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Limited effects of *Sargassum horneri*, an invasive alga, on temperate reef fish assemblages

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ABSTRACT: Biological invasions can dramatically affect the ecology of invaded regions, and globally have resulted in economic damages that total billions of dollars annually. In recent years, an invasive alga, *Sargassum horneri*, has become established and spread along the coast of southern California (USA). Using field observations and a field experiment, we explored how this nonnative alga influences the structure of fish assemblages on temperate reefs in southern California where *S. horneri* has become prolific. Fish and algal assemblages were quantified along transects on rocky reefs at depths of 3 and 6 m at 6–8 study sites spanning 5 km on 4 occasions over 1.5 yr. Spatiotemporal variation in the fish assemblage was not strongly correlated with the abundance of invasive *S. horneri* over this period, although it became less variable as native giant kelp *Macrocystis pyrifera* disappeared from the study sites due to a warm-water event, during which the invasive *S. horneri* became more dominant. An experiment removing a total of 4.25 t of *S. horneri* from 6 × 6 m plots (n = 14) revealed that the invasive alga did not affect fish abundance, species richness, species diversity (*H′*), or multivariate assemblage structure over a 5 mo period. Overall, we found little evidence of negative effects of *S. horneri* on fishes even though it drastically changed the underwater landscape. Nevertheless, we advise cautionary management actions to limit the movement of this invasive alga because its effects on other community members, such as other algal species, may be detrimental, and longer-term effects on fishes might develop.

KEY WORDS: *Sargassum horneri* · Fish assemblage · *Macrocystis pyrifera* · Santa Catalina Island · Invasive removal experiment · Kelp forest · Rocky reef · Field experiment

1. INTRODUCTION

Biological invasions may dramatically affect the ecology of invaded regions (Mack et al. 2000), and globally have resulted in economic damages and losses that total billions of dollars annually (Lovell & Stone 2005, Pimentel et al. 2005). Dramatic changes in populations of native species may directly result from predation, grazing, or competition by invasive species (Brown et al. 2002, Albins & Hixon 2008, Giakoumi 2014), and there are likely changes caused by indirect interactions that are more challenging to measure (Jordan et al. 2008, terHorst & Lau 2015). Humans depend on the stability of ecosystems to provide services, but when evolved relationships between native organisms are threatened by the introduction of exotic species, valuable economic entities like fisheries and outdoor recreation may be compromised (Ruiz et al. 1997, Eiswerth et al. 2005).

An invasive alga, *Sargassum horneri*, recently became established and spread along the coast and islands of southern California, USA (Miller et al. 2007, Marks et al. 2015). Native to northeastern Asia, this species was discovered in Long Beach Harbor in 2003 after presumably being transported in ballast water of large freighters. By 2006, it was found at Santa Catalina Island, California, and within a year had proliferated along the entire leeward coast of the

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island, forming dense stands in numerous areas (Miller & Engle 2009). Since that time, it has also been documented at the majority of the California Channel Islands, and along coastal areas of the Southern California Bight and Baja California (Aguilar-Rosas et al. 2007, Miller & Engle 2009, Marks et al. 2015). *S. horneri* is extremely fast growing (up to 4.46% d^{-1} in adult blade weight), and densities can exceed 1000 ind. m^{-2} for recruits and 100 ind. m^{-2} for adults (Choi et al. 2008, Marks et al. 2015). Thus, this introduced alga may compete against native algal species (Choi et al. 2008, Marks et al. 2015, Caselle et al. 2018, Marks 2018), although experimental evidence indicates it is usually not a strong competitor (Marks 2018).

As an annual species that changes dramatically in size over the course of a year (Yoshida et al. 1998, Marks 2018), the effects of *S. horneri* on fishes likely differ from those documented for perennial algal species, like giant kelp *Macrocystis pyrifera* (hereafter *Macrocystis*). Embryos of *S. horneri* are released during the late spring, which develop into small (<5 cm tall), fern-like, recruit thalli during the summer. As the water temperature begins to cool during the fall, recruits grow into much taller immature thalli (50–100 cm), which are supported by numerous gas bladders on vegetative blades. In its native range, *S. horneri* undergoes the greatest growth from October to November (Umezaki 1984), and a similar pattern of growth is evident along the coast of California (Marks 2018). Vertical growth slows as thalli reach maturity at 75–125 cm, signaled by the formation of elongated reproductive receptacles on blades. After the release of fertilized conceptacles attached to reproductive receptacles, the alga begins to decompose through the final senescent stage during the late winter and spring months.

In addition to changing in size and structure seasonally, *S. horneri* is much shorter than *Macrocystis*, the historically dominant macroalga in subtidal rocky habitats throughout southern California and northern Baja California (Dayton 1985). *Macrocystis* provides physical structure that is critical to a variety of organisms, including adult and juvenile fishes (Hobson & Chess 1976, Holbrook et al. 1990, Love et al. 1991), but it remains to be determined whether *S. horneri* provides similar ecological services. Because *S. horneri* does not extend as high into the water column as *Macrocystis* or form surface canopies, it is expected to affect fishes differently (Srednick & Steele 2019), as has been demonstrated for kelp bass *Paralabrax clathratus* (Ginther & Steele 2018).

The goal of our study was to determine how the fish assemblage is affected by the invasive *S. horneri*. First, we observationally quantified the relationship between the fish assemblage and the algal assemblage on reefs over a 1.5 yr period. During this period, the relative abundance of different life stages of *S. horneri* changed considerably (i.e. it was structurally different), allowing us to statistically evaluate the potential effect of this invasive alga on fishes. We then experimentally tested the effects of *S. horneri* on the fish assemblage by physically removing *S. horneri* from large plots on natural reefs and comparing these to unmanipulated plots on which *S. horneri* was the dominant space holder.

2. MATERIALS AND METHODS

2.1. Study area

We conducted our study along the leeward side of the western end of Santa Catalina Island, California, from Arrow Point (33° 28′ N, 118° 32′ W) to Lion Head (33° 27′ N, 118° 30′ W) (Fig. 1). These rocky reefs are dominated by large macroalgal beds, and are separated from each other by extensive areas of sandy bottom. The tides at Catalina are typically mixed semidiurnal and the tidal range is ~2 m at its maximum, which included the periods when we sampled reefs (Center for Operational Oceanographic Products and Services 2019). Historically, canopy-forming *Macrocystis* has been the dominant macroalga in this area, but during years when *Macrocystis* has been sparse, smaller, native understory macroalgae, like *Sargassum palmeri*, have blanketed reefs. In recent years, *S. horneri* has been ubiquitous in varying life stages throughout the year, often being the dominant space holder.

2.2. Observational study

We assessed the relationship between fish assemblages and habitat composition on several reefs during the summer (June and July) and fall (October and November) of 2014, summer (June) of 2015, and winter (January) of 2016. This period encompassed normal seasonal variation, plus the effects of an extreme warm-water period that started in late summer of 2014 and persisted through early 2016. Average sea surface temperatures during the four sampling periods were 19.0, 20.0, 17.3, and 15.2°C, respectively (National Data Buoy Center 2019). Our sampling

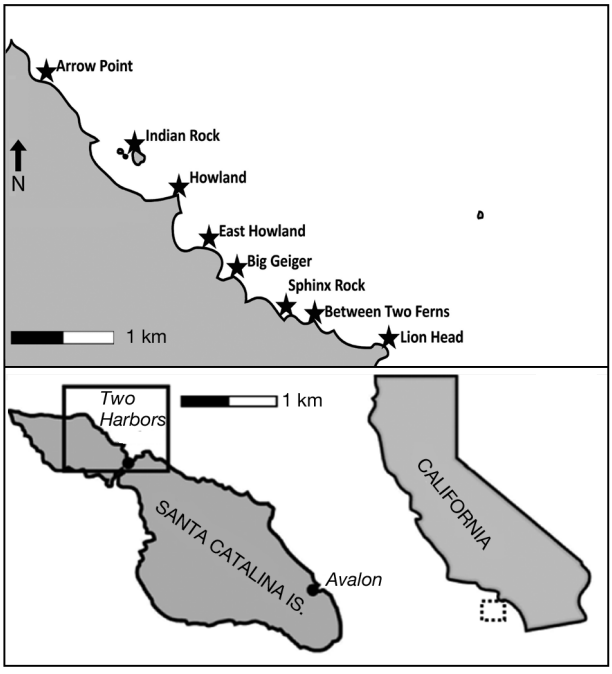

Fig. 1. Eight sites along the western leeward side of Santa Catalina Island, California, USA, were studied during summer and fall 2014, summer 2015, and winter 2016. Howland and Lion Head were used for the *Sargassum horneri* removal experiment starting in 2015, and so were not included in observational surveys during summer 2015 and winter 2016. The dashed and solid boxes indicate the location of Santa Catalina Island in reference to California and the location of the study sites along the coast of Santa Catalina Island, respectively

schedule encompassed distinct annual changes in size, structure, and biomass of *S. horneri* as it progressed through recruit, immature, mature, and senescent stages. It also encompassed a dramatic change from abundant *Macrocystis* in summer 2014 to historically low densities of this important native alga during the prolonged warm-water event of 2015–2016 in southern California (Zaba & Rudnick 2016). We sampled eight sites (Arrow Point, Indian Rock, Howland, East Howland, Big Geiger, Sphinx Rock, Between Two Ferns, and Lion Head; Fig. 1) during each sampling period, except that only six sites were sampled during summer 2015 and winter 2016 because two of the sites (Howland and Lion Head) were used as experimental sites (described in Section 2.4) starting in February 2015.

