Contributed Paper

Loss of Large Predatory Sharks from the Mediterranean Sea

FRANCESCO FERRETTI,*‡ RANSOM A. MYERS,*§ FABRIZIO SERENA,† AND HEIKE K. LOTZE*

*Department of Biology, Life Sciences Centre, 1355 Oxford Street, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada
†ARPAT (Agenzia Regionale per la Protezione Ambientale della Toscana), Via Marradi 114, 57100 Livorno, Italy

Abstract: *Evidence for severe declines in large predatory fishes is increasing around the world. Because of its long history of intense fishing, the Mediterranean Sea offers a unique perspective on fish population declines over historical timescales. We used a diverse set of records dating back to the early 19th and mid 20th century to reconstruct long-term population trends of large predatory sharks in the northwestern Mediterranean Sea. We 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. Only 5 of the 20 species we considered had sufficient records for analysis. Hammerhead (*Sphyrna *spp.), blue (*Prionace glauca*), mackerel (*Isurus oxyrinchus *and* Lamna nasus*), and thresher sharks (*Alopias vulpinus*) declined between 96 and 99.99% relative to their former abundance. According to World Conservation Union (IUCN) criteria, these species would be considered critically endangered. So far, the lack of quantitative population assessments has impeded shark conservation in the Mediterranean Sea. Our study fills this critical information gap, suggesting that current levels of exploitation put large sharks at risk of extinction in the Mediterranean Sea. Possible ecosystem effects of these losses involve a disruption of top-down control and a release of midlevel consumers.*

Keywords: elasmobranchs, extinction risk, generalized linear models, historical population trends, meta-analysis, overfishing, predatory sharks, top-down control

Pérdida de Tiburones Depredadores Grandes en el Mar Mediterráneo

Resumen: *La evidencia de declinaciones severas de peces depredadores grandes está incrementando alrededor del mundo. Debido a su larga historia de pesca intensiva, el Mar Mediterráneo ofrece una perspectiva única de las declinaciones de poblaciones de peces en escalas de tiempo histórico. Utilizamos un conjunto diverso de registros que datan de inicios del siglo XIX hasta mediados del siglo XX para reconstruir las tendencias poblacionales de largo plazo de tiburones depredadores en el noroeste del Mar Mediterráneo. Compilamos 9 series de tiempo de índices de abundancia de capturas comerciales y recreativas, muestreos científicos y registros visuales. Usamos modelos lineales generalizados para extraer tasas de cambio instantáneas de cada conjunto de datos, y realizamos un meta-análisis para comparar tendencias poblacionales. Solo 5 de las 20 especies consideradas tuvieron suficientes datos para el análisis.* Sphyrna *spp.,* Prionace glauca*,* Isurus oxyrinchus*,* Lamna nasu *y* Alopias vulpinus *declinaron entre 96 y 99.99% en relación con su abundancia anterior. De acuerdo con criterios de la Unión Mundial de Conservación (IUCN), estas especies serían consideradas en peligro crítico. Hasta ahora, la falta de evaluaciones poblacionales cuantitativas ha impedido la conservación de tiburones en el Mar Mediterráneo. Nuestro estudio llena este vacío de información crítico, lo cual sugiere que los niveles actuales de explotación han puesto en riesgo de extinción a los tiburones grandes en el Mar Mediterráneo. Los posibles efectos de estas pérdidas a nivel ecosistema implican una interferencia del* control arriba-abajo *y la detonación de consumidores primarios.*

‡*email ferretti@dal.ca*
§*Ransom A. Myers died during the writing of this paper. We will greatly miss his unique personality, passion, and intelligence.*
Paper submitted June 26, 2007; revised manuscript accepted November 15, 2007.

Conservation Biology, Volume 22, No. 4, 952–964

DOI: 10.1111/j.1523-1739.2008.00938.x

Palabras Clave: control arriba-abajo, elasmobranquios, modelos lineales generalizados, meta-análisis, riesgo de extinción, sobrepesca, tendencias poblacionales históricas, tiburones depredadores

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 & 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 & Worm 2005). In the Gulf of Mexico oceanic whitetip sharks (*Carcharhinus longimanus*) declined by >99% between the 1950s and 1990s (Baum & Myers 2004), and coastal elasmobranch species declined by 96–99% between 1972 and 2002 (Shepherd & Myers 2005). In the northwestern Atlantic several large shark species declined by >75% in just 15 years since 1986 (Baum et al. 2003). Little quantitative information is available from other regions, particularly 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 & Myers 2004; Shepherd & Myers 2005). In the northwestern 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 suggest 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 1884; Parona 1898; Ninni 1923). In the early 20th century many coastal fisheries targeted sharks or landed them as bycatch (e.g., Piaggio 1927; Arcidiacono 1931). In recent decades, however, large sharks seemed to be restricted to the eastern and southern Mediterranean coasts (Başusta et al. 2006) or to offshore pelagic waters, where they have been caught, albeit in very low numbers (Megalofonou et al. 2005; Tudela et al. 2005). Pelagic fisheries have caught only 3 species regularly: the blue shark, shortfin mako (*Isurus oxyrinchus*), and thresher shark, 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 landing 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 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 & 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 19th and 20th 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.

