Title: Evaluating the promise and pitfalls of a potential climate change-tolerant sea urchin fishery in southern California

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Abstract

Marine fishery stakeholders are beginning to consider and implement adaptation strategies in the face of growing consumer demand and potential deleterious climate change impacts such as ocean warming, ocean acidification, and deoxygenation. This study investigates the potential for development of a novel climate change-tolerant sea urchin fishery in southern California based on *Strongylocentrotus fragilis* (pink sea urchin), a deep-sea species whose peak density was found to coincide with a current trap-based spot prawn fishery (*Pandalus platyceros*) in the 200-300 m depth range. Here we outline potential criteria for a climate change-tolerant fishery by examining the distribution, life-history attributes, and marketable qualities of *S. fragilis* in southern California. We provide evidence of seasonality of marketable gonad production and demonstrate that peak gonad production occurs in the winter season and likely spawns in the spring season as evidenced by consistent minimum gonad indices in the spring/summer seasons across 4 years of sampling (2012-2016). The resiliency of *S. fragilis* to predicted future increases in acidity and decreases in oxygen was supported by high species abundance, albeit reduced relative growth rate estimates at water depths (485-510 m) subject to low oxygen (11.7-16.9 μmol kg^{-1}) and pH_{Total} (<7.44), which may provide assurances to stakeholders and managers regarding the suitability of this species for commercial exploitation. Some food quality properties of the *S. fragilis* roe (*e.g.*, color, texture) were comparable with those of the commercially exploited shallow-water red sea urchin (*Mesocentrotus franciscanus*), while other qualities (*e.g.*, 80% reduced gonad size by weight) limit the potential future marketability of *S. fragilis*. This case study highlights the potential future challenges and drawbacks of climate-tolerant fishery development in an attempt to inform future urchin fishery stakeholders.

Keywords: climate change, fisheries, sea urchin, California Current, *Strongylocentrotus fragilis*, *Mesocentrotus franciscanus*, climate-tolerant fishery

Introduction

Oxygen and pH regimes on the southern California shelf and slope are changing significantly with unknown consequences for the distributions and fitness of aerobic fishes and calcifying invertebrates (Bograd *et al.*, 2008, 2015; Gruber, 2011; Gruber *et al.*, 2012). Acidified zones (reduced pH, elevated CO_2) in the California Current System (CCS) are predicted to dramatically increase in magnitude and frequency in future decades (Fabry *et al.*, 2008), which can disproportionately impact certain slow or stationary species, like bivalves and urchins, in nearshore habitats that may not be as adapted to such conditions. For example, biogeochemical models in the CCS predict that 100% of water in the twilight zone (60-120m) may be undersaturated with respect to the aragonitic form of calcium carbonate by 2050 (Gruber *et al.*, 2012), making calcifying invertebrates of ecological and economic value particularly vulnerable. In addition, upwelling events, which are well known to bring deep, cold, and nutrient-rich water to shallower depths into coastal habitats are also characterized by relatively low oxygen, low pH, and low calcium carbonate saturation [Ω] (Feely *et al.*, 2008; Send and Nam, 2012; Booth *et al.*, 2014). Such events have been observed in nearshore kelp forests of San Diego (Frieder *et al.*, 2012), and potential sublethal effects on the reproductive output, structural integrity, and population dynamics of key calcifying resources are expected to become far more widespread (Gaylord *et al.*, 2011; Kelly *et al.*, 2013; Hofmann *et al.*, 2014). Recent corrosive upwelling events have caused mortality in several oyster hatcheries on the

U.S. west coast in Oregon, resulting in major environmental projects to mitigate the effects of ocean acidification (Barton *et al.*, 2012, 2015). Increased upwelling frequency over the next century may present challenges for fishery management due to unknown species-specific and ecosystem-wide effects of multiple climate drivers on fisheries (Gruber, 2011; Padilla-Gamiño *et al.*, 2013).

An important adaptive strategy under changing hydrographic conditions is to evaluate ways to shift fishery emphasis away from more vulnerable species to alternative resilient species (Ogier *et al.*, 2016). To reduce future harvest stress and synergistic climate effects on the red urchin (*M. franciscanus*), which makes up the vast majority of urchin fishery landings on the west coast of North America, it may be useful to consider an alternative, underutilized urchin species. The *M. franciscanus* fishery is vulnerable to overfishing, disease, thermal stress, poor spawning seasons, and the supply of and demand for its roe (known as *uni* in sushi restaurants) (Botsford *et al.*, 2004). Additionally, potential deleterious effects of CO_2-acidified water due to ocean acidification on fertilization, larval development, and gene expression in red urchins could negatively impact recruitment to the fishery, which depends on large, sexually mature individuals (O'Donnell *et al.*, 2009; Frieder, 2014; Hofmann *et al.*, 2014; Kapsenberg *et al.*, 2017). Early life-history stages of *M. franciscanus* have also been shown to be vulnerable to both acidification (Frieder, 2014) and thermal stress (O'Donnell *et al.*, 2009; Byrne and Przeslawski, 2013). While the demand for sea urchins has gone up domestically and internationally over recent years due to its increased popularity in various food markets worldwide (McBride, 2005), the landings and value produced by the *M. franciscanus* fishery has been in continuous decline since 2000 (Figure 1). While the currently harvested urchin species (*M. franciscanus*) may suffer under future climate change scenarios, the deep-dwelling pink urchin, *S. fragilis*, is highly tolerant of low oxygen and pH (Sato *et al.*, 2017; Taylor *et al.*, 2014). This species appears to be extending its distribution into shallower water as low oxygen zones in the NE Pacific expand (Sato *et al.*, 2017).

