus mormyrus	Sand steenbras	Marine migrant	Incidental	Temperate
Liza aurata	Golden grey mullet	Marine migrant	Target	Temperate
Liza ramada	Thinlip grey mullet	Catadromous	Incidental	Cold/Temperate
Liza saliens	Leaping mullet	Marine migrant	Incidental	Temperate

Table 3.1: (continued) Sampled species

Scientific name	Common name	Ecological guild	Fishery category	Climatic affinity
Mullus surmuletus	Surmullet	Marine migrant	Incidental	Cold/Temperate
Palaemon spp.	Rockpool prawn	Estuarine	Target	Cold
Parablennius sanguinolentus	Rusty blenny	Marine straggler	Discard	Temperate
Peneus spp.	Shrimp	Marine migrant	Incidental	Temperate
Platichthys flesus	European flounder	Marine migrant	Target	Cold
Pomatomus saltatrix	Bluefish	Marine straggler	Discard	Temperate/Warm
Pomatoschistus canestrinii	Canestrini's goby	Estuarine	Discard	Temperate
Pomatoschistus marmoratus	Marbled goby	Estuarine	Discard	Temperate
Pomatoschistus minutus	Sand goby	Marine migrant	Target	Cold
Salaria pavo	Peacock blenny	Estuarine	Discard	Temperate
Salmo trutta	Brown trout	Fresh water	Discard	Cold
Sardina pilchardus	European pilchard	Marine migrant	Discard	Temperate
Sepia officinalis	Common cuttlefish	Marine migrant	Target	Cold
Sepiola rondeletii	Dwarf bobtail squid	Marine straggler	Discard	Temperate
Solea solea	Common sole	Marine migrant	Incidental	Cold
Sparus aurata	Gilthead seabream	Marine migrant	Target	Temperate
Sprattus sprattus	Sprat	Marine migrant	Discard	Cold
Symphodus cinereus	Gray wrasse	Marine straggler	Discard	Temperate
Symphodus doderleini	Doderlein's wrasse	Marine straggler	Discard	Temperate
Symphodus roissali	Five-spotted wrasse	Estuarine	Discard	Temperate
Syngnathus abaster	Black-striped pipefish	Estuarine	Discard	Temperate
Syngnathus acus	Greater pipefish	Marine migrant	Discard	Cold
Syngnathus tenuirostris	Narrow-snouted pipefish	Estuarine	Discard	Temperate
Syngnathus typhle	Broadnosed pipefish	Estuarine	Discard	Cold
Trachurus trachurus	Atlantic horse mackerel	Marine straggler	Discard	Temperate
Umbrina cirrosa	Shi drum	Marine migrant	Discard	Warm
Zosterisessor ophiocephalus	Grass goby	Estuarine	Target	Temperate

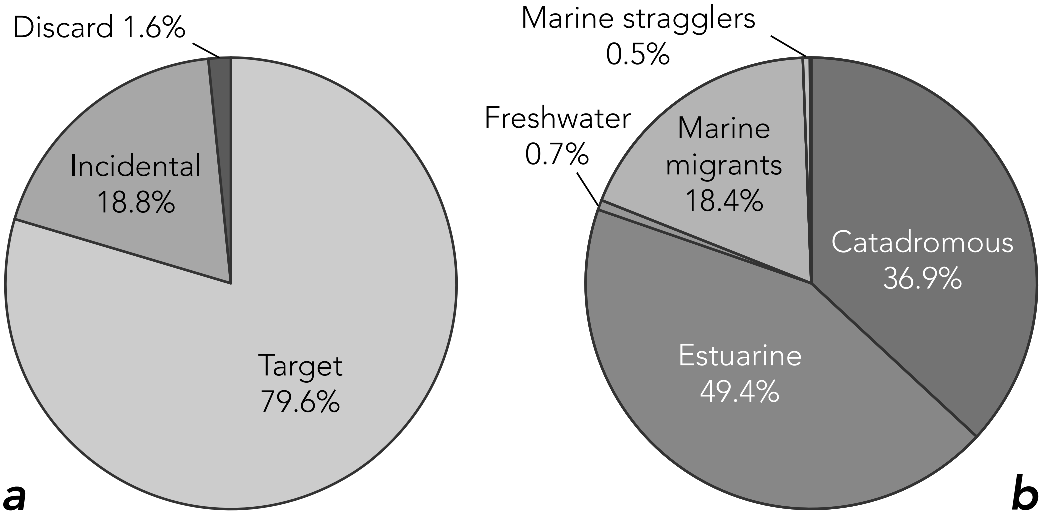

Figure 3.2: Catch composition (in biomass, standardised data) in relation to the interest for the fishing activity (*a*); and ecological guilds (*b*).

(European eel *Anguilla anguilla* (L. 1758) and thinlip grey mullet *Liza ramada* (Risso 1827)) (see also Table 3.1).

Data collected show some differences between the three basins, with significantly higher catches (Mann-Whitney U–test, $P < 0.05$) collected in the central part of the lagoon (Figure 3.3*a*). There is also a clear seasonality of catches, with significantly (Mann-Whitney U–test, $P < 0.05$) higher values recorded in autumn (Figure 3.3*b*).

In relation to thermal affinity groups, data collected show that in terms of target species, catches are entirely composed of cold and temperate species (28 and 72%); whereas incidental catches and discard species are more heterogeneous. Temporal analysis of thermal affinity groups showed an oscillating pattern with a negative peak recorded in 2003 (statistically significant in comparison with both 2009 and 2010, Mann-Whitney U–test, $P < 0.05$). This represented the warmest year of the time series, being characterised by a heat wave during the summer (Figure 3.4).

3.3.2 Time series analysis

In order to analyse long-term variations and possible relationships with climate parameters, starting from the target species list, the time series of landings from 1945 to 2011 has been reconstructed with fish market data (Figure 3.5). Different phases are recognisable: a sharp increasing trend between the 1950s and 1960s, culminating at the beginning of 1970s, then

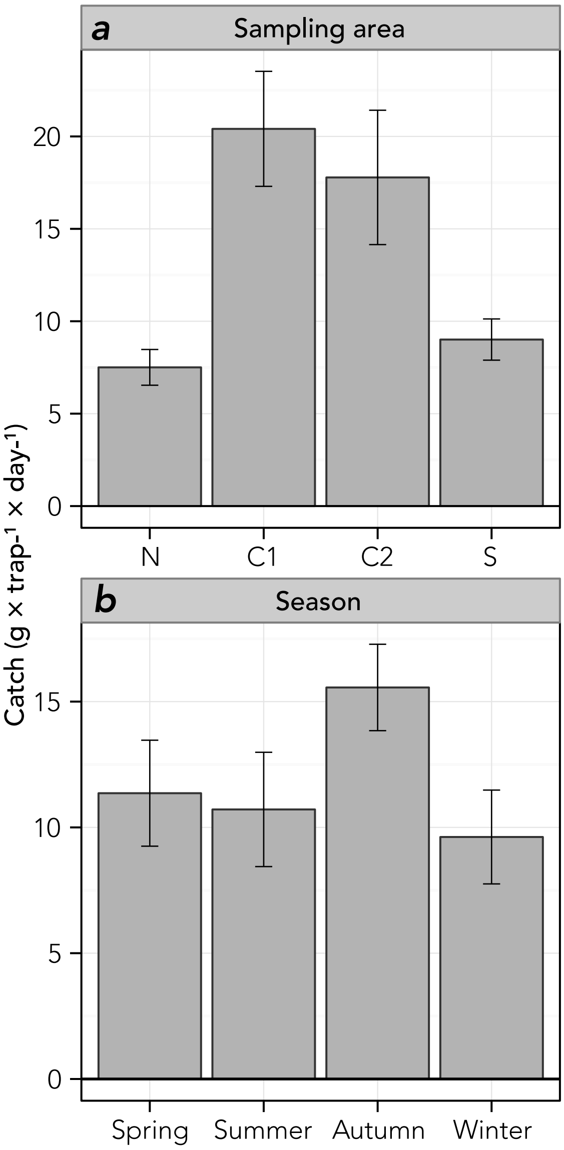

Figure 3.3: Mean catch values, with standard errors, for different areas (*a*) and season (*b*).

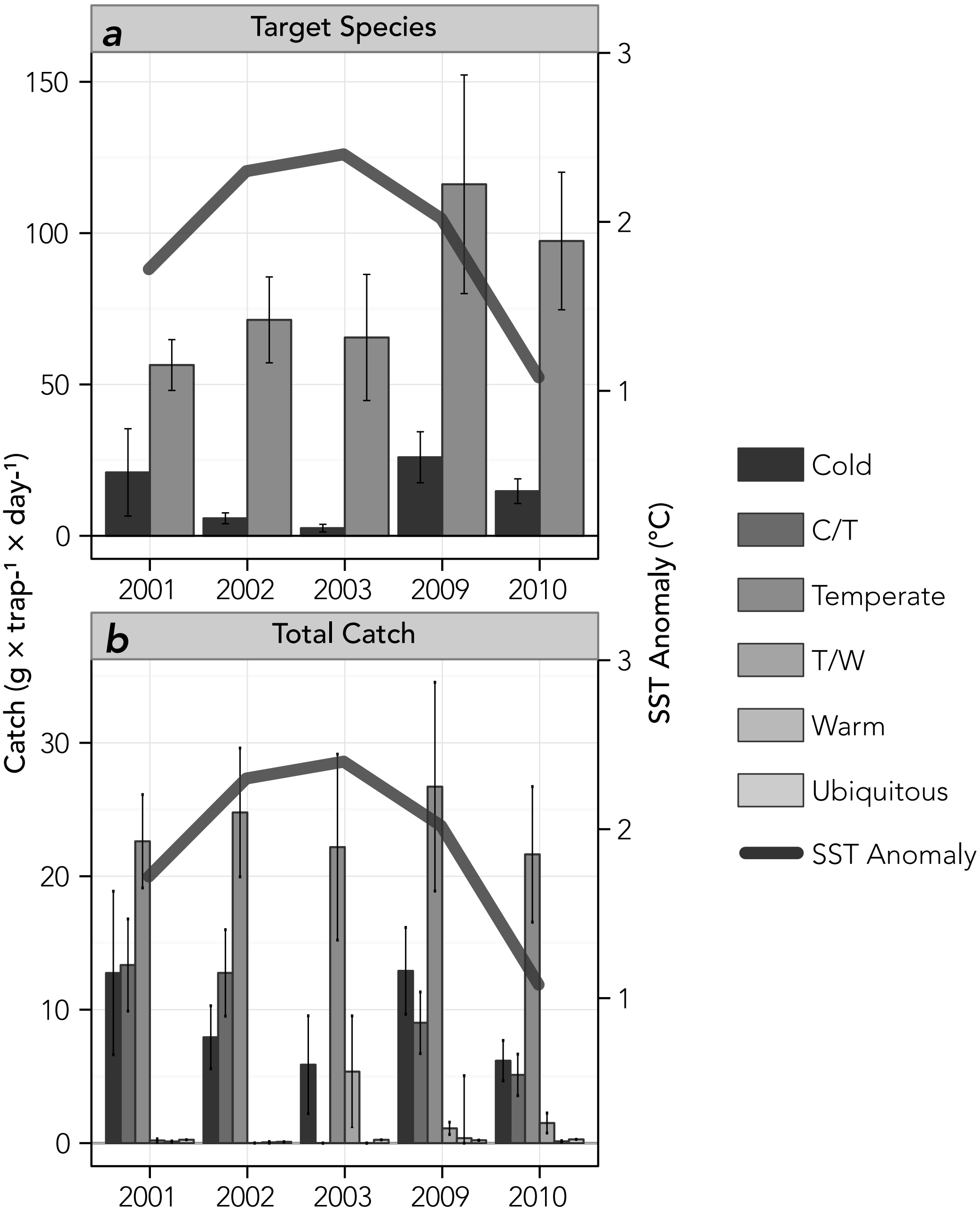

Figure 3.4: Temporal variations of the thermal affinity groups represented in (*a*) the target species and in (*b*) the total catch (target + incidental + discarded species) during the sampling periods. Standard errors are shown.

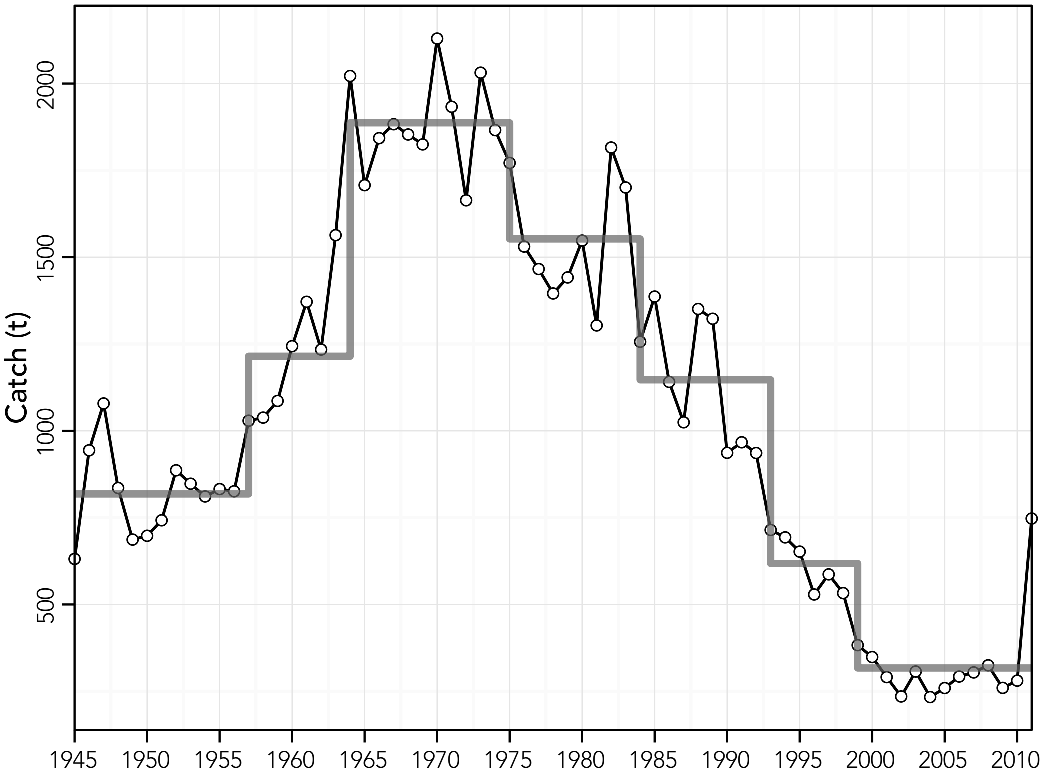

Figure 3.5: Temporal trend in landings of artisanal fishery target species from the Chioggia fish market (black line); different phases detected by the regime shift detector (STARS) are also reported (grey line).

a declining trend with the minimum value recorded in 1999, followed by a slight recovery. The presence of different phases was also confirmed by the application of the STARs (Figure 3.5). Given the temperature time series (1970–2011), a significant change of regime recorded in the second half of 1980s was clearly visible in terms of anomalies (Figure 3.6); thus, the attention has been focused on the transition recorded in the second half of the 1980s. For almost all series, total catches and the 12 target species highlight a significant decrease in values during this period (Table 3.2).

In terms of thermal affinity, a decreasing trend of both temperate and cold species abundance has been detected, more pronounced for the latter (Figure 3.7*a*).

Possible correlations between landings and climate variables were investigated by contrasting different groups and species v. water temperature and the NAO index. Both cold and temperate groups showed a significant (tested with GAM) negative correlation with the water temperature

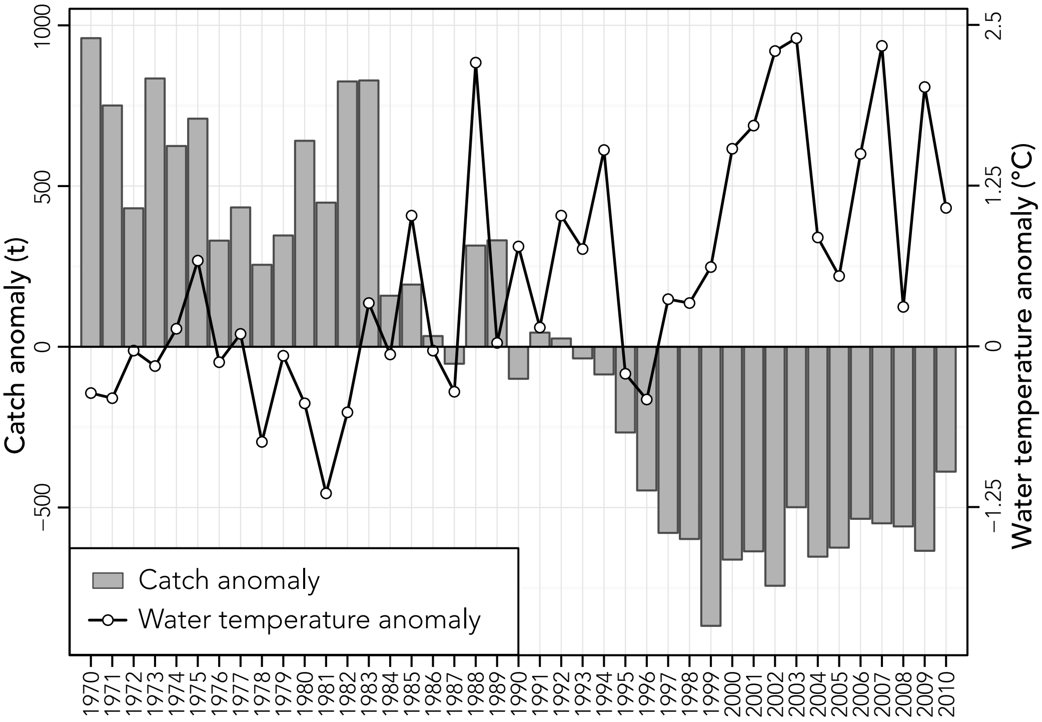

Figure 3.6: Time series of landings and temperature anomalies.

(Figure 3.7*a*); this was confirmed by all the target species with the exception of gilthead seabream *Sparus aurata* L. 1758 and golden grey mullet *Liza aurata* (Risso 1810) for which a positive and no relationship were detected (Figure 3.7*b*). The analysis contrasting landings v. the NAO index highlighted no significant correlation.

3.4 Discussion

Small-scale fisheries worldwide are recognised for their substantial contributions towards fish production and to be very relevant for their social, economic and ecological implications. Moreover, as underpinned also by the code of conduct for responsible fisheries [33], small-scale fisheries could represent, at least in some areas, a valid alternative to industrial fishery in terms of sustainable exploitation.

According to the results obtained, the artisanal fishery in the Venice Lagoon is configured as a small-scale fishery, characterised by a large variety of target species and a marked seasonality.

