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Original Article

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

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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 gonad production and demonstrate that peak gonad production occurs in the winter season. *S. fragilis* 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. colour, 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: California Current, climate change, climate-tolerant fishery, fisheries, *Mesocentrotus franciscanus*, sea urchin, *Strongylocentrotus fragilis*.

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 (60–120 m) 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 US west coast in Oregon, resulting in major environmental projects to mitigate the effects of ocean acidification (Barton *et al.*, 2012, 2015). Predicted increases in 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). Although 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 have been in continuous decline since 2000 (Figure 1). Although the currently harvested urchin species (*M. franciscanus*) may suffer under future climate change scenarios, the deep-dwelling pink urchin, *Strongylocentrotus fragilis*, appears to be highly tolerant of low oxygen and pH (Taylor *et al.*, 2014; Sato *et al.*, 2017). 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 (*Strongylocentrotus 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

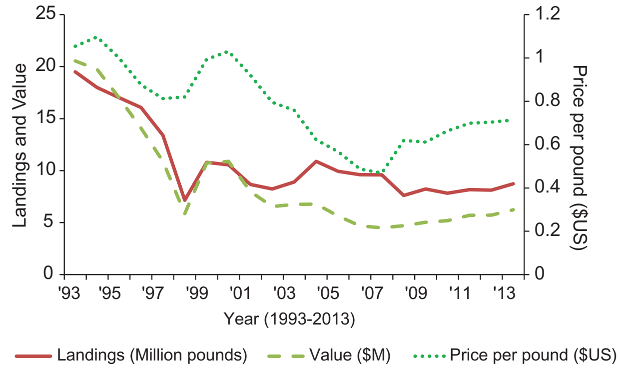

Figure 1. A 20-year time-series of *M. franciscanus* (red urchin) fishery data in southern CA. Commercial landings in million pounds (red line), ex-vessel value in millions of US dollars (green dashed line), and price per urchin pound (green dotted line). Data source: https://www.wildlife.ca.gov/Conservation/Marine/Invertebrates/Sea-Urchin.

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, management and fishing practice challenges will require further consideration among stakeholder groups. Previous efforts in the 1990s to enhance gonad yields for the development of a *S. purpuratus* commercial fishery by feeding caged outplants frozen kelp showed promising results (McBride, 2005). However, stakeholders prefer larger, wild-caught *M. franciscanus* urchins with higher gonad yields, which are also easier to harvest, process, and transport. *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 (P. Zerofski, pers. comm.). Although there may be additional costs incurred by fishers (e.g. fuel, gear-type) associated with switching fishing effort to a deep-urchin species from the current practice, the physical challenges of diving may be offset by a trap-based fishery. Furthermore, there are few studies that investigate life-history characteristics of *S. fragilis* (Sumich and McCauley, 1973) or the marketable food qualities of *S. fragilis* roe, such as gonad size, colour, and texture (McBride *et al.*, 2004). In addition to direct consumption, sea urchin roe is used as flavouring in sauces, soups, creams, and omelettes (Andrew *et al.*, 2002; Piñeiro-Sotelo *et al.*, 2002). We investigated the spatial variability of *S. fragilis* population density on the southern California outer shelf and slope, and compared food quality characteristics of *S. fragilis* gonads to current market standards (*M. franciscanus*) to evaluate the potential for developing this species as a climate change-tolerant fishery.

In this study, various fishery management criteria and food quality metrics of the pink urchin (*S. fragilis*) were evaluated in southern California in order to determine the feasibility of an emerging fishery. We addressed the following criteria to inform the potential future management of a new climate change-tolerant *S. fragilis* fishery in southern California: (i) Resiliency evaluated as distribution and relative growth rates in relation to multiple climate change variables, (ii) accessibility evaluated as abundance across space and time, (iii) habitat and ecosystems considered as habitat type, behaviour, and food preference, and (iv) acceptability standards (i.e. marketable gonad traits such as size, colour, and texture) relative to the currently fished urchin species (*M. franscianus*). 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 *S. 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 analysing 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 $\sim$10 min at 1.5–2.0 nm h^{-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) $\times$ 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 and 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 and 500 m was compared across survey years, while survey years (2003, 2008, and 2013) 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 three 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 behavioural observations

