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

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1 Abstract

Shark and ray populations appear to be extremely vulnerable to fishing pressure. In this paper, we investigated the dynamics of elasmobranch populations of the upper Tyrrhenian Sea over more than a century by analyzing data from commercial landings of fish traps, literature records and scientific trawl surveys. These data were integrated using generalized linear models, in which the change in abundance as well as depth distribution was modelled for each species. Of 36 species recognized to inhabit the coastal water of the investigated area in the 20^{th} century 17 have declined in abundance to undetectable levels in all depths. Others are still fished at deeper grounds, but even there they show signs of depletion due to fishing pressure. This paper analyzes a small sector of the Mediterranean Sea, but its results appear to agree with other investigations in the basin. We believe the magnitude of depletion of the elasmobranch community in the whole Mediterranean region be largely underestimated and require an immediate large scale reassessment to prevent multiple cases of local extinctions.

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2 Introduction

Elasmobranchs are declining worldwide because of fishing[14, 24, 8, 28]. In many parts of the world, even with relatively short periods of exploitation, elasmobranch populations have been greatly reduced. 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[13]. 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[17]. 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)[25, 9] 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[13] 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[26]. The IUCN has declared that 30% are data deficient, and roughly 70% require more thorough monitoring[1]. 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[3, 18].

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 by using 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 normal distributed. Normality is usually a weak assumption in fisheries, 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 [16]. Under this assumption the variance of the catches V is correlated to their mean μ by a quadratic function

$$V = \mu + \frac{\mu^2}{k} \tag{1}$$

where $1/k$ is a measure of population aggregation. Although the applicability of this parameter to all species at all densities has been questioned[30], shark species have been well fit by this approach[7, 8, 24, 28]. This paper is the first attempt to utilize the GRUND data in a generalized linear model framework.

2.1 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. Although the 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[4].

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[20, 22].

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 [22]. 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[5].

3 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[10]. 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 arrays 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[10, 32]. 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

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

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

$$\eta = log(\mu_i) = \beta_0 + \beta_y y_i \tag{3}$$

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. 2). 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[25]. 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. We modelled the chance of obtaining a number of specimens C_i in each tow$_i$ (eqn. 2), such that the linear predictor η is related to the mean μ_i by a log link function

$$\eta = log(\mu_i) = \beta_0 + \beta_y y_i + \beta_d d_i + \beta_{sj} S_{ji} + \beta_{zj} Z_{ji} + log(A_i) \tag{4}$$

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$_i$ where 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[19, 33]. 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

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 1: Summary of the Akiake Information Criterion comparing the linear model of eqn. 4 with the quadratic model of eqn. 5

or a related species from analyses performed by Shepherd and Myers in the Gulf of Mexico[28](Appendix 1-2).

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[3, 21, 18, 31].

4 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.9). 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. 9). For these species, a quadratic model, in which the square of the year y_i was added to the original model in eqn. 3

$$\eta = log(\mu_i) = \beta_0 + \beta_y y_i + \beta_y (y_i)^2 \tag{5}$$

gave a better fit (table 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 levels of statistical significance for their slope (p=0.05) (Fig. 10).

31 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. 6). 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). 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.6).

In the deep strata, we estimated trends in abundance for 22 species. 16 of them showed significant negative trends (fig. 5), 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 til 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[12, 10]. 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 by reducing its abundance by 91.07% (CI: 95.68% to 81.60%).

As *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*).

To attempt to explain for 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 parameter 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 correlation 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 (table 2). We expressed the lateness in maturity as the ratio between the female size at first maturity and the reported maximum length of the species. It appears that extremely vulnerable species are those that reach sexual maturity late in their life, while species that are relatively resistant, mature in earlier stages (fig. 1).

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 strata, sharks whose gradient of abundance over depth was steeper, declined faster than shark species more evenly distributed across depths (fig. 7). 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).

5 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 4). 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* [12], 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[32] 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[12]. 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. Cannibalism is a frequent behavior of many large sharks. For some species, adults constitutes the principal predators of juvenile specimens[15]. 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[11]. 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. *Squalus blainville* is increasing in coastal waters but shows negative trend in abundance offshore. This species could still suffer fishing pressure, interspecific competition and predation by populations still present in deep waters. This may also be true for *Dipturus oxyrhincus*, a large skate with a possibly high catchability, which is increasing in shallow water and declining in deep 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 surely play a major role on the vulnerability and sensitivity of species to increased fishing mortality. We detected an inverse relationship between the lateness in maturity and the year effect parameters of the change in abundance over time. More simply, all the species we lost in the area were relatively larger than those still present. However we can not find the same correlation for the relative response to fishing in the remaining species. We also could not detect statistically significant correlation between rate of change and age at maturity and depth range as well. Problem in parameter availability for many species and the restrictiveness of the analyzed data-set make it difficult to test these hypothesis.

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 appear 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 wrongly recognize 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 all misidentification of *Raja polystigma*[27]. Although we performed our analyses by relying on the data-set we had, since we don't have any evidence or test of this misidentifications, to look for eventual 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. The species that could 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 gear[2], 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[34]. Graham and coauthors in 2001, by comparing relative abundance of demersal sharks in the continental shelf and upper slope of NSW, 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[14].

The plot in fig.7 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 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 the exploitations.

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 [23, 2]. 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.

6 Conclusions

For managerial purposes finding clear patterns in multispecies fishery is a top requirement for preserving the functioning of the system and avoiding unexpected decreases in the profits. It is necessary to recognize the important components of the marine community and work on these to allow a long-term exploitation of its resources. To date it is still not clear what the role of sharks is in the marine community[29], whether or not as top predators they contribute to its structuring, through top down control effects. Recent results from food web model analyses, indicate that sharks depletion could play an important role in ecosystem shifts by triggering trophic cascades[6].

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 considered occasional and rare in the zone were instead abundant in the last century. 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 sector of the basin (Gulf of Lion and Adriatic sea)[3, 18], 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.

7 Acknowledgments

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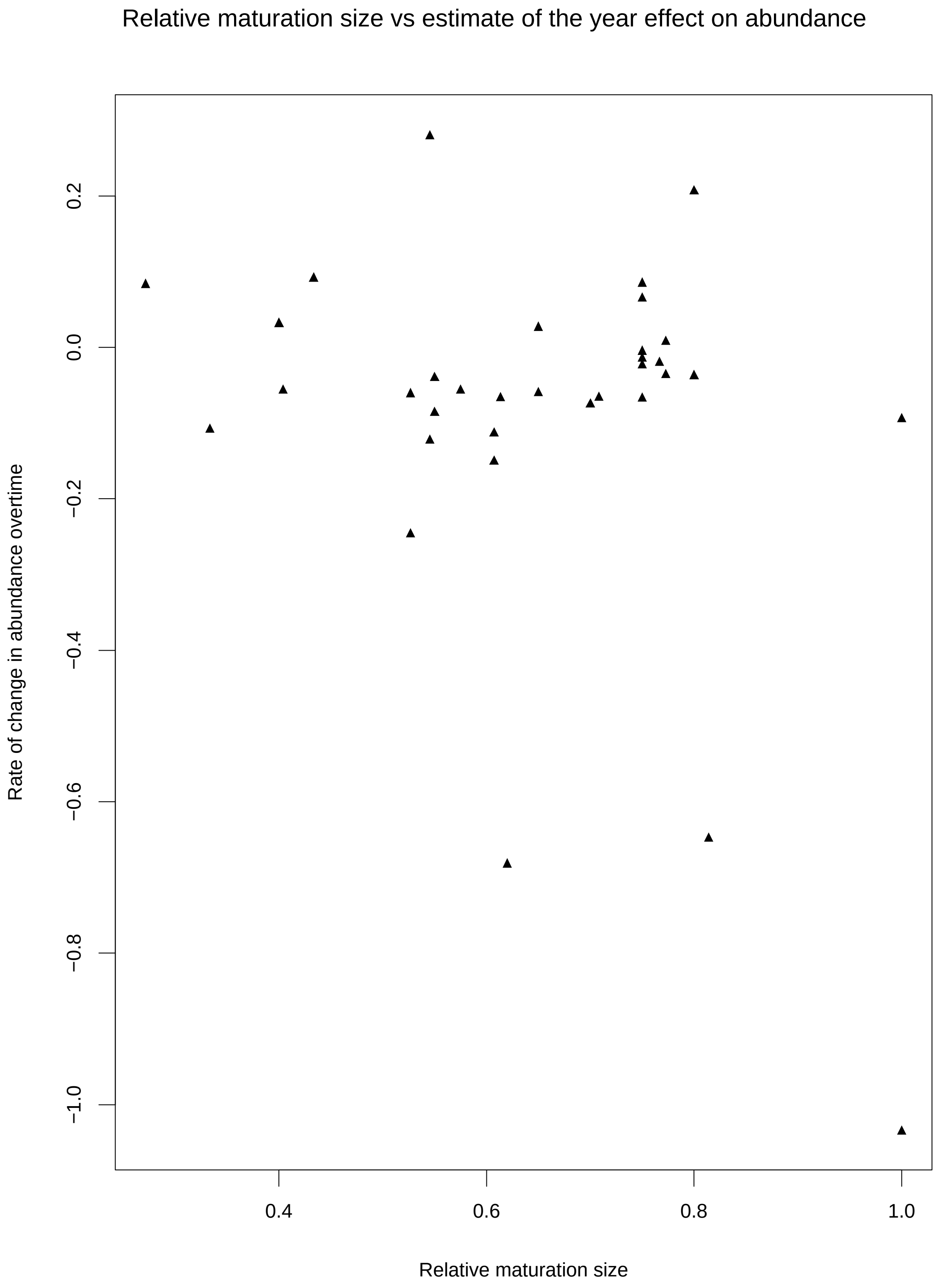

Figure 1: Weighted regression analysis between rate of change in abundance over time and the ratio between the female size at maturity and the maximum total size of the species.

