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Protection of large predators in a marine reserve alters size-dependent prey mortality

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Where predator–prey interactions are size-dependent, reductions in predator size owing to fishing has the potential to disrupt the ecological role of top predators in marine ecosystems. In southern California kelp forests, we investigated the size-dependence of the interaction between herbivorous sea urchins and one of their predators, California sheephead (*Semicossyphus pulcher*). Empirical tests examined how differences in predator size structure between reserve and fished areas affected size-specific urchin mortality. Sites inside marine reserves had greater sheephead size and biomass, while empirical feeding trials indicated that larger sheephead were required to successfully consume urchins of increasing test diameter. Evaluations of the selectivity of sheephead for two urchin species indicated that shorter-spined purple urchins were attacked more frequently and successfully than longer-spined red urchins of the same size class, particularly at the largest test diameters. As a result of these size-specific interactions and the higher biomass of large sheephead inside reserves, urchin mortality rates were three times higher inside the reserve for both species. In addition, urchin mortality rates decreased with urchin size, and very few large urchins were successfully consumed in fished areas. The truncation of sheephead size structure that commonly occurs owing to fishing will probably result in reductions in urchin mortality, which may reduce the resilience of kelp beds to urchin barren formation. By contrast, the recovery of predator size structure in marine reserves may restore this resilience, but may be delayed until fish grow to sizes capable of consuming larger urchins.

1. Introduction

Body size is an important driver of consumer–resource interactions, because it determines the amount and types of prey an individual can consume as well as the consumer's own vulnerability to other predators [1]. Variation in body-size distributions can therefore influence the interaction strength between predator and prey [2], with the loss of larger-bodied predators causing disruption of trophic control [3,4]. In aquatic systems, the size-selective nature of many fisheries has led to the disproportionate removal of larger-bodied fishes [5] and declines in body size of entire predator guilds [6]. In one marine ecosystem, reductions in predator body size alone were attributed with a 300% increase in prey abundance [6]. This suggests that truncations in predator size structure may lead to a loss of predator function even in the absence of changes in predator biomass.

Marine reserves have been proposed as one tool to reinstate key predator–prey interactions. In some instances, predator recovery in reserves has led to trophic cascades in which herbivorous prey populations decline, thereby allowing primary producers to flourish [7]. However, such indirect effects of marine reserve protection (i.e. population responses of non-fished species) are often difficult to detect [8,9] and, when present, often lag significantly behind direct effects

on fished species [10]. One potential explanation for observed time lags between predator recovery and reductions of prey abundance is size-dependent predation [10]. To predict how communities will respond to both fishing and protection in marine reserves, we need a more mechanistic understanding of how predator–prey interactions are affected by changes in both predator abundance and body size.

Much of the evidence for trophic cascades in marine reserves involves herbivorous sea urchin prey [7,10,11]. In the absence of predators, urchins can grow to very high abundances and potentially large sizes (if resources are sufficiently abundant). At high densities, urchins overgraze macroalgae and convert productive kelp forests to urchin barrens [11–13]. These barrens often persist for decades, even following reserve establishment, because urchins remain invulnerable to predation until the predators grow sufficiently large to consume them [10]. In some cases, prey that have grown very large may permanently escape predation and will persist until removed by other causes (e.g. storms [14] and disease [15]). As a result, understanding the size-dependence of the interactions between predators and urchins is critical to making accurate predictions about the consequences of management actions that affect predator size structure and the trajectory of recovery following the establishment of marine reserves.

In southern California, both the California sheephead (*Semicossyphus pulcher*) and spiny lobster (*Panulirus interruptus*) are important predators of sea urchins in kelp forests. The potential for sheephead to regulate urchin populations was corroborated by a 26% increase in urchin numbers and an increase in the proportion of urchins occupying exposed habitats when sheephead were experimentally removed [16]. Fishing on sheephead may reduce this important functional role [17]. Overharvest in the 1990s led to declines in sheephead biomass [18] and a significantly truncated size distribution [19]. If the interaction between sheephead and urchins depends on size, this truncation in size structure has the potential to affect the functional role of sheephead as urchin predators in kelp forests.

Here, we focus on how sheephead size and urchin size interact during *in situ* feeding trials to influence prey choice and examine consequences of fishing-induced changes in sheephead size structure for urchin demographics. We identify whether a threshold size for sheephead exists below which they are not capable of consuming urchins, and we evaluate how this urchin consumption threshold varies as a function of urchin size class for two urchin species that differ in their defensive abilities (i.e. spine length). Finally, we examine how spatial differences in sheephead size structure and density inside and outside of a marine reserve are translated into relative urchin mortality rates for urchins of different size classes and species.

2. Material and methods

(a) Study species

California sheephead are large sex-changing wrasses (family Labridae) occupying inshore rocky reefs and kelp beds from Monterey Bay to Baja California in the eastern Pacific [20]. Sheephead are generalist predators of benthic invertebrates [21], and purple urchin *Strongylocentrotus purpuratus*, and red urchin *Mesocentrotus franciscanus* are common prey. For a given test diameter (TD), red urchins have longer spines, and the disparity in spine length increases with size. Both factors increase the relative handling time of red versus purple urchins for predators and can thereby affect prey choice [22]. Both urchin species preferentially graze on attached and drift macroalgae, including the giant kelp *Macrocystis pyrifera* and many fleshy species.