Among the many calcified inhabitants of the California margin, sea urchins are important ecosystem engineers that efficiently graze on macroalgal species forming kelp forest habitat (Rogers-Bennett, 2007). These urchins experience a range of pH and oxygen conditions depending on depth and setting (Takeshita *et al.*, 2015; Chan *et al.*, 2017), with the red (*M. franciscanus*) and purple (*S. purpuratus*) urchins generally occupying the intertidal and inner shelf reefs (Kato and Schroeter, 1985; Rogers-Bennett, 2007), and pink urchins (*S. fragilis*) occurring throughout the outer shelf and upper slope (Sato *et al.*, 2017; Thompson *et al.*, 1993). Deep-sea fishery species (taken on the continental slope and seamounts) are conventionally thought to be non-sustainable due to long life spans, slow growth rates, and late maturity (Koslow *et al.*, 2000; Norse *et al.*, 2012). Indeed, most deep-sea fishery species have experienced significant declines and are thus not sustainable (Norse *et al.*, 2012; Clark *et al.*, 2016). However, species like *S. fragilis* that naturally occur in stressful environments with respect to climate-change variables such as oxygen and pH may be adapted to future conditions that are more hypoxic and acidic than at present.

Although supplementing the current urchin fishery by harvesting the less vulnerable, underutilized pink urchin species may seem reasonable, uncertain management and fishing practice challenges remain. In addition, there are few studies that investigate life-history of *S. fragilis* (Sumich and McCauley, 1973) or the marketable food qualities of *S. fragilis* roe, such as gonad size, color, and texture (McBride *et al.*, 2004). We investigated various adult characteristics of *S. fragilis* to evaluate the potential for developing this species as a climate change-tolerant fishery. *M. franciscanus* sea urchins are individually hand-picked by hookah divers throughout California, with most landings occurring primarily in southern California and secondarily in Mendocino County. *S. fragilis* is currently caught as bycatch in baited traps that target the valuable spot prawn (*Pandalus platyceros*) at a mean depth of 250 m (Phil Zerofski, Personal Communication). Indeed there may be additional costs incurred by fishers associated with fishing a deep-urchin species vs. the current practice (*e.g.*, fuel, gear-type). However, the physical challenges of diving may be offset by a trap-based fishery.

In this study, various fishery management criteria and food quality metrics of the pink urchin (*S. fragilis*) were evaluated in southern California populations in order to determine the feasibility of an emerging fishery. We addressed the following criteria for the potential management of a new climate change-tolerant *S. fragilis* fishery in southern California: (1) Resiliency evaluated as distribution and fitness traits in relation to multiple climate change variables, (2) accessibility evaluated as abundance across space and time, (3) habitat and ecosystems considered as habitat type, behavior, and food preference, and (4) acceptability (*i.e.*, marketable gonad traits such as size, color, and texture). In addition to these empirical data, we provide a rationale for the legalization of deep urchin bycatch take for urchin fishery stakeholders to consider as an alternative, long-term sustainable solution in the face of environmental variation and climate change.

Methods

Field Sampling

Distribution and density

Availability of *Strongylocentrotus fragilis* urchins (*e.g.*, to fishers) is partly a function of both their depth distribution and density in the Southern California Bight (SCB). These were determined by analyzing benthic megafauna trawl survey datasets collected during the summer months (July-September) of 2003, 2008, and 2013 by trained taxonomists associated with the regional *Bight* survey led by the Southern California Coastal Water Research Program. The gear type used during each survey year was a standardized 7.6 m head-rope semiballoon otter trawl net fitted with 1.25-cm cod-end mesh. Trawls were towed along open-coast isobaths for ~10 min at 1.5-2.0 nm hr^{-1} during daylight hours. Trawl distance was calculated from the start and stop fishing GPS coordinates, which acted as a proxy for the net's relative position. It was assumed the net remained on the bottom and was fishing the entire time (Allen *et al.*, 2011). Upon retrieval, catches were sorted, identified to species, and enumerated. Each station was sampled once. Bay sites and sites at water depths <10 m were removed from this analysis in order to minimize zero inflated data (Thompson *et al.*, 1993). The area swept by each trawl was calculated as the distance trawled (m) x 4.9 m (the width of the trawl) (Miller and Schiff, 2012). Densities of *S. fragilis* were obtained per trawl by dividing the species count by the calculated area swept.

