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Temporal and spatial patterns in behavioral responses of marine predators to a sudden influx of abalone prey (*Haliotis rufescens*)

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Abstract Predator–prey interactions exist on a variety of spatial and temporal scales; one of the earliest measurable responses to changes in these interactions is behavior. We examined the behavior of southern California kelp forest predators in response to a concentrated increase in the abundance of abalone during a restoration stocking experiment. We tested three hypotheses: (1) kelp forest predator density will increase following abalone stocking, (2) variations in predator characteristics will create an unequal impact on abalone, and (3) predation intensity will be greatest early in the experiment. Octopus discovered and exploited the influx of prey within the first week following stocking; their densities surged and then returned to pre-stocking levels after 2 months. This was not observed with any other predator. Damage from crustacean, fish, and octopus predation was observed on the recovered abalone shells, but were not correlated with predator densities. A larger percentage of recovered small shells had evidence of crustacean and fish predation, indicating there may be size-specific impacts of predators on abalone. Our results demonstrate that restoration stocking experiments can quantitatively test the predatory community's response to reintroductions, as well as predation risk of newly stocked prey species when exposed to a diverse suite of predators.

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Introduction

Predator–prey interactions exist on a variety of spatial and temporal scales. On short time scales, behavior is one of the earliest measurable responses and can be influenced by many components such as habitat heterogeneity, seasonality, predator characteristics, and prey anti-predator behavior and refugia (Sih et al., 2010; Wong & Candolin, 2015). Highly mobile predators have the capacity to respond behaviorally to sudden, large, and localized increases in prey populations and exploit that resource. The interactions between and importance of aggregating prey populations and their predators, such as spawning aggregations, are well studied in natural systems (Smale et al., 2001; Winder et al., 2001; Sigler et al., 2004). However, predator responses to artificial prey aggregations in systems unaccustomed to aggregation dynamics are less understood. This is particularly relevant for restoration ecology, reintroduction biology, and stock enhancement. Restoration strategies are centered on the reintroduction of depleted, endangered, or locally extinct species into environments where they once thrived (Dobson et al., 1997). These strategies can involve efforts to re-establish endangered or threatened species, as is typical in terrestrial ecosystems (Lipsey et al., 2007; Seddon et al., 2007; Armstrong & Seddon, 2008), or for the enhancement of fishery stocks, as is more common in marine ecosystems (Molony et al., 2005; Bell et al., 2006, 2008). Restoration projects have been criticized for not being experimentally rigorous, and thus limiting what can be learned about ecosystem function (Seddon et al., 2007). However, these projects offer a unique opportunity to test behavioral responses and community interactions on short and long time scales, providing a heuristic framework for learning about the system. Predation pressure on newly stocked populations is a common challenge to the success of restoration projects and requires careful understanding of the particular predator species and their responses to restoration actions.

Predation on newly stocked species of primary consumers, like abalone (*Haliotis* spp.) is considered one of the greatest barriers to the success of species and ecosystem restoration (Tegner & Butler, 1989; Banks et al., 2002; Moseby et al., 2011). Southern California kelp forest communities have high predator diversity, both in species and in functional groups.

Although the iconic abalone predator, the sea otter, *Enhydra lutris* (Linnaeus, 1758) has been locally extinct for over a century, southern California kelp forests have ecologically redundant predators, which help to maintain kelp forest ecosystems (Estes et al., 1978; Palumbi et al., 2008; Braje & Rick, 2011). The effects of predator diversity and its impact on prey predation risk can vary with predation method and habitat domain of both predators and prey (Schmitz, 2007; Pruitt et al., 2011). Generally, ecosystems that have predators with similar methods of predation (i.e., active hunters) and broader habitat domains than their prey have greater predation risk with increasing predator diversity (Hixon & Carr, 1997; Schmitz, 2007). The pool of potential abalone predators in southern California can be diverse, making the mitigation of predator effects for restoration ecology particularly challenging. However, it also provides an opportunity to evaluate temporal and spatial patterns in the behavioral response of a large suite of predators and the predation risk they impose on prey populations.

This study examined the behavior of southern California kelp forest predators in response to a sudden artificial and high-density influx of red abalone, *Haliotis rufescens* Swainson, 1822. The experimental design provided an opportunity to examine the predatory community response to the reintroduction of a previously abundant marine invertebrate genus, *Haliotis* spp. We tested the following hypotheses: (1) kelp forest predators will increase in number within the experimental areas immediately following abalone stocking, (2) variable foraging strategies and baseline populations of each predator species will create an unequal impact on the prey species, and (3) predation intensity will be greatest early in the experiment. Evidence to support or reject these hypotheses were measured in four ways: (1) the change in abundance of predators within the experimental areas; (2) the identification of active predation on juvenile abalone based on the types of shell damage of known mortalities; (3) differential predation pressure and predation type in relation to abalone size; and 4) the change in predator pressure through time.

Materials and methods

Study region

Three sites were established adjacent to a State Marine Conservation Area (SMCA) near Los Angeles in the southern California coastal region (Fig. 1). This area is dominated by a rocky reef kelp forest ecosystem. These sites were chosen because (1) the area was predicted to have an initial low density of abalone predators, (2) the area once supported high densities of abalone (particularly red abalone), and (3) recent surveys indicated few abalone of any species were present in the area. No wild red abalone were encountered in the area prior to stocking.