(b) Surveys and predation trials

Community surveys and predation trials were conducted at three sites inside the Catalina Marine Science Center Reserve (Chalk Cliffs 33°26′40″ N, 118°29′19″ W; Intakes 33°26′49″ N, 118°29′06″ W; Pumpernickel 33°26′54″ N, 118°28′48″ W) and three sites in the fished area outside the protection of the reserve (Lion's Head 33°27′13″ N, 118°30′05″ W; Isthmus 33°26′54″ N, 118°29′22″ W; Bird Rock 33°27′05″ N, 118°29′19″ W) (figure 1). The no-take marine reserve was established in 1988 and encompassed 0.13 km² [23] at the time of the study, prior to its expansion to 6.75 km² in 2012 as the Blue Cavern State Marine Conservation Area. This reserve was chosen because of documented differences in sheephead size structure inside and outside of the reserve [24] and the increased potential that predation could be observed directly via SCUBA owing to the high densities of sheephead relative to other locations in California [25].

Sites consisted of high relief (more than 1 m) boulder and rock cobble habitat with giant kelp (*M. pyrifera*) between 5 and 20 m depth. Locations within each site where empirical feeding trails were deployed were selected to standardize the substrate type and rugosity of the habitat.

Sheephead abundance and size distribution as well as urchin and kelp densities were quantified using SCUBA surveys in August 2010 and August 2011. Fish were surveyed on five 30 m × 2 m transects conducted in two reef zones (the inner (approx. 10 m depth) and outer (approx. 15 m depth) edges of the kelp bed at each site) in each year. Sizes were estimated visually to the nearest cm (total length (TL)) by divers experienced in estimating fish lengths. Our training using underwater calibration to fish models indicates sizing error for individual observations is less than 10%. Kelp and urchin densities were recorded on one 30 m × 2 m transect at each site in 2010 and two transects per site in 2011.

In August 2010, we used field predation trials to examine size-specific predation on two species of sea urchin: red (*M. franciscanus*) and purple (*S. purpuratus*). Urchins were collected at two sites outside of reserves (Isthmus and Lion's Head) by turning over boulders to reveal concealed urchins. Urchins were measured and assigned into one of three size classes: small (20–35 mm TD), medium (35–50 mm TD) and large (50–70 mm TD). Urchins were held in tanks of flowing seawater at the USC Wrigley Marine Science Center for 24 h prior to being returned to the field for use in feeding trials. The predation trials consisted of placing $n = 15$ urchins of each of the two species and three size classes within three 1 m² quadrats (i.e. prey choice arenas). Urchins were presented separately by size class but mixed for each species ($n = 30$ total urchins per quadrat) on rocky substrate (i.e. similar-sized large flat boulders) in each site. Quadrats were used solely to visually identify the area containing the transplanted urchins and were located approximately 1 m from each other. Within the quadrat, urchins were released onto exposed rocky substrates but were not prevented from seeking refuge during the predation trial. While urchins do occupy exposed habitats especially when food becomes limiting, by presenting urchins in this way, predation rates were probably artificially enhanced (urchin abundance is low at Catalina, and urchins are naturally restricted to crevices and concealed shelters there). However, our experiments were purposefully designed in this manner to quantify prey choice and concurrently to measure the relative mortality rates of free-ranging urchin prey of different sizes. A key issue is whether urchins of sufficient size can escape mortality even when fully exposed to potential predators. These experiments do not measure absolute predation rates at our study sites under natural
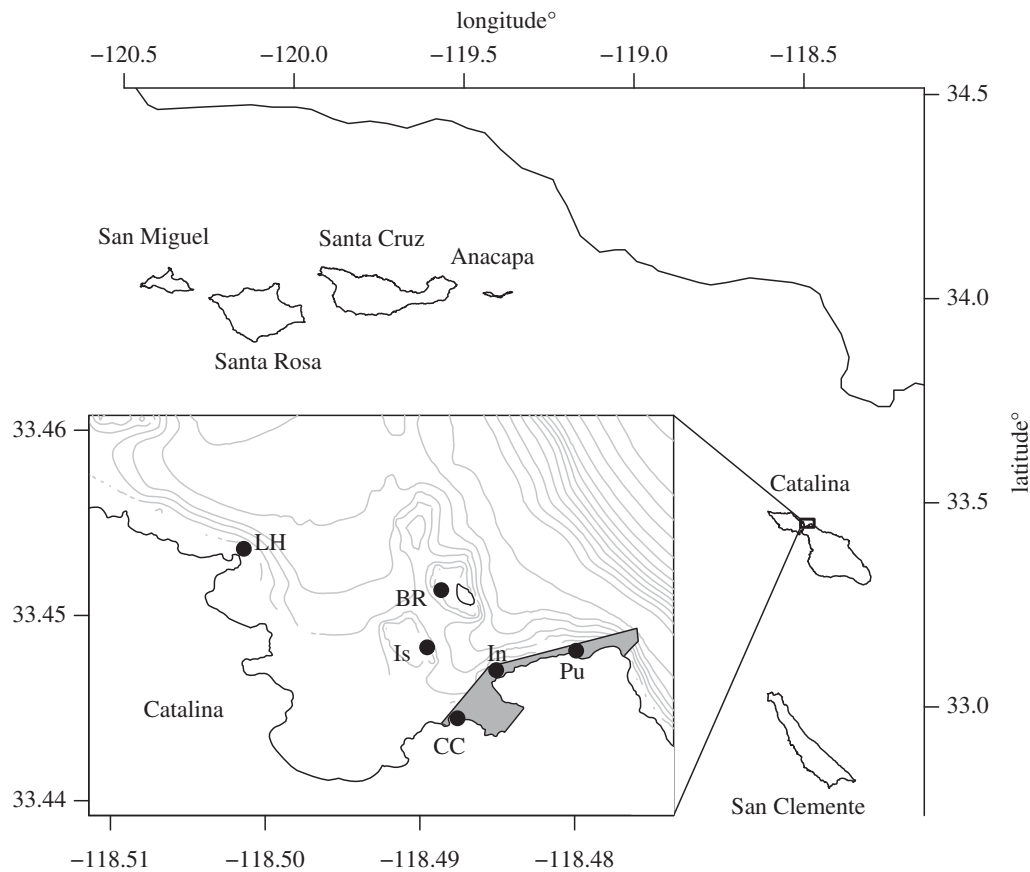
Figure 1. Greater study region in the southern California Bight, depicting the offshore Channel Islands (note: Santa Barbara and San Nicolas Islands not shown). Black rectangle highlights location of the specific study region on Catalina Island. Inset: filled black circles represent sites of surveys and predation trials at Catalina Island (fished sites: LH, Lion's Head; Is, Isthmus; BR, Bird Rock; reserve sites: CC, Chalk Cliffs; In Intakes; Pu, Pumpernickel). Dark grey shaded area is the Catalina Marine Science Center Reserve. Grey contour lines show 10 m depth contours from the California Seafloor Mapping Project.

