Title: Fished species uniformly reduced escape behaviors in response to protection

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Abstract

Predation is a critical ecological process that alters the structure and functioning of ecosystems through density-mediated and trait-mediated effects on lower trophic levels. Although studies have focused on harvest-driven reductions in abundances and sizes of targeted species, human harvest also alters species morphologies, life histories, and behaviors by selection, plasticity, and shifts in species interactions. Restricting harvest can recover the biomass of targeted species, but it is less clear how behavioral phenotypes recover, particularly relative to the impacts of potentially opposing pathways of human influence. We investigated the effects of protection on the behavioral traits of a marine fish assemblage, recording behavior of 1377 individual fishes of nine targeted kelp forest species across 16 California marine protected areas (MPAs) varying in age, protection level, and diver visitation. With long-term, full protection from harvest, all fish species exhibited shorter flight initiation distance (FID, or the distance at which an animal flees from an approaching threat) and longer time delays before fleeing, despite differences in trophic position, microhabitat use, and other ecological characteristics. These escape behaviors were amplified across new MPAs regardless of protection level, suggesting that recovery is slow and likely the result of differences in genetic or early-life experience among individuals in these long-lived species. Although the effects of full protection from harvest were partially offset by recovering populations of large piscivorous predators, the net effect of long-term, full protection on fish behavior was shorter FID. Additionally, all species had shorter FID at sites more frequently visited by divers, and this effect was greater in sites with long-term, full protection from fishing. To the extent that escape behavior is correlated with foraging behavior and predation rates, these results suggest that human-induced behavioral changes may affect ecosystem processes, even after abundances have recovered. If recovery of ecosystem functioning and services are the management goal, assessments should be broadened to include the recovery of functional traits (including behavior).

Key words: Behavior, Protected areas, Human harvest, Ecosystem function, Flight initiation distance, Fishing

Introduction

Human and natural predation impacts ecosystem processes through direct reductions of prey densities (Estes et al. 2011) and through indirect effects on prey traits including morphology, life history, and behavior (Breviglieri et al. 2017; Tollrian and Harvell 1999). Although conservation ecology has traditionally focused on the effects of human-driven declines in predator biomass on ecosystem function, the magnitude and direction of trait-mediated effects may differ from those of direct effects (Creel and Christianson 2008), and the strength of trait-mediated and indirect effects often exceeds that of density-mediated and direct effects of predation on ecosystems (Preisser et al. 2005; Schmitz et al. 2004; Werner and Peacor 2003). It is therefore important to consider trait-mediated and indirect pathways when assessing the impacts of extraction and predation on lower trophic levels (Peckarsky et al. 2008).

Humans have overexploited a wide range of ecologically important consumers, often targeting adult individuals with desirable phenotypes, and altering the morphological, size distribution, and behaviors of wild populations (Allendorf and Hard 2009). These unique patterns of extraction have important indirect consequences for prey populations (Darimont et al. 2015), communities (Madin et al. 2016), and ecosystems (Estes et al. 2011). Recent studies indicate that human-induced changes in the behavioral composition of targeted species may alter species interactions and the structure of entire ecosystems (Heithaus et al. 2008; Madin et al. 2010). Non-extractive human activities may also indirectly favor certain behavioral traits in wild populations, leading animals to favor flight or defense over foraging (Frid and Dill 2002), affecting the proportion of bold, aggressive and active phenotypes, and altering individual fitness, population dynamics, species interactions, and ecological functioning (Madin et al. 2016; Sih 2013; Wong and Candolin 2014).

Management strategies that regulate extractive and non-extractive recreational activities may likewise have direct and indirect effects on animal behavior and ecological processes. Restoring the densities of single top predatory species via gear restrictions or catch limits predictably strengthens behaviorally-mediated trophic cascades by enhancing anti-predator behavior and reducing foraging in prey (Estes et al. 2011; Ripple et al. 2014; Wirsing and Ripple 2011). Comparatively, protected areas that limit or prohibit hunting, fishing, and/or other human-related disturbances for entire ecological communities within their boundaries may remove the selective pressures and disturbances that alter the behavior of a range of targeted species (Bergseth et al. 2016; Harmelin et al. 1995; Lowry and Suthers 2004). By restoring natural densities of strongly interacting species (e.g., predators and prey), protected areas also indirectly impact species interactions and the behavioral composition of various trophic levels (Baskett and Barnett 2015). Protected areas that also promote non-extractive human activities such as ecotourism can alter habitat use and foraging of resident wildlife (Arlinghaus et al. 2016; Geffroy et al. 2015). These behaviorally-mediated direct and indirect effects have unforeseen consequences for ecological processes such as predation, competition, and herbivory in protected areas (Hebblewhite et al. 2005; Ripple and Beschta 2006), which have yet to be thoroughly investigated (Ford and Goheen 2015).

Within marine ecosystems, entire assemblages of species are harvested; yet the impacts of fishing on animal behavior have been well-studied solely for single species. Even less is known about the impacts of protection from fishing on the behaviors of targeted assemblages (Bergseth et al. 2016). Field studies of the impacts of fishing and protection from fishing have focused on flight initiation distance (FID), or the distance at which an animal flees from a perceived threat (Ydenberg and Dill 1986) as the central behavioral response (see Dickens et al.

(2011); Edgar et al. (2004); Watson and Harvey (2007)) and as a predictor of recovery (Goetze et al. 2017; Januchowski-Hartley et al. 2015). Since FID is correlated with anti-predator behavior (Stankowich and Blumstein 2005), it represents one side of the tradeoff between foraging versus risk of consumption by predators, which impacts individual fitness, population dynamics, and species interactions (Sih et al. 2004; Sih et al. 2012). Recent studies suggest that marine protected areas (MPAs) reduce FID (Feary et al. 2011; Gotanda et al. 2009; Januchowski-Hartley et al. 2011), though responses to protection can vary among species with distinct ecologies and life histories (Claudet et al. 2010; Januchowski-Hartley et al. 2014). Additionally, fishing (e.g., hook-and-line and spearfishing) influences ecologically important behaviors other than FID, including microhabitat use (Cote et al. 2014; Harmelin et al. 1995), activity level (Alos et al. 2012; Biro and Post 2008), and foraging (Biro and Post 2008; Gotanda et al. 2009; Walsh et al. 2006). Finally, non-extractive human activities in MPAs such as SCUBA diving and other water sports also impact fish behavior (Bergseth et al. 2016; Frid and Dill 2002; Kulbicki 1998; Pereira et al. 2016; Titus et al. 2015), in some cases serving as surrogates for extractive activities. Consequently, the net effects of multi-species management on animal behavior and the indirect effects of these behavioral changes on ecological processes in marine systems remain unknown.

California's kelp forests are highly productive ecosystems that support a diverse assemblage of commercially and recreationally harvested fishes. These targeted species constitute a range of trophic levels – piscivores, secondary carnivores, omnivores, and planktivores – some of which (i.e., piscivores) consume one another. They are also distributed across various microhabitats (e.g., kelp, flat reef, rocky caves and crevices), where they forage and shelter from predators. Kelp forest fishes are protected within California's state-designated MPA network, which consists of MPAs that vary in age and protection level, and also experience recreational SCUBA diving (Menzel et al. 2013). MPA monitoring efforts have thus far focused on the recovery of species composition and the biomass of fish, invertebrates, and algae, highlighting increases in the biomass of targeted species across southern California MPAs (Caselle et al. 2015). The rate of recovery of fish escape behaviors across entire assemblages of harvested species has not been assessed. Because these behaviors may affect predation rates on herbivorous invertebrates, an important ecological process maintaining kelp forests (Steneck et al. 2002; Tegner 2000), a better understanding of whether, how, and how quickly these behaviors respond to protection will also provide key insight into the recovery of ecosystem functioning in protected areas.

To investigate the impacts of protected areas on the behavioral traits and ecological function of a marine assemblage, we conducted field surveys of 1377 individual kelp forest fishes of nine different targeted species across sixteen sites within central California, which fall within MPAs of varying age, protection level, and SCUBA diver visitation level. We specifically asked how aspects of escape behavior (e.g., FID, time delay before flight) and habitat use varied among targeted species and as a function of MPA age, protection level, and SCUBA diver visitation. We hypothesized species at different trophic levels and with different habitat use may exhibit distinct direct and indirect behavioral responses to protection, with variable consequences for key ecological processes such as predation.

Materials and Methods

Study Sites. We conducted surveys from June to September 2014 on shallow, rocky reefs between the Breakwater in Monterey, CA, USA (36.609414 N, -121.8924 W) and Weston Cove in Carmel Highlands CA, USA (36.51103 N, -121.94486 W) (Figure 1; see additional information on sites in Table S.1 in Supplementary Information). All 16 surveyed sites were within Monterey Bay National Marine Sanctuary (MBNMS), a federally-designated MPA that manages prohibited activities (e.g., oil drilling and certain discharges). MBNMS contains smaller state-designated MPAs, which fall within the central region of California's statewide network of MPAs, established in 2007, which manage extraction of marine resources. These state-designated MPAs are regularly patrolled and enforced by wildlife officers, and consist of old, no-take MPAs (termed State Marine Reserves or SMRs, established in 1917 and 1973; no fishing permitted, n=6 study sites), new, no-take MPAs (also termed State Marine Reserves or SMRs, established in 2007; no fishing permitted; n=3 study sites), and new, partial-take MPAs (termed State Marine Conservation Areas or SMCAs, established in 2007; recreational fishing permitted, n=7 study sites). Old, partial-take MPAs in this region are absent. Since recreational harvest comprises a greater proportion of fishing relative to commercial harvest in central California kelp forests (Starr 2002; Wilson-Vandenberg et al. 2014), SMCAs surveyed in this region, which permit hook-and-line fishing and spearfishing, offer limited protection for fishes. However, all surveyed MPAs still prohibit commercial take of finfish, including the live fish component of the commercial nearshore fishery, which is data-limited. To the extent that the nearshore fishery may extracts resources from kelp forests in the Monterey region (CDFW 2015), SMCAs could offer some protection relative to unprotected areas. Thus, we continue to refer to SMRs as "no-take" and SMCAs as "partial-take", even though SMCAs are likely close to "full-take". Fully unprotected areas geographically adjacent to these MPAs are clustered along one area of highly exposed rocky coastline and are thus impossible to separate from geographic location, exposure, and inaccessibility to humans, and so these were excluded from this study.

Sites in this region are also visited by recreational divers, the majority of which are non-extractive SCUBA divers. Visitation is largely unregulated, with a few exceptions; only 15 dive teams are allowed per day at Point Lobos SMR, diving from shore is not permitted from Hopkins Marine Station at Lovers SMR, and fish feeding is not permitted at any site. For the purposes of this study, SCUBA diver visitation is divided into two categories: low diver visitation (0-10 divers per week) versus high diver visitation (10-100 divers per week), categorized based on independent personal observations (OKR, SIL). Categorizations were corroborated by consultation with active research and recreational divers in this region, do not distinguish among non-extractive and spearfishing divers, and largely refer to diver visitation by SCUBA divers during the summer season (diving is less frequent in the off-season due to weather conditions). We selected sites within MPAs of each age and protection level that experience low and high diver visitation, such that MPA type is not confounded with diver visitation level.

All MPAs are dominated by rocky substrates and giant kelp, *Macrocystis pyrifera*. Kelp cover was generally high across sites, and also includes other canopy-forming (*Nereocystis luetkeana*) and subcanopy species (*Pterygophora californica* and *Eisenia arborea*). Algal canopy and subcanopy cover did not vary among MPA types ($p=0.793$ and $p=0.688$), although canopy kelps are less abundant and subcanopy kelps are more abundant at sites with high relative to low diver visitation ($p<0.001$; Figures S.1 and S.2). Average visibility at the time of sampling naturally differed among sites; visibility did not significantly differ by MPA type ($p=0.364$), but it was significantly higher at sites with high relative to low diver visitation ($p=0.019$; Figure S.3). All sites are characterized by natural substrates except at the Breakwater site in Ed Ricketts SMCA, which is a manmade jetty constructed of natural riprap (large boulders and cobble).