The total catch composition, characterised by a high number of taxa,

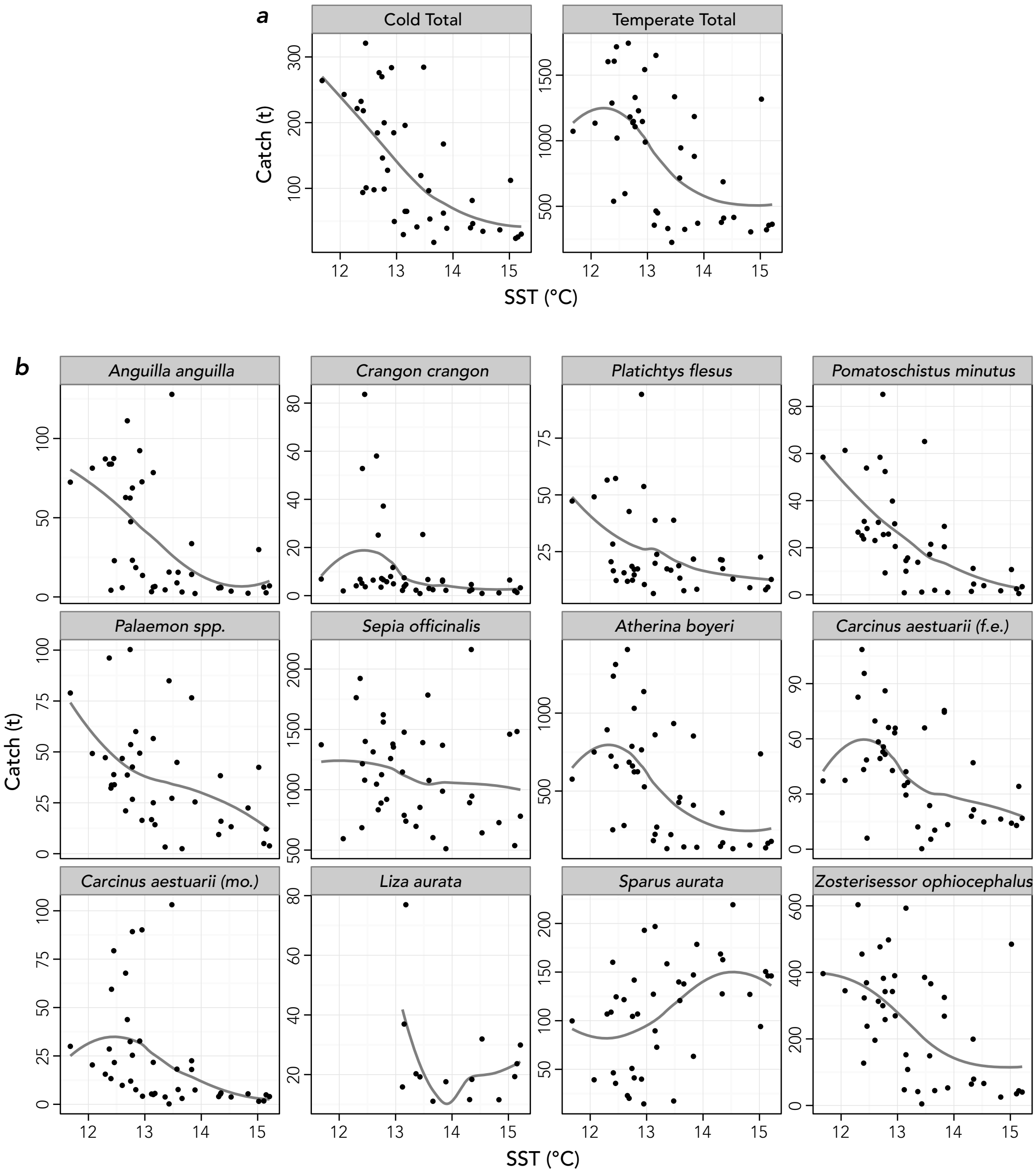

Figure 3.7: Relationship between landings (in terms of (*a*) thermal affinity groups in target species and (*b*) each target species) and water temperature; *Carcinus aestuarii* (f.e.) = female with eggs, *Carcinus aestuarii* (mo.) = specimens during the moulting phase; Loess smoothing.

Table 3.2: Significant regime shifts detected in the second half of '80s; downward arrow indicates decreasing trend from that year forward.

Year	1984	1985	1986	1987	1988
Anguilla anguilla		↓			
Crangon crangon				↓	
Platichtys flesus	↓				
Pomatoschistus minutus			↓		
Palaemon spp.		↓			
Sepia officinalis	↓				
Atherina boyeri			↓		
Carcinus aestuarii (f.e.)				↓	
Carcinus aestuarii (mo.)					↓
Liza aurata					
Sparus aurata					
Zosterisessor ophiocephalus	↓				
Total catches	↓				

completely reflects the nektonic assemblage described in the lagoon environment [26, 27], being composed of all the main ecological guilds typical of transitional waters. Targeted species represent the most abundant and regularly present groups in the lagoon, including resident species (estuarine), marine migrants and catadromous species. The marine stragglers by comparison, due to their random presence in the catches, are considered to be incidental or discard by local fishermen.

In relation to the economic classification of catches, the artisanal fishery is a low discard incidence activity ($< 2\%$ in biomass), as described for other small-scale Mediterranean fisheries [34, 35]. The fishery also shows a strong seasonality, both in terms of total catch and catch composition, confirming the ability of fishermen to change their habits according to the different environmental and ecological conditions in order to optimise catch and maximise profitability [25, 36–38]. The fishing activity in the lagoon is strongly related to habitat distribution (which, for example, can explain the spatial differences of catches in terms of different habitat configurations of fishing grounds), tidal currents and seasonal cycles. All of this directly requires the ecological knowledge of fishermen (in relation to life cycles of species, migrations, seasonality, feeding habits, influence of environmental factors such as tidal currents, morphology, salinity and temperature). Together with high cultural and heritage value [35], this knowledge represents an important source of diversity that has to be conserved [39, 40].

The combination of field and fish-market data, allowed the time series of landings of species targeted by artisanal fishery in the lagoon, from 1945 to today to be reconstructed. The time series analysis highlighted the presence of different phases that can be roughly summed up in an initial increasing phase, a stable period in the central part, and finally a long decreasing trend in landings.

All of the recognisable different phases are in accordance with those described by Libralato *et al.* [18], and are explainable in terms of: (1) increasing fishing effort, both in relation to the number of vessels and diffusion of engine-powered boats, and increasing ecosystem carrying capacity owing to the first effects of the eutrophication during the first expansion, (2) the reaching of the carrying capacity in the stable phase and (3) finally, synergic effects of different causes (*e.g.* anoxia events, dystrophic crises and explosion of the mechanical clam harvesting) in the decline recorded since the 1980s [18].

Within the context of describing possible effects of climate changes, attention was focused on the regime shift in total catches in the mid-1980s. Defined by deYoung [41], this shift is as an extensive and relatively abrupt change, happening within a few years, between contrasting persistent states of a system. It seemed to be related with changes in the thermal regime of the lagoon and with a regime shift (increasing variation) of the sea water temperature (SST) recorded both in 1984 and 1988. The presence of a negative shift in this period is confirmed by almost every target species. This was in agreement with other work from different areas in the Mediterranean Sea, showing a regime shift detected both in environmental (*i.e.* SST) and biological variables [42–44]. In the same period (late 1980s) abrupt changes have also been recorded in different Atlantic areas, such as the North Sea, Baltic Sea and Wadden Sea with a positive correlation both with water temperature and the NAO index, confirming a climate driver [45, 46]. This further confirms the presence of strong relationships (via teleconnection) between the Atlantic and Mediterranean Sea climate [47, 48].

In relation to thermal affinity of species, target catches, both in field and landings data, were almost entirely composed of cold and temperate species, with the temperate group largely dominating. It is interesting to note that among the target species, brown shrimp *Crangon crangon* and European flounder *Platichthys flesus* (L. 1758) can be considered Atlantic relicts of the Mediterranean Sea basin [49, 50], being distributed only in the coldest part (with boreal features), such as the northern Adriatic Sea. The time series analysis reveals a decreasing trend for both these groups and a significant inverse correlation with water temperature during recent decades. The same pattern has been detected for most target species, with the exception of *S. aurata*. These patterns can be explained by the effects of climate change on fish phenology, specific to recurrent temperature-dependent events, such as reproduction and migration, which can ultimately affect recruitment. Evidence of these effects is growing in the available literature, especially in terms of earlier breeding seasons, shift in migration dates, earlier larval appearance as a response to warming in commercially important freshwater and marine fishes [51–54]. Similar results have been recently shown for a resident estuarine fish in the Venice Lagoon, the grass goby *Zosterisessor ophiocephalus* (Pallas 1814) [55]. This work indicated that reproductive investment was positively correlated to temperature anomalies with breeding peaks occurring earlier in warmer years. This evidence suggests that temperature anomalies may determine a certain degree of mismatching between reproduction and food availability for larval and juvenile phases with possible negative impacts on recruitment. Accordingly, this may result in the negative trends observed by the present work.

The situation of *P. flesus* is heterogeneous. For areas located in the upper part of its range, a positive relationship with water temperature has been described [56]. Conversely, in proximity to the lower limits of distribution, negative effects of increasing temperature have been detected [56–58].

Sparus aurata is probably the warmest among the temperate species considered here and this could partially explain the recorded pattern. This species has experienced a large northward expansion in different places, in relation to water temperature increase [57, 59].

No significant correlations have been detected between species or groups and the NAO index. This is in contrast with findings by Conversi *et al.* [43]. They reported a significant influence of this index on the biological regime shifts recorded in some Mediterranean Sea areas such as the Gulf of Lion and Adriatic Sea. This discrepancy could be explained by the fact that, at present, evidence of NAO effects on Mediterranean meteorological and ecological conditions are weak and lack convergence [47, 60]. Additionally, as the NAO effects are mainly mediated by river discharges [61], no real effects could be detected in the lagoon due to the river's diversion over past centuries in order to counteract the filling in of the basin.

Globally, results obtained seem to confirm the hypothesis that the northern Adriatic Sea area represents a kind of refugium for cold species, but also highlight the vulnerability of this nektonic assemblage to climate change. Since the Mediterranean surface waters are expected to warm by an average of 3.1°C by the end of the 21st century [62], a general northward shift of fish ranges is expected, leading to the gradual replacement of cold and temperate species by thermophilic ones. In this process, semi-enclosed areas such as the Adriatic Sea and, inside it, the Venice Lagoon, might act as reservoirs, but may also become a *cul-de-sac* for species that simply cannot further migrate [8]. From a fishery perspective, however, this change in the nektonic assemblage composi- tion, with species substitution, may not be so deleterious, as fishermen usually can react very quickly to changes in resource exploitation. This was recently demonstrated in the Venice Lagoon with the Manila clam introduction and the following development of a fishing activity, producing $>$ 40000 t per year in less than a decade [21]. This substitution, however, could be partially blocked by habitat fragmentation [8]; lagoons, for example, are patchily distributed within the Mediterranean Sea basin and so migrations of estuarine species among them could be slow or almost impossible due to the presence of inhospitable areas.

In conclusion, in spite of the fact that northward shifts of thermophilic species are largely demonstrated in the Adriatic Sea [63–65], their presence in the lagoon has not been detected, which is possibly a sign of good resilience of the assemblage. A clear decreasing trend of both cold and temperate species, however, has been recorded, and a possible synergic effect of the increasing water temperature detected. All this highlights the vulnerability of artisanal fishery in the Venice Lagoon to climate change.

Chapter 4

Vulnerability of the northern Adriatic Sea Fishery to Climate Change

Abstract

Within marine environments, nekton assemblages are recognised to provide several kinds of ecosystem services, both fundamental and demand-derived. They contribute, indeed, to enhance the biodiversity, the ecological processes and finally the system resilience. They also directly support the production of goods, such as in the case of renewable resources exploited by commercial fisheries. The problem of the impacts of climate change on this component of marine ecosystems, with the related consequences on ecosystem services, becomes therefore an interesting issue. In this context, the northern Adriatic Sea, hosting several species adapted to boreal climatic conditions, can be considered a good case study. By analysing the composition of landings from fisheries in terms of thermal affinity groups, the potential vulnerability of these activities could be highlighted. Catches, indeed, were shown to be mainly composed of cold and temperate affinity species, whereas the contribution of warm ones proved to be very low. Given the significant negative relationships between the cold and temperate groups with the recorded variations of the thermal regime and the latest projections by the IPCC in terms of ocean temperature raise, fishing activities, both professional and recreational, can be expected to experience severe consequences.

4.1 Introduction

According to the latest projections by the IPCC, Ocean temperature has been raising in the last decades over most of the Globe, and it is predicted to raise further in the short as well as in the long term [1]. In particular, this general trend is expected to impact the Mediterranean Sea [2], where the nektonic communities are likely to undergo deep modifications, both in terms of structure and of distribution range [3]. Nektonic communities provide several kinds of ecosystem services, both fundamental and demand-derived [4]. Fundamental ecosystem services can be described as those that are essential for ecosystem function and resilience, such as the regulation of food web dynamics, ecosystem equilibrium and biodiversity, while demand-derived services consist, among others, in food production and recreational activities. These ecosystem services will likely be impacted by modifications in the nektonic communities. In particular, fishing activities, both professional and recreational, can be expected to experience severe consequences [4]. In this context the northern Adriatic Sea, which hosts several species adapted to boreal climatic conditions [5] and, due to its nature of semi-enclosed basin, configures as a *cul-de-sac* preventing northward migration of species [6], can prove a particularly vulnerable area.

In this chapter, the vulnerability of the northern Adriatic fisheries is characterised by analysing the trends of landings in relation to the composition in terms of climatic affinity groups (cold, temperate and warm climate-related species) and by studying possible correlations with thermal-regime indicators.

4.2 Materials and Methods

In analysing fish population dynamics, a choice has to be made whether to rely on data derived from scientifically conducted trawl survey campaigns (fishery-independent data), or on catch data provided by fish markets (fishery-dependent data). While fishery-independent data can theoretically provide the most accurate information, they often suffer from limitations due to the high costs of campaigns, and can be difficult to interpret because of unplanned variations in the procedures over the years [7]. Fishery-dependent data, on the other hand, are often the only data available over a large time scale, and when used with care, they can provide the necessary information to infer the size and status of the populations being exploited [8].

Therefore, for this work, time series of landings, spanning from 1970 to 2013 and comprising all the commercial species were retrieved from the official statistics of Chioggia fish market. Since Chioggia hosts the biggest fishing fleet in the northern Adriatic Sea, the data can be assumed to be representative of the whole basin.

Periodical observations on the quay of Chioggia harbour allowed identifying the fishing gear on-board each vessel (the three main types of gear used locally, otter trawl, *rapido* trawl and midwater pair trawl, are easily distinguishable). By integrating the fish market data with evidence from the observations on the quay, it was possible to quantify the average catch composition for each of the three main types (or métiers) of fishing gear in terms of contribution to total landings.

To account for the different sensitivity of the species to changes in temperature, the climatic affinity of each species recorded in the time-series was assessed according to the latitude-based method proposed by Pranovi *et al.* [9] (see section 3.2.2, on page 42). Each species was categorised according to the mean distribution area in terms of latitudinal range: species with a distribution above 45°N, species within the 30°N–45°N range, and species mainly found below 30°N. This allowed the identification of three climatic affinity groups, defined as cold, temperate and warm, respectively.

Monthly average sea-surface temperature (SST) time-series for the northern Adriatic was reconstructed using values from the U.S. National Oceanographic and Atmospheric Administration (NOAA) climate prediction centre website (`www.cpc.ncep.noaa.gov`). For each year a temperature curve was fitted, considering the months from February to August (usually the coldest and the warmest of the year, respectively), resulting in a sigmoid shape. For these curves, the slope of the tangent at the inflection point (s) was calculated (Figure 4.1), since this parameter can be considered a good proxy both for the annual temperature raise and for the suddenness of the transition from the cold to the warm season. Temporal trends have been analysed by plotting annual landings for each thermal affinity group against s. Statistical significance of correlations was tested through the application of generalised additive models (GAM [10]) in R v. 3.0.1 (R Core Development team; `www.r-project.org`). In addition, temporal trends were analysed taking into the account the landings composition of the three main métiers, to assess their vulnerability in relation to their composition in terms of climatic affinity groups. In order to assess

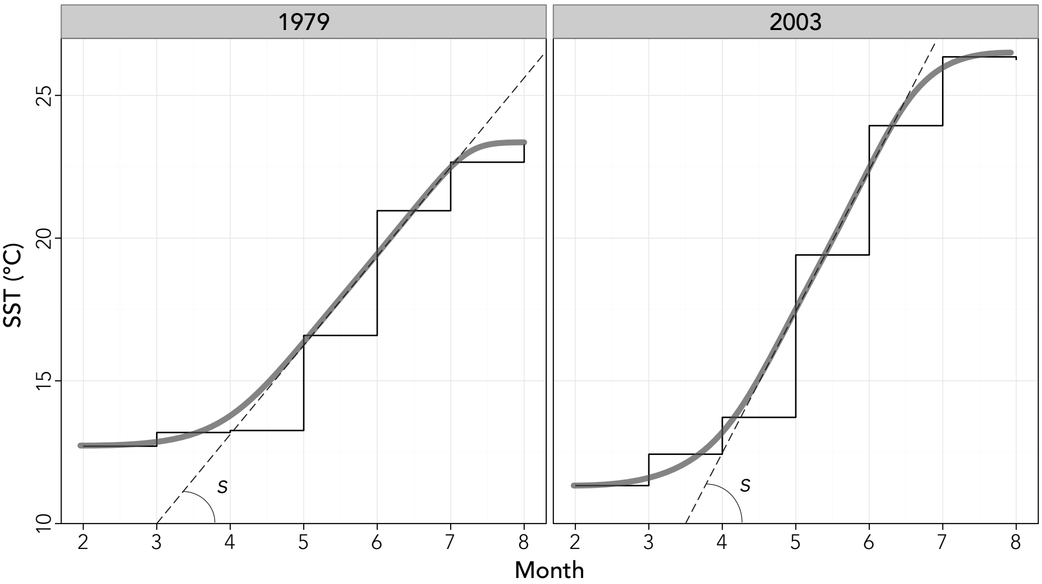

Figure 4.1: SST from February to August for 1979 and 2003. The *s* parameter is extrapolated by fitting a sigmoid curve (grey line) to the data (black stair-step line), and then calculating the slope of the tangent to the curve (dashed line) at the inflection point. Notice that *s* is much higher in 2003 ($s = 4.42$) than in 1979 ($s = 2.41$).

the presence of significant regime-shifts in the time-series of both landings (in terms of climatic affinity groups) and the *s* indicator the Regime Shift Detection method (STARS) was applied [11, 12].

4.3 Results

Total landings in the considered period showed an increasing trend with two peaks recorded at the end of ′70s and at the beginning of ′80s, followed by a sharp decrease at the end of ′80s and a fluctuating situation in the last part of the series (Figure 4.2). This pattern was mainly driven by the midwater pair trawl landings, which substantially contributed to the total values. The otter trawl and *rapido* showed both a declining trend through the time, with the highest values recorded again at the end of ′70s and at the beginning of ′80s. Considering the landings composition in terms of climatic affinity groups, the temperate one represented the main portion of the catch, amounting, on average, to about 57% in weight of the total landings; on the other hand, species with cold climatic preferences gave a contribution of about 41%, while the remaining 2% could be ascribed to warm climatic affinity species (Figure 4.3).

