

INDIRECT FOOD WEB INTERACTIONS: SEA OTTER PREDATION LINKED TO
INVASION SUCCESS IN A MARINE FOULING COMMUNITY

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ABSTRACT

Indirect Food Web Interactions: Sea Otter Predation Linked to Invasion Success in a Marine Fouling Community

Margaret Foster Jenkins

Humans have caused grave ecological and economic damage worldwide through the introduction of invasive species. Understanding the factors that influence community susceptibility to invasion are important for controlling further spread of invasive species. Predators have been found to provide biotic resistance to invasion in both terrestrial and marine systems. However, predators can also have the opposite effect, and facilitate invasion. Therefore, recovery or expansion of native predators could facilitate the spread of invasive species. Needles et al. (2015) demonstrated that the threatened southern sea otter (*Enhydra lutris nereis*) facilitated the invasion of an exotic bryozoan, *Watersipora subatra*. However, the underlying mechanism was not fully understood. We tested the hypothesis that sea otter predation on *Romaleon antennarium* crabs indirectly facilitated the abundance of *W. subatra*. To do this, we collected weekly data on sea otter foraging and quantified the abundance of crabs in the sea otter diet. We also conducted a caging experiment, where we experimentally manipulated crab densities and limited otter access using exclusion cages on pier pilings in Morro Bay, CA. We used photoQuad image processing software to calculate the abundance of *W. subatra* on PVC panels within each treatment group. We found that crabs were the second most abundant prey item in Morro Bay, comprising 25.1% of the otter diet. Through the caging experiment, we found that *W. subatra* abundance significantly increased as crab densities decreased. Our results indicated that sea otters indirectly facilitated the invasion of *W. subatra* by reducing *R. antennarium* crab densities and sizes. Removal of crabs may release *W. subatra* from the disturbance caused by crab foraging behavior. Understanding the impacts of top predators in invaded ecosystems has important management implications, as recovery of predator populations could unintentionally benefit some non-native species. Therefore, management should focus first on prevention and second on early detection and eradication of invasive species likely to benefit from predator recovery.

Keywords: invasive species, marine fouling community, trophic cascade, facilitation, indirect effects

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Chapter 1

1. INTRODUCTION

1.1 General Introduction

Humans have greatly altered ecosystems on a global scale through the introduction of invasive species (Vitousek et al. 1996,1997; Mack et al. 2000). In both terrestrial and marine systems, biological invasions pose a major ecological and economic threat (Pimentel et al. 2005). Invasive species can reduce the abundance of native species through direct predation, competition, (Williamson 1996, Suarez et al. 2000, Carlsson et al. 2009) or hybridization (Rhymer & Simberloff 1996), and can also have ecosystem-wide impacts by decreasing native habitat and biodiversity and altering nutrient cycling, fire regimes, and carbon sequestration (D'Antonio and Vitousek 1992, Kauffman et al. 1995, Vitousek et al. 1996, 1997; Mack et al. 2000, Bax et al. 2003). In the United States alone, invasive species cause approximately \$120 billion dollars of ecological damage per year (Pimentel et al. 2005). The economic impact of invasive species is also evident in local economies. Local fisheries in the Black Sea and Azov Sea collapsed due to the invasion of an exotic ctenophore, amounting to \$250 million in losses (Travis 1993). Given the widespread ecological and economic effects of invasive species (Vitousek et al. 1997), it is important to understand the underlying factors that influence invasion success (Bulleri 2008).

The success of exotic species depends on the attributes of the invader (Baker 1965, Ehrlich 1986), as well as physical and biological factors that either

act to facilitate or prevent invasion (Elton 1958, Byers 2002). Exotic species that are superior in resource acquisition, can tolerate variable or harsh environments, reproduce quickly, and have strong predatory defenses are more likely to become invasive (Rejmanek and Richardson 1996, Shea and Chesson 2002, Jensen et al. 2007). However, invader success is context dependent (Moulton & Pimm 1986, D'Antonio 1993) and regulated by a myriad of environmental constraints (e.g., temperature, salinity, wave exposure and other physical stressors) (Dethier & Hacker 2005, Moyle & Light 1996) and biotic factors within the recipient community (Elton 1958).

Communities with diverse species assemblages, including enemies of the invader (predators, competitors, or parasites), can be more resilient to invasion (Elton 1958, Kennedy et al. 2002, Juliano 2010). On a local scale, increased biodiversity reduces community susceptibility to invasion by reducing available niche space (Stachowicz et al. 1999, Shea and Chesson 2002, Kennedy et al. 2002), but in most large-scale observational surveys, the number of invaders increases with native diversity (Lonsdale 1999, Stohlgren et al. 1999, Stachowicz & Brynes 2006). This positive relationship may be explained by covarying environmental factors (Levine & D'Antonio 1999, Naeem et al. 2000, Shea & Chesson 2002), a lack of resource limitation, or presence of habitat forming species that increase resource availability for both native and invasive species (Stachowicz & Brynes 2006, Altieri et al. 2010, Bulleri et al. 2008, Tweedly et al. 2008, Bruno et al. 2003). Native species within the introduced range of the invader can provide biotic resistance to invasion through predation and

competition (Elton 1958, deRivera et al. 2005, Jensen et al. 2007, Walters & Mackay 2005, Going et al. 2009). Exotic species may be more susceptible to predation, because they have evolved independently from predators within the introduced range (Hokkanen & Pimentel 1984, Colautti et al. 2004 Parker & Hay 2005). However, ecosystems that lack native predators or competitors are more susceptible to invasion (Carlsson et al. 2009).

The global loss of top predators has exacerbated the spread of invasive species (Estes et al. 2011, Carlsson et al. 2009, Wallach et al. 2010). Direct harvest, habitat destruction, climate change, and pollution have led to defaunation in both terrestrial and marine systems (Young et al. 2016), with an estimated 11,000 to 54,000 species going extinct annually in recent years (Scheffers et al. 2012, Mora et al. 2013, Dirzo et al. 2014). Predators structure the communities they inhabit through direct predation and trophic cascades (Hairston et al. 1960, Paine 1969, Estes & Palmisano 1974, Ripple & Beschta 2012, Terborgh 2015), and enhance ecological resilience (Wilmers & Gertz 2005, Sandin et al. 2008, Wallach et al. 2010). In the absence of top predators, ecosystems can undergo changes in community composition (Terborgh 2001, Estes et al. 2011) and shift to alternative stable states dominated by invasive species (Wallach et al. 2010). For example, in Australia, removal of dingoes (*Canis lupus dingo*), a native apex predator, resulted in communities dominated by invasive mesopredators and herbivores (Wallach et al. 2010). Furthermore, when native birds were experimentally removed from small regions in Hawaii, the density of invasive spiders increased by 80-fold (Gruner et al. 2005).

When present, predators can reduce community susceptibility to invasion by directly consuming exotic species (Elton 1958, Reusch 1998, Parker et al. 2006, Carlsson et al. 2009, Carlsson et al. 2011, Morris et al. 2015). For example, native crabs (*Cancer productus*, *Romaleon antennarium*, *Callinectes sapidus*) limited abundance and distribution of the exotic European green crab (*Carcinus maenas*) through direct predation (Hunt & Yamada 2003, deRivera et al. 2005, Jensen et al. 2007), and native sea urchins (*Tetrapygus niger*) and shrimp (*Rhyncocinetes typus*) reduced abundance and settlement success of an exotic bryozoan (*Bugula neritna*) (Dumont et al. 2011). Predators can also limit the spread of invasive species through non-lethal means; invasive prey may change their behavior in response to a perceived risk of predation (Salo et al. 2008). For example, the invasive mink (*Mustela vison*) reduced movement between islands when the native predatory white-tailed sea eagle (*Haliaeetus albicilla*) was present (Salo et al. 2008). Predatory control of invasive species can abate negative impacts of invaders (Carlsson et al. 2009), release native species from interspecific competition (Juliano et al. 2010), and provide refuge for native species of lower trophic levels (Letnic et al. 2009). Recovery of native predators can also displace invasive predators, further mitigating the impacts of invaders (McDonald 2007).

Although native predators can be effective agents in resisting invasion, they can also facilitate the spread of invasive species. Predators that preferentially consume native prey species can release invaders from competition, and thereby allow invasive species to proliferate (Shea and Chesson 2002, Keane & Crawley

2002, Colautti et al. 2004, Maron & Vila 2001). Preferential consumption of native prey was first documented in terrestrial grasslands, where native mammals and insects facilitated the invasion of exotic grasses (Schierenbeck 1994, Joern 1989), but also occurs in marine systems (Veiga et al. 2011, Coma et al. 2011). For example, native urchins have preferentially consumed macroalgae and indirectly facilitated the invasion of an exotic coral (Coma et al. 2011).

Because of the variable effects of predators on exotic species, recovery of threatened or endangered top predators can be in conflict with invasive species management (Needles et al. 2015). The southern sea otter (*Enhydra lutris nereis*) was hunted to near extinction in the 19th century, but has since recovered from a remnant population of approximately 50 otters in 1938 (Riedman & Estes 1990) to 3,128 today (Hatfield et al. 2018). They historically ranged from Baja California, Mexico to Alaska, but their present range is constricted between Pigeon Point and Gaviota State Beach, California with slow expansion at the north and south ends of their range (Hatfield et al. 2018). Estuaries are emerging as important habitat for the recovery of the threatened southern sea otter within California (Lindsey 2016), as estuaries provide protection from wave action and shark predation, serve as important nursing grounds, and have abundant prey resources (Mccarthy 2010, Feinholz 1998). However, estuaries are highly susceptible to invasive species (Wasson et al. 2005).

Estuaries are particularly vulnerable to invasion (Ruiz et al. 1997), and are more invaded than open coastal environments (Wasson et al. 2005, Preisler et al. 2009) due to high input of invasive species through multiple vectors of

invasion and anthropogenic structures that support high abundances of invasive species (Glasby et al. 2007, Ruiz et al. 2009, Needles & Wendt 2013). The major vectors for introduction of exotic species include fisheries, aquaculture, aquarium and ornamental trade, plastic debris, fouling on hulls of ships, and ballast water (Carlton 1989, Carlton & Geller 1993, Cohen & Carlton 1998, Bax et al. 2003). Invasion rates are accelerating due increased international commerce (Cohen & Carlton 1998), and the effects have extended to smaller estuaries via transport on hulls of regional boats and currents (Wasson et al. 2001). Sea otter recolonization of estuaries provides an opportunity to study the effects of top predators on invasion.

Sea otters are known to structure nearshore communities and promote growth of both kelp forests and eelgrass through trophic cascades (Estes and Palmisano 1974, Hughes et al. 2013). Although the top-down effects of sea otters in both rocky and soft-bottom communities have been well documented (Estes and Palmisano 1974, Kvitek & Oliver 1988, Hughes et al. 2013), their effect on invaded fouling communities within estuaries and bays has received relatively little attention. Only one study, in Morro Bay, California, has investigated the indirect effects of sea otters in an invaded fouling community (Needles et al. 2015).