Methods

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 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; Supplementary Material) from 6 regions (Fig. 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

Table 1. Outline of data sets, study area, modeled species, and model details for the analyses of population abundance of large sharks in the Mediterranean Sea.

Data set	*Gear*	*Area (time span)*	*Species*	*Index of abundance*	*Regressing variables*	*Offset variable (distribution)*	*Source*
1	sighting records[a]	Adriatic Sea (1827–2000)	lamnids and *Sphyrna* spp.	sightings/year	year	none (Poisson)	Soldo & Jardas 2002
2	tuna trap	Tyrrhenian Sea (1898–1922)	*Alopias vulpinus,* lamnids,[b] and *Sphyrna* spp.	no. sharks/year; kg/year	year	none (negative binomial)	fisher logbooks
3	tuna trap	Ligurian Sea (1950–2006)	*A. vulpinus,* lamnids,[c] *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)	*A. vulpinus,* lamnids,[d] *P. glauca,* and *Sphyrna* spp.	no. sharks/year; kg/year	year	no. hooks/year (negative binomial)	Filanti et al. 1986 Megalofonou et al. 2000
5	pelagic longline	Strait of Sicily (1979–2001)	lamnids, *P. glauca,* and *Sphyrna* spp.[e]	kg/year	year	estimated total gross tonnage (gamma)	official statistics of Valletta's wholesale fish market
6	swordfish pelagic longline	Spanish Mediterranean waters[h] (1979–2004)	*A. vulpinus,* lamnids[f], *P. glauca,* and *Sphyrna* spp.[g]	kg/year	year, strata, year*strata	no. hooks/year (gamma)	Rey & 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)	*P. glauca*	no. sharks/year; kg/year	year	no. hooks/year (negative binomial)	De Zio et al. 2000; Megalofonou et al. 2000
8	swordfish pelagic longline	Ligurian Sea (1990–1998)	*A. vulpinus,* lamnids, and *P. glauca*	no. sharks/year; kg/year	year	no. hooks/year (negative binomial)	Garibaldi & Orsi Relini 2000
9	big game rod and reel fishing	Adriatic Sea (1995–2006)	*A. vulpinus*	no. sharks/year	year, tunas, year*tunas	no. club members/year (Poisson)	yacht-club logbooks

[a] *A genaral way to identify records of occasional sightings or catches obtained with different fishing gear.*
[b] *Most likely* Lamna nasus.
[c] *Most likely* Isurus oxyrinchus.
[d] L. nasus.
[e] *Most likely* Sphyrna zygaena.
[f] I. oxyrinchus.
[g] S. zygaena.
[h] Area fished by Spanish longliners.

Table 2. Large predatory sharks occurring in the Mediterranean Sea including their size, trophic level, habitat, and their World Conservation Union Red List extinction-risk category for the region.

Family	*Species*	*Common name*	*Maximum length (cm)*	*Trophic level*[a]	*Preferential habitat*[b]	*Red-list category*[c]
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	4.2[d]	benthopelagic, bathyal	EN
Alopidae (thresher sharks)	*Alopias superciliosus* (Lowe 1839)	bigeye thresher	461	4.2	pelagic, coastal/oceanic	DD
	A. 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 (Bonnaterre 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
	C. brachyurus (Günther 1870)	bronze whaler	292	4.2	benthopelagic, coastal/oceanic	DD
	C. brevipinna (Müller & Henle 1839)	spinner shark	280	4.2	bentopelagic, coastal	DD
	C. falciformis (Müller & Henle 1839)	silky shark	350	4.2	pelagic, coastal/oceanic	-
	C. limbatus (Müller & Henle 1839)	blacktip shark	255	4.2	benthopelagic, coastal	DD
	C. obscurus (Lesueur 1818)	dusky shark	420	4.2	benthopelagic, coastal/oceanic	DD
	C. 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	-
	S. mokarran (Rüppell 1837)	great hammerhead	600	4.3	benthopelagic, coastal/oceanic	DD
	S. zygaena (Linnaeus 1758)	smooth hammerhead	400	4.2	benthopelagic, coastal/oceanic	VU

[a] *According to Cortés (1999).*
[b] *According to Musick et al. (2004).*
[c] *Red-list category assessed by IUCN Shark Specialist Group (Cavanagh & Gibson 2007): CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; DD, data deficient (www.iucnredlist.org).*
[d] *From www.fishbase.org*

