



# Macroalgal physical structure predicts variation in some attributes of temperate fish assemblages better than macroalgal species composition

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Received: 20 December 2021 / Accepted: 14 October 2022 / Published online: 3 November 2022  
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## Abstract

The importance of vegetative habitat in influencing distribution patterns, species interactions, and biodiversity is well documented in marine ecosystems, yet most previous studies on macroalgal–fish relationships have focused on influences of density and identity of macroalgae, often ignoring how the unique physical structure provided by each alga contributes to patterns. We tested whether the distribution, abundance, and biomass of rocky reef fishes could be predicted as well or better by measures of physical structure of macroalgae than by species identity and abundance. Divers visually sampled fishes and macroalgae at seven sites spread over several km at Santa Catalina Island, California, over a 1-year period, to examine how the distribution patterns of fishes related to spatiotemporal differences in the macroalgal assemblage. We found that variation in the composition, density, and diversity of the fish assemblage was equally or better explained by macroalgal structure (total surface area and height) than by macroalgal species density. In contrast, biomass and vertical distribution of fishes were better predicted by macroalgal species identity and density than by macroalgal physical structure. Of the macroalgal attributes, surface area was the best predictor of fish abundance and multivariate assemblage structure (species and their densities). However, much of the spatiotemporal variation in the fish assemblage was not explained by macroalgae, indicating that even in habitats visually dominated by macroalgae, macrophytes are only one of many factors that drive spatiotemporal variation in community structure. Our results suggest that quantifying the physical structure provided by marine macroalgae can be more useful than macroalgal species identity in predicting some aspects of fish assemblage structure.

**Keywords** Habitat structure · Reef fish · Macroalgae · Kelp · Invasive species

## Introduction

Habitat structure is widely regarded as one of the cornerstones of ecosystem configuration (McCoy and Bell 1991). Complex, vertically oriented, living structures such as terrestrial forests (Franklin 1988; Noss 1990; Tews et al. 2004) and aquatic algal beds (Choat and Shiel 1985; Pérez-Matus and Shima 2010; Wilson et al. 2014; van Lier et al. 2018) provide foundational habitats that are important drivers of

biodiversity (Jones 1992; Graham 2004; Wilson et al. 2014), species interactions (Lawton 1983; McCoy and Bell 1991; Byrnes et al. 2011; O'Brien et al. 2018), and ecosystem processes (Graham et al. 2008; Arkema et al. 2009; Byrnes et al. 2011; Reed et al. 2016). The relationships between species diversity and the quantity and heterogeneity of vegetative habitat structure have been well documented in both terrestrial (Tews et al. 2004) and aquatic systems (Carr 1989; Holbrook et al. 1990; Levin and Hay 2002; Miller et al. 2018). Moreover, in some systems the structure provided by certain organisms (“ecosystem engineers”) may have important direct and indirect impacts on other organisms’ ability to access resources (Jones et al. 1997

Despite the clearly demonstrated importance of complex, living habitat structure, methods that summarize complex patterns of biogenic structures into simple, comparable units are not often used in marine systems (*see* McCoy and Bell 1991). In terrestrial forests, for example,

Responsible Editor: S. Hamilton.

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canopy cover, trunk diameter, stand biomass, stand size, foliage height, blade width, surface area, and volume are used to describe the amount, shape, and composition of vegetation (McElhinny et al. 2005). Analogous metrics (e.g., height, canopy cover, stipe density, thallus density, biomass) have been used in aquatic systems to examine how variation in physical structure within species of macroalgae influences associated organisms (Holbrook et al. 1990; Anderson 1994; Carr 1991; Boström et al. 2006; Pérez-Matus and Shima 2010; Miller et al. 2018; Lamy et al. 2020). Yet, a fundamental hurdle in assessing the effects of vegetative structure in marine systems is to compare the influence of living structure across species to determine if the patterns observed are (1) due to direct biological relationships between vegetation and organisms (e.g., food) or (2) simply the result of the physical arrangement of structural elements (Gregor and Anderson 2016). This topic is important because not all organisms use features of vegetative structures in the same way. For example, an amphipod may feed on the tissue of a macroalga, whereas a fish may hide from predators among the fronds of the same alga, as well as feed on the amphipods inhabiting it. The structural complexity of the alga can influence the activities of both species, but not necessarily in the same ways. Thus, understanding how variation in the physical quantity of vegetative habitat structure influences species interactions and subsequently drives the distribution and abundance of species is important in understanding how ecosystems are structured.

Measuring and comparing height, surface area, and volume of algae provides a useful way to quantify and differentiate the structural elements of macroalgae. Height is a commonly used measure of algal size and has demonstrated influence on various aspects of species abundance (Anderson 1994; Stelling-Wood et al. 2020). However, measures of height lack specific information about the structural complexity of an alga and fail to evaluate how differences in the cumulative amount of structural complexity across algae influence species abundance. Surface area has been used to summarize the structural complexity of objects (Parker et al. 2001; Stelling-Wood et al. 2020), where greater surface area indicates more complex branching and structural elements. Volume has been used to describe the amount of space that an object occupies (Ware et al. 2019) and can provide an additional dimension to quantifying the structure of macroalgae of similar height but different area. While height, surface area, and volume are all positively related to one another within a species, the slope of each relationship can differ meaningfully among species due to differences in physical structure among algae. Quantifying these attributes should improve our ability to discern why different algal species have different impacts on associated biota (Stelling-Wood et al. 2020).

In nearshore marine systems, algae form physical structure that provides important shelter from predators (Anderson 1994; Gutow et al. 2012) and increased access to food (Jones et al. 1997; Steneck et al. 2002; Hovel et al. 2016). Giant kelp (*Macrocystis pyrifera*), for instance, provides biogenic habitat for vertebrates and invertebrates, increasing the potential for species interactions (Holbrook et al. 1990; Sala and Graham 2002; Graham 2004; Steneck et al. 2002). Macroalgae are diverse structurally, both within and among species (Stewart and Carpenter 2003; Pérez-Matus and Shima 2010), and certain macroalgal morphologies may be more important for certain species or certain life history stages of a species (e.g., canopy shelter for small juveniles of some species). Moreover, where vegetation is dense, average biomass of fishes may be lower because it offers more refuge for smaller individuals and may be more challenging for larger individuals to navigate (Crowder and Cooper 1982). Variation in the size, morphology, and density of macroalgae can influence the distribution, behavior and subsequent interactions among associated fishes (Crowder and Cooper 1982; Levin and Hay 1996; Lewis and Anderson 2012), and in turn potentially can influence the stability of communities (Steneck et al. 2002; Castorani et al. 2018; Lamy et al. 2020).

Recent reductions in large stands of *Macrocystis pyrifera* triggered by increases in ocean temperatures and subsequent increases in the range and density of the exotic alga *Sargassum horneri* (Marks et al. 2015) have led to a significant change in the physical appearance of the macroalgal assemblage in parts of the Southern California Bight, USA and northern Baja California, Mexico. Specifically, whereas *M. pyrifera* forms tall, forest-like stands that span the water column, the structure provided by *S. horneri* is far shorter (<2.5 versus >20 m), more finely branched, and has much smaller blades. Recent examinations of the influence of the quantity of *M. pyrifera* suggest that the structure alone (measured as biomass) is responsible for 25% of the variation in the diversity of associated mobile species (Miller et al. 2018). Despite ample evidence of the importance of *M. pyrifera* as an ecosystem engineer (Castorani et al. 2018; Miller et al. 2018), there is uncertainty about how its unique physical structure relative to other macroalgae influences species distribution, interactions, and ecosystem processes. For example, a shift from it as the dominant macroalga on rocky reefs may have important implications for population dynamics of reef fishes (Ginther and Steele 2018, 2020).

Here, we test the hypothesis that variation in the fish assemblage, here described as the collective of fish populations within a location, can be predicted as well or better by just the quantity of physical structure provided by the macroalgae assemblage than by its composition (species identity and abundance). To do so, we first quantified the physical structure of a suite of abundant and morphologically diverse

macroalgal species, as well as their species-specific densities; and the abundance, distribution within the water column and biomass of the fish assemblage. Then we used a series of statistical models compare the relative success of macroalgal physical structure vs. macroalgal species identity and density as predictors of univariate and multivariate metrics of variation in the fish assemblage. Finally, we use the results of this exploration to help understand the impact of a change in dominant macroalgal structure from native to non-native macroalga.

