



# Variable fish habitat function in two open-coast eelgrass species

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**ABSTRACT:** Eelgrasses *Zostera* are foundation species that perform myriad ecosystem services, yet research into their habitat function is often focused on regions susceptible to intense anthropogenic disturbance. This trend has created a data gap on the role more remote eelgrass beds provide among the mosaic of other temperate marine habitats. In this study, we surveyed 15 *Z. marina* and *Z. pacifica* beds along Catalina Island and the Southern California Bight (SCB) mainland coast from 2018 to 2020 for areal coverage, structural components and fish assemblages, from which a relativized index of fish utilization was then created. We then evaluated the landscape and structural components that potentially drive fish utilization in *Z. marina* using the index as a response variable in a model selection procedure. *Zostera* beds ranged in size from 0.06 ha to >27.5 ha. Fish assemblages in *Z. marina* and *Z. pacifica* beds were significantly different, and in the case of fishes found in both, individuals were often below size at maturity in *Z. marina* and above size in *Z. pacifica*. Distance to the nearest reef and bed area, both positively related to the fish assemblage index, were the most important factors. The results suggest *Z. marina* beds function as a nursery habitat while *Z. pacifica* are used by mid-level predators for foraging. These data represent the first rigorous study of fish utilization of open-coast *Z. marina* and *Z. pacifica* beds, and are invaluable to marine spatial planning efforts that may incorporate a more holistic approach to habitat management in temperate regions.

**KEY WORDS:** Eelgrass · Habitat function · Fish assemblage

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## 1. INTRODUCTION

Understanding a habitat's function is integral for effective management in marine systems (Caldow et al. 2015). Habitat function is defined by how species assemblages utilize a specific area or biogenic structure to feed, mate or rear their offspring. Such information allows for the application of ecosystem-based marine spatial planning to balance the many natural and anthropogenic stressors that can affect species and ecosystems (Foley et al. 2010, Pinarbaşı et al. 2017). For example, foundation species in tropical and subtropical regions such as coral reefs, man-

groves and seagrasses play an important role in supporting the early life history stages of fishes (Barbier 2017). The overlap of fish species among each of these different ecosystems indicate a strong connection between the 3 habitats (Honda et al. 2013). These findings illustrate the need to conserve an entire habitat network rather than invoking a single-habitat management approach (Luo et al. 2009). It is difficult to tease apart the ecological function of one habitat from another, as well as to determine how landscape structure affects nearshore ecosystem functions such as refuge from predation and biological production, since relatively few studies have

recorded these behaviors occurring in nature (Able 2016, Munsch et al. 2016). Evaluating the function of nearshore environments *in situ* will improve our knowledge of the mechanisms that drive the differential use of these habitats and can inform the conservation and management of coastal ecosystems (Boström et al. 2006, Olson et al. 2019).

Seagrasses are marine flowering plants found worldwide in shallow waters and form the basis of one of the most productive ecosystems on Earth (Larkum et al. 2006). In the northern hemisphere, coastal eelgrass *Zostera* beds are the most widely distributed genera of seagrasses and provide a variety of ecosystem services, including the biogeochemical cycling of nutrients (Zarnoch et al. 2017), reducing the abundance of harmful bacteria in the water column (Lamb et al. 2017, Reusch et al. 2021) and providing nursery habitat for fishes (Beck et al. 2001, Heck et al. 2003, Tanner et al. 2019). The shallow coastal waters inhabited by eelgrass often brings it into conflict with anthropogenic actions that affect its ecological function and stability (Obaza et al. 2015, Shelton et al. 2017). For instance, coastal development and eutrophication can reduce the amount of sunlight available for photosynthesis (Eriander et al. 2017), directly remove vegetation and increase turbidity (Sabot et al. 2005) and may alter patterns of sedimentation, thus creating unsuitable conditions for the growth and survival (Patrick et al. 2016). In order to protect this biologically and economically valuable habitat, many resource agencies seek to achieve no net loss in the function of these systems (Levrel et al. 2012). This already daunting management feat is further challenged in areas where eelgrass is located along remote coastlines which are difficult to access, and in other cases in areas where there is limited information on eelgrass resources altogether (Long & Thom 2001).

The threats facing seagrass habitat, coupled with the knowledge that such areas are an important component in shaping the ecological connectivity amongst species, underscores the need to further understand the ecosystem function of open-coast *Zostera* beds relative to other temperate marine environments (Hauxwell et al. 2003, Ward et al. 2003, Lefcheck et al. 2017, McCune et al. 2020). However, temperate seagrasses such as *Zostera*, are often associated with estuarine habitats and not the open-coast environment (Moran et al. 2003, Park et al. 2013, Sherman & DeBruyckere 2018). The State of California, USA, for example, has not incorporated open-coast eelgrass beds into marine spatial planning efforts, as they have with other productive marine habitats including rocky reefs and kelp forests. The Southern California Bight (SCB),

which stretches along ~700 km of coastline from Point Conception in California to Ensenada in Mexico (Fig. 1), is host to 48 different marine protected areas (MPAs). Amongst these, <1% are listed as containing eelgrass, and half of those are located along open-coast environments (CDFW 2016). This focus on eelgrass habitats in estuaries is reasonable, as it is easier to find seagrass in shallow, low-energy areas, and this is where seagrass is likely to come into conflict with anthropogenic activities. There may also simply be more eelgrass in these sheltered environments, as was found in Nordic countries (Boström et al. 2014). Regardless, the physical setting of *Zostera* beds can affect response to stressors, and provides a basis for investigating differential habitat function (Cabello-Pasini et al. 2002, Fredericksen et al. 2004). As the SCB has 2 species of *Zostera* that are found on the open-coast and the region is consistent with the common inclination of temperate seagrass studies in estuarine environments (but see Altstatt 2003, Engle & Miller 2005, Coyer et al. 2008, Olsen et al. 2014), this setting is ideal to explore the question of differential habitat function.

