Contrasting Responses to Harvesting and Environmental Drivers of Fast and Slow Life History Species

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Abstract

According to their main life history traits, organisms can be arranged in a continuum from fast (species with small body size, short lifespan and high fecundity) to slow (species with opposite characteristics). Life history determines the responses of organisms to natural and anthropogenic factors, as slow species are expected to be more sensitive than fast species to perturbations. Owing to their contrasting traits, cephalopods and elasmobranchs are typical examples of fast and slow strategies, respectively. We investigated the responses of these two contrasting strategies to fishing exploitation and environmental conditions (temperature, productivity and depth) using generalized additive models. Our results confirmed the foreseen contrasting responses of cephalopods and elasmobranchs to natural (environment) and anthropogenic (harvesting) influences. Even though a priori foreseen, we did not expect neither the clear-cut differential responses between groups nor the homogeneous sensitivity to the same factors within the two taxonomic groups. Apart from depth, which affected both groups equally, cephalopods and elasmobranchs were exclusively affected by environmental conditions and fishing exploitation, respectively. Owing to its short, annual cycle, cephalopods do not have overlapping generations and consequently lack the buffering effects conferred by different age classes observed in multi-aged species such as elasmobranchs. We suggest that cephalopods are sensitive to short-term perturbations, such as seasonal environmental changes, because they lack this buffering effect but they are in turn not influenced by continuous, long-term moderate disturbances such as fishing because of its high population growth and turnover. The contrary would apply to elasmobranchs, whose multi-aged population structure would buffer the seasonal environmental effects, but they would display strong responses to uninterrupted harvesting due to its low population resilience. Besides providing empirical evidence to the theoretically predicted contrasting responses of cephalopods and elasmobranchs to disturbances, our results are useful for the sustainable exploitation of these resources.
Introduction

In ecology, organisms can be classified according to their main life history traits on a continuum from fast to slow. Fast life history species are characterized by small body size, short life-span, early reproduction, small offspring size, high fecundity and short generation time; opposite characteristics apply to slow life history species [1,2]. The fast-slow hypothesis is currently the most widely used classification scheme [2] given that the main assumptions of the traditional r-K strategies concept, from which the hypothesis derives, are considered no longer valid [3–5]. Organisms displaying the living fast and dying young strategy are, in general, more productive than those that live more slowly and die older [6,7]. The fast-slow hypothesis has been empirically tested across different taxonomic groups and highlights the interplay among physiology and life-history, ecology and evolution at broad scales [7–9]. Life history determines the responses of organisms to natural (e.g. climate) and anthropogenic (e.g. harvesting) factors, as slow species are expected to be more sensitive than fast species to perturbations [10–13].

In the marine environment, it is well documented that the intense fishing exploitation, with synergistic effects of environmental conditions in some cases, has induced more severe declines in abundance and more noticeable changes in life-history traits of large, slow-growing species than their smaller, faster-growing counterparts (e.g. [11,14–17]). In general, those species growing at slower rates and thus maturing later at greater sizes decreased in abundance compared to their counterparts as a result of harvesting; this entailed concomitant changes in the population structure of these species, such as lower mean individual size and lower maturation size. The fishery-induced truncation of size or age structure can reduce fecundity, elicit declines in harvestable biomass or instability in population growth, and eventually increase the vulnerability of fisheries through reduced resilience [18–21]. Harvested organisms have shown some of the most abrupt trait changes ever observed in wild populations, providing insight for how fast phenotypes can change [10]. Although fishing activity has been identified as the main cause of many marine populations depletions (e.g. [18,20,22]), it is recognised that both abiotic (climate and hydrodynamics) and biotic (trophic resources and predators) environmental variables can also induce intra- and inter-annual oscillations in the population dynamics of some exploited species (e.g. [23–25]).

Owing to their contrasting life histories, cephalopods and elasmobranchs are typical examples of fast and slow strategies, respectively. Cephalopods have short life spans (1.5–2 years at most) and high population growth rates; they have high production, high fecundity and high mortality rates [26]. By contrast, elasmobranchs are long-lived, slow growing and late-maturing, and have low production and low mortality rates [27,28]. As a consequence of these characteristics, cephalopod and elasmobranch populations have high and low resilience respectively.

The sensitivity of cephalopods to natural and human-induced perturbations suggests that they could act as good ecological indicators [29]. Cephalopod populations are more rapidly affected than longer-lived species by external drivers but they are also quicker to recover from perturbations [29–31]. In accordance with the high plasticity of cephalopod populations, substantial changes in biological traits have been reported at different time scales encompassing years [32], seasons [33], weeks [34] and even days [35]. Global cephalopod catch has quadrupled over the last four decades, which seems to be related to the severe decline of many fish stocks [31].

In elasmobranchs, population growth rate and thus recovery potential is, on average, significantly lower (reflecting increased extinction risk) than that of teleosts and terrestrial mammals [36]. The fact that more than half of all chondrichthyan species are predicted to be “Threatened or Near Threatened” according to the IUCN Red List reflects the high vulnerability of
elasmobranchs [27,37]. Elasmobranchs typically exhibit rapid declines in catch rates (boom and bust yields), with fisheries collapsing soon after the initiation of exploitation [38]. Although the knowledge on the stock status of elasmobranchs is limited, many populations around the world show dramatic declines or collapses, particularly the large-sized species [27,39].

