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Recreational angling intensity correlates with alteration of vulnerability to fishing in a carnivorous coastal fish species

Josep Alós, Miquel Palmer, Pedro Trías, Carlos Díaz-Gil, and Robert Arlinghaus

Abstract: Increased timidity is a behavioral response to exploitation caused by a combination of learning and fisheries-induced selection favoring shy fish. In our study, the potential for angling-induced change in fish behavior was examined in two marine coastal fishes exploited by boat recreational fishing in the Mediterranean (Mallorca, Spain). It was expected that the mean vulnerability to capture of surviving individuals would differ across a gradient of previous exposure to recreational angling and that this effect would be present in multiple species. The prediction received partial empirical support. Recreational angling intensity was correlated with enhanced gear-avoidance behavior in only one of the two study species, the carnivorous painted comber (*Serranus scriba*). By contrast, the omnivorous fish species in our study, the annular seabream (*Diplodus annularis*), did not differ in its behavior towards hooks in exploited compared with unexploited sites. These results suggest that recreational angling may contribute to patterns of hyperdepletion in catch rates because of increased timidity and associated reduced vulnerability to fishing gear in some exploited species. Such effects would lead to erroneous interpretations about the status of the fish stocks when assessed by fishery-dependent data and would negatively affect catch rates and quality of the fishery in the affected species.

Résumé : Une timidité accrue est une réaction comportementale à l'exploitation, causée par une combinaison d'apprentissage et de sélection induite par la pêche qui favorise les poissons timides. Dans notre étude, le potentiel de changement de comportement des poissons induit par la pêche à la ligne a été examiné chez deux poissons marins côtiers exploités par pêche sportive en bateau dans la Méditerranée (Majorque, Espagne). Il était prévu que la vulnérabilité moyenne à la capture des individus survivants varierait le long d'un gradient d'exposition passée à la pêche sportive à la ligne et que cet effet serait présent chez plus d'une espèce. Cette prédiction est partiellement appuyée par les observations empiriques. L'intensité de la pêche sportive à la ligne était corrélée à un comportement rehaussé d'évitement des engins chez seulement une des deux espèces étudiées, le serran écriture (*Serranus scriba*), un poisson carnivore. En revanche, il n'y avait pas de différence de comportement à l'égard des hameçons chez l'espèce omnivore étudiée, le sparaillon (*Diplodus annularis*), entre les sites exploités et non exploités. Ces résultats donnent à penser que la pêche sportive à la ligne pourrait contribuer aux motifs d'hyperdiminution des taux de prises en raison de l'augmentation de la timidité et de la diminution associée de la vulnérabilité aux engins de pêche chez certaines espèces exploitées. De tels effets mèneraient à des interprétations erronées concernant l'état des stocks de poissons évalué à partir de données dépendant de la pêche et auraient un effet négatif sur les taux de prises et la qualité de la pêche aux espèces touchées. [Traduit par la Rédaction]

Introduction

Fish behavior plays a key role in determining and moderating the impact of fishing on wild populations, inter alia, because it affects the vulnerability of individual fish to fishing gear (Walters and Martell 2004). The aggregated vulnerability of individuals in an exploited stock to fishing effort is subsumed in fisheries literature in the catchability coefficient (Arreguín-Sánchez 1996). Any change induced by fishing in the population-level catchability as a function of alteration of individual-level vulnerability to fishing will affect fishing quality because, for example, recreational anglers derive satisfaction from high catch rates (Arlinghaus 2006). Moreover, fishing-induced changes in vulnerability-related behavior, and consequently catchability, will affect fishery-dependent assessments because of the potential for decoupling fish abundance and catch rates (Pauly et al. 2013; Pine et al. 2009; Walters 2003). Despite its importance, the behavioral dimension of selective fisheries has been poorly explored (Arlinghaus et al. 2013; Olsen et al. 2012; Parsons et al. 2011).

Foraging arena theory provides a suitable framework for the mechanistic study of the consequences of behavior-based changes in response to fishing (Ahrens et al. 2012). It is assumed in foraging arena theory that predation risk caused by natural predators or fishing is one of the major selective forces leading to behavioral adaptation. Accordingly, to avoid predation, in any moment fish populations cluster into two mutually exclusive states of being vulnerable or invulnerable to predation (including fishing) (Ahrens et al. 2012; Walters and Martell 2004). The risk-sensitive behavioral decisions of fish (e.g., the decision to stay in safe refuges) ultimately will

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determine the proportion of fish that are vulnerable to fishing gear. The transition rate between the vulnerable and invulnerable pools in relation to risk of being harvested has been shown to have a genetic component in fish (Klefoth et al. 2013; Biro and Post 2008; Philipp et al. 2009), but can also be strongly affected by phenotypically plastic responses to a range of ecological processes (e.g., availability of refuges, presence of predators, Abrams et al. 2012; Inoue et al. 2005; Matsuda and Abrams 2004). Cox and Walters (2002) applied foraging arena theory to recreational angling, theorizing that foraging arenas also exist in relation to the fish reactions to the threat of angling. Indeed, similar to hunting (Ciuti et al. 2012), recreational fisheries may create a "landscape of fear" (Januchowski-Hartley et al. 2013*a*) that increasingly moves risk-sensitive fish into invulnerable pools (Klefoth et al. 2013). Assessing the proportions of vulnerable and invulnerable fish in different moments in time and studying how the proportions vary with fishing intensity therefore seems a suitable starting point to furthering our understanding about how fishing may alter behavior of fish.