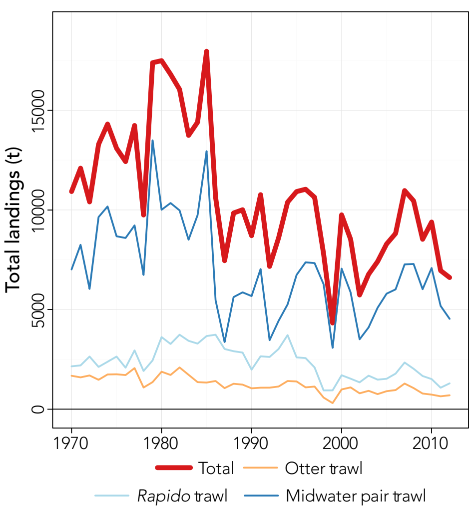

Figure 4.2: Time series of landings (total and by métiers); data reconstructed using Chioggia fish market official statistics.

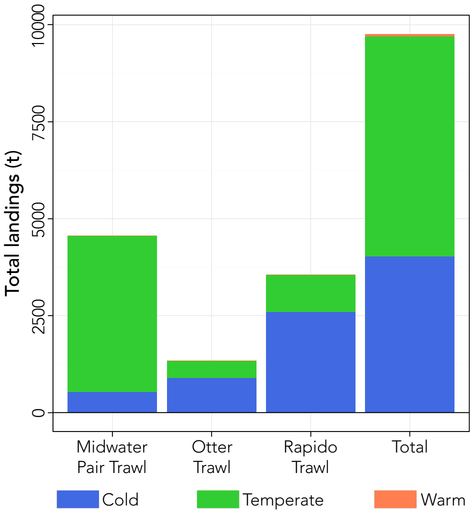

Figure 4.3: Landings composition in terms of climate affinity groups (total and by métiers).

Differentiating the landings based on the three métiers, it is noticeable that both otter trawl and *rapido* trawl catch mainly cold affinity species, while for the midwater pair trawl temperate species represent the most significant portion of the total landings. The temporal trends analysis highlighted the presence of a negative regime shift for both the cold and temperate affinity group, between the second half of the '80s and the first half of the '90s (Figure 4.4). On the contrary, warm affinity species showed a positive regime shift in 2001.

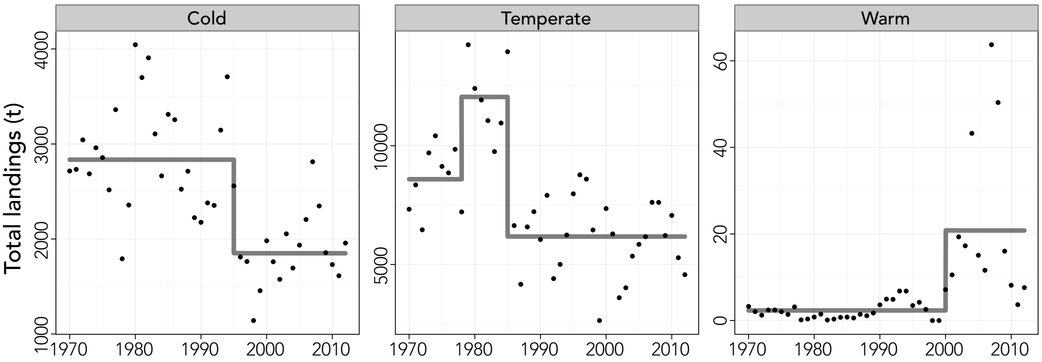

Figure 4.4: Time series of landings for the three climate affinity groups; grey lines mark the regime shifts according to the STARS method.

In relation to the thermal regime analysis, the temporal trend of the *s* indicator showed an increase through the time, with a positive shift in the early '90s, which roughly matches the negative one highlighted for the cold and temperate affinity groups (Figure 4.5).

The relationship between landings and the *s* indicator has been tested by modelling the correlation among the temporal trend of *s* and the different climatic affinity groups, using GAM. Results highlighted significant negative relationships for species of cold affinity ($p < 0.01$, 15.2% deviance explained), and of temperate affinity ($p < 0.001$, 30.6% deviance explained); no significant relationships have been detected for the warm group.

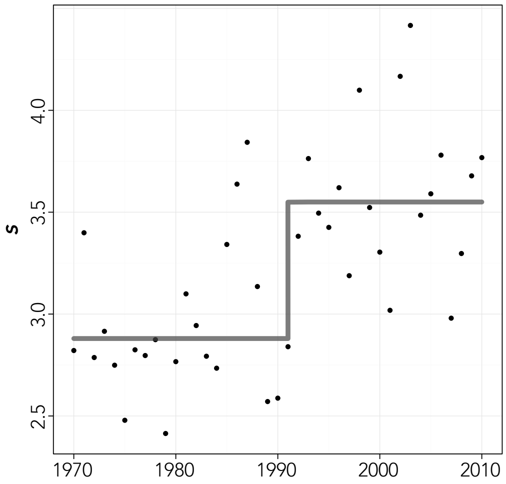

Figure 4.5: Time series of the *s* indicator; grey line marks the regime shift, according to the STARS method.

4.4 Discussion

Long term modifications in the structure and quantity of landings in the northern Adriatic Sea have been recently discussed by Barausse *et al.* [13], in terms of environmental drivers and life history of the different species. Findings in this chapter allow to suggest that the recorded decline in catches could be related, among other factors, to changes in the thermal regime of the area recorded during the last decades. During this period, indeed, an increase of the speed in the transition from the cold to the warm season has been pointed out, with a significant shift at the beginning of the '90s.

Globally, in relation to the composition in terms of climatic affinity groups, results seem to confirm on one side the hypothesis that the northern Adriatic Sea represents a kind of *refugium* for cold species, but on the other they highlight the high vulnerability of the nektonic assemblage to climate change. Since the Mediterranean surface waters are expected to warm by an average of 3.1°C by the end of the 21^{st} century [2], a general northward shift of fish ranges is expected, leading to a decrease of the cold and temperate species and a possible replacement by thermophilic ones. In this process, semi-enclosed areas located in the northern part of the basin, such as the Adriatic Sea, might act as reservoirs, but may also become a *cul-de-sac* for those species that simply cannot migrate further north [6].

Scientific evidence about the effects of climate change on fish phenology is growing in the available literature. In particular, shifts in the breeding seasons, migration timing and larval appearance in response to warming have been described in commercially relevant freshwater and marine fishes [14–17]. Similar effects have been recently described also for fish populations in the Venice lagoon [18]. All this is expected to directly influence the recruitment and ultimately the fish abundance and biomass.

These effects could be an explanation, at least for the last part of the time series, for the negative temporal trend shown by the cold and temperate affinity species of the northern Adriatic Sea, in relation to the change of the thermal regime.

The analysis of landings composition in terms of thermal affinity groups highlighted the high vulnerability of the fishing activities to climate changes in the northern Adriatic Sea, albeit with differences among the main métiers. Catches, indeed, proved to be almost entirely composed by cold and temperate species, which are the most exposed to temperature-related effects.

While recorded negative trends are certainly influenced by several factors such as increasing fishing effort and overfishing, it can be assumed that climate plays an important role in it, as confirmed by the significant negative relationship found between cold and temperate affinity groups and the thermal regime indicator.

On the other hand, in spite of the fact that northward shifts of thermophilic species are largely demonstrated in the Adriatic Sea [19–21], they still amount to just a marginal portion of the catches, even if they are increasing through time. The warm affinity species, however, showed no significant relationships with the thermal regime modifications. Their increase in the recent years can therefore be attributed to more complex dynamics possibly involving, for example, the reduced competition with local species, instead of a direct effect of temperature. All this reflected in terms of fishing activities, since landing data seem to indicate that the positive contribution from new species is not yet able to counterbalance the losses. Thus, even if fishing activity often proved to be able to adapt to the modifications in the nektonic assemblage composition by quickly turning to new exploitable resources (as shown in the case of the Manila clam in the Venice Lagoon [22]) it will still have to face an overall decrease in resources, augmenting, if possible, the overall vulnerability in relation to possible effects on the system resilience.

All the recorded modifications lead to the idea that the fish community in the northern Adriatic Sea is undergoing a deep change, with a significant decrease of native species and a gradual increase of new thermophilic ones.

Nektonic communities are recognised to provide several kinds of ecosystem services, both fundamental and demand-derived [4]. For example, fundamental services like regulation of trophic-web dynamics can be significantly altered if key, high-biomass planktivorous species such as sardine will decrease. Moreover, many species like mullet, seabream, or sardine itself are marine migrants, which spend part of their life-cycles in estuarine habitats, linking different systems in terms of energy. All this is expected to affect ecosystem functioning, finally reducing the long-term capacity to adapt [23].

All this is expected to deeply affect ecological processes going on in the northern Adriatic Sea with consequences also in terms of benefits for human populations [24]. Considering demand-derived services, other than the described effects on commercial fisheries, recreational fishing can also experience consequences, since many prized target species, like gilt-headed seabream, mackerel and bluefin tuna, belong to the temperate affinity group.

In conclusion, by analysing the nektonic composition in terms of thermal affinity groups it was possible to describe the vulnerability to climate changes of fisheries in the northern Adriatic Sea, discussing this issue in the light of possible implication in terms of ecosystem services provisioning.

Chapter 5

Marine food-webs and warming scenarios

Modelling a thermophilic species invasion in the northern Adriatic Sea

Abstract

Marine communities respond promptly to climate changes, with modifications ranging from an increased extinction rate for cold-climate adapted species to an increased risk of invasion of new areas by thermophilic ones. This will have direct consequences on human activities by redistributing the fisheries catch potential. Such effects might prove particularly significant in the Mediterranean Sea, where the temperature is predicted to increase more than the global average, and within the Mediterranean, the Northern Adriatic Sea is an highly vulnerable spot, due to the biological community composition reflecting its climatic peculiarities. In this work a dynamic food-web model is introduced, which takes into account the effects of temperature raise on the northern Adriatic community, at the same time simulating a thermophilic alien species invasion, with the aim of shedding some light on the dynamics regulating the system and providing some guidelines about the direction towards which it can evolve.

To simulate the effect of the arrival of non indigenous thermophilic species, dedicated functional groups, exclusively composed by alien species, were introduced in correspondence to the indigenous ones; to explicitly consider the effects of SST raise, the temperature range of every group in the system was estimated, and used in a forcing function to manipulate the predators search rates.

Results of the sensitivity tests highlighted nonlinear dynamics within the food-web, pointing out the soundness of the model; it also allowed to discriminate between the various drivers influencing the system components. Simulations based on realistic SST raise scenarios, on the other hand, suggest that the northern Adriatic ecosystem may be heading towards an impoverishment both in biomass and diversity, with potentially high impacts on commercial fisheries, and that future management requirements will be to deal with a reduction in the resources, rather than with changes in the composition of the marine community.

5.1 Introduction

As noted in the previous chapter, global Ocean temperatures have been subject to a raising trend over the last decades, and this tendency is predicted to continue in the future as well. The Mediterranean Sea is likely to be particularly affected by this phenomenon, since models associated to the IPCC warming scenarios prospect for this area a mean annual temperature raise higher than the global average [1].

Biologic systems have been found to respond to climate modifications in several ways, and at all levels [2–4]. Climate warming may induce shifts in species phenology, since many biological traits, such as migrations and spawning times, are triggered by temperature-related mechanisms; temperature changes may also determine shifts in genetic frequencies, morphology and behaviour [5]. Moreover, physiological traits like the rates of production and of respiration may change, possibly modifying community dynamics and ultimately influencing biodiversity [6]. Thermal variations can also modify the frequency of parasitic infestations and of diseases, and cause the appearance of new ones. More directly, changing temperatures can make previously inhospitable areas accessible to some species, while rendering old territories less suitable. All this can play a role in modifying the distributional ranges and density of species populations, through a poleward shift of habitats [2–4, 7].

The three main issues related to these modifications are:

- the increased risk of extinction for species with restricted temperature requirements and highly adapted to certain habitats , especially if they are characterised by small populations [7];
- the risk of an invasion by thermophilic alien species of ecosystems where they weren't historically recorded [8];
- the redistribution of fisheries catch potential, with a substantial increase in high-latitude regions and a significant drop around the tropics [9].

The trend of the introductions of nonindigenous, warm-climate marine species is presently increasing [10], and the outcome these introductions can have on a marine ecosystem can vary widely, from the almost unnoticeable to the irreversible shift of the original communities to a new equilibrium [11].

In the Mediterranean Sea, changes in the fish communities due to Non-Indigenous Species (NIS) invasions are a widespread issue, and have dramatically increased in the last decade, with 41% of the NIS recorded in the last century actually being signalled after 2001 [12]. The phenomenon of NIS introduction in the Mediterranean can be categorised into two main aspects: meridionalisation and tropicalisation [13]. In both cases, this consists in an increase in abundance of thermophilic species, accompanied by the extinction or rarefaction of native stenotherm ones adapted to colder climates [7]. In the case of meridionalisation, the invasive species originate from the warmer parts of the Mediterranean, while in tropicalisation they are allochthonous species, mainly of lessepsian origin.

Within the Mediterranean Sea, the northern Adriatic basin is a particularly vulnerable area to the effects of climate change. Unlike the rest of the Mediterranean, it is subject to a subatlantic climate, and therefore hosts a community comprising several species adapted to boreal conditions [14]. Being a semi-enclosed basin, it acts as a *cul-de-sac* for these species, preventing a further poleward migration as a response to temperature raise [15]. Moreover, it hosts a highly developed industrial fishery, with about 1800 vessels active in 2010, totalling a GT of 22900 tons and directly employing 3800 people [16], so that changes in the nektonic assemblages can have important socio-economic consequences.

In this context, new thermophilic NIS are being recorded ever more frequently [12, 17–22]. Some of the most striking examples include large pelagic predators such as the yellowmouth barracuda (*Sphyraena viridensis*), the bluefish (*Pomatomus saltatrix*) and the common dolphinfish (*Coryphaena hyppurus*), but also the small schooling pelagic round sardinella (*Sardinella aurita*) [18]. However, new records are not limited to these species, but encompass both vertebrates and invertebrates occupying a large spectrum of functional niches in the ecosystem.

To better understand the dynamics going on in marine ecosystems undergoing community structure modifications and alien species invasions due to the effects of climate change, and to develop and test scenarios to assist the management of a vulnerable system, providing a way to assess the possible development strategies, the modelling approach can prove a useful instrument, despite the many uncertainties related to the method, which make it impossible to predict with precision the impacts of a new species on a food-web, let alone its consequences on commercial fisheries [23]. This limit is common to the modelling approach, since the natural world is characterised by such a complexity that modelling must necessarily be reductionist [24], and precise predictions are seldom possible, because of the necessity of making assumptions and simplifications, making even the most complex models approximations of the real systems [25]. However, keeping these limitations in mind, applying models not to forecast, but rather to explore the possible consequences of the establishment of new species under climate change may have large benefits [24]

There have been some attempts at predicting the impacts of NIS on marine ecosystems over the world [23, 26–28]. However, all these works have focused just on one or a few species, and none of these have explicitly accounted for climatic drivers in the model design. Attempts at introducing climate-change related forcings in food-web models have also been made [29], but are limited to the impacts of such forcings on the existing communities, and don't account for potential climate change driven invasions. What is more, no such approach has ever been tried for the northern Adriatic ecosystem.

Thus, the goal of this chapter is to present the potential and the first results of a dynamic food-web model for the northern Adriatic Sea, built in Ecopath with Ecosim [30], explicitly accounting for the effects of Sea Surface Temperature raise on the system components, at the same time simulating an invasion from multiple thermophilic NIS, with the final aim of gaining a better knowledge of the dynamics going on in the system and providing some hints about the direction towards which it can evolve.

5.2 Materials and Methods

5.2.1 The study area

The Northern Adriatic Sea represents the northernmost region of the Mediterranean Sea, excluding the Black Sea [31]. It is a semi-enclosed basin, characterised on its western part by mainly sandy coasts, with the presence of lagoons and deltas, while the eastern coasts are constituted for the most part of rocky substrates [32]. It is a shallow basin, with an average depth of 33 m, consisting entirely of a continental shelf area. The maximum depth, reached in the middle of the basin, doesn't exceed 75 m [32]. Water circulation is mainly cyclonic, with an incoming current entering from the east, in a NW direction, and introducing relatively warm and high-salinity waters [33].

The area is characterised by highly diverse environmental conditions, which translate into high biodiversity [34]; moreover, due to the shallowness and to the consistent river runoff, the basin is trophically rich [35], and this is reflected in the fishery yields, which are among the highest in the entire Mediterranean Sea [36].

The modelled area consists of that part of the Northern Adriatic basin which ideally encompasses a 7100 km^2 surface, delimited southwards by the Po river delta, and eastwards by Croatian territorial waters.

5.2.2 The food-web model

The food-web model was built by using Ecopath with Ecosim (EwE) version 6.4 [37, 38]. It is based on the mass-balance assumption, *i.e.* it assumes that the biomass (or energy) input to any group in a model must equal the output from the group. This is mathematically described by the equation:

$$P_i = \sum_j B_j \cdot M2_{ji} + Y_i + E_i + BA_i + P_i \cdot (1 - EE_i) \tag{5.1}$$

where P is the production of each group (i) composing the modelled ecosystem, $M2_{ij}$ is the predation mortality caused by all the groups preying on i, B_j is the total biomass of these groups; Y_i represents the exports from the system due to fishing activity, while E_i accounts for all other exports; BA_i is the biomass accumulation in the ecosystem; finally, $(1 - EE_i)$ is the baseline mortality, and EE_i is the ecotrophic efficiency of the group within the system, *i.e.* the proportion of the production of the i^{th} group that is exported out of the ecosystem or consumed by predators within it. To explicitly consider the input parameters required by Ecopath, Equation 5.1 can be rewritten as follows:

$$B \cdot \left(\frac{P}{B}\right)_i = \sum_j B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ij} + Y_i + E_i + BA_j + B_i \cdot \left(\frac{P}{B}\right)_i \cdot (1 - EE_i) \tag{5.2}$$

where $(P/B)_i$ represents the production/biomass ratio for the group i and is equivalent to the total mortality Z under steady-state conditions [39]; $(Q/B)_j$ is the consumption/biomass ratio of j; DC_{ij} is the diet composition for each consumer group, *i.e.* the proportion in which i is present in the diet of the predator j.

The model is implemented by EwE in the form of a system of linear equations, one for every group in the model. In each equation, at least 3 out of the 4 basic parameters (B, P/B, Q/B and EE) must be known. Q/B can, if needed, be calculated from P/B and the gross food conversion efficiency (P/Q); usually, the parameter left unknown is EE, since it is very difficult, if not impossible, to estimate empirically [38]. The mass balance is ensured when for each group *i*, consumption equals the sum of production, respiration and unassimilated food.

The mass-balance model provides the initial conditions for the temporal dynamic module of EwE, called Ecosim [40], which is based on a system of ordinary differential equations where the biomass variation over time is expressed as follows:

$$\frac{dB}{dt} = \left(\frac{P}{Q}\right)_i \cdot \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i) \cdot B_i(t) \qquad (5.3)$$

where Q_{ji} is the consumption of group *i* by group *j*, Q_{ij} is the consumption of group *j* by group *i*, I_i is the immigration rate, M_i is the natural mortality rate (calculated as $P_i \cdot (1 - EE_i)$, with P_i being the production rate and EE_i the Ecotrophic efficiency of group *i* as derived from Ecopath), F_i is the fishing mortality rate (calculated as C_i/B_i, with C_i being the catch rate of group *i* as derived from Ecopath), e_i is the emigration rate and B_i is the biomass of the group *i*.