### Southern California kelp forest predators

The potential abalone predators in southern California kelp forests are variable in their mobility, prey detection method, microhabitat use, dietary flexibility, and fishery pressure, and thus they are variable in their predatory impact on stocked juvenile abalone. Benthic predators that have the most overlap with abalone habitat include the octopuses *Octopus bimaculatus* Verrill, 1883 and *O. bimaculoides* Pickford & McConnaughey, 1949, predatory sea stars (primarily

Fig. 1 **a** Relative locations of each of the three study sites and corresponding bathymetry, each indicated by the double-circle symbol. This double-circle symbol is also a generalization of the leadline array established at each site. **b** Regional location of our study (black box)

Pisaster spp.), California spiny lobsters, *Panulirus interruptus* (Randall, 1840), and Kellet's whelks, *Kelletia kelletii* (Forbes, 1850).

Octopuses have the ability to exploit and deplete prey populations (Ambrose, 1986; Rodhouse & Nigmatullin, 1996). Octopuses are chemotactile, exploratory foragers, and are not capable of long-distance detection of prey (Yarnall, 1969; Mather & O'Dor, 1991; Budelmann, 1996), therefore their ability to find and exploit prey resources is directly tied to their movement through their environment. There is no targeted fishery for octopus in California, and reported octopus landings are not common; only 89 lb valued at $85 were reported for the 2015 commercial fishery out of the Los Angeles Area (CDFW Commercial Landings CFIS, 2015). Previous research on Santa Catalina Island, located approximately 20 miles southwest of Long Beach, CA, suggested that octopus population density is at its lowest during December–March (Ambrose, 1988; Hofmeister, 2015). Using this information, we projected octopus population densities might also be relatively low during the abalone stocking study.

Sea stars (*Pisaster* spp.) are important keystone predators, especially in intertidal communities (Paine, 1966). They are a ubiquitous predator in kelp forest communities and can shape prey spatial dynamics (Duggins, 1983; Watanabe, 1984). Many prey species have evolved escape mechanisms in response, supporting the notion that *Pisaster* spp. are important predators that have driven the evolution of prey behavior (Harrold, 1982; Watanabe, 1983). However, this region had severely limited sea star predators due to a recent large-scale outbreak of sea star wasting disease, which caused massive mortality in 2013–2014 (Hewson et al., 2014).

California spiny lobsters (*P. interruptus*) exhibit high site fidelity and can use chemosensory signals to detect injured or dead prey, but are not necessarily useful for locating live prey (Zimmer-Faust & Case, 1982, 1983; Zimmer-Faust et al., 1985). They participate in short exploratory foraging excursions and rarely stray far from their shelter (Withy-Allen & Hovel, 2013). This southern California coastal region is an important area for commercial and recreational lobster fisheries. In 2015, the commercial fishery landed nearly 215,000 lb of California spiny lobster (*P. interruptus*) valued at approximately $4.5 million in the Los Angeles Area (CDFW Commercial
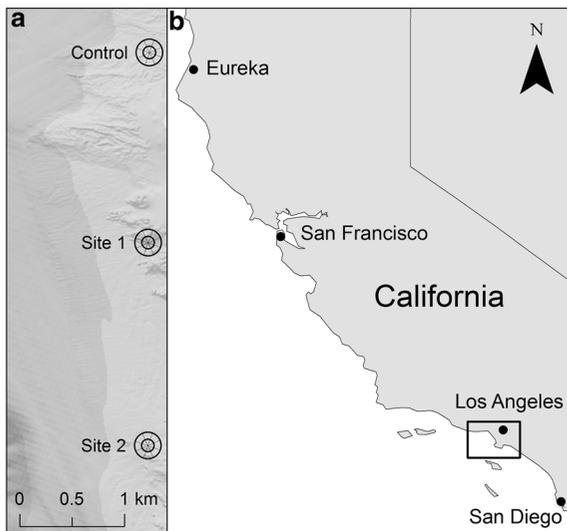
Landings CFIS, 2015). Additionally, there is an active recreational fishery in California that accounts for approximately 25% of all lobster take in the state (CDFW, 2017). Both the commercial and recreational lobster fishing season extends from October to March. Therefore, at the time of this study, lobster densities were expected to be relatively low as a direct result of the fishery.

Other benthic abalone predators include cabezon, *Scorpaenichthys marmoratus* (Ayres, 1854), scorpionfish, *Scorpaena guttata* Girard, 1854, and Kellet's whelks (*K. kelletii*) (Quast, 1968; Tegner & Butler, 1989; Beaudreau & Essington, 2007; Griffiths & Gosselin, 2008). While cabezon and scorpionfish are uncommon, Kellet's whelks are very common and could have a large predatory impact on seeded abalone. Little is known about the movement and predatory behavior of Kellet's whelks. While they are capable of drilling and have a drill hole shape distinguishable from octopus (Pilson & Taylor, 1961), they more typically scavenge or use their proboscis to get under the shell of already weakened or stressed abalone (Tegner & Butler, 1985).

