THE ROLE OF SHARKS IN MARINE ECOSYSTEMS: EVALUATING OVEREXPLOITED MARINE FISH COMMUNITIES TO DETECT LONG-TERM EFFECTS OF PREDATOR REMOVAL

by

Francesco Ferretti

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DEPARTMENT OF BIOLOGY

The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "THE ROLE OF SHARKS IN MARINE ECOSYSTEMS: EVALUATING OVEREXPLOITED MARINE FISH COMMUNITIES TO DETECT LONG-TERM EFFECTS OF PREDATOR REMOVAL" by Francesco Ferretti in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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External Examiner: ____________________

Research Supervisors: ____________________

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Examining Committee: ____________________

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Departmental Representative: ____________________

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Table of Contents

List of Tables

List of Figures

Abstract

Elasmobranchs are among the oldest and most successful predators in the ocean, yet one of the most vulnerable to the direct and indirect effects of fishing. Many populations are rapidly declining around the world, and an increasing number is listed as threatened or endangered. The broader ecosystem consequences of these declines, and whether other marine predators can replace sharks, are open questions. In this thesis, I used a diverse set of data and modeling techniques to analyze long-term changes in elasmobranch populations in the Mediterranean Sea, and the consequences of shark declines on marine ecosystems.

Because of its long history of fishing, the Mediterranean offers a unique perspective on the response of marine communities to exploitation over long time scales. Here, I reconstructed the history of elasmobranch exploitation over the past 200 years in pelagic, coastal and demersal communities. Results were combined meta-analytically to derive a general pattern of change for the entire region. Overall, I detected multiple cases of regional species extirpations, a strong correlation between historical intensity of exploitation and the stage of community degradation, and some cases of compensatory species increases. My results suggest that compared to other marine ecosystems worldwide, the Mediterranean Sea might be in an advanced stage of overexploitation.

To gain more general conclusions about the patterns and consequences of shark declines in the ocean, I reviewed and reanalyzed documented changes in exploited elasmobranch communities around the world, and synthesized the effects of sharks on their prey and wider communities. This work revealed that sharks are abundant and diverse in little exploited or unexploited marine ecosystems but vulnerable to even light levels of fishing. The decline in large sharks has reduced natural mortality in a range of their prey, contributing to changes in abundance, distribution, and behaviour of marine megafauna that have few other predators. In some cases, this has resulted in cascading changes in prey populations and food-web structure. Overall, my thesis greatly enhanced our knowledge about the critical state of elasmobranchs in the Mediterranean Sea and the consequences of the declines of these important marine predators on marine ecosystems.

To my grandfather Graziano, and RAM.

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Chapter 1

Introduction

1.1 The Problem

Chondrichthyans (sharks, rays and chimeras) are one of the oldest and most diverse groups of marine animals. They have evolved about 400 million years ago, have survived several mass extinctions, and undergone numerous adaptive radiations (Compagno 1990; Grogan and Lund 2004). About twelve hundred species have been described in a variety of habitats ranging from near-shore to the abyss in all oceans of the world. In most ecosystems, they are at the top of trophic chains, likely playing an important role in structuring and regulating marine ecosystems.

Although there are biological and ecological differences between species (Smith et al. 1998), most chondrichthyans are characterized by slow growth rate, late sexual maturity and low fecundity, resulting in low rates of biomass turnover (Hoening and Gruber 1990). These characteristics make elasmobranchs extremely vulnerable to current levels of direct and indirect exploitation (Walker 1998).

Over the last fifty years, fishing has increased enormously throughout the world's oceans, depleting many pelagic and coastal fish populations (Jackson et al. 2001; Pauly et al. 2002; Myers and Worm 2003). Large elasmobranchs showed some of the most dramatic declines in the Pacific Ocean (Ward and Myers 2005), Gulf of Mexico (Shepherd and Myers 2005), Northeast (Walker 1998; Stevens et al. 2000; Dulvy et al. 2000) and Northwest Atlantic (Casey and Myers 1998; Baum et al. 2003; Baum and Myers 2004). Yet population changes in one of the longest and most exploited large marine ecosystems, the Mediterranean Sea, have not been evaluated.

The rapid rates of decline in many elasmobranch populations raised concerns for their persistence as well as questions about how their disappearance may affect marine ecosystems. Today, many sharks and rays are listed on the Red List of threatened species by the International Union for the Conservation of Nature (IUCN); however the status of many species is unknown or data deficient (www.redlist.org, Dulvy et al. 2008; Field et al. 2009). Although the study of top-down control in marine ecosystems has gained increasing recognition over the past decade (Frank et al. 2005; 2006; 2007; Heithaus et al. 2008a; Baum and Worm 2009), it remains unclear whether elasmobranchs play a fundamental role in top-down control, or whether they can be replaced by other species with faster biomass turnover, such as tunas or billfishes, with minimal consequences for ecosystem functioning (Stevens et al. 2000; Kitchell et al. 2002).

Based on the above, the purpose of this thesis was threefold:

1. Determine the long-term changes in elasmobranch populations in one of the most depleted large marine ecosystems of the world, the Mediterranean Sea.
2. Evaluate the role or sharks in marine ecosystems and the consequences of their human-induced decline.
3. Compare the patterns and consequences of changes in exploited elasmobranch communities in the Mediterranean with those in other marine ecosystems of the world (see below).

Most of my analyses focus on the Mediterranean Sea. Here changes in exploited marine animals reach back centuries to millennia (Lotze et al. 2006). It was my goal to reconstruct the history of Mediterranean fisheries in different sectors of the basin and derive their impact on shark and ray populations over time.

1.2 The Mediterranean Sea

The Mediterranean Sea is a semi-enclosed marine basin characterized by complex and diverse marine communities (Tortonese 1964; Garibaldi and Caddy 1998). Compared to other oceanic regions, it is considerably richer in the number of species, many of which are endemic. Eighty four species are chondrichthyans with 49 sharks, 34 rays and skates, and 1 chimaera (Serena 2005).

Marine exploitation in the Mediterranean Sea dates back thousands of years (Lotze et al. 2006; Gertwagen et al. 2008). For most of its history, fisheries have remained coastal and largely artisanal, and industrial fishing only developed over the past 50 years (Farrugio et al. 1993). Today, Mediterranean marine resources are generally over-exploited (FAO 2005). Habitat degradation, coastal development, pollution and overpopulation contribute to make this region one of the most degraded in the world (Coll et al. 2010; Airoldi and Beck 2007; Claudet and Fraschetti 2010). Contemporarily, such a long history of perturbation makes the Mediterranean an ideal study systems to analyze long-term changes in marine populations and ecosystems (Pauly 1995; Dayton et al. 1998).

Unfortunately, there is a great lack of standardized data on the abundance of marine populations in the Mediterranean Sea. The largely artisanal aspect of its fisheries makes catches and fishing effort hard to monitor (FAO 2005). The 22 countries bordering the basin differ in culture, history and economic situations and lack a coordinated policy for fisheries management, which is only recently being established for European nations. Consequently, there is a heterogeneous (and often difficult to access and utilize) amount of scattered information, focusing on restricted portions of the basin, and in some regions limited to short periods of time. This has made it challenging to obtain a clear understanding of long-term changes in many Mediterranean ecosystems.

Many elasmobranchs are of little economic value, and detailed fishery statistics are scarce or aggregated in the Mediterranean, even though most species experience a constant fishing pressure as target and by-catch species (Costantini et al. 2000; Machias et al. 2001; Carbonell et al. 2003). About 46 species of demersal elasmobranchs are regularly caught in trawl fisheries (Anonymous 2003a), and at least 10 species of large pelagic sharks have been observed in catches of long-line and driftnet fisheries (di Natale et al. 1995; di Natale 1998; Megalofonou et al. 2000; Tudela et al. 2005). At least 9 species of large and small sharks (e.g *Alopias vulpinus*, *Prionace glauca* and *Mustelus* spp.) and 7 species of rays (e.g. *Pteroplatytrygon violacea*, *Milyobatis aquila* and *Raja clavata*) are also occasionally caught by pelagic trawlers and purse seiners (Anonymous 2003a; Fromentin and Farrugio 2005; Tudela 2004; Fortuna et al. 2010).

Official fisheries statistics report elasmobranch landings of 11,000 tonnes per year in the Mediterranean, about 1.1% of the total fish catch reported (Anonymous 2003a; Bonfil 1994) and likely a gross underestimation. Over the past decade, elasmobranch landings in the Mediterranean showed the strongest decline compared to other parts of the world (Bonfil 1994) (see Chapter 5), and many large elasmobranchs have disappeared from coastal zones of the Mediterranean basin (D'Ancona and Razzauti 1937; Aldebert 1997). However, the overall magnitude of population changes and shifts in community composition due to exploitation has not been examined.

1.3 Outline of Chapters

In Chapter 2, I used a diverse set of records dating back to the early 19^{th} and mid 20^{th} century to reconstruct long-term population trends of large predatory sharks in the north-western Mediterranean Sea including the Strait of Sicily, Ligurian, Tyrrhenian, Alboran, Balearic, Catalan, Ionian and Adriatic Seas. I compiled 9 time series of abundance indices from commercial and recreational fishery landings, scientific surveys, and sighting records. Generalized linear models were used to extract instantaneous rates of change from each data set, and a meta-analysis was conducted to compare population trends across regions.

In Chapter 3, I investigated the long-term dynamics of elasmobranch populations in the upper Tyrrhenian Sea over more than a century. For this purpose, I analyzed data from commercial landings of fish traps, literature records and scientific trawl surveys. These data were integrated with generalized linear models, in which the change in abundance as well as the depth distribution was modelled for each of 20 species.

In Chapter 4, I analyzed a demersal community of elasmobranchs in the Adriatic Sea, a large continental shelf of the Mediterranean Sea where marine ecosystems have been exploited for hundreds of years. I combined and standardized catches from five published and unpublished scientific trawl surveys carried out in the area since 1948, by using generalized linear models controlling for technological and environmental covariates. Within a multi-model, information theoretic approach, I estimated long-term trends in abundance and species-specific ecological requirements for 33 species of sharks and rays. Life histories, fish market and effort data, and historical fishing information from the 19^{th} century were used to explain relative changes in population abundance and possible predation and competition release effects.

In Chapter 5, I reviewed the documented changes in exploited elasmobranch communities in coastal, demersal, and pelagic habitats worldwide, and synthesized the effects of sharks on their prey and wider marine communities. This semi-quantitative synthesis summarized the most up-to-date research but also reanalyzed historical published and original data on the fishing effects on elasmobranch populations based on dive surveys, trawl surveys, long-line fisheries, and shark netting data. The ecological role of sharks in marine ecosystems was synthesized from observational, experimental, and modeling studies.

In Chapter 6, I derived major conclusions from the analyses described in Chapters 2 to 5. I further provide suggestions for future research that are priorities for shark conservation, for understanding the ecosystem gain in having sharks among its components, and for predicting major ecological changes ongoing in the global ocean.

Chapter 2

Loss of Large Predatory Sharks from the Mediterranean Sea

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2.1 Introduction

Over the last 50 years, fishing pressure has increased substantially in the world's oceans, resulting in rapid declines of large predatory fish communities (Myers and Worm 2003). Large elasmobranchs, which are particularly vulnerable to increased mortality rates because of their slow growth, late age of maturity, and low reproductive rate, have been of particular concern (Myers and Worm 2005). In the Gulf of Mexico, oceanic whitetip sharks (*Carcharhinus longimanus*) declined by > 99% between the 1950s and 1990s (Baum and Myers 2004) and coastal elasmobranch species declined by 96-99% between 1972 and 2002 (Shepherd and Myers 2005). In the NW Atlantic, several large shark species declined by > 75% in just 15 years since 1986 (Baum et al. 2003). Little quantitative information has been available from other regions, partcularly from Europe. Because of its long history of intense fishing (Farrugio et al. 1993; Lotze et al. 2006) and its current state of overexploitation (FAO 2005), we hypothesized that the Mediterranean Sea may have had similarly large declines in shark populations.

Usually at the apex of trophic chains, large sharks are expected to play an important role in the structure and functioning of marine ecosystems (Stevens et al. 2000). Thus, the decline of large sharks may have marked ecological consequences. In the Gulf of Mexico, predator and competitor release effects have been evident after the depletion of large sharks (Baum and Myers 2004; Shepherd and Myers 2005). In the NW Atlantic, the decline of great sharks from coastal ecosystems has triggered a trophic cascade that collapsed a century-old fishery for bay scallops (Myers et al. 2007). Moreover, food web models from the Caribbean suggested that large predatory sharks are among the most strongly interacting species, and that their overfishing may have caused trophic cascades that contributed to the degradation of Caribbean ecosystems (Bascompte et al. 2005).

In the Mediterranean Sea, 20 of the recorded 47 species of sharks (Serena 2005) can be considered top predators in coastal and pelagic ecosystems. Historically large sharks occurred throughout the Mediterranean Sea (e.g., Marchesetti 1882; Parona 1898; Ninni 1923). In the early 20th century, many coastal fisheries targeted sharks or landed them as by-catch (e.g., Piaggio 1927,Arcidiacono 1931). In recent decades, however, large sharks seemed to be restricted to the eastern and southern Mediterranean coasts (Basuşta et al. 2006) or to offshore pelagic waters where they have been caught, albeit in very low numbers (Tudela et al. 2005; Megalofonou et al. 2005). Pelagic fisheries have caught only 3 species regularly: the blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), and thresher shark (*Alopias vulpinus*), whereas the remaining species are caught only occasionally (Megalofonou et al. 2005).

A quantitative assessment of historical shark populations in the Mediterranean has not yet been attempted, probably because of a chronic lack of abundance data. Most fisheries are multispecific, and landings statistics are aggregated. In these cases, depletion of undervalued resources, such as sharks, can go unnoticed while extraction continues because yields are sustained by other, more-productive species (Graham et al. 2001). These factors have so far impeded the assessment of elasmobranch abundance and distribution in the Mediterranean Sea and prevented conservation actions. The IUCN has recently concluded that the Mediterranean region has some of the most threatened chondrichthyan populations in the world, and 26% of the species are data deficient (Cavanagh and Gibson 2007). Nevertheless, even those that have been classified differently have large uncertainties in terms of distribution, human-induced mortality, and resistance to exploitation.

We compiled a diverse set of historical records to reconstruct the history of shark exploitation and to evaluate trends in population abundance in the Mediterranean Sea during the 19^{th} and 20^{th} centuries. Different sources of information, including commercial and recreational fisheries landings, scientific surveys, and sightings records, were used to assemble 9 time series of abundance indices and to determine rates of population change in 6 regions of the basin. Regional estimates were then combined in a meta-analytical framework to quantify overall changes in abundance of large predatory sharks.

2.2 Methods

2.2.1 Data

We performed an extensive bibliographic search in the scientific literature and public and private archives for quantitative scientific and fisheries information on 20 species of large predatory sharks of the Mediterranean Sea (Table 2.1), here defined as species with a published maximum length > 2 m and estimated trophic level > 4. All data that directly or indirectly provided indices of abundance comparable across Mediterranean regions and over long periods of time were considered. We assembled 9 data sets (Table 2.2, Appendix) from 6 regions (Fig. 2.1). In our analyses, we included only shark species occurring in 2 or more data sets and more than 3 times within each. For data sets reporting only common names, we identified the most likely shark species on the basis of local historical literature. When we could not identify the species, we grouped 2 or more shark species into higher taxonomic groups (e.g., genus, family), as in the case of hammerhead (*Sphyrna* spp.) and mackerel sharks (Lamnidae).

2.2.2 Modelling Population Trends

For each data set, we extracted an appropriate index of abundance to be modelled over time with generalized linear models (GLM, Venables and Ripley 2001). In this framework such an index is assumed to follow a probability distribution of the exponential family. The specific probability distribution we chose depended on the type of data; a summary of data and models used is given in Table 2.2. The general model structure was

$$log(\mu_i) = \alpha + \beta_y y_i + XB + log(A_i) \tag{2.1}$$

where μ_i is the expected value of the index of abundance of sharks caught in the year_i (y_i), α is the intercept, β_y is a year-effect parameter or instantaneous rate of change of μ_i over time, X the matrix of covariates affecting the variability of μ_i, $\mathbf{B}$ the vector of their relative parameters, and $log(A_i)$ is an offset variable, usually a measure of effort for which we could standardize the index of abundance recorded under different sampling conditions. The offset term is included in the GLM as a regressing variable with parameter 1, rather than used as divisors of indices of abundance, to retain the probabilistic nature of the model. Covariates other than year were included in the model according to their level of statistical significance and the overall decrease of the Akaike information criterion (AIC, Venables and Ripley 2001). Parameter estimates and scale parameters (for negative binomial and gamma distributions) were obtained through maximum-likelihood fitting with a ridge-stabilized Newton-Raphson algorithm implemented in SAS 9.1 (SAS Institute, Cary, North Carolina).

After obtaining all local estimates of population change, we used a meta-analytical framework to calculate a weighted average of these estimates to extract a general rate of decline of the investigated shark species across different regions.

From large sample likelihood theory, the k local estimates of β_y will be approximately normally distributed with a known standard error and mean equal to the true β_y's. In fixed effects meta-analysis it is assumed that all of the regions have the same β_y (Cooper and Hedges 1994). Thus

$$\hat{\beta}_{yi} \sim N(\beta_y, s_i^2) \tag{2.2}$$

Our estimate of this common β_y is a weighted mean

$$\bar{\beta}_{y\cdot} = \frac{\sum w_i \hat{\beta}_{yi}}{\sum w_i} \tag{2.3}$$

where w_i is a weight assigned to each study, here the inverse of the variance s_i^2 of the year effect estimate, and the variance s^2 is given by,

$$s^2 = \frac{1}{\sum 1/s_i^2}. \tag{2.4}$$

The fixed effects model assumes $\beta_y = \beta_{y1} = \cdots = \beta_{yk}$. For our data this assumption may not be true because time periods and habitats investigated were quite different. It was more reasonable for us to assume that rates of change detected in coastal regions were different than those in oceanic environments. In addition, rates of change in the early 20^{th} century were likely different than those in recent times. In all regions and time periods considered, sharks have been subjected to different kinds of human perturbations at different levels of intensity.

As in the fixed effects model, the k local estimates of β_y will be approximately normally distributed with a known standard error. But now the true β_y values are random and allowed to be different across regions. Thus, given the true β_{yi} for the region, the conditional distribution of $\hat{\beta}_{yi}$ is

$$\hat{\beta}_{yi} \sim N(\beta_{yi}, s_i^2) \tag{2.5}$$

The random effects model additionally assumes that the β_{yi} is normally distributed with mean β_y and variance τ^2. Hence, similarly as in the fixed effects model, unconditionally, the $\hat{\beta}_{yi}$ are normally distributed with common mean β_y but variance $s_i^2 + \tau^2$. These are called hyper-parameters in random effects meta-analysis (Normand 1999).

We tested the appropriateness of a random- versus fixed-effect meta-analysis by performing a test of homogeneity,

$$Q = \sum w_i \beta_{yi}^2 - \frac{(\sum w_i \beta_{yi})^2}{\sum w_i}. \tag{2.6}$$

If Q exceeds the critical value of a chi-square distribution with $k - 1$ degrees of freedom, then the variance associated with a region-specific instantaneous rate of change is significantly greater that what one expects by chance if all regions share a common parameter. In this case it is appropriate to use random effects, and the estimate of within-region homogeneity is then incorporated to adjust the value of the variance associated with the hyper-parameter of interest as follow: $s_i^{2*} = s_i^2 + s_r^2$, where

$$s_r^2 = \frac{Q - (k-1)}{\sum w_i - \frac{\sum w_i^2}{\sum w_i}}. \tag{2.7}$$

Thus we used this new adjusted version of s_i^2 (s_i^{2*}) in eq. 2.4 and in the weights $w_i = 1/s_i^{2*}$ in eq. 2.3. We performed separate meta-analyses for landed biomass and landed numbers of sharks.

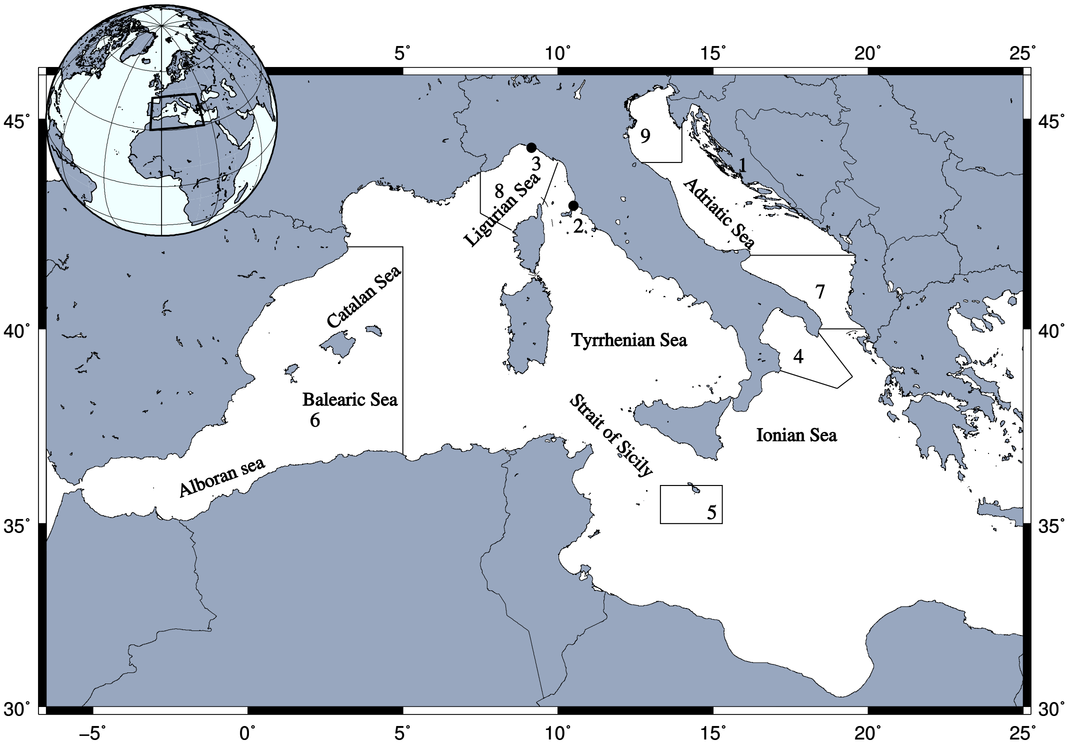

Figure 2.1: Study areas in the Mediterranean Sea. Data set 1 came from the coastal zone of the eastern Adriatic Sea; data sets 2 and 3 refer to the 2 fish-trap locations (dots); data sets 4-9 approximately represent the investigated pelagic longline and recreational fisheries (areas enclosed in lines, see Table 2.2 for details).

2.3 Results

Of 20 species of large sharks that occur in the Mediterranean basin 2.1, we could assess only five; these were two mackerel sharks (*Isurus oxyrinchus* and *Lamna nasus*), one requiem shark (*Prionace glauca*), one hammerhead shark (*Sphyrna zygaena*), and one thresher shark (*Alopias vulpinus*). All other species occurred only sporadically in our records, which was insufficient for analysis. In all regions and time periods considered, all 5 species showed high instantaneous rates of decline in landed numbers and biomass. Biomass generally declined more rapidly (Fig. 2.2).

Of the species investigated, hammerhead sharks (*Sphyrna* spp.) declined the fastest. In the early 1900s, declines were detected in coastal waters, where catches

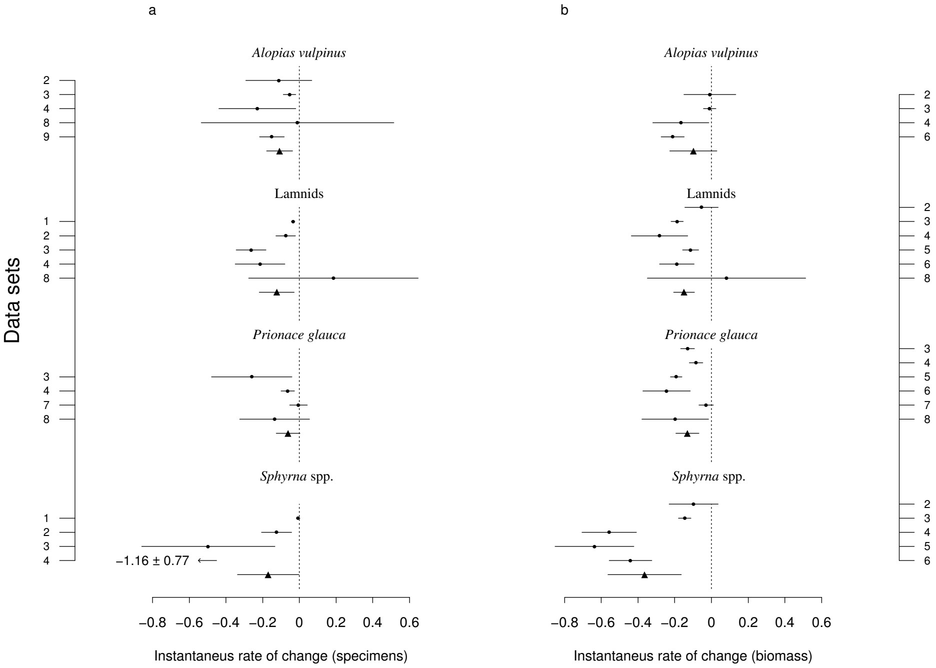

Figure 2.2: Meta-analysis of instantaneous rates of change in shark population abundance over time. Year-effect estimates for models fitted on (a) landed number of specimens and (b) landed biomass data. Dots are local estimates; triangles are meta-analytical averages over regions; numbers refer to data sets (see Table 2.2).

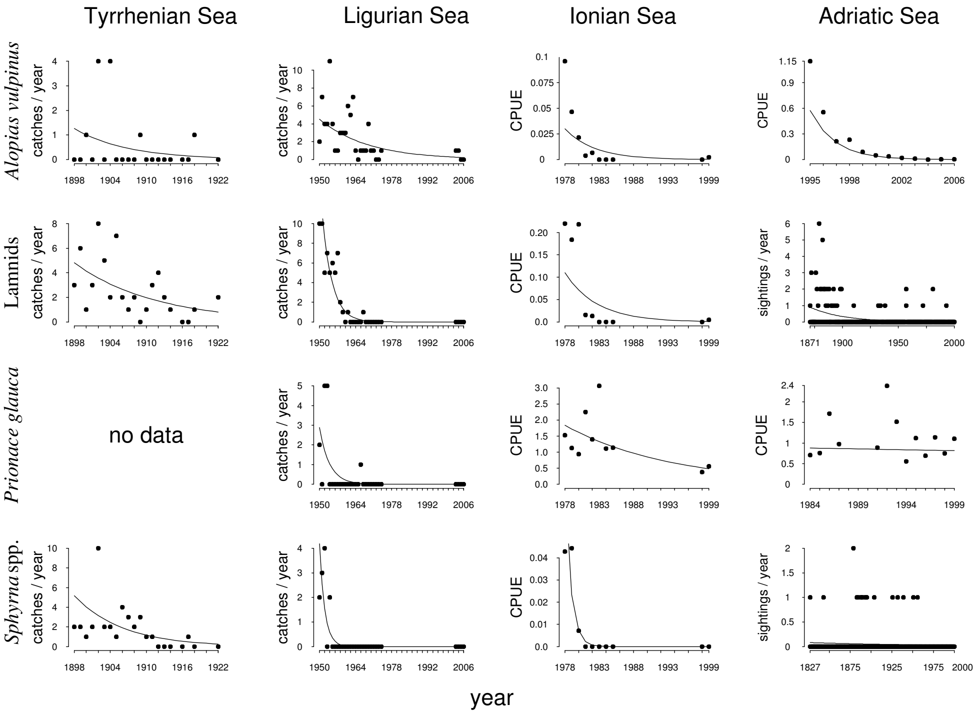

Figure 2.3: Trends in shark population abundance in the Mediterranean Sea. Dots represent standardized annual catches or annual sightings. Catch per unit effort (CPUE) for the Ionian and Adriatic *Prionace glauca* seas refer to sharks landed per 1000 hooks of fishing efforts, whereas CPUE for *Alopias vulpinus* in the Adriatic Sea are landed sharks per yacht-club member per year, standardized by a constant number of tuna catches (mean value over time period). Trends (solid lines) were calculated with the year-effect estimate (see Methods).

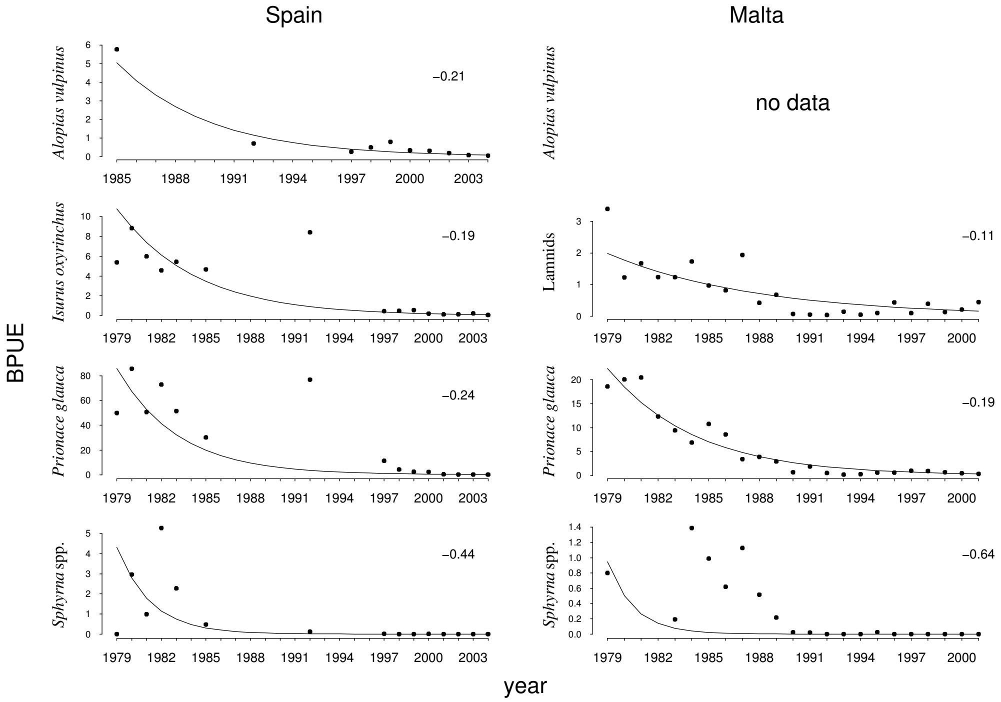

Figure 2.4: Trends in shark biomass (kg) in the western and central Mediterranean Sea. Dots are landed biomass per unit effort (BPUE). Biomass is expressed for Spain as kilograms per 1000 hooks and for Malta as kilograms per unit of gross tonnage (tons). Numbers on the right side of each plot are instantaneous rate of change in biomass.

and sightings were regular although not common (Fig. 2.3). After 1963 no hammerheads were caught or seen in coastal areas. In pelagic waters, catches declined consistently in the early 1980s in all sectors (Figs. 2.3 & 2.4). Longline catch rates were already low in 1978, with fewer than 0.05 specimens/1000 hooks in the Ionian Sea and < 4 kg/1000 hooks in Spanish waters. After 1995 we found no more records of hammerhead sharks. Meta-analysis revealed an average instantaneous rate of decline (IRD) of -0.17 (CI 95%: -0.34, -0.003; time range 178 years) in abundance and -0.36 (CI 95%: -0.56, -0.16; time range: 107 years) in biomass, which translate into an estimated species decline of >99.99% in both cases.

Family	Species	CN[1]	ML[2]	TL[3]	PH[4]	RLC[5]
Hexanchidae (cow sharks)	Hexanchus griseus (Bonnaterre, 1788)	bluntnose sixgill shark	480	4.3	benthopelagic, bathyal	NT
Echinorehinidae (bramble sharks)	Echinorhinus brucus (Bonnaterre, 1788)	bramble shark	300	4.4	benthopelagic, bathyal	DD
Odontaspididae (sand tiger sharks)	Carcharias taurus (Rafinesque, 1810)	sand tiger	320	4.4	benthopelagic, coastal	CR
	Odontaspis ferox (Risso, 1810)	smalltooth sand tiger	410	4.4[6]	benthopelagic, bathyal	EN
Alopidae (thresher sharks)	Alopias superciliosus (Lowe, 1839)	bigeye thresher	461	4.2	pelagic, coastal/oceanic	DD
	Alopias vulpinus (Bonnaterre, 1788)	thresher shark	246	4.2	pelagic, coastal/oceanic	VU
Lamnidae (mackerel sharks)	Isurus oxyrinchus (Rafinesque, 1810)	shortfin mako	400	4.3	pelagic, coastal/oceanic	CR
	Lamna nasus (Rafinesque, 1788)	porbeagle	417	4.2	pelagic, coastal/oceanic	CR
	Carcharodon carcharias (Linnaeus, 1758)	white shark	720	4.5	benthopelagic, coastal/oceanic	EN
Carcharhinidae (requiem sharks)	Carcharhinus altimus (Springer, 1950)	bignose shark	280	4.3	benthopelagic, coastal/oceanic	DD
	Carcharhinus brachyurus (Günther, 1870)	bronze whaler	292	4.2	benthopelagic, coastal/oceanic	DD
	Carcharhinus brevipinna (Müller & Henle, 1839)	spinner shark	280	4.2	bentopelagic, coastal	DD
	Carcharhinus falciformis (Müller & Henle, 1839)	silky shark	350	4.2	pelagic, coastal/oceanic	
	Carcharhinus limbatus (Müller & Henle, 1839)	blacktip shark	255	4.2	benthopelagic, coastal	DD
	Carcharhinus obscurus (Lesueur, 1818)	dusky shark	420	4.2	benthopelagic, coastal/oceanic	DD
	Carcharhinus plumbeus (Nardo, 1827)	sandbar shark	250	4.1	benthopelagic, coastal	EN
	Prionace glauca (Linnaeus, 1758)	blue shark	380	4.1	pelagic, oceanic	VU
Sphyrnidae (hammerhead sharks)	Sphyrna lewini (Griffith & Smith, 1834)	scalloped hammerhead	420	4.1	benthopelagic, coastal/oceanic	
	Sphyrna mokarran (Rüppell, 1837)	great hammerhead	600	4.3	benthopelagic, coastal/oceanic	DD
	Sphyrna zygaena (Linnaeus, 1758)	smooth hammerhead	400	4.2	benthopelagic, coastal/oceanic	VU

Table 2.1: List of large predatory sharks occurring in the Mediterranean Sea

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[1] common name

[2] maximum length in centimetres

[3] trophic level according to citeCortes.solo.1999

[4] red-list category assessed by IUCN Shark Specialist Groups (updated 14 February 2007, source IUCN Species Survival Commission, Shark Specialist Group, Newbury, UK): CR - Critically Endangered; VU - Vulnerable; NT - Near Threatened; LC - Least Concern - (www.iucnredlist.org)

[5] preferential habitat according to Musick et al. (2004)

[6] inferred

Data set	Gear	Area (timespan)	Species	Index of abundance	Regressing variables	Offset variable (distribution)	Source
1	sightings records	Adriatic Sea (1827-2000)	Lamnids and *Sphyrna* spp.	sightings/year	year	none (Poisson)	Soldo and Jardas (2002)
2	tuna trap	Tyrrhenian sea (1898-1922)	*Alopias vulpinus*, Lamnids,[1] *Sphyrna* spp.	no. sharks/year; kg/year	year	none (negative binomial)	fisher logbooks
3	tuna trap	Ligurian Sea (1950-2006)	*Alopias vulpinus*, Lamnids,[2] *Prionace glauca* and *Sphyrna* spp.	no. sharks/year; kg/year	year	fishing days (negative binomial)	fisher logbooks
4	swordfish pelagic longline	Ionian Sea (1978-1999)	*Alopias vulpinus*, Lamnids,[3] *Prionace glauca* and *Sphyrna* spp.	no. sharks/year; kg/year	year	no. hooks/year (negative binomial)	published data: Filanti et al. (1986); Megalofonou et al. (2000).
5	pelagic longline	Strait of Sicily (1979-2001)	Lamnids, *Prionace glauca* and *Sphyrna* spp.[4]	kg/year	year	estimated total gross tonnage (gamma)	official statistics of Valletta's wholesale fish market
6	swordfish pelagic longline	Spanish Mediterranean waters (1979-2004)	*Alopias vulpinus*,[5] Lamnids, *Prionace glauca* and *Sphyrna* spp.	kg/year	year, strata, year*strata	no. hooks/year (gamma)	published data: Rey and Alot (1984); Rey et al. (1987); Buenquerpo et al. (1998); Castro et al. (2000); Valerias et al. (2003); Mejuto et al. (2006)
7	swordfish pelagic longline	Adriatic Sea (1984-1999)	*Prionace glauca*	no. sharks/year; kg/year	year	no. hooks/year (negative binomial)	published data: De Zio et al. (2000); Megalofonou et al. (2000).
8	swordfish pelagic longline	Ligurian Sea (1990-1998)	*Alopias vulpinus*, Lamnids and *Prionace glauca*	no. sharks/year; kg/year	year	no. hooks/year (negative binomial)	published data: Garibaldi and Orsi Relini (2000)
9	big game rood and reel fishing	Adriatic Sea (1984-1999)	*Alopias vulpinus*	no. sharks/year	year, tunas, year*tunas	no. club members (Poisson)	yacht-club logbooks

Table 2.2: Outline of data sets, study area, modeled species, and model details for the analyses of population abundance of large sharks in the Mediterranean Sea.

Population factor and group	Area	Time range (yr)	Abundance estimate (%)	LowerWaldCL	UpperWaldCL	Data set
Abundance						
Alopias vulpinus	Ionian Sea	21	-99.19	-99.99	-33.88	4
	Ligurian Sea	55	-94.67	-99.18	-65.02	3
	Tyrrhenian Sea	24	-93.15	-99.91	408.96	2
	Adriatic Sea	11	-80.82	-90.86	-59.74	9
Lamnids	Ligurian Sea	55	<-99.99	<-99.99	<-99.99	3
	Adriatic Sea	129	-98.79	-99.67	-95.48	1
	Ionian Sea	21	-98.88	-99.93	-80.89	4
	Tyrrhenian Sea	24	-83.19	-95.27	-40.31	2
	Ligurian Sea	8	343.18	-89.02	17768.06	8
Prionace glauca	Ligurian Sea	55	<-99.99	<-99.99	-88.86	3
	Ionian Sea	21	-73.76	-87.91	-43.16	4
	Ligurian Sea	8	-65.8	-92.54	56.77	8
	Adriatic Sea	15	-6.95	-54.37	89.74	7
Sphyrna spp.	Ionian Sea	21	<-99.99	<-99.99	-99.97	4
	Ligurian Sea	55	<-99.99	<-99.99	-99.93	3
	Tyrrhenian Sea	24	-94.95	-99.31	-63.33	2
	Adriatic Sea	173	-68.08	-93.83	65.15	1
			Biomass estimate (%)			
Biomass						
Alopias vulpinus	Spanish waters	19	-98.2	-99.45	-94.03	6
	Ionian Sea	21	-96.96	-99.88	-24.69	4
	Ligurian Sea	55	-41.35	-91.11	284.78	3
	Tyrrhenian Sea	24	-18.84	-97.24	2287	2
Lamnids	Ligurian Sea	55	<-99.99	<-99.99	-99.98	3
	Ionian Sea	21	-99.73	-99.99	-93.26	4
	Spanish waters	25	-99.12	-99.92	-90.65	6
	Strait of Sicily	22	-91.58	-96.82	-77.7	5
	Tyrrhenian Sea	24	-72.9	-96.95	140	2
	Ligurian Sea	8	91.78	-93.92	5953	8
Prionace glauca	Ligurian Sea	55	-99.92	-99.99	-99.35	3
	Spanish waters	25	-99.78	-99.99	-94.36	6
	Strait of Sicily	22	-98.53	-99.28	-96.97	5
	Ionian Sea	21	-83.01	-92.1	-63.35	4
	Ligurian Sea	8	-79.48	-95.2	-12.3	8
	Adriatic Sea	15	-35.18	-64.16	17.06	7
Sphyrna spp.	Ionian Sea	21	<-99.99	<-99.99	-99.98	4
	Strait of Sicily	22	<-99.99	<-99.99	-99.99	5
	Spanish waters	25	<-99.99	<-99.99	-99.97	6
	Ligurian Sea	55	-99.97	-99.99	-99.79	3
	Tyrrhenian Sea	24	-90.32	-99.61	140	2

Table 2.3: Summary of estimated local change in population abundance and biomass and associated confidence intervals for the analyzed sharks over the considered time intervals[1].

Since the mid 20th century, blue shark (*P. glauca*) abundance is estimated to have declined by 3-4 orders of magnitude. In coastal waters, records in the tuna trap of Camogli (Ligurian Sea, data set 3,Table 2.2) starting in 1950 showed the highest rate of decline in abundance of >99.99% (Table 2.3). Here, *P. glauca* was one of the least frequent catches, with an average of 3 specimens/year at the beginning of the series (Fig. 2.3). There were no blue shark records in the tuna trap of Baratti (Tyrrhenian Sea, data set 2,Table 2.2), probably because of identification problems. *P. glauca* used to be very abundant in coastal waters of the Tuscan archipelago during the 19th century, specifically in the bay of Baratti, where fishers used to report nearshore

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[1] Upper Wald CI and lower Wald CI are, respectively, the upper and lower Wald confidence intervals at 95% level of statistical significance. A negative sign indicates a reduction over the indicated time period.

aggregations of this species (Biagi 1999). Nevertheless, *P. glauca* was commonly sold as smooth-hound (*Mustelus mustelus*, Foresi 1939), a highly valued commodity in Italian markets.

In the pelagic fisheries, *P. glauca* represented the most abundant shark catch (Figs. 2.3 & 2.4), but still declined considerably. In the northern Ionian Sea, landings of blue shark declined by 73.76% in abundance and 83.01% in biomass over 21 years, whereas in the Spanish waters, biomass declined by 99.78% in 25 years (Table 2.3). The Adriatic Sea had the lowest declines in abundance (-6.75%) and biomass (-35.18%), although neither estimate was statistically significant. Overall, the decline in blue sharks was 96.53% in abundance (IRD: -0.06; CI 95%: -0.13, -0.003; time range: 56 years) and 99.83% in biomass (IRD: -0.13; CI 95%: -0.19, -0.07; time range: 49 years).

For Lamnids (*I. oxyrinchus* and *L. nasus*) the largest declines where observed in the tuna trap of Camogli, with declines of >99.99% over 56 years in abundance and biomass. Similar rates of decline were observed in the northern Ionian Sea, where a large drop in mackerel sharks caught by pelagic longlines was observed in the early 1980s (Fig. 2.3). Nevertheless, catch rates were very low even at the beginning of the data series, with an average of 0.2 sharks/1000 hooks. The meta-analytical estimate of the rate of decline was >99.99% for biomass (IRD: -0.15; CI 95%: -0.21, -0.10; time range: 106 years) and abundance (IRD: -0.12; CI 95%: -0.22, -0.03; time range: 135 years).

The thresher shark (*Alopias vulpinus*) was the only species detected in coastal waters in recent times: 2 specimens were caught in 2003 and 2004 in the tuna trap of Camogli. Drastic declines were detected in the Ionian Sea (99.19% in abundance and 96.96% in biomass over 21 years) and in Spanish waters (98.20% in biomass over 19 years). In the northern Adriatic Sea, recreational catches of *A. vulpinus* declined by about 80.82% over 11 years. Overall the species declined >99.99% (IRD: -0.11; CI 95%:-0.18, -0.04; time range: 108 years) in abundance and biomass (IRD: -0.10; CI 95%: -0.23, 0.03; time range: 108 years), though the decline in biomass was not statistically significant (Fig. 2.2).

2.4 Discussion

In the Mediterranean Sea, large predatory sharks have declined dramatically in abundance over the last 2 centuries. Only 5 of the 20 large predatory sharks were detected at levels of abundance sufficient for analysis. Moreover, these 5 species showed rates of decline from > 96 to $> 99.99\%$, which may classify them as critically endangered according to IUCN criteria (IUCN 2001). At these low levels, large sharks may be considered functionally extinct in coastal and pelagic waters of the northwestern Mediterranean. For wide-ranging sharks, such as the species modelled in our study, these results may be indicative of a broader trend across the Mediterranean Sea.

Many historical records depicted the Mediterranean Sea with an abundance of large sharks. Sharks were considered a pest by fishers (Marchesetti 1882, F. S. unpublished data) or an impediment by those seeking to develop more productive fisheries over the continental slope (Arcidiacono 1931). In the early 20th century, many coastal fisheries regularly targeted or landed sharks (Rodríguez Santamaría 1923; Piaggio 1927; Arcidiacono 1931; D'Ancona and Razzauti 1937; Cannaviello 1942). For example, in the Tuscan Archipelago alone, there were about 51 shark gillnets (Bestinare and angel shark nets), 48 fish traps (similar to the one we analyzed in Baratti, dataset 2), and 11 tuna traps, all of them with a high incidence of shark catches (Mancini 1922; Gargiulo 1924). Consequently, declines in shark populations due to exploitation were noticed already in the early 20^{th} century (Fig. 2.3).

Sharks that prefer coastal habitats may have declined most precipitously and earlier. Not one species in the genus *Carcharhinus* (requiem sharks), a diverse group of predators characteristic of coastal environments, could be analyzed in our data sets because of insufficient records. Requiem sharks have been caught as target or by-catch in historical fisheries (Russo 1928; D'Ancona and Razzauti 1937), but have been below detectable levels in pelagic (our study) and demersal fisheries in the northwestern Mediterranean for at least 20-25 years (e.g., Bertrand et al. 2000; Relini et al. 2000). This is in contrast to the NW Atlantic and Gulf of Mexico, where requiem sharks are still being caught, albeit in much reduced numbers (Baum et al. 2003; Baum and Myers 2004; Shepherd and Myers 2005).

More wide-ranging sharks that occur in pelagic and coastal waters did have sufficient records for analyzing population trends. It is possible that these species found a refuge from intense historical coastal exploitation in offshore pelagic waters. Nevertheless, after pelagic fishing expanded in the Mediterranean Sea in the 1970s, all groups of sharks collapsed. In this period, drift netters and longliners began targeting tunas and swordfish, and sharks were regular by-catch (Silvani et al. 1999; Tudela et al. 2005; Megalofonou et al. 2005). Before their total ban for European fleets in 2002 (Tudela et al. 2005), about 700 boats were fishing with driftnets (SGFEN/STECF 2001), and between 1000 and 2000 boats may be still officially fishing with pelagic longlines in the Mediterranean (Appendix). Furthermore, a substantial illegal, unregistered, and unregulated fishing effort is deemed to exist throughout the basin (Tudela 2004). Data from the International Commission for the Conservation of Atlantic Tunas (ICCAT) indicate that the southwestern and central Mediterranean Sea are extremely exploited zones, where international fleets are deploying millions of hooks all year round (Appendix). Specifically, around the Strait of Gibraltar, a critical migration corridor for many pelagic species, Spain deploys most of its pelagic longliners and recently broadened its target on the Atlatic side to include *I. oxyrinchus* and *P. glauca* (Mejuto and de la Serna 2000). Such a pattern of fishing pressure could impair exchange and replenishment between Mediterranean and Atlantic parts of the shark populations, which may worsen population declines within the Mediterranean basin.

Populations of hammerhead sharks started to decline in the Tyrrhenian Sea in the early 20^{th} century and in the Ligurian Sea since the 1950s (Fig. 2.3), but were still detected in pelagic fisheries in the second half of the 20^{th} century. *S. zygaena* had the highest occurrences among the hammerhead sharks, and on the basis of its ecology may have found refuge in pelagic waters. Nevertheless, after the expansion of pelagic fishing populations of hammerheads collapsed (Fig. 2.3 & 2.4); they exhibited the highest rates of population decline among all species we analyzed (Fig. 2.2).

Lamnids had the second-largest declines after hammerhead sharks, with *L. nasus* probably facing the most serious depletion. Comparisons of our data with historical records suggest a strong reduction in abundance and geographical distribution in this species, which appears to be restricted to the central Mediterranean Sea around the Italian peninsula today. *L. nasus* is a slow-growing, stenotermic, and stenobathial shark that, compared with other lamnids, exhibits limited migration behavior with few exchanges between adjacent populations (Stevens et al. 2005). At the present rate of decline, its persistence in the basin has to be considered precarious.

In the Ligurian and Adriatic seas' pelagic waters, we repeatedly detected non significant population changes. This could be an artifact of our small sample size and degree of aggregation of the available data. Nevertheless, for pelagic fishing, these two areas are probably the least exploited among those we considered. The majority of pelagic longline fishing is concentrated in the southwestern and central Mediterranean Sea, whereas the Ligurian Sea up to 1997 was fished by about 27 longline fishers and has been under a driftnet ban since 1992 (Tudela 2004). In the Adriatic, pelagic longlining only began in the 1980s in the south (Marano et al. 1983) and was recently expanded to the rest of the basin (Tudela 2004). In our data, we detected a decline in *A. vulpinus* (Fig. 2.2), but trends in other species remained uncertain, such as for *P. glauca*, for which we had no quantitative information on pelagic by-catch after 1999. Anecdotal evidence indicates that, in the 1980s, anglers in the western Adriatic Sea landed hundreds of blue sharks in each fishing competition, whereas today such catches are sporadic (i.e., 1-3 specimens/tournament; F. F. unpublished data). In a recent chumming experiment in Croatia (eastern Adriatic), only 9 sightings of *P. glauca* were registered over 23 days spent releasing bait in the water (Soldo and Pierce 2005).

Overall, the instantaneous rates of decline we found for the 5 large sharks in parts of the Mediterranean were higher than those for comparable species groups analyzed in the Gulf of Mexico (Baum and Myers 2004), but similar to the NW Atlantic (Baum et al. 2003). Nevertheless, despite the high diversity of shark species listed for the Mediterranean Sea, the number of species that had sufficient records for analysis was much lower compared with other sectors of the Atlantic. For example, in pelagic waters of NW Atlantic, fishery-dependent and fishery-independent data showed substantial catches of 9 groups of large coastal and pelagic sharks (Simpfendorfer et al. 2002; Baum et al. 2003, for a total of 18 species). In the Gulf of Mexico, Baum and Myers (2004) could analyzed 11 groups of 14 species. In the Mediterranean, there were much fewer species to be analyzed, which may indicate not only strong declines in shark abundance but also diversity.

In our analyses, instantaneous rates of decline in biomass were generally higher than those for the corresponding landed numbers (Fig. 2.2), which reflects a reduction in mean size over time. The mean size of sharks landed in Mediterranean pelagic fisheries is among the lowest in the world (Megalofonou et al. 2005). Changes in biomass we detected in coastal fixed-gear fisheries were relatively low or not significant. Here, the majority of catches consisted of young immature sharks (Boero and Carli 1979), suggesting that coastal areas could have represented important nursery grounds.

Our analysis, combined with previously published information, indicates that the Mediterranean Sea is losing a wide range of its predator species. In addition to large predatory sharks, cetaceans, pinnipeds, turtles, and large bony fishes have declined similarly (Bearzi et al. 2004; Tudela 2004; FAO 2005; Fromentin and Powers 2005; Reeves and Notarbartolo di Sciara 2006; WWF 2006; Damalas et al. 2007). The wider ecosystem consequences remain to be investigated. Nevertheless, in various other systems, it has been demonstrated that predators can play an important role in structuring communities by controlling prey populations and preventing ecological dominance (Paine 1984; Heithaus et al. 2008a). Losing top predators can induce strong increases in mid-level consumers, shifts in species interactions, and trophic cascades (Estes et al. 1998; Pace et al. 1999; Worm and Myers 2003; Frank et al. 2005). So far, the depletion of large sharks has resulted in the release of mesopredators in the Gulf of Mexico (Baum and Myers 2004; Shepherd and Myers 2005) and trophic cascades in the coastal northwestern Atlantic and possibly the Caribbean (Bascompte et al. 2005; Myers et al. 2007). The decline of large sharks and other marine predators in the Mediterranean may entail similar ecological consequences.

Chapter 3

Long-Term Dynamics of the Chondrichthyan Fish Community in the Upper Tyrrhenian Sea

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3.1 Introduction

Many elasmobranch populations are declining worldwide because of fishing (Graham et al. 2001; Myers and Worm 2003; Baum and Myers 2004; Shepherd and Myers 2005). In many cases, population reductions have been substantial even after relatively short periods of exploitation. This is especially true in multi-species fisheries, where sharks (refers to sharks rays and chimeras) are usually a minor part of fishery landings. In these cases shark depletion often goes unnoticed and extraction may continue for many years, as the fishery is sustained by the more productive target fishes. The biological characteristics of sharks, such as low fertility, low growth rate and late sexual maturity, make them particularly vulnerable to drastic increases in mortality rates.

The Mediterranean fishery is one of the oldest on the planet. Humans along its coasts have been exploiting marine resources, including sharks, for thousands of years (Farrugio et al. 1993). It is a peculiar multi-species fishery, in that the spectrum of its resources is very broad, with no predominating species in the marine community (Jeftic et al. 1990). Due to these circumstances, we believe that collapses of shark populations may have occurred here in Mediterranean too, perhaps with even larger magnitudes. However evidence is scarce and controversial. Long-term sources of information to assess shark removals are very rare in this region. The present available time series coming from scientific surveys (GRUND and MEDITS, Relini 1998;

Bertrand et al. 2002b) have been often dismissed as a means for estimating trends because of the shortness of the covered period (MEDITS) and the heterogeneity of the sampling methods (GRUND). Fishery catch rates are unavailable since shark catches are rarely reported adequately. Furthermore, given the mainly artisanal aspect of the Mediterranean fisheries (Farrugio et al. 1993) and the scarce economic interest in shark species, most landings have never been reported, or if reported, records are hard to find.

At present, there are 84 known species of sharks and rays in the Mediterranean basin (Serena 2005). The IUCN has declared that 30% are data deficient, and roughly 70% require more thorough monitoring (Abdulla 2004). In previous analyses, in the Gulf of Lion and the Adriatic Sea, shark species diversity has dropped approximately 50% in less than 50 years due to fishing pressure (Aldebert 1997; Jukić-Peladic et al. 2001).

