Ocean conditions and bottom-up modifications of gonad development in the sea urchin *Strongylocentrotus purpuratus* over space and time

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ABSTRACT: Intraspecific life history attributes of growth, survival, and reproduction can vary in response to changes in the physical environment. These changes can induce a cascading effect across trophic levels. In marine systems, shifts in ocean conditions such as warm and cold phases of ENSO can change primary production in benthic algae, which in turn modify resources available to benthic omnivores. Monthly gonad samples of the purple sea urchin *Strongylocentrotus purpuratus* were taken from 2007 to mid-2009 at sites from Vancouver Island, Canada, to Punta Baja, Mexico. Although mean sea surface temperature (SST) changed by ~8°C from north to south, latitudinal patterns of size-specific gonad weight were not detected, although differences existed across sites. At individual sites, mean SST changed by <1°C from 2007 to 2009. Gonad index data from Yankee Point, California (USA), from 1952 to 1964 included mean annual temperatures that varied by 2.4°C and both strong El Niño and La Niña events. Yankee Point data showed significant ($p \leq 0.01$) correlations with the Multivariate ENSO Index, SST, the Northern Oscillation Index, and the Oceanic Niño Index. Dissections at other sites along the coast from mid-1960 to 2009 showed that size-specific gonad weights were lower during periods of El Niño than during periods of La Niña.

KEY WORDS: Allometry · Pacific coast · Gonad cycle · Intertidal · ENSO · Sea surface temperature · Multivariate ENSO Index · Latitudinal patterns

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INTRODUCTION

Patterns of density, growth, reproduction, and survival along environmental gradients or through time continue to be a mainstay of ecological studies of life histories. Availability of resources and their acquisition are of major importance, and resources in excess of what are required for maintenance can be used for somatic growth, reproduction, or storage (e.g. Levins 1968, Heino & Kaitala 1999, Kozłowski et al. 2004). Evolutionary pressures act on these trade-offs, and, given constraints of reaction norms, year to year environmental fluctuations can result in allocation changes.

Marine environments experience seasonal changes in physical conditions as well as variations that have a frequency of 5 to 10 yr (El Niño Southern Oscillation, ENSO) together with longer-period changes such as the Pacific Decadal Oscillation (PDO, Mantua & Hare 2002). The bottom-up effects of these physical changes on availability of nutrients and primary production are well known, as are the further links in pelagic systems to zooplankton, fish, sea birds, and marine mammals (e.g. Cowles et al. 1977, Barber & Chavez 1983, Glynn 1988, Peterson et al. 2002, 2010, Ware & Thomson 2005, Thiel et al. 2007, Tapia et al. 2009). Large-scale ocean conditions can also influence nearshore biological processes

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whereby macroalgae can be severely reduced or eliminated as a result of high coastal temperatures and reduced upwelling of nutrients during El Niño (e.g. Dayton et al. 1999, Edwards 2004, Parnell et al. 2010). Links between phytoplankton production and intertidal filter feeders have also been documented (e.g. Menge et al. 1997, Sanford 1999, Nielsen et al. 2008).

Increased upwelling and associated increased nutrients can stimulate production of benthic algae (Nielsen & Navarrete 2004), and Freidenburg (2003) showed that kelps along the Oregon coast responded negatively to the 1997 to 1998 El Niño. During El Niño, warm water depresses the thermocline so that even when upwelling occurs, warm water from above the thermocline is upwelled rather than cold, deep water (Barber & Chavez 1983). During El Niño, periods of downwelling can also occur. For shallow-water benthic grazers, detritivores, and omnivores, year to year changes in macroalgal production can be expected to drive changes in resource allocation. Algae can be grazed by benthic invertebrates or utilized as detritus and hence considered a nutritional subsidy.

As algae break down, the detritus can be a significant resource for a variety of near-shore benthic invertebrates such as barnacles and mussels (Duggins et al. 1989), amphipods (Crawley et al. 2009), limpets (Bustamante et al. 1995), abalone (Tutschulte & Connell 1988), and sea urchins (Ebert 1968, Rodriguez 2003, Kelly et al. 2012). The implication is that ocean conditions should have an important role in the amount of food available to benthic invertebrates and hence the amount of surplus resource above maintenance that is available for growth, reproduction, and storage.

Current oceanographic data permit exploration of links between ocean conditions and life-history traits over both temporal and spatial scales. There are various measures of ocean conditions that modify functions of marine organisms. Some of these conditions are focused on single features such as sea surface temperature (SST, e.g. Barnes et al. 2001) or upwelling (Bakun 1973; e.g. Peery et al. 2006) while most, such as the PDO (Mantua & Hare 2002) or the Multivariate ENSO Index (MEI, Wolter & Timlin 1993), use a principal components analysis to integrate environmental measurements. The MEI uses 6 variables (air temperatures, SST, sea level pressure, surface wind, and cloudiness) to characterize the state of ENSO conditions. Negative MEI values represent the cooler ENSO phase (La Niña) characterized by higher productivity, whereas positive MEI

values represent the less productive warm ENSO phase (El Niño). The MEI.ext (Wolter & Timlin 2011) uses only sea level pressure (SLP) and SST and with the original MEI (Wolter & Timlin 1993); the MEI.ext is the first principal component.

The PDO index uses North Pacific SSTs north of 20° latitude and the monthly anomaly from 1900 to 1993 as a baseline (Mantua & Hare 2002). The index is the first principal component of the difference between the anomaly and the mean global SST monthly anomaly. The Northern Oscillation Index (NOI, Schwing et al. 2002) is based on the difference in SLP anomalies in the northeast Pacific and near Darwin, Australia.

The North Pacific Gyre Oscillation (NPGO, Di Lorenzo et al. 2008) uses a principal components analysis of the anomalies of SST and sea surface height. The PDO pattern is found in the first principal component and the NPGO index is the second component. The North Pacific (NP) Index (Trenberth & Hurrell 1994) is the area-weighted mean SLP over the region 30° to 65° N, 160° E to 140° W. The Oceanic Niño Index (ONI) uses Niño 3.4 (120° to 170° W, 5° S to 5° N) SST anomalies relative to a base period climatology of 1950 to 1979 (Trenberth 1997) with a 3 mo running average. Finally, we used integrated annual upwelling based on Singular Spectral Analysis (Macias et al. 2012).

All of these measures and indices represent large-scale ocean processes that can influence the availability of nutrients to organisms, and all have been shown to correlate very well in various studies, although no index works best for all studies. We examined 9 measures and indices with respect to the 1953 to 1963 gonad index data. Our goal was to show how large-scale ocean events influence secondary production of an intertidal omnivore, a bottom-up process. As the precise causal linkages cannot be made, they are presented as hypotheses that remain to be tested.

The purple sea urchin *Strongylocentrotus purpuratus* (Stimpson 1857) is a common intertidal omnivore along the west coast of North America occurring from at least Torch Bay, Alaska, USA (58° 19' N, 136° 48' W, Duggins 1981) to Los Ojitos, Baja California del Norte, Mexico (28° 54.5' N, 114° 27' W; photo record obtained by JCH). Unlike its congener *S. franciscanus*, it is not the focus of a fishery. Early studies of gonad development of this species included monthly dissections of samples from Yankee Point, California, USA (36° 29' 32" N, 121° 56' 42" W) from 1952 to 1964 (Lasker & Giese 1954, Bennett & Giese 1955, Lawrence et al. 1965, Boolootian 1966) and pro-

duced the longest continuous dissection record of samples at 1 site. Additional historical records exist of gonad dissections along the coast, including sites in central Oregon (Ebert 1968, Gonor 1972, 1973), central California (Kenner 1992, Lester et al. 2007), southern California (Leighton & Jones 1968, Coleman 1993, Basch & Tegner 2007, Lester et al. 2007), and Mexico (Lester et al. 2007). Smaller data sets also exist from sites along the coast consisting of just a single or a few dissection dates. All of these data form a temporal and spatial record of allocation of resources to gonads that can be used for comparison with more recent data.