conditions. The advantage of this feeding trial approach is that the predators are presented with a standardized number and size distribution of prey in each trial at each site, which allowed us to calculate prey choice and metrics such as the probability of consumption of a given size of urchin after being encountered by a given size of sheephead. Feeding trials were repeated $n = 4$ times at each location, resulting in deployment of 2160 total urchins across all species, size classes and sites (4 replicates × 15 urchins × 2 species × 3 size classes × 6 sites).

Once urchins were released into the prey choice arenas, divers sat motionless at least 2 m away from the feeding trial and observed sheephead attacking and consuming urchins for 30 min at each site. Feeding trials were conducted randomly throughout the daylight hours at each site and nocturnal urchin predators like spiny lobster were not observed in these trials. The length of each sheephead observed to attack an urchin was estimated visually to the nearest centimetre TL for smaller sheephead and within 5 cm size bins for sheephead larger than 40 cm. Encounters were recorded when a sheephead attempted to attack a single urchin within the quadrat and were recorded as a 'success', if the attempted attack resulted in the consumption of an urchin.

(c) Statistical analyses

The total biomass, and the biomass of small (less than 20 cm TL) and large (greater than or equal to 20 cm TL) sheephead inside and outside of the reserve were compared using linear mixed effects models with site as a random effect using the 'lmer' function [26] in the R package lme4 [27]. Sheephead biomass was calculated from the observed size distribution, using the length–weight

relationship reported in Hamilton & Caselle ([28]; $W(g) = a\text{TL(cm)}^b$, where $a = 0.0144$ and $b = 3.04$). Significance of reserve fixed effects was assessed using the package lmerTest [29]. Significance of site random effects was assessed using simulation-based exact restricted likelihood ratio tests statistics with the package RLRsim [30]. The difference between the size distribution of sheephead observed in surveys and those observed eating urchins in feeding trials at each site was analysed using Monte Carlo simulations ($n = 1000$) of the Kolmogorov–Smirnov test with the 'ks.boot' function in the Matching R package [31] and adjusted for multiple comparisons with the Bonferroni correction.

The proportion of attacks that resulted in a successful urchin predation event was assessed as a function of sheephead and urchin size using a generalized linear mixed effects model with sheephead size and reserve status as fixed effects, site as a random effect and with binomial errors. Neither site nor reserve status significantly improved model fit (e.g. the simpler model without site or reserve status had lower Akaike information criterion in all cases). We therefore pooled the predation success data across sites and refit the model with sheephead size alone using a generalized linear model with binomial errors. We used the model to calculate the size at which the encounter was more than 10% successful and more than 50% successful, which we used to evaluate threshold size for consumptive ability.