Historical densities and distributions of *S. fragilis* urchins between 10-500 m in the SCB are reported in Sato *et al.* (2017). A reanalysis of these data was conducted to identify the depths where *S. fragilis* occurs at densities above 0.001 indiv. m^{-2}, within smaller 50-m depth bins. *S. fragilis* density between 10-500 m was compared across survey years, while survey years were pooled in the 50-m depth bin analysis. The upper and lower depth limits, as well as the median, 25% quartile and 75% quartile depths were calculated by pooling all trawls with densities greater than 0.001 indiv. m^{-2} from the 3 surveys. Urchins often form feeding aggregations on kelp falls, which may bias density estimates, but the high number of trawls conducted is likely to capture this variability (Sato *et al.*, 2017). One exception where kelp falls have been found to be more abundant is in submarine canyons (Harrold *et al.*, 1998), but in this study sites in canyons were avoided and sites were surveyed for flat, trawl-friendly ground prior to net deployment.

Abundance threshold depth and behavioral observations

Although *Strongylocentrotus fragilis* is present at depths of 100-1200 m in the SCB, the Oxygen Minimum Zone (OMZ) (O_2 < 20 μmol kg^{-1}) and associated food and climate variables limit most *S. fragilis* to the upper 500 m (Sato *et al.*, 2017). To identify the threshold depth (and associated climate variables) where urchins are subjectively more abundant, we analyzed video footage from two cross-slope Remotely Operated Vehicle (ROV) transects on the San Diego shelf and slope. ROV surveys were conducted in August 2015 (Dive #1448) and December 2016 (Dive J-093) using two ROVs, the *Hercules* (Ocean Exploration Trust) and the *Jason* (Woods Hole Oceanographic Institution), aboard the R/V *Nautilus* and R/V *Sally Ride*, respectively. Each ROV was equipped with a Sea-Bird Electronics, Inc., Conductivity-Temperature-Depth (CTD) and an Aanderaa oxygen sensor (see details below). For each upslope transect, ROV pilots were instructed to maintain speed of 0.2-0.5 nmph and altitude above the seafloor between 1-2 m. Video cameras maintained the same direction, angle, and zoom throughout the duration of each dive. Video footage was paused every 30 s to 20 mins (0.5-10 m seafloor depth), and still frames were visually analyzed, to identify the deepest depth within the OMZ where *S. fragilis* urchins first appeared at high density. Urchins were counted within the visible area of each paused frame and recorded. To compare results across dives, urchin counts were calculated as a proportion of the highest count recorded during that dive. Feeding aggregations were also observed, but not counted due to high uncertainty of urchin counts.

Spatiotemporal variability of edible gonads and growth

The spatial and seasonal variability of gonad production in *Strongylocentrotus fragilis* was compared across water depth zones on the shelf and slope in the SCB at various stations (N = 51 stations) and depths (Avg. depth ± SD = 351 ± 206 m) throughout the species' distribution (Table 1). Local differences in *S. fragilis* gonad production were determined by separating the stations geospatially by latitude into three subregions (*i.e.* San Diego, Los Angeles, and Santa Barbara). *S. fragilis* individuals used in this spatial analysis were collected *via* otter trawls on various research cruises between July 2012 and June 2016 (Table 1). Subregional gonad data were further separated into 100-m depth bins and compared among subregions in the upper 500 m of the continental shelf and slope. To compare relative growth rates of *S. fragilis*, individuals were collected *via* otter trawl surveys in the San Diego region between 2012 and 2014. To determine the seasonality of *S. fragilis* gonad production, individuals were sampled by otter trawl from a single station (~340 m) off of Point Loma, CA (32.6986 °N, -117.3765 °W), at various times throughout the year, with the first trawl taking place in Summer 2012 and the twelfth and final trawl occurring in Summer 2016 (Table 2). During each collection, ~25 intact individuals were haphazardly selected from the trawl catch, sealed in a plastic bag, immediately frozen in a -20°C freezer on each ship, and transported to -20°C freezer in the lab until further analysis.

To obtain gonads for food quality analysis, live *S. fragilis* urchins were collected from 305 m water depth *via* otter trawl by the Los Angeles County Sanitation District on the R/V *Ocean Sentinel* in February 2015, near Palos Verdes, CA (33.6787 °N, -118.3276 °W). Live urchins were transported to the Kaplan Experimental Aquarium at Scripps Institution of Oceanography (La Jolla, CA) where they were fed *ad libitum* fronds of giant kelp (*Macrocystis pyrifera*) in flow-through seawater tanks at 8°C for approximately 4 weeks.

Hydrography Data

Hydrographic data for the study area were obtained during a multidisciplinary research cruise carried out off the San Diego coast line on board the R/V *Melville* from 8-15 December, 2012 (see Nam *et al.*, 2015 for July 2012 data and seasonal results). A single profile of salinity, temperature, pressure, and dissolved oxygen (DO) at 1-m resolution was generated from the surface to 1,051 m (32.6901 °N, -117.5306 °W) using a Sea-Bird Electronics, Inc., CTD instrument (SBE9) and dissolved oxygen sensor (SBE43). Discrete water samples were collected every 50-100 m of water depth and analyzed for DO and pH following methods described by Nam *et al*. (2015). In brief, oxygen samples were analyzed following standard Winkler titration procedures (Dickson, 1996), and pH samples were analyzed spectrophotometrically at 20° C using a custom automated system with m-cresol purple without further purification (Nam *et al.*, 2015). Reported *in situ* pH was calculated from measured pH and dissolved inorganic carbon in CO2SYS (Van Heuven *et al.*, 2011) using dissociation constants from Lueker *et al.* (2000).