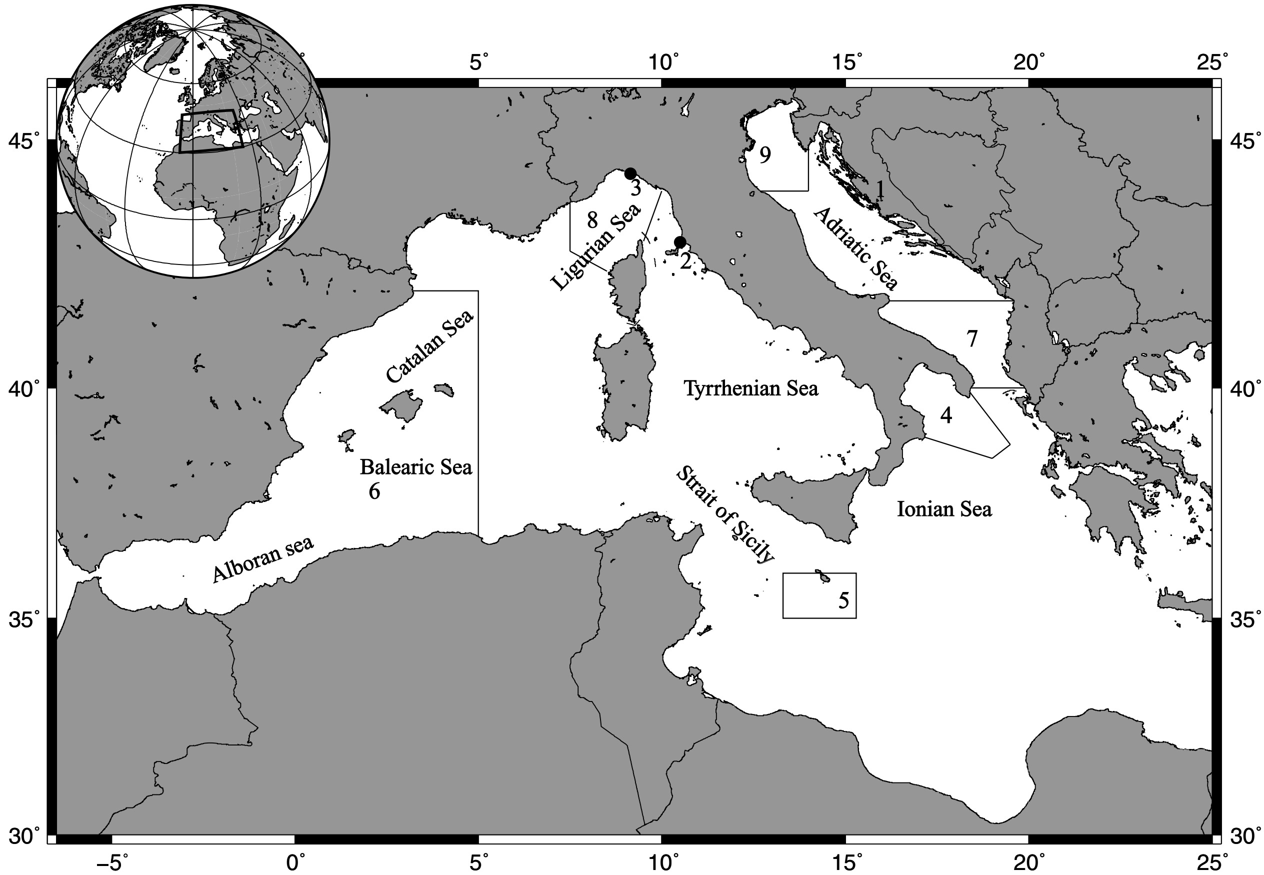

Figure 1. Study areas in the Mediterranean Sea. Data set 1 came from the coastal zone of the eastern Adriatic Sea; data sets 2 and 3 refer to the 2 fish-trap locations (dots); data sets 4–9 approximately represent the investigated pelagic longline and recreational fisheries (areas enclosed in lines,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

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).

Modeling Population Trends

For each data set we extracted an appropriate index of abundance to be modeled over time with generalized linear models (GLM; Venables & 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. The general model structure was

$$\log(\mu_i) = \alpha + \beta_y y_i + \mathbf{XB} + \log(A_i), \qquad (1)$$

where μ_i is the expected value of the index of abundance of sharks caught in the ith year (y_i), α is the intercept, β_y is a year-effect parameter or instantaneous rate of change of μ_i over time, $\mathbf{X}$ is the matrix of covariates affecting the variability of μ_i, $\mathbf{B}$ is 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 & 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. With fixed-effects meta-analysis, it is assumed that k local estimates of β_y are realizations of a normally distributed population of estimates,

$$\beta_{yi} \sim N(\bar{\beta}_y, s^2). \qquad (2)$$

The mean $\bar{\beta}_{y\bullet}$ is

$$\bar{\beta}_{y\bullet} = \frac{\sum w_i \beta_{yi}}{\sum w_i}, \tag{3}$$

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

$$s^2 = \frac{1}{\sum 1/s_i^2}. \tag{4}$$

This means that each local estimate predicts a common instantaneous rate of change across all regions, in other words, statistically $\beta_{y1} = \beta_{y2} = \cdots = \beta_{yk}$ (Cooper & Hedges 1994). Nevertheless, for our data, this may not be true because time periods and habitats investigated were quite different. It was more reasonable 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 20th 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. We therefore assumed that each local estimate β_{yi} was a realization of a normal distribution of region-specific estimates with mean $\bar{\beta}_{yi}$ and variance s_i^2 :

$$\beta_{yi} \sim N\left(\bar{\beta}_{yi}, s_i^2\right). \tag{5}$$

Then, each "study-specific" mean was assumed to be a draw of a superpopulation of parameters with mean, $\bar{\beta}_{y\bullet}$ and variance τ^2. Hence, all k β_{yi} were normally distributed with mean $\bar{\beta}_{y\bullet}$ and variance $s^2 = s_i^2 + \tau^2$. These are called hyperparameters 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,

$$Q = \sum w_i \beta_{yi}^2 - \frac{\left(\sum w_i \beta_{yi}\right)^2}{\sum w_i}. \tag{6}$$

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 than 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 hyperparameter of interest as follows: $s_i^{2^*} = s_i^{2^*} + s_r^{2^*}$, where

$$s_r^2 = \frac{Q-(k-1)}{\sum w_i - \frac{\sum w_i^2}{\sum w_i}} \quad \text{(Cooper \& Hedges 1994; Worm \& Myers 2003)}. \tag{7}$$

Thus, we used this new adjusted version of s_i^2 in Eq. 4. We performed separate meta-analyses for landed biomass and landed numbers of sharks.