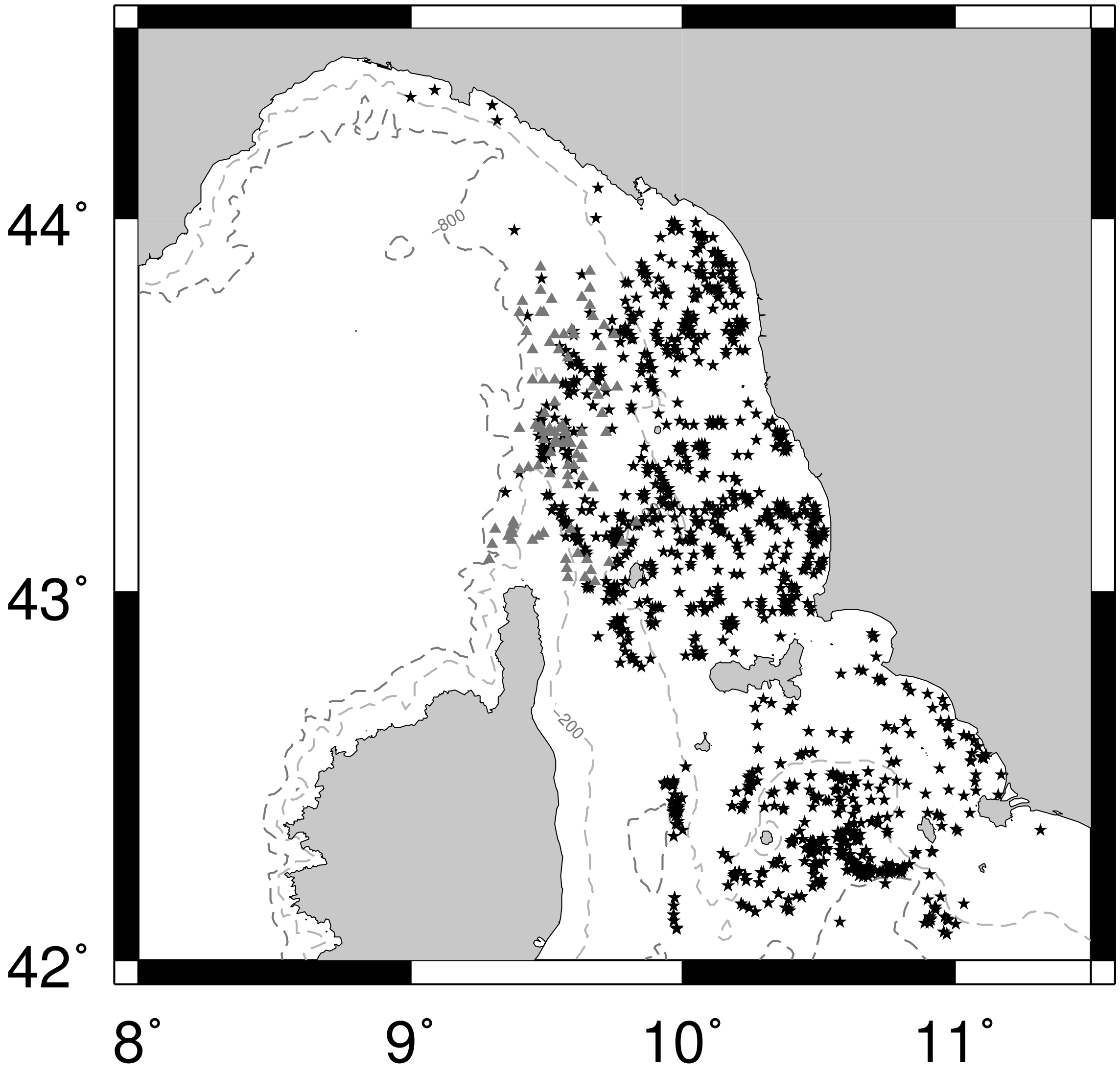

Figure 2: Map of the tows used as source of data in the investigated area. Triangles refer to the seventies surveys, stars refer to the GRUND surveys

Variable	DF	Estimate	St.Err	t value	Pr $>\lvert t\rvert$	R-Square
Intercept	1	0.399	0.228	1.75	0.0897	0.2215
L_{mf}/L_{max}	1	-1.007	0.329	-3.06	0.0043	

Table 2: Summary of the weighted regression analysis between the female lateness in maturity and the rate of change in abundance. L_{mf} is the size of females at first maturity , L_{max} is the maximum size. We expressed the ratio between these two parameters as the lateness in maturity of the species

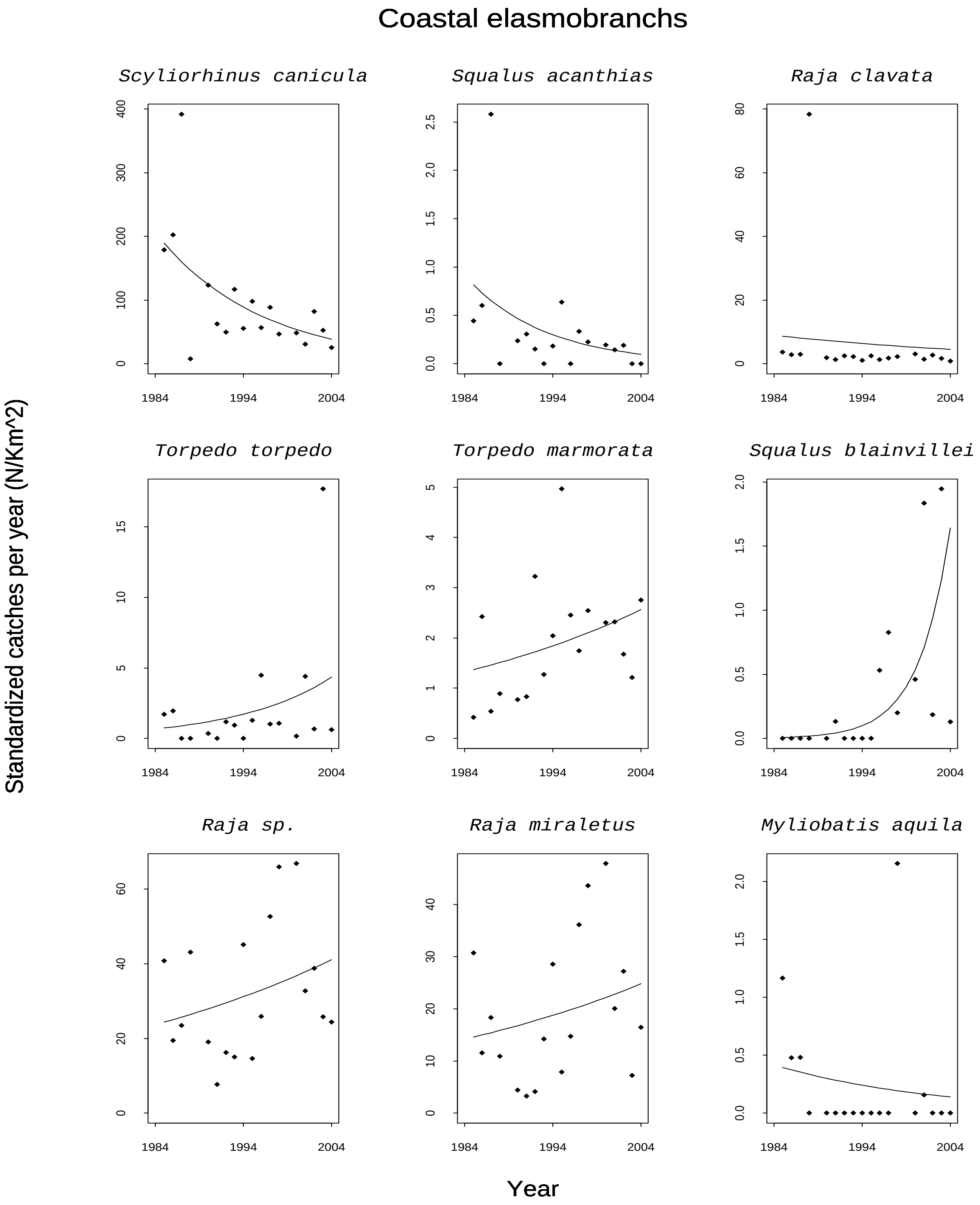

Figure 3: Variation in abundance of 9 coastal elasmobranch species. The models consider only the GRUND data series (1985-2004). The points refer to the yearly mean of the standardized catches in number of sharks per square kilometer.

