Limited recruitment of an ecologically and economically important fish, *Paralabrax clathratus*, to an invasive alga

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ABSTRACT: Some invasive species have devastating ecological impacts on native species, whereas others have little effect. The macroalga *Sargassum horneri* recently invaded the waters of California (USA) and Mexico, and in some places has largely replaced an important native macroalga, the giant kelp *Macrocystis pyrifera*. To explore the potential impacts of the invasive alga on populations of an ecologically and economically important fish, the kelp bass *Paralabrax clathratus*, we tested whether recruitment of kelp bass onto macroalgae differed between the invasive *S. horneri* and native *M. pyrifera*. Field surveys by scuba divers on naturally occurring *S. horneri* and *M. pyrifera* at Santa Catalina Island revealed that kelp bass recruits were ~30 times more abundant on individual *M. pyrifera* than on individual *S. horneri*. To assess the cause of this pattern, we conducted a field experiment in which plots containing 3 treatments (*M. pyrifera* only, *S. horneri* only, and *M. pyrifera* and *S. horneri* together) were isolated over a sandy bottom, which limited post-settlement movement of recently settled kelp bass among macroalgae. Kelp bass recruitment was similar for the 2 treatments containing *M. pyrifera*, but no recruits were observed on *S. horneri*, regardless of whether the alga was alone or paired with *M. pyrifera*. Additionally, we found a strong spatial gradient in recruitment among the experimental plots that was explained by the abundance of larger, cannibalistic conspecifics. This study presents the first evidence that invasive *S. horneri* may negatively impact an important reef fish.

KEY WORDS: *Sargassum horneri* · *Macrocystis pyrifera* · Kelp bass · Santa Catalina Island

INTRODUCTION

As technological advancements allow humans to travel to distant places with relative ease, they sometimes move organisms across physiological or ecological barriers that once served as natural population constraints (Parendes & Jones 2000, Courchamp et al. 2003, Haran et al. 2015). Despite the increased rate of transportation across barriers, most introduced organisms perish because they are not adapted to their new environment, or reproductive isolation hinders conspecifics from perpetuating the population (Lodge 1993, Bufford & Daehler 2014). However, when invasive species thrive and reproduce, their introduction into an ecosystem often results in major ecological or economic damages (Mack et al. 2000, Lovell & Stone 2005, Pimentel et al. 2005).

Sargassum horneri is a macroalga that is native to northeastern Asia and has recently invaded the waters of California (USA) and Mexico. Presumably transported in ballast water or by hull fouling, it was first discovered in Long Beach Harbor in 2003. By 2006 it had spread to the northwestern side of Santa Catalina Island, California, and within a year had proliferated along the entire leeward coast, forming dense stands in numerous areas (Miller & Engle 2009). Since then, it has been discovered at the majority of Channel Islands, and along coastal areas of the Southern California Bight and Baja California, spatially dominating many areas including reefs that

once supported large native kelp beds (Aguilar-Rosas et al. 2007, Miller & Engle 2009, Marks et al. 2015, Kaplanis et al. 2016). Similar to a relative that invaded California's water in the 1960s, i.e. *S. muticum*, *S. horneri* has buoyant conceptacles well suited for widespread dispersal and is monoecious (able to self-fertilize), traits that have likely contributed to its establishment and spread (Miller et al. 2007, Marks et al. 2015, Kaplanis et al. 2016).

Although not all exotic species are ecologically harmful, *S. horneri* has attributes that may allow it to outcompete marine flora that influence the community structure of fishes (Miller et al. 2007). As a recent invader, currently there is limited evidence that *S. horneri* outcompetes native macroalgae, including giant kelp *Macrocystis pyrifera* (hereafter *Macrocystis*), which historically has dominated shallow, subtidal, rocky habitats at Santa Catalina Island, and throughout California and Baja California (Miller & Engle 2009, Marks et al. 2015, Kaplanis et al. 2016), but it is not uncommon to see entire reefs dominated by this species. *S. horneri* is extremely fast-growing (up to 4.46% growth in biomass d^{-1}), and recruit and adult densities often exceed 1000 and 100 ind. m^{-2}, respectively, giving this alga the potential to be a formidable competitor against native algal species (Choi et al. 2008, Marks et al. 2015, Caselle et al. 2018). The invasive congener *S. muticum* may provide some insight into the possible effects of *S. horneri*. *S. muticum* negatively affects native algae (Stæhr et al. 2000, Britton-Simmons 2004), and in particular, inhibits recruitment of *Macrocystis* at Santa Catalina Island (Ambrose & Nelson 1982). In one of the few studies of the mechanisms of the *S. horneri* invasion in California, Caselle et al. (2018) concluded that invasion by *S. horneri* was suppressed by dense *Macrocystis* populations characteristic of a healthy kelp forest. Where native algae were sparse, invasion was more extensive. Because *Macrocystis* fluctuates in abundance widely from year to year, practically disappearing from large areas in some years (Dayton et al. 1992, 1999, Reed et al. 2011), it is reasonable to expect that *S. horneri* will flourish when native algae are sparse. Moreover, it may inhibit recovery of native algae through space occupation and shading, as was observed with *S. muticum* (Ambrose & Nelson 1982, Britton-Simmons 2004).

S. horneri is an annual alga, and its biomass changes predictably throughout the year, unlike native macroalgae, including *Macrocystis*. During the summer and early autumn, it is mostly 'lawn like' (≤5 cm tall) in its recruit phase, but predictably grows into a bushier (~2 m tall) morphology throughout the winter and spring. Some tall, senescing individuals persist into summer and early autumn. Its physical structure and predictable seasonal lifecycle differ greatly from *Macrocystis*, which is less physically complex but may exceed 45 m in length, and is a perennial that lives several years under favorable conditions (Foster 1975).

As a canopy-forming species, *Macrocystis* provides structure that is critical to a variety of organisms, including adult and juvenile fishes (Hobson & Chess 1976, Dayton 1985, Hallacher & Roberts 1985, Holbrook et al. 1990, Carr 1991a, Love et al. 1991, Anderson 2001). Specifically, recruitment of several common fishes depends upon *Macrocystis* (Carr 1989). Thus, if *Macrocystis* is displaced by *S. horneri*, several fish species are at risk. The important role of *Macrocystis* as recruitment habitat, however, may have more to do with its height, extending high into the water column, than other aspects of its morphology (Carr 1991b). Some *Sargassum* species, however, are also known to provide important recruitment habitat for reef fishes, such as leopard grouper *Mycteroperca rosacea* in the Gulf of California, which mainly uses *S. sinicola* (Aburto-Oropeza et al. 2007). *S. horneri* could be used in a similar way, potentially serving as a useful habitat for kelp forest fishes because of its high structural complexity. But because it does not extend high into the water column, it may not affect fish recruitment in the same way as *Macrocystis*.

