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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 6 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 ongoing 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 5 of the sites, the 2 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 7-year time series from La Jolla has revealed that spawning activity varies greatly among years, both in terms of 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

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 2000). Along the California coast, the diverse and abundant populations of marine fish serve as valuable resources for both commercial and recreational fisheries (Methot 1983, California Department of Fish and 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, Last et al. 2011, 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 nearshore 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

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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 to 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 to 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 accentuate 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, patterns or variability in larval fish assemblages have 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 6 study locations along the California coast: Santa Cruz, San Luis Obispo, Santa Barbara, Santa Monica, Newport Beach, and La Jolla (SIO). Sampling in La Jolla extends the work of Harada et al. (2015) and Duke et al. (2018), which was initiated in 2012 at the Scripps Pier (SIO), at the boundary of 2 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 in La Jolla and found a strong negative correlation between egg abundance and winter sea surface temperatures (SST). We continued sampling at the Scripps Pier through 2019 to determine the productivity of the 2018 and 2019 spawning seasons, evaluate whether the correlation between SST and egg abundance was 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 to 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 (505 µm 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 varied 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

Table 1. Comparison of sampling methodology across sites. The site abbreviations are as follows: SIO: La Jolla; NBP: Newport Beach; SM: Santa Monica; SB: Santa Barbara; CP: San Luis Obispo; and SC: Santa Cruz

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

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 laboratory (Scripps Institution of Oceanography), where they were promptly poured through a mesh screen (330 µm) to concentrate the plankton.

At the lab (Scripps Institution of Oceanography), the concentrated plankton sample was then placed in a Petri dish with seawater and immediately examined under a microscope at 7.5× 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 the lab at Scripps Institution of Oceanography, 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 h 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 95°C for 15 min and maintained in a 72°C 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 −20°C 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′-TTC TCA ACC AAC CAC AAA GAC ATT GG-3′ (forward) and 5′-ACT TCY GGG TGR CCR AAR AAT CA-3′ (reverse). Each sample was vortexed to ensure that the contents of each well were mixed. The samples were then placed in the thermocycler following the cycler conditions utilized by Harada et al. (2015) and Duke et al. (2018). 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′-CGC CTG TTA TCA AAA ACA T-3′ (forward) and 5′-CCG GTC TGA ACT CAG ATC ACG T-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 correctly sized band were purified and sent for sequencing.

PCR products were purified according to Harada et al. (2015) and Duke et al. (2018) and sent to Retrogen 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 compared our samples to all sequences available in GenBank. The addition of sequences from Hastings & Burton (2008) greatly contributed 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, 2 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 2 species, if sequences matched between 95% and 99%, they were recorded as ambiguous (one of the 2 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 were recorded approximately every 4 min from a sensor located 2 m 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 from 2013 to 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. For the temporal analysis, n was 17 and for the spatial analysis n was 29. 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 Figs 2 & 4.

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 ENS = exp(H) (Hill 1973), where H is the Shannon diversity index (Weaver & Shannon 1964). The Shannon diversity index was calculated using the vegan package in RStudio (Oksanen et al. 2013) with the formula:

$$H = -\sum_{i=1}^{S} p_i \ln p_i \quad (1)$$

where p_i is the proportional abundance of each species i and S is the number of species so that:

$$\sum_{i=1}^{S} p_i = 1 \quad (2)$$

3. RESULTS

During 2019, a total of 4277 eggs were identified, belonging to 32 different species across 6 sites, with only 2, speckled sanddab *Citharichthys stigmaeus*