Purple sea urchins live in what has been termed a fine-grained environment (Levins 1968). They are long-lived (Russell 1987, Ebert 2010) with generation times that span environmental variation within years, inter-annual changes over many years (El Niño–La Niña events), and even extended decadal shifts. Coupled with a long larval period (Strathmann 1978) and potential for long-range dispersal as indicated by a lack of genetic differentiation (e.g. Palumbi 1995, Flowers et al. 2002), substantial phenotypic plasticity is expected in fitness components (Levins 1968, Schlichting & Pigliucci 1998, Schoeppner & Relyea 2009).

The purpose of this paper was to explore bottom-up forcing by ocean conditions on annual gonad growth of *Strongylocentrotus purpuratus*. (1) Spatial patterns of gonad development are presented at coastal sites from 2007 to 2009 together with measures of SST and upwelling. (2) We present an analysis of a long series of monthly gonad index values based on collections from Yankee Point from 1953 to 1963. (3) The 2007 to 2009 study is placed in a historical context using the results of the 1953 to 1963 Yankee Point study together with other historic records that were gathered prior to 2007.

MATERIALS AND METHODS

From January 2007 to mid-2009, 20 *Strongylocentrotus purpuratus* were collected each month at intertidal locations along the North American west coast (Fig. 1). Monthly samples included a wide range of sizes, and total and gonad wet weights (WW) were determined to the nearest 0.01 g. Outliers were always checked with assistants and corrected when the problem had been data entry but at the end, remaining outliers always were included in analyses. To the extent possible, samples taken from 2007 to 2009 were gathered in the same pool or channel.

Some adjustments had to be made because removal of 20 ind. m^{-2} could deplete a pool, and a close pool or channel had to be selected. Length and width measurements of adjacent pools and channels were made and sea urchins were counted to give an estimate of density at each site.

It was not possible to sample at the historic Yankee Point site because it is now within a closed and gated community with no public access. The collection site we used at Garrapata is ~3 km south of Yankee Point. We also experienced problems at some sites. Maalth-sit, previously called 'Flat Top Rock' (Russell 1987) and 'Mabens Beach' (Ebert 1988), is ~5 km south

Fig. 1. *Strongylocentrotus purpuratus*. Underlined sites along the west coast of North America where monthly collections were made to determine changes in gonad size: Maalth-sit (48° 44.7' N, 125° 07.6' W); Boiler Bay (44° 49.9' N, 124° 03.6' W); Gregory Point (43° 20.4' N, 124° 22.5' W); Arena Cove (38° 55.0' N, 123° 42.8' W); Bodega Head (38° 18.2' N, 123° 03.9' W); Garrapata (36° 28.1' N, 121° 56.1' W); White Point (33° 42.9' N, 118° 19.2' W); Mission Bay (32° 45.7' N, 117° 14.9' W); Punta Baja (29° 57.2' N, 115° 48.7' W). Other sites shown are those for which historical data were available

(past bridge no. 11) along the Pacific Rim trail starting at the trailhead at Pachena Bay, which is 5 km south of Bamfield, British Columbia (Canada); winter storms can at times make the trail impassable. Selecting a site in San Diego, California, was difficult because intertidal *Strongylocentrotus purpuratus* have become very scarce. A site in Mission Bay was found in 2007 but was exhausted in 6 mo, and a replacement could not be located.

Because gonads do not begin to develop until sea urchins are larger than the size at settlement, an adjustment to weight was needed, which was estimated to be 0.5 g (Ebert et al. 2011). Also, this previous analysis showed that both β and α of the allometric equation of gonad versus total adjusted weight (Eq. 1) varied with season; consequently, these changes were also incorporated into the analysis.

Spatial differences were explored starting with an allometric equation for gonad WW, g , and total WW, w , that included the 0.5 g correction:

$$g = \alpha(w - 0.5)^\beta \quad (1)$$

or, using $G = \ln g$, $T = \ln(w - 0.5)$, and $A = \ln \alpha$,

$$G = A + \beta T \quad (2)$$

If a gonad index (GI) were to be used, β would be set equal to 1.0.

Analysis of the annual cyclic change in gonad size started with a modification of the model presented by Halberg et al. (1987):

$$y_i = A + M \cos[(2\pi/\tau)t_i + \phi] + \varepsilon_i \quad (3)$$

Starting with Eq. (2), Eq. (3) was written as appropriate for a gonad index, GI, with β fixed at 1.0 and with no seasonal variation in this parameter.

$$G = A + M \cos[(2\pi/\tau)t_i + \phi] + T + \varepsilon_i \quad (4)$$

Two additional parameters were then added to permit β to vary seasonally. Also, year to year variation in gonad development can occur, and so for 2007 to 2009, the pattern could be linear (increasing or decreasing), including 0 change, or quadratic. To model these additional complications, Eq. (4) was modified:

$$G = A + M \cos[(2\pi/\tau)t_i + \phi] + \beta T + C \cos[(2\pi/\tau)t_i + \phi]T + B_1 t_i + B_2 t_i^2 + \varepsilon_i \quad (5)$$

where $T = \ln$ -transformed total WW (g) adjusted by first subtracting 0.5 g, $A =$ the mean of $\ln \alpha$, which in Eq. (5) was seasonally adjusted by $M \cos[(2\pi/\tau)t_i + \phi]$, $M =$ the amplitude of half the total predicted change of $\ln \alpha$, $\tau =$ duration of 1 cycle, which was fixed at either 1.0 or 0.5 yr, $t_i =$ time when samples were collected starting with 0 on 1 January 2007, $\phi =$ lag from

reference time of the crest of the cycle, the 'arco-phase' (Halberg et al. 1987), $\beta =$ mean of the allometric exponent adjusted seasonally by $C \cos[(2\pi/\tau)t_i + \phi]$, $C =$ the amplitude of one-half predicted change in β ; and so similar to M , B_1 and $B_2 =$ coefficients of linear and quadratic changes with time, t_i , $\varepsilon_i =$ error.

Parameter estimates were made by nonlinear regression (NONLIN in SYSTAT 2004) using all data, including outliers, from each sample. Appropriateness of Eq. (5) versus Eq. (4) and addition of B_1 and B_2 was decided using Akaike's Information Criterion (AIC, Burnham & Anderson 2002).

Latitudinal differences in gonad development were explored by selecting a fixed total WW, arbitrarily selected to be 50 g, which is a size that was collected at all sites. Maximum gonad size and 95 % confidence limits were estimated for each site and year using fitted parameters in Eq. (5) (FUNPAR in NONLIN, SYSTAT 2004). Latitudinal change in maximum gonad size was then examined using linear regression.