Escape behavior. We conducted surveys on SCUBA during daylight hours at depths of 6-15 m, and with a minimum visibility of 3 m. Flight initiation distance (FID) surveys conducted on SCUBA and free diving have yielded similar results in tropical studies (Bergseth et al. 2016; Januchowski-Hartley et al. 2012); we therefore conducted surveys on SCUBA for ease of detection of fishes in a temperate system where high kelp cover and lower visibility made assessment by free diving impractical. Divers swam on a fixed bearing to select, approach, and measure FID of individual stationary or swimming fish using published methods (see Gotanda et al. (2009); Januchowski-Hartley et al. (2011)). The lead diver selected an unwary fish, approached the fish at a fixed speed, and assessed flight as the moment when the fish either exhibited a rapid escape reflex (C-start response from stand still) or accelerated away if already swimming. The lead diver dropped subsurface floats to mark the following three locations: (1) diver position at start of the approach, (2) diver position upon fish flight, and (3) fish position upon flight. Diver start distance was recorded as the horizontal distance between the first and third float, and FID was recorded as the horizontal distance between the second and third float. For those fishes that failed to flee immediately upon approach, we devised and recorded an additional measure of escape, flight initiation time (FIT), or time delay before flight. FIT was recorded using a stopwatch as the time delay between diver approach to within 0.5 m of the fish and fish flight, which occasionally lasted 10-60 seconds. If the fish did not move after 60 seconds, then the response was recorded as not having initiated flight. The lead diver also recorded fish species, estimated total length, and whether or not the fish returned to its original location within five minutes of displacement. Individual surveys of FID were of approximately five minutes duration, with successive individuals sampled at a minimum distance of 10-30 m (depending on visibility) to avoid surveying fish that had already witnessed previous surveys. To maintain consistency in approach, a single lead diver (OKR) conducted the majority of surveys (1301 of 1377 surveys). One other lead diver (SIL) conducted the remaining surveys. There were no significant differences in survey estimates of FID by observer (p=0.249).

Habitat use and availability. After the lead diver collected FID data, a second diver recorded the habitat characteristics within a one-meter horizontal radius of the location of each individual fish, prior to its flight. We quantified algal abundance by counting the total number of canopy-forming kelp stipes (1 m above the holdfast) and all other stipitate kelp plants using methods outlined in Hamilton et al. (2010) and by visually estimating the percent cover of foliose red algae (*Chondracanthus corymbiferus*, *Rhodymenia* spp., and others, excluding articulated coralline algae). We assessed refuge availability by measuring the horizontal distance between the fish and the entrance of the nearest rocky refuge (reef or boulder cracks, crevices, caves, or holes).

In total, we surveyed 1377 individuals of nine commonly harvested kelp forest fishes, including the following *Sebastes* species: *S. atrovirens* (kelp rockfish), *S. caurinus* (copper rockfish), *S. chrysomelas* (black and yellow rockfish), *S. melanops* (black rockfish), *S. miniatus* (vermilion rockfish) and *S. mystinus* (blue rockfish) (Family Sebastidae), as well as *Hexagrammos decagrammus* (kelp greenling) and *Ophiodon elongatus* (lingcod) (F. Hexagrammidae), and *Scorpaenichthys marmoratus* (cabezon) (F. Cottidae) (see Table S.2 for additional information on these species). We surveyed only subadults and adults (of approximately minimum size at maturity as described in Love (2011)). Of the nine species surveyed: eight exhibit high site fidelity, seven are predominantly diurnal, eight are late-maturing (6-15 years), and all are long-lived (lifespan of 30-100 years). All are generalist predators that ambush (sit-and-wait for), pursue (sit-and-pursue), or browse for (actively pursue) prey.

We surveyed each site until a target number of individuals (n=6) of each species was obtained (Figure S.4). Fish surveyed did not differ in body size across MPA types or diver visitation (p>0.5), with the exception of *O. elongatus,* which was 14% larger at old no-take relative to new, partial-take MPAs (p<0.001; Figure S.5). Two piscivorous fishes (*S. caurinus* and *S. miniatus*) that were fairly common at some of the old MPAs were almost entirely absent from new MPAs at surveyed depths (Figure S.4), we therefore removed these species from analyses of fish behavior by MPA type.

Abundance of piscivorous fishes. As a measure of the abundance of natural predators on the fishes surveyed for FID, we used subtidal fish survey data collected by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) Kelp Forest Monitoring Program (piscoweb.org) for each site. Specifically, we assessed the abundance of mature lingcod (*Ophiodon elongatus,* >56 cm total length), which are a dominant fish predator (Love 2011) and other large piscivores (*Scorpaenichthys marmoratus, Paralabrax clathratus*, and rockfishes of the *Sebastes* genus: *S. caurinus*, *S. miniatus*, *S. rastrelliger*, and *S. melanops,* >40 cm total length). We selected bottom and midwater surveys (height in the water column) conducted between 2007 and 2015, collected at the nearest locations to our survey sites (in most cases within 100 m), such that PISCO survey data should reflect piscivore abundance, size, and composition at our experimental sites. We extracted predictions of site-level piscivore abundance from the PISCO data using random effects models of abundance of these fish piscivores conditioned on site, with random effects of year, side (a subsection of site), and transect (nested within height in the water column, depth zone, side, and site). Data from these experiments are deposited to Mendeley Data (Rhoades et al. 2018).

Statistical methods. We described each fish species 'habitat niche' using a Multiple Factor Analysis (MFA) of survey data, treating each individual fish as a sample. Variables included aspects of habitat use (association with water column, rocky refuge, or algae, height above the substrate, and the distance to the nearest rocky refuge), and escape behaviors (FID, FIT, whether or not the fish fled in open water or to rocky refuges, and whether or not the fish returned to its original location after the initial disturbance). Dimensions 1 and 2 of the MFA account for 45% of the variation in the sample (Table S.3). We then calculated mean and confidence estimates around the behavioral characteristics of these dimensions (Table S.4) for fish species, MPA type, and SCUBA diver visitation (Table S.5).

Next, we constructed a statistical model to assess how the effects of MPA type and SCUBA diver visitation on FID varied among species. We used generalized linear mixed models fit to a gamma distribution with a log-link (for FID) using Bayesian Inference and Maximum Likelihood methods, which produced similar predictor estimates (see Results). We included random intercepts for site, individual dive, and species, and random slopes of fish total length and diver start distance for each species. We included MPA age, protection level, diver visitation, predator abundance, and the interaction between MPA age and diver visitation as fixed slopes, and as random slopes for each species. The significance of random effects was tested using model comparison.

We conducted statistical analyses in R version 3.2.4. Generalized linear mixed models were fit using the packages lme4 ((Bates 2015), Maximum Likelihood) and rethinking version 1.58 ((McElreath 2016), Bayesian Inference). We sampled from Bayesian Inference models using the Hamiltonian Monte Carlo method and using non-centered parameterization, using the R package RStan version 2.9.0.

Results

Fish displayed reduced escape behaviors at old relative to new MPAs (Figure 2A,C). All species at old, no-take MPAs were uniformly less likely to initiate flight in response to diver approach (p=0.002; Figure 2C). Flight initiation distance (FID) was 29% shorter at old, no-take MPAs relative to new MPAs (p<0.001; Figure 2A; Table S.6). This effect did not vary by species; model comparison indicates that there was no preference for the model including an interaction between MPA type and species on FID (Table S.7A; p=0.299).

Even accounting for the effects of MPA type, fish escape behaviors were also reduced at sites with high relative to low SCUBA diver visitation (p<0.001; Figure 2B,D). Species at popular dive sites were less likely to initiate flight at all in response to diver approach (p<0.001; Figure 2D). Those that did flee allowed divers to approach on average 16% closer at sites with high relative to low diver visitation (p<0.001; Figure 2B; Table S.6). Prior to initiating FID, diver start distances were shorter at popular dive sites (p<0.001; Figure S.6A), which likely contributed to shorter FID (Figure S.6B). The effect of diver visitation on FID also did not vary by species; model comparison indicates that there was no preference for the model including an interaction between MPA type and species on FID (Table S.7B; p=0.913).

There was a significant interaction between the effects of MPA age and SCUBA diver visitation level on FID, with fishes on average exhibiting a 5-10% decrease in FID due to higher diver visitation at old, no-take MPAs relative to new MPAs (p=0.020; Figure 2B; Table S.6). This effect was notably stronger for certain species; for example, the effect of high diver visitation no FID of *Ophiodon elongatus* and *Scorpaenichthys marmoratus* was 30% and 58% greater, respectively, at old relative to new MPAs (Figure 2B).

Piscivorous fish abundance varied significantly across sites, and was particularly high in old, no-take MPAs (Figure 3A; see also general fish abundance, Figure S.7). Piscivorous fish abundance was also a significant predictor of FID, resulting in 17% greater FID in targeted species when piscivores increased from <0.0001 to 0.23 individuals per transect (the full range in piscivore density across surveyed sites) ($p<0.001$, Figure 3B). Moreover, the effect of piscivore density on FID did not significantly differ by responding fish species ($p=0.995$). However, the effect size of MPA age on FID was greater than that of piscivore abundance (an average decrease in FID of 36% with greater MPA age as opposed to an increase in FID of 12% for a standard deviation change in piscivore density).

Species also varied in their habitat use as a function of SCUBA diver visitation, and to a lesser extent as a function of MPA type (Figure 4; Table S.8). Fishes at popular dive sites occurred closer to refuges ($p=0.050$; Figure 4A) as well as lower in the water column and closer to the benthos ($p<0.001$; Figure S.8), despite there being fewer refuges at popular dive sites ($p<0.001$; Figure 4B). Even though fishes exhibited shorter FID at sites with high diver visitation, their habitat choice was still suggestive of increased risk perception. Only one species' habitat use (*S. marmoratus*) was similar across areas of low and high diver visitation (likely due to its strong cryptic behavior and coloration). There was a marginally significant effect of MPA type on use of refuge ($p=0.056$), distance from the benthos ($p=0.222$) and refuge availability ($p=0.060$).

Despite similar behavioral responses to protected areas and level of diver visitation, surveyed species exhibited distinct responses to SCUBA diver approach during FID surveys, which corresponded with their different patterns of habitat use. Species found near refuges or complex habitats exhibited bolder behaviors than those typically found in more open or less complex environments (Figure 5A). Species that often occupied rocky refuges (*S. chrysomelas* and *S. caurinus*) or complex reef (*O. elongatus* and *S. marmoratus*) exhibited short FID or long FIT, and often fled to nearby crevices. By contrast, species that were frequently associated with open water or flat reef (*S. mystinus and H. decagrammus*) exhibited long FID and short FIT, tended to flee long distances in open water, and were among those species less likely to return shortly thereafter to their initial location ($p<0.001$; Figure S.9). Across species, mean FID ranged from 30-90 cm, and FIT spanned 1-16 seconds, and FID and FIT were marginally negatively correlated ($p=0.054$; Figure 5B). These observations of habitat use and escape behavior were generally consistent with previous qualitative observations of these species (Hallacher and Roberts 1985; Love 2011; Shaw and Hassler 1989; Stein and Hassler 1989).

Discussion

Although surveyed fishes exhibited unique ecological characteristics including distinct escape behaviors and habitat use, all species responded similarly to protection from harvest and exposure to high diver visitation. In particular, duration of protection has a strong effect on fish behavior, whereas there was little difference in fish escape behavior among new protected areas varying substantially in protection level. This suggests that the differences we observe may not be plastic behavioral responses, but instead indicate genetic or early-life experience driven differences, such that long time lags and new generations of recruits are required for behavioral trait change in these long-lived species. Although long-term, full protection from fishing favored bolder phenotypes, it also enhanced the density of natural fish predators, which in turn increased flight responses in protected areas. At our sites, the direct effects of protection outweighed the indirect effects of recovering predator densities, leading to a net positive effect of protection on boldness. This balance could be different in other ecosystems, complicating predictions of the effects of protection on ecosystem processes that are influenced by predator boldness. We separately discuss these direct and indirect effects, their ecological implications, and the implications of these behavioral changes for the management of ecosystems.

