

Regional productivity predicts individual growth and recruitment of rockfishes in a northern California upwelling system

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Abstract

Recruitment of marine fishes is largely determined by biological and environmental factors acting on early-life stages. Subtle changes in larval condition in response to their environment can result in order-of-magnitude differences in year-class-strength. Overlap of larval production and favorable feeding conditions drives recruitment for many temperate marine fishes, but challenges associated with studying marine larvae have made it difficult to assess how environmental processes act on individual larvae to affect their growth and survival. We conducted a 2-yr study in an upwelling system to assess the influence of regional productivity, temperature, and larval condition in explaining growth in rockfishes (*Sebastodes* spp.). We employed otolith microstructure and satellite imagery to measure initial larval growth and estimate the productivity and temperature experienced by individuals to determine their relative importance in subsequent growth at metamorphosis. We compared model performance using indexed environmental conditions scaled over three different regions. In both years, net primary productivity explained the most variation in pre-metamorphic growth relative to temperature and initial growth. This relationship was consistent across spatial regions, although model fit was highest using indices scaled to the south continental shelf region. Recent settlement, juvenile recruitment, and individual growth were significantly higher in a year when productivity bloomed earlier and individual larvae experienced higher levels of productivity. Thus, this link between regional scale productivity, growth, and subsequent year-class strength supports the hypothesis that large-scale oceanographic processes stimulating upwelling and secondary production are primary drivers of larval growth and recruitment in rockfishes.

Understanding recruitment variability of marine fishes has been a major focus of fisheries scientists for over a century. For most temperate marine fishes, extreme variation in annual recruitment (broadly defined as the input of new individuals to populations following a pelagic larval period) makes it difficult to predict year-class strength with stock-recruitment relationships alone. Variable survival of marine larvae is likely the key driver of recruitment for many fishes. Small changes in larval condition in response to environmental conditions have survival consequences that can

generate order-of-magnitude differences in year-class strength (Bailey and Houde 1989; Houde 2008). Recruitment to adult populations is largely influenced by density-independent environmental factors acting on early-life stages (Houde 2009; Zabel et al. 2011), in addition to the density-dependent processes that may modify or regulate late-larval (Jenkins et al. 1991; Duffy-Anderson et al. 2002) and juvenile abundances (see review by Hixon and Webster 2002; Zabel et al. 2011).

Since Hjort's "critical-period" hypothesis (1914), there have been a number of hypotheses regarding the conditions conducive to larval growth and recruitment. One of the most prominent of these is the "match-mismatch" hypothesis (Cushing 1974, 1990), which predicts that the timing of larval production relative to zooplankton abundance (or the overlap of larval durations with optimal feeding conditions)

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is the principal factor influencing larval survival. Recent evidence suggests small first-feeding larvae may be particularly sensitive to starvation by reduced feeding success (China and Holzman 2014). Theory and observation also provide evidence that the mortality of early life stages is size-specific and primarily a consequence of predation (Bailey and Houde 1989; Sogard 1997; Perez and Munch 2010). Thus, large size or rapid growth improve the likelihood of survival whereas small size or slow growth increase predation risk, either directly through size-dependent predation or indirectly through longer pelagic larval durations (Miller et al. 1988; Sogard 1997). The approach to testing these hypotheses has primarily been through mathematical modeling (Biktashev et al. 2003; James et al. 2003; Burrow et al. 2011; Zabel et al. 2011) and long-term studies of interannual recruitment variation relative to large-scale environmental conditions (Platt et al. 2003; Miller and Sydeman 2004; Ware and Thompson 2005; Ralston et al. 2013). Few studies, however, have evaluated how biologically relevant scales of oceanographic processes act on individual larvae (Meekan et al. 2003).

There are multiple biological and environmental factors that influence larval growth and stage duration. For many species, parental age and condition can have a strong influence on egg quality and larval condition, potentially influencing larval growth for several weeks post-hatch (Berkeley et al. 2004; Green and McCormick 2005; Sogard et al. 2008). Although there is considerable variation in the degree of maternal investment, the environment that larvae encounter can also have substantial impacts on growth and metamorphosis. For example, temperature may positively or negatively affect growth through changes in metabolism (Blaxter 1991; Takasuka et al. 2007; Comerford et al. 2013). In addition, the degree of overlap between larval production and spring productivity likely has a strong influence on growth and recruitment (Platt et al. 2003; Burrow et al. 2011; Kristiansen et al. 2011; Siddon et al. 2013). Several studies in the upwelling system along the west coast of the U.S.A. have found that year-class-strength is best predicted by the oceanographic patterns occurring during larval production and the early larval phase (Ralston and Howard 1995; Caselle et al. 2010b; Ralston et al. 2013), particularly conditions that influence upwelling and productivity. The underlying mechanism driving growth, however, is not fully understood because the relative contributions of multiple processes are rarely assessed. The primary objective of our study was to address this gap in knowledge and compare the relative importance of biological and environmental factors that might affect growth during the larval stage.

In this study, we use two rockfishes (genus *Sebastodes*) as model organisms to identify the primary drivers of larval growth. Rockfishes are well suited to investigate the relative importance of influential biological and environmental processes because they have a high degree of maternal investment (Sogard et al. 2008) and year-class strength appears to

be determined during the larval stage (Ralston and Howard 1995; Ralston et al. 2013). In addition, rockfishes inhabit a dynamic system in which ocean currents and food supply vary within and across years. There have been a number of studies correlating environmental conditions to pelagic juvenile abundance and juvenile recruitment of rockfishes. The main findings of these studies are that year-class strength is determined during the early larval phase and annual pelagic juvenile abundance is correlated with sea-level anomaly (an indicator of transport) and upwelling strength (Ralston and Howard 1995; Laidig et al. 2007; Ralston et al. 2013). In near shore surveys of recently settled rockfishes, there has been general synchrony in the annual abundance of rockfishes with a range of life history traits (Caselle et al. 2010aa,b; Jones and Mulligan 2014). Similarly, analyses of long-term mid-water trawl surveys targeting winter-spawning rockfishes have found synchrony among species in the size composition and annual abundance of pelagic juveniles (Ralston et al. 2013), suggesting that the drivers of growth and survival during early life-stages are common across many rockfish species and primarily sourced to large-scale density-independent environmental processes.