Using SCUBA, we quantified fish and algal abundance, as well as substratum composition, along depth-stratified (3 and 6 m), 30 m long transects at each site. Within a depth stratum, each transect was separated from the next nearest transect by 20 m. The horizontal distance between depth strata was typically 30–40 m. Both depth strata had virtually identical temperatures because they were above the thermocline at ~12–20 m depth. Transects were placed at 3 and 6 m depths because this depth difference incorporated a natural contrast in the abundance of *S. horneri*, which is more abundant at depths >5 m (Marks 2018). All fish species observed during our study are found at both depth strata. During the winter 2016, only the 6 m depth was surveyed due to logistical constraints. The number of transects placed at each site varied to ensure adequate coverage of each reef, with the smallest and largest sites having 3 and 7 transects per depth stratum, respectively.

During surveys, a diver first counted conspicuous, mobile fishes within a 4 m wide × 2 m high window while laying out each 30 m long transect (240 m^3), which has been shown to maximize fish counts and minimize diver disturbance (Dickens et al. 2011). The same diver then returned along the transect a second time to count less mobile, benthic fishes, which were less likely to be disturbed by other divers. Hereafter we refer to those two groups of fishes as 'conspicuous' and 'cryptic,' respectively, following Stephens & Larson (2006). The same person (S.C.G.) did all fish counts to avoid inter-observer bias (Thompson & Mapstone 2002). Fish counts were done between 08:00 and 14:00 h to limit variation in abundance caused by time of day (Galzin 1987). At a site, transects in different depth strata were typically surveyed on consecutive days, with transects at 3 m done the day after 6 m transects. Surveys at a site were not repeated within a sampling period because day-to-day variation appeared to be much smaller than seasonal variation, as has been noted for reef fishes elsewhere (Thompson & Mapstone 2002, Edgar et al. 2004).

Macrophytes (algae and surfgrass) were quantified in a few ways, depending on their size. Densities of *S. horneri* and other *Sargassum* species (*S. muticum* and *S. palmeri*) were estimated by counting individuals in 10 stratified-random 0.25 m^2 quadrats along each transect. One quadrat was placed in a random position within each 3 m long segment of the transect. Individuals of each species were classified as recruits (<5 cm), immature (>5 cm and without reproductive conceptacles), mature (>5 cm and with reproductive conceptacles), or senescent (>5 cm and reproductive conceptacles spent). Other understory macrophytes were sampled as percent dominant cover within the same quadrats, which were evenly divided into 25 squares, demarcated by strings. The taxon that occupied the majority of each square was recorded. From this, percent cover of each dominant

taxon was calculated. If no algae were present, then the square was classified as bare. Understory algae other than *Sargassum* spp. were classified to the level of genus. Due to time constraints during the winter of 2016, *Sargassum* spp. were quantified as percent cover rather than densities. Densities of adult *Macrocystis* (>1 m) were estimated by counting the number of individuals and stipes of each individual within a 2 m wide swath along each 30 m long transect, a standard method of measurement (see Caselle et al. 2018, Miller et al. 2018). Southern sea palm *Eisenia arborea* was also quantified within the 2 m swath, by counting blades on individuals with a thallus >20 cm tall.

Lastly, we estimated the percent cover of physical substrata using 16 point contacts within each randomly placed quadrat. At each of 16 uniformly spaced points within the quadrat, we recorded the presence of bedrock (>100 cm in longest dimension), large boulders (75–99.9 cm), medium boulders (50–74.9 cm), small boulders (25–49.9 cm), cobble (<25 cm), sand, or shell debris.

2.3. Statistical analyses of observational study

We used permutational multivariate analysis of variance (PERMANOVA) to test for differences in the multivariate fish assemblage among the factors sampling period, site, and depth. All sampling periods (i.e. summer 2014, fall 2014, summer 2015, and winter 2016), sites, and depths where surveys were completed were included in these analyses, and transect was treated as the fundamental unit of replication (n = 213 transects). All factors were treated as fixed, including site, because sites were chosen to be similar in reef structure, rather than chosen randomly or haphazardly. The multivariate fish assemblage was summarized by a Bray-Curtis dissimilarity matrix constructed from the density of each species. Non-metric multidimensional scaling (nMDS) plots were made to help interpret the results of the PERMANOVA. We also used univariate ANOVA (with factors sampling periods, sites, and depths), to test for differences in three univariate measures of the fish assemblage: total fish density, fish species richness, and fish species diversity (Shannon-Wiener index, *H'*). All multivariate analyses were conducted in PRIMER v6 with the PERMANOVA+ add-on package, and all univariate analyses were conducted in SYSTAT v13.

To evaluate the relationship between the multivariate fish assemblage and the abundance of *S. horneri*, *Macrocystis*, and other algae, we used distance based linear modeling (DistLM), which is the multivariate analog of linear regression. It was used to reveal which combination of habitat predictor variables best explained variation in the multivariate fish assemblage (as summarized by a Bray-Curtis dissimilarity matrix of the density of each fish species). Predictor variables included the densities of all stages of *S. horneri*, *S. muticum*, and *S. palmeri*, the densities of adult and juvenile *Macrocystis* stipes, the densities of the macroalgae *E. arborea* and *Egregia menziesii*, as well as the abundance of algal functional groups (derived from % cover) summarized by principal component analysis (PCA). Physical substratum (% cover) was also included in the model, summarized by PCA (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m643p115_supp.pdf). For the DistLM analysis, we used the best subsets procedure, Akaike's information criterion corrected for small sample sizes (AICc), and r^2 to identify which habitat variables were the best predictors of the multivariate fish assemblage structure. We also used multiple linear regression (MLR) analysis to determine which habitat variables were the best predictors of the univariate fish assemblage (total fish density, fish species richness, and diversity). To explore the potential influence of the full range of variation in the abundance of different stages of *S. horneri* on fishes, all sites and both depths surveyed during summer 2014, fall 2014, and summer 2015 were analyzed together (n = 180 transects). Winter 2016 was not included in this analysis because different methods were used to quantify algae (% cover rather than density), due to logistical constraints. Including data from different time periods confounds differences in algal assemblage structure with seasonal changes in other variables (e.g. temperature, day length, seasonal recruitment of fishes). To eliminate this confounding, separate DistLM analyses were also performed for each season: summer 2014 (n = 68), fall 2014 (n = 66), summer 2015 (n = 46), and winter 2016 (n = 33).

To determine which fish species contributed to most (90%) of the variation in the Bray-Curtis dissimilarity matrix of the fish assemblage across four time periods (summer and fall 2014, summer 2015, and winter 2016) and depths (3 and 6 m), we used the similarity percentages (SIMPER) function in PRIMER. To test the hypothesis that densities of fishes indicated by SIMPER analysis to be important in generating differences among times and depths were affected by *S. horneri*, we completed the equivalent univariate analysis, MLR, using significant predictor variables identified by the DistLM analysis described

above. Analyses of Winter 2016 were supplemented with additional habitat types, including biological and physical PCs, which were more representative of the overall reef landscape. As for the preceding analyses, we completed separate analyses for the first three sampling periods (summer 2014, fall 2014, and summer 2015) and for the final sampling period (winter 2016) because of differences in sampling methodology (i.e. % cover of algae in winter 2016).

To help us understand the possible causes of statistical relationships between the fish assemblage and the algal assemblage revealed by DistLM and multiple regression, we used Pearson's correlation to understand how the four life stages of the invasive *S. horneri* (recruit, immature, mature, and senescent) were correlated with the historically dominant *Macrocystis*. Transects were treated as replicates and pooled across all sites and depths, and across the summer 2014, fall 2014, and summer 2015 sampling periods (n = 180 transects). The winter 2016 sampling period was not included in this analysis because the sampling methods for *S. horneri* differed, and the data were not comparable.

Prior to performing all analyses, fish and algae density data were log (x + 1) transformed, and substrate and algae percent cover data were arcsine square root transformed after graphical analyses of residuals revealed that assumptions of normality and equality of variance were violated. To place variables measured as densities and percent cover on a common scale, we divided transformed values by the standard deviation for each variable (Sokal & Rohlf 1995).