Salinity, temperature, depth, and DO data were also collected from the ROV *Jason*, which was equipped with a CTD instrument (SBE19) that recorded data every second and an oxygen optode (Aanderaa 4831) that recorded dissolved oxygen every 30 seconds. The ROV *Hercules* was equipped with a CTD instrument (SBE FastCAT 49) and an oxygen optode (Aanderaa 3830), which recorded depth, salinity, temperature, and oxygen every second.

Lab Analyses

Gonad Index

Frozen *S. fragilis* urchins were thawed and rinsed clean of mud in the lab prior to dissection. Spines were removed prior to measurement of Total Length of the Diameter (TLD) via calibrated dial calipers to the nearest 0.1 mm. Wet weights of gonads (5 lobes) and each individual drained of its internal fluids were measured on a calibrated Sartorius digital balance (R160P) to the nearest 0.001 gram. The gonad index (GI) of a single individual was calculated by using the equation,

$$\mathrm{GI} = \frac{\mathrm{m_g}}{\mathrm{m}} \times 100,$$

where $\mathrm{m_g}$ is the total wet weight of the dissected gonads and m is the wet weight of the individual drained of its internal fluids.

Growth variability

Variability in relative growth was measured as a function of depth across the species' depth distribution (100-1200 m). Image analysis of growth bands was carried out on *Strongylocentrotus fragilis* individuals collected *via* otter trawl conducted at five depths (100 m, 300 m, 400 m, 700 m, 1096 m) in the San Diego region (Table 3). Frozen urchins were thawed in the laboratory, and individual ossicle plates from the interambulacral grooves of the aboral hemisphere were dissected using a scalpel under a dissecting microscope. Ossicle plates from each urchin were washed in a 2% bleach (NaClO) solution, placed on a shaker for 30 minutes to remove organic material from the plates, rinsed in DI water, and placed in a vial under a hood to dry for 24-48 hours. The ossicle plates were then charred in a muffled furnace for 3-5 minutes at 300°C and left to cool. Approximately 24 hours later, ossicles were set on a microscope slide and lightly coated with a clear epoxy for image analysis. Digital photographs were taken using a compound microscope fitted with a digital camera at 25x magnification. Images were digitally enhanced using Adobe Photoshop software in order to better identify alternating light and dark concentric bands on each ossicle (Figure 6).

The relative growth rate for each individual was calculated by using the equation,

$$\text{Rate of Growth} = \frac{x}{c},$$

where x is the TLD of the individual and c is the number of bands. Growth rate is reported as mm band^{-1} rather than mm year^{-1} because it is uncertain whether *S. fragilis* lays down annual or semiannual growth bands (Sumich and McCauley, 1973). Other studies have attempted calcein marking of growth bands in red urchins (Pearse and Pearse, 1975), but failed to determine urchin age due to inconsistencies of banding with seasonality (Kato and Schroeter, 1985). The growth zone analysis presented here provides a relative growth rate as a function of water depth, provided the assumption that *S. fragilis* from different depths lay down similar banding. The temperature, DO, and *in situ* pH values associated with each depth were determined using CTD data.

Roe Quality

To compare properties of *Strongylocentrotus fragilis* urchin roe quality to present seafood industry standards, freshly packaged *Mesocentrotus franciscanus* gonad lobes of the Grade B and B-minus quality were obtained from Catalina Offshore Products, Inc. (San Diego, CA). *M. franciscanus* individuals were collected from the wild by urchin divers, processed at Catalina Offshore Products, Inc., and gonad lobes were kept on ice until the moment of analysis. Prior to commercial sale, *M. franciscanus* gonads are typically placed in an anhydrous aluminum potassium sulfate ($AlK(SO_4)_2$), hereafter, Potassium Alum solution, which is used to commercially process urchin roe. The astringent is used for its ability to bind to proteins and prevent their breakdown, firming the roe (Kato and Schroeter, 1985). For this study, gonads from *S. fragilis* and *M. franciscanus* were soaked for 20 minutes in a 0.5% Potassium Alum solution. Excess moisture was removed from *S. fragilis* and *M. franciscanus* gonads using paper towels, and gonads were weighed immediately prior to color and texture analyses. Individual gonad lobes from *M. franciscanus* were also weighed immediately prior to color and texture analyses.

Gonad color, an important quality of marketable urchin roe, was compared between *S. fragilis* and *M. franciscanus* (also known as “California Gold *uni*”) using a Konica-Minolta Colorimeter C-400 and recorded using SpectraMagic NX software. Gonads were placed on transparent petri dishes and placed over the 8-mm diameter aperture of the colorimeter. Calibration of the colorimeter was carried out using a pure white color plate prior to each color measurement. The amount of red, the amount of yellow, and the lightness of the roe were measured 30 times per gonad lobe. The means of each color characteristic were used for statistical analysis. Red and yellow values represent on a scale of 0-100 the amount of red and yellow character a sample contains. Lightness is a measurement of how light or dark the sample is (white has the highest lightness character possible of $L = 60$). Total color change was recorded as the difference in overall color from pure white calibration plate (McBride *et al.*, 2004). The difference between the color of the urchin gonad (Sample) and the white color calibration plate (Target) was calculated using the following equation:

$$\Delta E = ((L_{Target} - L_{Sample})^2 + (a_{Target} - a_{Sample})^2 + (b_{Target} - b_{Sample})^2)^{0.5},$$

where ΔE = Total Color Change, L = Lightness, a = Redness, and b = Yellowness.