Benthopelagic predators can opportunistically predate on juvenile abalone when they are exposed while foraging or searching for shelter. Common benthopelagic predators include fish such as California sheephead, *Semicossyphus pulcher* (Ayres, 1854), and kelp bass, *Paralabrax clathratus* (Girard, 1854), though the predatory impact of each can be dependent on the relative location of stocked abalone to fish home ranges. Male California sheephead (*S. pulcher*) are highly territorial during the spawning season (July–September) but do not maintain feeding territories (Cowen, 1990; Adreani et al., 2004). However, both males and females exhibit high site fidelity and small home range size (Topping et al., 2005, 2006). Kelp bass (*P. clathratus*) also exhibit high site fidelity (Lowe et al., 2003). California bat rays, *Myliobatis californica* Gill, 1865, though relatively rare in southern California, are intense predators on mollusks and have been particularly impactful on molluscan aquaculture (Feder et al., 1974; Gray et al., 1997; Graham, 2004).

Artificial reefs for stocking

At each of the three sites, the California Department of Fish and Wildlife (CDFW) established a cluster of four artificial reefs composed of caged cinderblocks, called Baby Abalone Recruitment Traps (BARTs). BARTs have been used successfully in British Columbia to sample juvenile abalone that are typically cryptic and difficult to census (DeFreitas, 2003). BARTs each consist of a 92 cm (*L*) × 72 cm (*W*) × 36 cm (*H*) steel wire cage filled with 32 quarter-cut cinderblocks that create cryptic habitat for juvenile abalone. These BARTs were initially installed at each site in October 2014 to monitor natural abalone recruitment, and strategically placed to target historic white abalone habitat in depths ranging from 18 to 22 m. Three replicate sites of four BARTs each were located 1 km apart oriented parallel to shore approximately 0.3–0.6 km off the coastline. Sites were characterized by highly variable low-relief substrate, ranging from reef channels interspersed with sand to areas dominated by cobble and boulders. Algal canopy cover was characterized as sparse and primarily consisted of Giant kelp, *Macrocystis pyrifera* (Linnaeus) C. Agardh, 1820. Algal sub-canopy cover was robust and consisted mainly of *Laminaria* spp., *Pterygophora californica* Ruprecht, 1852, *Cystoseira* spp., and *Eisenia arborea* J.E. Areschoug, 1876. Foliose and turf algae was patchy, and there was a high percent cover of encrusting crustose and erect coralline algae.

Site design

The three clusters of BARTs were rearranged in preparation for abalone stocking January 2016 (Fig. 1). The central and southernmost sites were designated as experimental stocking sites, 'Site 1' and 'Site 2,' respectively, and the northernmost was left as the control (no stocked abalone). At all three sites, divers used railroad spikes and sledgehammers to secure a permanent leadline plot with 10-m spokes in the four cardinal (N, S, E, W) and intercardinal (NE, SE, NW, SW) directions from the center. The plot design delineated a series of zones ("pie slices") radiating from the center where four BARTs were positioned approximately 2–5 m apart. The area encompassed by the 0–5 m radius was the "inner zone" and the area encompassed by the 5–10 m radius was the "outer zone." Each inner zone wedge was approximately 9 m², and each outer zone wedge (e.g., A2) was approximately 27 m². Each site covered an area of approximately 300 m². Site plots not only

assisted divers in navigation and monitoring but also provided a method for approximating abalone dispersal from the stocked BARTs at the center of the plot.

Pre-stocking surveys

Before stocking abalone, divers conducted intensive predator surveys to quantify pre-stocking predator densities. The first dive team to descend conducted fish assemblage surveys in an area approximately 5 m wide and 3 m off the bottom over a 20 m swath across each site plot, covering a volume of 300 m^3. Divers recorded California sheephead (*Semicossyphus pulcher*), kelp bass (*Paralabrax clathratus*), and bat rays (*Myliobatis californica*). Benthic predator abundances, namely octopuses (*Octopus bimaculatus*), Kellet's whelks (*Kelletia kelletii*), California spiny lobster (*Panulirus interruptus*), and predatory sea stars (primarily *Pisaster* spp.), were counted by thoroughly searching the benthos of the entire plot area (300 m^2). Kellet's whelks, predatory sea stars, and octopuses were collected when possible and relocated at least 0.5 km away from the site since predator removal can decrease initial stocked abalone mortality (Tegner & Butler, 1989). Kellet's whelks and predatory sea stars were removed by hand, and octopuses were coerced from their dens with vinegar and then collected by hand.

Abalone stocking

On January 15, 2016, 3,200 red abalone (*Haliotis rufescens*) of two size classes, small (32.4 mm ± 2.6, $N = 2,400$) and large (55.9 mm ± 2.0, $N = 800$) were transported from The Cultured Abalone Farm (TCAF) in Goleta, CA to the Aquarium of the Pacific (AoP) in Long Beach, CA. Juvenile abalone were measured and tagged with oval Floy® Shellfish Tags 1/8 × ¼ in FTF-69, affixed with CorAffix™ cyanoacrylate adhesive after blotting the shell dry and submerging back into seawater after approximately 30 s. Tagged abalone were maintained with running seawater and fed kelp for six days until stocking. After tagging, abalone were moved into pre-assigned and numbered PVC tubes ("stocking modules") that were directly placed into the BARTs during stocking to reduce handling stress (Tegner & Butler, 1989). A total of 1,200 small abalone and 400 large abalone were stocked at Site 1 and Site 2 on January

20, 2016. The modules were not removed from the BARTs until < 5 abalone remained inside, which occurred at either 24 or 48 h after stocking. At this point, the remaining abalone were carefully removed by divers from the module and placed on bricks in the nearest BART.

