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Spatial and temporal variation in the species diversity of coastal California fish eggs

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Abstract

Ichthyoplankton studies can be used to assess the abundance, distribution, and reproductive activity of marine fishes, but few studies have monitored spawning activity at inshore sites. This study utilized weekly plankton sampling to construct a year long time series of fish spawning at six pier sites along the California coast – Santa Cruz, San Luis Obispo, Santa Barbara, Santa Monica, Newport Beach and La Jolla; sampling at the La Jolla site continues on-going monitoring initiated in 2012. Fish eggs were sorted from the collected plankton and identified to species level using DNA barcoding of the COI and 16S genes. While only one year of data has been collected from five of the sites, the two sites north of Point Conception show markedly reduced diversity compared to the southern sites. Although the species observed reflect the local environment of each site, this pattern of reduced diversity at the northern sites is consistent with the well documented decline in species richness with latitude along the California coast. The seven-year time series from La Jolla has revealed that spawning activity varies greatly among years, both in egg production and species diversity, with a continuing trend of highest egg numbers in years with colder average winter sea surface temperature.

Key Words
Spawning; fish eggs; species diversity; Point Conception

Main Text

1. INTRODUCTION

Nearshore ecosystems are highly productive and important contributors to the economy of coastal communities (Costanza et al. 1997, Beck et al. 2001, Barth et al. 2007, Mann 2009). Along the California coast, the diverse and abundant populations of marine fish serve as valuable resources for both commercial and recreational fisheries (Methot Jr 1983, Wildlife 2002). However, the dynamic conditions of the coastal marine environment and fishing pressures can lead to significant fluctuations in the abundance, diversity, and distributions of these species (Mann 2000, Perry et al. 2005, Anderson et al. 2008, Shelton & Mangel 2011). As a result, coastal populations need to be monitored across robust spatial and temporal scales in order to implement effective management and conservation strategies that will maintain both their economic and ecological viability. Despite this, only a limited number of studies have been conducted on these scales for fish communities in near-shore environments along the California coast.

Fish population survey methods usually require visual identification. This is reflected in the most common methods – diver surveys and trawls. However, these expensive and resource-intensive methods may miss cryptic species and generally fail to sample early life stages (Brock 1982, Stewart & Beukers 2000). Ichthyoplankton surveys, the collection of fish eggs and larvae, complement the traditional methods by accounting for some of the species at risk of being overlooked (Waugh 2007, Jaafar et al. 2012). Such surveys have been successfully employed to monitor the spawning activity of fishes in the California Current. For example, the California Cooperative Oceanic Fisheries Investigations (CalCOFI) survey cruises have produced notable temporally and spatially robust datasets for ichthyoplankton located in offshore communities in the California Current. As a complement to these surveys, Brewer & Smith (1982) deployed cruises for nearshore ichthyoplankton monitoring from 1978-1980, focusing on larvae from northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*). Barnett et al. (1984) also gathered coastal ichthyoplankton samples from 1977-1979, documenting shifts in ichthyoplankton as the distance from shore increased. Through these surveys, differences in larval abundance between the nearshore and offshore environments have been observed in commercially and ecologically important species. More recently, Suntsov et al. (2012) combined ichthyoplankton data from a variety of sources to evaluate the spatial structure of nearshore fish assemblages from San Diego to San Francisco. Their data accentuates shifts in species diversity with increasing depth and latitude. These surveys highlight the need for large-scale temporal and spatial monitoring of coastal areas, as there is not an active nearshore equivalent to CalCOFI's long-term monitoring program.

Species such as the northern anchovy and Pacific sardine have always been well-suited to ichthyoplankton surveys because their eggs can easily be identified morphologically, but most other species' eggs are not as distinct. However, through the use of molecular methods, a wide variety of ichthyoplankton can be accurately identified to species level (Ward et al. 2009, Gleason & Burton 2012, Harada et al. 2015, Duke et al. 2018). Ichthyoplankton sampling has been successfully employed to classify spawning seasons, estimate the abundance of adult spawning biomass, and assess the species composition of spawning communities, making it an excellent tool for fisheries management (Ahlstrom & Moser 1976, Hunter & Lo 1993, Harada et al. 2015, Duke et al. 2018). Additionally, identifying patterns or variability in larval fish assemblages has been used as ecosystem indicators to classify environmental changes, such as sea surface temperature anomalies (Brodeur et al. 2006).

This study explores how species diversity changes across a latitudinal gradient and provides baseline information as to which species are spawning at six study locations along the California coast: Santa Cruz (SC), San Luis Obispo (CP), Santa Barbara (SB), Santa Monica (SM), Newport Beach (NBP), and La Jolla (SIO). Sampling at SIO extends the work of Harada et al. (2015) and Duke et al. (2018), which was initiated in 2012 at the Scripps Pier (SIO) located in La Jolla, California at the boundary of two Marine Protected Areas (MPAs), the San Diego-Scripps Coastal State Marine Conservation Area (SMCA) and the Matlahuayl State Marine Reserve (SMR). Duke et al. (2018) documented extensive interannual variation in egg abundance during the summer spawning season at SIO and found a strong negative correlation between egg abundance and winter sea surface temperatures (SST). We continued sampling at SIO through 2019 to determine the productivity of the 2018 and 2019 spawning seasons, evaluate if the correlation between SST and egg abundance is upheld, and assess the relationship between egg abundance and species diversity. Unlike the majority of ichthyoplankton studies in the region, we attempted to sample each site on a weekly basis, giving greater temporal resolution of the spawning activity of each species found in our collections.