Direct effects of protection on animal behavior

Similar exploitation histories may contribute to similar behavioral responses to protection across taxonomically, morphologically, and behaviorally diverse species assemblages. Surveyed fishes in this study varied in body size, morphology, habitat choice, mobility, trophic position, and FID, all of which typically result in unique density-mediated responses to protection (Claudet et al. 2010) and different sensitivities to perceived risk (Abrahams 1995; Hulthen et al. 2014). Nevertheless, all surveyed species exhibited remarkably similar reductions in FID with long-term protection. Since all surveyed species share a similar local history as recreational and commercial nearshore fishery targets, they likely have similar haphazard encounter rates with hook-and-line gear as well as recreational SCUBA and free divers. These passive fishing methods uniformly encounter all species but selectively remove active, bold phenotypes (Biro and Post 2008; Ciuti et al. 2012a; Olsen et al. 2012; Uusi-Heikkila et al. 2008), suppress foraging (Askey et al. 2006; Biro and Post 2008; Walsh et al. 2006), and amplify anti-predator behaviors (Januchowski-Hartley et al. 2011; Tran et al. 2016). Therefore, the uniform imprint of fishing mortality may override variability in species ecologies in determining the behavioral response of heavily exploited species to protection.

In combination with similar exploitation histories, limited behavioral plasticity across such long-lived species assemblages may also result in delayed rates of change in behavioral traits. In contrast with rapid adjustments of FID of certain tropical species in response to fishery closures (Januchowski-Hartley et al. 2014; Januchowski-Hartley et al. 2011), reductions in FID in our study have not yet occurred with seven years of protection, as would be expected if traits were plastic. Indeed, FID was shorter at old protected areas (40-100 years old), but longer across new protected areas that vary in protection level (7 years old, no-take versus nearly full-take), suggesting that boldness traits may be genetically determined or the result of early conditioning, and therefore invariant (Reale et al. 2007). Since all surveyed species in our survey are resident (non-migratory) with minimum generation times of 6-15 years (Love 2011), changes in the frequencies of behavioral traits depend on species recruitment events from outside areas with greater trait diversity, slow growth of new individuals, and environmental tradeoffs within protected areas favoring foraging over hiding or fleeing from predators.

Indirect effects of protection on animal behavior

Protection increases natural fish predator densities, counteracting the direct effects of protection on behavioral recovery by selectively favoring individuals that are wary of larger piscivorous fishes. As the densities of predators and predatory interactions recover in new MPAs (Babcock et al. 1999; Guidetti 2006), the magnitude of escape behaviors in all trophic levels will also increase, particularly during periods of high risk (Ferrari et al. 2009; Sih and McCarthy 2002; Sih et al. 2000). However, the effect of natural predator densities and predation rates is offset by protection from human predation, with a net reduction in FID. Indeed, at sites in old, no-take MPAs where piscivorous fishes are already abundant, FID remains shorter than at new protected areas (where piscivores are generally less abundant).

In other systems, the balance between these direct and indirect effects might be different, especially where human harvest preferentially targets higher-order carnivores. In such situations, lower order consumers might exhibit magnified escape behaviors in protected areas, because the direct effect of humans on their behavior is small relative to the effect of recovery of natural predators (Creel et al. 2005). Whereas, in other systems in which lower-order consumers are targeted, these consumers might exhibit reduced escape behaviors in protected areas, because the direct effect of humans on their behavior is large relative to the effect of recovery of natural predators (Ciuti et al. 2012b; Proffitt et al. 2009). These results suggest that complex underlying mechanisms may drive behavioral trait change in a wide range of protected areas or conservation areas (e.g., savannah grasslands, temperate forests, and tropical reefs) in which multiple, strongly interacting trophic levels of previously targeted species are protected.

Impacts of human encounters on animal behavior

Below a certain threshold rate of neutral human encounters, wild animals may become partially habituated to the visual presence of humans, while still reacting to generalized disturbances associated with human activities. In our study, fishes exhibited uniformly shorter FID with high diver visitation, likely due to similar rates of benign encounters with divers (Geffroy et al. 2015; Stankowich and Coss 2006). Habituation to high rates of diver visitation was further amplified at old, no-take MPAs where SCUBA divers do not spearfish (Lindfield et al. 2014), highlighting that habituation is less likely where human recreation occurs concurrently with extraction (Arlinghaus et al. 2016). Nevertheless, despite shorter FID and regardless of microhabitat preference, all species remained closer to refuges at popular dive sites. This may be triggered by the pervasive, low-frequency noise of open-circuit SCUBA diving, to which fishes may be sensitive (Radford et al. 2005), causing avoidance or sheltering behavior (Dickens et al. 2011; Pereira et al. 2016). Indeed, a range of auditory disturbances caused by humans serve as part of the stimulus that elicits anti-predator responses, similar to those that would be expected for the approach of certain natural predators (Frid and Dill 2002).

Overall, fishes in kelp forests encounter fewer divers and spearfishers relative to those in many other regions (Frisch et al. 2012; Godoy et al. 2010), which may explain the shorter range in fish FID in our study relative to values recorded in the literature. Thus, our study provides a conservative estimate of animal response to human encounters, particularly when compared with heavily used managed areas (e.g., national parks, wildlife refuges, and dive destinations) in which highly concentrated, neutral and negative interactions between humans and animals provoke anti-predator responses and avoidance of humans (Arlinghaus et al. 2016) that suppress the recovery of wild populations (Sarmento and Berger 2017) and impact the ecological functions of these species (Hebblewhite et al. 2005; Ripple and Beschta 2006; Titus et al. 2015).

Ecological consequences of management-driven changes in animal behavior

FID in response to human approach is thought to reflect animal interactions with natural predators and prey (Parsons et al. 2010; Stankowich and Blumstein 2005), and natural tradeoffs between anti-predator behavior and foraging (Ydenberg and Dill 1986). If so, the impacts of management-driven changes in FID and other escape behaviors and habitat use may affect consumer ecological roles and key ecological processes. In our study system, long-term, full protection from harvest reduced escape behaviors and enhanced boldness across a diverse consumer assemblage. Boldness is linked to greater foraging success, higher energy gains (Reale et al. 2000), and to other traits such as egg production that increase individual fitness and population productivity (Biro and Post 2008; Walsh et al. 2006), which may accelerate the recovery of consumer abundance. Bolder, active phenotypes also disproportionately enhance prey mortality (Ioannou et al. 2008; Nannini et al. 2012), and exert stronger cascading effects on primary producers (Start and Gilbert 2017). Strong interactions among protected assemblages may further regulate changes in behavior. Bolder, active predators may also reduce prey foraging and enhance anti-predator behavior (Pruitt et al. 2017; Toscano and Griffen 2014), with cascading effects on basal trophic levels (Start and Gilbert 2017), as seen with behaviorally-mediated indirect effects (Creel et al. 2005; Schmitz 1997).

Even non-extractive human activities may also have unintended effects on consumer habitat use and function. In our study, moderate levels of human encounters caused all species but one to increasingly associate with safer habitats such as refuges (Anderson 2001; Carr 1991; Ebeling and Laur 1985; Holbrook et al. 1990). Given that the majority of species in this assemblage occupy residences or territories in distinct microhabitat types, displacement may alter their spatial foraging domain (see Figure 5) and thus their prey selection. In general, in avoiding areas heavily trafficked by humans (Coppes et al. 2017), consumers reduce foraging time (Ciuti et al. 2012b), displace from important foraging grounds, and select less palatable foods (Sarmento and Berger 2017), altering their ecological roles. In some cases, human-driven habitat shifts have cascading effects on lower trophic levels via changes in predation and herbivory (Hebblewhite et al. 2005; Ripple and Beschta 2006), although definitive evidence for this remains limited (Ford and Goheen 2015).

Conclusions: Incorporating escape behavior into ecosystem management

Resource managers have largely focused on abundance, size, and composition of target species within protected areas. From an extraction perspective this makes sense, yet from an ecosystem functioning perspective, we know that functional traits of a species assemblage more closely correlate with ecosystem processes than abundance or diversity of species alone (Cadotte et al. 2011; Coleman et al. 2015). Our study highlights that, due to the widespread presence of intraspecific variation in functional traits (Bolnick et al. 2003; Hughes et al. 2008; Violle et al. 2012), recovery of biomass and function may not completely coincide. If the goal is to recover ecosystem processes and services (and not simply abundance of targeted species), then monitoring and management requires looking beyond changes in density, isolating the causes and consequences of behavioral variation, and evaluating the direct and indirect behaviorally-mediated interactions within community assemblages.

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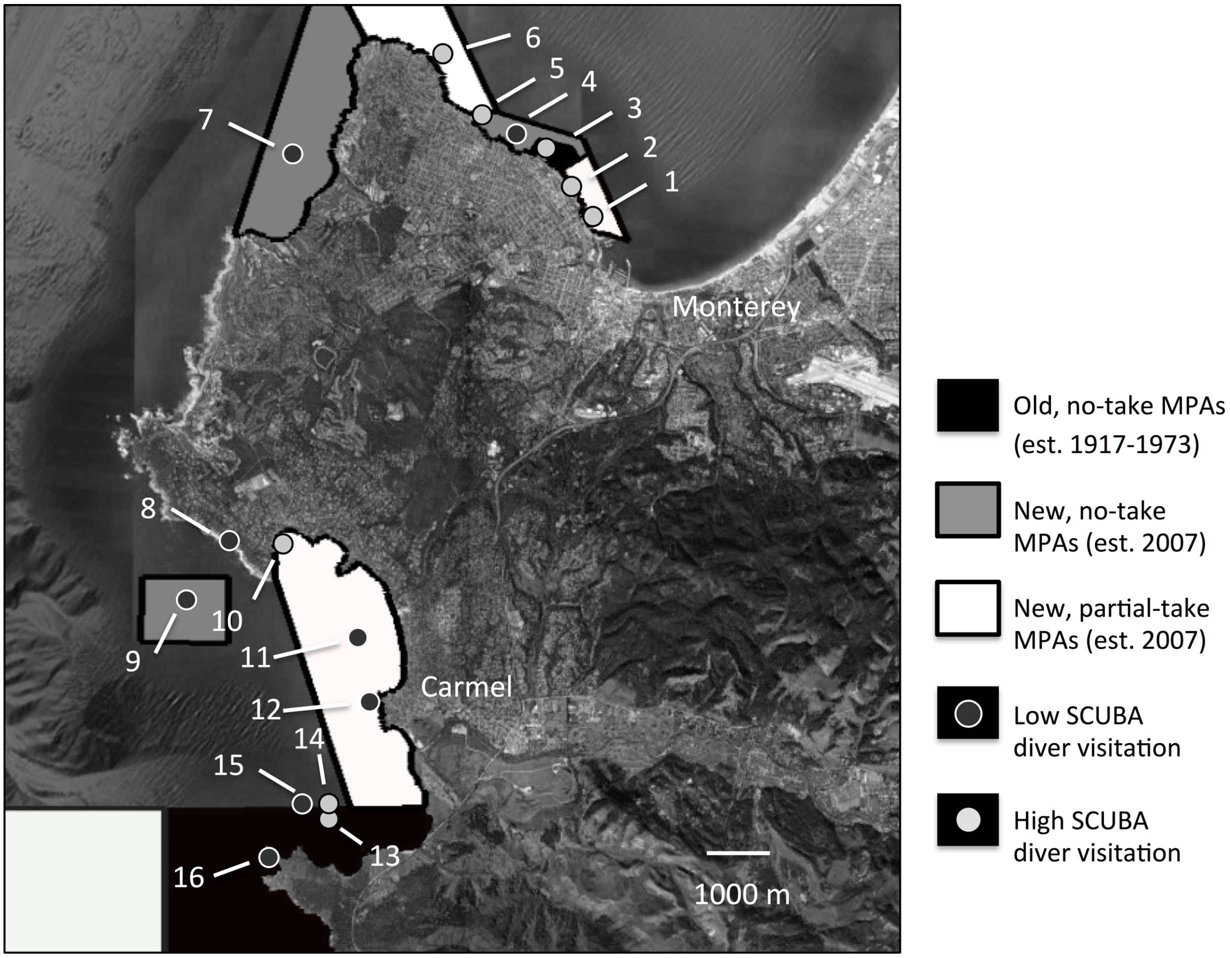

Figure 1. Map of flight initiation distance (FID) survey sites. Polygon shades refer to MPA type. Circles refer to surveyed sites, with circle shades of dark/light gray referring to low/high SCUBA diver visitation. Numbers indicate unique sites, which are also referenced in Table S.1 under 'Site (map ID)' which provides additional site information including names and MPA characteristics.