In this paper we investigate the dynamics of elasmobranch populations subject to fishing pressure in the upper Tyrrhenian Sea. We used commercial landings and scientific surveys to model trends in abundance of several demersal cartilaginous fishes with generalized linear models. These models allow us to detect trend in catch series even when the variability is not constant over time and when the errors are not normally distributed. The assumption of normality is often violated in fisheries data, especially for by-catch species where the probability of their occurrence in the catch is very low. In these cases it is reasonable to assume that the distribution of catches follow a negative binomial distribution (Hilborn and Mangel 1997). Under this assumption the variance of the catches V is correlated to their mean μ by a quadratic function

$$V = \mu + \mu^2 k \tag{3.1}$$

where k is a measure of population aggregation. Although the applicability of this parameter to all species at all densities has been questioned (Taylor et al. 1979), shark species have been well fit by this approach (Baum et al. 2003; Baum and Myers 2004; Myers and Worm 2003; Shepherd and Myers 2005). This paper is the first attempt to analyse the GRUND data in a generalized linear model framework.

3.1.1 History of the Tuscan Fishery

Along the Tuscan coast, there are currently about 700 boats with a total gross tonnage of 8000 tonnes. The most important fisheries are Viareggio, Porto Santo Stefano, Livorno and Porto Ercole (Fig. 3.1); However fishing effort is broadly distributed along the 25 ports of the coast. Of the total fleet, 74% of the fishing boats fish artisanally, 24 % trawl and 2% purse seine. However, trawlers account for 65% of the total gross tonnage and 57% of the total 80,000 horsepower of the Tuscan fleet. The principal trawl fisheries are located in the continental part of Tuscany, at such ports as Viareggio, Livorno, Piombino, Castiglione della Pescaia, Porto Santo Sefano and Porto Ercole (Anonymous 2003c).

The history of this fishery extends far into the past, although major exploitation of demersal stocks only began as late as the beginning of the 20th century. Then, only 15% of the available grounds was exploited by the fishery. Fishers worked in depths shallower than 150 meters and no farther than 7-8 miles from the coast. The fishery consisted of many sail powered boats, usually light in tonnage, employing many different kind of gears, and used by a great number of workers who remained very close to their ports (Mancini 1922; Matta 1958).

In the 1930's the fishery improved with technological advancements. Some engine boats began to be used in the zone and by the 1960's about 90% of the Tuscan Archipelago was exploited, an area of approximately 13,000 square kilometers (Matta 1958). Since that time, the area covered by fishing exploitation has remained approximately the same. Despite technological advancements and more powerful engines that have allowed trawlers to go further offshore and to deeper grounds, the bulk of the fishery still concentrates its effort closer to the major ports and at depths of less than 400 meters (Autieri et al. 1992).

3.2 Methods

We divided our analysis into two stages. First we assessed the dynamics of elasmobranch populations relative to the early period of the 20^{th} century. We used commercial landings from the tuna trap of Baratti. This fixed gear is conventionally called tuna trap, but despite its name it is quite different in shape from the classical tuna traps of the Mediterranean Sea (Biagi 1999). The gear consisted of a net 200 meters long, perpendicular to the coast and shaped as a hook in its final end. The net was 20 meters high and fished in depth from 2-3 meters near the coast to depths of 15 meters offshore. The mesh size was about 20 cm. It was originally intended to catch northern bluefin tunas (*Thunnus thynnus*), but the array of species composing its landings was quite diverse. It caught many other tuna-like fishes such as Atlantic bonito (*Sarda sarda*), bullet tuna (*Auxis rochei rochei*), little tunny (*Euthynnus alletteratus*), other pelagic and coastal fishes, and a great amount of elasmobranch species (Biagi 1999; Vacchi et al. 2000). We considered only demersal species of sharks for which comparisons were available in the scientific trawl surveys. Our trap data series starts in 1898 and end in 1922. Shark catches are reported monthly in number of individuals per species. We believe that catches for this kind of gear give us a reasonable index of population abundance for coastal fish species.

We modelled catch per month over time for 6 species and species groups: school shark (*Galeorhinus galeus*), smooth-hound (*Mustelus mustelus*), starry smooth-hound (*Mustelus asterias*), angel sharks (*Squatina spp.*), large-spotted dogfish (*Scyliorhinus stellaris*), and blunt-nose sixgill shark (*Hexanchus griseus*). We assumed that the chance of obtaining a certain number of individuals C_i each month followed a negative binomial distribution with mean μ_i

$$p(C_i; k; \mu_i) = \frac{\Gamma(C_i + \frac{1}{k})}{\Gamma(C_i + 1)\Gamma(\frac{1}{k})} \frac{(k\mu_i)^{C_i}}{(1 + k\mu_i)^{C_i + (\frac{1}{k})}}, forC_i = 0, 1, 2, ... \tag{3.2}$$

where Γ is the Gamma function and k is the dispersion parameter of the distribution. The linear predictor η is related to the mean μ_i by a log link function such that

$$\eta = log(\mu_i) = \beta_0 + \beta_y y_i \tag{3.3}$$

where y_i is the year of month_i. The dispersion parameter k was estimated by maximum likelihood.

The second stage of our analyses focused on the scientific trawl survey data. We combined two trawl surveys to construct a catch series ranging from 1972 to 2004. The first survey, a three years program of investigation of demersal resources carried out by the Italian Institute of Hydrobiology Fishery and Aquaculture, trawled 88 tows in the continental shelf and upper slope of the north part of the Tuscan archipelago (Fig. 3.1). The survey area was located between 43^oN and $43^o9'$N and between $9^o3'$E and $9^o83'$E. The area was divided into three statistical zones in which an equal number of tows were performed during the three years of operations (1972-1974). The boat used was a commercial trawler equipped with an Italian otter trawl net, and the majority of the tows were performed between 350 and 650 meters.

The second dataset came from the GRUND trawl surveys carried out in the statistical zones U2 and U3 in the upper Tyrrhenian sea. The GRUND program is an Italian trawl survey monitoring program of demersal resources conducted systematically each year along the Italian coasts (Relini 1998). The dataset consists of 1614 tows performed between the 42^{nd} and the 44^{th} parallel along the Tuscan coast, between 1985 and 2004. The tows were performed by using a random stratified sampling framework at depths between 0 and 800 meters.

We standardized the number of specimens caught in each tow by using the swept area of the net. As these two trawl surveys were not overlapping in time we could not test for a survey effect on catches. However, both the historical and GRUND surveys were carried out with commercial Italian trawls of a similar framework. Hence we assumed that differences in trawl performance between surveys were marginal with respect to the sampling variability of the species to model. We modelled the chance of obtaining a number of specimens C_i in each tow$_i$ (eqn. 3.2), such that the linear predictor η is related to the mean μ_i by a log link function

$$\eta = log(\mu_i) = \beta_0 + \beta_y y_i + \beta_d d_i + \beta_{sj} S_{ji} + \beta_{zj} Z_{ji} + log(A_i) \tag{3.4}$$

where y_i is the year of tow$_i$, d_i is the depth of tow$_i$, S_{ji} is the level j of the season for tow$_i$, and Z_{ji} is the level j of a categorical variable indicating the sector Z in which the tow$_i$ was performed. These two sectors reflect the working area of the GRUND operative units U2 and U3; β is the vector of parameters; A_i is the swept area which was treated as an offset variable.

Variables were removed from this full model by backward stepwise deletion according to the significance of the involved parameters, and the overall decrease of the Akiake Information Criterion (AIC) value for the model (Lindsey 2000; Venables and Ripley 2001). As above, the dispersion parameter k has been estimated by maximum likelihood for most species, however for some of these it was not possible due to the scarceness of the catches. In these cases we used dispersion parameters of a closely related species occurring in our dataset or a related species from analyses performed by Shepherd and Myers in the Gulf of Mexico (Shepherd and Myers 2005).

We analyzed the variation in abundance of the populations by dividing the species in two groups: those occurring in shallow water and those frequent in deeper grounds from 200 m to 800 m. In this way we were able to detect the effect of depth, and the consequent differential fishing pressure on the variation in abundance, and we could enclose most of the depth ranges of species characteristics of the two bathyal plains (Aldebert 1997; Massuti and Moranta 2003; Jukić-Peladic et al. 2001; Ungaro et al. 1998).

3.3 Results

All the considered species occurring in the tuna trap declined during the period by more than 90% in the 25 years of observations (Fig.3.2). The sharpest decline was that of *Galeorhinus galeus* which decreased in abundance by 99.97% (95%CI: more than 99.99% to 99.38%). The least declining species was *Mustelus mustelus* which declined by 94.38% (CI: 93.94% to 70.40%). The remaining group of sharks, except *Galeorhinus galeus* and *Mustelus asterias*, displayed an initial increasing trend in the early years of the tuna trap activity (Fig. 3.3). For these species, a quadratic model, in which the square of the year y_i was added to the original model in eqn. 3.3

$$\eta = log(\mu_i) = \beta_0 + \beta_y y_i + \beta_y (y_i)^2 \tag{3.5}$$

gave a better fit (table 3.1).

Nearly all the species started to decline after 1904. We ran the linear model from this point to calculate the degree of change over time. With this subset the instantaneous rate of change in abundance increased in magnitude for all the species. The relative change in abundance over time among the group of species varied too. The sharpest decline was shown by *Scyliorhinus stellaris.* All of the species except the group of angel sharks, which declined by 98.65%, declined by more than 99% their former abundance. *Galeorhinus galeus* and *Mustelus asterias* did not reach

Species	Original AIC	AIC
Hexanchus griseus	218.62	203.57
Mustelus mustelus	65.06	26.43
Squatina spp.	70.2	58.65
Scyliorhinus stellaris	64.58	62.3
Raja spp.	100.66	86.06

Table 3.1: Summary of the Akiake Information Criterion comparing the linear model of eqn. 3.4 with the quadratic model of eqn. 3.5

levels of statistical significance for their slope (p=0.05) (Fig. 3.4).

Thirty one species of elasmobranchs occurred in the series between 1972 and 2004. Most of them are strictly demersal species subject to fishing pressure by the local fisheries. We could not apply the model to a few species due to their rare occurrence in the surveys. We decided to analyze species that occurred in at least three years.

We estimated trends in abundance for 16 species of coastal elasmobranchs (Fig. 3.8). Due to the fact that the seventies' data were not representative of the continental shelf, we ran the analyses with the only GRUND surveys. In these 20 years of observations a total of 7 species declined significantly over time (Fig. 3.5). The sharpest decline was reached by speckled skate (*Raja polystigma*), which declined to extirpation; by large-spotted dogfish (*Scyliorhinus stellaris*) declining by 99.25% (95% CI: 99.61% to 98.54%) and by spiny dogfish (*Squalus acanthias*) declining by 89.27% (CI: 94.71% to 78.22%). Even species considered abundant in the region and assumed to be affected moderately by fishing pressure, showed fairly large rate of decline: small-spotted catshark (*Scyliorhinus canicula*) declined of 81.44% (CI: 90.44% to 63.87%), and blackmouth catshark (*Galeus melastomus*) by 73.07% (CI: 84.24% to 53.98%). In the same period, 7 other species increased in abundance. The largest increases were shown by longnose spurdog (*Squalus blainville*), longnosed skate (*Dipturus oxyrhincus*), bull ray (*Pteromylaeus bovinus*) and the common stingray (*Dasyatis pastinaca*). Moderate increases were detected for common torpedo (*Torpedo torpedo*) marbled torpedo (*Torpedo marmorata*) and brown skate (*Raja miraletus*) (Fig.3.8).

In the deep strata, we estimated trends in abundance for 22 species. Sixteen of them showed significant negative trends (Fig. 3.7), 7 species declined by more than 90% of their former abundance and a total of 13 species by more than 80% in 33 years.

The two species of angel sharks (*Squatina squatina* and *Squatina aculeata*) displayed the steepest negative rate of change by declining till extirpation. *S. squatina* and *S. aculeata* have not occurred in the series since the seventies surveys even though these constituted a big portion of elasmobranch landings in the region at the beginning of the last century (D'Ancona and Razzauti 1937; Biagi 1999).

Four species declined by more than 95% over the whole period: spiny dogfish (*Squalus acanthias*) by 99.26% (CI: 99.63% to 98.52%), longnose spurdog (*Squalus blainville*) by 98.16% (CI: 99.34% to 94.92%), angular roughshark (*Oxynotus centrina*) by 97.03% (CI: 98.61% to 93.68%) and speckled skate (*Raja polystigma*) by 95.31% (CI: 98.55% to 84.86%). Even non commercial species such as rabbit fish (*Chimaera montrosa*) declined precipitously in the period, with a reduction in abundance of 91.07% (CI: 95.68% to 81.60%).

As with *Squalus blainville*, two skates *Raja miraletus* and *Dipturus oxyrinchus* showed different trends than in shallower waters, by declining by 85.30% (CI: 95.12% to 55.89%) and 69.21% (CI: 83.06% to 44.05%) respectively. Only three species distinctly increased their population abundance: 9 times (CI: 1.86 to 43.61) for starry skate (*Raja asterias*), 16.25 times (CI: 7.81 to 38.09) for spotted skate (*Raja montagui*), 51.42 times (CI: 20.82 to 127.45) for shagreen skate (*Leucoraja fullonica*).

Variable	DF	Estimate	St.Err	t value	Pr $>\|t\|$	R-Square
Intercept	1	-0.01161	0.01320	-0.88	0.3864	0.3588
β_d	1	-1.73045	0.42957	-4.03	0.0004	

Table 3.2: Summary of the weighted regression analysis between the instantaneous rate of change in abundance per meter (β_d) and the instantaneous rate of change per year (β_y).

To attempt to explain the observed changes in the relative abundance of the species, we performed several correlation analyses between their biological traits and the rates of change over time. As often happens with elasmobranch species, we did not have all the required biological features for each investigated species, but maximum size, size at first maturity, and depth range of occurrence, are all easily retrievable parameters from the literature. These parameters are believed to strongly influence shark vulnerability since they affect the catchability, growth rate and availability to the fishery. Although most of the correlations were not significantly different from 0, a weighted linear regression analysis between the lateness of maturity of the species and their rate of change over time, where the weights of the variance were given by the standard errors of the rate of change estimates, gave a negative relationship for deep water elasmobranchs (Fig. 3.10), although the linear regression was substantially influenced by *Squatina squatina* (Cook's distance > 1, Montgomery et al. 2001). Lateness in maturity was expressed as the ratio between female size at first maturity and reported maximum length. No significant relationship was found for coastal species (Fig. 3.10). It appears that extremely vulnerable species are those that reach sexual maturity later in their life, while species that are relatively resistant, mature in earlier stages.

We were also concerned with the depth effect on the vulnerability of the species. Assuming that the fishing effort was more concentrated close to shore, we would have expected differential rate of changes in abundance over time for species occurring in shallow water and species more frequent in deeper grounds. By performing a weighted linear regression between the instantaneous rate of change per year β_y and the instantaneous rate of change per meter β_d, we found a negative relationship between the two parameters. In other words, within each stratum, sharks whose gradient of abundance over depth was steeper, declined faster than shark species more evenly distributed across depths (Fig. 3.9). However we did not reach levels of statistical significance at 95%. The regression was largely influenced by outliers such as *Raja polystigma*, *Squalus blainville*, and *Dipturus oxyrinchus*. Removing these species from the analysis produced a significant relationship between the two variables (table 3.2).

3.4 Discussion

During the last 100 years the Tuscan Archipelago has shown important changes in the elasmobranch community assemblage. The role of fishing appears quite evident from the results. The coastal aspect of fishing exploitation, shelf and upper slope grounds, is reflected by its effect on the elsmobranch populations. The elasmobranch community occurring in the coastal zones showed a drastic decrease in species diversity as well as decline in population abundance for the majority of species. In these waters declines in species abundance were already detectable as early as the beginning of the last century when the trawl fishing began to exploit the grounds off Tuscany. Among the 36 species occurring in the area before the 1930's, 17 species seem to be totally lost or declined under detectable levels (table 3.3). Most of the more abundantly landed species of the early century, *Squalus acanthias*, *Mustelus sp.*, *Squatina Squatina*, *Scyliorhinus sp. Dasyatis sp.*, *Myliobathis aquila*, *Pteromilaeus bovinus*, *Raja asterias* and *Raja clavata* (D'Ancona and Razzauti 1937), appear to to be the least occurring at the present. For many of them, the tuna trap landings showed strong decline in abundances, in some cases evidences of local extirpation.

When these data are compared with the analyses on trawl surveys, the resulting pictures is alarming. An entire family (Triakidae) seem to have disappeared from the zone. *Galeorhinus galeus* and *Mustelus asterias* were never reported in the trawl survey data. *Mustelus punctulatus* was captured only once in 1985. *Mustelus mustelus* occurred only in two years: once in 1985 and twice in 2001 only with juvenile specimens. The entire genus *Squatina* disappeared from the area about in the early 70's.

We were able to detect direct and indirect effects of fishing exploitation. Besides the decline in abundance of many species, we were able to detect increases in population abundance for others. In the first part of the century four demersal species occurring in the fish trap of Baratti initially increased in abundance as other species declined. Previous observations (Vacchi et al. 2000) and our unpublished analyses indicate that the fish trap landings also reported a drastic decline of big predators (Carcharhinids and Lamnids). *Carcharodon carcharias*, *Isurus oxyrhincus*, *Lamna nasus*, *Prionace galuca*, *Carcharhinus plumbeus* and *Carcharhinus melanopterus* were sporadically caught even by trawl fishing in the first half of the century (D'Ancona and Razzauti 1937). The pelagic ecology of most of them suggest a low catchability with trawl gears. Thus we can infer a greater abundance of these predators in the past given the fact that these species are never reported as by-catch by trawlers in recent years. Large sharks are among the most important predators of other sharks and rays (Cortés 1999; Cliff 1995; Cliff and Dudley 1991; Myers et al. 2007; Lucifora et al. 2009). Cannibalism is a frequent behavior of many large sharks. For some species, adults constitutes the principal predators of juvenile specimens (Heithaus 2004). Their decline could have favored the increase of habitual elasmobranch preys or could have increased their juvenile survival which constitutes one of the most sensitive life history parameters for response of shark to fishing exploitation (Cortés 2002). The increase of *Squalus blainville*, *Pteromylaeus bovinus*, *Dasiatis pastinaca* and the two eletric rays (*Torpedo torpedo* and *Torpedo marmorata*) detected by trawl surveys in the coastal waters could reflect a predator release effect as well as a reduction of competitors.

Those phenomena appeared buffered in deeper waters where we have a greater diversity in species, and the persistence of species extirpated in shallower waters. However, *Squalus blainville* is increasing in coastal waters but shows a negative trend in abundance offshore. Similarly, *Dipturus oxyrhincus*, a large skate with a possibly high catchability, is increasing in more exploited shallow waters and declining in the upper slope. These species may still suffer fishing pressure across the area, but benefit from changes in inter-specific competition and predation by overexploited populations in shallow waters.

To explain the differential response of all the species to fishing exploitation, different factors have to be taken into account. Life history parameters and size play a major role on species' vulnerability and exposure to fishing exploitation. We detected an inverse relationship between lateness in maturity and the year effect parameters of the change in abundance over time in deep waters. All species lost in the area were relatively larger than those still present. At the same time, such a loss in diversity restricted the ranges of variables to be tested for their influence in explaining patterns of change detected in the community. In fact, the effect of size appeared weaker in explaining the relative response to fishing of the remaining species, and no relationship between lateness of maturity and year effect was found in coastal areas. We could not detect statistically significant correlations between rates of change and age at maturity, and depth range as well. Limitations in the availability and reliability of life history parameters for many species of elasmobranchs, and the restrictiveness of the analyzed data-set might also reduce the validity of our analyses.

The strong reduction of *Raja polystigma* is indicative of this confluence of factors.

This is a small endemic species of the Mediterranean Sea. Its depth range appears limited from 100 to 400 meters. Its size at maturity appears to be close to its maximum size. These characteristics suggest that the species would be extremely sensitive to increases in its mortality rate and would not be able to "escape" fishing exploitation by shifting its center of occurrence to deeper grounds as well as other species may have done (*Raja asterias* and *Raja montagui*). All of its features would confirm the strong declining trend the species showed in the data.

It is worthwhile to mention that identification problems could also have contributed to the outcome for *Raja polystigma*. Morphologic similarity of this species and *Raja montagui* could contribute to misidentify the specimens during the surveys. Serena and coauthors claimed that all the samples of *Raja montagui* collected in the GRUND surveys, carried out in the Northern Tyrrhenian Sea, could be misidentified *Raja polystigma* (Serena et al. 2005).

We performed our analyses by relying on the data-set we had, since we don't have any evidence or test of this misidentification. However to look for possible differences in the results, we grouped together the two species in a unique group we called *Raja polystigma b*. The results confirm a negative trend in the coastal water and a positive change in deeper grounds. However the outcomes are largely driven by the greater abundance of *Raja montagui*. We believe that accurate monitoring programs, genetic analyses, a taxonomic reassessment of the species, and conservation action need to be taken for *Raja polystigma* in the immediate period.

Finally, fishermen behavior plays an important role on the outcome of the analyses. Species that could take refuge in less exploited zones, whether it was at deeper grounds or unexploited areas, resisted better to exploitation than more spatially constrained species. *Raja asterias* showed contrasting trends in shallow and deep waters. This is a heavily exploited species in coastal areas by several fishing gears (Abella and Serena 2002), but it benefits from low fishing pressure at deeper grounds and near the continental shelf of Corsica which could act as refuge area and recruitment reserve (Walker 1998). Graham and coauthors in 2001, by comparing relative abundance of demersal sharks in the continental shelf and upper slope of New South Wales (Australia), observed that the species that did not show outstanding declines in abundance were those whose area of occurrence was beyond the usual borders of the trawl fishing zones. Grounds difficult for trawling could act as recruitment zones for the nearby exploitable locations (Graham et al. 2001).

The plot in Fig. 3.9 suggests a negative correlation between the year effect and the depth effect in the explanation of the variability in abundance of the species. In other words the more the species is spatially constrained in depth the more it would suffer from fishing exploitation. The low R^2 in table 3.2 could be attributable to the indirect effect of fishing through the increase of some species taking advantages of the reduced competition and predation. Possibly a clearer pattern would have been detected if we analyzed the response of the community at the very beginning of exploitation.

The two electric rays (*Torpedo torpedo* and *Torpedo marmorata*) and *Galeus melastomus* could have benefitted from the fact they are being discarded at sea by fishermen (Minervini et al. 1985; Abella and Serena 2002). However other non targeted species such as *Chimaera monstrosa* and *Etmopterus spinax* do show significant declines in abundance over time. For those, interspecific relationships and a different degree of survival after release may be keys to understand their changing abundance over time.

3.5 Conclusions

For managerial purposes finding clear patterns in multispecies fisheries is paramount for preserving ecosystem structure and function. Recognizing important components of marine communities (e.g. keystone species) is necessary to develop efficient management actions toward those species recognized to have a structural role in the community, and whose conservation would ensure a long-term persistence of ecosystem function and services (Power et al. Sep 1996). To date, it is still not clear what the role of sharks is in the marine community (Stevens et al. 2000); whether or not as top predators, sharks contribute to ecosystem structuring through top-down control effects. Recent results from food-web model analyses indicate that shark overfishing could contribute to ecosystem regime shifts by triggering trophic cascades (Bascompte et al. 2005).

It is not easy to find clear patterns in the results of our analyses. We analyzed a small fraction of the Mediterranean Sea. The pool of data we were able to analyze didn't allow us to test many important ecological questions of the vulnerability of elasmobranch to fishing pressure. However our results are worrisome. We found cases of local extirpation before the beginning of the industrial fishing (*Mustelus asterias*, *Galeorhinus galeus*, *Dipturus batis*). In recent years, many of the species declined by more than 90% of their former abundance over 33 years in deep waters, and more than 80% over 20 years in coastal ecosystems. Others increased in abundance possibly through indirect effect of fishing exploitation (predator or competition release) and we are still unaware of the effect these changes could bring to the entire ecosystem.

We successfully applied generalized linear models to catch series coming from commercial landings and scientific surveys. We believe this is a useful tool for detecting trends otherwise obscured by the strong variability of the catches. We highlighted the need to use historical data to assess the impact of fishery on elasmobranch species. Important ecosystem changes were going on already at the beginning of the last century. Species abundant in the last century were rarely caught in recent surveys. Their decline could have significantly affected the species assemblage of the present elasmobranch community. These results would have appeared more puzzling by considering only recent data.

Therefore, considering ours and concordant results coming from other sectors of the basin (Gulf of Lion and Adriatic Sea) (Aldebert 1997; Jukić-Peladic et al. 2001), we believe elasmobranchs require immediate conservation action in the Mediterranean Sea. To accomplish this task we need to provide solid numbers about their status by performing analyses at basin scale. We need to use all the survey data available (GRUND and MEDITS) and all the historical scattered information we can find in all Mediterranean sectors. Also we need to fill the gap in biological and ecological parameters the chondrichthyans have in relation to other marine animals, especially for populations occurring in the basin which are thought to differ in their life history parameters from other sectors of the globe.

Species	Max size (cm)	Coastal waters	Deep waters	Mediterranean official status
Hexanchus griseus	500	absent	decline	vulnerable species
Dasyatis centroura	396	———- absent ———-		threatened species
Myliobatis aquila	260	decline	out of range	vulnerable species
Pteromylaeus bovinus	260	increase	out of range	threatened species
Dasyatis pastinaca	250	increase	out of range	vulnerable species
Dipturus batis	250	———- absent ———-		threatened species/locally disappeared
Galeorhinus galeus	200	———- absent ———-		vulnerable species
Rostroraja alba	200	—— disappeared ——		vulnerable species
Squatina aculeata	200	—— disappeared ——		threatened species
Squatina oculata	200	———- absent ———-		threatened species
Pteroplatytrygon violacea	190	———- absent ———-		vulnerable species
Dalatias licha	180	out of range	decline	vulnerable species
Mustelus punctulatus	180	—— disappeared ——		vulnerable species
Squatina squatina	180	—— disappeared ——		vulnerable species
Torpedo nobiliana	180	—— disappeared ——		vulnerable species
Mustelus mustelus	160	—— disappeared ——		vulnerable species
Centrophorus granulosus	150	absent	decline	vulnerable species
Dipturus oxyrinchus	150	increase	decline	vulnerable species
Oxynotus centrina	150	absent	disappeared	threatened species
Scyliorhinus stellaris	150	decline	decline	vulnerable species
Mustelus asterias	140	———- absent ———-		vulnerable species
Squalus acanthias	140	decline	decline	vulnerable species
Heptranchias perlo	138	—— disappeared ——		threatened species
Raja brachyura	125	———- absent ———-		occasional/rare species
Leucoraja circularis	120	absent	decline	occasional/rare species
Leucoraja undulata	120	———- absent ———-		occasional/rare species
Raja clavata	110	decline	increase*	stable biomass species
Raja fullonica	110	absent	increase	occasional/rare species
Squalus blainville	110	increase	decline	vulnerable species
Chimaera monstrosa	100	out of range	decline	stable biomass
Torpedo marmorata	100	increase	increase	vulnerable species
Raja asterias	80	decline*	increase	stable biomass species
Raja montagui	80	decline*	increase	stable biomass species
Scyliorhinus canicula	80	decline	decline	abundant not depleted
Etmopterus spinax	60	out of range	decline	stable biomass
Raja miraletus	60	increase	decline	stable biomass species
Raja polystigma	60	disappeared	disappeared	needs to be investigated
Torpedo torpedo	60	increase	out of range	vulnerable species
Galeus melastomus	52	decline	stable	very common not depleted

Table 3.3: Table showing the status of elasmobranch species observed in the investigated area since the beginning of the 20^{th} century. The term **absent** means the species was recorded in the literature but was not recorded in the analyzed trawl surveys; **out of range**: the species does not occur in the specified range of depths; **disappeared**: the species was recorded in the data series of trawl surveys but disappeared from the catches or are under detectable levels; **decline**: the species is declining in population abundance; **increase**: the species is increasing in population abundance. The species are sorted in descending order form the largest (maximum size) to the smallest. Asterisks denote not significant values. Mediterranean official status refer to the reported conservation and exploitation status of the considered species in the basin (Serena 2005)

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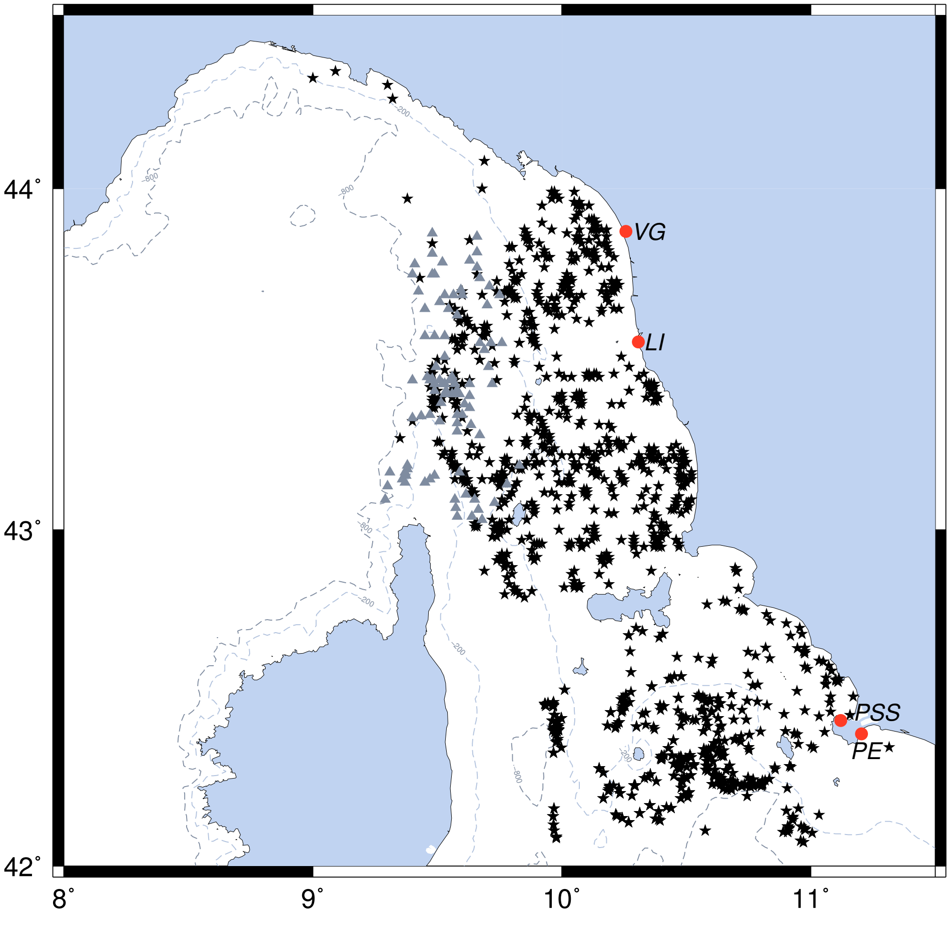
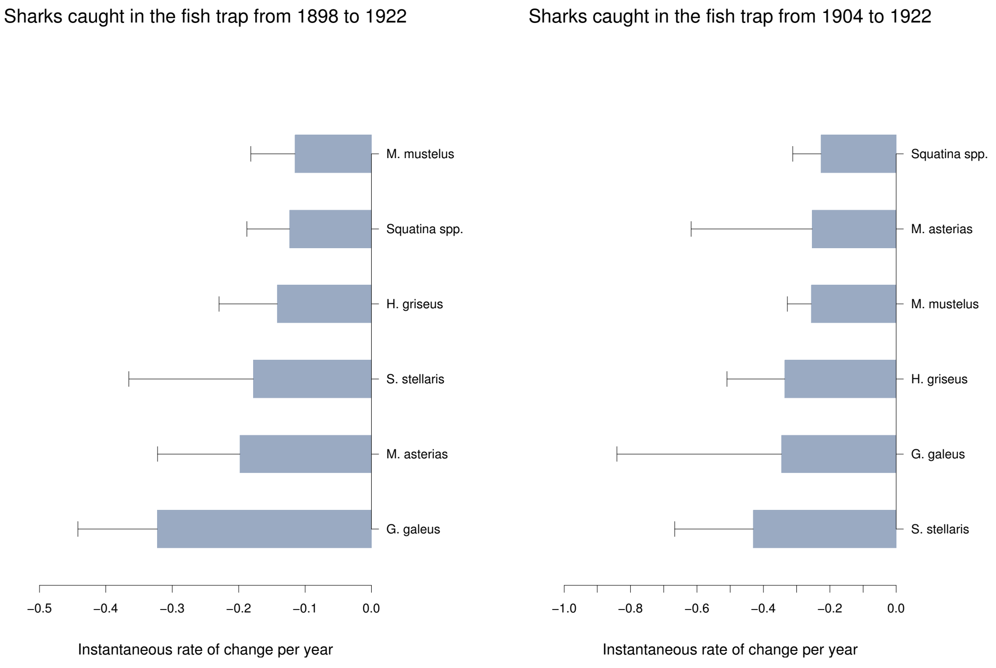


Figure 3.1: Map of the tows used as source of data in the investigated area. Triangles refer to the seventies surveys, stars refer to the GRUND surveys. Red dots indicate the major ports in the area: VG = Viareggio; LI = Livorno; PSS = Porto Santo Stefano; and PE = Porto Ercole.



(a) (b)

Figure 3.2: Rates of change in abundance per year of six demersal elasmobranchs occurring in the fish trap of Baratti. The horizontal segments at the end of the bars correspond to the 95% confidence interval of the relative rates. (a) refers to the whole time period, (b) from 1904 to 1922.

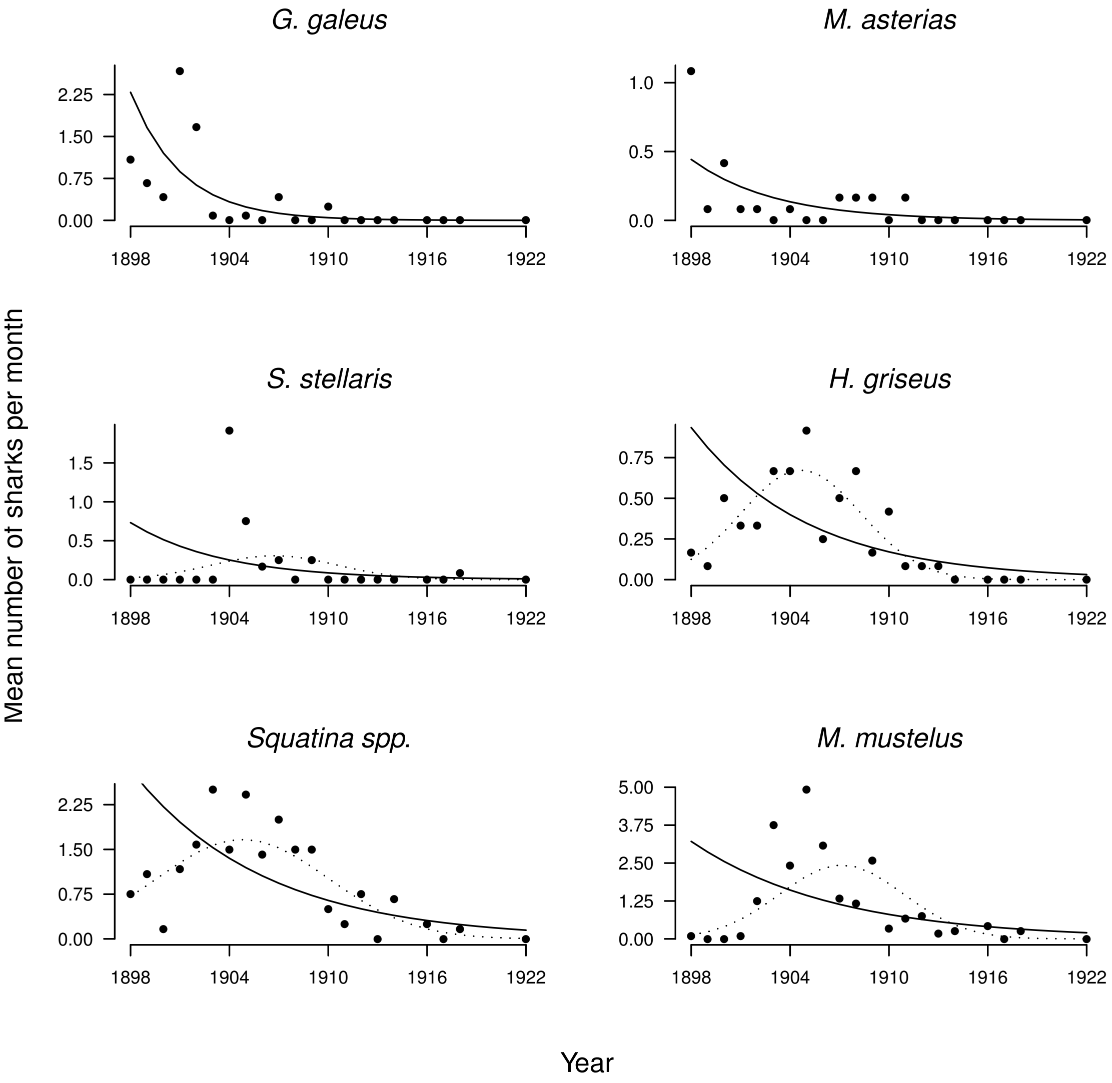


Figure 3.3: Estimated trends over time of the six demersal species of sharks occurred in the fish trap of Baratti from 1898 to 1922. Continuous lines represent the predicted values from the linear model; dotted lines represent the predicted values fom the quadratic model; points are the yearly means of the montly production for a given species.

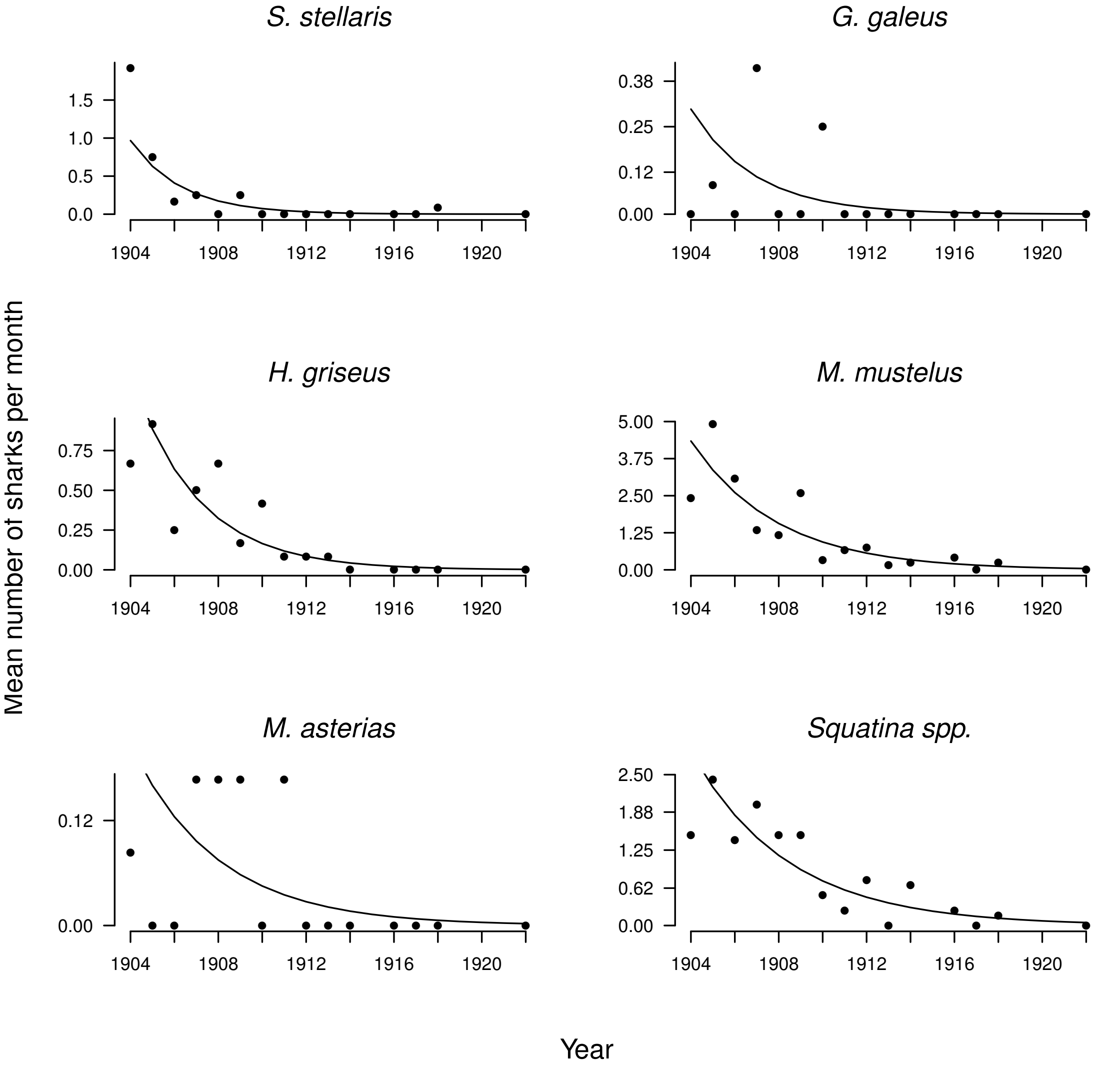


Figure 3.4: Estimated trends over time of the six demersal species of sharks occurred in the fish trap of Baratti from 1904 to 1922. Lines represent the estimated values of the linear model; points are the yearly means of the montly production for a given species.

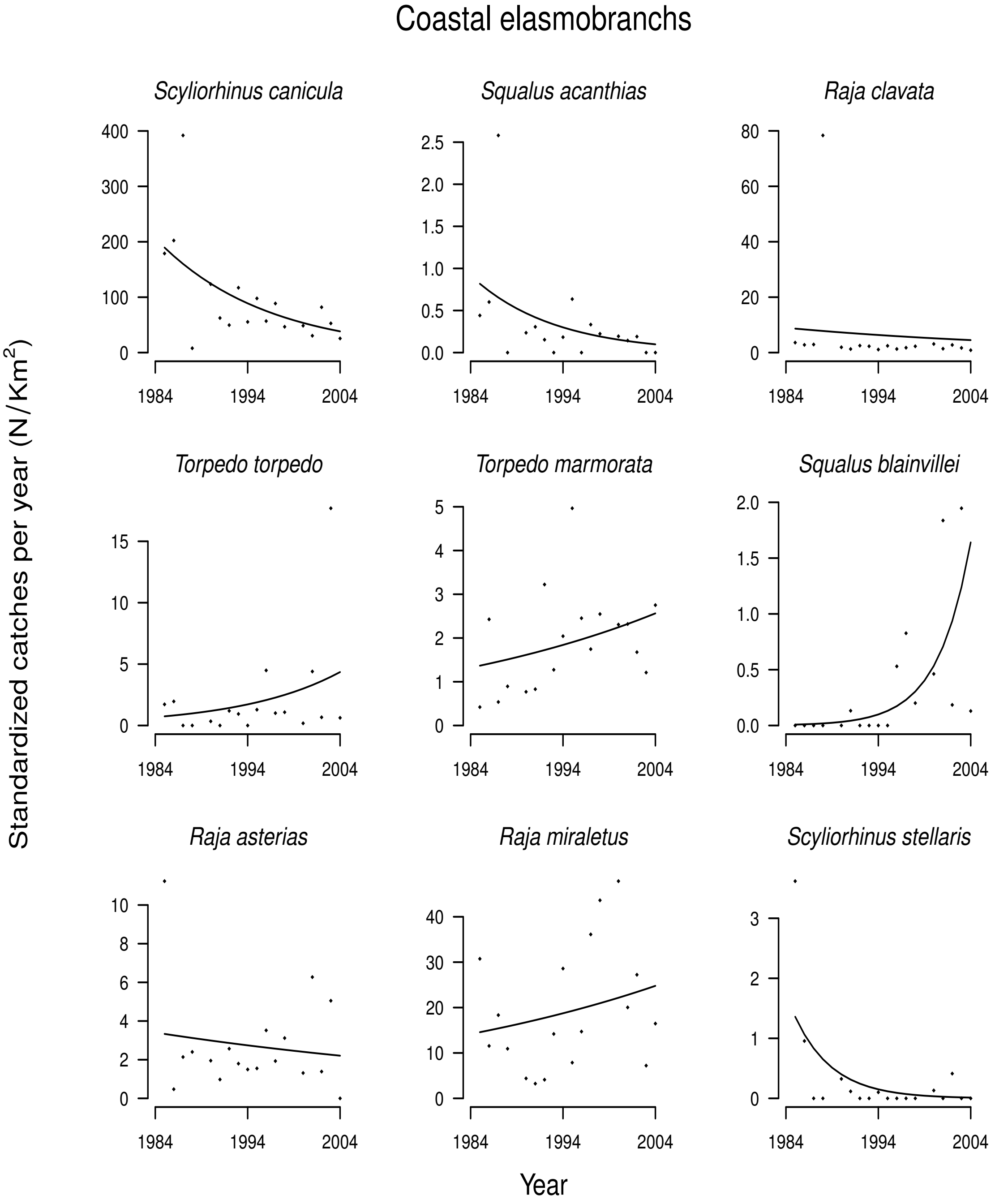


Figure 3.5: Variation in abundance of 9 coastal elasmobranch species (the most abundant and statistically significant). The models consider only the GRUND data series (1985-2004). Points refer to the yearly mean of the standardized catches in number of sharks per square kilometer.

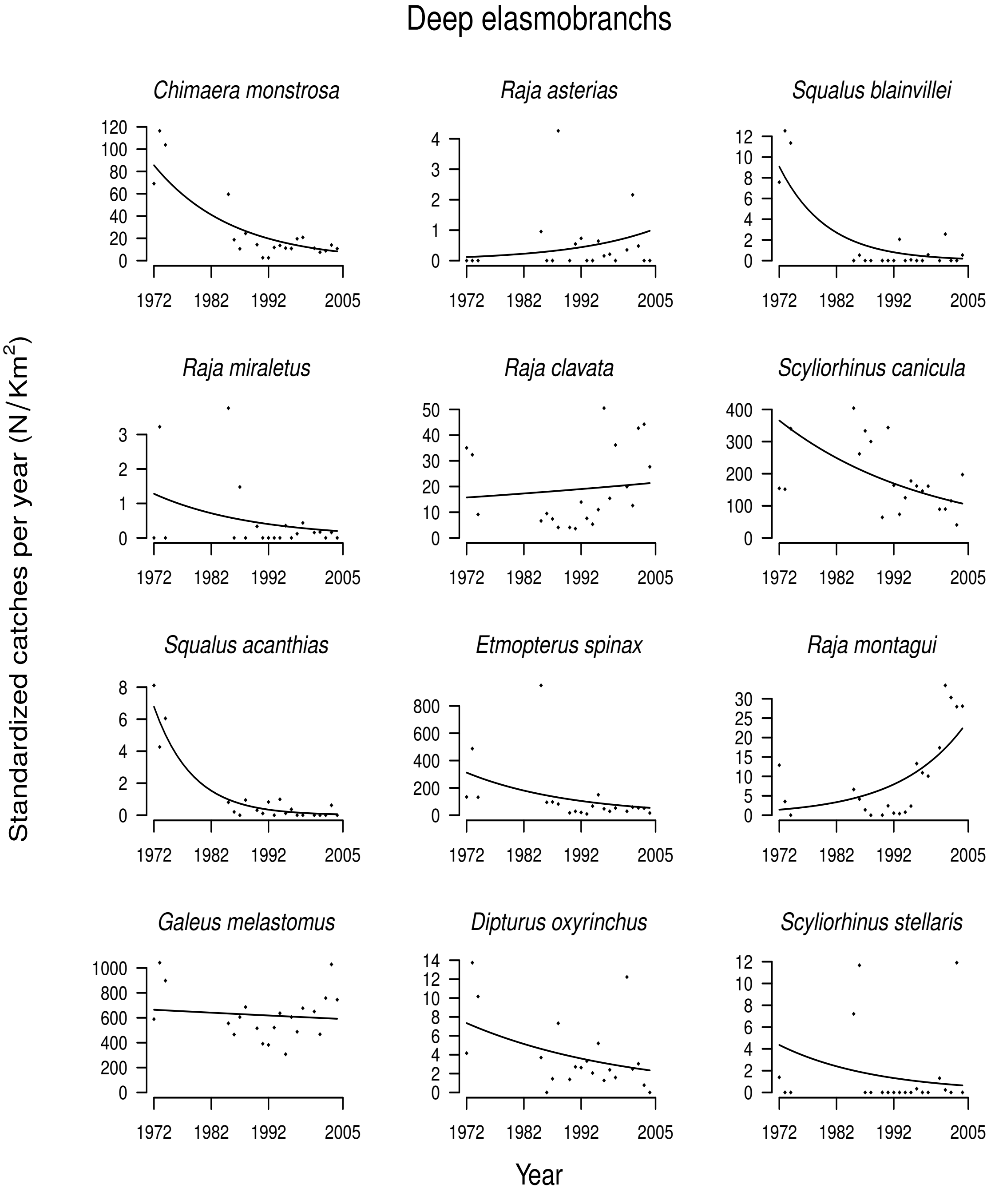


Figure 3.6: Variation in abundance of twelve elasmobranchs occurring in the deep strata (the most abundant and statistically significant). The models consider the whole data series coming from trawl surveys from 1972 to 2004. Points refer to the yearly mean of standardized catches in number of sharks per square kilometer.

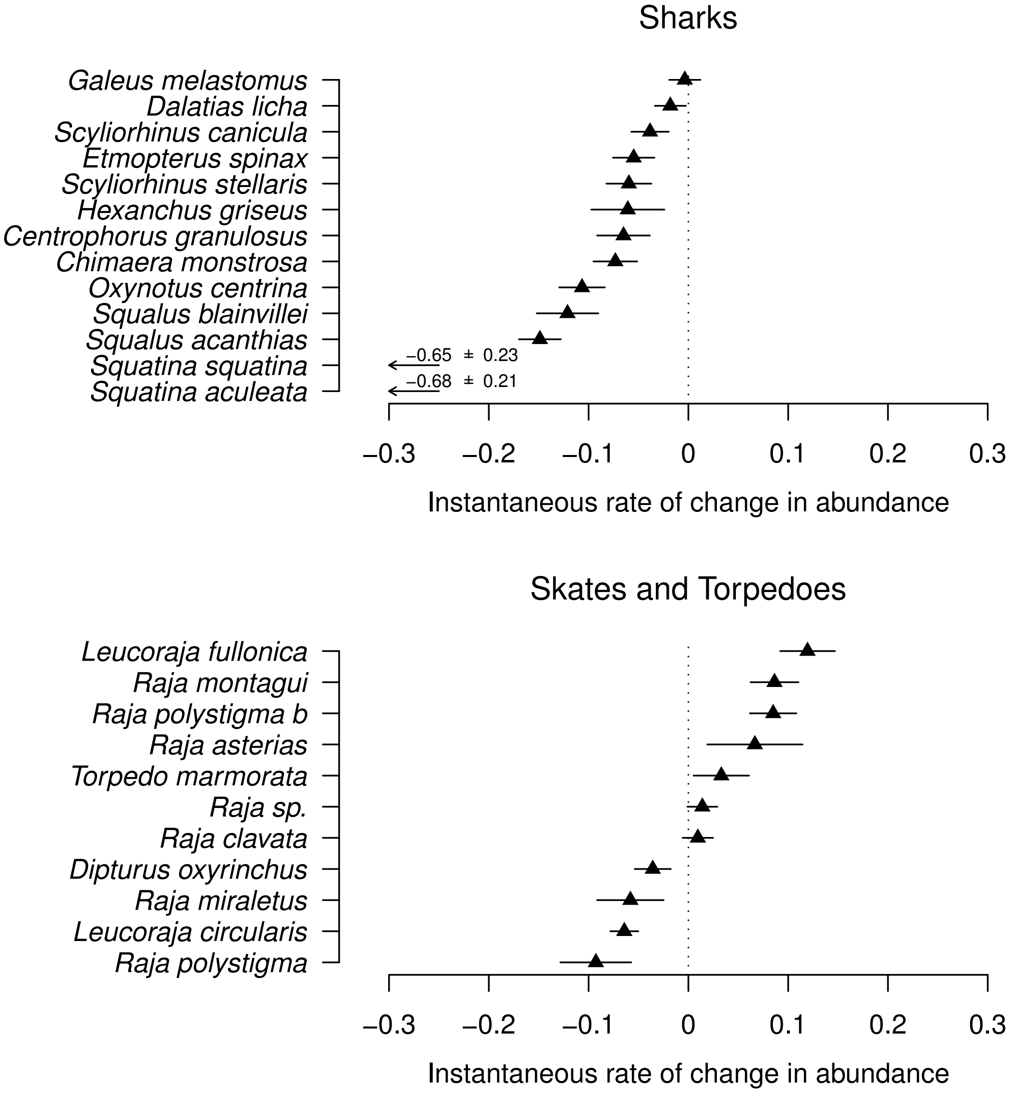


Figure 3.7: Instantaneus rate of change in abundance for elasmobranch species occurring in depths between 200 and 800 meters. The segments refer to the 95% Wald confidence intervals of the parameter estimates for the year effect.