The parameter Q_{ij} in Equation 3 is based on the foraging arena hypothesis [38, 41–43], which assumes that a given prey can be either accessible or inaccessible to a given predator at any given point in time: prey biomass is divided into vulnerable and non-vulnerable components, and the transfer rate between these two components is regulated by a vulnerability rate. The quantity of prey consumed by a predator will thus be:

$$Q_{ij} = \frac{f(T) \cdot a_{ij} \cdot v_{ij} \cdot B_i \cdot B_j}{2 \cdot v_{ij} + a_{ij} \cdot B_j} \qquad (5.4)$$

where a_{ij} is the search rate of predator *j* feeding on prey *i*, B_i and B_j are the biomasses of the prey and of the predator respectively, and v_{ij} is the vulnerability of prey *i* to predator *j*. To account for the action of external drivers that can affect the predator's ability to feed on a prey, the forcing function $f(T)$ can be used to modify the search rate [29], (see section 5.2.4 on page 78 for further detail).

5.2.3 Model outline

The model is an upgrade of an existing one from the 1990s [44, 45] with 2007–2008 data. It has a mid-complexity structure, accounting for the main functional groups constituting the system, rather than the individual species. This allows to provide a synthetic representation of the ecosystem, without reducing the capability to represent the main trophodynamic processes. Some taxa (namely Bluefin Tuna, Flatfish, Scallops and Venus clams), being of special interest in relation to their importance as target species for local fisheries, were nevertheless isolated in dedicated groups, in order to specifically monitor their role in the system. The detritus groups were differentiated in generic detritus and carcass, the latter collecting the dead organisms produced by fishing activity, as discard.

The main fishing activities carried out in the basin were taken into account with the inclusion of five fishing métiers: tuna fishing, mid-water pair trawl, otter-trawl, hydraulic dredge and *rapido* trawl (a typical fishing gear used in the Adriatic to harvest flatfish and scallops — see Pranovi *et al.* [46]).

To simulate the effect of the arrival of non indigenous thermophilic species, dedicated functional groups, exclusively composed by alien species, were introduced in correspondence to the indigenous ones. The thermophilic groups were defined based on species already observed in the basin, and on those whose arrival is likely in the immediate future [12]. Parameters for the new groups were calculated taking into account productivity and consumption rates of the invasive species, as well as the specific diets, which were derived from the data available on FishBase (`fishbase.org`) [47]. The initial biomass for the invasive groups was set to very low values, so to represent a sort of pre-invasion status.

The final model thus consisted of 30 living functional groups, plus 2 detritus groups and 5 commercial fishing fleets. The functional groups included in the model along with the input parameters are summarised in Table 5.1, while Table S.5.1 on page 105 details the sources used to determine the parameters, and Table S.5.2 on page 108 shows the diet composition matrix.

5.2.4 Dynamic simulations

Linking search rates to SST

To perform dynamic simulations based on Sea Surface Temperature raise scenarios, it was necessary to introduce the effects of climate change in the Ecosim base equations. The goal was to make the production rates of functional groups change accordingly with the assumed temperature trend. This was achieved by applying a function to manipulate the predators search rates ($f(T) \cdot a_{ij}$ in Equation 5.4), so that predators could consume more or less prey per unit energy spent searching, this way modifying their productivity; in the case of primary producers, the function directly modified primary production [29].

For consumer groups, the function used to modify the search rates was the one initially proposed by Lassiter and Kearns [48] to relate the growth rate of a population to temperature:

$$f(T) = \begin{cases} \left(\dfrac{T_{\text{max}} - T}{T_{\text{max}} - T_{\text{opt}}} \right)^{c\left(T_{\text{max}} - T_{\text{opt}}\right)} \cdot e^{c\left(T - T_{\text{opt}}\right)} & \text{if } T < T_{\text{max}} \\ 0 & \text{if } T \geq T_{\text{max}} \end{cases} \tag{5.5}$$

where T is the Sea Surface Temperature, T_{opt} is the optimum temperature for a given species, at which the search rate is maximum, T_{max} is the maximum tolerated temperature, above which the search rate is null, and c is a parameter accounting for the sensitivity of a species to temperature variations. For primary producers, two types of forcing functions were considered: a linear variation with temperature (see 'SST increase scenarios' on page 81 for details), and an exponential one [49]:

$$f(T) = 10^{0.0275 \cdot T - 0.07} \tag{5.6}$$

Estimating the parameters

To apply Equation 5.5 to the predators search rates, the parameters T_{opt}, T_{max} and c had to be estimated for each species composing each functional group of the model. Thus, as a first step, a yearly mean latitudinal SST profile was reconstructed for the northern Atlantic Ocean, using data from the online database `nodc.noaa.gov` and considering years from 1945 to 2000. Then for each considered species, the latitudinal distribution in the northern hemisphere was derived from the database `data.gbif.org`, considering occurrences up to year 2000 to avoid taking into the account possible range modifications due to climate change. For each species, the latitudes corresponding to the median and 5th percentile of the range were then extracted, and the T_{opt} was defined as the mean annual SST calculated at the latitude corresponding to the median of the distribution, while T_{max} was defined as the mean annual SST calculated at the latitude corresponding to the 5th percentile. Since, in estimating T_{opt} and T_{max} the surface temperature was used, the parameter c was attributed considering how a species related to the surface: this way pelagic species were assigned higher values, demersal species had lower values, and benthic species had even lower ones.

The parameters for the functional groups were calculated using weighted averages of the values of the species composing each group. To validate the results of this procedure, the parameters for the functional groups constituted of fish were calculated also using values of T_{opt} and T_{max} from Cheung *et al.* [50].

Sensitivity tests

The model was tested for sensitivity with regards to variability both in the SST trend, and in the parameters of Equation 5.5.

To test the effects of the variability of T, a set of 20 simulations over 30 years was run, applying a linear temperature raise for the first 10 years, and keeping it constant for the following 20 to allow the system to stabilise. The initial temperature was set to the mean SST registered in the basin in 2007 ($T_{\text{start}} = 18.4°\text{C}$); the final temperature variation was comprised between +0.8 and +1.2°C, in equal steps ($T_{\text{end}} = 19.2 \sim 19.6°\text{C}$). For each simulation, the final biomass (B_{end}), the relative biomass variation ($B_{\text{end}}/B_{\text{start}}$) and the value of the forcing function ($f(T)$) were calculated for each group; further, a relative sensitivity index S was calculated as follows:

$$S = \frac{\Delta B}{B_{\text{start}}} \cdot \frac{T_{\text{start}}}{\Delta T} \tag{5.7}$$

where $\Delta B = B_{\text{end}} - B_{\text{start}}$ and $\Delta T = T_{\text{end}} - T_{\text{start}}$.

To investigate the possibility of distinguishing the prevalence of trophic effects or of temperature-related effects on the various groups, the Mixed Trophic Impact (MTI) index was used [51], since it quantifies the direct and indirect trophic effects acting on each group as a consequence of the biomass variation of all the other groups in the system. Plotting MTI against the simulation results enables to distinguish between trophic and temperature-related effects on each functional group. To do so, the results of the simulation with $\Delta T = +1°\text{C}$ were used as the input for a new Ecopath model (Ecopath model from Ecosim plugin), from which the MTI matrix was extracted, and each value was normalised on the biomass of the group which received the effects.

To test the sensitivity of the model to the variability of the function linking temperature and search rates, 100 simulations were conducted. Each simulation considered different combinations of T_{opt}, T_{max} and c for every single group. Values were randomly extracted from a normal distribution centred on the actual estimated parameter. Simulations were performed also in this case over 30 years, applying a linear temperature raise from 18.4 to 19.4°C for the first 10 years.

SST increase scenarios

Simulations were then run in order to test temperature increase scenarios. The scenarios were based on the temperature projections by Somot *et al.* [52], considering the IPCC A2 scenario. Since this implied a 0.03°C SST raise per year, to obtain a temperature raise capable of producing significant results in the model, the forcing was applied for 30 years, and the results were taken at 50 years to allow the system to stabilise.

To gain deeper understanding of the dynamics influencing the system, 4 sets of simulations were performed:

a) applying the temperature-based forcing functions to the search rates of every group in the system;
b) applying the forcing functions only to indigenous groups;
c) introducing an interannual variability component in the forcing functions, in the form of a random factor 2 orders of magnitude smaller than the value of the forcing, which was added at each time-step; 100 simulations were run this way, changing the random components for each simulation;
d) taking into the account the indigenous species capability to adapt to temperature changes: this was performed by introducing an initial plateau in the forcing function for the indigenous groups.

For each set of simulations, three different primary production scenarios were tested:

a) no change in PP;
b) an exponential increase in production due to temperature;
c) a linear decrease of 20% in 30 years representing the actual oligotrophication trend detected in the basin [53].

To analyse the effects on the ecosystem of the different scenarios, three indices were applied. Kempton's Q [54] is the EwE built-in diversity index. It is derived from the Q_{75} index [55] and it represents the slope of the cumulative log-abundance curve, where the biomasses of the functional groups above TL III are employed as proxies for their abundances. Shannon's H [56] is one of the most applied diversity indices. Since in its original form it requires the functional groups abundances to be known, it was also modified to use the biomasses instead. Finally, the steepness of the $cumB - TL$ curve [57, 58] was calculated. This parameter is a good synthetic index providing an estimate of the effects of drivers acting on the ecosystem over time, since an heightening or stretching of the cumulative sigmoidal curve over time is associated with positive ecosystem responses, while a flattening of the curve indicates a perturbed ecosystem.

5.3 Results

5.3.1 Basic estimates

The model was balanced by using input values within the ranges found in literature (Table. S.5.1) for all functional groups with the exception of MZP and MDI. For these groups, values had to be slightly altered to obtain Ecotrophic Efficiencies less than 1.

The basic parameters calculated by the model are highlighted in bold in Table 5.1, and the resulting trophic web is represented in Figure. 5.1. The group with the highest trophic level is the Bluefin Tuna (BFT, TL = 4.33), while nekton feeding groups, both autochthonous and invasive, reach a slightly lower value (NFD, TL = 4.18; NFI, TL = 4.29). The majority of the biomass concentrates between TLs 2 and 3, mostly due to the benthic functional groups. P/B values vary widely, ranging from $219y^{-1}$ for the microzooplankton group to $0.43y^{-1}$ for Bluefin tuna; Q/B values also vary, reaching the highest values for the smallest organisms (BPL, $Q/B = 438y^{-1}$), while the lowest value, estimated by the software, is that of the local Nektonic feeding group ($2.13y^{-1}$). Ecotrophic Efficiencies, which were calculated by the software for all groups, range from a minimum of 0.18 for the invasive nekton feeding group to a maximum of 0.99 for Cephalopods. Globally, invasive groups show somewhat lower EE values, indicating that they are scarcely utilised in the system; on the contrary, local groups tend to have higher EE values, particularly those which are heavily targeted by the fishing activities (Planktivorous fish, with an EE of 0.29, make an exception). Phytoplankton has an EE of 0.82, indicating the important role played by primary production as an energy source in the trophic web. Concerning mortality rates (Figure S.5.1, page 109), medium and high trophic level, local groups show a significant fishing mortality, in some cases exceeding 50% of the total; conversely, invasive species consistently show

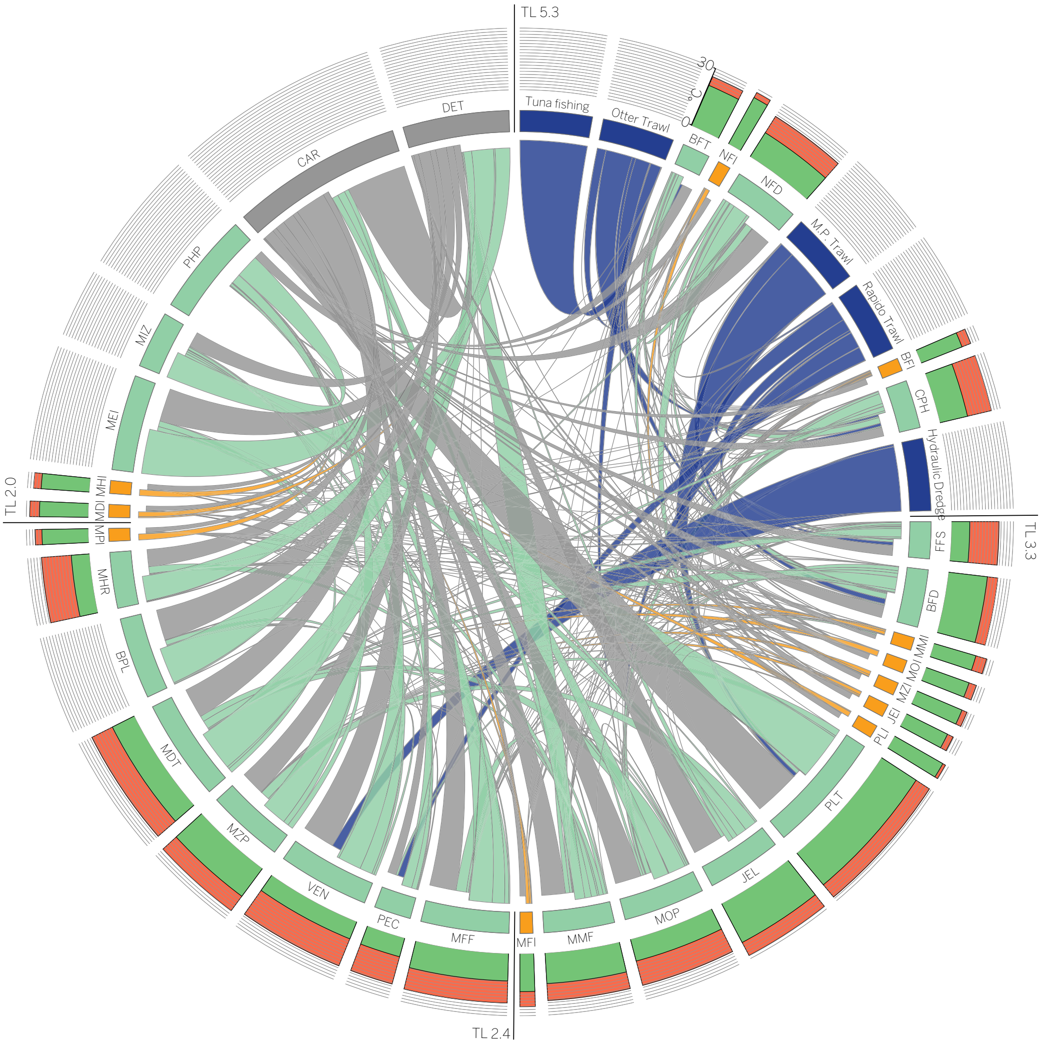

Figure 5.1: Scheme of the food-web structure resulting from the model. Functional groups are arranged counter-clockwise in decreasing order of TL. The width of the boxes representing the groups is proportional to their biomass, and the colour indicates the group type (Green=Autochthonous, Orange=Invasive, Blue=Fishery, Grey=Non-living). Links, representing trophic interactions, are proportional to the flow between two groups; inbound flows are those closest to each box. Barplots above boxes represent T_{opt} and T_{max} values for the respective groups.

Table 5.1: Functional groups included in the model, with input and output (in bold) parameters

		Basic Parameters						*Fishery catch ($t/km^2/y$)*					
	Group name	*TL*	*Biomass (t/km^2)*	*P/B (y^{-1})*	*Q/B (y^{-1})*	*EE*	*P/Q*	*Midwater pair trawl*	*Hydraulic dredge*	*Rapido trawl*	*Otter trawl*	*Tuna fishing*	*Total catch*
1	BFT	4.33	0.10	0.43	3.93	**0.54**	**0.11**					0.023	0.023
2	NFD	4.18	1.35	0.57	**2.13**	**0.69**	0.27	0.027		0.015	0.038		0.080
3	NFI	4.29	0.01	2.50	9.34	**0.02**	**0.27**	5 e-5			5 e-5		1 e-4
4	CPH	3.58	0.51	1.68	**5.60**	**1.00**	0.30	0.002		0.185	0.116		0.303
5	FFS	3.28	0.23	1.47	**7.35**	**0.85**	0.20	1 e-4		0.119	0.016		0.135
6	BFD	3.27	0.88	1.57	**4.92**	**0.94**	0.32	0.402		0.022	0.061		0.485
7	BFI	3.78	0.01	0.59	5.27	**0.32**	**0.11**	5 e-5		5 e-5	5 e-5		1.5 e-4
8	PLT	3.03	8.00	1.65	**4.95**	**0.29**	0.33	1.386		0.003	0.004		1.393
9	PLI	3.04	0.01	1.00	9.50	**0.40**	**0.11**	5 e-5			5 e-5		1 e-4
10	MOP	2.71	2.48	4.96	**12.40**	**0.92**	0.40	3.4 e-4		0.155	0.045		0.200
11	MOI	3.14	0.01	2.50	12.50	**0.31**	**0.20**			5 e-5	5 e-5		1 e-4
12	MMF	2.58	1.62	9.22	**46.10**	**0.97**	0.20						
13	MMI	3.23	0.01	2.50	8.50	**0.66**	**0.28**						
14	MFF	2.44	3.13	4.77	**23.85**	**0.92**	0.20			0.001			0.001
15	MFI	2.47	0.01	3.00	30.00	**0.15**	**0.10**			5 e-5			5 e-5
16	PEC	2.42	0.23	0.80	**4.00**	**0.99**	0.20	2.2 e-4		0.138	3 e-5		0.138
17	VEN	2.42	3.50	1.41	**7.05**	**0.51**	0.20		2.500				2.500
18	MZP	2.31	2.10	20.87	**104.35**	**0.97**	0.20						
19	MPI	2.00	0.01	39.08	80.00	**0.36**	**0.49**						
20	MDT	2.10	4.73	7.46	**37.30**	**0.80**	0.20						
21	MDI	2.00	0.01	10.00	50.00	**0.53**	**0.20**						
22	MHR	2.03	0.80	7.00	**35.00**	**0.84**	0.20						
23	MHI	2.00	0.01	3.00	15.00	**0.28**	**0.20**						
24	MEI	2.00	4.00	**13.70**	68.52	**0.61**	0.20						
25	JEL	2.85	1.90	14.60	50.48	**0.17**	**0.29**						
26	JEI	3.06	0.01	8.43	25.30	**0.11**	**0.33**						
27	MZI	3.08	0.01	18.00	38.00	**0.23**	**0.47**						
28	MIZ	2.00	0.85	219.00	**438.00**	**0.74**	0.50						
29	BPL	2.04	2.50	34.35	**171.74**	**0.53**	0.20						
30	PHP	1.00	4.85	152.13	**0.00**	**0.82**							
31	CAR	1.00	23.00			**0.23**							
32	DET	1.00	5.50			**1.00**							

negligible fishing mortalities, while in many cases the mortality due to predation is considerable, highlighting the important role these species could play in the food-web.

