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Authors

Koval, Gammon N.
Dugan, Jenifer E.
Hamilton, Scott L.

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Seasonal variation and response of surf zone fish assemblages to environmental variables in the Northeast Pacific

Gammon N. Koval [a,*], Jenifer E. Dugan [b], Scott L. Hamilton [a]

[a] Moss Landing Marine Laboratories, San Jose State University, Moss Landing, CA, 95039, USA
[b] Marine Science Institute, University of California, Santa Barbara, CA, 93106, USA

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ABSTRACT

Located at the land-sea interface, the highly dynamic sandy beach and surf zone ecosystem is one of the coastal zones used most intensely by humans (e.g., recreation, fishing, tourism). Surf zones are also important as fish habitat; however, the factors structuring fish assemblages in the surf zone are relatively understudied due to challenges associated with sampling this dynamic environment. To investigate temporal influences on surf zone fish communities, we evaluated seasonal trends in the fish assemblage and associations with environmental conditions using baited remote underwater video stations (BRUVS) at four beaches on the Northeast Pacific coast (California, USA) from July 2020 to June 2021. Our study region is characterized by strong seasonality in productivity (due to spring upwelling) and the wave climate (in response to winter storms), making it an ideal location for evaluating seasonal change in surf zone fish. We found that surf zone fish assemblages exhibited marked seasonality and site-to-site variability. Two species of surfperch (*Amphistichus argenteus* and *A. koelzi*) and leopard sharks (*Triakis semifasciata*) were more common in the winter and spring, corresponding with surfperch spawning, while flatfishes were more abundant in the summer. Fish species composition was most affected by distance from shore (as a proxy for surf zone width), visibility, water temperature, percent cover of combined macroalgae and surfgrass, and breaker wave height, with significant effects detected for distance from shore and breaker height. Fish species that exhibited higher abundance in the winter, including *A. argenteus*, *A. koelzi*, and *T. semifasciata*, were associated with larger waves and wider surf zones. Our results highlight the influence of seasonal variation in environmental conditions on fish communities in the dynamic, coastal surf zone ecosystem, with potential management implications for several highly abundant species targeted by recreational fisheries.

1. Introduction

The surf zone, the area extending from the first outermost breaking waves to the shore, is characterized by turbulent conditions including waves of various sizes and periodicity, constant turmoil, high tidal exchange, strong along-shore currents, and rip currents (Allen and Pondella, 2006; Olds et al., 2018). Surf and swash zone habitats are highly dynamic with varying conditions (Beyst et al., 2001), especially in temperate areas characterized by seasonal shifts in temperature, productivity, precipitation, and wave climate (Fiori et al., 2022). Studies of temporal variation in surf zones and associated species assemblages from around the world suggest these communities respond strongly to seasonal shifts in environmental conditions (Beyst et al., 2001; Layman, 2000; Marin Jarrin and Shanks, 2011; Nanami and Endo, 2007; Ross et al., 1987).

Evidence from previous studies indicates that changing oceanographic conditions have the potential to affect surf zone fish assemblages through a variety of environmental drivers. For surf zone fish, water temperature, breaker height, wave period, water velocity, the abundance of drift macrophytes, salinity, wind speed, and turbidity are the most studied environmental factors (Olds et al., 2018). In temperate ecosystems, greater abundance and diversity of fish species are typically reported in the surf zones as water temperatures increase (Harborne and Mumby, 2011), likely caused by transient species exhibiting seasonal migrations (Layman, 2000; Nanami and Endo, 2007). The biomass of drifting macrophytes has also been positively correlated with increased fish abundance in surf zones (Crawley et al., 2006), by providing shelter from predators and increased feeding opportunities on invertebrates associated with the algal subsidy (Hyndes et al., 2014). In contrast, studies have reported that the abundance of surf zone fish is negatively

* Corresponding author.
E-mail address: gkoval@faralloninstitute.org (G.N. Koval).

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correlated with breaking wave height, period, and speed (Clark, 1997). Many species occur more commonly in the surf zones of beaches with lower wave action, while some taxa are associated with higher wave action (Inui et al., 2010). Changes in oceanographic conditions, which influence productivity, prey availability, and the timing of reproduction, can drive temporal changes in surf zones and the fish communities that use them.

The California Current System is highly dynamic and characterized by strong seasonal variation in oceanographic conditions (García-Reyes and Sydeman, 2017), making it an ideal study system to better understand the effects of seasonality on surf zone fish assemblages. In terms of seasonality, summer, from June to August, is characterized by the calmest conditions, as water temperatures slowly rise (Ramp et al., 2011). Fall, from September to November, has the warmest ocean temperatures (Manzer et al., 2019) and the lowest productivity. Winter, from December to February, brings storms and high wave action, which dislodge kelps and other macroalgae that are transported into the surf zone as drift algae (Andrews, 1945; Krumhansl and Scheibling, 2012). Invertebrates transported on this drift macroalgae provide an important nutritional subsidy to the surf zone in central California (Allen and Pondella, 2006; Dugan et al., 2011). Spring, from March to May, is accompanied by strong winds and intense upwelling, reducing water temperatures and bringing nutrient-rich waters to the surface, which stimulate a range of primary producers (Thompson et al., 2012).

Common fish inhabitants of central California surf zones include the Embiotocidae (surfperch), Atherinopsidae (new world silversides), Paralichthyidae (sand flounders; Allen and Pondella, 2006), and elasmobranchs (Marraffini et al., 2024). The surfperch family, which includes 19 species in the eastern Pacific, is viviparous, leading to limited dispersal and localized populations (Carlisle et al., 1960; Bernardi et al., 2022). Fishing pressure can also impact surf zone fish populations with surfperch (Schroeder and Love, 2002) and elasmobranchs (Allen et al., 2002) being targeted by recreational and commercial anglers. Surfperch and some surf zone-associated elasmobranchs, such as *Triakis semifasciata* (leopard shark), exhibit high site fidelity in nearshore habitats (Carlisle et al., 1960; Carlisle and Starr, 2009). A 2018 literature review of 161 surf zone-related publications found only four from the Northeastern Pacific, highlighting the need for more studies of the factors influencing ecosystem structure and function in this region (Olds et al., 2018). Since then, additional studies have occurred investigating California surf zones (Marin Jarrin et al., 2022; Gold et al., 2023; Madden, 2023; Marraffini et al., 2024); however, these studies were generally limited to sampling during the calmer summer months. Due to the challenges of conducting surveys in dynamic, and potentially hazardous surf zones, little is known about how the biotic assemblage changes with season or how it may be affected by variation in environmental conditions.

This study was designed to fill gaps in our understanding of seasonal variation in the surf zone fish assemblage of the central California coast. We chose to focus on two questions: 1) how does the surf zone fish assemblage change seasonally? and 2) can the key environmental factors associated with temporal differences in surf zone assemblages be identified? For our first question, we predicted that there would be seasonal variation in diversity, with a peak in the spring to correspond with upwelling that results in high productivity and resource availability. We expected that abundance would be greatest in the summer and fall when conditions were calmest and warmest, associated with periods of fish recruitment. We also predicted that diversity and fish abundance would be lowest in the winter, when wave action and turbulence are highest in the surf zone, and at beaches with the widest surf zones that receive more wave action. For our second question, we predicted fish assemblages would be influenced by specific environmental factors associated with seasonality in a dynamic system, such as shifts in water temperature, salinity, drift algal percent cover, habitat features such as surf zone width, and other physical forcing factors, such as wind speed, wave period, and breaker height, often associated with exposed versus sheltered sampling locations.