Among successful urchin attacks, the relative consumption rates of urchin species and size class as a function of sheephead size and reserve status were assessed using a multinomial logistic regression with the 'multinom' function in the nnet package in R [32]. Including reserve status did not improve model fit (likelihood ratio = 6.29, $p = 0.27$), so prey choice data were pooled across sites. Sheephead less than 25 cm TL were only observed
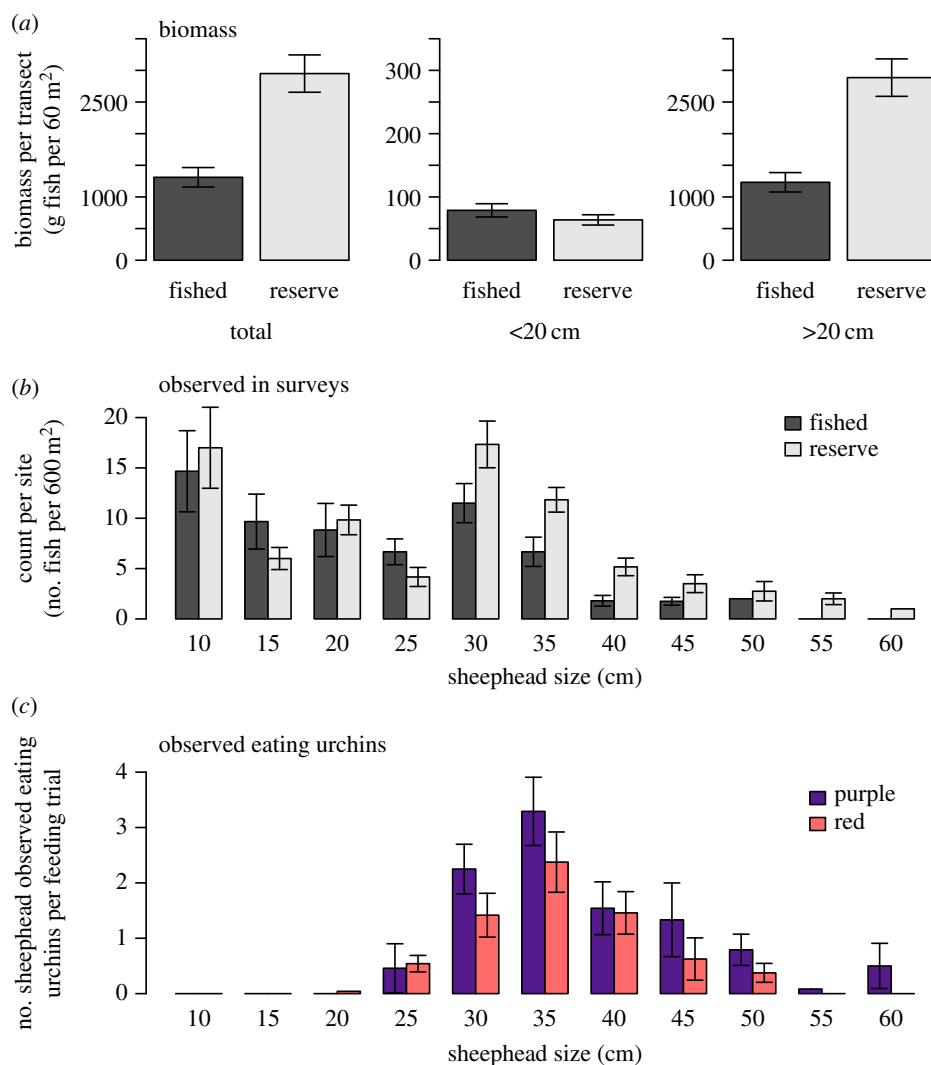
Figure 2. (a) Differences in the biomass of sheephead (g of fish per 60 m^2 transect) inside and outside of the reserve on Catalina Island. Shown are total biomass, the biomass of sheephead < 20 cm TL, and the biomass of sheephead > 20 cm TL. Error bars represent ±1 s.e. Size frequency distributions showing (b) the average (± s.e.) number of sheephead observed on visual surveys across all transects at each site and (c) the average (± s.e.) number of sheephead observed eating red or purple urchins in feeding trials. (Online version in colour.)

successfully attacking an urchin once and were therefore removed from the analysis of urchin prey choice.

Relative mortality rates for urchins in each size class were compared by fitting a generalized linear mixed effects model with binomial error terms to data on the proportion of urchins eaten within a feeding trial using the 'glmer' function in the R package *lme4* [26]. Urchin size, species and reserve status were treated as fixed effects, and site was a random effect. Differences in mortality between size classes were assessed using Tukey HSD comparisons using the R package *multcomp* [33]. Site effects were assessed by comparing models with and without random effects using χ^2 difference tests.