Kelp bass *Paralabrax clathratus*, the subject of this study, is one of the most economically and ecologically important fishes in southern California (Holbrook & Schmitt 1988, Anderson 2001, Southwick Associates 2009). This species is consistently ranked among the top 10 species caught by recreational anglers in southern California, a multi-billion-dollar industry (Horning 2009). Further, it is one of the most common local piscivores, affecting the abundance of other fish species (Holbrook & Schmitt 1988, Steele 1996, Anderson 2001). In the Southern California Bight, settlement of post-larval kelp bass (at ~13 mm total length, TL) occurs from July through September (Carr 1994, Cordes & Allen 1997), and is influenced by a number of physical factors, such as sea surface temperature, winds, tidal bores, and lunar cycles (Cordes & Allen 1997, Findlay & Allen 2002). However, much of the variation in recruitment of kelp bass is explained by biological factors, particularly variation in *Macrocystis* density (Carr 1994). Kelp bass preferentially recruit to structures (macroalgae or artificial algal mimics) positioned in the midwater portions of the water column, and become more ben-

thic associated as they age and grow (Carr 1991b, Findlay & Allen 2002).

The goal of this study was to determine if recruitment rates of kelp bass differed between *S. horneri* and *Macrocystis*. We expected that recruitment to *Macrocystis* would be greater than to *S. horneri*, in part because recruitment of kelp bass is highest in the middle of the water column (Carr 1991b, Findlay & Allen 2002) into which *Macrocystis* extends but *S. horneri* does not. Additionally, we explored whether the size of kelp bass recruits differed among strata in the water column to determine whether certain size classes are more likely to be found near the benthos where the non-native alga is prevalent. We anticipated that larger, older recruits would associate with *S. horneri* and small, recently settled kelp bass would associate with the midwater portion of *Macrocystis*.
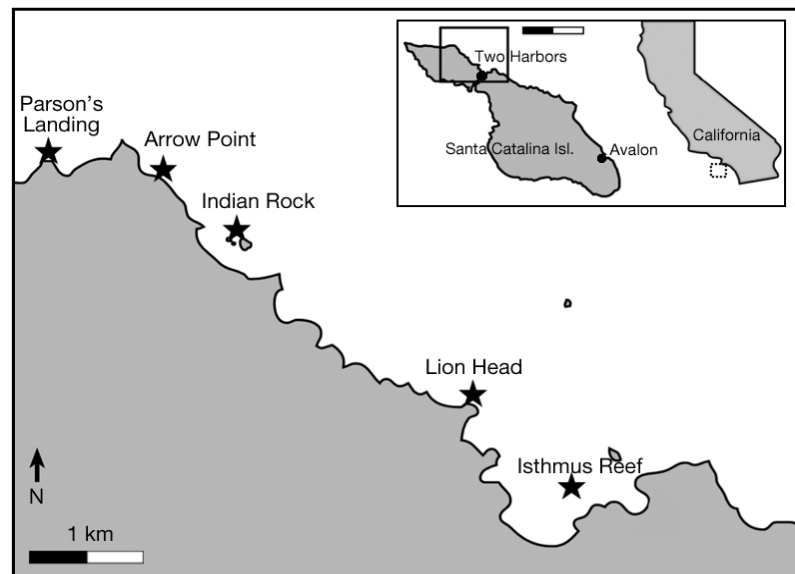

Fig. 1. Four observational study sites (Parson's Landing, Arrow Point, Indian Rock, and Isthmus Reef) and 1 experimental study site (Lion Head) on the western leeward side of Santa Catalina Island, California, USA. The dashed and solid boxes indicate the location of Santa Catalina Island in reference to California and the location of our study sites along the coast of Santa Catalina Island, respectively

MATERIALS AND METHODS

Observational study

To explore whether the invasive *Sargassum horneri* might impact recruitment of kelp bass on natural reefs, we compared recruit densities on *Macrocystis* with those on *S. horneri* at 4 sites on the northwestern, leeward, side of Santa Catalina Island, California, USA (33° 27' N, 118° 29' W): Parson's Landing, Arrow Point, Indian Rock, and Isthmus Reef (Fig. 1). These sites were chosen because *Macrocystis* and *S. horneri* were present at all of them and found at similar bottom depths. The abundance of kelp bass recruits was surveyed on individual *Macrocystis* and *S. horneri* from 3–6 August 2015, which is typically near the peak of the settlement period for kelp bass (Carr 1994, Cordes & Allen 1997). We defined recruits as individuals ≤5 cm TL, which would have settled during the 2015 settlement season.

Seven haphazardly selected 'plants' of each algal species were surveyed at each site, except that only 3 *S. horneri* plants of sufficient size (see below) were found and surveyed at 1 site, Parson's Landing (thus, total N = 28 for *Macrocystis* and 24 for *S. horneri*). To minimize disturbance to kelp bass recruits from diver bubbles, recruit abundance was surveyed sequentially from the top to the middle to the bottom third of each plant by descending along the entire length of a thallus while carefully searching through the fronds. To minimize the influence of other macrophytes in the area, all surveys were conducted on individuals >2 m away from other large (>0.5 m tall) macrophytes.

Surveys were made on *Macrocystis* and *S. horneri* of standardized sizes and with holdfasts anchored at ~10–18 m bottom depth (Fig. 2). *Macrocystis* surveyed averaged 5.7 ± 0.4 m (±SE) in length, and plants with approximately 16 stipes were selected. During our study, *Macrocystis* individuals at our study sites did not extend to the surface (i.e. no canopy): their tops were an average of 8.2 ± 0.4 m below the sea surface. *S. horneri* averaged 1.3 ± 0.1 m in length and were in the senescent stage, i.e. the tallest phase, and thus most likely to attract kelp bass recruits. These sizes of the 2 species were typical on the reefs studied at the time of our study.

To test whether the number of kelp bass recruits per thallus differed between *S. horneri* and *Macrocystis*, a paired *t*-test treating sites as replicates was used (n = 4 sites). Kelp bass might recruit more to *Macrocystis* than *S. horneri* because it extends higher into the water column. To assess this possibility, we tested whether the average number of recruits differed among 3 portions of *Macrocystis*
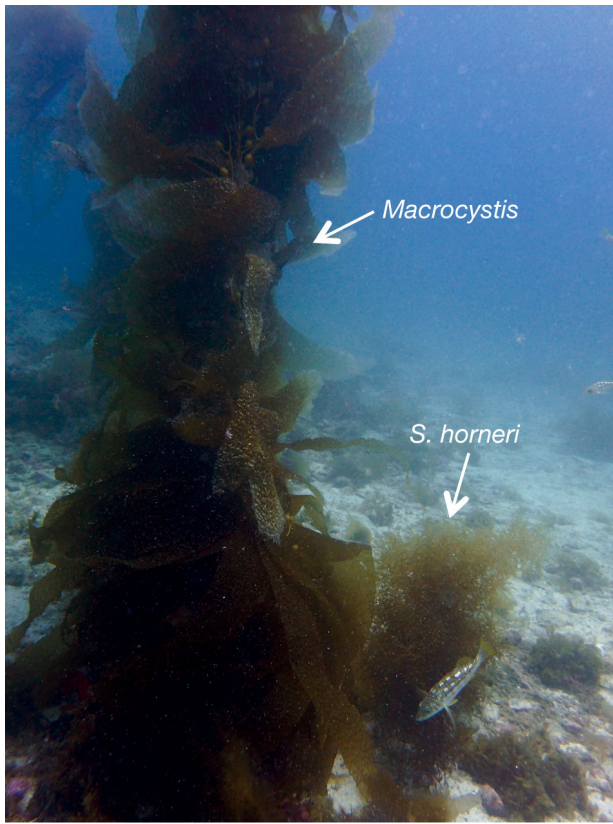
Fig. 2. *Macrocystis* and early senescent phase of *Sargassum horneri* observed at Isthmus Reef, Santa Catalina Island, California, USA. *S. horneri* in this photo is ~1.1 m tall