Characterizing habitat function requires the use of multiple survey approaches that maximize the trade-off between limited field resources and data utility. A review of seagrass monitoring plans reveals numerous tiered approaches with general characteristics (e.g. bed size) as the base requirement followed by increasingly specific data at fewer locations geared towards a function of interest (Neckles et al. 2011, Unsworth et al. 2014). Fish assemblages are commonly included as a more specific aim to characterize seagrass habitat given their value as indicator species and relationship to economic value (Araújo et al. 2000). Numerous methodologies exist to sample fishes in seagrass, and there are tradeoffs to each, making available resources and site-specific traits dictate the best approach (French et al. 2021). In areas with reliable visibility and low currents, underwater visual census on SCUBA is effective at collecting data suitable to delineating diversity, biomass and guild use (Murphy & Jenkins 2010, Nakamura 2010, Chirico et al. 2017). Beyond those metrics, the assemblage data may be applied to create an index useful in comparing relative habitat value (Harrison & Whitfield 2021). Applying a tiered survey approach to collect both broad information on seagrass characteristics and more specific data, such as fish utilization, will provide understanding of habitat function in understudied open-coast eelgrass beds.

The purpose of this study was to describe the fish habitat function of open-coast *Zostera* beds exposed to different physical forces, and likely different anthro-

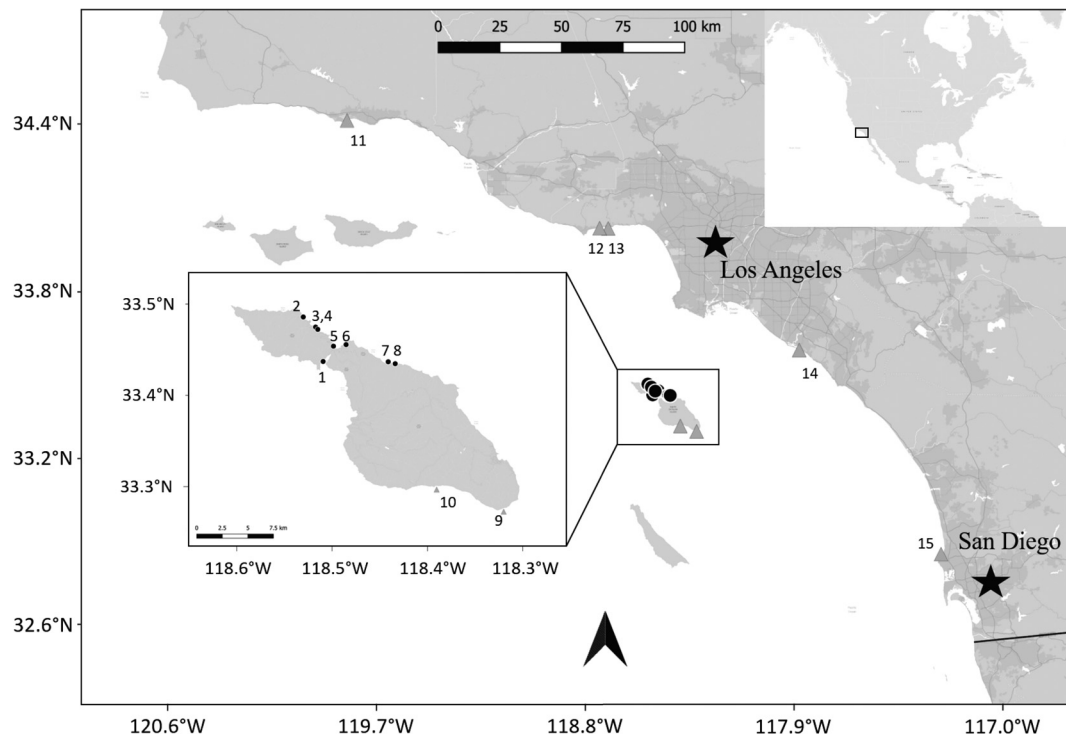


Fig. 1. Survey sites throughout the Southern California Bight (SCB) where eelgrass species is identified by shape. Starting on the most northern site on the windward side and moving clockwise around Catalina Island, survey locations were (1) Catalina Harbor, (2) Emerald Bay, (3) Big Geiger Cove, (4) Little Geiger Cove, (5) Isthmus Harbors, (6) Big Fisherman's Cove, (7) Empire Landing, (8) Ripper's Cove, (9) East End, and (10) Palisades. Moving from north to south on the mainland, survey locations were (11) Isla Vista, (12) Amarillo Beach, (13) Corral Canyon, (14) Newport Bay Entrance Channel and (15) La Jolla

pogenic stressors, than those found in estuaries. In particular, our goals were to determine the landscape and structural components of *Z. pacifica* and *Z. marina* that drive fish utilization, which occur as either overlapping or discrete beds off Catalina Island, located in the California Channel Islands, and along the mainland coast of the SCB. Habitat complexity was evaluated using a relativized fish utilization index based on *in situ* measurements of the (1) composition and size structure of fish assemblages and (2) areal coverage and structural complexity of open-coast *Z. marina* and *Z. pacifica* beds. These data will greatly improve the ability of scientists and policy makers to prepare for and respond to changes in marine habitats and their associated fauna both now and in the future.

