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Human-induced reductions in fish predator boldness decrease their predation rates in kelp forests

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Humans have restructured food webs and ecosystems by depleting biomass, reducing size structure and altering traits of consumers. However, few studies have examined the ecological impacts of human-induced trait changes across large spatial and temporal scales and species assemblages. We compared behavioural traits and predation rates by predatory fishes on standard squid prey in protected areas of different protection levels and ages, and found that predation rates were 6.5 times greater at old, no-take (greater than 40 years) relative to new, predominantly partial-take areas (approx. 8 years), even accounting for differences in predatory fish abundance, body size and composition across sites. Individual fishes in old protected areas consumed prey at nearly twice the rate of fishes of the same species and size at new protected areas. Predatory fish exhibited on average 50% longer flight initiation distance and lower willingness to forage at new protected areas, which partially explains lower foraging rates at new relative to old protected areas. Our experiments demonstrate that humans can effect changes in functionally important behavioural traits of predator guilds at large (30 km) spatial scales within managed areas, which require protection for multiple generations of predators to recover bold phenotypes and predation rates, even as abundance rebounds.

1. Background

Human activities have resulted in dramatic changes in the density and phenotypes of terrestrial and marine consumers, fundamentally altering the structure and functioning of ecosystems [1]. Management and conservation efforts have naturally focused on recovering numbers and sizes of key predators and herbivores, assuming these are sufficient proxies for the ecological functions that these species provide. Yet, human activities also alter a range of consumer traits, including morphology, life history and behaviour [2–5]. Of these traits, behaviours such as foraging and defence that directly influence rates of predation and herbivory have the potential to change rapidly in predators and prey, and their effects can quickly amplify across trophic levels and food webs [6–9]. Rapid and widespread human-induced evolution and phenotypic plasticity of foraging and defensive behaviours [3] might, therefore, alter species interactions as well as the recovery of populations, communities and ecological functioning under different management regimes [5].

To date, few empirical studies have quantified human-induced behavioural variation across species assemblages, or experimentally linked this variation to changes in rates of key species interactions such as predation. Instead, experiments have largely focused on short-term effects of human fishing, hunting and tourism on the behaviour and population dynamics of single species,

and frequently under controlled laboratory conditions, which may overestimate the impacts of human-induced changes in behaviour on species interactions and community structure [6,7]. Indeed, if behavioural shifts revert as soon as the stimulus is removed, their impact may rapidly attenuate [10], limiting the temporal extent of their impact. However, not all changes in behaviour are reversible, and population-level changes in behaviours can occur as a result of selection among distinct behavioural phenotypes [11] or early life conditioning of long-lived species [4,5,12]. In such cases, recovery of behaviours (and thus ecological role) of consumers may be incomplete even once population density and size structure recovers.

Despite this, the community consequences of human-induced changes in predator foraging and defence [13,14] and the concept of recovering consumer function by restoring these behaviours [15,16] have only recently been considered. Comparisons of consumer behaviour and foraging rates among protected areas that vary in age, extent or level of protection provide one approach to assessing the magnitude and duration of human-induced behavioural changes at larger spatial and temporal scales [8,17]. Such comparisons also offer the potential to determine whether recovery of predator density and size structure alone are sufficient to restore ecological interactions, or whether behavioural changes persist over longer time scales.

In marine ecosystems, overfishing has reduced predatory fish biomass by as much as 80–90% [18], weakening top-down control and modifying existing trophic cascades [19]. By limiting or prohibiting resource extraction within marine protected areas (MPAs), managers have rapidly recovered the biomass, diversity and individual body size of targeted species within as few as 3–5 years, depending on enforced protection level, age, size and degree of isolation [20]. However, fishing may also influence ecological functioning via changes in the behavioural traits of exploited species [12,14,21]. Spearfishing rapidly reduces exploratory behaviour and increases flight [22,23], and passive fishing gear selectively removes individuals with certain heritable traits including heightened boldness and activity [21,24], or selectively removes traits that are linked to these behaviours [25]. Whether learned or heritable, fishing-induced behavioural shifts may dramatically affect the rate of recovery of harvested consumer populations and consumer-driven ecological processes such as predation and herbivory. Some species rapidly adjust behaviour in response to short-term fishery closures [22], such that bold behaviour could quickly recover, while genetically based behaviours may be slow to change because of past depletion of bolder genotypes [26]. Moreover, low initial frequencies of bold phenotypes within consumer populations will further slow recovery of these species via low population growth rates [27] and altered life histories and other key ecological traits [28,29], also slowing the recovery of interactions of consumers with their prey. The probability and timeline of human-induced behavioural change in predator assemblages, how it varies across consumer assemblages and behavioural traits, and its contribution to restoring ecological processes such as predation across different management regimes remain unknown [30].

In this study, we investigated the recovery of fish behaviour, predator function and predation rates across MPAs of varying age and protection level in kelp forests in central California. We repeatedly deployed and video-recorded

over 200 feeding assays of standardized, tethered squid prey (highly palatable and commonly consumed prey for mobile marine carnivores [31,32]) at 78 locations across seven sites to compare relative predation rates and predator identity and composition across protected areas. We used our own field surveys of fish escape behaviour and independent data on fish abundance, body size and species composition to assess the relative importance of these factors in contributing to the effect of protection from human activities on predation rates.