Although *S. 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 analysed 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 no. 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 and 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 analysed, 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 *S. fragilis* was compared across water depth zones on the shelf and slope in the SCB at various stations (n = 51 stations) and depths (Average depth $\pm$ *SD* = 351 $\pm$ 206 m) throughout the species' distribution (Supplementary Table S1). 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 (Supplementary Table S1). 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 ($\sim$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 1). During each collection, $\sim$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 freezers 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

Table 1. Collection date, season, and mean GI ($\pm$ 1 *SE*) of *S. fragilis* collected *via* otter trawl at a single station (~340 m) off of Point Loma, San Diego, CA.

Year	Season	Date	GI ($\pm$ 1 *SE*)
2012	Summer	8 July 2011	3.114 $\pm$ 0.237
	Winter	12 December 2012	7.815 $\pm$ 0.913
2013	Summer	27 July 2013	3.547 $\pm$ 0.306
	Winter	13 February 2014	8.487 $\pm$ 0.825
2014	Spring	20 April 2014	3.923 $\pm$ 0.304
	Summer	26 July 2014	3.448 $\pm$ 0.487
	Fall	1 November 2014	5.583 $\pm$ 0.525
2015	Spring	12 April 2015	2.107 $\pm$ 0.226
	Summer	13 June 2015	2.402 $\pm$ 0.292
	Fall	18 October 2015	3.545 $\pm$ 0.274
2016	Spring	13 March 2016	2.880 $\pm$ 0.267

(La Jolla, CA) where they were fed *ad libitum* fronds of giant kelp (*Macrocystis pyrifera*) in flow-through seawater tanks at 8 °C for ~4 weeks.

Hydrography data

For growth analyses, 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 to 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 1051 m (32.6901°N, −117.5306°W) using a Sea-Bird Electronics, Inc., CTD instrument (SBE9) and DO sensor (SBE43). Discrete water samples were collected every 50–100 m of water depth and analysed for DO and pH following methods described by Nam *et al.* (2015). In brief, oxygen samples were analysed following standard Winkler titration procedures (Dickson, 1996), and pH samples were analysed 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).

Hydrographic data used for *S. fragilis* abundance threshold analysis included salinity, temperature, depth, and DO. The ROV *Jason* was equipped with a CTD instrument (SBE19) that recorded data every second and an oxygen optode (Aanderaa 4831) that recorded DO every 30 s. The ROV *Hercules* was equipped with a CTD instrument (SBE FastCAT 49) and an oxygen optode (Aanderaa 3830), which recorded salinity, temperature, depth, and DO 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 callipers to the nearest 0.1 mm. Wet weights of gonads (five lobes) and each individual drained of its internal fluids were measured on a calibrated Sartorius digital balance (R160P) to the nearest 0.001 g. The gonad index (GI) of a single individual was calculated by using the equation,

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

where 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 *S. fragilis* individuals collected *via* otter trawls conducted at five depths (100, 300, 400, 700, and 1096 m) in the San Diego region (n = 13–17 indiv. per depth; Table 2). 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 min to remove organic material from the plates, rinsed in DI water, and placed in a vial under a hood to dry for 24–48 h. The ossicle plates were then charred in a muffled furnace for 3–5 min at 300 °C and left to cool. Approximately 24 h 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 25× magnification. Images were digitally enhanced using Adobe Photoshop software in order to better identify alternating light and dark concentric bands on each ossicle (Figure 6d).

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 from the 1051 m December 2012 hydrocast.

Roe quality

To compare properties of *S. fragilis* urchin roe quality to present seafood industry standards, freshly packaged *M. 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 aluminium potassium sulphate ($AlK(SO_4)_2$), 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

Table 2. Collection sites of *S. fragilis* individuals in the SCB that were analysed in the lab for relative growth rate.