Post-stocking surveys

Sites were non-invasively surveyed for emergent predators and abalone at 24 h, 48 h, 1 week, 1 month post-stocking, and monthly after that using the same survey protocol as the pre-stocking surveys. Only Site 1 was surveyed at the 1-month time point due to boat and diver limitations. During each survey, predators were removed and relocated when possible, with the exception of lobsters and fishes. Abalone shells from deceased abalone were also collected during surveys, and subsequently assessed for growth and shell damage. Invasive surveys, where divers disassembled BARTs and looked under all moveable substrate for predators, live abalone, and abalone shells, were conducted after 3 months and 6 months. Expanded invasive 15 × 5 m swath surveys beyond the 300 m^2 leadline plot area were also conducted 3 and 6 months post-stocking off the ends of the north, east, south, and west plot lines.

Santa Catalina octopus surveys

To determine whether octopus population trends at the mainland stocking sites were similar to those at other southern California areas, complementary octopus surveys were completed on Santa Catalina Island, Los Angeles County where long-term density data are available for comparison (Hofmeister, 2015). All surveys were completed near the USC Wrigley Institute of Environmental Studies near the town of Two Harbors from February 16–18, 2016. Searches were conducted along a 20-m transect perpendicular to shore following the methods of Hofmeister (2015). Using lights, divers thoroughly searched for octopuses 2.5 m on each side of the transect, for a total search area of 100 m^2. Search time was recorded, as well as the species, estimated size, depth, and den type of any octopuses found.

Statistics

All statistical analyses were conducted using R (v. 3.3.3, R Core Team, 2017) or JMP® software (v.12, SAS Institute Inc., Cary, NC 1989–2017). Differences between shell mortality types across sites, abalone size classes, and survey time point were tested with Chi-square.

Results

Predator response to abalone stocking

Octopuses (*O. bimaculatus*) were present at all sites prior to stocking, and divers were successful in removing and relocating a subset of these individuals: two out of four, three out of five, and one out of four at the Control site, Site 1, and Site 2, respectively. One week after abalone stocking, a dramatic increase in the number of *O. bimaculatus* at Site 1 and Site 2, but not the Control (Fig. 2a) was observed. At 2 months after the abalone stocking, *O. bimaculatus* densities at the experimental sites decreased back to pre-stocking levels. No octopuses were successfully relocated during any post-stocking survey. In general, the observed octopus densities at this mainland site were higher than predicted by previous octopus survey work on Santa Catalina Island (Ambrose, 1988; Hofmeister, 2015). The mean ($\pm$ SE) densities of octopus at the stocking site on the mainland were 0.014 ± 0.001 m^{-2}; the mean ($\pm$ SE) density of octopuses was 0.007 ± 0.0026 m^{-2} on Santa Catalina Island. The octopus densities on Catalina Island were equivalent to measured densities at this island site in past years (Ambrose, 1988; Hofmeister, 2015). These results suggest that in January 2016, the stocking site on the mainland was relatively octopus-rich.

Kellet's whelks (*K. kelletii*) were the most abundant predators and the only predators consistently removed from each site prior to stocking. Densities of *K. kelletii* remained higher at the experimental sites than the control, but did not rapidly increase in response to stocking. (Fig. 2b). Because the vast majority of *K. kelletii* were removed from each plot at each survey, any density greater than zero indicates movement of that predator into the area. Additionally, average densities of *K. kelletii* remained higher at the two experimental sites than the control site. Densities

exceeded pre-stocking levels only at Site 2 during the 3-month survey, but no *K. kelletii* were found at that site during the 4-month survey.

Lobster (*P. interruptus*) densities were recorded prior to stocking and at the 6-month survey. Pre-stocking, baseline *P. interruptus* densities were six, zero, and ten lobsters at the Control site, Site 1, and Site 2, respectively. At the 6-month survey, two *P. interruptus* were present at Site 2 and no other sites had lobsters. Few predatory fish were observed at either the pre-stocking or 6-month survey, and no increase in fish density was observed. During the pre-stocking survey, four, two, and four California sheephead (*S. pulcher*) were seen, and at the 6-month survey three, one, and four were seen at the Control, Site 1, and Site 2, respectively. During the pre-stocking survey, zero, one, and zero kelp bass (*P. clathratus*) were seen, and at the 6-month survey two, one, and five were seen at the Control, Site 1, and Site 2, respectively. No bat rays, *Pisaster* spp., or any other predatory sea stars were observed at the sites.