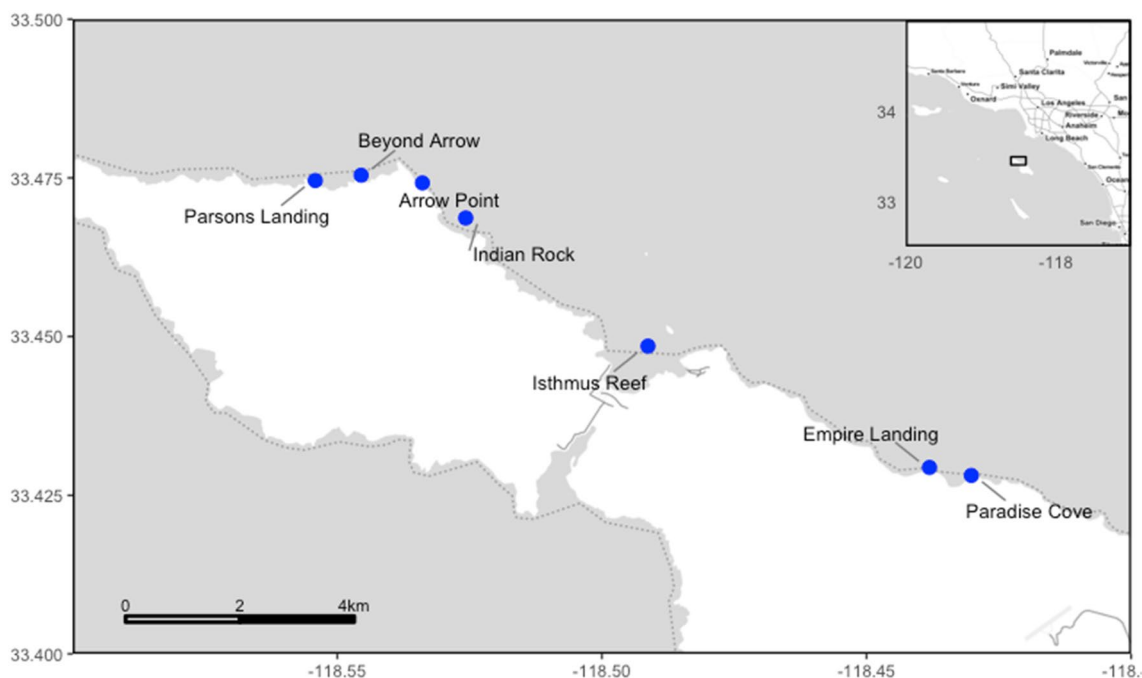
## Materials and methods

### Study system

We studied rocky reef communities along a 14-km stretch of the leeward coast of the west end of Santa Catalina Island, 32 km off the coast of California, U.S.A. (33°26'N, 118°28'W). These reefs harbor a temperate-subtropical fish assemblage composed of ~40 common species of reef-associated carnivores, herbivores, and generalists (Hobson & Chess 2001). Although they are considered kelp forest fishes, only a small fraction of the species in this assemblage have obligate associations with macroalgae, and some of these, only at certain points in their life history (Stephens et al. 2006). The reefs at Santa Catalina

Island historically have been characterized by large beds of the canopy forming (> 10 m tall) macroalgae *Macrocystis pyrifera*, with complex low-lying (< 1 m tall) algal understory on rocky reef substratum separated by sand plains. During the period of the present study (2015–2016), coinciding with end of north Pacific marine heatwave (Lorenzo and Matua 2016), *M. pyrifera* was much less common than it had been historically (with the exception of extreme El Niño events), and the invasive algae *Sargassum horneri* was the dominant space holder on the reefs.

Reefs at seven sites were chosen for this assessment: Paradise Cove, Empire Landing, Isthmus Reef, Indian Rock, Arrow Point, Beyond Arrow, and Parsons Landing (Fig. 1). All study sites were selected based on their similarity in the following factors: rocky or cobble reef extending horizontally at least 250 m at 8 m or greater depth, similar wind and swell exposure, and not within areas where fin-fishing was prohibited. The latter was important to avoid confounding effects that could be associated with comparing areas open versus closed to fishing (e.g., greater fish density and larger fish). Two of the study sites (Arrow Point and Indian Rock) were within a State Marine Conservation Area (SMCA), which prohibits harvest of invertebrates but allows take of fishes. Sites within the invertebrate reserves appeared comparable to sites outside of reserves. In particular, sea urchins, which are important grazers of kelps were sparse at all sites and there were no urchin barrens.



**Fig. 1** Study sites along the leeward coast of Santa Catalina Island, California, U.S.A

## Survey design

To evaluate how differences in the quantity of physical structure versus species identity and density of macroalgae accounted for variation in the identity, biomass, and abundance of fishes within rocky reef habitats, we visually sampled assemblages of fishes, macroalgae, and underlying rock substrata within distinct spatial zones. At each site, permanent anchors (1-m-long cable ties) were deployed along an 8–10 m isobath to mark the beginning and end of each of four permanent transects. Each transect measured 30-m long and 2-m wide, contained three separate water-column strata, and was separated from the next by 20 m to promote statistical independence. To explore the vertical distribution of fish, each transect was comprised of three sub-transects (each  $30 \times 2 \times 2$  m) in different strata of the water column: the upper-water column (2-m depth), mid-water ( $> 2$  m,  $\leq 5$  m depth), and benthic (8–10 m depth). Surveys were performed starting in the upper water column and working downward to avoid bubbles from divers disturbing fishes in areas above the divers.

We surveyed the seven study sites five times over a year between July 2015 and July 2016, at approximately 3-month intervals to observe temporal changes (including seasonal) in the macroalgal assemblage. Seasonality itself, however, was not tested in our analyses because seasons were not surveyed in subsequent years and thus lacked adequate replication. All surveys were performed during daylight hours (between 0800 and 1400) and completed over 10 days or less during each of the five periods.

## Underwater visual sampling of fishes and macroalgae

Visual surveys of the fish assemblage were performed in all three depth strata by identifying, counting, and estimating by eye the size (to the nearest cm standard length) of all fishes along each permanent transect. On the benthic portion, a second diver followed the first and recorded the identity, number, and size of small benthic fishes within ten  $0.5 \times 0.5$  m ( $0.25$  m<sup>2</sup>) quadrats, each deployed at a random position within each of ten 3-m-long sections along each transect. The first diver stayed 1 m above the bottom while surveying fishes to avoid disturbing the benthos.

Following surveys of small benthic fishes, the second diver recorded the number and height (to the nearest cm) of the macroalgae *Sargassum palmeri*, *S. muticum*, *S. horneri*, and *Stephanocystis neglecta* within the ten  $0.25$  m<sup>2</sup> quadrats (Table S1). Abundance of macroalgal recruits ( $< 5$  cm tall), as well as older stages of *Dictyopteris undulata* and *Zonaria farlowii*, were recorded as the percent of 25 marked cells (area:  $0.01$  m<sup>2</sup>) within each quadrat that were dominated ( $> 50\%$  of cell) by a species. We recorded the number and

height of *Eisenia arborea* and *M. pyrifer*a (number of stipes also recorded), respectively, within a 2-m-wide band centered on the transect.

Physical substratum type was recorded in each of the ten  $0.25$  m<sup>2</sup> quadrats on each benthic transect at 16 uniformly spaced points within the quadrat. Substratum was placed in one of six categories: sand, cobble ( $< 25$  cm diameter), small boulder (26–50 cm diameter), medium boulder (51–75 cm diameter), large boulder (76–100 cm diameter), and bed-rock ( $> 101$  cm diameter). Relief (i.e., the vertical change in benthic substratum height) was recorded every meter as the greatest vertical difference in substratum height over  $1\text{-m}^2$  area, centered on the transect. Substratum type was recorded during each sampling period, whereas relief was only recorded at the first sampling period (summer 2015), as it was not expected to change across periods on the permanent transects.

## Quantifying macroalgal structure

Of the eight species of macroalgae measured on reef surveys, four species, *Sargassum horneri*, *S. palmeri*, *Stephanocystis neglecta*, and *M. pyrifer*a, were the largest abundant macroalgae on reefs (Table S1), providing the majority of the biogenic structure, and were likely to be the most important to fishes, as noted by other studies on nearshore reef fishes at Santa Catalina Island (Anderson et al. 1989; 2001; Hobson and Chess 2001). Additionally, results of principal components analysis (PCA) indicated that these four species consistently contributed to variation in the macroalgal assemblage (Table S2a). Thus, we selected these species as potential predictors of variation in the fish assemblage.

To quantify the amount of physical structure that different macroalgae provide, we collected individuals of different sizes from the four species of macroalgae during June–August 2015 from the same study sites, but at least 50 m away from surveyed area. To increase samples sizes, in 2019 we collected additional individuals of *S. neglecta* and *S. palmeri* at the same sites. In total, we collected 33 thalli of *Stephanocystis neglecta*, 21 thalli of *M. pyrifer*a, 49 thalli of *Sargassum horneri*, and 29 thalli of *S. palmeri*. These individuals spanned the size range and reproductive stages observed on surveys across all seasons. All individuals were collected from depths of 6–9 m. For each individual thallus, we recorded the height (from base of thallus to apical tip), volume by displacement (rounded to nearest 20 mL) in a graduated cylinder (2000 mL) of water, and surface area via dye-dipping method in the laboratory (as modified from Hoegh-Guldberg 1988 and Stewart and Carpenter 2003). When the volume of an individual was measured as less than 20 mL (the graduation interval for 2000 mL cylinder) a 100 mL graduated cylinder was used to estimate volume to the nearest 1 mL. Additionally, when an entire thallus was