2. Materials and methods

2.1. Study sites and surveys

We assessed temporal variability in surf zone assemblages at four study locations along the Monterey Peninsula on the central California coast, in the northeast Pacific of the USA (Fig. 1). Spanish Bay and Carmel Beach represented exposed, sandy beaches that receive high wave action, while Whalers Cove and Stillwater Cove consisted of sheltered beaches receiving reduced wave action and harboring year-round kelp forests near each site (Fig. 1). Detailed descriptors of each site are included in Supplementary Table 1. Regular surveys were conducted at these sites from July 2020 to June 2021, with eleven surveys per site, approximately once a month. Though originally aiming for twelve surveys per site, a combination of weather conditions and safety concerns (2020 River Fire in Montrey County) limited access to the beaches, therefore Whalers Cove was not sampled in August, Carmel Beach and Stillwater Cove were not sampled in September, and Spanish Bay was not sampled in October. Based on the oceanographic seasonality of the region though, there is still sufficient data to draw conclusions based on seasonality.

2.2. Biological and environmental sampling of the surf zone

The surf zone fish assemblage was surveyed using Baited Remote Underwater Video Stations (BRUVS; Vargas-Fonseca et al., 2016) designed for this habitat and deployable in variable surf conditions. These BRUVS utilized a GoPro HERO7 Black camera recording at a resolution of 1080p and 60 frames per second, with the field of view set to "wide." The cameras were mounted to a 4.5-kg weight plate with a soft-mesh bait bag attached on a PVC pole and held 1 m from the camera (Supplemental Fig. 1). The bait used in each BRUVS was 500 g of frozen market squid (*Doryteuthis opalescens*). Six BRUVS were deployed at each site and left to record for at least 1 h and 15 min (Whitmarsh et al., 2017). The BRUVS were evenly spaced at least 50 m apart from each other traveling parallel along shore in a localized area to minimize spatial variability (Gold et al., 2023; Marraffini et al., 2024), and each BRUVS was swum out from shore and placed seaward of the outermost line of breaking waves and set on sandy substrate at a depth between 2 and 2.5 m. BRUVS were placed beyond the first line of breaking waves, as opposed to a specific distance offshore, to help control for differences in surf zone width (Supplemental Table 2). While deploying BRUVS, water visibility was estimated to the nearest 0.5 m around the deployment area. Distance from shore was also estimated based on the retrieval buoy location on the surface. Tide stage was not recorded because sampling was conducted within 2 h of low tide to avoid the bias from the daily migratory behavior of fish (McLachlan and Brown, 2006), and occurred between the hours of 6:00 and 18:00 to avoid the impact of crepuscular periods on fish abundance and behavior (Harvey et al., 2007).

Once the BRUVS were deployed, a series of environmental and physical measurements were recorded on three cross-shore transects that aimed to evaluate the environmental drivers of surf zone assemblages (Dugan et al., 2003). Water temperature was recorded in the surf with a handheld thermometer measured to the nearest 0.1 °C, while wind speed was measured at the swash zone for a 3-min period using a handheld anemometer measured to the nearest 0.1 m/s. The salinity of a water sample taken from the surf was measured using a handheld refractometer measured to the nearest 1 PSU. Significant breaker height was measured by placing a wave pole at the low swash point and aligning the top of the breaking wave with the horizon measured to the nearest 0.1 m. The average significant breaker period and time from breakpoint to swash was recorded for each transect for a 3-min period. Surf zone width, measured by the distance perpendicular from shore

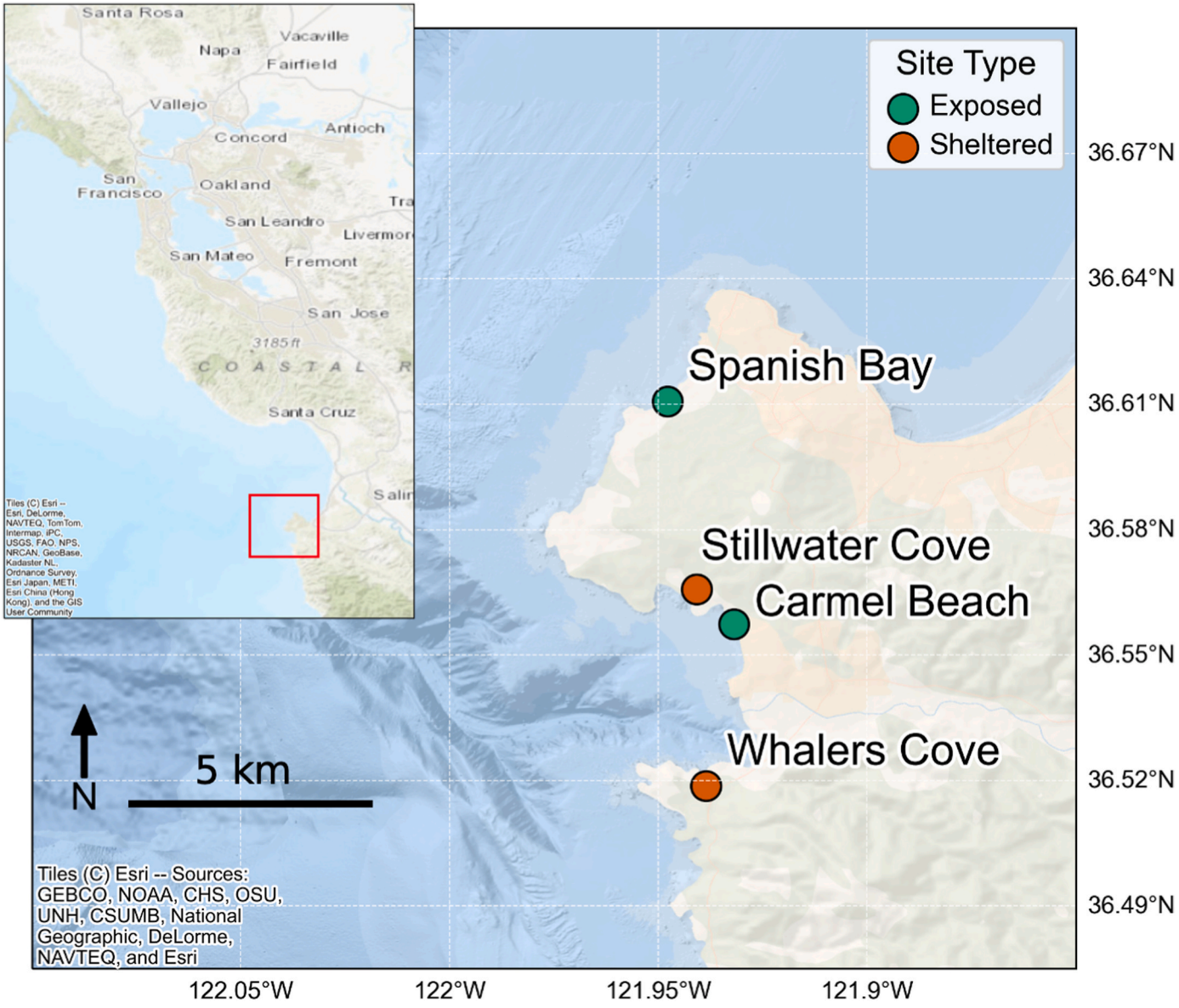

Fig. 1. Map of all four study sites with extent map. The four sites are labeled and colored based on the amount of beach exposure with Stillwater Cove and Whalers Cove being more sheltered and Carmel Beach and Spanish Bay being more exposed.

that each BRUVS was deployed, was estimated in meters by the swimmer deploying the BRUVS and confirmed by the spotter from shore.