2. Material and methods

(a) Study sites and organisms

We conducted field surveys and manipulations from June to September 2014 and 2015 on shallow, rocky reefs along a 30 km stretch of coast between the Breakwater in Monterey, CA, USA (36.609414 N, –121.8924 W) and Weston Cove in Big Sur, CA, USA (36.51103 N, –121.94486 W; see the electronic supplementary material, figure S1). All 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 into three categories according to age and protection level: old, no-take (ONT, established in 1917 and 1973; no fishing permitted), new, no-take (NNT, established in 2007; no fishing permitted) and new, partial-take (NPT, established in 2007; recreational fishing permitted) areas. Unprotected areas adjacent to state-designated protected areas are clustered along one area of highly wave-exposed rocky coastline. Since unprotected status was confounded with location, exposure and inaccessibility to humans, unprotected sites were excluded. Most of the deployments at new protected areas were in NPT areas (214 of 231 total feeding assays). We therefore principally compared predation rates and foraging behaviour between ONT and NPT areas.

Old and new protected areas in this region experience different levels of human extractive and non-extractive use. There is fairly good compliance with protected area regulations [33]; commercial and recreational fishing pressure is markedly reduced at no-take areas. Within NPT areas, recreational fishing (the dominant source of take) remains high; all size classes of rockfishes (*Sebastes* spp.) and larger, mature size classes of other species could be taken legally at the time this study was conducted. NPT areas, therefore, offer little to no protection for targeted fishes. We also surveyed sites that experience both high and low visitation of recreational SCUBA divers (the effects of which are discussed in [34]; also see diver visitation levels per site in the electronic supplementary material, tables S1 and S5), such that protected area characteristics were not confounded with diver visitation.

We conducted surveys and experiments on rocky substrate dominated by giant kelp, *Macrocystis pyrifera*. Transect-level patterns of topography and algal cover did not vary consistently across protected area age or protection level. Seawater temperature varied across the period of observations but did not vary as a function of protected area age or protection level. All sites are characterized by natural substrates except Breakwater, which is adjacent to and consists partly of a boulder jetty.

(b) Predation rate experiments

We assessed predation rates by natural assemblages of near shore reef fishes at seven sites in MBNMS from June to September 2015 (electronic supplementary material, figure S1 and table S1). These sites encompassed ONT ($n = 3$), NNT ($n = 1$) and NPT

($n = 3$) areas. At each site, we haphazardly selected locations on the reef to deploy feeding assays. A feeding assay consisted of 3 m of lead line strung between two cement anchors placed on the selected location on the reef. During deployment, divers attached 11 pieces of squid mantle (10 g each) at 25 cm intervals along the lead line, suspended 10–20 cm above the reef. Divers then clamped a GoPro Hero 3 video camera (GoPro, Inc., San Mateo, CA, USA) to one of the anchors and positioned it to video-record predatory fishes feeding along the baited line. After a short disturbance of 3 min, divers departed, and the baited line was left undisturbed for 1.5–3 h, after which divers returned to collect all equipment.

Feeding trials consisted of deploying feeding assays at a block of six locations on a single dive. Over the course of one to four weeks, we conducted a total of three feeding trials at the same block of six locations. We repeated this protocol one to six weeks later at a second block of six locations at the site. All sites therefore, consisted of six feeding trials across two blocks, except for Spanish Bay, which consisted of three feeding trials across a single block of five locations. Within a block, the six locations were separated from each other by 15–40 m. Within a site, the two blocks were separated from each other by 40–100 m.

We recorded and analysed predation events (including predator identity and behaviour) using SCUBA diver observations and GoPro video. We observed large predatory fishes (families Sebastidae, Hexagrammidae and Cottidae; electronic supplementary material, table S2) as well as smaller fishes (Percidae, Serranidae and Labridae) and invertebrates (classes Malacostraca, Asterozoa and Echinozoa; electronic supplementary material, table S3) feeding on standard squid prey at feeding assays (see life-history information in the electronic supplementary material, table S4). We also noted the presence/absence of a natural predator (seal, cormorant or large piscivore) at the feeding assay (which were more common at ONT areas, the impacts of which are generally discussed in [34]).

(c) Escape behaviour surveys

We surveyed fish escape behaviour at 16 sites within MBNMS from June to September 2014 (electronic supplementary material, figure S1 and table S5). These sites included ONT ($n = 6$), NNT ($n = 3$) and NPT ($n = 7$) protected areas. SCUBA divers swam unidirectional underwater transects and conducted surveys of flight initiation distance (FID) of individual fishes [22,35]. The lead diver approached unwary fishes at a fixed speed of approximately 1 m s^{-1} and recorded FID as the horizontal distance between a diver and a fish when the fish fled. Divers also recorded species, estimated total length and other aspects of the fish's escape behaviour. In total, we surveyed 1378 individuals of nine commonly harvested kelp forest fishes, including the following *Sebastes* species: *S. atrovirens*, *S. caurinus*, *S. chrysomelas*, *S. melanops*, *S. miniatus* and *S. mystinus* (Scorpaenidae), *Hexagrammos decagrammus* and *Ophiodon elongatus* (Hexagrammidae) and *Scorpaenichthys marmoratus* (Cottidae). We included only subadults and adults (above minimum size at maturity as described in [36]) in surveys. These species also comprised the majority of fishes observed consuming squid prey during feeding assays.