Two not mutually exclusive mechanisms can affect the flow of fish from vulnerable to invulnerable pools in response to fishing: (*i*) an evolutionary (i.e., genetic) response favoring invulnerable behavioral phenotypes caused by fisheries selectively capturing bold genotypes that actively forage outside refuges (Uusi-Heikkilä et al. 2008; Sutter et al. 2012; Wohlfarth et al. 1975), and (*ii*) acquisition of gear avoidance behavior through individual or social learning from previous experiences (Beukema 1968, 1970; Klefoth et al. 2013; Raat 1985; van Poorten and Post 2005). Selective capture of certain behavioral types has recently received some scientific attention owing to the growing evidence that fish, like many other vertebrates, show consistent individual differences in their behavioral patterns across time and contexts (i.e., personality or behavioural type; Conrad et al. 2011; Mittelbach et al. 2014). The assumption is that there is genetic variance associated with behavioral variation (Ariyomo et al. 2013) and that bolder and more explorative or active fish are more easily captured by many fishing gears than less bold, explorative, or active behavioral types (Biro and Post 2008; Côté et al. 2014; Sutter et al. 2012; but see Wilson et al. 2011). The second plasticity mechanism instead focuses on the ability of fish to quickly adjust their behavior due to learning, either by observing other fish being attacked by predators or from their own encounters with predators, which may include encounters with fishing gear as a form of human-induced predation threat (Brown et al. 2013; Klefoth et al. 2011; Warburton 2003). Both processes would leave behind individuals that are intrinsically harder to catch, thereby increasing the proportion of fish in invulnerable pools as fishing intensity magnifies.

The potential for species-specific behavioral responses to recreational angling gear in the wild and how these changes alter the proportion of vulnerable and invulnerable pools with increasing fishing pressure remain largely unexplored questions (for example, see Januchowski-Hartley et al. 2013*b*). The objective of the present work was to provide empirical evidence in relation to these questions by analyzing the vulnerability to recreational angling gear of two fish species with contrasting foraging ecology. We empirically tested the hypothesis that human predation risk (as induced by recreational boat angling) induces a change in behavior (Klefoth et al. 2011) that alters the proportion of fish in vulnerable and invulnerable pools in two exploited coastal fish species in the Mediterranean Sea. To test our hypotheses, we contrasted the fishes' risk-taking behavior as determined using an autonomous underwater video recording device in the wild and estimated the proportion of fish in vulnerable and invulnerable pools across a gradient of fisheries-induced risk in exploited and unexploited sites.

Materials and methods

Study species

We studied the popular recreational angling fishery above the *Posidonia oceanica* seagrass meadows in the Mediterranean Sea (March et al. 2014; Seytre and Francour 2014). The habitat supports a species-rich fish community that is primarily based on small-bodied species with confined home ranges, such as the annular seabream (*Diplodus annularis*), the painted comber (*Serranus scriba*), the Mediterranean rainbow wrasse (*Coris julis*), or the comber (*Serranus cabrilla*; see for details of the species composition in the fishery and its size structure in the catch; Alós and Arlinghaus 2013). The fishery is a low-skilled fishery that is based on the use of natural baits (shrimp) fished from anchored boats where the anglers distribute themselves over patches of seagrass, which are known from independent studies to concentrate the targeted species (March et al. 2014). Two of the most targeted fish species are two similar-sized species with different feeding ecologies: *D. annularis* and *S. scriba* (Morales-Nin et al. 2005). The seagrass is the preferred habitat for both species, offering refuge against large-bodied predators, while the use of refuge-free sand habitat is rare (March et al. 2010, 2011). Although the preferred prey of the two study species overlaps somewhat (Stergiou and Karpouzi 2001), both species tend to forage on different prey types within the seagrass habitat. Based on stable isotope studies, *S. scriba* is a carnivorous fish that primarily feeds on mobile prey, such as small fish or decapods (Stergiou and Karpouzi 2001). By contrast, *D. annularis* primarily feeds on small sessile prey, including algae and small bivalves (Pinnegar and Polunin 2000; Stergiou and Karpouzi 2001). Note that *S. scriba* does not feed on *D. annularis* directly, as both species have similar body sizes. Because the two species differ in their feeding ecologies while using the same habitat for refuge and foraging, we selected them as models of an omnivorous and a carnivorous exploited fish in the present work.

Study site and fishing pressure index

Along the 20 m isobath of the coastline of the inner Palma Bay in Mallorca (39°34′N, 2°38′E), northwestern Mediterranean (see online supplementary data, Fig. S1[1]), we randomly selected 54 sampling sites over the seagrass meadows of *P. oceanica*. Sites were separated from each other by a minimum distance of 250 m. The sampled area is regularly frequented by local anglers (Alós and Arlinghaus 2013; Alós et al. 2014*a*).

The probability for an individual fish of encountering a human predator can be considered an index of underlying predation risk (Lima and Dill 1990). For several reasons, the number of angling boats per area constituted a suitable surrogate of the number of encounters between the rather immobile species studied here and the mobile anglers in our study system. First, a larger number of recreational fishing boats per area should correlate with the angling gear density in the water body, thereby increasing the probability of encounter and capture. Second, as the fishery is characterized by low-skill techniques and is carried out in a particular habitat (i.e., seagrass of *P. oceanica*) located close to the shore, we expected the spatial distribution of the anglers and the typology of anglers (e.g., high- and low-skilled) to be uncorrelated. Hence, all sites should be fished by the same angler types because most of them use low-skill techniques in habitats that are accessible and well within the boat distance of harbors. Third, the fishery is predominantly located in the shallow seagrass habitat, and a larger number of boats per area should increase noise levels. This process can generate a change in fish behavior associated with the recreational fishing activity by signaling the presence of an angler (Holles et al. 2013). Hence, one angler-boat unit is likely to constitute a valid fishing pressure unit. Note that the number

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0183.