5.3.2 Summary statistics and transfer efficiency

The summary statistics of the model, including network flows and information indices are shown in Table 5.2. The global pedigree index for the model was 0.6, which indicates that the quality of the input data is adequate for ecosystem analysis [30].

Consumption made up for the largest portion of the Total System Throughput (TST, t/km^2/y), with a contribution of 38% to the total flows; production and flows into detritus contributed in similar proportions (25% and 21% respectively), while respiratory flows accounted for 15% of the total, and exports were negligible, contributing with less than 1% (Figure 5.2).

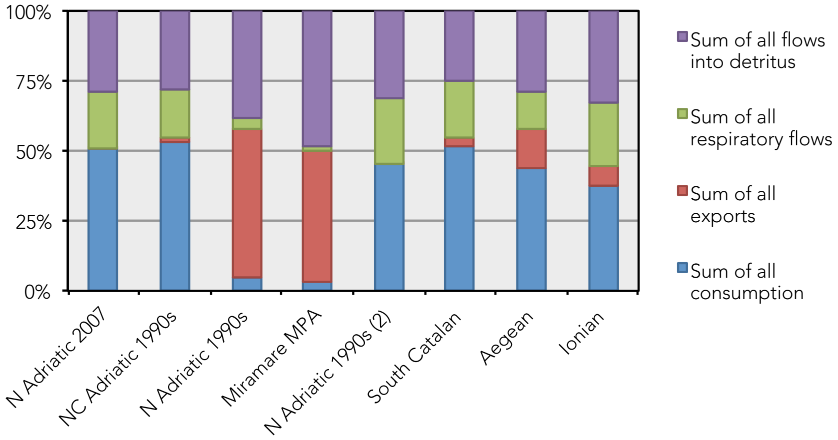

Figure 5.2: Flow composition for the northern Adriatic system, and comparison with those obtained from other models of the same area, and of other Mediterranean sites.

In Figure 5.3 the ecosystem is schematised in the form of a Lindeman spine, *i.e.* an integer trophic levels based flow diagram [59–61]. In the representation, primary producers and detritus are kept separated for clarity, and both are assigned a TL of 1. Main flows are included in TLs I, II and III, with the main portion generated in level II (42.3%), followed by level I (20.3%) and level III (7.7%). Figure 5.3 also highlights the important role played by TL II as a link between the food and the detritus part of the

Table 5.2: Summary statistics

Parameter	Value	Units
Sum of all consumption	1855.39	$t/km^2/y$
Sum of all exports	5.43	$t/km^2/y$
Sum of all respiratory flows	732.55	$t/km^2/y$
Sum of all flows into detritus	1052.35	$t/km^2/y$
Total system throughput	3645.71	$t/km^2/y$
Sum of all production	1241.91	$t/km^2/y$
Mean trophic level of the catch	2.79	
Gross efficiency (catch/net p.p.)	0.0073	
Calculated total net primary production	737.85	$t/km^2/y$
Total primary production/total respiration	1.01	
Net system production	5.3	$t/km^2/y$
Total primary production/total biomass	16.82	
Total biomass/total throughput	0.012	y^{-1}
Total biomass (excluding detritus)	43.87	t/km^2
Total catch	5.39	$t/km^2/y$
PPR (Primary Producers)	5.9	%
PPR (Detritus)	26.1	%
Connectance Index	0.22	
System Omnivory Index	0.15	
Ecopath pedigree index	0.6	
Measure of fit, t*	3.92	

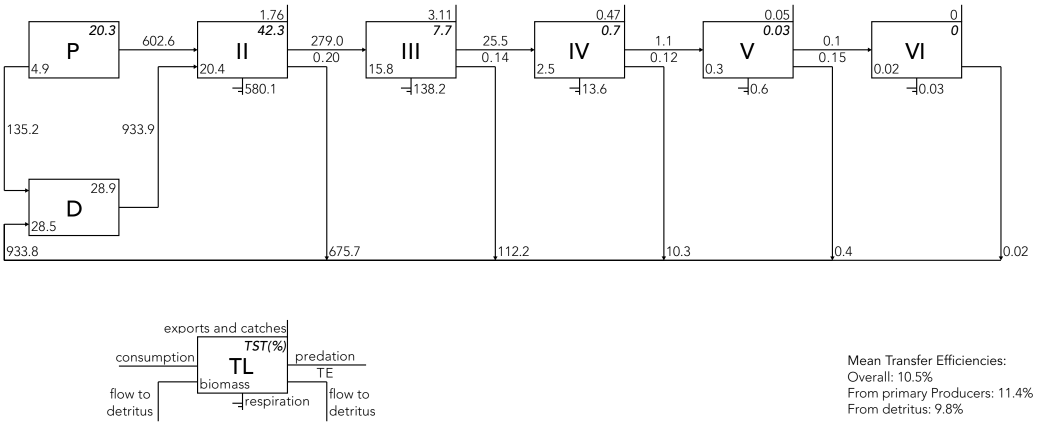

Figure 5.3: Lindeman spine for the northern Adriatic system. P = primary producers and D = Detritus. Flows in t/km^2/y and biomass in t/km^2

trophic web: TL II, mainly composed of benthic and planktonic invertebrates at the smallest side of the size-spectrum, produces and consumes the major part of the detritus. The mean transfer efficiency is of 12.5%, and it is slightly higher for the detritus part of the trophic web (13.0%) than for the food part (12.3%). Generally, it is maximum between TL II and III, and stabilises on lower values for higher TLs.

Figure S.5.2 on page 110 represents the analysis of consumption of ecosystem production. Excluding detritus groups (Figure S.5.2a), the system is dominated by zooplankton, accounting for about 55% of the total consumption; of the benthic groups, the one with the highest consumption is meiobenthos (15%). Leaving these groups aside (Figure S.5.2b), the importance of the local benthic groups, along with local jellyfish and planktivorous fish comes to evidence. When only the groups targeted by fishing activities are considered (Figure S.5.2c), planktivorous fish become the most important, followed by macrobenthic predators and venerids, while the consumption from high-TL fish groups is far less significant. Examining the invasive groups (Figure S.5.2d), which, due to their low biomasses, contribute only minimally to total consumption, macrobenthic groups have the largest impact, followed by jellyfish and planktivorous fish.

5.3.3 Mixed trophic impact analysis and keystoneness

Figure S.5.3 on page 111 shows direct and indirect impacts of each functional group on the system highlighted by the MTI index. Indirect impacts between groups due to partial niche overlapping can be observed, as in the

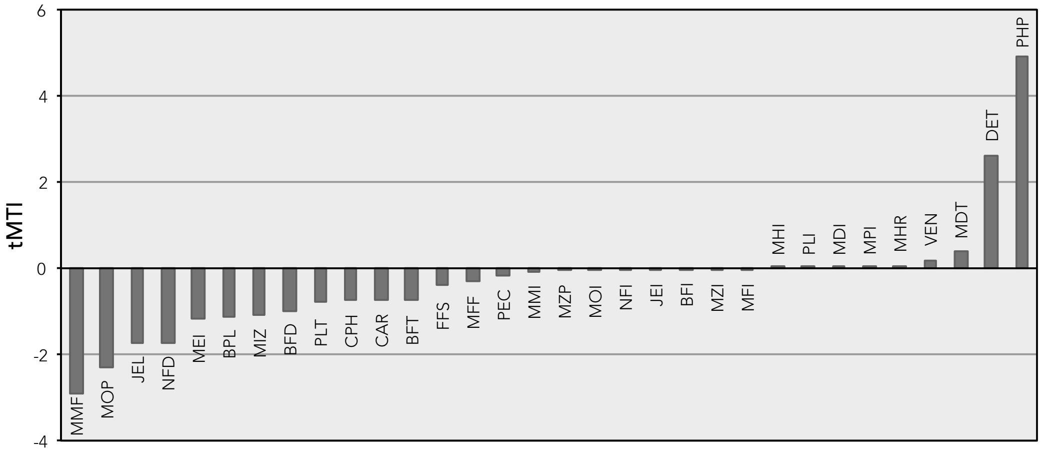

Figure 5.4: Total Mixed Trophic Impact (tMTI) of the impacting functional groups on all the other groups in the model.

case of an increase in nekton-feeding fish, which would impact negatively on Bluefin tuna and cephalopods. Indirect impacts due to trophic cascades can also be detected, for example an increment in planktivorous fish can impact negatively on benthic-feeding fish by favouring their predators, and an increase in clam harvesting would benefit invasive macrobenthic predators and mixed-feeders by reducing their autochthonous counterparts. Several groups throughout the system would be impacted by changes in the groups at the base of the food-web, like detritus, phytoplankton, various zooplankton groups and jellyfish. In particular, an increase in phytoplankton would have a beneficial effect on almost all groups. Concerning invasive groups, their impact on the system would be insignificant at this stage.

Figure 5.4 illustrates the result of total MTI analysis. Phytoplankton, detritus, detritivorous and herbivorous macrobenthos and venerids show the highest overall positive impacts on the food-web, while macrobenthic mixed feeders and nekton-feeding fish have the most negative impacts.

Figure 5.5 shows the estimated keystoneness of the functional groups. According to the Libralato *et al.* [62] keystoneness index (Figure 5.5*a*), phytoplankton, some macrobenthic groups (mixed feeders, predators, detritivores), zooplankton (jellyfish, micro– and mesozooplankton), and, among the nektonic groups, nekton feeders and planktivores, are the most likely to act as keystones. Conversely, invasive groups show the lowest values of keystoneness. On the other hand, the Power *et al* [63] version of the index (Figure 5.5*b*) substantially confirms these observations.

5.3.4 Fisheries

Calculated total landings and discards are shown in Table 5.1. The primary production required to sustain the fishery is 5.9% of total production when considering only the primary producers, and 26.1% when taking into the account detritus (Table 5.2). Moreover, the gross efficiency is high (0.04) and the mean trophic level of the catch is low (2.64).

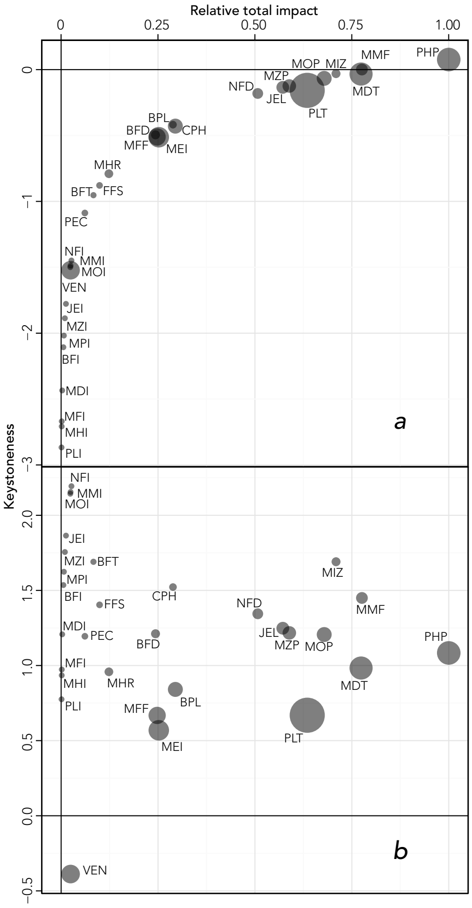

Figure 5.5: Keystoneness index vs. the relative total impact of the functional groups, according to (a) Libralato *et al.* [62] and to (b) Power *et al.* [63].

5.3.5 Dynamic simulations

Estimation of Temperature – Search Rate function parameters

Results of the estimation procedure of the parameters of Equation 5 for each functional group are shown in Table 5.3. For validation purposes, the table also gives T_{optC}, which indicates the optimum temperature values obtained from Cheung *et al.* [50] data, for those groups for which this parameter could be extrapolated; with the exception of the flatfish group (FFS), T_{opt} values obtained with the procedure presented in this chapter were within a ±20% range of those estimated from Cheung *et al.* [50] data.

Sensitivity tests

The analysis of sensitivity to the variability of T highlights the existence of nonlinear effects within the modelled food web. In particular, analysing the relationship between the value of $f(T)$ (Equation 5.5) calculated for T_{end} and the relative sensitivity index S (Equation 5.7), nonlinear changing rates are found for every functional group. As an example, Figure 5.6 illustrates these effects for the benthivorous nekton group (BFD).

Table 5.3: Temperature – Search Rate function parameters

	Group	T_{opt} (°C)	T_{max} (°C)	c	T_{optC} (°C)	$T_{\text{opt}}/T_{\text{optC}}$
1	BFT	21.21	25.80	0.7	24.00	113%
2	NFD	13.63	23.00	0.4	14.43	106%
3	NFI	25.55	28.34	0.7	27.00	106%
4	CPH	13.65	25.60	0.4	NA	
5	FFS	8.76	23.00	0.4	15.74	180%
6	BFD	18.90	24.02	0.4	18.71	99%
7	BFI	21.21	25.80	1.0	NA	
8	PLT	19.94	27.69	0.7	18.39	92%
9	PLI	26.85	28.32	0.7	25.00	93%
10	MOP	10.79	23.00	0.4	NA	
11	MOI	22.02	25.82	1.0	NA	
12	MMF	14.73	23.00	0.4	NA	
13	MMI	21.11	26.55	1.0	NA	
14	MFF	13.16	23.87	0.4	NA	
15	MFI	18.28	25.63	1.0	NA	
16	PEC	9.29	23.00	0.4	12.44	134%
17	VEN	8.86	23.00	0.4	NA	
18	MZP	16.67	25.38	0.7	NA	
19	MPI	22.46	25.82	1.0	NA	
20	MDT	11.83	23.00	0.4	NA	
21	MDI	23.64	28.37	1.0	NA	
22	MHR	8.76	23.29	0.4	NA	
23	MHI	23.36	27.08	1.0	NA	
25	JEL	21.21	28.37	0.7	NA	
26	JEI	22.15	25.17	0.7	NA	
27	MZI	23.64	26.29	0.7	NA	

Analysing the MTI from the +1°C scenario made it possible to highlight the model capabilities to discern the prevalence of climate-related or food-web related effects in influencing the results for each group. Plotting the relative biomass variation index against the normalised MTI index (Figure 5.7), 3 different groups could be detected:

A) Those with high biomass variation, but little affected by trophic effects, which were mainly dependent from temperature;
B) Those with little biomass variation, but with significant trophic interactions, which were mainly influenced by the food-web rather than by the temperature;
C) Those that showed mixed effects.

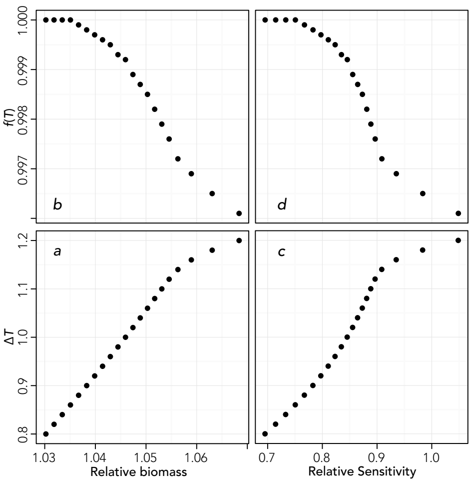

Figure 5.6: Relationship between T increase and relative biomass (a), forcing and relative biomass (b), T increase and relative sensitivity (c) and forcing and relative sensitivity (d) for the Benthic Feeders group (BFD).

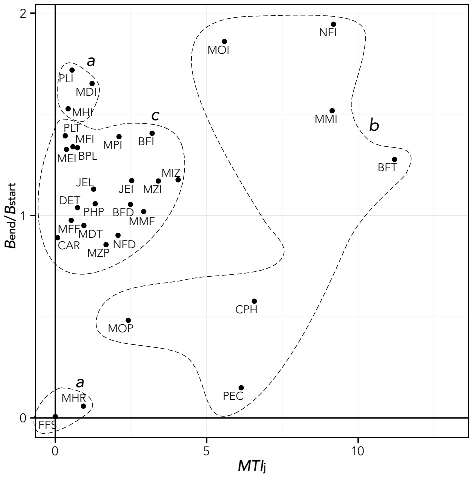

Figure 5.7: Relationship between relative biomass variation and relative impact index for all the trophic groups.

The results of sensitivity tests on the parameters of $f(T)$ (Equation 5.5) are illustrated in Figure 5.8. Variability in the parameters translates in a variability of the relative biomass estimated by the model, which is generally significant but not disproportionate, rarely exceeding ±30% of the median value. Moreover, medium-high TL groups were shown to be more sensitive than low TL groups, and autochthonous groups proved more sensitive than invasive groups.

SST increase scenarios

Figure 5.9 shows the results of the simulations based on the SST increase scenarios on autochthonous and invasive functional groups respectively. The effects on the autochthonous groups are mixed, reflecting the complex food-web interactions driving the system, as well as the different temperature requirements and tolerance of the various groups. Thus, while some groups suffer extremely negative impacts, to the point of extinction (CPH, FFS, MOP, PEC, VEN, MHR), others are less affected (NFD, BFD, MMF, MFF), and some show a biomass gain (BFT, PLT, MEI, JEL, MIZ, BPL). The phytoplankton raise scenario produces, in comparison, more significant gains and less drastic drops, while in the phytoplankton decrease scenario

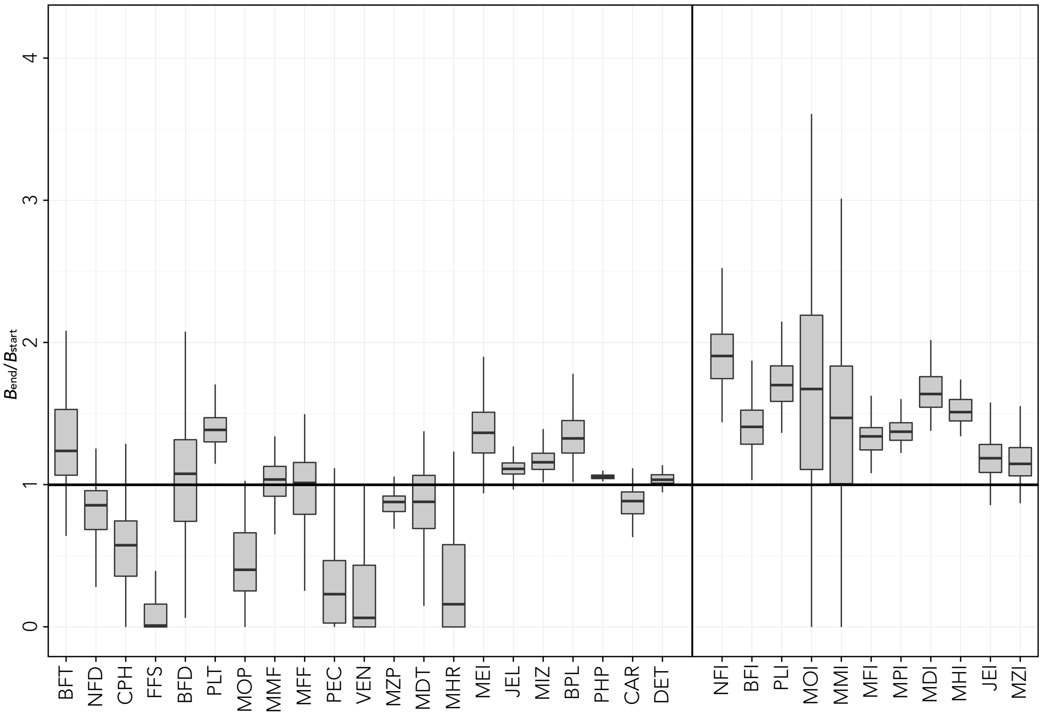

Figure 5.8: Results of the sensitivity tests on the *f(T)* parameters, in terms of relative biomass variation range for the functional groups. Autochthonous groups on the left, invasive groups on the right.

all groups undergo a biomass reduction, which is severe in most cases. Invasive groups show a simpler pattern, with all groups increasing their biomass at the end of the simulation. This effect is more significant when considering a phytoplankton increase, while a decrease in primary production tends to have a negative effect even on these groups.