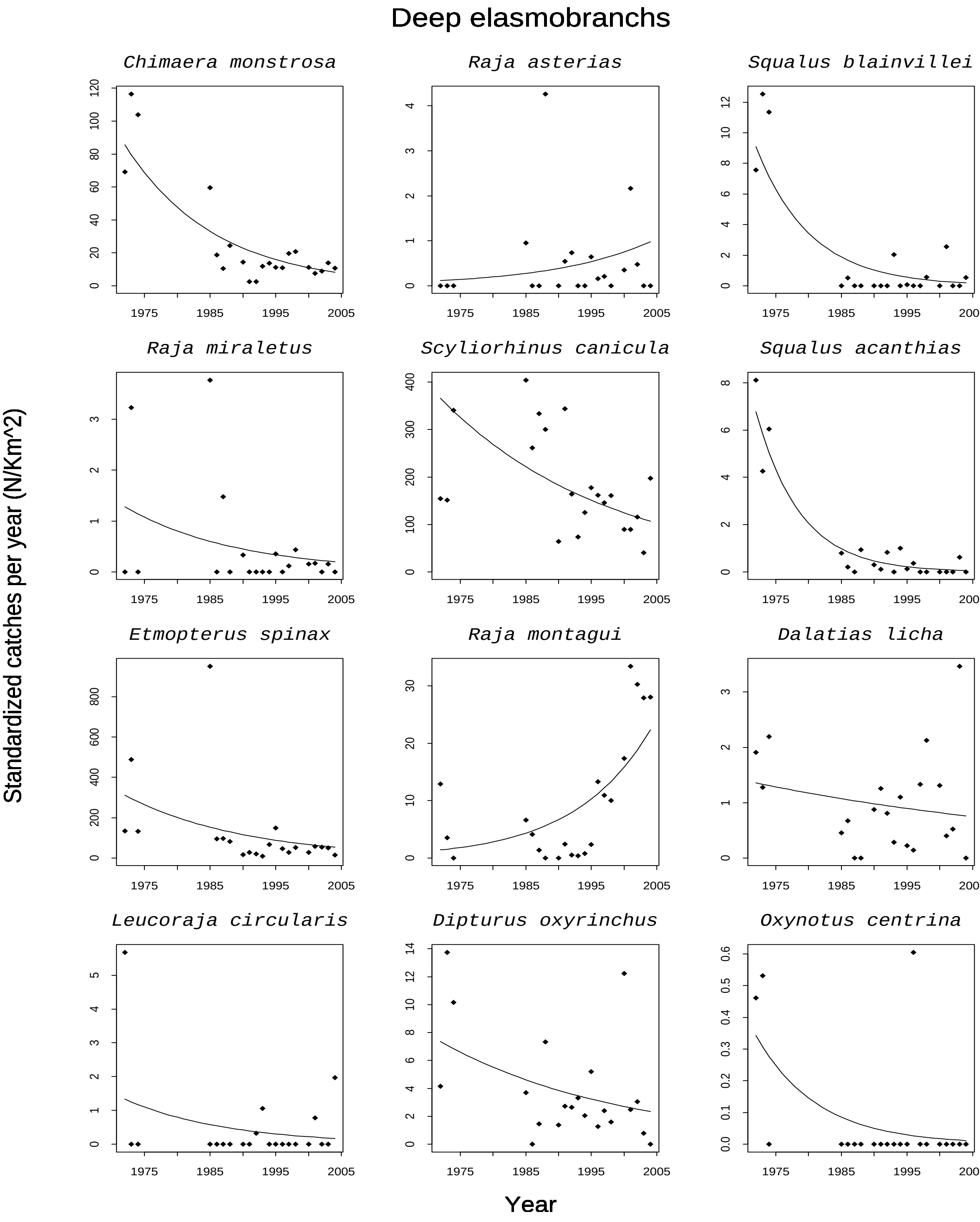

Figure 4: Variation in abundance of twelve elasmobranchs occurring in the deep strata. The models consider the whole data series coming from trawl surveys from 1972 to 2004. Points refer to the yearly mean of standardized catches in number of sharks per square kilometer.

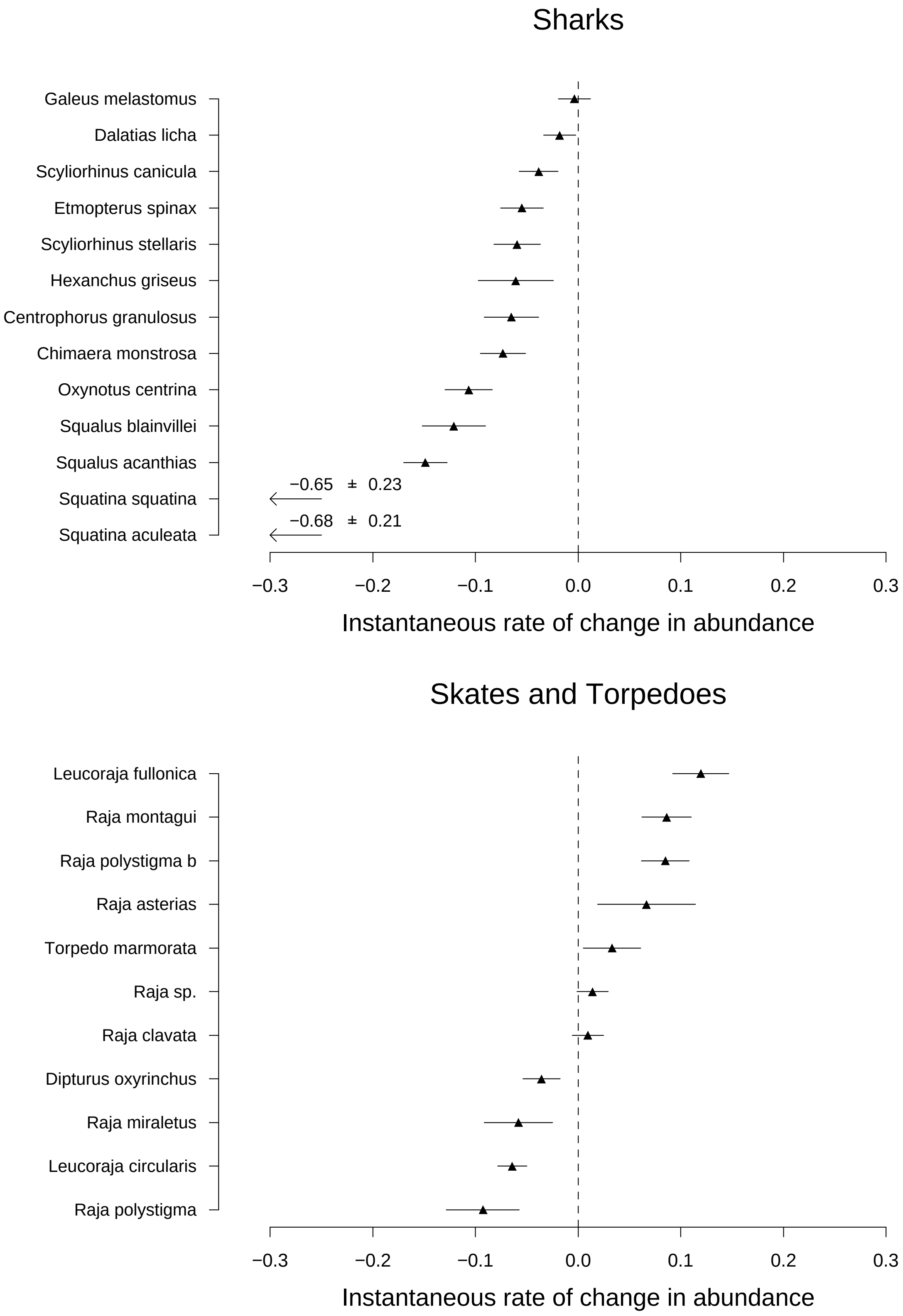

Figure 5: Instantaneus rate of change in abundance for elasmobranch species occurring in depths between 200 and 800 meters. The segments refer to the 95% Wald confidence intervals of the parameter estimates for the year effect.