Morro Bay is a small estuary in central California with a resident sea otter population (41 individuals) (Brian Hatfield, United States Geological Survey, unpublished data) and heavily fouled artificial structures dominated by exotic species (Needles & Wendt 2013). Archaeological evidence suggests that

southern sea otters historically occupied estuaries along California's coast prior to the fur trade (Woolfolk 2005; Jones et al. 2011), but today the only California estuaries that support resident sea otter populations are Elkhorn Slough and Morro Bay (McCarthy 2010). Sea otters first recolonized Morro Bay in 1982, and their population quickly peaked to 34 adult otters in 1985, before declining sharply to zero observed in 1993. Their population remained below 10 resident otters through 2010, but has since rebounded; the local population was 41 adult otters as of 2017 (Hatfield unpublished).

Southern sea otter recolonization of Morro Bay coincided with a dramatic increase in the abundance of an exotic encrusting bryozoan, *Watersipora subatra* (Needles & Wendt 2013; in which it was misidentified as *Watersipora subtorquata*). *Watersipora subatra* was previously misidentified throughout California as *Watersipora subtorquata* (Vieira 2014). *W. subatra* was first discovered in Morro Bay in 1989 (Ken Bondy photograph, Needles & Wendt 2013), and coverage remained low through 2000 (Needles et al. 2015), but by 2004, *W. subatra* occupied 86% of the artificial substrate surveyed (Needles & Wendt 2013). The increased abundance of *W. subatra* within Morro Bay was accompanied by a sharp decline in mussels, as well as declines in other known sea otter prey items such as crabs, chitons, and sea urchins on pier pilings (Ofstedal 2007, Needles & Wendt 2013).

Watersipora subatra is a widespread invasive bryozoan found on hard substrates across the Atlantic, Indo-West Pacific, and Pacific oceans (Ryland 1974, Ryland et al. 2009, Mackie et al. 2012, Viera et al. 2014). It was first

described in Japan (Ortman 1890) and has since spread via ballast water to larger ports (Carlton & Geller 1993; Drake & Lodge 2004) and to smaller estuaries, like Morro Bay, via hull fouling on smaller ships (Carlton & Hodder 1995, Wasson et al. 2001, Ashton et al. 2014, Zabin et al. 2014). Although *W. subatra* is predominantly found in fouling communities within estuaries, it recently colonized open coastal environments in California (Pister 2009, Zabin et al. 2018). The *Watersipora* spp. complex is problematic because it reproduces rapidly through asexual budding (Lonhart 2012), displaces native species (Needles & Wendt 2013), is resistant to copper anti-fouling paints (Floerl et al. 2004, Piola & Johnston 2006), and facilitates the spread of other exotic species by providing a non-toxic settlement surface (Floerl et al. 2004) and habitat for other invaders within its 3-dimensional foliose structure (Stachowicz & Brynes 2006).

Needles et al. (2015) found that both southern sea otters and sea stars facilitated the invasion of *W. subatra* by preying on mussels and thereby opening up space for *W. subatra* to colonize. However, they also observed a significant increase in *W. subatra* abundance in areas open to sea otter predation, even when mussels were not initially present in the system (Needles et al. 2015); this suggests that there is another mechanism by which southern sea otters facilitate the invasion of *W. subatra*. Needles et al. (2015) suggested that sea otter predation on chitons and crabs could play a role, as chitons bulldoze *W. subatra* (Nydham and Stachowicz 2007) and crabs break apart *W. subatra* while foraging for prey living within the interstitial spaces of the *W. subatra* colony (Aiken 2014).

Crabs seemed a more likely candidate, because crabs are more prevalent than chitons in the sea otter diet along the central coast of California (Oftedal 2007), and chitons were rarely observed on pier pilings in Morro Bay (pers obs.). Additionally, Hughes et al. (2013) demonstrated that sea otter predation on crabs can have cascading effects to lower trophic levels within an estuary. We therefore investigated how sea otter predation on crabs affects the abundance of *W. subatra*. We hypothesized that sea otter predation on crabs would facilitate the invasion of *W. subatra*, by releasing *W. subatra* from the disturbance caused by the crab foraging behavior. Elucidating the mechanisms by which sea otters facilitate the invasion of *W. subatra* is important for furthering our understanding of the indirect effects of predators in invaded communities.

1.2 Introduction for Publication

Humans have greatly altered ecosystems globally through the introduction of invasive species, resulting in changes in community composition, nutrient cycling, fire regimes, carbon sequestration, and biodiversity (D'Antonio and Vitousek 1992, Kauffman et al. 1995, Vitousek et al. 1996, 1997, Mack et al 2000, Bax et al. 2003). It is therefore important to understand the factors that influence community susceptibility to invasion (Bulleri 2008). Several studies have shown that native predators can reduce community susceptibility to invasion by directly consuming exotic species (Elton 1958, deRivera et al. 2005, Jensen et al. 2007, Letnic 2009, Dumont et al. 2011). Predators may also indirectly decrease abundance of an invader by consuming a native species that would otherwise facilitate invasion (Bulleri et al. 2008). Predatory control of

invasive species can mitigate the negative impacts of invaders (Carlsson et al. 2009), by releasing native species from interspecific competition with the invader (Juliano et al. 2010) and by providing refuge for native species of lower trophic levels (Letnic et al. 2009). However, predators do not always provide biotic resistance to invasion (Schierenbeck 1994, Joern 1989).

A growing body of evidence suggests that native predators can indirectly facilitate the spread of invasive species. Predators that preferentially consume native prey species can release invaders from competition and thereby allow invasive species to proliferate (Shea & Chesson 2002, Keane & Crawley 2002, Colautti et al. 2004, Maron & Vila 2001, Coma et al. 2011, Veiga et al. 2011, Needles et al. 2015). Through trophic cascades, top predators may indirectly increase abundance of habitat forming species (Estes & Palmisano 1974, Hughes et al. 2013), which may facilitate invasion in some cases (Tweedley et al. 2008, Bulleri et al. 2008, Gestoso et al. 2014). Given that apex predators exhibit strong top-down control (Estes & Palmisano 1974, Estes et al. 2011) and can facilitate invasion (Needles et al. 2015), recovery of top predators can be in conflict with invasive species management.

Recovery of the threatened southern sea otter has been linked to invasion success in the marine fouling community within Morro Bay, CA. Southern sea otter recolonization of Morro Bay coincided with a dramatic increase in the abundance of an exotic encrusting bryozoan, *Watersipora subatra* (previously misidentified as *Watersipora subtorquata* (Needles & Wendt 2013, Vieira 2014). *Watersipora subatra* originated in Japan (Ortman 1890), but has since spread via

ballast water to larger ports (Carlton & Geller 1993, Drake & Lodge 2004) and to smaller estuaries, like Morro Bay, via hull fouling on boats (Carlton & Hodder 1995, Wasson et al. 2001, Ashton et al. 2014). Although *W. subatra* is predominantly found in fouling communities within estuaries, it recently colonized open coastal environments in California (Pister 2009, Zabin et al. 2018). The *Watersipora* spp. complex is problematic because it displaces native species (Needles & Wendt 2013), is resistant to copper anti-fouling paints (Floerl et al. 2004, Piola & Johnston 2006), and facilitates the spread of other exotic species by providing a non-toxic settlement surface (Floerl et al. 2004) and habitat for other invaders within its 3-dimensional foliose structure (Stachowicz & Brynes 2006). It is a successful invader because it grows rapidly through asexual budding (Lonhart 2012), and can therefore quickly colonize open space (Clark & Johnston 2009). Needles et al. (2015) found that sea otter predation on mussels facilitated the invasion of *W. subatra* by opening up space for *W. subatra* to colonize. However, they also observed a significant increase in *W. subatra* abundance in areas open to sea otter predation, even when mussels were not initially present in the system (Needles et al. 2015); this suggests that there is another mechanism by which southern sea otters facilitate the invasion of *W. subatra*.

Elucidating the mechanisms by which sea otters facilitate the invasion of *W. subatra* is important for furthering our understanding of the indirect effects of predators in invaded communities (Needles et al. 2015). Needles et al. (2015) suggested two additional mechanisms by which sea otters could potentially

facilitate the invasion of *W. subatra*; sea otter predation on chitons and crabs could increase the abundance of *W. subatra*, as chitons bulldoze *W. subatra* (Nydam and Stachowicz 2007) and crabs break apart *W. subatra* while foraging for prey living within the interstitial spaces of the *W. subatra* colony (Aiken 2014). Crabs seemed a more likely candidate, because crabs are more prevalent than chitons in the sea otter diet along the central coast of California (Oftedal 2007), and chitons were rarely observed on pier pilings in Morro Bay (pers obs.). Additionally, Hughes et al. (2013) demonstrated that sea otter predation on crabs can have cascading effects to lower trophic levels within an estuary. We therefore investigated how sea otter predation on crabs affects the abundance of *W. subatra* within the Morro Bay fouling community. We hypothesized that sea otter predation on *Romaleon antennarium* crabs would facilitate the invasion of *W. subatra*, by releasing *W. subatra* from the disturbance caused by the crab foraging behavior. We aimed to: 1) determine the proportion of crabs in the sea otter diet within Morro Bay, 2) quantify changes in *W. subatra* abundance in response to varying *Romaleon antennarium* crab densities, and 3) quantify crab densities and *W. subatra* abundance in a system open to sea otter predation.

2. METHODS

2.1 Overview of Experimental Design

We conducted a subtidal cage exclusion experiment to test whether sea otter predation on crabs indirectly facilitated the abundance of the non-native bryozoan, *Watersipora subatra*, on pier pilings. We used cages to exclude sea otters and to manipulate crab densities on six pier pilings at the North T-Pier in Morro Bay, CA (35.370716, -120.858288) (Fig. 1). Morro Bay is tidally influenced with a tidal range of 1.62 m between the Mean Higher High Water and the Mean Lower Low Water, reaching flow velocities of 3.6 knots near the mouth of the bay (Morro Bay Power Plant 2001). Depth at the North T-Pier ranges from approximately 3m to 9m (pers obs.). We selected wooden cylindrical pilings on the interior of the pier to avoid contact with vessels anchored to the pier. Pilings were divided into four faces based on the cardinal directions. On each piling, three of the faces were caged and assigned to one of the following treatments: no crabs (0 crabs/m²), low crab density (1 crab/m²), and high crab density (3 crabs/m²). The fourth face of each piling remained uncaged, allowing a natural density of crabs in a system open to predation by sea otters and other predators. All four treatments were represented on each of the six pilings (Fig. 2). We ensured that each treatment faced each of the cardinal directions at least once by blocking for cardinal orientation on the first four pilings, and then randomly assigning the direction of treatments for the last two pilings (Supplementary material, Appendix 1, Table 3). For each of the treatments, six polyvinyl chloride (PVC) settlement plates were hung vertically against the piling surface (Fig. 2).

Prior to deploying the experimental setup, we performed point contact surveys on each face of the six pilings to determine the percent cover of *W. subatra* in the existing fouling community. The cage exclusion experiment commenced on May 18, 2017 and continued for ten months. We measured the percent cover of *W. subatra* on each settlement plate every other month from July 2017 through March 2018 using the photoQuad region count tool. We collected sea otter foraging data weekly from March 2016 to March 2018 at the North T-Pier to quantify the proportion of crab in the sea otter diet.



Figure 1. Map of Morro Bay, California, a tidally influenced estuary. The darker gray represents water and the light gray, green and white represent land. Our study site, the North T-Pier, is starred. Flow associated with tidal exchange runs along the channel.

2.1.1 Cages

We constructed eighteen cages (three per piling) using 16-gauge vinyl coated galvanized steel wire mesh with 1.27 x 1.27 cm openings (Fencer Wire).