Results

Of 20 species of large sharks that occur in the Mediterranean basin (Table 1), we could assess only 5: 2 mackerel sharks (*I. oxyrinchus* and *Lamna nasus*), 1 requiem shark (*Prionace glauca*), 1 hammerhead shark (*Sphyrna zygaena*), and 1 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).

Of the species investigated hammerhead sharks (*Sphyrna* spp.) declined the fastest. In the early 1900s declines were detected in coastal waters, where catches and sightings were regular, although not common (Fig. 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. 3 & 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 translated into an estimated species decline of >99.99% in both cases.

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) starting in 1950 showed the highest rate of decline in abundance, >99.99% (Table 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. 3). There were no blue shark records in the tuna trap of Baratti (Tyrrhenian Sea, data set 2; Table 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 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. 3 & 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 Spanish waters,

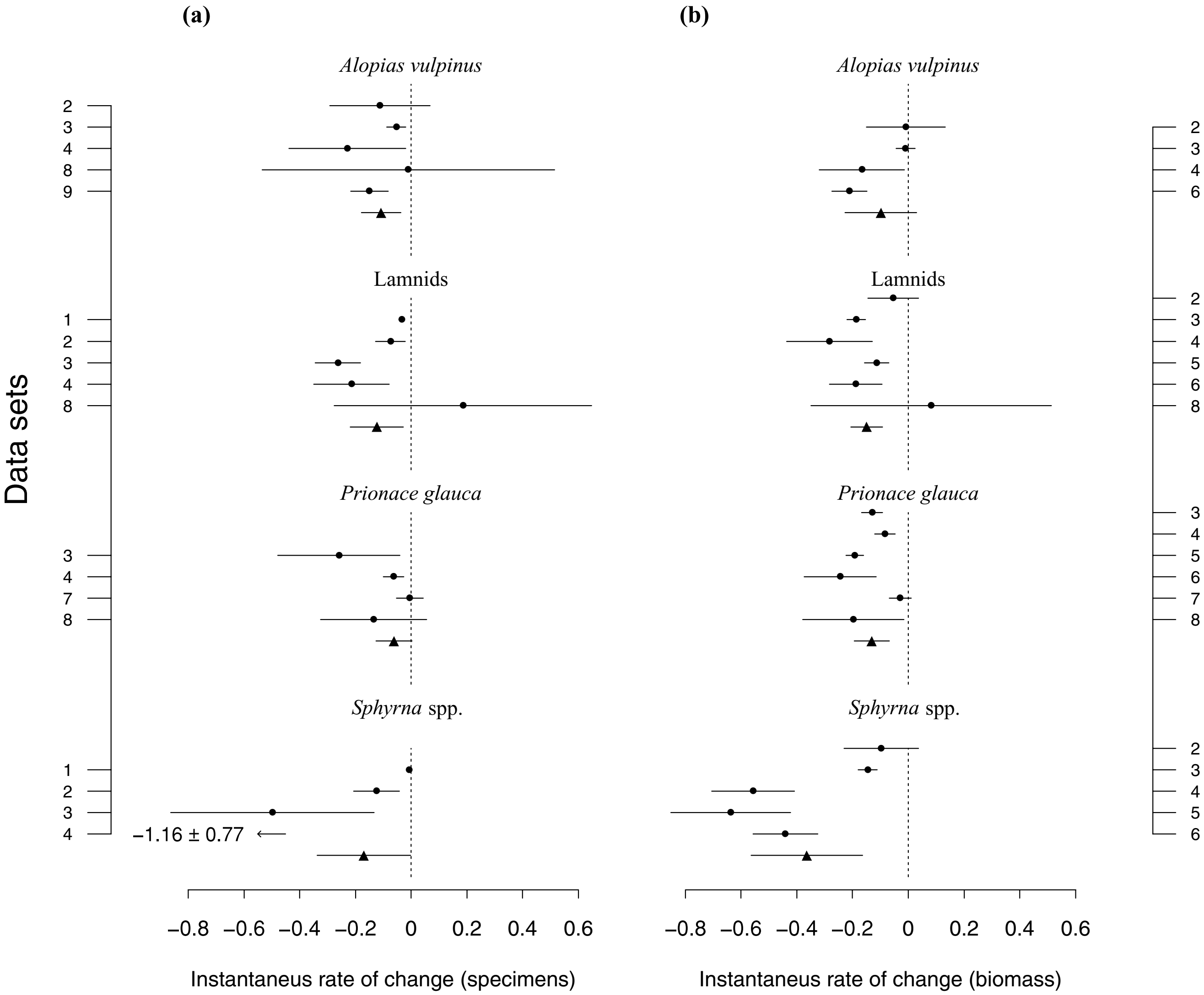

Figure 2. Meta-analysis of instantaneous rates of change in shark population abundance over time. Year-effect estimates for models fitted on (a) landed number of specimens and (b) landed biomass data. Dots are local estimates; triangles are meta-analytical averages over regions; numbers refer to data sets (see Table 2).