thalli (bottom, middle, and top third). The bottom third represents the zone in which *S. horneri* occurs. A mixed-model analysis of variance (ANOVA) with the factors stratum (bottom, middle, and top third; fixed), site (fixed), their interaction, and subject (*Macrocystis* individual surveyed; random) nested in site was used. We tested whether there was evidence of kelp bass settling in midwater and migrating down towards the seafloor as they grow by comparing kelp bass size among the top, middle, and bottom strata of *Macrocystis* with a 1-way ANOVA treating individual kelp thalli as replicates. For statistically significant results, a Tukey's HSD pairwise comparison test was used to determine which strata differed significantly. For all analyses, except the logistic regression described in the next section, numbers of kelp bass were transformed to square-root (x + 0.1) and lengths to log (x + 0.5) to satisfy the assumptions of normality and homoscedasticity (Sokal & Rohlf 1995). A p-value = 0.05 was considered significant. All statistical analyses were conducted using SYSTAT Version 13 software.

Experimental study

We also conducted a field experiment in Santa Catalina Island to assess whether patterns revealed in our observational study had a causal basis. The experiment was conducted in a sandy area near Lion Head reef (Fig. 1). Fifteen 1.5 × 1.5 m plots were established at 14–17 m bottom depth and arranged in a line parallel to shore. Plots were spaced 15 m apart and were at least that distance from any natural reef habitat. This spacing likely prevented any movement of recently settled kelp bass among plots, and between plots and the natural reef.

Three treatments were used: (1) *Macrocystis* alone (*M*), (2) *S. horneri* alone (*S*), and (3) *Macrocystis* and *S. horneri* together (*M+S*). The 15 plots were grouped into 5 blocks of 3 adjacent plots, and each treatment was assigned randomly to one of the 3 plots in each block. Both species of macroalgae were collected from nearby reefs, weighed on the surface to the nearest 0.05 kg, and secured to the bottom in their randomly assigned plots. *Macrocystis* (25–31 kg) and *S. horneri* (2–3 kg) biomass was standardized within species to achieve similar amounts of habitat structure among replicates. Thalli chosen for this experiment were typically the largest individuals observed at the collection site. The *Macrocystis* thalli used were ~4–6 m tall and *S. horneri* used were ~1–2 m tall. At the time of this experiment, no *Macrocystis* at our study sites were tall enough to reach the surface and form canopy. To ensure similarity among replicates of the 2 treatments using *S. horneri*, all thalli used were in the senescent phase. At the time of year of this study, the tallest *S. horneri* individuals are mostly in this phase. During the experiment, several *S. horneri* individuals broke free, but were replaced within 1–2 d.

The experiment ran from 15 July to 2 August 2015, a time period within the range of peak recruitment of kelp bass (Cordes & Allen 1997). Each plot was surveyed every 1–2 d, for a total of 13 surveys during the duration of the experiment. At the start of each survey, large, mobile fishes that could prey upon kelp bass recruits were counted to assess potential predators that could influence recruitment rates. Predatory kelp bass (>10 cm TL) that were within 1 m of *Macrocystis* or *S. horneri* were identified and counted as divers approached each plot. Recruits were surveyed as described previously. After the final survey, a total of 11 larger (12–27 cm TL) predatory kelp bass (the numerically dominant piscivore at Santa Catalina Island), were collected using a pole spear. Their sizes were typical of predatory individuals surveyed. Their guts

were examined using a dissecting microscope to determine whether they had consumed recently recruited conspecifics, likely from the experimental plots.

Because kelp bass recruits were absent in many plots, logistic regression was used to test for differences in kelp bass recruitment among the 3 treatments. Block (5 positions along the array from northwest to southeast) was also included in the model because there may have been a spatial difference in recruitment along the experimental array. The categorical dependent variable was presence or absence of kelp bass recruits, based on whether they were ever observed on a plot or not. Kelp bass recruited to all plots with *Macrocystis* on them, and if these recruits used the additional habitat structure provided by *S. horneri* on the *M+S* plots (relative to *M* plots), then one might expect to find more recruits near the bottom in the *S. horneri* zone on *M+S* plots than on *M* plots. To test this possibility, we compared the number of kelp bass recruits in bottom, middle, and top strata between *M* and *M+S* treatments. We used split-plot ANOVA with the factors stratum (bottom, middle, and top third of *Macrocystis*; fixed factor), block (5 positions; fixed factor), treatment (*M* and *M+S*; fixed factor), treatment × stratum interaction (fixed factor), and plot nested within block × treatment (random factor). The response variable was the number of kelp bass recruits within a stratum for each thallus averaged over the 13 observations. To evaluate whether there was evidence of kelp bass settling to the midwater portion of *Macrocystis* and later moving towards the benthos, we tested whether the size of kelp bass recruits differed among strata with a 1-way ANOVA; the average size was calculated at each stratum on each plot over the 13 observations.
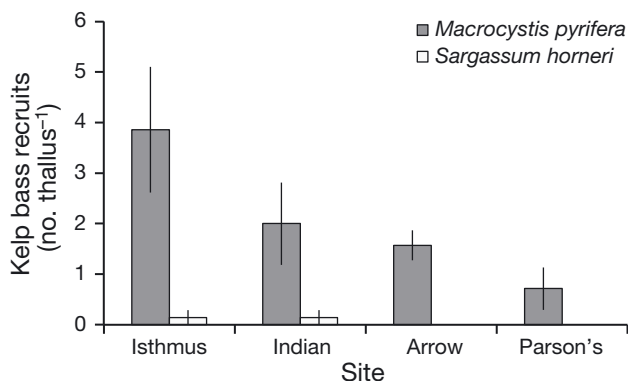
There was a distinct spatial gradient of recruitment across the array of experimental plots. We used linear regression to explore whether this pattern might have been caused by the presence of larger, predatory conspecifics by regressing the average number of recruits against predator density per plot. Only *M* and *M+S* plots were included in this analysis because predators were seldom present on the *S* plots, and kelp bass recruits were never found on them.

RESULTS

Observational study

Across the 4 study sites, 59 kelp bass recruits were encountered and 57 of these were associated with *Macrocystis pyrifera*; only 2 recruits were associated with *Sargassum horneri* (Fig. 3). Thus, numbers of recruit kelp bass per thallus were ~30 times greater on *Macrocystis* than on *S. horneri* (2.04 ± 0.66 vs. 0.07 ± 0.04, mean ± SE kelp bass recruits thallus^{-1}; paired *t*-test: $t = 4.34$, df = 3, p = 0.02). Kelp bass recruits were approximately evenly distributed among top, middle, and lower portions of *Macrocystis* (ANOVA testing for differences among strata: $F_{2,48} = 1.22$, p = 0.30); a pattern that was consistent among study sites (site × strata interaction: $F_{6,48} = 0.77$, p = 0.60). The size of kelp bass recruits, however, differed among strata of *Macrocystis* ($F_{2,56} = 13.72$, p < 0.001), with the smallest recruits in the top stratum (2.10 ± 0.09 cm) and larger ones in the middle (2.93 ± 0.20 cm) and bottom strata (3.14 ± 0.25 cm) (mean ± SE) (Fig. 4). The 2 recruits found associated with *S. horneri* were both larger, visually estimated to be 4 cm long.