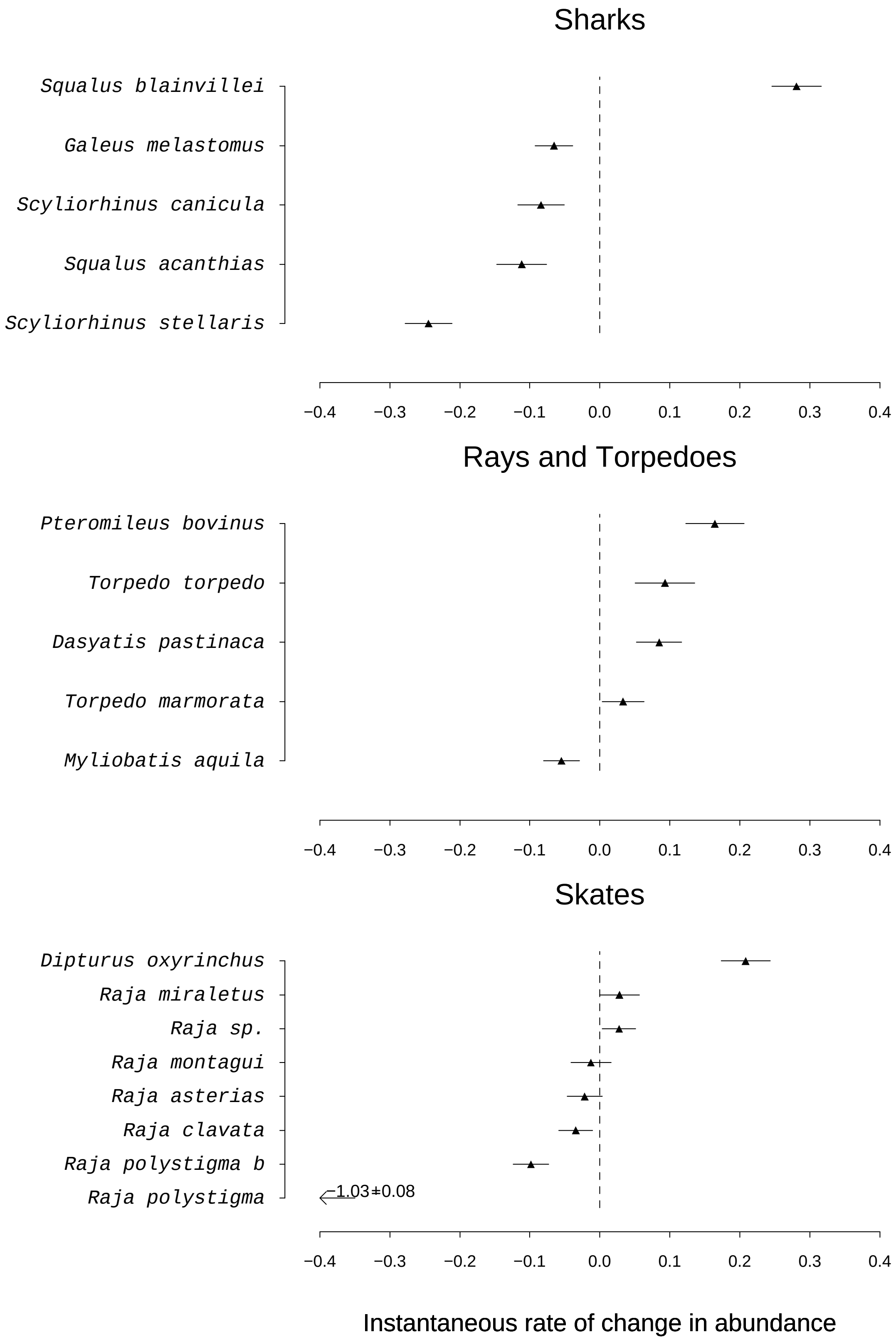

Figure 6: Instantaneous rate of change in abundance for elasmobranch species occurring in depths between 0 and 200 meters. The segments refer to the 95% Wald confidence intervals of the parameter estimates for the year effect.

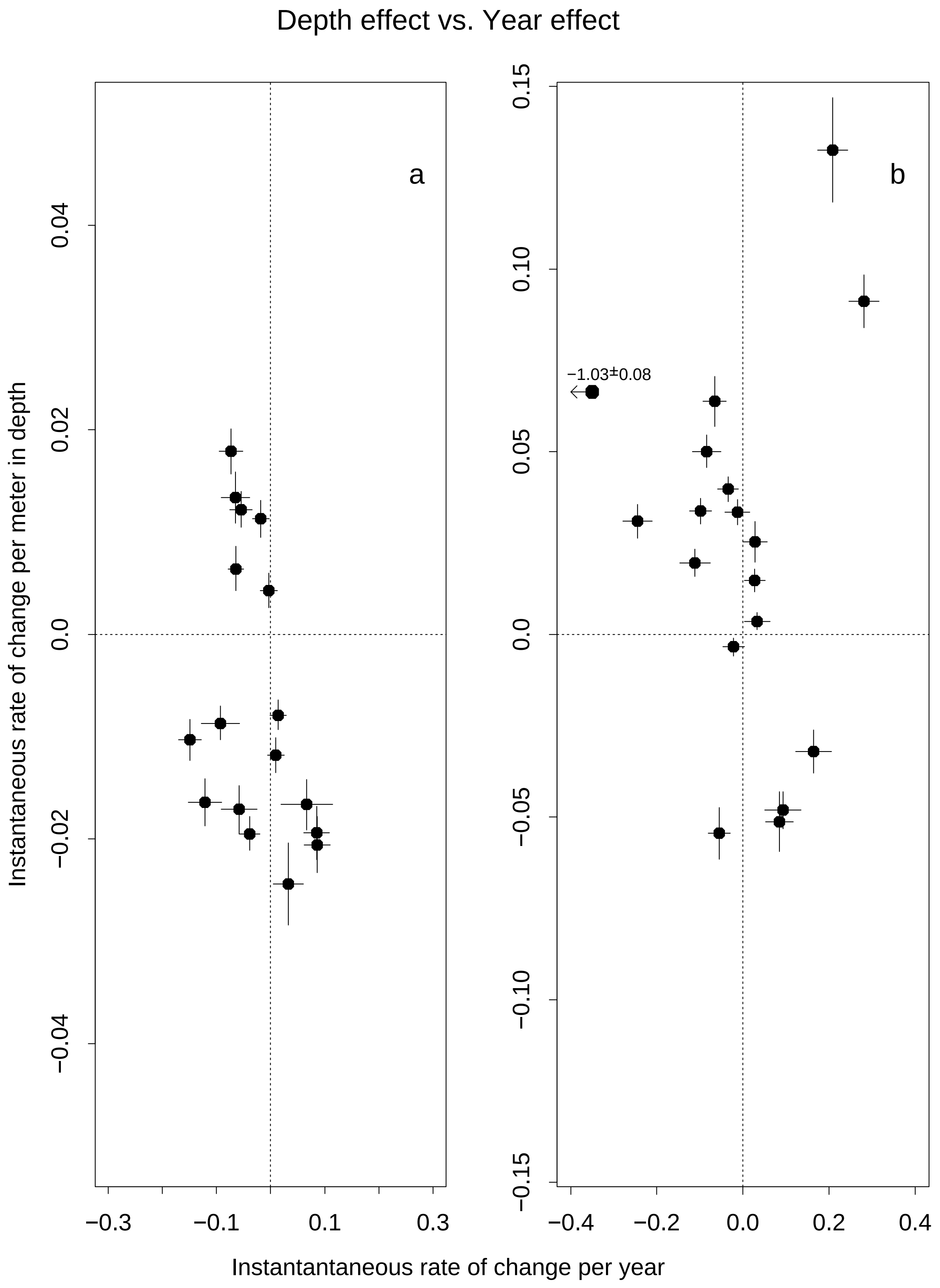

Figure 7: Rates of change in abundance per meter plotted against rates of change per year. Vertical and horizontal segments show the 95% confidence interval of the relative rates. In (a) points refer to deep water species, in (b) points refer to species occurring in shallow waters

Variable	DF	Estimate	St.Err	t value	Pr >$\lvert t\rvert$	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: 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).