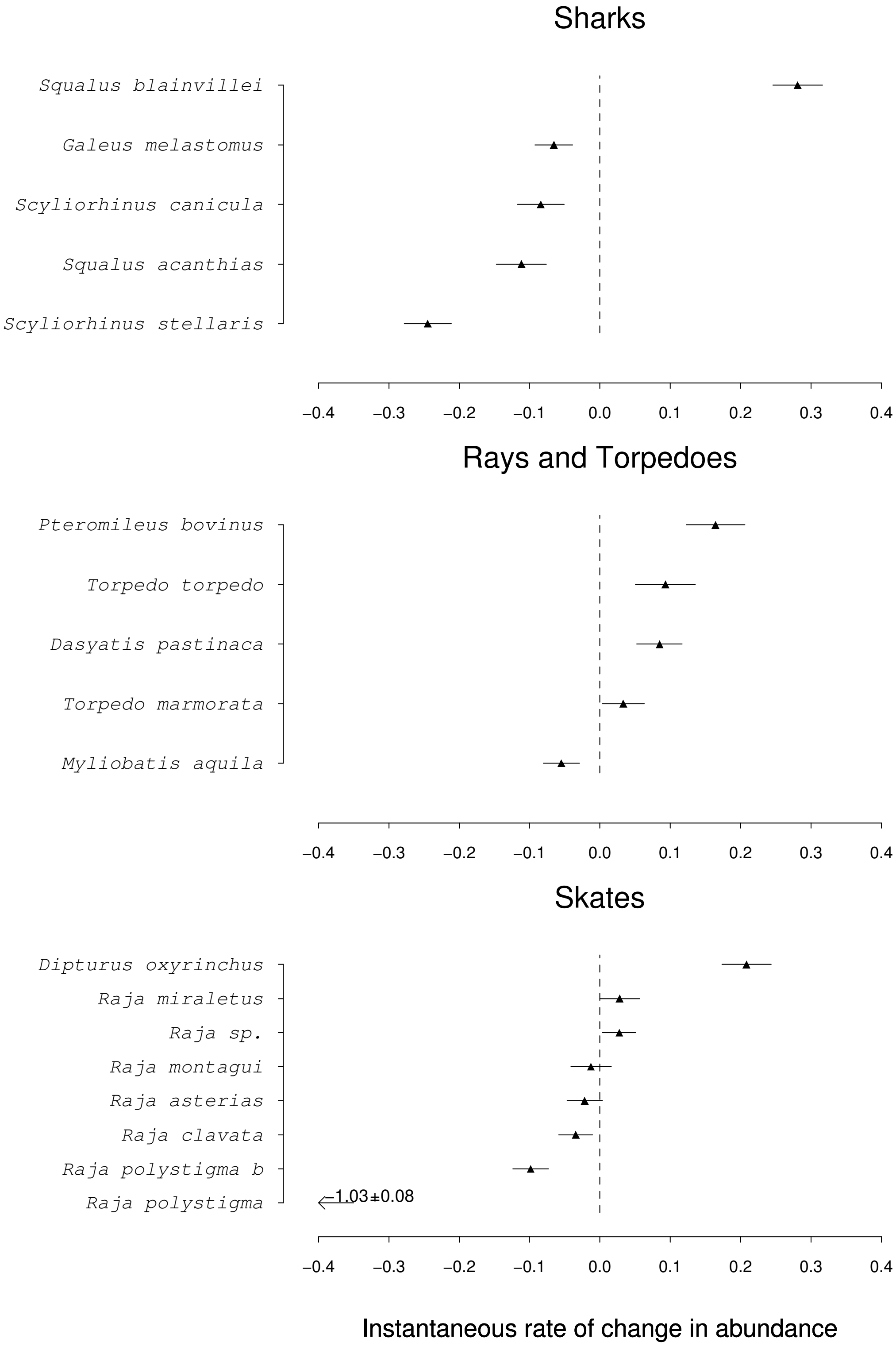


Figure 3.8: Instantaneous rate of change in abundance for elasmobranch species occurring in depths between 0 and 200 meters. The segments refer to the 95% Wald confidence intervals of the parameter estimates for the year effect.

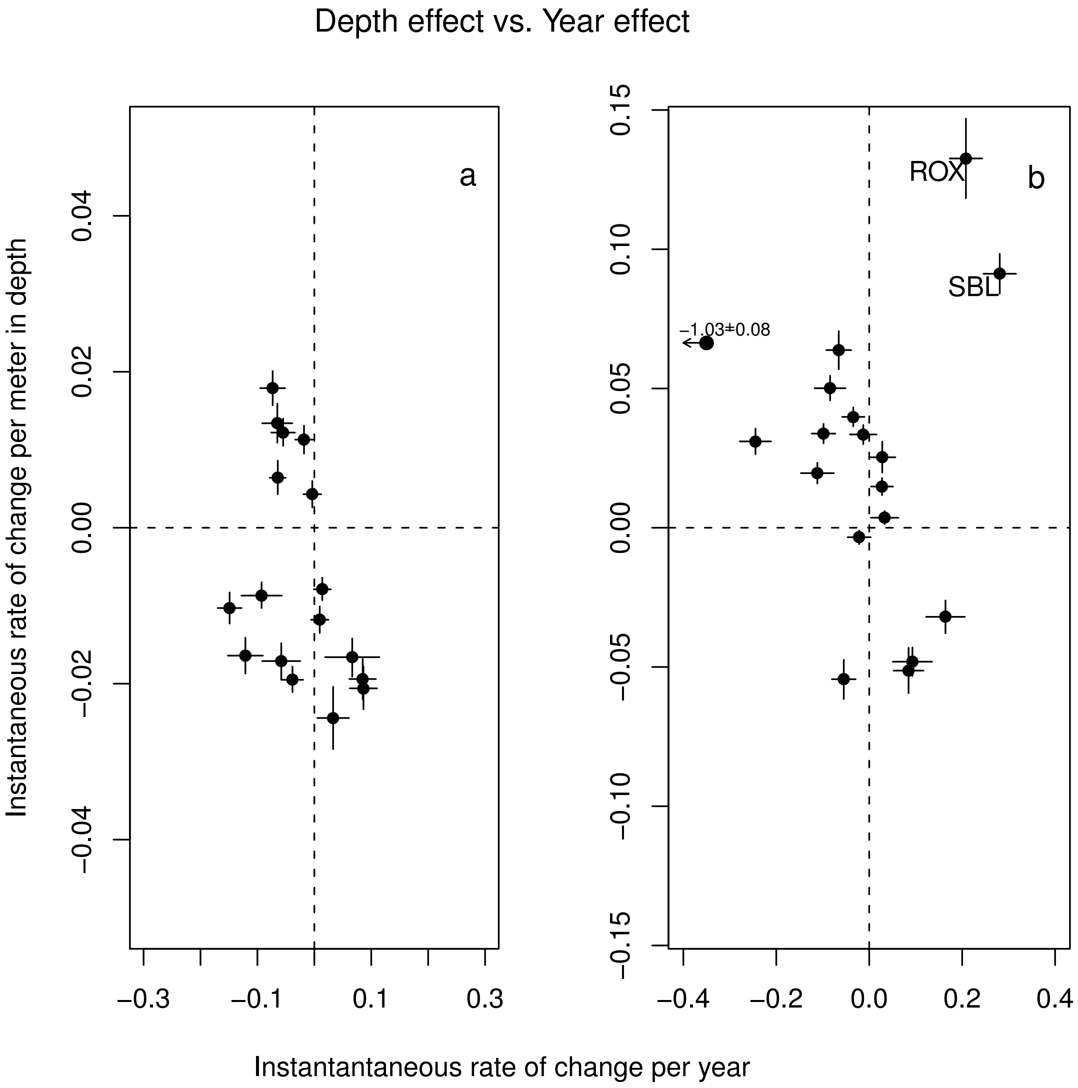


Figure 3.9: Rates of change in abundance per meter plotted against rates of change per year. Vertical and horizontal segments show the 95% confidence interval of the relative rates. In (a) points refer to deep water species, in (b) points refer to species occurring in shallow waters. Outliers are indicated by their species code: ROX - *Dipturus oxyrinchus*; SBL - *Squalus blainville.*

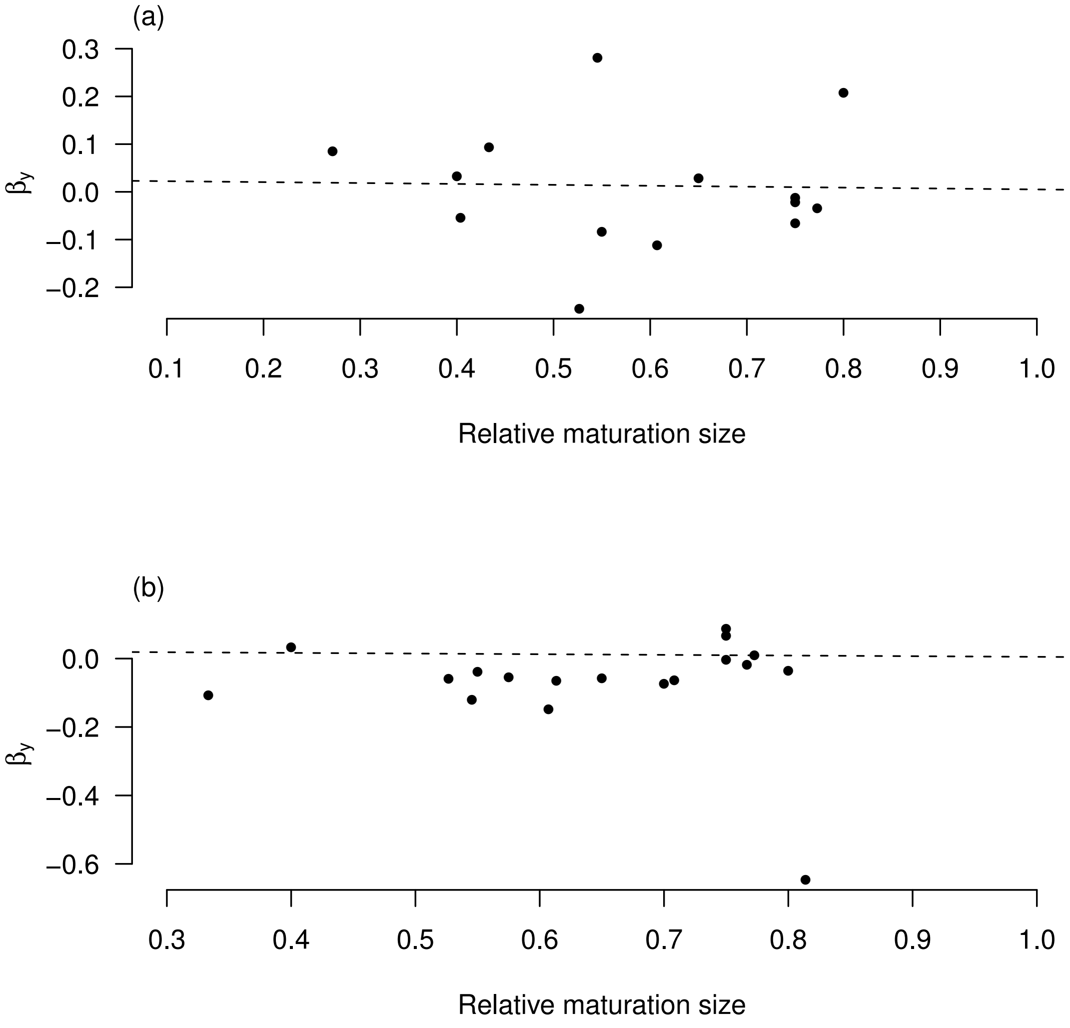


Figure 3.10: Weighted regression analyses between rate of change in abundance over time (β_y) and the ratio between the female size at maturity and the maximum total size of the species (Relative maturation size). (a) coastal elasmobranchs (R^2 = 0.0005, slope = -0.02, p-value = 0.93); (b) deep elasmobranchs (R^2 = 0.34, slope = -1.28, p-value = 0.01).

Chapter 4

Long-Term Ecological Change in a Meso-Predator Community in Response to Prolonged Human Disturbance

4.1 Introduction

Analyses of exploited fish communities in coastal, demersal and pelagic ecosystems have revealed that elasmobranch diversity and abundance can drop considerably after only short periods of fishing (Ferretti et al. 2010; Baum et al. 2003; Graham et al. 2001). In the northwest Atlantic, abundance of 18 large pelagic and coastal sharks declined by 49-89% in less than 15 years (Baum et al. 2003). In South Africa, populations of large coastal sharks were reduced by 27 to >99% after 20 years of shark netting programs (Ferretti et al. 2010). In Southeast Australia, demersal elasmobranch catch rates declined by >80% after 20 years of trawling (Graham et al. 2001). Industrial trawl fisheries in particular have strong direct and indirect effects on demersal communities by targeting a wide range of species, producing a high amount of by-catch, and destroying complex seafloor habitats (Watling and Norse 1998; Jennings and Kaiser 1998). However, not only exploitation itself but also different life-history characteristics and compensatory population responses such as predation and competition release can cause shifts in the overall community composition.

Elasmobranchs have generally low productivity due to their life-history characteristics. Most species have a late age at maturity, low fecundity, slow growth, and long gestation periods, which result in a very low intrinsic rate of population increase r and thus a low capacity to sustain exploitation (Smith et al. 1998; 2007; Myers and Worm 2005; García et al. 2008). However there is variability among species; some species such as *Mustelus californicus* have a value of r as high as 14% per year, while others such as *Squalus acanthias* as low as 1.7% (Smith et al. 1998). Differences in

r explained observed changes in abundance and composition of some exploited elasmobranch communities (Walker and Hislop 1998; Baum and Myers 2004). In others, however, r alone was not sufficient to explain observed changes. Rather, differential exposure to fishing (Shepherd and Myers 2005; Walker 1998; Graham et al. 2001), different catchability among species (Duvly et al. 2003), and release from predation (Shepherd and Myers 2005; Myers et al. 2007) and competition (Hobday et al. 1999; Dulvy et al. 2000) have been suggested to play an important role in population trajectories and shifts in community structure.

Predator declines are crucial in explaining the dynamics of meso-predators both in aquatic and terrestrial ecosystems (Ritchie and Johnson 2009). Among elasmobranchs, large sharks are the main predators of smaller species (Wetherbee and Cortes 2004). Thus in response to the decline of large predatory sharks, smaller elasmobranchs have been increasing on both sides of the North Atlantic (Fogarty and Murawski 1998; Dulvy et al. 2000; Myers et al. 2007), in the Gulf of Mexico (Shepherd and Myers 2005), Mediterranean Sea (Ferretti et al. 2005), North Pacific (Levin et al. 2006), Indian Ocean (van der Elst 1979; Pradervand et al. 2007) and around Australia (Graham et al. 2001). Yet, empirical evidence for a causal relationship is limited and controversial (Shepherd and Myers 2005; Myers et al. 2007; van der Elst 1979; Dudley and Cliff 1993), partly due to the unclear mechanism behind these changes. As predators decline, prey benefit from reduced direct killing (reduced natural mortality) but also from a reduced risk of being predated (Heithaus et al. 2008a; Ritchie and Johnson 2009). It has been suggested that risk effects may play a larger role on predator-prey dynamics than direct killing, especially for long-lived meso-predators (Heithaus et al. 2008a), yet they are difficult to study and quantify (Frid et al. 2008).

Competition has also been repeatedly suggested as the cause of changes in community structure in many demersal ecosystems (Fogarty and Murawski 1998; Hobday et al. 1999; Dulvy et al. 2000; Rogers and Ellis 2000). However, none of these studies tested the presence of such interspecific interactions empirically, and in some cases new empirical evidence confuted the occurrence of competitive effects (Frisk et al. 2008). Unfortunately, detecting competition in large marine ecosystems is a challenging task due to the impracticability to perform controlled experiments with large animals competing for food, space and other limiting resources (Connell 1983).

The Adriatic Sea is a semi-enclosed basin in the Mediterranean that has been exploited for thousands of years (Hoffmann 2005; Lotze et al. 2006). Over the past 50-200 years, the Adriatic Sea has experienced a dramatic reduction of large marine predators including large sharks, pinnipeds and cetaceans (Ninni 1912; Marchesetti 1882; Faber 1883; Ferretti et al. 2008; Bearzi et al. 2004) due to intensive exploitation, direct culling and pollution (Bearzi et al. 2004; Ferretti et al. 2008; Pastrovic 1913; Marchesetti 1882; Faber 1883). Moreover, its extensive continental shelf and accessible fishing grounds allowed the development of large fisheries for shellfish and groundfish (Bombace 1993; Mannini et al. 2005). Yet historically, fishing pressure has been unevenly distributed. While Italian waters on the western side have been enduring extremely high exploitation from high-capacity fishing fleets, the eastern side sustained a much lighter perturbation over past centuries (Fortibuoni 2010). Today the Adriatic demersal fleet (classified as trawlers and otter trawlers) counts 2437 boats. Italy registers 1420 boats, while 1017 are fishing in Slovenia, Croatia, Serbia and Montenegro, and Albania (Casale et al. 2004; Accadia and Franquesa 2006). Observer data revealed that Italian fishers tend to operate close to the Croatian borders where yields are higher (Casale et al. 2004).

The long history of exploitation, and spatio-temporal contrasts of perturbation between the eastern and western side, made the Adriatic Sea an ideal region to analyze the response of fish communities to exploitation over long time scales and across different exploitation regimes. Here, we used data from five published and unpublished scientific trawl surveys carried out in the Adriatic Sea since 1948 to analyze patterns of change in demersal elasmobranch populations. The different surveys were combined and standardized using generalized linear models controlling for technological and environmental covariates. Within a multi model information theoretic approach (Burnham and Anderson 2002), we extracted species-specific long-term trends of population abundance for 33 species of sharks and rays. We then used life-history characteristics, fishing effort data, and historical fishing information to explain the observed relative trajectories. We were interested in revealing the main drivers of change, whether the collapse of large predatory sharks triggered mesopredator releases as observed in other parts of the world, and if there was a reshuffling of the elasmobranch community composition due to competitive interactions.

4.2 Methods

We assembled a dataset of five bottom trawl surveys carried out in the Adriatic Sea between 1948 and 2005 for a total of 2670 tows. Three surveys named (or we identified as) Hvar (1948-1949), Grund (1994-1995), and Medits (1994-2005) covered large portions of the basin extending beyond national borders, while two we called Jukic (1963-1971) and Zupanovic (1956-1957) were more locally confined to Croatian waters of the central Adriatic Sea (Fig. 4.1)

Trawl surveys are sampling programs in which a certain number of fishing operations (tows) are performed over a designated area to collect biological information and indices of abundance of sampled species. Each sampling event consists in towing a cone shaped net for usually half an hour behind the vessel in contact with the seabed to collect all the organisms swimming over or firmly associated with the bottom. Sampling schemes as in Medits and Grund followed a random allocation of tows whose number was proportional to the spatial extent of each depth strata in the Adriatic. For the other programs, position of sampling operations were allocated homogeneously over the designated region and the number of tows reflected more logistics (e.g. ground suitability) and expenses in determining stations rather than sampling requirements. A brief description of each survey is given in the supplementary material (Appendix). Correspondent number of tows, time span, area coverage and technological details of vessels and gears used are given in Tables 4.1 and 4.2.

We extracted all data on elasmobranch species (sharks, rays, skates, and chimeras) detected in the different survey data sets.

4.2.1 Model Structure

Catch standardization was performed with Generalized Linear Models (GLMs) (McCullagh and Nelder 1999). We assumed that for any species, the chance of obtaining a certain number of individuals in a given tow_i followed a negative binomial distribution with mean μ_i and variance $\mu_i + \mu_i^2 k$ (Hilbe 2007), where k is a dispersion parameter estimated from the data. We modeled μ_i as a function of a number of covariates characterizing each tow, assuming a logarithmic function for the link between the linear predictor and μ,

$$\eta = log(\mu_i) = \alpha + XB + log(A_i), \tag{4.1}$$

where η is the linear predictor, α is the intercept, X the matrix of covariates affecting the variability of μ_i, B the vector of their relative parameters, and A_i is the swept area, treated as an offset. The area swept by each trawling operation was provided only in the Medits data. For the other surveys we estimated it by using technological gear configurations, trawling speed, and indirect measures of trawl efficiency extracted from the literature (Appendix).

We did not have the same set of covariates for each survey, and not all variables were expressed in the same format. Depth (m, identified by the mean point of each trawl path, continuous), latitude (decimal degrees, continuous), longitude (decimal degrees, continuous), season (linearized function of Julian day, see below) and bottom characteristics (categorical or continuous, details below) were available for all surveys. Year was included only in the Jukic and Medits models (continuous variable) while for the other surveys, given that we only had two years of observations each, we assumed that yearly differences in catches were negligible. Temperature (°C, continuous) and salinity (‰, continuous) were available only for Hvar surveys, and were measured at about 5 meters above the trawl stations (Karlovac 1956). Survey team (categorical) was included in the models for Medits catches to discriminate samples carried out by Slovenian, Croatian and Italian research institutes.

Since animal populations are expected to show higher densities around optimal values of environmental variables (Krebs 2001), we included quadratic functions of depth, temperature, salinity, latitude and longitude in the matrix of covariates. In addition, we included a similar function for year (in Medits) to test complex temporal trajectories of the species that might suggest responses to changing conditions of fishing, competition or predation. However, as we dealt with animals characterized by slow population dynamics, and had a relatively limited temporal observation window (11 years), we excluded the occurrence of more complex trajectories characterized by higher order polynomials.

Bottom characteristics for Hvar were extracted from Morovic (1951). These were proportions of four sediment granulometry categories sampled during the trawl operations: c1 = grains <0.01 mm; c2 = between 0.01 and 0.05 mm; c3 = between 0.05 and 2 mm; and c4 >2 mm. For Jukic, we used a categorical classification reported in Jukić (1975). Similar data were not available for Zupanovic, Grund and Medits. However, demersal species have strong reliance on seabed feature and substrate composition (Kaiser 1998; McConnaughey and Smith 2000; McConnaughey and Syrjala 2009). Therefore to avoid failing to account for a significant amount of variability in the catch standardization, we incorporated data of bottom characteristics from an external source. We used 11,500 measurements of sediment composition covering an extensive, albeit not complete, portion of the Adriatic Sea, extracted from the Seabed database (http://instaar.colorado.edu/ jenkinsc/dbseabed/). For unsampled areas, we interpolated sediment compositions by using a competent interpolator developed by Jenkins & Goff (unpublished). Then we projected a grid of 0.02 x 0.02 degrees of resolution over the Adriatic Sea, and for each pixel, we estimated log ratios of sediment compositions,

$$r_1 = log\left(\frac{m}{s}\right), r_2 = log\left(\frac{g}{s}\right). \tag{4.2}$$

s, m and g are percent composition of sand, mud and gravel respectively. We used log ratios to relax the restriction of having variables with bounded ranges (e.g. 0 to 1) and to deal with their lack of independence (Aitchison 1986). A D-part composition $(x_1, ..., x_D)$ where $(x_1 + .. + x_D = 1)$ has an additive logistic normal distribution $L^d(\mu, \Sigma)$, and $r = log(x_i/x_D)$ a d-dimensional normal distribution $N^d(\mu, \Sigma)$ with mean vector μ, and covariance matrix Σ (Aitchison 1986). We also used log ratios for the bottom compositions of the Hvar surveys. All log ratios were relative to the 4^{th} category (e.g. $r_1 = log(c1/c4), r_2 = log(c2/c4), r_3 = log(c3/c4)$).

Season was included to account for the common behavior of many elasmobranchs to undertake periodic migrations, or shift in distribution, in response to varying physical and biological habitat characteristics, or as effect of their reproductive behaviors (Walker et al. 1997). We included the seasonal effect in the models as a linearized sinusoidal function of the Julian day (J_{di}) of tow_i ($cos(2\pi J_d/365.25) + sin(2\pi J_d/365.25)$). In this way, we avoided increasing the model parameterization with the use of a multilevel factor. In general, whenever we had the choice between a continuous and a categorical variable expressing similar information, we preferred to use a continuous form to save degrees of freedom.

To avoid problems of collinearity, correlated variables were selected or combined to use unique forms of information. For example, $log(m/s)$ and $log(g/s)$ were expected to be independent, however, we detected a strong correlation between the two. Therefore we chose to use just relative $log(m/s)$. We included only main effects to avoid over-fitting, and difficulties in model interpretation in an ecological context.

4.2.2 Fitting Procedure

For each species in each survey we initially fitted a saturated model (e.g. all available variables together), and selected the best selection of covariates by backward elimination with a macro developed in SAS 9.1 (Appendix). The advantage of using a Newton-Raphson algorithm for maximum likelihood fitting of GLMs implemented in SAS was to reduce problems of model convergence. In this way, we could select a reasonable preliminary model structure, and then profile its likelihood function for the dispersion parameter estimation of more problematic species (i.e. those with the highest zero-inflation of catch data). Then we developed an exhaustive function in R to fit all the available variable combinations. Models having quadratic factors without their main effects were not evaluated. Continuous variables were standardized by using unit normal scaling:

$$x_j = \frac{(x_{ij}) - \bar{x}_j}{s_j} \tag{4.3}$$

where $\bar{x}$ is the mean of variable j, and s_j is its standard deviation. In this way we avoided computational problems due the different numerical scales of covariates. For each model$_i$ we calculated the Akiake Information Criterion (AIC), AIC differences ($\Delta_i = AIC_i - AIC_{min}$), Akaike weights,

$$w_i = \frac{exp(-1/2\Delta_i)}{\sum\limits_{r=1}^{R} exp(-1/2\Delta_r)}, \tag{4.4}$$

where R is the number of models fitted; and evidence ratios (w_{max}/w_i) (Burnham and

Anderson 2004). We then selected the best model corresponding to the minimum value of AIC, and the set of models with AIC differences < than $log(1/8) * 2$ to identify a 95% confidence set of models containing the estimated Kullback-Leibler best model (Burnham and Anderson 2002). We used this set of models to calculate the most important variables affecting the variability of the species, and the overall importance of these variables in explaining the catches of most species. To calculate the importance (w_+) of a variable (x_j) we summed the Akaike weights of all the models containing the variable among the 95% confidence set,

$$w_+ = \sum_{i=1}^{R} w_i I_j(g_i) \tag{4.5}$$

where

$$I_j(g_i) = \begin{cases} 1 & \text{if variable } x_j \text{ is in model } g_i \\ 0 & \text{otherwise.} \end{cases}$$

To evaluate the overall importance of the variables across species within each survey, we first ranked the variable importances for each species from 1 (the most important) to n ($n =<$ the maximum number of covariates used in a given survey). Then we averaged the ranks across all species.

4.2.3 Short-Term Trends

For Jukic and Medits surveys we estimated species-specific instantaneous changes in catch rates over time (β_y). Therefore we forced all the models to have a year effect, even if the selection process revealed that catches did not vary significantly over time. We profiled the likelihood function of the models for a range of β_y (-0.9,0.9), and selected the value corresponding to the maximum likelihood values and plotted the estimated profiles with a raindrop plot (Barrowman and Myers 2003)

4.2.4 Long-Term Trends

Long-term changes were estimated by comparing catches of tows carried out in overlapping survey domains to avoid unbalanced spatial comparisons. We made four long-term comparisons. In the area identified by the Hvar survey, we selected all tows of Hvar and Medits falling within the minimum convex polygon identified by the Hvar sampling locations. The others were performed over an area identified by the Jukic and Zupanovic surveys. Here we estimated long-term trends for the whole period (1948-2005) and for a historical period from 1948 to 1972. For these comparisons, we used a common model structure composed of the most important factors identified in the previous analytical stage,

$$\eta = log(\mu_i) = \alpha + \beta_y * Y_i + \beta_s S_i + \beta_n N_i + \beta_e E_i + \beta_d D_i + log(A_i). \tag{4.6}$$

and the dispersion parameters were held fixed to the values estimated from the Medits surveys.

4.2.5 Incorporating Uncertainty

Concerned with the effect of the uncertainty associated with the interpolation of bottom composition data, and lack of information on trawl performance for some surveys (Hvar, Zupanovic and Jukic) on the parameter estimates of our models, we made three tests of parameter robustness:

1. We explored the effect of a net horizontal opening mis-specification on the parameter estimates of the fitted models. We simulated 1000 datasets of 2575 trawl catches, from a negative binomial GLM of catch as a function of year, instantaneous rate of change β = -0.15, constant swept area of 0.057, and dispersion parameter $k = 1.06$. We used the sampled datasets to fit similar GLMs, which this time, had our empirical data (observed swept areas) in the offset parameter, and extracted the estimated year effect $\hat{\beta}$. To evaluate accuracy and precision of the estimated parameters, we calculated the Mean Squared Error, $E[(\hat{\beta} - \beta)^2]$ and the bias, $E(\hat{\beta} - \beta)$. In other words, we tested how much ignoring changes in swept areas among tows would bias the year effect estimate, or how sensible the year effect estimate is to systematic or random variations of the swept area values.

2. We recalculated the long-term instantaneous rate of change for *Scyliorhinus canicula* (the most common species) by generating 1000 vectors of swept area

correspondent to the tows used for the Hvar-Medits comparisons. This time swept area was estimated by using parameter estimates of an empirical relationship between horizontal opening (ho) and tow depth (D), obtained by regressing measured hos of tows carried out in the Medits surveys on depth ($ho = \alpha + \beta_d D + \varepsilon$). We fitted the GLM used for long-term comparisons to these new generated datasets, and estimated β_{yi} for each one of them. Here we simply compared the uncertainty that might come from the predictive model on the swept area, and the total variability associated with the year effect estimate.

3. Using the same method, we generated 1000 datasets of bottom composition correspondent to the Medits' tows, incorporating the uncertainty associated with $log(\frac{m}{s})$. Thus for each tow the new value of $log(\frac{m}{s})$ was a random variable $N(log(\frac{m}{s}), var[log(\frac{m}{s})])$. We fitted the best model of *S. canicula* (Tab. 4.9), and estimated mean and 95% confidence intervals as in test 2. Similarly to the above case, we compared the proportion of variability that would come from the uncertainty associated with each interpolated estimate of sediment composition and that associated with the year effect estimate.

4.2.6 Vulnerability to Fishing Exploitation

To evaluate the potential effect of exploitation on the observed patterns of species population change, we regressed the species-specific year effects estimated from Jukic and Medits surveys, and from the long-term analyses on the species' intrinsic rate of population increase r estimated following Smith et al. (1998). Life-history parameters necessary to estimate r (e.g. maximum size, size at maturity, age at maturity, fecundity - no. eggs/year, no. offsprings/year - and life span) were collected from the literature (Appendix). For missing observed information, we used estimates from empirical relationships (www.fishbase.org).

4.2.7 Effort Data

To explore the effect of fishing exploitation on the spatial patterns of abundance of the analyzed elasmobranch community, we visually compared the distribution of catches with the distribution of a predicted index of trawl fishing intensity projected over the area. We extracted and cross-checked the number, horse power (HP) and gross tonnage (GT) of boats fishing along the Italian, Slovenian, Croatian and Albanian coasts from the official statistics of the Italian National Institute of Statistics (ISTAT), the Italian Institute for Economic Research in Fishery and Aquaculture (IREPA), the statistical office of the European Community (EUROSTAT) and the General Fishery Commission for the Mediterranean (GFCM).

To estimate a likely scenario of fishing intensity, we assumed that the intensity of fishing per unit area of any point in the Adriatic Sea was given by the cumulative value of those exerted by all fishing fleets in the Adriatic. The contribution of each one would depend on the distance of the point to its harbouring port. We developed a working function between port distance and fishing intensity by analyzing empirical data of effort distribution of four Adriatic trawl fleets monitored by Casale et al. (2004). The data contained 1561 otter trawl tows observed on board of 12 boats fishing from Chioggia, Cesenatico, Fano and Ancona. For each fishing trip, observers recorded boat, port and the positions each trawl operation. After a preliminary analysis of spatial distribution of these fleets, we realized that Cesenatico, Fano, and Chioggia's effort allocation were deviating from our expectation of model fishery due to their vicinity to restricted areas (international borders or zone off limits to trawl, see below). Conversely, Ancona featured conditions virtually representative of most Adriatic fishing fleets (Appendix, Fig. B.5). Hence we selected the tows of this fishery for further analyses. This is a subset of 415 tows carried out by two vessels over 265 days. Boats had an average engine of 309 HP.

We divided the sea surface surrounding Ancona in a grid of 0.02 degrees of resolution. Then, we calculated the number of tows occurring in each pixel and assumed that the expected value followed a Poisson distribution. Hence, we fitted a GLM to the number of tows per pixel as a function of distance from port, depth, latitude and longitude to obtain the daily number of tows expected in each pixel by a unit of fishing effort (HP). We used the estimated parameters to predict the fishing intensity generated by the total capacity (in HPs) of all the Adriatic fleets in our data.

We calculated the distance between pixels and ports by using a function that looked for the shortest distance between two points while avoiding obstacles along the path (e.g. islands or any complex configuration of the coastline). This was meant to obtain a realistic estimate of the distance of fishing grounds from the Adriatic ports especially in the eastern coastal areas, characterized by complex systems of channels created by numerous archipelagos. This analysis only provided an approximate spatial picture of fishing effort. In reality, effort allocation is influenced by more factors than distance from port and fishing depth alone (see below). Nevertheless, for our purposes of distinguishing general patterns of fishing effort between the eastern and western, northern and southern parts of the Adriatic, our analysis should provide a sufficient approximation.

4.3 Results

4.3.1 Nominal Catches

In total, we analyzed 2736 trawl hauls carried out in the Adriatic Sea from 1948 to 2005. We detected 33 species including 12 sharks, 20 rays and 1 chimera (Table 4.3). Of these, 11 species disappeared during the period of observation (no more occurrences after the year 2000), while 4 were only recently detected by the Medits surveys. These included deep-water species such as *Chimera monstrosa* and *Etmopterus spinax* and small eurybathic species such as *Leucoraja melitensis.* All the species detected were bottom associated meso-predators smaller than 2 meters (TL). We compared our records from trawl surveys to other sources of information from the Adriatic Sea and found that between the end of the 19^{th} century and the beginning of the 20^{th}, there was a greater elasmobranch diversity observed than in recent decades (Table 4.4), including some larger bodied sharks such as *Sphyrna* spp., *Carcharias taurus* and *Odontaspis ferox* (Table 4.4).

Generally, there was higher species richness and abundance in the Hvar than the Medits survey (Fig.4.3), and during Medits, both indices were higher in the eastern coastal areas than elsewhere in the Adriatic (Fig. 4.2a and b). In particular, the high elasmobranch abundance in the central Adriatic in 1948-49 was absent in the Medits surveys (Fig. 4.2a). Conversely, in the Medits survey there was a relatively high-density zone in the northern Adriatic above the 50-meter isobath (Fig 4.2a), almost totally composed of three species: spiny dogfish (*Squalus acanthias*), smooth-hounds (*Mustelus mustelus*) and eagle ray (*Myliobatis aquila*). Hvar surveys revealed a well assembled meso-predator community of 23 species (Fig 4.3), dominated by the small spotted cat shark (*Scyliorhinus canicula*) and thorny ray (*Raja clavata*). *S. canicula* was caught in high numbers (426.8 individuals/km^2) and in 76% of the tows (Frequency of occurrence [FO] = 0.76). Similarly, *R. clavata* was present in 70.8% of the tows but with much lower density (76.8 ind/km^2). The other 21 species were caught in $< 21\%$ of tows with densities below 11 ind/km^2.

Over time, the species richness and abundance detected during the Hvar survey (Fig. 4.2a and 4.2b) decreased to a few dominant species and an increasing number of hardly detectable populations (Fig. 4.3). Spatial coverage and sampling intensity was lower for the Zupanovic and Jukic surveys (Table 4.1), but sample size in Medits increased six times compared to Hvar. *S. canicula* was still the most abundant species, but recorded a mean density of 62.1 ind./km^2 and FO of 0.20. *S. acanthias* and *M. mustelus* followed with 33.8 (FO = 0.14) and 15 ind./km^2 (FO = 0.07), respectively (Fig. 4.3e). In the Medits, 21 out of 27 species had FO < 0.021 and densities < 4 ind./km^2. There was a striking difference between the assemblages detected in the Croatian and Italian sectors (Appendix). Croatian waters had about one order of magnitude higher elasmobranch abundance than Italian areas. In Italy, *S. acanthias* was the most abundant species, although mostly relegated in the upper Adriatic. Frequency distribution in the Grund survey had the lowest diversity of species and abundance (Fig. 4.3d). It was comparable to densities and composition of the Italian Medits data (Appendix), with the most abundant shark also being *S. acanthias* (37.2 ind/km^2, FO: 0.25). *Galeus melastomus* was the second ranking species in terms of mean density (16.7 ind/km^2), though with a much lower FO of 0.02. The species was restricted to grounds deeper than 220 meters, and those few times the species was caught, it occurred in high numbers.

4.3.2 Standardized Catches

General Description of Species-Specific Models

To extract trends in abundance over time controlling for differences in sampling effort, environmental variables and technological factors deemed to affect species abundance, distribution and detection, we standardized catches with Generalized Linear Models (GLM). We fitted about 647 variable combinations for each species in Hvar, 215 in

Zupanovic, 430 in Jukic, 215 in Grund, and 1294 in Medits. Then we selected the one with the lowest value of AIC to be the candidate best model (Tables 4.5 - 4.9). We found considerable model selection uncertainty associated with the data available. More than half of the species in each survey had a selected best model with <10% chance (Akaike weight <0.1) to be the best one among the 95% confidence set (CS) of most plausible models (Table 4.5 - 4.9). However, we used the information contained in the whole set of models to extract a measure of relative importance of individual variables (numbers in brackets in Table 4.5 - 4.9). Ranking their importance across species and surveys (Table 4.10), we revealed that catches were mainly explained by spatial predictors such as mean depth, latitude and longitude. Temporal covariates (e.g. year, season) were less important (Table 4.10). For many species, catches were explained by quadratic functions of depth, latitude and longitude, indicating defined spatial structure of populations across the area (Table 4.5 - 4.9). Conversely, few species in Medits (*S. canicula*, *S. acanthias*, *M. aquila* and *E. spinax*) showed similar quadratic functions of the year effect (Table 4.5 - 4.9). Our interpolated index of sea floor composition outperformed similar measures (continuous or categorical) provided in the original data when these were available. The frequency of selection of log(m/s) was intermediate between spatial and temporal predictors (Table 4.10) and indicated that most modeled species preferred habitats with a greater percent of sand over mud (Figure 4.10). For a small portion of species in each survey, we estimated very high dispersion parameters (>1000, e.g. *Dipturus oxyrhincus* or *Dalatias licha* in Medits). Most of the times, these were associated with a very low number of positive catches (Table 4.5 - 4.9) and thus likely produced by a strong zero-inflation of the data.

Short-Term Temporal Trends

We analyzed short-term temporal trends from 1963 to 1972 in the eastern central Adriatic (Jukic data, Fig. 4.4) and from 1994 to 2005 across the entire area (Medits, Fig 4.5 and 4.6). In the Jukic surveys, nine species gave reliable trends in abundance. All except *Raja clavata* suggested an increase of standardized catches, however trends were statistically significant for only three species (*Scyliorhinus stellaris*, *Squalus blainville*, *Raja miraletus*).

In the Medits surveys, 16 of 27 species had detectable levels of abundance (occurring for three or more years and able to output an estimate of population change). Nine showed declines in catch trends of which three were statistically significantly (*S. blainville*, *C. monstrosa*, *S. acanthias*). Positive rates of change were mostly shown by meso-pelagic rays such as *Dasyatis pastinaca* and *M. aquila*, and small skates such as *R. clavata* and *R. miraletus*, although only *M. aquila* showed a statistically significant increase (2.77, CI: 0.06, 12.5). For sharks there was a general tendency to decline (e.g. *S. canicula*, *S. acanthias*, *S. blainville* etc), even if most of them did not reach levels of statistical significance (Fig. 4.6). For *E. spinax*, *S. canicula* and *R. clavata* the year effect was not significantly different from zero but improved the fit when included in the model. *S. canicula* showed a moderate decline, though its trajectory was not monotonic, initially increased, and then declined to lower levels than 1994. A similar quadratic trend with a steeper net decline was shown by *S. acanthias* (Fig 4.5). Some species were inefficiently sampled because they occurred at the margins of the survey domain (e.g. species living in the upper continental slope such as *G. melastomus*, *D. licha* and *E. spinax*. Others (*S. blainville* and *R. montagui*) were captured for three or more years but occurred with just one or two individuals each time producing extremely overdispersed catch distributions (Table 4.9).

Long-Term Comparisons

Comparisons between Hvar and Medits revealed that elasmobranchs declined by 92% over 57 years (Fig. 4.7), with sharks declining more (-95%) than rays (-83%). Thereby, the most abundant species *S. canicula* (-96.3%, CI: -97.8,-93.7) drove most of the patterns for all elasmobranchs. Among rays some shifts in species composition occurred. *R. clavata* was the most abundantly caught ray during Hvar, yet showed the strongest decline of all elasmobranchs (-97.1%, CI: -98.3, -95), while *R. miraletus* increased over time (1.8 times, CI: 0.3, 5) and became the most abundant ray in the Medits survey (Fig. 4.3 and 4.8a). There was a significant long-term increase for *M. aquila* (59 times, CI: 5.1, 594), *T. marmorata* (6.5 times, CI: 0.4, 40) and *S. acanthias* (5.8 times, CI: 1.02, 21.6), which matched a correspondent decline of closely related species such as *D. pastinaca* and *S. blainville* (Fig. 4.8). *G. melastomus* showed the strongest increase among all; however for this deep-water species sampling occurred at the margin of its range making the data less reliable.

Restricting the observations to a less exploited but much smaller coastal area of the Adriatic, the Jukic area, we could include tows carried out in the 1960s and 1970s. None of the nine species modeled increased significantly in abundance, and only *T. marmorata* showed some increase. In contrast, five species showed significant declines by more than 94% (Fig. 4.8b). When we restricted the series for tows carried out between 1948 and 1971 (Fig. 4.8c), *T. marmorata*, *S. acanthias* and *R. miraletus* increased significantly by 298 (CI: 0.18, 75703), 8.5 (1.1, 42), and 1.93 (CI: 0.3, 5.6) times, respectively, suggesting a temporary increase towards the 1970s followed by a decline in more recent times as depicted in the overall trend (Fig. 4.8b). In another coastal area off the eastern Adriatic, the Zupanovic area, several species showed a tendency to increase (Fig. 4.8d). *M. aquila*, *R. miraletus*, *M. mustelus* and *S. stellaris* increased significantly by 9.55 to 49 times from 1956-2005. *R. clavata* was the only species with a significant decline in catches (-64%, CI: -80, -35). While the trend for overall elasmobranchs and sharks were not significant, rays went through a general increase of 2.77 times (CI: 1.5, 4.7).

One of the main concerns of these cross-survey comparisons was the comparability of sampling gears. Trawls differed in framework and possibly performance during fishing operations (Table 4.2). A plot of swept areas, estimated from the net horizontal opening (ho), and time revealed a declining trend over the entire period (Appendix, Fig. B.2). Therefore, we tested the possible effect that a wrong specification of swept area calculated from ho would have on the estimated parameters of the models. Surprisingly, simulations revealed that the Mean Squared Error between the fixed and estimated year effect with misspecification of swept area was very low at 0.07. Year effect was underestimated by -0.008 (which is 38% over the entire period of 58 years, Fig. B.2). Accordingly, the use of predicted swept area based on an empirical relationship between tow depth and horizontal opening produced a very small variance of year effect estimates compared to the one associated with the parameter estimate assuming known swept area (Fig. B.3). Finally including uncertainty in the interpolated measure of sediment composition produced a relatively small variance of parameter estimates compared to the average standard error obtained if the year effect was estimated without measurement error in $log(s/m)$ (Fig. B.4).

Our projected distribution of fishing intensity (Fig. 4.9) revealed a strong difference between the Italian and Croatian side. Zones of greater fishing pressure were the northwestern regions between Chioggia and Ancona, and in southern Italy off the Apulia region. Croatia, Serbia and Montenegro had a much lower level of fishing. Here, however, our spatial resolution was limited by the coarse nature of input effort statistics. Most of the Croatian effort came from data aggregated by major fishing ports (Accadia and Franquesa 2006). This might have concentrated the spatial intensity of effort around the big maritime centers and underrepresented that fishing intensity occurring in areas between these cities. Nonetheless, the pattern roughly reflected the abundance and distribution of the catches detected in Medits with the exception of the upper Adriatic Sea (Fig. 4.2).

The importance of the spatial predictors used to standardize all the catches (Table 4.10) corroborated the strong differences between the Italian and the Croatian side of the Adriatic. Figure 4.10 reports the instantaneous rates of change of catches along latitude, longitude, depth and bottom composition gradients, evaluated over the largest survey areas we had available (Hvar and Medits). Most of the species had a greater abundance in the northeastern side of the Adriatic, which is the axis perpendicular to the main orientation of the Adriatic Sea, and thus to the Italian and Croatian coasts. Also, for most species, abundances decreased with depths suggesting a greater abundance in coastal areas rather than offshore. Exceptions were deep water species such as *G. melastomus*, *E. spinax* and *D. licha*.

Although there was a general consistency between areas of lower fishing pressure and detected abundance of elasmobranchs, at the species level relative changes in CPUEs were not explained by the intrinsic vulnerability of species to fishing. We found no significant relationships between the species' intrinsic maximum growth rate (r) and their instantaneous rate of change (β_y) estimated from the Medits (slope = 0.78, p-value: 0.661, R2: 0.015) and Jukic surveys (slope = 2.43, p-value 0.23, R^2: 0.2), and from historical comparisons in the Hvar area (slope = 0.45, p-value: 0.59, R^2: 0.03), Jukic area (slope = -0.81, p-value: 0.08, R^2: 0.37), Jukic area without the recent Medits surveys (slope = -0.55, p-value: 0.66, R^2: 0.03) and in the Zupanovic area (slope = 0.39, p-value: 0.3, R^2: 0.14).

4.4 Discussion

Understanding long-term ecological changes in exploited fish communities requires the consideration of the intrinsic vulnerability of different species to exploitation, changes in biological interactions (e.g. predators and competitors), different exposure to fishing (e.g. catchability, availability, and fisheries' interest), and other external factors (e.g. habitat degradation and pollution). All of these factors have the potential to alter the species-specific response to exploitation and thus might result in complex community responses that vary over time. Our goal was to take all of these factors into account when analyzing multiple trawl surveys carried out in the Adriatic Sea between 1948 and 2005 in order to characterize changes in an exploited elasmobranch community over six decades.

Overall, we found a community of predators and meso-predators in an advanced state of depletion. The 2736 tows carried out across the Adriatic Sea detected 33 species of small demersal (bottom associated) sharks and rays (Table 4.3) which declined in abundance by more than 92% over 58 years, and 11 species were not recorded at all after the year 2000. Contemporarily, the trawl surveys failed to detect 26 elasmobranch species recorded in earlier faunistic account (Table 4.4). Not a single large shark (>2 m length) was caught in any trawl survey. Although otter trawls are less efficient in catching large migratory, vagrant and fast swimming fish (Godo and Engas 1989), juveniles are more detectable because they are slower and more reliant on demersal environments, and virtually all those species or close relatives, when abundant, have been recorded in trawl by catch in the Mediterranean and elsewhere (Béchir and Nejmeddine 2009; Basuşta et al. 2006; Compagno et al. 1991).

The absence of large sharks in trawl surveys corroborated earlier reports indicating that some large predatory sharks in the Adriatic have declined by 68-99% over the past two centuries (Ferretti et al. 2008). However, other observations suggested the presence of nursery areas in the northern Adriatic for *Carcharhinus plumbeus* (Costantini and Affronte 2003; Mavrič et al. 2006), *Alopias vulpinus* (Notarbartolo di Sciara and Bianchi 1998), *Prionace glauca* (Bianchi et al. 1997; Politi 1997; Bello 1999) and possibly *Lamna nasus* (Soldo 2006), yet none of these species were detected in the trawl surveys. Excluding large sharks and strictly pelagic species, another nine bottom associated species were expected but not found in the trawl catches. These included large shallow water elasmobranchs such as *Pristis pristis*, *Squatina aculeata*, *Rhinobatos rhinobatos*, and *Gymnura altavela*, and species with broader habitat ranges such as *Echinorinus brucus* and *Centrophorus granulosus*, for which the high sampling effort and spatial coverage of the Medits surveys should have ensured a better chance of detection. If these species have disappeared, they would enlarge the list of extirpations proposed by Duvly et al. (2003) and revisited by Ferretti et al. (2010). Another seven species have only been detected in the recent Medits survey (1994-2005), although 3 of these *Raja radula*, *Dalatias licha* and *Raja polystigma* were not detected anymore after year 2000. The increased effort, spatial and depth range of the survey was likely determinant for some deep-water elasmobranchs such as *E. spinax*, *C. monstrosa* and *D. licha*. There is some concern that the new coming skates (*L. melitensis*, *R. radula* and *R. polystigma*) were not correctly identified in historical surveys (F. Tinti pers. comm., Mancusi *et al.* unpublished). However, the large depth distribution and high fecundity of *L. melitensis* in particular, would make a compensatory increase in distribution and abundance in response to declining less resilient competitors plausible.

The observed trends in abundance and diversity were the result of a long history of fishing in the Adriatic, and a strong spatial gradient of exploitation from the western to the eastern side. Likely, for some species, a low market value ensured lower exploitation rates. However, most easmobranchs are caught in multi-species trawl fisheries and almost all are landed if reaching a marketable size (Vannuccini 1999; Lanfredi 2003). Shark meat has always been marketed in Italy (Ninni 1912; D'Ancona 1926; Lanfredi 2003), and only few species (e.g. *Torpedo* spp.,*Myliobatis aquila*) are discarded due to lacking market value (Fortuna et al. 2010).

The window of observation we gained from the trawl surveys likely captured a final stage of the Adriatic exploitation history. Intense fishing in the area goes back to at least Roman and Medieval times, but was largely restricted to the coastal zone (Lotze et al. 2006; Hoffmann 2005). Spatial fisheries' expansion (especially Italian) begun by the end of the 18^{th} century, mostly lead by Chioggia (northwestern Adriatic) which, with 2500 boats in 1869, was the biggest fishing fleet in the Adriatic (Fortibuoni 2010). With two times the fishing capacity operating in the entire eastern Adriatic (Botter et al. 2006; Fortibuoni 2010), Chioggia spread its activities southwards along both sides of the basin (Levi Morenos 1916). Technological limitations (the fleet was mainly sail propelled and had to remain close to markets) confined fishing along coastal routes to less than 45 km away from the ports. Here stocks were heavily exploited, and local depletion was the main driver for many Italian fishers to venture seasonally into the eastern Adriatic where stocks were still abundant (Botter et al. 2006; Fortibuoni 2010).

From the late 19^{th} century until the end of the Second World War, fishing effort increased unevenly between the eastern and western sides. Trawling acquired popularity at the end to the 19^{th} century, but first only with light gear towed by sail boats (Faber 1883). Italy operated most fisheries, which predominated in the number and size of boats, the number of fishers, and gear efficiencies, while Austrians were mainly fishing locally for subsistence (Botter et al. 2006; Fortibuoni 2010). After the Second World War, trawling became mechanized, intense offshore fishing begun, and the gap between western and eastern exploitation became even larger. The Balkan territories joined into the Federal Republic of Yugoslavia, which was more concerned with the development of pelagic fishing than trawling the few available and difficult-to-fish grounds (Fortibuoni 2010). More importantly, Yugoslavia restricted the access of foreign boats to its territorial waters. While Yugoslavian fisheries remained largely artisanal, Italian fleets developed rapidly, increasing in capacity and technological efficiency, and exploited most Adriatic fish stocks (Fortibuoni 2010).

Thus when the Hvar survey started in 1948, the abundance and composition of coastal predator communities was already seriously depleted (Ferretti et al. 2008; Bearzi et al. 2004; Marchesetti 1882; Soldo and Jardas 2002). Where coastal trawling was common, even demersal elasmobranchs were nearly absent already in the 1930s (Zei 1949). Although offshore grounds (those sampled by Hvar) remained almost unexploited until the end of the Second World War, the surveyed fish community was characterized by small and residential elasmobranchs with *S. canicula* and *R. clavata* driving almost all estimated long-term changes. Large and less resilient demersal species (*D. batis*, *G.galeus*, *S. squatina* and eight others) were already scarce in Hvar (<5% of tows) (Table 4.3, Fig. 4.3), while most of them were considered common or seasonally abundant throughout the basin in the 19^th and early 20^th century (Faber 1883; Ninni 1912; Paolucci 1901). In the North Sea, similar characteristics of the elasmobranch community were evident after centuries of exploitation (Rijnsdorp et al. 1996; Walker and Hislop 1998; Rogers and Ellis 2000).

The overall history and spatial gradient in fishing pressure were the major explanatory factors for the long-term decline in elasmobranch abundance. The higher abundance and diversity of elasmobranchs on the eastern side of the Adriatic was related to the less intense history of exploitation and our projected distribution of lower fishing effort (Fig. 4.2 and 4.9). Sharks and rays mainly occurred in coastal Croatian waters where trawling is restricted or hardly practicable. Parameter estimates for species-specific models revealed quantitatively (Fig. 4.10) that the abundance of most species increased from the Italian to the Croatian coast and more specifically from offshore to coastal, less exploited, or protected areas. This partly explained the lack of significant relationships between intrinsic vulnerability of species, and estimated trends in population abundance for short- and long-term comparisons.

Similarly, we did not find relevant compensatory increases of elasmobranchs related to indirect effects of fishing such as competitor or predator release, as observed in other exploited continental shelves of the world (Fogarty and Murawski 1998; Link et al. 2002; Shepherd and Myers 2005; Myers et al. 2007). Nonetheless, in the least exploited sectors analyzed and in historical surveys (e.g. Jukic and Zupanovic areas, Fig. 4.8) we found multiple cases of temporal increases possibly related to changing interspecific interactions. This is where predator-prey dynamics and competitive interactions should be more evident as they are not confounded by high levels of fishing mortality. Nevertheless, the area of the observation was very limited and it was unclear whether observed increases resulted from shifts in distribution or a general increase in abundance over a larger area. When we compared historical and more recent surveys in the Jukic area (Fig, 4.8) most earlier increases were reversed, possibly in response to a recent increase in fishing pressure in offshore Croatian waters. Yet observed increases partly persisted in the Zupanovic area (Fig. 4.8) located in the more protected Croatian channels where exploitation has been much lower (Fig. 4.9).

Interestingly, historical information suggests substantial former abundance and increases of elasmobranchs in the Adriatic Sea in the late 19^{th} and the early 20^{th} century D'Ancona (1949). At the end of the 19^{th} century, there were many shark fisheries in the northern Adriatic suggesting high abundance (Marchesetti 1882). Squanere, large meshed gill nets targeting angel sharks (*Squatina spp.*) were among the most popular nets used in the area (Marchesetti 1882). A smaller version, Cagnolera, was used to catch dogfishes and smooth-hounds (*Squalus spp.* and *Mustelus spp.*) while skates were exploited with particular trammel nets called Cerbero and Palandara (Zolezzi 1946; Fortibuoni 2010). Increases in elasmobranch landings (relative to the total demersal fish produced) were detected in the most important fish market of the regions (Rijeka, Venezia, Chioggia and Trieste) (D'Ancona 1922; 1926; 1934; 1949), and were particularly evident after periods of reduced fishing operations during the two World Wars D'Ancona (1949), a pattern observed in the North Sea as well (Walker and Heessen 1996).

These accounts point to potential earlier compensatory increases in population abundance due to the decline in large predators or competitors (Ferretti et al. 2010) as well as to mechanisms through which sharks and rays, characterized by low biological rebound potentials (Smith et al. 1998; Myers and Worm 2005; García et al. 2008), experience rapid recoveries when exploitation temporally ceases. The exceptionally high catches recorded in years immediately after the wars (D'Ancona 1926; 1949) suggest that a combination of increases in abundance of residential sharks together with shifts in distribution and immigration of elasmobranchs from neighbouring, less-exploited areas may have enhanced local stocks. For example, D'Ancona (1949) reports unprecedented catches of *Mustelus* sp. in Chioggia where foot-seiners (Sciabica) recorded hauls of 160 and 70 smooth-hounds averaging 10 kg apiece, despite *M. mustelus* reaches such a size only when about 16 years old[1]. Those specimens were likely recruiting from elsewhere. Similarly, in the Northwest Atlantic, Frisk et al. (2008) showed that rapid increases of winter skate (*Leucoraja ocellata*) previously attributed to competition release (Fogarty and Murawski 1998) were explained by the species' migration, or shift in distribution, in response to changes in environmental regimes.