Our complementary approach in this study was to sample recently settled rockfishes over 2 yr and use otolith microstructure analysis to measure larval traits. We then used a multiple regression approach to determine how oceanographic conditions (as experienced by individual larvae) and early individual growth may influence growth near metamorphosis. To gain insight into the predictive power of remotely sensed oceanographic data, we compared model performance using indexed environmental conditions scaled over three different continental shelf regions, where new recruits may have undergone larval development (Petersen et al. 2010). We compared differences in annual juvenile recruitment, recent settlement, and growth and age at metamorphosis. We predicted that larval growth would be affected primarily by productivity and that interannual differences in recruitment and larval characteristics would be consistent with environmental differences between years.

Methods

Study system and species

We conducted this study in Bodega Bay, California, U.S.A., a region of strong and persistent upwelling with blooms in productivity during spring and summer. Temperature and productivity vary seasonally and annually, making this region well suited to evaluate influence of environmental variability on marine larvae. Rockfishes are abundant and ecologically important with species ranging from Baja to Alaska. Rockfishes are viviparous (Boehlert and Yoklavich 1984), with gestation periods of 30–40 d prior to parturition. Extruded larvae are approximately 4–6 mm, free swimming, and capable of capturing copepod nauplii prey (Love et al.

2002). The rockfishes (subgenus *Pteropodus*) used in this study were the copper rockfish (*S. caurinus*) and gopher rockfish (*S. carlsoni*), two nearshore species of rockfish that are evolutionarily closely related and difficult to identify to species in early life stages. Parturition occurs from December to March for copper rockfish and from March to late May for gopher rockfish (Echeverria 1987; Love et al. 2002). Pelagic larval durations last ~ 50–95 d, after which larvae metamorphose into juveniles of 15–25 mm standard length, and subsequently settle to demersal habitat (Love et al. 2002). Metamorphosis occurs 0–14 d prior to settlement (Wheeler 2015). The pelagic larval durations of these demersal rockfishes are shorter than those of deeper water shelf- or slope-associated species. Consequently they settle at smaller sizes (Love et al. 2002), which highlights the potential for these demersal species to have different experiences and responses to environmental conditions. Although the timing of parturition varies in copper and gopher rockfishes, their pelagic larval durations exhibit considerable overlap in northern California (Echeverria 1987; Love et al. 2002) and they have similar depth distributions as larvae (Lenarz et al. 1995). In addition, these species have strong morphological and genetic similarities (Narum et al. 2004). These species likely have similar larval trajectories and responses to environmental conditions as a result of these shared characteristics (Petersen et al. 2010). We tested whether species-specific traits were likely to confound our results and found that when our analysis was restricted to a single species, the results were generally consistent with the full dataset (see Supporting Information A). For these reasons, and to maintain consistency with other studies (Caselle et al. 2010a,b; Jones and Mulligan 2014), both species were included in our analyses. This approach also broadened the range of environmental conditions over which we evaluate larval traits.

Sampling protocol

Recently settled rockfishes were collected in two eelgrass beds located within Bodega Harbor, California. Collections occurred ~ weekly from April to August in 2010 and 2011 and for 3 months in 2012 (Fig. 1). No fish were caught in 2012, thus limiting our analysis to 2 yr. On each collection day, a 5-m long × 1.5-m deep beach seine was towed along two 8 m transects within each bed, after which rockfish were identified, enumerated, and measured. A subset of up to 25 live individuals was transported to the Bodega Marine Laboratory, University of California, Davis. We used coloration and size limits to confirm identifications and ensure that collected fish were recently settled (< 30 mm and within ~ 1 week) (Anderson 1983). Fish were subsequently euthanized using a concentration of 300 mg/L MS-222 and frozen until further analysis. Annual recruitment was measured as the abundance of surviving juveniles (> 30 mm) in a survey at the end of the sampling period (3rd September in 2010 and on 28th August in 2011) using the same survey protocol.

Catch-per-unit-effort (CPUE) was calculated as the total catch of recent settlers or surviving juveniles per beach seine tow per sampling day. All handling procedures adhered to University of California, Davis Institutional Animal Care and Use Committee standards (Protocol No. 16448).

Otolith analysis

Sagittal otoliths were extracted and mounted on glass slides in Crystalbond LT Mounting Wax (Buehler Brand, Illinois Tool Works, Lake Bluff, Illinois, U.S.A.). A right or left otolith was randomly selected and sanded in the sagittal plane to reveal daily growth rings. Deposition of daily growth bands has been validated for several larval rockfishes (Yoklavich and Boehlert 1987; Laidig and Sakuma 1998) and we assumed daily growth bands in these rockfishes. Otoliths were subsequently photographed using a Lumenera Infinity 2-3C CCD camera (Lumenera Corporation, Ottawa, Ontario, Canada) and images were analyzed using Image Premier 7.0 software (Media Cybernetics, Rockville, Maryland, U.S.A.) for a total of 209 samples (Table 1).