2.4. *S. horneri* removal experiment

We conducted an experiment removing *S. horneri* from replicate 6 × 6 m plots at two study sites that were similar in topography, biology, and exposure to oceanographic conditions: Howland and Lion Head reefs (Fig. 1). At each site, we marked 14 plots and designated half of them as 'removal' (complete removal of all *S. horneri*) and half as 'control' (no removal). Plots were placed haphazardly at shallow depths from 3.5 to 7.5 m where the cover of *S. horneri* was fairly uniform. *Macrocystis* was completely absent throughout the study areas at both sites. We removed all *S. horneri* from plots designated as 'removal' during winter (February 2015), when *S. horneri* individuals were large and there were few small recruits. Most *S. horneri* individuals were still immature, which reduced the chances of removal activities spreading reproductive propagules. Treatment assignments were alternated in space such that each plot was not immediately adjacent to a plot assigned the same treatment. Plots were separated by at least 8 m to limit quick movements of fishes among them. To reduce potential edge-effects, *S. horneri* was cleared beyond the 6 × 6 m boundaries of each plot: a circular area with a radius extending 8 m away from the center of each plot was cleared. In total, approximately 4.25 t of *S. horneri* were removed and transported to shore, air-dried, and disposed of properly.

Fishes were surveyed before and after removal of *S. horneri*. Mobile, conspicuous fishes were surveyed twice prior to removing *S. horneri* to obtain a baseline estimate of the fish assemblage. Benthic oriented, cryptic fishes were only surveyed once during this pre-manipulation period because they have smaller home ranges that are more closely associated with the seafloor (Allen et al. 1992), making their densities less likely to fluctuate over short time periods than those of more mobile species, which were frequently observed swimming in and out of experimental plots (S.C.G. pers. obs.). After removing *S. horneri*, we conducted monthly fish surveys in the plots from 27 February to 23 July 2015. We first counted and estimated the size (to the nearest cm) of mobile, conspicuous fishes by systematically swimming along the boundaries of each plot. Next, we counted benthic fishes in 1 m^2 quadrats (n = 8) placed in a stratified-random manner in each plot.

2.5. Statistical analysis: removal experiment

We used repeated-measures (RM) PERMANOVA to test whether the multivariate fish assemblage was affected by the removal of *S. horneri*, and whether the assemblage changed over time. The multivariate fish assemblage (density of each species found on the plots) was summarized with a Bray-Curtis dissimilarity matrix. We included the following factors and their interactions in the model: treatment (control vs. removal), time (sampling times 1–7), site (Lion Head and Howland), and plot (nested within site × treatment). Because the first sampling period (time 1) was prior to *S. horneri* removal, if the removal affected the fish assemblage, a time × treatment interaction would be expected. nMDS plots were generated to help interpret the results of the PERMANOVA. We also tested whether three univariate metrics of the fish assemblage, i.e. total fish density, species richness, and species diversity (H'), responded to removal of *S. horneri* using univariate RM ANOVA with the same factors used in the multivariate RM PERM-

ANOVA model. In all of the RM analyses, the average of the two counts of mobile fishes done prior to removal of *S. horneri* (time 1) was used; all other time periods had only a single count. Prior to performing analyses, fish density data were square root (x + 0.5) transformed after graphical analyses of residuals revealed that assumptions of normality and equality of variance were violated. Plots were used as the fundamental unit of replication (n = 7 treatment^{-1} site^{-1}).

3. RESULTS

3.1. Spatial and temporal variation in fish assemblage

The multivariate fish assemblage differed among time periods, but did so differently at the two depths (PERMANOVA: period × depth: pseudo-$F_{2,161}$ = 27.6, p = 0.001). In summer 2014 when *Macrocystis* was most abundant, the fish assemblage was most variable (Fig. 2a), whereas during fall 2014, summer 2015, and winter 2016, the assemblage was less variable within each period, and more similar among the time periods. Assemblage variability was greater at 3 m depth than 6 m (Fig. 2b). Due to time constraints during the winter 2016 sampling period, only the 6 m depth was sampled; the fish assemblage at this depth was similar between fall 2014, summer 2015, and winter 2016, but not summer 2014 (Fig. 2c). At the 3 m depth, summer 2014 differed from the other two time periods sampled at this depth, summer 2015 and fall 2015, which were similar to one another (Fig. 2d).

Total fish density was lower in summer 2014 than during fall 2014, summer 2015, and winter 2016, but these differences were inconsistent among sites (period × site; $F_{19,161}$ = 2.05; p = 0.01). Total fish density tended to be higher at 6 m depth than at 3 m, but not during summer 2014, when *Macrocystis* was most abundant (period × depth; $F_{2,161}$ = 63.5; p < 0.001; Fig. 3a). During summer (2014), fish densities were similar at 3 and 6 m depths.

Fish species richness tended to decline from summer 2014 through winter 2016 in a manner that was consistent among depths (period × depth: $F_{1,161}$ = 0.12, p = 0.73; Fig. 3b). Fish richness was notably different between the two summers (2014 and 2015); fish richness was higher during summer 2014 (when fish density was lowest) compared to summer 2015 (when fish density was second highest). Species richness changed through time, though not to the same extent at all sites (period × site; $F_{19,161}$ = 2.22; p = 0.004), but all sites showed a qualitatively similar pattern (data not shown).

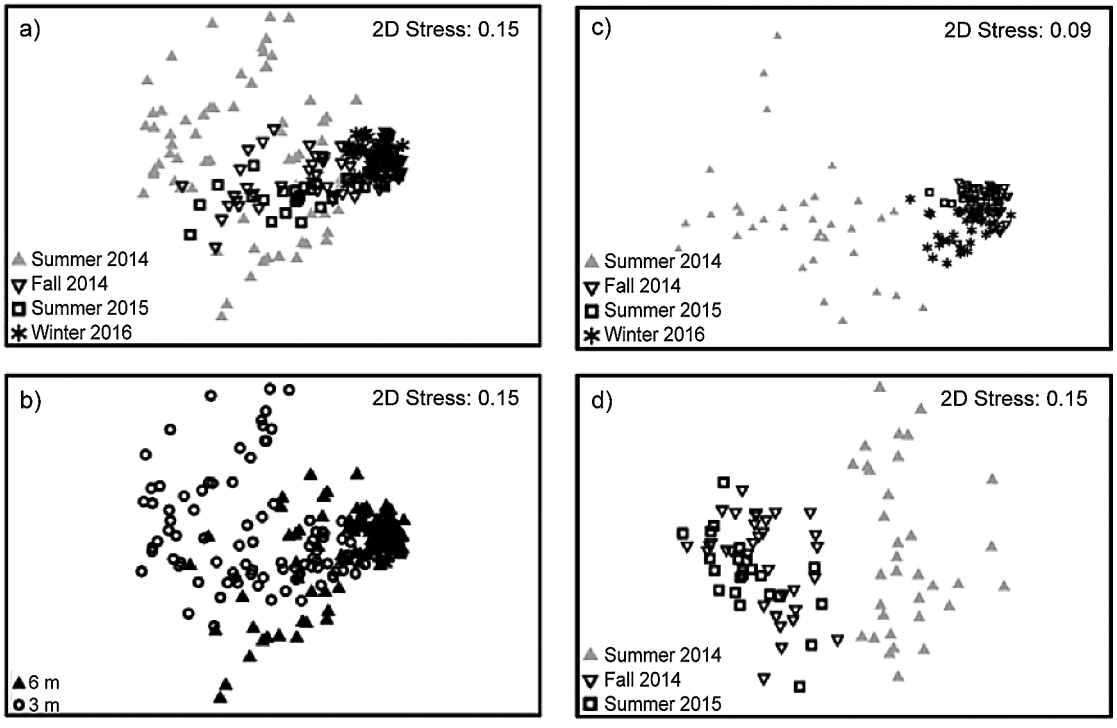

Fig. 2. Non-metric multidimensional scaling (nMDS) plots of the fish assemblage showing different (a) time periods, (b) depths, (c) only 6 m depth, and (d) only 3 m depth for the first 3 time periods surveyed (6 m depth was not surveyed during winter 2016)