## 2. MATERIALS AND METHODS

### 2.1. Study sites

Surveys were conducted annually during the summer and fall months from 2018–2020 at 15 sites com-

prised of either *Zostera marina* or *Z. pacifica* in the SCB (Fig. 1). Five sites were located along the mainland coast of the SCB (Isla Vista, Corral Canyon, Amarillo Beach, Newport Bay, and La Jolla), and 10 were situated off Catalina Island (Palisades, East End, Ripper's Cove, Empire Landing, Big Fisherman's Cove, Catalina Harbor, Isthmus Harbor, Emerald Bay, Little Geiger, and Big Geiger Cove), located ~35 km off the coast of Los Angeles. *Zostera* sites were selected based on reports from the scientific literature (Engle & Miller 2005, Santa Barbara Channelkeeper 2010, Bernstein et al. 2011), online databases (ecoatlas.org) and local knowledge on each of the different coastal and offshore locations. The presence and GPS locations of specific *Zostera* beds were confirmed using either a vessel-deployed, down-looking sonar system equipped with a remotely deployed camera or underwater visual surveys conducted by scuba divers. In California, eelgrass mitigation policies established by the National Oceanic and Atmospheric Administration (2014) require that the timing of *Zostera* field surveys coincide with the peak eelgrass growth season, which falls between the months of March and October. The seasonal timing of surveys in this study

was based on these guidelines as well as *Zostera* habitat structure and fish biomass data from Catalina Island reported by Tanner et al. (2019).

## 2.2. *Zostera* coverage and habitat structure

*Zostera* areal coverage was quantified using 2 separate data collection methods. For beds <10 ha in size, coverage was calculated using a handheld GPS receiver (Trimble® R1) interfaced with a smartphone. Both units were mounted onto a foam bodyboard, which was operated by a scuba diver at the water surface while a second diver was tracked swimming underwater along the perimeter of the *Zostera* bed. The GPS receiver, enabled with a Satellite-Based Augmentation System, provided real-time sub-meter accuracy during mapping. Larger *Zostera* beds (>10 ha) were mapped with a small boat using a sonar system (Lowrance® HDS Carbon 7) and a high-frequency (455/800 kHz) skimmer transducer (DownScan Imaging™). The structural complexity of *Zostera* habitat was recorded by scuba divers. Density was measured as the total number of leaf shoots counted inside a quadrat (0.07 m<sup>2</sup>) haphazardly placed along intervals (n = 30) ≥ 1 m apart within an eelgrass bed. Blade width and canopy height was measured to the nearest mm and cm, respectively, for ≥10 haphazardly selected leaf shoots in each bed (see Short & Duarte 2001).

## 2.3. Fish surveys

Timed, roving visual surveys were conducted by scuba divers to determine the abundance, total length (TL) and species identity of fishes following the protocols of Schmitt & Sullivan (1996) and modified by Looby & Ginsburg (2021). At most sites, divers performed a total of 6 visual surveys: 3 with *Zostera* (≥1 m) on either side of the diver and 3 along the edge of the *Zostera* bed adjacent to the unvegetated substrate. In some cases, *Zostera* beds were not large enough to accommodate all 6 surveys, and in this rare event divers completed as many surveys as feasible. Divers completed each survey in 3–6 min in which they observed and recorded the number and size of all conspicuous (>1 cm) fishes encountered within an estimated 1 m high × 2 m wide window while swimming ~1 m above the substrate. The TL of each fish was visually recorded to the nearest cm by scientific divers experienced in fish identification and sizing, and in accordance with the methods out-

lined in Bell et al. (1985) and Harvey et al. (2002). Underwater visibility of >2.5 m was required for surveys to be completed. See Pondella et al. (2019) and Tanner et al. (2019) for additional details on the utility of recording visual fish length data using SCUBA.

## 2.4. Data analysis

### 2.4.1. Fish assemblages

The mean TL of fishes recorded in *Z. marina* and *Z. pacifica* beds with normal distributions (*Heterostichus rostratus*, *Paralabrax nebulifer* and *Oxyjulis californica*) were compared using a 2-sample *t*-test, whereas comparison with length at maturity ( $L_m$ ) for fishes were analyzed with a 1-sample *t*-test. The 2 species with non-normally distributed lengths (*Paralabrax clathratus* and *Halichoeres semicinctus*) were compared across eelgrass species using the Mann-Whitney *U*-test and to  $L_m$  using the Wilcoxon Signed Rank test. Differences in the composition of fish assemblages were compared by creating a Bray-Curtis dissimilarity matrix from average relative species-specific encounter rates across individual surveys completed at each bed between 2018–2020. The dissimilarity matrix was used to create non-metric multi-dimensional scaling plots to visualize changes in fish assemblages across *Z. marina* and *Z. pacifica*, as well as a particular survey area (mainland coast of the SCB, leeward or windward side of Catalina Island). Assemblage differences were tested using permutation multivariate analysis of variance (PERMANOVA) (McCune et al. 2002). Differences in group dispersion were tested using the 'betadisper' function in the 'vegan' package and were not significant; therefore, no additional transformations on these data were conducted. To determine species-specific differences in fish assemblage, a similarity percentages (SIMPER) procedure was performed with both eelgrass species and region as factors. All multivariate statistical approaches were conducted using the 'vegan' package (Oksanen et al. 2019) in R (R Core Team 2017, v. 3.6.2).