Otolith microstructure analysis was used to determine age, parturition date, age and size at metamorphosis, and initial and pre-metamorphic growth (see Fig. 2). Age and parturition date were measured by counting the number of growth bands from the extrusion mark (parturition) to the edge of the otolith. Age at metamorphosis was calculated by counting the number of growth bands from the extrusion mark to the onset of the second accessory primordia, which marks metamorphosis (Laidig 2010). Size at metamorphosis was calculated by measuring the total distance from the core to the onset of the second accessory primordia. We found a strong, positive relationship between fish size (standard length) and otolith radius ($r^2 = 0.82$, $F_{1,82} = 373.71$, $p < 0.0001$), which provides the basis for predicting size at metamorphosis using otolith measurements. Mean daily growth for the first 10 d post-extrusion was estimated to index the initial condition of individuals (or “initial growth”), which we assume is at least in part influenced by parental investment (Berkeley et al. 2004). Pre-metamorphic growth (hereafter referred to as “growth”) was calculated by averaging the first 10-increment widths prior to the onset of the second accessory primordia and represents growth at the larval-juvenile transition. All otolith measurements correspond to explicit and relevant time-periods during the life history of each fish. Fish caught on the same day exhibit independent growth measurements because the day of metamorphosis and, therefore, the pelagic larval duration and date-range over which measurements occurred, is unique to each individual (Fig. 2). All otolith measurements were taken in the dorsal region, with transects beginning at the furthest distance from the core and subsequent measurements taken on a linear transect intersecting with the otolith core. This protocol ensures that increment widths reflect growth and not spatial variation in otolith morphology. To reduce

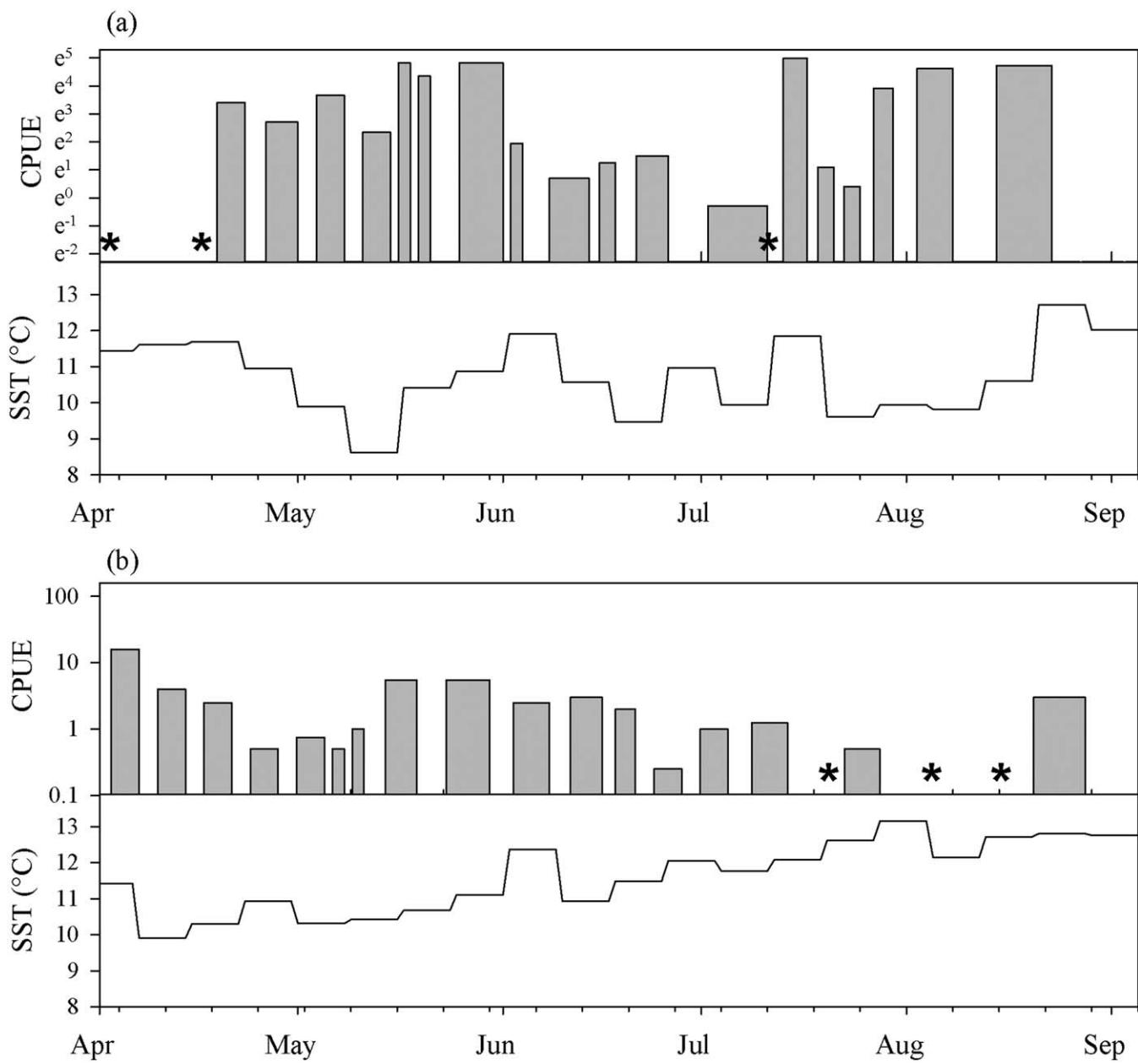


Fig. 1. Catch-per-unit-effort of recent settlers (gray bars) and “total shelf” sea surface temperature (SST) in 2010 (**a**) and 2012 (**b**). Asterisks indicate sampling dates when no recent settlers were caught (catch-per-unit-effort = 0).

measurement error, all observers were blind to sample identification, and an average of two measurements was used for each sample. Otoliths were removed from analysis if damaged during sample preparation.