2. MATERIALS & METHODS

2.1. Egg Collection and Quantification

Weekly fish egg collections were completed using vertical plankton tows conducted off the ends of Scripps Pier in La Jolla (SIO), Newport Beach Pier (NBP), Santa Monica Pier (SM), Stearns Wharf Pier in Santa Barbara (SB), Cal Poly Pier in San Luis Obispo (CP), and the Santa Cruz Wharf Pier (SC). Sampling at SIO occurred from 2013 – 2019, while sampling at the other 5 sites spanned 2019 only. The SIO, NBP, SM and SB sites are shore stations within the Southern California Coastal Ocean Observing System (SCCOOS) and CP and SC are within the Central and Northern California Coastal Ocean Observing System (CeNCOOS); the feasibility (logistically and economically) of our weekly collection schedule was possible due to collaborations with local personnel carrying out ongoing physical and biological measurements at these sites. For our ichthyoplankton sampling, a plankton net (505µ mesh) was lowered to the seafloor and raised back out of the water, funneling pelagic eggs into the bottle at the cod end as it rose. This process was repeated multiple times to increase the volume of water being sampled, however, due to local logistics, the number of tows and other sampling factors varies by location. A comparison of sampling sites and methods can be seen in Table 1. After the tows were completed, the net was lowered a final time, only until the rim touched the surface of the water, and then brought up to wash any residual eggs left in the net into the cod end. The contents of the cod end were transferred to a 1-liter container and brought back to the lab, where they were promptly poured through a mesh screen (330µm) to concentrate the plankton.

At SIO, the concentrated plankton sample was then placed in a petri dish with seawater and immediately examined under a microscope at 7.5x magnification. At the other 5 locations, the concentrated plankton sample was stored in 95% ethanol in a 50 mL conical Falcon tube and shipped to SIO, where it was poured into a petri dish and examined under a microscope. Fish eggs were removed and placed in 1.5 mL microtubes with 95% ethanol. The morphologically distinct eggs of the northern anchovy (*Engraulis mordax*) and the Pacific sardine (*Sardinops sagax*) were quantified and stored separately from the rest of the eggs. The eggs that remained to be identified were stored at -20°C for at least 24 hours until further processing.

2.2. DNA Extraction, Amplification, Sequencing, and Identification

The extraction, amplification, sequencing, and identification steps are in accordance with the protocols used by Harada et al. (2015) and Duke et al. (2018). Each egg was placed in an individual well of a 0.2 mL PCR strip tube. The ethanol was removed from each well and each egg was rinsed with 90 µL of nuclease-free water. The water was removed and 15 µL of a 66% AE buffer solution (Qiagen) was added to each well. The samples were then placed in a thermal cycler at 95ºC for 15 minutes and maintained in a 72ºC hold until their removal. A clean pipette tip was used to compress each egg until it burst, expelling the DNA into the AE buffer solution. The DNA was stored at -20ºC until further processing.

The DNA was thawed at room temperature. A 25 µL PCR reaction was prepared for each egg's DNA with 12.5 µL of GoTaq Green 2X Master Mix (Promega), 10.5 µL of molecular grade water, 0.5 µL of each primer, and 1 µL of DNA. The first primer pair used was the CO1 universal primers from Ivanova et al. (2007): 5' TTCTCAACCAACCACAAAGACATTGG 3' (forward) and 5' ACTTCYGGGTGRCCRAARAATCA 3' (reverse). Each sample was vortexed to ensure the contents of each well were mixed. The samples were then placed in the thermocycler following the cycler conditions utilized by Harada and Duke. The PCR product of each sample was checked on a 1.5% agarose gel for a band length of 710 base pairs. The samples with the correct band size were purified and sent for Sanger sequencing. The PCR step was repeated for the samples lacking bands using the 16S primer set: 5' CGCCTGTTATCAAAAACAT 3' (forward) and 5' CCGGTCTGAACTCAGATCACGT 3'' (reverse) from Palumbi (1996). The thermocycler conditions remain the same, with the exception of reducing the number of cycles from 35 to 30. The PCR products of the 16S PCR reaction were checked on a 1.5% agarose gel for a 570 base pair band. Samples with the correct sized band were purified and sent for sequencing.

PCR products were purified according to Harada and Duke and sent to Retrogen Inc. (San Diego) for Sanger sequencing in 10 µL reactions, with 9 µL of purified PCR product and 1 µL of either CO1 or 16S forward primer, depending on which primer was used in the corresponding PCR. The sequencing results were run through NCBI's Basic Local Alignment Search Tool (BLAST), which compares our samples to all sequences available on GenBank. The addition of sequences from Hastings and Burton (2008) greatly contribute to the robustness of the database for CO1 and 16S sequences of marine fish common to southern California waters. If our sequences matched a sequence in the database at 95% similarity or higher, it was classified as the species corresponding to that sequence. However, two closely related species, longfin sanddab (*Citharichthys xanthostigma*) and Pacific sanddab (*Citharichthys sordidus*), could only be differentiated from each other if the sequences matched at greater than 99% similarity. For these two species, if sequences matched between 95% and 99% they were recorded as ambiguous (one of the two species).

2.3. Temperature Data

The data used to calculate the average annual SST (°C) and the average annual winter SST (°C) were obtained from the Southern California Coastal Ocean Observing System (SCCOOS) website. Temperature measurements are recorded approximately every four minutes from a sensor located two meters below the surface. The annual and seasonal averages (and standard error) were calculated from daily averages.

2.4. Species Diversity Analysis

The temporal and spatial analyses for species diversity were performed on subsets of data from each year/site to mitigate the effects of variable sampling efforts. The minimum number of samples (n) collected in a year at SIO 2013-2019 (temporal analysis) and at a site during 2019 (spatial analysis) was identified. Then, n samples from each of the other years/sites were chosen at random, and the total egg abundance, species richness, and effective number of species (ENS) were calculated and stored in R. This process was repeated 1000 times and the mean, standard deviation, and standard error of the egg abundance, species richness, and ENS were calculated from the 1000 trials. The mean and standard deviation were used to create the plots displayed in the species diversity analysis section of the results.