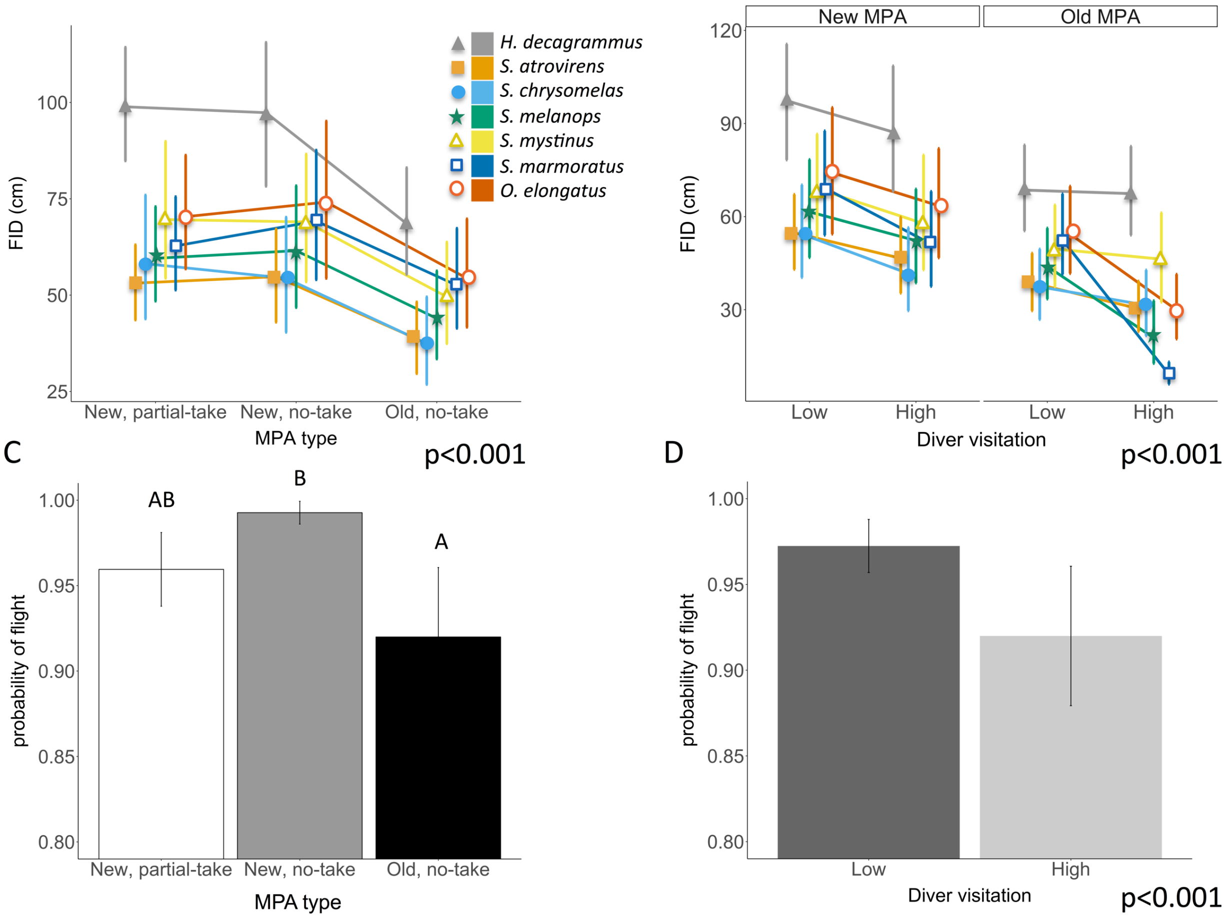

Figure 2. (A and B) Counterfactual predictions and 95% credible intervals from the generalized linear mixed models of species-level flight initiation distance (FID) by (A) MPA type and (B) low/high diver visitation. Color and symbol are indicative of fish species (see legend). Predictions are averaged across sites and dive replicates per site. (C and D) Predictions and standard errors from a generalized linear mixed model of probability of flight from approaching divers by (C) MPA type and (D) low/high diver visitation. Different letters indicate significant differences among MPA types ($p<0.05$).

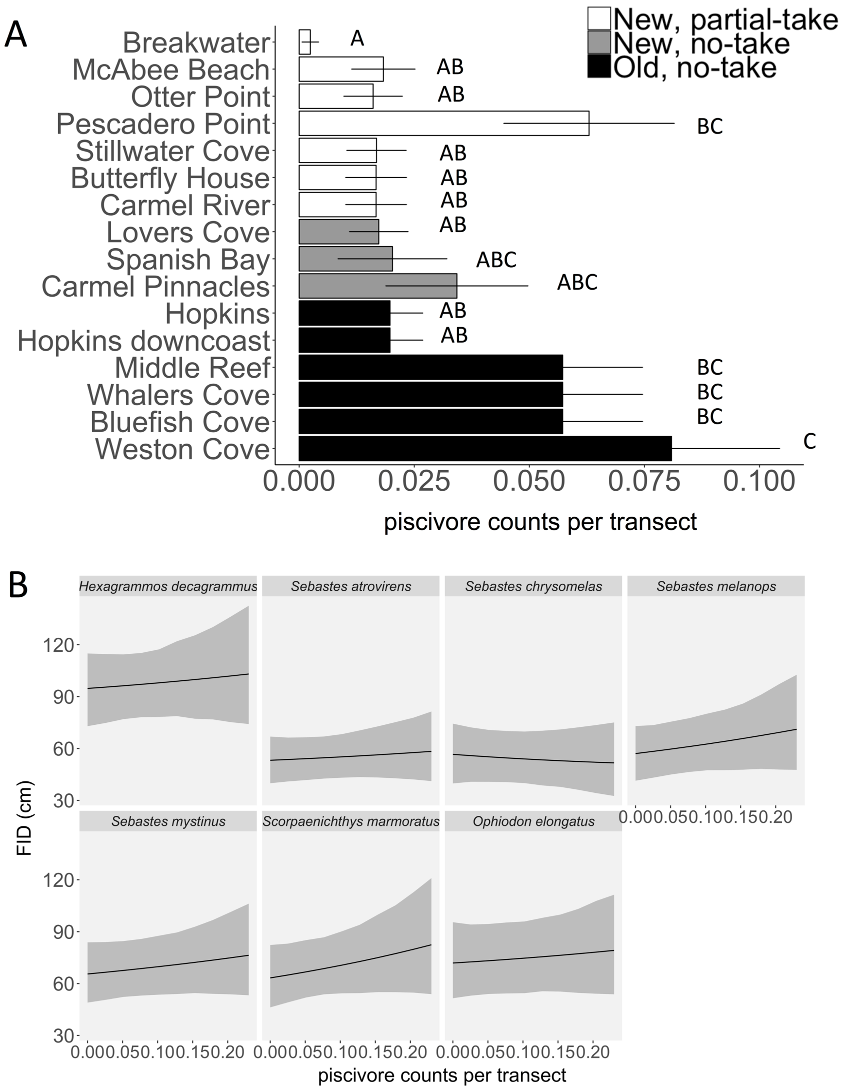

Figure 3. (A) Predictions and standard errors from a generalized linear mixed model of piscivorous fish abundance per transect, conditioned on site. Piscivorous fish abundance per transect is extracted from surveys collected by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) Kelp Forest Monitoring Program. Different letters indicate significant differences among sites ($p<0.05$), as determined through post-hoc pairwise comparisons of least square means. (B) Counterfactual predictions and 95% credible intervals from the generalized linear mixed model of FID by piscivore abundance, each separated by species. Predictions are averaged across sites and dive replicates per site.

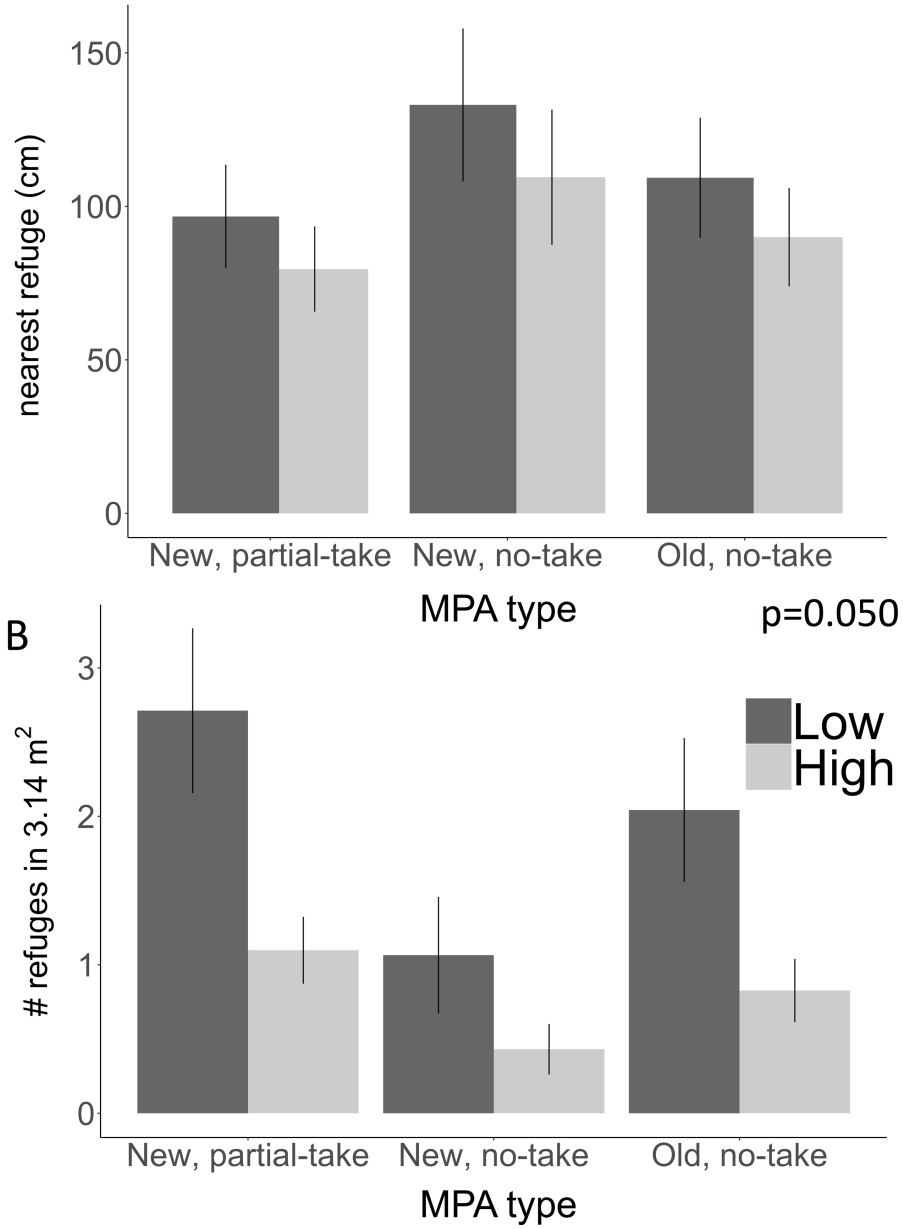

Figure 4. Predictions and standard errors from generalized mixed effects models of (A) distance to nearest refuge and (B) refuge density recorded surrounding each surveyed species, conditioned on MPA type and diver visitation level, with diver visitation level shown in dark/light gray (see legend).