Fig. 3. Abundance of kelp bass recruits (mean ± SE ind. thallus^{-1}) associated with *Macrocystis pyrifera* and *Sargassum horneri* at 4 sites: Isthmus Reef, Indian Rock, Arrow Point, and Parson's Landing, Santa Catalina Island, California, USA. Sites are listed from southeast to northwest
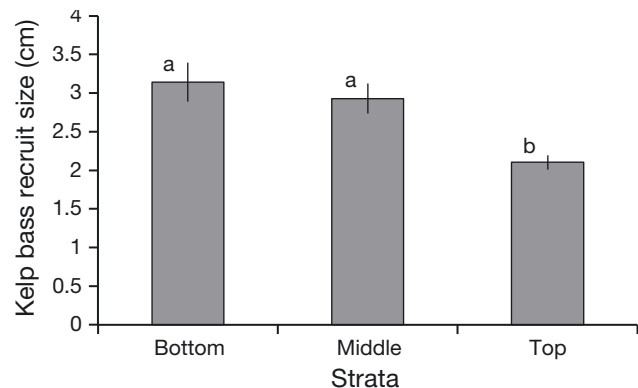

Fig. 4. Mean kelp bass recruit size (cm total length, TL) associated with the bottom, middle and top strata of macroalgae across 4 study sites (n = 14 fish for bottom and middle, n = 29 fish for top). Tukey's HSD post hoc groupings are shown with letters

Experimental study

No kelp bass recruits were observed on plots with only *S. horneri*, whereas all plots with *Macrocystis* received some recruitment (Fig. 5). Recruits were nearly evenly split between the *Macrocystis*-only treatment (2.26 ± 1.18 ind. plot^{-1}) and the *Macrocystis + S. horneri* treatment (2.23 ± 1.24 ind. plot^{-1}) (mean ± SE). Thus, there was a significant difference in kelp bass recruitment among the 3 treatments (logistic regression: $\chi^2 = 19.10$, df = 6, p = 0.004).

Recruitment differed among blocks ($F_{4,8} = 3.89$, p = 0.05), with the highest on plots in the northwest of the array and the lowest on plots in the southeast (Fig. 6a). This pattern was roughly the inverse of predator abundance (Fig. 6b). Linear regression revealed that kelp bass recruitment declined with the abundance of large, predatory kelp bass ($r^2 = 0.48$, p = 0.03), suggesting that predators created this spatial pattern in recruitment. In support of this notion, one of the 11 predatory kelp bass collected had 2 partially digested, but identifiable, kelp bass recruits (both ~1 cm TL) in its gut (Fig. 7). Large, predatory kelp bass were associated more closely with the *M* and *M+S* treatments than the *S* treatments (ANOVA: $F_{2,8} = 23.20$, p < 0.001; Fig. 8).

The number of recruits did not differ significantly among strata of *Macrocystis* ($F_{2,16} = 2.75$, p = 0.09), but the size of these recruits did ($F_{2,289} = 15.90$, p < 0.001). Kelp bass recruits were slightly larger in the bottom stratum (2.56 ± 0.05 cm) than in the middle (2.22 ± 0.07 cm) or top (2.23 ± 0.04 cm) portions of *Macrocystis* (Fig. 9). Based on their size and morphology, all recruits appeared to have settled from the plankton directly onto the experimental plots.

DISCUSSION

This study presents the first evidence that invasive *Sargassum horneri* is seldom used as a recruitment substratum by kelp bass and thus may negatively impact recruitment of this economically and ecologically impor-
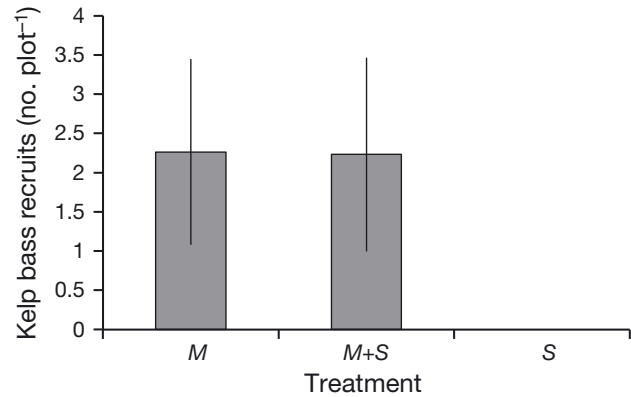
Fig. 5. Abundance of kelp bass recruits (mean ± SE ind. plot^{-1} per observation over 13 observations on separate days) associated with 3 treatments: *Macrocystis pyrifera* only (*M*), *Macrocystis pyrifera + Sargassum horneri* (*M+S*), and *Sargassum horneri* only (*S*)
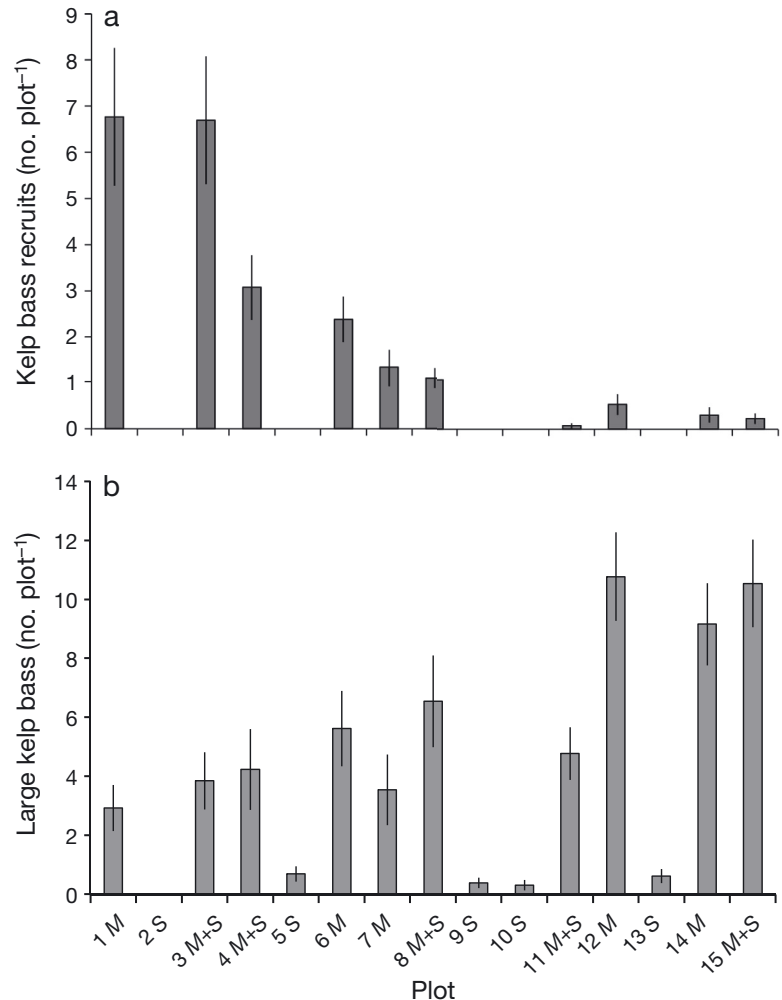
Fig. 6. Abundance of (a) kelp bass recruits and (b) large, predatory kelp bass (mean ± SE per plot over 13 observations on separate days) observed on each plot. Plot 1 was the furthest northwest and plot 15 was the furthest southeast; plots are labeled according to treatment type: *Macrocystis pyrifera* only (*M*), *Macrocystis pyrifera + Sargassum horneri* (*M+S*), and *Sargassum horneri* only (*S*)
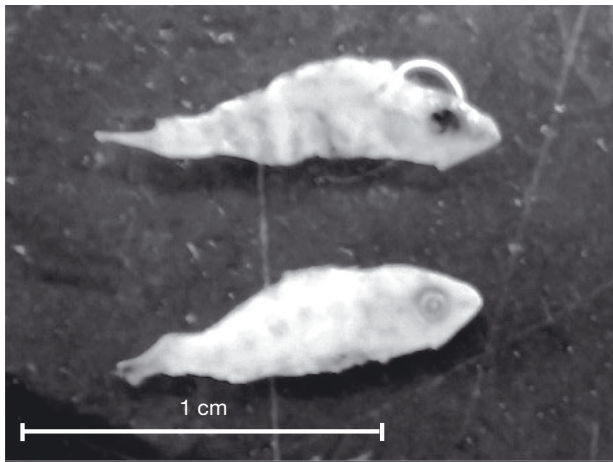
Fig. 7. Two partially digested, but identifiable, kelp bass recruits (~1 cm total length, TL) found in the gut of a kelp bass measuring 12.2 cm TL
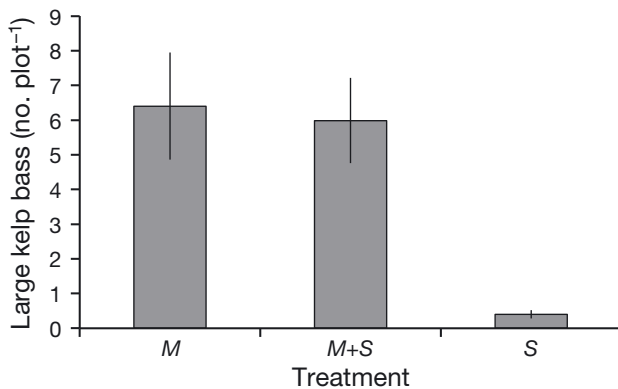