SSTs were recorded in the intertidal with loggers (Solinst levellogger Model 3001) set in tidepools or channels close to where sea urchins were collected for monthly dissections. Occasional problems, including malfunctions and vandalism, limited temperature measurements for the entire period of 2.5 yr. Intertidal temperatures are presented as minimum and maximum values for each day. Minimum estimates are taken as an estimate of SST, whereas maximum values occurred during low tide periods during sunny days. Loggers were not used at all sites, and in these cases, SST was obtained from shore stations maintained by NOAA or by educational institutions.

Sources of oceanographic data and indices were: SST (shorestation.ucsd.edu; bml.ucdavis.edu/boon/data_seawater_temperature.html; tidesandcurrents.noaa.gov/gmap3/), upwelling (pfeg.noaa.gov), MEI and MEI.ext (esrl.noaa.gov/psd/enso/mei/), PDO (jisao.washington.edu/pdo/PDO.latest), NPGO (o3d.org/npggo), and NOI, NP, and ONI (esrl.noaa.gov/psd/data/climateindices/list/). The annual total upwelling based on Singular Spectral Analysis was supplied by D. Macias (pers. comm.).

Historical data of gonad size were of 3 types. (1) We used gonad sizes determined by others that appeared in publications usually as gonad index (GI) values (gonad weight or volume/total WW $\times$ 100), but obtaining raw data was not possible (e.g. Lasker & Giese 1954, Bennett & Giese 1955, Boolootian 1966, Gonor 1973). Published GI graphs were scanned so correlations could be made with measures of ocean conditions. Unfortunately, it was not possible to reconstruct data from the GI in a form where statistical

comparisons could be made with samples from other sites or times (cf. Ebert et al. 2011). Three samples gathered by Gonor (1972) and presented as dry weights in figures were scanned so that raw data could be approximated. (2) We used original raw values from dissections (e.g. Lawrence et al. 1965, Ebert 1968, Leighton & Jones 1968, Coleman 1993, Lester et al. 2007, Basch & Tegner 2007). (3) We used data gathered at sites along the coast during the 1980s, but samples were taken just once or twice a year (e.g. Russell 1987).

RESULTS

Size structure at sites used for gonad samples

Sea urchins gathered during 2007 to 2009 differed in size structure across the latitudinal range of the study (Fig. 2). The largest individuals in the study were collected in Oregon and the smallest at Garrapata in central California. The interquantile ranges for Boiler Bay and Gregory Point (see Fig. 1 for site locations) did not overlap the interquantile ranges of Maalth-sit to the north or Garrapata and sites to the south. We also found differences in the presence of extreme values in the samples. Gregory Point collections were the only ones that included no individuals outside $1.5\times$ the interquantile range (Hspread). All other sites had some individuals that were between 1.5 and $3\times$ Hspread, and 3 sites (Bodega, Garrapata, and White Point) had some individuals that exceeded $3\times$ Hspread. Density estimates in 2007 to 2009 (Fig. 2) were similar to previous estimates (Ebert 2010) and showed no latitudinal pattern ($F_{1,29} = 3.004$, $p = 0.09$). The large sea urchins found at Gregory Point had an estimated density similar to that of the small sea urchins at Garrapata. Large standard deviations also indicated substantial variation in density within sites.

Temporal changes and latitudinal differences from 2007 to 2009

Sea urchins from Gregory Point spanned the greatest size range (Fig. 2) and are used to illustrate the importance of including allometry in analyses of the annual changes in gonad size. Individual regressions were used (Eq. 2) to determine β for each sample date, and a clear

pattern emerged (Fig. 3) showing an annual cycle of allometry. The significance of this cycle is important in application of Eqs. (4) or (5) to describe the pattern of annual gonad changes. Parameters were estimated for the Gregory Point data using Eqs. (4) and (5), without the coefficients B_1 and B_2 , and results showed smaller sum of squared error (SSE) with Eq. (5) compared to Eq. (4) (Table 1). The AIC was calculated for each model, and the difference, Δ_i , was 89. A difference >10 indicates essentially no support for a model (Burnham & Anderson 2002), and so we used cyclic allometry in further analyses.

Fig. 2. *Strongylocentrotus purpuratus*. Total wet weights of samples collected for gonad analysis; see Fig. 1 for locations. Vertical line inside a box is the median; boundaries of boxes (hinges) are at sample fractions of 0.25 (lower hinge) and 0.75 (upper hinge); whisker boundaries extend to $1.5\times$ the interquantile range or Hspread; weights between the whisker boundary and $3\times$ Hspread are shown by $\times$; weights $>3\times$ Hspread are shown by $\circ$; numbers show how many sea urchins were in the $3\times$ and $>3\times$ ranges; densities are the means in pools or channels with standard deviations; numbers of pools are shown in brackets

Fig. 3. *Strongylocentrotus purpuratus*. Cyclic change in the allometric exponent β (Eq. 2) at Gregory Point, Oregon, USA from 2007 to 2009. Most values of β are >1.0 , the value used with gonad index calculations

Temporal variation in gonad development is best shown using individual regressions for each site. Parameters (Eq. 5) were estimated (NONLIN, SYSTAT 2004) for the cyclical changes in $\ln$ gonad weight as a function of $\ln$ total WW adjusted by 0.5 g and time. With the exception of Punta Baja, sea urchins at all sites showed an annual cycle of gonad growth. For Punta Baja, 2 cycles yr^{-1} was supported versus just 1 cycle (Table 2). Mean total WW at each site was used with the estimated parameters (Table 3) to draw the fitted lines (Fig. 4). For plotting, data from each sample were used with Eq. (2) to estimate allometric parameters and adjusted to the common mean total WW (NONLIN, SYSTAT 2004) together with 95% confidence limits. The 95% confidence limits varied from site to site and were greatest for Arena Cove, although most sites had at least 1 sample with large confidence limits. In general, both linear and quadratic terms improved models (Table 3), so 'linear

alone' (just B_1) or 'no trend at all' had little or no support. The single exception was at White Point, where all 3 models had some support, although the best model was for 'no trend' ($p = 68.7\%$) followed by a slightly increasing linear trend ($p = 23.4\%$).

For purposes of comparison of sites, selecting a single characteristic total WW is difficult given the large differences in size structure (Fig. 2). We chose 50 g for total weight and, using a previous estimation of parameters (Eq. 5) for each site, selected a time, t , to correspond to the maximum gonad size. Across sites, this varied from $t = 0.84$ and 1.84 (White Point) to $t = 0.96$ and 1.96 (Garraapata). We used 50 g and the 2 values of t in the estimation of parameters (Eq. 5) which was done in SYSTAT using the FUNPAR function and estimates $\ln G$ at $\ln T$, where T is (50 g – 0.5 g). The 2 estimates for each site include 95% confidence limits (Fig. 5). Gonad size as a function of latitude was not significant ($F_{1,14} = 0.031$, $p = 0.86$), and we conclude that there is no latitudinal effect on gonad development.