The egg abundance, species richness, and ENS were calculated in the following ways: total egg abundance = the sum of eggs identified in each sample, species richness = the number of unique species identified, and the effective number of species (ENS) = exp(H) as described by Hill (1973) where H is the Shannon diversity index given by Shannon and Wiener (Weaver & Shannon 1964). The Shannon diversity index was calculated using the vegan package in RStudio (Oksanen et al. 2013) with the formula: $H = -\sum_{i=1}^{S} p_i \ln p_i$ where p_i is the proportional abundance of each species i and S is the number of species so that $\sum_{i=1}^{S} p_i = 1$.

3. RESULTS

During 2019, a total of 4,277 eggs were identified, belonging to 32 different species across six sites with only two, speckled sanddab (*Citharichthys stigmaeus*) and California halibut (*Paralichthys californicus*), being present at all sites (Figure 1). There are six species, California tonguefish *(Symphurus atricaudus)*, queenfish (*Seriphus politus*), California corbina (*Menticirrhus undulatus*), spotfin croaker (*Roncador stearnsii*), C-O sole (*Pleuronichthys coenosus*), and rock wrasse (*Halichoeres semicinctus*), present at all four sites south of Point Conception that are absent at the two northern sites. Meanwhile, there is one species, Pacific sand sole (*Psettichthys melanostictus*), that is only present at the two northern sites and absent from the other four. Interestingly, at SIO, the only location situated within an MPA (but also the most southern of the sites), there are nine species present that are absent from the other five locations.

In addition to the differences in species' distributions of eggs, the introduction of sampling at new locations revealed a wide variety of egg abundances between sites. SC, SM, and NBP lack large peaks in egg abundance, while CP, SB, and SIO all display distinct periods of elevated egg abundance (Figure 2A). At the three sites with large peaks in egg abundance, the peak at CP is during winter, whereas the peaks at SB and SIO occur during summer months.

Species richness and Shannon diversity were used to compare species diversity across the six sites, spanning four degrees of latitude along the California coast (Figures 2B and 2C). Despite this relatively short range of latitude, there is a strong, negative relationship between latitude and species richness ($\rho = - 0.84$), with SIO having the highest species richness ($N = 25$) by a large margin and CP ($N = 4$) and SC ($N = 4$) having the lowest species richness, also by a large margin (Figure 2B). This finding complements the distribution of species' eggs shown by the presence/absence chart (Figure 1), in which there are very few species observed at CP and SC. A similar, although weaker, trend ($\rho = - 0.66$) is given by the ENS defined through Shannon diversity (Figure 2C). It is significant that despite the limited number of eggs collected from NBP and SM, there are greater than 10 species identified, and regardless of the considerable number of eggs from CP, there are only four species identified. The ENS at SB is lower than both CP and SC due to the dominance of eggs from speckled sanddab (*Citharichthys stigmaeus*), however, the three most northern sites are still markedly less diverse than the three southern sites.

Over the seven-year monitoring period at SIO, 24,579 eggs have been identified to species level, representing 46 different species. Eighteen species were observed every year, with speckled sanddab (*Citharichthys stigmaeus*), señorita (*Oxyjulis californica*), Pacific sardine (*Sardinops sagax*), Californian salema (*Xenistius californiensis*), and northern anchovy (*Engraulis mordax*) being the most abundant (Figure 3). The spawning season, defined by a period of elevated egg abundance, occurs roughly from May 1st to August 31st each year (Figure 4A). However, the spawning seasons tend to vary in the timing of the peak egg abundance, the magnitude of peak egg abundance, and average egg production. The egg abundances observed in 2015, 2016, and 2019 lack large peaks in egg abundance and the average egg production during the spawning season (May 1st to August 31st) is lower than the seven-year average egg production during the spawning season, $x = 111$; in contrast, 2013, 2014, 2017, and 2018 exhibit large peaks in egg abundance and the average egg production during the spawning season is greater than the seven-year average egg production. As shown by Figure 3, there are fewer species present in the three years with lower egg abundance (2015, 2016, and 2019), but there are no instances of a species present in all of the higher egg abundance years and absent from the lower egg abundance years.

There is a strong, positive relationship ($\rho = 0.92$) between the total number of eggs identified during the spawning season and the species richness of the corresponding season (Figure 4B.). When using Shannon diversity (converted to ENS) to compare the relationship between egg abundance and species diversity (Figure 4C) the relationship weakens ($\rho = 0.7$). In particular, despite having much lower species richness than the high abundance years, the ENS of 2015 and 2019 (low abundance years) is nearly identical to the ENS of 2014 (high abundance year).

Lastly, the relationship between the average winter SST and the average spring-summer egg abundance reported in Duke et al. (2018) was upheld with the data from two additional years

(2018 and 2019). The weekly SST calculated over a 3-week rolling average is shown in Figure 5A with the additional 2018 and 2019 data in red and Figure 5B shows there is a negative correlation, ($\rho = -0.89$), between the average winter (December – February) SST and the average spring-summer (March – August) egg abundance.

4. DISCUSSION

When comparing the ichthyoplankton collected from different sites along the California coast, it is important to note that, in addition to its geographic location, each site differs in potentially important ecological parameters, such as depth and the characteristics of adjacent habitat. Also, local oceanography (i.e., current patterns) will impact the delivery of spawned eggs from nearby habitats to the collection site. Combined, these site-specific differences in habitat contribute to some of the variation we see in species diversity and abundance. In general, the sites are located on sandy bottoms, but the distance to rocky reefs, kelp forest, or other habitats varies. Species found at each of the sites are characteristic of their locality and habitats. For instance, at SB we observed eggs from señorita (*Oxyjulis californica*), kelp bass (*Paralabrax clathratus*), and various croakers complementing data from visual surveys done in the area (Ebeling et al. 1978). All of the species identified in our study from SM and NBP have been observed in the immediate, sandy bottom, or surrounding, rocky reef, habitats in these regions (Allen et al. 1985). The 2019 species composition of the eggs collected at SIO is in accord with the fish eggs observed in other years and by diver surveys conducted in the sandy bottom area under the SIO Pier (Harada et al. 2015, Duke et al. 2018, Craig et al. 2004, Hastings et al. 2014).