Depth of Urchin (m)	Mean Growth ($\pm$ *SD*)	Latitude (°)	Longitude (°)	Depth of CTD (m)	Oxygen (μmol kg^{-1})	Temperature (°C)	*in situ* pH
100	5.21 ± 1.63	32.9641	−117.3136	100	138.198	11.442	7.75
300	2.75 ± 0.69	32.9523	−117.3184	300	46.815	8.1301	7.46
400	2.12 ± 0.52	32.9471	−117.3416	400	26.355	7.2387	7.44
700	1.78 ± 0.39	32.8128	−117.4676	700	9.187	5.1982	7.39
1096	1.86 ± 0.41	33.2165	−118.2318	1051	19.336	4.0242	7.42

Hydrographic data (depth, DO, temperature, and *in situ* pH) were measured from a single vertical profile in December 2012 (32.69012° N, −117.53061° W) (Nam *et al.*, 2015).

M. franciscanus were soaked for 20 min 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 colour and texture analyses. Individual gonad lobes from *M. franciscanus* were also weighed immediately prior to colour and texture analyses.

Gonad colour, 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 colour plate prior to each colour 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 colour 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 colour change was recorded as the difference in overall colour from pure white calibration plate (McBride *et al.*, 2004). The difference between the colour of the urchin gonad (Sample) and the white colour calibration plate (Target) was calculated using the following equation:

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

where ΔE, total colour change; L, lightness, a, redness; and b, yellowness.

In additional to gonad colour, 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 analyser 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, GI, relative growth rate, gonad colour 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 GI 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 GI with depth. One-way analyses of variance (ANOVAs) were employed to test for differences between gonad colour metrics (i.e. lightness, yellowness, redness, and total colour 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 *S. 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 all trawls in 2003, 2008 and 2013 with *S. fragilis* densities >0.001 indiv. m^{-2} were 203 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) (Supplementary Figure S1). The mean density of *S. fragilis* between 10 and 500 m did not vary significantly among the three survey years (2003, 2008, and 2013) (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 (Figure 2) (Kruskal-Wallis Test: $\chi^2 = 8.263$, $p = 0.41$).

Abundance threshold and behavioural 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 *S. fragilis* abundance with depth (Figure 3). In each case, a shift from 0 to 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 and 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 and 510 m water depth. Table 3 shows the mean environmental conditions in which *S. fragilis* abundances were 25–75% of the maximum abundances counted during each dive.

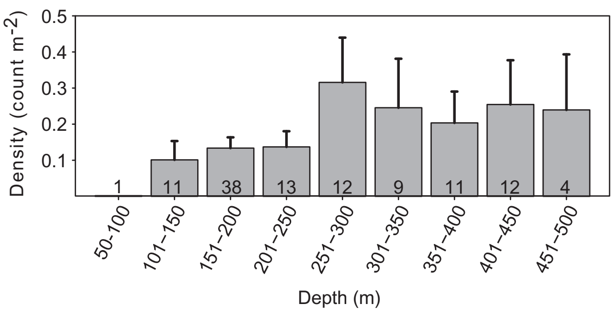

Figure 2. Pooled *S. fragilis* data collected during three trawl surveys throughout southern California (2003, 2008, and 2013). Mean density (± 1 *SE*) of *S. fragilis* across 50-m depth bins. Numbers inside bars represent number of trawls within each depth bin.

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} (Supplementary Figure S2). 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.

Spatiotemporal variability of edible gonads

Mean GI of *S. fragilis* collected in the upper 500 m varied significantly among all three subregions (Kruskal-Wallis Test: $\chi^2 = 56.89$, $p < 0.0001$). Although 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). GIs 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 (Supplementary Figure S3).