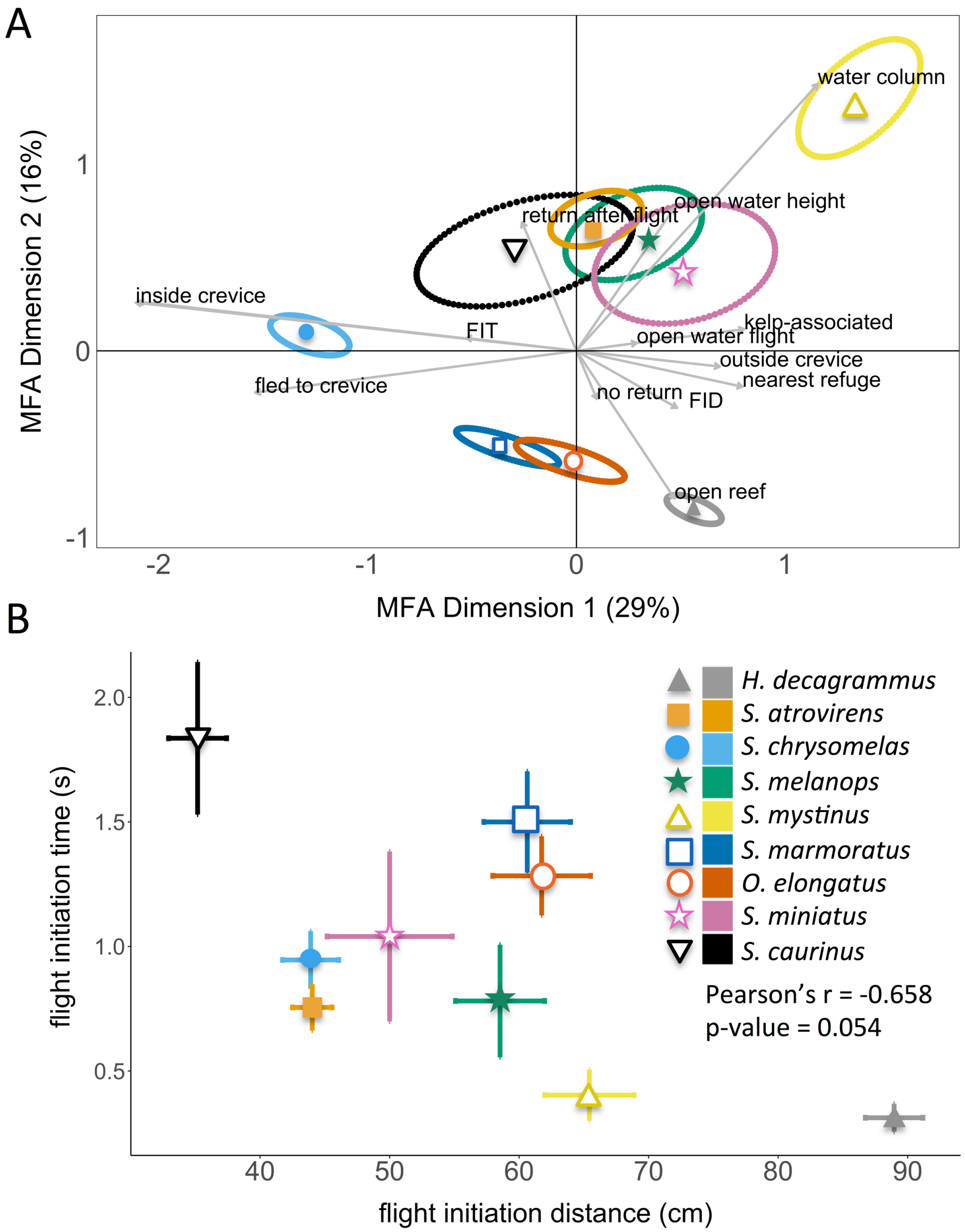

Figure 5. (A) Multifactor analysis of habitat use and escape behaviors of surveyed kelp forest fishes. The ellipses represent the region of confidence around the mean trait value for each surveyed species. The endpoints represent the values of the two dimensions for each behavioral trait that was surveyed. (B) Raw means and standard errors of FID in cm and flight initiation time (FIT) in seconds for each surveyed species.

Supplementary Information

Table S.1. GPS locations, MPA regulations, age, and diver visitation for flight initiation distance (FID) survey sites. Protect level refers to the MPA protection level.

Site (map ID)	MPA	MPA area (sq. km)	Age (est.)	Protect level	MPA regulations	Diver visitation level	Latitude (°N, °W)
Bluefish Cove (15)	Point Lobos SMR	9.927	old (1973)	No-take	No take permitted.	low	36.52206, 121.94376
Breakwater (1)	Ed Ricketts SMCA	0.145	new (2007)	Partial-take	Recreational take of finfish by hook-and-line permitted.	high	36.60941, 121.892398
Butterfly House (11)	Carmel Bay SMCA	1.979	new (2007)	Partial-take	Recreational take of finfish by hook-and-line and spear permitted.	low	36.54611, 121.932275
Carmel River (12)	Carmel Bay SMCA	1.979	new (2007)	Partial-take	Recreational take of finfish by hook-and-line and spear permitted.	low	36.537882, 121.932042
Hopkins (Down-coast) (4)	Lovers SMR	0.764	old (1917)	No-take	No take permitted.	low	36.623188, 121.905202
Hopkins (3)	Lovers SMR	0.764	old (1917)	No-take	No take permitted.	high	36.621003, 121.901555
Lovers Point (5)	Lovers SMR	0.764	new (2007)	No-take	No take permitted.	high	36.627069, 121.914063
McAbee (2)	Ed Ricketts SMCA	0.145	new (2007)	Partial-take	Recreational take of finfish by hook-and-line and spear permitted.	high	36.616758, 121.897551
Middle Reef (14)	Point Lobos SMR	9.927	old (1973)	No-take	No take permitted.	high	36.521433, 121.938802

Otter Point (6)	Pacific Grove Marine Gardens SMCA	1.722	new (2007)	Partial-take	Recreational take of finfish by hook-and-line and spear permitted.	high or low depending on area sampled	36.63556, 121.92209
Pescadero Point (8)	Carmel Bay SMCA	1.979	new (2007)	Partial-take	Recreational take of finfish by hook-and-line and spear permitted.	low	36.56205, 121.95766
Pinnacles (9)	Carmel Pinnacles SMR	2.285	new (2007)	No-take	No take permitted.	low	36.55853, 121.96709
Spanish Bay (7)	Asilomar SMR	3.929	new (2007)	No-take	No take permitted.	low	36.61717, 121.94887
Stillwater (10)	Carmel Bay SMCA	1.979	new (2007)	Partial-take	Recreational take of finfish by hook-and-line and spear permitted.	high	36.5618, 121.94731
Weston (16)	Point Lobos SMR	9.927	old (1973)	No-take	No take permitted.	low	36.51358, 121.94795
Whalers Cove (13)	Point Lobos SMR	9.927	old (1973)	No-take	No take permitted.	high	36.520665, 121.938493

Table S.2. Species surveyed, for which all individuals were >20 cm total length. Data on the behavior of surveyed species obtained from (Love 2011). Note that *Sebastes caurinus* and *Sebastes miniatus* were removed from MPA analyses as these species were virtually absent from new MPAs.

Species	**Common name**	**Functional group, predator mode**	**Habitat**	**Diurnal / Nocturnal**	**Movement**	**External References**
Ophiodon elongatus	lingcod	piscivore, ambush predator	Benthic, on complex rocky substrate (rocky refuges, ridges, and high relief). Also over soft seafloor.	Diurnal (forage deeper) and nocturnal (forage in shallow waters).	Solitary. High site fidelity. Average home range size: 0.25 square km.	Shaw & Hassler 1989; Starr et al. 2004; Bishop et al. 2010
Sebastes caurinus	copper rockfish	piscivore, territorial pursuer	Near bottom. Adults remain near complex structure, and often occur in rocky refuges.	Crepuscular and daytime feeders.	Solitary or in small schools. Display agonistic behavior to show territoriality. Limited movement. Average home range size: 30-400 square m. depending on site quality.	Matthews 1989; Stein & Hassler 1989; Murie 1995
Scorpaenichthys marmoratus	cabezon	piscivore, ambush predator	Benthic, most abundant over rocks and algae, but also found at cobble-mud interface.	Juveniles active at night.	Solitary. High site fidelity. Adults move less than 1000 square m.	Mireles et al. 2012
Sebastes miniatus	vermilion rockfish	piscivore, unknown predator mode	Subadults began to target high-relief areas, adults found in crevices caves, and sheltering spots. May school in water column or near bottom.	Juveniles active at night. Adults unknown.	Solitary or schooling. Anecdotal evidence that individuals have high site fidelity.	
Sebastes melanops	black rockfish	piscivore, browser	Remain around high relief, schooling in the water column or perched on rocks.	Inactive at night.	Schooling. Average home range size: 0.25 square km.	Stein & Hassler 1989; Green & Starr 2011

Sebastes mystinus	blue rockfish	carnivore, browser	Smaller individuals school near substrate. Larger individuals ascend into the water column over high relief seafloor, adjacent to kelp.	Remain in crevices or other shelters at night.	Schooling. High site fidelity. Average home range size: than 100 m from core location.	Jorgensen et al. 2006
Sebastes melanops	black rockfish	carnivore, browser	Remain around high relief, schooling in the water column or perched on rocks.	Inactive at night.	Schooling. Average home range size: 0.25 square km.	Stein & Hassler 1989; Green & Starr 2011
Sebastes chrysomelas	black and yellow rockfish	carnivore, territorial pursuer	Benthic, remain in rocks among high relief	Feed both during the day and at night.	Solitary. Territorial. High site fidelity.	Larson 1980a, Larson 1980b
Sebastes atrovirens	kelp rockfish	carnivore, ambush predator	Associated with kelp beds and rocky reefs.	Nocturnal ambush predators.	Solitary or schooling. Home ranges average 700 square m., but may remain within small areas.	Allen et al. 2011
Hexagrammos decagrammus	kelp greenling	carnivore, browser	Benthic, on rocky substrate, preferably near red algae.	Inactive at night.	Solitary. Average home range size: 1000 square m.	

Table S.3. Proportion of variance accounted for by each dimension from a Multiple Factor Analysis (MFA) of FID survey data on fish escape behavior and habitat use.

	Dim.1	Dim.2	Dim.3	Dim.4	Dim.5	Dim.6	Dim.7	Dim.8	Dim.9
Eigenvalue	2.018	1.104	1.007	0.850	0.598	0.503	0.353	0.296	0.167
% Variance	29.221	15.991	14.577	12.305	8.667	7.289	5.112	4.289	2.422
Cumulative % Variance	29.221	45.211	59.788	72.093	80.760	88.049	93.161	97.450	99.872

Table S.4. Category means (equivalent to loadings in a PCA analysis) for fish habitat use and behavioral traits for each dimension from a Multiple Factor Analysis (MFA) of FID survey data on fish escape behavior and habitat use.

Trait	Dim.1	Dim.2	Dim.3	Dim.4	Class
open water flight	0.289	0.030	-0.269	-0.169	categorical
fled to crevice	-1.525	-0.157	1.421	0.892	categorical
no return	0.119	-0.263	-0.350	0.361	categorical
return after flight	-0.334	0.742	0.985	-1.016	categorical
kelp-associated	0.753	0.130	-0.194	-0.299	categorical
crevice-associated	-2.089	0.264	-0.204	0.216	categorical
open reef	0.489	-0.780	0.144	-0.233	categorical
water column	1.184	1.507	-0.057	0.357	categorical
outside crevice	0.694	-0.085	0.066	-0.075	categorical
inside crevice	-2.101	0.258	-0.198	0.228	categorical
FID	0.491	-0.268	0.311	0.329	continuous
FIT	-0.524	0.035	-0.589	-0.229	continuous
open water height	0.462	0.777	-0.113	0.301	continuous
nearest refuge	0.798	-0.191	-0.040	-0.174	continuous

Table S.5. Subcategory means including species, MPA age, diver visitation, and all combinations of these subcategories for each dimension from a Multiple Factor Analysis (MFA) of FID survey data on fish escape behavior and habitat use.