Fig. 8. Abundance of large, predatory kelp bass (mean ± SE ind. plot^{-1} over 13 observations on separate days) in 3 treatments: *Macrocystis pyrifera* only (*M*), *Macrocystis pyrifera* + *Sargassum horneri* (*M+S*), and *Sargassum horneri* only (*S*)
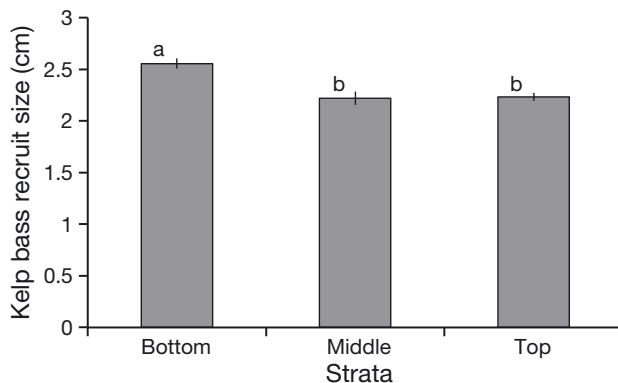

Fig. 9. Mean kelp bass recruit size (cm total length, TL) in the bottom, middle and top strata of macroalgae across all treatments (n = 117 fish for bottom, n = 50 for middle, n = 125 for top). Tukey's HSD post hoc groupings are shown with letters

tant fish species through the potential displacement of native giant kelp *Macrocystis pyrifera*. Kelp bass recruitment was vastly lower on *S. horneri* than on native *Macrocystis*: across our observational study and experiment, only 2 kelp bass recruits were observed associated with *S. horneri*. The height of the 2 algae is a likely cause of the difference in kelp bass recruitment between them. Kelp bass settle at higher rates to settlement substrata presented in the middle of the water column than to those near the bottom (Carr 1991b, Findlay & Allen 2002). *Macrocystis* extends up into this midwater zone, but *S. horneri* does not. The pattern of size differences we found in kelp bass recruits is also consistent with this hypothesis: recruits were smallest in the top strata of *Macrocystis*, which was located in midwater, suggesting that they settled in the middle of the water column and later moved down the thallus to the lower portions of the kelp, where we found larger recruits. Carr (1991b) reached the same conclusion about post-settlement movement of kelp bass recruits, and this pattern is also consistent with other studies, which found that several species of kelp forest fish move down from the upper strata of kelp and become more benthic associated as they age and grow (Carr 1991a, Anderson 1994, Nelson 2001). Whether kelp bass would settle on *S. horneri* if they encountered it in the middle of the water column remains to be tested, but Carr (1991b) found that *S. palmeri*, a California native and a relative of *S. horneri* that is broadly similar in morphology, was preferred by kelp bass as a settlement substratum when placed alongside *Macrocystis* in the middle of the water column. Settling kelp bass might perceive the 2 complex, bushy algal congeners as similar.

Although the short height of *S. horneri* relative to *Macrocystis* and its absence from the middle of the water column is a potential cause of the differences in recruitment of kelp bass to these 2 macroalgae, there are other differences between them that could influence fish recruitment. Morphologically, these 2 macroalgae are very different; they may differ chemically; and they might harbor different assemblages of invertebrate prey for kelp bass recruits, or predators of the recruits. High habitat complexity attracts and benefits prey fishes in a variety of different environments (Schmitt & Holbrook 1985, Kingsford 1995, Levin & Hay 1996, Forrester & Steele 2004, Scharf et al. 2006). *Macrocystis* may provide better habitat than *S. horneri*, particularly at the time of year when kelp bass settle from the plankton. By this time, late summer, senescent *S. horneri* begins to deteriorate as it dies, having already shed its conceptacles, leaving

the once bushy thallus now only with small pinnatifid blades (<5 cm width) (Marks et al. 2015). Although still providing vertical structure low in the water column, senescent *S. horneri* may not be as attractive to young kelp bass as the luxuriant pre-senescent stage. *Macrocystis* may provide better refuge from predators than senescing *S. horneri* because kelp bass can easily stay completely out of sight of predators by sheltering between its large blades (often >15 cm width). Additionally, during our study, most *Macrocystis* were in the reproductive stage and had lush sporophyll blades just above the holdfast, which provided abundant shelter for young kelp bass. It is also possible that *S. horneri* and *Macrocystis* harbor different numbers or types of predators of recent recruits, which could contribute to different recruitment patterns between them. The only difference in predators associating with the 2 species that we noticed was more predatory, large kelp bass associating with *Macrocystis* than *S. horneri*, which would create a pattern opposite to what we documented.