In additional to gonad color, texture is another important urchin roe quality used to assess the marketable grade level (McBride *et al*. 2004). Gonad texture was determined as a combination of gonad hardness and resilience using a TA.XT*Plus* texture analyzer with a 2" diameter metal cylinder probe. Hardness was recorded as the peak force (Newtons, kg m s^{-2}) required to compress the roe to half of its original height. Height of each gonad lobe was noted prior to texture analysis. The samples were compressed to a fixed distance of half their original height at a speed of 0.55 mm s^{-1} for a fixed duration of time. Resilience was then recorded as a function of the amount of time required for the roe to return to half of its original height after the roe's compression. Resilience was calculated by dividing the area under the curve during the probe's withdrawal by the area under the curve during compression. The curve during withdrawal represented the decline in force as the probe returned to its starting height. The maximum force of the TA.XT*Plus* was set to its lowest setting (5 kg Load Cell), allowing for a force sensitivity of 0.1 g. The instrument was calibrated before every measurement using a 100 g weight.

Statistical Analyses

All response metrics (density, gonad index, relative growth rate, gonad color and texture) were tested for normality using the Shapiro-Wilk test and homogeneity of variances using the Breusch–Pagan test. In most cases, assumptions of normality and homoscedasticity were violated, so a Box-Cox power transformation was used to attempt to correct the data. If the transformation did not improve normality or homoscedasticity of the data, then non-parametric tests were used. A Kruskal-Wallis test was used to compare density and gonad index across subregion, depth bin or season. If a significant difference was detected, a *post hoc* Dunn's test treated with a Bonferroni correction was conducted using the Pairwise Multiple Comparison of Mean Ranks Package in R. The Pearson product-moment correlation coefficient was determined for mean relative growth rate (evaluated as urchin test diameter in mm per band) with each depth-dependent environmental variable (*i.e.*, temperature, DO, and pH) and for gonad index with depth. One-way ANOVAs were employed to test for differences between gonad color metrics (*i.e.*, lightness, yellowness, redness, and total color change) across urchin species. To determine *S. fragilis* thresholds from ROV footage, mean environmental data (*i.e.*, depth, salinity, temperature, and DO) were calculated from data where abundances proportional to the maximum abundance were between 0.25 and 0.75.

Results

Distribution and density of *Strongylocentrotus fragilis*

Reasonably high density is a prerequisite for a viable fishery species, so we identified the depth distribution of *S. fragilis* in trawls where density exceeded 0.001 indiv. m^{-2}. The median and mean depths of trawls between 2003 and 2013 with *S. fragilis* densities >0.001 indiv. m^{-2} were 203 m and 250 m, respectively. Fifty percent of the trawls with these densities were found between depths 180.8 m (25% quartile) and 339 m (75% quartile) (Figure 2a). The mean density of *S. fragilis* between 10 and 500 m did not vary significantly among the three survey years (Kruskal-Wallis Test: $\chi^2 = 5.967$, $p = 0.051$). As a result, the density data were pooled prior to further depth bin analysis. Density did not vary significantly across 50-m depth bins in the upper 500 m (Kruskal-Wallis Test: $\chi^2 = 8.263$, $p = 0.41$).

Abundance threshold and behavioral observations

Video analysis of two cross-slope benthic transects between ~450 and 650 m water depth using ship-based ROV deployments off San Diego, CA, revealed a consistent dramatic shift in *Strongylocentrotus fragilis* abundance with depth (Figure 3a). In each case, a shift from 0-5 urchins per frame to a considerable abundance of 33-38 urchins per frame occurred over a short change in depth of <5 m. During the ROV *Hercules* dive in August 2015, this increase in *S. fragilis* occurred between 485-490 m water depth. During the ROV *Jason* dive in December 2016, the community changed abruptly to a *S. fragilis* urchin-dominated community from an asteroid-dominated community between 505-510 m water depth. Table 4 shows the mean environmental conditions in which *S. fragilis* abundances were 25-75% of the maximum abundances counted during each dive.

We observed *S. fragilis* urchins aggregating around kelp falls (<500 m) consistently during both dives with estimated densities of up to ~200 indiv. m^{-2} (Figure 3b). Active feeding on giant kelp (*Macrocystis pyrifera*) was confirmed by collections of urchins clinging to the kelp. However, drift *M. pyrifera* was observed without aggregating urchins at ~600 m where no *S. fragilis* urchins were present (Figure 3b).

Spatiotemporal variability of edible gonads

Mean gonad index (GI) of *Strongylocentrotus fragilis* collected in the upper 500 m varied significantly among all three subregions (Kruskal-Wallis Test: $\chi^2 = 56.89$, $p < 0.0001$). While the mean depths from which the urchins originated significantly differed among subregions (Kruskal-Wallis Test: $\chi^2 = 74.18$, $p < 0.0001$), these depths did not differ between Los Angeles and San Diego (*post hoc* Dunn's test: $p = 0.76$). The mean depth of trawls in the Santa Barbara subregion was significantly shallower (219 m) than Los Angeles (302 m) and San Diego (310 m). The mean GI from Santa Barbara was 26% greater than those from Los Angeles and 94% greater than those from San Diego (Figure 4a). Gonad indices decreased linearly with increasing depth (75-1100 m) in the SCB (Pearson: $r_{37} = -0.43$, $p = 0.007$) (Figure 4b). When separated into 100-m depth bins, peak GI was found in different depth bins for each subregion with the highest mean GI occurring in Santa Barbara between 200 and 300 m water depth (Figure 4c).