When a phase of adaptation of the autochthonous groups to the temperature raise is taken into the account, biomass variations are somewhat less than those registered in the no-adaptation scenario. However, due to trophic interactions, there are some exceptions to this, particularly when phytoplankton variations are considered.

Effects on fisheries reflect the biomass variations in the target groups.

Interannual variability (Figure 5.10) affects the results only little, highlighting the robustness of the model.

Finally, if the forcing function is applied only to indigenous groups, biomass variations don't change significantly when compared to previous cases.

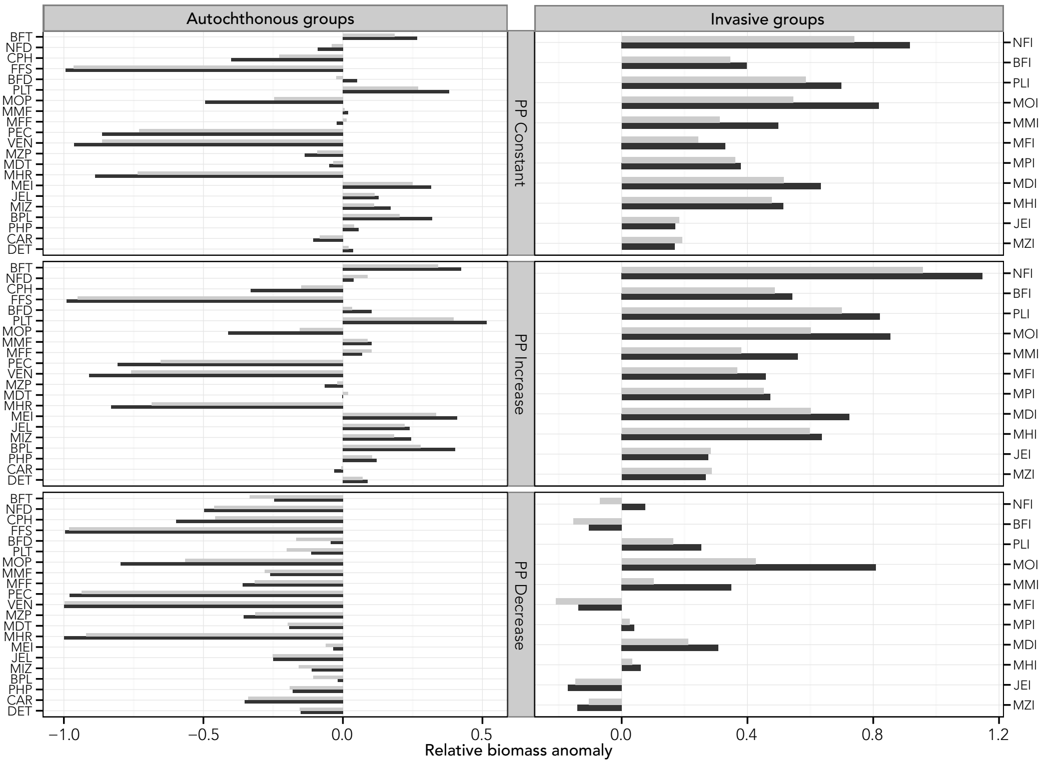

Figure 5.9: Results of the simulations based on the SST increase scenarios, in terms of relative biomass anomaly. Black bars indicate scenarios considering an adaptation phase for autochthonous groups, grey ones represent scenarios not considering it.

Ecosystem indices

The ecosystem indices time trends obtained from the SST increasing simulations are shown in Figure 5.11. The Kempton's Q index (Figure 5.11*a*) shows a common trend in all cases, which can be described as follows:

1. an initial steady raise, more pronounced when not considering the adaptation phase for indigenous groups;
2. a maximum attained after the forcing function stops acting; the peak is reached quickly in scenarios without adaptation phase, and significantly later when the adaptation is considered;
3. a drop, after which the index stabilises along a plateau.

Shannon's diversity index (Figure 5.11*b*) follows a seemingly opposite trend:

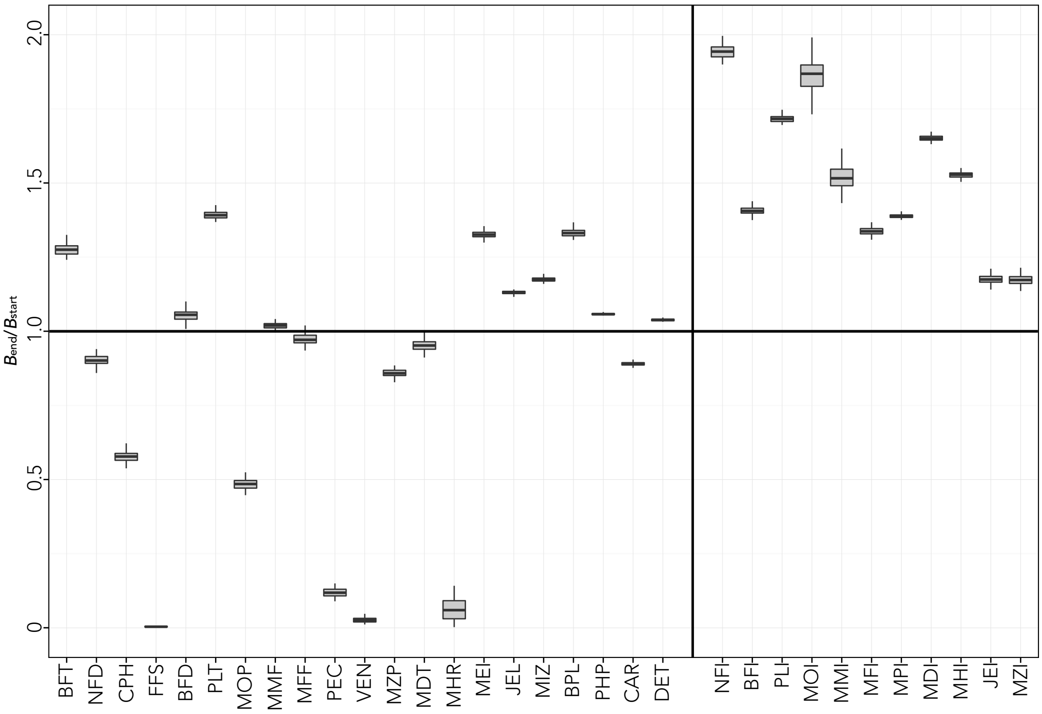

Figure 5.10: Results of the simulations based on the SST increase scenarios considering an interannual variability component, in terms of relative biomass variation range for the functional groups. Autochthonous groups on the left, invasive groups on the right.

1. an initial moderate drop, becoming steeper while the forcing is applied; in this case too, the drop is more pronounced when no adaptation phase is considered;
2. a plateau reached after the forcing function stops acting.

Finally, the trend of the $cumB - TL$ steepness curve (Figure 5.11*c*) can be distinguished as follows:

1. in the case of the application of the temperature forcing alone, and with the addition of the phytoplankton raise, the index initially decreases, but the trend is inverted towards the end of the forcing application period, and a plateau is reached afterwards:
2. in the phytoplankton decrease scenarios, the initial drop is far more pronounced, and is not followed by a significant rebound, resulting in a stabilisation around values much lower than the initial ones.

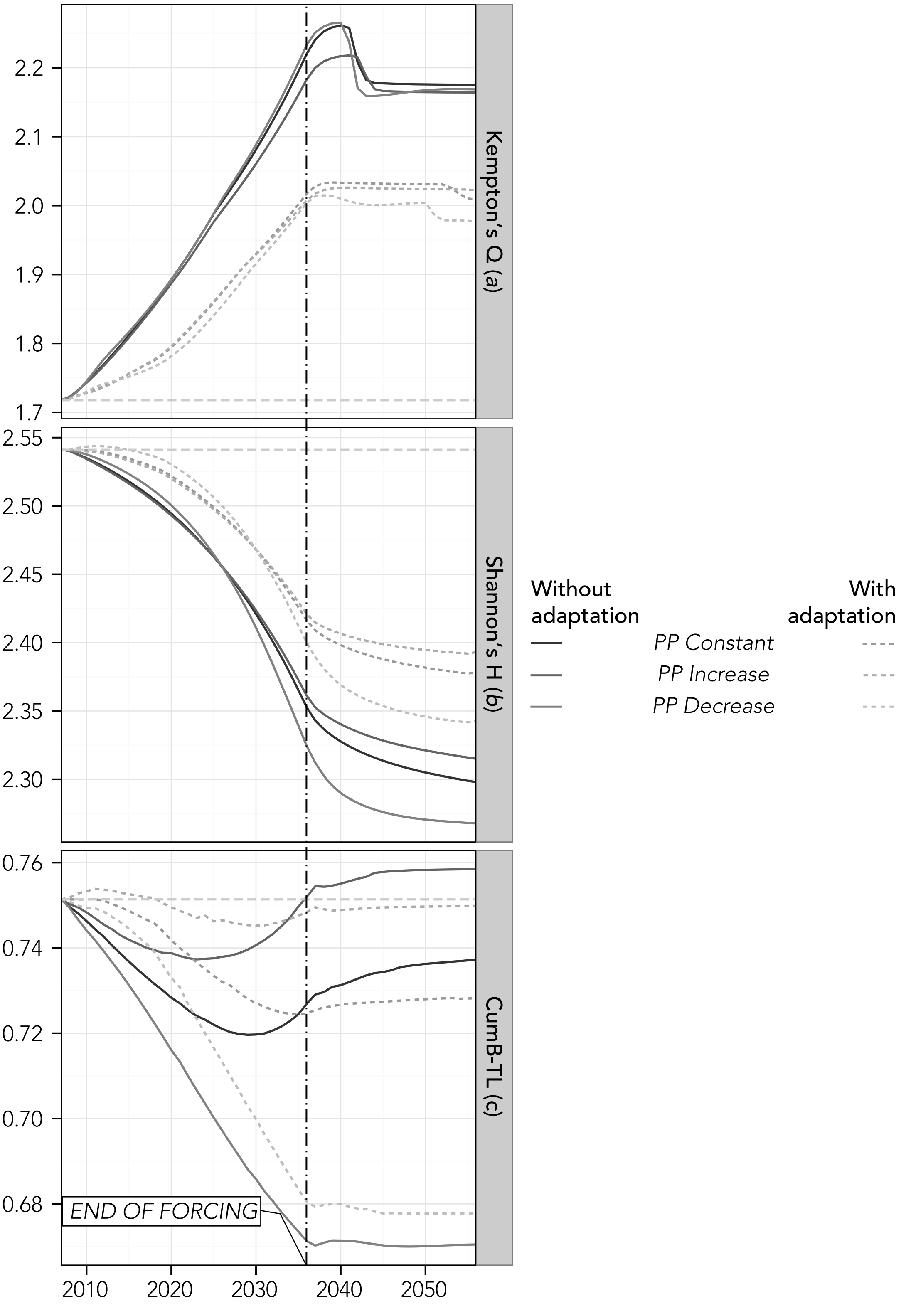

Figure 5.11: The ecosystem indices time trends obtained from the SST increasing simulations.

5.4 Discussion

5.4.1 Food-web and ecosystem structure

Data availability played a major role in the building of the food-web model, and this led to the exclusion of some component from the system (for example, marine mammals, seabirds, and the recreational fishery). However, globally all most relevant functional groups have been represented, and for many of these it has been possible to identify a matching group of invasive thermophilic species. Moreover, the quality of the data was good enough to produce a pedigree index of 0.6. This allowed to perform detailed analysis of the potential impacts of these invasive species in a scenario of climate warming.

Results regarding trophic flows are in line with those highlighted by other EwE models for the Northern Adriatic Sea [64, 65], while differences emerge with other areas of the Mediterranean Sea because of the very high contribution of consumption to TST, and of the almost negligible proportion of the respiratory flows [66–68] (Figure 5.2). Most notably, the composition of TST differs substantially from the results of the model used as the base for the present work, showing a substantially closed system, dominated by consumption flows, in contrast with the open one in which detritus played a major role described by Zucchetta [44] and Pranovi & Link [45] for the 1990s. This could mean that either limitations in the available data along with design choices dictated by the specific purposes of that model contributed to an anomalous output, as noted by the author himself [44], or that the dynamics of the system have changed considerably over a decade. The fact that the results of other works also based on 1990s data are congruent with those presented here apparently opposes this hypothesis, but it retains some validity nonetheless, since the areas covered by the models aren't completely coincident, and some changes in the drivers affecting the system have actually taken place [53]. Moreover, the proportions of trophic flows differ also with those found for the Miramare MPA [69, 70], which is located in the Gulf of Trieste, in the northernmost corner of the northern Adriatic Sea. In this case, however, the differences are easily explained with the peculiarities associated with an MPA, which is necessarily a very small area in open exchange with the surrounding waters, and thus naturally subject to significant export flows.

In terms of flows and biomasses, it is clear from the Lindeman Spine diagram (Figure 5.3) that TL II is the most important, contributing for more than 40% to the TST, and for about 50% to the total living biomass of the system. This means that the Northern Adriatic ecosystem is dominated by low TL planktonic and macrobenthic invertebrate groups. Mean TEs match the 10% value usually found in literature [71], and they highlight a good coupling between these invertebrates and their predators. In more detail, the decrease of TE values from TL II to IV, due to the inefficiencies along the food chain, is in accordance with ecological theory, but its increase between levels IV and V is not. This phenomenon can be detected in the other northern Adriatic models as well [44, 64, 65], an can be related to the effects of the fishing activity [72]. This is confirmed by the fact that such discontinuity in TE is absent in the Miramare MPA model [69, 70], which obviously doesn't account for fishing.

Analysis of the flows also points out a good bentho-pelagic coupling, mainly because of the strong link between detritus and benthic and pelagic groups, respectively. This is in line with the results of other models of the same area [45, 64], and has been explained with the limited average depth of the basin and its oceanographic features, which drive the nutrient recirculation dynamics. This, as an example, causes a large part of zooplankton production to be directed to detritus, thus sustaining benthic production. On the other hand, a significant part of production from benthic invertebrates also flows into detritus. Furthermore, fishing activity plays a major role in enhancing the bentho-pelagic coupling, since the large amount of discard it generates (CAR group in the model) is only partly directly used as a food by fish and macrobenthic invertebrates, and what remains is converted into detritus. As a matter of fact, a strong bentho-pelagic coupling has been described as a common characteristic of heavily exploited basins [45].

Mean TLs are consistent with those found in Zucchetta [44] for corresponding groups, while it is worth noting that, because of differences in the diet, invasive thermophilic groups don't always have TLs comparable with those of their autochthonous counterparts (for example BFI, MMI and MZI), suggesting that an invasion of NIS wouldn't resolve into a mere overlap of corresponding functional groups.

Groups at the bottom of the trophic web, namely phytoplankton, planktonic invertebrate groups, meiobenthos and herbivorous and detritivorous macrozoobenthos, show impacts on many other groups in the system, highlighting the existence of a bottom-up flow control [73]. Some medium-TL groups have also high impacts on the system (macrobenthic predators and mixed feeders, and, to a lesser extent, planktivorous fish), highlighting the importance of these groups in the analysed food-web, and likely indicating the existence of wasp-waist effects [74, 75]. Nekton feeders impact on the higher portion of the food-web, which comprises both competing species and preys of the group, is also considerable, but it can be considered as minor from a global perspective. Overall however, since, as noted before, the system is dominated by zooplankton and macrobenthos, the prevailing effects controlling the food-web are of the bottom-up type.

According to Libralato *et al.* [62], some keystone groups can be identified (KS_i values close to or greater than 0): PHP, MMF, MOP, MDT and MIZ. Moreover, two of these (MIZ and MMF) are also identified as keystones by the Power *et al.* [63] version of the index, and have low biomasses, pointing to an intrinsic significant effect of those groups on all the others. This confirms the importance of low and medium TL invertebrate groups, and emphasising the crucial ecological role played by macrobenthos [45].

Concerning the fishing activity in the basin, the mean TL of the catch is practically equal to the one found by both Zucchetta [44] / Pranovi & Link [45] and Barausse *et al.* [65] for the 1990s, and lower than the results from Coll *et al.* [64] for the same area and period, which can be explained with the latter model not taking into the account the coastal zone, thus excluding clam harvesting. In facts, the low TL is comparable to the value specified by Pauly and Christensen [71] for coastal areas, and it is to be attributed to the high incidence of invertebrate groups and small pelagic planktivores in the total catch, as well as to the high level of exploitation.

The Primary Production Required to sustain the fishery (PPR%) falls within the range for this type of ecosystem when taking into account the primary producers, but it exceeds the upper limit when considering also detritus, again highlighting the role played in the catch by the venerids group.

The gross efficiency of the fishery is high compared to the models from the 1990s, which in their turn estimated a GE_f value significantly higher than the global average. This, together with the Ecotrophic Efficiency and mortality rate estimates suggest a heavy influence of predators (both natural ones ad the fishery) on the dynamics of the system. Despite this, exploitation rates don't show critical situations for any fished group, with the possible exception of scallops (PEC). This is not surprising since the stock of Pectinidae in the northern Adriatic Sea is overfished, and has been greatly reduced since the early 1990s [76].

Finally, indicators of ecosystem development signal that the northern Adriatic Sea system is at a medium stage of development [77]. For example, the primary production/respiration ratio shows that the energy produced is very efficiently utilised, but the primary production/biomass ratio indicates a considerable level of biomass accumulation. Moreover, the System Omnivory Index is low, pointing to linear tendencies in the food web [37]. Ascendency is comparable to results for other Mediterranean systems and confirms a medium stage of development, and a moderate capacity of resistance to perturbations. This can translate in a medium-high vulnerability to changes in the fishery compartment, but also, more interestingly for the scopes of this chapter, to modifications due to the effects of climate change.