In this paper, we analyse the responses of fast (cephalopods) and slow (elasmobranchs) life history strategies to fishing exploitation and environmental conditions. According to the contrasting life histories of these two taxonomical groups, the starting hypothesis is that elasmobranch populations will be more highly impacted by harvesting than cephalopod populations owing to the lower resilience of the formers. We further hypothesize that the semelparous, short-lived cephalopods will be, by contrast, more influenced by environmental conditions than the iteroparous, multi-aged elasmobranch populations. Assessing differential responses to harvesting of species with contrasting strategies within an ecological community is essential to manage mixed fisheries under the current Ecosystem Approach to Fisheries [40,41].

Material and Methods

Ethic statement

Biological data were obtained from the annual trawl surveys carried out as part of the Mediterranean International Trawl Survey (MEDITS) project. The sampling was performed under repeated international standardized protocol (see [42] for details of the survey methodology). The surveys were conducted across the Spanish territorial waters in the Mediterranean Sea. The research vessels had full permission from national (Fisheries General Secretariat) and international authorities (General Fisheries Commission for the Mediterranean) to sample in territorial and Mediterranean community waters. No approval by an ethics committee was required, as common exploited species were targeted and trawling did not affect endangered or protected species or marine protected areas. Most of the authors participate consistently in the surveys of the MEDITS programme. As most individuals taken by bottom trawl gears arrive dead or in very bad condition on board, it was not necessary to sacrifice them; the most resistant species such as sharks and rays were thrown back to sea alive.

Sampling and data analysis

Data on cephalopod and elasmobranch abundances were collected during the MEDITS bottom trawl surveys [42] conducted from 2007 to 2012 around the Balearic Islands (western Mediterranean; Fig 1). These surveys are carried out annually at late spring, following a depth stratified random sampling scheme in which a set of approximately 50 stations are sampled. The following four depth strata are considered: A (50–100 m), B (101–200 m), C (201–500 m) and D (501–800 m). The sampling gear is the experimental bottom trawl GOC 73, with a 20 mm mesh codend and average horizontal and vertical net openings of 16.0 and 2.7–3.2 m, respectively. The towing speed is around 2.7–3.0 knots to ensure the best trawl geometry, and the effective trawling duration varies between 20 and 60 min depending on the depth-strata. For each sampling station, the position (latitude, longitude) and depth (m) were taken. The mean density of each studied species was estimated as the total number of individuals by swept area (n Km^-2). The three most abundant cephalopod (common octopus Octopus vulgaris, horned octopus Eledone cirrhosa and southern shortfin squid Illex coindetii) and elasmobranch (small-spotted catshark Scyliorhinus canicula, thornback skate Raja clavata and blackmouth shark Galeus melastomus) species were selected.

To avoid bias in the results caused by sporadic species occurrences in marginal habitats, only the sampling stations located in the main bathymetric distributional range of each species.
were considered (Fig 2). In order to show the contrasting life-history traits of cephalopods and elasmobranchs, the main population characteristics of each studied species were summarized from literature (Table 1). All three cephalopods live 2 years at most, while elasmobranchs life-spans range between 7 (G. melastomus) and 15 (R. clavata) years. The length of first maturity has been estimated between 10 and 15 cm mantle length for cephalopods and between 40 and 81 cm total length for elasmobranchs. Fecundity is very high in cephalopods (up to hundred thousands oocytes) and hatchlings are planktonic larvae spending a few months on pelagic waters before adopting adult morphology. By contrast, fecundity is very low in elasmobranchs (11–74 eggs) and the eggs give rise to young fish already displaying the main adult characteristics; as a consequence, population resilience in the three investigated elasmobranchs is relatively low (4.5–14 yr; http://www.fishbase.org/).

Vessel Monitoring System (VMS) records of bottom trawlers, which is the main fleet targeting the selected species, were used to estimate the fishing effort for the study area from 2007 to 2012. VMS records have been used as a proxy of the fishing exploitation in many previous works (e.g. [54–56]). None of the cephalopods and elasmobranchs analysed here are target
species of the bottom trawl fishery, since all of them are taken as a by-catch [57]. This entails that the fishing effort exerted on each of the six species is the same and, in case of finding contrasting responses between groups or among species, these would not be related to contrasting fishing mortalities. Only VMS records with speeds between 1.5 and 5.0 knots, revealing fishing

![Diagram showing frequency of occurrence (F%) by depth strata of the fast (cephalopods) and slow (elasmobranchs) life history species analysed. Numbers between brackets are the sampling size and the arrows indicate the datasets removed from the analysis (see Material and methods).]

**Table 1.** Main population traits of the fast (cephalopods) and slow (elasmobranchs) life history species analyzed in this study obtained from the literature: maximum age (in years), maximum individual size, size at first maturity (L$_{50}$) and fecundity. Size and L$_{50}$ (both in cm mantle and total length for cephalopods and elasmobranchs, respectively) are shown for females (F) and males (M) separately.

| Taxonomical group | Species                | Age (yr) | Size (F/M) | L$_{50}$ (F/M) | Fecundity       | Source |
|-------------------|------------------------|----------|------------|----------------|-----------------|--------|
| Cephalopods       | Octopus vulgaris       | 1$^a$    | 27/27$^b$ | 18/10$^b$      | 70,000–650,000$^b$ | $^[43]$; $^[44]$ |
|                   | Eledone cirrhosa       | 1.5$^a$ | 19/15$^b$ | 10/12$^b$      | 550–6500$^b$     | $^[45]$; $^[46]$ |
|                   | Illex coindetii        | 1.5      | 17/14      | 15/12          | 30,000–200,000   | [47]   |
| Elasmobranchs     | Scyliorhinus canicula  | 12$^a$   | 47/49$^b$ | 40/40$^b$      | 18$^b$          | $^[48]$; $^[49]$ |
|                   | Raja clavata           | 15$^a$   | 110/89$^b$| 81/67$^b$      | 48/74$^b$       | $^[50]$; $^[51]$ |
|                   | Galeus melastomus      | 7$^a$    | 64/62$^b$ | >51/>52$^b$    | 11/30$^b$       | $^[52]$; $^[53]$ |

For each species, symbols “a” and “b” refer to the papers reported on the Source column.