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of anglers per boat did not vary significantly among the high and low exploited fishing areas we surveyed (ANOVA, $F = 1.403$, p value = 0.245), so that an angler-boat unit seemed an appropriate effort index. It should be noted that there were few if any pleasure boats in the area, and it is thus easy to identify angler boats during censuses (see below for details).

For the reasons given, we approximated the number of encounters between fish and anglers in each sampling site through visual census of recreational fishing boats (Cabanellas-Reboredo et al. 2014). To that end, we considered an area of 1 km^2 around each sampling site, which corresponded to the mean home range size of the two study species (March et al. 2010, 2011), and we visited each field sampling station at least once a month over a 2-year period (2009 and 2010). We first counted the total number of fishing boats on the 54 sampling sites and calculated the total number of fishing boats per square kilometre per census-day. Second, we determined the mean number of fishing boats per square kilometre for each sampling site as a fishing predation risk index. We categorized the fishing predation risk of each sampling site as either low or high based on a median split of mean site-specific fishing boats per square kilometre per day. Fish exposed to the high fishing predation risk were exploited by a mean ± SD (range) of 1.3 ± 0.6 (0.41–3.04) fishing boats per square kilometre per day, whereas the sampling locations categorized as having low fishing risk had a mean ± SD of 0.16 ± 0.13 (0–0.39) fishing boats per square kilometre per day. Accordingly, the fishing predation risk was on average 87% lower in the low-risk sites.

Assessment of fish behavior in the field

We used an autonomous underwater video recording device to record the behavior of the fish when they were exposed to baited hooks (Fig. S2[1]) that represented conventional fishing gear used by recreational fishers in the study area. Underwater video has previously been successfully used to record the behavior of wild marine fish around baited hooks (e.g., Løkkeberg et al. 1989; Mallet and Pelletier 2014). We measured vulnerability-related behavior using the latency time to attack a natural bait as a potential food object presented above the seagrass habitat. Variants of "open field tests" where a bait is offered outside a refuge are sometimes considered a measure of feeding under risk of predation in laboratory trials (Carter et al. 2012; Réale et al. 2007). In our case, the seagrass was both refuge and foraging habitat for both study species (Deudero et al. 2008). The choice of offering the bait above the seagrass or immediate vicinity close to the seagrass was simply convenient to receive good visual enumeration of attack frequencies and latencies, and we cautiously did not interpret the results as a measure of boldness (i.e., feeding under risk of predation) per se. Instead, we called our behavioral measure "vulnerability to fishing".

The experimental protocol was based on simultaneously deploying three different camera devices and baited hooks in each of the 54 sampling stations. The three cameras were identical; they were deployed 50 m apart to ensure that there would be no overlap between the cameras. The cameras continuously recorded (in full high definition) over the seagrass for a period of 10 min. In each 10 min video, all identifiable individuals of *D. annularis* and *S. scriba* were continuously monitored. No cameras were deployed when anglers were present in the sampling site. We recorded the latency time as the duration in seconds from the time at which a focal fish appeared in the video field to the time until the fish potentially approached and ingested one of five baited hooks with a piece of shrimp (*Penaeus vannamei*, the commonly bait and gear used in the fishery; Alós and Arlinghaus 2013). The hook shank was cut to prevent hooking the fish. Instead, we assumed a "theoretical capture" event whenever an individual fish ingested the bait and the individual was not tracked in the video any longer. We considered the individuals that did not ingest the bait to be right-censored data. The use of underwater video cameras usually do not allow for identification of the individual (Mallet and Pelletier 2014). Therefore, we could not discard the existence of some bias of measuring the latency time twice in an individual that left the field of the camera (right-censored data) and reentered in the field after. We accounted for this potential bias by testing through ANOVA if the number of fish measured per video was independent of the fishing pressure (high or low). We found a nonsignificant effect of the fishing pressure in the number of fish measured in both species (*D. annularis*: ANOVA, $F = 0.267$, $p = 0.61$; and *S. scriba*: ANOVA, $F = 0.127$, $p = 0.724$). We therefore disregarded the fact that the number of potential individuals measured for more than one time affected the intraspecific individual behavior differences in low and high fishing intensity environments. We performed a survival analysis on the latency times of noncaptured and hypothetically captured fish (see below). All of the *S. scriba* ($n = 62$ fish) sampled and a random representative sample of the whole of the sampling stations of *D. annularis* ($n = 119$ fish) were analyzed (Fig. 1).

Once the three experimental trials in one site station were completed, we visited another sampling site until all of the sites were sampled at random. For logistical reasons, it was impossible to sample all 54 sites in 1 day. Therefore, we structured the sampling into 4 days (sampling time from 0900 to 1300). On each sampling day, we visited a number of different sampling stations ($n = 12$, 13, 14, and 15 sampling sites per day), but the order of sampling within days was fully randomized. This meant that we visited sampling stations spaced across the entire field site and covering both harvesting pressure sites on each sampling day. Overall, a total of 162 experimental trials (videos of 10 min duration) were collected.