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 (Supplementary

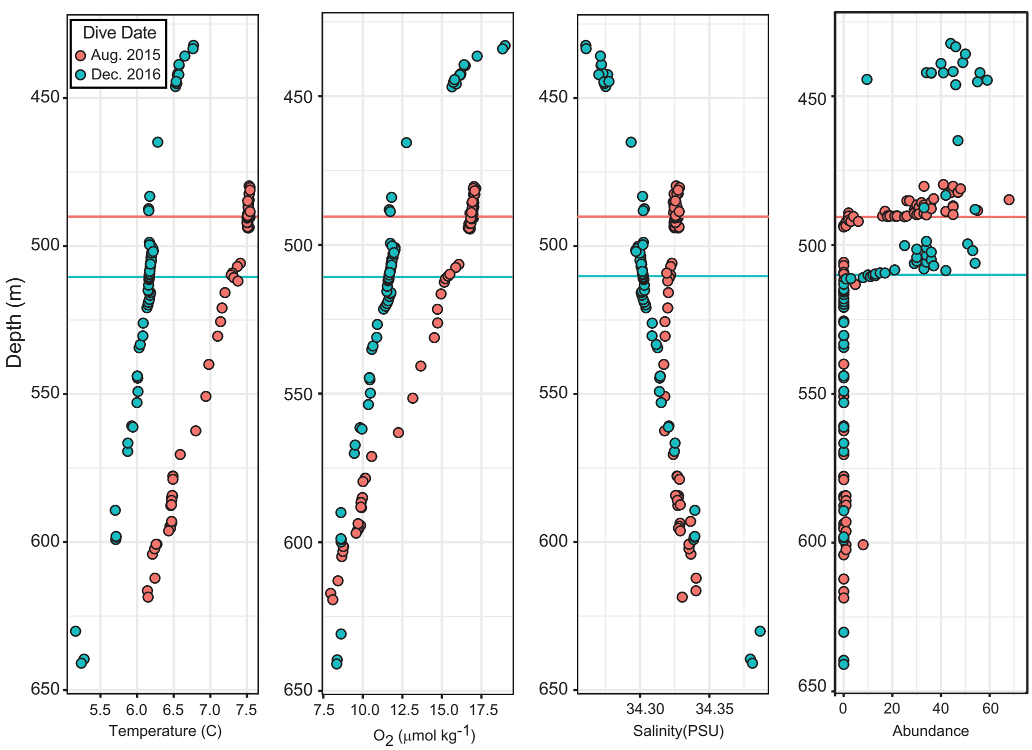

Figure 3. Abundance thresholds of *S. fragilis* from two ROV dives conducted on the San Diego slope. Depth of *S. fragilis* observations as functions of water temperature (°C), DO (μmol kg^{-1}), salinity (Practical Salinity Units; PSU), and *S. fragilis* abundance determined during the ROV *Hercules* dive in August 2015 (red circles) and the ROV *Jason* dive in December 2016 (blue circles). Horizontal coloured lines indicate depths at which *S. fragilis* abundance dramatically increased. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

Table 3. *Strongylocentrotus fragilis* threshold results from *in situ* visual surveys conducted by ROVs.

Vehicles	Vessel	Date	Mean Latitude (°)	Mean Longitude (°)	Depth (m)	Salinity (PSU)	Temperature (°C)	O_2 (μmol kg^{-1})	Proportion of max abundance	No. of frames analysed
Hercules	E/V *Nautilus*	1 August 2015	32.8134	−117.4121	487.1 [3.3]	34.326 [0.001]	7.52 [0.01]	16.945 [0.077]	0.46 [0.14]	38
Jason	R/V *Sally Ride*	3 December 2016	32.7085	−117.4144	478.6 [30.7]	34.290 [0.015]	6.34 [0.21]	13.614 [2.467]	0.54 [0.11]	31

Mean environmental conditions over which *S. fragilis* abundances were 25–75% of the maximum abundances counted during each dive. Values in brackets are SDs.