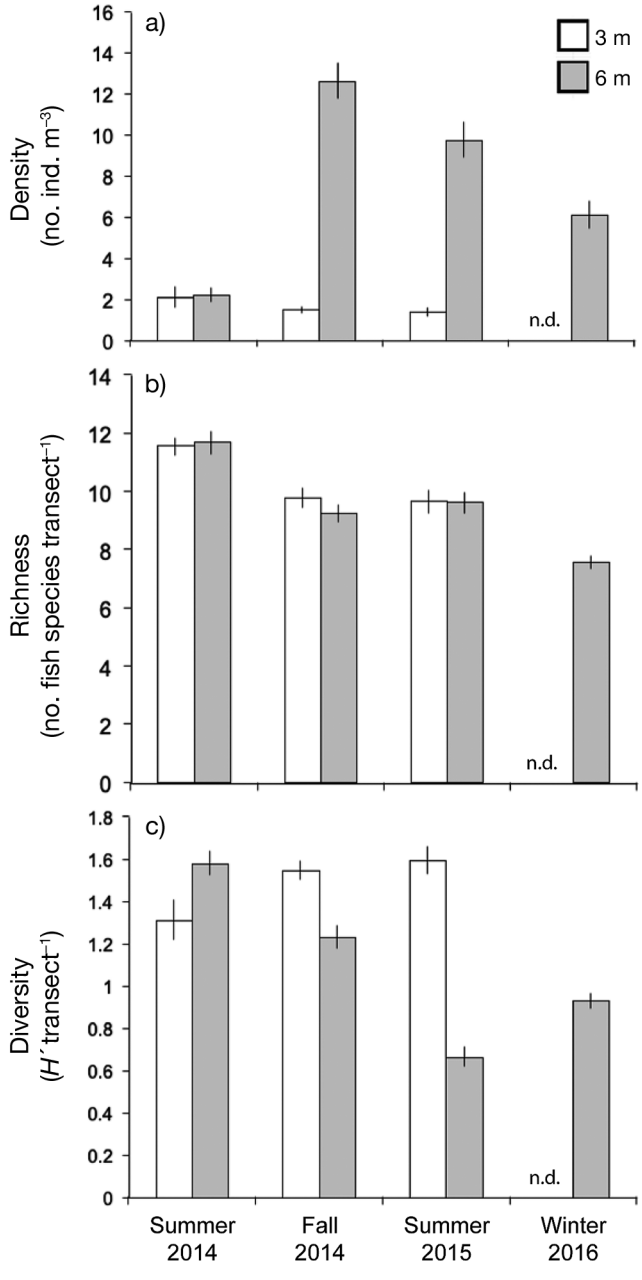

Fig. 3. Fish (a) density (mean ± SE), (b) richness (mean ± SE), and (c) diversity (mean ± SE, *H′*: Shannon index) during different periods at 2 depths. n = 8 sites in summer and fall 2014, and n = 6 for summer 2015 and winter 2016. No data (nd) were collected at Lion Head and Howland reefs during summer 2015 and winter 2016, or at 3 m depth during winter 2016

Fish diversity (*H′*) was fairly consistent over time at 3 m depth, slightly increasing, but it declined over time at 6 m depth (period × depth; $F_{2,161}$ = 43.21; p < 0.001; Fig. 3c). *H′* was highest and fairly similar at both 3 and 6 m depths during summer 2014 and fall 2014.

3.2. Predictors of fish assemblage structure

To determine whether the significant variation observed in the fish assemblage across time periods or study sites could be predicted by algal abundance or physical substrate, we reduced the number of habitat variables using PCA. The variation in habitats across the four different sampling periods is summarized in Table 1.

Pooled across summer 2014, fall 2014, and summer 2015, DistLM analysis indicated that about half of the variation in the multivariate fish assemblage was explained by several similarly-supported habitat predictor models (Table 2). Notably, models that included the invasive *Sargassum horneri* were no better at predicting the structure of the fish assemblage than models from which it was absent. When sampling periods (seasons) were analyzed separately, relationships between the fish assemblage and the algal assemblage were consistent with trends that emerged from pooled analyses (Table S2), suggesting that predictors of the fish assemblage were not confounded with temporal differences in other factors.

MLR analysis was used to determine which habitat types predicted variation in three univariate measures of the fish assemblage: total density, species richness, and species diversity. Six habitat variables significantly predicted total fish density during summer and fall 2014, and summer 2015 (adjusted r^2 = 0.62, p < 0.001). During the same time period, four habitat variables also significantly predicted fish species richness, although they explained less variation (adjusted r^2 = 0.25, p < 0.001). Fish species diversity (*H′*) was predicted by five habitat variables during summer and fall 2014, and summer 2015 (adjusted r^2 = 0.26, p = 0.01). Table 3 gives a complete list of the significant habitat predictor variables of the MLR analyses. During the winter 2016, habitat variables did not significantly predict total fish density (r^2 = 0.37, p = 0.07) or fish species richness (r^2 < 0.01 p = 0.93). Two habitat variables significantly predicted diversity during winter 2016 (adjusted r^2 = 0.56, p = 0.01) (Table 3).

3.3. Species-specific responses of fishes to habitat predictor variables

SIMPER analysis revealed that of the 38 fish species seen on 213 transects (Table 4), seven accounted for 90% the overall fish assemblage dissimilarity across time periods and depths (Table 5). The seven

Table 1. Principal components analyses (PCA) on (a) algal functional groups and (b) physical substratum across reefs during the first 3 (summer 2014, fall 2014, and summer 2015) and last (winter 2016) survey periods. Algal functional groups were AC: articulated coralline; EC: encrusting coralline; fol. brown: foliose brown algae; fol. red: foliose red algae; fili. red: filiform red algae; fol. green: *Codium* spp.; *Phyllospadix* spp.; turf; and bare substrate. The amount of variation explained by each of the first 3 principal components and coefficients is listed

(a) Algal functional groups

Time period	PC	% variation	AC	EC	Fol. brown	Fol. red	Fili. red	Fol. green	*Phyllo-spadix*	Turf	Bare
Summer 2014	1	27.2	0.43	−0.32	0.40	0.02	0.38	0.10	0.27	−0.50	−0.28
Fall 2014	2	22.1	0.10	0.50	0.19	−0.52	−0.34	0.17	−0.14	−0.14	−0.50
Summer 2015	3	12.6	−0.23	−0.02	0.29	0.23	0.31	0.20	−0.81	−0.06	−0.09
Winter 2016	1	39.0	0.03	−0.07	0.09	−0.05	0.01	−0.98	0.00	0.01	0.08
	2	23.9	−0.11	0.63	−0.58	−0.10	−0.04	−0.05	0.00	0.10	0.48
	3	15.0	−0.04	−0.17	0.52	0.06	−0.03	0.13	0.00	0.14	0.82

(b) Physical substratum

Time period	PC	% variation	Bedrock	Large boulder	Medium boulder	Small boulder	Cobble	Sand	Shell
Summer 2014	1	35.2	0.62	−0.33	−0.52	−0.45	−0.12	−0.09	0.10
Fall 2014	2	18.9	−0.02	−0.02	−0.13	−0.01	0.34	−0.55	−0.75
Summer 2015	3	16.3	−0.18	−0.17	−0.20	−0.20	0.80	0.48	0.05
Winter 2016	1	33.1	0.25	0.64	−0.46	0.00	−0.43	−0.36	0.00
	2	26.1	0.25	−0.17	0.55	−0.53	−0.53	−0.22	0.00
	3	14.4	−0.36	0.27	0.44	0.58	−0.47	0.23	0.00

Table 2. Habitat predictor models of the multivariate fish assemblage from DistLM analysis of the first 3 sampling periods (summer 2014, fall 2014, and summer 2015) pooled. Predictor variables were (1) algal principal component (PC) 1, (2) algal PC2, (3) algal PC3, (4) algal PC4, (5) physical substrate PC1, (6) physical substrate PC2, (7) physical substrate PC3, and densities of (8) *Macrocystis*, (9) *Eisenia arborea*, (10) *Sargassum horneri* recruits, (11) *S. horneri* immature, (12) *S. muticum* immature, (13) *S. palmeri* immature, (14) *S. palmeri* mature, and (15) *S. palmeri* senescent. AICc: Akaike's information criterion corrected for small sample size

AICc	r^2	Predictor variables
1284.0	0.49	1, 2, 5, 8, 9, 10, 13, 14, 15
1284.3	0.50	1, 2, 5, 6, 8, 9, 10, 13, 14, 15
1284.4	0.50	1, 2, 5, 8, 9, 16, 11, 13, 14, 15
1284.4	0.50	1, 2, 3, 5, 8, 9, 10, 13, 14, 15
1284.7	0.50	1, 2, 3, 5, 6, 8, 9, 10, 13, 14, 15
1284.7	0.50	1, 2, 3, 5, 8, 9, 16, 10, 13, 14, 15
1284.8	0.50	1, 2, 5, 6, 8, 9, 16, 10, 13, 14, 15
1284.9	0.49	1, 2, 5, 6, 8, 10, 13, 14, 15
1285.0	0.50	1, 2, 5, 8, 9, 10, 12, 13, 14, 15
1285.1	0.49	1, 2, 3, 5, 8, 9, 13, 14, 15

species included four conspicuous species (blacksmith, señorita, rock wrasse, and kelp bass) and three cryptic species (bluebanded goby, blackeye goby, and spotted kelpfish). How these seven species, plus the ubiquitous garibaldi found on every transect except one, were related to macroalgae and physical habitat was evaluated with MLR analysis. As predictors, MLR included the nine variables from the DistLM model that best predicted the multivariate fish assemblage during the first three sampling periods, plus an additional *S. horneri* stage that was prevalent. Two life stages of *S. horneri* (recruit and immature) significantly predicted densities of some fish species, but the relationships between density of these fishes and *S. horneri* was generally weak (low standardized regression coefficient, β, or low model r^2) or inconsistent (i.e. positive over one time period but negative over another) (Table 6). Density of *S. horneri* recruits significantly predicted densities of señorita ($\beta = -0.32$ $p = 0.003$), rock wrasse ($\beta = 0.20$, $p = 0.02$), garibaldi ($\beta = 0.21$, $p = 0.04$), bluebanded goby ($\beta = 0.32$, $p < 0.001$), blackeye goby ($\beta = -0.17$, $p = 0.003$), and spotted kelpfish ($\beta = -0.39$, $p < 0$ .001). Density of immature *S. horneri* only predicted bluebanded goby densities ($\beta = 0.13$, $p = 0.01$; Table 6a). Only cover of immature *S. horneri* significantly predicted the density of any fish species during winter 2016, and this was for only a single species, the bluebanded goby, and the direction of the relationship was the opposite to that during the preceding time period ($\beta = -0.69$, $p = 0.02$; Table 6b). In general, abundance of *Macrocystis* and other algae (summarized by algal PC1) were more strongly related (larger β) to density of the eight fish species.