Differences in chemical composition between *Macrocystis* and *S. horneri* could also contribute to differences in recruitment rates of kelp bass between them. Many tropical fishes use chemical cues to settle in preferred areas (Sweatman 1988, Atema et al. 2002, Wilson et al. 2010, Dixson et al. 2014). In temperate kelp forests, the role of chemical cues in structuring settlement patterns of fishes is far less studied, but there is evidence that algal chemical cues induce settlement of invertebrates, such as abalone (Morse & Morse 1984). Carr (1991b) found that more kelp bass settled on natural *Macrocystis* and *S. palmeri* than on artificial mimics, which implies that chemical cues affect recruitment of our study species in some capacity. It is unclear whether algal cues (chemical) or cues of prey of kelp bass that reside in algae (various invertebrates) are the primary source of attraction of kelp bass recruits to macroalgae over artificial mimics. For kelp forest species, a body of evidence suggests that prey availability is important in post-settlement processes (Holbrook & Schmitt 1984, 1988, Anderson & Sabado 1995). Furthermore, during our study *S. horneri* may have been exuding chemicals that deterred kelp bass or their prey. *S. horneri* was senescing, and may have been exuding secondary metabolites, such as phenols, that are known to deter grazers (Hay et al. 1988, Van Alstyne & Paul 1990, Steele & Valentine 2015).

Macrocystis and *S. horneri* have fundamentally different life cycles that may interact with the seasonality of kelp bass recruitment. *Macrocystis* is a perennial that is capable of living multiple years if conditions are favorable (Foster 1975). Although *Macrocystis* grows most rapidly during winter and spring, and slowest during summer and autumn (Wheeler & North 1981, Zimmerman & Kremer 1986), it is not uncommon for it to form canopies on the surface during summer and early autumn (Graham et al. 1997) when kelp bass settle from plankton (Carr 1994, Cordes & Allen 1997). Although typically a canopy-forming species, the *Macrocystis* individuals in our study did not reach the surface and form canopy. Kelp canopy can be important in explaining variation in the distribution and abundance of fishes (Carr 1983, Anderson 2001). During our study, however, there were no *Macrocystis* that reached the surface on most reefs near our study sites at Santa Catalina Island, presumably due to the very warm surface waters during that El Niño period. Our findings are representative of a situation that is not uncommon, particularly in the warmer parts of the range of *Macrocystis*, where kelp canopies often come and go (Dayton et al. 1984, Tegner & Dayton 1987, Wernberg et al. 2010). As an annual species, *S. horneri* predictably changes dramatically in size over the course of a year (Yoshida et al. 1998), and when kelp bass are settling it is primarily found in 2 stages: ~5 cm tall recruits and 1–2 m tall senescent adults. We can only speculate that the differences in kelp bass recruitment between *Macrocystis* and *S. horneri* would be even greater in those situations because the difference in size and position in the water column between the 2 macroalgae would be larger. A logical next step would be to conduct experiments aimed at understanding the mechanism for why kelp bass preferred *Macrocystis* over *S. horneri*.

Across both portions of our study, we only observed 2 kelp bass recruits associated with *S. horneri*, and these were relatively large (estimated to be 4 cm TL), not recent settlers. These larger individuals may have moved from their original settlement habitat (i.e. *Macrocystis*) to *S. horneri*. Our experiment supports the notion that only larger recruits will move away from their settlement habitat because none of the small, recently settled kelp bass observed were found in *S. horneri*, even on plots where it was only 1 m away from *Macrocystis*. The presence of abundant predators (larger conspecifics) on natural reefs (~16 kelp bass per 120 m^3 on the 4 natural reefs; G. Srednick unpubl. data) and associated with *Macrocystis* plots in our experiment may have discouraged small, recently settled kelp bass from venturing away from the shelter provided by the *Macrocystis* to which they settled, even when *S. horneri* was nearby.

The present study clearly documents much higher recruitment of kelp bass to the native *Macrocystis* than to the invasive *S. horneri*, but our studies were done at the scale of individual 'plants,' at which settling kelp bass were likely able to choose among plants to settle on. Whether our findings extrapolate to larger scales is unknown. If extrapolated, our results suggest that kelp bass would not recruit to reefs dominated by *S. horneri* and that lack *Macrocystis*. Yet such reefs do have young-of-the-year kelp bass on them (authors' pers. obs.). Given the distance of these reefs to other reefs with *Macrocystis*, it is unlikely these young kelp bass moved to them from areas with *Macrocystis*. More likely, either these kelp bass settled to the invasive alga, or given the results of the present study, perhaps settled to another substratum on those reefs and then moved to *S. horneri* later. For instance, kelp bass will settle to rocky areas devoid of any macroalgae (Steele et al. 2002). Discrepancies in fish recruitment between small scales at which habitat selection may occur and site-scale patterns do occur (Caselle & Warner 1996, Munday 2002), including with kelp bass and *Macrocystis*. White & Caselle (2008) found that kelp bass recruitment was positively related to *Macrocystis* density at small scales but not at larger scales. Further research on the effects of *S. horneri* on kelp bass recruitment at the reef scale, particularly where *Macrocystis* is rare or absent, as has happened recently at Santa Catalina Island, would be valuable for predicting the effects of this invasive alga as it spreads.

The strong spatial pattern in recruitment of kelp bass, with decreasing recruitment from the northwest to southeast, may have been due to 2 non-exclusive processes: (1) post-settlement mortality caused by larger, predatory conspecifics, and (2) a settlement shadow (Gaines et al. 1985). The negative relationship we found between recruitment and predator abundance supports the first hypothesis, especially given the observation of recently settled kelp bass in the gut of a larger, predatory conspecific. Along with predation, the swift southeasterly current often encountered at the experimental site may have set the stage for upstream settlement depleting the supply of larvae available for settlement on downstream plots.

Invasive biogenic habitat often has drastic community effects. Biogenic invasives may aid native organisms, as in the case with the red alga *Gracillaria vermiculophylla* (Thomsen 2010), and a mussel, *Musculista senhousia* (Crooks & Khim 1999), which both positively affect numerous native invertebrates in their respective invaded regions. However, invasive habitat-forming species are more frequently associated with negative effects. They are either detrimental to native species (Reusch & Williams 1998, Hedge & Kriwoken 2000, Longepierre et al. 2005, Gribben et al. 2009), or are associated with increases in other non-native species (Heiman et al. 2008). For example, the highly invasive green alga *Caulerpa taxifolia* was found to threaten important seagrass habitats, which altered fish assemblages in southeast Australia (York et al. 2006), and it lowered species richness and abundances of invertebrates (Santini-Bellan et al. 1996) as well as biomass and abundance of fishes (Francour et al. 1995) in invaded regions of the Mediterranean.

The population explosion of *S. horneri* in recent years makes eradicating this alga highly improbable. Eradication of a similar invasive species, *S. muticum*, in southern California proved to be futile despite adding native algal canopies and herbivorous urchins to limit the recovery of the invasive alga (Smith 2016). Similarly, a recent experiment removing *S. horneri* at Santa Catalina Island resulted in re-colonization of large, cleared plots within months (L. Marks unpubl. data). Rather than focus efforts on total eradication of this invasive alga, it would be better to target control efforts at the most ecologically valuable areas, while continuing to develop a sound understanding of the ecological impacts of *S. horneri* so that its effects can be predicted as it spreads. As a highly complex and fairly low-lying alga, *S. horneri* may offer more cover and protection to benthic, cryptic fishes from roving predators. In contrast, fishes or invertebrates that depend on the native algal assemblage may suffer indirectly because the introduction may alter algal assemblages by space preemption or shading. The present study clearly demonstrates that recruitment of an ecologically and economically important fish, kelp bass, is much higher to native *Macrocystis* than to invasive *S. horneri*, but further studies that generate a more comprehensive understanding of the impact of this alga on kelp forest organisms are needed to predict its long-term, large-scale effects.