### 2.4.2. Fish utilization index

Two separate indices were created to quantify the utilization value of *Zostera* habitat to fishes. Survey metrics used to evaluate *Z. marina* included the encounter rate of individual feeding guilds, species richness and nursery function. The first 2 metrics

used for *Z. marina* were also used to create the *Z. pacifica* index; however, fishery function, or the percentage of fishes above the minimum catch limit size for commercial and recreational fisheries established by the California Department of Fish and Wildlife (CDFW) (CDFW 2020), was substituted for nursery function. This substitution was made to account for differences in fish size and assemblage composition between the 2 *Zostera* species. Fish species were matched with their corresponding guild using a modified version of the protocol reported by Bond et al. (1999), summed by each transect within a given bed (*Z. marina* or *Z. pacifica*) and year and divided by survey time to determine the guild encounter (GE) rate. Guilds were defined by foraging mode and may be found in Appendix A of Bond et al. (1999). The number of feeding guilds recorded at each *Zostera* bed was averaged across all transects and summed to calculate the overall GE rate for each sampling event. Species richness was calculated as the number of fish taxa recorded on each transect as a function of the total survey time. The nursery function of *Z. marina* was estimated using the ratio of the combined sum of fishes smaller than their predicted  $L_m$  to the total number of fish observed in each bed. For *Z. pacifica*, the minimum take size for all fish species listed by CDFW was applied as a data filter to include only those individuals that belonged to a recognized fishery. The ratio of this value to the amount of time required to complete the survey was used to measure the rates of each GE on a given survey, and thus determine the fishery function of *Z. pacifica*. Data for all survey metrics were standardized by subtracting off its mean and dividing by its standard deviation, and then summed according to the site and year it was collected to establish a fish assemblage index for *Z. marina* ( $Z_m$ ) and *Z. pacifica* ( $Z_p$ ) as follows:

$$Z_m = \sum \text{GE} + \text{Richness} + \text{Nursery Function} \quad (\text{Eq. 1})$$

$$Z_p = \sum \text{GE} + \text{Richness} + \text{Fishery Function} \quad (\text{Eq. 2})$$

#### 2.4.3. Habitat structure model selection

To determine the most important factors driving fishes to utilize open-coast *Zostera* habitat, a model selection procedure (corrected Akaike's information criterion [AICc]; Burnham & Anderson 2002) was used to evaluate the following variables: areal coverage, perimeter, perimeter-to-area ratio, density, blade length, blade width, whether a bed was located in-

side or outside of a MPA and distance to the closest rocky reef. This process was not undertaken for *Z. pacifica* beds given the limited amount of areal coverage data known for these field sites. The proximity of each *Z. marina* bed to a given reef habitat was calculated using Google Earth (earth.google.com/web) as the linear distance from the edge of a *Z. marina* site to the closest rocky reef boundary. These data were compared to one another using a linear model to determine the variables that best explain fish community composition. A reduced maximum likelihood linear mixed-effects model was used to account for variation in the fish assemblage index introduced via a relatively small number of sample locations and times. Residual distribution was checked to confirm normality, and a Gaussian distribution was presumed. The explanatory variables chosen during AICc model selection were used as fixed effects in a mixed effects model in which site and year were randomly selected. Variance inflation factors (VIFs) were produced for all fixed effects to evaluate the influence of multicollinearity. All data were analyzed using R Statistical Software (R Core Team 2017, v. 3.6.2) with the 'vegan' (Oksanen et al. 2019) and 'lmerTest' (Kuznetsova et al. 2017) packages.

## 3. RESULTS

### 3.1. *Zostera* coverage and structure

A total of 39 surveys of areal coverage and habitat structure of *Zostera marina* and *Z. pacifica* beds were recorded over the course of this study. Areal coverage of *Zostera* beds ranged from 0.06–27.74 ha with an annual median size of 0.25 ha in 2018, 0.27 ha in 2019 and 0.28 ha in 2020 (Table 1). For *Zostera* sites surveyed across multiple years, mean inter-annual standard deviation of bed area was approximately 21% of bed size. Although slight changes in distribution and size were evident in beds surveyed across all years, no marked shifts were observed, save for a reduction in *Z. marina* bed size at Empire Landing of 0.06 ha or 47% coverage loss. The mean density of *Z. marina* leaf shoots was more than 4 times greater than those from *Z. pacifica* beds, averaging  $414.1 \pm 205.5$  and  $89.5 \pm 42.6$  shoots  $\text{m}^2$ , respectively. Mean blade width, however, was 3.4 times greater for *Z. pacifica* leaf shoots ( $1 \pm 0.25$  cm) than *Z. marina* ( $0.29 \pm 0.1$  cm). The mean length of *Z. marina* and *Z. pacifica* leaf shoots ( $46.2 \pm 15.3$  and  $55.9 \pm 25.3$  cm, respectively) did not substantially differ.

Table 1. Location and abundance of *Zostera* habitat recorded 2018–2020 off Catalina Island and the coastal mainland of California. Map numbers correspond to survey sites outlined in Fig. 1. Latitude and longitude represent the approximate center of the habitat area; depth is the mean of all transects for all years surveyed. Areal coverage and fish assemblage index data are listed for both *Zostera marina* (*Zm*) and *Z. pacifica* (*Zp*) for each year surveyed. –: no data were collected; na: insufficient data were collected for analysis. Fish indices were calculated separately for eelgrass species; both included 2 survey metrics, encounter rate by feeding guild, and species richness; the third metric used was either a measure of nursery (*Zm*) or fishery function (*Zp*)