(d) Fish abundance, size and species composition

We used subtidal fish survey data (2007–2015) collected by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) Kelp Forest Monitoring Program (standard procedures used to assess the abundance of kelp forest fish stocks in MPAs, both state-wide and globally [37]) to estimate total abundance and mean size of all fishes greater than 20 cm observed on survey transects (including bottom, mid-water and

canopy surveys). We selected fishes greater than 20 cm total length for analyses because they were able to handle, remove and consume entire pieces of squid mantle. Principal components analysis (PCA) did not indicate any clustering of fish species composition by year of PISCO survey (electronic supplementary material, figure S2), however, abundance and body size moderately increased within sites across years (electronic supplementary material, figures S3 and S4).

We estimated site-level fish abundance and mean total length using PISCO data by estimating predicted values of these variables in a generalized linear mixed model (GLMM) including site as a fixed effect and side (location within site), zone (depth location) and transect (single location at three levels, canopy, mid-water and bottom), year, and fish species (when estimating mean total length) as random effects (intercepts). We estimated species composition of fishes that consumed standard squid prey during our field assays (hereafter termed 'feeders') by conducting a PCA of fish species observed at the assay that consumed squid, using feeding assays as samples (PC1 and PC2 accounted for 41% of variation in the sample). Site, assay and species scores were obtained to interpret differences in feeder assemblages with respect to PC1 and PC2 (electronic supplementary material, figure S5).

We selected experimental sites for proximity (in most cases within 100 m) to PISCO monitoring sites, such that PISCO survey data should reflect differences in fish abundance, size and composition among experimental sites. For the two experimental sites greater than 100 m from PISCO sites but less than 100 m from Reef Check sites (which employs PISCO protocols), PISCO and Reef Check abundance estimates were compared, confirming that PISCO data were also accurate representations of those more distant experimental sites (electronic supplementary material, figure S6).

(e) Statistical methods

We calculated the predation rate (number of standard squid prey consumed min^{-1}) at each of the 231 feeding assays by fitting a linear model to the number of squid prey consumed as a function of time and used the linear slope as the predation rate. We calculated per capita feeding rates for individual fishes feeding on squid prey at a single feeding assay by fitting a linear model to the number of squid prey consumed by that fish as a function of time, and using the linear slope as the per capita feeding rate. Attempted nonlinear fits (logarithmic and Poisson) performed poorly relative to linear fit, which better represented the consumption of squid prey for the majority of assays and individual fishes.

We fitted a series of GLMMs to estimate predation rates per feeding assay and per individual fish. Models for predation rate by feeding assay included feeding assay and block as random effects (intercepts), and sequence of repeated deployments as random slopes fitted to each feeding assay and block, respectively. These models also contained site-level estimates of fish abundance and total length, assay-level feeder species composition and predator presence/absence, as well as either protected area age (model 1) or site-level predictor of FID (model 4) as fixed effects. The model of predation rate by individual fish included feeding assay, feeding trial, block, site, the sequence of repeated deployments at each assay and fish species as random effects (intercepts), and protected area age and feeder abundance as random slopes fitted to each fish species.

We also fitted a model of FID for individual fish to test the importance of protected area age in influencing FID (model 3), which included site, individual dive and surveyed fish species as random effects (intercepts), and fish total length, diver start distance and diver visitation as random slopes fitted to each

fish species, and protected area age and protection level as fixed effects.

We fitted GLMMs to a gamma distribution with a log-link using both Bayesian inference (BI) and maximum-likelihood methods, which produced qualitatively and quantitatively similar predictor estimates (see Results). We conducted statistical analyses in R v. 3.2.4. GLMMs were fitted using the packages lme4 (maximum-likelihood) [38] and rethinking v. 1.58 (BI) [39]. We sampled from BI models using the Hamiltonian Monte Carlo method and using non-centred parametrization, using the R package RStan v. 2.9.0 [40].

3. Results

Predation rates were consistently higher at ONT areas relative to NPT and NNT areas (figure 1; also see the electronic supplementary material, figure S7A). Analysis of over 600 h of underwater video footage from 231 feeding assays indicates that on average, time to more than 50% consumption of standard squid prey was nearly three times greater at new relative to old protected areas (figure 1a). Large predatory fishes consumed the majority of squid prey (98 versus 76% of squid prey at ONT versus predominantly NPT areas), and these predatory fishes were more abundant and larger at ONT areas relative to new protected areas ($p < 0.001$; figure 2a,b), probably contributing to greater predation rates. However, even accounting for fish abundance and body size across sites and fish feeder composition across feeding assays as predictors in the GLMM, predation rates were 6.5 times higher in old relative to new protected areas (model 1; electronic supplementary material, table S6; $p < 0.001$; figure 1b). These data suggest that there is an additional effect of protected area age on predation rates that is not explained by estimated site-level differences in fish abundance and body size. Moreover, our model of per capita feeding rates (model 2; electronic supplementary material, table S6) indicates that individual feeders, though of similar body size across sites (figure 2d), consumed squid prey 1.9 times faster at old relative to new protected areas ($p < 0.001$; figure 1c).