Table 3. Results of multiple linear regressions testing whether habitat variables predicted variation in fish density, species richness, and diversity during summer 2014, fall 2014, and summer 2015, and winter 2016. β is the standardized regression coefficient. **Bold:** significant at $p < 0.05$

	Density		Richness		Diversity	
	β	p	β	p	β	p
Summer 2014, Fall 2014, and Summer 2015						
Physical PC 1	0.04	0.61	0.06	0.59	−0.15	0.14
Physical PC 2	−0.05	0.35	0.14	0.05	0.07	0.31
Physical PC 3	−0.07	0.25	−0.21	**0.01**	0.02	0.75
Physical PC 4	0.02	0.76	−0.02	0.77	0.02	0.83
Physical PC 5	0.07	0.17	−0.03	0.65	−0.12	0.09
Algal PC 1	−0.61	**<0.001**	0.12	0.29	0.27	**0.02**
Algal PC 2	−0.01	0.92	0.10	0.39	0.09	0.42
Algal PC 3	−0.02	0.67	0.03	0.71	0.01	0.89
Algal PC 4	−0.04	0.47	−0.05	0.53	−0.05	0.58
Algal PC 5	−0.06	0.25	0.03	0.71	0.15	**0.04**
Macrocystis	−0.63	**<0.001**	0.38	**<0.01**	0.70	**<0.001**
Egregia menziesii	0.07	0.17	0.05	0.49	−0.08	0.28
Eisenia arborea	0.01	0.90	0.07	0.46	−0.14	0.15
S. horneri recruits	0.16	**0.02**	−0.10	0.27	−0.34	**<0.001**
S. horneri immature	0.11	0.19	−0.16	0.16	0.17	0.15
S. horneri mature	−0.09	0.11	−0.04	0.55	0.00	0.97
S. horneri senescent	0.01	0.83	0.06	0.47	−0.14	0.08
S. muticum recruits	−0.01	0.81	0.06	0.47	0.04	0.57
S. muticum immature	0.03	0.65	−0.20	**0.04**	−0.02	0.80
S. muticum senescent	0.13	**0.01**	−0.09	0.20	0.07	0.32
S. palmeri recruits	0.05	0.34	−0.01	0.89	0.02	0.72
S. palmeri immature	−0.24	**<0.001**	0.06	0.49	0.18	**0.04**
S. palmeri mature	−0.01	0.80	0.01	0.86	−0.01	0.93
S. palmeri senescent	−0.14	**0.03**	−0.22	**0.01**	0.05	0.55
Winter 2016						
Physical PC 1	0.08	0.69	0.04	0.88	0.09	0.60
Physical PC 2	0.22	0.35	−0.11	0.74	0.32	0.11
Physical PC 3	−0.12	0.50	−0.10	0.71	0.06	0.70
Physical PC 4	−0.18	0.33	−0.03	0.92	0.31	0.06
Physical PC 5	0.03	0.87	−0.38	0.16	0.14	0.36
Algal PC 1	−0.29	0.14	0.04	0.88	0.47	**0.01**
Algal PC 2	0.11	0.76	−0.18	0.74	0.36	0.24
Algal PC 3	−0.39	0.38	−0.73	0.26	0.05	0.89
Algal PC 4	−0.35	0.29	−0.37	0.44	0.00	1.0
Algal PC 5	0.00	0.99	−0.11	0.70	0.02	0.93
S. horneri recruits	0.03	0.88	0.12	0.71	0.17	0.35
S. horneri immature	−1.09	0.07	−0.45	0.58	0.46	0.33
S. muticum recruits	0.18	0.41	0.00	0.99	0.45	**0.03**
S. muticum immature	−0.16	0.47	0.09	0.77	0.13	0.49
S. palmeri recruits	−0.02	0.93	0.03	0.91	0.02	0.89
S. palmeri immature	0.22	0.38	−0.19	0.59	0.03	0.88

3.4. Correlations between *S. horneri* and *Macrocystis*

Although there were statistically significant correlations between densities of the four stages of the invasive *S. horneri* and densities of native *Macrocystis*, none of these were very strong (Table 7). During the summer 2015, when *Macrocystis* was absent, *S. horneri* recruits were ~2.5× more abundant compared to during summer 2014 when *Macrocystis* was present, but the senescent stage of *S. horneri* occurred in similar abundances in those two summers (Fig. 4).

3.5. *S. horneri* removal experiment

We observed 31 fish species during our *S. horneri* removal experiment from February–July 2015 (Table S3). We found no evidence that removing *S. horneri* affected the fish assemblage. Prior to removing *S. horneri* (6 February 2015), the multivariate fish assemblage did not differ between the two treatments (pseudo-$F_{1,24}$ = 0.58, p = 0.63), and there was no interaction between treatment and site (pseudo-$F_{1,24}$ = 1.42, p = 0.25). Although the two sites used in this portion of the study were chosen based on similarities in visual landscape (depth, biotic and abiotic substrate, and orientation along coast), the multivariate fish assemblage differed between them (pseudo-$F_{1,24}$ = 10.83, p = 0.001). An nMDS plot showed clear overlap of assemblage structure between plots assigned to the two treatments, but data points grouped by site (Fig. 5a,b).

For the multivariate fish assemblage across the duration of the *S. horneri* removal experiment, there was no treatment × time interaction (Table 8), which would have indicated that *S. horneri* affected the fish assemblage (Fig. 5c). For a complete summary of the results of the multivariate and univariate analyses of our *S. horneri* removal experiment, see Table 8. Total fish density also did not respond to removal of *S. horneri*. There was no significant site × time × treatment interaction or time × treatment interaction, indicating that total fish density was not affected by the removal of *S. horneri* (Fig. 6a). Total fish density changed in a different pattern at the two sites; immediately after removing *S. horneri*, fish density decreased in both removal and control plots at Howland but increased in both plot types at Lion Head (6–27 February); thereafter, changes in fish density were fairly similar between the two sites.

Table 4. Fish species and total numbers observed on 213 transects on reefs at Santa Catalina, California. No. transects: total number of transects on which a species was observed (n = 213 total transects). Sites observed indicates where at least 1 individual of a species was observed. Study sites were Arrow Point (AR), Indian Rock (IR), Howland (HO), East Howland (EH), Big Geiger (BG), Sphinx Rock (SR), Between Two Ferns (BTF), and Lion Head (LI). 'All' indicates the species was observed at every study site

Species	Common name	Total abundance	No. of transects	Sites observed
Alloclinus holderi	Island kelpfish	8	7	AR, BTF, SR, IR, LI
Hermosilla azurea	Zebra-perch sea chub	3	2	BTF, IR
Anisotremus davidsonii	Sargo	1	1	HO
Apogon guadalupensis	Guadalupe cardinalfish	2	2	EH, HO
Atherinops affinis	Topsmelt	99	10	AR, BG, BTF, SR, EH, LI, HO
Brachyistius frenatus	Kelp surfperch	160	44	All
Chromis punctipinnis	Blacksmith	23785	177	All
Cymatogaster aggregata	Shiner surfperch	957	16	All
Embiotoca jacksoni	Black surfperch	127	66	All
Gibbonsia elegans	Spotted kelpfish	672	122	All
Girella nigricans	Opaleye	250	73	All
Gymnothorax mordax	California moray	116	78	All
Halichoeres semicinctus	Rock wrasse	3055	204	All
Heterodontus francisci	Horn shark	35	24	All
Heterostichus rostratus	Giant kelpfish	298	110	All
Hyposoblennius gentilis	Bay blenny	1	1	IR
Hypsypops rubicundus	Garibaldi	2012	212	All
Lythrypnus dalli	Bluebanded goby	26347	138	All
Lythrypnus zebra	Zebra goby	45	29	AR, BTF, SR, EH, IR, LI, HO
Medialuna californiensis	Halfmoon	147	33	All
Oxyjulis californica	Señorita	3723	130	All
Oxylebius pictus	Painted greenling	10	9	AR, BG, BTF, EH, LI, HO
Paralabrax clathratus	Kelp bass	3505	213	All
Rhacochilus toxotes	Rubberlip surfperch	1	1	HO
Rhacochilus vacca	Pile surfperch	5	3	IR, HO
Rhinogobiops nicholsii	Blackeye goby	1411	84	All
Scorpaena guttata	California scorpionfish	98	71	All
Scorpaenodes xyris	Rainbow scorpionfish	12	10	AR, BG, EH, IR, LI, HO
Sebastes atrovirens	Kelp rockfish	11	8	AR, BTF, SR
Sebastes rastrelliger	Grass rockfish	29	26	All
Sebastes serriceps	Treefish	6	6	AR, BG, EH, IR
Semicossyphus pulcher	California sheephead	255	107	All
Seriola lalandi	Yellowtail	5	3	BG, HO
Trachurus symmetricus	Pacific jack mackerel	2045	2	LI
Triakis semifasciata	Leopard shark	3	3	IR
Unknown Blenniiformes	Unknown blenny sp.	1	1	SR
Urobatis halleri	Round stingray	3	3	BG, BTF, LI
Xenistius californiensis	Salema	357	8	SR, LI