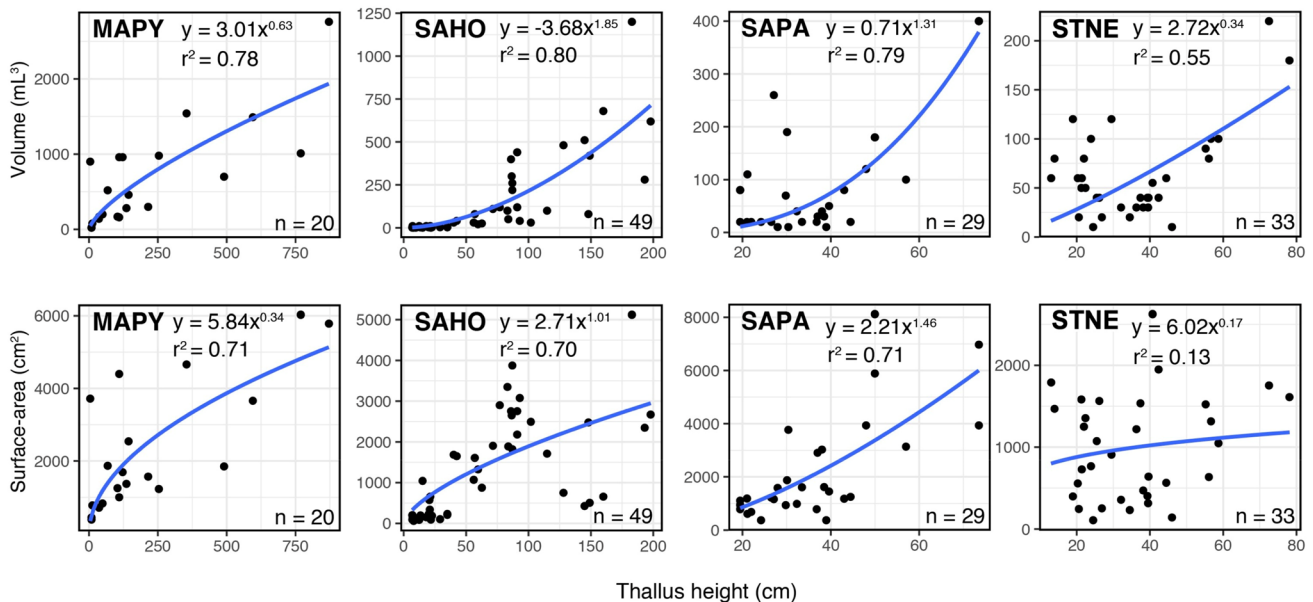
too large to fit in the 2000 mL graduated cylinder (e.g., *M. pyrifera*), the thallus was separated into smaller portions, measured, and then summed to calculate the overall thallus volume. The dye-dipping method consisted of dipping an alga in a solution of 5% Triton X100 detergent and fresh water to prevent absorption of dye, then dipping it in 0.1% methylene-blue dye and fresh water for 5 s. The dyed alga then was placed in a salad spinner and spun for ten rotations to remove excess dye. The alga then was placed into a container with 800 mL of filtered seawater and rinsed for 20 shakes. We then took a 12-mL subsample of the rinsed fluid and measured its absorbance on a spectrophotometer at a wavelength of 520 nm (Beckman DU 640). Surface area then was estimated using a calibration line established using the same method on eight pieces of waterproof paper cut to known area ( $r^2 = 0.99$ ). Dye-dipping was used to estimate surface area without confounding estimates with variation in texture and porosity among species, which might occur if image analysis was used.

Using macroalgal height and density data from the transect surveys, we calculated the volume and surface area of macroalgae on each transect with power equations for each of the four macroalgae, after which we summed across species to estimate total macroalgal volume and surface area along each transect (Fig. 2). Power equations for each species were generated with 'nls' function of the 'stats' package in R studio (Rstudio team 2020), using estimated start coefficients, and assessed for goodness of fit. Macroalgal volume and surface area were calculated as the values predicted from the power equations when applied to the height

of each thallus measured in the field for each species on each transect, and then summed across all of the four species of interest on the transect resulting in a single number for each of summed height, surface area, and volume of macroalgae for each transect. Using this summation of macroalgal structural complexity (measured as height, surface area, or volume) across species allowed us to separate species-specific effects of macroalgae from physical structure, and enabled us to evaluate how the distribution of fishes is related to certain macroalgae species versus the quantity of structure they provide.

### Predicting variation in the fish assemblage from macroalgae: macroalgal structure or macroalgal identity?

To test the hypothesis that variation in the fish assemblage was predicted as well or better by macroalgal structure than macroalgal identity and density, we compared models that predicted attributes of the fish assemblage from data on the density of different, large, abundant macroalgal species, with those that ignored species identity and instead used data on macroalgal structure (height, surface area, or volume) summed over the macroalgal species (*Sargassum horneri*, *S. palmeri*, *Stephanocystis neglecta*, and *M. pyrifera*). The models also included study site, as well as abiotic habitat variables measured at the benthic stratum, which were summarized as principal components. To account for the non-independence of observations made along the same permanent transects, models included transect ID as a random



**Fig. 2** Predictive relationships between macroalgal height and volume or surface area generated from power equations for four species *Macrocystis pyrifera* (MAPY), *Sargassum horneri* (SAHO), *Sargassum palmeri* (SAPA), and *Stephanocystis neglecta* (STNE)



factor. Linear mixed-effects modeling (Bates et al. 2015) was used to construct all univariate models with the abiotic principle components (PCs), sampling site and transect ID, plus one of the following metrics of macroalgal density or quantity: density of each of the four common macroalgal species, or their height, volume, or surface area summed across the four species. These models that included macroalgal attributes were also compared with a model including just physical substratum, transect ID, and sampling site to assess how much physical substratum and site-specific characteristics unrelated to macroalgae contributed to observed variation in the fish assemblage.

The fish assemblage response variables analyzed were the multivariate fish assemblage (density and identity of each fish species), total density (all fishes summed), individual species density (for six abundant species), fish diversity per transect, vertical distribution of fishes, and fish biomass. Fish assemblage diversity transect<sup>-1</sup> was calculated as Shannon–Wiener H' using the 'diversity' function in the R package 'vegan'. Density of fishes was analyzed as number transect<sup>-1</sup>. The multivariate fish assemblage was analyzed with distance-based redundancy analysis (dbRDA) on a Euclidian-distance matrix of the density of each fish species using the *vegan* package in R (Oksanen et al. 2020) with 999 permutations for each test, which was treated as the multivariate-analog to linear mixed-effects modeling. Multi-dimensional scaling (MDS) was used to visualize variation in the multivariate fish assemblage and correlation bi-plots were used to assess how macroalgal attributes and species explained variation in the fish assemblage.

To understand which fish species were driving the patterns in the overall fish assemblage, we generated mixed-effects models using the same models on individually on each of six kelp forest fishes that were abundant and known to be influenced by variation in the algal community and abiotic habitat characteristics (Larson & Demartini 1985; Anderson 1994; Carr 1991). These species were *Chromis punctipinnis*, *Halichoeres semicinctus*, *Hypsypops rubicundus*, *Lythrypnus dalli*, *Oxyjulis californica*, and *Paralabrax clathratus*. The tightly kelp-associated *Brachyistius frenatus* and macrophyte- (macroalgae and surfgrass) associated *Heterostichus rostratus* were not evaluated because they were too rare during our study for meaningful analysis (Table S3).

To evaluate how macroalgae might influence vertical distribution of fishes in the water column (Carr 1989, 1991; Holbrook et al. 1990), we calculated the proportion of fish in the water-column portions of each transect (hereafter vertical distribution of fishes), and considered both mid- and upper-water-column transects to represent the water column (i.e., [mid-water + upper-water] / [benthic + mid-water + upper-water density]). Thus, this metric was simple, univariate index of the proportion of fish on a transect that were in the water column versus near the seafloor.

The biomass (g) of all fish (species pooled) on each transect was calculated from fish body size (cm total length) for each species using established length–weight relationships from Fishbase in the R package 'rfishbase' (Boettiger et al. 2012), after which individual species biomass was summed for each transect.

Our analyses pooled time periods (i.e., it was not a factor in the analyses) to evaluate how well the combination of temporal and spatial (spatiotemporal) variation in the fish assemblage was predicted by spatiotemporal variation in macroalgal attributes. Spatiotemporal variation in both the fish assemblage and macroalgal attributes stemmed from differences among transects (spatial) and time periods (temporal), and the analyses tested which attributes of macroalgae best predicted the spatiotemporal variation in fish assemblage attributes. Transects were used as the unit of replication, resulting in  $n = 140$  (5 sampling periods  $\times$  7 study sites  $\times$  4 transects per site) for all analyses.

The best model for each univariate response variable was selected by comparing AICc values, with models within two AICc units being considered indistinguishable (Burnham and Anderson 2004); and the relative utility in explaining variation in each response variable was explored by comparing  $r^2$  values. For the multivariate fish assemblage, the best model for each response variable was selected by comparing  $r^2$  values.

## Data transformation and statistical software

Prior to performing all analyses, data were transformed as needed to satisfy assumptions of normality and homogeneity of variances (Sokal and Rohlf 1995), and to reduce the influence of highly abundant species. Macroalgae density data (thallus/m<sup>2</sup>) were square-root transformed except for *M. pyrifera*, which was log ( $x + 1$ ) transformed. For algal structure data, summed surface area was square-root transformed, and summed height and summed volume data were log ( $x + 1$ ) transformed. Fish species diversity (H'), the multivariate fish assemblage, overall and individual fish density, and fish biomass, were log ( $x + 1$ ) transformed. Multivariate homogeneity of dispersions was confirmed for the fish assemblage data using *betadisper* (in *vegan*) and a permutation-test (999 permutations).

All analyses were performed in R studio v1.3.1093 (RStudio Team 2020) with additional packages 'lme4' (Bates et al. 2015), 'dotwhisker' (Solt and Hu 2018), 'ggmap' (Kahle and Wickham 2013), 'patchwork' (Pedersen 2020), 'tidyverse' (Wickham et al. 2019), 'vegan' (Oksanen et al. 2020), and 'broom,mixed' (Bolker and Robinson 2021).

## Results

### Predicting macroalgal surface area and volume from height

The strength of the relationship between macroalgal height and surface area or volume varied among species. Height was a good predictor of surface area for *Macrocystis* ( $r^2=0.71$ ), *S. horneri* ( $r^2=0.70$ ), and *S. palmeri* ( $r^2=0.70$ ) (Fig. 2), but not for *S. neglecta* ( $r^2=0.13$ ). Likewise, height was a good predictor of volume for *Macrocystis* ( $r^2=0.78$ ), *S. horneri* ( $r^2=0.80$ ), and *S. palmeri* ( $r^2=0.79$ ), but less so for *S. neglecta* ( $r^2=0.55$ ).