3. Results

Despite having similar total densities ($t = 1.4$, $p = 0.23$; electronic supplementary material, figure S1), sheephead had higher biomass inside the reserve, with significant site-to-site variation in biomass (reserve: $t = 3.280$, $p = 0.047$; site: likelihood ratio = 3.7, $p = 0.0154$; figure 2a). This site variability was primarily driven by high sheephead biomass at the centrally located reserve site (Intakes) relative to the two reserve sites at the edge of the reserve (Chalk Cliffs and Pumpernickel), as well as higher biomass at Isthmus relative to the two other

fished sites (electronic supplementary material, figure S2). Sheephead smaller than 20 cm TL had equal biomass inside and outside of the reserve (figure 2a; reserve: $t = -0.759$, $p = 0.48$, site: likelihood ratio = 2.2, $p = 0.04$) with slightly higher biomass at Isthmus (electronic supplementary material, figure S2). The biomass of sheephead greater than or equal to 20 cm TL was on average more than 2× greater in the reserve (figure 2a; reserve: $t = 3.2$, $p = 0.03$, site: likelihood ratio = 2.71, $p = 0.03$) and was consistently higher across all reserve sites (electronic supplementary material, figure S2). This elevated biomass is driven by the larger individual body size observed for fish of this size category inside the reserves.

The sizes of sheephead observed eating both red and purple urchins were skewed towards larger-sized individuals relative to the population as a whole, as recorded on visual surveys (bootstrap K-S test, $D > 0.43$ and $p < 0.001$ for red urchins at all sites; $D > 0.42$ and $p < 0.001$ for purple urchins at all sites; figure 2b,c). Sheephead smaller than 20 cm TL did not consume urchins, despite the high relative abundance of these small sheephead. By contrast, sheephead more than 25 cm TL were disproportionately involved as urchin predators (figure 2b,c).

Urchin species identity did not affect the frequency at which an observed attack resulted in a successful predation event (Wald $Z = -0.49$, $p = 0.62$ for small urchins, Wald
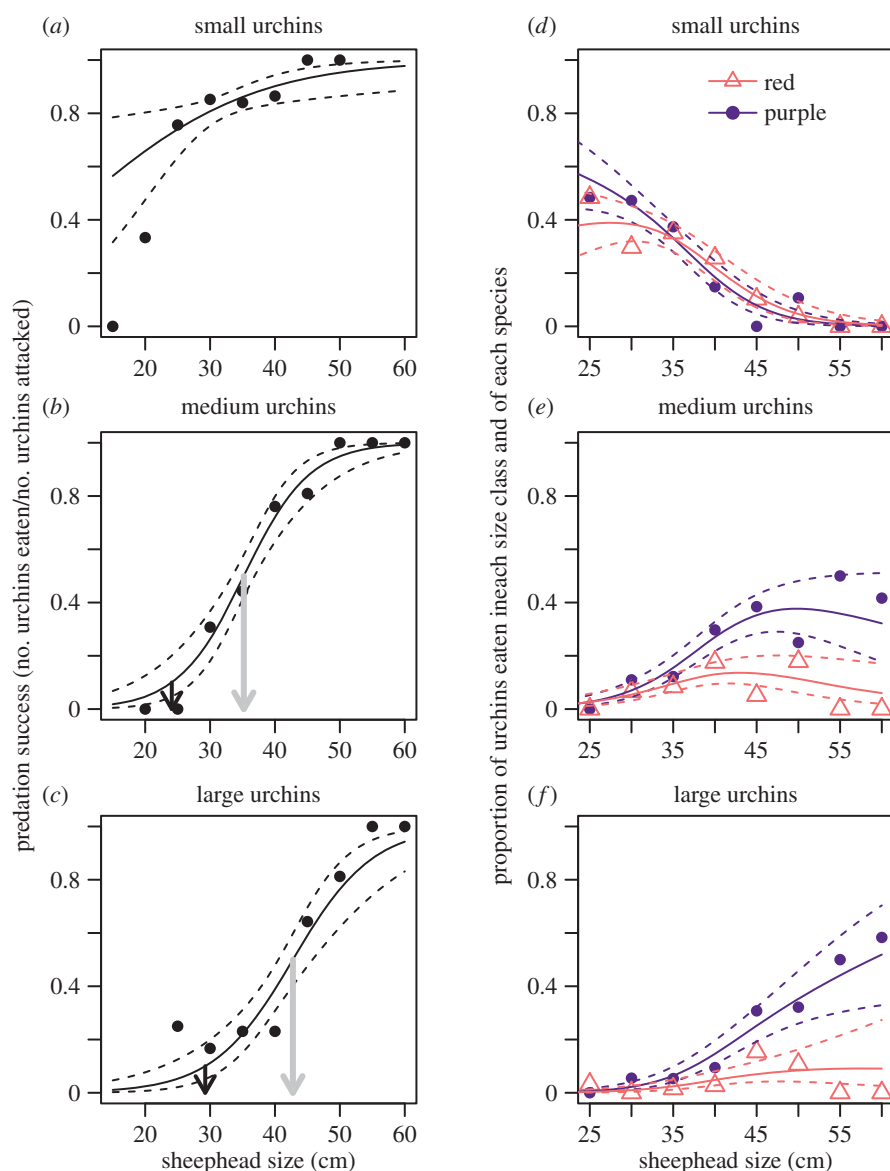
Figure 3. (a – c) Observed predation success (number of successful attacks/total observed attacks) for a given sheephead size class during experimental predation trials (filled circles). The mean (solid lines) and 95% CIs (dashed lines) are predicted probability of success in a given attack from a logistic regression. The vertical black arrow represents the size at which attacks were 10% successful and the thick grey arrow represents the size at which 50% of attacks are successful. (d – f) Observed proportion of each urchin size class and urchin species (red: open triangles; purple: filled circles) eaten within a given sheephead size class. Also shown are the mean (solid lines) and 95% CIs (dashed lines) of the predicted proportions from a multinomial regression. (a,d) small urchins (20 – 35 mm TD), (b,e) medium urchins (35 – 50 mm TD) and (c,f) large urchins (50 – 70 mm TD). (Online version in colour.)