| Location/survey site            | Map no. | Latitude N  | Longitude W  | Species   | Depth (m) | Area (ha) |      |      | Fish index |      |       |
|---------------------------------|---------|-------------|--------------|-----------|-----------|-----------|------|------|------------|------|-------|
|                                 |         |             |              |           |           | 2018      | 2019 | 2020 | 2018       | 2019 | 2020  |
| <b>Catalina Island</b>          |         |             |              |           |           |           |      |      |            |      |       |
| Catalina Harbor <sup>a</sup>    | 1       | 33° 25' 40" | 118° 30' 40" | <i>Zm</i> | 7.2       | 0.25      | 0.21 | 0.22 | 4.87       | 4.23 | 3.99  |
| Emerald Bay                     | 2       | 33° 28' 04" | 118° 31' 41" | <i>Zm</i> | 4.6       | –         | 0.19 | 0.18 | –          | 5.07 | 5.43  |
| Big Geiger Cove <sup>b</sup>    | 3       | 33° 27' 33" | 118° 31' 04" | <i>Zm</i> | 8.0       | 0.56      | 0.55 | 0.54 | 6.42       | 5.12 | 6.85  |
| Little Geiger Cove <sup>b</sup> | 4       | 33° 27' 26" | 118° 30' 55" | <i>Zm</i> | 7.5       | 0.18      | 0.19 | 0.23 | 5.62       | 4.94 | 6.69  |
| Isthmus Harbor                  | 5       | 33° 26' 36" | 118° 29' 56" | <i>Zm</i> | 3.7       | 0.36      | 0.50 | 0.46 | 6.46       | 8.61 | 10.44 |
| Big Fisherman Cove <sup>c</sup> | 6       | 33° 26' 38" | 118° 29' 07" | <i>Zm</i> | 7.8       | 0.24      | 0.28 | 0.29 | 5.53       | 5.53 | 7.42  |
| Empire Landing                  | 7       | 33° 25' 44" | 118° 26' 27" | <i>Zm</i> | 7.2       | 0.12      | 0.10 | 0.06 | 6.57       | 3.83 | 5.68  |
| Rippers Cove                    | 8       | 33° 25' 38" | 118° 26' 01" | <i>Zm</i> | 7.8       | 0.05      | 1.58 | 1.60 | 8.00       | 5.21 | 5.37  |
| East End                        | 9       | 33° 19' 03" | 118° 18' 12" | <i>Zp</i> | 16.8      | 10.48     | –    | –    | 6.48       | 4.80 | 7.40  |
| Palisades                       | 10      | 33° 18' 08" | 118° 20' 21" | <i>Zp</i> | 14.7      | 27.74     | –    | –    | 3.54       | 2.27 | 2.47  |
| <b>Santa Barbara</b>            |         |             |              |           |           |           |      |      |            |      |       |
| Isla Vista                      | 11      | 34° 24' 44" | 119° 49' 37" | <i>Zp</i> | 7.3       | –         | –    | –    | na         | –    | –     |
| <b>Malibu</b>                   |         |             |              |           |           |           |      |      |            |      |       |
| Corral Canyon                   | 12      | 34° 01' 42" | 118° 44' 55" | <i>Zp</i> | 9.1       | –         | –    | –    | 7.80       | –    | –     |
| Amarillo Beach                  | 13      | 34° 01' 41" | 118° 42' 08" | <i>Zp</i> | 9.7       | –         | 0.46 | 0.29 | 7.59       | 3.56 | 3.59  |
| <b>Newport Beach</b>            |         |             |              |           |           |           |      |      |            |      |       |
| Newport Bay                     | 14      | 33° 35' 59" | 117° 53' 01" | <i>Zp</i> | 7.0       | –         | –    | –    | –          | 6.66 | 10.02 |
| <b>San Diego</b>                |         |             |              |           |           |           |      |      |            |      |       |
| La Jolla <sup>d</sup>           | 15      | 32° 51' 15" | 117° 15' 59" | <i>Zp</i> | 10.3      | 0.22      | 0.25 | 0.26 | 3.93       | 5.00 | 4.53  |

<sup>a</sup>Cat Harbor State Marine Conservation Area; <sup>b</sup>Arrow Point to Lion Head Point State Marine Conservation Area; <sup>c</sup>Blue Cavern Onshore State Marine Conservation Area; <sup>d</sup>Matlahuayl State Marine Reserve

### 3.2. Fish surveys

Overall, scientific divers completed 219 roving visual fish surveys in which they spent 17.6 h underwater. During these surveys, 13 747 individual fishes from 38 different species were recorded. Seven species (*Atherinopsis affinis*, *Cymatogaster aggregata*, *Halichoeres semicinctus*, *Oxyjulis californica*, *Paralabrax clathratus*, *Trachurus symmetricus* and *Xenistius californiensis*) accounted for >90% of fishes encountered. Five species (*H. semicinctus*, *Heterostichus rostratus*, *O. californica*, *P. clathratus* and *P. nebulifer*) were regularly observed on both *Z. marina* and *Z. pacifica* beds (Fig. 2). Estimates of TL recorded for *H. semicinctus*, *O. californica*, *P. clathratus*, *P. nebulifer* on *Z. pacifica* beds were typically larger than those measured on *Z. marina*. Moreover, TL measurements for *H. semicinctus*, *O. californica* and *P. clathratus* were often smaller than  $L_m$  when observed at sites with *Z. marina* but not for any of these species recorded at sites with *Z. pacifica*. The  $L_m$  for only one species (*P. nebulifer*) was significantly larger when amongst *Z. pacifica* habitat.

### 3.3. Fish assemblages

Thirteen different fish guilds were recorded in *Z. marina* habitat, whereas a total of 10 guilds were present at *Z. pacifica* sites. Benthic schooling foragers (*O. californica*, *Brachyistius frenatus* and *C. aggregata*), non-schooling diurnal engulfers (*P. clathratus*, *P. nebulifer* and *H. rostratus*), benthic foragers (*Embiotoca jacksoni*, *Hypsurus caryi*, *Girella nigricans* <100 mm and *Hypsypops rubicundus*) and crushers (*H. semicinctus*) were observed in ≥50% of all *Z. marina* and *Z. pacifica* beds surveyed. Herbivores (*G. nigricans* >100 mm and *Medialuna californiensis*) and diggers (*Pleuronichthys coenosus* and *Urolophus halleri*) were recorded amongst ≥40% of *Z. marina* sites, but not at *Z. pacifica* sites. PERMANOVA results indicated that the composition of fish assemblages observed at *Z. marina* and *Z. pacifica* sites were significantly different from one another ( $F_{1,14} = 11.45$ ,  $p < 0.01$ ; Fig. 3). According to results from the SIMPER analysis, differences were driven by the presence of greater numbers of *H. semicinctus* and *X. californiensis* in *Z. marina* habitat and *O. califor-*