Data analysis

Two possible confounding variables were assessed and subsequently controlled in the modelling process: the effect of habitat characteristics and the density of potential competitors for food. First, although all of the experimental trials were conducted in seagrass meadows, we explicitly considered the presence of microhabitats (e.g., the presence of a rock in the seagrass, patchy sandy or muddy sediment within the seagrass; Fig. S3[1]). We categorized the habitat as absence or presence (0 or 1) of seagrass, rocks, sand, or mud and obtained a matrix of multiple habitat combinations (up to eight combinations of absence and presence of the specific habitats). We reduced these multiple combinations of habitats using a principal component analysis (PCA; Fig. S3[1]). The first two axes of the habitat-specific PCA explained 82% of the total variability. One main microhabitat gradient was identified for each of the axes (Fig. S3[1]; PC1: gradient involving the presence of rocks (negative scores) and PC2: presence of mud (positive scores) in the seagrass). We used the first two PCA components instead the eight combinations of habitats in all further analyses by adopting the PCA scores of the first and second axes as variables. Second, using the video footage, we also measured the density of potential competitors by counting the total number of fish of the same and any other species located in the sampling area at the moment a focal individual of either one of the two species appeared in the camera field. Both potentially confounding variables were considered as covariates in further data analyses.

We used survival analysis on latency time to ingest a bait as surrogate for being vulnerable to harvest to investigate the factors that affected the time at which the particular event occurred (Hougaard 1999). Survival analysis of the sort tackled here has to deal with an important challenge; not all fish ingested the bait within the duration of an experimental trial. Therefore, the exact latency time is unknown for some fish that did not reach the endpoint of the event (i.e., theoretical capture). These partially missing data are called right-censored data (Hougaard 1999). To account for this, specific likelihood functions have been developed in past survival analysis applications (Crawley 2007). From

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Fig. 1. Histogram of the latency times (in seconds) observed in *S. scriba* (left panel, *n* in low fishing intensity sites = 37 and *n* in high fishing intensity site = 25) and *D. annularis* (right panel, *n* in low fishing intensity sites = 60 and *n* in high fishing intensity sites = 59). The inset panels show the proportion of captured (black) and noncaptured (grey) fish for both species defining the group (pool) sizes of vulnerable and invulnerable fish in high and low fishing intensities. Note the decrease in the proportion of captured fish in high fishing intensity sites in *S. scriba*.

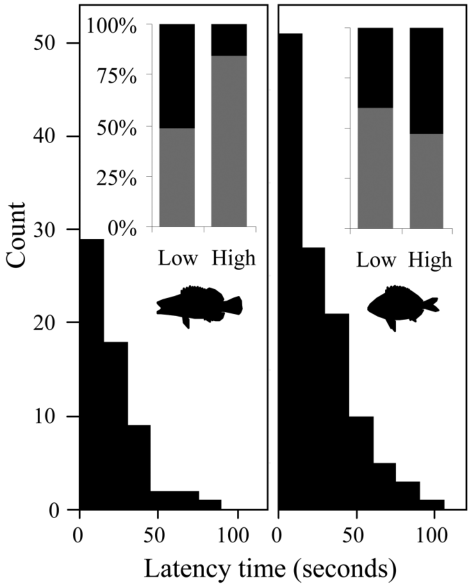


Table 1. Minimal adequate survival models fitted to explore inter- and intraspecies differences in survivorship (i.e., noncapture) and multiple predictors.

	Coef	exp (coef)	SE (coef)	*z* value	Pr(>|*z*|)
Between-species comparison (*n* = 93)					
Species (*S. scriba*)	0.945	2.572	0.306	3.091	0.002
PC1	−0.294	0.745	0.156	−1.882	0.060
Likelihood ratio test = 13.59 on 2 df, *p* = 0.0011					
Within-species comparison					
D. annularis (*n* = 119)					
PC1	−0.461	0.631	0.162	−2.897	0.004
PC2	0.250	1.285	0.140	2.061	0.039
Likelihood ratio test = 8.13 on 2 df, *p* = 0.017					
S. scriba (*n* = 62)					
Fishing predation risk (high)	−1.756	0.173	0.653	−2.690	0.007
PC1	−0.968	0.380	0.517	−1.870	0.061
PC2	−3.521	0.030	1.030	−3.420	0.001
Likelihood ratio test = 28.42 on 3 df, *p* < 0.001					

Note: Cox regression coefficients (coef), standard error (SE), *z* value, and *p* value of the minimal adequate survival models fitted to explore inter- and intraspecies differences in the survivorship (i.e., noncapture) and multiple predictors. The full model included species in the case of interspecies comparison, harvesting pressure in the case of intraspecies comparison, habitat characteristics (PC1: gradient from the presence of rocks (negative score) to the presence of sand (positive scores) in the seagrass; and PC2: the presence of mud in the seagrass (positive scores)), and the density of competitors. The table shows the fixed factors that are included in the minimally adequate model as well as the likelihood ratio test. In all cases, random effects were not significant and not included in the model.

these, we chose a Cox regression model for describing the probability of noncapture (survivorship) against a set of explanatory variables. The sample unit for a survival analysis was each individual fish censored, and the full survival model included the fixed properties of the treatments (i.e., harvesting pressure, habitat type using the PCA scores, and the abundance of conspecifics or heterospecifics) and the random effect of day. We performed two different types of analyses: (*i*) a test for assessing the existence of interspecies differences (*S. scriba* versus *D. annularis*) in relation to the intrinsic vulnerability to capture based on a scenario of low harvesting pressure (which was assumed to represent a more natural situation with less intensive human-induced disturbances) and (*ii*) two intraspecies models for assessing the effects on capture probability attributable to the harvesting pressure (high versus low) and all relevant covariates. We used the "coxph" function in the survival library of the R package (developed by T. Therneau and T. Lumleyat; http://cran.r-project.org/web/packages/survival/survival) to estimate the model parameters of the minimally adequate model (Akaike information criterion (AIC)-based stepwise selection using the function "step") and the likelihood ratios of the model. The predicted capture rates at different times and for different factors (species or harvesting pressure) were estimated using the function "survfit" from the same library to visualize the results. The stabilization of the survival probability over time was useful to explore the proportion of fish that remained invulnerable to the fishing gear, and this information was used to test the clustering of fish into invulnerable and vulnerable components, as predicted by foraging arena theory (Ahrens et al. 2012).