biomass declined by 99.78% in 25 years (Table 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 were 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. 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 (*A. 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),

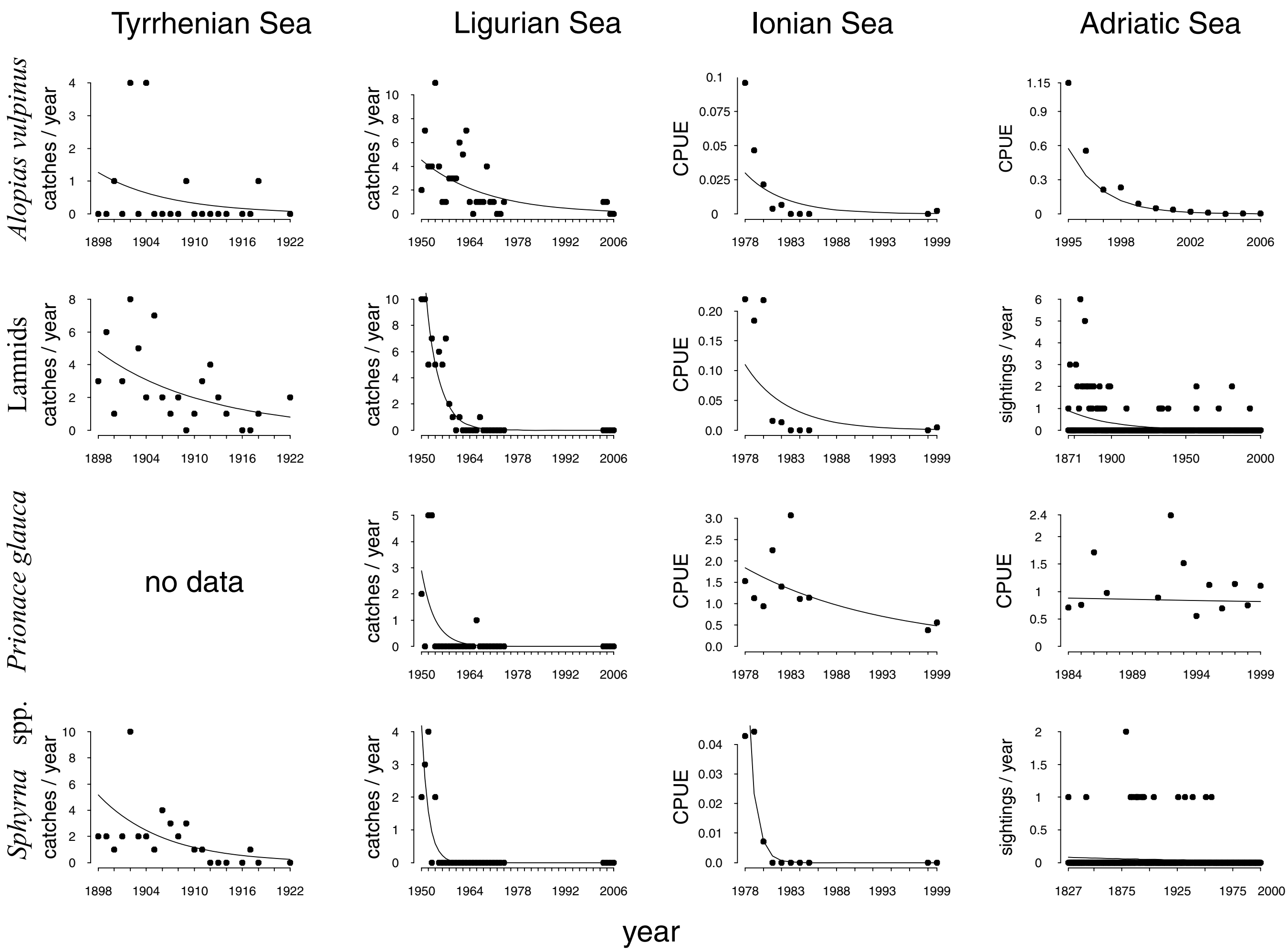

*Figure 3. Trends in shark population abundance in the Mediterranean Sea. Dots represent standardized annual catches or annual sightings. Catch per unit effort (CPUE) for the Ionian and Adriatic (*Prionace glauca*) seas refer to sharks landed per 1000 hooks of fishing efforts, whereas CPUE for* Alopias 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).*

although the decline in biomass was not statistically significant (Fig. 2).

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 we modeled, these results may be indicative of a broader trend across the Mediterranean Sea.

Many historical records show the Mediterranean Sea as having an abundance of large sharks. Sharks were considered a pest by fishers (Marchesetti 1884; 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 (Rodriguez Santamaria 1923; Piaggio 1927; Arcidiacono 1931; D'Ancona & Razzauti 1937; Cannaviello 1942). For example, in the Tuscan Archipelago alone, there were about 51 shark gill nets (bestinare and angel shark nets), 48 fish traps (similar to the one we analyzed in Baratti, data set 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 20th century (Fig. 3).