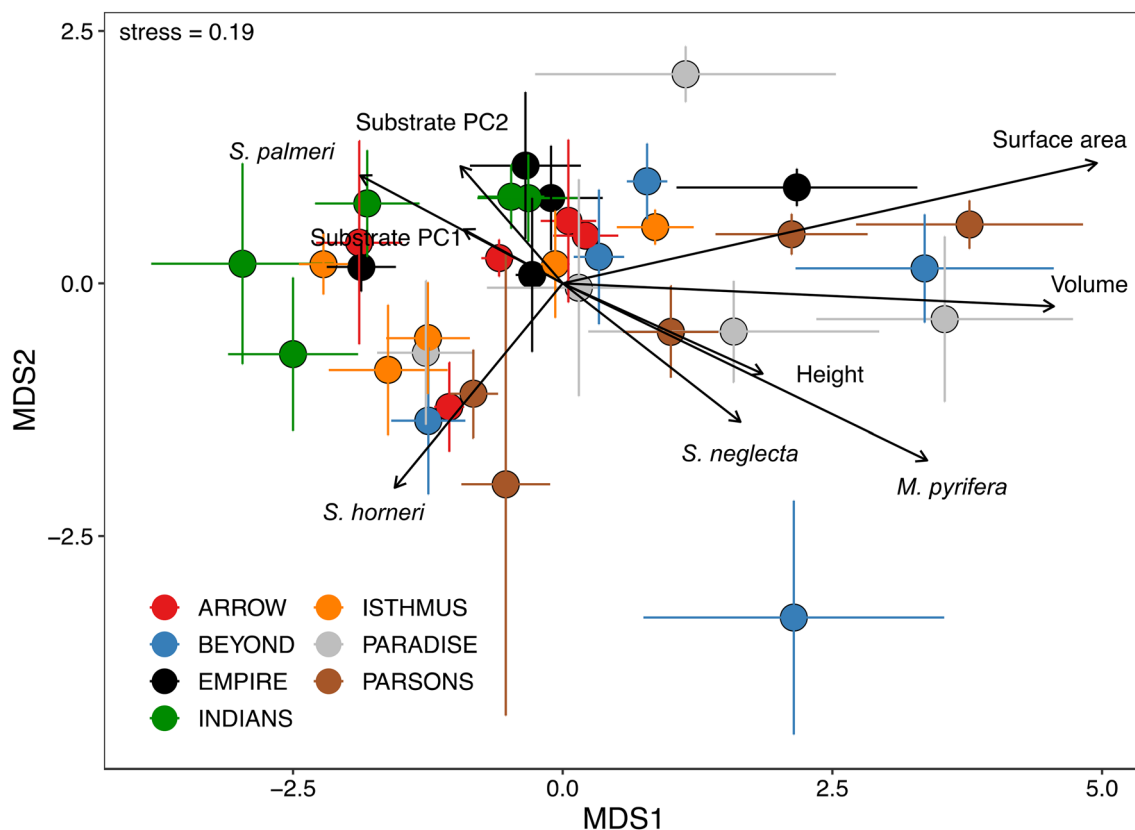
### Summarizing abiotic habitat attributes

Two PC's summarized 88.0% of the variation in the physical substratum (65.4% and 22.6%, respectively) (Table S2b). Substratum PC 1 was moderately positively correlated with bedrock, and moderately negatively correlated with large boulders and cobble. PC 2 was most strongly correlated with

large boulders (positively) and cobble (negatively). Neither of the two PCs were strongly correlated with relief.

### Predicting variation in the fish assemblage from macroalgae: physical structure vs. species identity

Variation in the multivariate fish assemblage (identity and density of each species) was best and similarly predicted by models containing macroalgal surface area ( $r^2=0.40$ ;  $Pseudo-F=15.77$ ;  $p=0.001$ ) or volume ( $r^2=0.38$ ;  $Pseudo-F=12.56$ ;  $p=0.001$ ), as determined through dbRDA models (Tables 1 & S4, Fig. 3). The model containing macroalgal species identities and densities explained slightly less (36%) of the variation in the fish assemblage but with more predictors (7 vs. 4). Within that model, site ( $Pseudo-F=1.69$   $p=0.001$ ), substratum PC 1 ( $Pseudo-F=3.92$ ;  $p=0.005$ ), density of *S. palmeri* ( $Pseudo-F=2.46$ ;  $p=0.03$ ), and density of *M. pyrifera* ( $Pseudo-F=3.46$ ;  $p=0.004$ ) were statistically significant, indicating that site-specific differences, rocky habitat, and densities of the macroalga *S. palmeri*, and *M. pyrifera*



**Fig. 3** Similarities in the fish assemblage pooled across seasons (sites as colors) with arrows representing the correlation with the MDS axes for density of the macroalgal species *M. pyrifera*, *S. horneri*, *S. palmeri*, and *S. neglecta*, for the two principle components summarizing physical habitat at sites, and for summed structural parameters of these algae: height, surface area, and volume. Multidimensional scaling (MDS) plot based on Euclidean distance.  $N=140$  transects

izing physical habitat at sites, and for summed structural parameters of these algae: height, surface area, and volume. Multidimensional scaling (MDS) plot based on Euclidean distance.  $N=140$  transects

**Table 1** Comparisons of models testing how well the multivariate fish assemblage, total fish density, diversity ( $H'$ ), vertical distribution, and biomass were predicted by physical substratum and site (together called “Habitat”) combined with either the densities of the four dominant macroalgal species (*M. pyrifera*, *Sargassum horneri*, *S. muticum*, and *Stephanocystis neglecta*), or macroalgal height, volume, or surface area summed across the four species; and also alone with just physical substratum and site (“Habitat”)

Model	Number of parameters	AICc	$\Delta_i$	$r^2$
<b>Fish assemblage</b>				
Macroalgal species	7	...	...	0.36
Height	4	...	...	0.32
Volume	4	...	...	0.38
Surface area	4	...	...	0.40
Habitat	3	...	...	0.30
<b>Fish density</b>				
Macroalgal species	15	350.82	27.46	0.09
Height	12	347.27	23.91	0.07
Volume	12	335.44	12.08	0.15
Surface area	12	323.36	0	0.22
Habitat	11	345.22	21.86	0.07
<b>Fish diversity</b>				
Macroalgal species	15	87.35	5.14	0.24
Height	12	82.22	0	0.23
Volume	12	86.73	4.52	0.20
Surface area	12	90.20	7.98	0.18
Habitat	11	95.46	13.24	0.14
<b>Vertical distribution</b>				
Macroalgal species	15	445.58	0	0.19
Height	12	446.41	0.83	0.14
Volume	12	450.64	5.06	0.11
Surface area	12	450.57	4.99	0.11
Habitat	11	448.48	2.90	0.11
<b>Fish biomass</b>				
Macroalgal species	15	327.45	0	0.35
Height	12	335.16	7.71	0.28
Volume	12	333.01	5.55	0.29
Surface area	12	332.38	4.93	0.30
Habitat	11	333.12	5.66	0.28

Results are from dbRDA for the multivariate fish assemblage (density and identity of each fish species) and general linear models for all other response variables. Samples were pooled across sites and time points ( $n = 140$ ). Density results are shown without highly abundant species *L. dalli* and *C. punctipinnis*. Proportion of fish density in the water column is shown as “Vertical distribution”. Best model (in gray shading) determined by AICc except for multivariate results for which only  $r^2$  is reported

were the primary predictors of the overall fish assemblage when considering macroalgal species. The “habitat”-only model (which included site and two PCs summarizing the rocky substratum, but no macroalgae variables as predictors) was the worst model, but still explained 75% of the

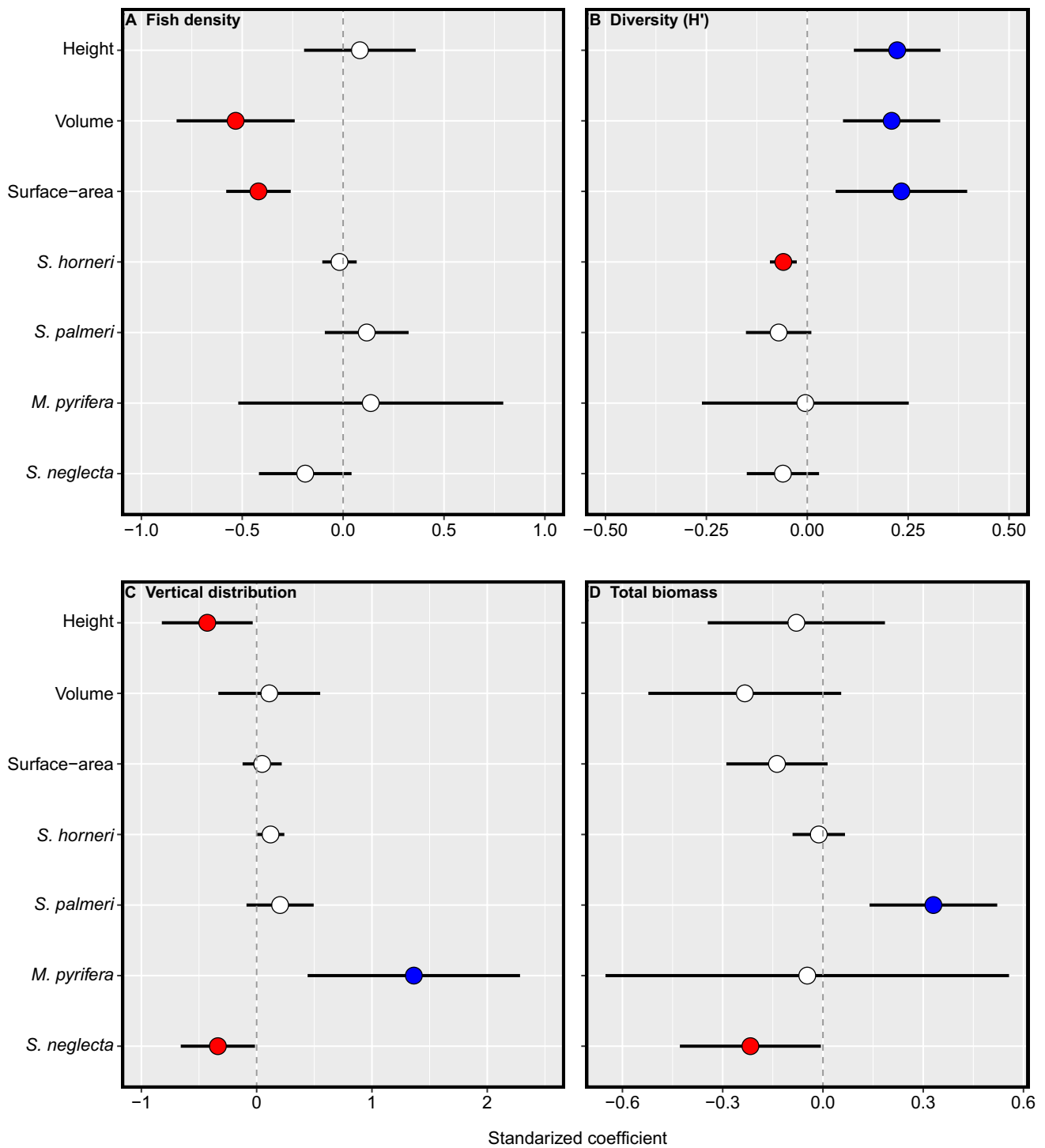
variance explained by the best model with macroalgae predictor variables ( $r^2 = 0.30$  vs 0.40) of the multivariate fish assemblage.