Our behavioural observations suggest that these stark differences in predation rates and per capita feeding rates among protected areas are partially accounted for by enhanced boldness in individual fishes at old protected areas (see the electronic supplementary material, videos S1–S6). At new protected areas, abundant species (*S. chrysomelas*, *O. elongatus*, *H. decagrammus* and *Sc. marmoratus*) initiated brief attempts but failed to remove squid prey while divers were present (electronic supplementary material, videos S1 and S3), and fed successfully only after divers had departed, mouthing or biting (handling) and removing single prey and fleeing to shelter after short feeding events (electronic supplementary material, videos S2 and S4). By contrast, these same species as well as rarer species (e.g. *S. caurinus* and *S. miniatus*) rapidly approached and remained at baited lines to handle and successfully remove prey at old protected areas while divers were present (electronic supplementary material, video S5). Fishes that encountered baited lines after divers had departed remained to handle and remove multiple prey consecutively (electronic supplementary material, video S6). These data demonstrate variation in willingness to forage despite apparent threats. Likewise, our surveys of fish escape behaviour indicate that fishes at old protected areas exhibited

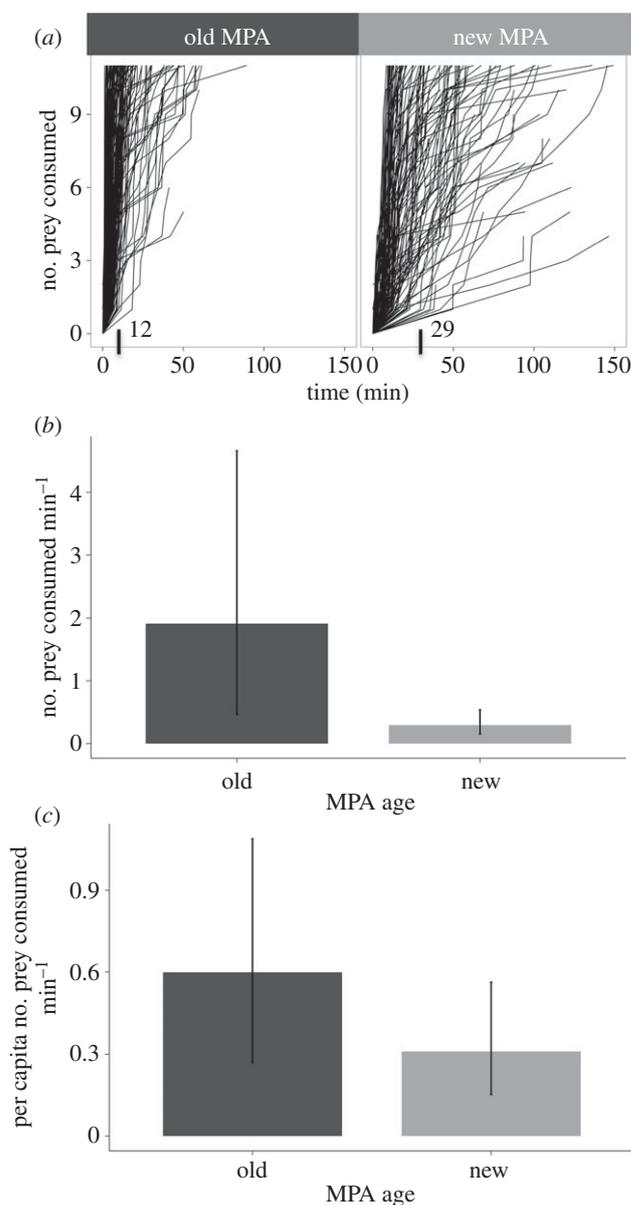


Figure 1. Fish consumption of standard squid prey, separated by protected area age. (a) Prey consumed per feeding assay since the time of deployment, recorded from video footage. The vertical line on the x-axis indicates the time in minutes to over 50% consumption (six of 11 prey consumed). Counterfactual predictive plot of (b) predation rate and (c) per capita feeding rate by protected area age, both with 95% credible intervals from the GLMM and with raw data overlaid on predictions.

shorter FID (40–60 cm) compared to fishes at NNT and NPT areas (35–85 cm), allowing divers to approach closer before fleeing. Even accounting for species identity, body size and other sources of site-level variation as predictors in the GLMM, fish FID was 50% longer at new relative to old protected areas ($p > 0.001$; figure 3a; model 3; electronic supplementary material, table S6 and also figure S7B).