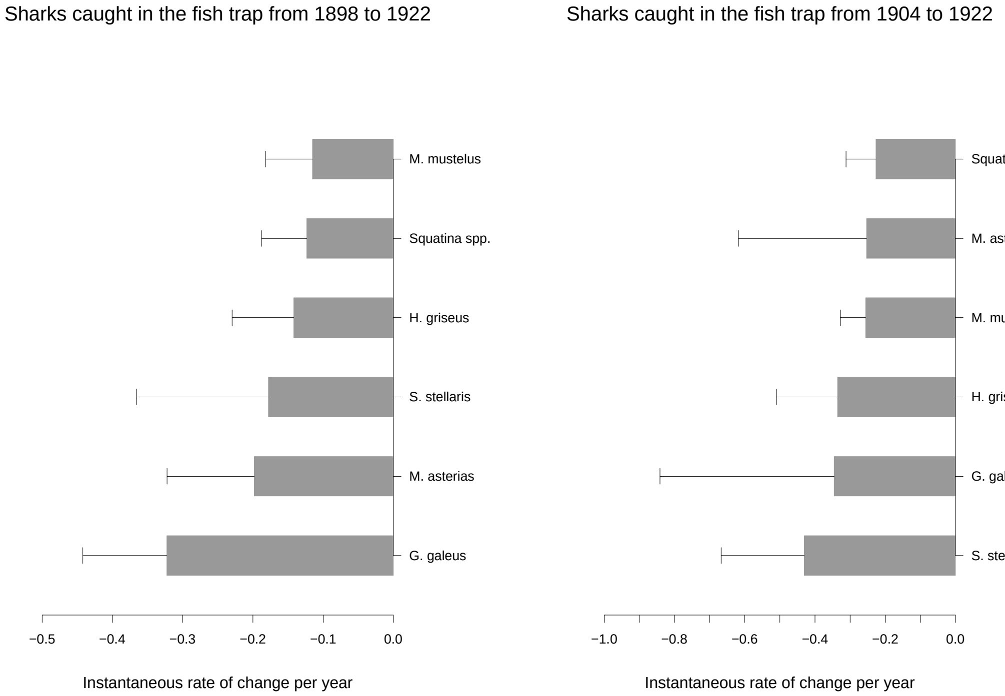

Figure 8: Rates of change in abundance per year of six demersal elasmobranchs occurring in the fish trap of Baratti. The horizontal segments at the end of the bars correspond to the 95% confidence interval of the relative rates.

<table>
<tr><th>Species</th><th>Max size (cm)</th><th>Coastal waters</th><th>Deep waters</th><th>Mediterranean official status</th></tr>
<tr><td><i>Hexanchus griseus</i></td><td>500</td><td>absent</td><td>decline</td><td>vulnerable species</td></tr>
<tr><td><i>Dasyatis centroura</i></td><td>396</td><td colspan="2">absent</td><td>threatened species</td></tr>
<tr><td><i>Myliobatis aquila</i></td><td>260</td><td>decline</td><td>out of range</td><td>vulnerable species</td></tr>
<tr><td><i>Pteromylaeus bovinus</i></td><td>260</td><td>increase</td><td>out of range</td><td>threatened species</td></tr>
<tr><td><i>Dasyatis pastinaca</i></td><td>250</td><td>increase</td><td>out of range</td><td>vulnerable species</td></tr>
<tr><td><i>Dipturus batis</i></td><td>250</td><td colspan="2">absent</td><td>threatened species/locally disappeared</td></tr>
<tr><td><i>Galeorhinus galeus</i></td><td>200</td><td colspan="2">absent</td><td>vulnerable species</td></tr>
<tr><td><i>Rostroraja alba</i></td><td>200</td><td colspan="2">disappeared</td><td>vulnerable species</td></tr>
<tr><td><i>Squatina aculeata</i></td><td>200</td><td colspan="2">disappeared</td><td>threatened species</td></tr>
<tr><td><i>Squatina oculata</i></td><td>200</td><td colspan="2">absent</td><td>threatened species</td></tr>
<tr><td><i>Pteroplatytrygon violacea</i></td><td>190</td><td colspan="2">absent</td><td>vulnerable species</td></tr>
<tr><td><i>Dalatias licha</i></td><td>180</td><td>out of range</td><td>decline</td><td>vulnerable species</td></tr>
<tr><td><i>Mustelus punctulatus</i></td><td>180</td><td colspan="2">disappeared</td><td>vulnerable species</td></tr>
<tr><td><i>Squatina squatina</i></td><td>180</td><td colspan="2">disappeared</td><td>vulnerable species</td></tr>
<tr><td><i>Torpedo nobiliana</i></td><td>180</td><td colspan="2">disappeared</td><td>vulnerable species</td></tr>
<tr><td><i>Mustelus mustelus</i></td><td>160</td><td colspan="2">disappeared</td><td>vulnerable species</td></tr>
<tr><td><i>Centrophorus granulosus</i></td><td>150</td><td>absent</td><td>decline</td><td>vulnerable species</td></tr>
<tr><td><i>Dipturus oxyrinchus</i></td><td>150</td><td>increase</td><td>decline</td><td>vulnerable species</td></tr>
<tr><td><i>Oxynotus centrina</i></td><td>150</td><td>absent</td><td>disappeared</td><td>threatened species</td></tr>
<tr><td><i>Scyliorhinus stellaris</i></td><td>150</td><td>decline</td><td>decline</td><td>vulnerable species</td></tr>
<tr><td><i>Mustelus asterias</i></td><td>140</td><td colspan="2">absent</td><td>vulnerable species</td></tr>
<tr><td><i>Squalus acanthias</i></td><td>140</td><td>decline</td><td>decline</td><td>vulnerable species</td></tr>
<tr><td><i>Heptranchias perlo</i></td><td>138</td><td colspan="2">disappeared</td><td>threatened species</td></tr>
<tr><td><i>Raja brachyura</i></td><td>125</td><td colspan="2">absent</td><td>occasional/rare species</td></tr>
<tr><td><i>Leucoraja circularis</i></td><td>120</td><td>absent</td><td>decline</td><td>occasional/rare species</td></tr>
</table>

Species	Max size (cm)	Coastal waters	Deep waters	Mediterranean official status
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 4: Table showing the status of elasmobranch species observed in the investigated area since the beginning of the 20^{th} century. The term **absent** mean 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 [26]

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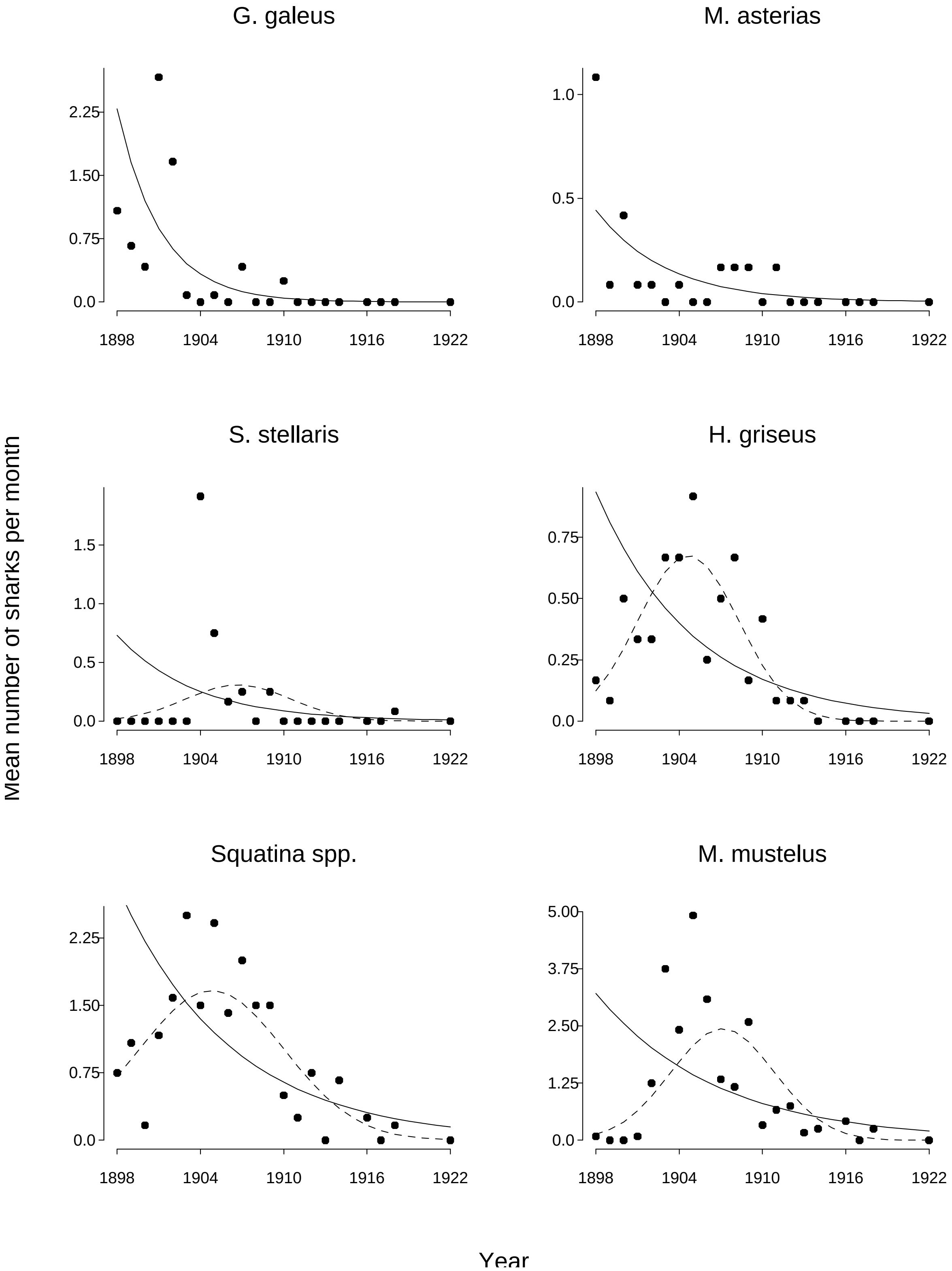