Fig. 2. Dotplot of fish size in *Zostera pacifica* (orange) and *Z. marina* (green) where each point represents a recorded individual. Horizontal lines are length at maturity. ✂: fish lengths significantly different in *Z. marina* to length at maturity;  $\Psi$ : fish lengths significantly different in *Z. marina* and *Z. pacifica*;  $\ominus$ : fish lengths significantly different in *Z. pacifica* to length at maturity

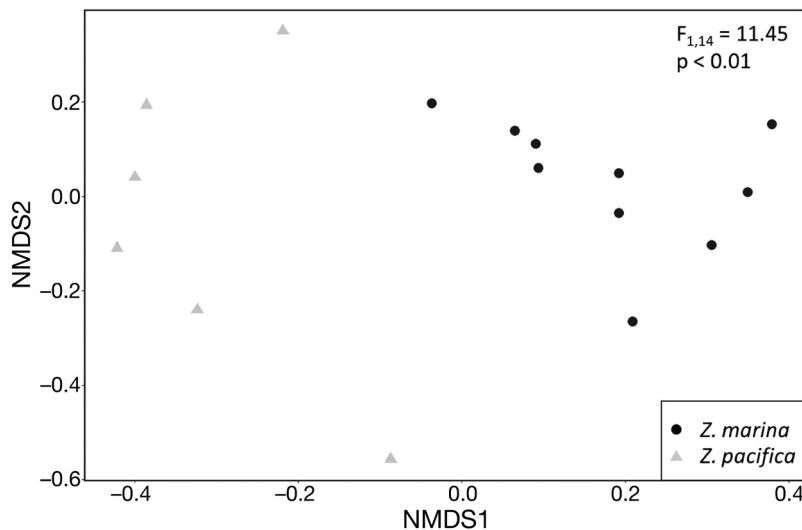
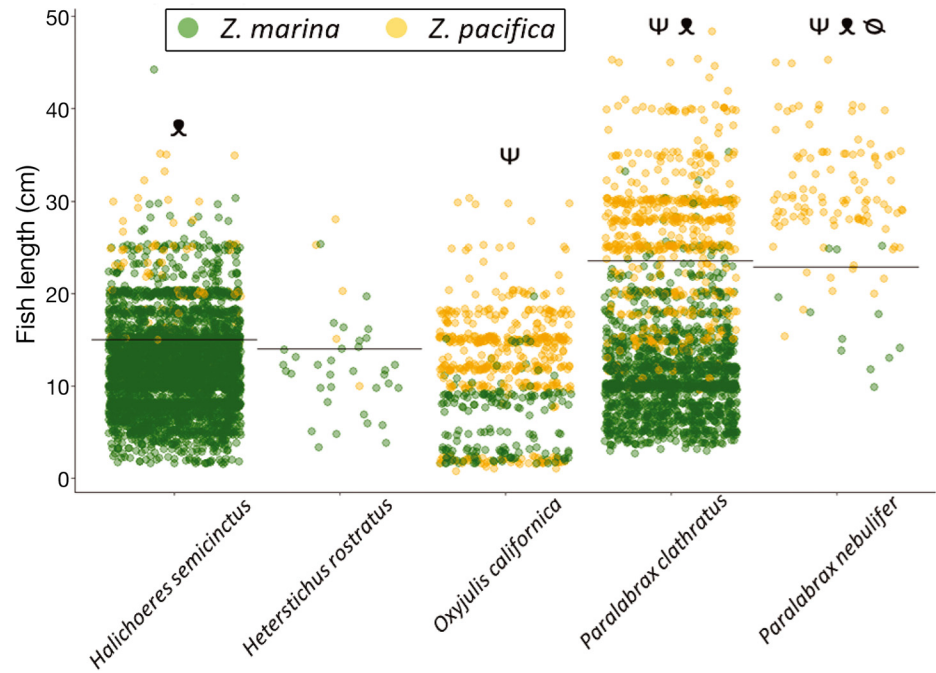


Fig. 3. Non-metric multidimensional scaling (NMDS) plot where each point is the averaged fish assemblage from each sampled bed by eelgrass species (stress = 0.11). Permutation multivariate analysis of variance (PERMANOVA) results reported on plot

*nica*, *P. nebulifer* and *Syngnathus leptorhynchus* in *Z. pacifica* beds. Likewise, the composition of fish assemblages recorded at separate *Zostera* sites along the windward side of Catalina Island were markedly different from those on the SCB mainland ( $F_{2,13} = 7.13$ ,  $p < 0.01$ ; Fig. 4). SIMPER results showed fish assemblages off Catalina contained greater numbers of *O. californica* and *H. semicinctus*, whereas *P. nebulifer* and *Phanerodon furcatus* were more prevalent along coastal sites off the mainland.

### 3.4. Fish index

The highest ranked fish assemblage composition from 2018–2020 was recorded at the Isthmus Harbor eelgrass site (Table 1). Temporal patterns in the size of fish assemblages had little to no impact on the estimated index values. For example, fish index values at some *Zostera* sites (La Jolla, Palisades, Isthmus Harbor and Catalina Harbor) remained relatively unchanged, while at other sites (East End, Empire Landing and Amarillo Beach) these values fluctuated across years. The model of best fit from AICc selection, which was only conducted on *Z. marina* beds, included 3 predictor variables: bed area, bed perimeter and distance to the nearest rocky reef (AIC = 81.88). The next best model included the 3 predictor

variables from above, as well as *Zostera* blade length (AIC = 84.56). A review of VIFs conducted after running the linear mixed effects model indicated multicollinearity in the perimeter fixed effect, indicating it was highly correlated to other variables in the model. This factor was removed from the model, leaving 2 fixed effects with VIFs between 1 and 2, thus demonstrating evidence that multicollinearity did not affect these data. Results of the revised linear mixed effects model are depicted in

