Fished species uniformly reduced escape behaviors in response to protection

O. Kennedy Rhoades, Steve I. Lonhart, John J. Stachowicz

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 fish 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).

1. 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 (Cree 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).
which impacts individual behavior (Stankowich and Blumstein, 2005), it represents one side of the story of life histories (Claudet et al., 2010; Januchowski-Hartley et al., 2015). Responses to protection can vary among species with distinct ecologies and as a predictor of recovery (Goetze et al., 2017; Januchowski-Hartley et al., 2015). Since FID is correlated with anti-predator behavior (Stankovich 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 that 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.

2. Materials and methods

2.1. 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) (Fig. 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 policed by MPA managers, 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 SMCA, 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 et al., 2002; Wilson-Vandenberg et al., 2014), SMCA 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 fish, including the live fish component of the commercial nearshore fishery, which is data-limited. To the extent that the nearshore fishery may extract resources from kelp forests in the Monterey region (CDFW, 2015), SMCA could offer some protection relative to unprotected areas. Thus, we continue to refer to SMCA as “no-take” and SMCA as “partial-take,” even though SMCA 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 accessibility 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. Visitations are 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; Figs. 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; Fig. 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).

### 2.2. 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 s. If the fish did not move after 60 s, 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 5 min of displacement. Individual surveys of FID were of approximately 5 min 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).

### 2.3. 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.

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**Fig. 1.** Map of flight initiation distance (FID) survey sites. Polygon shades (black, gray, and white) 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.
(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. atrovires (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 (ca-bezon) (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 (Fig. 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; Fig. 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 (Fig. S.4), so we therefore removed these species from analyses of fish behavior by MPA type.

2.4. 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 in Mendeley Data (Rhoades et al., 2018).

2.5. 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 et al., 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.

3. Results

Fish displayed reduced escape behaviors at old relative to new MPAs (Fig. 2A, C). All species at old, no-take MPAs were uniformly less likely to initiate flight in response to diver approach (p = 0.002; Fig. 2C). Flight initiation distance (FID) was 29% shorter at old, no-take MPAs relative to new MPAs (p < 0.001; Fig. 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; Fig. 2B, D). Species at popular dive sites were less likely to initiate flight at all in response to diver approach (p < 0.001; Fig. 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; Fig. 2B; Table S.6). Prior to initiating FID, diver start distances were shorter at popular dive sites (p < 0.001; Fig. S.6A), which likely contributed to shorter FID (Fig. 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; Fig. 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 (Fig. 2B).

Piscivorous fish abundance varied significantly across sites, and was particularly high in old, no-take MPAs (Fig. 3A; see also general fish abundance, Fig. 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, Fig. 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 (Fig. 4; Table S.5). Fishes at popular dive sites occurred closer to refuges (p = 0.050; Fig. 4A) as well as lower in the water column and closer to the benthos.
pied rocky refuges (originally signi-
dificant due to its strong cryptic behavior and coloration). There was a mar-
times (p < 0.001; Fig. 4B). Even though
(p < 0.001; Fig. S.8), despite there being fewer refuges at popular dive
sites, their habitat choice was still suggestive of increased risk perception. Only one species’ habitat use (S. marmor-
atus) was similar across areas of low and high dive visitation (likely
due to its strong cryptic behavior and coloration). There was a mar-
ginally 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
dive 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 (Fig. 5A). Species that often occu-
pied rocky refuges (S. chrysomelas and S. carinus) 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 asso-
ciated 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; Fig. 5B; Table 1). Across species,
mean FID ranged from 30 to 90 cm, and FIT spanned 1–16 s, and FID
and FIT were marginally negatively correlated (p = 0.054; Fig. 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).

4. Discussion

Although surveyed fishes exhibited unique ecological characteristics
including distinct escape behaviors and habitat use, all species re-
sponded similarly to protection from harvest and exposure to high dive
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 be-
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 re-
covering 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 dis-
uss these direct and indirect effects, their ecological implications, and
the implications of these behavioral changes for the management of
ecosystems.

4.1. 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 po-
sition, 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-pre-
dator 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.

Fig. 2. (A and B) Counterfactual predictions and 95% credible intervals from the general-
ized linear mixed models of species-level flight initiation distance (FID) by (A) MPA type and (B) low/high diver visitation. Symbols and colors 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).
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.

4.2. 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 piscivores 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.

4.3. 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 (Geoffroy 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).

4.4. 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 et al., 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 Fig. 5) and thus their prey selection. In general, in avoiding areas heavily trafficked by humans (Coppes et al., 2017), consumers reduce foraging time (Guti 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).

4.5. 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; Viole 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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.bioccon.2018.06.030.

References