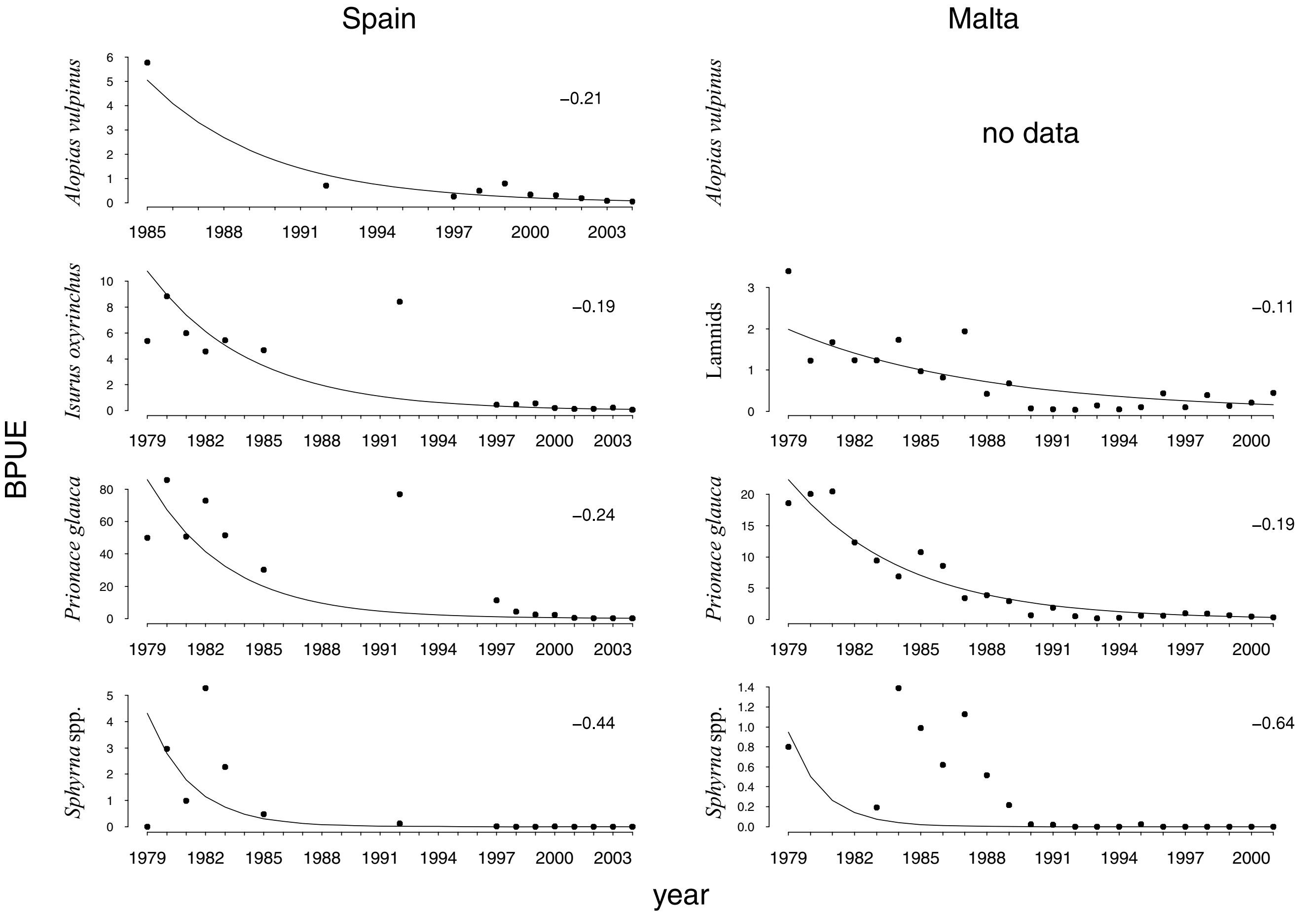

Figure 4. Trends in shark biomass (kg) in the western and central Mediterranean Sea. Dots are landed biomass per unit effort (BPUE). Biomass is expressed for Spain as kilograms per 1000 hooks and for Malta as kilograms per unit of gross tonnage (tons). Numbers on the right side of each plot are instantaneous rate of change in biomass.