For univariate descriptors of the fish assemblage, the best models for predicting total fish density (all species combined minus the highly abundant *L. dalli*) contained the significant predictor variables macroalgal surface area (negatively related) and substratum PC 2 (positively related to large boulders and negatively related to cobble) (AICc =  $-118.80$ ,  $p < 0.001$ ; Tables 1 & S4). When the very abundant *C. punctipinnis* and *L. dalli* were removed from fish density, the model including macroalgal surface area was still the best predictor of variation in fish density, with which it was negatively related, but neither substratum PC was statistically significant; and this model explained only 22% total variation in fish density (AICc =  $-160.40$ ,  $p < 0.001$ ; Fig. 4; Tables 1 & S4). The model including macroalgal species identity and density explained less variance in fish density ( $r^2 = 0.09$  vs. 0.22) and consequently was much poorer than the macroalgal surface area model ( $\Delta\text{AIC} = 27.5$ ). The habitat only model explained only 7% ( $r^2 = 0.07$ ) of the variation in fish density. Fish species diversity ( $H'$ ) was best predicted by the model including summed macroalgal height, to which it was positively related (AICc =  $-27.88$ ,  $p < 0.001$ ; Fig. 4; Tables 1 & S4). The model including macroalgal species identity and density explained slightly more variance in fish diversity ( $r^2 = 0.24$  vs. 0.23) but included three more predictors, and consequently was a poorer model than the macroalgal surface area model ( $\Delta\text{AIC} = 5.1$ ). The habitat-only model was the least supported model ( $\Delta\text{AIC} = 13.2$ ), explaining only 14% ( $r^2 = 0.14$ ) of the variation in fish diversity.

In contrast to the preceding attributes of the fish assemblage, the vertical distribution of fish was best predicted by the macroalgal species identity and density rather than macroalgal structural attributes (AICc =  $-205.85$ ;  $r^2 = 0.19$ ; Fig. 4; Tables 1 & S4). Vertical distribution was lower in habitats with *S. neglecta* ( $\beta = -0.36$ ) and greater in habitats with *M. pyrifera*, *S. palmeri*, and *S. horneri*. This relationship was strong for *M. pyrifera*, but moderate to weak for *S. palmeri* and *S. horneri* ( $\beta = 1.36$ ,  $\beta = 0.20$  and  $\beta = 0.12$ , respectively). Of the models containing macroalgal structural attributes, height was the best predictor of variation in the vertical distribution of fishes, and this model had similar support as the macroalgal species identity and density model ( $\Delta\text{AIC} = 0.8$ ), but explained 5% less variance ( $r^2 = 0.14$ ; AICc =  $-209.97$ ; Tables 1 & 4; Fig. 4). The habitat-only model was the next best supported model ( $\Delta\text{AIC} = 2.9$ ), explaining 11% ( $r^2 = 0.11$ ) in fish vertical distribution.

Total fish biomass was also best explained by the model containing macroalgal species identity and density (AICc = 327.45,  $r^2 = 0.35$ ; Tables 1 & S4; Fig. 4), in which total biomass was positively related to density of *S. palmeri* ( $\beta = 0.33$ ) and negatively related to density of *S. neglecta*





**Fig. 4** Influence of summed macroalgal height, volume, surface area, or mean density of *S. horneri*, *S. palmeri*, *M. pyrifera*, or *S. neglecta*, on (A) fish density (without *L. dalli* and *C. punctipinnis*), (B) fish species diversity ( $H'$ ), (C) proportion of total fish density in the water

( $\beta = -0.22$ ). All of the models containing macroalgal structural attributes were poorer than the species identity and density models ( $\Delta AIC > 4.9$ ) and they explained virtually

column (i.e., vertical distribution of fish), and (D) biomass of fishes. Colored circles differ statistically significantly from zero whereas white circles do not. Standardized coefficients ( $\beta \pm 95\%$  confidence intervals) from general linear models are shown

no more variance ( $r^2 = 0.28-0.30$ ) than the model containing only “habitat” ( $r^2 = 0.28$ ; Table 1).

Densities of the six fish species we examined individually were better predicted by models containing structural

measures of macroalgae rather than species identity and density of macroalgae (Tables S5 and S6). For five of six species (*P. clathratus*, *H. semicinctus*, *O. californica*, *H. rubicundus*, and *L. dalli*), the model containing summed surface area of macroalgae was the best model (lowest AICc); and for the 6<sup>th</sup> species (*C. punctipinnis*), the model with summed height of macroalgae was best (though essentially statistically indistinguishable from any other model:  $\Delta\text{AIC} < 2$ ). For *P. clathratus*, the macroalgae surface area and volume models were indistinguishable ( $\Delta\text{AIC} = 0.7$ ); and for *H. semicinctus*, all models using summed structural attributes of macroalgae were indistinguishable ( $\Delta\text{AIC} < 2$ ). Notably, in the best supported models, density of each of the six species was negatively related to the quantity of macroalgae structure.

## Discussion

Heterogeneity in the physical arrangement of habitat structure can have important and complicated ecological effects (McCoy and Bell 1991; Kovalenko et al. 2012; Farina et al. 2014). In nearshore marine systems where macroalgal stands can transform the underwater landscape, spatial, and temporal variability in structural components of these biogenic habitats can influence distribution patterns and ecological processes (Mattila et al. 2008; Dijkstra et al. 2017; Miller et al. 2018). The goal of the present study was to determine if the physical structure of macroalgae was a better predictor of attributes of the fish assemblage than macroalgal species identity and density. Our results show that some of the complex influences of macroalgae on fish assemblages may be simplified by quantifying the physical dimensions of macroalgae rather than focusing on their species identity. However, other attributes of fish assemblages (e.g., biomass) were better predicted by macroalgal species identity and density, highlighting the importance of considering how macroalgae influence multiple attributes of the fish assemblage.

We found that total macroalgal surface area was the best predictor of the multivariate structure of the fish assemblage (identity and density of each fish species), total fish density (summed across species), and the densities of five of the six abundant fish species that we analyzed individually (and for the 6<sup>th</sup> species, the total surface area was as good as any other model, based on  $\Delta\text{AIC} < 2$ ). Surface area, the two-dimensional estimate of physical structure, was likely the best predictor of fish densities because algal surfaces (e.g., blades) are what fishes orient to for shelter (e.g., *Paralabrax clathratus*, Carr 1991), foraging (e.g., *Oxyjulis californica*, Bray and Ebeling 1975), or that they avoid (e.g., *Lythrypnus dalli*, authors' personal observations). Surface area likely better estimates the quantity of biogenic structure that influences fish than does macroalgal height or volume. Regarding

volume, for example, a long stretch of bladeless stipe may have considerable volume but little surface area. And for height, it is intuitive that a tall, skinny macroalga would be perceived by a fish as providing less biogenic habitat than a bushy macroalgae with more surface area. Thus, surface area may best predict differences in fish abundance caused by variation in the abundance of different macroalgal species because it is the physical characteristic of macroalgae that most influences fishes (Mattila et al. 2008; Stelling-Wood et al. 2020).

Volume, rather than surface area, has been used to quantify structural complexity (Hacker and Steneck 1990; Warfe et al. 2008) and reef size (Steele 1996) in other studies. In the present study, it was never the best predictor of any fish-assemblage response variable, though in most cases, its predictive power was similar to that of macroalgal surface area. This is no surprise given that volume and surface area were tightly correlated (Fig. S3). But our results suggest that effort spent quantifying habitat volume would better be spent on quantifying surface area.

Of the three physical attributes of macroalgae that we quantified, only one can readily be measured in the field: height. Summed height of macroalgae was a poorer predictor of density-related fish assemblage variables than were summed surface area or volume, but it was the best predictor of fish species diversity ( $H'$ ), which was positively related to height. No single macroalgal species had a significant positive relationship with fish diversity, so we interpret the positive influence of summed macroalgal height as indicating that areas (transects) with more macroalgae in the water column supported more diverse fish assemblages.