We tested whether the effect of protected area (model 1) could be accounted for by reduced fish escape behaviours in old protected areas (model 4) by replacing protected area age with site-level estimates of FID for an abundant predatory rockfish species (*S. chrysomelas*) that consumed standard squid prey at all sites (figure 5c). FID estimates for *S. chrysomelas* were calculated by fitting a GLMM of FID by site for this fish species. In this model (model 4, electronic supplementary material, table S6), a 33% reduction in FID from new to old protected areas (which is the average increase

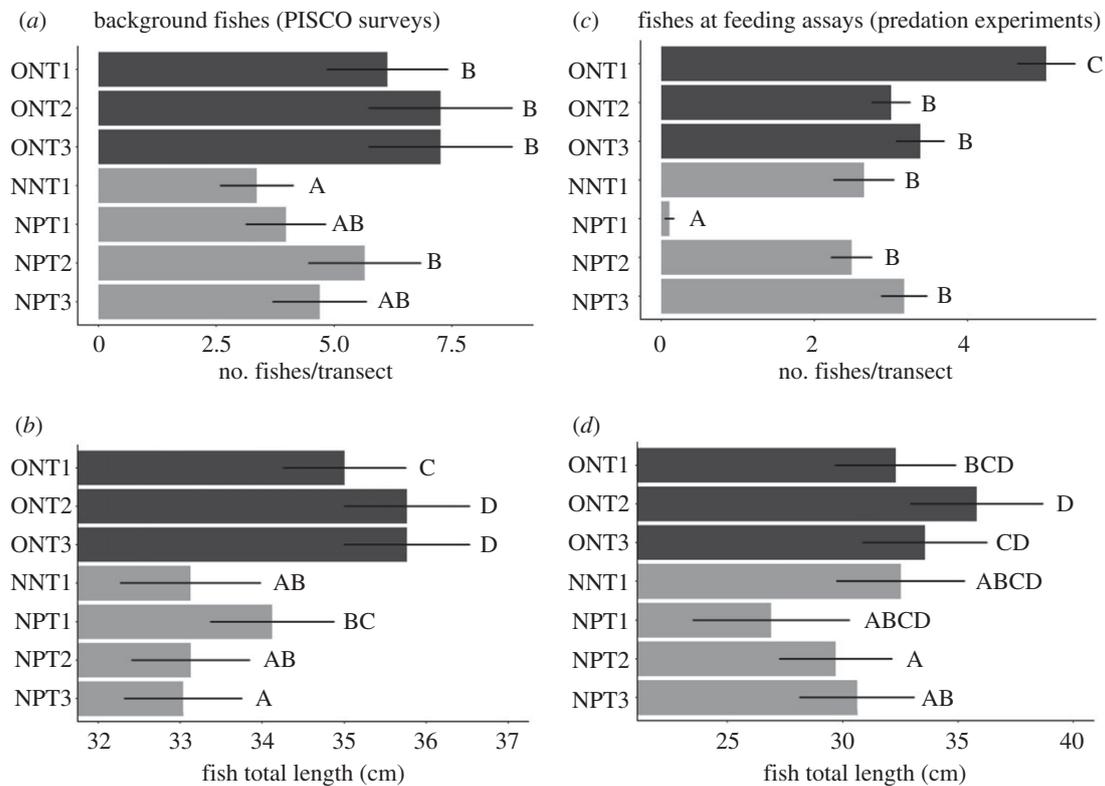


Figure 2. Abundance and total length of fishes obtained from diver-recorded data from PISCO surveys (a,b), and video-recorded data on fishes that consumed prey during feeding assays (c,d) across sites. Mean estimates are shown with 95% credible intervals from the GLMM.

in FID across all fish species from old to new protected areas, see the electronic supplementary material, figure S8 for site-level differences in FID for *S. chrysomelas*) increases predation rates by 3.4 times. Moreover, the effect of FID on predation rates was greater in magnitude than that of fish abundance, size and feeder composition ($p < 0.001$; figure 4), and model comparisons (Akaike information criterion, Bayesian information criterion, and widely applicable information criterion) indicate that the model containing FID has the same or better predictive accuracy for predation rates as the model containing protected area age (electronic supplementary material, table S7). Given that protected area age and FID are highly correlated if included in the same model, FID probably provides one mechanistic explanation for the effect of protected area age on predation rates.

Feeder species composition also differed among ONT areas and between ONT and NPT areas, potentially contributing to differences in predation rates. Although background fish species composition did not differ among sites (figure 5a,b), the species composition of predatory fishes that fed on squid prey varied significantly across sites and by protected area age (figure 5c,d). Species of feeders varied significantly between ONT area sites, and specifically at ONT2 relative to ONT1 and ONT3 (with a 95% bootstrap probability that these sites cluster separately; electronic supplementary material, figure S9), and between old and new protected areas (with a 89% bootstrap probability that these sites cluster separately, see the electronic supplementary material, figure S10; see also figure 5d and the electronic supplementary material, figure S5 for explanation of PCA species scores). Feeders were top piscivores (*S. caurinus*, *O. elongatus* and *Sebastes carnatus*) at ONT2, in comparison with secondary carnivores (*S. mystinus*, *S. atrovirens* and *S. chrysomelas*) at ONT1. Feeders at the four new protected area sites consisted of some distinct species (*Sc. marmoratus* and