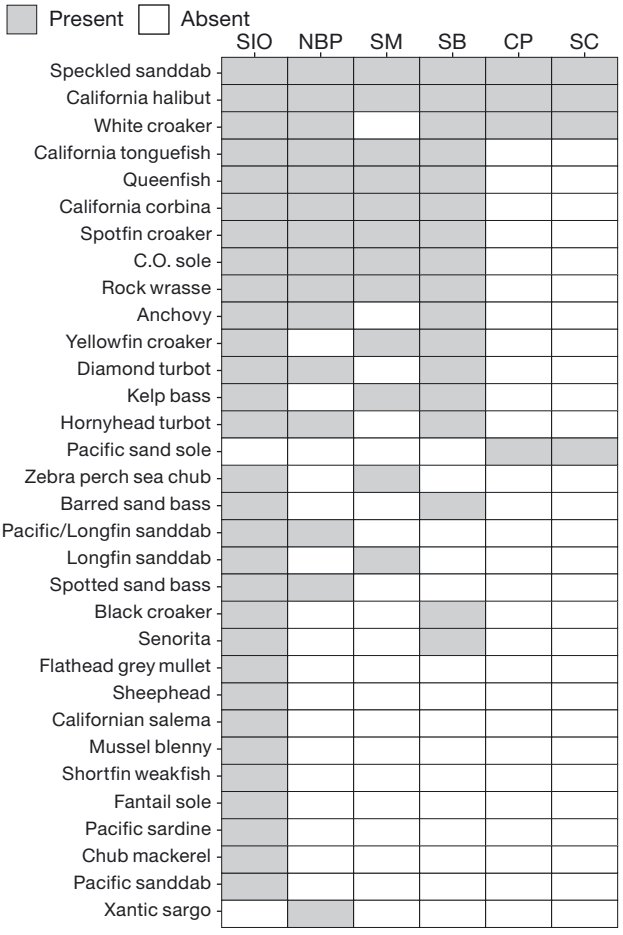

Fig. 1. Species present at each location during 2019. SIO: La Jolla; NBP: Newport Beach; SM: Santa Monica; SB: Santa Barbara; CP: San Luis Obispo; and SC: Santa Cruz. The scientific names for these species can be found in Tables S1 and S2 in the Supplement at www.int-res.com/articles/suppl/m669p139_supp.pdf

and California halibut *Paralichthys californicus*, being present at all sites (Fig. 1). There were 6 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 4 sites south of Point Conception that were absent at the 2 northern sites. Meanwhile, one species, Pacific sand sole *Psettichthys melanostictus*, was only present at the 2 northern sites and absent from the other 4. Interestingly, at SIO, the only location situated within an MPA (but also the most southern of the sites), there were 9 species present that were absent from the other 5 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 lacked large peaks in egg abundance, while CP, SB, and SIO all displayed distinct periods of elevated egg abundance (Fig. 2A). At the 3 sites with large peaks in egg abundance, the peak at CP was during winter, whereas the peaks at SB and SIO occurred during summer months.