$Z = -0.11$, $p = 0.729$ for medium urchins and Wald $Z = 0.713$, $p = 0.476$ for large urchins). Thus, observations of predation success were pooled across urchin species. Sheephead size increased the likelihood that an attack would be successful for all urchin size classes (Wald $Z = 2.564$, $p = 0.0103$ for small urchins, Wald $Z = 5.974$, $p < 0.001$ for medium urchins, and Wald $Z = 5.510$, $p < 0.001$ for large urchins; figure 3a–c). All sizes of sheephead larger than 20 cm TL were capable of consuming the smallest urchin size class (20–35 mm TD) of urchins (figure 3a). However, as urchin size increased, the minimum threshold size at which sheephead was capable of consuming urchins also increased. For medium-sized urchins (35–50 mm TD), sheephead needed to be larger than 24 mm TL to be successful in at least 10% of their attacks, while a sheephead size of 35 cm TL was required for encounters to be at least 50% successful. For large urchins (50–70 mm TD), only sheephead larger than 29 cm TL were successful in at least 10% of their attacks, while only sheephead larger than

43 cm TL were successful in more than half of their attacks (figure 3b,c).

The empirical feeding trials revealed that sheephead size also influenced the relative rate at which the three urchin size classes and two urchin species were consumed (figure 3d–f). At the onset of including urchins in the diet at approximately 20 cm TL, sheephead only consumed small urchins. Larger sheephead were more likely to consume medium and large urchins (Wald $Z = 8.06$, $p < 0.001$ and Wald $Z = 8.95$, $p < 0.001$ for medium and large urchins, respectively). The largest sheephead consumed ever larger urchins and at a size larger than 53 cm TL, 50% of the sheephead diet was comprised large purple or red urchins (figure 3f). The relative selection of purple urchins also varied as a function of urchin size. Small purple and red urchins were attacked and consumed at similar rates. However, as urchin test size increased, purple urchins were consumed at higher rates relative to red urchins of the same TD, especially by the large sheephead size classes (figure 3d–f, Wald
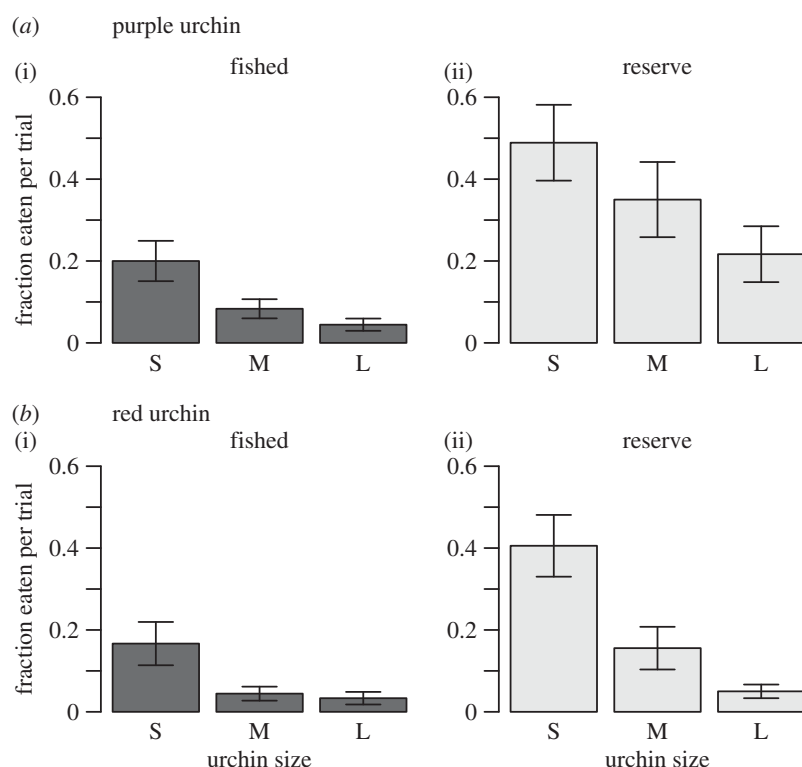
Figure 4. Size-specific urchin mortality (fraction eaten during a feeding trial) outside (a(i),b(i)) and inside (a(ii),b(ii)) of the marine reserve for (a) purple urchins and (b) red urchins during 30 min feeding trials. Error bars represent ± 1 s.e.

$Z = -2.64$, $p = 0.008$ and Wald $Z = -2.98$, $p = 0.003$ for medium and large urchins, respectively).