2.3. Video analysis

Video recordings from each deployed BRUVS were analyzed using EventMeasure software (©2020 SeaGIS). For each video, 1 h of footage was selected. The first 10 min of the collected 75-min video consisted of an acclimation window and therefore was not analyzed, allowing sufficient time for the environment to recover from the disturbance of placing the BRUVS on the benthos. The remaining 60 min of video were watched fully, and all species of fishes observed were counted and identified to the lowest taxonomic level. The relative abundance of each species was calculated using the MaxN statistic as the maximum number of individuals of a single species present in a single video frame. MaxN is a standard metric used when analyzing BRUVS footage as it prevents double counting individuals that might have dropped out of the field of view and then reappeared (Murphy and Jenkins, 2010). While MaxN represents the most accurate measure of abundance, it is conservative, leading to a potentially deflated estimate of relative abundance. The Shannon-Weiner diversity index (H') was calculated for each BRUVS using the MaxN value for each species, where p_i is the proportion of the total sample represented by species i (equation (1)).

$$H' = \sum p_i \times \ln(p_i) \quad (1)$$

To measure the relative abundance of drift macroalgal wrack in the surf zone, three images were captured throughout the video (one at the beginning, one at the 30-min interval, and one at the 60-min interval), and 24 points were randomly overlaid across the image (with a 50-pixel margin on all sides) using ImageJ software (view Supplemental Fig. 2 for an example image). Overlaying the points over the whole image, as opposed to only the substrate, allowed us to capture any drift or attached macroalgae and surfgrass that might be in the frame. Any species of macrophyte underneath each point was used to classify percent cover for each image still, and this information was added to the environmental data as a potential factor influencing surf zone species assemblages.

2.4. Statistical analysis

All statistical analyses were conducted in R v4.0.2 (R Core Team, 2017) using the vegan R package v2.5–6. The first question focused on how the surf zone assemblage changed seasonally and spatially by site. The MaxN values for each species were summed for each BRUVS and then those summed MaxN values per BRUVS were averaged for a survey day, also referred to as total MaxN. This resulted in three or four points per season per site and was used as the lowest level of replication for analysis. The Shannon-Wiener diversity (calculated with the *diversity* function in the vegan package) and total MaxN were analyzed with separate two-way analysis of variance (ANOVA) using season, site, and their interaction as fixed effects. This tested both spatial and temporal differences and allowed us to determine if the seasonal differences were consistent across sites throughout the year. Significant effects were determined with a standard alpha level of 0.05, and a Tukey's honest significance post-hoc test was run on significant effects to determine group differences.

To further analyze seasonal trends in community composition, the MaxN data were square root transformed to down-weight the importance of highly abundant species, and the results were used to calculate a Bray-Curtis dissimilarity matrix (calculated using the *vegdist* function from vegan; Clarke and Warwick, 1994). The matrix was then used to create a non-metric multidimensional scaling ordination (nMDS) plot with two dimensions (using the *metaMDS* function in the vegan package) to visualize differences in community composition among sites and seasons, along with vector overlays to depict which species were driving the differences among samples (calculated using *envfit* from the vegan package). The stress score for an nMDS is a goodness-of-fit metric that shows the difference between distances in the reduced dimension versus the complete multidimensional space. A stress score of around 0.1 or lower corresponds to an accurate ordination (Clarke and Warwick, 1994). To test statistical significance of the fish community data, a two-way permutational analysis of variance (PERMANOVA) was used to analyze the effect of site, season, and their interaction on the abundances of all species in the community, using the *adonis* function (Attwood et al., 2016). Significant effects from the PERMANOVA were further tested with a Tukey pairwise test using the *pairwise.adonis* function from the pairwiseAdonis package v0.4.1 (Martinez Arbizu, 2020).

The second question investigated how environmental factors affect the surf zone assemblage, including: tide height at the time of deployment, water temperature, salinity, average wind speed, the water depth at BRUVS deployment, visibility, distance from shore, breaker height, wave period, and the total percent cover of attached and drift macrophytes (summed into a single variable). The environmental data were averaged per sampling day and matched with the corresponding total MaxN data based on the sampling month and site (one point per site per month with the summarized environmental variables and average MaxN). A partial distance-based redundancy analysis (dbRDA) was used to evaluate the association of the environmental predictors with the fish community abundance data (Currey-Randall et al., 2021). The dbRDA was run using the *capscale* function from the vegan package with site set as a conditional effect to partial out the spatial effects before constraints. Before running the dbRDA, variable selection of all environmental variables was conducted using forward and backward propagation with the *ordistep* function in the vegan package (Blanchet et al., 2008). After the final model was run, multicollinearity was examined for the selected environmental variables using variance inflation factors (VIF). This was done with the *vif.cca* function from the vegan package and all variables were ensured to have a VIF score of less than 10 (Zuur et al., 2010). The model allows for the determination of significant environmental factors ($p < 0.05$ based on a correlation between each environmental variable and the results from the dbRDA) and the resulting influence of each factor on each species.

3. Results

In total, 264 BRUVS were analyzed, and 25 species of fish were identified. Only two individuals from the *Sebastes* genus were not definitively identified down to the species level and were removed from the analysis. The four most observed species were in the family Embiotocidae (i.e., surfperch; Supplemental Table 3). Detailed statistical results for all analyses can be found in Supplementary Table 4, only p-values are reported in the text.

3.1. Effects of season and site on surf zone assemblages

Fish diversity differed significantly among sites, but not among seasons, with a marginally non-significant interaction of site and season (site $p < 0.01$; season $p = 0.244$; site × season: $p = 0.051$). Diversity was higher at Stillwater Cove and Whalers Cove compared to Carmel Beach and Spanish Bay ($p < 0.05$; Fig. 2A), with Spanish Bay exhibiting distinct seasonal trends compared to the other sites. Since no two-way interactions were significant, those were not analyzed with a post-hoc test. For total fish abundance (MaxN), only sites differed significantly from each other ($p = 0.011$), while season (Fig. 2B; $p = 0.560$) and the interaction of site and season ($p = 0.513$) were not significant sources of variation. Carmel Beach had a significantly higher abundance of fish than Stillwater Cove, while Spanish Bay and Whalers Cove did not differ significantly from any other sites ($p < 0.05$; Fig. 2B). Overall, the more exposed sites tended to be characterized by higher MaxN compared to the sheltered sites, a result opposite the observed spatial patterns in diversity.

Further insights into seasonal and site variation in surf zone fish composition were revealed by the results of multivariate approaches. We detected significant differences in fish communities among seasons ($p = 0.011$) and sites ($p = 0.001$), but the interaction of site and season was not significant ($p = 0.293$). The nMDS for season indicated a relatively high overlap of surf zone fish community composition across the year (Fig. 3A), due to the strong site-to-site differences. However, the significant seasonal effect can be attributed to the winter assemblages being most distinct from those in the summer ($p = 0.012$). With species vectors overlaid, *Citharichthys stigmaeus* (speckled sanddab) and *Platyrhinoidis triserata* (thornback ray) were relatively more abundant in summer and fall than winter and spring, while *Amphistichus argenteus* (barred surfperch), *A. koelzi* (calico surfperch), and *T. semifasciata* were strongly associated with the winter and spring seasons (Fig. 3A). When the same data were viewed as a function of site, distinct assemblages appear for Whalers Cove and Stillwater Cove, with high overlap between the assemblages in Spanish Bay and Carmel Beach (Fig. 3B; $p < 0.05$). Among sites, *A. argenteus*, *A. koelzi*, and *T. semifasciata* were more common at the exposed sites of Spanish Bay and Carmel Beach. At Whalers Cove, we observed more *Hypsurus caryi* (rainbow seaperch), *Embiotoca lateralis* (striped surfperch), and *E. jacksoni* (black perch), while at Stillwater Cove there were more *P. triserata* (thornback ray), *Micrometrus minimus* (dwarf perch), and *Sebastes rastrelliger* (grass rockfish; Fig. 3B).