The contrast between relatively higher Medits' catch rates of bentho-pelagic elasmobranchs (*S. acanthias*, *M. mustelus* and *M. aquila*), and a projected high level of exploitation in the upper Adriatic was a drawback of the simplistic nature of our

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[1] We applied the von Bertanlaffy growth function by using $L\infty = 200/95$, $k = 0.12$, $To = -0.93$, and length weight relationship parameters extracted from www.fishbase.org.

projected spatial fishing effort. Although useful to depict a coarse figure of effort allocation, our model neglected other predictors of the spatial distribution of fishing pressure that might be important at local scales, such as avoidance of fisheries competition, resource abundance, and compliance with spatial and seasonal management restrictions (Baro et al. 2004; Caddy and Carocci 1999). Indeed, bottom trawling is restricted in most of the upper Adriatic (faoadriamed.org). Fishing is mainly operated by artisanal fixed gears (Costantini et al. 2000), pelagic trawlers (Fortuna et al. 2010), and small and localized beam trawl fisheries (Hall-Spencer et al. 1999; Franceschini et al. 1999; Pranovi et al. 2001). Additionally, historically trawlers avoided fishing in the area for the danger of collecting unexploited world war mines (D'Ancona 1949; Karlovac 1956), and more recently, given the complex division of territorial waters among Italy, Croatia and Slovenia, for the risk of trespassing international boarders resulting in law enforcement actions (Fortibuoni 2010). All of this buffered the degree of habitat destruction and fish stock depletion that occurred elsewhere. Thus, this area may have acted as a buffer zone between the highly exploited Italian sectors and less exploited Croatian waters, which may explain a spillover effect from Istria (Forcada et al. 2009).

Elasmobranchs can rapidly shift their distribution in response to changes in environmental and ecological conditions (Frisk et al. 2008; Bowen et al. 2003; Hobday et al. 1999). However, lacking pelagic stages, their migration relies on available ecological corridors (Veríssimo et al. 2010) and intrinsic mobility, usually a function of body size (Musick et al. 2004). While small demersal elasmobranchs such as *S. canicula* and other skates seem to be quite sedentary (home ranges <50 km Walker and Heessen 1996; Pawson and Ellis 2005; Rodríguez-Cabello et al. 2008), bentho-pelagic species such as *S. acanthias* and *Mustelus sp.* have been observed to undertake transoceanic movements (Francis 1988; Pawson and Ellis 2005; Veríssimo et al. 2010), and eagle rays (Myliobatidae) are known for their long seasonal migrations (Myers et al. 2007). Thus, mobility seems a key factor to explain the abundance and composition patterns observed in the Adriatic. Although the Italian side was almost barren of elasmobranchs, three (*S. acanthias*, *M mustelus* and *M aquila*) of the four most abundant species in the upper Adriatic were highly mobile. Consequently, their populations are only partially susceptible to localized stressors, and they may be able to benefit from recruitment from areas outside the Adriatic, possibly utilizing a partially sheltered gateway (or ecological corridor) represented by Croatian waters. Similarly, in the highly exploited North Sea, recent increases in resilient elasmobranchs (e.g. *S. canicula*) as well as persistence of overexploited species (e.g. *S. acanthias*, Pawson and Ellis 2005; Ellis et al. 2005) seemed to be related to their opportunity to recruit from less exploited areas such as the Celtic and Irish Seas (Ellis et al. 2004) or nursery areas between Scotland and the Faroe islands (Ellis et al. 2004). On the other hand, the persistence of several elasmobranchs in the less exploited eastern part of the Adriatic may be explained by their sedentary nature (e.g *R. miraletus* or *R. clavata*) that helped them to be not exposed to high exploitation levels in the western Adriatic.

In our dataset, 11 vessels and 7 gears were used for sampling (Table 4.2), and even though all retained the framework of a conventional otter trawl, there is concern for the potential bias that modification in technological components added to the estimated trends (Godo and Engas 1989). Unfortunately, such modifications covaried with year in a non-overlapping fashion, thus we could not disentangle their individual effect from the undergoing population change. Nonetheless we accounted for changes is swept area, which is the most used index to standardize trawl catches (Maunder and Punt 2004), and for potential unaccounted measurement error associated due to its estimation for many tows. Yet simulations revealed the year effect would be minimally biased by an unaccounted systematic change of swept area. The variability generated by a random or a systematic change of swept area was negligible compared to the inherent sampling variability. Furthermore, in addition to the horizontal opening, the higher vertical spread of the Medits gears has been suggested to increase the gear efficiency for species associated with the water column (Fiorentini et al. 1999), i.e. for bentho-pelagic sharks in our case (*Mustelus sp.* and *Squalus sp.*), and less for bottom associated fish such as rays. Yet, the estimated trends suggest that if bias occurred this was negligible compared to the magnitude of undergoing population change. In fact, while sharks displayed a general decline in abundance, rays in multiple cases went through temporal increases. We suggest this depended on the relative scale between the inherent variability of sampled populations and changes in gear catchability. Organisms characterized by low population densities such as sharks and rays show catch distributions highly skewed and zero inflated that are successfully modeled with the negative binomial distribution. This accounts for the quadratic relationship between sampled density and variance ($\mu + \mu^2 k$) (Hilborn and Mangel 1997; Cunningam and Lindanmayer 2005), a pattern demonstrated for a large array of natural populations (Taylor 1961). Therefore, for a fixed k, when animal density increases, sampling error becomes so large that any other source of error becomes negligible compared to the overall observed variability (Taylor 1953). Hence, within large orders of magnitude, differences in gear configuration might be less relevant for estimating overall population trends. Nonetheless, empirical tests on the effect of trawl modifications on catchability of rare species are virtually nonexistent and should be encouraged in the future to increase the efficiency and confidence of analyses obtained from the integration of multiple sets of independent trawl survey data, which are essential to define baselines for exploited marine ecosystems.

4.5 Conclusion

Our analysis revealed strong declines in the abundance of elasmobranchs from 1948-2005, a sequential disappearance of 11 species in the trawl surveys and the absence of another 26 species present in other historical accounts. We detected only few temporal increases, possibly due to predator or competitor release, which were mostly evident in less exploited coastal areas of Croatia and in historical surveys.

Historical and current patterns of fishing explained most of the observed trends in population abundance and diversity. The strong gradient of fishing intensity from the Italian to the Croatian side allowed the persistence of a more diverse and abundant elasmobranch community in the eastern Adriatic. This was mostly composed of small resilient and resident elasmobranchs together with more broad-ranging species. For the latter, spillover from less exploited Croatian waters to heavily exploited Italian grounds may explain the abundance of some highly mobile species in the upper Adriatic. Thus Croatian waters may represent a source and Italian waters a sink for elasmobranch populations (Pulliam 2000), and an ecological corridor connecting less exploited and more biodiverse southeastern Adriatic areas (southern Croatia, Montenegro and Albania) (Bello 1999; Basuşta et al. 2006) to the broader central and Northern Adriatic shelf. In fact, recent exceptional catches of very rare elasmobranchs occurred in these peripheral sectors (e.g. *Dasyatis centroura* and *Gymnura altavela*, Dulcic et al. 2003).

In 2003, Croatia proposed the establishment of a 23,870 km^2 Ecological and Fisheries Protection Zone (EFPZ) extending its jurisdiction over international Adriatic waters (to outer limits allowed by international law) where foreign boats, including European community members, would not be allowed to fish ((Chevalier 2005; Anonymous 2003b)). The area was enforced in January 2008, but re-opened on March 15, 2008 after harsh opposition of bordering countries, especially Italy which lands >300 million Euros worth of fish from the proposed EFPZ annually, ten times the production of Croatia (Radic 2008). Based on our analyses, such a management action may protect Croatian resources from further depletion and promote recovery of elasmobranch abundance and diversity in the overall Adriatic Sea. Despite their slow population dynamics, elasmobranchs can show relatively rapid recovery when mortality decreases. Therefore, in order to sustain and restore fishing grounds and biodiversity in the Adriatic Sea an integrated management of the entire basin would be beneficial that includes the protection of important source areas and the creation of buffer zones with reduced fishing pressure.

Survey	Time range	Sampling design	Depth range	Tows	Stations	Species	Index of abundance	Source
Hvar	1948-49	ASBS	0-400	277	167	23	n/tow	Karlovac (1959)
Zupanovic	1956-57	RA	68-106	126	10	17	n/tow	Županović (1961)
Jukic	1963-71	Hvar stations	38-262	197	24	15	n/tow	Jukić (1975)
GRUND	1994-95	Transects SRS	84-421	307		13	n/hour	Piccinetti (1996)
MEDITS	1994-2007	SRS	9.5-840	1667	144	27	n/tow	Jukić-Peladic et al. (2001)

Table 4.1: Summary of trawl surveys used for analyses listing the time range of surveys, sampling design (ASBS: Adapted to Seabed Suitability; RA: random allocation within the survey domain; SRS: Stratified Random Sampling), depth range in meters, number of tows and stations, number of elasmobranch species, the index of abundance recorded, and the source.

Survey	Vessel	Length	HP	Gear	WM	SM	FR	HR	Source
Hvar	Hvar	25.00	250	OT	55	26	44.00	35.00	Karlovac (1959)
Zupanovic	Zupanovic			OT	57		34.00	28.00	Županović (1961)
Jukic	Prevodnik		200	OT	55	20	46.10	34.10	Jukić (1975)
-	Bios		300	OT	55	20	36.30	29.10	Jukić (1975)
-	Bios II		300	OT	50	20	40.00	37.00	Jukić (1975)
GRUND	Pipeta	26.00	300	OT		20	41.00	32.00	Piccinetti (1996)
MEDITS	Fulmine	29.00	986	GOC 73	70	10	40.00	35.70	Jukić-Peladic et al. (2001)
-	Elisa Guidotti	29.00	442	GOC 73	70	10	40.00	35.70	Bertrand et al. (1996); Anonymous (2007a)
-	Andrea	29.50	1742	GOC 73	70	10	40.00	35.70	Bertrand et al. (1996); Anonymous (2007a)
-	Principessa I	32.00	540	GOC 73	70	10	40.00	35.70	Bertrand et al. (1996); Anonymous (2007a)

Table 4.2: Summary of vessels and trawl gears used in the analyzed surveys. Vessels are identified by name, length (m) and horse power (HP); gear is described by gear type (OT: conventional otter trawl; GOC 73, specific trawl gear used in the Medits surveys), WM: Wing Mesh (mm), SM: Sack Mesh (mm), FR: Foot Rope (m), HR: Head Rope (m).

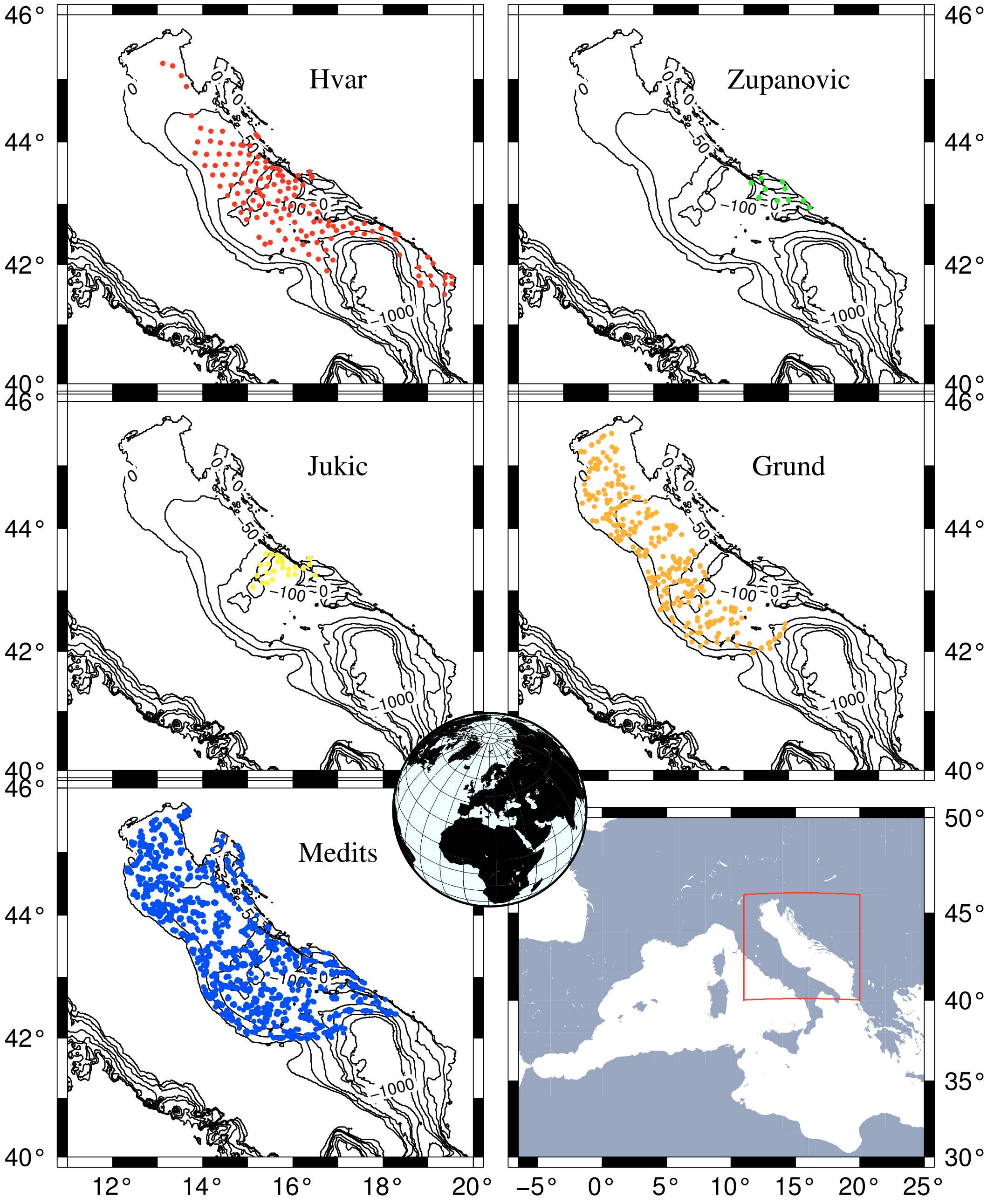


Figure 4.1: Positions of trawl operations carried out during the five analyzed surveys and a map of the Adriatic Sea. Survey details are shown in Table 4.1 and 4.2.

Species	Tows	Individuals	Last	Drange	Length
Heptranchias perlo	2	2	1948	27–1000	138
Leucoraja circularis	2	2	1948	70–900	120
Pteromylaeus bovinus	1	44	1948	10–150	250
Galeorhinus galeus	15	18	1957	2–450	186
Squatina squatina	11	16	1958	0–150	180
Dipturus batis	14	17	1968	100–1000	242
Raja radula	8	8	1994	40–450	70
Rhinoptera marginata	2	2	1994	30-100	
Dasyatis centroura	4	4	1996	3–270	247
Dalatias licha	3	7	1997	40–1800	181
Raja polystigma	2	2	2000	100–400	60
Dipturus oxyrinchus	30	60	2001	0–900	150
Torpedo nobiliana	1	1	2001	2–800	180
Oxynotus centrina	17	48	2003	60–660	150
Torpedo torpedo	2	2	2003	0–150	50
Chimaera monstrosa	11	71	2004	200–1000	87
Etmopterus spinax	11	57	2004	70–2000	53
Rostroraja alba	16	18	2004	40–500	200
Squalus blainville	79	348	2004	14–400	110
Dasyatis pastinaca	45	94	2005	60–200	150
Galeus melastomus	41	1147	2005	50–1000	68
Leucoraja melitensis	1	1	2005	60–800	50
Mustelus asterias	63	94	2005	0–100	140
Mustelus mustelus	186	1302	2005	0–350	162
Myliobatis aquila	133	539	2005	0–200	150
Raja asterias	55	129	2005	10–300	72
Raja clavata	536	3612	2005	0–700	107
Raja miraletus	327	1780	2005	50–150	66
Raja montagui	9	9	2005	0–550	77
Scyliorhinus canicula	812	24401	2005	0–400	76
Scyliorhinus stellaris	139	396	2005	0–100	150
Squalus acanthias	425	3632	2005	10–200	125
Torpedo marmorata	68	92	2005	20–350	82

Table 4.3: Species detected in the Adriatic trawl surveys analyzed (1948-2005). "Tows" is the number of trawl tows that caught the species. "Individuals" is the cumulative number of specimens detected in all the positive catches. "Last" is the year of the last catch. Drange and Length are the depth distribution range and maximum length of the species reported in the literature.

Species	Reported	Last	Ref
Carcharhinus brachiurus	1		Lipej et al. (2004)
Carcharhinus brachiurus or leucas	1		Faber (1883)
Carcharhinus brevipinna	1		Bello (1999)
Carcharhinus limbatus	2		Lipej et al. (2004)
Leucoraja fullonica	1		Bello (1999)
Mobula mobular	1		Jardas (1984)
Raja naevus	1		Bello (1999)
Rhinobatos cemiculus	1		Bello (1999)
Somnius rostratus	1		Bello (1999)
Squatina aculeata	1		Bello (1999)
Carcharhinus leucas	2	1882	Marchesetti (1882)
Cephaloptera giorna	2	1888	Ninni (1912)
Pristis pectinata	2	1906	Bello (1999)
Odontaspis ferox	5	1912	Ninni (1912)
Raja fullonica	3	1912	Paolucci (1923)
Sphyrna tudes	5	1912	Ninni (1912)
Sphyrna zygaena	9	1956	Soldo and Jardas (2002)
Carcharias taurus	5	1975	Bello (1999)
Glyphis glyphis	3	1975	Bello (1999)
Isurus oxyrhincus	8	1975	Bello (1999)
Raja undulata	3	1975	Bello (1999)
Rhinobatos rhinobatos	2	1975	Bello (1999)
Squatina oculata	5	1975	Bello (1999)
Carcharhinus longimanus	2	1978	Lipej et al. (2004)
Echinorhinus brucus	6	1985	Bello (1999)
Centrophorus granulosus	4	1998	Bello (1999)
Gymnura altavela	4	2000	Dulcic et al. (2003)
Lamna nasus	7	2002	Lipej et al. (2004)
Carcharodon carcharias	9	2003	Soldo and Dulčić (2005)
Hexanchus griseus	8	2003	Lipej et al. (2004)
Cetorhinus maximus	5	2004	Lipej et al. (2004)
Alopias vulpinus	9	2008	Fortuna et al. (2010)
Carcharhinus plumbeus	9	2008	Fortuna et al. (2010)
Mustelus punctulatus	5	2008	Fortuna et al. (2010)
Prionace glauca	11	2008	Fortuna et al. (2010)
Pteroplatytrygon violacea	3	2008	Fortuna et al. (2010)

Table 4.4: Additional elasmobranch species that have been identified in the Adriatic Sea historically or recently but were not detected in the trawl surveys. “Reported” refers to the number of references that have listed the species.“Last” is the year of the most recent demonstrated record, or reference mentioning the occurrence.“Ref” is the corresponding publication tracking the source.

Species	Terms	AIC	Weight	Theta	Tows	CS
Dasyatis pastinaca	$\mathbf{D}$(0.69, <0.0001) $\mathbf{D}^2$(0.58, <0.0001) $\mathbf{E}$(0.55, <0.0001) $\mathbf{S}_1$(0.66, <0.0001)	93.28	0.05	0.11	11	46
Mustelus asterias	$\mathbf{N}$(0.41, 0.092) $\mathbf{N}^2$(0.4, 0.008) $\mathbf{E}$(0.51, 0.007) $\mathbf{E}^2$(0.51, 0.018) $\mathbf{S}_1$(0.42, 0.078)	191.16	0.05	0.43	27	34
Mustelus mustelus	$\mathbf{D}$(0.84, <0.0001) $\mathbf{N}$(0.83, 0.082) $\mathbf{N}^2$(0.83, <0.0001) $\mathbf{E}$(0.84, <0.0001) $\mathbf{E}^2$(0.84, <0.0001) $\mathbf{T}$(0.67, 0.423) $\mathbf{T}^2$(0.38, 0.178)	119.00	0.06	0.95	17	42
Myliobatis aquila	$\mathbf{D}$(0.88, 0.002) $\mathbf{D}^2$(0.69, 0.02) $\mathbf{N}$(0.88, 0.001) $\mathbf{S}_2$(0.63, 0.06) $\mathbf{R}_1$(0.88, 0.003) $\mathbf{T}$(0.72, 0.48) $\mathbf{T}^2$(0.3, 0.299)	51.53	0.06	673.36	7	40
Oxynotus centrina	$\mathbf{D}$(0.81, 0.254) $\mathbf{D}^2$(0.81, 0.021) $\mathbf{N}$(0.81, 0.015) $\mathbf{E}$(0.81, 0.065)	67.95	0.06	0.26	10	44
Rostroraja alba	$\mathbf{D}$(0.35, 0.015) $\mathbf{R}_1$(0.53, 0.001)	87.09	0.04	553.10	13	56
Raja asterias	$\mathbf{D}$(0.75, <0.0001) $\mathbf{D}^2$(0.75, <0.0001) $\mathbf{N}$(0.75, <0.0001) $\mathbf{N}^2$(0.42, <0.0001) $\mathbf{E}$(0.43, <0.0001) $\mathbf{S}_1$(0.31, <0.0001) $\mathbf{R}_1$(0.42, <0.0001) $\mathbf{T}$(0.31, <0.0001) $\mathbf{T}^2$(0.18, <0.0001)	55.14	0.04	13.07	10	62
Dipturus batis	$\mathbf{D}$(0.28, 0.188) $\mathbf{E}$(0.42, 0.094) $\mathbf{S}_2$(0.68, 0.012)	97.88	0.03	0.77	11	89
Raja clavata	$\mathbf{E}$(0.68, 0.036) $\mathbf{E}^2$(0.68, <0.0001) $\mathbf{S}_1$(0.68, 0.005) $\mathbf{T}$(0.68, <0.0001) $\mathbf{T}^2$(0.68, 0.002)	1325.16	0.12	0.68	196	17
Raja miraletus	$\mathbf{D}$(0.76, <0.0001) $\mathbf{D}^2$(0.58, 0.001) $\mathbf{N}$(0.74, <0.0001) $\mathbf{E}$(0.76, <0.0001) $\mathbf{R}_1$(0.76, <0.0001)	414.28	0.05	0.30	57	46
Dipturus oxyrinchus	$\mathbf{D}$(0.72, <0.0001) $\mathbf{D}^2$(0.49, 0.068) $\mathbf{T}$(0.37, 0.1)	143.72	0.02	0.92	20	168
Scyliorhinus canicula	$\mathbf{D}$(0.65, 0.627) $\mathbf{D}^2$(0.29, 0.066) $\mathbf{S}_1$(0.83, <0.0001) $\mathbf{R}_1$(0.83, <0.0001) $\mathbf{T}$(0.83, <0.0001) $\mathbf{T}^2$(0.83, <0.0001)	2033.81	0.07	0.48	212	36
Scyliorhinus stellaris	$\mathbf{D}$(0.68, 0.026) $\mathbf{D}^2$(0.44, 0.106) $\mathbf{N}$(0.75, 0.747) $\mathbf{N}^2$(0.75, <0.0001) $\mathbf{E}$(0.75, 0.464) $\mathbf{E}^2$(0.75, <0.0001) $\mathbf{S}_1$(0.67, 0.011) $\mathbf{R}_1$(0.47, 0.115) $\mathbf{T}$(0.6, 0.037)	310.89	0.12	0.33	47	20
Squalus acanthias	$\mathbf{N}$(0.48, 0.005) $\mathbf{E}$(0.4, 0.021) $\mathbf{E}^2$(0.31, 0.077) $\mathbf{S}_1$(0.3, 0.013)	158.88	0.03	0.19	21	64
Squalus blainville	$\mathbf{N}$(0.8, 0.855) $\mathbf{N}^2$(0.68, 0.022) $\mathbf{E}$(0.8, <0.0001) $\mathbf{E}^2$(0.8, <0.0001) $\mathbf{S}_1$(0.4, 0.092)	275.16	0.04	0.39	39	62

Table 4.5: Summary of the best models for each species caught during the 5 analyzed trawl surveys. Terms indicate the best selection of variables, which are depth (D), longitude east (E), latitude north (N), temperature (T), cosine component of the seasonal term (S1), sine component of the seasonal term (S2), and composition of bottom sediments (R1 = $log(\frac{c1}{c2})$ for Hvar, Rm = $log(\frac{m}{s})$ for Zupanovic, Grund and Medits, and B for Jukic) as specified in the text. Relative variable importance, and correspondent p-values in the best variable selection, are indicated in brackets. Akaike Information Coefficient (AIC), Akaike weights, and dispersion parameter (Theta = $1/k$) refer to the best model. Tows are the number of positive trawl taws where the species was caught. CS is the confidence set of models containing the Kullback-Leibler best model (Burnham and Anderson 2002).

Species	Terms	AIC	Weight	Theta	Tows	CS
Dasyatis centroura	$\mathbf{D}$(0.34, 0.993) $\mathbf{N}$(0.57, 0.993)	25.57	0.03	7982.70	3	74
Dasyatis pastinaca	$\mathbf{N}$(0.7, 0.011) $\mathbf{N}^2$(0.67, 0.015) $\mathbf{E}$(0.37, 0.165)	98.06	0.05	0.62	12	47
Galeorhinus galeus	$\mathbf{N}$(0.35, 0.013) $\mathbf{S}_2$(0.67, 0.005)	27.06	0.05	3555.40	3	47
Mustelus asterias	$\mathbf{D}$(0.68, 0.991) $\mathbf{N}$(0.68, 0.991) $\mathbf{N}^2$(0.59, 0.991) $\mathbf{E}$(0.68, 0.991) $\mathbf{E}^2$(0.55, 0.991)	79.66	0.13	5.60	11	19
Mustelus mustelus	$\mathbf{N}$(0.67, 0.089) $\mathbf{N}^2$(0.29, 0.145) $\mathbf{E}$(0.45, 0.139) $\mathbf{Rm}$(0.64, 0.124)	92.57	0.05	13.08	15	56
Myliobatis aquila	$\mathbf{D}$(0.52, 0.993) $\mathbf{D}^2$(0.32, 0.993) $\mathbf{E}$(0.59, 0.993) $\mathbf{E}^2$(0.35, 0.993)	104.63	0.04	0.22	11	70
Oxynotus centrina	$\mathbf{N}$(0.49, 0.979) $\mathbf{N}^2$(0.41, 0.979)	26.62	0.08	7174.65	3	27
Rostroraja alba	$\mathbf{E}$(0.43, 0.969) $\mathbf{E}^2$(0.19, 0.97)	19.49	0.04	12307.52	2	73
Raja clavata	$\mathbf{D}$(0.94, <0.0001) $\mathbf{D}^2$(0.94, <0.0001) $\mathbf{N}$(0.94, <0.0001) $\mathbf{N}^2$(0.94, 0.009) $\mathbf{E}$(0.94, <0.0001) $\mathbf{E}^2$(0.94, <0.0001) $\mathbf{Rm}$(0.94, <0.0001)	500.21	0.34	5.06	96	4
Raja miraletus	$\mathbf{D}$(0.96, 0.013) $\mathbf{D}^2$(0.96, 0.004) $\mathbf{N}$(0.96, 0.002) $\mathbf{N}^2$(0.53, 0.137) $\mathbf{E}$(0.96, 0.003) $\mathbf{E}^2$(0.96, 0.005) $\mathbf{Rm}$(0.96, 0.003)	247.71	0.16	1.46	40	8
Dipturus oxyrinchus	$\mathbf{N}$(0.44, 0.992) $\mathbf{E}$(0.53, 0.992)	26.62	0.03	7174.67	3	114
Scyliorhinus canicula	$\mathbf{D}$(0.89, <0.0001) $\mathbf{D}^2$(0.65, 0.041) $\mathbf{N}$(0.89, 0.01) $\mathbf{N}^2$(0.89, <0.0001) $\mathbf{E}$(0.89, <0.0001) $\mathbf{E}^2$(0.83, 0.004) $\mathbf{S}_2$(0.89, 0.001) $\mathbf{Rm}$(0.83, 0.004)	875.28	0.42	1.73	96	5
Scyliorhinus stellaris	$\mathbf{N}$(0.87, <0.0001) $\mathbf{N}^2$(0.54, 0.039) $\mathbf{E}$(0.93, <0.0001) $\mathbf{E}^2$(0.77, 0.001) $\mathbf{S}_1$(0.93, 0.002) $\mathbf{Rm}$(0.44, 0.205)	190.84	0.08	12.20	37	28
Squalus acanthias	$\mathbf{D}$(0.6, 0.006) $\mathbf{D}^2$(0.45, 0.024) $\mathbf{N}$(0.55, 0.14) $\mathbf{E}$(0.47, 0.033) $\mathbf{E}^2$(0.42, 0.019) $\mathbf{Rm}$(0.42, 0.093)	323.34	0.06	0.34	43	39
Squalus blainville	$\mathbf{N}$(0.81, 0.997) $\mathbf{N}^2$(0.81, 0.991) $\mathbf{E}$(0.63, 0.981) $\mathbf{E}^2$(0.58, 0.99) $\mathbf{S}_1$(0.7, 0.001) $\mathbf{Rm}$(0.43, 0.987)	127.12	0.10	0.40	16	20
Torpedo marmorata	$\mathbf{D}$(0.46, 0.097) $\mathbf{N}$(0.69, 0.017)	86.06	0.04	2046.45	13	63

Table 4.6: Summary of best models in Zupanovic. See caption in Table 4.5 for details.

Species	Terms	AIC	Weight	Theta	Tows	CS
Dasyatis pastinaca	**D**(0.6, 0.665) **E**(0.7, 0.664) $\mathbf{E}^2$(0.7, 0.664)	42.52	0.12	1.78	6	22
Mustelus asterias	**N**(0.87, 0.106) $\mathbf{N}^2$(0.87, 0.001) **E**(0.87, 0.001) $\mathbf{E}^2$(0.87, 0.003)	101.72	0.17	1.35	13	16
Mustelus mustelus	**Y**(0.77, <0.0001) **N**(0.77, <0.0001) **E**(0.74, <0.0001) $\mathbf{S}_2$(0.77, <0.0001)	48.03	0.21	18030.94	7	13
Myliobatis aquila	**D**(0.56, 0.982) $\mathbf{S}_1$(0.75, <0.0001)	46.44	0.12	37.35	9	26
Oxynotus centrina	**Y**(0.34, <0.0001) **D**(0.65, 0.799) $\mathbf{D}^2$(0.65, 0.798) **E**(0.63, 0.811) $\mathbf{S}_1$(0.49, <0.0001)	25.41	0.11	17434.60	3	18
Dipturus batis	**Y**(0.33, 0.003) **D**(0.44, 0.001) **N**(0.41, <0.0001) **E**(0.43, 0.004) $\mathbf{E}^2$(0.41, 0.002)	37.30	0.07	0.41	3	28
Raja clavata	**D**(0.97, <0.0001) $\mathbf{D}^2$(0.97, <0.0001) **N**(0.97, <0.0001) $\mathbf{N}^2$(0.97, 0.001) **E**(0.97, <0.0001) $\mathbf{E}^2$(0.97, <0.0001) $\mathbf{S}_1$(0.97, 0.002) $\mathbf{S}_2$(0.5, 0.067) **B**(0.97, <0.0001)	814.50	0.50	0.85	105	3
Raja miraletus	**Y**(0.7, <0.0001) **D**(0.67, 0.901) **N**(0.49, 0.882) $\mathbf{N}^2$(0.28, 0.904) **E**(0.69, 0.998) $\mathbf{E}^2$(0.6, 0.985) **B**(0.7, <0.0001)	305.06	0.08	2.94	40	22
Raja radula	**E**(0.61, 0.055) $\mathbf{E}^2$(0.49, 0.02) $\mathbf{S}_1$(0.64, 0.009)	49.64	0.07	1157.40	7	32
Scyliorhinus canicula	**D**(0.87, 0.321) $\mathbf{D}^2$(0.87, <0.0001) **N**(0.87, 0.001) $\mathbf{N}^2$(0.87, <0.0001) **E**(0.87, <0.0001) $\mathbf{E}^2$(0.87, 0.006) **B**(0.87, <0.0001)	1037.55	0.26	0.62	110	7
Scyliorhinus stellaris	**Y**(0.44, 0.027) **D**(0.39, 0.205) $\mathbf{D}^2$(0.21, 0.039) **E**(0.51, 0.029) $\mathbf{E}^2$(0.41, 0.018) $\mathbf{S}_1$(0.55, 0.021)	126.35	0.05	1.77	19	40
Squalus acanthias	**D**(0.53, 0.099) **N**(0.76, <0.0001) **E**(0.76, 0.003) $\mathbf{E}^2$(0.63, 0.029) $\mathbf{S}_2$(0.76, 0.001)	322.76	0.07	0.29	42	30
Squalus blainville	**Y**(0.43, <0.0001) **N**(0.61, 0.987) $\mathbf{N}^2$(0.31, 0.988) **E**(0.66, 0.988) $\mathbf{E}^2$(0.51, 0.988) $\mathbf{S}_2$(0.6, <0.0001) **B**(0.66, <0.0001)	127.01	0.07	1.71	17	32
Torpedo marmorata	**D**(0.51, 0.001) $\mathbf{D}^2$(0.47, 0.002) **N**(0.44, 0.009) **E**(0.54, 0.001) $\mathbf{E}^2$(0.51, 0.001)	105.16	0.11	1.21	13	17

Table 4.7: Summary of best models in Jukic. See caption in Table 4.5 for details.

Species	Terms	AIC	Weight	Theta	Tows	CS
Dasyatis pastinaca	**N**(0.53, <0.0001) $\mathbf{N}^2$(0.51, <0.0001)	12.00	0.13	21438.62	3	24
Galeus melastomus	**D**(0.75, <0.0001) $\mathbf{D}^2$(0.67, <0.0001) **N**(0.77, <0.0001) $\mathbf{N}^2$(0.35, <0.0001)	38.77	0.07	109468.99	6	45
Mustelus mustelus	**N**(0.75, <0.0001) $\mathbf{S}_2$(0.75, 0.001) **Rm**(0.7, 0.006)	236.73	0.12	0.18	43	19
Myliobatis aquila	**E**(0.45, <0.0001) $\mathbf{E}^2$(0.36, <0.0001) $\mathbf{S}_1$(0.77, 0.171)	59.96	0.06	5533.65	14	45
Raja asterias	**D**(0.52, 0.004) **N**(0.71, 0.001) **E**(0.76, 0.019) $\mathbf{E}^2$(0.73, <0.0001) **Rm**(0.77, <0.0001)	104.93	0.09	0.11	17	30
Raja clavata	**D**(0.82, <0.0001) $\mathbf{D}^2$(0.82, <0.0001) **N**(0.82, <0.0001) **E**(0.82, 0.225) $\mathbf{E}^2$(0.82, <0.0001) $\mathbf{S}_2$(0.59, 0.003) **Rm**(0.57, 0.001)	105.59	0.16	0.34	18	13
Raja miraletus	**D**(0.87, <0.0001) $\mathbf{D}^2$(0.87, <0.0001) **N**(0.87, <0.0001) **E**(0.87, <0.0001)	91.40	0.12	39.64	15	22
Scyliorhinus canicula	**D**(0.57, 0.478) $\mathbf{D}^2$(0.4, 0.153) **N**(0.94, <0.0001) $\mathbf{N}^2$(0.94, <0.0001) **E**(0.94, 0.01) $\mathbf{E}^2$(0.94, 0.011) **Rm**(0.94, 0.005)	385.67	0.16	0.47	61	11
Squalus acanthias	**D**(0.94, 0.007) $\mathbf{D}^2$(0.94, 0.004) **N**(0.57, 0.231) **E**(0.94, 0.004) $\mathbf{E}^2$(0.94, 0.008) **Rm**(0.94, 0.001)	706.23	0.20	0.19	103	11
Torpedo marmorata	**D**(0.51, <0.0001) $\mathbf{D}^2$(0.45, <0.0001) **N**(0.67, <0.0001) $\mathbf{N}^2$(0.67, <0.0001) $\mathbf{S}_1$(0.64, 0.001)	35.52	0.08	15458.91	9	33

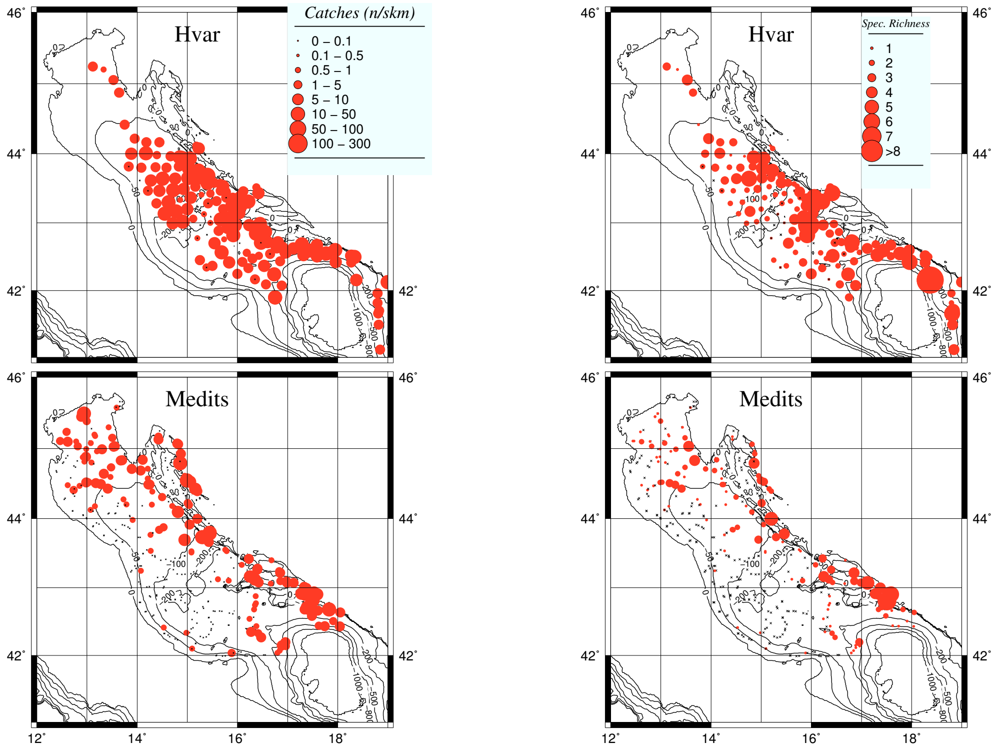
Table 4.8: Summary of best models in Grund. See caption in Table 4.5 for details.

Species	Terms	AIC	Weight	Theta	Tows	CS
Chimaera monstrosa	**Y**(1, <0.0001) **E**(1, <0.0001) **Rm**(1, <0.0001)	128.12	0.53	0.07	11	4
Dasyatis pastinaca	**D**(0.65, 0.003) **E**(0.65, 0.019) $\mathbf{E}^2$(0.4, 0.135) $\mathbf{S}_2$(0.36, 0.091)	159.06	0.02	0.28	14	115
Etmopterus spinax	**Y**(0.64, <0.0001) $\mathbf{Y}^2$(0.52, <0.0001) **D**(0.71, <0.0001) $\mathbf{D}^2$(0.71, <0.0001) $\mathbf{S}_2$(0.65, <0.0001)	95.21	0.06	0.50	11	45
Galeus melastomus	**D**(0.68, <0.0001) $\mathbf{D}^2$(0.68, <0.0001) **N**(0.42, <0.0001) **E**(0.68, <0.0001)	301.56	0.05	0.40	32	43
Mustelus asterias	**N**(0.64, <0.0001) $\mathbf{N}^2$(0.39, <0.0001) **E**(0.64, <0.0001) $\mathbf{E}^2$(0.32, <0.0001) $\mathbf{S}_2$(0.43, 0.003)	130.04	0.02	0.03	10	146
Mustelus mustelus	**D**(0.85, <0.0001) **N**(0.85, <0.0001) **E**(0.85, <0.0001) $\mathbf{E}^2$(0.85, 0.007) **C**(0.85, <0.0001) **Rm**(0.85, 0.001)	1085.05	0.08	0.17	119	30
Myliobatis aquila	**Y**(0.88, 0.13) $\mathbf{Y}^2$(0.6, 0.036) **D**(0.91, 0.001) $\mathbf{D}^2$(0.91, 0.011) **N**(0.91, 0.957) $\mathbf{N}^2$(0.91, 0.001) $\mathbf{S}_2$(0.62, 0.103) **C**(0.91, <0.0001) **Rm**(0.58, 0.03)	927.42	0.22	0.12	98	10
Raja asterias	**D**(0.46, 0.018) **N**(0.34, 0.058) $\mathbf{N}^2$(0.25, 0.089) $\mathbf{S}_2$(0.26, 0.128) **Rm**(0.2, 0.122)	434.03	0.02	0.02	35	122
Raja clavata	**Y**(0.53, 0.226) **D**(0.8, 0.492) $\mathbf{D}^2$(0.78, 0.063) **N**(0.8, <0.0001) $\mathbf{N}^2$(0.8, 0.007) **E**(0.8, <0.0001) **C**(0.8, 0.001) **Rm**(0.55, 0.195)	1136.41	0.06	0.16	126	41
Raja miraletus	**D**(0.9, <0.0001) $\mathbf{D}^2$(0.9, <0.0001) **E**(0.9, <0.0001) $\mathbf{E}^2$(0.9, <0.0001) **C**(0.9, <0.0001) **Rm**(0.9, <0.0001)	1499.88	0.21	0.29	177	8
Raja montagui	**N**(0.33, 0.081) **Rm**(0.21, 0.184)	69.69	0.03	54.00	5	71
Dipturus oxyrinchus	**D**(0.53, <0.0001) $\mathbf{D}^2$(0.41, <0.0001) **N**(0.57, <0.0001) $\mathbf{N}^2$(0.5, <0.0001) **E**(0.42, <0.0001)	25.58	0.06	31211.22	4	52
Dalatias licha	**D**(0.57, <0.0001) $\mathbf{D}^2$(0.49, <0.0001) **N**(0.51, <0.0001) $\mathbf{S}_1$(0.65, <0.0001) $\mathbf{S}_2$(0.67, <0.0001)	21.48	0.10	28515.83	3	30
Scyliorhinus canicula	**Y**(0.7, 0.08) $\mathbf{Y}^2$(0.7, 0.011) **D**(0.7, 0.81) $\mathbf{D}^2$(0.65, 0.005) **N**(0.7, <0.0001) $\mathbf{N}^2$(0.7, <0.0001) **E**(0.7, <0.0001) $\mathbf{E}^2$(0.7, 0.001) **C**(0.7, <0.0001) **Rm**(0.7, <0.0001)	3180.23	0.35	0.24	340	4
Scyliorhinus stellaris	**D**(0.62, <0.0001) $\mathbf{D}^2$(0.27, 0.047) **E**(0.62, 0.769) $\mathbf{E}^2$(0.55, 0.001) **C**(0.62, <0.0001)	381.84	0.04	0.06	34	55
Squalus acanthias	**Y**(0.84, <0.0001) $\mathbf{Y}^2$(0.84, 0.005) **D**(0.8, 0.277) $\mathbf{D}^2$(0.76, 0.11) **N**(0.84, <0.0001) **E**(0.84, 0.253) $\mathbf{E}^2$(0.84, <0.0001) $\mathbf{S}_2$(0.6, 0.089) **C**(0.84, <0.0001) **Rm**(0.84, <0.0001)	2242.73	0.28	0.12	243	9
Squalus blainville	**Y**(0.56, <0.0001) **D**(0.42, 0.49) $\mathbf{D}^2$(0.32, <0.0001) **N**(0.54, <0.0001) **E**(0.68, <0.0001) $\mathbf{S}_1$(0.52, <0.0001) $\mathbf{S}_2$(0.54, <0.0001) **Rm**(0.68, <0.0001)	89.30	0.07	43909.46	7	33
Torpedo marmorata	**D**(0.58, 0.008) **N**(0.68, <0.0001) $\mathbf{N}^2$(0.68, <0.0001) **E**(0.68, <0.0001) $\mathbf{E}^2$(0.62, 0.01)	300.96	0.05	0.31	33	47

Table 4.9: Summary of best models in Medits. See caption in Table 4.5 for details.

	Hvar	Zupanovic	Jukic	Grund	Medits
E	2.62	2.53	1.87	2.55	2.89
D	3.19	2.71	3.33	3.36	2.58
N	3.56	1.41	3.33	1.91	3.32
T	5.38				
E^2	5.56	6.12	3.93	4.64	6.37
R_1	5.69				
S_1	5.75	6.65	5.80	6.91	8.26
D^2	6.94	6.71	6.20	5.27	6.16
N^2	7.69	4.94	6.67	5.82	6.95
S_2	8.25	6.59	6.47	6.55	6.89
T^2	8.56				
Rm		4.29		4.55	5.58
Y			5.60		5.26
B			7.40		
C					6.79
Y^2					9.26
Models	647.00	215.00	430.00	215.00	1294.00

Table 4.10: Mean rank of covariates selected from the 95% confidence set of models (CS) for the different surveys. E = Longitude E, N = Latitude N, D = Depth, T = Temperature, S = Salinity, B = Bottom sediment, $R_1 = log(\frac{c1}{c4})$, Rm = $log(\frac{m}{s})$, $S_1 = cos(2\pi J_d/365.25)$, $S_2 = sin(2\pi J_d/365.25)$ and C - Country. These express the average rank of variables across species based on their relative importance (see methods, equation 4.5). In the last row we reported the number of model combinations fitted to the data to select the best set of plausible models.



(a)

(b)

Figure 4.2: Comparisons of nominal catches (numbers per square kilometre) (a), and species richness (b), recorded in the Hvar and Medits' surveys. For Medits we selected only the last two years of the series (2004-05) to allow a balanced temporal comparison.

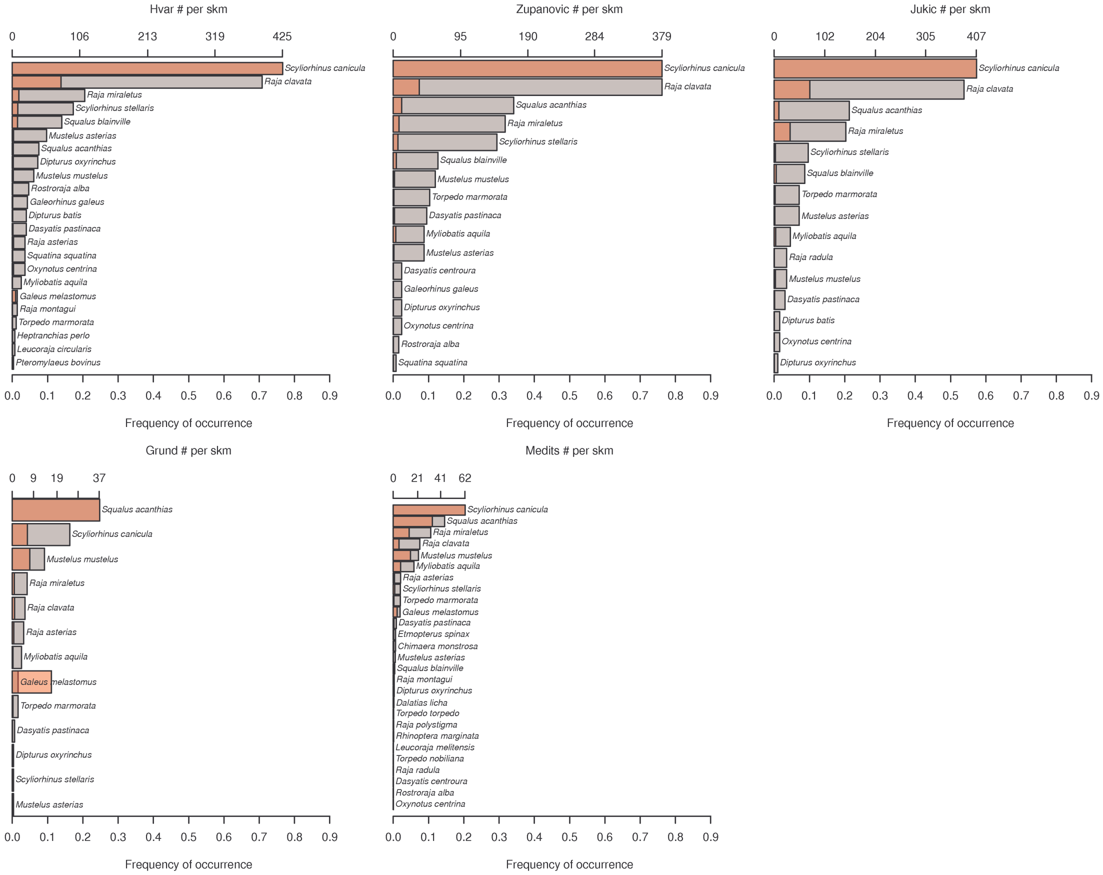


Figure 4.3: Frequency of occurrence (f_i) of elasmobranchs caught in trawl surveys (grey bars). F_i is the number of tows that caught species$_i$ divided by the total number of tows performed. Red filling indicates the species mean density in number per square kilometre (nominal catches).

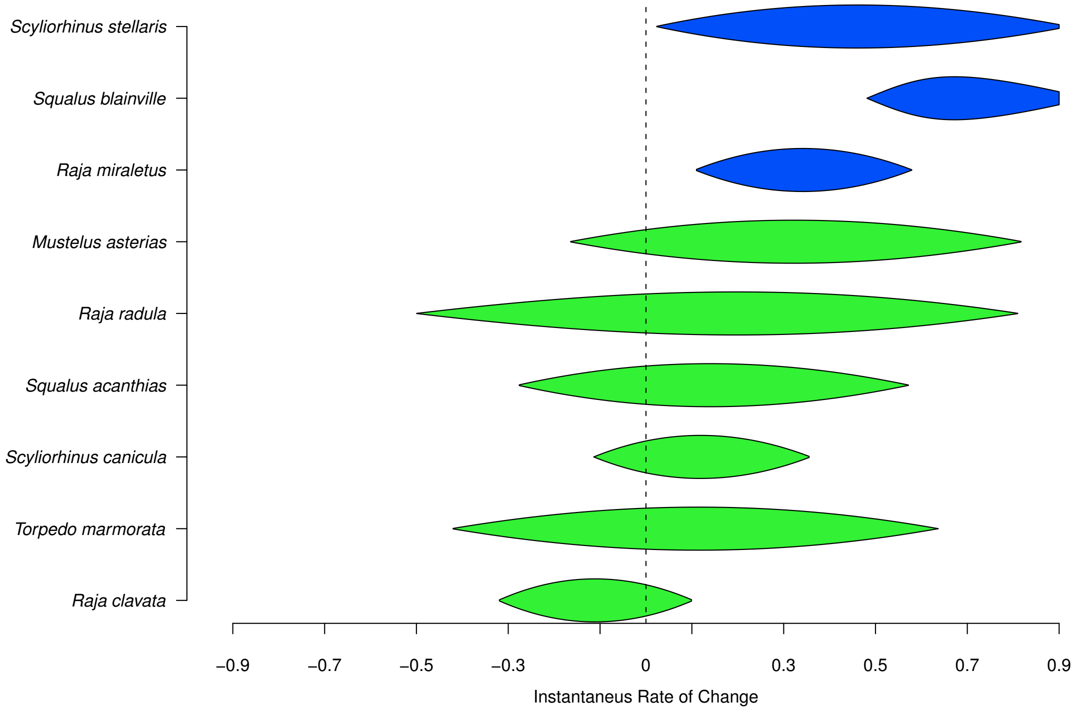


Figure 4.4: Raindrop plot of the instantaneous rate of change (β_y)' profile likelihoods for elasmobranchs detected during the Jukic surveys (1963-1972). Drop widths indicate the 95% confidence interval for the β_y. The thickness of the drop at a particular value of β_y indicates the relative plausibility of that value. Blue raindrops indicate that the models did have "year" as a significant term, while green raindrops indicate non-significant year-effects.

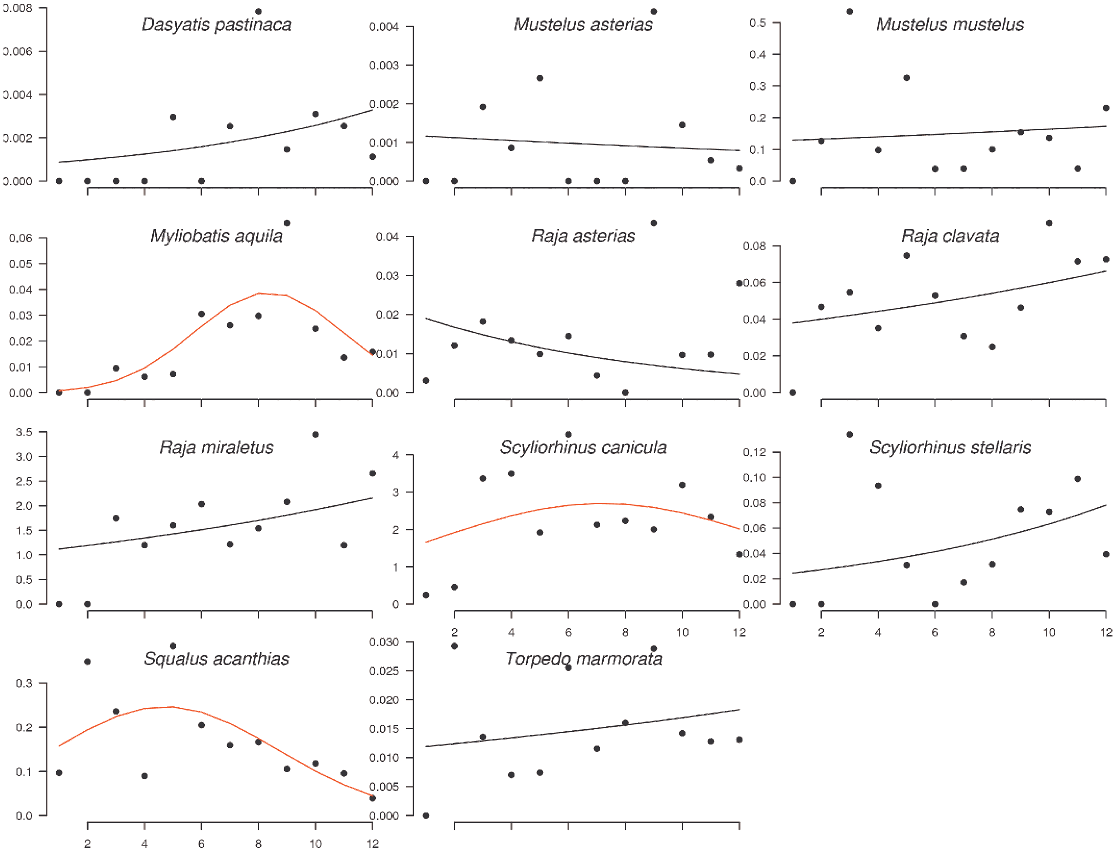


Figure 4.5: Trends of standardized catch per unit effort (CPUE, number per square kilometre) of elasmobranchs detected during the Medits surveys (1994-2005). Species with cumulative CPUE >0.001 km^2 are shown. All other standardizing variables (including the offset) were held fixed at their average value. Trend lines were predicted by using the year-effect value; red lines indicate quadratic trends.