Consistent with the dominant role of large sheephead in urchin predation, the higher biomass of large sheephead inside the reserve led to greater numbers of urchin attacks (electronic supplementary material, figure S3) and on average three times higher relative urchin mortality ($\chi^2_1 = 9.409$, $p = 0.0022$; figure 4). The particular site location within reserve or fished areas also influenced attack and mortality rates ($\chi^2_1 = 77.2$, $p < 0.001$), with higher rates at the centrally located reserve site with the highest sheephead biomass (electronic supplementary material, figures S2–S5). Overall, reserve sites consistently experienced higher mortality rates compared to fished sites (electronic supplementary material, figures S4 and S5).

Purple urchins had a higher relative mortality rate than red urchins ($\chi^2_1 = 32.77$, $p < 0.001$), and this difference was driven by greater mortality of purple urchins in the medium and large size classes. Because fewer sheephead were capable of consuming large urchins, mortality decreased with urchin size for both urchin species ($\chi^2_2 = 133.27$, $p < 0.001$). Consistent with the higher relative urchin mortality for purple urchins and the relative increase in mortality inside reserves, purple urchin densities were also lower inside the reserve (electronic supplementary material, figure S6; $t = -2.215$, $p = 0.05$). Red urchin densities were similar inside and outside the reserves ($t = -0.8$, $p = 0.44$), and giant kelp densities were also similar inside and outside of the reserves ($t = 0.653$, $p = 0.523$).

4. Discussion

The predator–prey interaction between California sheephead and sea urchins was strongly size-dependent. Despite their high relative abundance, small sheephead (less than 20 cm TL) were not involved in consuming urchins. This size-

dependent predator–prey interaction is probably controlled by the functional limitations of the sheephead jaw needed to break open an urchin test; crushing ability typically increases with the size of the fish [34,35]. Sheephead switch their diet from small crustaceans and bivalves to urchins and larger mobile prey as they grow in size and their crushing capacity increases [21,28]. At the size threshold where urchins were first added into the diet, sheephead only consumed small urchins. The ability to consume larger urchins required ever larger sheephead. Interestingly, the minimum threshold sheephead size required to consume large urchins is near the minimum size limit in the sheephead fishery (30 cm TL for the recreational fishery and 33 cm TL for the commercial fishery). Sheephead larger than the minimum size limit for the fishery consumed urchins at a rate greater than that expected from their relative abundance. They also were more likely to consume the largest urchins, especially the smaller-spined *S. purpuratus*. As a result, current fishery regulations focus harvest pressure on the sheephead size classes that are the most effective urchin predators. On the other hand, our results suggest that restoration of sheephead size structure will increase the number of individuals that are capable of eating urchins. This is corroborated by gut content analyses from San Nicolas Island which show that an increase in the number of large sheephead following a reduction in fishing pressure led to greater consumption of urchins as a fraction of the overall diet [36].

Because of these size-dependent predation patterns, biomass of the largest sheephead was more important than total density in driving patterns in urchin mortality. The higher biomass of large sheephead inside the reserve resulted in relatively higher urchin mortality. Our study represents, to our knowledge, the first *in situ* experimental demonstration relating the well-known effects of reserve protection on predator sizes to size-specific urchin mortality rates in California kelp forests. These results suggest that by reducing the abundance

and size structure of urchin predators, fishing not only reduces overall urchin mortality but also shifts this mortality to smaller urchin sizes. The relative increase in predation in the reserve was more pronounced for larger purple urchins, which differed from red urchins in having relatively shorter spines and higher gonad weight [37] for the same TD. The higher potential reward and lower handling time may underlie the greater consumption rates of purple urchins. As purple urchins more commonly form barrens than red urchins in southern California [38,39], restoring sheephead size structure in marine reserves may have significant ecosystem benefits in preventing urchin barren formation.

Where size-dependent predator feeding preferences have been invoked to explain size-specific urchin mortality, that prey choice has typically been inferred from the size of urchin body parts recovered in gut contents [40] (but see [41,42] for a notable exception). Given the propensity among many fish predators to scavenge upon urchins previously opened by other individuals [43] (R. Selden 2010–2011, personal observation), such indirect measures may not represent true predation capability and may instead over-estimate the role of these smaller individuals in urchin consumption. In addition, the feeding trial approach employed here is unique in that it presented a standardized and replicated array of prey to sheephead in the field, permitting us to detect the characteristics that influence prey choice and consumptive abilities. For example, we were able to measure precisely the minimum size thresholds at which sheephead become capable of preying on different sized urchins, which is a significant refinement over previous indirect measures of these relationships based on gut contents [22,28,42]. Direct observations of size-specific prey choice like those demonstrated in this study are rare owing to the difficulty of observing predation over ecologically relevant time scales. However, empirical studies of size-dependent predation are critical to predicting how prey populations will respond to management measures that affect the size structure of their predators.