3.2. Environmental drivers of seasonal and spatial variation in surf zone assemblages

A detailed description of the seasonal patterns for environmental variables is included in Supplementary Table 2. Generally, winter was characterized by large waves and low visibility, spring had strong onshore winds, and summer and fall had smaller waves, warmer waters, and the BRUVS were deployed closer to shore on average, due to the narrower surf zone. The final dbRDA model based off forward and backward propagation model selection included distance from shore, wave height, water temperature, water visibility, and total percent cover of macrophytes (removing tide height, wind speed, wind direction, salinity, depth, wave period, and wave direction). This array of

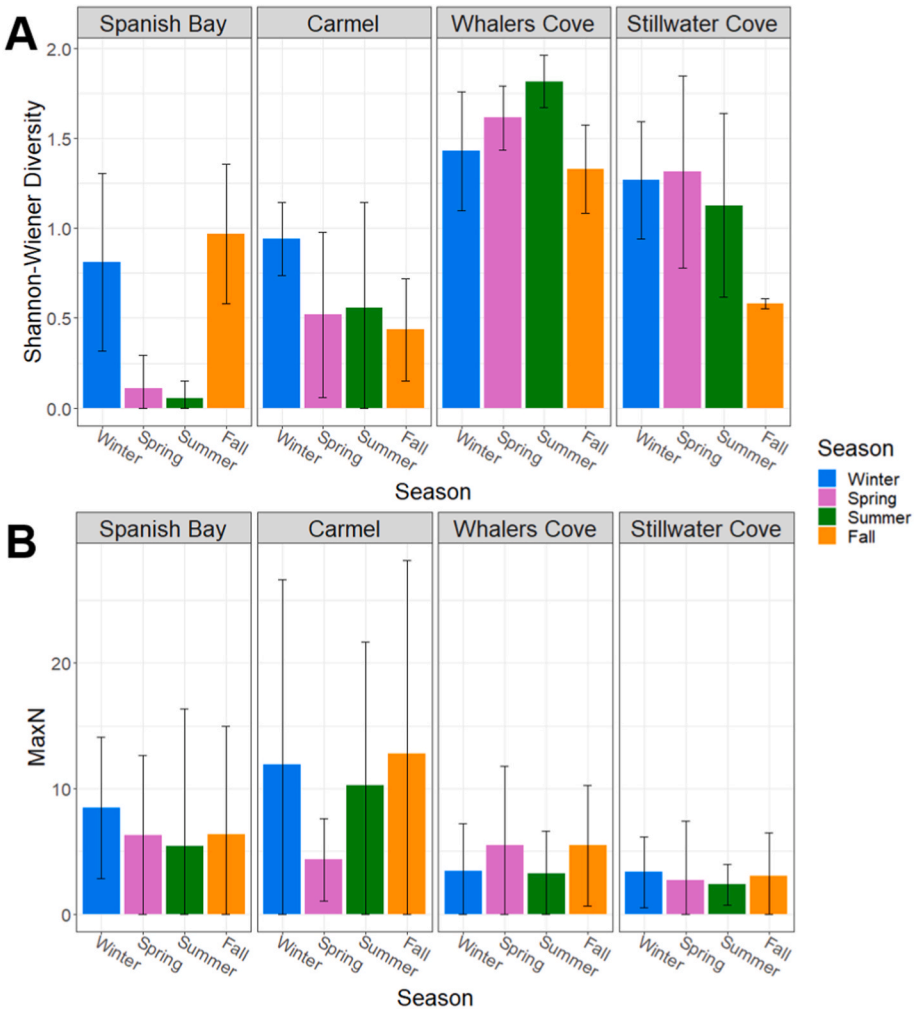

Fig. 2. Diversity and abundance of surf zone fish by site and season. A) Shannon-Wiener diversity of fish assemblage by site and season. B) Fish abundance as averaged MaxN for each BRUVS. Bars are mean values ± 1 standard deviation.

environmental variables explained a significant amount of the variation in the surf zone fish assemblage when controlling for site-to-site differences ($p = 0.001$), with distance from shore as an indicator of surf zone width and wave breaker height being the only two significant predictors of fish community composition ($p < 0.05$; Fig. 4A; Table 1). Surf zone width and breaker height were more strongly associated with the winter and spring fish assemblage, while water temperature and percent cover of macrophytes were strongly associated with summer and fall. Several fish species, *T. semifasciata*, *A. koelzi*, and *A. argenteus*, were more likely to occur at sites and during seasons when breaker height and surf zone width were greater, while *C. stigmaeus* tended to be found at sites with less wave action and a narrow surf zone. Three species (*H. caryi*, *P. triserata*, and *M. minimus*) were associated with warmer water temperatures, typical of summer and fall, while *E. lateralis* and *E. jacksoni* were more associated with cooler water temperatures found in winter and spring. *P. triserata* also occurred more frequently in conditions containing a higher percent cover of macrophytes (Fig. 4B).

4. Discussion

4.1. Effects of season and site on surf zone assemblages

For surf zone fish assemblages, we detected strong differences in diversity and abundance among the four sites and identified trends in assemblage composition across seasons using multivariate approaches. The significant differences we observed in diversity, abundance, and composition of surf zone fish among sites aligned with the strong geophysical differences between the wave-exposed and sheltered study sites. The narrow, sheltered surf zones at Whalers Cove and Stillwater Cove exhibited greater diversity, but lower fish abundance compared to the wider wave-exposed surf zones at Spanish Bay and Carmel Beach. Our diversity results align with Valesini et al. (2004), who reported that fish species diversity was greater in highly sheltered sites versus those exposed to moderate wave activity, when sampling with seine nets in Australian surf zones. In contrast, the pattern of increased environmental stress, such as increased wave exposure, has been reported to result in increased diversity of species in rocky nearshore habitats in other studies (Scrosati et al., 2011). The sheltered sites in our study were also in closer proximity to subtidal rocky reefs, which has been shown to increase functional diversity and functional niche space (Henderson et al., 2022). The trend of lower diversity but greater abundance of surf zone fish at the exposed sites indicates that although fewer species were present at Carmel Beach and Spanish Bay, they could be highly abundant in winter. Our findings agree with results of studies from other regions in California using a combination of BRUVS and seine nets, where the surf zone community is typically dominated by a few highly abundant species (Marraffini et al., 2024).

Some species of fish, including the surfperches *A. argenteus* and *A. koelzi*, were observed throughout the year but had greater abundances during the winter and spring, likely due to seasonality in prey availability. These two surfperch species feed on invertebrates, such as low intertidal sand crabs and amphipods (Schooler et al., 2024; Madden,

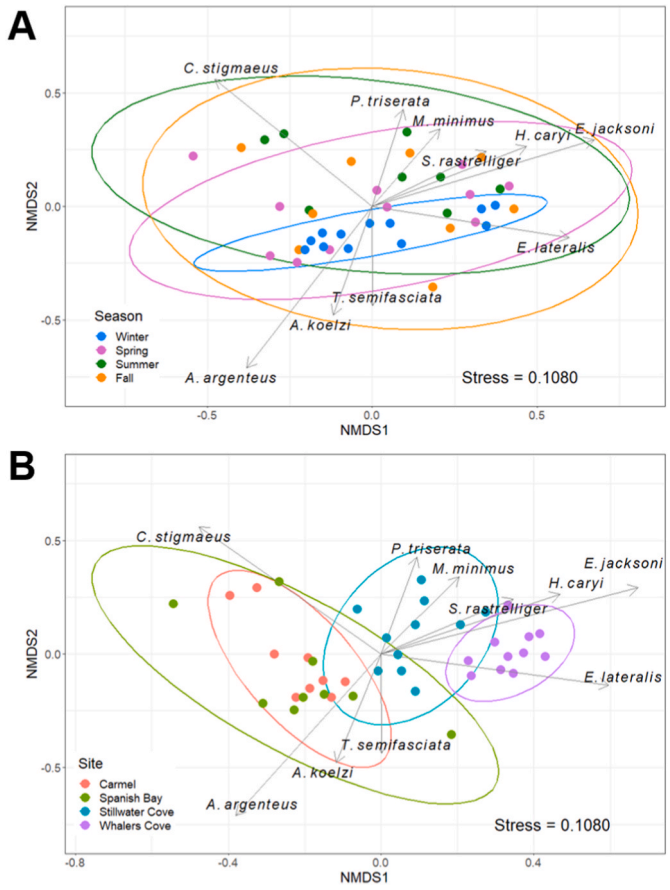

Fig. 3. Results from nonmetric multidimensional scaling (nMDS) analysis of surf zone fish assemblages (detailed species details are included in Supplemental Table 3). A) Separation of sampling days by season. B) Separation of sampling days by site. Ellipses are 95 % confidence intervals and include species vectors for the 10 most common species labeled.