Figure 9: Estimated trends over time of the six demersal species of sharks occurred in the fish trap of Baratti from 1898 to 1922. Continuous lines represent the predicted values from the linear model; dotted lines represent the predicted values fom the quadratic model; points are the yearly means of the montly production for a given species.

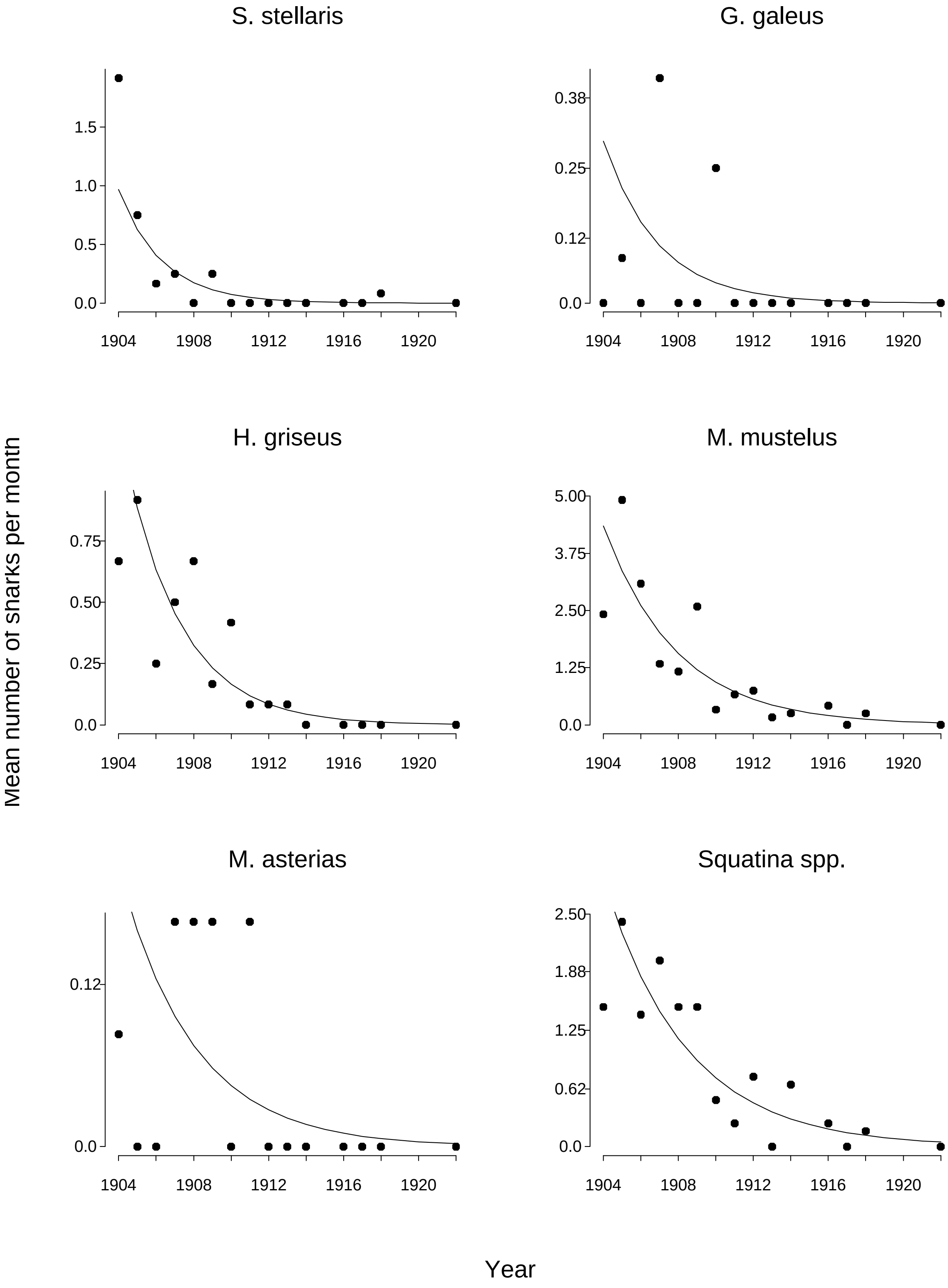

Figure 10: Estimated trends over time of the six demersal species of sharks occurred in the fish trap of Baratti from 1904 to 1922. Lines represent the estimated values of the linear model; points are the yearly means of the montly production for a given species.

Appendix 1

species	DF	Estimate	Level	Parameter	ChiSq	ProbChiSq	StdEr
S. canicula	1	165.1049		Intercept	23.79	<.0001	33.84
S. canicula	1	-0.0842		year	24.59	<.0001	0.01
S. canicula	1	0.0501		depth	485.59	<.0001	0.002
S. canicula	1	2.7815	uo2	uo	332.95	<.0001	0.152
S. canicula	0	0	uo3	uo	.	.	
S. canicula	1	-0.7789	fall	season	5.85	0.0155	0.321
S. canicula	1	-0.7213	spring	season	3.96	0.0466	0.362
S. canicula	1	-1.4693	summer	season	15.03	0.0001	0.37
S. canicula	0	0	winter	season	.	.	
S. canicula	1	4.2627		Dispersion			0.237
R. polystigma	1	2032.286		Intercept	609.69	<.0001	82.305
R. polystigma	1	-1.0337		year	618.49	<.0001	0.041
R. polystigma	1	0.0664		depth	503.36	<.0001	0.00
R. polystigma	1	8.4634	uo2	uo	520.92	<.0001	0.370
R. polystigma	0	0	uo3	uo	.	.	
R. polystigma	1	3.8555	fall	season	11.34	0.0008	1.144
R. polystigma	1	-0.7094	spring	season	0.34	0.5584	1.212
R. polystigma	1	6.8598	summer	season	36.07	<.0001	1.142
R. polystigma	0	0	winter	season	.	.	
R. polystigma	1	11.0904		Dispersion			0.823
S. acanthias	1	194.3175		Intercept	29.22	<.0001	35.948
S. acanthias	1	-0.1116		year	38.19	<.0001	0.018
S. acanthias	1	0.0196		depth	109.17	<.0001	0.001
S. acanthias	1	2.1336	uo2	uo	112.66	<.0001	0.20
S. acanthias	0	0	uo3	uo	.	.	
S. acanthias	1	22.9725	fall	season	7199.2	<.0001	0.270
S. acanthias	1	23.6565	spring	season	10070.1	<.0001	0.235
S. acanthias	0	22.4549	summer	season	.	.	
S. acanthias	0	0	winter	season	.	.	
S. acanthias	1	14.3151		Dispersion			1.74
R. clavata	1	63.6053		Intercept	6.75	0.0094	24.482
R. clavata	1	-0.0343		year	7.83	0.0052	0.012
R. clavata	1	0.0398		depth	533.04	<.0001	0.001
R. clavata	1	2.8377	uo2	uo	340.25	<.0001	0.153
R. clavata	0	0	uo3	uo	.	.	
R. clavata	1	-0.5562	fall	season	3.79	0.0516	0.285
R. clavata	1	-0.9103	spring	season	9.05	0.0026	0.302
R. clavata	1	-1.189	summer	season	13.64	0.0002	0.32
R. clavata	0	0	winter	season	.	.	
R. clavata	1	1.6307		Dispersion			0.169
T. torpedo	1	-183.997		Intercept	18.34	<.0001	42.962
T. torpedo	1	0.093		year	18.59	<.0001	0.021
T. torpedo	1	-0.0481		depth	343.47	<.0001	0.002
T. torpedo	1	0.8304	uo2	uo	15.22	<.0001	0.212
T. torpedo	0	0	uo3	uo	.	.	
T. torpedo	1	0.6989	fall	season	2.88	0.0896	0.411
T. torpedo	1	0.0176	spring	season	0	0.9678	0.436
T. torpedo	1	-1.6504	summer	season	10.56	0.0012	0.507
T. torpedo	0	0	winter	season	.	.	
T. torpedo	1	9.9466		Dispersion			0.927