Estimation of environmental conditions

We used data products produced from the Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua and Terra sensors. Sea surface temperature (SST; 1 km spatial scale resolution: website: http://spg.ucsd.edu/Satellite_data/California_Current/) and net primary productivity (NPP; 1/12° spatial

scale resolution; website: <http://www.science.oregonstate.edu/ocean.productivity>) were assessed in discrete 8-d time bins to estimate the environmental conditions experienced by individual larvae. We acknowledge that there are challenges to remote sensing in coastal marine systems (Santer and Schmechtig 2000; Toole and Siegel 2001). However, we found no anomalous patterns in model pixels close to the coast that deviated from the observed regional patterns. NPP products were calculated by a vertically generalized production model outlined by Behrenfeld and Falkowski (1997). For each time bin, SST and NPP values were averaged over the

Table 1. Monthly otolith sample size and average standard length (mm) of samples used in multiple regression analyses.

Month	2010		2011	
	n	SL	n	SL
April	19	22.2	21	24.8
May	29	24	25	25
June	25	26.9	33	27.4
July	17	27.5	7	27.6
Aug	18	26.6	15	26.3
Total	108		101	

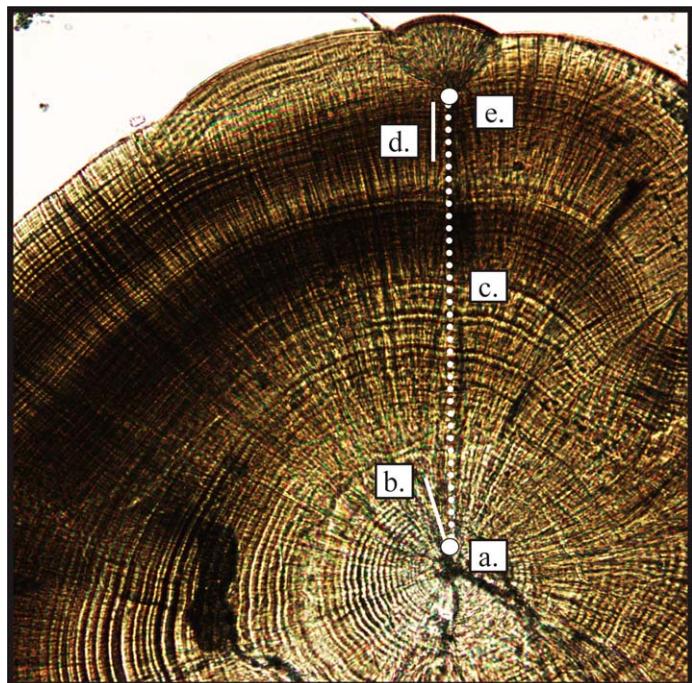


Fig. 2. Measurements of otolith microstructure: parturition date (**a**), early growth (**b**), the region of otolith growth that represents the pelagic larval duration, age and size at metamorphosis, and the date range over which sea surface temperature and NPP (before 24-d lag) are averaged for each fish sample (**c**), pre-metamorphic growth (**d**), metamorphosis date (**e**).

continental shelf (140 m isobath), extending 200 km north and south of the collection site in Bodega Harbor. (“total shelf” spatial region, Fig. 3). There is sufficient oceanographic evidence to assume larvae are primarily retained within the continental shelf and alongshore transport is likely within 200 km north or south of settlement sites (Miller and Shanks 2004; Petersen et al. 2010), qualifying this spatial scale as ecologically relevant. In our analysis, we compared three spatial regions over which environmental indices were averaged: the “total shelf” (defined above), north shelf, and south shelf. We defined the north shelf and south shelf

spatial regions as the continental shelf area extending either 200 km north (“north shelf”) or south (“south shelf”) of Bodega Harbor.

In our analysis, we estimated the temperature and food supply experienced by individuals by averaging SST and NPP over the dates associated with larval durations for each fish at each spatial region. These temperatures were calculated by taking the weighted average of SST from the dates of parturition to metamorphosis, which correspond to pelagic larval duration (Fig. 2). The food supply expected to be encountered by individual larvae was indexed in a similar fashion, using NPP lagged by 24 d, which is an ecologically relevant time lag for primary productivity to translate into zooplankton abundance (Botsford et al. 2003). This approach measures these environmental factors (SST and NPP) as they affect individual larvae, while also scaling these factors to appropriate temporal (pelagic larval duration) and spatial scales (continental shelf scaled explicitly to the region adjacent to the collection site). Given the 24 d temporal lag between calculated NPP and SST indices, we conclude it is valid to assume that these factors are independent. Similarly, given that we use independent measures of SST and NPP for each fish, these factors do not represent time-series datasets.

In an effort to verify the effectiveness of NPP as an index of larval food supply, we compared NPP to zooplankton biomass near our study region (see Supporting Information B). We compared the performance of sea surface chlorophyll and NPP values to predict measured zooplankton biomass from California Cooperative Oceanic Fisheries Investigation survey data (<http://www.data.calcofi.org/publications/calcofi-data-reports.html>) between 37°N and 40°N and in years 1983–2013. In summary, a cross-correlation analysis revealed that NPP lagged three 8-d time steps (total of ~24 d) exhibited the highest significant *r* value (*r*=0.47, *p*<0.001) and was therefore selected to index food supply.

We conducted a correlation analysis between parturition date and individual larval NPP values for each year to determine whether NPP reflects the seasonal timing of larval release in addition to the overlap with favorable feeding conditions. This established the relationship between seasonal productivity and seasonal timing of birth.