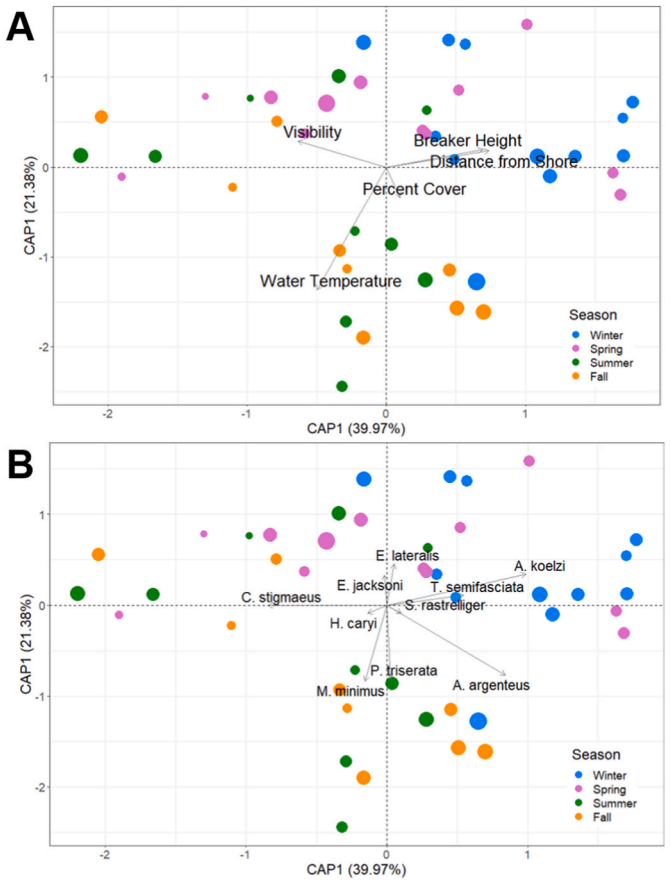

Fig. 4. Results from distance-based redundancy analysis of fish species at all sites with the proportion of variance explained on each axis. Points represent a sampling day and are colored by season and scaled by relative abundance of fish (MaxN). A) Overlay of environmental variable vectors. B) Overlay of all species vectors for 10 most common species.

2023). Kelp subsidies transported from offshore in the winter and spring, due to dislodgement by storms, typically harbor amphipods (Hyndes et al., 2014) that are a seasonally important prey resource for surf zone fish (Schooler et al., 2024). A similar trend of predatory fish seasonally shifting their forging grounds to feed on pulsed prey abundance has been observed in subtropical estuaries (Livernois et al., 2021). The Pacific sand crab, *Emerita analoga*, is also a key resource for surfperch and populations of sand crabs contain a wide range of sizes (3 to >30 mm carapace length) whose abundance varies seasonally in the surf zone (Dugan et al., 1994). The smaller size classes, including megalopae, juveniles, and males, are consumed by numerous surfperch species (Carlisle et al., 1960; Madden, 2023; Schooler et al., 2024), with young-of-the-year *E. analoga* being most abundant in winter, spring, and early summer (Dugan et al., 1994). In contrast, larger overwintering *E. analoga* are prey for the larger surfperch (*A. argenteus* and *A. koelzi*), particularly during the fall and winter (Madden, 2023). The abundance and high nutritional quality of *Emerita* may help to fuel the energetic needs of surfperch reproduction, as it ramps up from winter to spring (Izumiyama et al., 2020). Seasonal trends of the dominant surfperch species can likely be explained by prey availability and resource acquisition.

In terms of elasmobranchs, the leopard shark, *T. semifasciata*, also exhibited higher abundances within the surf zone in the winter and spring. Leopard sharks are an active and mobile species, and their metabolism and behavior are less strongly affected by temperature compared to other temperate elasmobranch species (Skelton et al., 2023). Within central California, leopard sharks inhabit the nearby

Table 1
Results for environmental factors from the partial distance-based redundancy analysis. CAP1 and CAP2 values represent the correlation between the environmental variable and the constrained ordination (axis 1 and 2 respectively).

Variable	CAP1	CAP2	p-value
Distance from shore/Surf Zone Width (m)	0.479	0.109	0.013
Breaker height (m)	0.451	0.116	0.008
Water temperature (°C)	−0.324	−0.821	0.059
Visibility (m)	−0.411	0.174	0.082
Algae percent cover (%)	0.066	−0.205	0.130

Elkhorn Slough in Monterey Bay, but have been observed vacating the slough during the winter due to lower salinity, dissolved oxygen, and cooler water temperatures relative to the ocean (Carlisle and Starr, 2009), potentially resulting in higher visitation of surf zone habitats. Leopard sharks also exhibit seasonal foraging patterns (Talent, 1976), focusing on fish eggs (*Atherinopsis californiensis)* in early May and Cancridae crabs in late May (Ebert and Ebert, 2005). Although these sharks are observed in the surf zone through summer and fall (Marraffini et al., 2024), our results suggest they are likely migrating into the surf zone in the winter when conditions become less ideal in the estuaries in central California.

4.2. *Environmental variables driving changes in surf zone assemblages*

Our results on the influence of environmental variables on surf zone fish assemblages were generally consistent with those from previous surf

zone studies using a variety of methods (Olds et al., 2018, Ortodossi et al., 2019). We found that water temperature had mixed effects on the surf zone fish community with two surfperch species (*H. caryi* and *M. minimus*) and *P. triserata* being associated with warmer waters, while *E. lateralis* and *E. jacksoni* were associated with cooler waters, though not strongly. Generally, past studies have indicated that water temperature influences surf zone fish abundance and distribution, with some species declining while others increase their range or abundance in warmer conditions (Harborne and Mumby, 2011, Rodrigues and Vieira, 2013). Embiotocids typically associate with cooler ocean temperatures and increasing temperatures have been predicted to result in population declines (Froeschke et al., 2007). California fish communities are known to be affected by dramatic shifts in ocean temperatures related to marine heatwaves. During the intense marine heatwave of 2015, twenty-nine species in the eastern Pacific Ocean were observed to expand their geographic range, including two species that shifted into new habitats (Lonhart et al., 2019). A recent northern range extension of *Zapteryx exasperata* (banded guitarfish) that we observed on BRUVS in Whalers Cove has been attributed to these warm water events (Aitchison et al., 2021). Similarly, the intense marine heatwave of 2014–2016 was associated with a decrease in species and trophic diversity of nearshore rocky reefs in central California (Ziegler et al., 2023). These extreme events are predicted to increase in frequency (Holbrook et al., 2019), and coupled with global increases in ocean temperature, surf zone fish communities are likely to respond to these events. Additionally, central California and the Monterey Bay region have been identified as important transition zones for both warm- and cool-water adapted species, so increases in the frequency and intensity of marine heatwaves may disrupt this system (Sanford et al., 2019). Continued warming of ocean temperatures could allow additional fish species with southern affinities to move north into central California, while those with cold-water affinities may shift their ranges out of the region.

Exposure of beaches to prevailing wind and swell leads to differences in the surf zone reflected in factors such as wave height, surf zone width, and the amount of macroalgal wrack. In this study, two distinct types of surf zones were investigated: sheltered and exposed. Although the sheltered sites typically had a higher percent cover of macrophytes on the BRUVs, this was more commonly in the form of attached macrophytes. In contrast, the exposed sites were characterized by a higher cover of drift macroalgae. Some fish species weakly co-occurred with the total percent cover of macrophytes, but this variable was not significant in the dbRDA. To try to further control for the effects of microhabitat and differing wave effects, all BRUVS were placed seaward of the breaking waves. This allowed us to use the distance the BRUVS were deployed from shore as a proxy for surf zone width and therefore beach exposure (Borland et al., 2017). Distance from shore and breaker height co-occurred in the dbRDA. These variables were significant explanatory factors for surf zone fish assemblages, specifically two surfperch species, *A. argenteus* and *A. koelzi*, and leopard sharks, *T. semifasciata*, which were positively associated with both breaker height and distance from shore. The surfperch family (Embiotocidae) evolved in the temperate North Pacific, and many species in this family have adapted to live in the exposed surf zone (Longo and Bernardi, 2015). Other studies have identified the influence of breaker height on surf zone fish; fish abundance was negatively correlated with larger waves in South Africa and Brazil, and larger individuals were found in more exposed sites (Clark, 1997, Shah Esmaeili et al., 2022). Our study did not include a component of fish length, but additional studies using stereo-BRUVS could evaluate the influence of waves on size structure of fish populations. The frequency of large, storm-driven wave events are predicted to triple by the end of the century in central California (Poujol et al., 2021), leading to more significant wave events in the surf zone seasonally. These changes in wave climate could shift the surf zone assemblage toward the surfperch and elasmobranch species that favor larger waves and more exposed beaches.