Predation modes and shell damage

A total of 511 empty abalone shells were found during the eight months of surveys post-stocking over the course of seven surveys (1 week, 1 month, 2 month, 3 month, 4 month, 6 month, 8 month). Abalone shells were separated into five visual damage categories to infer the primary predator causing mortality: (1) chipped = portion of the shell missing (either on the edge or in the middle) with no single piece larger than a 0.5×0.5 mm area; (2) smashed = portion of the shell missing and a single missing piece is larger than a 0.5×0.5 mm area; (3) Octopus drill hole; (4) exposed nacre; or (5) no visible damage (Tegner & Butler, 1989; Fig. 3). Any shells with drill holes or exposed nacre that also were chipped or smashed were defined as having primary and secondary types of shell damage. Octopus drill holes that fully penetrated the shell were considered a primary source of mortality since it is highly unlikely that an octopus would infiltrate the shell and reach the abalone tissue but not successfully kill the abalone (Pilson & Taylor, 1961). Likewise, exposed nacre was defined as the primary source of mortality since the shell could have been chipped or smashed in the process of the fish removing the abalone from the substrate, but the cause of death would be fish digestion. Of the 511 shells found, 276
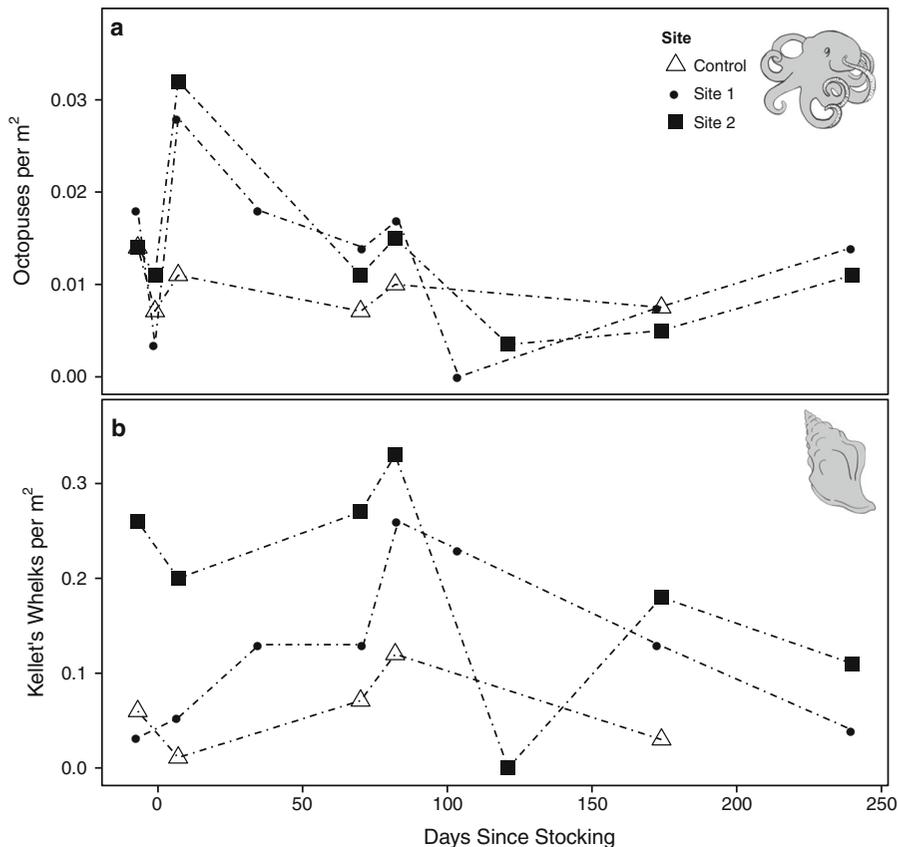
Fig. 2 Numbers of **a** octopuses and **b** Kellet's whelks m^{-2} pre- and post-abalone stocking at each site. Day 0 is stocking day, January 20, 2016. There was a clear increase in the density of octopuses immediately following the abalone stocking as compared to the control site. Kellet's whelk densities returned to pre-stocking levels but did not increase beyond their initial densities. Surveys were not completed at the Control or Site 2 at the 1-month time point

(54.0%) shells had at least one type of shell damage, and 35 (6.8%) had two types of shell damage. Of the types of shell damage, chipped was the most common (114 shells; 22.3% of all shells found), followed by drill holes (78; 15.3%), smashed (43; 8.4%), and exposed nacre (41; 8.0%). Of the shells with drill holes, 70 (89.7%) had one hole, 7 (9.0%) had two holes, and 1 (1.3%) had three holes.

Evidence of abalone mortality on recovered shells

Similar numbers of shells were found of each size class (252 small; 259 large), so that a smaller percentage of the small shells were recovered (10.5% of small abalone; 32.3% of large abalone). Small and large abalone shells had significantly different proportions of shell damage types (χ^2 test, $X4 = 59.89, P < 0.0001$; Fig. 4). A larger percentage

of small shells were smashed and had exposed nacre than large shells. Primary shell damage counts were marginally insignificantly different between sites (χ^2 test, $X4 = 8.80, P = 0.07$). More shells were recovered at Site 1 (317) than Site 2 (194), possibly due to the increased survey effort at Site 1.