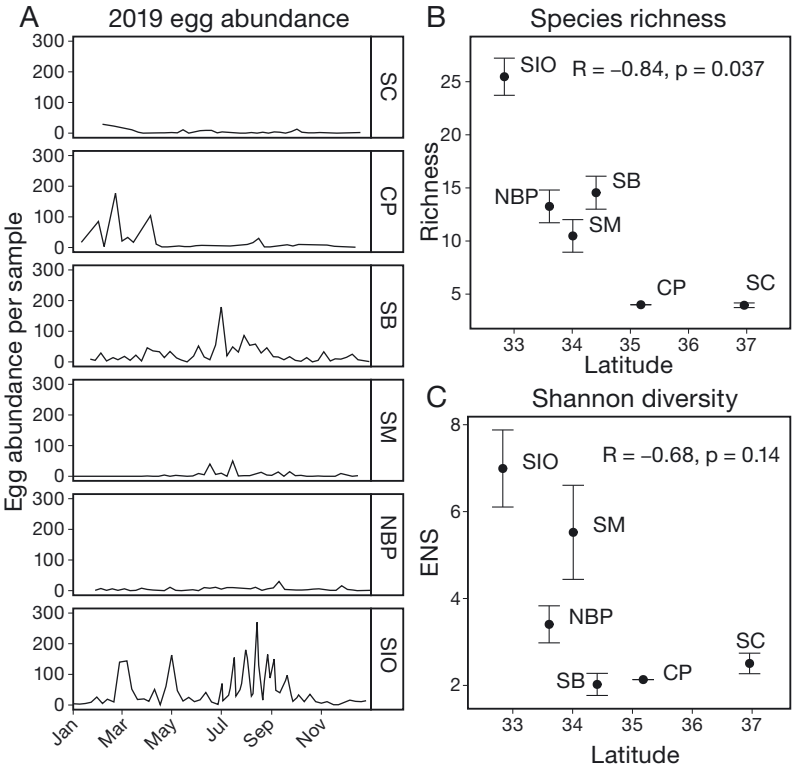

Fig. 2. Spatial variation in egg abundance and species diversity. (A) Number of eggs collected in each sample during 2019, separated by location (presented in descending latitude). SC: Santa Cruz; CP: San Luis Obispo; SB: Santa Barbara; SM: Santa Monica; NBP: Newport Beach; SIO: La Jolla. (B) Relationship between latitude and species richness of the eggs collected at each site. Latitude serves as a proxy for the other factors unique to each site that may give rise to this trend (e.g. temperature, productivity, etc.). (C) Relationship between latitude and effective number of species (ENS), calculated from exp(H), where H is the Shannon diversity. Data in B and C are shown as means ± SD

Species richness and Shannon diversity were used to compare species diversity across the 6 sites, spanning 4 degrees of latitude along the California coast (Fig. 2B,C). Despite this relatively short range of latitude, there was a strong, negative relationship between latitude and species richness ($R = -0.84$, $p = 0.037$), 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 (Fig. 2B). This finding complements the distribution of species' eggs shown by the presence/absence chart (Fig. 1), in which there were very few species observed at CP and SC. A similar, although weaker, trend ($R = -0.66$, $p = 0.14$) is given by the ENS defined through Shannon diversity (Fig. 2C). It is significant that despite the limited number of eggs collected from NBP and SM, there were greater than 10 species identified at these sites, and regardless of the considerable number of eggs from CP there were only 4 species identified here. The ENS at SB was lower than that at both CP and SC due to the dominance of eggs from speckled sanddab *Citharichthys stigmaeus*; however, the 3 most northern sites still had markedly less species diversity than the 3 southern sites.

Over the 7-yr monitoring period at SIO, 24 579 eggs were 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 (Fig. 3). The spawning season, defined by a period of elevated egg abundance, occurred roughly from 1 May to 31 August in each year (Fig. 4A). However, the spawning seasons tended 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,

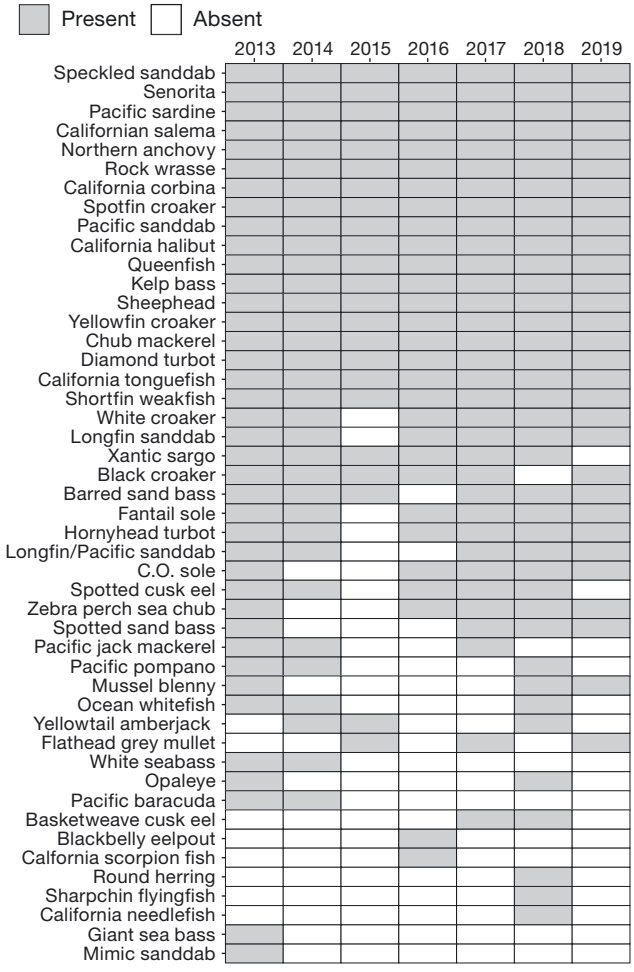

Fig. 3. SIO annual species presence. A gray box indicates the presence of at least one egg from the given species in our samples in the given year, while a white box indicates the absence of eggs from that species. The scientific names for these species can be found in Tables S3 and S4 in the Supplement