A primary physical feature of latitude is SST, a factor that can change from year to year (Fig. 6) and hence can potentially modify gonad growth. Temperature estimates for sites without loggers or where loggers failed to collect data from 2007 to mid-2009 relied on data from shore stations. The Neah Bay station at 48.37°N is near the mouth of the Strait of Juan de Fuca and only 0.375° south of Maalth-sit. The Yaquina Bay site (44.63°N) is close to Boiler Bay (44.83°N), and Newport Harbor (33.60°N) is close to White Point (33.72°N). Plotted temperatures are daily values and show maximum and minimum temperatures for loggers and mean values for other stations. Intertidal logger measurements of temperature

Table 1. *Strongylocentrotus purpuratus*. Comparison of seasonal gonad development at Gregory Point, Oregon, USA, with and without cyclic changes in the allometric exponent β , using Eqs. (4) and (5) (without the coefficients B_1 or B_2); k is the number of parameters and includes the sum of squared error (SSE); fixed $\beta = 1$ is equivalent to using the gonad index, GI; AIC: Akaike's Information Criterion; AICc: corrected AIC; Δ_i : Akaike difference

Gonad allometry	SSE	k	n	σ^2	AIC	AICc	Δ_i	Conclusion
Cyclic	169.24	6	620	0.273	-793.01	-792.88	0.00	Supported
Fixed $\beta = 1$ (GI)	195.70	4	620	0.316	-706.95	-706.89	85.99	Not supported

Table 2. *Strongylocentrotus purpuratus*. Comparison of gonad development with 1 or 2 cycles yr^{-1} at Punta Baja, Baja California, Mexico. k is the number of parameters and includes the sum of squared error (SSE); AIC: Akaike's Information Criterion; AICc: corrected AIC; Δ_i : Akaike difference

No. cycles yr^{-1}	SSE	k	n	σ^2	AIC	AICc	Δ_i	Conclusion
2	149.93	6	619	0.242	-865.72	-865.58	0.00	Supported
1	160.33	6	619	0.259	-824.19	-824.06	41.53	Not supported

Table 3. *Strongylocentrotus purpuratus*. Parameters for cycles of ln gonad wet weight as a function of ln adjusted total wet weight (Eq. 5) with levels of support of models with a change from 2007 to 2009. A = the mean of $\ln\alpha$, which in Eq. 5 was seasonally adjusted by $M\cos[(2\pi/\tau)t_i + \phi]$; τ = duration of 1 cycle, which was fixed at 1 yr for all sites except Punta Baja where 2 cycles were supported (Table 2) so τ was fixed at 0.5; M = the amplitude of half the total predicted change of $\ln\alpha$; ϕ = lag from reference time of the crest of the cycle; β = mean of the allometric exponent adjusted seasonally by $C\cos[(2\pi/\tau)t_i + \phi]$; C = the amplitude of one-half predicted change in β ; B_1 and B_2 = coefficients of linear and quadratic changes with time, t_i ; t_i = time when samples were collected starting with 0 at 1 January 2007 (see Eq. 5). B_1 is linear change, B_2 adds a quadratic term, 'Neither' means neither B_1 nor B_2 ; k : number of parameters including the sum of squared error (SSE); AICc: corrected Akaike Information Criterion; Δ_i : Akaike difference; w_i : Akaike weight; ASE: asymptotic standard error of the estimate; L 95 % and U 95 %: lower and upper 95 % confidence limits, respectively. The model with the most support shown in **bold**. See Fig. 1 for site locations

Site	N	SSE	k	AICc	Δ_i	w_i	Parameter	Estimate	ASE	L 95 %	U 95 %
Maalth-sit	405						A	-2.8390	0.1716	-3.1763	-2.5017
							M	1.4379	0.2123	1.0206	1.8551
							ϕ	0.6394	0.0595	0.5223	0.7564
							β	1.1780	0.0417	1.0961	1.2599
							C	-0.2257	0.0579	-0.3394	-0.1119
							B_1	-0.4974	0.1376	-0.7678	-0.2269
							B_2	0.2503	0.0487	0.1547	0.3460
							B_1 only	0.1914	0.0332	0.1262	0.2566
							Neither				
Boiler Bay	598						A	-2.8737	0.1569	-3.1819	-2.5655
							M	0.6444	0.1958	0.2599	1.0288
							ϕ	0.3516	0.0520	0.2495	0.4538
							β	1.2177	0.0295	1.1598	1.2756
							C	-0.0139	0.0441	-0.1005	0.0727
							B_1	-1.0057	0.1513	-1.3029	-0.7085
							B_2	0.3477	0.0544	0.2410	0.4545
							B_1 only	-0.0579	0.0318	-0.1203	0.0045
							Neither				
Gregory Pt	620						A	-3.1486	0.1379	-3.4193	-2.8778
							M	1.1471	0.1921	0.7698	1.5245
							ϕ	0.7736	0.0476	0.6801	0.8670
							β	1.2666	0.0279	1.2118	1.3214
							C	-0.1216	0.0414	-0.2030	-0.0403
							B_1	-0.8892	0.1135	-1.1121	-0.6663
							B_2	0.3463	0.0427	0.2625	0.4300
							B_1 only	0.0057	0.0285	-0.0501	0.0616
							Neither				
Arena	506						A	-5.5741	0.2182	-6.0029	-5.1453
							M	-1.2038	0.2259	-1.6478	-0.7599
							ϕ	-2.2291	0.1016	-2.4288	-2.0294
							β	1.9409	0.0452	1.8521	2.0296
							C	0.1434	0.0598	0.0260	0.2608
							B_1	-1.1743	0.2785	-1.7215	-0.6271
							B_2	0.3106	0.0985	0.1171	0.5042
							B_1 only	-0.3158	0.0563	-0.4264	-0.2051
							Neither				
Bodega	619						A	-4.4711	0.1884	-4.8410	-4.1011
							M	1.1641	0.2335	0.7055	1.6228
							ϕ	0.0293	0.0538	-0.0764	0.1350
							β	1.4388	0.0454	1.3498	1.5279
							C	-0.1530	0.0594	-0.2696	-0.0364
							B_1	0.4904	0.1154	0.2638	0.7171
							B_2	-0.1773	0.0429	-0.2617	-0.0930
							B_1 only	0.0283	0.0284	-0.0275	0.0840
							Neither				
Garrapata	616						A	-3.5423	0.1789	-3.8937	-3.1909
							M	0.7509	0.2573	0.2457	1.2562
							ϕ	0.3051	0.0955	0.1175	0.4926
							β	1.3100	0.0590	1.1940	1.4259
							C	-0.1335	0.0799	-0.2905	0.0234
							B_1	0.1299	0.0321	0.0668	0.1930

(Table continued on next page)

Table 3 (continued)

Site	N	SSE	k	AICc	Δ_i	w_i	Parameter	Estimate	ASE	L 95 %	U 95 %
White Pt	620	190.48 195.95	8 6	-706.75 -693.41	0.91 14.25	0.39 0.00	A	-3.4706	0.1914	-3.8464	-3.0947
							M	0.6810	0.2686	0.1535	1.2084
							ϕ	0.3287	0.0971	0.1381	0.5193
							β	1.3084	0.0590	1.1924	1.4243
							C	-0.1087	0.0843	-0.2743	0.0569
							B_1	-0.0132	0.1401	-0.2882	0.2618
							B_2	0.0544	0.0518	-0.0473	0.1561
							Neither				
							A	-3.7937	0.1709	-4.1292	-3.4581
							M	-0.5999	0.2509	-1.0925	-0.1073
							ϕ	1.0072	0.0595	0.8903	1.1241
							β	1.3702	0.0480	1.2760	1.4644
							C	0.3114	0.0694	0.1750	0.4477
							Neither				
Pt Baja	619	176.81 176.61	7 8	-763.7 -762.34	2.04 3.39	0.23 0.12	A	-3.7962	0.1730	-4.1359	-3.4565
							M	-0.6017	0.2522	-1.0969	-0.1065
							ϕ	1.0063	0.0604	0.8876	1.1250
							β	1.3699	0.0481	1.2754	1.4644
							C	0.3118	0.0698	0.1748	0.4489
							B_1	0.0028	0.0295	-0.0552	0.0607
							B_2				
							A	-3.5029	0.1760	-3.8486	-3.1572
							M	1.4688	0.2532	0.9715	1.9661
							ϕ	1.1889	0.1163	0.9606	1.4172
							β	1.3005	0.0459	1.2103	1.3907
							C	-0.3446	0.0672	-0.4766	-0.2126
							B_1	0.2070	0.0263	0.1554	0.2587
							A	-3.4884	0.1771	-3.8363	-3.1405
							M	1.4641	0.2526	0.9679	1.9602
		135.94 149.93	8 6	-922.12 -865.58	1.57 58.11	0.31 0.00	ϕ	1.2047	0.1169	0.9752	1.4343
							β	1.3053	0.0465	1.2140	1.3966
							C	-0.3425	0.0670	-0.4741	-0.2108
							B_1	0.1340	0.1087	-0.0794	0.3474
							B_2	0.0282	0.0406	-0.0516	0.1079
							Neither				