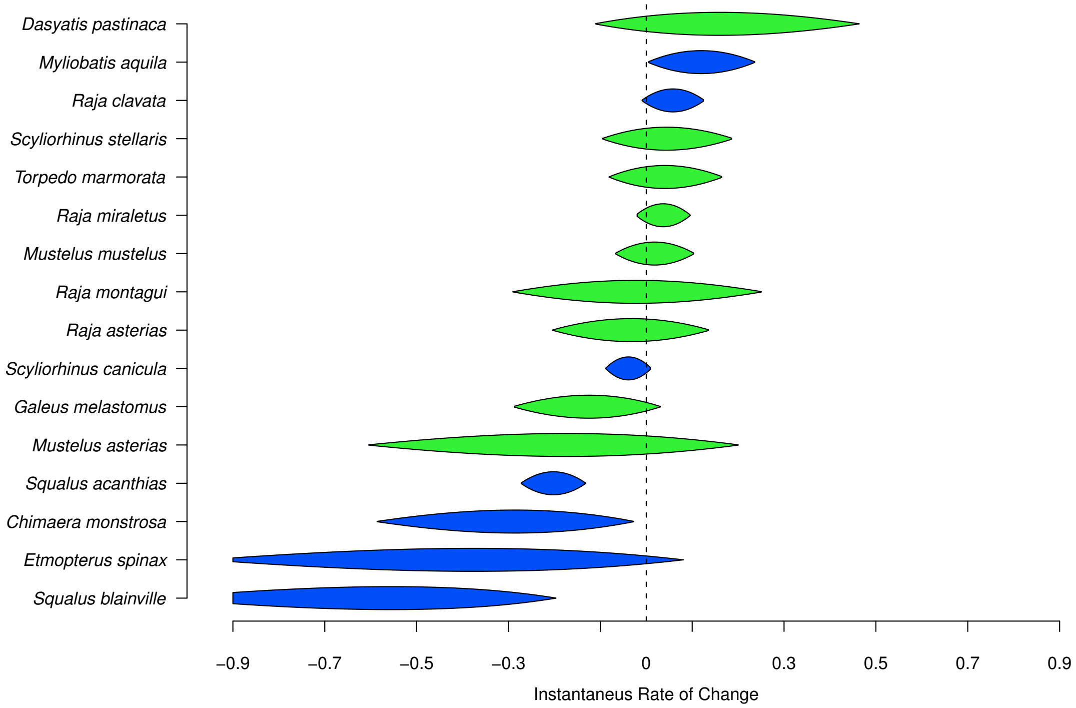


Figure 4.6: Raindrop plot of elasmobranchs in Medits as specified in Fig. 4.4.

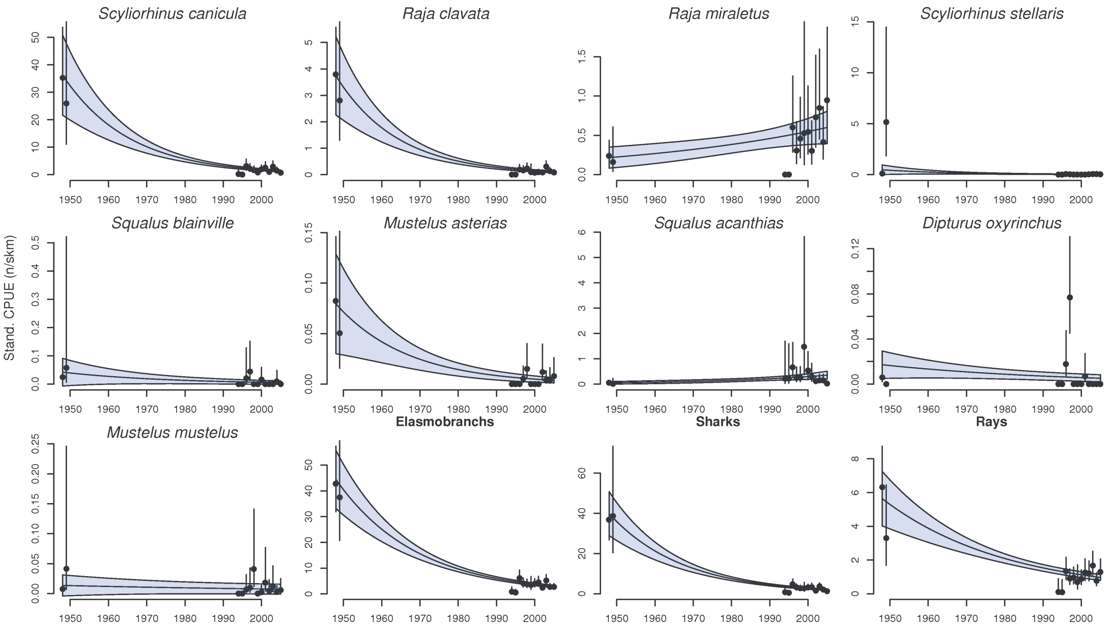


Figure 4.7: Trends of standardized catch per unit effort (CPUE) of the nine most abundant elasmobranch species and three groups (elasmobranchs, sharks, rays) detected in the Hvar surveys. We combined tows recorded in Hvar and Medits falling into the region sampled by the Hvar surveys (Fig 4.1). Dots and associated bars are standardized CPUEs and 95% confidence intervals estimated by using year as a categorical variable, and keeping all the other covariates constant to their average value. Lines and shaded areas are trend lines estimated by using year as a continuous variable and 95% confidence intervals.

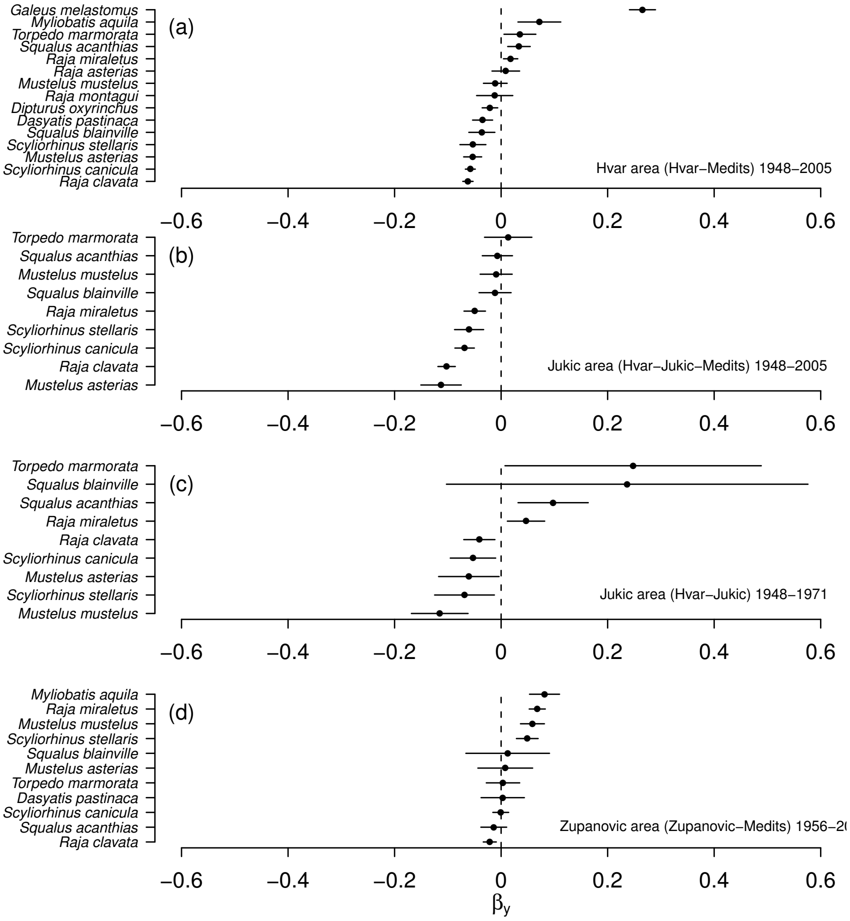


Figure 4.8: Centipede plots of year effects estimated for all elasmobranchs occurring in three or more years in each respective long-term period considered.

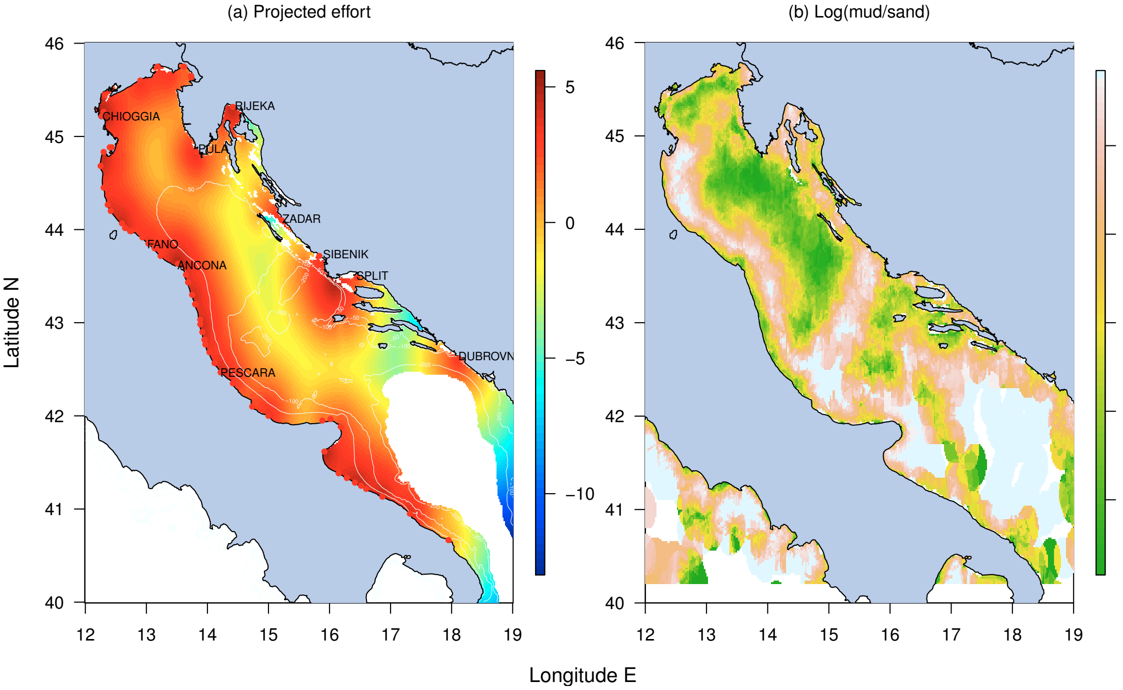


Figure 4.9: (a) Projected distribution of fishing effort in the Adriatic Sea. Color scale refers to the logarithm of the expected horse powers (HPs) deployed per day in a given 0.02 x 0.02 degree cell. (b) Distribution of interpolated seabed composition data for the fraction $log(\frac{m}{s})$

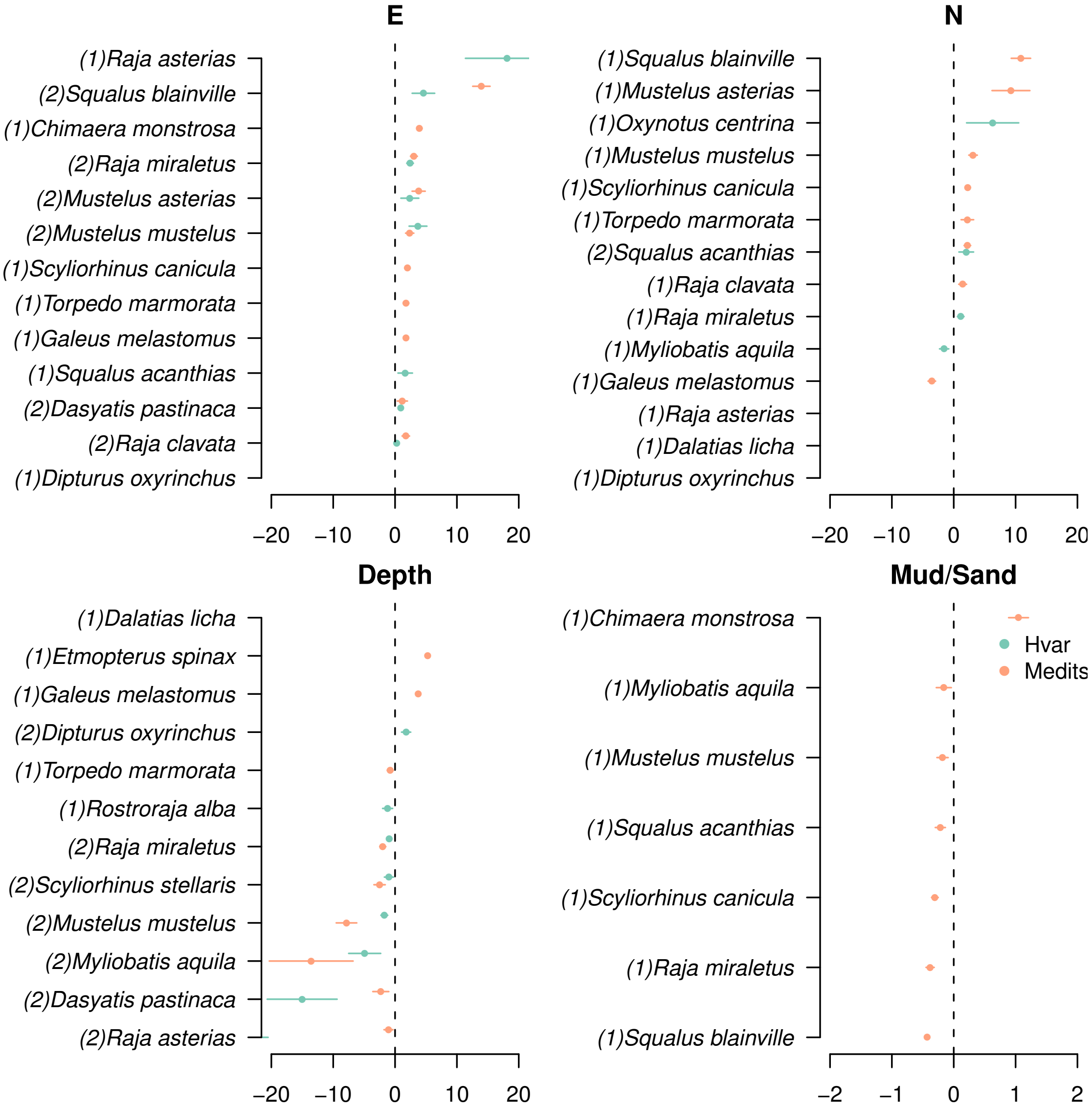


Figure 4.10: Effect plot for four spatial variables included in the models standardizing catches in Medits and Hvar surveys. Numbers in parentheses before the species name indicate the number of estimats available (e.g. 2 means that the parameter was estimated for both surveys). E is longitude east. N is latitude north.

Chapter 5

Patterns and Ecosystem Consequences of Shark Declines in the Ocean

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5.1 Introduction

Ecologists have long been intrigued by the often strong effects of predation on community structure (Paine 1966; Schmitz et al. 2004; Knight et al. 2005; Ritchie and Johnson 2009). Predator effects, however, do vary considerably among different species and ecosystems. For example, a meta-analysis of 102 field experiments indicated strong cascading effects, on average, in lakes and marine benthos and weaker effects in marine plankton and terrestrial food webs (Shurin et al. 2002). Classic work on the effects of predation often concerns relatively small-bodied, slow-moving predators such as starfish (Paine 1966) or spiders (Schmitz et al. 2004), that are easily manipulated and controlled. Recent studies on large-bodied and highly mobile terrestrial predators (e.g. wolves, *Canis lupus*,Ripple & Beschta 2007) suggest that they exert similar or even more powerful effects; yet large marine predators have been much less studied, mainly for logistical reasons (Heithaus et al. 2008a; Baum and Worm 2009).

Here we attempt to synthesize what is known about the ecological role of sharks, which are among the largest and most wide-ranging predators in the ocean. This topic has received urgent attention over the past decade, as studies have indicated rapid and widespread declines, particularly of large sharks, due to the direct and indirect effects of fishing (Baum et al. 2003; Dulvy et al. 2008; Ferretti et al. 2008). This has prompted questions about the nature and scale of the ecological consequences. In this context, marine biologists have debated the patterns of decline for different species, the apparent community changes, and whether sharks do play a unique and fundamental role (Stevens et al. 2000; Kitchell et al. 2002; Baum et al. 2005; Burgess et al. 2005; Myers et al. 2007; Heithaus et al. 2008a). While sharks have distinct ecological features that could lead to strong structuring roles in marine environments, such effects are not necessarily ubiquitous because other marine predators may potentially take sharks' place when functionally removed by fishing (e.g.,Kitchell *et al.* 2002). Also there is considerable diversity in body sizes and trophic interactions among sharks and other elasmobranchs, hence some variation in ecological roles might be expected.

In this study, we begin by briefly reviewing the ecological features of sharks, highlighting differences from other marine predators. We then analyze the current state and history of shark exploitation, searching for general patterns of community change in coastal, demersal, and pelagic ecosystems. Finally, we synthesize the expected and observed effects of sharks on marine ecosystems from experimental, empirical, and modeling studies. In the conclusion, we attempt to explain under which conditions sharks are expected to play a unique role, and how that role may depend on the ecosystem context. This study is largely based on all major peer-reviewed papers published on this topic over the past decade, but also includes important earlier work.

5.2 Ecological Features

5.2.1 Primordial Predators

Sharks constitute about half of all contemporary chondrichthyans (492 sharks, 621 bathoids, 46 chimeras, www.catalogueoflife.org), a monophyletic group of predatory fishes that originated about 423 million years ago (Fig. 5.1), before any other extant vertebrate predators.

Evolving initially as small coastal consumers, over evolutionary time, selection favoured larger body sizes, continuous growth, delayed age at maturity, and the ability to colonize deeper oceanic waters (Grogan and Lund 2004). The group acquired ecological niches previously occupied by now extinct predatory vertebrates (Walker

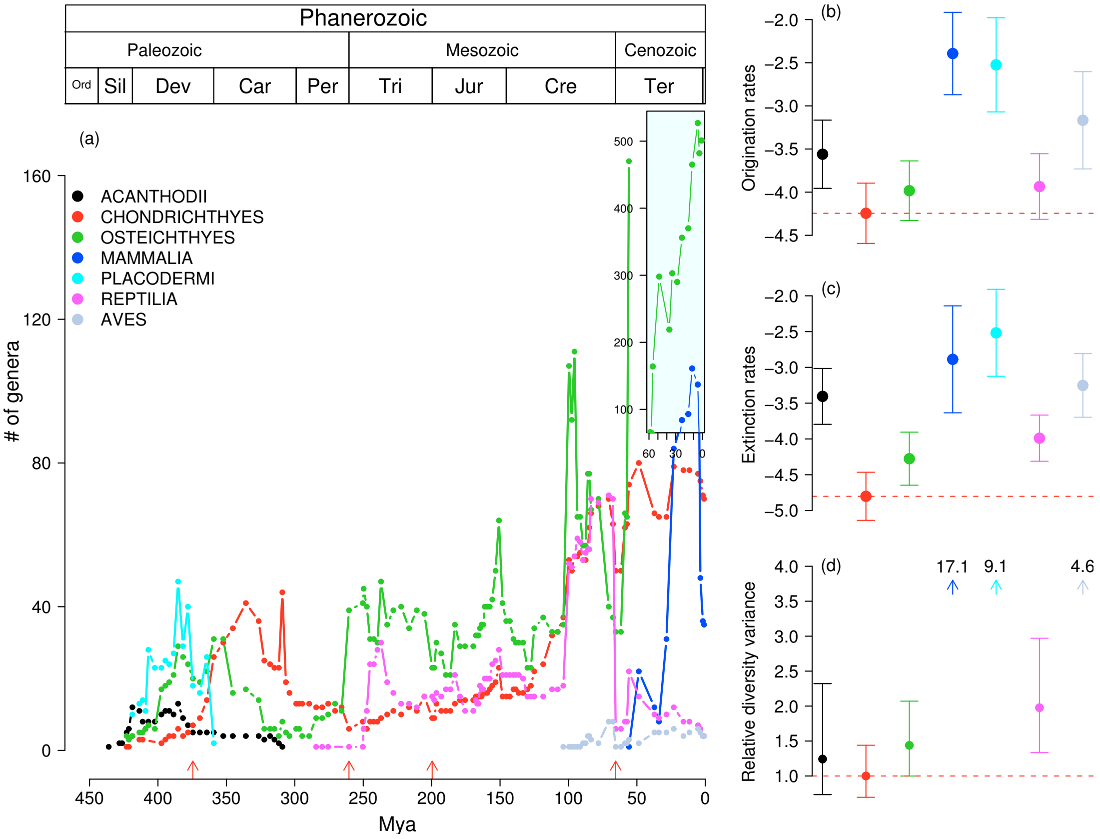

Figure 5.1: Diversification of chondrichthyans and other marine vertebrates. (a) Time trend in genus diversity from the fossil record; geological eras and periods are indicated at the top; red arrows indicate major mass extinction events. (b) Origination and (c) extinction rates are expressed as $y = log(x/z)$, where x is the number of genus extinctions or originations in each geological era, and z is the contemporary genus richness. Bars represent 95% confidence intervals. The relative diversity variance (d) for each taxon was obtained by detrending each time series in panel (a) with a moving average of the order 1, and calculating the variance of the residuals. We tested the null-hypothesis that the ratio between the variance in genus richness of chondrichthyans and other taxa was equal to 1. Symbols represent the ratio between the variance of a given taxon and that of chondrichthyans. Confidence intervals were off-scale for mammals (8.11–50.28), placoderms (4.74– 21.71) and marine birds (2.73–8.78). Data from Sepkoski (2002) compiled in http://geology.isu.edu/FossilPlot/

and Brett 2002), and have influenced the diversification and distribution of prey and competitor species (Lindberg and Pyenson 2006). One spectacular example is the extinct *Carcharodon megalodon*, the largest predatory fish ever recorded, which may have caused substantial changes in the evolutionary history of marine mammals, its preferred prey (Lindberg and Pyenson 2006). Compared to other marine vertebrates, the trajectory of chondrichthyan evolution appears steadier, with lower origination and extinction rates (Fig. 5.1). This resilience has been related to a high evolutionary adaptability and ecological generalism (Grogan and Lund 2004; Kriwet et al. 2009).

Contemporary sharks inhabit coastal, demersal, and pelagic habitats in all oceans (Compagno 1990). While most species are limited to the continental shelves, there is a small number of fully oceanic species (e.g. blue, oceanic whitetip, mako), and a larger count that migrates between coastal and oceanic waters (e.g. hammerhead, silky, tiger, white). Sharks are carnivores with body sizes from 0.2 to >20 m (fishbase.org) and feeding types ranging from filter-feeding (basking, whale shark) to suction crushing (carpet sharks) and effective raptorial mechanisms (white, tiger sharks) (Compagno 1990). While most larger species (>3 m total length) function as top predators, there is a high diversity of mesopredatory elasmobranchs (typically <1.5 m total length) that are prey to larger sharks. Many sharks are generalists, feeding on a wide variety of prey items. This explains the high connectivity of sharks seen in food-web models (Bascompte et al. 2005), and the likely limited effects on any particular prey species (Ellis and Musick 2007).

Sharks feeding is not gape-limited as in bony fish; the hyostylic suspension of their jaw, a consequent powerful bite, and efficient cutting dentition allow sharks to cut large prey into chunks (Wilga et al. 2007) and thus to attack larger prey than bony fishes of the same size. For this reason, large megafauna, including marine reptiles, mammals, and elasmobranchs often have large sharks as their major or exclusive predators. These species often show strong behavioural responses to the risk of shark predation that could result in lower population sizes through non-consumptive mechanisms (Heithaus et al. 2008a). Finally, through their high mobility, large sharks may connect widely spaced food webs (Musick et al. 2004).

5.2.2 Vulnerability to Fishing

Most chondrichthyans are characterized by low growth rates, late sexual maturity, and low fecundity compared to bony fish (Frisk et al. 2001; Myers and Worm 2005), which makes them vulnerable to fishing mortality. A comparison of 26 shark and 151 bony fish populations found that sharks show twice the fishing extinction risk of bony fishes (Myers and Worm 2005). Also their ability to recover after depletion is low on average: rebound potential of 26 shark populations ranged between 14% (*Mustelus californicus*) and 1.7% (*Squalus acanthias*) per year (Smith et al. 1998) with variability explained by a combined effect of size and preferred habitat. In fact, it was highest for small coastal sharks, intermediate for pelagic and minimal for large coastal species (Smith et al. 1998). Deep-water sharks may be among the most vulnerable to fishing, with population growth rates 40-60% lower compared to pelagic, and 55-63% lower compared to coastal species (García et al. 2008).

As a life history trade-off, most elasmobranchs invest more into juvenile survival and growth (Frisk et al. 2001) rather than fecundity (Cortés 2002). Elasticity analyses show that changes in juvenile and adult survival and age at maturity have the highest contributions to population growth rate (Cortés 2002; Frisk et al. 2005). This explains why elasmobranch populations generally respond strongly to changes in both predation and fishing. While exploitation often leads to decreased ages at maturity and increased fecundities in teleosts (Jorgensen et al. 2007), there is little evidence for such compensating responses in elasmobranchs (Frisk et al. 2005).

Finally, while life history determines the level of mortality sharks can sustain, their vulnerability depends on the combination of life history, sensitivity to habitat loss (Heupel et al. 2007) and exposure to perturbations such as catchability and availability to fisheries. The latter relates to many factors including geographic range (Dulvy and Reynolds 2002; Shepherd and Myers 2005), habitat use (García et al. 2008), behaviour (Ward and Myers 2005; Gilman et al. 2008), and body size (Duvly et al. 2003; Field et al. 2009).

5.3 Patterns of Change

5.3.1 Global Fisheries and Conservation Status

Historically, many sharks had low commercial value, and were not regularly recorded in fisheries statistics. Thus, detailed catch or survey data are often lacking (Dulvy and Reynolds 2002; Clarke et al. 2006), and population changes for many species have not been well documented until recently (Stevens et al. 2000; Graham et al. 2001; Myers and Worm 2005; Dulvy et al. 2008; Ferretti et al. 2008). On a global scale, elasmobranch landings reported to the United Nations Food and Agriculture Organization (FAO) are often aggregated. Only 15% are reported at the species level, the rest as larger taxonomic groups (e.g., dogfishes, skates) or more often 'sharks and rays' (Clarke et al. 2006; Dulvy et al. 2008). Reliability and resolution of these data vary among nations (Watson and Pauly 2001), and underreporting is probably severe for many shark species (Clarke et al. 2006). Nonetheless, some interesting patterns emerge.

In general, industrial fisheries commenced in the NW Pacific, NE Atlantic and Mediterranean before the 1950s. These three areas, in decreasing order, recorded the highest initial catches per unit shelf area (Fig. 5.2). Over time, these fisheries expanded to other regions (Myers and Worm 2003; Pauly et al. 2005), and elasmobranch catches increased in many areas (Fig. 5.2). However, individual shark fisheries have often been depleted within a few decades after their onset (Hurley 1998; Stevens et al. 2000). Thus, the increase in total catches may mask local population depletions, changes in species composition, and fisheries expansions into newly exploited regions and deeper waters.

Different catch trajectories may reflect local histories of exploitation. The NW Pacific shows a steady decline in elasmobranch catches since 1950. Here, landings have been driven by Japan with some of the largest elasmobranch fisheries (Stevens et al. 2000). Japan was already trading shark fins with China >200 years ago and had well-developed trawl fisheries with signs of overexploitation before World War II (Nakano 1999). Thus, in the NW Pacific, elasmobranch exploitation may have

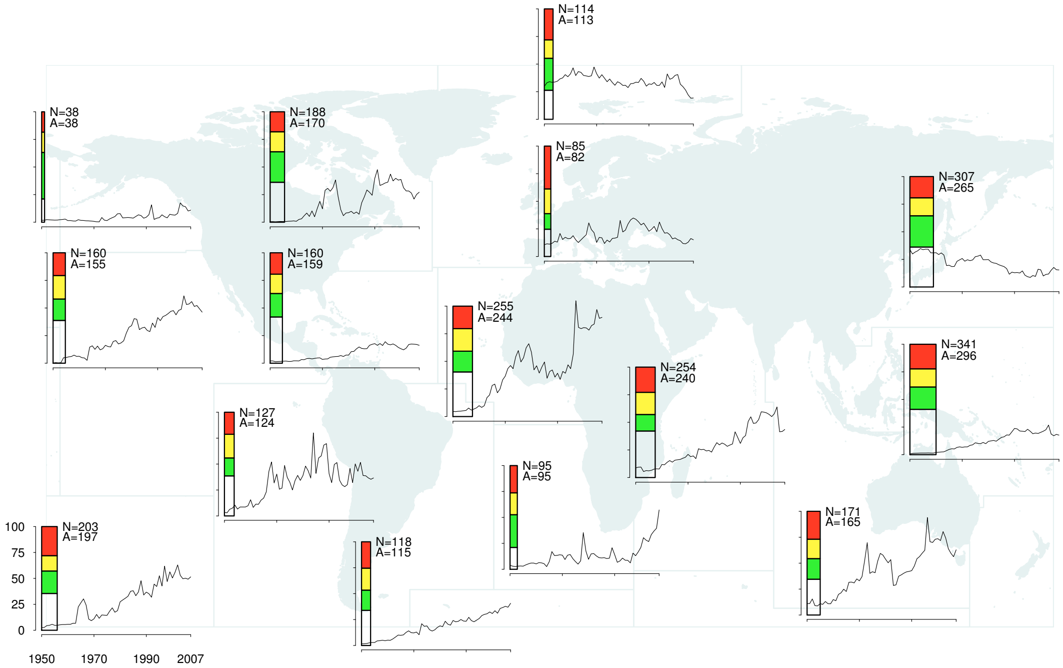

Figure 5.2: Global fisheries trends and conservation status of chondrichthyans. Time series refer to landings of sharks, rays and chimeras in thousands of metric tonnes per km^2 of shelf area since 1950, as reported to the United Nations Food and Agriculture Organization (FAO). Stacked bars represent the global conservation status of all chondrichthyans assessed by the International Union for the Conservation of Nature (IUCN) Shark Specialist Group (Appendix C.1, Camhi *et al.* 2009, http://www.redlist.org). Red indicates the percentage of species that occur in a particular FAO area and that are globally assessed as critically endangered (CR), endangered (EN), and vulnerable (VU); yellow indicates near threatened (NT) status and green the percentage of species assessed as least concern (LC). Transparent bars refer to species that are assessed data deficient (DD) or that have not been assessed yet. FAO assessment areas are outlined in light blue on the background map. A list of chondrichthyans occurring in each FAO area was derived from FishBase (http://www.fishbase.org). N, total number of species occurring in that area; A, number of species assessed by IUCN.

peaked at or before the 1950s. The NE Atlantic and Mediterranean have also experienced long exploitation histories (Lotze et al. 2006). Both show fluctuating landing trajectories with recent downward trends and relatively low catch per unit shelf area today (Fig. 5.2). Independent data suggest that these areas have experienced exceptional elasmobranch population depletions (Ferretti *et al.* 2008, see Appendix Fig. C.1).

Only over the past 5-10 years has the conservation status of many elasmobranchs been systematically evaluated by the International Union for the Conservation of Nature (IUCN). Its shark specialist groups concluded that elasmobranchs are primarily threatened by fishing (96.1%) including directed commercial (31.7%), bycatch (57.9%), recreational (0.7%) and artisanal/subsistence fishing (5.8%), followed by habitat destruction (2.9%) and pollution (0.4%, www.redlist.org). Of the 1159 chondrichthyans known, 881 species have been evaluated globally with 42.8% listed as data deficient (DD), 25.7% least concern (LC), 13.9% near threatened (NT), 11.2% vulnerable (VU), 4.1% endangered (EN) and 2.4% critically endangered (CR, www.redlist.org). Status varies by region, with the highest proportion of threatened (VU, EN, CR) species in the Mediterranean and NE Atlantic (Fig. 5.2), while in the NW Pacific the situation appears less critical. However, there is considerable uncertainty as many species are listed as data deficient or not yet assessed (Fig. 5.2). Three regional IUCN assessments further highlight the critical situation in the Mediterranean and NE Atlantic, while providing a more optimistic assessment for Australia (Appendix Fig. C.1).

5.3.2 Coastal Ecosystems

Coastal ecosystems have been exploited throughout history and few have remained unaffected by human activities (Lotze et al. 2006). Hence, reconstructing pre-exploitation abundances and historical changes of coastal sharks is difficult (Ferretti et al. 2008). However, spatial gradients of human impacts can be used to gain insight into the structure of near-pristine ecosystems and their response to human disturbance. DeMartini et al. (2008) surveyed the fish assemblage in the remote Northern Line Islands (Fig. 5.3a). On uninhabited Kingman Reef, the bulk of fish biomass was composed by predators, 74% of which were reef sharks (*Triaenodon* *obesus*, *Carcharhinus amblyrhinchos*, *C. limbatus*). The proportion and biomass of sharks gradually declined with increasing human presence on neighbouring atolls (Fig. 5.3a). Similarly, the proportion of sharks (*T. obesus*, *C. amblyrhinchos*, *C. galapagensis*) to total fish biomass in the protected North Western Hawaiian Islands (NWHI) was 13% compared to almost zero in the densely populated Main Hawaiian Islands (MHI) (Fig. 5.3b, Friedlander & DeMartini 2002). On the Great Barrier Reef, no-entry marine reserves had higher shark densities (*T. obesus*, *C. amblyrhinchos*) than a near-pristine control site (Cocos Island), while sharks were greatly depleted in fished and even unfished areas where people were allowed to enter (Fig. 5.3c,Robbins *et al.* 2006). Interestingly, there was a sharp difference in overall shark abundance across these case studies. Shark biomass in Kingman Reef was an order of magnitude higher than in NWHI, which had variable fishing regulations over time (Friedlander and DeMartini 2002). Yet NWHI had still twice the sharks than the most protected portions of the Great Barrier Reef (Fig. 5.3), around which commercial fishing for sharks occurs (Robbins et al. 2006). These results suggest that the overall human footprint, including historical and current fishing in surrounding areas, may affect the structure of even protected ecosystems; yet differences in environmental factors or sampling methods may also have played a role (Ward-Paige 2010).

Another valuable source of data on coastal ecosystems comes from shark netting programs, which were developed in South Africa and Australia to protect swimmers. These programs provide long-term time series of shark catches-per-unit-effort (CPUE) in a region. They often pre-dated commercial exploitation and revealed high initial diversity and abundance of large sharks in inshore areas. At least 14 species were caught in netting programs in South Africa (Dudley and Simpfendorfer 2006), 25 in New South Wales (Reid and Krogh 1992) and 11 in Queensland, Australia (Appendix Fig. C.2). Most species were coastal carcharhinids such as bull (*Carcharhinus leucas*) and blacktip sharks (*C. limbatus*). Soon after netting programs began, shark CPUE dropped dramatically. In New South Wales, 10 years after the first nets were installed in the late 1930s, catch rates had declined by 94% (Reid and Krogh 1992). In South Africa, shark netting started in the early 1950s. From 1961-1972 species-specific catch rates declined between 27% and >99% (Fig. 5.4, Appendix Table C.1), yet anecdotal information suggested that severe declines

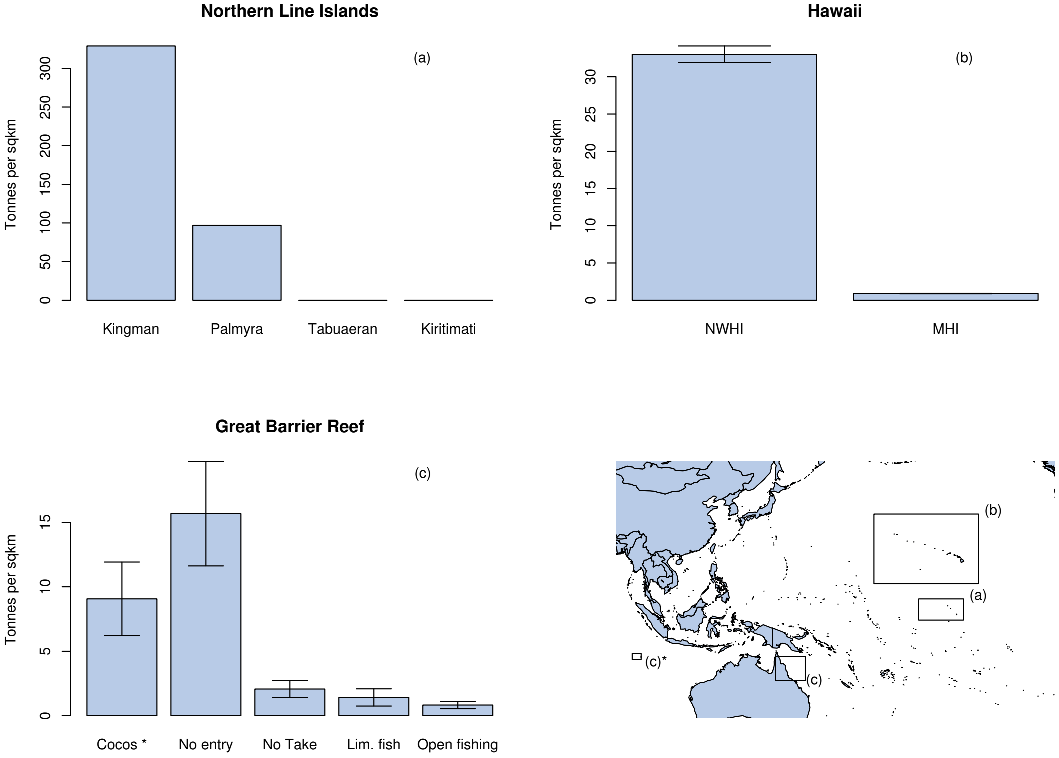

Figure 5.3: Estimates of shark biomass on tropical reefs across gradients of human impacts. These were derived from dive transect surveys in the (a) Northern Line islands (DeMartini et al. 2008), (b) Northwest Hawaiian (NWHI) and Main Hawaiian (MHI) Islands (Friedlander and DeMartini 2002), and (c) different management zones on the Great Barrier Reef and Cocos Island (Robbins et al. 2006). Sample areas are outlined by black boxes on the map. To obtain indices of abundance from (Robbins et al. 2006) comparable to the other studies, we transformed abundance from number per m^2 to weight per km^2. Using information on survival and fecundity provided in the study, we first estimated a stable age distribution for the recorded species. Then, we used species-specific parameters of the von Bertanlaffy growth function (http://www.fishbase.org) to estimate a frequency distribution of lengths at age. From this, we calculated the average length of the population and, using published length-weight relationships (http://www.fishbase.org), estimated the mean weight of the population.

had already occurred before systematic data collection (Holden 1977). Queensland developed its program in the 1960s, and catches decreased by 85% over 45 years (Appendix Fig. C.2). Generally, the nets were only installed on a fraction of the shoreline. South Africa had a maximum of 32 km of nets along 267 km of coastline in 1975. Yet, this was sufficient to affect large sharks across the whole region (van der Elst 1979). In Queensland, newly installed nets recorded similarly low CPUEs as established ones (Appendix Fig. C.2), indicating that shark declines were not just localized phenomena.

These studies suggest that even light fishing pressure by artisanal and subsistence fishing on remote islands or shark-netting programs along continental shores can be sufficient to cause dramatic declines in populations of large coastal sharks. This would explain why such populations are now rare or absent in more impacted systems such as the Gulf of Mexico, Caribbean, and Mediterranean Sea (Shepherd and Myers 2005; Ferretti et al. 2008; Ward-Paige 2010). Moreover, shark-netting data suggest some patterns of ecological reorganisation. As large coastal sharks declined, catch rates of more fecund and wide-ranging species such as tiger (Galeocerdo cuvier) or hammerhead sharks (*Sphyrna* spp.) increased, at least temporarily, in shark nets in New South Wales (Reid and Krogh 1992), South Africa (Dudley and Simpfendorfer 2006), and Queensland (Paterson 1990, Appendix Fig. C.2), However, it is unclear at this point to which extent these reflect changes in abundance, distribution, or behaviour (Simpfendorfer 1992).

5.3.3 Demersal Ecosystems

More than 90% of elasmobranch species worldwide inhabit demersal ecosystems on continental shelves and slopes (Compagno 1990), which makes them vulnerable to trawl fishing (Shepherd and Myers 2005). When trawling begins, catches of elasmobranchs are usually abundant and diverse including both small and large species despite the lower catchability of the latter. For example, scientific trawl surveys in recently exploited shelf regions off South Africa, detected 4 species of large predatory sharks and 51 small elasmobranchs in 1986-1990 (Compagno et al. 1991). On a small shallow bank in eastern South Africa, 6 large coastal sharks and 21 small elasmobranchs were recorded in 1989-1992, as by-catch in a prawn fishery that developed

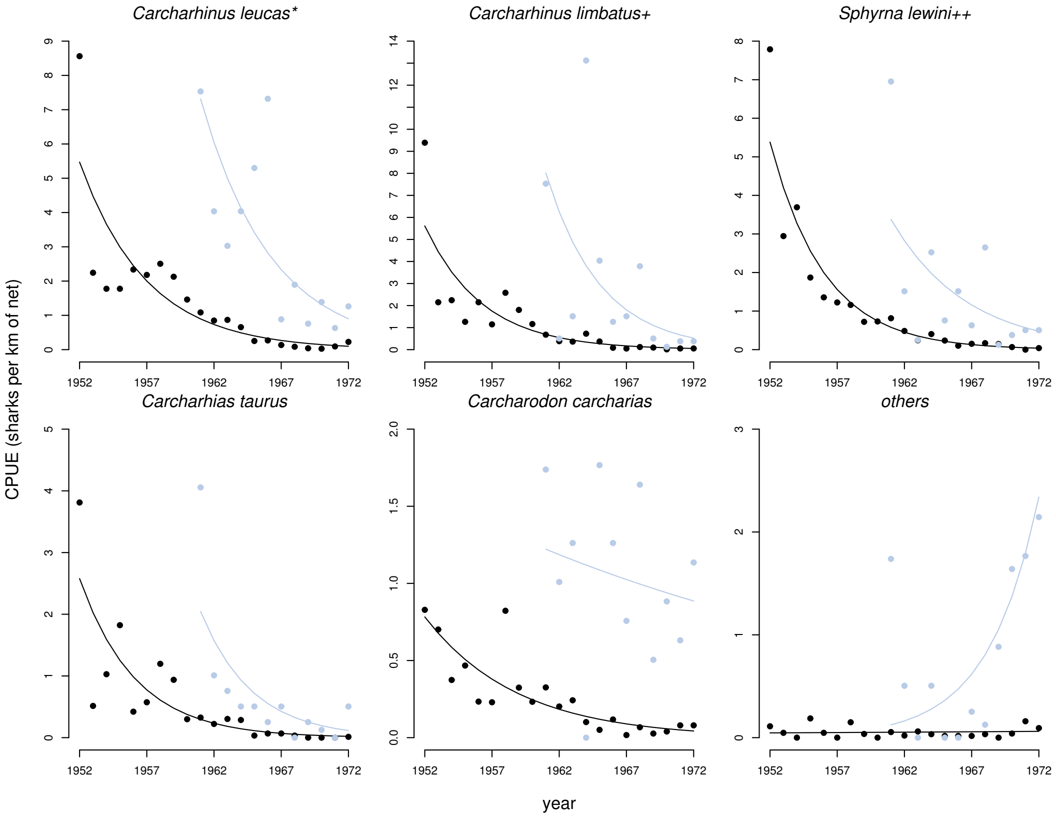

Figure 5.4: Depletion of large coastal sharks. Shown are catches per unit effort (CPUE) of sharks caught by the shark netting program in Main Beach (1952–1972, black symbols) and Brighton Beach (1961–1972, grey symbols) near Durban, South Africa. Data were extracted from Holden (1977). Generalized linear models were fit to the data assuming a Poisson distribution and a log link. Fishing effort in terms of meters of nets per location was treated as an offset variable. Species names refer to the most common species; *few *C. obscurus*; +some *S. tudes*; ++some *C. brevipinna*. Parameter estimates of the models are reported in Appendix Table C.1. 'Others' were mainly pelagic species such as shortfin mako (*Isurus oxyrinchus*), blue shark (*Prionace glauca*) and tiger shark (*Galeocerdo cuvier*).

in the late 1970s (Fennessy 1994). Similarly, in the Gulf of Carpentaria, another recently exploited region of Australia, prawn trawl surveys recorded 10 large coastal sharks and 46 small elasmobranchs in 1990-1998 (Stobutzki et al. 2002).

As fishing proceeds, this initial diversity and abundance can be eroded very quickly. Large sharks often disappear from catches, and the community becomes dominated by smaller elasmobranch mesopredators (e.g. in the NE Atlantic,Ellis *et al.* 2005). Moreover, major restructuring of elasmobranch communities can occur through differential vulnerabilities to fishing gears, variation in spatial occurrence relative to fishing areas, and release from predation and competition. Scientific trawl surveys in the Gulf of Mexico in 1972-2002 revealed substantial changes in the relative abundance of 31 elasmobranch species that are by-catch in the U.S. shrimp fishery (Shepherd and Myers 2005). Catch rates of shallow-water species such as *Dasyatis say* and *Gymnura micrura* declined by 60% and 99% respectively, while those of deeper-water species declined less or even increased, from 6- (*Squatina dumeril*) to 13-fold (*Mustelus canis*). For deeper-water species, shrimp fishing in depths <20 m was less detrimental (Shepherd and Myers 2005). In the Tyrrhenian Sea, trawl surveys in 1974-2005 indicated strong declines in most sharks (e.g. *Scyliorhinus stellaris* 99%, *Squalus acanthias* 89%, *Galeus melastomus* 73%), while bathoids were less affected; again catch rates of deeper-water species declined less or even increased (Ferretti et al. 2005).

Over time, trawl fisheries often expand towards further offshore and deeper grounds (Aldebert 1997; Klaer 2001) where elasmobranch communities are composed of less resilient species (García et al. 2008). In SE Australia, offshore trawling developed in the 1970s, and elasmobranchs made up almost 50% of total fish biomass. After 20 years, elasmobranch catch rates were reduced by 80% (90% if *Squalus megalops* is excluded, Graham *et al.* 2001).

At this stage, domains of developed trawl fisheries often exceed the habitat and dispersal range of many elasmobranch species (Dulvy and Reynolds 2002), leaving no spatial refuges. This is the case of the Mediterranean, where a century of trawl fishing led to the loss of 16 of 31 recorded elasmobranch species in the Tyrrhenian Sea, 6 of 33 species in the Adriatic Sea (Appendix Table C.2) and half of the elasmobranch species recorded in trawl fisheries in the Gulf of Lion since the 1950s

(Aldebert 1997, Appendix S4). Similarly, in the North Sea, a diverse elasmobranch assemblage changed to one dominated by few small, highly productive species such as small spotted cat sharks (*Scyliorhinus canicula*) and little skates (*Raja naevus*, *R. montaguy*, Rogers & Ellis 2000).

5.3.4 Pelagic Ecosystems

Industrial fisheries in the open ocean started in the 1950s (Ward et al. 2000) primarily to catch tuna and swordfish on the high seas. Fisheries statistics and scientific surveys were available from the beginning, and early catch rates essentially reflect unexploited fish communities (Myers and Worm 2003; Baum and Myers 2004; Ward and Myers 2005). Sharks constituted a substantial by-catch (Ward et al. 2000), and often a nuisance in causing damage to hooked target fish (Myers and Worm 2003; Baum and Myers 2004). In the Gulf of Mexico and Pacific Ocean, longliners caught about one shark for every two yellowfin tuna (*Thunnus albacores*, Baum and Myers 2004; Ward and Myers 2005) and in the Atlantic, 2-3 sharks for every swordfish (Brodie and Beck 1983). This led to rapid declines in shark catches over the last 50 years. In the Pacific, standardized catch rates of *Carcharhinus falciformis* decreased by 91.7%, while in the Gulf of Mexico those of *C. longimanus* were reduced by >99% (Baum and Myers 2004). In the NW Atlantic, 18 coastal and pelagic sharks showed declines in catch rates of 49-89% in <15 years (Baum *et al.* 2003, Fig. 5.5). We note here that trend estimates depend on accurate interpretation of commercial longline CPUE data, which can be prone to both hyperdepletion (CPUE declines faster than the population) or hyperstability (population declines faster than CPUE) (Harley et al. 2001). These problems can be alleviated by standardizing for changes in fishing practises, area covered, and other factors. Also using different statistical frameworks can bias trend estimates in different ways (Minami et al. 2007). However, substantial uncertainties remain in some cases, and are the source of considerable debate (Burgess et al. 2005; Baum et al. 2005; da Silva et al. 2008).

At the community level, declines are not uniform across species. Less resilient carcharhinids usually declined first potentially benefiting more prolific species such as blue and mako sharks (*Isurus oxyrinchus*). From 1977-1994, pelagic fisheries landings in Brazil revealed the disappearance of 14 species of carcharhinids (dominated by *C.*

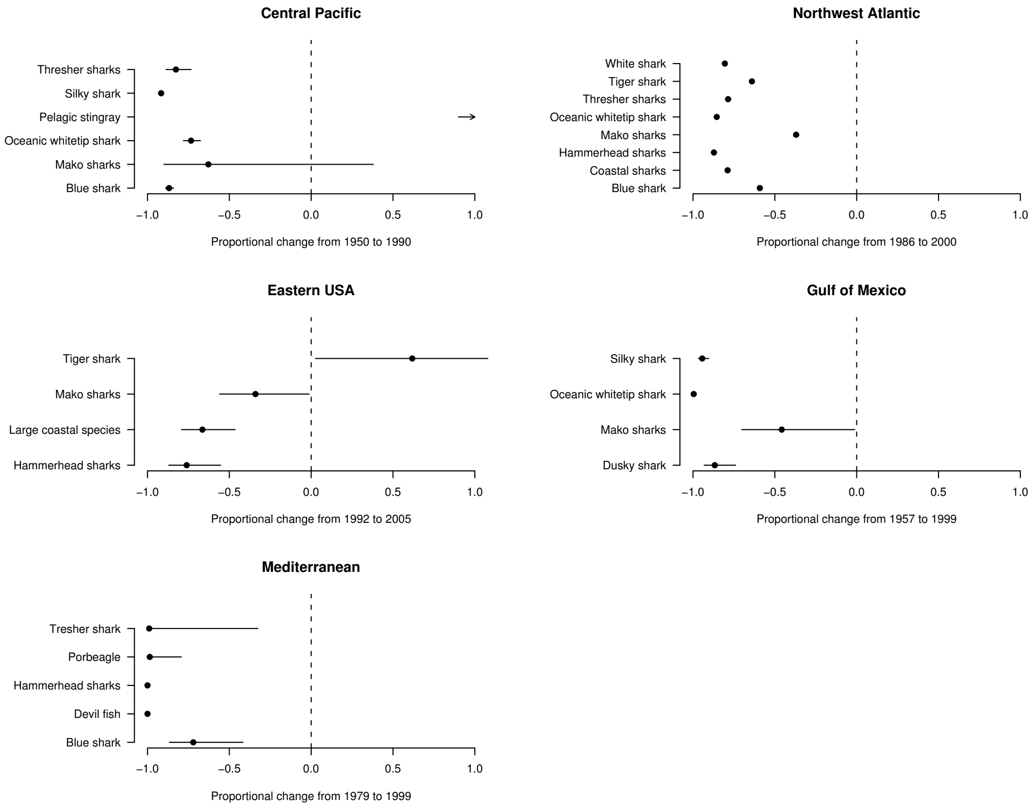

Figure 5.5: Relative changes in population abundance of pelagic sharks in the Central Pacific (Ward and Myers 2005), Northwest Atlantic (Baum et al. 2003), Eastern USA (Myers et al. 2007), Gulf of Mexico (Baum and Myers 2004), and the Mediterranean (Ferretti et al. 2008), based on the analyses of the Ionian Sea pelagic fishery).

signatus), and a concomitant increase of mako and blue sharks (Amorim et al. 1998). Likewise, in the North Pacific, blue shark biomass is estimated to have increased by 20% relative to the 1970s (Sibert et al. 2006), and this species is now considered the most abundant shark in pelagic ecosystems (Dulvy et al. 2008). Mako sharks appear to have declined less than other large species in the Gulf of Mexico, Central Pacific and NW Atlantic (Fig. 5.5). However, when intense exploitation continues, all large sharks can be virtually eliminated such as in the Mediterranean Sea (Ferretti et al. 2008).

Approximately 21 oceanic elasmobranch species are commonly caught in high seas fisheries; these are broad-ranging species with circumglobal distribution (Dulvy et al. 2008). Although there are no documented cases of local species extinctions, 58% of pelagic species are considered threatened by IUCN, more than any other listed group of chondrichthyans (Dulvy et al. 2008). The high demand for shark fins in Asian markets (Schindler et al. 2002) is an important factor in the decline of pelagic species, which are often highly priced for their fins. This has motivated new shark fisheries, and prompted others to switch from bony fish to sharks (Amorim et al. 1998; da Silva et al. 2008). Pelagic sharks range across extensive, poorly monitored areas (Gilman et al. 2008); thus the amount of sharks taken globally for their fins is estimated to be four times higher than that reported to FAO (Clarke et al. 2006).

In summary, sharks have been increasingly threatened by the direct and indirect effects of fishing worldwide. This threat has caused marked declines in shark populations, particularly larger and less resilient species such as carcharhinids. These declines have coincided with substantial reorganisation of elasmobranch communities, including the rise of smaller sharks and rays in some regions. Next, we examine possible mechanisms that can lead to ecological reorganisation while evaluating the wider ecosystem consequences of shark declines.