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activity [58], were included in the calculations. The sum of records within a radius of 3 km around each sampling station was averaged to account for the specific effect of fishing effort intensity at each station. Due to the clear depth gradient in the area (Fig 1), only the VMS records situated within the same depth strata than the corresponding sampling station were used. As a result of the contrasting life-histories of cephalopods and elasmobranchs, different sensitivities to fishing pressure between groups were expected. As aforementioned, whereas cephalopods are short-lived species dying shortly after reproduction during its first year of life, elasmobranchs are long-lived species with life-spans of several years (see Table 1). Consequently, fishing effort exerted around each station during the previous 3 and 12 months were calculated for cephalopods and elasmobranchs, respectively.

To investigate putative environmental drivers affecting the abundance of both taxonomic groups, we tested the effect of two environmental indicators providing information about the local spatiotemporal changes of sea surface temperature (SST) and chlorophyll-a concentration (Chla; mg m^{-2}). In order to capture local variations among the different sampling stations, the average Chla within a 9 km radius of the five months previous to the survey (1st January-31st May) was calculated. This period includes the spring bloom, occurring between January and March in the study area [59]. The spatiotemporal average of Chla was computed from weekly means (at 0.05 degrees of spatial resolution) downloaded from the MODIS sensor from the web site of NOAA Coast Watch Program and NASA’s Goddard Space Flight Center (http://coastwatch.noaa.gov/). The SST data were obtained from the NCEP/NCAR reanalysis fields provided by the NOAA/OAR/ESRL PSD [60]. As previous works reported lagged responses to Chla in fish and cephalopod populations from the western Mediterranean (e.g. [61,62]), two different series of monthly records, spring data contemporary to the survey and data from the previous winter, were used.

In order to estimate the effect of harvesting (VMS records) and environmental conditions (Chla and SST) on the population densities (N km^{-2}) of the six selected species, Generalized Additive Models (GAMs) and Generalized Additive Mixed Models (GAMMs) were used. To account for spatial and bathymetric effects, sampling location (latitude, longitude) and depth were also used as covariates. A backward approach, in which only the significant explanatory variables were retained, was used to get the best model. Model selection was based on the Akaike’s information criterion (AIC), which was used as a measure of the goodness of fit as well as the optimal number of model parameters, the best one having the smallest AIC value. Model performance was measured as the proportion of the null deviance explained (DE) or the adjusted regression coefficient (R2) when using GAM or GAMM, respectively. Finally, model residuals were checked to fulfill the normality assumption and absence of spatial and temporal autocorrelation. All analyses were implemented with the mgcv library [63] using the R version 3.0.2 (www.R-project.org/).

Results

The spatial distribution of the sampling stations covered most trawling grounds around the two major Balearic Islands (Mallorca and Menorca) between 50 and 800 m depth, where the commercial fleet works all the year round (Fig 1). The total number of sampling stations analyzed during the study period ranged between 133 (O. vulgaris) and 188 (E. cirrhosa) in cephalopods and between 84 (G. melastomus) and 232 (S. canicula) in elasmobranchs (Fig 2). There were clear bathymetric differences in the frequency of occurrence of the selected species, being O. vulgaris and G. melastomus the species showing the shallower and deepest distribution, respectively (Fig 2). A first set of exploratory scatterplots representing the densities of each species against the VMS records showed clear contrasting responses between cephalopods and
elasmobranchs to the fishing pressure (Fig 3). Whereas the graph did not show any relationship in the former group, the densities of elasmobranchs decreased noticeably with increasing fishing intensity, especially in *R. clavata* and *G. melastomus*.

The full list of GAM and GAMM models used to test the species densities against fishing effort (VMS), environmental conditions (SST, Chla and depth) and spatial distribution is shown in the Supporting Information; the best model for each species was selected based on the AIC (Table 2). These models gave rise to significant effects in all cases except for *E. cirrhosa*, whose mean density in the area was not affected by any of the selected explanatory variables. As we were not able to find a suitable model describing this octopus’ densities using those set of covariates, the following findings refer to the remaining five species.

The deviance explained (expressed as proportions), or $R^2$ (expressed as percentages), was high in elasmobranchs (*S. canicula*, 0.38; *R. clavata*, 44.8%; *G. melastomus*, 55.4%) as well as in *O. vulgaris* (0.65), but much lower in *I. coindetii* (0.08). Depth was statistically significant for all species and, interestingly, its effect was linear in cephalopods but non-linear in elasmobranchs (Fig 4). Population densities gradually increased and decreased with depth in *I. coindetii* and *O. vulgaris*, respectively. Whereas densities of *S. canicula* and *R. clavata* also decreased with depth, *G. melastomus* effect was hump-shaped with a maximum at about 400 m. The sampling location was significant for *O. vulgaris*, *S. canicula* and *R. clavata* and it had no effect for *I. coindetii* and *G. melastomus*.

Regarding the remaining factors (fishing effort and environmental variables), the best models differed clearly between groups since cephalopods and elasmobranchs were exclusively driven by environmental variables, namely SST, and fishing exploitation (VMS) respectively. Densities of *I. coindetii* decreased linearly with increasing SST, whereas *O. vulgaris* densities also showed a hump-shaped trend with a maximum at around 21–22°C. The response of elasmobranchs to fishing exploitation (VMS) was homogeneous, as their population densities decreased linearly with increasing harvesting in all three species.