Only two of the 32 species found in this study were observed at all 6 sites. We, of course, do not conclude that our observations are tightly correlated to the geographic ranges of the species. Rather, our data reflect local abundances and spawning activity (Zwiefel & Lasker 1976, Garrison et al. 2002, Craig et al. 2004). Particular species may be locally low in abundance or distant from their regional spawning grounds, leading to no eggs in our collections. However, we do see patterns consistent with known geographic distributions. For example, 8 species - California corbina (*Menticirrhus undulatus*), spotfin croaker (*Roncador stearnsii*), rock wrasse (*Halichoeres semicinctus*), yellowfin croaker (*Umbrina roncador*), black croaker (*Cheilotrema saturnum)*, mussel blenny (*Hypsoblennius jenkinsi)*, shortfin weakfish (*Cynoscion parvipinnis)*, xantic sargo (*Anisotremus davidsonii)* - have northern range limits at Point Conception (Miller & Lea 1972, Hastings et al. 2014), a well-known biogeographic barrier (Horn & Allen 1978, Gaylord & Gaines 2000, Hohenlohe 2004) and, as would be expected, none of these species were observed at CP or SC. Although ocean warming over the past several decades has led to documented northward shifts in a variety of shallow water species in California (e.g., Barry et al. 1995) and phenological shifts in reproductive behavior in the California Current ecosystem (Asch 2015), our data suggest that none of these fish species have yet extended their spawning ranges north of Point Conception.

Our observation of decreasing species diversity with increasing latitude is consistent with literature documenting a sharp decline in species diversity across the Point Conception biogeographic boundary (Valentine 1966, Hayden et al. 1976, Horn & Allen 1978, Suntsov et al. 2012). The low species diversity and the winter timing of peak eggs at SC and CP are also consistent with previous observations noting low resident fish catch and February peak spawning for fish in this region (Parish et al. 2013). Further sampling is required to determine if the baseline data shown here are representative of long-term trends at each site.

The addition of 2018-2019 data at SIO supports the previous observation by Duke et al. (2018) that there is extensive interannual variation in the egg abundance exhibited among spawning seasons at SIO. Interannual variation in ichthyoplankton abundance is quite common and has been well documented in Pacific sardine and northern anchovy (Ahlstrom 1966, Van der Lingen & Huggett 2003), as well as other larval fish assemblages (Loeb et al. 1983, Chiu & Hsyu 1994, Duke et al. 2018). Both seasonal and annual variation observed has been attributed to a number of abiotic stressors including salinity, upwelling, anomalous water temperatures, decreased nutrient availability, and global events such as El Niño or La Niña (De Vlaming 1972, Fiedler 1984, Cury & Roy 1989, Doyle et al. 2009, Pankhurst & Munday 2011, Duke et al. 2018). The effects of water temperature and photoperiod on the reproductive processes of fish have been extensively studied and anomalous sea surface temperatures have been linked to numerous reproductive difficulties (reviewed in Pankhurst & Munday 2011, Wang et al. 2010).

The seven years of data from the La Jolla site shows that warm winter SST is correlated with reduced total egg abundance in the subsequent summer. The depressed egg abundance seen in 2015 and 2016 is associated with the El Niño/Warm Blob events, explored by Duke et al. (2018); however, SST alone cannot explain the reduced egg abundance in 2019 because those events had subsided. SST higher than the typical range a species is exposed to, especially if outside its physiological limits, could lead to reproductive failure or shifts in species' ranges (Munday et al. 2008, Cavole et al. 2016). In order to conclusively determine how SST can influence the productivity of a spawning season, more needs to be understood about all the species contributing to the spawning season.

The relationship between warm winter SST and reduced total egg abundance in summer could be due to either reduced productivity of many of the contributing species or failure of specific species to spawn in years with warm winters. Analysis of the temporal changes in species richness indicate that there are, in fact, fewer species contributing to the total egg abundance of the spawning season during less productive years. However, even an equal reduction in the number of eggs produced by each species, such that the proportion of eggs from each species remained the same, would likely result in decreased representation of rarer species in our samples. The weakened trend between total egg abundance and ENS, given by Shannon diversity, suggests that the reduction in total egg abundance is not purely a result of the absence of certain species. The nearly equivalent ENS values of 2015, 2019 (low egg abundance years), and 2014 (high egg abundance year) indicates that regardless of the disparities in species richness, the diversity, defined by both species richness and evenness, is very similar. The presence/absence chart (Figure 3) shows there is not a single species contributing to the egg abundance in high abundance years (2013, 2014, 2017, and 2018), that is absent from all the low egg abundance years (2015, 2016, and 2019); hence the decrease in egg abundance is not caused by the same species failing to spawn in each warm year. Based on the limited available data, we conclude that the observed low egg numbers in warm winter years is the result of a broad effect impacting the productivity of many of the resident species.

In summary, our spatial sampling provides some insight into the range of species' spawning grounds along the California coast. Although our study sites span less than half the length of California's 1350 km coastline, only two of 32 species detected in our year-long study were observed to spawn at all six study sites. Species diversity among spawners was low at sites north of Point Conception relative to those in the south, consistent with both the nature of Point Conception as a biogeographic boundary and with the well-documented gradient in species diversity with latitude along the Pacific coast of North America (Wares et al. 2001, Horn et al. 2006). As patterns of climate change suggest continued warming of the oceans, maintaining spatial and temporal monitoring of fish spawning across biogeographic barriers such as Point Conception may provide important insights into the ecological consequences of environmental change.