Table 5. Fish species contributing to 90% of the dissimilarity (Bray-Curtis) in multivariate fish assemblage among 4 time periods (summer and fall 2014, summer 2015, and winter 2016) and depths (3 and 6 m) as revealed by SIMPER analysis. *Benthic oriented, cryptic fish species. Garibaldi did not contribute to 90% of the total dissimilarities, but was observed on 99% of all transects (n = 213)

Fish species	Common name	% Contribution dissimilarity
*Lythrypnus dalli**	Bluebanded goby	56.4
Chromis punctipinnis	Blacksmith	14.2
*Rhinogobiops nicholsii**	Blackeye goby	7.9
*Gibbonsia elegans**	Spotted kelpfish	4.4
Oxyjulis californica	Señorita	4.3
Halichoeres semicinctus	Rock wrasse	2.3
Paralabrax clathratus	Kelp bass	1.9
Hypsypops rubicundus	Garibaldi	0.0

Table 6. Multiple linear regressions testing whether habitat variables predicted spatiotemporal variation in density of 8 fishes during (a) summer 2014, fall 2014, and summer 2015, and (b) winter 2016. **Bolded** terms are significant at $p < 0.05$. β is the standardized regression coefficient; rec: recruit; imm: immature; mat: mature; sen: senescent

(a) Summer 2014, Fall 2014, and Summer 2015		Algal PC 1	Algal PC 2	Physical PC 1	*Macrocystis*	*E. arborea*	*Sargassum horneri* (rec)	*S. horneri* (imm)	*S. horneri* (sen)	*S. palmeri* (imm)	*S. palmeri* (mat)	*S. palmeri* (sen)	Adj. r^2
Blacksmith	β	−0.13	−0.08	0.24	−0.19	−0.07	−0.13	0.04	0.08	−0.09	−0.04	−0.01	
	p	0.23	0.44	**0.01**	0.12	0.42	0.25	0.71	0.38	0.30	0.67	0.93	0.06
Señorita	β	0.15	0.02	−0.03	0.20	−0.13	−0.32	−0.03	0.13	−0.04	−0.10	−0.01	
	p	0.16	0.82	0.74	0.09	0.11	**0.003**	0.77	0.11	0.63	0.24	0.95	0.10
Rock wrasse	β	0.03	0.29	0.03	−0.17	0.18	0.20	0.09	−0.10	0.10	0.27	0.07	
	p	0.75	**<0.001**	0.73	0.05	**0.01**	**0.02**	0.25	0.11	0.16	**<0.001**	0.29	0.46
Kelp bass	β	−0.52	0.08	−0.05	0.11	0.03	−0.03	0.12	−0.11	0.00	0.03	−0.06	
	p	**<0.001**	0.41	0.53	0.28	0.68	0.73	0.18	0.15	0.97	0.74	0.40	0.28
Garibaldi	β	0.07	0.27	0.19	−0.19	0.04	0.21	0.01	−0.06	0.07	0.24	−0.09	
	p	0.48	**0.004**	**0.02**	0.07	0.59	**0.04**	0.90	0.41	0.41	**0.001**	0.25	0.27
Bluebanded goby	β	−0.54	0.18	0.07	−0.57	−0.08	0.32	0.13	−0.03	−0.10	0.03	0.05	
	p	**<0.001**	**0.001**	0.12	**<0.001**	**0.04**	**<0.001**	**0.01**	0.46	**0.03**	0.45	0.24	0.77
Blackeye goby	β	−0.22	0.15	−0.07	0.71	−0.06	−0.17	0.00	0.07	0.01	−0.11	0.04	
	p	**<0.001**	**−0.01**	0.13	**<0.001**	0.19	**0.003**	0.97	0.11	0.82	**0.02**	0.42	0.75
Spotted kelpfish	β	0.35	0.01	0.01	−0.04	0.04	−0.39	−0.13	0.01	−0.06	0.01	−0.06	
	p	**<0.001**	0.86	0.93	0.61	0.54	**<0.001**	0.08	0.88	0.33	0.83	0.36	0.53

(b) Winter 2016		Algal PC 1	Algal PC 2	Algal PC 3	Physical PC 1	Physical PC 2	Physical PC 3	*S. horneri* (recruit)	*S. horneri* (immature)	*S. palmeri* (immature)	Adj. r^2
Blacksmith	β	0.14	0.20	−0.13	0.01	0.34	−0.29	−0.06	0.16	0.27	
	p	0.50	0.53	0.71	0.97	0.17	0.16	0.42	0.89	0.30	<0.01
Señorita	β	0.07	−0.10	0.01	−0.11	0.27	−0.17	−0.06	0.07	0.14	
	p	0.75	0.75	0.98	0.61	0.30	0.42	0.74	0.90	0.61	<0.01
Rock wrasse	β	0.00	0.22	0.32	−0.22	−0.31	−0.05	0.31	0.15	0.42	
	p	0.98	0.39	0.26	0.20	0.12	0.76	0.36	0.37	0.06	0.27
Kelp bass	β	0.01	−0.27	0.06	−0.26	−0.31	−0.02	0.12	0.03	0.22	
	p	0.94	0.34	0.84	0.16	0.16	0.90	0.85	0.74	0.35	0.13
Garibaldi	β	0.16	0.56	0.31	0.10	0.20	0.03	0.02	−0.01	0.44	
	p	0.36	0.05	0.30	0.57	0.33	0.86	0.97	0.96	0.06	0.21
Bluebanded goby	β	−0.16	0.31	−0.06	0.05	0.19	0.03	−0.69	0.04	0.19	
	p	0.26	0.17	0.80	0.73	0.26	0.85	**0.02**	0.80	0.29	0.49
Blackeye goby	β	0.08	0.05	0.05	−0.10	0.16	−0.07	0.33	0.08	−0.14	
	p	0.70	0.87	0.88	0.62	0.51	0.72	0.70	0.44	0.58	<0.01
Spotted kelpfish	β	0.18	−0.14	−0.17	0.17	−0.22	0.17	0.16	−0.31	−0.09	
	p	0.40	0.67	0.63	0.43	0.37	0.43	0.14	0.70	0.73	<0.01

Table 7. Correlations among phases of invasive *Sargassum horneri* and native *Macrocystis pyrifera* on reefs at Santa Catalina Island, pooled across sites for summer 2014, fall 2014, and summer 2015 survey periods (n = 180), and summer 2014 only (n = 68 transects), when *Macrocystis* was most prevalent. Pearson correlation coefficients (r) are given, and statistically significant values ($p < 0.01$) are in **bold**

	Macrocystis	Recruit *S. horneri*	Immature *S. horneri*	Mature *S. horneri*	Senescent *S. horneri*
Summer 2014, Fall 2014, and Summer 2015					
Macrocystis	1				
Recruit *S. horneri*	0.14	1			
Immature *S. horneri*	**–0.33**	–0.09	1		
Mature *S. horneri*	**0.26**	0.13	–0.14	1	
Senescent *S. horneri*	**0.27**	**0.29**	–0.13	**0.37**	1
Summer 2014					
Macrocystis	1				
Recruit *S. horneri*	**0.38**	1			
Immature *S. horneri*	0.23	0.21	1		
Mature *S. horneri*	0.18	0.09	**0.44**	1	
Senescent *S. horneri*	**0.39**	0.18	**0.34**	0.15	1

Species richness and species diversity (*H′*) of fishes were also not affected by the removal of *S. horneri* (Fig. 6b,c). Species richness was slightly higher at Howland compared to Lion Head (7.0 ± 0.2 vs. 6.1 ± 0.1 fish species plot^{-1}, respectively). Richness also differed significantly among times, decreasing after removing *S. horneri* (i.e. time 1) and staying relatively constant thereafter (Fig. 6b). The six most common fishes observed among all plots were blacksmith, garibaldi, kelp bass, rock wrasse, señorita, and bluebanded goby. Overall, fish diversity (*H′*) was higher at Howland than at Lion Head (1.14 ± 0.3 vs. 0.93 ± 0.03), and differed significantly among times (Fig. 6c).

4. DISCUSSION

We found little evidence that rocky reef fishes were affected by *Sargassum horneri*, even though this invasive alga dominated the reef landscape throughout our study. Our field experiment, in which *S. horneri* was completely removed from 6 × 6 m plots on natural reefs, provided the most compelling evidence that fishes were not much affected by the invasive alga, given the lack of differences in fish density, species richness, diversity, and multivariate assemblage structure between plots with and without *S. horneri*. Our observational results from surveys of unmanipulated natural reefs that differed in the abundance of the various life stages of *S. horneri* revealed that statistical models including the abundance of *S. horneri* were no better at predicting the multivariate fish assemblage than a model lacking any data on *S. horneri* abundance. Furthermore, we observed mostly weak relationships between the abundance of *S. horneri* and the density of fish species that contributed most to spatiotemporal dissimilarity in the multivariate fish assemblage. Taken together, these results suggest that the invasive *S. horneri* had little direct effect on the temperate reef fishes studied. Thus, we would expect few changes in the fish assemblage if *S. horneri* invades rocky reefs without displacing important native algae, like *Macrocystis*, or invades a landscape lacking native algae (analogous to our experiment, in which *Macrocystis* was absent on both control and *S. horneri* removal plots).