5.4 Ecosystem Consequences

We are just beginning to understand the potential ecological consequences of shark declines, largely because of the difficulties in studying sharks and their prey in their natural environments. Ecosystem models predict that in some situations sharks will exert considerable top-down impacts on their prey, while not in others

(Stevens et al. 2000; Kitchell et al. 2002; Okey et al. 2004). Unfortunately, a paucity of empircal studies makes it difficult to draw strong conclusions from some of these predictions. For example, we found little data on the effects of shark removals on teleosts and cephalopods, which constitute a large portion of their diets. This scarcity of information likely stems from the difficulties in studying population responses of these prey to variation in shark abundances, but it is also possible (and expected based on models decribed below) that these taxa would be less impacted by shark predation (Jennings and Kaiser 1998; Stevens et al. 2000). Larger-bodied and longer-lived prey species, however, are more likely to respond behaviourally and numerically to shark predation (Heithaus et al. 2008a). Indeed, both theoretical and empirical studies indicate that the decline of large sharks in particular can contribute to observed increases in the abundance of elsasmobranch mesopredators, marine mammals and reptiles and that this can induce cascading effects in some ecosystems. Similar to terrestrial predators (Creel and Christianson 2008), these effects are driven by both consumptive (direct predation) and non-consumptive (behavioural or ‘risk’) mechanisms, (Heithaus et al. 2008a). Therein, risk effects act on the entire population, can be at least as influential as consumptive effects, and may be substantial even for prey that are rarely consumed (Creel and Christianson 2008; Heithaus et al. 2008a). In general, risk effects are expected to be greater when prey are in good body condition and in long-lived species that might invest more in predator avoidance than short-lived ones (Heithaus et al. 2008a). In the following, we are first documenting the theoretical, then the empirical evidence for the ecosystem effects of sharks and their respective mechanisms.

5.4.1 Insights from Food-Web Models

Partly due to a scarcity of empirical data on community changes due to fishing, food-web models based on diet data have been employed to explore possible effects of shark declines on food-web structure. For example, Bascompte et al. (2005) compiled data on trophic interactions of 249 species or trophic groups in the Caribbean, including ten shark species, and analyzed the occurrence of strong and weak interactions in the resulting food web. Sharks were represented in 48% of the trophic chains with strong interactions, and 31% of these were characterized by some degree of omnivory. Bioenergetic models showed that the removal of sharks could induce trophic cascades and make communities more prone to perturbations by reducing the degree of omnivory (Bascompte et al. 2005). The authors hypothesized that overfishing of sharks could have indirectly contributed to an observed shift from coral- to seaweed-dominated reefs, via an increase of fish consumers, which depressed herbivore density. However, others have suggested that predation on groupers and herbivorous parrotfish would occur simultaneously and therefore weaken the indirect effects of sharks on coral reef ecosystems (Mumby et al. 2006).

Mass-balance trophodynamic models (Ecopath with Ecosim, EwE) have been widely used to explore the potential effects of shark declines (Stevens et al. 2000). These models have sometimes been controversial, mainly because current applications do not adequately address uncertainty in data inputs and model structure (Plagányi and Butterworth 2004). Yet they allow us to frame hypotheses about the potential ecosystem effects of fishing. Regarding sharks, EwE models have suggested that effects of shark removal depend on the species involved and the ecosystem context (Stevens et al. 2000). Strong effects were seen particularly for large sharks in coastal environments. For example, in French Frigate Shoals (NW Hawaiian Islands), a simulated decline of tiger sharks caused increases in a range of prey species, including seabirds, turtles, monk seals and reef sharks, which in turn led to rapid declines of tuna and jacks. In contrast, removing reef sharks from the same ecosystem model had little effect (Stevens et al. 2000). One possible explanation is that reef sharks feed on fish and invertebrates that have relatively high turnover rates, as compared to the birds, turtles, seals, and sharks consumed by tiger sharks. Moreover, jacks and other predatory fish may functionally replace reef sharks that feed on similar species, whereas tiger sharks are the only major predator on turtles, for example. In a similar model of Floreana Island (Galapagos), the loss of all sharks led to increased abundance in toothed cetaceans, sea lions, and non-commercial reef predators, which forced decreases in a number of commercial reef fishes, and an increase in small invertebrates via a four-level trophic cascade (Okey et al. 2004). While the increase in marine mammals and decrease in commercial fishes is similar to what was seen in the Hawaiian model, it is unfortunate that the effects of larger sharks (mostly

Carcharhinus galapagensis) and reef sharks could not be separated.

With respect to demersal systems, on the NE Venezuelan shelf, the simulated removal of smaller demersal sharks (mesopredators feeding on fish and invertebrates) caused complex and persistent changes in the abundance of many species groups, some of which had weak trophic interactions with sharks (Stevens et al. 2000). However, it is unclear which mechanisms caused those complex effects. Less strong and persistent effects were seen in pelagic systems. In the Alaska Gyre, the modeled depletion of pelagic blue and salmon sharks (*Lamna ditropis*) had mostly transient effects on pinnipeds and large fish (Stevens et al. 2000). Similarly, in the Central North Pacific, Kitchell et al. (2002) did not identify sharks as keystone predators of the pelagic community. In their model, the effect of pelagic sharks on the fish community was limited because of sharks' restricted diets and low consumption rates. Predatory fishes such as tuna and billfishes, characterized by faster biomass turnover, could substitute sharks without significantly affecting the dynamics of other species (Kitchell et al. 2002). Thus, based on these trophodynamic models we would predict that the effects of shark declines should be more pronounced in coastal and demersal than pelagic systems. We also would expect larger effects in sharks that feed on long-lived prey species.

Behaviourally-explicit models suggest that the risk of shark predation could also be important in driving community dynamics. For example in Prince William Sound, Alaska, harbour seals (*Phoca vitulina richardsi*) are preyed upon by killer whales (*Orcinus orca*) near the surface and sleeper sharks (*Somnius pacificus*) in deeper waters. Seal prey resources are segregated in the water column as well; Pacific herring (*Clupea pallasi*) occur towards the surface while walleye pollock (*Theragra chalcogramma*) overlap with sleeper shark distribution at depth. Modelling shark, orca, seal and prey depth distribution from fisheries data and tagging experiments, Frid et al. (2007) predicted that both orcas and sharks influenced seals' diving behaviour and resource use. However, sharks elicited a stronger behavioural response than killer whales, even though seals were only a minor portion of their diets (Frid et al. 2007). In the presence of sharks, seals reduced foraging on abundant pollock, unless herring was scarce or seals were in poor energy condition (Frid et al. 2007).

5.4.2 Effects on Elasmobranch Mesopredators

Large sharks are important, and sometimes the only consumers of smaller elasmobranchs (Wetherbee & Cortés 2004 and references therein). An increase in these species following declines of large sharks has been documented in several coastal and demersal habitats, but rarely in pelagic ecosystems. Above we discussed the increases in small demersal sharks and rays in the Gulf of Mexico and Mediterranean (Shepherd and Myers 2005; Ferretti et al. 2005). Likewise, along the eastern U.S., catch rates of 14 small elasmobranch species in research surveys increased from 1.2% to 25.6% per year from 1959-2005, possibly in response to large predatory shark declines (Myers et al. 2007). Similarly, on the U.S. west coast, from California to Canada, 7 small chondrichthyans species increased from 1977-2001 (Levin et al. 2006).

Dogfishes (*Squalus* spp.) in particular have shown strong increases in many regions. *S. acanthias* increased 20- and 17-fold in the Gulf of Alaska and Prince William Sound, respectively (Fowler et al. 2004), and *S. megalops* increased 5-fold in SE Australia from 1976-1997 (Graham et al. 2001). Dogfishes and other small demersal elasmobranchs also increased sharply in New England in the 1970s-1990s (Rago et al. 1998), a trend that coincided with the overfishing of groundfish (Fogarty and Murawski 1998) and the depletion of large sharks (Hurley 1998; Baum et al. 2003). They are now the most abundant demersal sharks on the shelf and upper slope of New Zealand (Beentjes et al. 2002) and South Africa (Kroese and Sauer 1998). In contrast, dogfishes have been driven to very low levels in the NE Atlantic because of intense target exploitation, and a similar overfishing trend has been seen where directed fisheries developed in the NW Atlantic (Rago et al. 1998; Fowler et al. 2004). These observations suggest that small elasmobranchs show widespread increases which could be partly linked to predator release. However, such increases can be reversed quickly by fishing, because of the high sensitivity of elasmobranchs to any changes in survival (Shepherd and Myers 2005). Note that most examples of local extinctions in Table A1 also concern smaller mesopredatory elasmobranchs.

In pelagic ecosystems, information about mesopredator changes is more limited, probably because those species have little commercial value, are not recorded, or are not susceptible to longline gear. Scientific survey and observer data from the Central Pacific (Ward and Myers 2005), however, do suggest large increases in pelagic stingray

(*Pteroplatytrygon violacea*) and small teleosts, e.g. slender sunfish (*Ranzania laevis*) and pomfrets (Bramidae), from 1950s-1990s. In addition to changing population size, increases may also be due to changes in habitat use; the removal of large sharks may allow small species to move into sunlit epipelagic waters during the day, which once were the domain of large predators (Ward and Myers 2005). Because sharks and other predatory fish such as tuna and billfish declined at the same time, the apparent increase in mesopredators cannot be attributed to sharks alone.

5.4.3 Effects on Marine Mammals and Sea Turtles

A number of large sharks commonly prey on marine mammals and reptiles, exerting both direct predation and risk effects (Heithaus 2001; Heithaus et al. 2008b). The preferential distribution of predatory sharks in tropical and temperate latitudes is thought to be one of the limiting factors for the expansion of pinnipeds and pursue-diving birds in these regions (Cairns et al. 2008). For example, tiger sharks are primary predators of some sirenians, dolphins, sea turtles, sea snakes and cormorants (Heithaus 2001; Heithaus et al. 2008b). Detailed studies in Shark Bay, Australia have shown how seasonal occurrence of tiger sharks influences the distribution, habitat use, and feeding behaviour of multiple preys (*Chelonia mydas*, *Dugong dugong*, *Tursiops aduncus*) with population and ecosystem-level consequences (Heithaus *et al.* 2008, and references therein). Tiger sharks increase in abundance in warmer months yet almost disappear in the cold season. Their preference for productive shallow habitats causes even infrequent prey such as dolphins and dugongs to give up foraging opportunities in order to enhance safety. Not all individuals, however, abandon profitable but dangerous foraging locations. For example, green turtles in poor energetic condition are more frequently observed in the interior of seagrass beds, where the highest-quality plants are found, despite increased predation risk (Heithaus et al. 2007).

Relaxation of shark predation may have partially contributed to the recovery of some megafauna populations. In the NW Atlantic, the recovering grey seal (*Halichoerus grypus*) population on Sable Island experienced an increase in pup production of 12.6% per year in 1962-1982. Reduced shark predation on juveniles has been proposed as a contributing factor (Brodie and Beck 1983), since large-scale declines of predatory sharks have occurred since the 1960s (Brodie and Beck 1983; Hurley 1998; Baum et al. 2003). Likewise, the harbour seal population increased by 6% per year throughout the 1980s (Lucas and Stobo 2000; Bowen et al. 2003), but strongly declined in the 1990s due to increased mortality (Lucas and Stobo 2000; Bowen et al. 2003). Bite morphologies suggested Greenland sharks (*Somniosus microcephalus*) as possible predators (Z. Lucas unpublished work), and it was suggested that a water temperature decline caused these cold-water sharks to expand to Sable Island (Bowen et al. 2003). Grey seals were also preyed upon, but seemed less affected for their high abundance. This likely contributed to the decline of the reduced harbour seals population through increased competition (Lucas and Stobo 2000; Bowen et al. 2003). A conservative estimate suggests that sharks might have contributed to about 50% of the harbour seal decline (Lucas and Stobo 2000).

Finally, the endangered Hawaiian monk seal (*Monachus schauinslandi*) is preyed upon by both tiger and Galapagos sharks. Monk seal populations at French Frigate Shoals experienced sudden increases in juvenile mortality in the early 1990s enhancing ongoing population declines (Antonelis et al. 2006). An experimental removal of 10 Galapagos sharks from pupping beaches reduced annual shark-inflicted pup mortality from 28 in 1997 to 3 in 2003 (Antonelis et al. 2006), suggesting that sharks could play an important role in seal population dynamics.

5.4.4 Empirical Evidence of Trophic Cascades

Several recent studies support the idea that changes in large shark abundance can induce trophic cascades through changes in prey abundance or behaviour. Data from 17 research surveys from Florida to Maine revealed increases of 12 small sharks, skates and rays that coincided with declines in large sharks from 1970-2005 (Myers et al. 2007). One ray, *Rhinoptera bonasus*, strongly increased in abundance and in turn reduced its prey, the bay scallop *Agropecten irradians*, in North Carolina (Myers et al. 2007). While the effects of rays on scallops were confirmed by exclusion experiments (Myers et al. 2007), the effect of sharks on rays is less well documented. There is an active debate concerning the magnitude of predation release and possible mechanisms. For example, some increases in catch rates of small elasmobranchs may not only reflect changes in population size but also changes in migration patterns, range shifts, or habitat expansions.

The 50-year shark netting program along the Kwala-Zulu Natal shore in South Africa provides another good example of possible cascading effects (Fig. 5.6). In 1956-1976, while large shark CPUE declined in netting programs (Fig. 5.6a) recreational fishing tournaments revealed a proliferation of smaller elasmobranchs in inshore waters and a decline of bony fish (Fig. 5.6b-d, van der Elst 1979). The increase in smaller sharks was dominated by two species: juvenile *Carcharhinus obscurus* and *Rhizoprionodon acutus*. These were only lightly affected by shark nets, but preyed upon by larger sharks. Although *C. obscurus* can grow to large size (maximum length 4.2 m), it uses those inshore waters as nursery areas (van der Elst 1979) and the reduced presence of large predatory sharks may have benefited its pup survival. van der Elst (1979) proposed that the increase in these mesopredators contributed to observed declines of bony fish, which constitute a large portion of their diet. Independent projections estimated that between 419,000 and 2.8 million small sharks, and about 5000 dolphins would have escaped shark predation in the period 1956-1976 (van der Elst 1979; Dudley and Cliff 1993). Data collected after 1977 from the same fisheries provide an intriguing temporal contrast. Since the 1990s, C. obscurus and R. acutus (representing 69% of elasmobranch catches) showed an overall decline (Fig. 5.6f). Angling pressure for these species was elevated (Pradervand et al. 2007) and likely overcompensated for the previous decrease in natural mortality. At the same time, catches of rays and bony fish increased (Fig. 5.6g, h), likely benefitting from reduced predation and competition from sharks. Pradervand et al. (2007) cautioned that these trends may have been influenced by changes in fishing technology or attitude, yet clear evidence for these mechanisms is missing.

Risk effects can also initiate trophic cascades. For example, green turtles and dugongs affect the spatial distribution and species composition of seagrass beds through foraging and excavation (Preen 1995; Aragones 2000). In Shark Bay, Australia, the spatial patterns of seagrass nutrient composition suggest that tiger shark-induced shifts in foraging locations and behaviours of green turtles and dugongs cascade to seagrasses (Heithaus et al. 2007; 2008a). Recent studies in other areas, where tiger shark populations have declined but green turtles have begun to recover, also suggest indirect effects of sharks on seagrass, mediated by the release of large

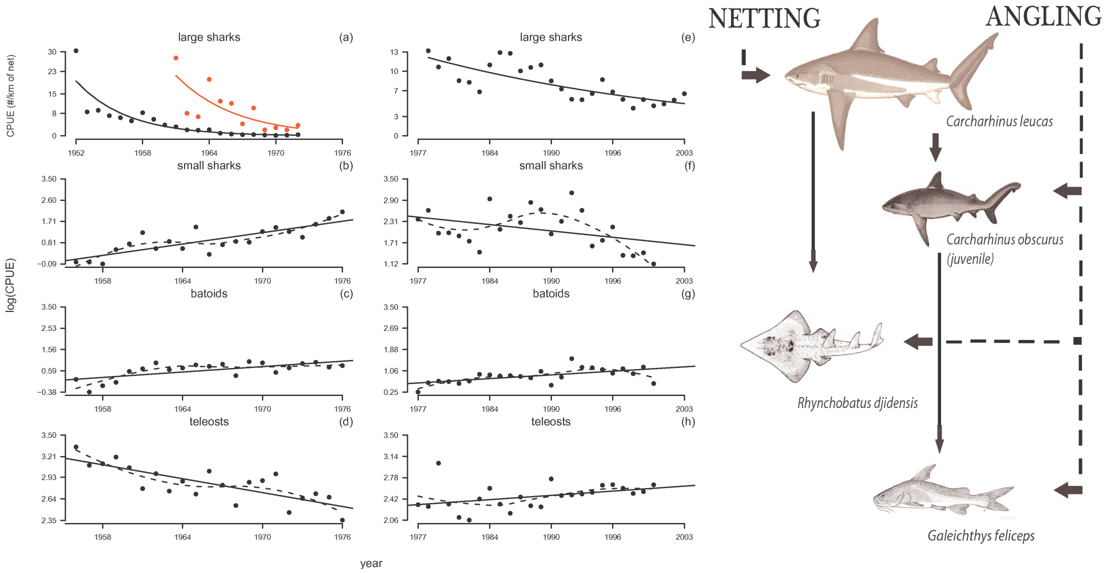

Figure 5.6: A possible trophic cascade in the inshore waters of Kwa-Zulu Natal, South Africa. Two periods are contrasted: 1952–1977 and 1978–2003. (a, e) Large sharks caught in shark netting programs (black: Main Beach, grey: Brighton Beach); data were derived from aggregated catches of large sharks species reported in Holden (1977) and Dudley and Simpfendorfer (2006). To be consistent between time periods, the species included in this group in both panels (a, e) are those reported by Holden (1977). Regression lines are: (a) generalized linear models as specified in Fig. 5.4, and (e) linear models of $log(CPUE)\ year$. Panels (b–d) and (f–h) are time series of log CPUE of small sharks (mostly juvenile dusky sharks), batoids (skates and rays) and teleost fishes from the recreational fishery, as reported by van der Elst (1979) and Pradervand et al. (2007). As the fraction of teleosts was not explicitly reported in Pradervand et al. (2007), we estimated it by subtracting the elasmobranchs from the total number of fish caught. Solid lines depict linear regressions fitted to log transformed data. Dashed lines represent local regressions (LOESS). The diagram shows common species caught by shark nets and recreational angling, respectively, as well as their trophic relationships. The initial increase of small sharks was thought to be due to predatory release, and their later decline because of increased angling pressure.

grazers (Murdoch et al. 2007; Heithaus et al. 2008b).

It seems likely that trophic cascades driven by the depletion of large sharks may play out in other parts of the world, but have so far remained undocumented because of a lack of data on non-commercial species (Myers et al. 2007) or missing connections between separate studies that involve many species and broad temporal and spatial scales. Clearly, there is a need to find out whether the above examples represent isolated cases or common patterns that shape contemporary marine ecosystems.

5.5 Conclusions

Our overview shows that in natural, unexploited systems, sharks often exhibit high abundance and diversity. Yet even light fishing pressure is sufficient to cause strong population declines in vulnerable species, particularly large sharks. Such trends have been shown for artisanal and subsistence fishing on remote islands, shark netting programs, and in trawl and long-line fisheries in many regions, resulting in community shifts from large- to small-bodied species. Population declines of large species often exceeded one, sometimes two orders of magnitude with some local extinctions. Yet some more resilient species have not declined as drastically or have even increased, possibly via reduced competition or predation. Larger shark populations are still seen in some remote or protected areas, particularly in the Pacific, and may provide valuable opportunities to further understand the ecological role of sharks. Yet, reported catches of sharks and other elasmobranchs are still increasing in most regions, possibly indicating that more fisheries target sharks where they have not been historically exploited, a trend partially driven by the rising demand for highly prized shark fins on Asian markets.

Our brief review of shark evolution and life history suggests that sharks have been a relatively stable force in ocean ecosystems over evolutionary time, and possess a unique combination of ecological traits. They are morphologically and phylogenetically related to bony fish, but their life-histories may be more comparable to marine mammals, specifically with respect to their large size, low rate of reproduction, and late maturity. This renders sharks highly sensitive to changes in survival, either through predation or fishing. Many large sharks are the sole predators of smaller elasmobranchs and other marine megafauna, and the depletion of large sharks has likely contributed to considerable increases in these species in some regions. With their wide-ranging distribution and predatory role, large sharks in particular can spread their impacts across different ecosystems. Such spatial connectivity has also been shown to be important in freshwater and terrestrial ecosystems (Knight et al. 2005), and may increase the connectivity and stability of ocean food webs.

Ecosystem models predict that the loss of sharks should result in complex community changes, including trophic cascades, mesopredator release, and consequent declines in some commercial fish. The strength and persistence of these effects, however, appears to decrease from coastal and reef to demersal and pelagic environments. Observational studies suggest the presence of strong species interactions in some regions, mediated by direct consumption and risk effects, sometimes leading to trophic cascades. Figure 7 attempts to conceptualize observed top-down links, and broad abundance trends across coastal and demersal ecosystems in different regions: as fishing and netting effort has increased, declines in large apex-predatory sharks have coincided with widely documented increases in smaller sharks and rays, as well as mammals and turtles. These mesopredator increases may be partly explained by decreased predation mortality and risk effects, and have in some cases led to increased pressure on prey species, such as invertebrates and teleost fishes or even seagrasses (Fig. 5.7). We must caution that many of the interactions displayed in Figure 5.7 are supported by limited empirical evidence. We are only beginning to study the complex ecological roles that large-bodied, wide-ranging predators such as sharks play. An important consideration for further research is the context-dependence of these interactions, which undoubtedly are mediated by a number of factors. These may include, among others:

1. Food web properties: the diversity of available prey species will determine whether sharks can easily switch to alternative prey, and could limit the effects on any particular species. Furthermore the presence and strength of intraguild predation in which sharks are involved could affect their role as a group (Kitchell et al. 2002; Kondoh 2008). Finally, whether particular prey species of sharks have other predators (such as billfish or tuna in pelagic systems), and

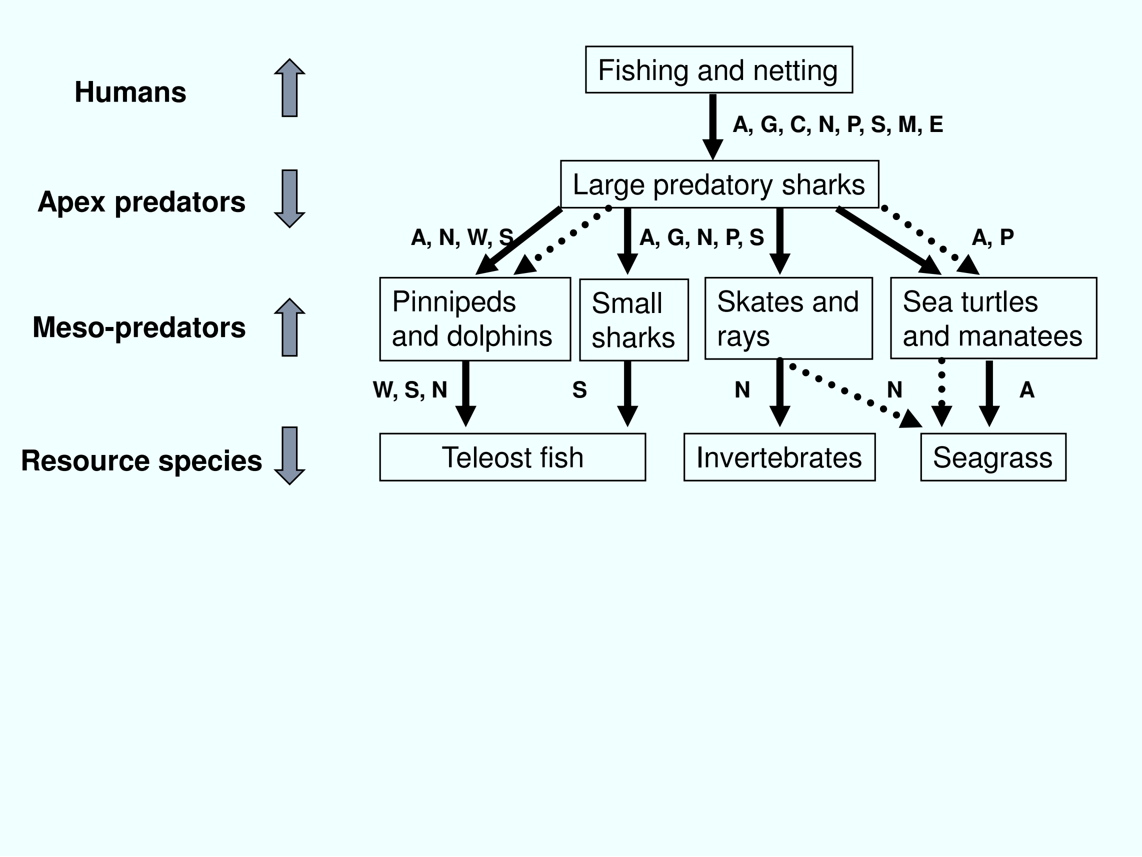

Figure 5.7: Documented ecosystem effects of fishing large sharks. Depicted are trophic (solid arrows) and behavioural (dotted arrows) interactions between humans, large and mesopredator elasmobranchs and their prey species. Block arrows represent overall population trends of the various functional groups. Regions in which particular interactions have been documented (see text) are indicated by letters (A, Australia; C, Caribbean; E, Europe; G, Gulf of Mexico; M, Mediterranean Sea; N, North American East Coast; P, Central Pacific; S, South Africa; W, North American West Coast). Note that few studies have documented effects on teleost and cephalopod prey.

whether these prey are strong interactors themselves (such as large-bodied grazers in coastal systems), will affect the propagation of shark predatory effects through the food web.

2. The life-history attributes of mesopredator and prey species: long-lived species and those which cannot compensate for increased mortality through growth or reproduction should be most affected by shark predation and risk effects. Also, the scope for effective anti-predator behaviour varies among species and individuals (Heithaus et al. 2008a). Separating direct predation and risk effects and understanding their potential interactions for different prey species poses a fascinating challenge for the study of large mobile predators.

3. The interplay of fishing and predation: fishing affects not just sharks, but a wide range of target and bycatch species, and continues to change the nature of top-down regulation in the ocean (Heithaus et al. 2008a; Baum and Worm 2009). Any assessment of the effects of sharks needs to take into account changes in both natural (predation and environmental factors) and fishing mortality. While ecologists tend to focus on natural mortality, fisheries and conservation biologists tend to concentrate on human-related threats. In reality, however, natural and fishing mortality interact such that they both drive observed changes. For example, the decrease in both human and shark-inflicted mortality may have affected the rapid increase in grey seals in Eastern Canada (Brodie and Beck 1983), whereas both fishing and increased natural mortality from cownose rays may have contributed to the collapse of bay scallops in North Carolina (Myers et al. 2007). We suggest that these drivers, along with their direct, indirect and interactive effects should pose a ripe challenge for theoretical and empirical research. The objective would be to quantify and visualize spatially and temporally dynamic landscapes of risk and mortality, integrating the complex effects of human and non-human predators.

Chapter 6

Conclusions

6.1 Main conclusions

Overall, my thesis had a threefold objective: (i) determine the long-term changes in elasmobranch populations in one of the most depleted large marine ecosystems of the world, the Mediterranean Sea, (ii) evaluate the role of sharks in marine ecosystems and the consequences of their human-induced decline, and (iii) compare the patterns and consequences of changes in exploited elasmobranch communities in the Mediterranean with those in other marine ecosystems of the world. In the following, I briefly summarize the main conclusions from the different chapters, then highlight the management implications of my results, and provide an outlook on potential future directions of my research.

The work presented in Chapter 2 filled a critical information gap on the status of large sharks in the Mediterranean Sea by providing the first large-scale evaluation of historical changes in remaining shark populations. Declines of the analyzed species ranged between 96% and 99.9%, yet concerned only 5 of 20 species historically recorded to inhabit the Mediterranean basin. Based on the species life-history and ecological characteristics, the history of Mediterranean fisheries, and old catch records, I concluded that large coastal sharks (Carcharinids) have substantially declined during earlier time periods, while sharks able to range from littoral to pelagic habitats were temporarily sheltered from intense historical coastal exploitation when remaining in offshore waters until high-sea exploitation begun in the 1950s. The analyses performed in Chapter 2 completed previous qualitative accounts of predator declines in the Mediterranean (Bearzi et al. 2004; Tudela 2004; FAO 2005; Fromentin and Powers 2005; Reeves and Notarbartolo di Sciara 2006; WWF 2006; Damalas et al. 2007) and raised concerns for the entailed ecological consequences of these changes.

In Chapter 3 and 4, I focused on analyses of trawl survey data in two sectors of the Mediterranean Sea. Chapter 3 dealt with demersal ecosystems of the upper Tyrrhenian Sea, a historically exploited region on the Northwest coast of Italy. Here I demonstrated the decline to below detectable levels of 17 elasmobranch species from a pool of 36 that were described in trawl fishery landings in the early 20^{th} century. Many of the local extirpations occurred before the beginning of industrial fishing in the 1950s, and remained unnoticed because of failure to compare recent with historical data, with the use of appropriate analytical frameworks to analyze trawl surveys. By assuming a negative binomial distribution of catches within a generalized linear modeling framework, I could fit trends in abundance of 26 demersal elasmobranchs. Responses of the exploited elasmobranchs were closely related to spatial patterns of fishing intensity and its overlap with the species distribution. Species occurring in deeper waters declined less or even increased in abundance because of the lower fishing effort in these habitats. However, by analyzing the ecology and life history of detected populations, I could show that the dynamics of exploited elasmobranch communities are complex and influenced by several other factors, including species intrinsic vulnerability, habitat range, and size.

Chapter 4 dealt with another heavily depleted sector of the Mediterranean basin, the Adriatic Sea. The location was chosen for its long exploitation history, peculiar ecological setting, and spatiotemporal contrasts of perturbation, which was ideal to analyze population dynamics over long time scales and across different exploitation regimes. By analyzing 5 separate demersal research surveys from 1948 to 2005, I found that sharks and rays have been depleted by >92% and at least 37 of 69 formerly described species have locally disappeared due to fishing. The spatial heterogeneity of fishing effort provided insights into different patterns of change in the highly exploited western compared to the less exploited eastern part of the Adriatic. I was also able to show that the variable level of mobility among species explained spatial patterns of community change in response to exploitation. While wide-ranging species persisted and spilled over from less to highly depleted regions, more sedentary species only sustained populations in areas of light exploitation. Thus, the spill-over and redistribution of highly mobile species may contribute to population recovery after fishing ceases. Recovery, however, requires the protection of ecological corridors between exploited and unexploited areas. Results of this chapter suggested the potential benefit of large area closures for the conservation and recovery of depleted marine communities. If portions of suitable habitats for elasmobranchs are left unperturbed, or critical habitats are protected, elasmobranch resistance and resilience to exploitation can increase substantially.

Both Chapters 3 and 4 confirmed the extreme degree of depletion of exploited Mediterranean fish communities, especially those subjected to commercial trawling. Analyzing fishery independent data from unselective fishing gears was useful to describe multiple population trajectories in response to exploitation, and thus gain insight into the magnitude of depletion and extinction risk across a broad range of species. I confirmed that large and low productive animals are among the most vulnerable to exploitation. Nonetheless, the species ecology and distribution have a strong effect on extinction risk because they influence the exposure and vulnerability to fisheries. As most of the species detected in trawl surveys have home ranges comparable with fisheries' extensions, I found a close correspondence between landscapes of fishing intensity and abundance and diversity of exploited species. Furthermore, I found that differences in intrinsic vulnerability among species are often masked by interspecific interactions, such as predator-prey and competitive interactions. Although these are evident in the initial stages of depletion or where fishing is light, such patterns are masked or reversed by the overwhelming effect of increasing fishing later on.

In Chapter 5, results of previous chapters dealing with the Mediterranean were placed in a global context. I provided evidence of a great abundance and diversity of large sharks where exploitation pressure is zero or very light. However, this biodiversity is extremely vulnerable to even minimal levels of fishing, explaining the low levels or absence of many species from the Mediterranean Sea and other highly exploited marine ecosystems. I compiled evidence that the decline of large predatory sharks contributed to changes in the abundance, distribution, and behavior of smaller elasmobranchs as well as marine mammals and sea turtles that have few other predators. Synthesizing theoretical and empirical research, it emerges that sharks affect their prey not only by direct consumption-induced mortality but also through mechanisms of fear. I added new perspectives on observed increases of mega fauna and trophic cascades in several sectors of the world. Large sharks can exert strong top-down control that may shape marine communities over large spatial and temporal scales. Yet more empirical evidence is needed to test the generality of these effects throughout the ocean. In many large ecosystems, fishing pressure on mesopredators might mask or even reverse some of the ecosystem effects of large shark declines.

Throughout my thesis, I showed that assessments of depleted populations can be carried out with scattered, inconsistent and unbalanced data sets on animal abundance. Thereby, it is crucial to use appropriate statistical techniques that are able to deal with peculiar probability distributions of data characterizing rare animal populations. Meta-analysis can be very useful to quantitatively combine multiple sources of data that would produce contrasting and unconvincing results if analyzed individually because of their limited spatial coverage or temporal extension. In this regard, historical research is important to discover and integrate unconventional data that are the only source of information for many rare and endangered species and can help to hindcast ecological baselines (Lotze and Worm 2009). Incomplete historical data can be incorporated and combined with recent information by borrowing strength from their higher resolution statistics. For example, in Chapter 4, I used distribution parameters of the negative binomial distribution of species caught in recent high resolution trawl surveys to incorporate old surveys characterized by smaller sample sizes for the estimation of long-term trends in abundance of elasmobranchs caught in the Adriatic Sea. Here, I foresee an increasing use of Bayesian statistics. Available data in the Mediterranean is scattered, often qualitative, and therefore, challenging to combine with recent high resolution information. However, recent data can be used as priors to increase the amount of information that could be extracted from incomplete historical material (Gerber 2006).

6.2 Management Implications of the Work

This thesis increased our understanding on the status of sharks and rays in the Mediterranean Sea by providing sound scientific evidence on the magnitude and patterns of decline over the last two centuries. The alarming results of multiple local disappearances and >90% of population depletions call for immediate conservation actions, especially because the causes of decline have not halted but rather increased in efficiency and spatial extent over time. Conservation actions aimed at non-commercial species, such as sharks and rays, are often problematic because of the entailed costs of fishing restrictions and regulations of other human activities. These need to be weighted against the predictable long-term benefits of elasmobranch conservation for marine ecosystems and human society. This process relies on effective communication of reliable scientific results to the public and policy makers.

I worked in close collaboration with the Lenfest Ocean Program for disseminating the results of Chapters 2 and 5. We have produced plain language research syntheses targeted to the general public and decision makers (Anonymous 2008b; 2010). For communicating the results of Chapter 2, we further organized a press conference in Rome on June 10 2008, which received wide national and international media interest. I gave interviews to many newspapers, radio and television agencies worldwide, including BBC News, Washington Post, the New York Times, the Times of London, and Le Monde. It is my hope, that these outreach efforts contribute to change the public perception of the status of sharks and marine ecosystems.

In July 2008, the European Commission requested the Scientific, Technical and Economic Committee for Fisheries (STECF) to review the results of Chapter 2 published in Ferretti et al. (2008), evaluate the findings and make appropriate comments and recommendations. STECF recognized the challenge in compiling, combining and analyzing the heterogeneous pool of data used. It recognized that the approach based on historic records, bibliographic search, and combining different kinds of information was the only feasible strategy to pursue in the Mediterranean. STECF encouraged the undertaking of similar analyses with more focus on reducing uncertainty noting that additional time series are available and should be analyzed in the future. Based on the evidence provided by my analyses, STECF recommended that an EU Action Plan for Sharks should be agreed upon and implemented as soon as possible. This should include the possibility to establish by-catch reduction programs for elasmobranch species considered Critically Endangered or Endangered by IUCN. By-catch reduction programs for elasmobranchs are desirable, where a zero Total Allowable Catch (TAC) or prohibited status is not in force for these species (Anonymous 2008a).

On February 5th 2009, the European Commission adopted the first ever EU

Plan of Action for the Conservation and Management of Sharks (http://europa.eu). Although the adoption of this policy framework is the result of the work of many NGOs, international conservation bodies and advice of many scientists, the results of my work provided strong empirical evidence to accelerate the formalization of the Commission's commitment toward the conservation of cartilaginous fish.

One challenge I faced during my doctoral research was the difficulty to access publicly-funded data on research surveys of marine resources in many Mediterranean countries. The European Commission is investing large quantities of public money to evaluate the status of exploited fish population in its waters. In the Mediterranean, these data are not readily available for scientific use. Data regarding elasmobranchs should be considered highly important and urgently needed to determine their status and trends. Effective management and conservation actions require accessible information and sound scientific analysis. Such information should not be withheld from scientific use.

6.3 Future Research

The work outlined in this thesis raised multiple research questions and lines of investigation that should have high research priority because of their potential to produce original and important results on top-down regulation of marine ecosystems and shark conservation.

1. Analyzing the structure of pristine marine ecosystems: The analyses of recently exploited coastal ecosystems and remote islands revealed interesting insights into the structure and composition of natural communities. Predators were mostly composed of large sharks, while in the Mediterranean, and other large marine ecosystems, scientific observations were late to capture the onset of human induced ecosystem change. Similarly, unpopulated and protected areas in Africa feature high diversity and abundance of large cats (Felidae) and canids (Sinclair et al. 2003), that in the majority of terrestrial ecosystems were eradicated thousands of years ago (Roberts et al. 2001; Lyons et al. 2004). Investigating the conditions that allow the persistence of large predators, and their effect on ecosystem structure and functioning could reveal important insights into understanding the ecological role of sharks. More broadly, it could

reveal generalizations on top-down control of natural ecosystems with practical implications of placing current conservation efforts and restoration targets in a meaningful perspective.

2. Synthesizing long-term changes in demersal elasmobranch communities: Analyses of Chapters 3 and 4 revealed patterns of change in exploited demersal communities characterized by steep population declines and multiple species eradications. Similar studies adopting different analytical techniques reached comparable results in other western Mediterranean sectors (Aldebert 1997; Gerber 2006). Conversely, observations from the eastern and southern Mediterranean suggest lighter ecosystem depletion (Basuşta et al. 2006). Future research should incorporate all historical and recent trawl survey data from the Mediterranean to produce an overall assessment of the Mediterranean Sea. Increasing the spatial coverage of analyses carried out in the Adriatic and Tyrrhenian Sea would clarify the extent of elasmobranch depletion in the basin, explain dynamics of species recovery and resistance to exploitation, and evaluate whether cases of mesopredator release observed in other parts of the world could be detected in areas of lighter exploitation in the Mediterranean.

3. Characterizing top-down control of sharks: Many large sharks are important or even sole predators of smaller elasmobranchs, marine mammals, seabirds and other megafauna, and have contributed to shape the abundance and distribution of many wide ranging organisms in the ocean over evolutionary times (Cairns et al. 2008). The magnitude and mechanisms of sharks top-down control and its propagating effects on other ecosystem components have been little quantified across broader spatial and temporal scales. In this thesis, I have been able to describe such top-down effects based on circumstantial evidence, yet most examples have been of correlative nature. Cause-effect relationships were inferred mostly based on theory. Future research should aim to address causation. In particular, characterizing quantitatively the relative effects of fear and direct predation in controlled experiments would gain useful insights into the magnitude of sharks' influence on the distribution and abundance of their preys. Simulations of multiple scenarios of changes in mesopredators'

natural mortality and survival, entailed by large predators overfishing and by conservation actions, within different regimes of fishing mortality; analysis of competitive interactions at large scales; and finally identifying the scale of action of these mechanisms in space and through time are top-priorities to achieve this goal. This would be a prerequisite to test the generality of trophic cascades across marine realms and predict the scale of observations necessary to capture these phenomena. A multiple hypothesis- testing framework would be essential to factor out alternative mechanisms, and evaluate the relative proportion of different driving factors. The meta-analytical approach used in Chapter 2 could be applied to test the occurrence of these processes and extend the scale by combining information coming from multiple oceanic sectors into a unique global analysis.

4. Developing criteria for shark extinction risk: The absence of monitoring for about half of all known elasmobranch species worldwide is one of the most pressing problems for their conservation and management (Chapter 5). Of the 1159 chondrichthyans known, 881 species have been evaluated globally with 42.8% listed as data deficient (DD). In most of the cases, these species are unregulated by-catch in commercial fisheries. Developing general paradigms of chondrichthyan extinction risk by using data of evaluated species would help to predict priors of extinction for the others and thus prevent further inclusions in the list of threatened species. The global status of chondrichthyan fishes would become more robust and reliable to encourage conservation actions.

Bibliography

Abdulla, A., 2004. Status and conservation of sharks in the Mediterranean Sea. IUCN Technical Paper. pp 7.

Abella, A. J. and F. Serena, 2002. Comparison of elasmobranch catches from research trawl surveys and commercial landings at port of Viareggio (Italy in the last decade). *J. Northw. Atl. Fish. Sci.* **35**:345–356.

Accadia, P. and R. Franquesa, 2006. The operational units approach for fisheries management in the mediterranean sea. Studies and Reviews. General Fisheries Commission for the Mediterranean. 80, 36 p., FAO, Rome.

Airoldi, L. and M. Beck, 2007. Loss, status and trends for coastal marine habitats of Europe. *Oceanogr. Mar. Biol.* **45**:345–405.

Aitchison, J., 1986. The statistical analysis of compositional data. Chapman and Hall, New YorK, NY.

Aldebert, Y., 1997. Demersal resources of the Gulf of Lions (NW Mediterranean). Impact of exploitation on fish diversity. *Vie Milieu* **47**:275–285.

Amorim, A., C. Arfelli, and L. Fagundes, 1998. Pelagic elasmobranchs caught by longliners off southern Brazil during 1974-97: an overview. *Mar. Freshwater Res.* **49**:621–632.

Anonymous, 2003a. Commission staff working paper report of ad working group elasmobranchs fisheries. Sec(2003)1427, Commission of the European Communities, Brussels.

Anonymous, 2003b. Decision on the extension of the jurisdiction of the Republic of Croatia in the Adriatic Sea. Text note verbale No. 331/2003 dated 29 October 2003 from the permanent mission of Croatia.

Anonymous, 2003c. Realizzazioni di indagini per la conoscenza e la valorizzazione delle attivita' di pesca e maricoltura in Toscana. CD rom.

Anonymous, 2007a. International bottom trawl survey in the Mediterranean (Medits). Instruction manual, version 5.

Anonymous, 2007b. The Republic of Malta. FAO. Fishery Country Profile.

Anonymous, 2008a. 28th plenary meeting report of the scientific, technical and economic committee for fisheries. Commission staff working document Plen-08-02, Commission of the European Communities, Helsinki.

Anonymous, 2008b. Shark declines in the mediterranean sea. Lenfest Ocean Program Research Series, Washington, DC.

Anonymous, 2010. Global consequences of shark declines. Lenfest Ocean Program Research Series, Washington, DC.

Antonelis, G., J. Baker, T. Johanos, R. Braun, and A. Harting, 2006. Hawaiian monk seal(*Monachus schauinslandi*): status and conservation issues. *Atoll Res. Bull.* **543**:75–101.

Aragones, L. V., 2000. A review of the role of the green turtle in tropical seagrass ecosystems. In N. Pilcher and G. Ismail, editors, *Sea turtles of the Indo-Pacific: research, management and conservation*, page 69–85. Academic Press Ltd, London, UK.

Arcidiacono, F., 1931. La pesca del pesce vacca (*Hexanchus griseus* L.) nella marina di Riposto. *Boll. Pesca Pisc. Idrobiol.* **7**:608–612.

Autieri, R., A. Abella, R. Baino, P. Righini, F. Serena, R. Silvestri, and A. Voliani, 1992. Gestione della fauna ittica le principali specie demersali dell'Alto Tirreno. Technical report, Regione Toscana.

Axiak, V., V. Gauci, M. Mallia, E. Mallia, P. J. Schembri, A. J. Vella, and L. Vella, 2002. State of the environment report for Malta. Technical report, Ministry for Home Affairs and the Environment.

Baro, J., J. M. Serna-Quintero, I. Sobrino, M. P. Jimenez, and L. . M. Fernández-Salas, 2004. An approach to the spatial distribution of fishing effort in the Gulf of Cadiz. *Thalassas* **20**:17–21.

Barrowman, N. J. and R. A. Myers, 2003. Raindrop plots: a new way to display collections of likelihoods and distributions. *Am. Stat.* **57**:268–275.

Bascompte, J., C. J. Melián, and E. Sala, 2005. Interaction strength combinations and the overfishing of a marine food web. *Proc. Natl. Acad. Sci. U. S. A.* **102**:5443–5447.

Basuşta, N., Ç. Keskin, F. Serena, and B. Serét, editors, 2006. Proceedings of the Workshop on Mediterranean Cartilaginous Fish with emphasis on Southern and Eastern Mediterranean, 14-16 October 2005, Instanbul - Tutkey. Turkish Marine Research Foundation.

Baum, J. K., D. Kehler, and R. A. Myers, 2005. Robust estimates of decline for pelagic shark populations in the Northwest Atlantic and Gulf of Mexico. *Fisheries* **30**:27–29.

Baum, J. K. and R. A. Myers, 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecol. Lett.* **7**:135–145.

Baum, J. K., R. A. Myers, D. G. Kehler, B. Worm, S. J. Harley, and P. A. Doherty, 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science* **299**:389–392.

Baum, J. K. and B. Worm, 2009. Cascading top-down effects of changing oceanic predator abundances. *J. Anim. Ecol.* **78**:699–714.

Bearzi, G., D. Holcer, and G. Notarbartolo di Sciara, 2004. The role of historical dolphin takes and habitat degradation in shaping the present status of northern Adriatic cetaceans. *Aquat. Conserv.: Mar. Freshwat. Ecosyst.* **14**:363–379.

Béchir, S. and B. M. Nejmeddine, 2009. Captures accidentelles des elasmobranches en Mediterranee: synthese bibliographique. Technical report, GFCM.

Beentjes, M., B. Bull, R. Hurst, and N. Bagley, 2002. Demersal fish assemblages along the continental shelf and upper slope of the east coast of the South Island, New Zealand. *N.Z. J. Mar. Freshwat. Res* **36**:197–223.

Bello, G., 1999. The chondrichthyans of the Adriatic Sea. *Acta Adriat.* **40**:65–76.

Bertrand, J., G. De Sola, C. Papakostantinou, G. Relini, and A. Souplet, 2000. Contribution on the distribution of elasmobranchs in the Mediterranean (from the MEDITS surveys). *Biol. Mar. Medit.* **7**:385–399.

Bertrand, J., L. Gil de Sola, C. Papaconstantinou, G. Relini, and A. Souplet, 1996. Campagne internationale de chalutage démersal en Méditerranée (MEDITS 1995). campagne 1995. *Rapport géneral (vol. I) et manuel des protocoles (vol. II), Rapport de contrat CEE-IFREMER-IEO-SIBM-NCMR (Étude 94/047, 011, 057, 051)* .

Bertrand, J., I. Leonori, P. Dremiére, and G. Cosimi, 2002a. Depth trajectory and performance of a trawl used for an international bottom trawl survey in the Mediterranean. *Sci. Mar.* **66**:169–182.

Bertrand, J. A., L. Gil De Sola, C. Papaconstantinou, G. Relini, and A. Souplet, 2002b. The general specifications of the MEDITS surveys. *Sci. Mar.* **66**:9–17.

Biagi, V., 1999. Memorie della Tonnara di Baratti. 2^a ed. Circolo Nautico e Pesca Sportiva di Baratti., Baratti, Italy.

Bianchi, I., S. Cl*ó*, and M. Costantini, 1997. Med-Tag e baby shark: due progetti per la marcatura degli squali. Primi risultati, riflessioni e prospettive. *Quad. Civ. Staz. Idrobiol.* **22**:51–64.

Boero, F. and A. Carli, 1979. Catture di elasmobranchi nella tonnarella di Camogli (Genova) dal 1950 al 1974. *Boll. Mus. Ist. Biol. Univ. Genova* **47**:27–34.

Bombace, G., 1993. Ecological and fishing features of the Adriatic Sea. In K. Sherman and G. B. Alexander, L. M., editors, *Large marine ecosystems: stress, mitigation and sustainability*, pages 119–136. AAAS, Press.

Bonfil, R., 1994. Overview of world elasmobranch fisheries. FAO Fisheries Technical Paper 341, FAO.

Botter, L., O. Giovanardi, and S. Raicevich, 2006. Chioggia's Fleet Fishery Migration in the Adriatic Sea between the 19^{th} and the early 20^{th} centuries. *J. Marit. Hist.* **16**:27–44.

Bowen, W., S. Ellis, S. Iverson, and D. Boness, 2003. Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. *J. Zool.* **261**:155–163.

Brodie, P. and B. Beck, 1983. Predation by sharks on the grey seal (*Halichoerus grypus*) in Eastern Canada. *Can. J. Fish. Aquat. Sci.* **40**:267–271.

Buenquerpo, V., S. Rios, and J. Moron, 1998. Pelagic sharks associated with the swordfish, Xiphias gladius, fishery in the eastern North Atlantic Ocean and the Strait of Gibraltar. *Fish. Bull.* **96**:667–685.

Burgess, G., L. Beerkircher, G. Cailliet, J. Carlson, E. Cortés, K. Goldman, R. Grubbs, J. Musick, M. Musyl, and C. Simpfendorfer, 2005. Is the collapse of shark populations in the Northwest Atlantic Ocean and Gulf of Mexico real? *Fisheries* **30**:19–26.

Burnham, K. and D. Anderson, 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociol. Method. Res.* **33**:261.

Burnham, K. P. and D. R. Anderson, 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Caddy, J. F. and F. Carocci, 1999. The spatial allocation of fishing intensity by port-based inshore fleets: a GIS application. *ICES J. Mar. Sci.* **56**:388.

Cairns, D., A. Gaston, and F. Huettmann, 2008. Endothermy, ectothermy and the global structure of marine vertebrate communities. *Mar. Ecol. Prog. Ser.* **356**:239.

Camhi, M. D., S. V. Valenti, F. S. V., F. S. L., and G. C., 2009. The conservation status of pelagic sharks and rays: report of the IUCN Shark Specialist Group pelagic shark red list workshop. Technical report, IUCN Species Survival Commission Shark Specialist Group.

Cannaviello, E. F., 1942. Calendario delle pesche del golfo di Napoli. *Boll. Pesca Pisc. Idrobiol.* **18**:23–85.

Carbonell, A., F. Alemany, P. Merella, A. Quetglas, and E. Roman, 2003. The by-catch of sharks in the western Mediterranean (Balearic Islands) trawl fishery. *Fish. Res.* **61**:7–18.

Casale, P., L. Laurent, and G. De Metrio, 2004. Incidental capture of marine turtles by the Italian trawl fishery in the north Adriatic Sea. *Biol. Conserv.* **119**:287–295.

Casey, J. M. and R. A. Myers, 1998. Near extinction of a large, widely distributed fish. *Science* **281**:690–692.

Castro, J., J. M. de la Serna, D. Macías, and J. Mejuto, 2000. Estimaciones científícas preliminares de los desembarcos de especies associadas realizados por la flota Española de palangre de superficie en 1997 y 1998. *ICCAT. Col. Vol. Sci. Pap.* **51**:1882–1893.

Cavanagh, R. and C. Gibson, 2007. Overview of the conservation status of cartilaginous fishes (Chondrichthyans) in the Mediterranean Sea. *World Conservation Union, Gland, Switzerland, and Malaga, Spain.* .

Cavanagh, R. D., P. M. Kyne, S. L. Fowler, J. A. Musick, and M. B. Bennett, 2003. The conservation status of Australian Chondrichthyans. Report of the IUCN Shark Specialist Group Australia and Oceania regional Red List workshop, The University of Queensland, School of Biomedical Sciences, Brisbane, Australia.

Chevalier, C., 2005. Governance of the Mediterranean Sea. Outlook for the legal regime. Technical report, IUCN-Med, Málaga (Spain).

Clarke, S. C., M. K. McAllister, E. J. Milner-Gulland, G. P. Kirkwood, C. G. J. Michielsens, D. J. Agnew, E. K. Pikitch, H. Nakano, and M. S. Shivji, 2006. Global estimates of shark catches using trade records from commercial markets. *Ecol. Lett.* **9**:1115–1126.

Claudet, J. and S. Fraschetti, 2010. Human-driven impacts on marine habitats: A regional meta-analysis in the Mediterranean Sea. *Biol. Conserv.* **143**:2195–2206.

Cliff, G., 1995. Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 8. The Great hammerhead shark *Sphyrna mokarran* (Ruppell). *South African Journal of Marine Science* **15**:105–114.

Cliff, G. and S. Dudley, 1991. Sharks caught in the protective gill nets off Natal, South Africa. 4. The bull shark *Carcharhinus leucas* (Valenciennes). *South African Journal of Marine Science* **10**:253–270.

Coll, M., C. Piroddi, J. Steenbeek, K. Kaschner, F. Lasram, J. Aguzzi, E. Ballesteros, C. Bianchi, J. Corbera, T. Dailianis, et al., 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PLoS One* **5**:e11842.

Compagno, L. J. V., 1990. Alternative life-history styles of cartilaginous fishes in time and space. *Environ. Biol. Fish.* **28**:33–75.

Compagno, L. J. V., D. A. Ebert, and P. D. Cowley, 1991. Distribution of offshore demersal cartilaginous fish (class Chondrichthyes) off the west coast of southern Africa, with notes on their systematics. *S. Afr. J. Marine Sci.* **11**:43–139.

Connell, J., 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* **122**:661.

Cortés, E., 1999. Standardized diet compositions and trophic levels of sharks. *ICES J. Mar. Sci.* **56**:707–717.

Cortés, E., 2002. Incorporating Uncertainity into Demographic Modelling: Application to Shark Populations and Their Conservation. *Cons. Biol.* **16**:1048–1062.

Costa, M., K. Erzini, and T. Borges, 2005. Reproductive biology of the blackmouth catshark, *Galeus melastomus* (Chondrichthyes: Scyliorhinidae) off the south coast of Portugal. *J. Mar. Biol. Assoc. UK* **85**:1173–1183.

Costantini, M. and M. Affronte, 2003. Neonatal and juvenile sand bar sharks in northern Adriatic Sea. *J. Fish Biol.* **62**:740–743.

Costantini, M., M. Bernardini, P. Cordone, P. G. Giuliani, and G. Orel, 2000. Osservazioni sulla pesca, la biologia riproduttiva ed alimentare di *Mustelus mustelus* (Chondrichtyes, Triakidae) in alto Adriatico). *Biol. Mar. Medit.* **7**:427–432.

Creel, S. and D. Christianson, 2008. Relationships between direct predation and risk effects. *Trends Ecol. Evol.* **23**:194–201.

Cunningam, R. B. and D. B. Lindanmayer, 2005. Modelling count data of rare species. *Ecology* **86**:1135–1142.

da Silva, A. A., J. Hoey, and V. Gallucci, 2008. A historical index of abundance for the blue shark *Prionace glauca* in the western north atlantic. *Fish. Res.* **92**:41 – 52.