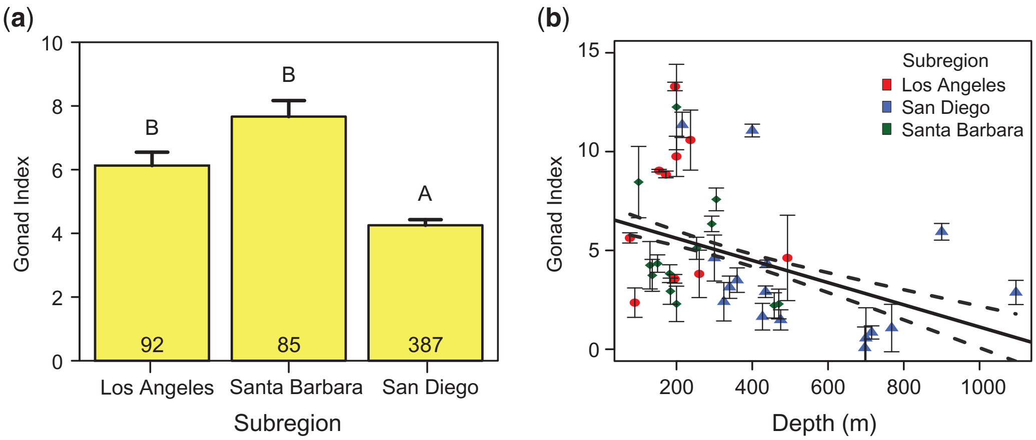

Figure 4. *Strongylocentrotus fragilis* GIs collected from Los Angeles, Santa Barbara, and San Diego subregions in the SCB. Numbers inside bars indicate replicate number of urchins dissected. (a) Mean (+1 *SE*) GI from urchins collected in the upper 500 m. Letters indicate significant differences among means based on Dunn's test treated with a Bonferroni correction ($p < 0.05$). (b) Relationship between GI (±1 *SE*) and depth in Los Angeles (red circles), San Diego (blue triangles), and Santa Barbara (green diamonds). Linear regression (solid line) and 95% *CIs* (dashed lines) represents trend across all data.

Figure S4). 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 overall mean GI was reduced by 62–64% in the Spring and Summer (Figure 5a). 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 5b). Mean GI data for two Winter and two Fall seasons were grouped into a Fall/Winter season group to demonstrate the differences among years relative to Summer GI (Figure 5b). In addition, mean GI in Fall of 2015 was 58% lower than in Winter 2014 and 55% lower than in Winter 2012 (*post hoc* Dunn's test: $p < 0.001$).

Growth variability

Relative growth rate analysis of *S. 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 700 m was 66% lower than at 100 m (Table 2). Relative growth rate was positively correlated with DO (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—colour and texture

Strongylocentrotus fragilis mean gonad lobe weight (2.38 g ± 0.33 *SE*) was 80% lower than the weight of gonad lobes of *Mesocentrotus franciscanus* (11.95 g ± 0.76 *SE*; Kruskal-Wallis Test: $\chi^2 = 14.778$, $p = 0.0001$). Colour 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 colour change than *S. fragilis* gonads (one-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 and 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 (*S. fragilis*) and describes relevant food quality properties in order to inform various stakeholders about the feasibility of developing a *S. fragilis*