We applied an additional anti-corrosion protective coating (Si-COAT 579 Polysiloxane) to the caging material, which is environmentally benign once cured (CSL Silicones Inc. 2012). Each cage measured 4 m high x 0.25 m wide x 0.18 m deep (Fig. 2). The boundary of the un-caged treatment was delineated by the sides of the neighboring cages, and ranged between 0.25 m and 0.35 m wide depending on the circumference of the piling (between 1 m and 1.1 m). We chose these cage dimensions to allow for a block design, including all four treatments on one piling, and to accommodate the low-density crab treatment of one crab per m².

The cages were five sided, with an open back to allow the crabs to be in direct contact with the piling surface. The top and bottom of the cages were cut to match the curvature of the pier pilings, allowing the cages to lay flush against the piling surface. All cages had six side doors, three front doors, and doors on both the top and bottom (Fig. 2). These doors were all attached to the caging material using zip ties and fastened shut with a bungee cord to prevent crabs from escaping. The doors hinged open to allow access for cleaning the cages. Buildup of fouling organisms on the cages could alter the composition of the fouling community on the settlement plates, either by preventing the flow of water and larvae into the cage, or by decreasing flow and trapping larvae within the cages (Miller and Gaylord 2007, Nowell and Jumars 1984). In order to prevent potential cage effects, SCUBA divers cleaned the cages every other week using scrub brushes and metal scrapers.

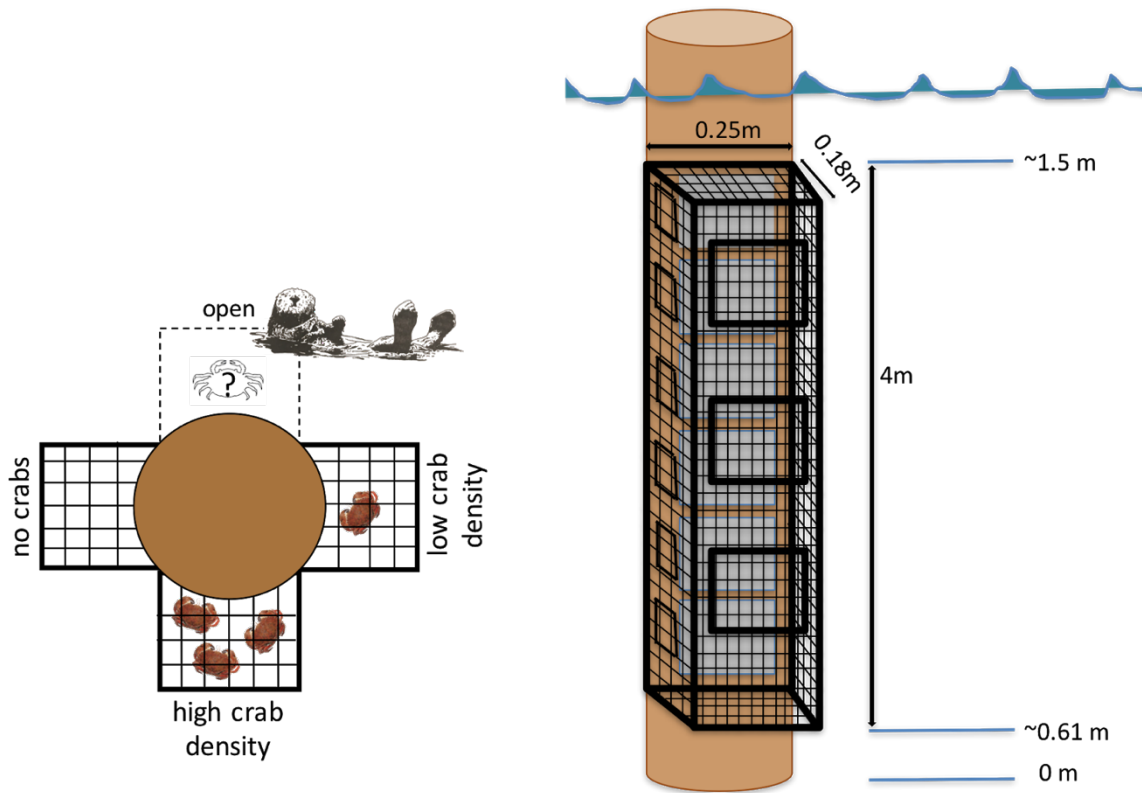


Figure 2. Diagram depicting experimental design. Left is a bird's eye view of a pier piling with all 4 treatments represented on a single piling. Three faces of the piling were caged and assigned to one of the following treatments: no crab treatment (0 crabs/m^2), low crab density (1 crab/m^2), and high crab density (3 crabs/m^2). The fourth face of each piling remained uncaged, allowing a natural density of crabs (N) in a system open to sea otter predation. Right is a representation of the predatory exclusion cages. The cages measured 4 m tall x .25 m wide x .18 m deep and had 6 side doors, 3 front doors, and doors on both the top and bottom that all hinged open. The cages were 5 sided so that crabs could be directly exposed to the piling surface. The six grey squares represent settlement plates. The cages were secured 0.61 m above the benthos.

We attached three cages to each pier piling using twelve, 1.83 m long high tensile strength cable ties, which fed through the caging material of all three cages and cinched the cages tightly against the piling surface. The bottoms of the cages were secured 0.61 m above the benthos, such that at high tide the tops of the cages were submerged between 1.5-3 m below the surface, and at a 0.15 m low tide, all cages remained fully submerged. However, the upper parts of

some cages were exposed at negative low tides. To minimize gaps between the cage and piling, a 0.25 m long piece of Gutter Guard plastic mesh (Miners Ace Hardware) was zip tied to the caging material at the top and bottom of the cages. We also used Gutter Guard plastic mesh and recycled bicycle tubing to minimize gaps on the sides of the cages.

2.1.2. Settlement Plates

To measure any differences in the abundance of *W. subatra* across treatments and over time, we deployed six, 24.7 cm x 24.1 cm grey PVC settlement plates within each treatment group. Prior to deploying the settlement plates, we roughened the plate surface with sandpaper to encourage settlement (Marshall and Keough 2004). We drilled a small hole in each corner of each settlement plate, 1.5 cm in from each side, for a zip tie anchor point. A handle and a small notch extended out from the 24.7 cm x 24.1 cm area to reduce disturbance of the fouling community during handling of the settlement plates (Supplementary material, Appendix 1, Fig. 8). For the caged treatments, the settlement plates slid into a PVC track that was zip tied to the cage. The notch and handle stuck out through the caging material, functioning to hold the settlement plate in place. For the un-caged treatment, we secured the settlement plates to the wire mesh material of the neighboring cages using zip ties. The settlement plates were placed 38.1 cm from the top and bottom of the cage and were evenly spaced 30.5 cm apart. A small gap remained between the settlement plates and piling surface for all treatment groups, which allowed crabs to fit behind the settlement plates.

2.1.3. Crabs

We chose to use *Romaleon antennarium* (formerly *Cancer antennarius*) crabs in the field experiment because: (1) they are a known sea otter prey item (Oftedal 2007, Hughes et al. 2013), (2) they are relatively abundant on the pier pilings at the Morro Bay North T-Pier (Supplementary material, Appendix 1, Fig. 9), and (3) they occur in higher densities on vertical man-made structures than on the surrounding benthos (Page and Dugan 1999). The low-density crab treatment of one crab per m² was based on the naturally occurring *R. antennarium* crab density on the pier pilings at the North T-Pier in Morro Bay, which is subject to sea otter predation (Hatfield et al. 2018). We initially selected four crabs per m² for the high-density treatment, based on the highest published *R. antennarium* densities found on an oil platform structure in the waters offshore of Goleta, California (Page and Dugan 1999), which is outside the range of the southern sea otter (Hatfield et al. 2018). However, these densities were not sustainable over the long-term, as cannibalism at these densities was high and survival rates of the smallest crabs were low. Therefore, we reduced the high-density treatment to three crabs per m² within the first four weeks of the field experiment.

All *R. antennarium* crabs were collected from the Cal Poly Pier in Avila Beach, CA. The crabs were housed in a flow-through sea water system and fed squid every 2-3 days until we amassed enough crabs to start the field experiment. We systematically assigned crabs to each treatment group to account for differences in crab size. All low-density treatments initially had a crab

between 84 and 92 mm, and all high-density treatments had an even distribution of small (61-72 mm) medium (76-97 mm) and large (>98 mm) crabs. All crabs were transported from the Cal Poly Pier in Avila Beach, CA to the Morro Bay North T-Pier and deployed into their respective low-density or high-density crab treatment cages.

We checked the density of crabs within all the caged treatments every other week to ensure that the crab densities remained consistent for each treatment. Although the cages were secured tightly against the piling, small gaps allowed some small juvenile crabs (approximately 10-50mm) to move freely in and out of the cages. Octopus were able to fit through the caging material as well. We removed any octopus and extra crabs found in the cages and replaced any missing or dead crabs with a similarly sized crab (minimum crab size 60 mm). To prevent double counting of crabs within the high-density crab treatment, we attached different colored rhinestones to the carapace of each crab using Super Glue (ethyl cyanoacrylate) (Stachowicz and Hay 1999). For the un-caged treatment, we measured both the density and sizes of all species of crabs on the un-caged area of each piling every other month for the entire duration of the experiment. Sea otters, octopus, and sea stars had access to the un-caged treatment area.

2.1.4. *Watersipora subatra* sampling method and photo analysis

We photographed all settlement plates on the surface to measure the abundance of *W. subatra* in July 2017, September 2017, November 2017, January 2018, and March 2018. SCUBA divers attached settlement plates to a

1.3 m high x 1.7 m wide x 0.3 m deep frame constructed of PVC and plastic netting (Ace Hardware Tenax Snow Guard Fence) affixed with carabiner clips. The frame enabled divers to pull up all 24 settlement plates from a single piling at one time. A surface support team photographed the settlement plates using a DSLR camera (Canon EOS 70D(W) 20.2 megapixels) with a macro lens (Canon EFS 60 mm) and immediately returned the settlement plates to the water. In order to reduce edge effects, we set the quadrat boundary 1.5 cm in from all sides of the settlement plates, creating a 21.7 cm x 21.1 cm quadrat boundary. Percent cover of *W. subatra* on each settlement plate was calculated using the photoQuad region count tool. We calibrated each image, delineated the quadrat boundary, and identified all *W. subatra* species regions by outlining all *W. subatra* colonies within the quadrat boundary. The photoQuad program calculated the percent cover of *W. subatra* based on the number of pixels assigned to *W. subatra* divided by the total number of pixels within the quadrat boundary (Trygonis and Sini 2012).

2.1.5. Sea Otter Foraging

We collected sea otter foraging data weekly from March 2016 to March 2018 using land-based high power (50x) Questar field telescopes and binoculars (8-24x). We recorded foraging observations on untagged sea otters in close proximity to our study site. Most observations were made within 5-80 m of the study site and all observations were made within 200 m. Following standard methods developed by Watt et al. (2000) and Ralls et al. (1995), we identified each sea otter prey item to the lowest taxonomic level possible for all successful

dives. We calculated the proportion of crab in the sea otter diet by dividing the total number of crabs caught across all feeding observations by the total number of prey items caught. We also collected opportunistic data on the number of otters foraging near the study site while diving and performing other fieldwork at the study site.