2016, and 2019 lacked large peaks, and the average egg production during the spawning season (1 May to 31 August) was lower than the 7-yr average egg production during the spawning season, $\bar{x}$ = 111; in contrast, 2013, 2014, 2017, and 2018 exhibited large peaks in egg abundance and the average egg production during the spawning season was greater than the 7-yr average egg production. As shown in Fig. 3, there were fewer species present in the 3 yr with lower egg abundance (2015, 2016, and 2019), but there were no instances of a species present in all of the higher egg abundance years and absent from the lower egg abundance years.

There was a strong, positive relationship (R = 0.92, p = 0.0031) between the total number of eggs identified during the spawning season and the species richness of the corresponding season (Fig. 4B). When using Shannon diversity (converted to ENS) to compare the relationship between egg abundance and species diversity (Fig. 4C), the relationship weakened (R = 0.7, p = 0.08). In particular, despite having much lower species richness than the high abundance years, the ENS of 2015 and 2019 (low abundance years) was 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 2 additional years (2018 and 2019). The weekly SST calculated over a 3-wk rolling average is shown in Fig. 5A with the additional 2018 and 2019 data in red, and Fig. 5B shows that there was a negative correlation (R = −0.89, p = 0.0075) 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 affect 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. 1980). 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 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 (Craig et al. 2004, Hastings et al. 2014, Harada et al. 2015, Duke et al. 2018).