Statistical analyses

We used a multiple regression approach to determine the primary driver of growth at the larval-juvenile transition. The independent factors in this study (initial growth, SST, and 24-d lagged NPP) were linearly correlated and exhibited elevated Variance Inflation Factors (VIF) in full regression models at the total and south spatial regions in 2010 (Tables 2–4). To manage multicollinearity in these two instances and maintain an unbiased comparison of the variance explained by these factors, we employed a statistical analysis using a combination of three approaches following recommendations by Neter et al. (1996). The relative importance

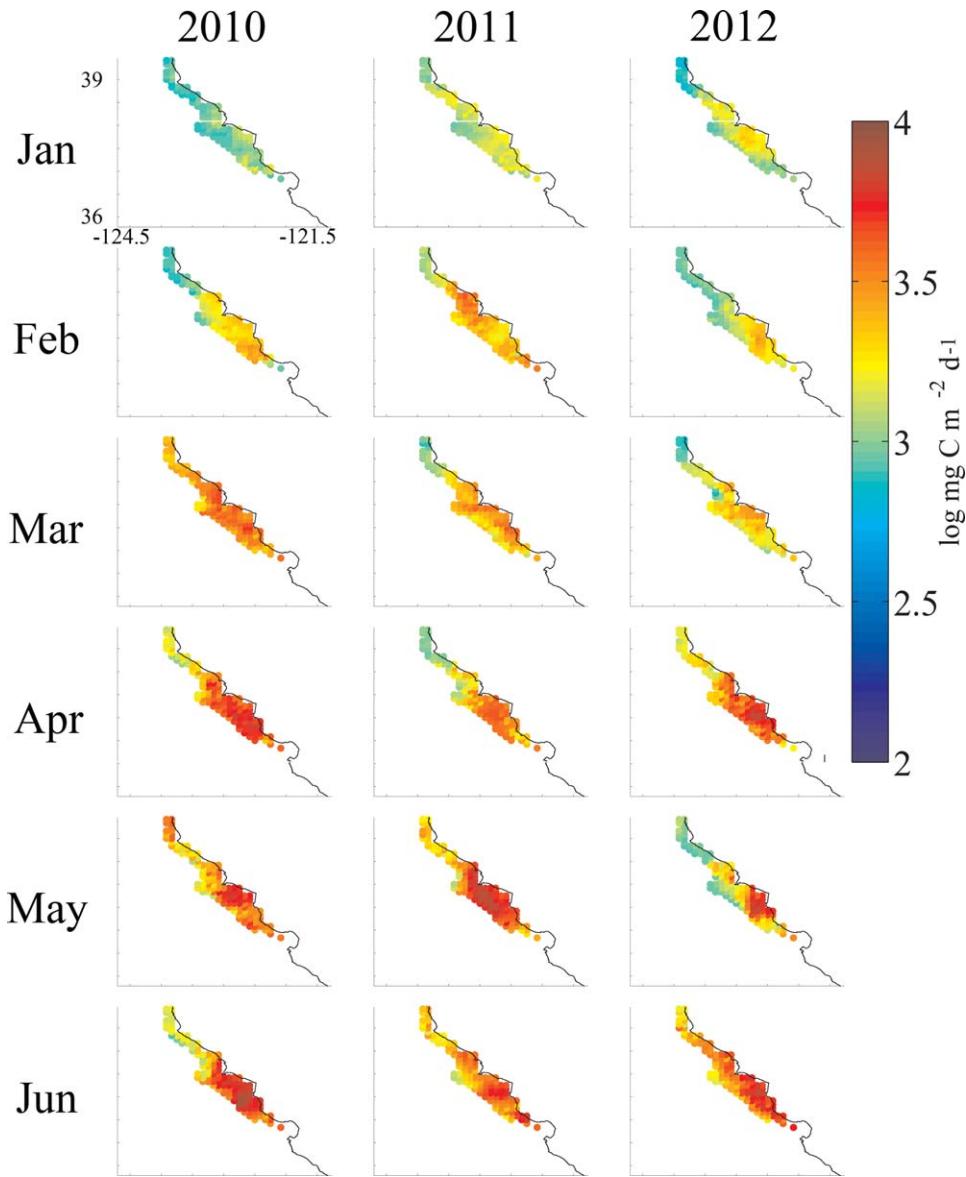


Fig. 3. Monthly net primary productivity ($\log \text{mg C m}^{-2} \text{d}^{-1}$) in 2010, 2011, and 2012 along the continental shelf (140 m isobath) or “total shelf” in our study region.

of independent factors was evaluated by comparing model fit among a full multiple regression, individual bivariate regressions, and a step-forward type I sums of squares (SS) regression. In the full multiple regression model, initial growth, SST, and NPP were used as independent factors to explain growth. Individual bivariate regressions were conducted between each independent factor and growth. The step-forward Type I SS regression was conducted in sequential bivariate regressions. First, we used coefficients of determination (r^2) to determine the best-fit bivariate individual predictor, identified as NPP in all cases. Residuals from this model, Type I SS, were used as the dependent variable in a subsequent regression with the factor exhibiting the second highest bivariate regression r^2 value,

which was SST in all models. In the final step, initial growth was regressed against the Type I SS from the second step in the regression. Data were log-transformed and met the assumptions of normality and homoscedasticity. Assumptions were tested using Levene’s test for equal variances and a Shapiro-Wilk test of normality for residuals binned across values of independent variables. Residuals were also evaluated visually and in probability plots following Neter et al. (1996). We determined that a multiple linear regression was an appropriate analysis because we found no evidence of non-linear relationships in growth. The distributions of residuals were normal across the domain for each independent variable when related to growth in a bivariate regression.

Table 2. Pearson product-moment correlations (r) among independent factors measured along the total continental shelf, south shelf, and north shelf in 2010 and 2011.

Variable pairs	2010			2011		
	Total shelf	South shelf	North shelf	Total shelf	South shelf	North shelf
NPP and SST	-0.799	-0.799	-0.587	0.287	0.331	0.321
NPP and initial growth	0.222	-0.207	0.276	-0.120	-0.140	0.010
SST and initial growth	-0.162	-0.161	-0.164	0.152	0.120	0.212
NPP and parturition date	0.867	0.858	0.770	0.914	0.903	0.858

Table 3. Full multiple regression, individual bivariate regressions, and step-forward type I sums of squares regression models, with net primary productivity (NPP), sea surface temperature (SST) initial growth as sources of variation for pre-metamorphic growth in 2010. Predictor variables SST and NPP scaled to the total shelf.