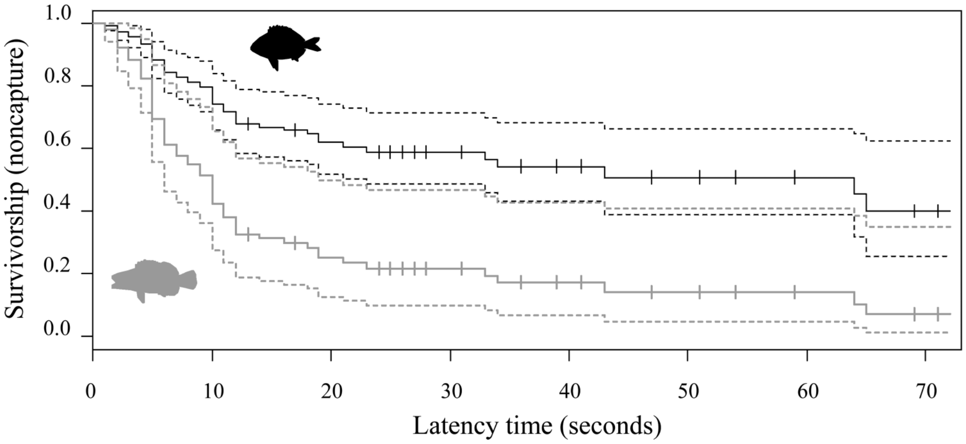
To assess the relationship of harvesting pressure and true fish abundance and to appreciate whether alterations of fishing vulnerability may decouple catch rates from abundance, we derived an index of relative abundance to compare the number of fish of each species that appeared on the videos in relation to the two types of fishing pressure while controlling for all potentially confounding variables. We used all fish (*S. scriba* and *D. annularis*) that appeared on the videotape during the 10 min and treated this measure as a fishery-independent measure of the relative abundance (number of fish per 10 min). We obtained a total of 162 measures (i.e., 162 videos that were 10 min in length) of relative abundance to explore patterns of abundance in relation to harvesting pressure (high versus low). Differences in the index of relative abundance at sites with different harvesting pressure were explored via a generalized linear mixed model (GLMM; Zuur et al. 2009). A Poisson distribution was assumed because the relative abundance was expressed as count data (number of fish in 10 min). The relative abundance values of *S. scriba* and *D. annularis* were considered dependent variables. The sample unit was the video, and the harvesting pressure (low versus high), habitat type (PC1 and PC2), and depth (m) were included as explanatory variables (fixed factors). The design was nested and fully balanced; the three replicates (three videos) per site obtained were incorporated as random nested factors (videos nested in site and day because the whole of the sites were sampled over 4 different days) in the model. The effects of the fixed and random factors were eventually included in the minimally adequate model following a forward step-by-step approach by comparing the model with and without the factors using a likelihood-ratio test (Zuur et al. 2009). The parameter estimates were generated using the "lme4" library (by D. Bates and M. Maechler; http://cran.r-project.org/web/packages/lme4) in the R package.

Results

Interspecific comparison of behavior in low fishing intensity environments

In the sites that experienced low fishing (harvesting) pressure, *S. scriba* (*n* = 37) showed a shorter mean latency time to approach and ingest a baited hook compared with *D. annularis* (Table 1). The fraction of noncaptured *S. scriba* individuals declined within the first 10 s of the experiment trial, indicating vulnerable individuals. Over 60% of the *S. scriba* individuals were "captured" within a few seconds after the presentation of the baited stimulus (Fig. 2).

Fig. 2. Predicted survivorship of the Cox regression fitted to explore changes in the latency time (seconds) and the probability to theoretical survival (noncapture) in the two species studied in low fishing intensity sites. The solid lines show the survival distribution, and the broken lines show the confidence intervals (±95%) in *S. scriba* (grey, $n = 37$) and *D. annularis* (black, $n = 60$). Note the minimum overlap of the confidence intervals (95%), which indicates significant differences ($p < 0.001$).



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The probability of avoiding capture stabilized at a value of approximately 10% (i.e., only one-tenth of *S. scriba* were invulnerable to harvest within 10 min of gear deployment; Fig. 2).

The behavioral response of *D. annularis* ($n = 60$) to baited gear in low fishing-induced predation risk environments was different; it was characterized by a longer mean latency time and a smoother decrease in the noncapture probability compared with *S. scriba* (Table 1; Fig. 2). Only approximately 30% of the *D. annularis* individuals were captured within the first 10 s of gear deployment, and the probability of avoiding capture stabilized at 50%, meaning that half of the *D. annularis* remained invulnerable to harvest within 10 min of gear deployment (Fig. 2). The percentage of *D. annularis* captured in the first 10 s of gear deployment was much less than *S. scriba*, which confirmed the higher intrinsic capture vulnerability of *S. scriba*.