Only 2 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

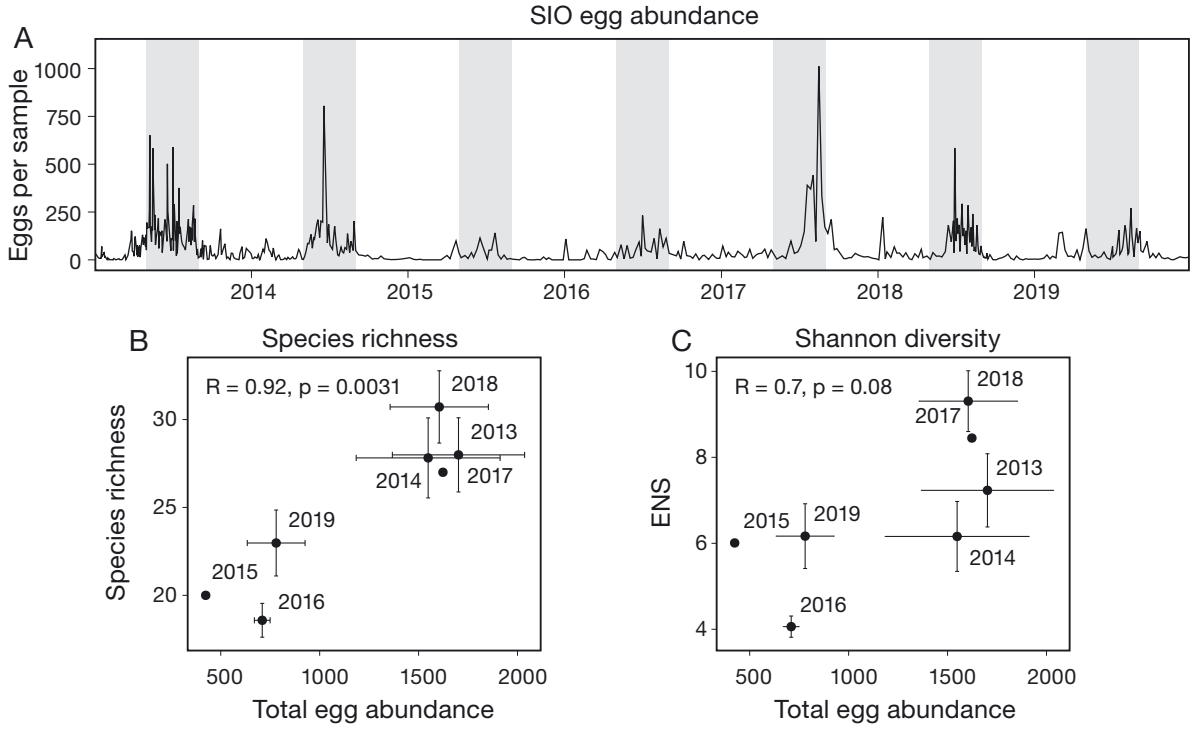

Fig. 4. SIO egg abundance and diversity 2013–2019. (A) Distribution of the number of eggs present in each sample (eggs per ~16 m^3 seawater collected ~weekly) from La Jolla (SIO). Shading: spawning season. (B) The relationship between the average total egg abundance and species richness of those eggs within the spawning season of each year. (C) Relationship between total egg abundance and ENS, calculated through the Shannon diversity index, within the spawning season of each year. Data in B and C are shown as means ± SD

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*, and xantic sargo *Anisotremus davidsonii* — have northern range limits at Point Conception (Miller & Lea 1972, Hastings et al. 2014), a well-known biogeographic barrier (Hayden & Dolan 1976, Horn & Allen 1978, Burton 1998, Gaylord & Gaines 2000, Hohenlohe 2004, Blanchette et al. 2007), 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 & Dolan 1976, Horn & Allen 1978, Allen et al. 2006, 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 (Parrish et al. 1981). 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,

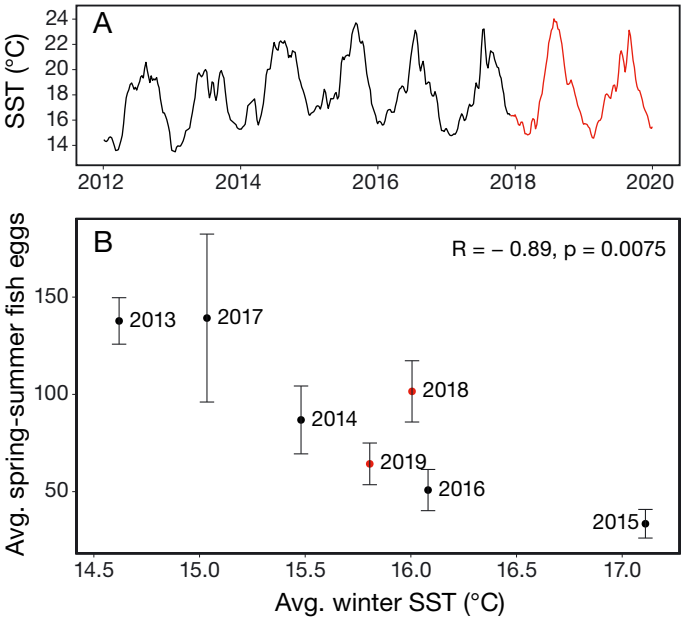

Fig. 5. SIO pier sea surface temperature (SST). (A) Weekly averages of SST in La Jolla calculated on a 3-wk rolling average; the additional 2018 and 2019 data are in red. The SST measurements were recorded by the SCCOOS sensors located at 2 m depth on Scripps Pier. (B) Correlation between the average winter (December–February) SST and the average spring–summer (March–August) fish egg abundance. 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 et al. (2018) and the red points are the additional 2018 and 2019 data

Lluch-Belda et al. 1992, Van der Lingen & Huggett 2003), as well as in other larval fish assemblages (Loeb et al. 1983, Chiu & Hsyu 1994, Beare et al. 2005, Duke et al. 2018). Observed seasonal and annual variation have both 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, Bye 1984, Fiedler et al. 1986, Cury & Roy 1989, Platt et al. 2003, Sims et al. 2004, Takasuka et al. 2008, Doyle et al. 2009, Donelson et al. 2010, Pankhurst & Munday 2011, Fincham et al. 2013, Duke et al. 2018). The effects of water temperature and photoperiod on the reproductive processes of fish have been extensively studied and anomalous SSTs have been linked to numerous reproductive difficulties (reviewed in Pankhurst & Munday 2011, Wang et al. 2010).