Model type (dependent variable)	Sources of variation	VIF	Std. slope	F	p	r^2	AIC
Full regression (Log growth)	Total model			16.53	<0.001	0.323	-229.8
	NPP	2.83	0.3		0.029		
	SST	2.76	-2.85		0.036		
	Initial growth	1.05	0.055		0.509		
Individual regression (Log growth)	NPP		0.54	43.55	<0.001	0.291	-228.9
	SST		-0.533	42.11	<0.001	0.284	-227.8
	Initial growth		0.168	3.08	0.082	0.028	-194.8
Type 1 SS regression (Log growth residuals)	SST		-0.121	1.59	0.211	0.015	-230.5
Type 1 SS regression (SST residuals)	Initial growth		0.037	0.15	0.703	0.001	-230.6

VIF, variance inflation factor.

Table 4. Full multiple regression, individual bivariate regressions, and step-forward type I sums of squares regression models, with net primary productivity (NPP), sea surface temperature (SST) initial growth as sources of variation for pre-metamorphic growth in 2010. Predictor variables SST and NPP scaled to the south shelf.

Model type (dependent variable)	Sources of variation	VIF	Std. slope	F	p	r^2	AIC
Full regression (Log growth)	Total model			16.27	<0.001	0.319	-229.3
	NPP	2.82	0.329		0.017		
	SST	2.77	-0.25		0.066		
	Initial growth	1.05	0.059		0.474		
Individual regression (Log growth)	NPP		0.542	44.03	<0.001	0.293	-229.2
	SST		-0.523	39.93	<0.001	0.274	-226.2
	Initial growth		0.168	3.08	0.082	0.028	-194.8
Type 1 SS regression (log growth residuals)	SST		-0.107	1.24	0.269	0.012	-230.5
Type 1 SS regression (SST residuals)	Initial growth		0.049	0.26	0.613	0.002	-230.7

VIF, variance inflation factor.

Model fit was evaluated using r^2 values and Akaike's Information Criterion (AIC). We compared AIC and AIC corrected for small samples sizes (AICc), and found negligible differences in their values for all models run in our analysis, which indicated sample size had a negligible effect on AIC. This finding confirmed AIC as an appropriate measure of model fit (Burnham and Anderson 2002). Regression models

were conducted for each year and spatial region separately to reveal if the primary driver of growth differed between years and spatial region. All statistical analyses were conducted using SYSTAT 12 software (2007, SYSTAT Software, ver. 12.02.00).

Interannual differences in larval traits were compared using analysis of covariance (ANCOVA). Growth was

Table 5. Full multiple regression, individual bivariate regressions, and step-forward type I sums of squares regression models, with net primary productivity (NPP), sea surface temperature (SST) initial growth as sources of variation for pre-metamorphic growth in 2010. Predictor variables SST and NPP scaled to the north shelf.

Sources of variation	VIF	Std. slope	F	p	r ²	AIC
Total model			14.23	<0.001	0.291	-224.8
NPP		0.185		0.081		
	1.61					
SST		-0.396		<0.001		
	1.53					
Initial growth		0.052		0.547		
	1.08					

VIF, variance inflation factor.

compared between years using “total shelf NPP” as a covariate. Annual differences in mean age at metamorphosis were evaluated using ANCOVA with size at metamorphosis as a covariate. Adjusted means were compared between years using Student–Newman–Keuls pairwise comparison tests for the factor year. Assumptions of ANCOVA were evaluated for residuals within each year using the same method described for regression analyses in combination with testing for equal slopes. Parallelism was determined by testing for the presence of a significant interaction between the factor year and the covariate using generalized linear models and confirmed by negligible changes to r^2 and AIC values with and without the interaction term. Annual abundance of recent settlers was calculated as mean CPUE and compared between years using a two-sample Z-test used for heterogeneous variances between groups. Annual recruitment was measured by the CPUE of surviving juveniles from surveys on 3rd September in 2010 and 28th August in 2011 ($n = 1$ survey per year).

Results

Recent settlers were collected ~weekly from eelgrass beds in Bodega Harbor, California (Fig. 1). We found a strong correlation between parturition date and NPP in both years (Table 2), establishing the relationship between seasonal timing of birth and seasonal timing of productivity. Correlation analysis identified multicollinearity among the three independent factors in our study (Table 2). At all spatial regions, there was a strong negative correlation between NPP and SST in 2010 and a weaker positive correlation in 2011. Initial growth ($\mu\text{m d}^{-1}$ of otolith growth) was weakly correlated with the other factors and there were no consistent relationships across years or spatial region.

Of the three factors measured, NPP was a consistent predictor of growth ($\mu\text{m d}^{-1}$ of otolith growth) in both 2010 and 2011. NPP exhibited a positive relationship with growth

Table 6. Full multiple regressions scaled to the total shelf, south shelf, and north shelf with net primary productivity (NPP), sea surface temperature (SST) and initial growth as sources of variation for pre-metamorphic growth in 2011.

Model	VIF	Std. slope	F	p	r^2	AIC
Total shelf			5.87	0.001	0.154	-190.2
NPP	1.12	0.374		<0.001		
SST	1.13	-0.261		0.01		
Initial growth	1.05	-0.009		0.928		
South shelf			5.94	0.001	0.155	-190.4
NPP	1.17	0.4		<0.001		
SST	1.16	-0.238		0.020		
Initial growth	1.05	-0.009		0.923		
North shelf			5.12	0.002	0.137	-188.2
NPP	1.12	0.241		0.017		
SST	1.17	-0.362		0.001		
Initial growth	1.05	0.019		0.844		

VIF, variance inflation factor.

and explained the greatest amount of variability in 2010 and 2011 at the “total shelf” and “south shelf” spatial regions (Tables 3–6; Fig. 4). NPP had the highest predictive ability of growth when averaged over the “south shelf,” with negligible differences in r^2 values and AIC when scaled to the “total shelf” (Tables 3, 4). In addition to NPP, SST exhibited a negative effect on growth in the full and bivariate regressions, but this relationship was absent in 2010 when multicollinearity with NPP was taken into account in the step forward Type 1 SS regression models. Of the remaining factors, SST explained more variation in growth relative to initial growth. Initial growth did not predict pre-metamorphic growth in any model tested. Models scaled over the “south shelf” described the most variation in growth, although the “total shelf” scale r^2 and AIC values were very similar.