Seasonal variability of gonad production in *S. fragilis* was observed over the sampling period (2012-2016) at a 340-m water depth site near Point Loma, San Diego, CA (Figure 5a). When seasons were pooled across years, GI in *S. fragilis* exhibited significant seasonality (Kruskal-Wallis Test: $\chi^2 = 79.822$, $p < 0.001$) (Figure 5b). Mean Winter GI was 86% higher than the global mean (4.11 ± 0.18 SE) and was reduced by 62-64% in the Spring and Summer (Figure 5b). Mean Summer GI was significantly different across years (Kruskal-Wallis Test: $\chi^2 = 10.851$, $p = 0.013$), with Summer 2013 GI 48% higher than in Summer 2015 (*post hoc* Dunn's test: $p = 0.01$) (Figure 5c). In addition, GI in Fall of 2015 was 58% lower than in 2013 and 55% lower than in 2012 (*post hoc* Dunn's test: $p < 0.001$).

Growth variability

Relative growth rate analysis of *Strongylocentrotus fragilis*, as determined from band counts, demonstrated positive growth at all depths. *S. fragilis* collected from 100-m water depth had the highest growth rate relative to those urchins living at greater water depths (Figure 6). The mean relative growth rate at 700m was 66% lower than at 100m (Table 3). Relative growth rate was positively correlated with dissolved oxygen (Pearson's correlation: $r_3 = 0.93$, $p = 0.022$) (Figure 6a) and pH (Pearson's correlation: $r_3 = 0.95$, $p = 0.014$) (Figure 6b), but there was no significant relationship with temperature (Pearson's correlation: $r_3 = 0.71$, $p = 0.183$) (Figure 6c) or depth (Pearson's correlation: $r_3 = -0.74$, $p = 0.152$).

Roe Quality – Color and Texture

Strongylocentrotus fragilis mean gonad lobe weight (2.38 g ± 0.33 S.E.) was 80% lower than the weight of gonad lobes of *Mesocentrotus franciscanus* (11.95 g ± 0.76 S.E.; Kruskal-Wallis Test: $\chi^2 = 14.778$, $p = 0.0001$). Color differences among the three types of gonad (*i.e. S. fragilis*, *M. fransciscanus* Grade B and B-minus) were observed (Figure 7a-d), with *M. fransicanus* gonads exhibiting more total color change than *S. fragilis* gonads (1-way ANOVA: $F_{2, 29} = 32.49$, $p < 0.001$; Figure 7d). *S. fragilis* gonads did not significantly differ in lightness and redness from *M. franciscanus* B-grade gonads (Figure 7a, c), nor did they significantly differ in yellowness from *M. franciscanus* B-minus grade gonads (Figure 7b). The most distinctive difference in texture between the two species was the peak hardness of their gonads (Figure 7e). On average, *S. fragilis* gonads were 85% softer than *M. franciscanus* B-grade gonads (Kruskal-Wallis Test: $\chi^2 = 12.231$, $p < 0.001$; Figure 7e), but there was no significant difference in the resilience between the species (Kruskal-Wallis Test: $\chi^2 = 3.316$, $p = 0.07$; Figure 7f).

Discussion

The development of sustainable climate-tolerant fisheries is one of several management adaptation strategies that stakeholders may pursue to limit the deleterious negative effects of climate change (FAO, 2016). This study uniquely provides spatiotemporal analyses of an unfished species of sea urchin (*Strongylocentrotus fragilis*) and describes relevant food quality properties in order to inform various stakeholders about the feasibility of developing a *S. fragilis* fishery in southern California. The management criteria that we investigated (resiliency, accessibility, *S. fragilis* habitat and behavior, and acceptability) may inform the sea urchin industry, management, and scientific communities about *S. fragilis* should it be considered as a viable fishery in the future. The sheer abundance (Figure 3b) of *S. fragilis* urchins throughout its vast spatial distribution at water depths (485-510 m) subject to low oxygen (11.7-16.9 μmol kg^{-1}) and pH (<7.44) in southern California (Bograd *et al.*, 2008; Gruber *et al.*, 2012; Nam *et al.*, 2015) demonstrate the species' tolerance to stressful environments with respect to climate change variables. As a species tolerant to relatively acidic and hypoxic conditions, *S. fragilis* may become more accessible at shallower depths as the OMZ expands into shallower waters (Sato *et al.*, 2017).