5. Acknowledgements

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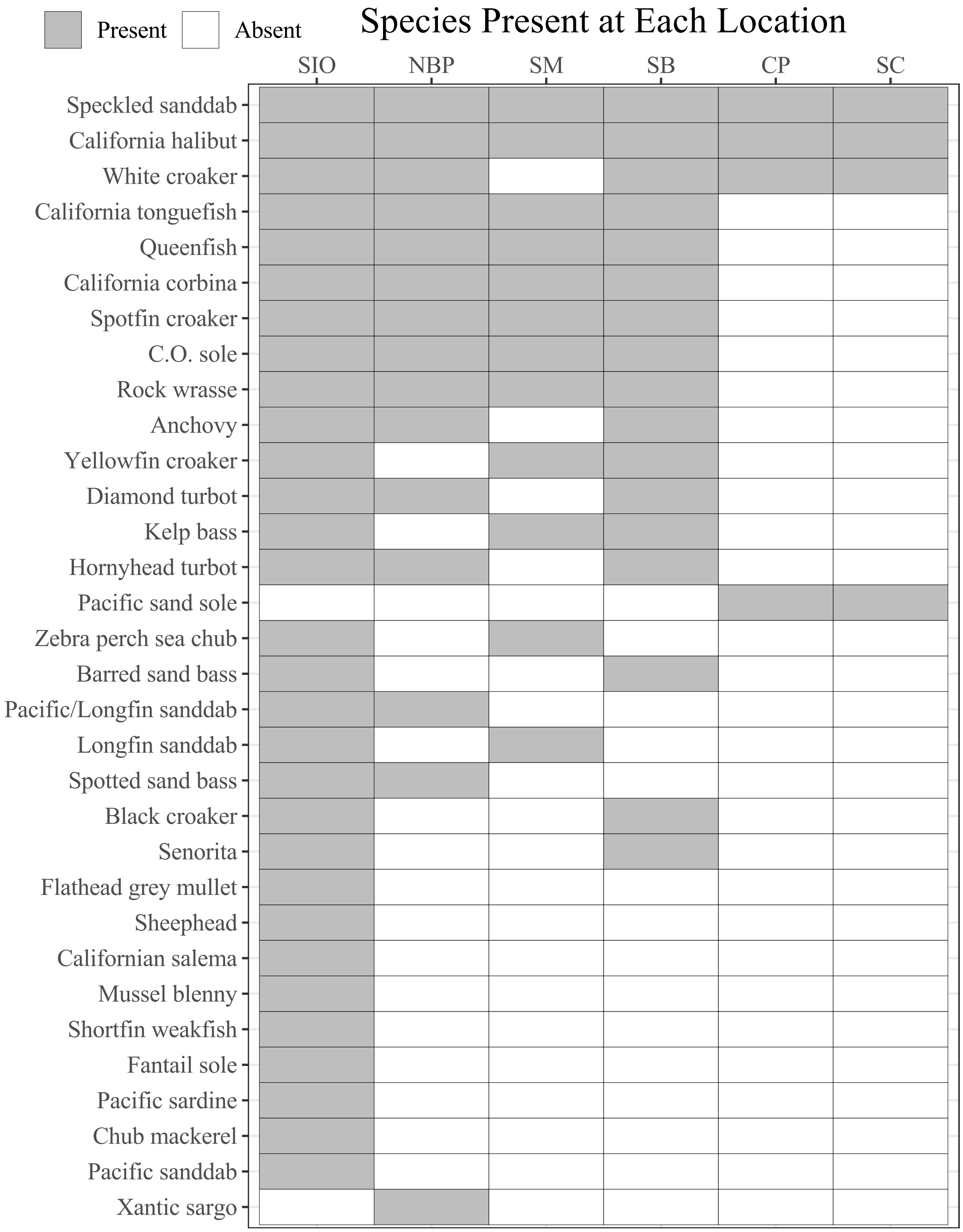
Table 1: Comparison of Sampling Methodology Across Sites. The site abbreviations are as follows: La Jolla = SIO, Newport Beach = NBP, Santa Monica = SM, Santa Barbara = SB, San Luis Obispo = CP, and Santa Cruz = SC.

Location	SIO	NBP	SM	SB	CP	SC
Sampling Start Date	1-2-2019	1-28-2019	1-2-2019	1-22-2019	1-11-2019	2-6-2019
Sampling End Date	12-26-2019	12-31-2019	12-23-2019	12-30-2019	12-13-2019	12-19-2019
Sampling Effort (Number of Collections)	65	44	45	49	29	34
Latitude	32° 52’ 2” N	33°36'21.7"N	34°00'27.0"N	34°24'29.1"N	35°10'12.6"N	36°57'26.2"N
Longitude	117° 15’ 26” W	117°55'52.0" W	118°29'60.0"W	119°41'05.9"W	120°44'26.4" W	122°01'02.2"W
Net Diameter (m)	1	0.5	0.75	0.5	1	0.75
Number of Tows	4	4	4	16	4	4
Depth (m)	5	7	6	6	9	5
Sample Volume (m^3)	64	30	44	64	112	45
Tow Method	Crane	Hand	Hand	Hand	Crane	Hand

Figure 1: Species Present at Each Location. The figure below shows which species were identified in the samples from each of the locations during 2019. The location abbreviations are as follows: SIO = La Jolla, NBP = Newport Beach, SM = Santa Monica, SB = Santa Barbara, CP = San Luis Obispo, SC = Santa Cruz. The scientific names for these species can be found in Supplemental Tables 1 and 2.