at Punta Baja (29.95° N, 115.81° W) were consistently lower than the daily measurements at Newport Harbor. Maximum measurements during low tide periods at Punta Baja only once exceeded 21°C, whereas daily SST measurements at Newport Harbor were consistently >21°C from July to September and reached highs close to 23°C. Mean annual temperatures at sites from 2007 to 2009 varied very little. At Neah Bay, annual SST varied by ~0.5° and ~0.2°C at Newport Harbor. Latitudinal variation from north to south was 8°C.

Estimates of maximum gonad size at a total weight of 50 g changed from 2007 to 2008 at sites, as did annual mean temperature. There was no relationship between changes in gonad size and changes in temperature ($p = 0.8$) or upwelling ($p = 0.90$) or with changes in gonad size and latitude ($p = 0.7$). Changes in both gonad size and physical factors from 2007 to 2008 were modest, and statistically

not significant. A longer time series would be needed to resolve possible effects.

Gonad indices at Yankee Point and ocean conditions

A GI was determined for *Strongylocentrotus purpuratus* at Yankee Point from 1952 to 1955 (Fig. 7A). The GI increased from 1952 to a high in 1955, which was followed by a decline to a low in 1958 and then a rise. GI values based on raw data gathered by Lawrence et al. (1965) showed a time displacement of the values in 1963 and may represent a problem with transferring information from the graph in Boolootian (1966) to data values. Adjustment of ~1 mo aligns the data points. The raw dissection data for 1963 to 1964 include actual dates of collection and so are correct with respect to the time axis.

Fig. 4. *Strongylocentrotus purpuratus*. Annual cycles of gonadal weight (means $\pm$ 95 % confidence limit) for the 8 monthly sampled sites (see Fig. 1). Fitted lines used all raw dissection data with Eq. (4) and plots are with mean total weights for each site; lines for 2 annual cycles are shown for Punta Baja

The annual mean GI at Yankee Point showed correlations ≥ 0.71 with $p \leq 0.01$ for 5 measures of ocean conditions: NP, MEI, ONI, MEI.ext, and SST (Table 4). The PDO, with $r = -0.57$, had $p = 0.06$. SST was based on measurements made at Hopkins Marine Station,

very close to Yankee Point, but other indices used large-scale and distant measures and so illustrate the significant teleconnections that exist. The pattern of monthly GI values (Fig. 7A) shows a high in 1955 and a low in 1958, which are La Niña and El Niño events,

Fig. 5. *Strongylocentrotus purpuratus*. Maximum annual gonad size adjusted to a common total wet weight of 50 g as a function of latitude. Error bars: 95 % confidence limits

respectively. The annual mean GI was plotted versus annual mean values of 4 indicators of ocean conditions (Fig. 7B–E). Patterns show that as the Aleutian Low intensifies (NP), gonad size goes down; the lowest mean value, 1011.5 mb, was for 1958 which was also the year of the highest mean SST, 14.6°C, at Hopkins Marine Station. NP, MEI, ONI, and SST were all associated with the patterns of upwelling of nutrients along the coast, but total annual upwelling (Table 4) was poorly correlated with the GI ($r = 0.32$, $p = 0.34$) and also poorly correlated with SST ($r = -0.42$), but much better with NP ($r = 0.63$). The signs of the correlations, however, all are in the expected direction, indicating large gonads during years of increased upwelling. This analysis supports a bottom-up influence on gonad growth in *Strongylocentrotus purpuratus* and indicates that any of the top 5 indices could be used as proxies for ocean conditions that promote development. It is important that the difference between the highest and lowest SST is about 2.4°C and between the greatest and smallest GI is about 6.4, so the range of values is much greater than SST and gonad size found for 2007 to 2008. Having a long run of data that includes a wide range of environmental conditions is important.

Ocean conditions and historical comparisons

Historical data were compared with dissection data from 2007 to 2009 and placed in the context of ocean conditions as summarized with the Multivariate ENSO Index MEI (Fig. 8) and major El Niño/La Niña events (see esrl.noaa.gov/psd/enso/mei/ and cpc.ncep.noaa.gov/products/analysis_monitoring/enso_stuff/ensoyears.shtml). Strength of El Niño (warm) and La Niña (cool) events was measured using the ONI and summarized by J. Null (ggweather.com/

enso/oni.htm). Events were defined as 5 consecutive months at or above/below the 5° anomaly for warm or cool events. Weak, moderate, and strong events have SST anomalies of 0.5 to 0.9, 1.0 to 1.4, and ≥ 1.5 , respectively. Over the past 50+ yr, ocean conditions have changed both relatively as shown by the MEI or ONI but also absolutely, as mean SST has increased in southern and central California at the Scripps Institution of Oceanography in La Jolla and at the Hopkins Marine Station in Pacific Grove (see shore-station.ucsd.edu).

The relationship between ocean conditions at Yankee Point and the GI can be seen in other data gathered along the coast. Boolootian (1966, his Figs. 25–28, p. 588) showed gonad cycles at 15 sites along the coast from 1958 to 1961. Northern sites such as Shell Beach, California, and ‘Coos Bay’ (in fact Sunset Bay), Oregon, showed the same general increase over time as Yankee Point during those years. Southern sites did not show a pattern, and ‘Corona del Mar’ in southern California failed to show a seasonal signal. The important point is that there was a clear negative relationship between the MEI and the GI at Yankee Point and many other northern sites along the coast.

Gonad size data for each site, including original data from all historical sites, were analyzed (Eq. 2) month by month to determine gonad size using the grand mean of total body WW adjusted by 0.5 g. The pairwise comparisons of means within months used the Bonferroni procedure at $\alpha = 0.05$.

Sea urchins were dissected at 2 sites on southwest Vancouver Island in the 1980s: Maalth-sit, near the mouth of Pachena Bay, and Seppings Island in Barkely Sound. All historical dissections in the 1980s were point samples rather than part of a monthly program. Gonad development during the 2007 to 2009 period was greater than during the 1980s (Fig. 9A), and 2007 and 2008 were moderate La Niña years. Strong El Niño conditions were present in 1982 and moderate in 1987. Weak La Niña (cool) conditions were recorded in 1985 (Fig. 8). Gonad WW estimated for *Strongylocentrotus purpuratus* at Seppings Island in March 1985 did not differ from the 2007 or 2009 samples. Sea urchins at Seppings Island had gonad sizes that were slightly larger than those in the 1985–1987 samples from Maalth-sit but not significantly so ($p > 0.05$). Sea urchins sampled at Maalth-sit from 1985 to 1987, during a long, moderate El Niño period, had small gonads compared with those in samples from 2007 to 2009.