**Discussion**

Our results confirmed the foreseen contrasting responses of fast (cephalopods) and slow (elasmobranchs) life history species to natural (environment) and anthropogenic (harvesting) influences. Even though a priori foreseen, we did expect neither the clear-cut differential responses between groups nor the homogeneous sensitivity to the same factors within the two taxonomic groups. Apart from depth, which affected both groups, cephalopods and elasmobranchs were exclusively affected by environmental conditions (namely SST) and fishing exploitation, respectively. Besides providing empirical evidence to the theoretically predicted contrasting responses of cephalopods and elasmobranchs to disturbances, our study also reveals useful information for the sustainable exploitation of these resources under the current Ecosystem Approach to Fisheries Management (EAFM).

Main life history traits determine population responses to disturbances, as the fast-life history species are more able to withstand them than the slow life history strategists. The fast-slow continuum in life-history not only applies to taxonomic groups with strong differences in life cycles. Strategies can be quite diverse within a taxon or even within populations of the same species [64], whereas distantly related taxa can display similar strategies [65]. Consequently it is inappropriate to generalize a specific strategy to an entire class or family [66], which might explain the lack of significant responses in the horned octopus in contrast with the remaining two cephalopod species analysed. As this octopus was found to be affected by environmental variables in nearby areas [61,62], the lack of significant responses in our study might be related with the highly complex oceanographic conditions at relatively small spatial scales from the
western Mediterranean, which has been reported to induce differences in the spatial distribution and life cycles of this species [67,68]. An entire fast-slow continuum also occurs within elasmobranchs [39,69], as they encompass a broad range of life-histories from the small-sized sharks and rays to the giant species (e.g. white shark, whale-shark). Since in our study we analyzed relatively small-sized elasmobranchs situated in the fast corner of this fast-slow

Table 2. Best GAM models obtained for the fast (cephalopods) and slow (elasmobranchs) life history species analysed in this study. Species densities (N km⁻²) were modelled against different covariates (environmental parameters and fishing effort; see Material and methods). Significant covariates, degrees of freedom (DF), goodness of fit (AIC), model performance (DE/R²) and sampling size (N) are shown. AIC: Akaike Information Criterion; DE/R²: deviance explained (DE, in percentage) or regression coefficient (R²) in case of using GAM or GAMM respectively.

| Taxonomical group | Species            | Covariates                                                        | DF | AIC   | DE/R² | N   |
|-------------------|--------------------|-------------------------------------------------------------------|-----|-------|-------|-----|
| Cephalopods       | *Octopus vulgaris* | s(SST, k = 4)+s(depth, k = 4)+s(lon, lat, k = 10),random = list(station = ~1) | 10  | 258.8 | 0.65  | 108 |
|                   | *Illex coindetii*  | s(SST, k = 4)+s(depth, k = 4),random = list(year = ~1)            | 7   | 410.4 | 0.08  | 150 |
| Elasmobranchs     | *Scyliorhinus canicula* | s(VMS)+s(depth, k = 4)+s(lon, lat, k = 10),correlation = corAR1() | 10  | 630.8 | 0.38  | 229 |
|                   | *Raja clavata*     | s(VMS)+s(depth, k = 4)+s(lon, lat, k = 10)                        | 11.4| 396.4 | 44.8  | 158 |
|                   | *Galeus melastomus*| s(VMS)+s(depth, k = 4)                                            | 5.9 | 279.3 | 55.4  | 83  |

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continuum, we did not expect the strong responses to harvesting we finally found, as it would have been expected in typical slow living, larger-sized species. Such strong responses to harvesting, however, fully agree with the dramatic declines of these species reported either in our study area [70] and other nearby Mediterranean areas such as the Adriatic Sea [71–74]. To give some figures, elasmobranchs declined by 94.5% over 57 years in the Adriatic [73], with sharks declining more than rays (95.6% vs 87.7%); the small-spotted shark drove most of the patterns (96.2%) and the thornback skate, the most abundant ray in the 1940s, recorded the steepest decline (97.2%). Elasmobranchs are the most endangered group of marine fishes in the Mediterranean, with 31 species assessed as critically endangered, endangered or vulnerable [75].

The observed responses of such comparatively small-sized elasmobranchs agree with the view that body size is not a good indicator of life-history strategies [17,76–79]. In the marine environment, tunas and their relatives constitute good case studies for this view. Time related traits describing the speed of life, rather than size-related traits, better explained the extend and rate of declines and current exploitation status of this taxonomical group [77].
relatively large (>200 cm), yellowfin tuna is a fast-growing and short lived tropical species that can cope with relatively high fishing mortality rates compared with the similar-sized temperate bluefin tuna. Similar results were obtained when comparing yellowfin tuna with the smaller and lighter elasmobranch blue shark [17]. Blue shark was highly sensitive to low exploitation rates, while yellowfin populations were extremely robust across a wide range of exploitation rates. 

In our study, cephalopods were affected by environmental conditions but not by fishing, which tallies with the ecological change in global landings hypothesized by Caddy and Rodhouse [30]. According to these authors, as most coastal and shelf cephalopod fisheries are likely to be fully exploited or overexploited (as is the case in our populations [80]), the current annual fluctuations in their landings are probably largely environmentally-driven. The high sensitivity of cephalopods to environmental conditions is well-know, despite the underlying causes of the links between environment and population dynamics are poorly understood [31]. As a result, cephalopods have been suggested as good ecological indicators of environmental change [29], especially climate change [33], which agrees with the significant sensitivity to sea surface temperature found in our study (but see [81]). In contrast to this view, however, our results indicate that cephalopods would not be good indicators of moderate fishing exploitation. It should be stressed that our results would not imply that cephalopods could cope with any level of harvesting because the fishing exploitation in our study area is moderate compared to nearby areas [82] and responses might be triggered under higher rates. As we hypothesize below, the contrasting responses of cephalopods to environment and harvesting might be related to the fast life history characteristics of this taxonomic group. The lack of response to moderate fishing might also reflect the positive effect that the overfishing of groundfish stocks has had on many cephalopod populations worldwide [30].