Larval traits and abundance differed between years. Pre-metamorphic growth differed annually after correction for NPP (Table 7; Fig. 4). Adjusted mean growth was higher in 2010 than in 2011 (Student–Newman–Keuls adjusted means for log(growth) 0.744 and 0.709, respectively). We found no significant interaction between NPP and log(pre-metamorphic growth); there were negligible changes to AIC ($\delta\text{AIC} = 0.791$) and r^2 values ($\delta r^2 = 0.01$) with and without the interaction term. We found no significant interaction between size at metamorphosis and age at metamorphosis; there were negligible changes to AIC ($\delta\text{AIC} = 0.005$) and r^2 values ($\delta r^2 = 0.00$) with and without the interaction term. We were unable to compare adjusted mean age at metamorphosis due to heterogeneous variances of residuals between years. The variance in age at metamorphosis was two times higher in 2011 relative to 2010 ($F_{1,186} = 0.344$, $p < 0.001$; residual $s^2 = 0.002$ and 0.004, respectively), which was primarily driven by the presence of many older fish in 2011 (Fig. 4). Average CPUE of

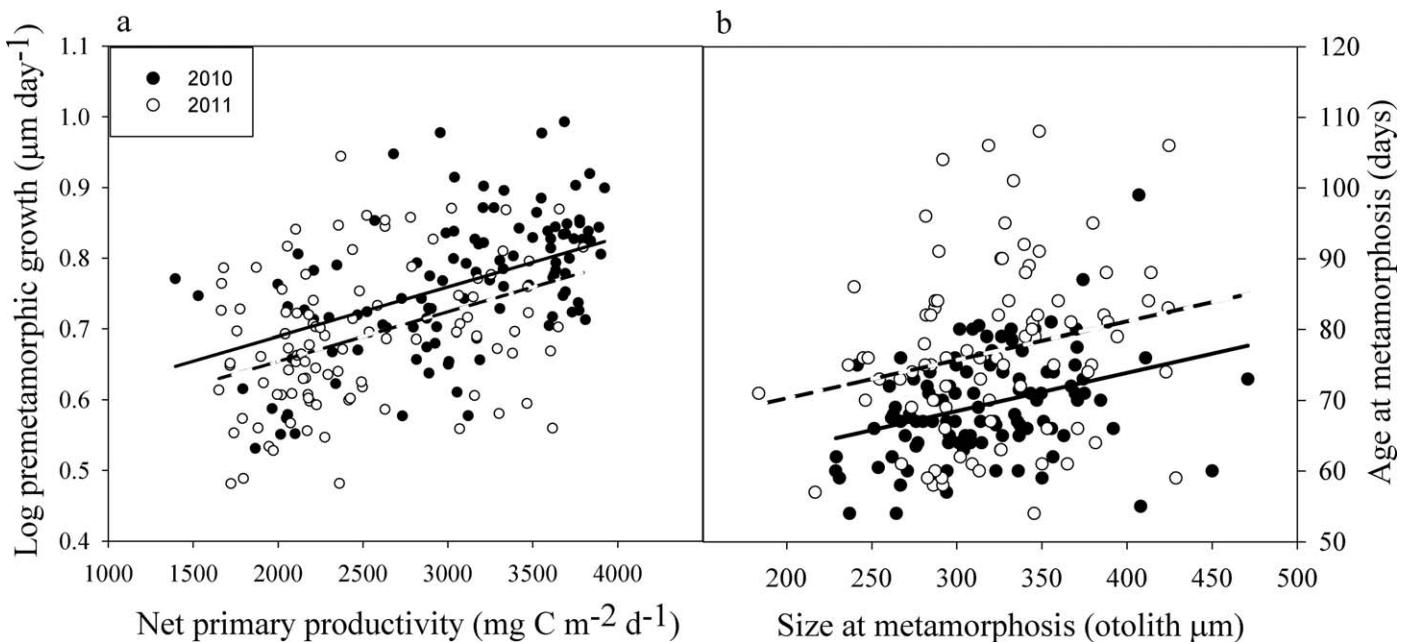


Fig. 4. Relationship between (a) net primary productivity (“total shelf” NPP) and pre-metamorphic growth (otolith increment width, $\mu\text{m}/\text{d}$) and (b) size at metamorphosis (otolith radius μm) and age at metamorphosis in 2010 (filled circles, solid line) and 2011 (open circles, dashed line).

Table 7. ANCOVA results for pre-metamorphic growth and age at metamorphosis, with year as the main factor and net primary productivity (NPP) or fish size as covariates, respectively.

Dependent variable	Sources of variation	df	F	p	Model r^2
Log (growth)	Year	1	6.663	0.011	0.291
	NPP	1	45.962	<0.001	
	Error	206			
Log (age at metamorphosis)	Year	1	25.353	<0.001	0.164
	Size	1	13.724	0.003	
	Error	186			

recent settlers was higher in 2010 than 2011 (Fig. 1, $Z = 3.187$, $p < 0.001$, $df = 1$) and no individuals were caught from April through June in 2012. Juvenile recruitment was higher in 2010 relative to 2011 (CPUE: 03 September 2010 = 67.25 and 28 August 2011 = 1.5).