2.2 Statistical Analyses

To account for the repeated measures aspect of our experimental design, we performed a general linear mixed model with compound symmetry covariance structure to test for differences in the percent cover of *W. subatra* across treatments and over time. The percent cover of *W. subatra* was logit percent transformed to homogenize variance and normalize the distribution of residuals (Supplementary material, Appendix 1, Fig. 10). The logit percent transformation corrected for the severe non-normality of the un-transformed residuals, but was still non-normal based on a Shapiro Wilk's test ($p < 0.0001$). However, we proceeded with the analysis using the logit transformation, because residuals using the transformation more closely followed a normal distribution, with less skew, fewer outliers, and no obvious deviations from the expected values (Supplementary material, Appendix 1, Fig. 11). We included treatment, sample month, vertical panel position, orientation of each treatment group, and interactions between month and treatment, month and vertical panel position, and treatment and vertical panel position as fixed effects. Because *W. subatra* has non-feeding larvae with a short larval duration after being released from the source colony (Marshall and Keough 2003), we accounted for natural variation in

W. subatra abundance on the pier pilings by including the initial percent cover of *W. subatra* on the piling surface within each treatment area as a fixed effect covariate. We transformed the initial percent cover of *W. subatra* to correct for skewness by adding a constant of 1.5 and performing a logit percent transformation. The constant of 1.5 was chosen because it was half of the smallest non-zero value for the initial percent cover of *W. subatra*. We considered a higher order model that included a quadratic term for the initial percent cover of *W. subatra*, but the quadratic term was non-significant, so was excluded in our final analysis. Piling and panel ID were included as random effects: piling as a block and panel ID for the repeated measures.

We compared the compound symmetry mixed model to models with autoregressive and Toeplitz covariance structures. There was little difference in both AIC and BIC across the models. The autoregressive model was the poorest fitting model, as the AIC was the same as the compound symmetry model, and the BIC was higher. The Toeplitz model had a marginally smaller AIC than the compound symmetry model, but the BIC was the same. We decided to proceed with the simpler model, with compound symmetry covariance structure, because the AIC for the Toeplitz model only differed by 1.5% (Supplementary material, Appendix 1, Table 4).

3. RESULTS

3.1 Patterns in *Watersipora subatra* abundance across treatments and over time

Treatment, month, and the interaction between treatment and month were significant predictors of the percent cover of *W. subatra* (Table 1). We observed a trend of decreasing percent cover of *W. subatra* with increasing crab density within the caged treatments for each month (Fig. 3A). Although the pattern was consistent across months, results from the post hoc comparisons using a Bonferroni correction ($\alpha = 0.0083$) indicated that the differences in the percent cover of *W. subatra* across the caged treatments were not significant for every month. The high crab density treatment had a significantly lower percent cover of *W. subatra* than the no crab treatment in September and November, and significantly lower percent cover of *W. subatra* than the low crab density treatment in September only ($p < 0.0001$, Fig. 3A).

Table 1. Summary of the fixed effects tests for the linear mixed model analyzing logit transformed *Watersipora subatra* percent cover across several predictor variables. Significant p-values at $\alpha = 0.05$ are in bold font.

Predictor Variable	DF	DF Denominator	F Ratio	Prob > F
Treatment	3	113.79	29.01	<.0001
Month	3	405.00	53.15	<.0001
Position	5	111.62	5.93	<.0001
Orientation	3	112.16	7.57	<.0001
Position*Treatment	15	111.62	0.77	0.7068
Position*Month	15	405.00	2.39	<.0001
Month*Treatment	9	405.00	7.85	<.0001
Logit[initial_ws% +1.5]	1	26.04	2.75	0.1091

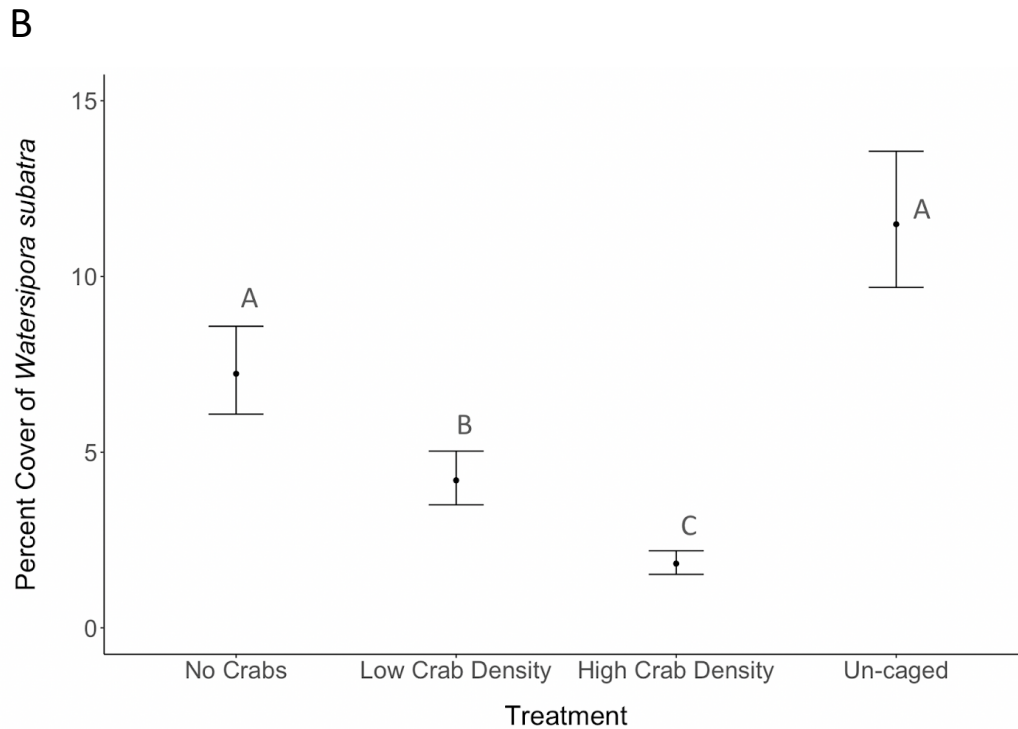
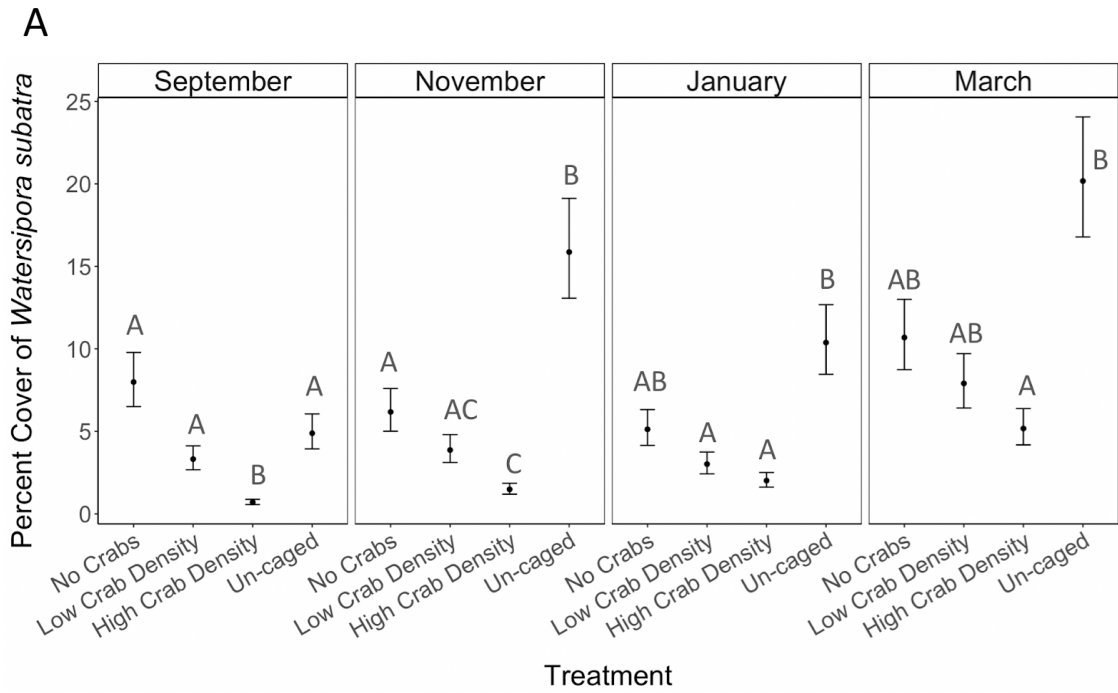


Figure 3. A) Plot of modeled mean percent cover of *Watersipora subatra* across treatment groups by month. Values have been back transformed from the logit percent scale to the standard percent scale. Error bars represent standard error about the mean. Different letters denote significantly different means based on a post hoc test with $\alpha = 0.0083$ using a Bonferroni correction. Statistical

comparisons were only done between treatment groups within the same month. B) Modeled mean percent cover of *Watersipora subatra* across treatment groups, including data from September, November, January, and March. Values have been back transformed from the logit percent scale to the standard percent scale. Error bars represent standard error about the mean. Different letters denote significantly different means based on a post hoc Tukey test with $\alpha = 0.05$.

We observed the highest abundance of *W. subatra* in the un-caged treatment for all months, except September, which was the first month of sampling (Fig. 3A). The un-caged treatment had a significantly greater abundance of *W. subatra* than the high crab density treatment for all months ($p < 0.0001$, Fig. 3A). Additionally, the percent cover of *W. subatra* in the un-caged treatment was significantly greater than all other treatments in November, and greater than both the low and high crab density treatments in January (Fig. 3A).

The percent cover of *W. subatra* varied significantly across treatments ($p < 0.0001$, Table 1), reflecting the trends observed within each month (Fig. 3A). Within the caged treatments, the percent cover of *W. subatra* significantly decreased with increasing crab density (Fig. 3B). Overall, the un-caged treatment had significantly greater abundance of *W. subatra* than both the low and high crab density treatments ($p < 0.0001$), but was not significantly different from the no-crab treatment ($p = 0.059$, Fig. 3B).

There was a significant increase in the overall abundance of *W. subatra* (averaged across all treatments) over time, except between November and January (Fig. 4). However, the relationship between month and the percent cover of *W. subatra* varied significantly by treatment group ($p < 0.0001$, Table 1). The

high crab density treatment had a steady increase in *W. subatra* abundance over time, whereas all other treatments experienced a decline in *W. subatra* abundance in January.