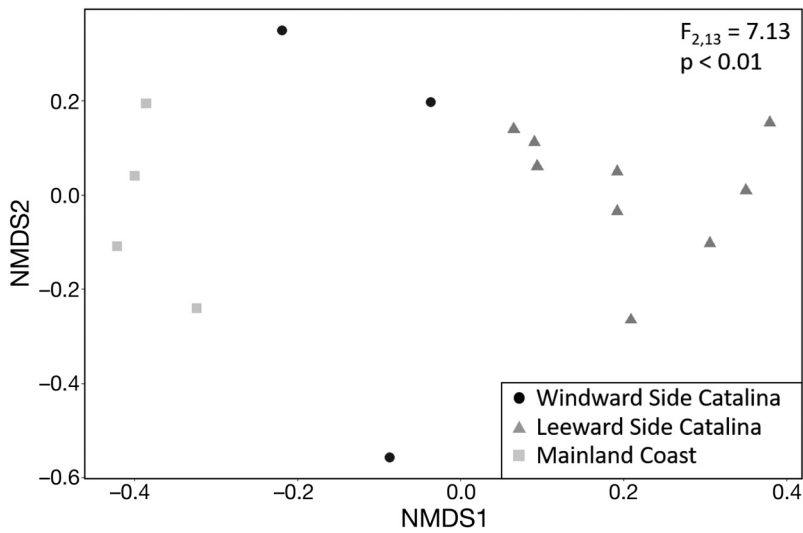


Fig. 4. Non-metric multidimensional scaling (NMDS) plot where each point is the averaged fish assemblage from each sampled bed by survey region (stress = 0.11). Circular point furthest left on plot represent Catalina Harbor; this plot shows how similar this site's assemblage is to those on the leeward side of the island. Permutation multivariate analysis of variance (PERMANOVA) results are reported on plot

Table 2. Statistical results of linear mixed effects model using eelgrass *Zostera marina* habitat metrics identified during model selection procedure to predict fish index

| Fixed effect     | Estimate | SE      | df   | t      | p    |
|------------------|----------|---------|------|--------|------|
| Bed area         | 0.000009 | 0.00007 | 12.1 | -0.124 | 0.9  |
| Distance to reef | 0.011    | 0.004   | 3.34 | 3.094  | 0.04 |

Table 2. According to the model, distance to reef was a significant driver of the fish index in which the study site and survey year accounted for 13.3 and 26.8% of the variance, respectively.

## 4. DISCUSSION

### 4.1. Habitat function

The conventional wisdom that seagrass beds serve as nursery habitat (McDevitt-Irwin et al. 2016) is supported by data from *Zostera marina* beds evaluated in this study. However, the lack of data upholding this paradigm in *Z. pacifica* beds indicate that habitat function should be limited to individual species. Specifically, the high encounter rates of juvenile fishes in *Z. marina* beds, particularly when coupled with juvenile *Paralabrax clathratus* secondary productivity data from an open-coast *Z. marina* bed (Tanner et al. 2019), meet several nursery-role require-

ments (see Beck et al. 2001). Differences in the fish assemblage composition and nursery function of *Zostera* may be driven by the physical environment and not by any trait of the seagrass itself. As demonstrated here, *Z. pacifica* beds were often located in deeper, more exposed environments than *Z. marina*. Depth and energy influence fish assemblage composition on reefs (Fulton & Bellwood 2004, Love et al. 2009, Parsons et al. 2016), as well as in seagrass habitat in other regions (Hutchinson et al. 2014). However, the lower leaf shoot density in *Z. pacifica* beds may limit predator avoidance by juvenile fishes, leading to higher rates of mortality and fewer observations during surveys (Hyndes et al. 2003). Future studies of the ecosystem function of *Zostera* habitat may disentangle whether the physical environment in *Z. pacifica* beds drives

fish assemblage differences rather than another aspect of *Zostera* itself. This, however, does not obviate the result that *Z. pacifica* performs separate habitat functions from that of open-coast *Z. marina* in the SCB. Such findings are vital to the development of effective conservation and management policies.

### 4.2. Fish assemblage composition

The greater relative abundance of digging and herbivorous fish guilds in *Z. marina* beds provide further evidence of the bioenergetic impacts on the structure of fish assemblages. Few herbivores directly consume eelgrass, instead preferring the epiphytes growing on seagrass blades (Mittermayr et al. 2014), which are more abundant in low energy seagrass environments (Lavery et al. 2007). Therefore, the presence of greater numbers of herbivores in *Z. marina* beds fits with the expected availability of more abundant epiphyte resources. Concomitantly, increased wave exposure also affects sediment composition and lowers sediment organic matter in seagrass beds (Fonseca & Bell 1998), which may drive the higher abundances of the digging fish guild found amongst *Z. marina* beds in this study. Adult, non-schooling, diurnal engulfers such as *P. clathratus* and *P. nebulifer* were the most frequently encountered fish guild in *Z. pacifica* beds and may indicate that mid-level predators forage in this habitat. If that



is the case, foraging behavior may also influence the limited number of juvenile fishes present (Hynes et al. 2003). Other commonly encountered guilds such as crushers and benthic foragers, suggest a high-production value of the epibenthos within *Z. pacifica* beds.

The distribution of *Zostera* off the California coast makes the separation of region and species as drivers of fish assemblages impossible. However, assemblage differences on the windward side of Catalina Island, where 2 of 3 beds are comprised of *Z. pacifica*, and along the mainland coast, where all 4 beds are comprised of *Z. pacifica*, may be worth exploring in more detail. For instance, the higher abundance of crushers and pickers on the windward side of the island suggest more productive epibenthos on those beds while the higher abundance of a generalist forager (*Phanerodon furcatus*) may imply those beds do not have the diversity of prey items to support specialists. Mainland beds were often shallower than their counterparts on the windward side of Catalina Island, potentially leading to a higher energy environment and fewer opportunities to develop healthy epibiota.