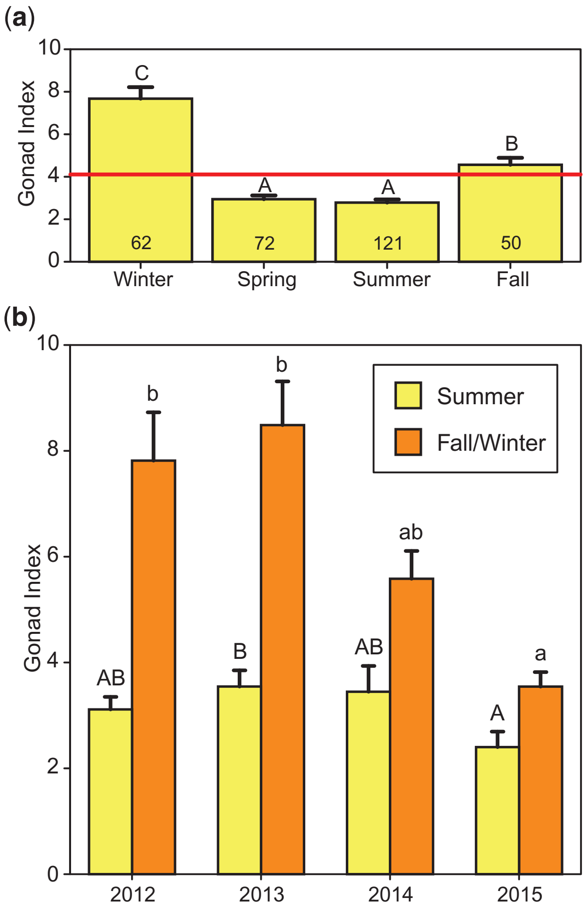

Figure 5. GIs of *S. fragilis* collected from a repeat trawl station at 340 m water depth near Point Loma, San Diego, CA. Red line indicates the dataset mean measured across 12 collections spanning 4.5 years. Letters represent significant differences ($p < 0.05$) among means as determined from *post hoc* Dunn's tests. Numbers inside bars indicate replicate number of urchins dissected. (a) Seasonality of GI (+1 *SE*) pooled across years. (b) 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.

fishery in southern California. The management criteria that we investigated (resiliency, accessibility, *S. fragilis* habitat, and behaviour, 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 3) 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 early life stages of the red urchin fishery species (*M. franciscanus*) are potentially vulnerable to the effects of climate change and ocean acidification (O'Donnell *et al.*, 2009; Reuter *et al.*, 2011; Frieder, 2014), while the purple urchin (*S. purpuratus*) may have the capacity to adapt to these conditions over evolutionary timescales (Kelly *et al.*, 2013; Frieder, 2014; Kapsenberg *et al.*, 2017). Although the limited hydrography data used in this study do not reflect natural variability, DO concentration at 700 m was 93% lower than at 100 m (Table 2), and our results suggest that *S. fragilis* currently exhibits reduced relative growth rates in the OMZ core (700 m) where DO and pH in December 2012 were 9.187 µmol kg^{-1} and 7.39, respectively (Figure 6b and c). This trend may potentially constrain the proposed fishery to fish for *S. fragilis* at shallower depths where relative growth rates are highest, and as the reduced pH and DO conditions in the OMZ are predicted to shoal simultaneously (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 in central CA 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 also possible that differences in food availability at different depths can contribute to the greater relative growth rates at shallower depths (Figure 6), which has been found to explain growth rate variability in other urchin species (Ebert, 1968, 2007; Ebert *et al.*, 1999; Britton-Simmons *et al.*, 2012). Ranges of pH and DO concentrations at the ROV sites in San Diego where abundant populations of *S. fragilis* persist at different seasons (Figure 3; Table 3) further 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 *M. 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 Dayton, 1977, 1991; Tegner and Levin, 1983), while younger urchins may not be reproductive. We were unable to observe this behaviour in *S. fragilis* using trawl and ROV imagery, and this possibility warrants further investigation. Although the average age of *M. fransicanus* in the fishery is ~4–5 years (Kato and Schroeter, 1985), the absolute age of *S. fragilis* remains uncertain (Sumich and McCauley, 1973), and a study on *S. fragilis* absolute growth rates and gonad production (i.e. age at maturity) would be required to inform a stock assessment. 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 unfavourable 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 (*M. pyrifera*) (Reed *et al.*, 2016). In northern CA, bull kelp (*Nereocystis luetkeana*) declines in 2014 and