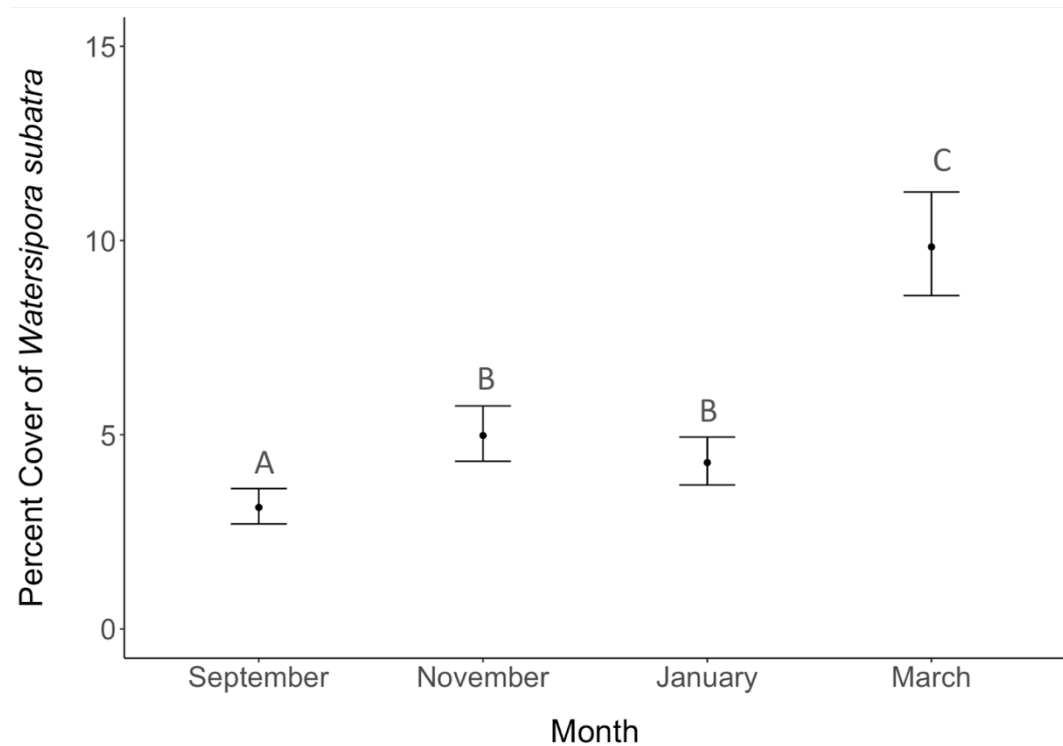


Figure 4. Modeled mean percent cover of *Watersipora subatra* across months, including data for all treatment groups. Months are listed in chronological order from September 2017 through March 2018. Values have been back transformed from the logit percent scale to the standard percent scale. Error bars represent standard error about the mean. Different letters denote significantly different means based on a post hoc Tukey test with $\alpha = 0.05$.

3.2 Patterns in *Watersipora subatra* abundance across vertical panel position and cage orientation

The percent cover of *W. subatra* varied significantly across cage orientation and vertical panel position ($p < 0.0001$, Table 1). The percent cover of *W. subatra* within the west facing treatment groups was significantly higher than

both north and south facing treatments, but did not differ from east facing treatments (Fig. 5). The relationship between the percent cover of *W. subatra* and vertical panel position varied significantly across months ($p < 0.0001$), but not across treatments ($p = 0.7068$, Table 1). Although the interaction between position and month was significant ($p < 0.0001$), we observed a similar pattern across months, where the shallowest settlement plate (position 1) consistently had the lowest abundance of *W. subatra* (Fig. 6A). Based on *post hoc* comparisons using a Bonferroni correction ($\alpha = 0.0033$), position 1 (shallowest) had a significantly lower abundance of *W. subatra* than position 5 in November and position 6 (deepest) in September (Fig. 6A). Overall, the shallowest settlement plate (position 1) had a significantly lower abundance of *W. subatra* than all other settlement plates (Fig. 6B), which reflected the pattern observed across vertical positions within each month.

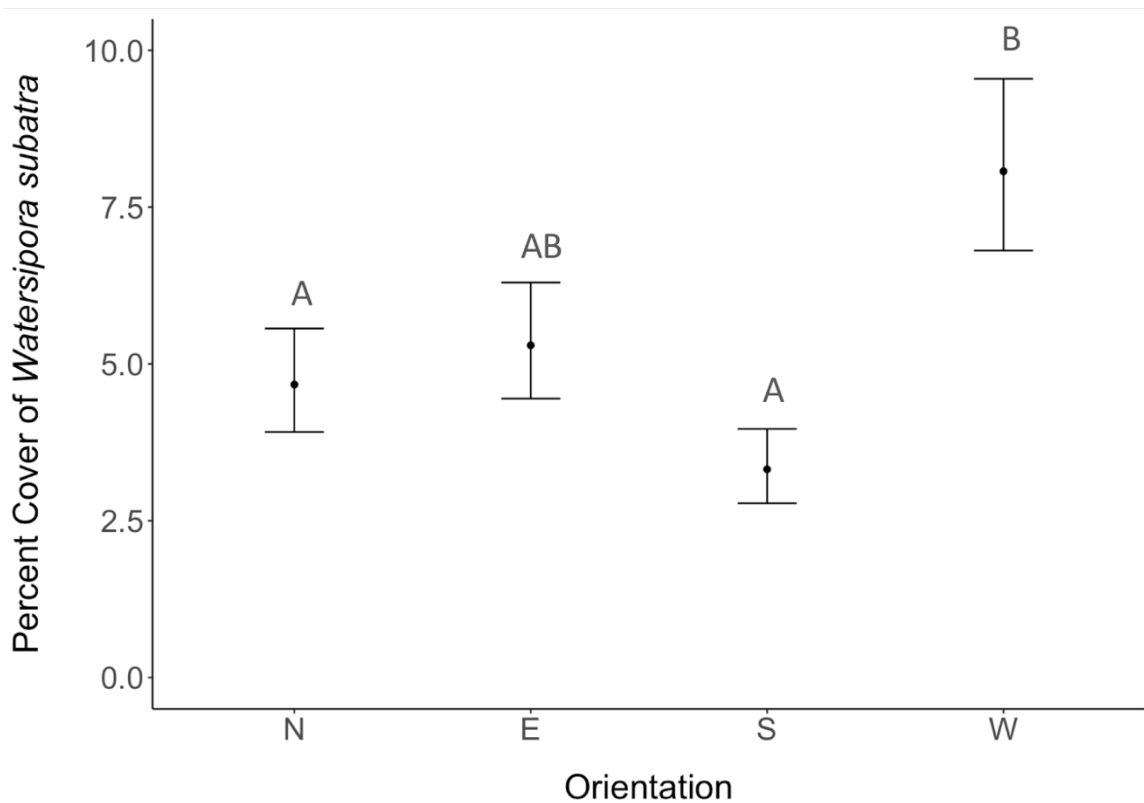


Figure 5. Modeled mean percent cover of *Watersipora subatra* by cage orientation (cardinal directions: North, East, South and West) across the entire duration of the experiment and across all treatments. Values have been back transformed from the logit percent scale to the standard percent scale. Error bars represent standard error about the mean. Different letters denote significantly different means based on post hoc Tukey test with $\alpha = 0.05$.

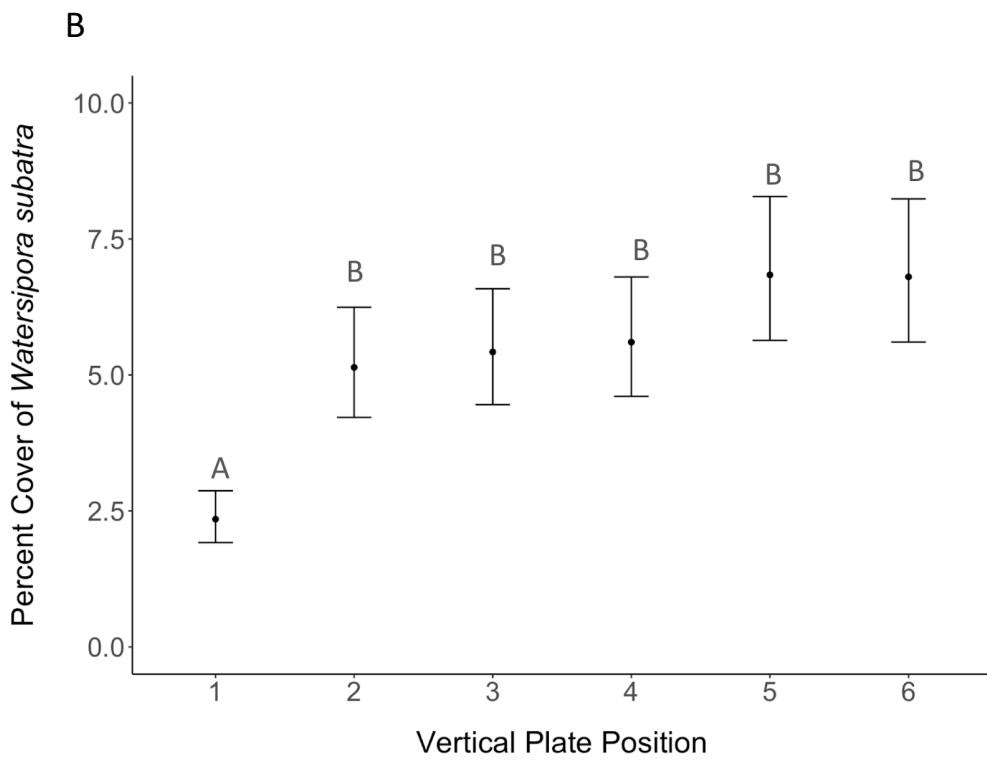
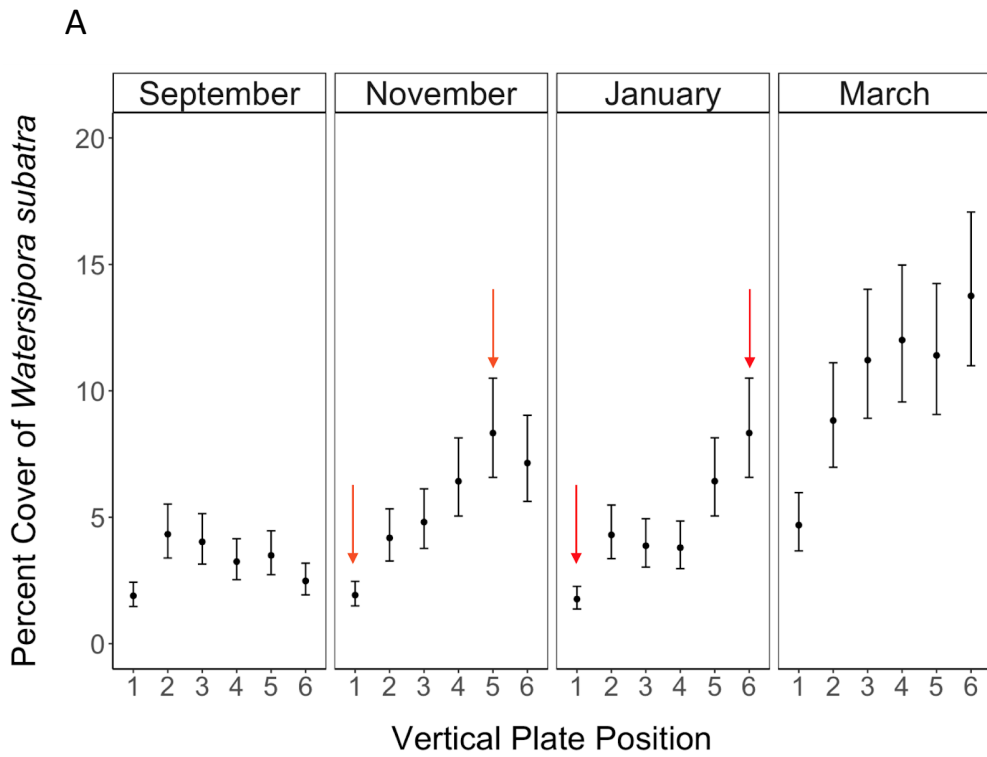


Figure 6. A) Plot of modeled mean percent cover of *Watersipora subatra* across vertical panel positions by month, including data from all treatments. Position 1 is

the shallowest settlement plate, and position 6 is the deepest. Values have been back transformed from the logit percent scale to the standard percent scale. Error bars represent standard error about the mean. Red arrows denote means that are significantly different from one another based on a post hoc test with $\alpha = 0.0033$ using a Bonferroni correction. Statistical comparisons were only done between vertical panel positions within the same month. B) Modeled mean percent cover of *Watersipora subatra* by vertical panel positions (1=shallowest, 6=deepest) across the entire duration of the experiment, including data from all treatments. Values have been back transformed from the logit percent scale to the standard percent scale. Error bars represent standard error about the mean. Different letters denote significantly different means based on post hoc test with $\alpha = 0.05$.