Two attributes of the fish assemblage we studied were best predicted by models that contained macroalgal species identity and abundance: fish distribution within the water column and fish biomass, highlighting the importance of considering the context of the effects of macroalgae on the fish assemblage. For vertical distribution of fishes, the proportion of fish in the water column was strongly positively related to the density of giant kelp (*Macrocystis pyrifera*) and more weakly negatively related to the density of *Stephanocystis neglecta*. Previous studies have shown that the vertical distribution of fishes within the water column is linked to the presence of *Macrocystis* extending into it (Holbrook et al. 1990; Anderson 1994; Carr 1991), which is typically the tallest species of macroalgae on temperate reefs in our study area. Anyone who has dived on a rocky reef with giant kelp will not be surprised that a greater fraction of the fishes are found up off the bottom, in the water column, where giant kelp is present. It provides biogenic structure with which several species associate, even if their relationship with giant kelp is not obligate. This finding indicates that *Macrocystis* does have a unique role on the rocky reefs we studied (e.g., it had the strongest effect on

vertical distribution), and it does so by virtue of its height in the water column, not by any other special morphological feature (Srednick & Steele 2019).

Fish biomass ( $\text{g transect}^{-1}$ ) was best predicted by a model with macroalgal species density and identity, in which fish biomass was most strongly related to the density of the native macroalgae *Sargassum palmeri*, which harbors dense invertebrate populations upon which several reef fishes feed (Scafidi 2020). It is not generally used as shelter by fishes (authors' personal observations). Giant kelp was not a significant predictor of fish biomass; and the strongest predictor of fish biomass was the rocky habitat, primarily large boulders (PC2), which provide shelter for many rock reef fishes (Stephens et al. 2006). The finding that fish biomass was less strongly related to macroalgal densities or attributes (e.g., surface area) fits the prevailing hypothesis that in areas with complex rocky reefs, biogenic structure of macroalgae has limited effects on fish assemblages, whereas on simple, low-relief and low-shelter reefs, macroalgae more strongly influence fishes (DeMartini and Roberts 1990; Stephens et al. 2006).

The present study was conducted during the longest and most extreme warm-water period ever recorded in the study region, a regional marine heatwave from 2014 to 2016 that increased regional average sea-surface temperature by  $\sim 3^\circ\text{C}$ , nicknamed “the Blob” (Lorenzo and Mantua 2016). During this period, giant kelp at our study sites was much less dense than the long-term average, and was similar to what was present during past extreme El Niño events (Bell et al. 2015). Although we did encounter *Macrocystis* at a number of study sites, the densities observed during the present study were not comparable to those observed in other studies on the influence of giant kelp on fishes at Santa Catalina Island (e.g., Holbrook et al. 1990; Carr 1991; Anderson 1994). Additionally, during the period of our study, the invasive macroalga *Sargassum horneri* had become a dominant space holder. Thus, our findings may not relate well to times or places with more abundant giant kelp, or to areas lacking *Sargassum horneri*. However, given the expected, continued anthropogenic warming of the ocean and the spread of *S. horneri*, our study may provide insight into future conditions on rocky reefs.

In contrast to previous assessments of the effects of macroalgal structure on fish assemblages (Carr 1989; DeMartini and Roberts 1990; Holbrook et al. 1990; Anderson 2001; Miller et al. 2018), in the present study, total fish density was negatively related to the amount of macroalgal structure. This result seems counterintuitive in light of the demonstrated positive effects of macroalgal structure (*but see* Shelamoff et al. 2020). A likely cause of the negative associations between fishes and abundance and quantity of macroalgae is that most of the fishes in the assemblage present during our study do not associate closely with macroalgae,

and instead rely more on the abiotic physical structure provided by the rocky sea floor. The numerically dominant species on the reefs studied was *Lythrypnus dalli*, a rock-crevice-dwelling goby that does not use macroalgae and was negatively associated with density of *Macrocystis* as well as all three measures of algal quantity (height, surface area, and volume; Table S6). Although some species known to associate tightly with macroalgae were exceedingly rare during the present study (e.g., *Brachyistius frenatus* and *Heterostichus rostratus*; Table S3), another species that associates with macroalgae, *Oxyjulis californica*, was strongly positively associated with density of the invasive *S. horneri*. Another species sufficiently abundant for statistical analysis *Paralabrax clathratus* and with a demonstrated algal association in the recently settled stage (Carr 1989, 1991; Holbrook et al. 1990), was in fact more closely tied to physical substratum (PC 2; i.e., high cover of large boulders) than abundance of any particular macroalgal species or unique structure provided by macroalgae. As an adult, this species is not tightly linked to giant kelp (Holbrook et al. 1990) and we pooled all life stages of this species, which emphasized the older life stages that are less tied to giant kelp because they were more abundant than recent recruits during our study. Thus, the high numerical abundance of habitat generalists that can rely on the complex physical structure of rocky reefs we studied, as well as potentially the behavioral plasticity of rocky reef fishes (Angel and Ojeda 2001; Perez-Matus et al. 2012), likely resulted in the negative relationship between fish density and quantity of algal structure that we document here. Similarly, Holbrook et al. (1990) documented negative relationships between fish density and giant kelp abundance for several rocky reef fishes that inhabit kelp forests.

In the present study, we describe differences in the explanatory power of different attributes of the macroalgal assemblage in predicting aspects of the fish assemblage. Our statistical models, however, explained  $< 40\%$  of the variation in various descriptors of the fish assemblage. That our relatively simple statistical models could not predict a larger portion of the spatiotemporal variation in the fish assemblage is no surprise and is a frequent outcome in studies of comparable design and scope (Witman et al. 2015; Ginther and Steele 2020). The limited explanatory power of our models is likely due to a variety of factors, notably including variation in larval delivery among our study sites (e.g., Steele et al. 2002; Krug and Steele 2013), our sampling across seasonal settlement (i.e., we collected data before, during, and after strong pulses of settlement, across which densities of a species at a site varied dramatically), and the influence of physical substratum in driving variation in the fish and algal assemblages (Randell et al. 2022). The modest to low explained variance in our study is not, however, likely due to limiting our statistical exploration to only four species of macroalgae. These four species (*Macrocystis pyrifera*,

*Sargassum horneri*, *S. palmeri*, and *Stephanocystis neglecta*) provided the majority of macroalgal physical structure on our study reefs. Moreover, including all macroalgae on our study reefs as predictors in models did not result in better-supported models that explained much more variance in fish assemblage attributes than the models presented here (Srednick 2018 and additional analyses not shown).

Similar to Ginther and Steele (2020), we found little evidence that the invasive macroalga *Sargassum horneri* affects the fish assemblage at our study sites. Diversity ( $H'$ ) was significantly but only weakly (i.e., low  $\beta$ ) negatively related to the abundance of this species. ( $H'$  was also weakly, though not statistically significantly, negatively related to abundance of the three native macroalgae species.) And the density of *O. californica* was positively related to this invasive alga. We suggest that any impacts of this invasive species on fishes in our study area are due to the biogenic structure it creates. Of the four macroalgae we focused on, abundance of *S. horneri* was most strongly (positively) correlated with summed surface area of macroalgae, and thus, it may be most responsible for the negative relationships between fish density and surface area of macroalgae as also evidenced by a significant negative correlation between fish density and the surface area of *S. horneri* ( $r = -0.37$ ,  $p < 0.001$ ). Elsewhere we have shown experimentally that some attributes of the fish assemblage appear to be more linked to the quantity of algal structure rather than the species composition (Srednick and Steele 2019).

The present study, however, is limited in its assessment of how a change in the dominant macroalgae (e.g., a shift from *Macrocystis pyrifera* to *S. horneri*) might influence ecological interactions. Moreover, the long-term effects of a change in macroalgal structure on population and community dynamics (e.g., fish recruitment, community and trophic web stability) may differ from what is observed over shorter periods, such as during this study, and lag effects may be important drivers of ecosystem change (Dayton 1985). Over the long term, sea-surface temperatures and the frequencies of storms and heatwave events are expected to increase (Easterling et al. 2000; Hansen et al. 2007). Kelp forest communities are particularly vulnerable to these stressors (Wernberg et al. 2013; Filbee-Dexter et al. 2016; Simonson et al. 2015; Reed et al. 2016), and reduction in kelp cover and increases in invasive species may have lasting effects on the community (Steneck et al. 2002; Graham 2004; Caselle et al. 2018).

This study highlights the value of assessing the physical structure that biogenic habitats provide, instead of only the identities and densities of habitat forming species (e.g., macroalgae and corals). In this study, we illustrate that physical, structural attributes of biotic habitat can be at least as important to measure as species identity and density for understanding how animals respond to vegetative components of

the community. Likely, this will be most true of communities composed primarily of animals that are vegetative habitat generalists, rather than ones with many tightly coevolved relationships between animals and plants. Future studies that incorporate estimates of the quantity of biogenic habitat (e.g., surface area of macroalgae or corals), rather than just species abundance, may improve our ability to predict how marine communities will respond to changes in the composition of the biotic habitat formers.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00227-022-04135-7>.

**Acknowledgements** We thank Sam Ginther, Russell Dauksis, Malek Al-Marayati, Juan Aguilar, Trevor Oudin, Lauren Czarnecki Oudin, and the entire staff of the Wrigley Marine Science Center (WMSC) for assistance with this project. This research was conducted in partial fulfillment of a Master of Science degree by G.S. at California State University Northridge (CSUN). We thank Larry Allen, Robert Carpenter, Peter Edmunds for advice and for reviewing drafts of this manuscript. Mark Carr, Scott Hamilton, and four anonymous reviewers also provided helpful comments on drafts of this manuscript. This research was funded by the Myers Oceanographic Trust, Lerner Gray Memorial Fund, the PADI Foundation Scholarship, CSU Northridge Graduate Thesis Support, and the International Women's Fishing Association. This is contribution number 371 of the CSUN Marine Biology program and 260 of WMSC.