Damalas, D., P. Megalofonou, and M. Apostolopolou, 2007. Environmental, spatial, temporal and operational effects on swordfish (*Xiphias gladius*) catch rates of eastern Mediterranean Sea longline fisheries. *Fish. Res.* **84**:233–246.

D'Ancona, U., 1922. Notizie sulla pesca nel Golfo di Fiume. *R. Com. Talass. Ital.* **XCIV**:1–30.

D'Ancona, U., 1926. Dell'influenza della stasi peschereccia del periodo 1914–1918 sul patrimonio ittico dell'Alto Adriatico. *R. Com. Talass. Ital.* **CXXVI**:1–95.

D'Ancona, U., 1934. Ulteriori osservazioni sulle statistiche della pesca dell'Alto Adriatico. *R. Com. Talass. Ital.* **CCXV**:1–27.

D'Ancona, U., 1949. Rilievi statistici sulla pesca nell'alto Adriatico. *Atti Ist. Ven. Sci. Lett. Art.* **CVIII**:41–53. CVIII.

D'Ancona, U. and A. Razzauti, 1937. Pesci e pesca nelle acque dell'Arcipelago Toscano. *R. Comm. Explor. Méditerranée* **11**:129–144.

Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser, 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecol. Appl.* **8**:309–322.

De Metrio, G., M. Caucci, M. Deflorio, S. Desantis, and N. Santamaria, 1999. Incidenza della pesca ai grandi pelagici sulle catture di squali. *Biol. Mar. Medit.* **7**:334–345.

De Zio, V., A. M. Pastorelli, and L. Rositani, 2000. By catch of blue shark *Prionace glauca* (L.) durante la pesca dei grandi pelagici nel basso Adriatico. *Biol. Mar. Medit.* **7**:444–446.

DeMartini, E. E., A. M. Friedlander, S. A. Sandin, and E. Sala, 2008. Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. *Mar. Ecol. Prog. Ser.* **365**:199–215.

di Natale, A., 1998. By-catch of shark species in surface gear used by the Italian fleet for large pelagic species. *Col. Vol. Sci. Pap. ICCAT* **48**:138–140.

di Natale, A., A. Mangano, A. Maurizi, L. Montaldo, E. Navarra, S. Pinca, G. Schimenti, G. Torchia, and M. Valastro, 1995. A review of driftnet catches by the Italian fleet: species composition, observers data and distribution along the net. *Col. Vol. Sci. Pap. ICCAT* **44**:226–235.

Dudley, S. and C. Simpfendorfer, 2006. Population status of 14 shark species caught in the protective gillnets off KwaZulu-Natal beaches, South Africa, 1978-2003. *Mar. Freshwater Res.* **57**:225.

Dudley, S. F. J. and G. Cliff, 1993. Some effect of shark nets in the Natal nearshore environment. *Environ. Biol. Fishes* **36**:243–255. Africa.

Dulcic, J., I. Jardas, V. Onofri, and J. Bolotin, 2003. The roughtail stingray *Dasyatis centroura* (Pisces: Dasyatidae) and spiny butterfly ray *Gymnura altavela* (Pisces: Gymnuridae) from the southern Adriatic. *J. Mar. Biol. Assoc. UK* **83**:871–872.

Dulvy, N. and J. Reynolds, 2002. Predicting extinction vulnerability in skates. *Conserv. Biol.* **16**:440–450.

Dulvy, N. K., J. K. Baum, S. Clarke, L. J. V. Compagno, E. Cortés, A. Domingo, S. Fordham, S. Fowler, M. P. Francis, C. Gibson, J. Martínez, J. A. Musick, A. Soldo, J. D. Stevens, and S. Valenti, 2008. You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquat. Conserv.* **18**:459–482.

Dulvy, N. K., J. D. Metcalfe, J. Glanville, M. G. Pawson, and J. D. Reynolds, 2000. Fishery stability, local extinctions, and shifts in community structure in skates. *Conserv. Biol.* **14**:283–293.

Duvly, N. K., Y. Sadovy, and J. D. Reynolds, 2003. Extintion vulnerability in marine populations. *Fish Fish.* **4**:25–64.

Ellis, J., N. Dulvy, S. Jennings, M. Parker-Humphreys, and S. Rogers, 2005. Assessing the status of demersal elasmobranchs in UK waters: a review. *J. Mar. Biol. Assoc. UK* **85**:1025–1047.

Ellis, J. and J. Musick, 2007. Ontogenetic changes in the diet of the sandbar shark, Carcharhinus plumbeus, in lower Chesapeake Bay and Virginia (USA) coastal waters. *Environ. Biol. Fish.* **80**:51–67.

Ellis, J. R., A. Cruz-Martinez, B. D. Rackham, and S. I. Rogers, 2004. The distribution of chondrichthyan fishes around the British Isles and implications for conservation. *J. Northwest Atl. Fish. Sci.* **35**:195–213.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak, 1998. Killer whale predation on sea otter linking oceanic and nearshore ecosystems. *Science* **282**:473–475.

Faber, G. L., 1883. The fisheries of the Adriatic and the fish thereof: a report of the Austro-Hungarian Sea-fisheries, with a detailed description of the Marine fauna of the Adriatic Gulf. B. Quaritch, London, UK.

FAO, 2005. Review of the state of world marine resources. FAO Fisheries Technical Papers 457, FAO.

Farrugio, H., P. Oliver, and F. Biagi, 1993. An overview of the history, knowledge, recent and future research trend in Mediterranean fisheries. *Sci. Mar.* **57**:105–119.

Fennessy, S. T., 1994. Incidental capture of elasmobranchs by commercial prawn trawlers on the Tugela Bank, Natal, South Africa. *S. Afr. J. Marine Sci.* **14**:287–296.

Fergusson, I. K. and M. A. Marks, 1996. Commercial landings of sharks within Maltese fisheries. Interim report to the IUCN Shark Specialist Group North-eastern Atlantic and Mediterranean region, IUCN (Species Survival Commission) Shark Specialist Group.

Ferretti, F., R. Myers, F. Serena, and H. Lotze, 2008. Loss of large predatory sharks from the Mediterranean Sea. *Conserv. Biol.* **22**:952–964.

Ferretti, F., R. A. Myers, P. Sartor, and F. Serena, 2005. Long term dynamics of the chondrichthyan fish community in the upper Tyrrhenian Sea. In *ICES. 2005. Theme session on elasmobranch fisheries science (N).ICES Document CM 2005/N:25. 25 pp.*

Ferretti, F., B. Worm, G. L. Britten, M. R. Heithaus, and H. K. Lotze, 2010. Patterns and ecosystem consequences of shark declines in the ocean. *Ecol. Lett.* **13**:1055–1071.

Field, I. C., M. G. Meekan, R. C. Buckworth, and C. J. A. Bradshaw, 2009. Susceptibility of sharks, rays and chimaeras to global extinction. In D. W. Sims, editor, *Advances in Marine Biology*, volume 56, pages 275 – 363. Academic Press.

Filanti, T., P. Megalofonou, G. Petrosino, and G. De Metrio, 1986. Incidenza dei selaci nella pesca del pesce spada con long-line nel Golfo di Taranto. *Nova Thalassia* **8**:667–669.

Fiorentini, L., P. Dremiere, I. Leonori, A. Sala, and V. Palumbo, 1999. Efficiency of the bottom trawl used for the Mediterranean international trawl survey (MEDITS): Efficacite du chalut de fond utilise pour le programme international d'evaluation des ressources halieutiques de Mediterranee (MEDITS). *Aquat. Living Resour.* **12**:187–205.

Fogarty, M. and S. Murawski, 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. *Ecol. Appl.* **8**:6–22.

Forcada, A., C. Valle, P. Bonhomme, G. Criquet, G. Cadiou, P. Lenfant, and J. L. Sánchez-Lizaso, 2009. Effects of habitat on spillover from marine protected areas to artisanal fisheries. *Mar. Ecol. Prog. Ser.* **379**:197–211.

Foresi, S., 1939. Pesci, Pesca e Pescatori nel mare dell'Elba. Tipo-grafia Popolare, Portoferraio, 113 pp.

Fortibuoni, T., 2010. La pesca in alto Adriatico dalla caduta della Serenissima ad oggi: un analisi storica ed ecologica. Master's thesis, Università degli studi di Trieste.

Fortuna, C., C. Vallini, E. Filidei Jr, M. Ruffino, I. Consalvo, S. Di Muccio, C. Gion, U. Scacco, E. Tarulli, O. Giovanardi, and A. Mazzola, 2010. By-catch of cetaceans and other species of conservation concern during pair trawl fishing operations in the Adriatic Sea (Italy). *Chem. Ecol.* **26**:65–76.

Fowler, S., C. Raymakers, and U. Grimm, 2004. Trade in and conservation of two shark species, Porbeagle (*Lamna nasus*) and spiny dogfish (*Squalus acanthias*). *BfN - Skripten 118* .

Franceschini, G., F. Pranovi, S. Raicevich, M. Farrace, and O. Giovanardi, 1999. "Rapido" trawl fishing In the northern Adriatic: direct impact on epifauna. *Giovanardi, O., Editor* pages 49–61.

Francis, M. P., 1988. Movement patterns of rig (*Mustelus lenticulatus*) tagged in southern New Zealand. *N.Z. J. Mar. Freshwat. Res* **22**:259–272.

Frank, K., B. Petrie, J. Choi, and W. Leggett, 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* **308**:1621–1623.

Frank, K., B. Petrie, and N. Shackell, 2007. The ups and downs of trophic control in continental shelf ecosystems. *Trends Ecol. Evol.* **22**:236–242.

Frank, K., B. Petrie, N. Shackell, and J. Choi, 2006. Reconciling differences in trophic control in mid-latitude marine ecosystems. *Ecol. Lett.* **9**:1096–1105.

Frid, A., L. Dill, R. Thorne, and G. Blundell, 2007. Inferring prey perception of relative danger in large-scale marine systems. *Evol. Ecol. Res.* **9**:635.

Frid, A., G. G. Baker, and L. M. Dill, 2008. Do shark declines create fear-released systems? *Oikos* **117**:191–201.

Friedlander, A. M. and E. E. DeMartini, 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Mar. Ecol. Prog. Ser.* **230**:253–264.

Frisk, M., T. Miller, and M. Fogarty, 2001. Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. *Can. J. Fish. Aquat. Sci.* **58**:969–981.

Frisk, M. G., T. J. Miller, and N. K. Dulvy, 2005. Life histories and vulnerability to exploitation of elasmobranchs: inferences from elasticity, perturbation and phylogenetic analyses. *J. Northw. Atl. Fish. Sci* **35**:27–45.

Frisk, M. G., T. J. Miller, S. J. D. Martell, and K. Sosebee, 2008. New hypothesis helps explain elasmobranch "outburst" on Georges Bank in the 1980s. *Ecol. Appl.* **18**:234–245.

Fromentin, J. and H. Farrugio, 2005. Results of the 2003 observer program on board the French purse seiner targeting Atlantic bluefin tuna in the Mediterranean Sea. *Col. Vol. Sci. Pap. ICCAT* **58**:779–782.

Fromentin, J. and J. Powers, 2005. Atlantic bluefin tuna: population dynamics, ecology, fisheries and management. *Fish Fish.* **6**:281–306.

García, V., L. Lucifora, and R. Myers, 2008. The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. *P. R. Soc. B* **275**:83–89.

Gargiulo, M., 1924. La pesca nel Tirreno. Tipografia G. Raho, Monteleone di Calabria, Italy.

Gargiulo, M., 1926. La pesca Lungo il Promontorio Argentario e nelle isole dell'Arcipelago Toscano. Tipografia G. Raho, Monteleone di Calabria.

Garibaldi, F. and L. Orsi Relini, 2000. Summer abundance, size, and feeding habits of the blue shark, *Prionace glauca*, in the pelagic sanctuary of the Ligurian Sea. *Biol. Mar. Medit.* **7**:324–333.

Garibaldi, L. and J. F. Caddy, 1998. Biogeographic characterization of Mediterranean and Black Seas faunal provinces using GIS procedures. *Oce. Coa. Man.* **39**:211–227.

Gerber, L., 2006. A Bayesian method for determining trends in abundance from negative binomial count data. Master's thesis, Dalhousie University.

Gertwagen, S., R. ane Raicevich, T. Fortibuoni, and O. Giovanardi, editors, 2008. Il mare com'era. Proceedings of the II HMAP Mediterranean and the Black Sea project Chioggia (Italy), 27^{th}-29^{th} September 2006.

Gibson, C., S. V. Valenti, S. V. Fordham, and S. L. Fowler, 2008. The conservation of Northeast Atlantic Chondrichthyans. Report of the IUCN Shark Specialist Group Northeast Atlantic Red List workshop.

Gilman, E., S. Clarke, N. Brothers, J. Alfaro-Shigueto, J. Mandelman, J. Mangel, S. Petersen, S. Piovano, N. Thomson, P. Dalzell, M. Donoso, M. Goren, and T. Werner, 2008. Shark interactions in pelagic longline fisheries. *Mar. Policy* **32**:1 – 18.

Godo, O. R. and A. Engas, 1989. Swept area variation with depth and its influence on abundance indices of groudfish from trawl surveys. *J. North. Atl. Fish. Sci.* **9**:133–139.

Graham, K., N. Andrew, and K. Hodgson, 2001. Changes in relative abundance of sharks and rays on Australian south east fishery trawl grounds after twenty years of fishing. *Mar. Freshwater Res.* **52**:549–61.

Grogan, E. D. and R. Lund, 2004. The origin and relationships of early chondrichthyes. In J. C. Carrier, J. A. Musick, and M. R. Heithaus, editors, *Biology of sharks and their relatives*, pages 3–31. CRC press, Boca Raton, FL.

Hall-Spencer, J., C. Froglia, R. Atkinson, and P. Moore, 1999. The impact of Rapido trawling for scallops, *Pecten jacobaeus* (L.), on the benthos of the Gulf of Venice. *ICES J. Mar. Sci.* **56**:111.

Harley, S. J., R. A. Myers, and A. Dunn, 2001. Is catch-per-unit-effort proportional to abundance? *Can. J. Fish. Aquat. Sci.* **58**:1760–1772.

Heithaus, M. R., 2001. Predator-prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review. *J. Zool.* **253**:53–68.

Heithaus, M. R., 2004. Predator-prey interactions. In J. C. Carrier, J. A. Musick, and M. R. Heithaus, editors, *Biology of Sharks and Their Relatives*, pages 487–521. CRC Press.

Heithaus, M. R., A. Frid, A. J. Wirsing, L. M. Dill, J. W. Fourqueran, D. Burkholder, J. Thomson, and L. Bejder, 2007. State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *J. Anim. Ecol.* **76**:837–844.

Heithaus, M. R., A. Frid, A. J. Wirsing, and B. Worm, 2008a. Predicting ecological consequences of marine top predator declines. *Trends Ecol. Evol.* **4**:202–210.

Heithaus, M. R., A. J. Wirsing, J. A. Thomson, and D. A. Burkholder, 2008b. A review of lethal and non-lethal effects of predators on adult marine turtles. *J. Exp. Mar. Biol. Ecol.* **356**:43 – 51.

Heupel, M. R., J. K. Carlson, and C. A. Simpfendorfer, 2007. Shark nursery areas: concepts, definition, characterization and assumptions. *Mar. Ecol. Prog. Ser.* **337**:287.

Hilbe, J., 2007. Negative binomial regression. Cambridge University Press, New York, NY.

Hilborn, R. and M. Mangel, 1997. The Ecological Detective. Princeton University Press, Princeton, NJ.

Hobday, D. K., R. A. Officer, and G. D. Parry, 1999. Changes to demersal fish communities in Port Phillip Bay, Australia, over two decades, 1970-91. *Mar. Freshwater Res.* **50**:397–407.

Hoening, J. M. and S. H. Gruber, 1990. Life-history patterns in the elasmobranchs: implications for fisheries management. In H. L. J. Pratt, S. H. Gruber, and T. Taniuchi, editors, *Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of fisheries*, volume NOAA Tech. Rep. NMFS 90. U. S. Department of Commerce, Washington.

Hoffmann, R., 2005. A brief history of aquatic resource use in medieval Europe. *Helgoland Mar. Res.* **59**:22–30.

Holden, M. J., 1977. Elasmobranchs. In J. A. Gulland, editor, *Fish Population Dynamics*, pages 187–215. John Wiley & sons.

Hurley, P. C. F., 1998. A review of the fishery for pelagic sharks in Atlantic Canada. *Fish. Res.* **39**:107–113.

Ivory, P., F. Jeal, and C. P. Nolan, 2004. Age determination, growth and reproduction in the lesser-spotted dogfish, *Scyliorhinus canicula* (L.). *J. Northwest Atl. Fish. Sci.* **35**.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, et al., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**:629–638.

Jardas, I., 1984. Adriatic chondrichthyes by the biogeographicl standpoint. *Inst. Ocean. Rib.* **59**:1–7.

Jeftic, L., M. Bernhard, A. Demetropulos, F. Fernex, G. P. Gabrielides, F. Gasparovic, Y. Halim, D. Orhon, and L. J. Saliba, 1990. State of the marine environment in the Mediterranean region. UNEP Regional Seas Reports and Studies 132, UNEP.

Jennings, S. and M. J. Kaiser, 1998. The effects of fishing on marine ecosystems. *Adv. Mar. Biol.* **34**:201–212.

Jorgensen, C., K. Enberg, E. Dunlop, R. Arlinghaus, D. Boukal, K. Brander, B. Ernande, A. Gardmark, F. Johnston, S. Matsumura, et al., 2007. Ecology: managing evolving fish stocks. *Science* **318**:1247.

Jukić, S., 1975. Trawl fishing grounds in the central Adriatic. *Acta Adriat.* **17**:1–86.

Jukić-Peladic, S., N. Vrgoc, S. Krustulovic-Sifner, C. Piccinetti, G. Piccinetti-Manfrin, G. Marano, and N. Ungaro, 2001. Long-term changes in demersal resources of the Adriatic Sea: comparison between trawl surveys carried out in 1948 and 1998. *Fish. Res.* **53**:95–104.

Kaiser, M. J., 1998. Significance of bottom-fishing disturbance. *Conserv. Biol.* **12**:1230–1235.

Karlovac, O., 1956. Station list of the M.V. "HVAR" Fishery-Biological cruises 1948-1949. *R. Inst. Oceanogr. Ribarst. Split SFR Jug.* **1**:1–177.

Karlovac, O., 1959. Exploration of fish stocks and edible invertebrata carried out by trawling in open adriatic. istraživanja naselja riba i jestivih beskralježnjaka vucom u otvorenom jadranu. Technical report, Svz. Inst. Oceanogr. Ribarst., Split.

Kitchell, J. F., T. E. Essington, C. H. Boggs, D. E. Schindler, and C. J. Walters, 2002. The role of sharks and longline fisheries in a pelagic ecosystem of the Central Pacific. *Ecosystems* **5**:202–216.

Klaer, N. L., 2001. Steam trawl catches from south-eastern Australia from 1918 to 1957: trends in catch rates and species composition. *Mar. Freshwater Res.* **52**:399–410.

Knight, T., M. McCoy, J. Chase, K. McCoy, and R. Holt, 2005. Trophic cascades across ecosystems. *Nature* **437**:880–883.

Kondoh, M., 2008. Building trophic modules into a persistent food web. *Proc. Natl. Acad. Sci. U. S. A.* **105**:16631.

Krebs, C. J., 2001. Ecology. Benjamin Cummings, San Francisco.

Kriwet, J., W. Kiessling, and S. Klug, 2009. Diversification trajectories and evolutionary life-history traits in early sharks and batoids. *P. R. Soc. B* **276**:945–951.

Kroese, M. and W. Sauer, 1998. Elasmobranch exploitation in Africa. *Mar. Freshwater Res.* **49**:573–578.

Lanfredi, C., 2003. Valutazione del pescato di elasmobranchi nel mercato ittico di Chioggia. Firts degree Laurea Thesis. Università degli Studi di Padova. Anno Accademico 2002/2003.

Leiva, I., C. Busuttil, M. Darmanin, and M. Camilleri, 1998. Artisnal fisheries in the western Mediterranean. FAO COPEMED, The Department of Fisheries and Aquaculture of Malta.

Levi Morenos, D., 1916. L'emigrazione peschereccia pel lavoro nell'Adriatico. *R. Com. Talass.* **32**:9–14.

Levin, P. S., E. E. Holmes, K. R. Piner, and C. J. Harvey, 2006. Shifts in a Pacific Ocean fish assemblage: the potential influence of exploitation. *Conserv. Biol.* **20**:1181–1190.

Lindberg, D. R. and N. D. Pyenson, 2006. Evolutionary patterns in Cetacea. Fishing up prey size through deep time. In J. A. Estes, D. P. Demaster, D. F. Doak, T. M. Williams, and R. L. J. Brownell, editors, *Whales, whaling, and ocean ecosystems*, pages 67–81. University of California Press, Berkeley, CA.

Lindsey, J. K., 2000. Applying Generalized Linear Models. Springer-Verlag, New York, NY.

Link, J., L. Garrison, and F. Almeida, 2002. Ecological interactions between elasmobranchs and groundfish species on the northeastern US continental shelf. I. Evaluating predation. *N. Am. J. Fish. Manage.* **22**:550–562.

Lipej, L., A. De Maddalena, and A. Soldo, 2004. Sharks of the Adriatic Sea. Univerza na Primorskem, Znanstveno-raziskovalno središče Koper.

Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, and J. B. C. Jackson, 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* **312**:1806–1809.

Lotze, H. K. and B. Worm, 2009. Historical baselines for large marine animals. *Trends Ecol. Evol.* **24**:254–262.

Lucas, Z. and W. T. Stobo, 2000. Shark-inflicted mortality on a population of harbour seals (*Phoca vitulina*) at Sable Island, Nova Scotia. *J. Zool.* **252**:405–414.

Lucifora, L., V. García, R. Menni, A. Escalante, and N. Hozbor, 2009. Effects of body size, age and maturity stage on diet in a large shark: ecological and applied implications. *Ecological Research* **24**:109–118.

Lyons, S., F. Smith, and J. Brown, 2004. Of mice, mastodons and men: human-mediated extinctions on four continents. *Evol. Ecol. Res.* **6**:339–358.

Machias, A., V. Vassilopoulou, D. Vatsos, P. Bekas, A. Kallianiotis, C. Papaconstantinou, and N. Tsimenides, 2001. Bottom trawl discards in the northwestern Mediterranean Sea. *Fish. Res.* **53**:181–195.

Mancini, R., 1922. L'arcipelago Toscano. Seconda crociera di pesca marittima. Ministero per l'Agricoltura. Ispettorato Generale della Pesca.

Mannini, P., F. Massa, and N. Milone, 2005. Adriatic Sea fisheries: outline of some main facts. In *Interactions between aquaculture and capture fisheries: a methodological perspective*, page 124. FAO.

Marano, G., R. Vaccarella, G. Bello, and A. M. Pastorelli, 1983. Prime osservazioni sulla pesca di *Xiphias gladius* L. (Osteichthyes) nel basso Adriatico. *Thalassia Salent.* **13**:50–59.

Marchesetti, C., 1882. La pesca lungo le coste orientali dell'Adria. *Atti Mus. Civ. Stor. Nat., Trieste* **7**:1–234.

Massuti, E. and J. Moranta, 2003. Demersal assemblages and depth distribution of elasmobranchs from the continental shelf and slope off the Balearic Island (western Mediterranean). *ICES J. Mar. Sci.* **60**:753–766.

Matta, F., 1958. La pesca a strascico nell'Arcipelago Toscano. *Boll. Pesca. Pisc. Idrobiol.* **XXXIV**:1–365.

Maunder, M. N. and A. E. Punt, 2004. Standardizing catch and effort data: a review of recent approaches. *Fish. Res.* **70**:141–159.

Mavrič, B., R. Turk, and L. Lipej, 2006. Elasmobranch research in Slovenia. In N. Basuşta, c. Keskin, F. Serena, and B. Serét, editors, *Proceedings of the workshop on Mediterranean cartilaginous fish with emphasis on southern and eastern Mediterranean*, 14-16 October 2005, Instanbul - Turkey. Turkish Marine Research Foundation.

McConnaughey, R. A. and K. R. Smith, 2000. Associations between flatfish abundance and surficial sediments in the eastern Bering Sea. *Can. J. Fish. Aquat. Sci.* **57**:2410–2419.

McConnaughey, R. A. and S. E. Syrjala, 2009. Statistical relationships between the distributions of groundfish and crabs in the eastern Bering Sea and processed returns from a single-beam echosounder. *ICES J. Mar. Sci.* **66**:1425–1432.

McCullagh, P. and J. A. Nelder, 1999. Generalized Linear Models, volume 37 of *Monographs on Statistics and Applied Probability*. Chapman & Hall/CRC, second edition.

Megalofonou, P., D. Damalas, C. Yannopoulos, G. De Metrio, M. Deflorio, J. M. de la Serna, and D. Macias, 2000. By-catches and discards of sharks in the large pelagic fisheries in the Mediterranean Sea. Final Report of the Project No 97/50 Directorate General for Fisheries and Maritime Affair XIV/C1, Community of Mediterranean Universities.

Megalofonou, P., C. Yannopoulos, D. Damalas, G. De Metrio, M. Deflorio, and J. M. de la Serna, 2005. Incidental catch and estimated discards of pelagic sharks from the swordfish and tuna fisheries in the Mediterranean Sea. *Fish. Bull.* **103**:620–634.

Mejuto, J. and J. M. de la Serna, 2000. Standardized catch rates by age and biomass, from the North Atlantic swordfish (*Xiphias gladius*) from the Spanish longline fleet for the period 1983-1998 and bias produced by changes in the fishing strategy. *Col. Vol. Sci. Pap. ICCAT* **51**:1387–1410.

Mejuto, J., B. García-Cortés, J. M. de la Serna, and A. Ramos-Cartelle, 2006. Scientific estimations of by-catch landed by the Spanish surface longline fleet targeting swordfish (*Xiphias gladius*) in the Atlantic Ocean: 2000-2004 period. *Col. Vol. Sci. Pap. ICCAT* **59**:1014–1024.

Minami, M., C. E. Lennert-Cody, W. Gao, and M. Román-Verdesoto, 2007. Modeling shark bycatch: the zero-inflated negative binomial regression model with smoothing. *Fish. Res.* **84**:210 – 221.

Minervini, A., M. Giannotta, and M. L. Bianchini, 1985. Observation on the fishery of Rajformes in central Tyrrhenian Sea. *Oebalia* **XI**:583–591.

Mollet, H. F., 2005. Elasticity patterns for sharks, turtles, mammals, and birds: the importance of age at first reproduction, mean, age of reproducing females, and survival in the discounted fertilities of the Leslie matrix. *Unpublished manuscript [http://homepage.mac.com/mollet/Demography/molletMSApr92005WithMinorCorr.pdf]* .

Monte-Luna, P., D. Lluch-Belda, E. Serviere-Zaragoza, R. Carmona, H. Reyes-Bonilla, D. Aurioles-Gamboa, J. L. Castro-Aguirre, S. A. Próo, O. Trujillo-Millán, and B. W. Brook, 2007. Marine extinctions revisited. *Fish and Fisheries* **8**:107–122.

Montgomery, D., E. Peck, and G. Vining, 2001. Introduction to Linear Regression Analysis. John Wiley & Sons, Inc.

Morovic, D., 1951. Composition mecanique des sediments au large de l'Adriatique. *R. Inst. Oceanogr. Ribarst. Split SFR Jug.* **3**:1–18.

Moura, T., I. Figueiredo, P. B. Machado, and L. S. Gordo, 2004. Growth pattern and reproductive strategy of the holocephalan *Chimaera monstrosa* along the Portuguese continental slope. *J. Mar. Biol. Assoc. UK* **84**:801–804.

Mumby, P., C. Dahlgren, A. Harborne, C. Kappel, F. Micheli, D. Brumbaugh, K. Holmes, J. Mendes, K. Broad, J. Sanchirico, et al., 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* **311**:98–101.

Murdoch, T. J. T., A. F. Glasspool, M. Outerbridge, J. Ward, S. Manuel, and J. e. Gray, 2007. Large-scale decline in offshore seagrass meadows in Bermuda. *Mar. Ecol. Prog. Ser.* **339**:123–130.

Musick, J., M. Harbin, and L. Compagno, 2004. Historical zoogeography of the Selachii. In *The biology of sharks and their relatives*, pages 33–78. CRC Press, Boca Raton, FL.

Myers, R. A., J. K. Baum, T. Shepherd, S. P. Powers, and C. H. Peterson, 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* **315**:1846–1850.

Myers, R. A. and B. Worm, 2003. Rapid worldwide depletion of predatory fish communities. *Nature* **423**:280–283.

Myers, R. A. and B. Worm, 2005. Extinction, survival or recovery of large predatory fishes. *Philos. Trans. R. Soc. Lond., B* **360**:13–20.

Nakano, H., 1999. Case studies of the management of elasmobranch fisheries, volume 378/2, chapter 19. Fishery management of sharks in Japan, page 552. FAO Fisheries Technical Paper.

Ninni, E., 1912. Catalogo dei pesci del Mare Adriatico. Tip. Carlo Bertotti, Venezia.

Ninni, E., 1923. Primo contributo allo studio dei pesci e della pesca nelle acque dell'Impero Ottomanno. Missione Italiana per l'esplorazione dei mari di Levante, Vol. V. Premiate officine grafiche Carlo Ferrari, Venezia, Italy.

Normand, S. T., 1999. Tutorial in biostatistics. Meta-analysis: formulating, evaluating, combining, and reporting. *Stat. Med.* **18**:321–359.

Notarbartolo di Sciara, G. and I. Bianchi, 1998. Guida degli squali e delle razze del Mediterraneo. ARIES.

Okey, T. A., S. Banks, A. F. Born, R. H. Bustamante, M. C. na, G. J. Edgar, E. Espinoza, J. M. F. na, L. E. Garske, G. K. Reck, S. Salazar, S. Shepherd, V. Toral-Granda, and P. Wallem, 2004. A trophic model of a galápagos subtidal rocky reef for evaluating fisheries and conservation strategies. *Ecol. Model.* **172**:383 – 401.

Orsi Relini, L., 2000. Pesche professionali d'altura, catture di verdesca, *Prionace glauca* L., e problemi di conservazione. *Biol. Mar. Medit.* **7**:313–323.

Orsi Relini, L., C. Cima, F. Garibaldi, G. Palandri, M. Relini, and G. Torchia, 1999. La pesca professionale con i palamiti galleggianti nel "Sautuario dei cetacei" del Mar Ligure: si tratta di attivita' ecocompatibili? *Biol. Mar. Medit.* **6**:100–109.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell, 1999. Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.* **14**:483–488.

Paine, R., 1966. Food web complexity and species diversity. *Amer. Nat.* **100**:65–75.

Paine, R. T., 1984. Ecological determinism in the competition for space: the Robert H. MacArthur Award Lecture. *Ecology* **65**:1339–1348.

Paolucci, C., 1923. Il primo esperimento governativo di pesca con battello a vapore in Adriatico. *Riv. Pesca Idrobiol.* pages 33–48.

Paolucci, L., 1901. Le pescagioni nella zona Italiana del medio Adriatico. In A. Camera di Commercio, editor, *Secondo congresso nazionale di pesca di Palermo*. Dip. Maritt. Di Ancona.

Parona, C., 1898. La pesca maritima in Liguria. *Atti Soc. Ligustica Sci. Nat. Geogr.* **IX**:1–69.

Pastrovic, G., 1913. Manuale del Pescatore per l'anno 1913. Ed. Caprin, Trieste.

Paterson, R., 1990. Effects of long-term anti-shark measures on target and non-target species in Queensland, Australia. *Biol. Conserv.* **52**:147–159.

Pauly, D., 1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends Ecol. Evol.* **10**:430–430.

Pauly, D., R. Watson, and J. Alder, 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. *Philos. Trans. R. Soc. Lond., B* **360**:5–12.

Pauly, D. L., V. Christensen, S. Guenette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson, and D. Zeller, 2002. Towards sustainability in world fisheries. *Nature* **418**:689–695.

Pawson, M. G. and J. R. Ellis, 2005. Stock Identity of Elasmobranchs in the Northeast Atlantic in Relation to Assessment and Management. *J. Northwest Atl. Fish. Sci.* **35**:173–193.

Piaggio, C., 1927. Metodi ed usi di pesca nelle acque del circondario marittimo di Santa Margerita Ligure. *Boll. Pesca Pisc. idrobiol.* **3**:3–41.

Piccinetti, C., 1996. Valutazione delle risorse demersali nell'alto e medio Adriatico. Technical report, Laboratorio di Biologia Marina e Pesca - Fano, Universitá di Bologna.

Plagányi, É. E. and D. S. Butterworth, 2004. A critical look at the potential of ECOPATH with ECOSIM to assist in practical fisheries management. *Afr. J. Mar. Sci.* **26**:261–287.

Politi, E., 1997. Analisis dei contenuti gastrici di *Prionace glauca* nell'Alto e medio Adriatico. *Quad. Civ. Staz. Idrobiol.* **22**:65–78.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, and e. al, Sep 1996. Challenges in the quest for keystones. *Bioscience* **46**:609–.

Pradervand, P., B. Q. Mann, and M. F. Bellis, 2007. Long-term trends in the competitive shore fishery along the KwaZulu-Natal coast, South Africa. *Afr. Zool.* **42**:216–236.

Pranovi, F., S. Raicevich, G. Franceschini, P. Torricelli, and O. Giovanardi, 2001. Discard analysis and damage to non-target species in the "rapido" trawl fishery. *Mar. Biol.* **139**:863–875.

Preen, A., 1995. Impacts of dugong foraging on seagrass habitats: observational and experimental evidence for cultivation grazing. *Mar. Ecol. Prog. Ser.* **124**:201–213.

Pulliam, H., 2000. On the relationship between niche and distribution. *Ecol. Lett.* **3**:349–361.

Radic, N., 2008. Croatia seizes Italian boat days after fishery zone comes into force. Southeast European Times. Accessed on 15/09/2010.

Rago, P. J., K. A. Sosebee, J. K. T. Brodziak, S. A. Murawski, and E. D. Anderson, 1998. Implications of recent increases in catches on the dynamics of Northwest Atlantic spiny dogfish (*Squalus acanthias*). *Fish. Res.* **39**:165–181.

Ravier, C. and J. M. Fromentin, 2001. Long-term fluctuations in the eastern Atlantic and Mediterranean tuna populations. *ICES J. Mar. Sci.* **58**:1299–1317.

Reed, J. M., 1996. Using statistical probability to increase confidence of inferring species extinction. *Conserv. Biol.* **10**:1283–1285.

Reeves, R. and G. Notarbartolo di Sciara, 2006. The status and distribution of cetaceans in the Black Sea and Mediterranean Sea. Technical report, IUCN.

Reid, D. D. and M. Krogh, 1992. Assessment of catches from protective shark meshing of new south wales between 1950 and 1990. *Aust. J. Mar. Freshwater Res.* **43**:283–296. Australia.

Relini, G., 1998. Valutazione delle risorse demersali in Italia. *Biol. Mar. Medit.* **5**:3–19.

Relini, G., J. Bertrand, and A. Zamboni, 1999. Syntesis of the knowledge on bottom fishery resources in central Mediterranean (Italy and Corsica). *Biol. Mar. Medit.* **6**:1–868.

Relini, G., F. Biagi, F. Serena, A. Belluscio, M. T. Spedicato, P. Rinelli, M. Follesa, C. Piccinetti, N. Ungaro, L. Sion, and D. Levi, 2000. I selaci pescati con lo strascico nei mari Italiani. *Biol. Mar. Medit.* **7**:347–384.

Rey, J. C. and E. Alot, 1984. Contribution al estudio de la pesqueria de palangre del pez espada (*Xiphias gladius*) en el Mediterraneo occidental. *Col. Vol. Sci. Pap. ICCAT* **20**:428–434.

Rey, J. C., E. Alot, E. Ramos, and J. A. Camiñas, 1987. La pesqueria Española de pez espada con palangre en el Mediterraneo en 1985. *Col. Vol. Sci. Pap. ICCAT* **26**:402–408.

Rijnsdorp, A., P. van Leeuwen, N. Daan, and H. Heessen, 1996. Changes in abundance of demersal fish species in the North Sea between 1906-1909 and 1990-1995. *ICES J. Mar. Sci.* **53**:1054.

Ripple, W. and R. Beschta, 2007. Restoring Yellowstone's aspen with wolves. *Biol. Conserv.* **138**:514–519.

Ritchie, E. G. and C. N. Johnson, 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecol. Lett.* **12**:982–998.

Robbins, W. D., M. Hisano, S. R. Connolly, and J. H. Choat, 2006. Ongoing collapse of coral-reef shark populations. *Curr. Biol.* **16**:2314–2319.

Roberts, R., T. Flannery, L. Ayliffe, H. Yoshida, J. Olley, G. Prideaux, G. Laslett, A. Baynes, M. Smith, R. Jones, et al., 2001. New ages for the last Australian megafauna: continent-wide extinction about 46,000 years ago. *Science* **292**:1888.

Rodríguez-Cabello, C., F. Sánchez, A. Serrano, and I. Olaso, 2008. Effects of closed trawl fishery areas on some elasmobranch species in the Cantabrian Sea. *J. Mar. Syst.* **72**:418–428.

Rodríguez Santamaría, B., 1923. Diccionario de artes de pesca de España y sus posesiones. Madrid, Sucesoes de Rivadeneyra (s.a.).

Rogers, S. I. and J. R. Ellis, 2000. Changes in the demersal fish assemblages of British coastal waters during the 20^{th} century. *ICES J. Mar. Sci.* **57**:866–881.

Russo, A., 1928. Studi sulla pesca nel Golfo di Catania. *Boll. Pesca Pisc. Idrobiol.* **4**:495–543.

Schembri, T., 2006. Conservation management of sharks and rays (Vertebrata: Chondrichthyes) in the Maltese Islands (central Mediterranean) - a review of status and trends. In N. Basuşta, c. Keskin, F. Serena, and B. Serét, editors, *Proceedings of the workshop on Mediterranean cartilaginous fish with emphasis on southern and eastern Mediterranean*, pages 177–187, 14-16 October 2005, Istanbul - Turkey. Turkish Marine Research Foundation.

Schindler, D. E., T. E. Essington, J. F. Kitchell, C. Boggs, and R. Hilborn, 2002. Sharks and tunas: fisheries impacts on predators with contrasting life histories. *Ecol. Appl.* **12**:735–748.

Schmitz, O. J., V. Krivan, and O. Ovadia, 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.* **7**:153–163.

Sepkoski, J. J., 2002. A compendium of fossil marine animal genera. *Bull. Am. Paleontol.* **363**:1–560.

Serena, F., 2005. Field identification guide to the sharks and rays of Mediterranean and Black Sea. FAO Species Identification Guide for Fishery Purposes. FAO. Rome.

Serena, F., C. Mancusi, M. Barone, and A. A. J., 2005. Abundance and distribution of rays in the south ligurian and north tyrrhenian sea. In *ICES. 2005. Theme session on elasmobranch fisheries science (N).ICES Document CM 2005/N:20. 16 pp.*

SGFEN/STECF, 2001. Incidental catches of small cetaceans. Working paper of the subgroup on fishery and environment (SGFEN) of the Scientific, Technical and Economic Committee for Fisheries (STECF) of the EC. Document SEC(2002) 376, Brussels, 81 pp.

Shepherd, T. D. and R. A. Myers, 2005. Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico. *Ecol. Lett.* **8**:1095–1104.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern, 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.* **5**:785–791.

Sibert, J., J. Hampton, P. Kleiber, and M. Maunder, 2006. Biomass, size, and trophic status of top predators in the Pacific Ocean. *Science* **314**:1773.

Silvani, L., M. Gazo, and A. Aguilar, 1999. Spanish driftnet fishing and incidental catches in the western Mediterranean. *Biol. Conserv.* **90**:79–85.

Simpfendorfer, C., 1992. Biology of tiger sharks (*Galeocerdo cuvier*) caught by the Queensland shark meshing program off Townsville, Australia. *Aust. J. Mar. Freshwater Res* **43**:33–43.

Simpfendorfer, C. A., R. E. Hueter, U. Bergman, and S. M. H. Connett, 2002. Results of a fishery-independent survey for pelagic sharks in the western North Atlantic, 1977-1994. *Fish. Res.* **55**:175–192.

Sinclair, A. R. E., S. Mduma, and J. S. Brashares, 2003. Patterns of predation in a diverse predator-prey system. *Nature* **425**:288–290.

Smith, S. E., D. W. Au, and C. Show, 1998. Intrinsic rebound potentials of 26 species of pacific sharks. *Mar. Freshwater Res.* **49**:663–678.

Smith, W. O., D. G. Ainley, and R. Cattaneo-Vietti, 2007. Trophic interactions within the Ross Sea continental shelf ecosystem. *Philos. Trans. R. Soc. Lond., B* **362**:95–111.

Soldo, A., 2006. Status of the sharks in the Adriatic. In N. Basuşta, c. Keskin, F. Serena, and B. Serét, editors, *Proceedings of the workshop on Mediterranean cartilaginous fish with emphasis on southern and eastern Mediterranean*, pages 128–134, 14-16 October 2005, Instanbul - Turkey. Turkish Marine Research Foundation.

Soldo, A. and J. Dulčić, 2005. New record of a great white shark, *Carcharodon carcharias* (Lamnidae) from the eastern Adriatic Sea. *Cybium* **1**:89–90.

Soldo, A. and I. Jardas, 2002. Occurrence of great white shark, *Carcharodon carcharias* (Linnaeus, 1758) and basking shark, *Cetorhinus maximus* in the eastern Adriatic and their protection. *Periodicum Biologorum* **104**:195–201.

Soldo, A. and R. Pierce, 2005. Shark chumming in the eastern Adriatic. *Annales, Ser. Ist. Nat.* **15**:203–208.

Stevens, J., S. L. Fowler, A. Soldo, M. McCord, J. Baum, E. Acuña, and A. Domingo, 2005. *Lamna nasus* (Mediterranean subpopulation). IUCN 2006. 2006 IUCN Red List of Threatened Species. [WWW document] URL http://www.iucnredlist.org/search/details.php/61420/all.

Stevens, J. D., R. Bonfil, N. K. Duvly, and P. A. Walker, 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystem. *ICES J. Mar. Sci.* **57**:476–494.

Stobutzki, I. C., M. J. Miller, D. S. Heales, and D. T. Brewer, 2002. Sustainability of elasmobranchs caught as bycatch in a tropical prawn (shrimp) trawl fishery. *Fish. Bull.* **100**:800–821.

Taylor, C., 1953. Nature of variability in trawl catches. *Fish. Bull.* **54**:145–166.

Taylor, L. R., 1961. Aggregation, variance and the mean. *Nature* **189**:732–735.

Taylor, L. R., I. P. Woiwod, and J. N. Perry, 1979. The negative binomial as a dynamic ecological model for aggregation, and the density dependence of *k*. *J. Anim. Ecol.* **48**:289–304.

Tortonese, E., 1964. The main biogeographical features and problems of the Mediterranean fish fauna. *Copeia* **1**:98–107.

Tudela, S., 2004. Ecosystem effects of fishing in the Mediterranean: an analysis of the major threats of fishing gear and practices to biodiversity and marine habitats. *Studies and reviews. General Fisheries Commission for the Mediterranean* page 44.

Tudela, S., A. Kai Kai, F. Maynou, M. E. Andalossi, and P. Guglielmi, 2005. Driftnet fishing and biodiversity conservation: the case study of the large-scale Moroccan driftnet fleet operating in the Alboran Sea (SW Mediterranean). *Biol. Cons.* **121**:65–78.

Ungaro, N., G. Marano, A. Vlora, and M. Martino, 1998. Space-time variations of demersal fish assemblages in southwestern Adriatic Sea. *Vie Milieu* **48**:191–201.

Vacchi, M., V. Biagi, R. Pajetta, R. Fiordiponti, F. Serena, and G. Notorbartolo Di Sciara, 2000. Elasmobranch catches by tuna trap of Baratti (Northern Tyrrhenian Sea) from 1898 to 1922. In M. Vacchi, G. La Mesa, F. Serena, and Séret, editors, *Proc. 4th Europ. Elasm. Assoc. Meet., Livorno (Italy) 27-30 September 2000*, pages 177–183.

Valerias, J., J. M. de la Serna, D. Macías, and E. Alot, 2003. Nuevos datos científicos sobre desembarcos de especies asociadas realizados por la flota Española de palangre de superficie en el Mediterráneo en 1999 y 2000. *Col. Vol. Sci. Pap. ICCAT* **5**:149–153.

van der Elst, R. P., 1979. A proliferation of small sharks in the shore-based Natal sport fishery. *Environ. Biol. Fishes* **4**:349–362.

Vannuccini, S., 1999. Shark utilization, marketing and trade. FAO Fisheries Technical Paper 389, FAO, Rome.

Venables, W. N. and B. D. Ripley, 2001. Modern applied statistics with S-Plus. Statistics and computing. Springer, New York, third edition.

Veríssimo, A., J. R. McDowell, and J. E. Graves, 2010. Global population structure of the spiny dogfish Squalus acanthias, a temperate shark with an antitropical distribution. *Mol. Ecol.* **19**:1651–1662.

Šimunović, A., 1997. Quantitative and qualitative investigations of benthic communities in areas of mobile bottoms of the Adriatic Sea. *Acta Adriat.* **38**:77–194.

Šimunović, A., C. Piccinetti, M. Despalatović, and I. Grubelić, 2002. Experimental catches and distribution of Queen scallop *Aequipecten opercularis* (LINNAEUS, 1758) (Pectinidae, Mollusca Bivalvia) in the Adriatic Sea. *Acta Adriat.* **43**:49–57.

Županović, v., 1961. Kvantitativno-kvalitativna analiza ribljih naselja kanala sednjeg jadrana. *Acta Adriat.* **9**:1–151.

Walker, P., G. Howlett, and R. Millner, 1997. Distribution, movement and stock structure of three ray species in the North Sea and eastern English Channel. *ICES J. Mar. Sci.* **54**:797.

Walker, P. A. and H. J. L. Heessen, 1996. Long-term changes in ray populations in the North Sea. *ICES J. Mar. Sci.* **53**:1085.

Walker, P. A. and J. R. G. Hislop, 1998. Sensitive skates or resilient rays? Spatial and temporal shifts in ray species composition in the central and north-western North Sea between 1930 and the present day. *ICES J. Mar. Sci.* **55**:392–402.

Walker, S. E. and C. E. Brett, 2002. Post-Paleozoic patterns in marine predation: was there a Mesozoic and Cenozoic marine predatory revolution? *Paleontol. Soc. Paper.* **8**:119–194.

Walker, T., 1998. Can shark resources be harvested sustainably? *Mar. Freshwater Res.* **49**:553–72.

Ward, P. and R. A. Myers, 2005. Inferring the depth distribution of catchability for pelagic fishes and correcting for variations in the depth of longline fishing gear. *Can. J. Fish. Aquat. Sci.* **62**:1130–1142.

Ward, P., J. M. Porter, and S. Elscot, 2000. Broadbill swordfish: status of established fisheries and lessons for developing fisheries. *Fish Fish.* **1**:317–336.

Ward-Paige, C. A., 2010. Monitoring elasmobranch populations using scuba divers: patterns, trends and potential biases. Ph.D. thesis, Dalhousie University, Halifax, Canada.

Watling, L. and E. A. Norse, 1998. Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. *Conserv. Biol.* **12**:1180–1197.

Watson, R. and D. Pauly, 2001. Systematic distortions in world fisheries catch trends. *Nature* **414**:534–536.

Wetherbee, B. M. and E. Cortes, 2004. Food consumption and feeding habits. In J. Carrier, J. A. Misick, and M. R. Heithaus, editors, *Biology of sharks and their relatives*. CRC Press, Boca Raton, FL.

Wilga, C. D., P. J. Motta, and C. P. Sanford, 2007. Evolution and ecology of feeding in elasmobranchs. *Integr. Comp. Biol.* **47**:55–69.

Worm, B. and R. A. Myers, 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology* **84**:162–173.

WWF, 2006. The plunder of bluefin tuna in the Mediterranean and East Atlantic in 2004 and 2005. Uncovering the real story. [WWW document]. URL http://assets.panda.org/downloads/wwfbftreportfinaleditionreducido_final.pdf.

Zei, N. M., 1949. Raziskovanje s travlom na ribolovnem prodrocju vzhodnega Jadrana (Investigation with trawl in the north eastern part of the Adriatic. Contribution to the knowledge of the biology and ecology of the benthonic fishes of eastern Adriatic). *Slov. Akad. Ljubljana* **IV**:89.

Zolezzi, G., 1946. La pesca nella provincia di Venezia. *Boll. Pesca Piscicolt. Idrobiol.* **22**:155–231.

Appendix A

Loss of Large Predatory Sharks from the Mediterranean Sea

A.1 Datasets

A.1.1 Dataset 1: Sighting Records

Published sighting records of hammerhead and mackerel sharks in the eastern Adriatic Sea (Soldo and Jardas 2002). Data counted 76 records of *Isurus oxyrinchus*, *Lamna nasus*, *Sphyrna tudes* and *Sphyrna zygaena* from 1827 to 2000. Records refer to specimens in museum collections; trawl, purse seine and longline catches; and occasional sightings, with information on date, location, sex, length, weight and bibliographic reference. Not all information was available for each record. For incomplete dates (e.g. 198.., 19..), suggesting just a time interval (e.g. 1980-1989, 1900-1999), we used the last year of such an interval, or the year of the publication, whichever was earlier.

We analyzed the time-series by assuming that sightings followed a Poisson distribution, meaning that sighting frequencies are rare events with the same chance of occurrence for constant population densities. Such probability depends on the observation effort, propensity to report a sighting, population abundance, and detectability of animals (Reed 1996, McPherson & Myers, unpublished). Instantaneous rates of change of sighting resulting from the above model is a proxy of population change if all but the population abundance remained constant.

We acknowledge that this assumption can be easily violated. Observation effort may change over time, depending on fishing pressure, pattern of fishing, employed fishing gears, with more or less catchability toward sharks; or with the level of coastal development and use, for recreation purposes (e.g. tourism). Propensity to report a sighting may increase as the species became less abundant, but also may be largely affected and decrease during war periods (e.g. World War I and II, Yugoslavian civil wars). Museum collection records may have different probabilities of occurrence over time. Policy for new acquisitions may change as species become available the first time. Further occurrences may have lower probabilities to enter the collection, depending on the need to replace items, or having duplicates according to display characteristics of the new ones.

We did not have any detailed information on the dynamics of the above mentioned factors, which in our opinion may have likely coacted in both directions (to decline and increase sighting probability of records) for most of the period. We applied a simple model on the basis of the statistical distribution of data. We explored the presence of any major trend of the data to be included in the context of the multiple analyses we performed in several other regions of the Mediterranean Sea. The uncertainty associated with the resulting estimate has been weighted in the meta-analytical stage and consistency or discrepancy with the rest of the data has been evaluated.

A.1.2 Dataset 2: Fish trap of Baratti

Landing records of a fish trap operating between 1898 and 1922 in the bay of Baratti (Tuscan Archipelago), The gear consisted of a hook-shaped net, 200 m long and 20 m high, perpendicular to the coast. It fished from depths of 2-3 m near to the coast to 15 m offshore (Biagi 1999; Vacchi et al. 2000). It was a very popular type of fish trap used in several places of the Tyrrhenian Sea (Gargiulo 1926).

Data counted 250 monthly records of elasmobranch catches extracted from fisher logbooks. Records provided information on species, number of specimens, total biomass, month and year of landing. The gear did not have any significant changes in netting material, fishing position and fishing methods over the considered time period.

As no consistent measure of effort was available (e.g. fishing days per year), we assumed that the trap fished about the same amount of days each year. This is a reasonable assumption, as these kinds of gear fished all year round except during bad weather.

A.1.3 Dataset 3: Tuna Trap of Camogli

Landing records of a tuna trap placed off the town of Camogli (Ligurian Sea, Fig. 2.1) extracted from original fishers logbooks.

A tuna trap is a fixed gear composed by many chambers made of net. It has been used since medieval time in the Mediterranean Sea to catch large schools of bluefin tunas. It is a floating labyrinth placed in strategic places of the basin, not too far from the coasts, that tunas encounter in their migration route (Ravier and Fromentin 2001). The tuna trap of Camogli is a modification of the above framework, as it is composed by just 3 chambers. It targets a broad array of species including migrating fish, coastal fish, and elasmobranchs. Fishers usually collect catch three times a day.

The data set counted 4099 daily landings from 1950 to 1974, and about 454 from 2003 to 2006. Records provided information on species, number of specimens, total biomass, time and date of landing. The trap did not have any major change in netting materials, fishing position, or fishing methodology over time.

We had raw data for all years except 2003 and 2006. For these, we had only information on landed sharks, provided by interviews with the secretary and accountant (Mr. Gardella) of the tuna trap, a local writer and expert on the tuna trap history (Anna Maria Mariotti), and a marine biologist (Simone Bava) who monitors the gear's landings. All catches were cross-checked by photographic proofs. Since we used the number of fishing days as offset variable, we assumed that 2003 and 2006 had a minimum of 105 fishing days on the basis of the records for 2004 and 2005, 105 and 139 respectively.

A.1.4 Dataset 4: Swordfish Pelagic Long Line Catches in the Northern Ionian Sea

Published shark landings of the swordfish longline fishery, operating in the Gulf of Taranto and in the northern Ionian Sea (Filanti et al. 1986; Megalofonou et al. 2000). Data refers to catch and effort of the Porto Cesareo fishing fleet. Characteristics of the fleet, fishing location and season are described in De Metrio et al. (1999).

A.1.5 Dataset 5: Maltese Fishery Landings

Large predatory sharks landed at the wholesale fish market of Valletta in Malta. These sharks are mainly landed by the local pelagic longline fishery targeting tunas and swordfish (Schembri 2006). This is a small-scale fishery, composed by small-size longliners and multipurpose vessels, localized between the 35 to 36 degree north and 13.30 to 15.30 degree east (Fig. 2.1 Leiva et al. 1998; Axiak et al. 2002). We assumed that such statistics were a good estimator of shark abundance in the surroundings of the Maltese islands, as catches performed by Maltese fishers are mandatorily reported in the Valletta's wholesale market, and the discard rate of sharks is negligible, or relegated to some well identified species (Fergusson and Marks 1996; Leiva et al. 1998).