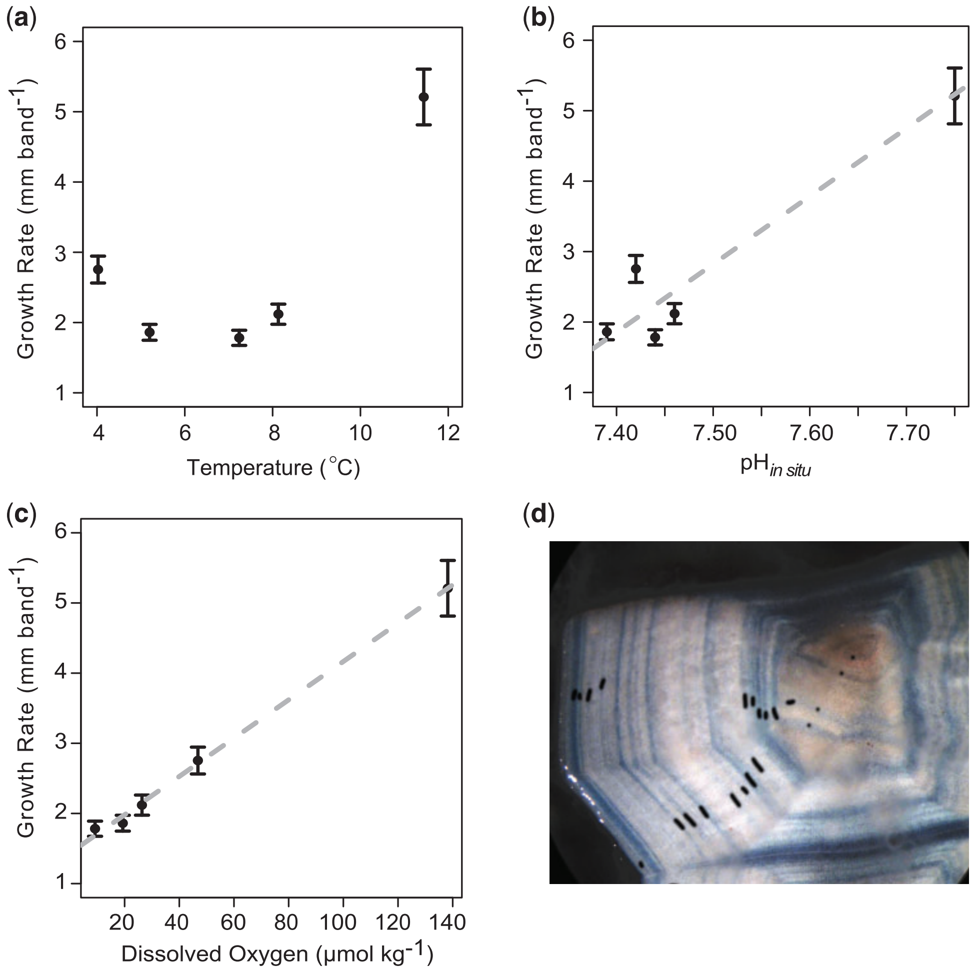

Figure 6. Mean growth rates (n = 13–17 indiv. per depth) of *S. fragilis* ($\pm$ 1 *SE*) as functions of (a) temperature (°C), (b) DO (µmol O_2 kg^{-1}), and (c) *in situ* pH. (d) Growth rates are presented as diameter length (mm) per growth band by counting the number of dark bands within treated interambulacral plate ossicles. Depths of each trawl and CTD cast are presented in Table 2. Grey dashed line indicates a significant correlation between growth rate and environmental variable (see text for details).

2015 forced urchin divers to fish for suitable roe as far north as Alaska. 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 5b). 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; Takagi *et al.*, 2017). This enhanced flexibility could provide stakeholders with adaptive management strategies (e.g. alternation or supplementation of fishery species) necessary to inform ecosystem-based fishery management frameworks (Botsford *et al.*, 1997; Shelton *et al.*, 2014; Stephenson *et al.*, 2017).

The United States currently imports ~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 (Le Cornu *et al.*, n.d.; Katsukawa and Matsuda, 2003). Based on the criteria we present, *S. fragilis* may be a possible viable alternative fishery to supplement the current southern CA red urchin fishery; however, despite previously rejected attempts to commercialize purple urchins, further consideration should be given to *S. purpuratus* as another potential climate-tolerant species (Kelly *et al.*, 2013). Marketable sea urchin products depend on GIs around 5–15% (McBride, 2005), and thus an abundance of food in the wild is required to meet this standard (Ebert *et al.*, 1999; 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 colour 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 flavouring (e.g. for sauces, creams, and seasonings) could be possible. A study on how *S. fragilis* roe size and qualities (including taste) compare to similarly sized urchin species (e.g. *S. purpuratus*, *Strongylocentrotus droebachiensis*, *Loxechinus albus*, and others) would also be helpful to better understand the potential for developing *S. fragilis* as a new fishery.