Historical data for Boiler Bay were recovered from graphs in Gonor (1972) and are for Boiler Bay in 1970

Fig. 6. *Strongylocentrotus purpuratus*. Sea surface temperature (SST) at sites along the coast including intertidal loggers at sites showing daily minimum (solid lines) and maximum (dashed lines) (A,C,D,F,H); sites without loggers (B,E,G) are from websites given in the text. See Fig. 1 for site locations

and Yaquina Head in 1970 and 1971. Dissections from Yaquina Head were made in 1985 (6 June) and 1987 (17 May) (Fig. 9B). The sample from June 1985 did not differ from the 2007 and 2008 samples from

Boiler Bay, but all other historical samples had sea urchins with smaller gonads than found in the 2008 to 2009 samples ($p < 0.05$). Moderate La Niña existed during 1970 and 1971, and so we expected that

results would be similar to 2007 and 2008. Dissection data from 1985 and 1987 were collected during weak La Niña and moderate El Niño, respectively, and the 1985 dissections were similar to 2008 and 2009 results. The low estimates for 1970 and 1971 may contain errors associated with translating Gonor's graphs using dry weights to WW, or differences may be due to site-specific details of Boiler Bay and Yaquina Head during this time period.

Historical data for comparison with Gregory Point (Fig. 10A) come from the south side of Sunset Bay at a site called the Boulder Field (Ebert 1968). Sea urchins at this site were of comparable size to those at Gregory Point, which is 0.7 km northwest. Data from September 1964 (weak La Niña) to the end of the year did not differ from this annual period in 2007 but gonads were smaller than in 2008. In general, the 1964-65 data did not differ from dissections made in 2007 to 2009 other than in early 2007. Dissections made during weak La Niña conditions in 1985 (8 June) and during an El Niño in 1987 (15 May) showed sea urchins with smaller gonads compared with those sampled from 2007 to 2009 ($p < 0.05$).

Historical data for both Arena Cove and Bodega Head are single samples gathered on 14 April 1985 at Arena Cove and 13 November 2004 at Bodega Marine Reserve (Lester et al. 2007). The Arena Cove sample had sea urchins with smaller gonad weights than those in the 2007 and 2009 April samples (no April sample was taken in 2008) but not significantly so ($p = 0.7$). Sea urchins in the November 2004 sample at Bodega had significantly smaller gonads than in November samples from 2007 and 2008 ($p < 0.01$). The 2004 sample was gathered in the Bodega Marine Reserve (Lester et al. 2007), whereas the 2007 to 2009 samples were from Bodega Head ~2 km to the south.

Historical data for Garrapata include raw dissection data gathered by R. Lasker on 2 March 1954 at Yankee Point, 15 October 1962 to 23 February 1964 by J. and A. Lawrence, and 17 October 1984 to 5 November 1985 at Stillwater Cove, a subtidal site on the south side of the Monterey Peninsula, by M. Kenner. The 1962 to 1964 dissections were made mostly during 1963, an El Niño period, and in general had

Fig. 7. *Strongylocentrotus purpuratus*. (A) Monthly gonad index (GI) changes from 1952 to 1964 starting in October 1952. ●: from 1952 to August 1953, dissections shown in Lasker & Giese (1954); ○: from 1953 to August 1954, from Bennett & Giese (1955); ○: from 1954 to August 1962, from Boolootian (1966); ●: from 1962 to 1964, based on raw dissection data from J. Lawrence (pers. comm.). (B–E) Mean annual GI vs. measures of ocean conditions 1954 to 1963; (B) North Pacific (NP); (C) Multivariate ENSO Index (MEI); (D) Oceanic Niño Index (ONI); (E) sea surface temperature (SST)

Table 4. *Strongylocentrotus purpuratus*. Mean annual gonad index (GI) for Yankee Point, CA, and measures of ocean conditions with correlation coefficients (r). NP: North Pacific, MEI: Multivariate ENSO Index, ONI: Oceanic Niño Index, MEI.ext: MEI using only sea level pressure and SST, SST: sea surface temperature, PDO: Pacific Decadal Oscillation, NOI: Northern Oscillation Index, SLP: Standardized Darwin Sea Level Pressure, NPGO: North Pacific Gyre Oscillation. Significant values ($p < 0.05$) are shown in **bold**

Year	GI	NP	MEI	ONI	MEI.ext	SST	PDO	NOI	SLP	Upwelling	NPGO
1953	7.395	1011.78	0.336	0.692	0.460	12.735	-0.157	1.546	0.217	2.861×10^8	1.082
1954	12.141	1013.14	-0.941	-0.350	-0.534	12.971	-0.291	0.391	-0.750	-2.406×10^9	0.207
1955	12.093	1014.55	-1.622	-0.975	-1.548	12.253	-1.948	2.416	-1.192	3.806×10^9	-0.075
1956	8.556	1013.55	-1.291	-0.592	-1.262	12.699	-1.804	2.735	-1.442	-5.170×10^8	0.070
1957	8.742	1012.57	0.622	0.900	0.811	13.748	0.228	-1.073	0.067	1.397×10^9	-1.147
1958	5.737	1011.47	0.792	0.783	1.116	14.557	0.643	-1.878	-0.350	-3.712×10^9	-0.548
1959	8.194	1013.14	0.119	0.133	0.484	13.535	-0.027	0.526	-0.425	3.517×10^9	-0.204
1960	9.106	1012.73	-0.286	0.008	-0.071	13.114	0.058	0.795	-0.683	-1.756×10^9	0.748
1961	9.924	1012.84	-0.277	0.000	-0.056	13.047	-0.818	1.512	-0.092	-7.307×10^8	0.971
1962	10.870	1013.46	-0.762	-0.242	-0.615	12.605	-1.158	1.330	-0.617	7.268×10^7	-0.093
1963	8.179	1012.02	0.053	0.633	0.355	13.444	-0.686	-0.561	0.058	-3.595×10^9	-0.235
r		0.80	-0.78	-0.76	-0.74	-0.71	-0.57	0.50	-0.46	0.32	0.14
p		<0.01	<0.01	0.01	0.01	0.01	0.06	0.11	0.16	0.34	0.69

Fig. 8. *Strongylocentrotus purpuratus*. Multivariate ENSO Index (MEI) values from 1950 to 2010 indicating historical data used in this study. Yankee Point, CA, USA: Bennett & Giese (1955) (including data from Lasker & Giese 1954), Boolootian (1966), Lawrence et al. (1965); Sunset Bay, OR, USA: Ebert (1968); White Point, CA: Leighton & Jones (1968); Boiler Bay, OR: Gonor (1972); Punta Baja, Mexico, La Jolla, CA, and Maalth-sit, Canada: Russell (1987); Mission Bay, La Jolla, CA: Coleman (1993), Bash & Tegner (2007); Punta Baja, Mexico, and Bodega Marine Reserve, CA: Lester et al. (2007). Solid lines show periods during which gonad size data were gathered

significantly lower gonad weights ($p < 0.05$) than dissections from other time periods that were dominated by La Niña conditions. The October 1984 to November 1985 collections at Stillwater Cove were made during a weak La Niña period and so were similar to the samples of 2007, but gonad weights were larger in samples from 2008 and 2009.