Summary of the model results for species occurring in coastal waters

species	DF	Estimate	Level	Parameter	ChiSq	ProbChiSq	StdEr
T. marmorata	1	-64.938		Intercept	4.61	0.0318	30.251
T. marmorata	1	0.0331		year	4.75	0.0292	0.015
T. marmorata	1	0.0036		depth	8.94	0.0028	0.001
T. marmorata	1	-0.8254	fall	season	9.03	0.0027	0.274
T. marmorata	1	-0.8041	spring	season	7.67	0.0056	0.290
T. marmorata	1	-0.7192	summer	season	5.65	0.0174	0.302
T. marmorata	0	0	winter	season	.	.	
T. marmorata	1	1.9062		Dispersion			0.329
G. melastomus	1	120.0063		Intercept	19.21	<.0001	27.383
G. melastomus	1	-0.0656		year	23.02	<.0001	0.013
G. melastomus	1	0.0638		depth	333.74	<.0001	0.003
G. melastomus	1	-2.0639	uo2	uo	106.42	<.0001	0.200
G. melastomus	0	0	uo3	uo	.	.	
G. melastomus	1	37.2897		Dispersion			3.396
S. blainville	1	-578.016		Intercept	258.67	<.0001	35.938
S. blainville	1	0.2809		year	246.09	<.0001	0.017
S. blainville	1	0.0912		depth	611.26	<.0001	0.003
S. blainville	1	1.808	uo2	uo	146.75	<.0001	0.149
S. blainville	0	0	uo3	uo	.	.	
S. blainville	1	2.9563		Dispersion			0.343
R. montagui	1	20.8959		Intercept	0.51	0.4732	29.130
R. montagui	1	-0.0128		year	0.77	0.3805	0.014
R. montagui	1	0.0335		depth	361.6	<.0001	0.001
R. montagui	1	1.3223	uo2	uo	61.95	<.0001	0.16
R. montagui	0	0	uo3	uo	.	.	
R. montagui	1	11.0652		Dispersion			1.058
R. polystigma b	1	191.3845		Intercept	55.15	<.0001	25.770
R. polystigma b	1	-0.0984		year	57.63	<.0001	0.01
R. polystigma b	1	0.0338		depth	359.11	<.0001	0.001
R. polystigma b	1	1.7923	uo2	uo	99.16	<.0001	0.1
R. polystigma b	0	0	uo3	uo	.	.	
R. polystigma b	1	14.3872		Dispersion			1.209
R. asterias	1	43.7589		Intercept	2.97	0.0846	25.37
R. asterias	1	-0.0217		year	2.92	0.0875	0.012
R. asterias	1	-0.0034		depth	7.63	0.0058	0.001
R. asterias	1	1.0135	uo2	uo	35.02	<.0001	0.171
R. asterias	0	0	uo3	uo	.	.	
R. asterias	1	10.7313		Dispersion			0.893

Appendix 1 continued

species	DF	Estimate	Level	Parameter	ChiSq	ProbChiSq	StdEr
Raja spp.	1	-53.544		Intercept	4.89	0.0271	24.222
Raja spp.	1	0.0275		year	5.15	0.0233	0.012
Raja spp.	1	0.0148		depth	87.41	<.0001	0.001
Raja spp.	1	0.753	uo2	uo	25.27	<.0001	0.149
Raja spp.	0	0	uo3	uo	.	.	
Raja spp.	1	5.6913		Dispersion			0.328
R. miraletus	1	-55.4556		Intercept	3.69	0.0547	28.870
R. miraletus	1	0.028		year	3.73	0.0535	0.014
R. miraletus	1	0.0253		depth	80.26	<.0001	0.002
R. miraletus	1	20.5013		Dispersion			1.164
S. stellaris	1	481.7732		Intercept	200.88	<.0001	33.991
S. stellaris	1	-0.2448		year	204.45	<.0001	0.017
S. stellaris	1	0.031		depth	173.2	<.0001	0.002
S. stellaris	1	0.4009	uo2	uo	5.84	0.0156	0.165
S. stellaris	0	0	uo3	uo	.	.	
S. stellaris	0	6.22		Dispersion			
M. aquila	1	109.3002		Intercept	17.62	<.0001	26.040
M. aquila	1	-0.0548		year	17.59	<.0001	0.013
M. aquila	1	-0.0544		depth	227.52	<.0001	0.003
M. aquila	1	1.1067	uo2	uo	30.3	<.0001	0.20
M. aquila	0	0	uo3	uo	.	.	
M. aquila	1	27.7519		Dispersion			2.912
D. oxyrinchus	1	-439.846		Intercept	153.58	<.0001	35.492
D. oxyrinchus	1	0.2081		year	135.77	<.0001	0.017
D. oxyrinchus	1	0.1326		depth	329.99	<.0001	0.007
D. oxyrinchus	1	-1.3556	uo2	uo	69.34	<.0001	0.162
D. oxyrinchus	0	0	uo3	uo	.	.	
D. oxyrinchus	1	1.81		Dispersion			0.254
P. bovinus	1	-329.369		Intercept	60.24	<.0001	42.436
P. bovinus	1	0.1641		year	59.74	<.0001	0.021
P. bovinus	1	-0.032		depth	113.89	<.0001	0.00
P. bovinus	0	1.7787		Dispersion			
D. pastinaca	1	-169.813		Intercept	26.82	<.0001	32.789
D. pastinaca	1	0.0847		year	26.59	<.0001	0.016
D. pastinaca	1	-0.0513		depth	150.49	<.0001	0.004
D. pastinaca	0	12		Dispersion			

Appendix 1 continued

Appendix 2

species	DF	Estimate	Level	Parameter	ChiSq	ProbChiSq	StdEr
C. monstrosa	1	140.7166		Intercept	39.92	<.0001	22.272
C. monstrosa	1	-0.0732		year	42.68	<.0001	0.011
C. monstrosa	1	0.0179		depth	258.35	<.0001	0.001
C. monstrosa	1	-1.7576	fall	season	13.04	0.0003	0.486
C. monstrosa	1	-0.4631	spring	season	0.89	0.3448	0.490
C. monstrosa	1	-1.5549	summer	season	9.93	0.0016	0.493
C. monstrosa	0	0	winter	season	.	.	
C. monstrosa	1	1.8306	uo2	uo	102.27	<.0001	0.18
C. monstrosa	0	0	uo3	uo	.	.	
C. monstrosa	1	3.7223		Dispersion			0.258
R. aterias	1	-150.139		Intercept	9.56	0.002	48.5
R. aterias	1	0.0666		year	7.47	0.0063	0.024
R. aterias	1	-0.0166		depth	177.8	<.0001	0.001
R. aterias	1	22.792	fall	season	5251.91	<.0001	0.314
R. aterias	1	19.9575	spring	season	2109.56	<.0001	0.434
R. aterias	0	22.908	summer	season	.	.	
R. aterias	0	0	winter	season	.	.	
R. aterias	1	-1.7274	uo2	uo	52.32	<.0001	0.238
R. aterias	0	0	uo3	uo	.	.	
R. aterias	1	17.2361		Dispersion			1.785
S. blainville	1	222.7784		Intercept	50.32	<.0001	31.405
S. blainville	1	-0.1211		year	59.39	<.0001	0.015
S. blainville	1	-0.0164		depth	188.83	<.0001	0.001
S. blainville	1	25.307	fall	season	4563.98	<.0001	0.374
S. blainville	1	20.4024	spring	season	2521.61	<.0001	0.406
S. blainville	0	22.8954	summer	season	.	.	
S. blainville	0	0	winter	season	.	.	
S. blainville	1	1.1741	uo2	uo	16.86	<.0001	0.28
S. blainville	0	0	uo3	uo	.	.	
S. blainville	1	69.6851		Dispersion			5.214
R. miraletus	1	97.7954		Intercept	8.35	0.0039	33.840
R. miraletus	1	-0.0581		year	11.68	0.0006	0.01
R. miraletus	1	-0.0171		depth	198.52	<.0001	0.001
R. miraletus	1	22.9369	fall	season	4157.23	<.0001	0.355
R. miraletus	1	22.5592	spring	season	4955.88	<.0001	0.320
R. miraletus	0	21.8405	summer	season	.	.	
R. miraletus	0	0	winter	season	.	.	
R. miraletus	1	0.1962	uo2	uo	0.86	0.3542	0.211
R. miraletus	0	0	uo3	uo	.	.	
R. miraletus	1	22.0568		Dispersion			2.566
C. granulosus	1	121.0383		Intercept	20.33	<.0001	26.84
C. granulosus	1	-0.065		year	23.26	<.0001	0.013
C. granulosus	1	0.0134		depth	111.82	<.0001	0.001
C. granulosus	1	2.7808	uo2	uo	111.32	<.0001	0.263
C. granulosus	0	0	uo3	uo	.	.	
C. granulosus	1	29.8899		Dispersion			2.613
R. polystigma	1	158.2756		Intercept	19.35	<.0001	35.976
R. polystigma	1	-0.0927		year	26.12	<.0001	0.018
R. polystigma	1	-0.0087		depth	104.3	<.0001	0.000
R. polystigma	0	27.6659	uo2	uo	.	.	
R. polystigma	0	0	uo3	uo	.	.	
R. polystigma	1	155.93		Dispersion			17.273