**Author contributions** Griffin Srednick and Mark Steele contributed to the study conception and design. Material preparation, data collection and analysis were performed by Griffin Srednick and Mark Steele. The first draft of the manuscript was written by Griffin Srednick and both authors commented on previous versions of the manuscript. Both authors read and approved the final manuscript.

**Funding** Open Access funding enabled and organized by CAUL and its Member Institutions. Myers Oceanographic Trust, Lerner Gray Memorial Fund, PADI Foundation, International Women's Fishing Association, CSU Northridge Graduate Thesis Support

**Data availability** Datasets analyzed for this study are available on Zenodo: <https://doi.org/10.5281/zenodo.7251212>.

**Code availability** Code available at [github.com/gredsrednick/algalstructure\\_pub](https://github.com/gredsrednick/algalstructure_pub).

## Declarations

**Conflict of interest** The authors have not disclosed any competing interests.

**Ethical approval** This work was conducted in compliance with all ethical standards and necessary permitting. Authors declare no conflict of interest.

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## References

- Anderson TW (1994) Role of macroalgal structure in the distribution and abundance of a temperate reef fish. *Mar Ecol Prog Ser* 113(279):290. <https://doi.org/10.3354/meps113279>
- Anderson TW (2001) Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecol* 82:245–257. [https://doi.org/10.1890/0012-9658\(2001\)082%5B0245:PRPRAD%5D2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082%5B0245:PRPRAD%5D2.0.CO;2)
- Anderson TW, Demartini EE, Roberts DA (1989) The relationship between habitat structure, body size and distribution of fishes at a temperate artificial reef. *Bull Mar Sci* 44(2):681–697
- Angel A, Ojeda FP (2001) Structure and trophic organization of subtidal fish assemblages on the northern Chilean coast: The effect of habitat complexity. *Mar Ecol Prog Ser* 217(81):91. <https://doi.org/10.3354/meps217081>
- Arkema KK, Reed DC, Schroeter SC (2009) Direct and indirect effects of giant kelp determine benthic community structure and dynamics. *Ecol* 90:3126–3137. <https://doi.org/10.1890/08-1213.1>
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67(1):1–48
- Bell TW, Cavanaugh KC, Siegel DA (2015) Remote monitoring of giant kelp biomass and physiological condition: an evaluation of the potential for the hyperspectral Infrared Imager (HypSIIRI) mission. *Remote Sens Environ* 167(218):228
- Boettiger C, Temple Lang D, Wainwright P (2012) rfishbase: exploring, manipulating and visualizing fishbase data from r. *J of Fish Biol.* <https://doi.org/10.1111/j.1095-8649.2012.03464.x>
- Bolker B, Robinson D (2021). broom.mixed: tidying methods for mixed models. r package version 0.2.7. <https://CRAN.R-project.org/package=broom.mixed>
- Boström C, Jackson EL, Simenstad CA (2006) Seagrass landscapes and their effects on associated fauna: a review. *Estuar Coast Shelf Sci* 68:383–403. <https://doi.org/10.1016/j.ecss.2006.01.026>
- Bray RN, Ebeling AW (1975) Food, activity, and habitat of three “picker-type” microcarnivorous fishes in kelp forests off Santa Barbara, California. *Fish Bull* 73:815–829
- Burnham KP, Anderson DR (2004) Model selection and multimodel inference, a practical information-theoretic approach. 437–454.
- Byrnes JE, Reed DC, Cardinale BJ, Cavanaugh KC, Holbrook SJ, Schmitt RJ (2011) Climate-driven increases in storm frequency simplify kelp forest food webs. *Global Change Biol* 17:2513–2524. <https://doi.org/10.1111/j.1365-2486.2011.02409.x>
- Carr MH (1989) Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. *J Exp Mar Biol Ecol* 126:59–76. [https://doi.org/10.1016/0022-0981\(89\)90124-X](https://doi.org/10.1016/0022-0981(89)90124-X)
- Carr MH (1991) Habitat selection and recruitment of an assemblage of temperate zone reef fishes. *J Exp Mar Biol Ecol* 146:113–137. [https://doi.org/10.1016/0022-0981\(91\)90257-W](https://doi.org/10.1016/0022-0981(91)90257-W)
- 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. <https://doi.org/10.1111/ele.12869>
- Castorani MCN, Reed DC, Miller RJ (2018) Loss of foundation species: disturbance frequency outweighs severity in structuring kelp forest communities. *Ecology* 99:2442–2454. <https://doi.org/10.1002/ecs.2485>
- Choat JH, Schiel DR (1985) Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. *J Exp Mar Biol Ecol* 60:129–162. [https://doi.org/10.1016/0022-0981\(82\)90155-1](https://doi.org/10.1016/0022-0981(82)90155-1)
- Crowder LB, Cooper WE (1982) Habitat structural complexity and the interaction between bluegills and their prey (*Lepomis macrochirus*). *Ecology* 63:1802
- Dayton PK (1985) Ecology of kelp communities. *Annu Rev Ecol Syst* 16:215–245. <https://doi.org/10.1146/annurev.es.16.110185.001243>
- Demartini EE, Roberts DA (1990) Effects of giant kelp (*Macrocystis*) on the density and abundance of fishes in a cobble-bottom kelp forest. *Bulletin of Marine* 46(287):300
- Dijkstra JA, Harris LG, Mello K, Litterer A, Wells C, Ware C (2017) Invasive seaweeds transform habitat structure and increase biodiversity of associated species. *J Ecol* 105:1668–1678. <https://doi.org/10.1111/1365-2745.12775>
- Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. *Science* 289:2068–2074. <https://doi.org/10.1126/science.289.5487.2068>
- Farina S, Arthur R, Pagès JF, Prado P, Romero J, Vergés A, Hyndes G, Heck KL, Glenos S, Alcoverro T (2014) Differences in predator composition alter the direction of structure-mediated predation risk in macrophyte communities. *Oikos* 123(1311):1322
- Filbee-Dexter K, Feehan C, Scheibling R (2016) Large-scale degradation of a kelp ecosystem in an ocean warming hotspot. *Mar Ecol Prog Ser* 543:141–152. <https://doi.org/10.3354/meps11554>
- Franklin JF (1988) Structural and functional diversity in temperate forests. Biodiversity. – National Academy Press, Washington, DC, 166–175.
- Ginther S, Steele M (2018) Limited recruitment of an ecologically and economically important fish, *Paralabrax clathratus*, to an invasive alga. *Mar Ecol Prog Ser* 602:213–224. <https://doi.org/10.3354/meps12673>
- Ginther S, Steele M (2020) Limited effects of *Sargassum horneri*, an invasive alga, on temperate reef fish assemblages. *Mar Ecol Prog Ser* 643:115–131. <https://doi.org/10.3354/meps13321>
- Graham MH (2004) Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. *Ecosystems* 7:341–357. <https://doi.org/10.1007/s10021-003-0245-6>
- Graham MH, Halpern BS, Carr MH (2008) Diversity and dynamics of Californian subtidal kelp forests. Food webs and the dynamics of marine reefs. Oxford University Press, New York, pp 103–134
- Gregor CA, Anderson TW (2016) Relative importance of habitat attributes to predation risk in a temperate reef fish. *Environ Biol Fish* 99:539–556. <https://doi.org/10.1007/s10641-016-0496-7>
- Gutow L, Long JD, Cerda O, Hinojosa IA, Rothäusler E, Tala F, Thiel M (2012) Herbivorous amphipods inhabit protective microhabitats within thalli of giant kelp *Macrocystis pyrifera*. *Mar Biol* 159:141–149. <https://doi.org/10.1007/s00227-011-1794-4>
- Hacker SD, Steneck RS (1990) Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. *Ecology* 71:2269–2285. <https://doi.org/10.2307/1938638>
- Hansen J, Sato M, Ruedy R, Lo K, Lea DW, Medina-elizade M (2007) Global temperature change. *Proc National Acad Sci.* <https://doi.org/10.1073/pnas.0606291103>
- Hobson ES, Chess JR (2001) Influence of trophic relations on form and behavior among fishes and benthic invertebrates in some California marine communities. *Environ Biol Fish* 60:411–457. <https://doi.org/10.1023/A:1011027312001>
- Hoegh-Guldberg O (1988) A method for determining the surface area of corals. *Coral Reefs* 7(113):116. <https://doi.org/10.1007/BF00300970>