The 7 yr of data from the La Jolla site show 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 of 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) indicate that regardless of the disparities in species richness, the diversity, defined by both species richness and evenness, is very similar. The presence/absence chart (Fig. 3) shows that 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 on 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 2 of 32 species detected in our yearlong study were observed to spawn at all 6 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 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.

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LITERATURE CITED

Ahlstrom EH (1966) Distribution and abundance of sardine and anchovy larvae in the california current region off California and Baja, California, 1951–64: a summary. US Department of the Interior, Fish and Wildlife Service, Special Scientific Report – Fisheries No 534.

Ahlstrom EH, Moser HG (1976) Eggs and larvae of fishes and their role in systematic investigations and in fisheries. Rev Trav Inst Peches Marit 40:379–398

Allen L (1985) A habitat analysis of the nearshore marine fishes from Southern California. Bull South Calif Acad Sci 84:133–155

Allen LG, Pondella DJ, Horn MH (2006) The ecology of marine fishes: California and adjacent waters. University of California Press, Berkeley, CA

Anderson CN, Hsieh Ch, Sandin SA, Hewitt R and others (2008) Why fishing magnifies fluctuations in fish abundance. Nature 452:835–839

Asch RG (2015) Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. Proc Natl Acad Sci USA 112:E4065–E4074

Barnett A, Jahn A, Sertic P, Watson W (1984) Distribution of ichthyoplankton off San Onofre, California, and methods for sampling very shallow coastal waters. Fish Bull 82: 97–111

Barry JP, Baxter CH, Sagarin RD, Gilman SE (1995) Climate-related, long-term faunal changes in a California rocky intertidal community. Science 267:672–675

Barth JA, Menge BA, Lubchenco J, Chan F and others (2007) Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. Proc Natl Acad Sci USA 104:3719–3724

Beare D, Burns F, Jones E, Peach K, Reid D (2005) Red mullet migration into the northern North Sea during late winter. J Sea Res 53:205–212

Beck MW, Heck KL, Able KW, Childers DL and others (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: a better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. BioScience 51:633–641

Blanchette CA, Helmuth B, Gaines SD (2007) Spatial patterns of growth in the mussel, *Mytilus californianus*, across a major oceanographic and biogeographic boundary at Point Conception, California, USA. J Exp Mar Biol Ecol 340:126–148

Brewer GD, Smith P (1982) Northern anchovy and Pacific sardine spawning off southern California during 1978-80: preliminary observations on the importance of the nearshore coastal region. CCOFI Rep 23:160–171

Brock RE (1982) A critique of the visual census method for assessing coral reef fish populations. Bull Mar Sci 32: 269–276

Brodeur RD, Ralston S, Emmett RL, Trudel M, Auth TD, Phillips AJ (2006) Anomalous pelagic nekton abundance, distribution, and apparent recruitment in the northern California Current in 2004 and 2005. Geophys Res Lett 33:L22S08

Burton RS (1998) Intraspecific phylogeography across the Point Conception biogeographic boundary. Evolution 52: 734–745

Bye V (1984) The role of environmental factors in the timing of reproductive cycles. Fish reproduction: strategies and tactics

California Department of Fish and Wildlife (2002) Nearshore fishery management plan. California Department of Fish and Wildlife, Monterey, CA

Cavole LM, Demko AM, Diner RE, Giddings A and others (2016) Biological impacts of the 2013–2015 warm-water anomaly in the Northeast Pacific: winners, losers, and the future. Oceanography 29:273–285

Chiu TS, Hsyu YH (1994) Interannual variation of ichthyoplankton density and species composition in the waters off northeastern Taiwan. Mar Biol 119:441–448