Summary of the model results for species occurring in deep waters.

species	DF	Estimate	Level	Parameter	ChiSq	ProbChiSq	StdEr
R. clavata	1	-14.8231		Intercept	0.89	0.3442	15.672
R. clavata	1	0.0095		year	1.49	0.2227	0.007
R. clavata	1	-0.0118		depth	189.4	<.0001	0.000
R. clavata	1	3.5763	uo2	uo	357.07	<.0001	0.189
R. clavata	0	0	uo3	uo	.	.	
R. clavata	1	5.0516		Dispersion			0.387
Raja spp.	1	-23.3817		Intercept	2.31	0.1289	15.398
Raja spp.	1	0.014		year	3.36	0.0669	0.007
Raja spp.	1	-0.0079		depth	113.12	<.0001	0.000
Raja spp.	1	2.3713	uo2	uo	191.22	<.0001	0.171
Raja spp.	0	0	uo3	uo	.	.	
Raja spp.	1	4.0076		Dispersion			0.287
S. canicula	1	86.8499		Intercept	20.56	<.0001	19.152
S. canicula	1	-0.0384		year	16.05	<.0001	0.009
S. canicula	1	-0.0195		depth	536.77	<.0001	0.000
S. canicula	1	1.6541	uo2	uo	102.85	<.0001	0.163
S. canicula	0	0	uo3	uo	.	.	
S. canicula	1	3.951		Dispersion			0.260
S. acanthias	1	298.9027		Intercept	193.38	<.0001	21.494
S. acanthias	1	-0.1488		year	193	<.0001	0.010
S. acanthias	1	-0.0103		depth	100.9	<.0001	0.00
S. acanthias	1	0.6221	uo2	uo	7.89	0.005	0.221
S. acanthias	0	0	uo3	uo	.	.	
S. acanthias	1	12.0022		Dispersion			1.382
E. spinax	1	107.8034		Intercept	26.19	<.0001	21.064
E. spinax	1	-0.0548		year	26.74	<.0001	0.010
E. spinax	1	0.0122		depth	178.57	<.0001	0.000
E. spinax	1	1.0509	uo2	uo	29.76	<.0001	0.192
E. spinax	0	0	uo3	uo	.	.	
E. spinax	1	4.7654		Dispersion			0.298
R. montagui	1	-165.868		Intercept	45.77	<.0001	24.517
R. montagui	1	0.0863		year	49.65	<.0001	0.012
R. montagui	1	-0.0206		depth	214	<.0001	0.001
R. montagui	1	3.1925	uo2	uo	206.7	<.0001	0.222
R. montagui	0	0	uo3	uo	.	.	
R. montagui	1	12.9069		Dispersion			1.057
R. polystigma b	1	-163.579		Intercept	47.01	<.0001	23.856
R. polystigma b	1	0.085		year	50.81	<.0001	0.011
R. polystigma b	1	-0.0194		depth	216.37	<.0001	0.001
R. polystigma b	1	3.2021	uo2	uo	214.15	<.0001	0.218
R. polystigma b	0	0	uo3	uo	.	.	
R. polystigma b	1	12.5826		Dispersion			1.041
G. melastomus	1	11.308		Intercept	0.5	0.4781	15.940
G. melastomus	1	-0.0036		year	0.2	0.6525	0.00
G. melastomus	1	0.0043		depth	24.09	<.0001	0.000
G. melastomus	1	0.7333	uo2	uo	22.5	<.0001	0.154
G. melastomus	0	0	uo3	uo	.	.	
G. melastomus	1	2.807		Dispersion			0.158

Appendix 2 continued

species	DF	Estimate	Level	Parameter	ChiSq	ProbChiSq	StdEr
D. licha	1	30.2265		Intercept	3.67	0.0555	15.78
D. licha	1	-0.0181		year	5.2	0.0226	0.007
D. licha	1	0.0113		depth	149.21	<.0001	0.000
D. licha	1	0.5063	uo2	uo	8.87	0.0029	0.169
D. licha	0	0	uo3	uo	.	.	
D. licha	1	2.3626		Dispersion			0.424
L. circularis	1	97.8419		Intercept	47.7	<.0001	14.166
L. circularis	1	-0.0642		year	80.48	<.0001	0.007
L. circularis	1	0.0064		depth	34.48	<.0001	0.001
L. circularis	0	26.7969	uo2	uo	.	.	
L. circularis	0	0	uo3	uo	.	.	
L. circularis	1	40.0913		Dispersion			3.700
D. oxyrinchus	1	71.9802		Intercept	15.17	<.0001	18.4
D. oxyrinchus	1	-0.0357		year	14.9	0.0001	0.009
D. oxyrinchus	1	0.665	uo2	uo	12.58	0.0004	0.187
D. oxyrinchus	0	0	uo3	uo	.	.	
D. oxyrinchus	1	6.5715		Dispersion			0.614
T. marmorata	1	-59.7649		Intercept	4.48	0.0343	28.239
T. marmorata	1	0.033		year	5.41	0.02	0.014
T. marmorata	1	-0.0244		depth	144.43	<.0001	0.00
T. marmorata	1	-0.1083	uo2	uo	0.44	0.5077	0.163
T. marmorata	0	0	uo3	uo	.	.	
T. marmorata	0	1.94		Dispersion			
S. stellaris	1	119.757		Intercept	27.24	<.0001	22.943
S. stellaris	1	-0.0596		year	26.81	<.0001	0.011
S. stellaris	1	-3.1349	uo2	uo	114.13	<.0001	0.293
S. stellaris	0	0	uo3	uo	.	.	
S. stellaris	0	6.22		Dispersion			
S. squatina	1	1261.595		Intercept	30.62	<.0001	228.003
S. squatina	1	-0.6467		year	31.31	<.0001	0.115
S. squatina	0	13.799	uo2	uo	.	.	
S. squatina	0	0	uo3	uo	.	.	
S. squatina	0	1.33		Dispersion			
S. aculeata	1	1329.574		Intercept	38.13	<.0001	215.323
S. aculeata	1	-0.6807		year	38.88	<.0001	0.109
S. aculeata	0	12.9299	uo2	uo	.	.	
S. aculeata	0	0	uo3	uo	.	.	
S. aculeata	0	1.33		Dispersion			
O. centrina	1	184.5764		Intercept	64.01	<.0001	23.070
O. centrina	1	-0.1066		year	83.49	<.0001	0.011
O. centrina	0	24.6248	uo2	uo	.	.	
O. centrina	0	0	uo3	uo	.	.	
O. centrina	0	2.45		Dispersion			
L. fullonica	1	-265.711		Intercept	90.14	<.0001	27.98
L. fullonica	1	0.1194		year	72.59	<.0001	0.01
L. fullonica	0	26.445	uo2	uo	.	.	
L. fullonica	0	0	uo3	uo	.	.	
L. fullonica	0	4.93		Dispersion			
H. griseus	1	119.0296		Intercept	10.2	0.0014	37.268
H. griseus	1	-0.0607		year	10.54	0.0012	0.018
H. griseus	1	-26.1464	uo2	uo	0	0.9995	38234.9
H. griseus	0	0	uo3	uo	.	.	
H. griseus	0	1		Dispersion			

Appendix 2 continued

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