H. decagrammus) and some shared species (*S. mystinus* and *S. chrysomelas*) relative to ONT areas.

4. Discussion

The intensity of consumer–prey interactions in communities is often assessed by consumer abundance and body size, implicitly assuming these are the dominant drivers of predation, herbivory and cascading effects on lower trophic levels. Our field experiments and surveys across a network of protected areas demonstrate that human-induced changes in escape and foraging behaviour of a predator guild contribute to substantial variation in predation rates in the field. By altering predator behavioural traits, humans indirectly alter predation rates, thereby influencing the outcome and intensity of species interactions and their importance for community structure and resilience from anthropogenic disturbances. Our work complements controlled experiments by showing that human-induced changes in multiple functionally important behaviours occur in open, natural systems and across entire consumer assemblages, and persist over long time scales and large (30 km) spatial scales. Predator and prey behaviours are often assumed to recover faster than density, such that behaviourally mediated effects could be quickly reversed with protection and removal of human predation risk [5]. This is probably true when behavioural effects involve *individuals* changing behaviour in response to changing threat conditions. In our study, the reverse was true: differences in foraging, defence and predation rates remained long after densities recovered, potentially because the shifts we observed were *population-level* changes caused by selection shifting the relative abundances of individuals with different behavioural phenotypes. Our work shows that it may be incorrect to assume that the impacts of human-induced behavioural shifts on predator function are either short-lived and/or small-scale [5,12,14,17].

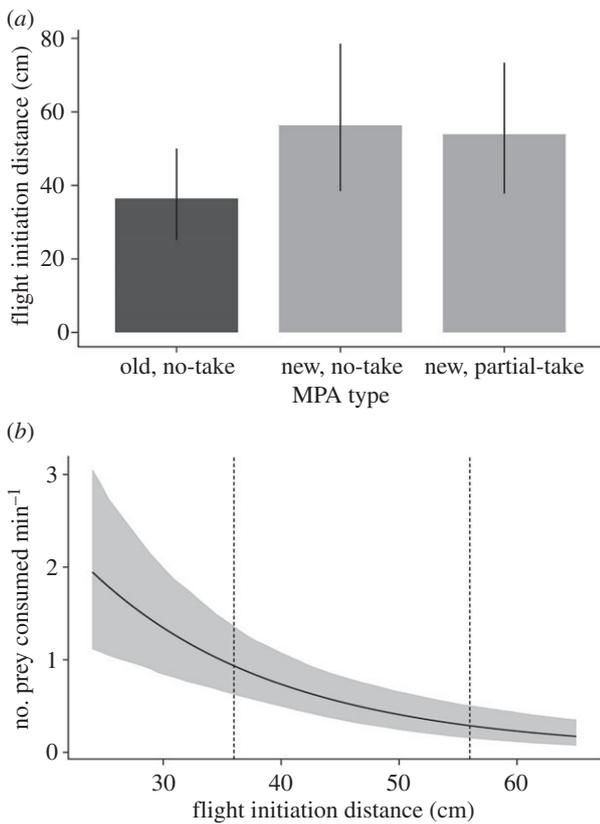


Figure 3. (a) Counterfactual predictive plot of FID across protected area age and protection level, with 95% credible intervals from the GLMM, and with raw data overlaid on predictions. (b) Counterfactual predictive plot of predation rate by FID for *Sebastes chrysomelas* with the mean line and shaded 95% credible intervals. Vertical dotted lines indicate the lower and upper limits of the average difference in fish FID between new and old protected areas.

Predation rates on standard squid prey were 6.5 times higher, and per capita feeding rates were 1.9 times higher at old relative to new protected areas, even accounting for variation in predator abundance and body size across sites. Higher predation rates on squid prey at ONT areas were partly explained by reduced flight responses of individuals of the same species at these sites relative to new protected areas. Higher individual feeding rates, greater willingness to forage (particularly in piscivores) and longer feeding times across the predator assemblage probably also contributed to higher predation rates at ONT areas, which experience the low risk of human predation relative to new protected areas.

Human predation risk-induced changes in the defensive behaviours of key predators and herbivores have a range of predictable consequences for populations, communities and ecosystems. Bold behaviour is linked to enhanced foraging success, higher energy gains and other traits that increase individual fitness and population productivity [25–27,41,42], such that increases in the frequency of bold phenotypes may increase population growth rates. Boldness is also linked to variation in activity level, habitat use and foraging [41,43], which impact competitive interactions among or within predatory species [44] and among predators and prey [45], strengthening their direct and indirect effects on lower trophic levels. In our kelp forest study system, fish predation can reduce abundances of intermediate carnivores (other fishes) or herbivorous invertebrates (crabs, snails and