	SIO	NBP	SM	SB	CP	SC
Speckled sanddab	▨	▨	▨	▨	▨	▨
California halibut	▨	▨	▨	▨	▨	▨
White croaker	▨	▨	☐	▨	▨	▨
California tonguefish	▨	▨	▨	▨	☐	☐
Queenfish	▨	▨	▨	▨	☐	☐
California corbina	▨	▨	▨	▨	☐	☐
Spotfin croaker	▨	▨	▨	▨	☐	☐
C.O. sole	▨	▨	▨	▨	☐	☐
Rock wrasse	▨	▨	▨	▨	☐	☐
Anchovy	▨	▨	☐	▨	☐	☐
Yellowfin croaker	▨	☐	▨	▨	☐	☐
Diamond turbot	▨	▨	☐	▨	☐	☐
Kelp bass	▨	☐	▨	▨	☐	☐
Hornyhead turbot	▨	▨	☐	▨	☐	☐
Pacific sand sole	☐	☐	☐	☐	▨	▨
Zebra perch sea chub	▨	☐	▨	☐	☐	☐
Barred sand bass	▨	☐	☐	▨	☐	☐
Pacific/Longfin sanddab	▨	▨	☐	☐	☐	☐
Longfin sanddab	▨	☐	▨	☐	☐	☐
Spotted sand bass	▨	▨	☐	☐	☐	☐
Black croaker	▨	☐	☐	▨	☐	☐
Senorita	▨	☐	☐	▨	☐	☐
Flathead grey mullet	▨	☐	☐	☐	☐	☐
Sheephead	▨	☐	☐	☐	☐	☐
Californian salema	▨	☐	☐	☐	☐	☐
Mussel blenny	▨	☐	☐	☐	☐	☐
Shortfin weakfish	▨	☐	☐	☐	☐	☐
Fantail sole	▨	☐	☐	☐	☐	☐
Pacific sardine	▨	☐	☐	☐	☐	☐
Chub mackerel	▨	☐	☐	☐	☐	☐
Pacific sanddab	▨	☐	☐	☐	☐	☐
Xantic sargo	☐	▨	☐	☐	☐	☐

Figure 2: Spatial Variation in Egg Abundance and Species Diversity. 2A. The number of eggs collected in each sample during 2019, separated by location. The locations are presented in descending latitude. The location labels are as follows: SC = Santa Cruz, CP = Cal Poly San Luis Obispo, SB = Santa Barbara, SM = Santa Monica, NBP = Newport Beach, SIO = La Jolla. 2B. The relationship between latitude and species richness (ρ = 0.84) of the eggs collected at each site. The latitude refers to the coordinates of each site and serves as a proxy for the other factors unique to each site that may give rise to this trend (e.g. temperature, productivity, etc.). The samples at each site were subset to contain 29 random samples (the minimum sampling effort of the sampling done at the 6 sites) before calculating the species richness. This process was repeat 1000 times and the average and standard deviation of those trials is reported here. 2C. The relationship between latitude and effective number of species (ENS) is ρ = 0.92, calculated from exp(H) where H is the Shannon diversity. The mean ENS was calculated using the same 1000 trials of 29 random samples used for richness and the error bars represent the standard deviation of those trials.