Although other environmental factors, such as wind speed and salinity, can be important factors in influencing surf zone assemblages, results from our study and others have yielded a variety of contrasting results. Our study detected little effect of either variable on surf zone fish in central California, likely tied to only conducting surveys on days with relatively smaller waves and less wind, due to safety concerns. This constraint on survey conditions reduced our ability to detect an effect of these variables on surf zone fish. Beaches near freshwater outflows have been reported to exhibit a strong negative correlation between surf zone fish abundance and salinity in certain areas, such as Brazil (do Nascimento et al., 2021), but not in other temperate surf zones such as Japan (Inui et al., 2010). However, none of our study sites were located near significant riverine or estuarine outflows and our study region was undergoing extreme drought conditions during the study period (Williams et al., 2022). These combined effects may have contributed to the lack of detection of any association between salinity and fish assemblage composition in our study.

The monthly temporal resolution of this study was necessary to analyze seasonal variability, but having longer term, multi-year data would yield more information on the composition of the surf zone community and how it is influenced by the changing environment. Future studies should aim to gather additional temporal data at more sites. Longer studies that cover multiple years have been shown to document greater numbers of species in the surf zone (Olds et al., 2018). For example, the winter of 2020 and spring of 2021 were classified as a mild La Niña in our study region, meaning there were changes in the typical ocean trends. Many wildfires occurred in our region during the fall of 2020, including the Carmel and River Fires, which were close to the Monterey Peninsula. Increased soil erosion and run-off after wildfires into rivers and estuaries that flow to the ocean can negatively alter water quality (Benda et al., 2003). Having additional years of replicated sampling would help to evaluate the extent of these large-scale, long--lasting environmental events. Additionally, adding a broader scale of study sites and species could further tease apart the differences between sheltered and exposed beaches to determine if the differences we detected are consistent. Although only fish were examined in this study, the prey for most of the highly abundant fish were small invertebrates. Combining investigations of the seasonal distribution of surf zone fish and prey invertebrates (specifically *E. analoga*), would be useful to continue explaining the seasonal trends observed here. Following recommendations from Harvey et al. (2021), further standardizing the sampling methods used (BRUVS in this study) can provide invaluable tools for larger scale investigations of fish populations for management. More study of surf zone biota is needed to inform coastal management and conservation as limited efforts have gone into understanding its ichthyological residents.

5. Conclusion

Sandy beaches and surf zones provide many cultural, economic, and recreational resources; however, ecological studies of the drivers of these highly dynamic systems are underrepresented within the scientific literature. This study investigated the impact of seasonality on fish assemblages in the surf zone at four beaches in central California using BRUVS. Wave height was the strongest driver of species composition within the surf zone, and predicted changes in large wave events with winter storms in California will likely lead to beach and shoreline erosion and changes in the surf zone communities. Resource managers frequently overlook the surf zone, as less information is available from this ecosystem, even though several recreationally targeted species of fish are found in high abundance and utilize the surf zone as a nursery habitat. Our finding of strong seasonal variability in fish use of central California surf zones at both sheltered and exposed beaches provides new insights on the dynamics of these understudied coastal resources.

CRediT authorship contribution statement

Gammon N. Koval: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jenifer E. Dugan:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Scott L. Hamilton:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.csr.2025.105526.

Data availability

The data and code are available at GitHub: https://github.com/gkoval11/Koval_etal_2025_SurfZoneFish

References

Aitchison, R.M., Koval, G.N., Ebert, D.A., 2021. First record of the banded guitarfish, *Zapteryx exasperata* (Rhinopristiformes: trygonorrhinidae), in central California, USA. J. Ocean Sci. Found. 38, 131–137. https://doi.org/10.5281/zenodo.5807911.

Allen, L.G., Pondella, I.I.D.J., 2006a. Chapter 6. Surf zone, coastal pelagic zone, and harbors. The Ecology of Marine Fishes: California and Adjacent Waters. University of California Press, Berkeley, pp. 149–166. https://doi.org/10.1525/9780520932470-008.

Allen, L.G., Findlay, A.M., Phalen, C.M., 2002. Structure and standing stock of the fish assemblages of San Diego Bay, California from 1994 to 1999. Bull. South Calif. Acad. Sci. 101 (2), 49–85.

Andrews, H.L., 1945. The kelp beds of the monterey region. Ecology 26, 24–37. https://doi.org/10.2307/1931912.

Attwood, C.G., van Zyl, C.S., Lombard, A.T., McCagh, C., 2016. Seasonally and spatially referenced estimates of recreational shore-angling effort, catch composition, catch rates and total catch in the Goukamma Marine Protected Area, South Africa. Afr. J. Mar. Sci. 38, 563–579. https://doi.org/10.2989/1814232X.2016.1256837.

Benda, L., Miller, D., Bigelow, P., Andras, K., 2003. Effects of post-wildfire erosion on channel environments, Boise River, Idaho. For. Ecol. Manag. 178 (1–2), 105–119. https://doi.org/10.1016/S0378-1127(03)00056-2.

Bernardi, G., Toy, J.A., Escalona, M., Marimuthu, M., Sahasrabudhe, R., Nguyen, O., Sacco, S., Beraut, E., Toffelmier, E., Miller, C., Shaffer, H.B., 2022. Reference genome of the Black surfperch, *Embiotoca jacksoni* (Embiotocidae, Perciformes), a California kelp forest fish that lacks a pelagic larval stage. J. Hered., Esac034 https://doi.org/10.1093/jhered/esac034.

Beyst, B., Buysse, D., Dewicke, A., Mees, J., 2001. Surf zone hyperbenthos of Belgian sandy beaches: seasonal patterns. Estuar. Coast Shelf Sci. 53, 877–896. https://doi.org/10.1006/ecss.2001.0808.

Blanchet, F.G., Legendre, P., Borcard, D., 2008. Forward selection of explanatory variables. Ecology 89 (9), 2623–2632. https://doi.org/10.1890/07-0986.1.

Borland, H.P., Schlacher, T.A., Gilby, B.L., Connolly, R.M., Yabsley, N.A., Olds, A.D., 2017. Habitat type and beach exposure shape fish assemblages in the surf zones of ocean beaches. Mar. Ecol. Prog. Ser. 570, 203–211. https://doi.org/10.3354/meps12115.

Carlisle, A.B., Starr, R.M., 2009. Habitat use, residency, and seasonal distribution of female leopard sharks *Triakis semifasciata* in Elkhorn Slough, California. Mar. Ecol. Prog. Ser. 380, 213–228. https://doi.org/10.3354/meps07907.

Carlisle, J.G., Schott, J.W., Abramson, N.J., 1960. The barred surfperch (*Amphistichus argenteus* Agassiz) in southern California (No. 109). State of California. Department of fish and game. Marine Res. Op. 1–78.

Clark, B.M., 1997. Variation in surf-zone fish community structure across a wave-exposure gradient. Estuar. Coast Shelf Sci. 44, 659–674. https://doi.org/10.1006/ecss.1996.0151.