Increased overall urchin mortality and higher mortality of large urchins where large sheephead are abundant should lead to lower urchin abundance and fewer large reproductive individuals, reducing both grazing pressure and future reproductive output. As a result, the restoration of sheephead size structure and abundance in reserves may serve to enhance the resilience of kelp forest ecosystems. While our results suggest a greater relative capacity for sheephead to control urchins within the reserves, this control is likely to be strongest for purple urchins, which they consumed at a higher rate. Only purple urchins had a significantly lower density inside the reserves at Catalina. Densities of both urchin species at Catalina, even in the fished areas (approx. 0.2 m^{-2}), are also at least an order of magnitude lower than that found at the northern Channel Islands [37], and those urchins that were present were concealed under boulders and not actively grazing kelp. Urchin outbreaks in fished areas on Catalina Island may be rare because urchin recruitment is low, and/or because even the current predation pressure on urchins is sufficient to regulate urchin populations. Recruitment of sheephead is 6.4 times higher at Catalina than that in the northern Channel Islands (J. Claisse 2004, 2008, 2011, 2012, unpublished data), and the density of large fish we observed at all sites was still at least two times the maximum density observed in the reserves in the northern Channel Islands [28] (electronic supplementary material, figure S1). This suggests the unusually

high density of sheephead at Catalina may keep urchin populations in check even when fishing reduces the abundance and size of these predators. However, the resilience of other sites with lower sheephead recruitment may be more sensitive to fishing removals of the larger size classes of sheephead that serve this important ecological function.

The size-dependent nature of the interaction between sheephead and urchins may also explain some of the lag in community responses to newly established marine reserves in the southern California Bight. Ten years after the establishment of many newer marine reserves in the northern Channel Islands, both sheephead densities and biomass were higher in reserves across the islands [28] and sheephead biomass was negatively correlated with urchin densities regardless of reserve status. In many of these reserves, urchin abundance is low and kelp abundance is high [28], but urchin barrens still persist within others a decade after fishing on sheephead ceased [44]. Our finding that sheephead do not eat urchins until they reach a critical size suggests that the potential for sheephead to constrain urchin populations may lag behind reserve establishment significantly. Interestingly, variation in demography and growth rates among populations across southern California [45] may alter the duration of this lag. Relatively fast-growing populations at the northern Channel Islands reach the minimum size threshold for eating urchins of any size at approximately 3 years of age, while sheephead at Catalina do not reach this size until age 4 [45]. To achieve the larger sizes required to be effective predators of larger urchins (35–45 cm TL sheephead), an additional 2–4 years would be required for the sheephead on the northern islands, and 7 more years would be needed for sheephead at Catalina.

The resilience of kelp forest ecosystems may be further augmented by the recovery of other fished urchin predators inside marine reserves, such as spiny lobster (*P. interruptus*). Laboratory studies demonstrate that predation by spiny lobster on sea urchins is likewise size-dependent [22,46], suggesting predation pressure on urchins may similarly depend on lobster size structure. Indeed, truncations in size compromised the capacity for a similar lobster species to control the spread of an invasive sea urchin in Tasmanian kelp forests [41]. Marine reserves in southern California have been particularly effective in restoring the abundance and size structure of spiny lobster [47], and some studies have suggested that *P. interruptus* may be even more important predators than sheephead in regulating urchin abundance [15,48]. Therefore, the increased abundance of large sheephead and lobster within reserves may confer greater resilience than either predator alone.

We show that size-dependent predation is a potential mechanism that may help explain observed delays between recovery of predator abundance in marine reserves and consequent impacts on urchin populations. Other temperate reefs in which urchins are key herbivores may show similar patterns. In fact, differences in size-specific urchin mortality between reserves and fished areas have also been found in the Mediterranean [40], Tasmania [41,42] and New Zealand [49], and lags between predator recovery and changes in urchin demographic rates are common [10]. In cases where prey achieve a size refuge from the largest predators, size-dependent predation may further impede the cascading effects of reserve protection on basal algal resources. In New Zealand, recovery of lobster and sparid fish inside reserves led to elevated urchin mortality for small urchins, but at some sites a fraction of the sea urchin

population had grown large enough to be invulnerable to even the largest predators [44]. As a result, the increased predation pressure did not result in reduced grazing pressure until these largest urchins died of other causes 25 years after reserve protection, after which the site quickly transitioned from urchin barren to kelp forest. We found that the large urchins of the longer-spined *M. franciscanus* were similarly less affected by predation; these may have been difficult to handle even for large sheephead. This suggests that the degree to which reserves cause trophic cascades will depend on whether prey achieve a size refuge, even in the presence of the largest predators.

5. Conclusion

The size-dependent interaction between urchins and their predators will influence the relative effect of fisheries management strategies on the capacity for predators to regulate urchin populations. Marine reserves are particularly successful in restoring the interaction between sheephead and urchins, although delays in recovery of kelp forest ecosystems may be observed until sufficient numbers of sheephead are large enough to be effective large urchin predators. Because many predator–prey interactions in aquatic systems are size-structured [50], truncations in predator size structure may cascade to prey populations in other systems in ways that would not have been predicted from changes in predator abundance alone. As a result, monitoring predator size structure in conjunction with metrics of abundance may improve our ability to assess the success of marine reserves and predict where fishing may have the greatest impact on marine ecosystems. Where predation is size-dependent, increasing the proportion of large individuals in the population may increase the resilience of marine ecosystems in which they serve a key role.

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