Multiple studies have suggested that important sea urchin fishery species are vulnerable to the effects of climate change and ocean acidification (O'Donnell *et al.*, 2009; Reuter *et al.*, 2011; Frieder, 2014). In contrast to the conclusions of these experiments on currently fished sea urchin species, our results suggest that *S. fragilis* currently exhibits reduced relative growth rates in the OMZ core (700 m) where dissolved oxygen and pH in December 2012 were 9.187 μmol kg^{-1} and 7.39, respectively (Figure 6b, c). The DO concentration at 700 m was 93% lower than at 100m (Table 3), and the simultaneously reduced pH and dissolved oxygen conditions in the OMZ are predicted to shoal as the ocean becomes increasingly more acidic and deoxygenated (Bograd *et al.*, 2008; Gruber *et al.*, 2012). Our findings support the results of a study by Taylor *et al.* (2014), which demonstrated that *S. fragilis* collected from the OMZ has limited ability to regulate internal acid-base balance under simulated ocean acidification conditions (pH <7.5), with little effect on their feeding rates and righting times. It is possible that differences in food availability at different depths can contribute to the greater relative growth rates at shallower depths (Britton-Simmons *et al.*, 2012). Ranges of pH and dissolved oxygen concentrations at the ROV sites in San Diego where abundant populations of *S. fragilis* persist at different seasons (Figure 3; Table 4) demonstrate the resilience of this species to extreme pH and oxygen conditions.

However, there are lessons to consider from the existing urchin fisheries. Understanding the size- and age-dependent responses to low oxygen and low pH environments is important for setting or changing size limits for the *Mesocentrotus franciscanus* urchin fishery (Kato and Schroeter, 1985; Rogers-Bennett, 2007). Larger *M. franciscanus* serve as nursery habitat for younger urchins that are more vulnerable to predation (Tegner and Levin, 1983; Tegner and Dayton, 1991), while younger urchins may not be reproductive. We were unable to observe this behavior in *S. fragilis* using trawl and ROV imagery, and this possibility warrants further investigation. While the average age of *M. fransicanus* in the fishery is approximately 4-5 years (Kato and Schroeter, 1985), the absolute age of *S. fragilis* remains uncertain (Sumich and McCauley, 1973), and a comparative study to test effects on absolute growth rates and gonad production would be required. These important environmental and *S. fragilis* life-history data are additional management criteria that would need to be investigated in further detail, which further highlights the need to expand continental margin ocean observations into the deep ocean (Thurber *et al.*, 2014; Sweetman *et al.*, 2017).

Although sea urchin gonads are often considered delicacies in various cuisines worldwide (McBride, 2005), the demand for and fishing pressure on sea urchins continues to increase (Andrew *et al.*, 2002; Botsford *et al.*, 2004; Knapp and Rubino, 2016). In order to provide enough sea urchins for this growing demand, finding alternative sources of supply should be a priority for managers and stakeholders, especially given the known vulnerability of sea urchin populations to overfishing (Andrew *et al.*, 2002; Botsford *et al.*, 2004) and unfavorable environmental conditions. For example, El Niño or anomalously warm ocean conditions (*e.g.*, 2014/15 "warm blob" or 2015/16 El Niño in the Southern CA Bight) reduce the availability of nutrients and inhibit the growth of the primary urchin food source of harvested sea urchins, giant kelp (*Macrocystis pyrifera*) (Reed *et al.*, 2016). These warm ocean conditions can subsequently affect the gonad production and recruitment of sea urchins into the fishery (Tegner and Dayton, 1991; Arntz *et al.*, 2006; Rogers-Bennett, 2007; Vasquez, 2007; Teck *et al.*, 2017) and may have explained the decrease in *S. fragilis* gonad production in Fall 2015 (Figure 5a, c). As these conditions are predicted to become more frequent due to ocean warming (Sweetman *et al.*, 2017), it is critical for stakeholders to consider alternative sources of sea urchins including increased imports, aquaculture, or other alternative food production techniques (McBride, 2005).

The United States currently imports approximately 90% of its seafood (by value), and the country's trade deficit continues to increase (Kite-Powell *et al.*, 2013; Knapp and Rubino, 2016). In the face of climate change, increasing domestic fishery production (*via* alternative species or aquaculture) may provide some economic relief. Based on the criteria we present, *S.*

fragilis may be a possible viable alternative fishery to supplement the current southern CA fishery, but further consideration and research will be required. Marketable sea urchin products depend on gonad indices around 5-15% (McBride, 2005), and thus an abundance of food in the wild is required to meet this standard (Teck *et al.*, 2017). Although the gonad weight of *S. fragilis* gonads was on average 80% lower than *M. franciscanus* gonads and significantly softer (Figure 7e), the color and resilience was comparable. These results suggest that *S. fragilis* gonads may not be suitable for direct consumption as *uni*, as smaller and softer gonads may be more difficult to process and transport, but other potential uses for *S. fragilis* gonads such as garnish and flavoring (*e.g.*, for pasta dishes) could be possible. A study on how *S. fragilis* roe size and qualities (including taste) compare to other smaller, commercially-fished urchin species (*e.g.*, *Strongylocentrotus purpuratus*, *S. droebachiensis*, *Loxechinus albus*, and others) would also be helpful to better understand the potential for developing *S. fragilis* as a new fishery.