3.3 Patterns in *Watersipora* abundance across pilings and settlement plates

The initial percent cover of *W. subatra* within each treatment area ($p=0.1091$, Table 1) and the random effect of piling ($p=0.2485$, Table 2) were not significant predictors of the abundance of *W. subatra*. There was significant variation in the abundance of *W. subatra* across settlement plates ($p<0.0001$, Table 2).

Table 2. Summary statistics of the random effects for the linear mixed model analyzing logit transformed *Watersipora subatra* percent cover across piling and individual settlement plates. Significant p-values at $\alpha=0.05$ are in bold font.

Random Effect	Variance Ratio	Variance Component	Std Error	Wald p-Value	Percent of Total Variation
Piling	0.1169	0.0839	0.0727	0.2485	6.40
Settlement Plate.ID	0.7107	0.5101	0.0932	<.0001	38.88
Residual		0.7178	0.0504		54.72
Total		1.3118	0.1211		100

3.4 Crab density surveys

Romaleon antennarium (pacific rock crab), *Loxorhynchus* spp., *Loxorhynchus crispatus* (decorator crab), and *Pachygrapsus crassipes* (striped

shore crab) were observed on the piling surface and settlement plates within the un-caged treatments. We were not able to distinguish between juvenile *L. crispatus* (decorator crab) and *L. grandis* (sheep crab), so they were both categorized as *Loxorhynchus* spp. The overall mean crab density in the un-caged treatment was 3.08 crabs/m² with a mean size of 26.4 mm. While the overall mean density of the un-caged treatment resembled the high crab density treatment of 3 crabs/m², the mean crab size was substantially smaller in the un-caged treatment. The smallest crab placed in the high crab density treatment was 60 mm. The mean *R. antennarium* crab density in the un-caged treatment was 1.33 crabs/m², and the mean size was 32.6 mm, with a range from 14 mm to 78 mm. The mean *R. antennarium* density in the uncaged treatment more closely resembled the density of crabs in the low crab density treatment (1 crab/m²); however, the size of the *R. antennarium* crabs in the low crab density treatment ranged between 60 mm and 112 mm. The overall mean crab density and the mean *R. antennarium* crab density decreased over time, with the exception of a slight increase in the mean *R. antennarium* crab density from January to March.

3.5 Sea Otter Diet and Predator Presence

Sea otters were observed foraging at the study site throughout the entire duration of the experiment. Based on data collected from 851 sea otter foraging dives, we found that sea otters primarily consumed clams and crabs, comprising 45.9% and 25.1% of their diet, respectively (Fig. 7). We confirmed the Needles et al. (2015) observations of sea otters preying on mussels within Morro Bay, and found that mussels comprised 12.2% of the otter diet. Octopus, other bivalves,

urchins, worms, sea stars, barnacles, and non-prey items (i.e., empty shells, litter) collectively comprised 4.1% of the otter diet. The remainder of the otter diet (12.7%) consisted of unknown prey items (Fig. 7), which we were not able to identify due to small sizes, obstructed view, or rapid handling times. Although not all crabs were identified to species level, *R. antennarium*, other rock crabs (*Cancer productus*), shore crabs (*Pachygrapsus crassipes*, *Hemigrapsus oregonensis*), kelp crabs (*Pugettia producta*), and decorator crabs (*Loxorhynchus crispatus*) were present in the otter diet. We observed one foraging bout in which the otter consumed crabs almost exclusively, eating 47 crabs in 60 minutes. On several occasions while diving and performing other fieldwork, we observed sea otters surfacing with *R. antennarium* crabs next to pier pilings at the study site, but these observations were not included in the diet calculations.

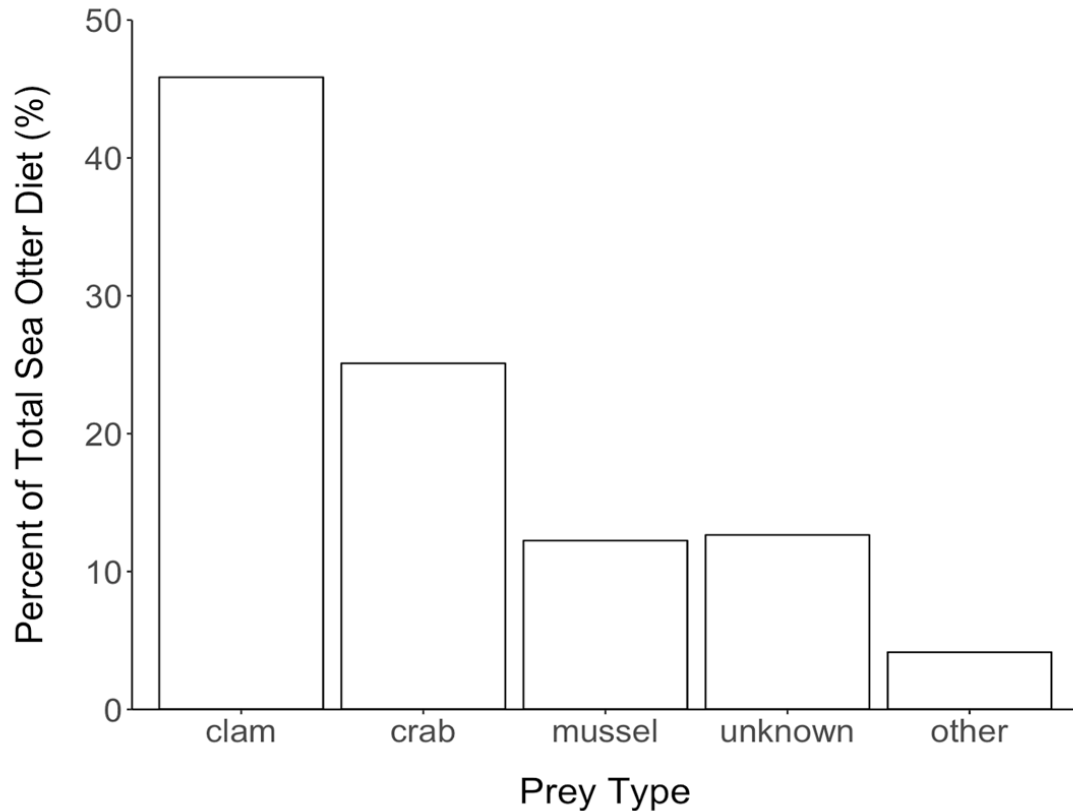


Figure 7. Relative percent of each prey type in the sea otter diet at the Morro Bay North T-Pier based on observational foraging data collected from May 2016 through March 2018, including 851 foraging dives. The “other” prey category consists of prey items rarely eaten, including octopus, sea stars, other bivalves (i.e. cockles, scallops), worms, urchins, barnacles, sea stars, and non-prey items (i.e., empty shells, litter).

In addition to otters actively foraging at the study site, we observed *Pisaster ochraceus* sea stars present on the un-caged surface of the pier pilings and *Octopus* spp. both near the un-caged treatments and occasionally within the caged treatments. On one occasion, we observed an octopus within the high crab density caged treatment consuming a *Romaleon antennarium* crab. All octopus were removed from the cages to prevent crab mortality. No sea stars were observed within the caged treatments, because the small openings prevented their access.

4. DISCUSSION

Several studies have highlighted the importance of predators in providing biotic resistance to invasion (Elton 1958, Reusch 1998, Carlsson et al. 2009, Carlsson et al. 2011, Morris et al. 2015). However, there is a growing body of literature that suggests that predators could also indirectly facilitate the invasion of exotic species by preferentially consuming native species, and thereby releasing invaders from predation pressure and competition for resources (Shea and Chesson 2002, Keane & Crawley 2002, Colautti et al. 2004, Maron & Vila 2001, Needles et al. 2015). Our study demonstrates that predators can also indirectly increase the abundance of invasive species by removing mesopredators that would otherwise reduce the abundance of the invader. The results of the sea otter foraging surveys and the caging experiment indicated that removal of crabs by sea otters can indirectly increase the abundance of *W. subatra* within the Morro Bay fouling community.

The sea otter foraging surveys indicated that sea otters can limit the abundance of crabs on pier pilings through direct predation. Crabs were a main prey item in the sea otter diet within Morro Bay, comprising 25.1% of their diet. While we were not able to identify all crabs to the species level, we observed sea otters consuming *Romaleon antennarium* crabs at the study site. Even a few otters at a site could have large impacts. We suspect that at our study site, some sea otters specialize on crabs, since we observed several foraging bouts where otters consumed crabs almost exclusively. *Cancer* crab specialization (including *Romanelon antennarium*- formerly *Cancer*) is well documented within Central

California (Estes et al. 2003, Tinker et al. 2006, Oftedal 2007). Moreover, the percentage of crabs in the sea otter diet within Morro Bay may be underrepresented due to the timing of our observations. Sea otters do actively forage at night when *Cancer* crabs are active, but our foraging surveys only included diurnal observations (Ostfeld 1982).

While our foraging studies demonstrated the impact of otters on crab populations, our caging experiment demonstrated that *Romaleon antennarium* crabs reduce the abundance of *W. subatra*. This was supported by the significantly lower abundance of *W. subatra* in the high crab density treatment compared to the other caged treatments for all months combined (Fig. 3B) and an inverse relationship between crab density and *W. subatra* abundance within each month (Fig. 3A). Although the mechanism behind why *Romaleon antennarium* crabs reduce *W. subatra* abundance is unknown, Aiken (2014) observed *Metacarcinus gracilis* crabs (formerly *Cancer gracilis*) destroying *W. subatra* bryoliths (large un-attached free-living colonies) while foraging for invertebrates (shrimp, annelids, and flatworms) living within the *W. subatra* colonies. *Romaleon antennarium* crabs are also scavengers (Carroll & Winn 1989) and likely reduced the abundance of *W. subatra* on pier pilings through a similar mechanism. Although large *W. subatra* bryoliths may facilitate further spread of *W. subatra* (Aiken 2014), small fragments resulting from crab destruction of existing colonies are unlikely to aid in *W. subatra* dispersal, because small *W. subatra* fragments cannot reattach to hard substrates (Hopkins et al. 2011). Another mechanism by which *Romaleon antennarium* crabs could

reduce *W. subatra* abundance is through trampling newly settled *W. subatra* recruits, preventing successful establishment of *W. subatra*; we observed significant differences in *W. subatra* abundance across treatments before large 3-dimensional foliose *W. subatra* structures had formed (Fig 3A). While this has not been studied in crabs, studies of limpets show that limpets bulldoze *W. subatra* recruits (Nydem & Stachowicz 2007).