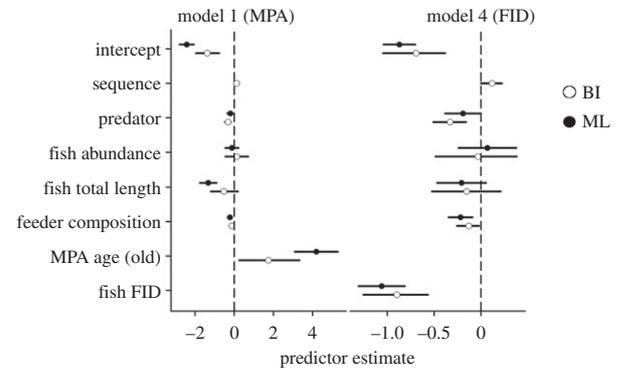


Figure 4. Model estimates of fixed effects (predictors) from GLMMs of predation rate by protected area age (model 1) versus by fish FID (model 4). Mean estimates are shown with 95% confidence intervals (maximum-likelihood, ML), and 95% credible intervals (Bayesian inference, BI). These models were fitted using a gamma distribution, such that per unit increase in a predictor, the predation rate is the exponentiated mean predictor estimate multiplied by the current predation rate. Continuous predictors are centred and standardized, such that their full range is 2 units (compared to 1 unit for binary predictors). A prediction interval containing 0 is equivalent to no effect. Sequence refers to the ordered sequence of deployments of standard squid prey at a single block. Predator refers to the presence of a predator at a feeding assay.

urchins) [46]. With lower human predation risk, bolder fishes emerge more frequently into open areas [47], encounter and consume more prey [42], and alter prey foraging and hiding behaviour [43]. However, since these fishes are generalists that feed across trophic levels, the net ecological impacts of variation in predator boldness and predation rates across sites are difficult to predict [48], and may result in suppression or enhancement of feeding on basal trophic levels, potentially increasing or decreasing primary producer biomass.

In other systems, human alteration of consumer behaviour may also alter the strength of predator–prey interactions, with potential consequences for community structure and ecosystem functioning. On coral reefs, spearfishing of key bioeroders and herbivores increases FID and may reduce foraging time, which could indirectly enhance algal overgrowth and reduce coral settlement, growth and survival more than expected based solely on reductions in fish biomass [15]. In terrestrial forests, human activities displace wolves and cougars from heavily trafficked areas, impacting deer and elk foraging, and indirectly altering the composition of trees and shrubs, the distribution of riparian areas, and associated birds and mammals [13,49,50], although evidence for this remains controversial [51]. Humans impact consumer defensive behaviours across marine [16,22,25,35] and terrestrial habitats [2,5,13,49,50], influencing a wide range of trophic levels and taxa. These studies highlight human-induced changes in a range of defences (habitat displacement, temporal or spatial foraging shifts and activity level), many of which are probably more costly than FID in terms of energetic or foraging trade-offs. Thus, we expect that differences in rates of predation or herbivory as a result of human-caused behavioural changes in consumers are likely to be important in a broad range of ecosystems.

Additionally, we used standardized, undefended prey to facilitate comparisons of predation rates in the field across many sites. Predation rates on tethered squid mantle are