Over the course of the post-stocking surveys, the number of recovered shells decreased (Fig. 4). During the 1-week post-stocking surveys, 195 empty shells were found: 86 small and 109 large. Primary shell damage counts were significantly different between survey times (χ^2 test, $X24 = 49.38, P = 0.0017$; Fig. 5). The proportion of shells with no shell damage decreased over time. The proportion of shells with octopus drill holes remained relatively constant over time suggesting octopus predation was more consistent than other predatory types (Fig. 5).
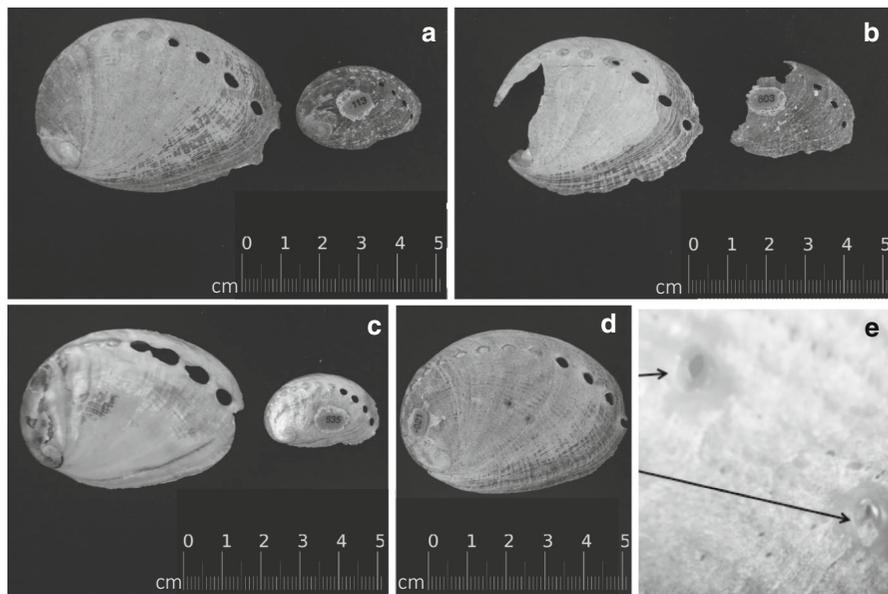
Fig. 3 Examples of the types of stocked red abalone shell damage of each shell size category. **a** Smashed; **b** chipped; **c** exposed nacre (the small abalone pictured is also chipped); **d** Octopus drill holes on a large red abalone; and **e** drill holes from the same abalone in panel d at ×20 magnification

Discussion

Predators in southern California kelp forests responded differently to the sudden artificial influx of prey, which occurred during an abalone restoration stocking effort. This differential pattern of predation is important to quantify and understand both for enhancing understanding of predator–prey interactions and for the conservation of depleted and endangered shellfish species. Our study demonstrates that octopuses (*O. bimaculatus*) are highly capable of responding quickly to the introduction of juvenile abalone into their habitat. Hofmeister & Voss (2017) have demonstrated that *O. bimaculatus* is highly mobile relative to other octopus species of similar size, which has direct implications for their prey discovery behavior. It is unknown how octopuses navigate within their environment to find food items or what influences their variability in foraging strategy. Many experiments have established the cognitive abilities of octopus in the lab, but very few have explored the application of these behaviors in a natural setting (Mather, 1995; Hanlon & Messenger, 1996; Darmaillacq et al., 2014). It is realistic to expect that these organisms are utilizing learned abilities to navigate through their environment and perform tasks such as foraging and avoiding predation. Bony fishes and sharks can learn to incorporate new food items into their diet based on encounter rate, and can learn to adopt the most efficient feeding strategy in different environments (Kieffer & Colgan, 1992; Guttridge et al., 2009). In addition, learning can be especially advantageous in habitats with spatial and temporal variability (Hughes et al., 1992).

A surprising discovery within this study was the difference in octopus population densities between mainland southern California and Santa Catalina Island. All previously published knowledge about octopus population dynamics and seasonal fluctuations of *O. bimaculatus* have resulted from studies on the lee side of Santa Catalina Island (Ambrose, 1988; Hofmeister, 2015). These past studies consistently revealed lower densities and smaller octopus sizes in December–March, and the island surveys presented as part of the current study yielded similar results. It is possible that the populations on the mainland cycle differently than on coastal islands, or the 2015–2016 El Niño affected synchronicity of southern California octopus populations, since several cephalopod species are affected by large El Niño events (Zeidberg et al., 2006; Jacox et al., 2016). Regardless, this observation warrants further investigation.