Contrary to cephalopods, elasmobranchs were found to be affected by fishing but not by environmental conditions. This is in accordance with the general agreement that the dominant factor in the decline of elasmobranchs has been the fishing exploitation, although probably acting together with synergistic effects of environmental conditions [27,71,72,83,84]. Owing to its slow life history traits (slow growth rate, late maturity, low fecundity), which are more similar to those of large mammals than to other fishes, elasmobranchs are particularly vulnerable to harvesting [27,38,39]. A recent review estimated that one-quarter of elasmobranch species are threatened due to overfishing and that the population depletion is particularly prevalent in the Indo-Pacific Biodiversity Triangle and Mediterranean Sea [27]. The severe decline of large sharks in the Mediterranean during the last two centuries would reflect its long history of intense fishing exploitation [85].

In accordance with previous works (e.g. [11,13,14]), our results indicate that the differential responses of fast (cephalopods) and slow (elasmobranchs) species to harvesting and environmental conditions are governed by their contrasting life history characteristics. Owing to its short, annual cycle, cephalopod populations do not have overlapping generations and consequently lack the buffering effects conferred by different age classes observed in multi-aged species such as elasmobranchs. We suggest that cephalopods are sensitive to short-term perturbations, such as seasonal environmental changes, because they lack this buffering effect but they are in turn not influenced by continuous, long-term disturbances such as moderate fishing, because of its high population growth and turnover. The contrary would apply to elasmobranchs, whose multi-aged population structure would buffer the seasonal environmental effects, but they would display strong responses to uninterrupted harvesting due to its low population resilience. This explanation is in line with Saether et al. [86], when stating that perturbations will affect many age classes in long-lived species, which is likely to result in delayed responses in the dynamics because of covariation in environmental stochasticity producing
fluctuations in age structure. In contrast, short-lived species will show far more immediate responses to environmental perturbations, because changes in population size will be caused by demographic variations across most parts of the life cycle.

All cephalopod and elasmobranch species analysed in this study are important by-catch resources from the Mediterranean bottom trawl mixed-fisheries, which take a large number of species having different sensitivities to harvesting. The management of mixed-fisheries constitutes an important challenge, especially in the framework of the Ecosystem Approach to Fisheries, which goes beyond the single-stock strategy, and current approaches based on the maximum sustainable yield (MSY) concept. The MSY has been adopted as the primary management goal by several inter-government fishery organisations (e.g. IWC, ICCAT, IATTC) and has been the cornerstone of the federal fishery policy in the United States for decades [87]. In Europe, the concept has been integrated into the Common Fisheries Policy, with the commitment to maintain or restore their fish stocks to MSY levels by 2020 (EU Regulation N. 1380/2013). The MSY concept, however, has been criticized [88,89] and is especially problematic in the case of mixed-fisheries because it is not possible to simultaneously obtain MSY values for more than one species at a time and alternative approaches are thus required [90–92]. The existence of complex ecological interactions involving the impacts of both the environmental conditions, such as climate change, and the fishing exploitation complicates even further seeking MSY targets at mixed-fisheries or ecosystem levels [90–92]. According to Mackinson et al. [90], taking account of the effect of environmental change and fishing on species dynamics and determining their relative influence is challenging research of vital importance to developing robust long-term fisheries management plans. Our work is in line with this claim since it demonstrates, together with other many studies already reported here, the existence of contrasting sensitivities to natural or anthropogenic disturbances at different taxonomical levels (species, class) that should be taken into account for management purposes and highlights the need for specific strategies adapted to those differential sensitivities.

Supporting Information

S1 Table. List of GAM and GAMM tested in this study to model population density against environmental parameters (SST, Chla, depth) and fishing exploitation (VMS). The degrees of freedom (df), Akaike Information Criteria (AIC), percentage of deviance explained (%DE) or regression coefficient (R²) and the number of samples (n) are also shown. The best model number is highlighted with an asterisk.

(DOCX)

Author Contributions

Conceived and designed the experiments: AQ LR BG EM. Performed the experiments: AQ LR BG EM. Analyzed the data: AQ LR. Contributed reagents/materials/analysis tools: AQ LR DAB. Wrote the paper: AQ LR DAB BG EM.

References

1. Reynolds JD. (2003) Life histories and extinction risk. In: Blackburn TM, Gaston KJ, editors. Macroecology: concepts and consequences. Oxford: Blackwell. pp. 195–217.
2. Jeschke JM, Kokko H. (2009) The roles of body size and phylogeny in fast and slow life histories. Evol Ecol 23: 867–878.
3. Jeschke JM, Gabriel W, Kokko H. (2008) Population dynamics: r-strategists / K-strategists. In: Jorgensen SE, Fath BD, editors. Encyclopedia of ecology. Oxford: Elsevier B.V. pp. 3113–3122.
4. Roff DA (2002) Life history evolution. Sunderland: Sinauer Associates Inc., U.S.
5. Rueffler C, Egas M, Metz JA. (2006) Evolutionary predictions should be based on individual-level traits. Am Nat 168: E148–E162. PMID: 17080357

6. Stearns SC. (1989) Trade-Offs in Life-History Evolution. Funct Ecol 3: 259–268.

7. Sibly RM, Brown JH. (2007) Effects of body size and lifestyle on evolution of mammal life histories. P Natl Acad Sci USA 104: 17707–17712.