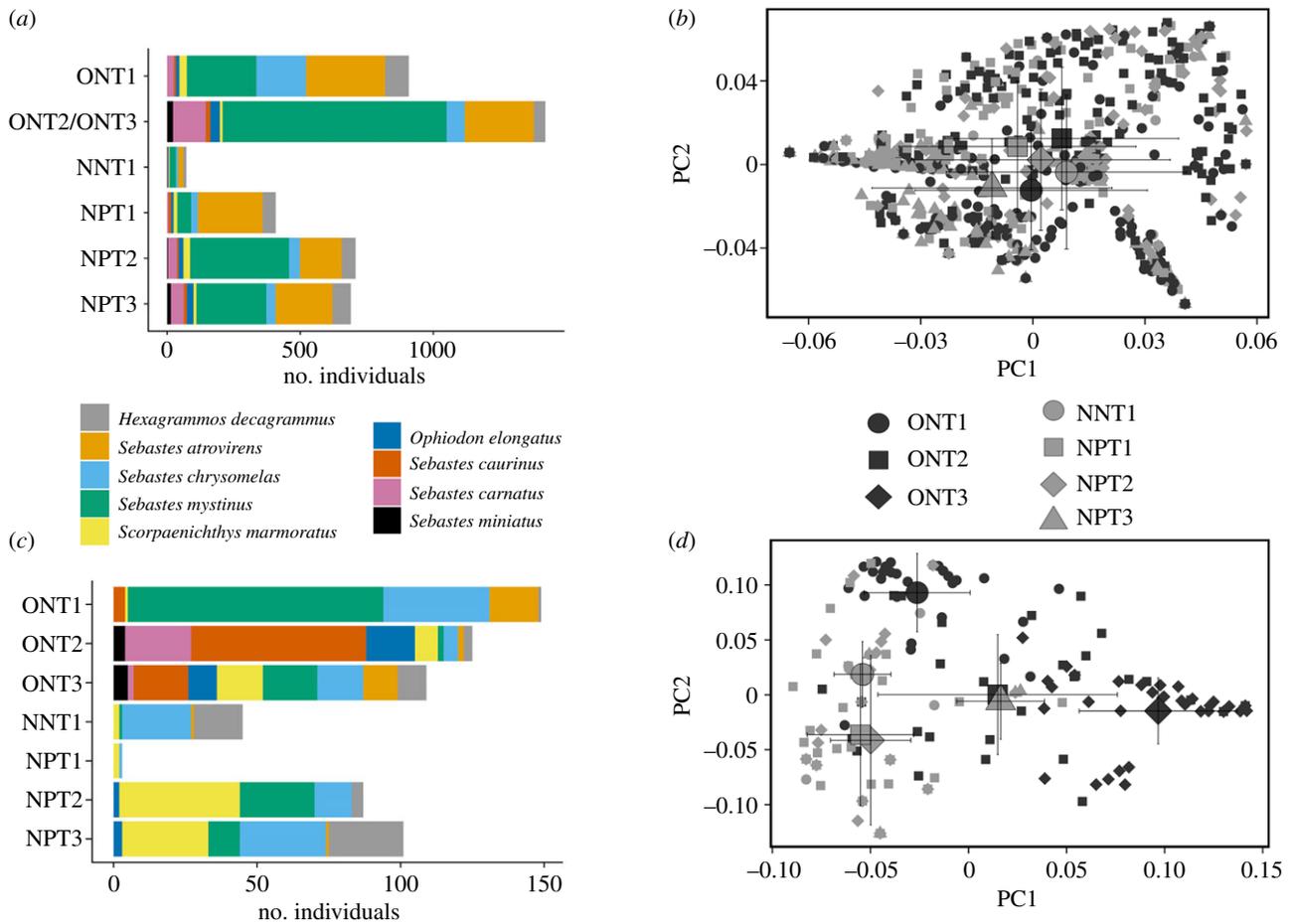


Figure 5. Background fish and feeder abundance and composition by site-based diver-recorded PISCO surveys (*a* and *b*), versus video-recorded data on fishes that consumed standard squid prey during feeding assays (*c*, *d*) across sites. (*a*, *c*) Raw fish abundance by site. (*b*, *d*) Sites scores for principal component 1 (PC1) and principal component 2 (PC2) from PCA analysis using community abundance data, with the symbol represented by the mean and lines representing the standard error in PC1 and PC2 for each site. (Online version in colour.)

correlated with predation on tethered live organisms [31], but real prey require extensive search, pursuit or handling time. Consequently, bold phenotypes, which forage more frequently and for longer lengths of time, generally have greater capture success of behaviourally and morphologically defended live prey. We, therefore, believe that our experiments probably provide a reasonable, if not conservative estimate of changes in rates of prey consumption under variable human predation risk, even within this system.

Recent studies suggest that protecting large areas from extraction and other human activities can restore consumer behaviour and function [13,16], eliminating human predation risk by preventing selective removals of bold individuals and by suppressing behavioural shifts due to encounters with humans. However, our study suggests that long-term protection across multiple generations of consumers could be required to restore natural predator behaviours and predation rates on prey. FID did not vary between recently fully protected and partially protected areas, and protected area age significantly reduced FID (figure 3*a*), suggesting that recovery of behaviours occurs quite slowly. This suggests that differences in behaviour among sites are the result of selection on behavioural types altering the frequency of bold genotypes [26] across multiple generations rather than the result of rapidly induced behavioural plasticity. Only old protected areas have prohibited human extraction of predators for sufficient time (40+ years) to allow recruitment and growth-to-maturity of new individuals of bold phenotypes.

Although our experimental design (at primarily NPT and ONT areas) prevents us from fully distinguishing between the effects of protection level and age on predation rates, escape and foraging are closely linked, and full protection from human predation risk across multiple generations of key consumers is probably required to re-establish consumer behavioural traits and rates of predation.

To date, the majority of studies of the consequences of human impacts on consumer behaviour for population- and community-level processes have been conducted in controlled, short-term laboratory experiments with a few species, or in large-scale correlative field studies. Our study assesses the magnitude and extent of human-induced changes in predator behaviour and directly measures rates of consumption of prey by these predators across protected areas, encompassing 30 km of coastline and natural environmental variation, and with substantial differences in history (8 versus 40+ years) and intensity of human predation. We conclude that humans significantly impact functionally important escape and foraging behaviours of an entire assemblage of predatory fishes, with predictable impacts on predation rates and therefore on predator function that continues even after abundance and size structure of consumers recover with protection. These results not only support theory on the spatial and temporal extent of human-induced behavioural shifts in nature, but also highlight the ecological significance of these behavioural changes for predation pressure, and therefore for food webs

and ecosystems [9,14,17]. If we seek to recover key ecological processes and functions in natural systems, we must look beyond simple metrics of consumer abundance and size to restore the key traits that define consumer function.

Ethics. Deployment of field experiments was approved by Monterey Bay National Marine Sanctuary, MBNMS-2015-019 and the State of California Department of Parks and Recreation, 20150528_085801. Field experiments and fish surveys were non-invasive and strictly adhered to the laws of the United States of America.

Data accessibility. Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5nq06fj> [52]. Escape behaviour survey data available at: <https://data.mendeley.com/datasets/8hxc7hr7m4/1>.

Authors' contributions. All authors conceived of the study and designed research; O.K.R. and S.I.L. collected field data; O.K.R. and J.J.S. analysed data; and O.K.R., J.J.S. and S.I.L. wrote the manuscript. All authors gave final approval for publication.

Competing interests. We have no competing interests.

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