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 bycatch in historical fisheries (Russo 1928; D'Ancona & 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 northwestern Atlantic and Gulf of Mexico, where requiem sharks are still being caught, albeit in much reduced numbers (Baum et al. 2003; Baum & Myers 2004; Shepherd & 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 the considered sharks collapsed. In this period, drift netters and longliners began targeting tuna and swordfish, and sharks were regular bycatch (Silvani et al. 1999; Megalofonou et al. 2005; Tudela 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 fishing with pelagic longlines in the Mediterranean (Supplementary Material). Furthermore, a substantial illegal, unregistered, and unregulated fishing effort is thought 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 (Supplementary Material). Specifically, around the Strait of Gibraltar, a critical migration corridor for many pelagic species, Spain deploys most of its pelagic longlines and recently broadened its target on the Atlantic side to include *I. oxyrinchus* and *P. glauca* (Mejuto & de la Serna 2000). Such patterns of fishing

Table 3. Summary of estimated local change in population abundance and biomass and associated confidence intervals for the analyzed sharks over the considered time intervals.*

Population factor and group	*Area*	*Time range (year)*	*Abundance estimate (%)*	*Lower Wald CI*	*Upper Wald CI*	*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
	Ligurian Sea	8	−7.76	−98.61	60.26	8
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	−65.80	−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						
A. vulpinus	Spanish waters	19	−98.20	−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	2287.00	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	−77.70	5
	Tyrrhenian Sea	24	−72.90	−96.95	140.00	2
	Ligurian Sea	8	91.78	−93.92	5953.00	8
P. 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	−92.10	−63.35	4
	Ligurian Sea	8	−79.48	−95.20	−12.30	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	140.00	2

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.

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 20th century and in the Ligurian Sea since the 1950s (Fig. 3), but were still detected in pelagic fisheries in the second half of the 20th 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. 3 & 4); they exhibited the highest rates of population decline among all the species we analyzed (Fig. 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, stenothermic, and stenobathial shark that, compared with other lamnids, exhibits limited migration behavior with few exchanges between adjacent populations (Stevens et al. 2006). 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 nonsignificant 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 2 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 longline fishing 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. 3), but trends in other species remained uncertain, such as for *P. glauca*, for which we had no quantitative information on pelagic bycatch 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 & 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 & Myers 2004), but similar to the northwestern 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 the northwestern Atlantic, fishery-dependent and fishery-independent data showed substantial catches of 9 groups of large coastal and pelagic sharks (Simpfendorer et al. 2002; Baum et al. 2003, for a total of 18 species). In the Gulf of Mexico, Baum and Myers (2004) could analyze 11 groups of 14 species. For the Mediterranean, because there were so few species to be analyzed, this 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), 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 & 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 & Powers 2005; Reeves & Notorbartolo 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. 2008). Losing top predators can induce strong increases in midlevel consumers, shifts in species interactions, and trophic cascades (Estes et al. 1998; Pace et al. 1999; Worm & 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 & Myers 2004; Shepherd & 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.

Acknowledgments

We are grateful to W. Blanchard for statistical advice; F. Boero, B. Worm, G. Fitzgerald, L. Lucifora, V. Garcia, A. Rosenberg, and C. Osio for comments and discussion; F. Micheli and 2 anonymous reviewers for their helpful comments; and A. Rosetti, A. Mariotti, S. Bersanetti, L. Lasi, and T. Schembri for help with data gathering. Financial support was provided by the Pew Foundation's Global Shark Assessment, the Lenfest Ocean Program, the Oak Foundation, and the Future of Marine Animal Populations Program of the Census of Marine Life.

Supplementary Material

A detailed description of data sets 1–9 including original references and a map showing fishing effort registered in ICCAT referred to in the discussion are available as part of the on-line article from http://www.blackwell-synergy.com/ (Appendix S1). The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Arcidiacono, F. 1931. La pesca del pesce vacca (*Hexanchus griseus* L.) nella marina di Riposto. Bollettino di Pesca, Piscicoltura e Idrobiologia **7:**608–612.

Bascompte, J., C. J. Melián, and E. Sala. 2005. Interaction strength combinations and the overfishing of a marine food web. Proceedings of the National Academy of Sciences of the United States of America **102:**5443–5447.

Başusta, 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. Turkish Marine Research Foundation, Istanbul.

Baum, J. K., and R. A. Myers. 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. Ecology Letters **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.

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. Aquatic Conservation: Marine and Freshwater Ecosystems **14:**363–379.

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). Biologia Marina Mediterranea **7:**385–399.

Biagi, V. 1999. Memorie della Tonnara di Baratti. 2nd edition. Circolo Nautico e Pesca Sportiva di Baratti, Baratti, Italy.

Boero, F., and A. Carli. 1979. Catture di elasmobranchi nella tonnarella di Camogli (Genova) dal 1950 al 1974. Bollettino dei Musei e degli Istituti Biologici della Regia Università di Genova **47:**27–34.

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. Fishery Bulletin **96:**667–685.

Cannaviello, E. 1942. Calendario delle pesche del golfo di Napoli. Bollettino di Pesca, Piscicoltura e Idrobiologia **18:**23–85.

Castro, J., J. M. de la Serna, D. Macías, and J. Mejuto. 2000. Estimaciones cientifícas preliminares de los desembarcos de especies associadas realizados por la flota Española de palangre de superficie en 1997 y 1998. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers **51:**1882–1893.

Cavanagh, R. D., 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.

Cooper, H., and L. V. Hedges. 1994. The handbook of research synthesis. Russell Sage Foundation, New York.

Cortés, E. 1999. Standardized diet compositions and trophic levels of sharks. ICES Journal of Marine Science **56:**707–717.

D'Ancona, U., and A. Razzauti. 1937. Pesci e pesca nelle acque dell'Arcipelago Toscano. Rapport de la Commission International Exploration de la Mer Méditerranée **11:**129–144.