8. Ricklefs RE, Wikelski M. (2002) The physiology/life-history nexus. Trends Ecol Evol 17: 462–468.

9. Okie JG, Boyer AG, Brown JH, Costa DP, Ernest S, Evans AR, et al. (2013) Effects of allometry, productivity and lifestyle on rates and limits of body size evolution. P Roy Soc B-Biol Sci 280.

10. Le Quesne WJ, Jennings S. (2012) Predicting species vulnerability with minimal data to support rapid risk assessment of fishing impacts on biodiversity. J Appl Ecol 49: 20–28.

11. Sibly RM, Brown JH. (2007) Effects of body size and lifestyle on evolution of mammal life histories. P Natl Acad Sci USA 104: 17707–17712.

12. Suding KN, Lavorel S, Chapin F, Cornelissen JH, Diaz S, Garnier E, et al. (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Glob Change Biol 14: 1125–1140.

13. Schindler DE, Essington TE, Kitchell JF, Boggs C, Hilborn R. (2002) Sharks and Tunas: Fisheries Impacts on Predators with Contrasting Life Histories. Ecol Appl 12: 735–748.

14. Anderson CNK, Hsieh CH, Sandin SA, Hewitt R, Beddington A, Kitchell JF, Boggs C, Hilborn R. (2008) Why fishing magnifies fluctuations in fish abundance. Nature 452: 835–839. doi: 10.1038/nature06851 PMID: 18421346

15. Hoegh-Guldberg O, Bruno JF. (2010) The impact of climate change on the world's marine ecosystems. Science 328: 1523–1528. doi: 10.1126/science.1189930 PMID: 20558709

16. McGowan JA, Cayan DR, Dorman LM. (1998) Climate-ocean variability and ecosystem response in the northeast Pacific. Science 281: 210–217. PMID: 9660743

17. Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan KS, Lima M. (2002) Ecological effects of climate fluctuations. Science 297: 1292–1296. PMID: 12193777

18. Boyle PR, Rodhouse PG (2005) Cephalopods: Ecology and Fisheries. Oxford: Blackwell Science Ltd.

19. Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM, Harrison LR, et al. (2014) Extinction risk and conservation of the world's sharks and rays. Elife 3: e00590. doi: 10.7554/eLife.00590 PMID: 24448405

20. Field IC, Meekan MG, Buckworth RC, Bradshaw CJ. (2009) Susceptibility of Sharks, Rays and Chimaeras to Global Extinction. Adv Mar Biol 56: 275–363. doi: 10.1016/S0065-2881(09)56004-X PMID: 19895977

21. Pierce GJ, Valavanis VD, Guerra A, Jereb P, Orsi-Relini L, Bellido JM, et al. (2008) A review of cephalopod-environment interactions in European Seas. Hydrobiologia 612: 49–70.