5.4.2 Dynamic simulations

Forecasts based on ecological models are inherently affected by a high degree of uncertainty, due to the high level of approximation implied by model-building, and to the many assumptions which are necessarily made during implementation. Yet, they can constitute a powerful resource in decision-making, by providing useful insight into future scenarios [78]. In studying the effects of introduced species on food-webs, moreover, numerous approaches have been tried, but many of these are retrospective, focusing on the explanation of what already happened, rather than on the assessment of the future consequences of the arrival of new species [79]. Some studies have applied a retrospective approach in Ecopath with Ecosim, comparing models built for periods before the introduction of an alien species in a new environment, and after the new species became established, to assess the possibility of making an accurate prediction in advance [79, 80]. A few attempts have also been made to actually predict the possible consequences of the introduction of an invasive alien species, by directly forcing an increase of its biomass: Pinnegar *et al.* [23] applied this technique to determine the effects on the food-web of the introduction of the predator *Fistularia commersonii* in the Bay of Calvi (Corsica), and Arias-González *et al.* [28] used it to predict the impact of the invasive Indo-Pacific lionfish *Pterois volitans* on the Caribbean reef food-webs. Applications of EwE exist also with regards to the prediction of the effects of climate change on marine food-webs. Ainsworth *et al.* [29] assessed the effects of modifications in various drivers related to climate change (primary productivity, zooplankton community structure, range shifts of species, ocean acidification and deoxygenation) on Northeast Pacific marine food-webs and fisheries, by applying forcing functions to manipulate the predator search rates. However, the forcings were applied to pre-existing models, that weren't built in the first place to account for the introduction of invasive new species, which is very likely in a climate change scenario [2, 4].

In this work, through an approach similar to the one introduced by Ainsworth *et al.* [29], it was possible to demonstrate for the first time the capabilities of using EwE to make predictions about the effects of an invasion of thermophilic alien species driven by climate change.

The estimation procedure for the parameters of the search rate forcing function (equation 5.5) was arbitrary to a certain extent. Nevertheless, considering that the output for the nektonic groups was consistent with the values given by Cheung *et al.* [50], the results of the method can be regarded as satisfying.

The results from sensitivity tests point out the soundness of the model. In particular, the nonlinear effects within the modelled food-web emerging from the analysis of sensitivity to the variability of T are evidence that the output of the simulations conducted using the model is not banal, but it is rather the outcome of complex dynamics, and cannot be inferred from the initial conditions alone. Studying the sensitivity to the parameters of $f(T)$ (equation 5.5), on the other hand, reveals that, while an accurate estimate of these parameters is fundamental, the model is not over-sensitive to small variations, thus allowing for a certain level of approximation. However, despite this general robustness, the sensitivity tests allow also to point out some criticalities: two invasive groups, namely macrobenthic predators and mixed feeders exhibit extreme variability in their biomass at the end of the simulations, depending on the combination of parameters used in $f(T)$. These two groups may require further investigation, in terms of species composition and of temperature dependency, in order to obtain more reliable results from the whole model.

The sensitivity analysis allowed also to investigate the impact of the main drivers affecting the system by studying the MTI index of the functional groups at the end of the simulation period in relation to their biomass variation. This way it was possible to notice that, while the components of the system are subject for the most part to the mixed action of the temperature forcing and of trophic interaction (group *c*, Figure 5.7), many of the components, both autochthonous and invasive, exhibiting a significant biomass variation are actually driven by the food-web dynamics (group *b*): this means that, even if the arrival of new species, such as nektonic predators, may be due to changes in the climatic conditions of the area, the success of a possible invasion will depend mostly on the availability of the suitable trophic niche and on the competition with local species. On the other hand, some invasive groups seem to be actually mainly influenced by the temperature driver (group *a*).

In the simulations using the SST raise projections based on the IPCC A2 scenario [52] it is possible to distinguish 3 different types of response by the autochthonous groups:

1. Groups that suffer extremely negative impacts: this response is the effect of a group being particularly vulnerable to both drivers affecting the system. All the groups in this category have significant fishery + predation mortality, with 5 out of 6 actually being heavily fished. In addition, each group contains a high proportion of species adapted to cold climates, thus being extremely sensitive to temperature raises.
2. Groups undergoing mild effects: while many of these groups show mortalities comparable with those of the previous case, they are also adapted less strictly to cold climate conditions, which allows them to suffer less severe impacts from the temperature raise. In the case of nektivorous and benthivorous fish, they also benefit from trophic cascades, since their main prey groups show a positive biomass variation.
3. Groups showing positive biomass variations: these groups can be further subdivided in low TL groups, which are not impacted by the fishery and substantially benefit from a reduced natural predation, and high TL groups (BFT and PLT) which, despite being autochthonous, are partly or entirely composed of warm affinity species, thus benefiting directly from the temperature raise.

As noted in section 5.3.5, invasive groups follow a simpler pattern, predictably increasing their biomass at the end of the simulations. It is important to stress, however, that the biomass variations considered are relative, and that the absolute biomasses of the invasive groups remain very low when compared with those of the local ones.

When a phytoplankton raise is introduced, the final output changes little in comparison to the previous case. Basically, the increased primary production tends to favour those groups which already showed a biomass increase or a mild decrease (cases 2 and 3), while groups suffering significant negative impacts perform no better in the presence of more phytoplankton. The opposite situation, when a reduction in phytoplankton is considered, is more interesting since in this case all autochthonous groups undergo a biomass decrease; the impact of an oligotrophication is so significant that many thermophilic groups too show a biomass drop, actually reducing greatly the risk of an invasion. This scenario is of particular importance because, while being the most negative for the marine community and consequently for the fishing activity relying on it, it is also the most likely to happen, since an oligotrophication trend has actually been detected [53].

Further variants introduced in the simulations add little to what has been observed so far, with the exception of the application of the search-rate forcing function to the autochthonous groups only. In this case, the results don't differ significantly from those obtained by applying it to all groups. This means that, while through the analysis of the MTI, some invasive thermophilic groups have been found to be affected mainly by the climatic drivers, the temperature raise has basically the function of opening an invasion window, *i.e.* setting the proper combination of environmental variables, this way creating an 'opening' for invasive species to enter the new region [81]. In this case, the arrival of new organisms in an already vulnerable system (see section 5.4.1) is made possible thanks to the temperature increase creating suitable living conditions for thermophilic species, and most importantly reducing the competition from the local ones. In this context, the invaders have then the possibility to increase their biomass through food-web dynamics. This hypothesis is confirmed when considering the oligotrophication scenarios (Figure 5.9): since in this case the SST warming is not accompanied by an adequate primary production, the invasion window (to stick with this metaphor) presents a narrower opening, into which only some thermophilic species are capable of fitting, so increasing their biomasses.

Finally, the observation of the diversity index trends give contrasting messages at a first glance. In facts, while the diversity seems to raise in all cases according to Kempton's Q, Shannon's index suggests an almost symmetrical diversity drop during time in all cases. This apparent contradiction can depend from the construction of the indexes in relation to the peculiarities of the model described in this work. In more detail, Shannon's diversity index primarily describes changes in evenness, since the number of functional groups in the model is fixed [29], and the results of the model clearly reflect a decrease in evenness since many of the groups showing the most dramatic changes over time are also high-biomass groups. On the other hand, Kempton's index tracks changes in both evenness and richness [29], by describing the slope of the cumulative log abundance curve, where the biomasses of the functional groups serve as proxies for their abundances. To calculate the slope, the inter-quartile portion of the sigmoid curve is considered, in order to avoid problems arising from the inclusion of tails [55]. In the present case, where a part of the system is made of very low biomass groups (the invaders) and the rest is constituted of high-biomass ones (the autochthonous groups), excluding the tails causes the index to raise during time, since invasive groups may enter the interquartile range of the curve because of their increasing biomass, but especially because the autochthonous groups enter it too while their biomass decreases.

Thus the two indexes are probably showing the same phenomenon from different perspectives, and the result is a drop in the diversity caused by a decrease in the biomasses of autochthonous groups which is not balanced by the raise in the invading thermophilic ones, ultimately translating in a net biomass decline and in a more vulnerable system in all scenarios. This is further confirmed when the trend of the steepness of the $cumB - TL$ curve is considered. In accordance with the stress-stretching theory [57, 58], its decrease in 5 out of 6 scenarios is evidence of an increasing importance of intermediate TLs in the system, related to the net biomass drop in high-TL local group which is not compensated by a rise in invasive ones. This effect, again, is more dramatic in the oligotrophication scenarios.

Reading through the results of Ecosim simulations, the assumptions, and consequently the limitations, underlying the method have to be taken into careful consideration [23]. For instance, Ecosim shares the mass-balance assumption with Ecopath, which may be no longer verified when making simulations far into the future [40]. Moreover, the longer the term of a simulation, the higher the probability of unpredictable exogenous factors perturbing the system, such as deviations of the temperature from the predicted trend, arrival of different new species or variations in the fishing pressure.

Keeping all this in mind, with this work it was possible to provide a useful insight into the dynamics which can drive an invasion of thermophilic species in the northern Adriatic basin under climate change, and given some hint about the direction towards which the system can be expected to evolve. In conclusion, results from the simulations seem to show that the northern Adriatic ecosystem may be heading towards an impoverishment in terms of biomass and diversity, affecting especially functional groups targeted by the commercial fishery. Considering that the worst-case scenario, with a reduction in primary production occurring, is the most likely to happen, may also mean that in the near future a consistent management effort will be required, and the main focus of it will not be in dealing with changes in the composition of community, but rather with a reduction of the resources.

Table S. 5.1: List of the functional groups included in the Ecopath model, detailing the species composition and the sources used to derive the basic input parameters.

Functional group	Original value		Source	Species
1 – Bluefin Tuna (BFT)				*Thunnus thynnus*
Biomass	0.1	t/km^2	[82]	
P/B	0.43	y^{-1}	[83]	
Q/B	3.93	y^{-1}	[47]	
2 – Nekton Feeders (NFD)				*Alopias vulpinus, Belone belone, Conger conger, Dicentrarchus labrax, Lichia amia, Lophius piscatorius, Merlangius merlangius, Merluccius merluccius, Mustelus asterias, Sarda sarda, Sciaena umbra, Scyliorhinus canicula, Squalus acanthias, Xyphias gladius, Zeus faber*
Biomass	1.35	t/km^2	[84, 85]	
P/B	0.57	y^{-1}	[86]	
P/Q	0.27		[45]	
3 – Nekton Feeders Invasive (NFI)				*Coryphaena hyppurus, Pomatomus saltatrix, Sphyraena viridensis*
Biomass	0.01	t/km^2		
P/B	2.5	y^{-1}	[87]	
Q/B	9.34	y^{-1}	[47]	
4 – Cephalopods (CPH)				*Alloteuthis media, Eledone moschata, Loligo vulgaris, Octopus vulgaris, Sepia officinalis, Sepiola rondeletii, Todarodes sagittatus*
Biomass	0.51	t/km^2	[84, 85]	
P/B	1.68	y^{-1}	[87]	
P/Q	0.3		[45]	
5 – Flatfish (FFS)				*Platichthys flesus, Psetta maxima, Scophthalmus rhombus, Solea solea*
Biomass	0.23	t/km^2	[84, 85]	
P/B	1.47	y^{-1}	[86]	
P/Q	0.2		[45]	
6 – Benthic Feeders (BFD)				*Cepola macrophtalma, Gobius niger, Lithognathus mormyrus, Mullus barbatus, Mullus surmuletus, Ophidion barbatum, Pomatoschistus minutus, Sarpa salpa, Sparus aurata, Trisopterus minutus capelanus, Umbrina cirrosa, Zosterisessor ophiocephalus*
Biomass	0.88	t/km^2	[84, 85]	
P/B	1.57	y^{-1}	[86]	
P/Q	0.32		[45]	
7 – Benthic Feeders Invasive (BFI)				*Pagrus major*
Biomass	0.01	t/km^2		
P/B	0.59	y^{-1}	[88]	
Q/B	5.27	y^{-1}	[88]	
8 – Planktivorous fish (PLT)				*Boops boops, Engraulis encrasicolus, Sardina pilchardus, Scomber colias, Scomber scombrus, Sprattus sprattus*
Biomass	8	t/km^2	[84, 85]	
P/B	1.65	y^{-1}	[86]	
P/Q	0.33		[45]	
9 – Planktivorous fish Invasive (PLI)				*Sardinella aurita*
Biomass	0.01	t/km^2		
P/B	1	y^{-1}	[64]	
Q/B	9.5	y^{-1}	[47]	
10 – Macrobenthic Predators (MOP)				Asteroidea, Decapoda, Gastropoda, Polychaeta, Stomatopoda
Biomass	2.48	t/km^2	[84, 85, 89]	
P/B	4.96	y^{-1}	[90]	
P/Q	0.4		[45]	
11 – Macrobenthic Predators Invasive (MOI)				*Callinectes sapidus, Marsupenaeus japonicus, Rapana venosa*
Biomass	0.01	t/km^2		
P/B	2.5	y^{-1}	[91]	
Q/B	12.5	y^{-1}	[91]	
12 – Macrobenthic Mixed-Feeders (MMF)				Crustacea, Gastropoda, Ophiuroidea, Polychaeta
Biomass	1.62	t/km^2	[89]	
P/B	9.22	y^{-1}	[90]	
P/Q	0.2		[45]	

Table S. 5.1: (continued) List of the functional groups included in the Ecopath model

Functional group	Original value		Source	Species
13 – Macrobenthic Mixed-Feeders Invasive (MMI)				*Halgerda willeyi, Hemigrapsus sanguineus*
Biomass	0.01	t/km^2		
P/B	2.5	y^{-1}	[92]	
Q/B	8.5	y^{-1}	[92]	
14 – Macrobenthic Filter-Feeders (MFF)				Bivalvia, Crustacea, Polychaeta
Biomass	3.13	t/km^2	[89]	
P/B	4.77	y^{-1}	[90]	
P/Q	0.2		[45]	
15 – Macrobenthic Filter-Feeders Invasive (MFI)				*Anadara inaequivalvis, Anadara transversa, Ficopomatus enigmaticus, Musculista senhousia, Saccostrea commercialis*
Biomass	0.01	t/km^2		
P/B	3	y^{-1}	[93]	
Q/B	30	y^{-1}	[93]	
16 – Pectinidae (PEC)				*Aequipecten opercularis, Pecten jacobeus*
Biomass	0.23	t/km^2	[84, 85]	
P/B	0.8	y^{-1}	[94]	
P/Q	0.2		[45]	
17 – Veneridae (VEN)				*Chamelea gallina, Venus verrucosa*
Biomass	3.5	t/km^2	[95]	
P/B	1.41	y^{-1}	[96–98]	
P/Q	0.2	y^{-1}	[45]	
18 – Mesozooplankton (MZP)				Crustacea
Biomass	2.1	t/km^2	[99]	
P/B	20.87	y^{-1}	[100]	
P/Q	0.2		[45]	
19 – Mesozooplankton Invasive (MPI)				*Arietellus pavoninus*
Biomass	0.01	t/km^2		
P/B	39.08	y^{-1}	[101]	
Q/B	80	y^{-1}	[101]	
20 – Macrobenthic Detritivores (MDT)				Crustacea, Gastropoda, Holoturoidea, Polychaeta, Sipunculida
Biomass	4.73	t/km^2	[89]	
P/B	7.46	y^{-1}	[90]	
P/Q	0.2		[45]	
21 – Macrobenthic Detritivores Invasive (MDI)				*Bursatella leachii*
Biomass	0.01	t/km^2		
P/B	1.03	y^{-1}	[102]	
Q/B	4.41	y^{-1}	[102]	
22 – Macrobenthic Herbivores (MHR)				Crustacea, Echinata, Gastropoda, Polychaeta
Biomass	0.8	t/km^2	[89]	
P/B	7	y^{-1}	[90]	
P/Q	0.2		[45]	
23 – Macrobenthic Herbivores Invasive (MHI)				*Aplysia dactilomela, Haminoea callidegenita, Siphonaria pectinata*
Biomass	0.01	t/km^2		
P/B	3	y^{-1}	[103]	
Q/B	15	y^{-1}	[103]	
24 – Meiobenthos (MEI)				Crustacea, Echinata, Gastropoda, Polychaeta
Biomass	4	t/km^2	[104, 105]	
Q/B	68.52	y^{-1}	[106]	
P/Q	0.2		[45]	

Table S. 5.1: (continued) List of the functional groups included in the Ecopath model

Functional group	Original value		Source	Species
25 – Jellyfish (JEL)				
Biomass	1.9	t/km^2	[89]	*Pelagia noctiluca*
P/B	14.6	y^{-1}	[107]	
Q/B	50.48	y^{-1}	[107]	
26 – Jellyfish Invasive (JEI)				*Mnemiopsis leidyi, Carybdea marsupialis, Clytia hummelincki, Arctapodema australis, Niobia dendrotentaculata*
Biomass	0.01	t/km^2		
P/B	8.43	y^{-1}	[101]	
Q/B	25.3	y^{-1}	[101]	
27 – Macrozooplankton Invasive (MZI)				
Biomass	0.01	t/km^2		*Pontodora pelagica, Thalia orientalis*
P/B	18	y^{-1}	[108]	
Q/B	38	y^{-1}	[108]	
28 – Microzooplankton (MIZ)				
Biomass	0.85	t/km^2	[99]	
P/B	219	y^{-1}	[100]	
P/Q	0.5		[45]	
29 – Bacterioplankton (BPL)				
Biomass	2.5	t/km^2	[99]	
Q/B	34.35	y^{-1}	[109]	
P/Q	0.2		[45]	
30 – Phytoplankton (PHP)				
Biomass	4.85	t/km^2	[89]	
Q/B	152.13	y^{-1}	[110, 111]	
31 – Carcass (CAR)				
Biomass	23	t/km^2	[46]	
32 – Detritus (DET)				
Biomass	5.5	t/km^2	[112]	

Table S. 5.2: Diet composition matrix for the consumer groups

		Predator Groups																												
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Prey Groups	1 BFT																													
	2 NFD	9.99%	9.99%	19.99%																										
	3 NFI	0.01%	0.01%	0.01%																										
	4 CPH	22.00%	13.00%	4.00%	3.00%			5.00%																						
	5 FFS	8.00%	3.00%																											
	6 BFD	20.00%	15.00%	4.99%			1.99%	9.99%																						
	7 BFI	0.10%	0.03%	0.01%			0.01%	0.01%																						
	8 PLT	39.80%	49.90%	69.85%	9.99%	2.99%		19.95%																						
	9 PLI	0.10%	0.10%	0.15%	0.01%	0.01%		0.05%																						
	10 MOP		0.96%		44.90%	13.98%	13.98%	13.98%			1.99%	1.99%		1.90%																
	11 MOI		0.01%		0.10%	0.02%	0.02%	0.02%			0.01%	0.01%		0.10%																
	12 MMF			0.99%	12.98%	7.99%	9.99%	19.97%			4.99%		3.96%	5.90%																
	13 MMI			0.01%	0.02%	0.01%	0.01%	0.03%			0.01%		0.01%	0.10%																
	14 MFF				1.99%	4.99%	13.98%	4.99%			4.99%	4.99%	10.00%	26.80%																
	15 MFI				0.01%	0.01%	0.02%	0.01%			0.01%	0.01%		0.20%																
	16 PEC						1.00%																							
	17 VEN																													
	18 MZP					9.99%	0.99%		11.90%	15.98%		1.99%			3.00%	8.99%	4.99%	4.99%								34.90%	54.00%	59.70%		
	19 MPI					0.01%	0.01%		0.10%	0.02%		0.01%				0.01%	0.01%	0.01%								0.10%	1.00%	0.30%		
	20 MDT		7.99%		18.97%	49.90%	44.90%	7.99%			45.90%	86.70%	13.00%	52.70%																
	21 MDI		0.01%		0.03%	0.10%	0.10%	0.01%			0.10%	0.30%	0.02%	0.30%																
	22 MHR				7.99%	9.99%	9.99%	3.99%				2.98%	5.00%	11.80%																
	23 MHI				0.01%	0.01%	0.01%	0.01%				0.02%	0.01%	0.20%																
	24 MEI								3.00%		2.00%		18.00%								10.00%		2.50%							
	25 JEL							13.98%																		4.99%	4.99%			
	26 JEI							0.02%																		0.01%	0.01%			
	27 MZI								0.10%			1.00%																		
	28 MIZ								83.90%	83.00%					30.00%	30.00%	30.00%	30.00%	15.00%							30.00%	25.00%	30.00%		3.00%
	29 BPL														10.00%	5.00%	5.00%	5.00%	15.00%											1.00%
	30 PHP								1.00%	1.00%					56.00%	56.00%	59.00%	55.00%	70.00%	100.00%		20.00%	2.50%	100.00%		15.00%		10.00%	100.00%	1.00%
	31 CAR						3.00%				40.00%		20.00%								5.00%									
	32 DET												30.00%		1.00%		1.00%	5.00%			85.00%	80.00%	95.00%		100.00%	15.00%	15.00%			95.00%