#### 4.3. Fish index

The higher fish index values in beds further from reef habitats found in this study runs counter to evidence in tropical locations (Jelbart et al. 2007, Gullström et al. 2008). One possible explanation for this result is the tendency towards more frequent movements between adjacent eelgrass and reef habitats. Swadling et al. (2019) found greater fish density and diversity on temperate reefs near seagrass beds, and Obaza et al. (2015) noted higher piscine predator abundance in nighttime surveys of eelgrass beds. Therefore, fishes found in eelgrass beds further from reef habitats may not travel to nearby reef areas. The distance might also prevent primarily reef-dwelling predators from conducting diel foraging activity in eelgrass beds. Both restrictions may lead to an increase in overall fish utilization of more isolated beds due to reduced emigration and predation. This explanation for higher fish index values further from reefs does not preclude the use of *Z. marina* beds as nursery habitat. Juvenile *P. clathratus* abundance declines dramatically in *Z. marina* beds during winter months (Tanner et al. 2019), with emigration being the most plausible explanation. It would then follow that many of the fishes recorded rearing in *Z. marina* during these surveys, which were conducted

primarily in summer and fall, would emigrate during the winter. These results show fish utilization of temperate seagrass beds, as in tropical locations, needs to incorporate a larger landscape context, keeping in mind that habitat relationships likely change across regions.

Other factors driving fish utilization within open-coast *Z. marina* beds are consistent with those reported in the literature. The importance of perimeter may be related to the influence of edge effects, where greater foraging or resource availability may exist at the seagrass/soft bottom interface. This phenomenon has been documented through greater fish diversity and abundance in these microhabitats elsewhere (Jelbart et al. 2006, Smith et al. 2008, Hori-nouchi et al. 2009). Edge effects and bed area may also interact in structuring fish utilization (Smith et al. 2008), providing further evidence beyond the geometric relationship of why multicollinearity existed between the 2 factors. Bed area's influence on fish assemblages may be as simple as a species–area relationship, where increasing available habitat creates more niche space, allowing for additional species diversity (Arrhenius 1921). That is likely too simplistic, however, as bed size may also cause a decrease in the presence of herbivorous fishes (Prado et al. 2008). Given the herbivorous fish guild was commonly found in *Z. marina*, the trend identified by Prado et al. (2008), a negative relationship between seagrass bed size and herbivore abundance, may also exist in these beds. Blade length is frequently reported as the most important structural element (e.g. physical component of seagrass) driving fish utilization in seagrass beds (Gullström et al. 2008, Tanner et al. 2019). While length was not part of the highest performing model selected in this study, it was still a stronger driver than other structural elements.

#### 4.4. Eelgrass bed characteristics

Though not a central component of this study, there remains a paucity of spatial data on open-coast eelgrass beds. Coupled with the worldwide concern for seagrass losses (Orth et al. 2006, Waycott et al. 2009), and fluctuations evident during this study, some discussion of bed size is merited. The dynamic nature of seagrass beds is well established and is consistent with the changes in eelgrass bed size documented in this study (Frederiksen et al. 2004, Costello & Kenworthy 2011). However, the loss of eelgrass beds documented on the eastern lee side of Catalina Island as compared with the sizes reported

by Engle & Miller (2005) is cause for concern. There are no conspicuous anthropogenic activities in the region that might drive these widespread changes. Because the island's eastern lee side has a different orientation than the western lee side, it is possible that a large swell event removed beds on the eastern lee side while not having the same force further west. Potentially confounding this hypothesis is the steady reduction in eelgrass coverage at Empire Landing, also without a conspicuous anthropogenic cause, located on the eastern edge of extant beds on the lee side of Catalina. The only bed further east of Empire Landing is Ripper's Cove, the largest *Z. marina* bed documented on Catalina, which is maintaining steady coverage. Therefore, no single factor explains these reductions. A source-sink metapopulation construct might explain eelgrass patches on Catalina, with several robust beds on the western lee side serving as a source, and the island's many coves on its eastern lee side serving as sinks being variably occupied over time (Bell 2006). Eelgrass exhibits high dispersal and colonization potential that would be consistent with a metapopulation structure (Harwell & Orth 2002). While definitive determination of possible metapopulation dynamics in open-coast eelgrass beds is beyond the scope of this paper, circumstantial evidence may be useful in guiding potential restoration efforts and/or protection of unvegetated coves that support suitable soft-bottom habitat for eelgrass colonization.

## 5. CONCLUSIONS

Given the results of this study, we strongly encourage further research that distinguishes between the function of open-coast and sheltered eelgrass beds (in bays and estuarine habitats) and investigates the connection of open-coast beds to nearby habitats such as reefs and kelp forests. Locally in California, precise mapping of larger *Zostera pacifica* beds would provide crucial data to conduct a similar model selection exercise to determine the factors that drive fish utilization of *Z. pacifica* beds, and may further close this data gap. There are also more remote open-coast eelgrass beds worldwide that must be included in future comparisons to better understand the differences between mainland and open-coast beds. Finally, targeted fish tagging studies and telemetry should further clarify the interactions between reef and seagrass habitats in temperate regions, providing insight on the degree and frequency of fish biomass transport between habitat types. The differing func-

tions for *Z. marina* as nursery and *Z. pacifica* as fishery habitat, respectively, as well as the driving structural and physical factors of higher fish utilization presented in this study are valuable for regional conservation efforts and as part of the broader marine ecology literature.

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