Combination category	Single category	Dim.1	Dim.2	Dim.3	Dim.4
new MPA	black rockfish	0.312	0.790	0.053	0.296
old MPA	black rockfish	0.147	0.298	-0.100	-0.328
new MPA	blue rockfish	1.634	1.459	-0.247	0.741
old MPA	blue rockfish	0.980	1.309	-0.468	0.663
new MPA	black and yellow rockfish	-1.262	0.111	0.416	-0.062
old MPA	black and yellow rockfish	-1.304	0.070	-0.027	-0.346
new MPA	cabezon	-0.310	-0.516	-0.277	-0.035
old MPA	cabezon	-0.331	-0.534	-0.692	-0.320
new MPA	kelp greenling	0.646	-0.823	0.220	0.057
old MPA	kelp greenling	0.402	-0.753	0.169	-0.033
new MPA	kelp rockfish	0.114	0.796	0.174	0.040
old MPA	kelp rockfish	0.031	0.618	-0.128	-0.145
new MPA	lingcod	0.038	-0.618	-0.077	-0.043
old MPA	lingcod	-0.110	-0.517	-0.350	-0.333
low diver visitation	black rockfish	0.617	0.682	0.102	0.239
high diver visitation	black rockfish	-0.226	0.625	-0.115	-0.026
low diver visitation	blue rockfish	1.788	1.624	-0.443	1.044
high diver visitation	blue rockfish	0.711	1.063	-0.206	0.224
low diver visitation	black and yellow rockfish	-1.040	0.059	0.460	-0.169
high diver visitation	black and yellow rockfish	-1.569	0.144	0.022	-0.147
low diver visitation	cabezon	-0.207	-0.579	-0.085	0.125
high diver visitation	cabezon	-0.420	-0.471	-0.760	-0.393
low diver visitation	kelp greenling	0.655	-0.823	0.227	0.055
high diver visitation	kelp greenling	0.449	-0.770	0.172	-0.009
low diver visitation	kelp rockfish	0.776	0.899	-0.052	-0.002
high diver visitation	kelp rockfish	-0.494	0.600	0.177	-0.040
low diver visitation	lingcod	0.131	-0.573	-0.039	-0.182
high diver visitation	lingcod	-0.209	-0.584	-0.368	-0.129
	black rockfish	0.267	0.658	0.012	0.129
	blue rockfish	1.344	1.393	-0.345	0.706
	black and yellow rockfish	-1.276	0.097	0.264	-0.159
	cabezon	-0.318	-0.523	-0.437	-0.144
	kelp greenling	0.568	-0.801	0.203	0.028
	kelp rockfish	0.086	0.736	0.072	-0.022

	lingcod	-0.021	-0.578	-0.186	-0.159
	new MPA	0.051	0.019	0.103	0.078
	old MPA	-0.096	-0.036	-0.193	-0.146
	low diver visitation	0.292	0.015	0.088	0.082
	high diver visitation	-0.338	-0.018	-0.102	-0.095

Table S.6. (A) Model estimates (fixed effects) and variance (random effects), and (B) statistical significance of fixed effects using the Wald test, from the generalized mixed model of individual FID, calculated using Maximum Likelihood. This model was fit using a gamma distribution, such that per unit increase in a predictor, FID is the exponentiated mean predictor estimate multiplied by the current FID. Continuous predictors are centered and standardized, such that the full range of a continuous predictor is 2 units (compared to 1 unit for categorical predictors).

(A)

Predictor	Fixed / Random	Estimate	Standard Error	Variance	SD
Intercept (New, partial-take, low diver visitation)	Intercept	4.403	0.065		
Piscivore abundance	Fixed slope	0.089	0.027		
MPA age (old)	Fixed slope	-0.384	0.077		
MPA protection level (no-take)	Fixed slope	-0.043	0.059		
Diver visitation	Fixed slope	-0.235	0.054		
MPA age (old) * Diver visitation (high)	Fixed slope	-0.214	0.092		
Dive replicate	Random intercept			0.005	0.073
Site	Random intercept			0.004	0.062
Species	Random intercept			0.020	0.142
Initial distance	Random slope			0.008	0.093
Fish total length	Random slope			0.011	0.103
SCUBA diver visitation	Random slope			0.003	0.051
MPA age (old)	Random slope			0.002	0.043
MPA protection level (high)	Random slope			<0.001	0.029
Piscivore abundance	Random slope			<0.001	0.027
MPA age (old) * SCUBA diver visitation level (high)	Random slope			0.022	0.147
Residual				0.204	0.452

(B)

Predictor	Chi Square	DF	Probability >(Chi square)
Piscivore abundance	10.96	1	<0.001
MPA age (old)	44.88	1	<0.001
MPA protection level (no-take)	0.53	1	0.468
Diver visitation	46.29	1	<0.001
MPA age (old) * Diver visitation (high)	5.37	1	0.020

Table S.7. Pairwise model comparisons of the generalized mixed model of FID including all interactions (Original model), versus models (A) without an interaction between MPA type and species (Model A), and (B) without an interaction between diver visitation and species (Model B), compared using Akaike Information Criteria (AIC) and Bayesian Information Criteria (BIC).

(A)

Model	**DF**	**AIC**	**BIC**	**Log Likelihood**	**Deviance**	**Chi Square**	**Chi DF**	**Chi Square Test**
Model A	36	11705	11888	-5816.4	11633			
Original model	45	11712	11942	-5811.1	11622	10.67	9	0.299

(B)

Model	**DF**	**AIC**	**BIC**	**Log Likelihood**	**Deviance**	**Chi Square**	**Chi DF**	**Chi Square Test**
Model B	24	11683	11805	-5817.5	11635			
Original model	45	11712	11942	-5811.1	11622	12.86	21	0.913

Table S.8. (A) Model estimates (fixed effects) and variance (random effects), and (B) statistical significance of fixed effects using the Wald test, from the generalized mixed models of nearest refuge, refuge density, and distance above benthos, calculated using Maximum Likelihood. These models were fit using the gamma (nearest refuge) and Poisson (refuge density and distance above benthos) distributions, such that per unit increase in a predictor, the response variable is the exponentiated mean predictor estimate multiplied by the current response variable. Continuous predictors are centered and standardized, such that the full range of a continuous predictor is 2 units (compared to 1 unit for categorical predictors).

(A)

Model (response variable)	Predictor	Fixed / Random	Estimate	Standard Deviation	Variance	SD
Nearest refuge	Intercept (new, no-take MPA, high diver visitation)	Intercept	4.696	0.199		
Nearest refuge	MPA type (new, partial-take)	Fixed slope	-0.319	0.134		
Nearest refuge	MPA type (old, no-take)	Fixed slope	-0.197	0.139		
Nearest refuge	Diver visitation (low)	Fixed slope	0.195	0.099		
Nearest refuge	Site	Random intercept			0.000	0.000
Nearest refuge	Species	Random intercept			0.152	0.390
Nearest refuge	Residual				0.949	0.974
Refuge density	Intercept (new, no-take MPA, high diver visitation)	Fixed slope	-0.841	0.385		
Refuge density	MPA type (new, partial-take)	Fixed slope	0.934	0.400		
Refuge density	MPA type (old, no-take)	Fixed slope	0.651	1.548		
Refuge density	Diver visitation (low)	Fixed slope	0.904	4.349		
Refuge density	Site	Random intercept			0.369	0.607
Distance above benthos	Intercept (new, no-take MPA, high diver visitation)	Intercept	0.184	1.348		
Distance above benthos	MPA type (new, partial-take)	Fixed slope	-0.071	0.295		
Distance above benthos	MPA type (old, no-take)	Fixed slope	-0.429	0.302		
Distance above benthos	Diver visitation (low)	Fixed slope	0.628	0.063		
Distance above benthos	Site	Random intercept			0.183	0.428

Distance above benthos	Species	Random intercept			12.679	3.561

(B)

Model (response variable)	Predictor	Chi Square	DF	Probability >(Chi square)
Nearest refuge	MPA type	5.76	2	0.056
Nearest refuge	Diver visitation	18.91	1	0.050
Refuge density	MPA type	5.61	2	0.060
Refuge density	Diver visitation	18.91	1	<0.001
Distance above benthos	MPA type	3.01	2	0.222
Distance above benthos	Diver visitation	99.81	1	<0.001

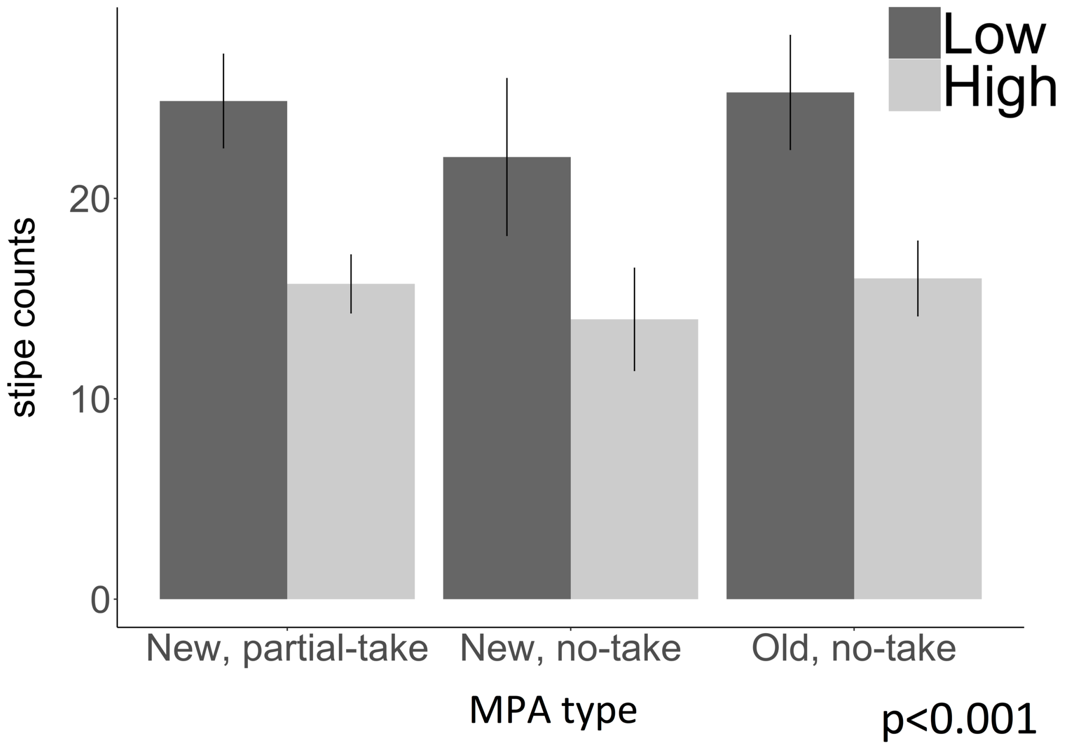

Figure S.1. Predictions and standard errors from a generalized mixed effects model of the number of stipes of the giant kelp *Macrocystis pyrifera* within 1 m radius of fishes surveyed, conditioned on MPA type and diver visitation, with diver visitation level shown in dark/light gray (see legend).