- Holbrook SJ, Schmitt RJ, Ambrose RF (1990) Biogenic habitat structure and characteristics of temperate reef fish assemblages. *Aust J Ecol* 15:489–503. <https://doi.org/10.1111/j.1442-9993.1990.tb01473.x>
- Hovel KA, Warneke AM, Virtue-Hilborn SP, Sanchez AE (2016) Mesopredator foraging success in eelgrass (*Zostera marina* L.): Relative effects of epiphytes, shoot density, and prey abundance. *J Exp Mar Biol Ecol* 474:142–147. <https://doi.org/10.1016/j.jembe.2015.10.014>
- Jones GP (1992) Interactions between herbivorous fishes and macro-algae on a temperate rocky reef. *J Exp Mar Biol Ecol* 159(217):235. [https://doi.org/10.1016/0022-0981\(92\)90038-C](https://doi.org/10.1016/0022-0981(92)90038-C)
- Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecol* 78:1946–1957. [https://doi.org/10.1890/0012-9658\(1997\)078%5B1946:PA NEO%5D2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078%5B1946:PA NEO%5D2.0.CO;2)
- Kahle D, Wickham H (2013) ggmap: Spatial Visualization with ggplot2. *R J* 5(1):144–161. <http://journal.r-project.org/archive/2013-1/kahle-wickham.pdf>
- Kovalenko KE, Thomaz SM, Warfe DM (2012) Habitat complexity: approaches and future directions. *Hydrobiologia* 685:1–17
- Krug J, Steele M (2013) Larval exposure to shared oceanography does not cause spatially correlated recruitment in kelp forest fishes. *Mar Ecol Prog Ser* 477:177–188. <https://doi.org/10.3354/meps10144>
- Lamy T, Koenigs C, Holbrook SJ, Miller RJ, Stier AC, Reed DC (2020) Foundation species promote community stability by increasing diversity in a giant kelp forest. *Ecol* 101:e02987. <https://doi.org/10.1002/ecy.2987>
- Larson RJ, Demartini EE (1985) Abundance and vertical distribution of fishes in a cobble-bottom kelp forest off San-Onofre California USA. *Fish Bull* 82(37):54
- Lawton JH (1983) Plant architecture and the diversity of phytophagous insects. *Annu Rev Entomol* 28:23–39. <https://doi.org/10.1146/annurev.en.28.010183.000323>
- Pauly D, Morgan GR (ed) (1987) Length-based methods in fisheries research. *WorldFish*, 13
- Levin P, Hay M (1996) Responses of temperate reef fishes to alterations in algal structure and species composition. *Mar Ecol Prog Ser* 134:37–47. <https://doi.org/10.3354/meps134037>
- Levin PS, Hay ME (2002) Fish-seaweed association on temperate reefs: do small-scale experiments predict large-scale patterns? *Mar Ecol Prog Ser* 232(239):246. <https://doi.org/10.3354/meps232239>
- Lewis LS, Anderson TW (2012) Top-down control of epifauna by fishes enhances seagrass production. *Ecol* 93:2746–2757. <https://doi.org/10.1890/12-0038.1>
- Lorenzo ED, Mantua N (2016) Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nat Clim Change* 6:1042–1047. <https://doi.org/10.1038/nclimate3082>
- Marks L, Salinas-Ruiz P, Reed D, Holbrook S, Culver C, Engle J, Kushner D, Caselle J, Freiwald J, Williams J, Smith J, Aguilar-Rosas L, Kaplanis N (2015) Range expansion of a non-native, invasive macroalga *Sargassum horneri* (Turner) C. agardh, 1820 in the eastern Pacific. *Bioinvasions Rec* 4:243–248. <https://doi.org/10.3391/bir.2015.4.4.02>
- Mattila J, Heck KL, Millstein E, Miller E, Gustafsson C, Williams S, Byron D (2008) Increased habitat structure does not always provide increased refuge from predation. *Mar Ecol Prog Ser* 361(15):20. <https://doi.org/10.3354/meps07392>
- McCoy ED, Bell SS (1991) Habitat structure: the evolution and diversification of a complex topic. *Habitat structure*. Springer, Dordrecht, pp 3–2
- McElhinny C, Gibbons P, Brack C, Bauhus J (2005) Forest and woodland stand structural complexity: Its definition and measurement. *Forest Ecol Manag* 218:1–24. <https://doi.org/10.1016/j.foreco.2005.08.034>
- Miller RJ, Lafferty KD, Lamy T, Kui L, Rassweiler A, Reed DC (2018) Giant kelp, *Macrocystis pyrifera*, increases faunal diversity through physical engineering. *Proc Royal Soc B* 285:2017–2571. <https://doi.org/10.1098/rspb.2017.2571>
- Noss RF (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conserv Biol* 4:355–364. <https://doi.org/10.1111/j.1523-1739.1990.tb00309.x>
- O'Brien BS, Mello K, Litterer A, Dijkstra JA (2018) Seaweed structure shapes trophic interactions: a case study using a mid-trophic level fish species. *J Exp Mar Biol Ecol* 506:1–8. <https://doi.org/10.1016/j.jembe.2018.05.003>
- Oksanen JF, Blanchet G, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry Stevens MH, Szoecs E, Wagner H (2020). *vegan: community ecology package*. R package version 2.5–7. <https://CRAN.R-project.org/package=vegan>
- Parker J, Duffy J, Orth R (2001) Plant species diversity and composition: experimental effects on marine epifaunal assemblages. *Mar Ecol Prog Ser* 224:55–67. <https://doi.org/10.3354/meps224055>
- Pedersen TL (2010) Patchwork: The Composer of Plots. R package version 1.1.1. –<<https://CRAN.R-project.org/package=patchwork>>
- Pérez-Matus A, Shima JS (2010a) Disentangling the effects of macroalgae on the abundance of temperate reef fishes. *J Exp Mar Biol Ecol* 388:1–10. <https://doi.org/10.1016/j.jembe.2010.03.013>
- Pérez-Matus A, Pledger S, Daz FJ, Ferry LA, Vsquez JA (2012) Plasticity in feeding selectivity and trophic structure of kelp forest associated fishes from northern Chile. *Rev Chil Hist Nat* 85:29–48. <https://doi.org/10.4067/s0716-078x2012000100003>
- Randell Z, Kenner M, Tomoleoni J, Yee J, Novak M (2022) Kelp-forest dynamics controlled by substrate complexity. *Proc National Acad Sci* 119:e2103483119. <https://doi.org/10.1073/pnas.2103483119>
- Reed DC, Rassweiler AR, Miller RJ, Page HM, Holbrook SJ (2016) The value of a broad temporal and spatial perspective in understanding dynamics of kelp forest ecosystems. *Mar Freshwater Res.* <https://doi.org/10.1071/MF14158>
- Rstudio Team (2020) Rstudio: Integrated Development for R. Rstudio, Inc., Boston, MA – <<http://www.rstudio.com/>>
- Sala E, Graham MH (2002) Community-wide distribution of predator–prey interaction strength in kelp forests. *Proc National Acad Sci* 99(3678):3683. <https://doi.org/10.1073/pnas.052028499>
- Scafidi K (2020) Trophic effects of an invasive alga in a temperate reef system. California State University Northridge, Northridge, CA, USA
- Shelamoff V, Layton C, Tatsumi M, Cameron MJ, J JTW, Edgar GJ, Johnson CR (2020) High kelp density attracts fishes except for recruiting cryptobenthic species. *Mar Environ Res* 161:105127. <https://doi.org/10.1016/j.marenvres.2020.105127>
- Simonson E, Scheibling R, Metaxas A (2015) Kelp in hot water: i. Warming seawater temperature induces weakening and loss of kelp tissue. *Mar Ecol Prog Ser* 537:89–104. <https://doi.org/10.3354/meps11438>
- Sokal RR, Rohlf FJ (1995) *Biometry: the principles and practice of statistics in biological research*. – Macmillan.
- Solt F, Hu Y (2018) Dotwhisker: Dot-and-whisker plots of regression results. r package version 0.5.0. –<<https://CRAN.R-project.org/package=dotwhisker>>
- Srednick G (2018) The influence of the structure of an invasive alga on the distribution of temperate reef fishes. California State University Northridge, Northridge, CA, USA
- Srednick G, Steele M (2019) Macroalgal height is more important than species identity in driving differences in the distribution and behavior of fishes. *Mar Ecol Prog Ser* 613:139–149. <https://doi.org/10.3354/meps12898>
- Steele MA (1996) Effects of predators on reef fishes: separating cage artifacts from effects of predation. *J Exp Mar Biol Ecol* 198:249–267. [https://doi.org/10.1016/0022-0981\(96\)00011-1](https://doi.org/10.1016/0022-0981(96)00011-1)

- 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. <https://doi.org/10.3354/meps235195>
- Stelling-Wood TP, Gribben PE, Poore AGB (2020) Habitat variability in an underwater forest: using a trait-based approach to predict associated communities. *Funct Ecol* 34:888–898. <https://doi.org/10.1111/1365-2435.13523>
- Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ Conserv* 29(436):459. <https://doi.org/10.1017/S0376892902000322>
- Stephens JS, Larson RJ, Pondella DJ (2006) The ecology of marine fishes. *California Adjacent Waters*. <https://doi.org/10.1525/9780520932470-011>
- Stewart HL, Carpenter RC (2003) The effects of morphology and water flow on photosynthesis of marine macroalgae. *Ecol* 84(2999):3012. <https://doi.org/10.1890/02-0092>
- Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J Biogeogr* 31(79):92. <https://doi.org/10.1046/j.0305-0270.2003.00994.x>
- van Lier JR, Wilson SK, Depczynski M, Wenger LN, Fulton CJ (2018) Habitat connectivity and complexity underpin fish community structure across a seascape of tropical macroalgae meadows. *Landscape Ecol* 33:1287–1300. <https://doi.org/10.1007/s10980-018-0682-4>
- Ware C, Dijkstra J, Mello K, Stevens A, O'Brien B, Ikedo W (2019) A novel three dimensional analysis of functional-architecture that describes the properties of macroalgae as refuge. *Mar Ecol Prog Ser* 608:93–103. <https://doi.org/10.3354/meps12800>
- Warfe DM, Barmuta LA, Wotherspoon S (2008) Quantifying habitat structure: surface convolution and living space for species in complex environments. *Oikos* 117:1764–1773. <https://doi.org/10.1111/j.1600-0706.2008.16836.x>
- Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, Bettignies TD, Bennett S, Rousseaux CS (2013) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nat Clim Change* 3(78):82. <https://doi.org/10.1038/nclimate1627>
- Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Bache SM, Müller K, Ooms J, Robinson D, Seidel DP, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019) Welcome to the tidyverse. *J Open Sour Software*. <https://doi.org/10.21105/joss.01686>
- Wilson SK, Fulton CJ, Depczynski M, Holmes TH, Noble MM, Radford B, Tinkler P (2014) Seasonal changes in habitat structure underpin shifts in macroalgae-associated tropical fish communities. *Mar Biol* 161(2597):2607. <https://doi.org/10.1007/s00227-014-2531-6>
- Witman JD, Lamb RW, Byrnes JEK (2015) Towards an integration of scale and complexity in marine ecology. *Ecol Monogr* 85:475–504. <https://doi.org/10.1890/14-2265.1>

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