Historical intertidal data at or near White Point along the Palos Verdes coast were collected during a weak La Niña from 26 April 1966 to 17 May 1967 (D. Leighton) and a weak El Niño from 26 October 2003 to 2 May 2005 (S. Lester). Gonad sizes overlapped somewhat with the 2007 to 2009 data, but overall, the historical dissections had sea urchins with smaller gonads compared with measurements made in 2007 to 2009. Additional historical intertidal dissection data from other sites along the Palos Verdes peninsula collected during 1966 to 1967 (D. Leighton) were combined with the 2007 to 2009 dissections to determine whether gonad sizes were different across time. Monthly trends are evident (Fig. 11B), as well as differences across studies and samples. Sites sampled by D. Leighton were on both sides of White Point (Fig. 11A), although mostly to the west and north. The 2 sites farthest from White Point, Flat Rock Point and Lunada Bay, did not show the greatest difference from White Point, and some samples from 1966 to 1967 had sea urchins with gonad weights equal to or greater than those at White Point in 2007 to 2009. Intertidal sea urchins sampled at Cabrillo Beach to the east of White Point had some of the largest gonads that were measured. The dissections from 2007 to 2009 showed consistently larger gonad sizes than samples from 2003 to 2005. The gonad sizes during 2007 to 2009 reflect these changes, with the largest gonad sizes occurring during the moderate La Niña or late 2007 and early 2008.

Samples from Mission Bay (Fig. 12A) had 4 months where mean gonad sizes were not different ($p > 0.05$): June, July, August, and November. The distribution of months when dissections were made was

Fig. 9. *Strongylocentrotus purpuratus*. Gonad weights in 2007 to 2009 adjusted to common mean total wet weights at (A) Maalth-sit and (B) Boiler Bay plotted with historical dissection data; Maalth-sit 1982 from Russell (1987); Boiler Bay 1970 and Yaquina Head 1970 to 1971 extracted from graphs in Gonor (1972). El Niño years: 1982 (strong), 1987 (moderate); La Niña years: 1970 to 1971 (moderate); 1985 (weak); 2007 to 2008 (moderate). See Fig. 1 for site locations

Fig. 10. *Strongylocentrotus purpuratus*. Gonad weights in 2007 to 2009 adjusted to common mean total wet weights at (A) Gregory Point and (B) Garrapata plotted with historical dissection data; Sunset Bay (Boulder Field area) September 1964 to June 1965 (Ebert 1968); Yankee Point 1954 from R. Lasker (unpubl.), October 1962 to February 1964 (Lawrence et al. 1965), Stillwater Cove October 1984 to November 1985 (Kenner 1992). El Niño: 1963 (moderate); La Niña: 1962 (weak), 1964 to mid-1965 (weak), 1984 to 1985 (weak); 2007 to 2008 (moderate). See Fig. 1 for site locations

not consistent across studies, and the only study that covered all months was from 1989 to 1990 (Basch & Tegner 2007). The trend was for sea urchins in samples from 2007 to have gonads weights equal to those from 1994 to 1996, which covered months from February to July, and for sea urchins in the 1989 to 1990 samples to have smaller gonad weights than in 1994 to 1996, which covered July to December. Both of the periods 1989 to 1990 and 1994 to 1996 were mixtures of weak El Niño and weak La Niña conditions.

Historical data gathered at Punta Baja were scattered single samples from the 1980s and samples gathered during 2003 to 2005 (Lester et al. 2007) with gaps from 1 to 5 mo. Historical dissections (Fig. 12B). In general, the historical data showed (Fig. 12B) that sea urchins had smaller gonads than observed in 2007 to 2009. ENSO conditions were neutral in 2003, turning towards weak El Niño conditions by mid-2004 before turning neutral again by early 2005.

Fig. 11. *Strongylocentrotus purpuratus*. Gonad weights in 2007 to 2009 at White Point, CA, USA adjusted to a common mean total wet weight and plotted with historical dissection data at intertidal sites along the Palos Verdes Peninsula, Los Angeles, CA. (A) White Point, showing sewer outfall pipes and sites sampled together with symbols used in panel B. (B) 1966 to 1967 (Leighton & Jones 1968); October 2003 to May 2005 (Lester et al. 2007). El Niño: 2004 (weak); La Niña: 1967 (weak), 2007 to 2008 (moderate)

Differences in the ENSO conditions may be related to the overall higher values of gonad size during our study. Mostly, historical studies covered periods of strong to weak El Niño or weak La Niña. Only 1955 (Yankee Point), 1970 (Boiler Bay and Yaquina Head), and 2007 (this study) had modest La Niña conditions. Unfortunately, it is not possible to reanalyze the historical data from Yankee Point, but the size structure of the samples (mode = 72 g, range 23–191 g) gathered by J. and A. Lawrence compared to the size

Fig. 12. *Strongylocentrotus purpuratus*. Gonad weights adjusted to common mean total wet weights at (A) Mission Bay and (B) Punta Baja plotted with historical dissection data; La Jolla 1982 (Russell 1987); Mission Bay July 1989 to 1990 (Coleman 1993); 1994 to 1996 (Basch & Tegner 2007); and 2004 (Lester et al. 2007). El Niño: 1982, 1994 to early 1995; La Niña: 1985, 1989, mid-1995 to 1996, 2007. See Fig. 1 for site locations

structure of samples from Garrapata (mode = 25 g, range 4–76 g) suggests that these sites, despite their proximity, were very different with respect to potential productivity.

DISCUSSION

Ocean conditions summarized by the MEI resulted in modifications of gonad growth in the west coast purple sea urchin *Strongylocentrotus purpuratus*. When the MEI was positive (El Niño conditions),

size-specific gonad growth was less than when the MEI was negative (cool La Niña conditions). This association is most evident in the 11 yr data set at Yankee Point, California (Fig. 7B), and emphasizes the importance of long-term studies in exploring demographic patterns. The proposed mechanism for the linkage between ocean conditions and gonad growth is the bottom-up effect of nutrient availability to benthic algae production and hence food for the sea urchins. The annual cyclical pattern of gonad growth during a year is not changed by ocean conditions (Fig. 4). Sea urchins at all sites showed peak gonad size in about December and the smallest gonads by June, as described by various workers (e.g. Boolootian 1966, Pearse 1981, Pearse & Cameron 1991). Gametogenesis responds to photoperiod (Pearse 1981, Pearse et al. 1986) and appears to be independent of other environmental signals such as temperature (reviewed by Pearse & Cameron 1991). Accordingly, the annual cycle is an aspect of the reaction norms of gonad growth that is fixed with respect to photoperiod. Cues for initiation of spawning are less clear (Pearse & Cameron 1991), although once maximum gonad size has been attained, spawning in the field appears to follow soon as indicated by the decline in size-specific gonad weight (Fig. 4). Observations of *S. purpuratus* spawning in the field, however, are very rare (Pennington 1985, Mercier & Hamel 2009). The importance of an increase in temperature to initiate spawning (Himmelman et al. 2008) seems unlikely in our study because sites from north to south all had maximum gonad size in November and December followed by a decrease in size. Furthermore, spikes in intertidal temperatures recorded by loggers (Fig. 6) failed to show temperature fluctuations in late fall.