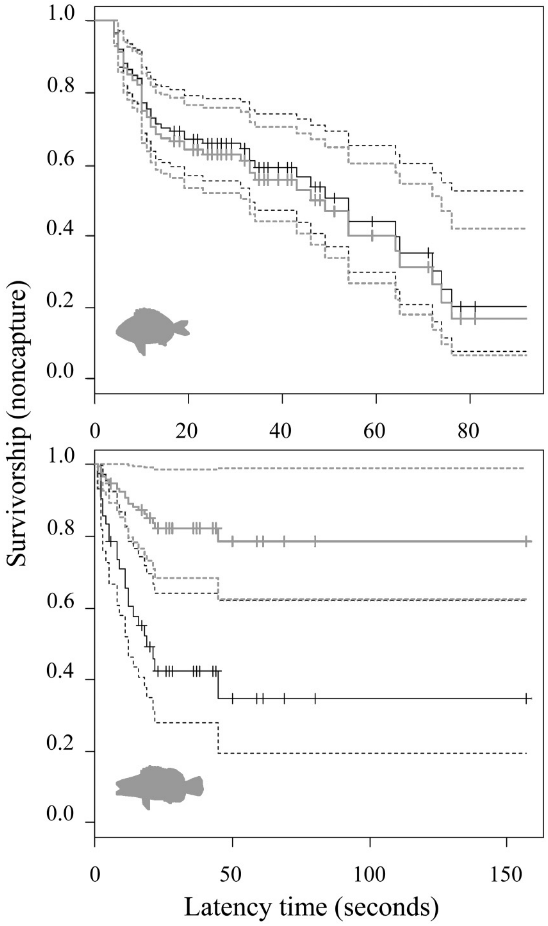
Environmental variables exerted insignificant effects in the interspecific comparison of behavior in low fishing intensity environments. Although the habitat characteristics defined by the PC1 remained in the final model, the final effect on the latency time of this variable was not significant (Table 1). The habitat characteristics defined by the PC2, the number of competitors of the same or other species, and the random variance of the day of sampling had no effect on the latency time in both species and were thus dropped from the final model (Table 1).

Intraspecific individual behavior in low and high fishing intensity environments

Individuals of *D. annularis* inhabiting either low or high fishing-induced predation risk environments did not differ in their latency times, and no evidence for fishery-related effects on behavior towards baited hooks was found (Table 1; Fig. 3). Only the habitat characteristics affected the behavior of *D. annularis* (Table 1). The presence of sand and the absence of rocks or mud in the seagrass increased the latency times (i.e., lowered vulnerability; Table 1). The number of competitors of the same or other species and the random variance of the day of sampling had no effect on the latency time in both species, and these variables were thus dropped from the final model (Table 1).

In *S. scriba*, both fishing-induced predation risk and habitat characteristics had a significant effect on the vulnerability to capture (Table 1). As elaborated before, the behavior of individuals inhabiting low harvesting sites was characterized by short latency times and large probabilities to be rapidly captured (Fig. 3). In the high fishing intensity sites, however, the behavior of *S. scriba* was characterized by long latency times (low vulnerability to fishing) and a smaller overall probability to be captured (Table 1; Fig. 3).

Fig. 3. Predicted survivorship of the Cox regression results fitted to explore changes in the latency time (seconds) and the probability to theoretical survival (noncapture) between the two fishing predation risks: low (black) and high (grey). The solid lines show the survival distribution, and the broken lines show the confidence intervals (±95%) in *D. annularis* (upper panel) and *S. scriba* (lower panel).



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The results revealed that the pools of vulnerable and invulnerable *S. scriba* varied among sites with contrasting fisheries intensity. Although the vulnerable pool of *S. scriba* in low-risk sites represented 70% of the population, only 20% of the individuals were in the vulnerable pool in the high-risk sites at the moment of sampling (Fig. 3). Therefore, we accepted the hypothesis that heavily harvested populations of *S. scriba* were dominated by invulnerable fish. Although PC1 and PC2 remained in the final model of *S. scriba* after AIC-based model reduction, only the presence of mud in the field, denoted by positive values of PC2, had a significant effect by increasing the latency time and hence decreasing the vulnerability to angling (Table 1). Both the number of competitors of the same or other species and the random variance of the day of sampling had no effect on the latency time and were also dropped from the final model (Table 1).

Relative abundance of *S. scriba* and *D. annularis* in low and high fishing intensity sites

Minimal adequate GLMMs only retained variables related to the habitat type to explain the relative abundance of both study species as revealed by video recordings (Table 2). In the case of *D. annularis*, only the habitat variable PC2 (the presence of muddy sediment in the seagrass) was significant, and the abundance of fish decreased with an increasing presence of mud (Table 2). By contrast, the presence of rocks in the seagrass favoured the presence of *S. scriba* (Table 2). Depth (m), fishing intensity, and the random variance of days did not affect the abundance of either species.

Table 2. Estimates, standard error (SE), z values, and p value of the minimally adequate generalized linear mixed models fitted to explore differences between the relative abundance (fish count per 10 min) and multiple predictors in *D. annularis* and *S. scriba*.