Strongylocentrotus fragilis is currently caught as bycatch in baited traps that target the valuable spot prawn (*P. platyceros*) at a

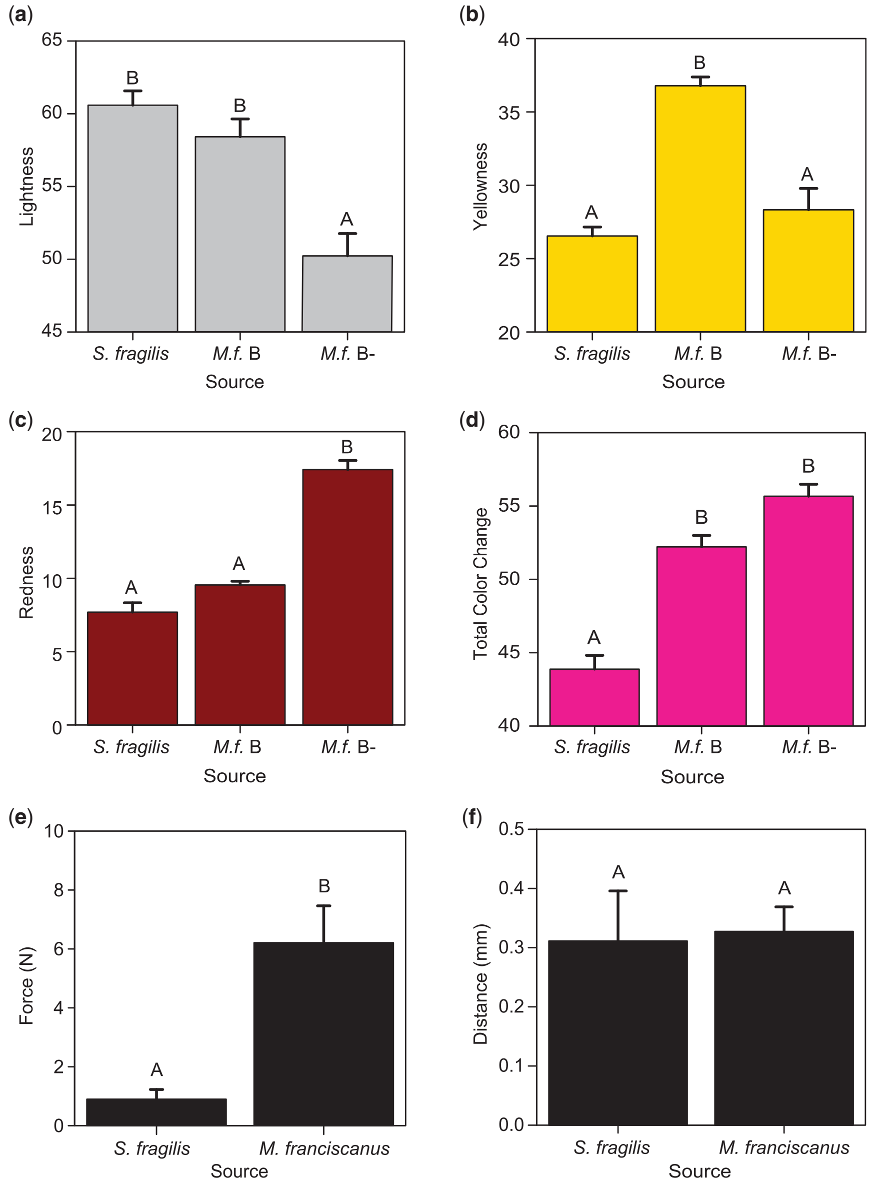

Figure 7. Mean (+1 *SE*) colour and texture properties of individual gonad lobes from *S. fragilis* and *M. franciscanus* (B and B-minus grade). (a) Lightness, (b) yellowness, (c) redness, and (d) total colour change. Letters indicate significant differences among sources of gonads as indicated by Dunn's tests. (e) Mean peak hardness (+1 *SE*) and (f) resilience (+1 *SE*) 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 one-way ANOVA (peak hardness) or Kruskal-Wallis test (resilience).

mean depth of 250 m (P. Zerofski, pers. comm.). Our results suggest that the highest densities of *S. fragilis* also occur 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 5a). 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 favourable *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 similar to previously mentioned challenges, warrant further investigation.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the article.

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