The gonad changes at Punta Baja (Fig. 4) indicate 2 events of gonad increase and decline during a year, which is not consistent with the primary importance of photoperiod in gonad growth. Pearse (1981) showed a single spawning season for *Strongylocentrotus purpuratus* at Papalote Bay (31°43'N, 116°43'W), Baja California del Norte, and using small *S. purpuratus* collected at this site, Pearse et al. (1986) experimentally showed the importance of photoperiod. Papalote Bay is only ~215 km north of Punta Baja, so if the annual cycle is determined by photoperiod, only 1 cycle of gametogenesis would be expected at Punta Baja. However, Pearse et al. (1986) did not observe changes in gonad size associated with the changes in the percent of ripe sea urchins, and thus no spawning event was observed under laboratory conditions. We did not examine sections of

gonad tissue to measure progression of a reproductive cycle, so decreases in gonad size might be a result of resorption without spawning. However, this would create a problem of explaining why such a decrease would occur twice each year. Leahy et al. (1981), however, observed 2 peaks of fertility in subtidal *S. purpuratus* at Victoria Point off Goff Island in Laguna Beach, southern California (33°30'44" N, 117°45'37" W). Other than sea urchins at Punta Baja, temporal changes along the coast from 2007 to 2009 showed the expected annual cycles with 1 cycle yr⁻¹.

A number of patterns of gonad development have emerged from the data of 2007 to 2009 together with historical dissections of *Strongylocentrotus purpuratus* along the Pacific coast of North America. The spatial differences from Maalth-sit, British Columbia, to Punta Baja, Baja California del Norte, showed no latitudinal trend of size-specific gonad size and thus do not support the conclusion of Lester et al. (2007) that reproduction is better at the southern edge of the distribution of *S. purpuratus*. Size structure was different across sites, and the sea urchins collected at Garrapata in central California were very small compared to those collected in central Oregon at Gregory Point and Boiler Bay. Size structure of intertidal populations at the latitudinal extremes in our study, Maalth-sit and Punta Baja, however, were similar.

Individual growth in test diameter at sites from Maalth-sit to Punta Baja (Russell 1987, Ebert 2010) showed no latitudinal pattern, which has also been reported for red sea urchins *Strongylocentrotus franciscanus* (now *Mesocentrotus franciscanus*, see Vinikova & Drozdov 2011) from Alaska to southern California (Ebert et al. 1999). The lack of clear latitudinal patterns shows consistent resource allocation in this species. Although size structure varied, there were no regions along the coast where allocation was preferentially directed towards growth, so available space inside the test was not filled with gonads to the same extent as at other regions; large sea urchins have large gonads. Gonad development along the coast, as we have shown here, is consistent with these growth patterns. Both individual growth and gonad development appear independent of temperature changes associated with latitude, which is contrary to laboratory studies with *S. purpuratus* (Azad 2011) as well as other sea urchin species (e.g. Spirlet et al. 2000). Physiological responses of purple sea urchins to temperature show acclimation under laboratory conditions (e.g. Farmanfarmanian & Giese 1963, Ulbricht 1973), and Percy (1972, 1973) found seasonal acclimatization in both respiratory metabo-

lism and activity measured by the righting response of an inverted individual of the congener *S. droebachiensis*. Reaction norms of growth and gonad development can be similar across many degrees of latitude if food resources are available. Although many marine invertebrates show growth responses to latitude (e.g. Weymouth et al. 1931, Hall et al. 1974), others do not (e.g. Gilman 2006). Tarr (1995) showed a clear adaptive response to temperature adaptation in the field. We hypothesize that the lack of a latitudinal pattern in gonad development in *S. purpuratus* is a consequence of physiologically plastic adjustment to the latitudinal changes in temperature and so is similar to the lack of a latitudinal pattern of growth (Russell 1987, Ebert 2010).

Differences in the seasonal progression of benthic algal production and subsequent production of detritus along the coast provide environmental variation in addition to seasonal changes in temperature. The algal cycle in Oregon had a high summer standing crop followed by a breakdown during the fall and barren rocks in winter (Ebert 1968). Pearse (1981) and Rogers-Bennett et al. (1995) reported a similar pattern in central California where standing stocks of giant kelp accumulate in summer both as attached fronds and broken pieces but much of this is carried away by winter storms. In southern California, however, the seasonal variation is less, although an increase in summer and decline in winter has been reported (Basch & Tegner 2007). ZoBell (1971) showed seasonal variation in drift of algae and seagrasses on beaches in southern California over a 12 yr period (1945 to 1957). For total quantity, 27.4 % of drift mass was found from April through September and 56.3 % from November through February. The transition months of March and October had 16.1 %. Littler (1980) calculated seasonal means of percent cover of macrophytes for 10 sites in the California Bight but found a very slight lowering during winter months.

Differences in the latitudinal distribution of algal species along the coast also contribute to the differences in food types that are available. Point Conception is a breakpoint for groups of algal species (Abbott & Hollenberg 1976), and biomass is lower south of the point compared with sites to the north. Large laminarians and fleshy red algae are abundant north of Point Conception, but to the south, smaller fucoids and branched red algae are more abundant. We speculate that the availability of algae differs from north to south. Northern populations of sea urchins benefit from a large pulse of detritus in the fall that is followed by a lack of food during the win-

ter, whereas in the south, food is more evenly distributed throughout the year. However, such latitudinal measurements have not been made. Given differences in food type and seasonal availability, detrital pulses, and temperature differences, lack of a latitudinal trend in size-specific gonad size (Fig. 5) is an indication of substantial phenotypic plasticity in *Strongylocentrotus purpuratus*.

Comparing historical data at White Point to data from 2007 to 2009 is complicated by changes in water quality that have taken place since the dissections made by D. Leighton in 1966 and 1967. Extensions of the sewer outfall at White Point on the Palos Verdes Peninsula in Los Angeles were made in 1956, with a second larger extension in 1966, but emissions of effluent solids did not reach a peak until 1971, after which there was a dramatic drop due to improved treatment (Stull et al. 1996). Kelp cover off the Palos Verdes peninsula did not begin to recover until 1977 (Schiff et al. 2000). Historical data from sites on the Palos Verdes peninsula were all gathered while the area was still highly polluted; it is therefore important to note that intertidal samples from Cabrillo Beach gathered during 1966 to 1970 showed gonad development comparable to that of samples collected in 2007 to 2009. Pearse et al. (1970) speculated that sea urchins at White Point benefited from sewage. There are also sulfur springs in the intertidal at White Point, and bacterial production may contribute to sea urchin nutrition.

Reproductive studies of species that span edges as well as the middle portion of a geographic range contribute to understanding mechanisms that determine limits. We found no evidence for any latitudinal pattern for size-specific gonad production in *Strongylocentrotus purpuratus* and infer that reproductive output does not act as a mechanism for range limitation. Size structure, however, may be useful in identifying regions of particular significance for gamete production. Purple sea urchin populations along the southern and central coast of Oregon (Gregory Point/Sunset Bay and Boiler Bay) may be important sources of gametes, although it would have to be determined whether gametes released at these sites had an impact on recruitment anywhere along the coast. A lack of knowledge concerning connectivity of sites continues to represent a major unsolved problem in understanding ranges and limits. We have shown that gonad growth does not change with latitude and contribute to establishing the geographic range limits of *S. purpuratus*, and we have shown the importance of bottom-up forcing by ocean conditions on size-specific gonad development.

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