Costanza R, d'Arge R, De Groot R, Farber S and others (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260

Craig MT, Fodrie FJ, Hastings PA (2004) The nearshore fish assemblage of the Scripps coastal reserve, San Diego, California. Coast Manage 32:341–351

Cury P, Roy C (1989) Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can J Fish Aquat Sci 46:670–680

De Vlaming VL (1972) Environmental control of teolost reproductive cycles: a brief introduction. J Fish Biol 4:131–140

Donelson JM, Munday PL, McCormick MI, Pankhurst NW, Pankhurst PM (2010) Effects of elevated water temperature and food availability on the reproductive performance of a coral reef fish. Mar Ecol Prog Ser 401:233–243

Doyle MJ, Picquelle SJ, Mier KL, Spillane MC, Bond NA (2009) Larval fish abundance and physical forcing in the Gulf of Alaska, 1981-2003. Prog Oceanogr 80: 163–187

Duke EM, Harada AE, Burton RS (2018) Large interannual variation in spawning in San Diego marine protected areas captured by molecular identification of fish eggs. Mar Ecol Prog Ser 604:199–210

Ebeling AW, Larson RJ, Alevizon WS (1980) Habitat groups and island-mainland distribution of kelp-bed fishes off Santa Barbara, California. In: Power DM (ed) The California Islands: Proc Multidisciplinary Symp. Santa Barbara (CA), Santa Barbara Museum of Natural History. p 403–431

Fiedler PC, Methot RD, Hewitt RP (1986) Effects of California El Niño 1982–1984 on the northern anchovy. J Mar Res 44:317–338

Fincham JI, Rijnsdorp AD, Engelhard GH (2013) Shifts in the timing of spawning in sole linked to warming sea temperatures. J Sea Res 75:69–76

Gaylord B, Gaines SD (2000) Temperature or transport? Range limits in marine species mediated solely by flow. Am Nat 155:769–789

Gleason LU, Burton RS (2012) High-throughput molecular identification of fish eggs using multiplex suspension bead arrays. Mol Ecol Resour 12:57–66

Harada AE, Lindgren EA, Hermsmeier MC, Rogowski PA, Terrill E, Burton RS (2015) Monitoring spawning activity in a Southern California marine protected area using molecular identification of fish eggs. PLOS ONE 10: e0134647

Hastings PA, Burton RS (2008) Establishing a DNA sequence database for the marine fish fauna of California. UC San Diego, California Sea Grant College Program. (Retrieved from https://escholarship.org/uc/item/1ck9b3qs)

Hastings PA, Craig MT, Erisman BE, Hyde JR, Walker HJ (2014) Fishes of marine protected areas near La Jolla, California. Bull South Calif Acad Sci 113:200–231

Hayden BP, Dolan R (1976) Coastal marine fauna and marine climates of the Americas. J Biogeogr 3:71–81

Hill M (1973) Diversity and evenness: a unifying notation and its consequences. Ecology 54:427–432

Hohenlohe PA (2004) Limits to gene flow in marine animals with planktonic larvae: models of *Littorina* species around Point Conception, California. Biol J Linn Soc 82: 169–187

Horn M, Allen L (1978) A distributional analysis of California coastal marine fishes. J Biogeogr 5:23–42

Horn MH, Allen LG, Lea RN (2006) Biogeography. In: Allen LG, Pondella DJ, Horn MH (eds) The ecology of marine fishes: California and adjacent waters. University of California Press, Berkeley, CA, p 3–25

Hunter JR, Lo NH (1993) Ichthyoplankton methods for estimating fish biomass introduction and terminology. Bull Mar Sci 53:723–727

Ivanova NV, Zemlak TS, Hanner RH, Hebert PD (2007) Universal primer cocktails for fish DNA barcoding. Mol Ecol Notes 7:544–548

Jaafar TNAM, Taylor MI, Nor SAM, De Bruyn M, Carvalho GR (2012) DNA barcoding reveals cryptic diversity within commercially exploited Indo-Malay Carangidae (Teleosteii: Perciformes). PLOS ONE 7:e49623