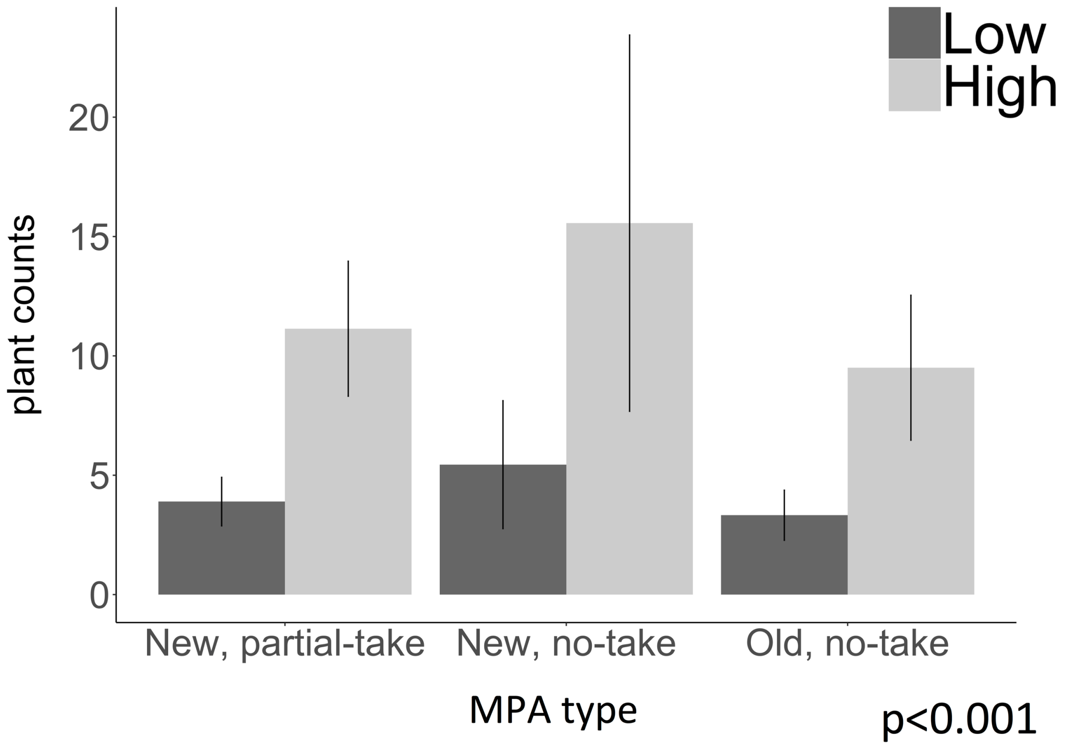

Figure S.2. Predictions and standard errors from a generalized mixed effects model of the number of plants of the subcanopy kelps *Pterygophora californica* and *Eisenia arborea* within 1 m radius of fishes surveyed, conditioned on MPA type and diver visitation, with diver visitation level shown in dark/light gray (see legend).

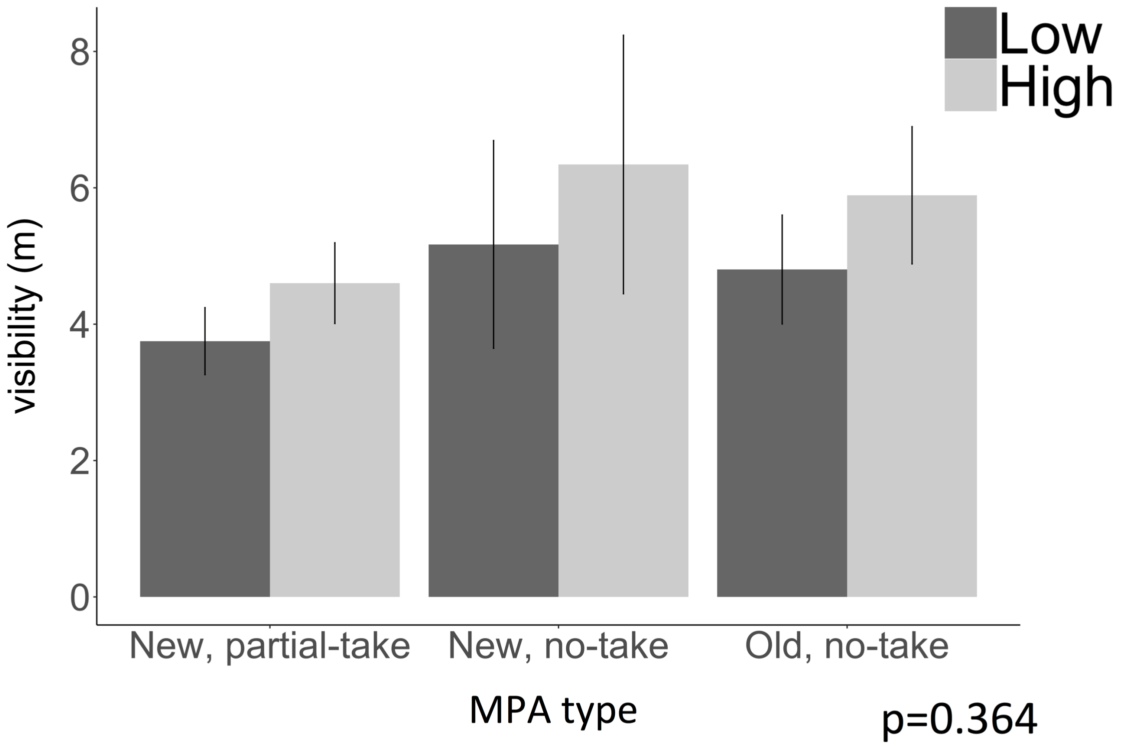

Figure S.3. Predictions and standard errors from a generalized mixed effects model of water visibility recorded during each dive after fishes were surveyed, conditioned on MPA type and diver visitation, with diver visitation level shown in dark/light gray (see legend).

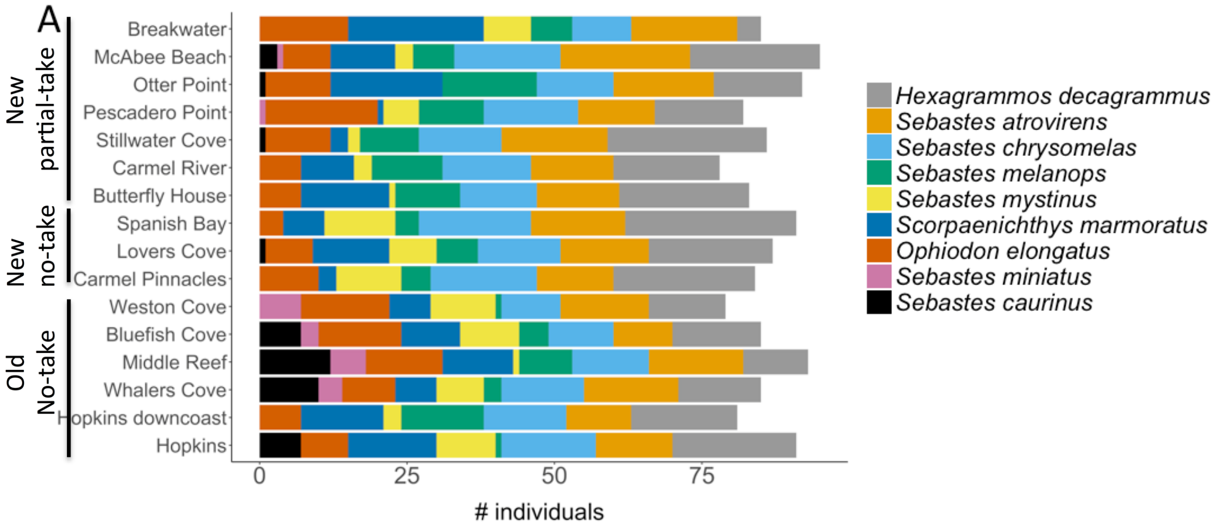

Figure S.4. Abundance and composition of fishes surveyed, separated by site. MPA type of each site is also indicated. Color is indicative of fish species (see legend).

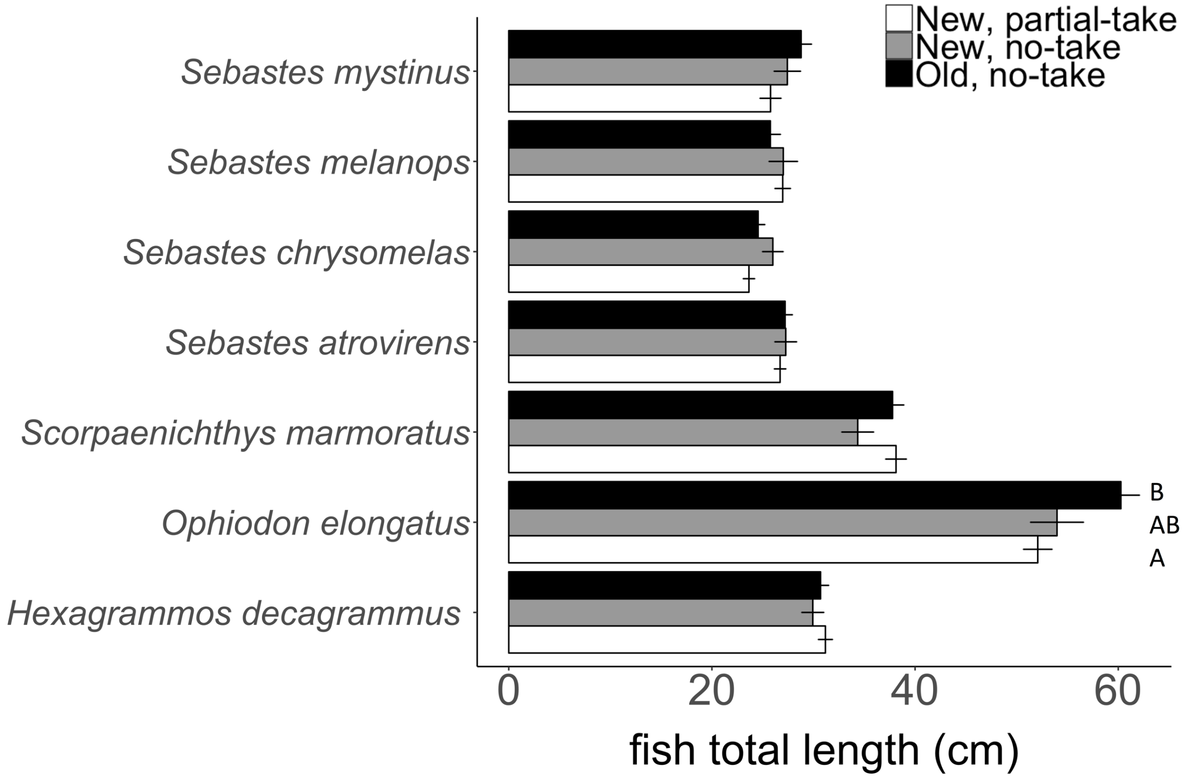

Figure S.5. Predictions and standard errors from a generalized mixed effects model of fish total length recorded during surveys, conditioned on species, MPA type, and diver visitation level. Shade is indicative of MPA type (see legend). Different letters indicate significant differences in fish total length among MPA type within a species ($p<0.05$).