Clarke, K.R., Warwick, R.M., 1994. An approach to statistical analysis and interpretation. Change Marine Commun. 2, 117–143. https://doi.org/10.3354/meps307233.

Crawley, K.R., Hyndes, G.A., Suzanne, G.A., 2006. Influence of different volumes and types of detached macrophytes on fish community structure in surf zones of sandy beaches. Mar. Ecol. Prog. Ser. 307, 233–246. https://doi.org/10.3354/meps307233.

Currey-Randall, L.M., Galaiduk, R., Stowar, M., Vaughn, B.I., Miller, K.J., 2021. Mesophotic fish communities of the ancient coastline in Western Australia. PLoS One 16 (4), e0250427. https://doi.org/10.1371/journal.pone.0250427.

Dugan, J.E., Hubbard, D.M., Wenner, A.M., 1994. Geographic variation in life history in populations of the sand crab *Emerita analoga* Stimpson, on the California coast: relationships to environmental variables. J. Exp. Mar. Biol. Ecol. 181, 255–278. https://doi.org/10.1016/0022-0981(94)90132-5.

do Nascimento, CG, da Costa, MR, de Almeida Tubino, R, Monteiro-Neto, C, 2021. Spatial and seasonal patterns of the surf-zone ichthyofauna on a tropical Atlantic dissipative coastline. Reg. Stud. Marine Sci. 48, 101981. https://doi.org/10.1016/j.rsma.2021.101981.

Dugan, J.E., Hubbard, D.M., McCrary, M.D., Pierson, M.O., 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. Estuar. Coast Shelf Sci. 58, 25–40. https://doi.org/10.1016/S0272-7714(03)00045-3.

Dugan, J.E., Hubbard, D.M., Page, H.M., Schimel, J.P., 2011. Marine macrophyte wrack inputs and dissolved nutrients in beach sands. Estuaries Coasts 34, 839–850. https://doi.org/10.1007/s12237-011-9375-9.

Ebert, D.A., Ebert, T.B., 2005. Reproduction, diet and habitat use of leopard sharks, *Triakis semifasciata* (Girard), in Humboldt Bay, California, USA. Mar. Freshw. Res. 56 (8), 1089–1098. https://doi.org/10.1071/MF05069.

Fiori, S.M., Cazorla, A.L., Martínez, A., Carcedo, M.C., Blasina, G., Molina, J.M., Cardona, J.G., Moyano, J., Menéndez, M.C., 2022. Life in the surf-zone: variations of faunal assemblage structure in temperate sandy beaches of the Southwestern Atlantic coast. Cont. Shelf Res., 104781. https://doi.org/10.1016/j.csr.2022.104781.

Froeschke, B., Allen, L.G., Pondella, D.J., 2007. Life history and courtship behavior of black perch, Embiotoca jacksoni (Teleostomi: embiotocidae), from Southern California. Pac. Sci. 61 (4), 521–531. https://doi.org/10.2984/1534-6188(2007)61[521:LHACBO]2.0.CO;2.

García-Reyes, M., Sydeman, W.J., 2017. California multivariate ocean climate indicator (MOCI) and marine ecosystem dynamics. Ecol. Indic. 72, 521–529. https://doi.org/10.1016/j.ecolind.2016.08.045.

Gold, Z., Koch, M.Q., Schooler, N.K., Emery, K.A., Dugan, J.E., Miller, R.J., Page, H.M., Schroeder, D.M., Hubbard, D.M., Madden, J.R., Whitaker, S.G., 2023. A comparison of biomonitoring methodologies for surf zone fish communities. PLoS One 18 (6), e0260903. https://doi.org/10.1371/journal.pone.0260903.

Harborne, A.R., Mumby, P.J., 2011. Novel ecosystems: altering fish assemblages in warming waters. Curr. Biol. 21 (19), R822–R824. https://doi.org/10.1016/j.cub.2011.08.043.

Harvey, E.S., Cappo, M., Butler, J.J., Hall, N., Kendrick, G.A., 2007. Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure. Mar. Ecol. Prog. Ser. 350, 245–254. https://doi.org/10.3354/meps07192.

Harvey, E.S., McLean, D.L., Goetze, J.S., Saunders, B.J., Langlois, T.J., Monk, J., Barrett, N., Wilson, S.K., Holmes, T.H., Ierodiaconou, D., Jordan, A.R., 2021. The BRUVs workshop–An Australia-wide synthesis of baited remote underwater video data to answer broad-scale ecological questions about fish, sharks and rays. Mar. Pol. 127, 104430. https://doi.org/10.1016/j.marpol.2021.104430.

Henderson, C.J., Gilby, B.L., Olds, A.D., Mosman, J., Connolly, R.M., Hyndes, G., Kelaher, B., Maslo, B., Williams, A., Schlacher, T.A., 2022. Connectivity shapes functional diversity and maintains complementarity in surf zones on exposed coasts. Estuaries Coasts 45 (6), 1534–1544. https://doi.org/10.1007/s12237-022-01046-0.

Holbrook, N.J., Scannell, H.A., Gupta, A.S., Benthuysen, J.A., Feng, M., Oliver, E.C.J., Alexander, L.V., Burrows, M.T., Donat, M.G., Hobday, A.J., Moore, P.J., Perkins-Krikpatrick, S.E., Smale, D.A., Straub, S.C., Wernberg, T., 2019. A global assessment of marine heatwaves and their drivers. Nat. Commun. 10, 2624. https://doi.org/10.1038/s41467-019-10206-z.

Hyndes, G.A., Nagelkerken, I., McLeod, R.J., Connolly, R.M., Lavery, P.S., Vanderklift, M.A., 2014. Mechanisms and ecological role of carbon transfer within coastal seascapes. Biol. Rev. 89 (1), 234–254.

Inui, R., Nishida, T., Onikura, N., Eguchi, K., Kawagishi, M., NakataniM, Oikawa S., 2010. Physical factors influencing immature-fish communities in the surf zones of