	Estimate	SE (estimate)	z value	Pr(>|z|)
***Diplodus annularis* (n = 162, groups = 54)**				
Fixed effects				
(Intercept)	–1.251	0.395	–3.170	0.0015
PC1	–0.307	0.182	–1.694	0.090
PC2	–0.978	0.226	–4.325	$p < 0.001$
Random effects				
Sampling station ($\sigma^2 = 6.47$)				
Likelihood ratio test= 825.84 on 2 df, $p < 0.001$				
***Serranus scriba* (n = 162, groups = 54)**				
Fixed effects				
(Intercept)	–3.544	0.539	–6.581	$p < 0.001$
PC1	–1.318	0.282	–4.667	$p < 0.001$
Random effects				
Sampling station ($\sigma^2 = 5.966$)				
Likelihood ratio test = 187.8 on 1 df, $p < 0.001$				

Note: The full model included depth (m), harvesting pressure (high versus low), and habitat characteristics (PC1: gradient from the presence of rocks (negative score) to the presence of sand (positive scores) in the seagrass; and PC2: the presence of mud in the seagrass (positive scores)). The table shows the fixed and random factors included in the minimally adequate model as well as the likelihood ratio test. The number of groups denoted by the random effects included in the model is shown as well as its variance (σ^2).

Discussion

In our comparative field study, we found evidence of correlation of risk-taking behavior in *S. scriba* in relation to angling intensity. In particular, we found the proportion of fish that were vulnerable to angling to be different in sites varying by fishing intensity levels while controlling for relevant environmental variables related to habitat structure, depth, and competitor density (of conspecifics or heterospecifics). By contrast, no evidence of such variation in behavior was found in *D. annularis*. Irrespective of the exact mechanism (selection or learning) that could cause the alteration in fishing vulnerability in *S. scriba*, our results agree with previous studies (e.g., Biro and Post 2008; Philipp et al. 2009; Sutter et al. 2012) that suggest that at least some exploited fish species respond to fishing by becoming more risk-averse. Such change in behavior increases the pool of invulnerable fish and may contribute to the decoupling of catch rates and fish abundance. The latter statement received some support in our work because we did not detect any differences in relative abundances of either species among fishing risk levels despite the differences in vulnerability to fishing gear detected in *S. scriba*.

A growing body of literature documents the existence of personality and behavioral types in fish, defined as consistent individual differences in behaviors (Sih et al. 2012). There is also growing evidence that fishing selects for some of these behavioral traits; usually bold and aggressive individuals were found to be more vulnerable to capture than shy fish (Alós et al. 2014*b*; Biro and Post 2008; Klefoth et al. 2012, 2013). Accordingly, harvesting with recreational hook-and-line can be expected to generally select for shy and less active phenotypes (Alós et al. 2014*a*; Härkönen et al. 2014), traits that may also be associated with lower life history productivity (Biro and Stamps 2008). In our study, we were not able to directly assess activity in low and highly exploited sites, and we were also unable to generate an independent measure of boldness. Moreover, we did not measure repeatability and consistency of the “latency to bite” measure across different ecological contexts, which prevented us from interpreting our behavioral measure as a personality trait. However, it is undisputed that we found vulnerability to fishing to be substantially different in *S. scriba* that inhabited highly exploited sites compared with individuals living in lower-exploited areas. In this respect, our findings were consistent with previous experimental studies on fishing vulnerability (Alós et al. 2012; Biro and Post 2008; Sutter et al. 2012), and selection of vulnerable behavioral types could explain the results we obtained.

Learning from previous experiences is the other mechanism that may contribute to the patterns we found in *S. scriba* (Anderson and LeRoy Heman 1969; Askey et al. 2006; Young and Hayes 2004). Experiential learning to avoid capture certainly is an important contributor to the expression of risk-taking behavior in fish in response to predation risk by humans (Januchowski-Hartley et al. 2013*a*; Klefoth et al. 2013). Moreover, in addition to plasticity, learning ability has a genetic basis in fishes (Huntingford and Wright 1992). Askey et al. (2006) demonstrated that an exploited catch-and-release fishery of rainbow trout (*Oncorhynchus mykiss*) contained a group of fish that quickly learned to avoid hooks in just 1 week of exploitation, while others continued to be readily captured. Overall, catch rates drastically dropped when rainbow trout fishing started (Askey et al. 2006), mirroring findings previously reported for northern pike (*Esox lucius*) fished with lures (Beukema 1968) and carp (*Cyprinus carpio*) fished with natural bait (Raat 1985). Therefore, declining angling catch rates with increasing angling effort can be expected for some species even when the number of fish remains constant (Askey et al. 2006; Klefoth et al. 2013). Although fisheries-induced evolution of behavior as well as plastic learning might be involved in the results we reported, without common garden experiments we cannot definitively determine whether fishery-induced behavioral change in *S. scriba* was caused by genetic selection acting on the risk-taking behavior trait directly, by genetic selection of learning ability, or by plastic learning from previous hooking or through the observations of conspecifics being hooked and possibly removed. However, irrespective of the mechanism, our work suggests that exploitation can drive populations of *S. scriba* to become more risk-averse, which will decouple angling catch rates and fish abundance as the proportion of invulnerable fish increases.