Fig. 4 a Percent of recovered empty shells from all stocked small abalone ($N = 2{,}400$) by shell damage category, and **b** percent of all stocked large abalone ($N = 800$) by shell damage category. **a**, **b** have different scales on the Y-axis
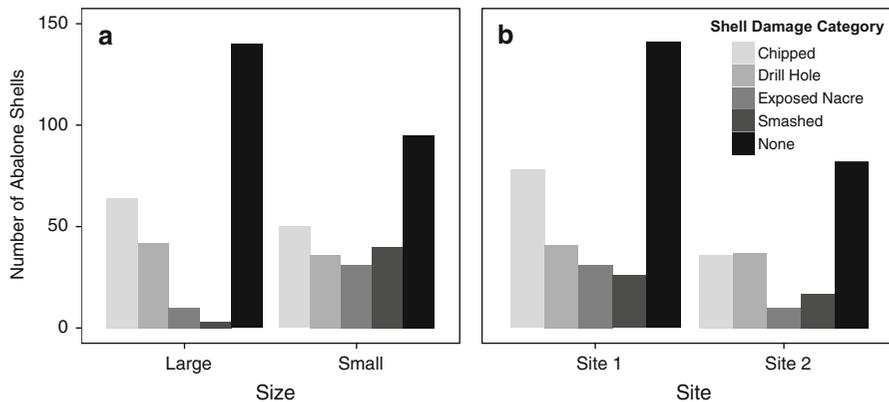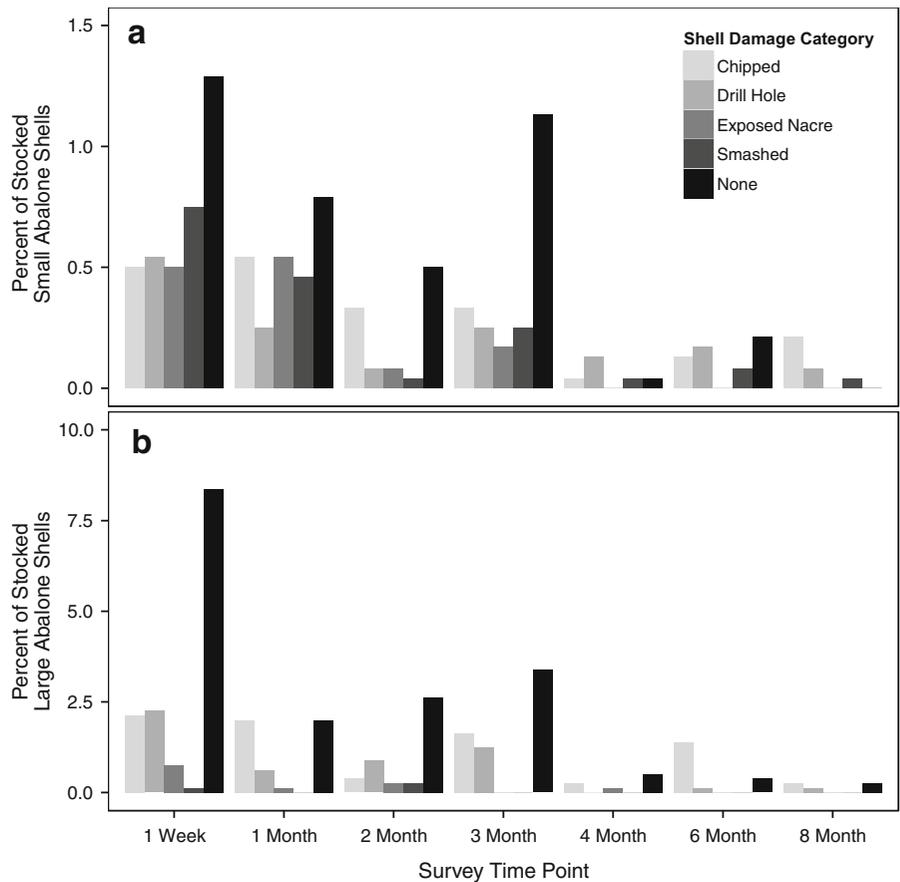
Fig. 5 a Number of stocked red abalone shells found with each shell damage category separated by shell size where small = 32.4 mm ± 2.6 and large = 55.9 mm ± 2.0, and **b** number of stocked red abalone shells found with each shell

damage category separated by site. Proportions of shell damage categories were significantly different between shell sizes and not site, but only marginally

We observed no obvious behavioral response from other potential abalone predators in this experiment. Counts of *K. kelletii* post-abalone stocking did not

show a rapid increase in response to the addition of juvenile abalone (Fig. 2b). Other potential predators, such as California spiny lobsters (*P. interruptus*) and

sheephead (*S. pulcher*), are difficult for divers to track with only a few hours of bottom time per day. It is, however, unlikely that they would have aggregated, since neither species was qualitatively observed to have increased in density within our sites. Additionally, there is no evidence suggesting abalone can cause *P. interruptus* to aggregate (Zimmer-Faust et al., 1985), and since *S. pulcher* exhibit high site fidelity, juvenile abalone placed within a home range or spanning across several home ranges have the potential to be heavily predated on by the resident fish. Divers observed that *S. pulcher*, especially large males, were attracted to diver activity and increased in numbers relative to our initial fish surveys. It is likely that the fish surveys were not an accurate representation of the number of *S. pulcher* in the area over the course of the days, weeks, and months that followed abalone stocking, and therefore predation by fish could be much higher than our data suggest. We also do not know the predatory response of another well-known and highly impactful predator, sea stars of the genus *Pisaster*. These sea stars were absent from our study area due to large-scale outbreak of sea star wasting disease, which depleted the populations (Hewson et al., 2014; Eisenlord et al., 2016; Montecino-Latorre et al., 2016). It can be assumed that prior to this massive mortality event, sea stars would have had a larger predatory impact (Tegner & Butler, 1985; Schiel & Welden, 1987; Rogers-Bennett & Pearse, 1998; Dixon et al., 2006).