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LITERATURE CITED

Aburto-Oropeza O, Sala E, Paredes G, Mendoza A, Ballesteros E (2007) Predictability of reef fish recruitment in a highly variable nursery habitat. Ecology 88:2220–2228

Aguilar-Rosas LE, Aguilar-Rosas R, Kawai H, Uwai S, Valenzuela-Espinoza E (2007) New record of *Sargassum filicinum* Harvey (Fucales, Phaeophyceae) in the Pacific Coast of Mexico. Algae 22:17–21

Ambrose RF, Nelson BV (1982) Inhibition of giant kelp recruitment by an introduced brown alga. Bot Mar 25:265–267

Anderson TW (1994) Role of macroalgal structure in the distribution and abundance of a temperate reef fish. Mar Ecol Prog Ser 113:279–290

Anderson TW (2001) Predator responses, prey refuges, and density-dependent mortality of a marine fish. Ecology 82:245–257

Anderson TW, Sabado BD (1995) Correspondence between food availability and growth of a planktivorous temperate reef fish. J Exp Mar Biol Ecol 189:65–76

Atema J, Kingsford MJ, Gerlach G (2002) Larval reef fish could use odour for detection, retention and orientation to reefs. Mar Ecol Prog Ser 241:151–160

Britton-Simmons KH (2004) Direct and indirect effects of the introduced alga *Sargassum muticum* on benthic, subtidal communities of Washington State, USA. Mar Ecol Prog Ser 277:61–78

Bufford JL, Daehler CC (2014) Sterility and lack of pollinator services explain reproductive failure in non-invasive ornamental plants. Divers Distrib 20:975–985

Carr MH (1983) Spatial and temporal patterns of recruitment of young of the year rockfishes (genus *Sebastes*) into a central California kelp forest. MSc thesis, San Francisco State University, San Francisco, CA

Carr MH (1989) Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. J Exp Mar Biol Ecol 126:59–76

Carr MH (1991a) Habitat selection and recruitment of an assemblage of temperate zone reef fishes. J Exp Mar Biol Ecol 146:113–137

Carr MH (1991b) Patterns, mechanisms, and consequences of recruitment of a temperate marine reef fish. PhD dissertation, University of California, Santa Barbara, CA

Carr MH (1994) Effects of macroalgal dynamics on recruitment of a temperate reef fish. Ecology 75:1320–1333

Caselle JE, Warner RR (1996) Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. Ecology 77:2488–2504

Caselle JE, Davis K, Marks LM (2018) Marine management affects the invasion success of a non-native species in a temperate reef system in California, USA. Ecol Lett 21:43–53

Choi HG, Lee KH, Yoo HI, Kang PJ, Kim YS, Nam KW (2008) Physiological differences in the growth of *Sargassum horneri* between the germling and adult stages. J Appl Phycol 20:729–735

Cordes JF, Allen LG (1997) Estimates of age, growth, and settlement from otoliths of young-of-the-year kelp bass (*Paralabrax clathratus*). Bull South Calif Acad Sci 96:43–60

Courchamp F, Chapuis J, Pascal M (2003) Mammal invaders on islands: impact, control and control impact. Biol Rev Camb Philos Soc 78:347–383

Crooks JA, Khim HS (1999) Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia.* J Exp Mar Biol Ecol 240:53–75

Dayton PK (1985) Ecology of kelp communities. Annu Rev Ecol Syst 16:215–245

Dayton PK, Currie V, Gerrodette T, Keller BD, Rosenthaland R, Ven Tresca D (1984) Patch dynamics and stability of some California kelp communities. Ecol Monogr 54:253–289

Dayton PK, Tegner MJ, Parnell PE, Edwards PB (1992) Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecol Monogr 62:421–445

Dayton PK, Tegner MJ, Edwards PB, Riser KL (1999) Temporal and spatial scales of kelp demography: the role of oceanographic climate. Ecol Monogr 69:219–250

Dixson DL, Abrego D, Hay ME (2014) Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery. Science 345:892–897

Findlay AM, Allen LG (2002) Temporal patterns of settlement in the temperate reef fish *Paralabrax clathratus.* Mar Ecol Prog Ser 238:237–248

Forrester GE, Steele MA (2004) Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. Ecology 85:1332–1342

Foster MS (1975) Algal succession in a *Macrocystis pyrifera* forest. Mar Biol 32:313–329

Francour P, Harmelin-Vivien M, Harmelin JG, Duclerc J (1995) Impact of *Caulerpa taxifolia* colonization on the littoral ichthyofauna of north-western Mediterranean Sea: preliminary results. Hydrobiologia 300:345–353

Gaines S, Brown S, Roughgarden J (1985) Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula.* Oecologia 67:267–272

Graham MH, Harrold C, Lisin S, Light K, Watanabe JM, Foster MS (1997) Population dynamics of giant kelp *Macrocystis pyrifera* along a wave exposure gradient. Mar Ecol Prog Ser 148:269–279

Gribben PE, Wright JT, O'Connor WA, Doblin MA, Eyre B, Steinberg PD (2009) Reduced performance of native infauna following recruitment to a habitat-forming invasive marine alga. Oecologia 158:733–745

Hallacher LE, Roberts DA (1985) Differential utilization of space and food by the inshore rockfishes (Scorpaenidae: *Sebastes*) of Carmel Bay, California. Environ Biol Fishes 12:91–110

Haran J, Roques A, Bernard A, Robinet C, Roux G (2015) Altitudinal barrier to the spread of an invasive species: Could the Pyrenean chain slow the natural spread of the pinewood nematode? PLOS ONE 10:e0134126

Hay ME, Duffy JE, Fenical W, Gustafson K (1988) Chemical defense in the seaweed *Dictyopteris delicatula*: differential effects against reef fishes and amphipods. Mar Ecol Prog Ser 48:185–192

Hedge P, Kriwoken LK (2000) Evidence for effects of *Spartina anglica* invasion on benthic macrofauna in Little Swanport estuary, Tasmania. Austral Ecol 25:150–159

Heiman KW, Vidargas N, Micheli F (2008) Non-native habitat as home for non-native species: comparison of communities associated with invasive tubeworm and native oyster reefs. Aquat Biol 2:47−56

Hobson ES, Chess JR (1976) Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish Bull 74:567−598

Holbrook SJ, Schmitt RJ (1984) Experimental analyses of patch selection by foraging black surfperch (*Embiotoca jacksoni* Agazzi). J Exp Mar Biol Ecol 79:39−64

Holbrook SJ, Schmitt RJ (1988) The combined effects of predation risk and food reward on patch selection. Ecology 69:125−134

Holbrook SJ, Carr MH, Schmitt RJ, Coyer JA (1990) Effect of giant kelp on local abundance of reef fishes: the importance of ontogenetic resource requirements. Bull Mar Sci 47:104−114

Horning O (2009) Review of selected California fisheries for 2008: coastal pelagic finfish, market squid, ocean salmon, groundfish, California spiny lobster, spot prawn, white seabass, kelp bass, thresher shark, skates and rays, Kellet's whelk and sea cucumber. Calif Coop Ocean Fish Invest Rep 50:30−32