sandy beaches in northwestern Kyushu Island, Japan. Estuar. Coast Shelf Sci. 86 (3), 467–476. https://doi.org/10.1016/j.ecss.2009.09.034.
Izumiyama, M., Westphal, M.F., Crow, K.D., 2020. In the surf zone: reproductive strategy of the calico surfperch (*Amphistichus koelzi*) in a comparative context. J. Fish. Biol. 96 (4), 939–949. https://doi.org/10.1111/jfb.14283.
Krumhansl, K.A., Scheibling, R.E., 2012. Production and fate of kelp detritus. Mar. Ecol. Prog. Ser. 467, 281–302. https://doi.org/10.3354/meps09940.
Layman, C.A., 2000. Fish assemblage structure of the shallow ocean surf-zone on the eastern shore of Virginia Barrier Islands. Estuar. Coast Shelf Sci. 51, 201–213. https://doi.org/10.1006/ecss.2000.0636.
Livernois, M.C., Fujiwara, M., Fisher, M., Wells, R.D., 2021. Seasonal patterns of habitat suitability and spatiotemporal overlap within an assemblage of estuarine predators and prey. Mar. Ecol. Prog. Ser. 668, 39–55. https://doi.org/10.3354/meps13700.
Longo, G., Bernardi, G., 2015. The evolutionary history of the embiotocid surfperch radiation based on genome-wide RAD sequence data. Mol. Phylogenet. Evol. 88, 55–63. https://doi.org/10.1016/j.ympev.2015.03.027.
Lonhart, S.I., Jeppesen, R., Beas-Luna, R., Crooks, J.A., Lorda, J., 2019. Shifts in the distribution and abundance of coastal marine species along the eastern Pacific Ocean during marine heatwaves from 2013 to 2018. Marine Biodiversity Rec. 12 (1), 1–15. https://doi.org/10.1186/s41200-019-0171-8.
Madden, J.R., 2023. *Temporal Variation and Ontogenetic Shifts in the Diet of a Surf Zone Fish, the Barred Surfperch, Amphistichus argenteus* (Doctoral Dissertation, UC Santa Barbara).
Manzer, C.R., Connoly, T.P., McPhee-Shaw, E., Smith, G.J., 2019. Physical factors influencing phytoplankton abundance in southern Monterey Bay. Cont. Shelf Res. 180, 1–13. https://doi.org/10.1016/j.csr.2019.04.007.
Marraffini, M.L., Hamilton, S.L., Marin Jarrin, J.R., Ladd, M., Koval, G., Madden, J.R., Mangino, I., Parker, L.M., Emery, K.A., Terhaar, K., Hubbard, D.M., 2024. Evaluating the influence of marine protected areas on surf zone fish. Conserv. Biol., e14296 https://doi.org/10.1111/cobi.14296.
Marin Jarrin, J.R., Shanks, A.L., 2011. Spatio-temporal dynamics of the surf-zone faunal assemblages at a southern Oregon sandy beach. Mar. Ecol. 32, 232–242. https://doi.org/10.1111/j.1439-0485.2010.00414.x.
Marin Jarrin, J.R., Shanks, A.L., Miller, J.A., 2022. The biology and ecology of sandy beach surf zones. In: Sandy Beaches as Endangered Ecosystems. CRC Press, pp. 26–53.
Martinez Arbizu, P., 2020. Pairwiseadonis: Pairwise Multilevel Comparison Using Adonis. R package version 0.4.
McLachlan, A., Brown, A., 2006. The Ecology of Sandy Shores, second ed. Elsevier-Academic Press, Burlington, MA.
Murphy, H.M., Jenkins, G.P., 2010. Observational methods used in marine spatial monitoring of fishes and associated habitats: a review. Mar. Freshw. Res. 61, 236–252. https://doi.org/10.1071/MF09068.
Nanami, A., Endo, T., 2007. Seasonal dynamics of fish assemblage structures in a surf zone on an exposed sandy beach in Japan. Ichthyol. Res. 54, 277–286. https://doi.org/10.1007/s10228-007-0402-6.
Olds, A.D., Vargas-Fonseca, E., Connolly, R.M., Gilby, B.L., Huijbers, C.M., Hyndes, G.A., Layman, C.A., Whitfield, A.K., Schlacher, T.A., 2018. The ecology of fish in the surf zones of ocean beaches: a global review. Fish Fish. 19, 78–89. https://doi.org/10.1111/faf.12237.
Ortodossi, N.L., Gilby, B.L., Schlacher, T.A., Connolly, R.M., Yabsley, N.A., Henderson, C. J., Olds, A.D., 2019. Effects of seascape connectivity on reserve performance along exposed coastlines. Conserv. Biol. 33 (3), 580–589. https://doi.org/10.1111/cobi.13237.
Poujol, B., Prien, A.F., Molina, M.J., Muller, C., 2021. Dynamic and thermodynamic impacts of climate change on organized convection in Alaska. Clim. Dyn. 56 (7), 2569–2593. https://doi.org/10.1007/s00382-020-05606-7.
R Core Team, 2017. R: a language and environment for statistical computing. https://www.R-project.org.
Ramp, S.R., Lermusiaux, P.F., Shulman, I., Chao, Y., Wolf, R.E., Bahr, F.L., 2011. Oceanographic and atmospheric conditions on the continental shelf north of the monterey Bay during August 2006. Dynam. Atmos. Oceans 52, 192–223. https://doi.org/10.1016/j.dynatmoce.2011.04.005.
Rodrigues, F.L., Vieira, J.P., 2013. Surf zone fish abundance and diversity at two sandy beaches separated by long rocky jetties. J. Mar. Biol. Assoc. U. K. 93 (4), 867–875. https://doi.org/10.1017/S0025315412001531.
Ross, S.T., McMichael, Jr.RH., Ruple, D.L., 1987. Seasonal and diel variation in the standing crop of fishes and macroinvertebrates from a Gulf of Mexico surf zone. Estuar. Coast Shelf Sci. 25, 391–412. https://doi.org/10.1016/0272-7714(87)90033-3.
Sanford, E., Sones, J.L., García-Reyes, M., Goddard, J.H., Largier, J.L., 2019. Widespread shifts in the coastal biota of northern California during the 2014–2016 marine heatwaves. Sci. Rep. 9 (1), 4216. https://doi.org/10.1038/s41598-019-40784-3.
Schooler, N.K., Emery, K.A., Dugan, J.E., Miller, R.J., Schroeder, D.M., Madden, J.R., Page, H.M., 2024. Cross-ecosystem trophic subsidies to sandy beaches support surf zone fish. Mar. Biol. 171 (9), 184. https://doi.org/10.1007/s00227-024-04499-y.
Schroeder, D.M., Love, M.S., 2002. Recreational fishing and marine fish populations in California. Calif. Coop. Ocean. Fish. Investig. Rep. 182–190.
Scrosati, R.A., van Genne, B., Heaven, C.S., Watt, C.A., 2011. Species richness and diversity in different functional groups across environmental stress gradients: a model for marine rocky shores. Ecography 34 (1), 151–161. https://doi.org/10.1111/j.1600-0587.2010.06119.x.
Shah Esmaeili, Y., Corte, G.N., Checon, H.H., Bilatto, C.G., Lefcheck, J.S., Zacagnini Amaral, A.C., Turra, A., 2022. Revealing the drivers of taxonomic and functional diversity of nearshore fish assemblages: implications for conservation priorities. Divers. Distrib. 28 (8), 1597–1609. https://doi.org/10.1111/ddi.13453.
Skelton, Z.R., Prinzing, T.S., Hastings, P.A., Wegner, N.C., 2023. Laboratory-based measures of temperature preference and metabolic thermal sensitivity provide insight into the habitat utilisation of juvenile California horn shark (Heterodontus francisci) and leopard shark (Triakis semifasciata). J. Fish Biol. 102 (4), 829–843. https://doi.org/10.1111/jfb.15307.
Talent, L.G., 1976. Food habits of the leopard shark, Triakis semifasciata. In: Slough, Elkhorn, Bay, Monterey (Eds.), California. *California Fish and Game*, 62, pp. 286–298, 4.
Thompson, S.A., Sydeman, W.J., Santora, J.A., Black, B.A., Suryan, R.M., Calambokidis, J., Peterson, W.T., Bograd, S.J., 2012. Linking predators to seasonality of upwelling: using food web indicators and path analysis to infer trophic connections. Prog. Oceanogr. 101, 106–120. https://doi.org/10.1016/j.pocean.2012.02.001.
Valesini, F.J., Potter, I.C., Clarke, K.R., 2004. To what extent are the fish compositions at nearshore sites along a heterogeneous coast related to habitat type. Estuar. Coast Shelf Sci. 60 (4), 737–754. https://doi.org/10.1016/j.ecss.2004.03.012.
Vargas-Fonseca, E., Olds, A.D., Gilby, B.L., Connolly, R.M., Schoeman, D.S., Huijbers, C. M., Hyndes, G.A., Schlacher, T.A., 2016. Combined effects of urbanization and connectivity on iconic coastal fishes. Divers. Distrib. 22, 1328–1341. https://doi.org/10.1111/ddi.12495.
Whitmarsh, S.K., Fairweather, P.G., Huveneers, C., 2017. What is big BRUVver up to? Methods and uses of baited underwater video. Rev. Fish Biol. Fish. 27, 53–73. https://doi.org/10.1007/s11160-016-9450-1.
Williams, A.P., Cook, B.I., Smerdon, J.E., 2022. Rapid intensification of the emerging Southwestern North American megadrought in 2020–2021. Nat. Clim. Change 12 (3), 232–234. https://doi.org/10.1038/s41558-022-01290-z.
Ziegler, S.L., Johnson, J.M., Brooks, R.O., Johnston, E.M., Mohay, J.L., Ruttenberg, B.I., Starr, R.M., Waltz, D.E., Hamilton, S.L., 2023. Marine protected areas, marine heatwaves, and the resilience of nearshore fish communities. Sci. Rep. 13, 1405. https://doi.org/10.1038/s41598-023-28507-1.
Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1 (1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.