The significantly greater abundance of *W. subatra* in the un-caged treatment compared to the low and high crab density treatments (Fig 3B) could potentially be attributed to the presence of other crab species in the un-caged treatment or to smaller sized crabs in the un-caged treatment. In the caged treatments, all other species of crabs were removed from the cages every 2 weeks and the average carapace size of *R. antennarium* was similar among the 3 caged treatments (average size >60 mm). However, other crab species were present in our surveys of the uncaged treatment area and the crabs found had a much smaller carapace size (average size 26.4 mm). To understand whether other crab species affected the *W. subatra* abundance found in the uncaged treatment, we compared the low-density crab treatment to the uncaged treatment, as they had similar *R. antennarium* densities (uncaged *R. antennarium* density: 1.33/m², low: 1/m²). If other crab species were negatively impacting *W. subatra* abundance, we would expect that the un-caged treatment would have a lower abundance of *W. subatra* than the low crab density treatment. However, if other crab species are not impacting *W. subatra*, we would expect there to be a similar abundance of *W. subatra* between the low

crab density and the un-caged treatment. We observed neither of these patterns. Instead, the un-caged treatment had a significantly greater abundance of *W. subatra* than the low crab density treatment, indicating that either other crab species have a positive effect on *W. subatra* abundance, or that some other factor is contributing to the increased abundance of *W. subatra* in the un-caged treatment. It is unlikely that other crab species would have a positive effect on *W. subatra* abundance, because Aiken (2014) found that another species, *Metacarcinus gracilis*, destroys *W. subatra* bryoliths. The underlying mechanism behind the destruction of *W. subatra* colonies was mechanical – crabs walking on and breaking apart pieces of the colony while foraging (Aiken 2014), which is likely a shared behavior across other crab species.

The most parsimonious explanation for the higher abundance of *W. subatra* in the un-caged treatment is that the crabs found in the uncaged treatment were smaller than crabs in the caged treatments. We can look at the effect of size by comparing the high crab density treatment with the uncaged treatment, as they have similar overall crab densities (not just *R. antennarium* densities as in the above comparison to the low crab density treatment, uncaged: 3.08/m², high: 3/m²) but different crab sizes. The average carapace size for the high crab density treatments was >60 mm, compared to the average carapace size for the un-caged treatment of 26.4 mm. The increased abundance of *W. subatra* in the un-caged treatment compared to the high crab density treatment suggests that larger sized crabs have a greater ability to decrease *W. subatra* than smaller crabs.

Otters have been shown to reduce both crab populations and decrease average carapace size (California Department of Fish and Game 1976, Ostfeld 1982, Oftedal 2007, Hughes et al. 2013). Sea otters preferentially consume larger, more calorically rich prey to maximize their rate of energy intake (Ostfeld 1982). Their preference for larger prey sizes can provide refuge for smaller juvenile prey (Ostfeld 1982). It is likely that sea otters indirectly increase *W. subatra* coverage by reducing sizes of crabs present on the pier pilings, in addition to controlling crab densities.

While sea otter predation on crabs clearly plays a role in increasing *W. subatra* abundance, other predators may also influence fouling community composition. The uncaged treatment allowed other predators (e.g. octopus, cabezon (*Scorpaenichthys marmoratus*) and sea stars) access to the settlement plates, which may explain the increased abundance of *W. subatra* in the uncaged treatment compared to the low and high crab density treatments. Cabezon prey on juvenile *R. antennarium* crabs (Carroll & Winn 1989) and octopus prey on both juveniles and adults (Ambrose 1984). Therefore, cabezon and octopus may be contributing to the reduced *R. antennarium* density. We observed an octopus consuming an *R. antennarium* crab on one occasion. In addition, we observed *Pisaster ochraceus* sea stars within the un-caged treatments, and sea stars are known to increase *W. subatra* abundance by removing native space competitors (Needles et al. 2015). If octopus and sea stars also indirectly increase the abundance of *W. subatra*, sea otter predation on octopus and sea stars could potentially reduce the facilitative effects of sea otters on *W. subatra*

abundance. However, octopus and sea stars are rarely consumed by sea otters along the central coast (Oftedal 2007) and in Morro Bay specifically (Fig. 7); therefore, sea otters likely do not limit the top-down effects of octopus and sea stars.

The cages themselves could potentially have had an effect on *W. subatra* abundance as well. However, it is unlikely that cage effects were responsible for the difference between the caged treatments and un-caged treatment, as cages would be expected to promote *W. subatra* growth (Needles 2015). The cages reduced flow velocities and increased larval retention, which would increase abundance of *W. subatra* within the caged treatments (Needles et al. 2015). We used the same caging material and mesh size, and conducted the experiment at the same site as Needles et al. (2015), so we would expect a similar effect. Additionally, the caged treatments were more shaded than the un-caged treatments. Low light conditions favor bryozoans (Pomerat & Reiner 1942, Jokiel 1980, Baynes 1999), and *W. subatra* abundance is greater on shaded areas of pier pilings and settlement plates (Glasby 1999, Connell 1999). Given that the cages likely promoted *W. subatra* growth to some extent, the difference in *W. subatra* abundance between the un-caged and low and high crab density treatments may be underestimated.

Differences in light and flow velocity may have impacted *W. subatra* abundance across depths. The shallowest settlement plate (position 1) consistently had the lowest abundance of *W. subatra* across months (Fig. 6A). This pattern was reflected in the significantly lower overall abundance of *W.*

subatra in position 1 compared to all other positions (Fig. 6A). The deeper settlement plates had decreased light and flow velocity (pers. obs.), which favors *W. subatra* growth (Glasby 1999, Connell 1999, Svanfeldt 2017).

The differences in *W. subatra* abundance across cage orientations (Fig. 5) were likely an artifact of our experimental design rather than due to directional flow velocities. Morro Bay has mixed semidiurnal tides and the flow direction follows the channel (Walter et al. 2018), running Northwest (incoming) and Southeast (outgoing) along the North T-Pier (Fig. 1). Although *W. subatra* is generally more abundant in protected areas and low flow environments (Davis et al. 2002, Svanfeldt 2017), all orientations should be equally impacted by current. Therefore, the differences across orientations were likely due to an uneven distribution of treatments across orientations (Supplementary material, Appendix 1, Table 3); the north and south facing sides had more high crab density treatments, which are associated with a lower abundance of *W. subatra*.

The overall cover of *W. subatra* and the impact of treatments varied over time. The overall percent cover of *W. subatra* was lowest in September and generally increased over time with die-back in January (Fig. 4). This pattern was also reflected when comparing treatment impacts over time. The difference in *W. subatra* abundance between the high crab density and un-caged treatments was smallest in September and January. In addition, the un-caged treatment had a substantially higher percent cover of *W. subatra* than the low crab density treatment in every month except September. Run-off associated with seasonal variation in rainfall may influence fouling community composition (Rodriguez &

Ibarra-Obando 2008), and storm water run-off enters Morro Bay near the North-T pier (Morro Bay Power Plant 2001). However, the seasonal trends in rainfall (NOAA 2018) did not coincide with seasonal patterns in *W. subatra* abundance. Temporally variable recruitment may explain die back in January, but likely did not contribute to the low abundance of *W. subatra* in September (Nydam & Stachowicz 2007); *W. subatra* recruitment peaks September-November (Nydam & Stachowicz 2007). The lower abundance of *W. subatra* in September may instead be due to the timing of the experiment. September was the first measure of *W. subatra* abundance and the settlement plates had only been deployed for 3 months. In addition, the relatively low abundance of *W. subatra* in the un-caged treatment in September may be explained by seasonal patterns in the abundance of *R. antennarium* crabs, which peak in the fall (Carroll 1982). The *R. antennarium* crab density within the un-caged treatment was highest in September (2.9 crabs/m²), and higher *R. antennarium* densities are associated with lower abundances of *W. subatra*. The seasonal patterns in *W. subatra* abundance are likely not linked to temporal variation in sea otter foraging, because sea otters actively foraged at the study site throughout the entire duration of the experiment.

Sea otter predation has the potential to dramatically increase *W. subatra* abundance, because sea otters can facilitate the spread of *W. subatra* through two mechanisms. Sea otters can increase the abundance of *W. subatra* by removing *R. antennarium* crabs, which would otherwise reduce the abundance of *W. subatra*. Additionally, the relatively large proportion of mussels (12.2%) in the

sea otter diet supports the Needles et al. (2015) finding that sea otter predation on mussels facilitates the invasion of *W. subatra* by freeing up settlement space. Therefore, a large portion of the sea otter diet (>35% crabs and mussels combined) could contribute to the increased abundance of *W. subatra* in Morro Bay, potentially creating a conflict between sea otter recovery and management of invasive *W. subatra*.

4.1 Implications for management of *Watersipora subatra*

Adopting preventative strategies and improving early detection of invaders is important for minimizing the conflict between sea otter recovery and invasive species management. Sea otters can indirectly increase the abundance of *Watersipora subatra* on pier pilings within Morro Bay through multiple mechanisms, and may therefore contribute to further spread of *W. subatra*. Harbors and estuaries serve as potential source populations for the spread of invasive species to the outer-coast (Zabin et al. 2018) and to other estuaries (Wasson et al. 2001; Ruiz et al. 2011; Zabin et al. 2014). *Watersipora subatra* populations within Morro Bay may contribute to further spread of *W. subatra* into the open coast and other estuaries. Thus, it is important for managers to focus on preventative measures (Hewitt et al. 2004, Hunsucker et al. 2019), and early detection and rapid response (Secord 2003, Williams & Grosholz 2008, Williams 2007) to limit further spread of *W. subatra*. Specialized grooming, which involves regularly wiping hulls to dislodge newly settled fouling species before they can become established, can limit the spread of the *Watersipora* sp. complex via hull-fouling (Hunsucker et al. 2019).

In addition, monitoring areas with high invasion risk has been suggested as an effective preventative strategy (Lodge et al. 2006, Simberloff et al. 2013). Monitoring *W. subatra* abundance in regions just outside of the southern sea otter range could improve early detection, and thereby increase the likelihood of eradication before sea otter arrival. For example, this strategy may be applied in the Half Moon Bay region, which is in close proximity to San Francisco Bay – a potential source for many invaders (Wasson et al. 2001); *W. subatra* has not yet been detected on the outer-coast adjacent to Half Moon Bay (Zabin et al. 2018), and this region is just beyond the current range of southern sea otters (Hatfield et al. 2018). Therefore, continued monitoring of the Half-Moon Bay region for *W. subatra*, may be a worthwhile investment to prevent further spread of *W. subatra*.

4.2 Future work & implications for general invasive species management

While our study demonstrates that sea otters can facilitate the invasion of *W. subatra*, top predators, including sea otters, could promote biotic resistance to invasion as well (Needles et al. 2015, Kremer & da Rocha 2016). Predators can increase the abundance of a particular invasive species, yet reduce abundance of another invader, and therefore may not change the overall proportion of invasive species present (Kremer & da Rocha 2016). The impact of top predators on invasive species depends on the prey preferences of the predator (Needles et al. 2015) and existing biotic interactions in the community (Bulleri et al. 2008). Given the variable effects of top predators on invasive species, we cannot reliably predict the impact of sea otters on other invasive fouling organisms, on *W. subatra* populations along the rocky open coast, or on invasive

mesopredators (such as the European green crab). Therefore, further study is needed to assess the net impact of sea otters, and other top predators, on community susceptibility to invasion.