The fish assemblage we studied was most variable during summer 2014, the only time period when *Macrocystis* was present at most sites. Afterwards it became less variable within time periods and more similar across periods, despite *S. horneri* occurring in different life stages that vary greatly in height, e.g. <5 cm for recruits and 1–2 m for late immature through senescent stages. This result, combined with *Macrocystis* explaining a statistically significant amount of variation in multivariate and univariate fish assemblage, is consistent with this key native species having important effects on the fish assemblage, but the invasive *S. horneri* having relatively small effects on fishes. The presence of *Macrocystis* often coincides with a greater numbers of fish species or higher abundance of particular species (Stephens et al. 1984, Anderson 1994, Deza & Anderson 2010, Srednick & Steele 2019). Although many species that are affected positively by *Macrocystis* typically reside in the canopy or midwater (Carr 1983, Bodkin 1988, Deza & Anderson 2010), our surveys would not have quantified fishes associated with the upper portions of the water column, because they were conducted within 2 m of the seafloor. When *Macrocystis* is not present, many of these reef fishes will associate with understory algae or the physical substratum. This would cause the fish assemblages quantified along our benthic transects to appear more dense and more uniform from one to another, as happened

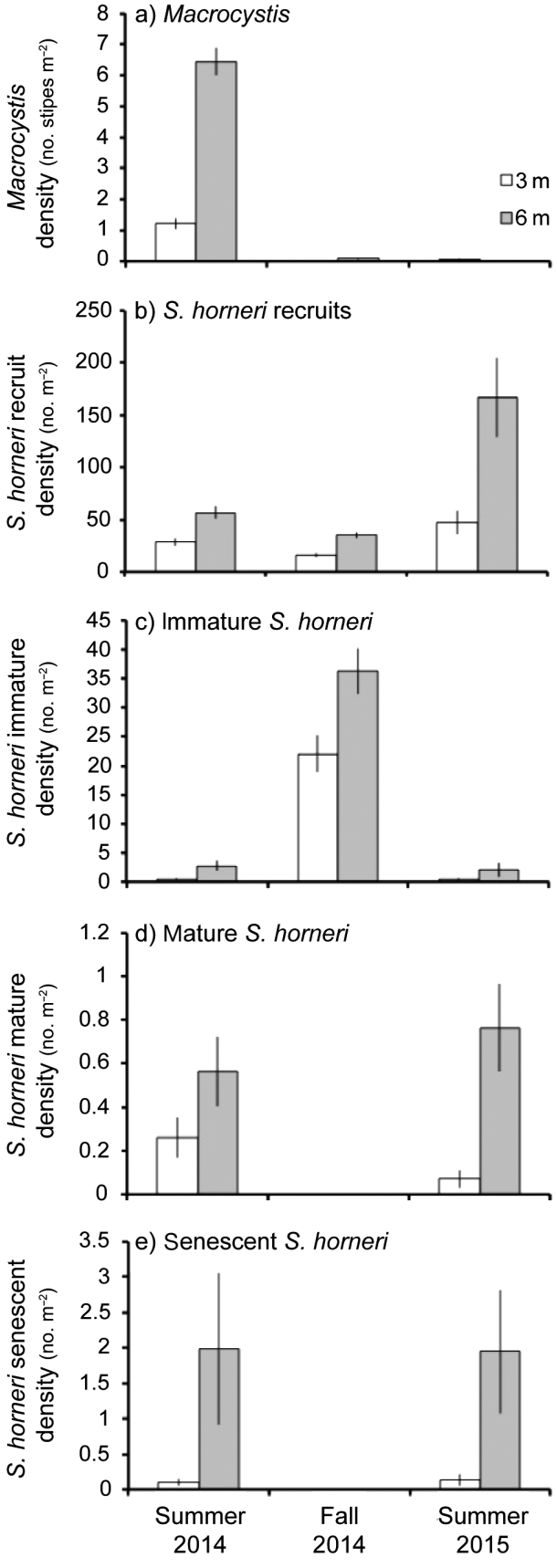

Fig. 4. Algal density (mean ± SE ind. m^{-2}) during 3 sampling periods at 2 depths for (a) *Macrocystis*, (b) *Sargassum horneri* recruits, (c) immature *S. horneri*, (d) mature *S. horneri*, and (e) senescent *S. horneri*. No data were collected at Lion Head and Howland during summer 2015

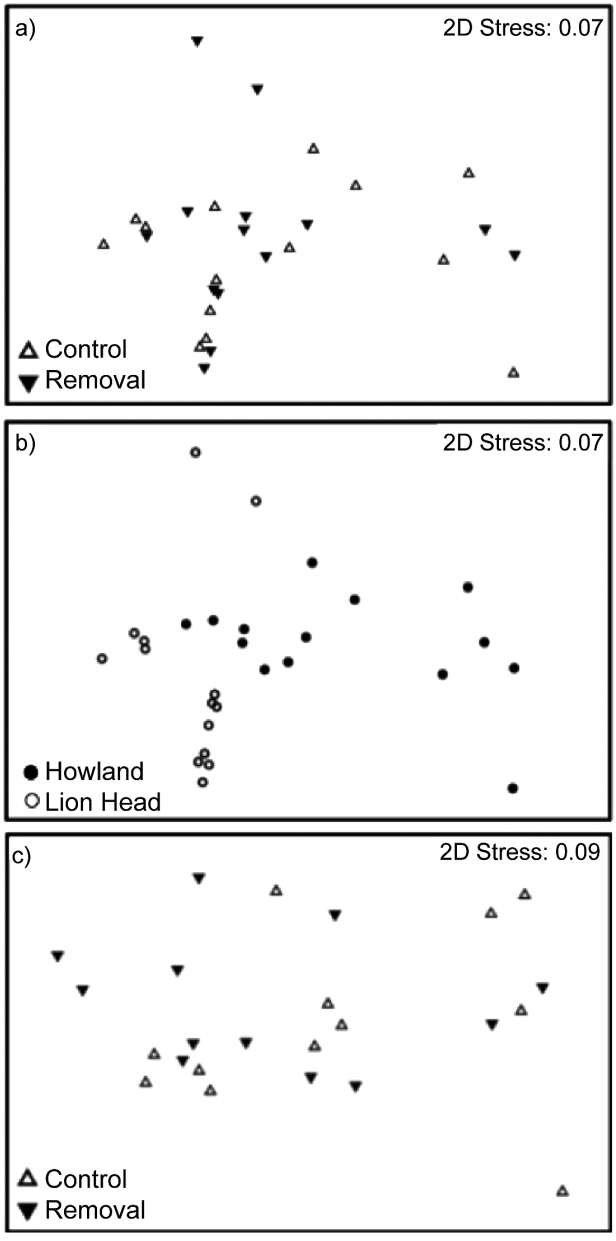

Fig. 5. Non-metric multidimensional scaling (nMDS) plots of the fish assemblage prior to removal of *Sargassum horneri* (trip 1; 6 February) displaying the factors (a) treatment, (b) site; and (c) after removal of *S. horneri* (trips 2–7; 27 February–23 July). Each point represents an experimental plot. Densities of each fish species were averaged over trips 2–7 to make the dissimilarity matrix used to generate panel c

Table 8. Results of repeated-measures PERMANOVA and ANOVA testing for effects of removing *Sargassum horneri* from experimental plots (6 × 6 m) on the fish assemblage at 2 study sites at Santa Catalina Island over time (7 sampling periods over 5 mo). Effects on the multivariate fish assemblage, total fish density, fish species richness, and fish species diversity (*H′*) were tested. n = 7 for both removal and control plots at both study sites; total N = 28 plots

Factor	df	Multiv. Assemblage		Total density		Richness		Diversity (*H′*)	
		pseudo-*F*	p-perm	*F*	p	*F*	p	*F*	p
Treatment (Tr)	1, 24	1.47	0.23	1.13	0.30	0.51	0.48	0.45	0.51
Site (S)	1, 24	5.90	0.01	5.30	0.03	21.24	<0.001	14.37	<0.001
Time (Ti)	6, 144	9.56	0.001	41.42	<0.001	17.02	<0.001	9.12	<0.001
Tr × Ti	6, 144	0.65	0.87	0.54	0.78	0.91	0.49	0.62	0.72
Tr × S	1, 24	1.57	0.22	0.42	0.52	0.17	0.69	0.98	0.33
S × Ti	6, 144	3.02	0.001	7.90	<0.001	1.96	0.07	1.67	0.13
Tr × S × Ti	6, 144	0.84	0.65	0.68	0.67	0.97	0.45	0.11	0.99