Last PR, White WT, Gledhill DC, Hobday AJ, Brown R, Edgar GJ, Pecl G (2011) Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. Glob Ecol Biogeogr 20:58–72

Lluch-Belda D, Lluch-Cota DB, Hernández-Vázquez S, Salinas-Zavala CA (1992) Sardine population expansion in eastern boundary systems of the Pacific Ocean as related to sea surface temperature. S Afr J Mar Sci 12:147–155

Loeb VJ, Smith PE, Moser HG (1983) Ichthyoplankton and zooplankton abundance patterns in the California current area, 1975. CCOFI Rep 24:109–131

Mann KH (2000) Ecology of coastal waters: with implications for management. Blackwell Science, Malden, MA

Methot RD Jr (1983) Management of California's nearshore fishes. Rec Fish 8:161–172

Miller DJ, Lea RN (1972) Guide to the coastal marine fishes of California. Fish Bull 157:1–249

Munday PL, Jones GP, Pratchett MS, Williams AJ (2008) Climate change and the future for coral reef fishes. Fish Fish 9:261–285

Oksanen J, Blanchet FG, Kindt R, Legendre P and others (2013) Package 'vegan'. Community ecology package, version 2. Available at https://cran.r-project.org/web/packages/vegan/vegan.pdf

Palumbi SR (1996) Nucleic Acids II: The polymerase chain reaction. In: Hillis DM, Moritz C, Mable BK (eds) Molecular systematics, 2nd edn. Sinauer Associates, Sunderland, MA, p 205–247

Pankhurst NW, Munday PL (2011) Effects of climate change on fish reproduction and early life history stages. Mar Freshw Res 62:1015–1026

Parrish RH, Nelson CS, Bakun A (1981) Transport mechanisms and reproductive success of fishes in the California Current. Biol Oceanogr 1:175–203

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308:1912–1915

Platt T, Fuentes-Yaco C, Frank KT (2003) Spring algal bloom and larval fish survival. Nature 423:398–399

Shelton AO, Mangel M (2011) Fluctuations of fish populations and the magnifying effects of fishing. Proc Natl Acad Sci USA 108:7075–7080

Sims DW, Wearmouth VJ, Genner MJ, Southward AJ, Hawkins SJ (2004) Low-temperature-driven early spawning migration of a temperate marine fish. J Anim Ecol 73: 333–341

Stewart BD, Beukers JS (2000) Baited technique improves censuses of cryptic fish in complex habitats. Mar Ecol Prog Ser 197:259–272

Suntsov A, Koslow JA, Watson W (2012) The spatial structure of coastal ichthyoplankton assemblages off central and southern California. CCOFI Rep 53:153–170

Takasuka A, Oozeki Y, Kubota H (2008) Multi-species regime shifts reflected in spawning temperature optima of small pelagic fish in the western North Pacific. Mar Ecol Prog Ser 360:211–217

Valentine JW (1966) Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf. Limnol Oceanogr 11:198–211

Van der Lingen C, Huggett J (2003) The role of ichthyoplankton surveys in recruitment research and management of South African anchovy and sardine. The big fish bang: proceedings of the 26th annual larval fish conference. Institute of Marine Research, Bergen, Norway

Wang N, Teletchea F, Kestemont P, Milla S, Fontaine P (2010) Photothermal control of the reproductive cycle in temperate fishes. Rev Aquacult 2:209–222

Ward RD, Hanner R, Hebert PD (2009) The campaign to DNA barcode all fishes, FISH-BOL. J Fish Biol 74: 329–356

Wares JP, Gaines S, Cunningham CW (2001) A comparative study of asymmetric migration events across a marine biogeographic boundary. Evolution 55:295–306

Waugh J (2007) DNA barcoding in animal species: progress, potential and pitfalls. BioEssays 29:188–197

Weaver W, Shannon C (1964) The mathematical theory of information. Illinois Press, Urbana, IL

Zwiefel JR, Lasker R (1976) Prehatch and posthatch growth of fishes: a general model. Fish Bull 74:609–621

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