We can apply knowledge gained from studying the impacts of top predators on invasive species to develop effective management strategies and better predict future invasions (Bulleri et al. 2008, Kremer & da Rocha 2016). Augmentative biocontrol, which involves increasing abundance of native predators to control invasive species, has been suggested as a lower risk alternative to traditional biocontrol in marine environments (Secord 2003). Native predators that reduce overall community susceptibility to invasive species could be good candidates for augmentative biocontrol. Moreover, further study on the effects of top predators in invaded systems can also be applied to improve early detection, by identifying invaders likely to increase with predator recovery. Focusing eradication efforts on invasive species likely to benefit from predator recovery could help to minimize the potential conflict between predatory recovery and invasive species management.

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APPENDIX A – SUPPLEMENTARY MATERIAL

Table 3. Assignment of the orientation for each of the four treatments on all 6 pier pilings. We ensured that each treatment faced each of the cardinal directions at least one time by blocking for cardinal orientation on the first 4 pilings, and then randomly assigning the direction of treatments for the last two pilings.

Piling	Direction			
	N	E	S	W
1	low crab density	un-caged	high crab density	no crabs
2	un-caged	no crabs	high crab density	low crab density
3	un-caged	low crab density	no crabs	high crab density
4	no crabs	high crab density	low crab density	un-caged
5	high crab density	un-caged	low crab density	no crabs
6	high crab density	no crabs	un-caged	low crab density

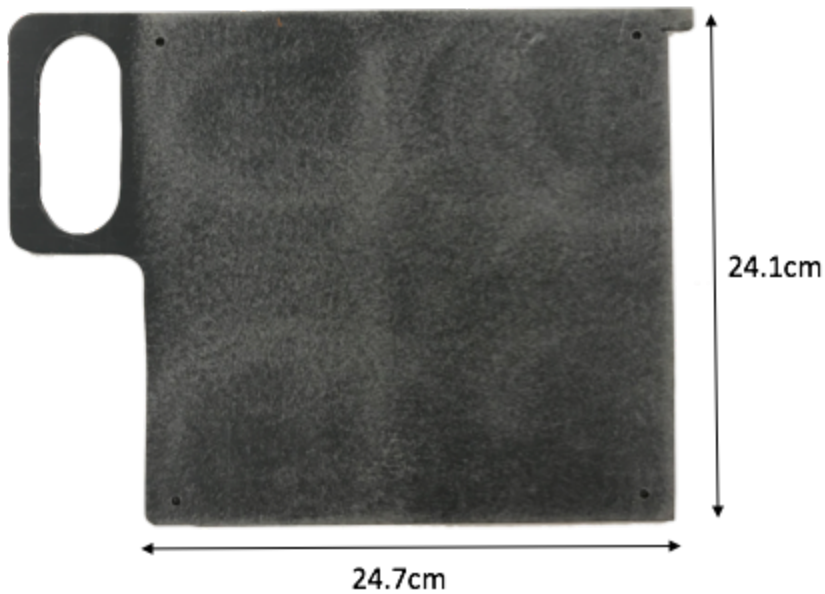


Figure 8. PVC settlement plate with handle and small notch extending outward from the 24.7cm x 24.1 cm panel area.

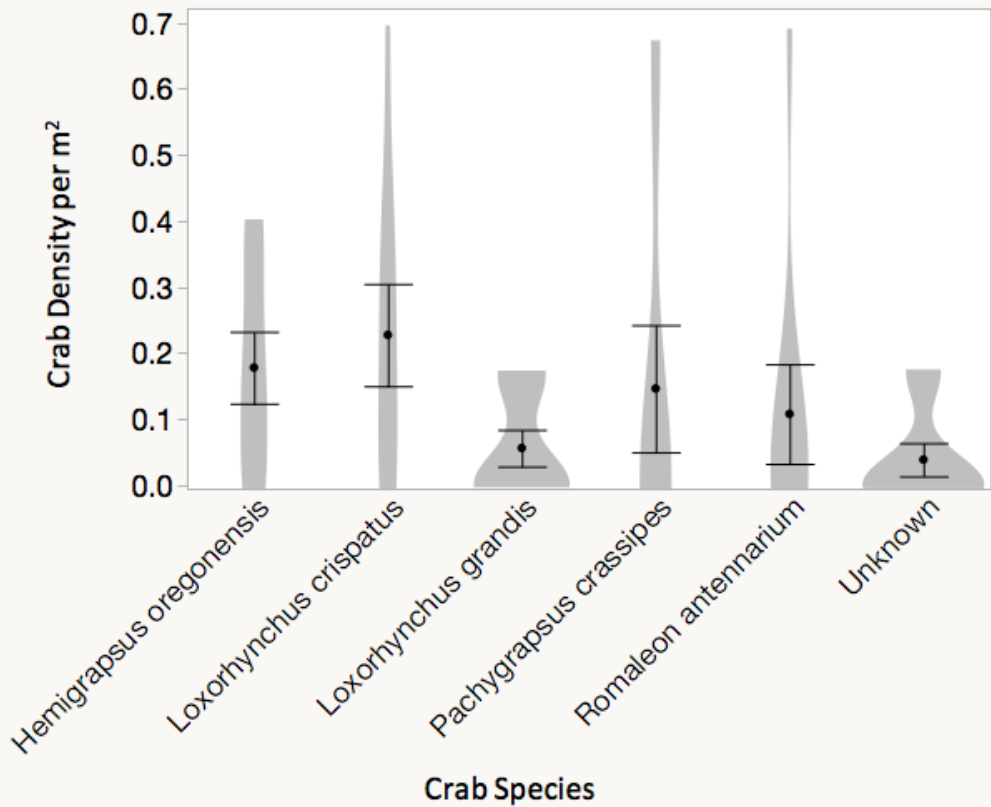
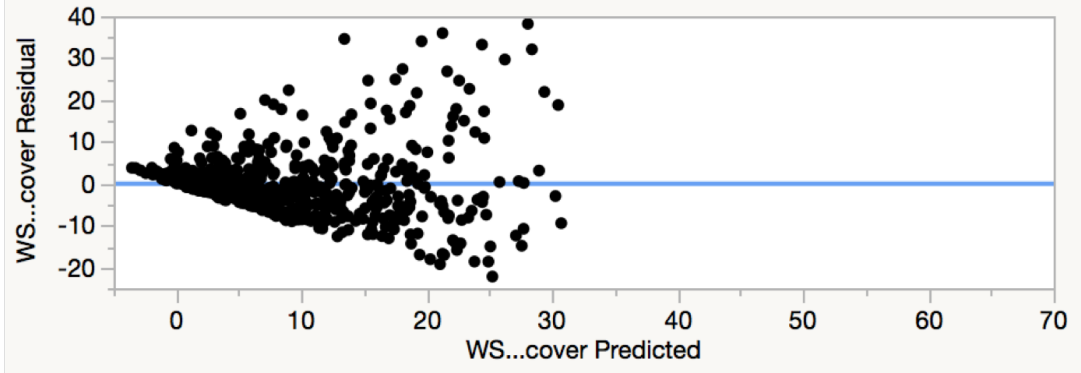


Figure 9. Mean crab density per m² for all species observed in preliminary crab density surveys conducted in February 2016 prior to the caging experiment. We surveyed 9 pier pilings at the North T-Pier in Morro Bay using SCUBA. The gray shaded regions represent the distribution of the data and error bars represent standard error about the mean. The common names for the species list are as follows (from left to right): yellow shore crab, decorator crab, sheep crab, lined shore crab, pacific rock crab.

A Residual by Predicted Plot



B Residual by Predicted Plot

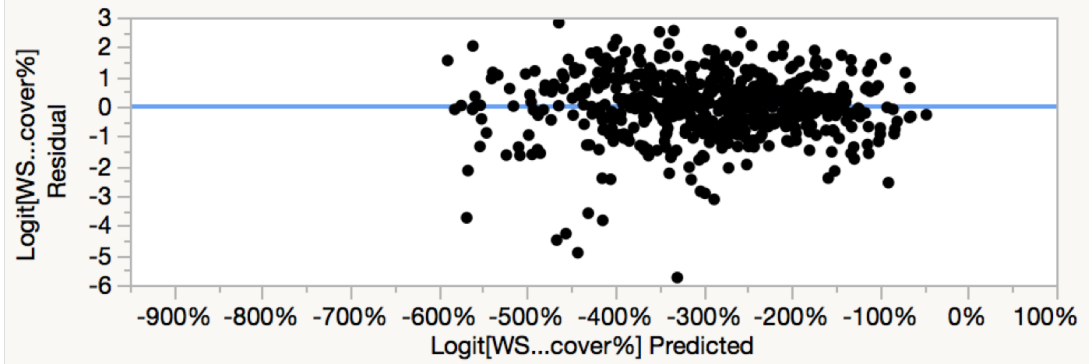


Figure 10. A) Plot of residuals vs. predicted values for model with percent *Watersipora subatra* as the response variable. B) Plot of residuals vs. predicted values for model with logit percent transformed *Watersipora subatra* as the response variable.

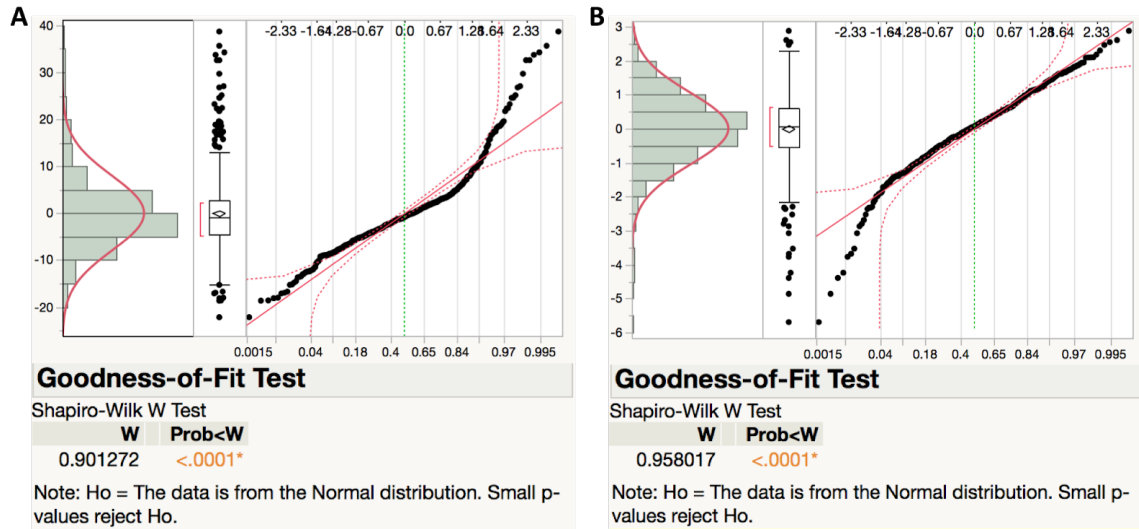


Figure 11. Distribution of residuals, normal quantile plot, and Shapiro Wilk test for A) model with percent cover of *Watersipora subatra* as the response and B) model with logit percent transformed percent cover of *Watersipora subatra* as the response.

Table 4. Model comparison table showing AIC and BIC values for models with compound symmetry, autoregressive, and Toeplitz covariance structures.

	Compound Symmetry	Autoregressive	Toeplitz
AIC	1719.9079	1719.7274	1693.6021
BIC	1959.3242	1978.4121	1959.9225