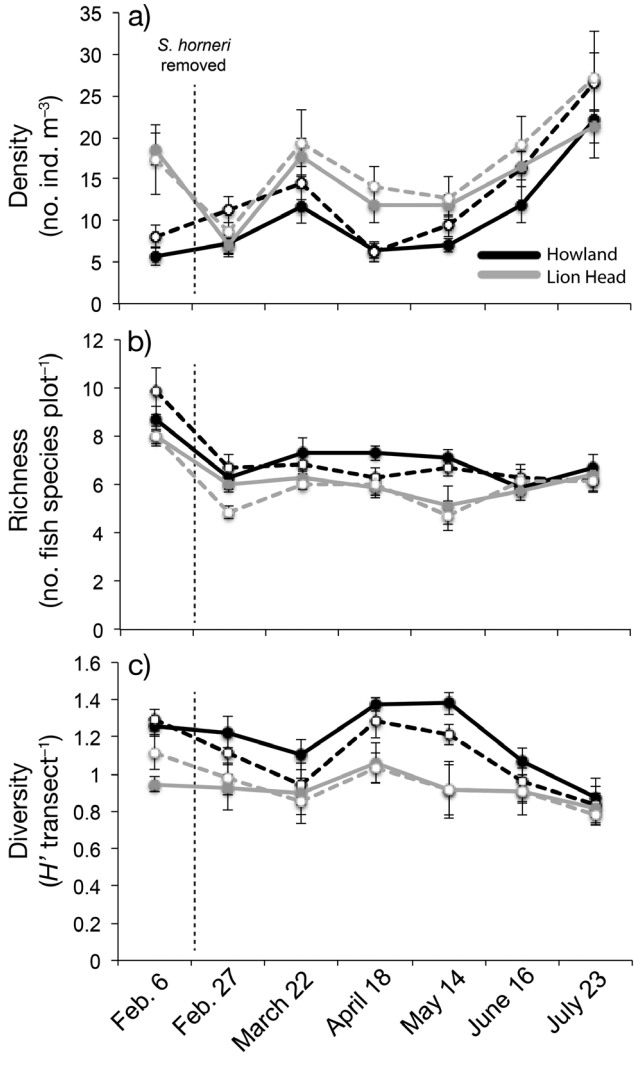

Fig. 6. Fish (a) density (mean ± SE ind. of all species), (b) richness (± SE), and (c) diversity on control (closed points) and removal (open points) plots at Lion Head and Howland reefs during all survey trips. *Sargassum horneri* was removed during 19–22 February. n = 7 plots per point (pooled between 2 sites)

between summer and fall of 2014 when *Macrocystis* disappeared. The results of our experiment also suggested that tall forms (i.e. immature, mature, and senescent) of *S. horneri* (i.e. what was removed from plots) do not drive fish distribution patterns. However, tall forms of the invasive alga did not occur in high abundances at a similar time as when *Macrocystis* was present on reefs during summer 2014. Thus, our inference of how tall stages of *S. horneri* (and *Macrocystis*) may have affected the fish assemblage is more limited than if both species of algae coincided in high abundances in one or more of our survey periods.

Another likely reason why this study revealed little evidence of impacts of the invasive *S. horneri* on the fish assemblage is that most of the fishes present on our experimental plots and along our transects do not associate tightly with macrophytes. In the *S. horneri* removal experiment, four fishes that composed 90% of the total fish abundance observed within our plots were species that do not typically associate with macroalgae: bluebanded goby, blacksmith, rock wrasse, and garibaldi. Similarly, the vast majority of the 69 600 fish counted in the observational study do not associate with macroalgae, and the main fishes that drove spatiotemporal differences in the fish assemblage, as revealed by the SIMPER analysis, were primarily species that are not typically associated with macroalgae. Of species that made up >1% of all the fishes counted, only kelp bass (5%) and señorita (5%) are commonly associated with macroalgae, but even those associations are fairly loose and certainly not obligate. Only two species we observed have obligate associations with macrophytes, namely kelp perch and giant kelp fish, but combined these species made up <1% of all fish counted. In communities with more obligate associations between fishes and macrophytes, one might expect to see a bigger

impact of an invasive macrophyte than we found at Santa Catalina Island.

We examined the correlative relationship between *Macrocystis* and several stages of *S. horneri* to explore how fishes might be indirectly affected by their relationship. We found that *Macrocystis* abundance was correlated with, but likely not influenced by, the abundance of several stages of *S. horneri*. Overall, the mix of negative and positive correlations between *Macrocystis* and *S. horneri* over the course of the first three sampling periods (summer and fall 2014, and summer 2015), over which *Macrocystis* went from being abundant to virtually absent at our study sites, suggested no strong interactions between the two macroalgae. For example, the density of *Macrocystis* was negatively correlated with immature *S. horneri* over the course of the first three sampling periods, but immature *S. horneri* occurred in similar densities when *Macrocystis* was present and absent from reefs (i.e. <5 ind. m^{-2} during summer 2014 and 2015). From our results and basic knowledge of the life history of the invasive *S. horneri*, it is reasonable to conclude that the change in fish assemblage structure throughout our study was not indirectly driven by the relationship between *Macrocystis* and *S. horneri*.

The large changes we documented in multivariate and univariate descriptors of the fish assemblage after summer 2014 were likely due to direct and indirect effects of anomalously high sea surface temperatures from an El Niño Southern Oscillation event combined with 'The Blob' (Bond et al. 2015), and local conditions. It is well known that increased temperatures and nutrient depletion from the surface layers of waters off the southern California coast during warm water events can negatively affect *Macrocystis* abundance and production (Zimmerman & Robertson 1985, Dean & Jacobsen 1986). *Macrocystis* that we observed at Catalina Island appeared to be negatively affected by those abiotic attributes of warm water starting in late summer 2014, and densities of *Macrocystis* were dramatically reduced by fall 2014. Warmer and nutrient poor surface water surrounding Catalina Island likely indirectly affected some fishes at our study sites by negatively affecting an important habitat, giant kelp. Additionally, warmer water temperatures are also directly associated with greater recruitment of certain fishes in California (Ebeling & Laur 1988, Stephens et al. 1984, Lenarz et al. 1995). Densities of some fish species that have an affinity for warm water increased markedly over the course of this study. For example, rock wrasse density increased ~5-fold from summer 2014 to summer 2015, and bluebanded goby densities increased by ~12-fold during that same time period (Ginther & Steele unpubl. data), both apparently due to high recruitment. In contrast, some normally abundant species were virtually absent from reefs following the summer 2014, such as the blackeye goby, which prefers cooler waters (Love & Schroeder 2007), and this was evident in the observed decline in fish species richness and diversity after summer 2014.

The recurrent disappearance of native canopy-forming *Macrocystis* (Dayton et al. 1984, Ebeling et al. 1985) over evolutionary time scales may have selected for fishes that are capable of quickly adjusting their behavior to successfully associate with a variety of understory algae. This may limit the impacts of invasive macroalgae, such as *S. horneri*. Castorani et al. (2018) found that fish biomass did not change in reef patches that experienced natural fluctuations in kelp in an approximately decade-long study. Similarly, we found that in an *S. horneri*-dominated landscape, despite natural and manipulated changes in *S. horneri* structure, the fish assemblage was fairly similar across sampling periods.

Changes in animal populations often occur over longer time scales than that of our study (Jones 1990, Thompson & Ollason 2001, Rodriguez-Sanchez et al. 2002), and even though we studied changes over 1.5 yr and 5 mo for our observational field study and field experiment, respectively, these periods are short relative to the generation times of many species of fish. Exploring how *S. horneri* affects vulnerable life stages of fishes (e.g. recently settled individuals) may aid in predicting long-term consequences that have not yet been realized. For example, at the scale of individual alga, an important predatory kelp forest fish, the kelp bass *Paralabrax clathratus*, preferentially recruits to *Macrocystis* compared to *S. horneri* (Ginther & Steele 2018), but over larger spatial scales, the present study suggests this pattern may not hold. Whether kelp bass (or other fishes) recruit to a reef landscape completely dominated by *S. horneri* and absent of *Macrocystis* remains to be determined empirically. Understanding the consequence of prolonged oceanic regimes (i.e. warm water) that appear to be more conducive to the proliferation of *S. horneri* and detrimental to *Macrocystis*, and that span multiple generations, will require longer-term studies.

S. horneri has been established at Santa Catalina Island for approximately 10 yr, but this study is the first to focus on the effects of the invasive alga on the rocky reef fish assemblage. Despite a striking change in underwater landscape over our nearly 2 yr study, and complete removal of *S. horneri* in a large field experiment, we found little evidence of effects of

S. horneri on the fish assemblage at Santa Catalina Island. The changes we observed in the fish assemblage are better explained by other factors, such as that direct and indirect effects of warm-water events, including the die-off of *Macrocystis*. Although our study found little evidence of negative effects of the non-native *S. horneri* on fishes, we still advise cautionary management actions to limit the movement of *S. horneri*, since its effects on other community members, such as other algal species, may be detrimental, and effects on fishes may occur over longer time periods or at different spatial scales than studied here.

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