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

De Zio, V., A. Pastorelli, and L. Rositani. 2000. Catture accessorie di *Prionace glauca* (L.) durante la pesca dei grandi pelagici nel basso Adriatico (1984-1998). Biologia Marina Mediterranea **7:**444–446.

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

FAO (Food and Agriculture Organization). 2005. Review of the state of world marine resources. Fisheries technical paper 457. Fishery Resource Division, FAO, Rome.

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

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.

Foresi, S. 1939. Pesci, Pesca e Pescatori nel mare dell'Elba. Tipografia Popolare, Portoferraio, Italy.

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

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

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

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. Biologia Marina Mediterranea **7:**324–333.

Graham, K. J., N. L. Andrew, and K. E. Hodgson. 2001. Changes in relative abundance of sharks and rays on Australian south east fishery trawl grounds after twenty years of fishing. Marine and Freshwater Research **52:**549–561.

Heithaus, M. R., A. Frid, A. J. Wirsing, and B. Worm. 2008. Predicting ecological consequences of marine top predator declines. Trends in Ecology & Evolution **23:**202–210.

IUCN (World Conservation Union). 2001. IUCN red list categories and criteria: version 3.1. IUCN, Gland, Switzerland, and Cambridge, United Kingdom.

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. B. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science **312:**1806–1809.

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

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

Marchesetti, C. 1884. La pesca lungo le coste orientali dell'Adria. Atti del Museo Civico di Storia Naturale, Trieste **7:**1–234.

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 DG XIV/C1. Community of Mediterranean Universities, Bari, Italy.

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. Fishery Bulletin **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. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers **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. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers **59:**1014–1024.

Musick, J. A., M. M. Harbin, and L. J. V. Compagno. 2004. Historical zoogeography of the Selachii. Pages 33–78 in J. C. Carrier, J. A. Musick, and M. R. Heithaus, editors. Biology of sharks and their relatives. CRC Press, Boca Raton, Florida.

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. Philosophical Transactions of the Royal Society B: Biological Sciences **360:**13–20.

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.

Ninni, E. 1923. Primo contributo allo studio dei pesci e della pesca dell'impero Ottomanno. Premiate officine grafiche Carlo Ferrari, Venezia, Italy.

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

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

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

Parona, C. 1898. La pesca marittima in Liguria. Atti della Società Ligustica di Scienze Naturali e Geografiche **9:**1–69.

Piaggio, C. 1927. Metodi ed usi di pesca nelle acque del circondario marittimo di Santa Margerita Ligure. Bollettino di Pesca, Piscicoltura e Idrobiologia **3:**3–41.

Reeves, R., and G. Notarbartolo di Sciara. 2006. The status and distribution of cetaceans in the Black Sea and Mediterranean Sea. World Conservation Union, Centre for Mediterranean Cooperation, Malaga, Spain.

Relini, G., et al. 2000. I selaci pescati con lo strascico nei mari Italiani. Biologia Marina Mediterranea **7:**347–384.

Rey, J., and E. Alot. 1984. Contribution al estudio de la pesqueria de palangre del pez espada (*Xiphias gladius*) en el Mediterraneo occidental. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers **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. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers **26:**402–408.

Rodriguez Santamaria, B. 1923. Diccionario de artes de pesca de España y sus posesiones. Sucesores de Rivadeneyra, Madrid.

Russo, A. 1928. Studi sulla pesca nel Golfo di Catania. Bollettino di Pesca, Piscicoltura e Idrobiologia **4:**495–543.

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.

SGFEN/STECF (Scientific, Technical and Economic Committee for Fisheries). 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. EC, Brussels.

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

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

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. Fisheries Research **55:**175–192.

Soldo, A., and I. Jardas. 2002. Large sharks in the eastern Adriatic. Pages 141–155 in M. Vacchi, G. La Mesa, F. Serena, and Séret, editors. Proceedings of the 4th European elasmobranch association meeting, ICRAM, ARPAT & SFI, Livorno, Italy.

Soldo, A., and R. Pierce. 2005. Shark chumming in the eastern Adriatic. Annales, Series Historia Naturalis **15:**203–208.

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 Journal of Marine Science **57:**476–494.

Stevens, J. D., S. L. Fowler, A. Soldo, M. McCord, J. K. Baum, E. Acuña, and A. Domingo. 2006. *Lamna nasus* (Mediterranean subpopulation). 2007 IUCN red list of threatened species. World Conservation Union, Gland, Switzerland. Available from http://www.iucnredlist.org/search/details.php/61420/all (accessed April 2007).

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 no. 74. General Fisheries Commission for the Mediterranean, Food and Agriculture Organization, Rome.

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). Biological Conservation **121:**65–78.

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. International Commission for the Conservation of Atlantic Tunas. Collective Volume of Scientific Papers **5:**149–153.

Venables, W. N., and B. D. Ripley. 2001. Modern applied statistics with S-Plus. 3rd edition. Springer-Verlag, New York.

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 (World Wildlife Fund). 2006. The plunder of bluefin tuna in the Mediterranean and East Atlantic in 2004 and 2005. Uncovering the real story. WWF Mediterranean Program Office, Rome. Available from http://assets.panda.org/downloads/wwfbftreport finaleditionreducido_final.pdf (accessed November 2007).