22. Caddy JF, Rodhouse PG. (1998) Cephalopod and groundfish landings: evidence for ecological change in global fisheries? Rev Fish Biol Fisher 8: 431–444.
31. Rodhouse PGK, Pierce GJ, Nichols OC, Sauer WHH, Arkhipkin AI, Laptikhovsky VV, et al. (2014) Environmental effects on cephalopod population dynamics: implications for management of fisheries. Adv Mar Biol 67: 99–233. doi: 10.1016/B978-0-12-800287-2.00002-0 PMID: 24880795
32. Smith JM, Pierce GJ, Zuur AF, Boyle PR. (2005) Seasonal patterns of investment in reproductive and somatic tissues in the squid Loligo forbesi. Aquat Living Resour 18: 341–351.
33. Hoving HJ, Gilly WF, Markaida U, Benoît-Bird KJ, Brown ZW, Daniel P, et al. (2013) Extreme plasticity in life-history strategy allows a migratory predator (jumbo squid) to cope with a changing climate. Glob Change Biol 19: 2089–2103.
34. Jackson GD, Pecl GT. (2003) The dynamics of the summer-spawning population of the loliginid squid (Sepioteuthis australis) in Tasmania, Australia—a conveyor belt of recruits. ICES J Mar Sci 60: 290–296.
35. Molschaniwskyj NA, Pecl GT, Lyle J. (2002) An assessment of the use of short-term closures to protect spawning southern calamy aggregations from fishing pressure in Tasmania, Australia. B Mar Sci 71: 501–514.
36. Hutchings JA, Myers RA, Garcia VB, Lucifora LO, Kuparinen A. (2012) Life-history correlates of extinction risk and recovery potential. Ecol Appl 22: 1061–1067. PMID: 22827118
37. Bradley D, Gaines SD. (2014) Counting the cost of overfishing on sharks and rays. Elife 3: e02199. doi: 10.7554/eLife.02199 PMID: 24499984
38. Dulvy NK, Metcalfe JD, Gianvillle J, Pawson MG, Reynolds JD. (2000) Fishery stability, local extinctions, and shifts in community structure in skates. Conserv Biol 14: 283–293.
39. Worm B, Davis B, Kettemer L, Ward-Paige CA, Chapman D, Heithaus MR, et al. (2013) Global catches, exploitation rates, and rebuilding options for sharks. Mar Policy 40: 194–204.
40. Link JS. (2013) Ecosystem Approaches to Fisheries: A Global Perspective. Fisheries 38: 463.
41. Jennings S, Rice J. (2011) Towards an ecosystem approach to fisheries in Europe: a perspective on existing progress and future directions. Fish Fish 12: 125–137.
42. Bertrand JA, de Sola LG, Papaconstantinou C, Relini G, Souplet A. (2002) The general specifications of the MEDITS surveys. Sci Mar 66: 9–17.
43. Cuccu D, Mereu M, Cau A, Pesci P, Cau A. (2013) Reproductive development versus estimated age and size in a wild Mediterranean population of Octopus vulgaris (Cephalopoda: Octopodidae). J Mar Biol Assoc U K 93: 843–849.
44. Silva L, Sobrino I, Ramos F. (2002) Reproductive biology of the common octopus, Octopus vulgaris Cuvier, 1797 (Cephalopoda: Octopodidae) in the Gulf of Cadiz (SW Spain). B Mar Sci 71: 837–850.
45. Regueira M, Gonzalez AF, Guerra A. (2015) Determination of age and growth of the horned octopus Eledone cirrhosa (Cephalopoda: Octopoda) using stylet increment analysis. Sci Mar 79: 71–78.
46. Regueira M, Gonzalez AF, Guerra A, Soares A. (2013) Reproductive traits of horned octopus Eledone cirrhosa in Atlantic Iberian waters. J Mar Biol Assoc U K 93: 1641–1652.
47. Gonzalez AF, Guerra A. (2013) Illex coindetii, broadtail shortfin squid. In: Rosa R, Pierce GJ, O’Dor R, editors. Advances in squid biology, ecology and fisheries. Part II: Oegopsid squids. New York: Nova Science Publishers. pp. 49–71.
48. Ivory P, Jeal F, Nolan CP. (2004) Age Determination, Growth and Reproduction in the Lesser-spotted Dogfish, Scyliorhinus canicula (L.). J North Atl Fish Sci 35: 89–106.
49. Kousteni V, Kontopoulou M, Megalofonou P. (2010) Sexual maturity and fecundity of Scyliorhinus canicula (Linnaeus, 1758) in the Aegean Sea. Mar Biol Res 6: 390–398.
50. Kadri H, Marouani S, Saidi B, Bradai MN, Bouain A, Morize E. (2014) Age, growth, sexual maturity and reproduction of the thornback ray, Raja clavata (L.), of the Gulf of Gabes (south-central Mediterranean Sea). Mar Biol Res 10: 416–425.
51. Ellis JR, Shackley SE. (1995) Observations on egg-laying in the thornback ray. J Fish Biol 46: 903–904.
52. Moore D, Neat F, Mccarthy I. (2013) Population biology and ageing of the deep water sharks Galeus melastomus, Centroseelachus crepidater and Apristurus aphyodes from the Rockall Trough, north-east Atlantic. J Mar Biol Assoc U K 93: 1941–1950.
53. Capape C, Guelorget O, Vergne Y, Reynaud C. (2008) Reproductive biology of the blackmouth cat shark, Galeus melastomus (Chondrichthyes:Scyllorhinidae) off the Languedocian coast (southern France, northern Mediterranean). J Mar Biol Assoc U K 88: 415–421.
54. Witt MJ, Godley BJ. (2007) A Step Towards Seascape Scale Conservation: Using Vessel Monitoring Systems (VMS) to Map Fishing Activity. Plos One 2: e1111. PMID: 17971874
55. Lee J, South AB, Jennings S. (2010) Developing reliable, repeatable, and accessible methods to provide high-resolution estimates of fishing-effort distributions from vessel monitoring system (VMS) data. ICES J Mar Sci 67: 1260–1271.

56. Chang SK, Yuan TL. (2014) Deriving high-resolution spatiotemporal fishing effort of large-scale longline fishery from vessel monitoring system (VMS) data and validated by observer data. Can J Fish Aquat Sci 71: 1363–1370.

57. Merino G, Quetglas A, Maynou F, Garau A, Arrizabalaga H, Murua H, et al. (2015) Improving the performance of a Mediterranean demersal fishery toward economic objectives beyond MSY. Fish Res 161: 131–144.

58. Eastwood P, Mills C, Aldridge J, Houghton C, Rogers SI. (2007) Human activities in UK offshore waters: an assessment of direct, physical pressure on the seabed. ICES J Mar Sci 64: 453–463.

59. Fernandez de Puelles ML, Alenamy F, Janss J. (2007) Zooplankton time-series in the Balearic Sea (Western Mediterranean): Variability during the decade 1994–2003. Prog Oceanogr 74: 329–354.

60. Kalnay E, Kanamitsu M, Kistler R, Collins W, Deaven D, Gandin L, et al. (1996) The NCEP/NCAR 40-year reanalysis project. B Am Meteorol Soc 77: 437–471.

61. Lloret J, Leonart J, Sole I, Fromentin JM. (2001) Fluctuations of landings and environmental conditions in the north-western Mediterranean Sea. Fish Oceanogr 10: 33–50.

62. Quetglas A, Ordines F, Valls M. (2011) What drives seasonal fluctuations of body condition in a semelparous income breeder octopus? Acta Oecol 37: 476–483.

63. Wood SN. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J R STAT SOC B 73: 3–36.

64. Schultner J, Kitatsky A, Gabrielsen G, Hatch S, Bech C. (2013) Differential reproductive responses to stress reveal the role of life-history strategies within a species. P Roy Soc B-Biol Sci 280: 20132090.

65. Heppell SS, Caswell H, Crowder LB. (2000) Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. Ecology 81: 654–665.

66. Barnett LA, Winton MV, Ainsley SM, Cailliet GM, Ebert DA. (2013) Comparative Demography of Skates: Life-History Correlates of Productivity and Implications for Management. Plos One 8: e65000. doi: 10.1371/journal.pone.0065000 PMID: 23741442

67. Puerta P, Hidalgo M, Gonzalez M, Esteban A, Quetglas A. (2014) Role of hydro-climatic and demographic processes on the spatio-temporal distribution of cephalopods in the western Mediterranean. Mar Ecol Progr Ser 514: 105–118.