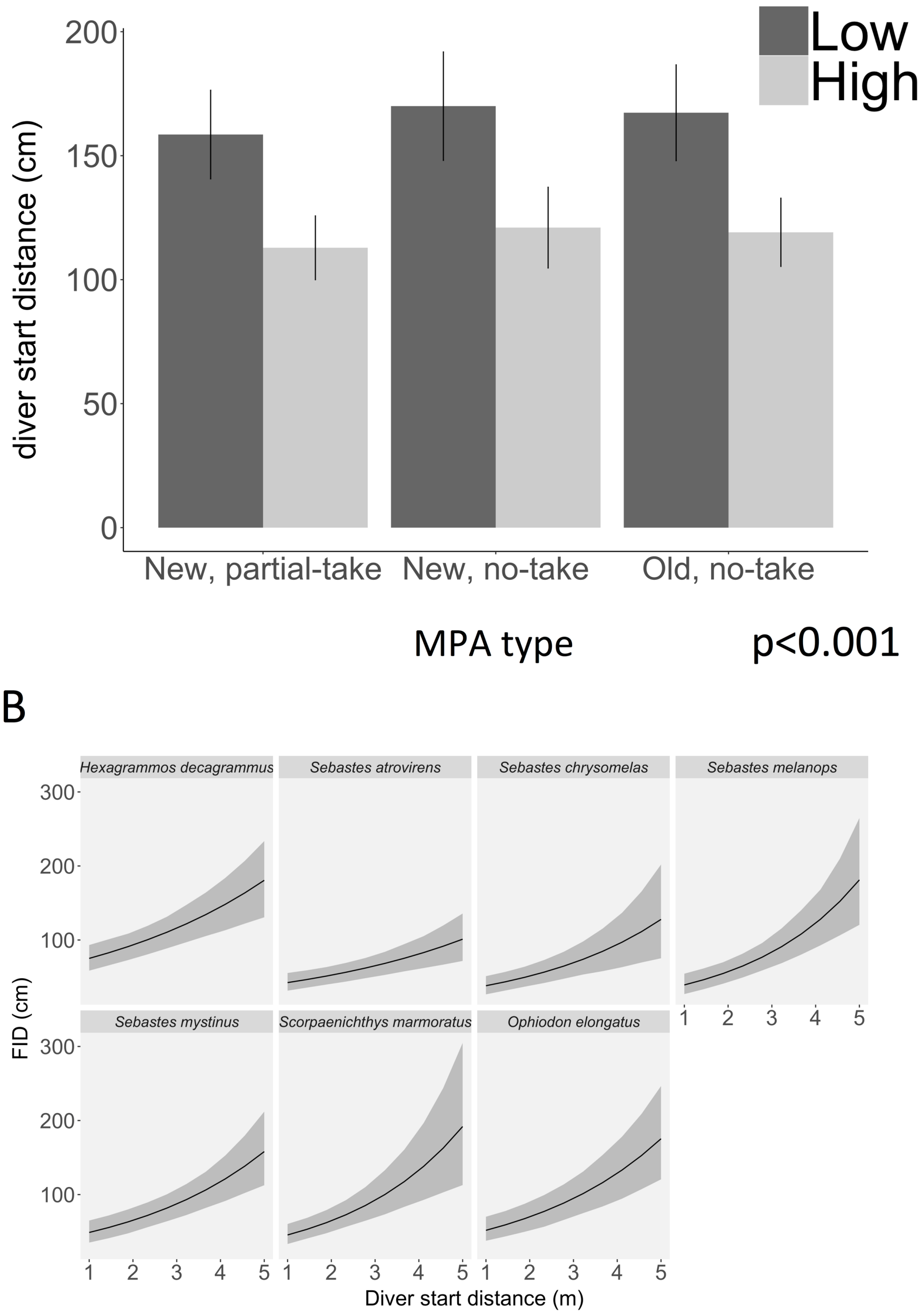

Figure S.6. Predictions and standard error bars from a generalized mixed effects model of diver start distance, conditioned on MPA type and diver visitation, with diver visitation level shown in dark/light gray (see legend). (B) Counterfactual predictions and 95% credible intervals of FID by diver start distance, separated by species, from the linear mixed model. Predictions are averaged across sites and dive replicates per site.

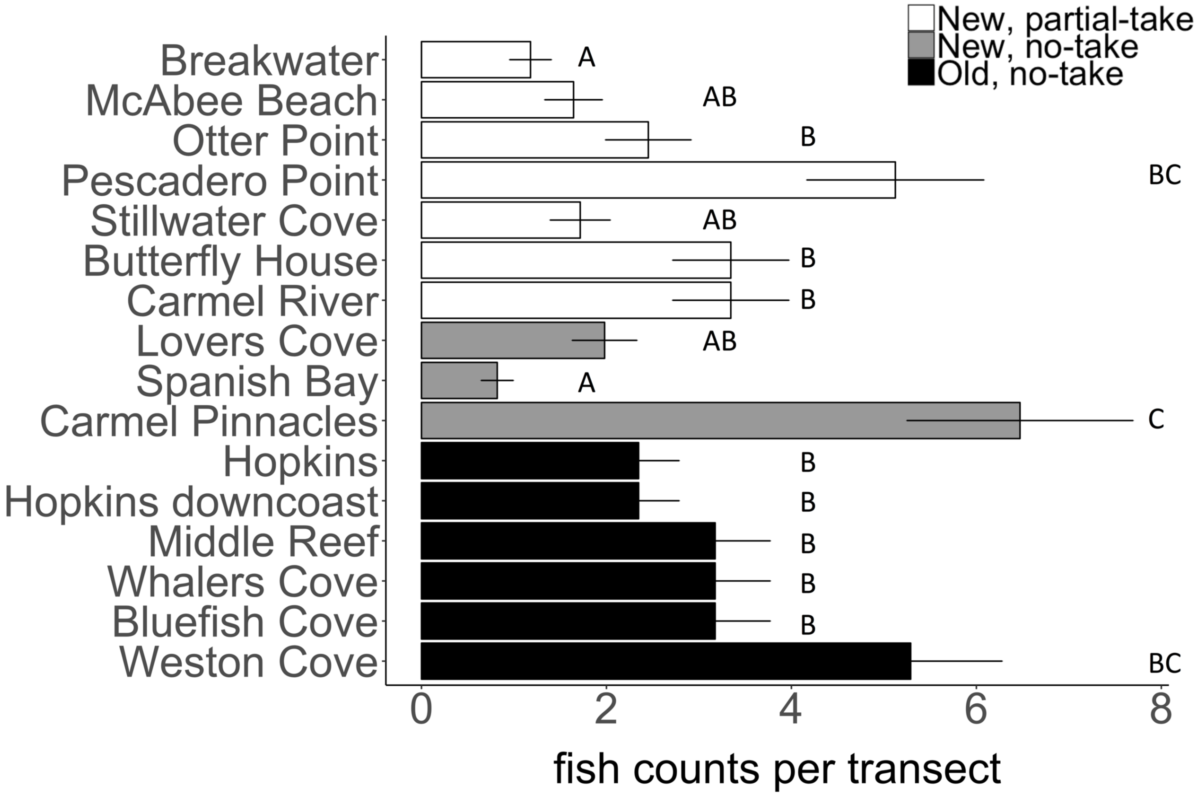

Figure S.7. Predictions and standard errors from a generalized mixed effects model of abundance of medium and large fishes (>20 cm total length) per transect, conditioned on site. Fish abundance per transect is extracted from surveys collected by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) Kelp Forest Monitoring Program. Shade is indicative of MPA type (see legend). Different letters indicate significant differences among sites ($p<0.05$), as determined through post-hoc pairwise comparisons of least square means among sites.

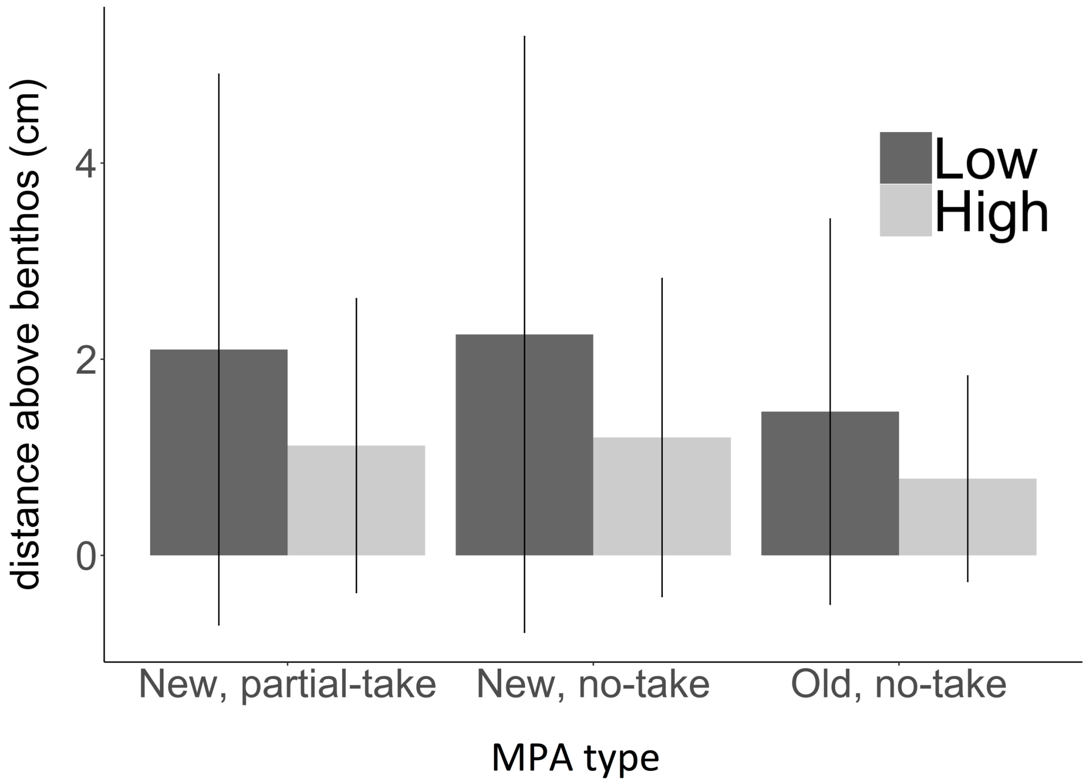

Figure S.8. Predictions and standard errors from a generalized mixed effects model of fish distance above the benthos, conditioned on diver visitation level, with diver visitation level shown in dark/light gray (see legend).

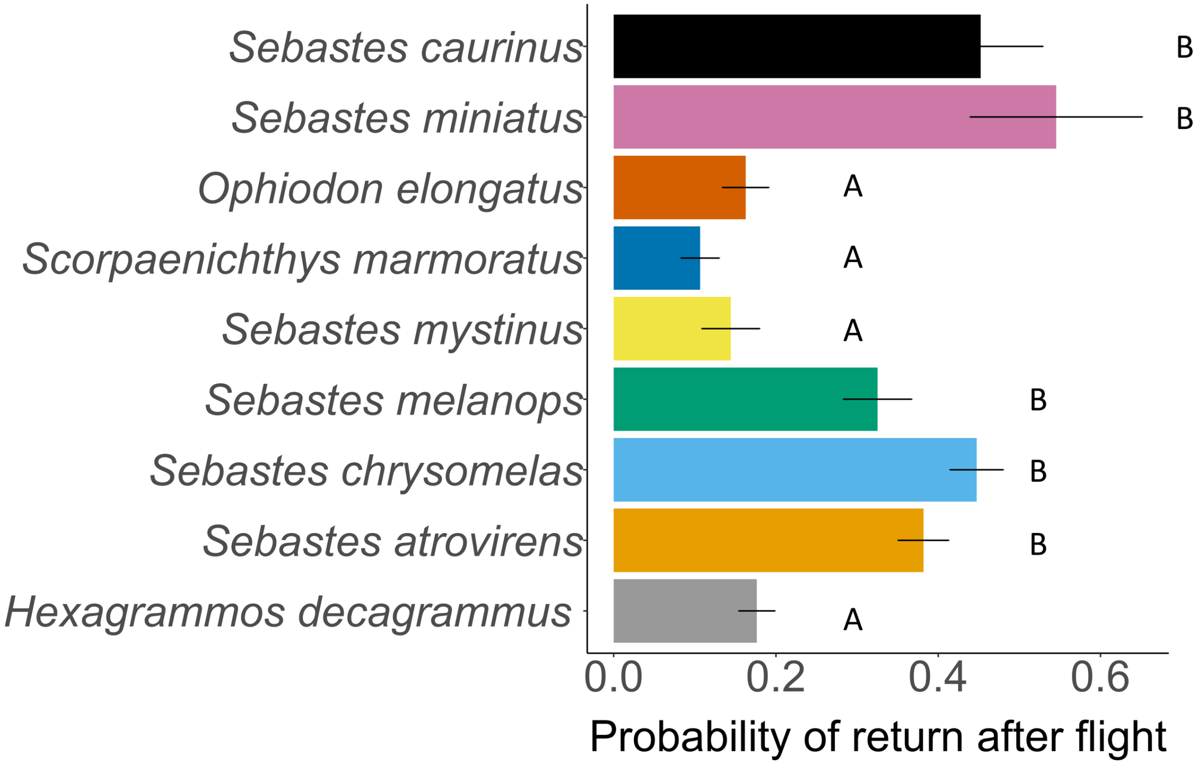

Figure S.9. Predictions and standard errors from a generalized mixed effects model of fish return to original location after flight, conditioned on fish species. Different letters indicate significant differences in probability of return among species ($p<0.05$).