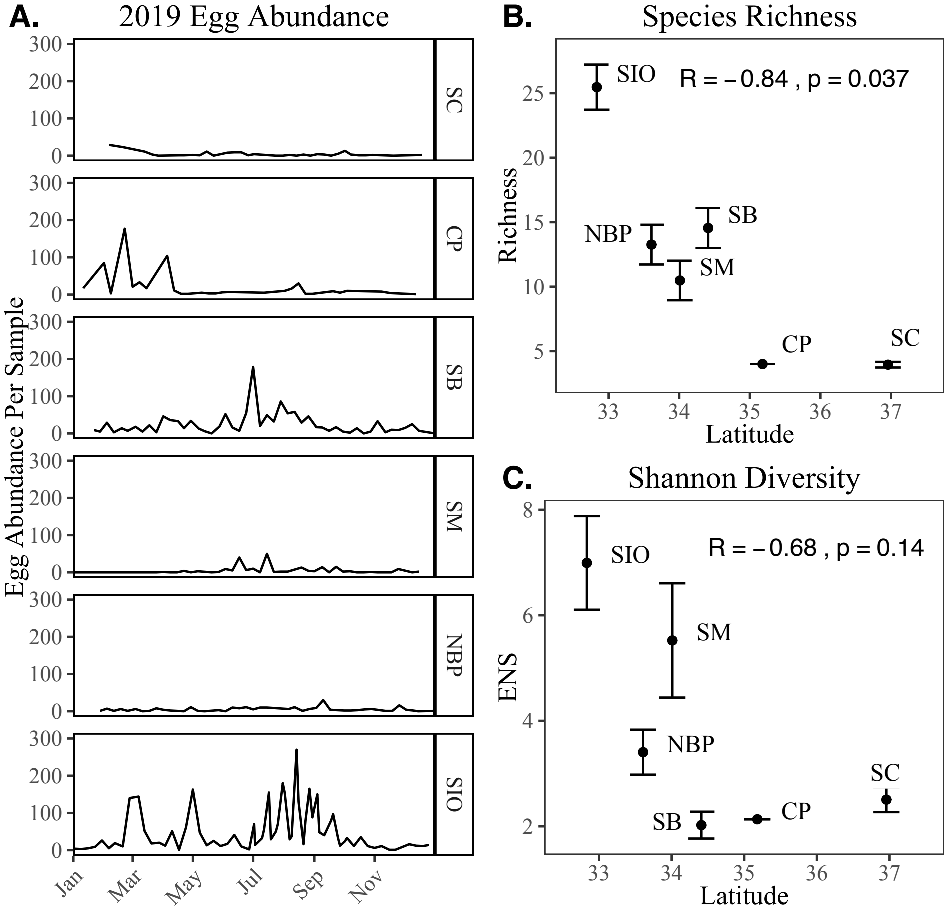
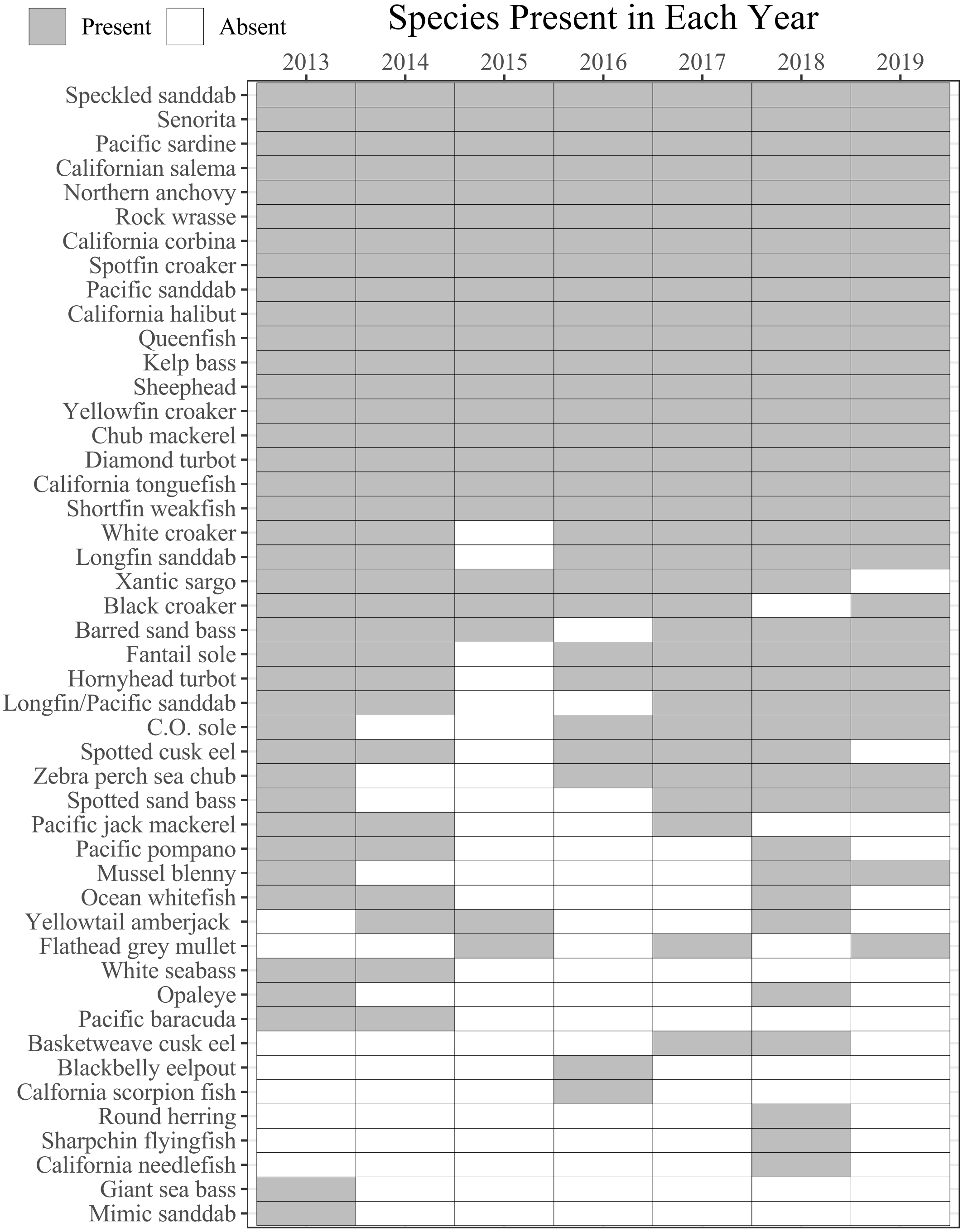


Figure 3: SIO Annual Species Presence. The chart below displays the species present in our samples from La Jolla (SIO) in each year. A gray box indicates the presence of at least one egg from the given species in our samples in the given year, while a white box indicates the absence of eggs from that species. The scientific names for these species can be found in Supplemental Tables 3 and 4.



	2013	2014	2015	2016	2017	2018	2019
Speckled sanddab	▨	▨	▨	▨	▨	▨	▨
Senorita	▨	▨	▨	▨	▨	▨	▨
Pacific sardine	▨	▨	▨	▨	▨	▨	▨
Californian salema	▨	▨	▨	▨	▨	▨	▨
Northern anchovy	▨	▨	▨	▨	▨	▨	▨
Rock wrasse	▨	▨	▨	▨	▨	▨	▨
California corbina	▨	▨	▨	▨	▨	▨	▨
Spotfin croaker	▨	▨	▨	▨	▨	▨	▨
Pacific sanddab	▨	▨	▨	▨	▨	▨	▨
California halibut	▨	▨	▨	▨	▨	▨	▨
Queenfish	▨	▨	▨	▨	▨	▨	▨
Kelp bass	▨	▨	▨	▨	▨	▨	▨
Sheephead	▨	▨	▨	▨	▨	▨	▨
Yellowfin croaker	▨	▨	▨	▨	▨	▨	▨
Chub mackerel	▨	▨	▨	▨	▨	▨	▨
Diamond turbot	▨	▨	▨	▨	▨	▨	▨
California tonguefish	▨	▨	▨	▨	▨	▨	▨
Shortfin weakfish	▨	▨	▨	▨	▨	▨	▨
White croaker	▨	▨	□	▨	▨	▨	▨
Longfin sanddab	▨	▨	□	▨	▨	▨	▨
Xantic sargo	▨	▨	▨	▨	▨	▨	□
Black croaker	▨	▨	▨	▨	▨	□	▨
Barred sand bass	▨	▨	▨	□	▨	▨	▨
Fantail sole	▨	▨	□	▨	▨	▨	▨
Hornyhead turbot	▨	▨	□	▨	▨	▨	▨
Longfin/Pacific sanddab	▨	▨	□	□	▨	▨	▨
C.O. sole	▨	□	□	▨	▨	▨	▨
Spotted cusk eel	▨	▨	□	▨	▨	▨	□
Zebra perch sea chub	▨	□	□	▨	▨	▨	▨
Spotted sand bass	▨	□	□	□	▨	▨	▨
Pacific jack mackerel	▨	▨	□	□	▨	□	□
Pacific pompano	▨	▨	□	□	□	▨	□
Mussel blenny	▨	□	□	□	□	▨	▨
Ocean whitefish	▨	▨	□	□	□	▨	□
Yellowtail amberjack	□	▨	▨	□	□	▨	□
Flathead grey mullet	□	□	▨	□	▨	□	▨
White seabass	▨	▨	□	□	□	□	□
Opaleye	▨	□	□	□	□	▨	□
Pacific baracuda	▨	▨	□	□	□	□	□
Basketweave cusk eel	□	□	□	□	▨	▨	□
Blackbelly eelpout	□	□	□	▨	□	□	□
Calfornia scorpion fish	□	□	□	▨	□	□	□
Round herring	□	□	□	□	□	▨	□
Sharpchin flyingfish	□	□	□	□	□	▨	□
California needlefish	□	□	□	□	□	▨	□
Giant sea bass	▨	□	□	□	□	□	□
Mimic sanddab	▨	□	□	□	□	□	□