Kaplanis NJ, Harris JL, Smith JE (2016) Distribution patterns of the non-native seaweeds *Sargassum horneri* (Turner) C. Agardh and *Undaria pinnatifida* (Harvey) Suringar on the San Diego and Pacific coast of North America. Aquat Invasions 11:111−124

Kingsford MJ (1995) Drift algae: a contribution to near-shore habitat complexity in the pelagic environment and an attractant for fish. Mar Ecol Prog Ser 116:297−301

Levin PS, Hay ME (1996) Responses of temperate reef fishes to alterations in algal structure and species composition. Mar Ecol Prog Ser 134:37−47

Lodge DM (1993) Biological invasions: lessons for ecology. Trends Ecol Evol 8:133−137

Longepierre SA, Robert A, Levi F, Francour P (2005) How an invasive alga species (*Caulerpa taxifolia*) induces changes in foraging strategies of the benthivorous fish *Mullus surmuletus* in coastal Mediterranean ecosystems. Biodivers Conserv 14:365−376

Love MS, Carr MH, Haldorson LJ (1991) The ecology of substrate-associated juveniles of the genus *Sebastes.* Environ Biol Fishes 30:225−243

Lovell SJ, Stone SF (2005) The economic impacts of aquatic invasive species: a review of the literature. NCEE Working Paper 05-02. U.S. Environmental Protection Agency, Washington, DC

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689−710

Marks LM, Salinas-Ruiz P, Reed DC, Holbrook SJ and others (2015) Range expansion of a non-native, invasive macroalga *Sargassum horneri* (Turner) C. Agardh, 1820 in the eastern Pacific. BioInvasions Rec 4:243−248

Miller KA, Engle JM (2009) The natural history of *Undaria pinnatifida* and *Sargassum filicinum* at the California Channel Islands: non-native seaweeds with different invasion styles. In: Damiani CC, Garcelon DK (eds) Proc 7th CA Island Symp. Institute for Wildlife Studies, Arcata, CA, p 281−289

Miller KA, Engle JM, Uwai S, Kawai H (2007) First report of the Asian seaweed *Sargassum filicinum* Harvey (Fucales) in California, USA. Biol Invasions 9:609−613

Morse ANC, Morse DE (1984) Recruitment and metamorphosis of *Haliotis* larvae induced by molecules uniquely available at the surfaces of crustose red algae. J Exp Mar Biol Ecol 75:191−215

Munday PL (2002) Does habitat availability determine geographical-scale abundances of coral-dwelling fishes? Coral Reefs 21:105−116

Nelson PA (2001) Behavioral ecology of young-of-the-year kelp rockfish *Sebastes atrovirens* Jordan and Gilbert (Pisces: Scorpaenidae). J Exp Mar Biol Ecol 256:33−50

Parendes LA, Jones JA (2000) Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andres experimental forest, Oregon. Conserv Biol 14:64−75

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol Econ 52: 273−288

Reed DC, Rassweiler A, Carr MH, Cavanaugh KC, Malone DP, Siegel DA (2011) Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. Ecology 92:2108−2116

Reusch TBH, Williams SL (1998) Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia.* Oecologia 113:428−441

Santini-Bellan D, Arnaud PM, Bellan G, Verlaque M (1996) The influence of the introduced tropical alga *Caulerpa taxifolia*, on the biodiversity of the Mediterranean marine biota. J Mar Biol Assoc UK 76:235−237

Scharf FS, Manderson JP, Fabrizio MC (2006) The effects of seafloor habitat complexity on survival of juvenile fishes: species-specific interactions with structural refuge. J Exp Mar Biol Ecol 335:167−176

Schmitt RJ, Holbrook SJ (1985) Patch selection by juvenile black surfperch (Embiotocidae) under variable risk: interactive influence of food quality and structural complexity. J Exp Mar Biol Ecol 85:269−285

Smith JR (2016) The putative impacts of the non-native seaweed *Sargassum muticum* on the native communities in tidepools of southern California and investigation into the feasibility of local eradication. Mar Ecol 37:645−667

Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological research, 3rd edn. WH Freeman, New York, NY

Southwick Associates (2009) The potential economic and conservation impacts of proposed marine recreational fishing closures in southern California. Southwick Associates, Fernandina Beach, FL. http://www.southwickassociates.com/wp-content/uploads/2011/10/CA_2009.pdf

Stæhr PA, Pedersen MF, Thomsen MS, Wernberg T, Krause-Jensen D (2000) Invasion of *Sargassum muticum* in Limfjorden (Denmark) and its possible impact on the indigenous macroalgal community. Mar Ecol Prog Ser 207:79−88

Steele L, Valentine JF (2015) Seagrass deterrence to meso-grazer herbivory: evidence from mesocosm experiments and feeding preference trials. Mar Ecol Prog Ser 524: 83−94

Steele MA (1996) Effects of predators on reef fishes: separating cage artifacts from effects of predation. J Exp Mar Biol Ecol 198:249−267

Steele MA, Malone JC, Findlay AM, Carr MH, Forrester GE (2002) A simple method for estimating larval supply in reef fishes and a preliminary test of population limitation by larval delivery in the kelp bass *Paralabrax clathratus.* Mar Ecol Prog Ser 235:195−203

Sweatman H (1988) Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. J Exp Mar Biol Ecol 124:163–174

Tegner MJ, Dayton PK (1987) El Niño effects on Southern California kelp forest communities. Adv Ecol Res 17: 243–279

Thomsen MS (2010) Experimental evidence for positive effects of invasive seaweed on native invertebrates via habitat-formation in a seagrass bed. Aquat Invasions 5: 341–346

Van Alstyne KL, Paul VJ (1990) The biogeography of polyphenolic compounds in marine macroalgae: temperate brown algal defenses deter feeding by tropical herbivorous fishes. Oecologia 84:158–163

Wernberg T, Thomsen MS, Tuya F, Kendrick GA, Staehr PA, Toohey BD (2010) Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. Ecol Lett 13:685–694

Wheeler PA, North WJ (1981) Nitrogen supply, tissue composition and frond growth rates for *Macrocystis pyrifera*

off the coast of Southern California. Mar Biol 64:59–69

White JW, Caselle JE (2008) Scale-dependent changes in the importance of larval supply and habitat to abundance of reef fish. Ecology 89:1323–1333

Wilson SK, Depczynski M, Fisher R, Homes TH, O'Leary RA, Tinkler P (2010) Habitat associations of juvenile fish at Ningaloo Reef, Western Australia: the importance of coral and algae. PLOS ONE 5:e15185

York PH, Booth DJ, Glasby TM, Pease BC (2006) Fish assemblages in habitats dominated by *Caulerpa taxifolia* and native seagrasses in south-eastern Australia. Mar Ecol Prog Ser 312:223–234

Yoshida G, Arima S, Terawaki T (1998) Growth and maturation of the 'autumn-fruiting type' of *Sargassum horneri* (Fucales, Phaeophyta) and comparisons with the 'spring-fruiting type'. Phycol Res 46:183–189

Zimmerman RC, Kremer JN (1986) *In situ* growth and chemical composition of the giant kelp, *Macrocystis pyrifera*: response to temporal changes in ambient nutrient availability. Mar Ecol Prog Ser 27:277–285