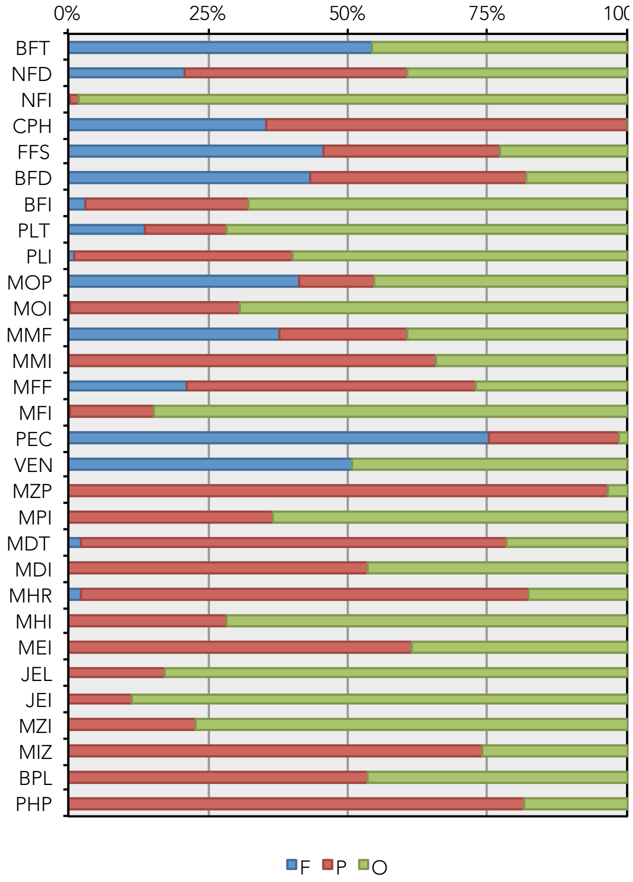

Figure S. 5.1: Distribution of the mortality rates. F=Fishing, P=Predation, O=Other.

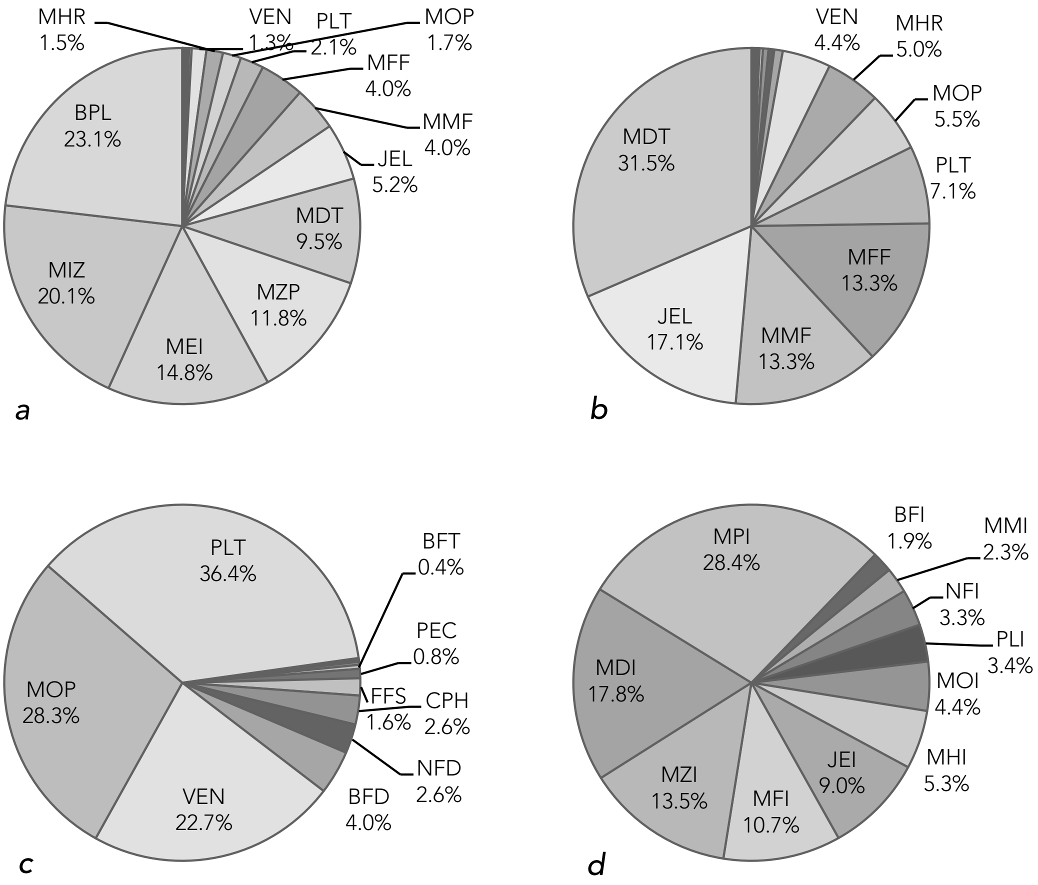

Figure S. 5.2: Main partitioning of (a) total consumption of production, (b) total consumption excluding zooplankton and benthic invertebrates, (c) total consumption of fished groups and (d) total consumption of invasive groups).

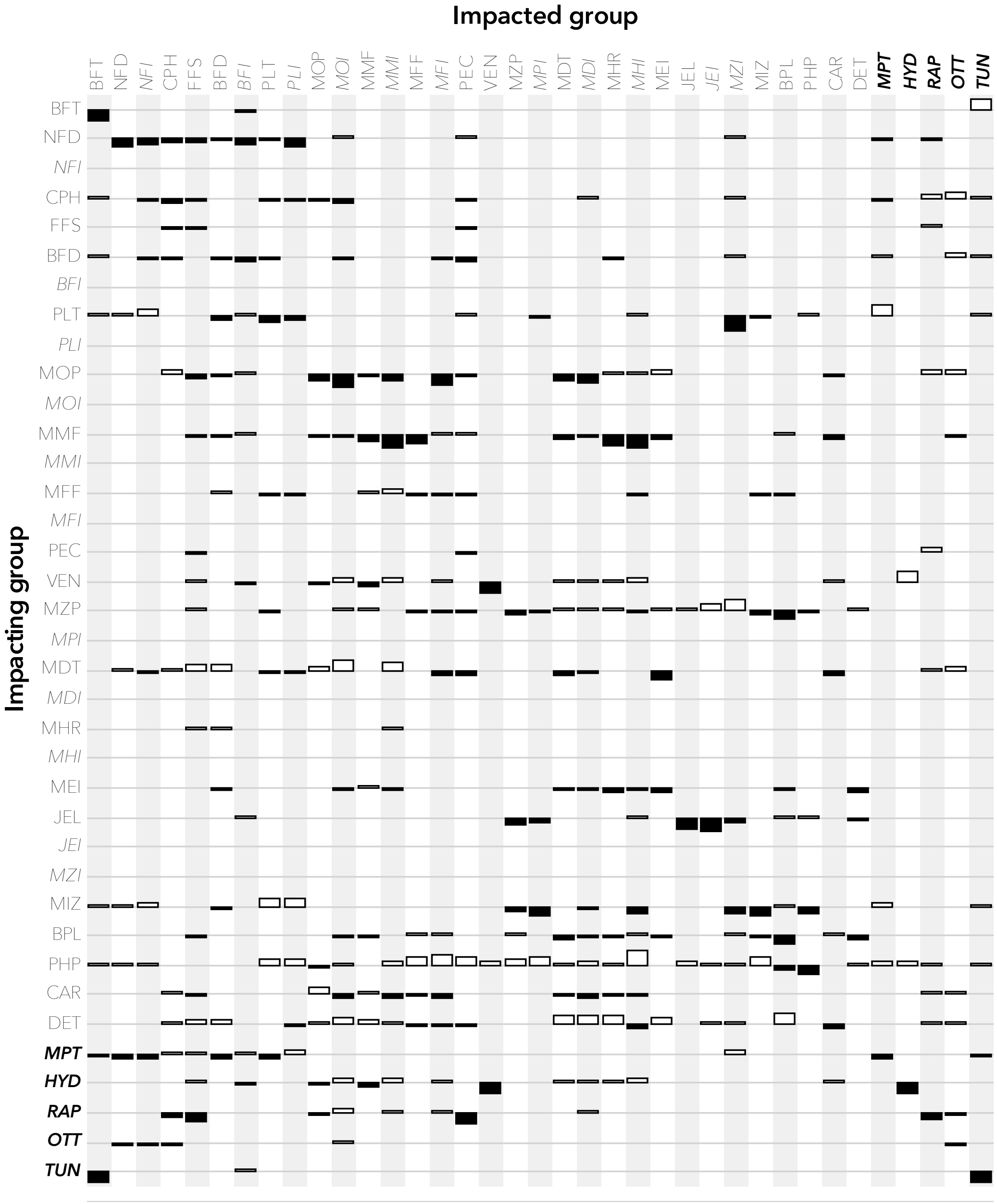

Figure S. 5.3: Mixed Trophic Impact analysis. The bars indicate relative impact.

Chapter 6

Conclusions

The key hypothesis around which this work revolved was the possibility of investigating the effects of climate change over the Mediterranean nektonic communities by focusing on the northern Adriatic basin, since this area presented, in theory, all the characteristics to be regarded as an hotspot in this perspective.

The first step in this direction was thus to validate such an hypothesis by gathering the available knowledge about how biological communities reflected the climatic peculiarities of the area. This allowed to define a baseline against which early signs of climate-related modifications of the communities could be detected. What emerged was the existence of a very 'boreal enclosure', whose communities, both terrestrial and marine, are characterised by the presence of elements typically associated with cold-temperate climates. This was indirectly implied by the findings of early studies, that characterised the area as the 'Venetian Lacuna' [1–5], referring to the attenuation of Mediterranean features. In particular, it was highlighted the presence of plant communities, as well as terrestrial and marine animal species typically found along the northern Atlantic coasts of Europe, that in some cases can be considered as endemic in the Mediterranean context. These species often exhibited phenological adaptations in response to the extreme climatic conditions found close to the limits of their respective distributional ranges. This alone proves well enough the fragility of the northern Adriatic ecosystem, since even slight climatic modifications could severely impact species already subject to limit conditions, potentially disrupting important ecological processes and leading to completely new equilibriums [6–18]. In addition, time-series analysis clearly showed that the area is presently experiencing modifications that can be related to climate change, with a raise in temperatures (in the form of a disappearance of the 7°C winter SST isotherm, which historically drew the boundaries of the so-called lacuna [5]), associated with a NIS diffusion in the terrestrial plant communities, and, more strikingly, with a clear change in the composition of the nektonic assemblage, in favour of warm-climate related species. What is more, those species that were identified as glacial relicts of boreal affinity, and endemic for the northern Adriatic, exhibited during time phenological shifts, as well as biomass reductions, that, while certainly tied also to other factors, can be regarded as adaptations to a warming environment.

In synthesis, the picture that emerged from this study was that of a biodiversity hotspot [19], particularly sensitive to early signs of climate change, and for this reason well suited to be used as a case study for detecting the possible impacts that may affect the whole Mediterranean basin. What also emerges clearly, though, is that, because of this very sensitivity to climate, united to the typical anthropogenic factors associated with a well-developed coastal area, the system presents an extreme vulnerability to further modifications.

Such a vulnerable system requires managing, and in order to devise effective management strategies, a detailed understanding of the dynamics going on in the system is necessary. The study on the artisanal fishery in the Venice lagoon provided a first insight on these dynamics. Besides uncovering the importance of artisanal fisheries and of the vast ecological knowledge they imply as a means to support local diversity and resource sustainability [20–22], it also allowed to describe the impacts of climate change over the nektonic assemblage. These were evident in the simultaneous and opposing regime shifts registered in the water temperature and in the fishery landings, and in the significant negative relationships tying the landings of several local species (particularly those constituting glacial relicts) with the mean annual temperature. Also, while the fact that no warm-affinity species were found to be present is a sign of a good underlying resilience of the lagoon system, the negative temporal trend of both cold and temperate affinity species confirms the vulnerability to climate change.

The study of the vulnerability of the northern Adriatic Sea completed the picture. By introducing a synthetic indicator that provides a measure of both the suddenness of the transition from the cold to the warm season as well as of the annual temperature raise, based on the slope (s) of the sigmoidal monthly mean SST curve, it allowed to disentangle the climatic impacts from the other drivers that may influence the biomasses of nektonic species, and ultimately fishery landings [23, 24]. Thus it was possible to prove the statistically significant negative impact of climate drivers on fishery catch, whose declining trend had already been described also for the Venice lagoon, where it was found to be significantly related to temperature. Moreover, differentiating the landings based on the climatic affinity of the species and on the different métiers helped to describe in further detail the drivers acting on the system, leading to two major findings:

1. Species of different climatic affinity aren't influenced by climate drivers in the same way: the negative relationship between the s indicator and landings is stronger for temperate affinity species than for the cold group, while warm affinity species show no correlation

at all.

2. Fishery landings at present are almost entirely composed of species of cold and temperate affinity, with the latter group representing the larger part of the catch, while warm species play a negligible role; moreover, the three main métiers catch the different climatic affinity groups in different proportions.

This, in turn, made it possible to highlight two main aspects of the vulnerability of the northern Adriatic system, and in particular of the fishery:

1. The shifting climatic regime is inducing deep modifications in the nektonic community, reducing the biomass of native species, particularly of the temperate affinity ones; this is accompanied by a steady increase in the incidence of thermophilic alien species, which are able to colonise the system not as a direct consequence of the warmer temperatures, but possibly because of the opening of an 'invasion window' [6]. The appearance of new species, however, doesn't seem to be likely to counterbalance the loss in biomass of the autochthonous ones.
2. While modifications in the nektonic community may not constitute a relevant threat to the fishery by itself, since fisheries have generally shown the capacity to adapt to changes in the exploited communities [23, 25], with examples to be found even in the northern Adriatic area [26], still it will have to face a general decrease in resources, since, as noted before, the main target species don't seem likely to be replaced by new ones in terms of biomass.

Having determined the capabilities of the northern Adriatic Sea to provide early signs of the effects of climate change in the Mediterranean, and having assessed the vulnerability of the ecosystem and of human activities alike related to this high sensitivity, the construction and application of a dynamic food-web model allowed a better understanding of the processes driving the system, and made it possible to give a hint about the possible scenarios that may develop. The choice of building such a model, despite the considerable amount of uncertainty inherently affecting its results because of the high level of approximation and of the many assumptions required by the implementation process, was dictated in facts by the useful insights into the system dynamics and the future scenarios it could provide [27]. Moreover, it must be noted that the model constituted the first attempt at representing the effects of climate change on a community in Ecopath with Ecosim, at the same time simulating the introduction and potential invasion of new non-indigenous thermophilic species [28], thus adding to the value of the results.

From an ecosystem structure and functioning perspective, results from the model described a benthos-dominated system, substantially subject to a bottom-up type of control, as can be expected from a shallow marine environment [29]. The system is subject to a significant but not critical level of exploitation by the fishery compartment. Most notably, the model confirmed the observations previously made about the vulnerability, picturing an ecosystem at an intermediate stage of development [30], with a moderate capacity of resistance to perturbations, which translates in a considerable vulnerability both to fishery impacts and to climate change effects.

The consequence of this was shown by the dynamic simulations according to temperature raise scenarios, which ultimately confirm the hypotheses made when analysing the vulnerability of the northern Adriatic Sea fishery to climate change, prospecting an impoverishment in terms of biomass and diversity, particularly in those functional groups mostly targeted by commercial fisheries, with invasive species incrementing their presence in the basin thanks to the availability of an 'invasion window' created by the reduced competition with autochthonous groups, but failing to counterbalance the loss in biomass.

These results make clear the need for management efforts. In dealing with the effects of climate change, which are mostly inevitable at least in the short and medium term, the two main strategies for an effective management become mitigation and adaptation [25, 31], and in a marine ecosystem, one of the few ways to attain these goals is by reducing the fishing mortalities. The means to do so are many, ranging from livelihood diversification measures for people presently employed in the fishery, to vessel buybacks, to restriction on some gear types [25]. The latter option can prove interesting in the present case, since midwater pair trawl has been shown to exert a particularly significant impact over the segment of the nektonic community most sensitive to climatic drivers. So, a restriction on this métier can help to relieve some pressure from the system, and such a measure wouldn't be too hard to apply, since the vessels employing the midwater pair trawl can easily switch to *rapido* trawls, and already do so in some periods during the year. Another possible way to reduce fishing mortality could be the introduction of protected areas where fishing isn't allowed. These areas would act as refugia, where species would be able to feed, reproduce and survive, thus maintaining vital populations [32]. Similar solutions have already been put into action, and show encouraging results [33]. The effects of both measures could be tested by acting on the fishery compartment in the food web model, so to obtain valuable information about the effectiveness of these actions, and to fine-tune them before the actual implementation.

In order to provide more detailed insight on the ecosystem dynamics related to climate change, the model itself has a wide margin of improvement. Without altering its complexity, which was purposefully kept at an intermediate level to guarantee an adequate degree of synthesis and to produce more general results, it will certainly be possible to enhance it, for example by including functional groups that were left out from the present implementation, such as marine mammals and seabirds. Above all, the accuracy of the results would benefit from the inclusion of the recreational fishery compartment. Recent observations, in facts, lead to believe that for many species the landings from recreational fishing rival, and in some cases outweigh, professional catches [34]. As a consequence, recreational fishing becomes an aspect that cannot be overlooked in an effort towards an effective management of the northern Adriatic ecosystem, and it will require further study. Another significant improvement would come from the application of the Ecospace module in Ecopath with Ecosim [35]. Integrating the spatial component in the model would be possible, for example, by using data from trawl surveys [36], or even by using information from the VMS system to reconstruct the main fishing grounds and commercial species ranges [37, 38], and would add to the realism of the results, as well as making it possible to test the effects of spatially-based management measures like those proposed here.

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Chapter 3: Vulnerability of Artisanal Fisheries to Climate Changes in the Venice Lagoon

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