To standardize landings, we used a proxy of fishing effort exploiting large sharks. Number of hooks, fishing days, or any other detailed measure of effort was consistently unavailable for the whole time series. Therefore, we assumed that the annual value of total Gross Registered Tonnage (GRT) of Maltese longliners may be proportional to the local fishing pressure on large pelagic fish. Data, matching our catch series, were available from the FAO online fishery statistics database (`http://www.fao.org/fi/statist/statist.asp`) until 1995. More recent information was missing or reported in an inconsistent way. Data for 1979 was missing and we assumed an average value between 1970, 1975, and 1980. For years following 1995, we estimated a constant increase of about 1.5% per year of the 1995 fleet tonnage value, on the basis of published literature on Maltese fisheries (Leiva et al. 1998; Axiak et al. 2002; Anonymous 2007b) and recent information on Maltese fishing fleets extracted from Eurostat Fishing Fleet Statistics online database (`http://epp.eurostat.ec.europa.eu`).

A.1.6 Dataset 6: Spanish Swordfish Fisheries

Shark landings reported by Spanish swordfish longline fisheries. We combined three datasets:

- Catch and effort (number of hooks deployed at sea) of a pelagic long-line survey carried out in the eAlboran Sea from 1979 to 1983 published in Rey and Alot

(1984).

- Landings (in numbers) and effort of the Mediterranean Spanish swordfish fishery monitored by Buenquerpo et al. (1998) in 1992. Numbers were converted to biomass by converting the reported average length of each species to weight through length-size relationships in: Kohler et al. (2002) for *Alopias vulpinus*, *Prionace glauca* and *Isurus oxyrinchus*; and in Stevens (1984) for *Sphyrna zygaena*.

- Landed biomass of large pelagic sharks recorded by the Mediterranean Spanish swordfish fishery from 1985 to 2004. Data was extracted from Rey et al. (1987) for 1985; from Castro et al. (2000) for 1997 and 1998; from Valerias et al. (2003) for 1999; and from (Mejuto et al. 2006) for 2000 to 2004. Species with reported dressed weight (fish gutted and finned before landing) were reported to round weight by using conversion factors in Mejuto et al. (2006). Effort (number of hooks deployed at sea each year) was extracted from the ICCAT Task II Catch-Effort database (`http://www.iccat.es/t2ce.asp`, version 1.0, Oct 2007), and cross-checked with all fishery reports that provided information on pelagic fishing effort for the considered period.

As dataset 1 and 2 referred to the Alboran Sea, and dataset 3 to the whole Mediterranean Spanish fishery, we stratified the data in two categories: “Alboran” for dataset 1 and 2, and “ICCAT” for dataset 3 (referred as strata in Table 1, main text). Landed sharks registered by the Spanish swordfish fishery is a good proxy of real catches performed at sea, especially for the analyzed species, as the discard rate for these sharks is negligible (Castro et al. 2000; Megalofonou et al. 2005).

A.1.7 Dataset 7: Adriatic Swordfish Pelagic Fishery

Landings of *Prionace glauca* associated with the surface longline fishery of the southern Adriatic Sea. The fishery is directed to swordfish (*Xiphias gladius*) and albacore

(*Thunnus alalunga*). The fishing region is located from 30 to 70 miles off the Apulian coast (Marano et al. 1983, area 7 in Fig. 2.1). We analyzed landings and effort, recorded in the port of Monopoli, for 1984 to 1997 (De Zio et al. 2000), which we combined with data for the same fishery for 1998-1999 reported in (Megalofonou et al. 2000). Monopoli represents the most important fishing port of the southern Adriatic Sea. Data coming from this fishery is representative for the whole southern Adriatic longline fishery. It covers most of the southern Adriatic Sea and concerns the 80% of the total fish biomass landed in the region (De Zio et al. 2000).

A.1.8 Dataset 8: Ligurian Swordfish Pelagic Fishery

Landings and relative effort of large sharks caught by the Ligurian pelagic longline fishery (Garibaldi and Orsi Relini 2000). Data refer to a small fleet composed by 3-7 longliners of small size (30% are less then 10 meters long) from the port of San Remo. Fishing is usually conducted in an area 6 to 30 miles away from the port (Fig. 2.1). The main target of this fishery is swordfish (Garibaldi and Orsi Relini 2000; Orsi Relini 2000). The discard rate is low, limited to loggerhead turtles, sunfishes, pelagic stingrays, and manta rays (Garibaldi and Orsi Relini 2000; Orsi Relini et al. 1999). Sharks are landed dressed (headed, gutted and deprived of their fin). Observations ranged from 1990 to 1998.

A.1.9 Dataset 9: Recreational Fishing Data

Landings records of *Alopias vulpinus* compiled by two sport fishing clubs located around the Po delta, in the towns of Albarella and Barricata (area 9 in Fig. 2.1). These are among the biggest recreational fishing clubs in Italy, accounting for the highest number of recreational fishers in the region. Both clubs keep logbooks of catches to compile internal ranking of anglers, and to regulate their fishing activity according to the associations' deontological rules. We had number of tunas and threshers landed each year, together with technical information on used gears and date of catch. Data ranged from 1995 to 2006.

A.1.10 Pelagic Effort

ICCAT Pelagic longline effort

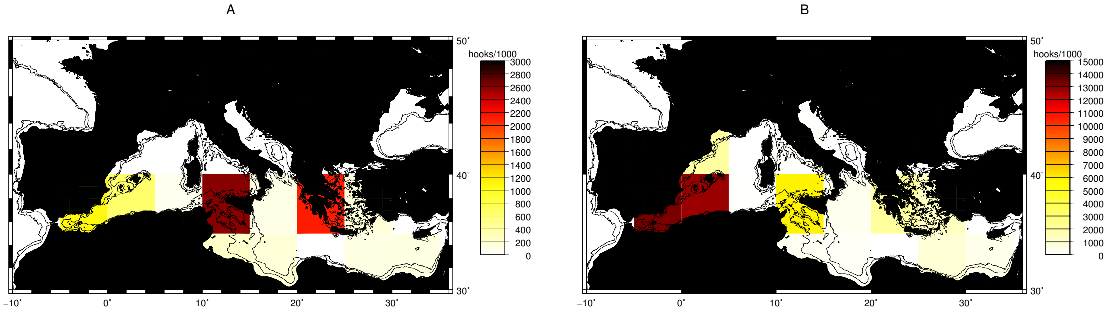

Figure A.1: Maps show an indication of areas and intensity of pelagic longline fishing effort in the Mediterranean Sea according to ICCAT. We accessed the Task II catch-effort online database at `http://www.iccat.es/t2ce.asp` (version 1.0,Oct.solo.2007). Of countries fishing in the Mediterranean Sea, we extracted data for Italy, Greece, Malta, Cyprus, Lybia, Spain, Japan, and Chinese Taipei. Croatia, France, Morocco, Serbia & Montenegro, Turkey and Tunisia had no reported longlining in the ICCAT database, and China and Korea had no data for year 2000 which was used for this graphical representation. We discarded records that did not report catches of bluefin tuna (*Tunnus thynnus*), swordfish (*Xiphias gladius*) or albacore (*Tunnus alalunga*). In this way we had a good proxy of the total effort of bluefin tuna, swordfish and albacore longlining, which are the major large pelagic fisheries in the Mediterranean Sea. In plot A we show the total number of hooks deployed by the international fleet in May 2000 on a geographical grid of 5 by 5 degrees. In plot B we show the number of hooks deployed by the same fleet for the entire year 2000. 2000 was the most recent year when all the above fleets where fishing at the same time.

Longliners in the Mediterranean Sea

Estimating the number of boats fishing with pelagic longlines in the Mediterranean Sea is very hard. Fisheries are not monitored on a regular basis, most are artisanal and thus difficult to regulate, and there is a high incidence of illegal and unregistered effort (Tudela 2004; FAO 2005; WWF 2006). Tudela (2004) reports about 1500 longliners for Italy, 400 for Greece, 245 for Spain, 100 fishing with flags of convenience or illegally, and 30 for Japan. Megalofonou and coauthors (2000) surveyed about 1400 boats from Italy, Spain and Greece to which 52 registered in the Ligurian Sea

(Orsi Relini et al. 1999) can be added. The Scientific, Technical and Economic Committee for Fisheries SGFEN/STECF (2001) reported data of 690-1041 boats operating in Italy, Spain and Greece, whereas Garibaldi (2006) estimated about 1000 longliners only for Italian waters. As these fleets are only a part of the overall international fleet exploiting pelagic waters in the Mediterranean we assume that 1000-2000 fishing boats is a conservative estimate.

Appendix B

Long-Term Ecological Change in a Meso-Predator Community in Response to Prolonged Human Disturbance

B.1 Data

B.1.1 Hvar

This is the first large scale trawl survey of the Adriatic. From February 16th 1948 to March 31st 1949 the national and international waters off former Yugoslavia and Albania to about twenty nautical miles off the Italian coast were sampled. 167 stations were surveyed with an American style otter trawl bottom trawl, allocated homogeneously over the designated region. Depth ranged from 5 to 400 meters. In total we extracted data for 278 tows. Gear specifications are given in Table 4.2. Tow duration was often 1 hour as a rule. However, sometimes tows lasted for 2, 3 or 4 hours. Data were extracted from Karlovac (1959). For each sampling event we had data on latitude, longitude, depth of the beginning and end of the tow, direction in degrees, duration in hours, characteristics of the bottom, chlorophyll, temperature and salinity of a water sample taken usually 5 meters above the sea floor. From these we calculated the mean depth (and position) of each tow. Trawling speed was 2.5 knots from February 26th to April 9th, and 3 knots for the rest of the survey. Number of specimens and cumulative weight per tow were recorded for each species. We cross-checked and validated misspelled, invalid or archaic species names by using Fish Base (`www.fishbase.org`) and the Interim Register of Marine and Nonmarine Genera (`http://www.cmar.csiro.au/datacentre/irmng/`). As otter trawl mouth geometry changes as the gear operates at different depths (Godo and Engas 1989), we calculated the area swept by each tow by using parameter estimates of a linear regression between horizontal opening and towing depth of a traditional Italian otter trawl used in Tuscany (headrope: 35 m; footrope: 40 m) for which performance experiment data were available (F. Serena unpublished data).

B.1.2 Zupanovic

From 1957 to 1958, 126 trawl fishing operations were carried out on 10 stations in the Croatian channels. Tows were performed once a month in all of the 10 fixed stations by two motorboats, ”Bios” and ”Predvodnik”. Catches were extracted from Županović (1961). Indices of abundance were expressed in numbers. For each tow, date and mean depth were reported. We geolocated the tow stations (latitude and longitude identified) by using ARCinfo on Županović (1961)’s map. Tow duration was reported as one hour for all. Trawl horizontal opening was estimated by using the estimated values of swept areas observad in the Jukic surveys (see below). Zupanovic and Jukic used the same trawl and vessel. Swept area was calculated by multiplying tow duration by the estimated horizontal opening.

B.1.3 Jukic

Data were extracted from Jukić (1975). Tows were performed at different times of the day, from 5 in the morning to 8 in the evening, and were normally distributed around the mean of this time range. Tows were carried out between 32 and 262 meters with and uniform distribution of tows along this depth range. Trawl horizontal opening (OP) was not reported. Hence swept area was inferred from reported indices of production such as kg/hectar and kg/hour, which were reported for each station. We estimated swept area per hour $km^2/hour$ by using the ratio of the two indices and dividing by 100. Such proxy was indicative of trawl performance. Type of trawl and vessels differed across stations. From 1963 to 1967, a 180-hp cotton trawl was towed by m/b ”Prevodnik” of 200 hp (46 tows). In the channel stations, from 1967 to 1970, a 250-hp cotton trawl with knots was towed by m/b (motor boat) ”Bios” (300 hp, 136 tows). Finally, in 1971, a syntectic 180 hp trawl towed by m/b ”Bios” was used (15 tows Jukić 1975). The average tow speed was 3 knots. Sampling design was substantially unbalanced. Vessel changed across stations and over time. Consequently, latitude, longitude and sampling depth changed as well. Estimating changes in abundance of fish populations controlling for tow position and sampling

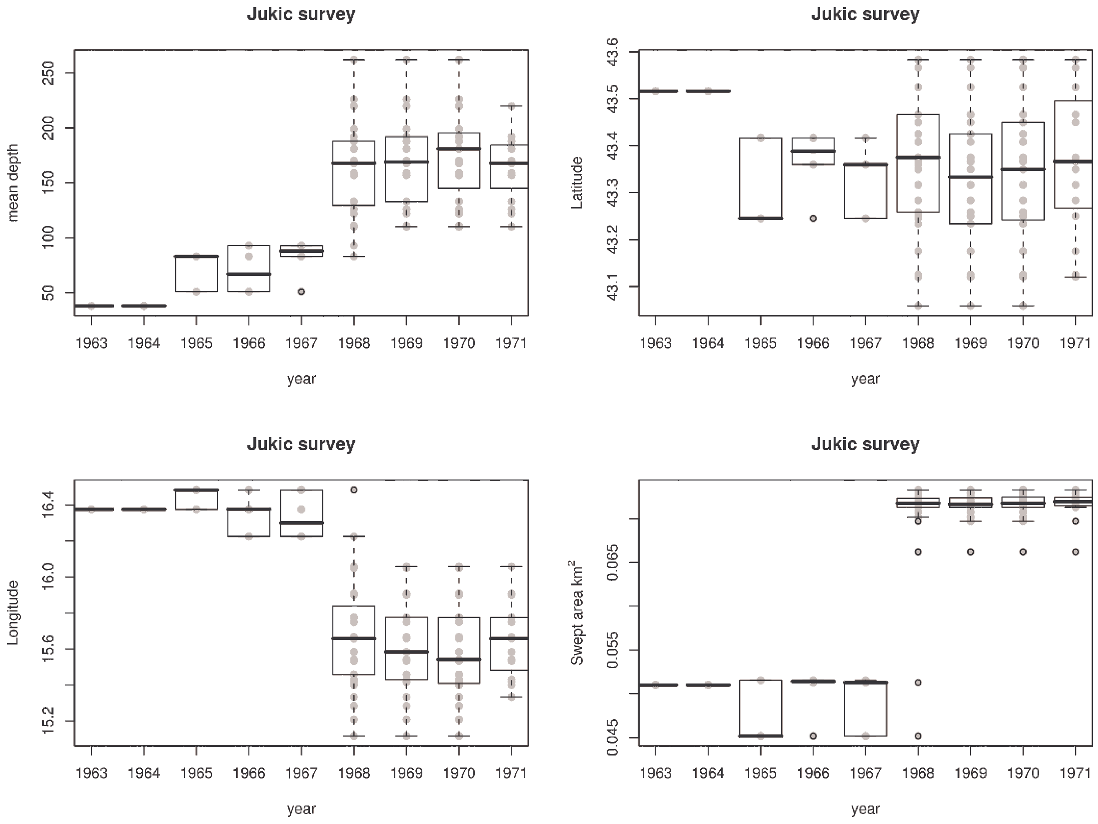

Figure B.1: Depth, latitide, longitude and swept area ranges relative to the tows carried out with the "Jukic" survey framework (1963-1971) depth was therefore challenging for lack contrasts.

B.1.4 GRUND

GRUND is an Italian national trawl survey program that started in 1985 (Relini et al. 1999). In the Adriatic Sea sampling design followed a transept framework (Relini et al. 2000). Number of stations were allocated proportionally to depth strata's extension (Piccinetti 1996). We could not access raw data but survey reports held in the archive of the Ministry of Forestry and Agriculture. Data for the period 1994-96 was reported as n/hour and kg/hour for each tow. Latitude, longitude, date, time of start and end of the operation, and mean depth were reported as well. We calculated tow duration, and the expected number and biomass of sharks caught by each tow multiplying the indices of abundance by tow durations and rounding the values to integers (i.e. we applied the inverse function used to aggregate the data for the report). Sampling operations were carried out with m/b "Pipeta". Technical specifications of boat and gear are in Table 4.1. Average trawl speed was 3.25 knots (between 2.5 and 4 knots, depending on depth, type of bottom, catch, etc. Piccinetti 1996). Swept area was estimated by multiplying the average $km^2/hour$ of swept reported in Šimunović (1997); Šimunović et al. (2002), by tow duration in hours. Tow duration was meant to be one hour. However, depending on the bottom conditions, tow duration varied.

B.1.5 MEDITS

The Mediterranean International Trawl Survey program (MEDITS) is a European sampling program of demersal resources that begun in 1994. Initially it involved Spain, France, Italy and Greece. Later, other Mediterranean European countries joined the effort (Bertrand et al. 2002a). In the Adriatic Sea, the program extended the sampling operations in the eastern Adriatic waters when Albania, Slovenia and Croatia joined the effort (Bertrand et al. 2002a). In 1999, Croatia did not carry out its sampling operation due to the Yugoslavian war. Tows were performed between May and September, from 2.25 in the morning to 19.13 in the evening. Depth ranged between 9.5 and 850 meters, with an average of 92.29 meters. 91.36 % of tows were carried out in daylight. Data have been checked for typing errors. Trawl gear has been substantially the same for the whole period, although during the first years, minor adjustment to gears were done to optimize its performance Bertrand et al. (2002a). Different countries used their own boats (which have been always the same within nations). 5 vessels have been employed for the surveys: FUL (1994, 1995), EGU (1995, 1996), PRI (1997), IGO (1997, 1998) and AND (1999-2005) (Table 4.2).

Swept area was calculated by multiplying horizontal opening provided in decimeters with tow duration. Croatia reported a constant horizontal opening (*ho*) for years 2003 and 2004. Therefore swept areas likely carried higher measurement error in these years (e.g. it was constant regardless the sampled depth). Not all *ho* were always measured with the use of SCANMAR. However we could not distinguish which one was estimated from the others.

MEDITS followed a stratified random sampling design with proportional allocation of tows. The stratifying parameter was depth, and the sampling rate was one station every 200 square nautical miles (Bertrand et al. 2002b).

B.2 Analysis

B.2.1 SAS Macro

Step by step, we removed the variable with the highest p-value of the likelihood ratio test for the significance level. The macro initially searched non significant values among higher order interactions, then proceeded with those of lower order, finally with main effects. If a main effect was selected as not significant, all its interactions were removed as well, regardless of their statistical significance.

For class variables, statistical significance was assessed according to a type III analysis. If models were not converging, thus resulting in the absence of type III analysis results, we coerced the program to count the number of statistically significant levels for the considered class from type I analysis . If these were more than half the number of levels, then it retained the variable.

Sometimes, the fitting iteration process resulted in negative dispersion parameters, meaning problems in parameter estimation. In these cases, a profile likelihood analysis was carried out. We specified a parameter space of 110 values from 0.1 to 100, fitting a first sequence from 0.1 to 1 by steps of 0.1, and then a sequence of steps by 1. k was held constant at any given value for each model. In these cases, the stepwise variable selection process picked the worst variable from the corresponded model resulting with the best log likelihood value, and corresponding k values. Running a profile likelihood in these cases is necessary as the negative binomial likelihood function does not always have a simple solution. It requires a very intensive parameter estimation process. By fitting models holding k fixed, we reduced the likelihood function complexity allowing the fitting algorithm to estimate fewer parameters. We selected the best fit according to the maximum value of the log likelihood estimation for the data. Finally, we identified the best model over the pool of all the fitted ones, according to the associated AIC (Akaike Information Criterion).

B.2.2 Incorporating Uncertainty

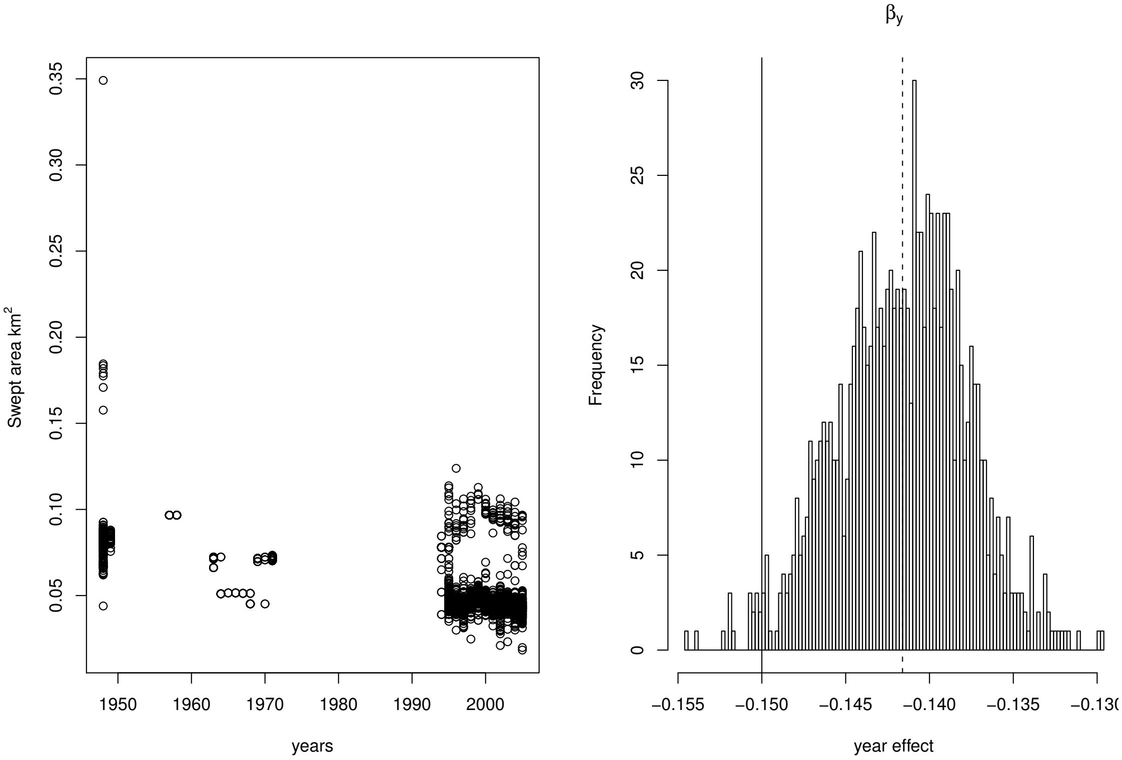

Figure B.2: (a) Scatter plot of swept areas associated to the tows present in the dataset; (b) distribution of year effect estimates obtained. The vertical line indicates the expected value for β_y (true known year effect). The dashed line indicates the mean β_y of the distribution of 1000 estimates (see section 4.2.5)

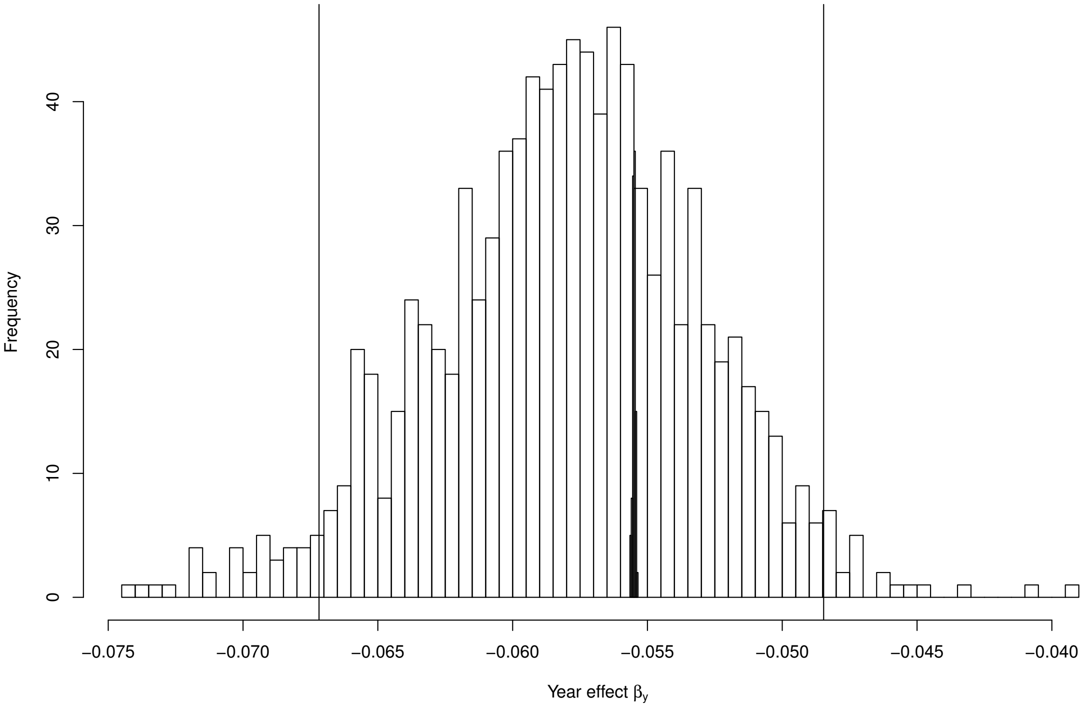

Figure B.3: Simulated distribution of year effect estimates drawing from a normal distribution with mean equal to the parameter estimate obtained for *S. canicula* in the long-term comparison in the Hvar area Fig. 4.8 and variance equal to the square of its associated standard error. The two vertical lines refer to the lower and upper limit of the confidence interval. Black depicts the distribution of parameter estimates obtained from estimating swept area from the empirical relationship of horizontal opening and depth as described in methods (section 4.2.5).

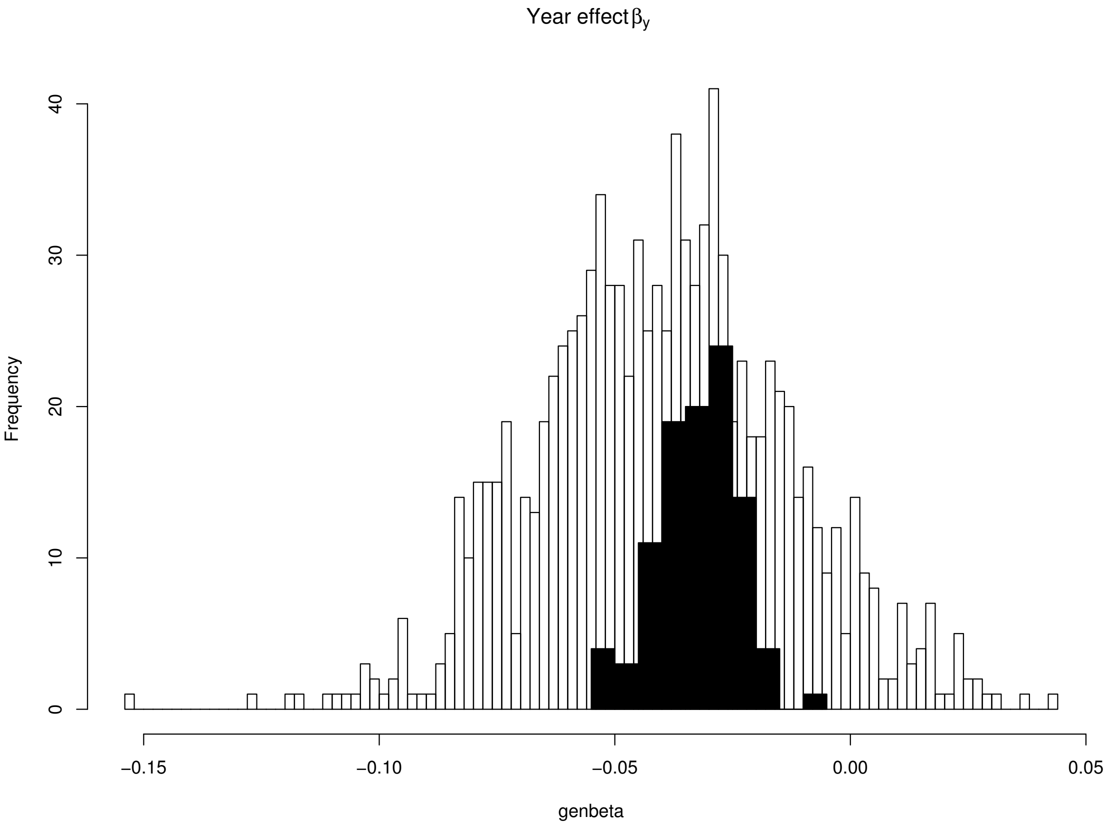

Figure B.4: Simulated distribution of year effect estimates obtained by drawing 1000 values from a normal distribution with mean equal to the best estimate of year effect for *S. canicula* obtained in the short-term analyses of Medits data (Fig. 4.6), and variance equal to the square of its associated standard error. Black depicts the distribution of year effect estimates obtained including sediment composition with measurement error (see section 4.2.5).

B.2.3 Vulnerability to Fishing Exploitation

Life history parameters were collected from:

fishbase.org, www.redlist.org, Moura et al. (2004); García et al. (2008); Dulcic et al. (2003); Frisk et al. (2005); Smith et al. (1998); Costa et al. (2005); Pawson and Ellis (2005); Ivory et al. (2004); Mollet (2005); Graham et al. (2001), and references therein.

B.2.4 Effort

The choice of Ancona as training fishing fleet to develop the fishing effort model was related to the observed distributions of the available tows. Ancona showed an expected spatial distribution of fishing operations based on their distance from port and fishing depth. The distribution patterns for the other fisheries seemed influenced by local factors unlikely to be shared by most Adriatic fleets. Chioggia had an insufficient number of tows to train the model. Fano's trawl tows were mostly in proximity of the Croatian border, perhaps to increase fishing yields and to avoid competitions with surrounding fisheries. In fact, Cesenatico, Fano's neighboring fleet seemed to allocate its effort on a narrow strip between where Chioggia would be expected to deploy most of its effort and where Fano is fishing in the south.

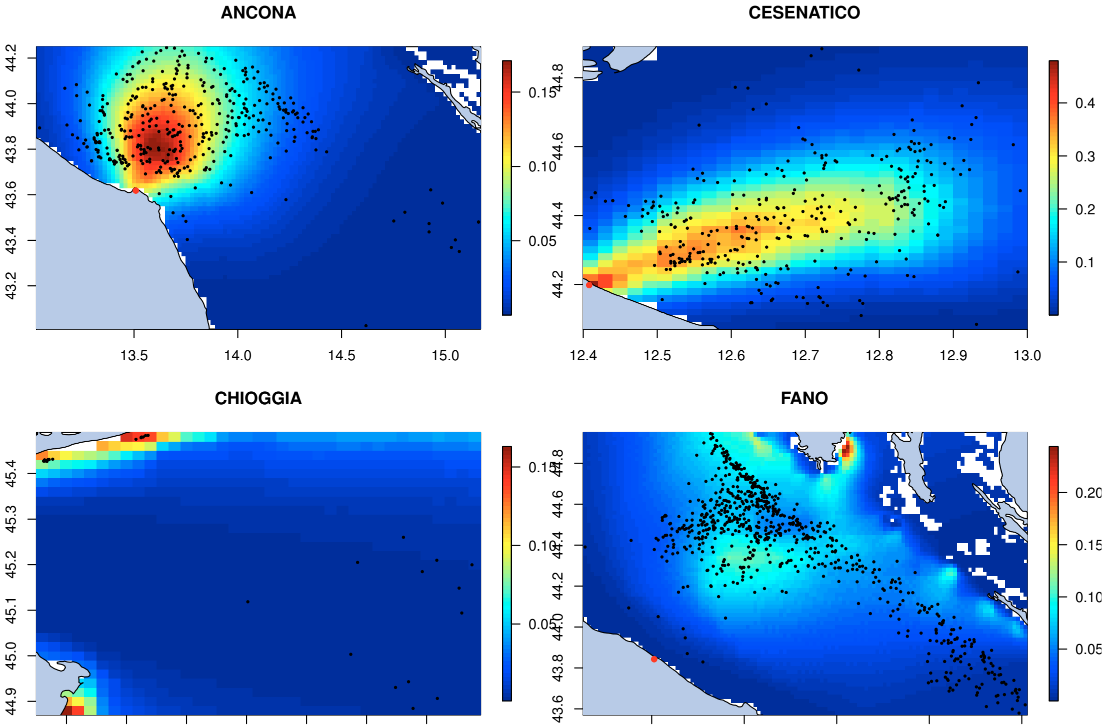

Figure B.5: Dsitribution of commercial trawl tows used to develop the model of effort distribution represented in Figure 4.9 (a). Black dots are tow locations. Color intensity is the predicted index of effort expressed as the number of tows expected in any pixel over a year

B.3 Spatial Comparison of Medits' Nominal Catches

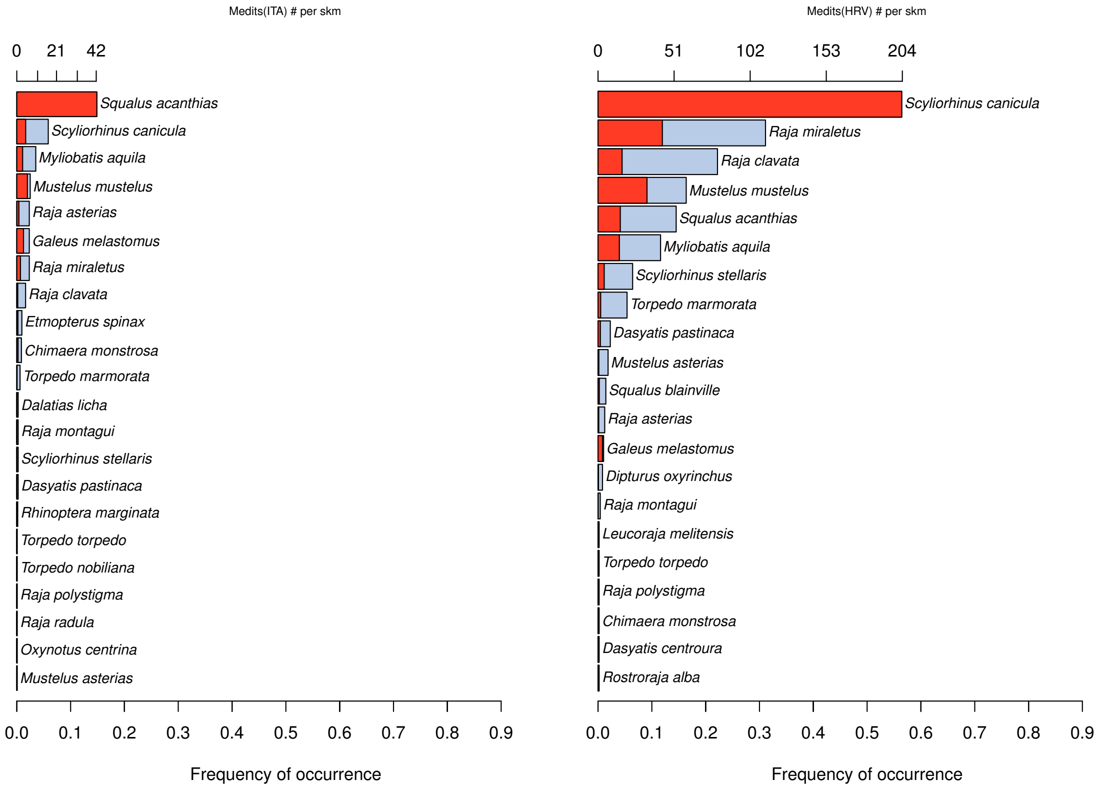

Figure B.6: Frequency of occurrence (f_i) of elasmobranchs caught in the Medits' survey (grey bars) for Italy (ITA) and Croatia (HRV). F_i is the number of tows that caught species$_i$ divided by the total number of tows performed. Red filling indicates the species mean density in number per square kilometre (nominal catches).

Appendix C

Patterns and Ecosystem Consequences of Shark Declines in the Ocean

Species	Slope	p-value	Deviance	Location	Percent change	Period
*Carcharhinus leucas**	-0.2	< 0.001	178.55	Main Beach	-98.2	1952-1972
Carcharhinus limbatus+	-0.23	< 0.001	189.6	Main Beach	-99.1	1952-1972
Sphyrna lewini++	-0.25	< 0.001	63.52	Main Beach	-99.3	1952-1972
Carcharhias Taurus	-0.24	< 0.001	117	Main Beach	-99.2	1952-1972
Carcharodon carcharias	-0.14	< 0.001	39.2	Main Beach	-94.5	1952-1972
Others	0.01	0.61	45.26	Main Beach	-31.7	1952-1972
*Carcharhinus leucas**	-0.19	< 0.001	44.66	Brighton Beach	-87.7	1961-1972
Carcharhinus limbatus+	-0.25	< 0.001	122.05	Brighton Beach	-93.5	1961-1972
Sphyrna lewini++	-0.18	< 0.001	47.79	Brighton Beach	-85.9	1961-1972
Carcharhias Taurus	-0.26	< 0.001	18.99	Brighton Beach	-94.4	1961-1972
Carcharodon carcharias	-0.03	0.46	17.64	Brighton Beach	-27.5	1961-1972
Others	0.27	< 0.001	28.82	Brighton Beach	17.8	1961-1972

Table C.1: Parameter estimates of Generalized Linear Models (GLM) applied to shark netting data in South Africa from 1952-72 extracted from (Holden 1977) and shown in Fig. 4. GLM were fitted to the data assuming a Poisson distribution and a log link. Fishing effort in term of meters of nets per location has been treated as an offset variable. Species names refer to the most common species; * included few *Carcharinus obscurus*; + included some *Sphyrna tudes*; ++ included some *C. brevipinna*; Parameter estimates of the models are reported in SM. "Others" were mainly pelagic species such as shortfin mako (*Isurus oxyrhinchus*), blue shark (*Prionace glauca*) and tiger sharks (*Galeocerdo cuvier*).

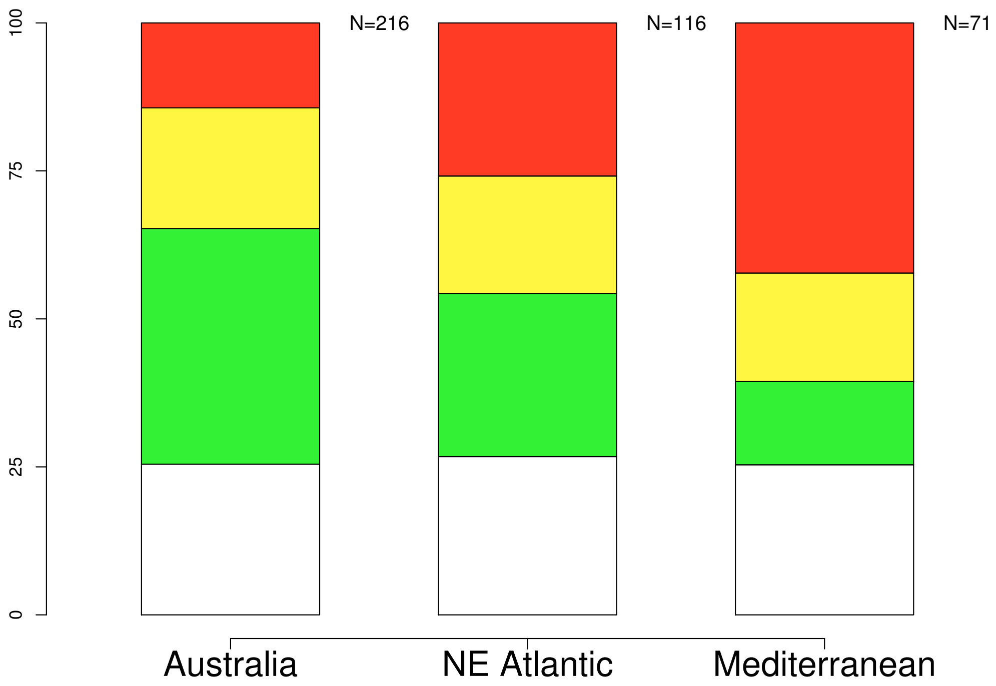

Figure C.1: Conservation status of Australian, NE Atlantic and Mediterranean chondrichthyans as assessed by the International Union for the Conservation of Nature (IUCN). Red indicates the percentage of species regionally assessed as Critically Endangered (CR), Endangered (EN), and Vulnerable (VU); yellow indicates Near Threatened (NT) status; green the percentage of species assessed as Least Concern (LC); transparent bars refer to species that are assessed Data Deficient (DD). Number of species assessed (N) is reported. Data have been extracted from the regional reports available (Cavanagh et al. 2003; Cavanagh and Gibson 2007; Gibson et al. 2008).

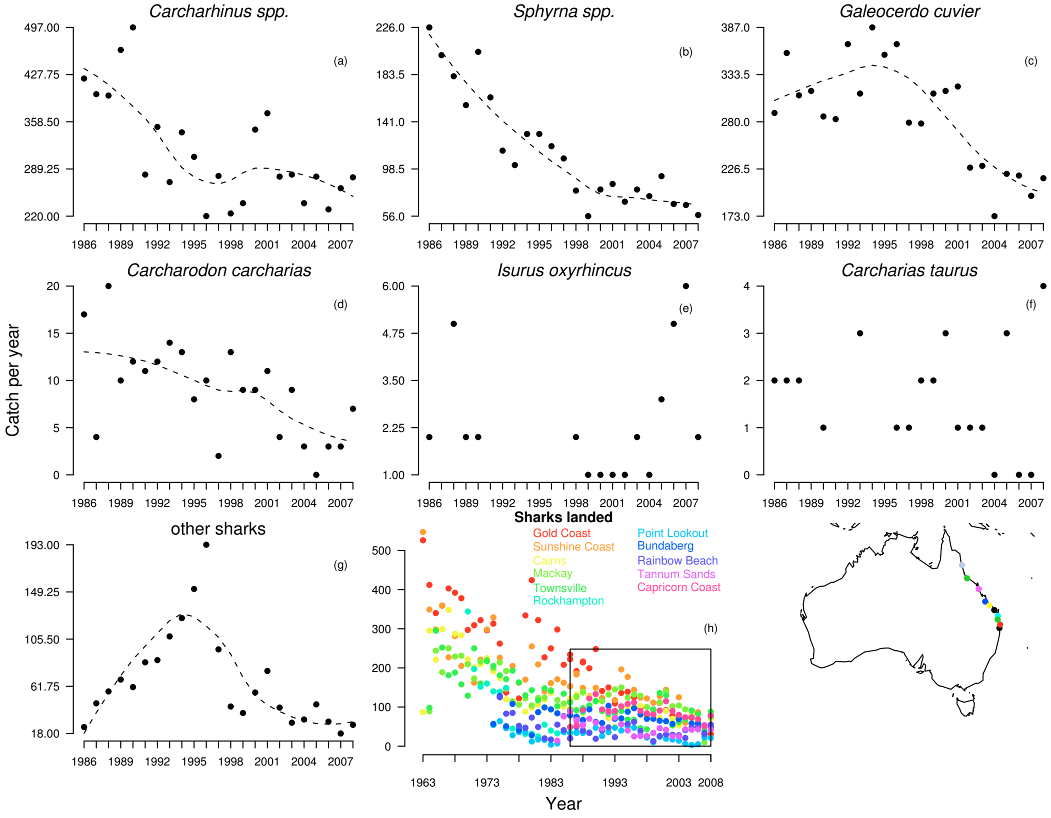

Figure C.2: Trends in the shark landings of the shark control program in Queensland, Australia. For the species specific trajectories (a-g) and cumulative catch per location (h) after 1986, data have been extracted from official statistics of the Queensland Department of Primary Industries and Fisheries available at http://www.oesr.qld.gov.au/queensland-by-theme/industry/agriculture-forestry-fishing/tables/shark-control-program-caught-area/index.shtml. For the cumulative catch per location in years prior to 1986, data were extracted from Paterson (1990). Dashed lines represent predicted values of local regressions.

Species	Region	FAO area	Last caught	Period	Reference and notes	Confirmed
Dipturus batis	Adriatic Sea	Mediterranean and Black Sea	1966	1948-2005	Analyzed trawl surveys in the Adriatic Sea from 1948 to 2005 (Ferretti unpublished data)	yes
Galeorhinus galeus			1956			
Squatina squatina			1958			
Heptranchias perlo			1948			
Leucoraja circularis			1948			
Pteromilaeus bovinus			1948			
Rostroraja alba	Adriatic Sea	Mediterranean and Black Sea	2004	1948-2005		no
Oxynotus centrina			2003			
Oxynotus centrina	Gulf of Lions	Mediterranean and Black sea	1992	1957-1995	Species disappeared from trawl survey data used by Aldebert (1997) . Monte-Luna et al. (2007) cautions for further investigation given the qualitative nature of some surveys used by Aldebert (1997)	Further investigation required
Dipturus batis			1960			
Dipturus oxyrhincus			1984			
Galeorhinus galeus			1957			
Mustelus mustelus			1989			
Mustelus asterias			1970			
Leucoraja naevus			1989			
Raja microcellata			1960			
Scyliorhinus stellaris			1987			
Myliobatis Aquila			1976			
Leucoraja circularis			1960			
Leucoraja miraletus			1989			
Leucoraja undulata	Tyrrhenian Sea	Mediterranean and Black Sea		1972-2005	Species absent or disappeared from trawl survey data (Ferretti et al. 2005)	yes
Raja polystigma			1990			
Dasyatis centroura						
Dipturus batis						
Galeorhinus galeus						
Rostroraja alba			1993			
Squatina aculeate			1973			
Squatina oculata						
Pteroplatytrygon violacea						
Mustelus punctulatus						
Squatina squatina			1974			
Torpedo nobiliana			1993			
Mustelus mustelus			2001			
Mustelus asterias						
Heptranchias perlo			1974			
Raja brachyura						
Dipturus batis	Irish Sea	Northeast Atlantic	1981	1957-1995	(Duvly et al. 2003)	yes
Dipturus oxyrhincus			1880			
Rostroraja alba			1880			
Squatina squatina			1998			
Dipturus batis	North Sea	Northeast Atlantic	1991	1982-2002	(Ellis et al. 2005)	yes
Mustelus mustelus	Wadden Sea	Northeast Atlantic	1990		(Duvly et al. 2003)	yes
Dasyatis pastinaca			1966			
Raja clavata			1960			
Scyliorhinus canicula			1955			
Squatina squatina	Bay of Biscay	Northeast Atlantic			(Duvly et al. 2003)	yes
Echinorhinus brucus			1981			
Rostroraja alba	English channel	Northeast Atlantic	1880		(Duvly et al. 2003)	yes
Pristis pesctinata	W Atlantic	Atlantic western Central			Although population number below viable levels, updated analyses rejected such claim (Monte-Luna et al. 2007)	no
Pristis pectinata	Bermuda					
Pristis perotteti	Gulf of California	Pacific Eastern Central			Synonymous of *Pristis pristis* which is claimed to not occur in the Gulf of California (Monte-Luna et al. 2007)	no

Table C.2: Updated list of elasmobranch local extinctions after Duvly et al. (2003). The most recent year the species was caught or observed in the period considered by the reference is indicated. Confirmed indicates whether the claim of local extirpation by Duvly et al. (2003) can be dismissed or accepted on the basis of further information.

Group	Slope	p-value	R2
small sharks	0.079987	< 0.001	0.68
Batoids	0.04106	< 0.001	0.45
Teleosts	-0.03124	< 0.001	0.61

Table C.3: Coefficients of linear models fitted to data depicted in Fig. 5.6 (b-d).

Group	Slope	p-value	R2
small sharks	-0.02961	0.06	0.15
Batoids	0.02361	0.002	0.35
Teleosts	0.012006	0.06	0.15

Table C.4: Coefficients of linear regression models fitted to data depicted in Fig. 5.6 (f-h)

Appendix D

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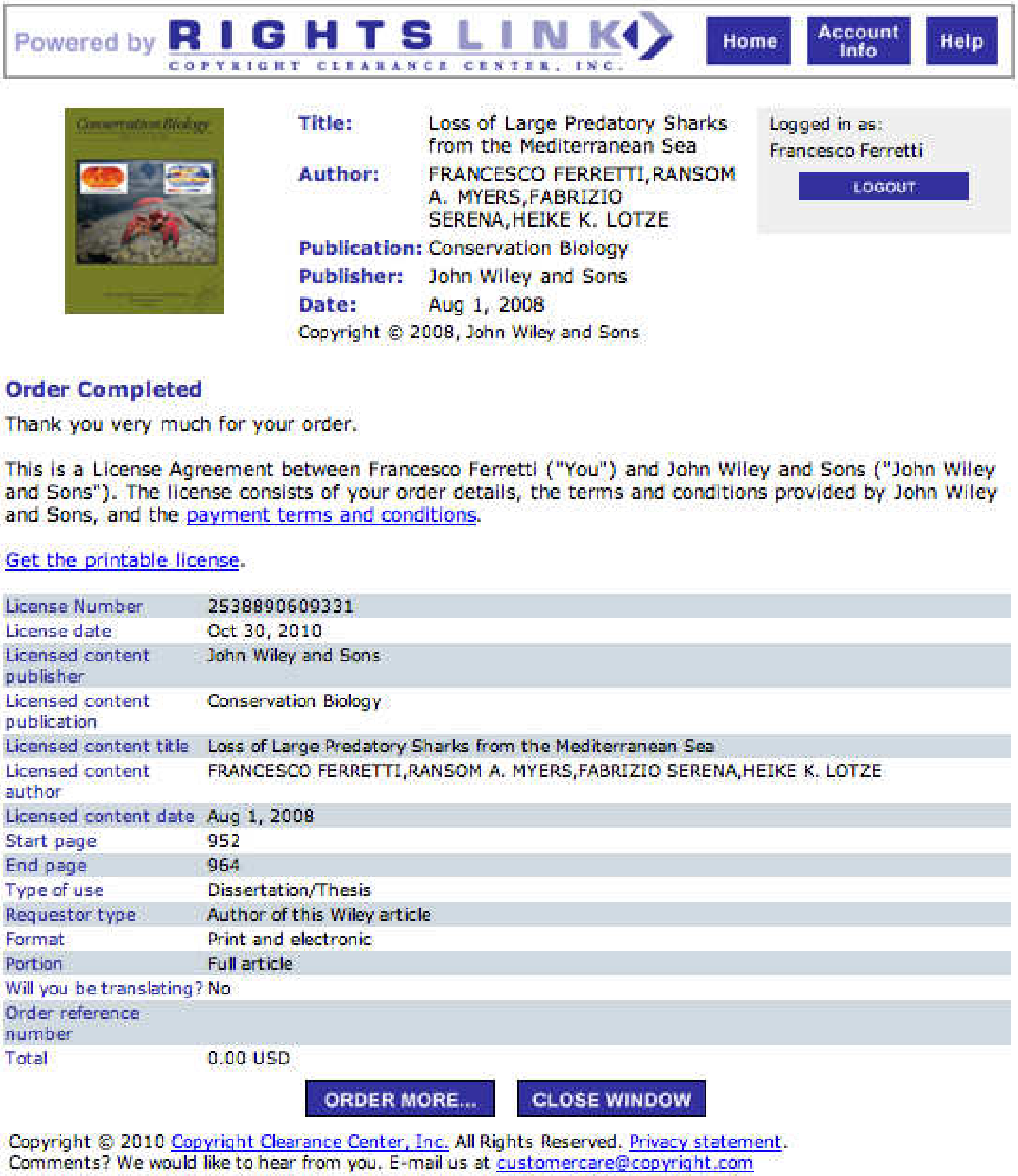

Title: Loss of Large Predatory Sharks from the Mediterranean Sea

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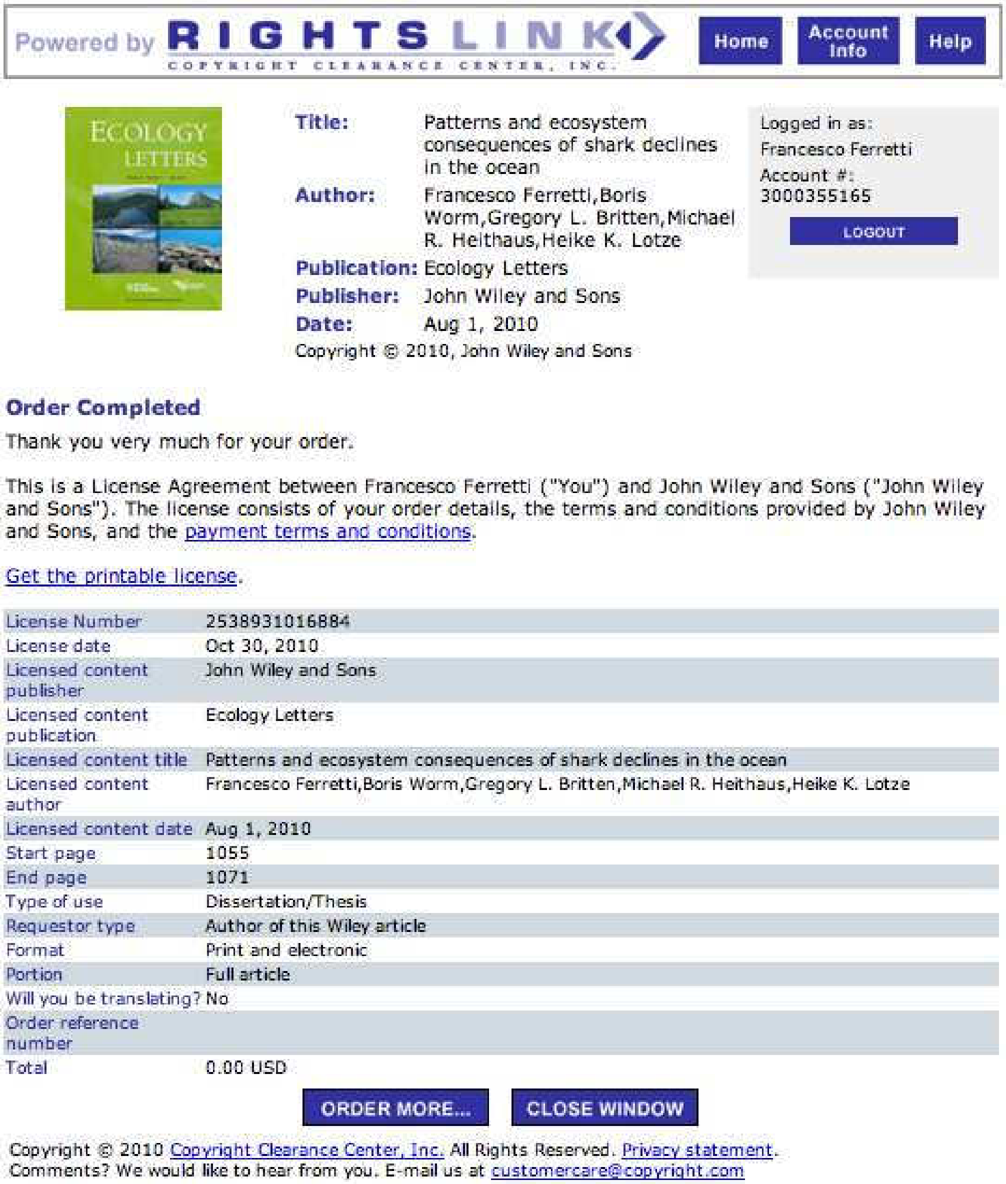

Title: Patterns and ecosystem consequences of shark declines in the ocean

Author: Francesco Ferretti,Boris Worm,Gregory L. Britten,Michael R. Heithaus,Heike K. Lotze

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