S. fragilis is currently caught as bycatch in baited traps that target the valuable spot prawn (*Pandalus platyceros*) at a mean depth of 250 m (Phil Zerofski, Personal Communication). Our results suggest that the highest densities of *S. fragilis* also occurs in the 251-300 m depth bin, which coincides with the targeted depth range for *P. platyceros* (Figure 3b). Spot prawn fishers however, are not permitted to catch sea urchins and are prohibited from taking non-target species (CDFG, 2008). The *P. platyceros* fishery season in southern CA is open during the spring and summer months when *S. fragilis* gonad production is low and closed during the fall and winter months when *S. fragilis* gonad production is high (Figure 5). Legalizing *S. fragilis* bycatch or opening a *S. fragilis* fishery during fall and winter months could provide an additional source of income for fishers in the region. Baited traps are a less destructive type of gear than bottom trawls and would minimize costs to fishers and ecosystem impact (Clark *et al.*, 2016). Additionally, we documented on several occasions using ROVs that *S. fragilis* aggregated in large numbers on *M. pyrifera*, the seemingly most important and favorable *S. fragilis* food source. Therefore, the type of bait used for *S. fragilis* could be switched to *M. pyrifera* kelp in order to minimize impact on *P. platyceros* during its closure season. These issues could complicate the development of future fishery activity for *S. fragilis* and warrant further investigation.

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Figure Captions

Figure 1. 20-year time series of *Mesocentrotus franciscanus* (red urchin) fishery data in southern CA. Commercial landings in million pounds (red line), ex-vessel value in millions of US dollars (green dashed line), and price per urchin pound (green dotted line). Data source: http://www.dfg.ca.gov/marine/seaurchin/index.asp.

Figure 2. Pooled *Strongylocentrotus fragilis* data collected during three trawl surveys throughout southern California (2003, 2008, and 2013). (a) Depth distribution of otter trawls with *S. fragilis* densities >0.001 indiv. m^{-2}. Boxplot shows upper and lower limits, 25% and 75% quartile depths, and median depth of trawls. (b). Mean density (± 1 SE) of *S. fragilis* across 50-m depth bins. Numbers inside bars represent number of trawls within each depth bin.

Figure 3. Abundance thresholds of *Strongylocentrotus fragilis* from two remotely operated vehicle (ROV) dives conducted on the San Diego slope. (a) Depth of *S. fragilis* observations as functions of water temperature (°C), dissolved oxygen (μmol kg^{-1}), salinity (PSU), and *S. fragilis* abundance determined during the ROV *Hercules* dive in August 2015 (red circles) and the ROV *Jason* dive in December 2016 (blue circles). Horizontal colored lines indicate depths at which *S. fragilis* abundance dramatically increased. (b) All images were taken during the ROV *Jason* dive. Left: feeding aggregation of *S. fragilis* at 485 m was estimated to have an approximate density of 200 indiv. m^{-2}. Right: holdfast of *Macrocystis pyrifera* kelp at ~625 m unoccupied by *S. fragilis*.

Figure 4. *Strongylocentrotus fragilis* gonad indices collected from Los Angeles, Santa Barbara, and San Diego subregions in the Southern California Bight. Numbers inside bars indicate replicate number of urchins dissected. (a) Mean (+1 S.E.) gonad index from urchins collected in the upper 500 m. Letters indicate significant difference based on Dunn's test treated with a Bonferroni correction ($p < 0.05$). (b) Relationship between gonad index (±1 S.E.) and depth in Los Angeles (red circles), San Diego (blue triangles), and Santa Barbara (green diamonds). Linear regression (solid line) and 95% confidence intervals (dashed lines) represents trend across all data. (c) Mean GI (+1 S.E.) separated into 100 m depth bins across subregions.

Figure 5. Gonad indices (GI) of *Strongylocentrotus fragilis* collected from a repeat trawl station at 340 m water depth near Point Loma, San Diego, CA. Red line indicates the dataset mean measured across 12 collections spanning 4.5 years. Letters represent significant differences ($p < 0.05$) as determined from *post hoc* Dunn's tests. Numbers inside bars indicate replicate number of urchins dissected. (a) Seasonality of GI (+1 S.E.) from Winter 2012 to Summer 2016. (b) Seasonality of GI (+1 S.E.) pooled across years. (c) Comparison of GI between Summer and either Fall or Winter seasons across years to show the difference between seasons with relatively high and low GI.

Figure 6. Mean growth rates of *Strongylocentrotus fragilis* (± 1 S.E.) as functions of (a) temperature (C°), (b) dissolved oxygen (μmol O_2 kg^{-1}), and (c) *in situ* pH. (d) Growth rates are presented as diameter length (mm) per growth band by counting the number of dark bands within treated interambulacral plate ossicles. Depths of each trawl and CTD cast are presented in Table 3. Gray dashed line indicates a significant correlation between growth rate and environmental variable (see text for details).

Figure 7. Mean (+1 S.E.) color and texture properties of individual gonad lobes from *Strongylocentrotus fragilis* and *Mesocentrotus franciscanus* (B and B-minus grade). (a) Lightness, (b) yellowness, (c) redness, and (d) total color change. Letters indicate significant differences among sources of gonads as indicated by Dunn's tests. (e) Mean peak hardness (+1 S.E.) and (f) resilience (+1 S.E.) of individual lobes from *S. fragilis* and *M. franciscanus* (B grade). Letters indicate significant differences between the two sources as the results of either a 1-way analysis of variance (peak hardness) or Kruskal-Wallis test (resilience).