Based on our study, no generalization across species in terms of fishery-induced decrease in risk-taking behavior is possible. In fact, it is expected that fishery-induced, behavior-based changes may be species-specific by reflecting the evolutionary history of

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fishes (Blowes et al. 2013; Feary et al. 2011; Januchowski-Hartley et al. 2011). We did not find the same responses in *D. annularis* (an omnivorous fish) as we did in *S. scriba* (a carnivorous fish), and the vulnerable proportion of *D. annularis* fish was generally low, independent of angling risk. Species-dependent results could be explained by the feeding ecology of the species (Stoner 2004), assuming that the more aggressive carnivorous fish species would be intrinsically more vulnerable to fishing and hence show stronger responses to the omnivorous species (Abesamis et al. 2014; Donaldson et al. 2011). However, Wilson et al. (2011) noted that shy, omnivorous bluegill (*Lepomis macrochirus*) were preferentially harvested by angling compared with fish that were seined, but these findings do not discount the possibility that angled fish are bolder than the average fish in the population. Indeed, Klefoth et al. (2012, 2013) studied the omnivorous carp (*C. carpio*), revealing a positive relationship between boldness and vulnerability. Therefore, in the three omnivorous fish studied so far, varying scenarios of angling-induced adaptive change in behavior were reported, involving scenarios of increasingly shy (carp) or unaltered (*D. annularis*) behavioral phenotypes. There seems to be limited room for generalization as to which behavioral response to expect towards fishing. By contrast, the available evidence is more consistent in carnivorous fish species, such as largemouth bass (*Micropterus salmoides*) (Cooke et al. 2007) or rainbow trout (Biro and Post 2008). All these studies documented that bolder, more aggressive, and more active fish to be preferentially harvested, similar to the outcomes shown in *S. scriba* in the present work.

We also found species-specific differences in terms of how abundance and latency time to bite varied along microhabitats. Uniform seagrass microhabitats and those scattered with patches of sand decreased the latency time to bite (e.g., theoretical capture was quicker) in *D. annularis* while also increasing its abundance compared with seagrass microhabitats with a presence of rocks (PC1) or mud (PC2). Uniform seagrass habitat corresponds to the preferred foraging habitat of *D. annularis*, presumably because it offers optimal conditions for feeding on small, nonmobile prey types, such as small crustaceans or epiphytes attached to *P. oceanica* (Giakoumi 2013). The habitat effects on abundance and vulnerability to fishing were different in the carnivorous *S. scriba*. In this species, the presence of rocks breaking the uniformity of the seagrass habitat increased the abundance of *S. scriba*, which was consistent with the literature reporting more structured seagrasses to be the preferred habitat of this species (Giakoumi 2013). Interestingly, decreased latency time to attack the bait was found in the less preferred seagrass habitat with muddy patches, presumably because the less structured muddy habitat promoted predation risk assessment, in turn fostering more rapid attacks after deployment of the bait. Our data collectively showed that vulnerability to fishing is not only a function of the fishing pressure and the intrinsic biology of exploited species, but is moderated by habitat features in a species-specific fashion. In light of these findings, further studies of the two species outside *P. oceanica* might be worthwhile to analyze whether the differential fishing pressure found in the present study holds for even less structured habitat. Obviously, more studies with other species are also a worthwhile endeavor.

Our work has four relevant limitations that should be mentioned and ideally addressed in future work. First, we only assessed two species, and inferences expressed towards behavioral change across species in our study must be treated with extreme caution and as tentative at best. Second, our experimental design was designated to assess the behavior of fish above seagrasses. Further work is needed to fully understand the fish behaviors in more open habitat (e.g., rocky or sandy habitats). Third, interspecific behavioral differences should be studied across time and different contexts to infer whether the behavioral change truly has a personality basis. This is an interesting question that has to be addressed in further investigations by incorporating different habitat (ecological context) in the proper assessment of behavioral and temperamental traits, ideally replicating the assessments on individually marked fish over time. The fourth limitation is that we have focused our work on a specific rod-and-reel fishery. Similar work could be done with other passive gear where the same behavioral traits may play a key role determining the fate of the fish. This includes other recreational fishing gears that uses artificial baits, but also commercial fisheries such as longline or trammel nets. We are, however, unsure how fishes would respond to more actively operated gear or how other species inhabiting different habitats (e.g., open water) respond in front of the fishing gears. Our work will hopefully stimulate other groups to perform field experiments such as ours to better understand the role of fishing in the alteration of fish behavior and how this translates to catch rates and hyperdepletion (Hilborn and Walters 1992) and therefore the reliability of stock assessments that are based on fishery-dependent data.

Despite these limitations, we can draw three implications of our study. First, increasing proportions of fish in invulnerable pools in response to fishing in some species can have implications for population dynamics, food web interactions, the productivity of the fishery, and individual fitness. Second, reliably inferring population abundance data from hook-and-line-based catch rate indices will be a challenge with some species, and this challenge likely holds true for other passive harvesting techniques where the capture success strongly depends on fish behavior (e.g., longline, gill netting, or trapping fish). An example from our own work shall illustrate the issue. We did not find any differences in the abundances of the two species in the low and high fishing intensity sites. This finding calls into question our own previous conclusions about the conservation value offered by partial marine protected areas in the Mediterranean (Alós and Arlinghaus 2013). Indeed, we reported earlier that the abundances of *S. scriba* in exploited areas were lower than that in protected areas, but we inferred these results from angling-based catch rate indices. Based on the present work, we might have wrongly equated catch rates to an index of underlying abundance, at least in *S. scriba*. Third and finally, because behavior and life history traits such as growth will often be correlated (Biro and Stamps 2008), one should pay attention to the potential for sampling bias caused by the preferential capture of certain behavioral types that carry phenotypic traits of interest (e.g., growth, Ricker 1969). Active sampling methods may avoid some of this bias but can also suffer from trait-selective sampling (e.g., with respect to swimming speed or schooling tendency). Because this key uncertainty cannot be resolved without fish tracking studies in the wild, we echo Walters and Bonfil (1999) and recommend better experimental studies to further our understanding about the exchange processes between vulnerable and invulnerable arenas. Adding to this challenge, studies are needed to improve our understanding regarding how vulnerability arenas change over time and how this varies across fish species. Shedding light on these questions is not only of academic interest but has important implications for fisheries and its assessments.

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