Figure 4: SIO Egg Abundance and Diversity 2013 – 2019. 4A. The distribution of the number of eggs present in each sample (eggs per ~16m^3 seawater collected ~weekly) from La Jolla (SIO). Figure 4B. The relationship between the average total egg abundance and species richness (ρ = 0.70) of those eggs within the spawning season of each year. The samples in each year were subset to contain 17 random samples (the minimum sampling effort during a spawning season throughout the seven years) before calculating the total egg abundance and species richness. This process was repeated 1000 times and the average and standard deviation of those trials is reported here. 4C. The relationship between total egg abundance and the effective number of species (ENS), calculated through the Shannon diversity index, within the spawning season of each year. The total egg abundance and Shannon diversity index were calculated using the same repeated subset method used for B.

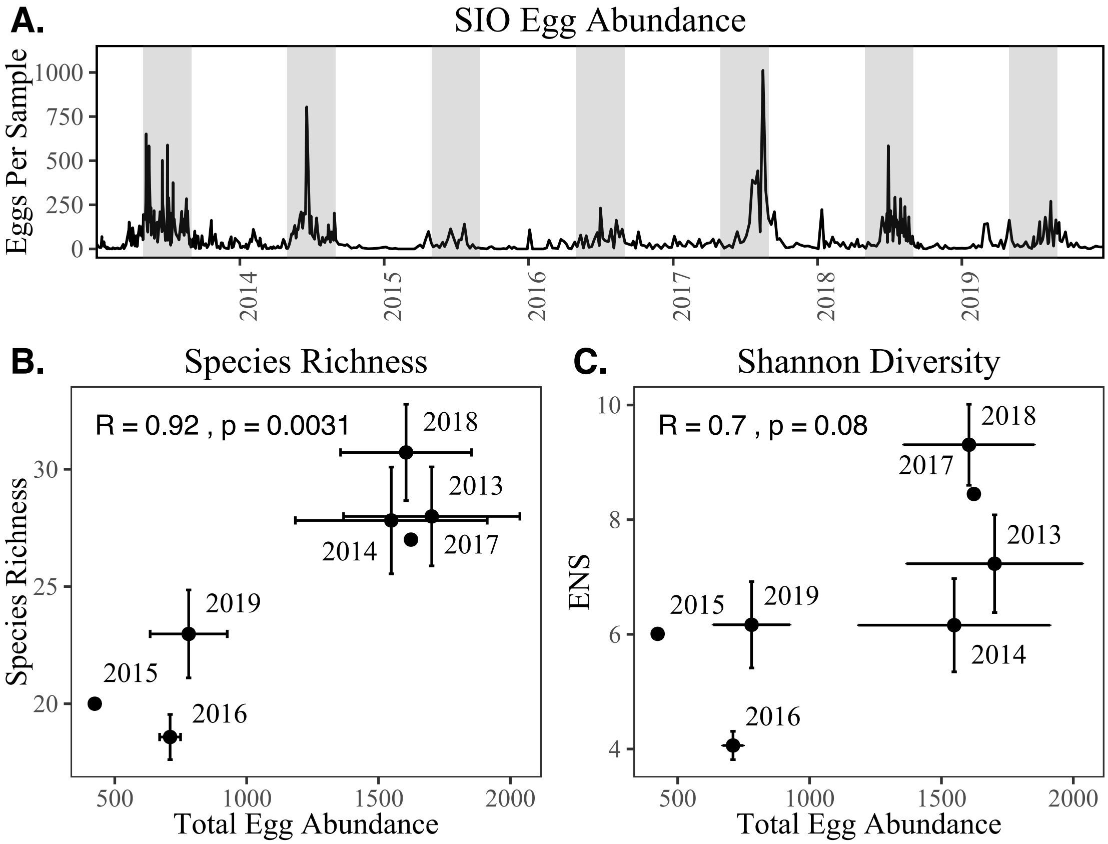


Figure 5: SIO Pier SST. 5A. The weekly averages of sea surface temperature (SST) in La Jolla (SIO) calculated on a three-week rolling average and the additional 2018 and 2019 data is in red. The SST measurements were recorded by the SCCOOS sensors located at 2m depth on the Scripps Pier. 5B. The correlation (ρ = -0.89) between the average winter (December – February) SST and the average spring – summer (March – August) fish eggs. The error bars represent the standard error of the annual spring – summer mean in fish egg abundance. The black points (2013 – 2017) are data points originally identified and calculated by Duke (2018) and the red points are the additional 2018 and 2019 data.