We were able to attribute shell damage to predator groups but not specific species of predators, with the exception of those shells with octopus drill holes which were consistent in size and concave in shape (Pilson & Taylor, 1961; Tegner & Butler, 1985, 1989). These drill holes are likely a low estimate of octopus predation since it is possible that octopuses pulled juvenile abalone off the substrate due to their small size without drilling, leaving no visible shell damage (Emmett & Jamieson, 1989; Hansen & Gosselin, 2013). Many of the shells were chipped along the shell lip, which is indicative of lobsters, crabs, or other crustaceans attempting to remove the abalone from the substrate (Kojima, 1981; Tegner & Butler, 1985; Schiel & Welden, 1987; Emmett & Jamieson, 1989; Rogers-Bennett & Pearse, 1998; Dixon et al., 2006; Hansen & Gosselin, 2013). Smashed shells could be a result of lobster predation, but could also be attributed to sheephead or bat rays (Tegner & Butler, 1989).

Exposed nacre shells are most certainly from fish predation, such as cabezon, with the possible inclusion of sheephead and kelp bass (*P. clathratus*). These fish can ingest the abalone whole, digest the tissue, and spit out the remaining shell, which has been partially dissolved and only the colorful nacre remains (Feder et al., 1974; Emmett & Jamieson, 1989; Tegner & Butler, 1989; Griffiths & Gosselin, 2008). The majority of recovered shells (46%) had no evidence of shell damage, and these mortalities could not be attributed to any specific predator group. As hypothesized, types of predation were unequal and the predatory impact was highest immediately post-stocking.

There is evidence of differential susceptibility to particular predators between size classes of abalone. Very few large abalone shells that were recovered were smashed ($N = 3$) or had exposed nacre ($N = 10$), suggesting that this size class may be less vulnerable to predation from bony fishes, bat rays, or lobsters. Small shells had a relatively even representation of shell damage, suggesting this size of abalone may be equally susceptible to multiple types of predators. A total of 32% of stocked large shells were recovered, which is a considerably higher percentage than recovered small shells (11%). These findings may indicate increased predation on larger abalone, increased susceptibility of larger abalone to early mortality, or increased detectability because these shells are larger, easier to see, and less likely to be swept away by water movement or crushed into indiscernible pieces.

Fluctuations of predator and prey populations can happen on many temporal and spatial scales. On short time scales, as evidenced through this study, the behavioral responses of predators contribute to a measurable impact on the prey population. On longer time scales, relationships between predators and their prey are often revealed through fluctuations in population sizes and densities (Barbosa & Castellanos, 2005). It is not difficult to scale up from these short-term behavioral responses to these larger-scale population ones. Given the long-term goals of the abalone restoration efforts, pulsed reintroductions in abalone of high densities will become more frequent and widespread, evoking possible changes in predator–prey interactions and population fluctuations. The majority of targeted species reintroductions have been of top predators in terrestrial ecosystems, which often serve as drivers of biodiversity and ecosystem health

(Hayward & Somers, 2009), though there have been a few key case studies in marine systems (Tinker et al., 2008a, b). The establishment of marine protected areas has allowed for the recovery of overfished species from many trophic levels (Babcock et al., 1999; Gell & Roberts, 2003). Much less understood are the effects of directed efforts to restore lower trophic level species and the resulting interactions between predators and competitors. Our results demonstrate that restoration stocking experiments provide an opportunity to quantitatively test the predatory community's response to such a reintroduction, as well as the predation risk of these newly stocked prey species when exposed to a diverse suite of predators (Schmitz, 2007).

Application of results: predator mitigation and site selection

Restoration of red abalone populations is needed in southern California, as there is now a lack of both adults and juveniles in areas that once supported dense populations and a valuable fishery (Rogers-Bennett et al., 2002). The results of this study provide further evidence of the need to plan for and mitigate predation impacts for shellfish restoration stocking (Read et al., 2013). Tegner and Butler (1989) demonstrated that the number of initial mortalities is lower when predators are removed, but that this requires constant efforts to reduce predator impact. An alternative to predator relocation is strategic site selection and timing to reduce predatory impact, such as targeting heavily fished sites or sites and seasons with naturally low predator densities. Selecting sites with low predator densities will be especially important at the beginning of a restoration stocking effort when abalone are most stressed, vulnerable, and densities are high before dispersal into natural habitat occurs. These decisions also have to be weighed against the benefit of selecting restoration sites within protected areas, which may provide additional protection against anthropogenic activities such as anchoring and poaching, but where predator densities may be higher. Reducing initial mortalities also improves the overall effectiveness of establishing long-term self-sustaining populations (Catton et al., 2016) through restoration stocking efforts. Additionally, the seeding densities used here and in most restoration stocking studies represent an unnaturally high density of prey, which could increase the intensity of the predatory response. Given the quick response of predators, especially octopus, to the stocking of red abalone in this study, future work should explicitly test the relationship between abalone stocking densities and predatory response. The ultimate application of these efforts is to restore endangered, threatened, and depleted species of abalone, such as the white abalone, *Haliotis sorenseni* Bartsch, 1940, and preserve the biodiversity of southern California kelp forests (Davis et al., 1992; Rogers-Bennet et al., 2016).

Compliance with ethical standards

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were followed.

Conflict of interest The authors have no conflicts of interest to disclose.

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