68. Puerta P, Hunsicker ME, Quetglas A, Alvarez-Berastegui D, Esteban A, Gonzalez M, et al. (2015) Spatially Explicit Modeling Reveals Cephalopod Distributions Match Contrasting Trophic Pathways in the Western Mediterranean Sea. Plos One 10.

69. Dulvy NK, Baum JK, Clarke S, Compagno LJV, Cortes E, Domingo A, et al. (2008) You can swim but you can’t hide: the global status and conservation of oceanic pelagic sharks and rays. Aquat Conserv 18: 459–482.

70. Guijarro B, Quetglas A, Moranta J, Ordines F, Valls M, Gonzalez N, et al. (2012) Inter- and intra-annual trends and status indicators of nektobenthic elasmobranchs off the Balearic Islands (northwestern Mediterranean). Sci Mar 76: 87–96.

71. Barausse A, Micheli A, Riginella E, Palmeri L, Mazzioli C. (2011) Long-term changes in community composition and life-history traits in a highly exploited basin (northern Adriatic Sea): the role of environment and anthropogenic pressures. J Fish Biol 79: 1453–1486. doi: 10.1111/j.1095-8649.2011.03139. x PMID: 22136236

72. Barausse A, Correale V, Curkovic A, Finotto L, Riginella E, Visentin E, et al. (2014) The role of fisheries and the environment in driving the decline of elasmobranchs in the northern Adriatic Sea. ICES J Mar Sci 71: 1593–1603.

73. Ferretti F, Osio GC, Jenkins CJ, Rosenberg AA, Lotze HK. (2013) Long-term change in a meso-predator community in response to prolonged and heterogeneous human impact. Sci Rep 3: 1057. doi: 10.1038/srep01057 PMID: 23309344

74. Fortiboni T, Libralato S, Raicevich S, Giovanardi O, Solidoro C. (2010) Coding Early Naturalists’ Accounts into Long-Term Fish Community Changes in the Adriatic Sea (1800–2000). Plos One 5: e15502. doi: 10.1371/journal.pone.0015502 PMID: 21109349

75. Cavanagh RD, Gibson C (2007) Overview of the conservation status of cartilaginous fishes (Chondrichthys) in the Mediterranean Sea. IUCN, Gland, Switzerland and Malaga, Spain. vi + 42 pp.

76. Bromham L. (2011) The genome as a life-history character: why rate of molecular evolution varies between mammal species. Philos T R Soc B 366: 2503–2513.
77. Juan-Jorda MJ, Mosqueira I, Freire J, Dulvy NK. (2015) Population declines of tuna and relatives depend on their speed of life. P Roy Soc B-Biol Sci 282: 20150322.
78. Oli MK. (2004) The fast-slow continuum and mammalian life-history patterns: an empirical evaluation. Basic Appl Ecol 5: 449–463.
79. Rochet MJ, Cornillon PA, Sabatier R, Pontier D. (2000) Comparative analysis of phylogenetic and fishing effects in life history patterns of teleost fishes. Oikos 91: 255–270.
80. Quetglas A, Keller S, Massuti E. (2015) Can Mediterranean cephalopod stocks be managed at MSY by 2020? The Balearic Islands as a case study. Fish Manag Ecol 22: 349–358.
81. Andre J, Haddon M, Pecl GT. (2010) Modelling climate-change-induced nonlinear thresholds in cephalopod population dynamics. Glob Change Biol 16: 2866–2875.
82. Quetglas A, Guijarro B, Ordines F, Massuti E. (2012) Stock boundaries for fisheries assessment and management in the Mediterranean: the Balearic Islands as a case study. Sci Mar 76: 17–28.
83. Rogers SI, Clarke KR, Reynolds JD. (1999) The taxonomic distinctness of coastal bottom-dwelling fish communities of the North-east Atlantic. J Anim Ecol 68: 769–782.
84. Stevens JD, Bontli R, Dulvy NK, Walker PA. (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthysans), and the implications for marine ecosystems. ICES J Mar Sci 57: 476–494.
85. Ferretti F, Myers RA, Serena F, Lotze HK. (2008) Loss of large predatory sharks from the Mediterranean Sea. Conserv Biol 22: 952–964. doi: 10.1111/j.1523-1739.2008.00938.x PMID: 18544092
86. Saether BE, Coulson T, Grotan V, Engen S, Altwegg R, Armitage KB, et al. (2013) How Life History Influences Population Dynamics in Fluctuating Environments. Am Nat 182: 743–759. doi: 10.1086/673497 PMID: 24231536
87. Scott RD, Sampson DB. (2011) The sensitivity of long-term yield targets to changes in fishery age-selectivity. Mar Policy 35: 79–84.
88. Finley C, Oreskes N. (2013) Maximum sustained yield: a policy disguised as science. ICES J Mar Sci 70: 245–250.
89. Larkin PA. (1977) An epitaph for the concept of Maximum Sustainable Yield. T Am Fish Soc 106: 1–11.
90. Mackinson S, Deas B, Beveridge D, Casey J. (2009) Mixed-fishery or ecosystem conundrum? Multi-species considerations inform thinking on long-term management of North Sea demersal stocks. Can J Fish Aquat Sci 66: 1107–1129.
91. Mueter FJ, Megrey BA. (2006) Using multi-species surplus production models to estimate ecosystem-level maximum sustainable yields. Fish Res 81: 189–201.
92. Walters CJ, Christensen V, Martell SJ, Kitchell JF. (2005) Possible ecosystem impacts of applying MSY policies from single-species assessment. ICES J Mar Sci 62: 558–568.