Discussion

This study provides evidence that regional productivity drives growth and recruitment of rockfishes. In both years, net primary productivity, an index of zooplankton biomass, explained more variation in individual growth relative to temperature and initial growth. The seasonal timing of reproduction was strongly related to productivity in each year. In addition, both settlement and recruitment were

significantly higher in 2010 when productivity occurred earlier in the season, thereby increasing the overlap of pelagic larval durations with optimal feeding conditions. The extent that larvae experienced favorable feeding conditions (i.e., higher NPP) predicted growth and survival potential of rockfishes, which is consistent with “match-mismatch” dynamics. These results support the hypothesis that large-scale oceanographic processes that stimulate upwelling and secondary production are key drivers of larval growth and subsequent year-class-strength in rockfishes. Long-term records of annual juvenile recruitment, coastal oceanography, and the size and abundance of pelagic juvenile rockfish are consistent with these findings (Ainley et al. 1993; Laidig et al. 2007; Ralston et al. 2013; Jones and Mulligan 2014).

The effect of biological and environmental factors acting on individual larvae is understudied in wild fish populations, primarily due to logistical challenges in measuring the environmental conditions experienced by individuals within a season. This study compared the relative importance of both biological and environmental factors in predicting growth using a multiple regression approach. NPP exhibited a consistent positive relationship to growth relative to other factors, which demonstrates that favorable feeding conditions play a key role in determining rockfish larval growth.

We identified strong explanatory power of SST in 2011 and in the 2010 bivariate models and those scaled to the “north shelf,” with SST consistently exhibiting a negative relationship to growth. The strong negative correlation (multicollinearity) between NPP and SST in 2010 is not surprising in this system as upwelling brings cold nutrient-rich waters

to the surface and stimulates productivity. In 2011, however, we found a weaker positive correlation between NPP and SST and found that SST, generally, increased throughout the season, with considerably warmer temperatures in the late summer. A negative relationship between SST and growth could be a result of physiological stress from warmer temperatures (Takasuka et al. 2007), even though the range of temperatures experienced by individuals for any spatial region was minimal in this study (minimum SST = 9.62°C, maximum SST = 12.3°C) and the range did not exceed a difference of 1.5°C with any model. Although it is possible that temperature may have reduced growth via physiological stress, the negative relationship between SST and growth may also reflect an indirect effect through environmental conditions associated with upwelling and productivity. The SST r^2 values < 0.02 from 2010 Type I SS regression models indicates that SST explains relatively little variation in growth after NPP has been taken into account, suggesting that SST is likely reflective of upwelling driven productivity.

The negative relationship between SST and growth may also reflect changes in prey quality associated with temperature. In this system, temperature can influence the species composition of zooplankton, with lipid-rich copepods associated with colder waters and lipid-poor copepods associated with warmer waters (Peterson et al. 2014; Fontana et al. 2016). Additionally, the presence of lipid-rich copepods has been shown to explain up to 42% of the variability of rockfish recruitment in the central California Current (Peterson et al. 2014), highlighting the potential for SST to indirectly affect growth and survival via changes to feeding conditions. The negative relationships found between SST and growth in this study suggests that prey composition may have differed seasonally or annually. SST was higher in 2011 relative to 2010, particularly during the summer (Bjorkstedt et al. 2011, 2012; Jones and Mulligan 2014). Unfavorable environmental conditions and possibly lower prey quality in 2011 may have resulted in a weaker relationship between NPP and growth, slower overall growth relative to 2010, and reduced recruitment. Conversely, colder temperatures in 2010 may have favored a lipid-rich prey community (Peterson et al. 2014; Fontana et al. 2016), which may have benefitted growth and survival of rockfishes in 2010. Although the NPP index was unable to directly capture differences in prey quality, the relationships among intra- and inter-annual patterns in SST, NPP, and growth suggest that coastal oceanography, productivity and prey composition are related processes affecting growth and survival in larval rockfishes. Future studies would benefit from field observations of prey density and quality in combination with regional indices of environmental conditions to evaluate these complex relationships.

The underlying mechanisms driving growth in larval fish are not fully understood in marine systems because the relative contributions of multiple factors are rarely assessed. Previous studies have evaluated the drivers of larval growth

using mathematical models (Pitchford et al. 2005; Burrow et al. 2011), laboratory experiments (Berkeley et al. 2004), and by correlating biological or environmental parameters to larval traits (Meekan et al. 2003; Baumann et al. 2006; Takasuka et al. 2007; Shima and Sweare 2009; Comerford et al. 2013; Paulsen et al. 2014). Our study contributes to the limited number of studies comparing the relative effects of initial condition, temperature, and food availability on individual larval growth in the marine environment (Meekan et al. 2003). A strength of this study is its ability to measure biological and environmental factors as they affect individual larvae, measuring these at appropriate temporal scales (pelagic larval duration) and spatial scales (continental shelf scaled to the region adjacent to collection site), and linking these factors to growth at an explicit and relevant time-period during the life history of each fish (at the larval-juvenile transition).

Understanding the spatial region at which oceanographic processes influence larval growth provides valuable insight into the scale that environmental conditions influence larval traits. The relationship between NPP and pre-metamorphic growth was consistent in all spatial regions, with small differences in model fit between the "total shelf," "south shelf," and "north shelf regions." These results identify a measurable effect of coastal oceanographic processes on larval traits at a spatial scale of 200–400 km, providing evidence that growth is related to regional patterns in productivity. NPP had the highest predictive ability of growth when averaged over the "south shelf," with negligible differences in r^2 values and AIC when scaled to the "total shelf." Although differences in model fit among spatial regions were small, these results align with model estimates of larval dispersal trajectories in Northern California. In this region, northward movement and south-shelf residencies of rockfish larvae are consistent with predictions for larvae released at all depths in the winter and depths ≥ 20 m in the spring (Petersen et al. 2010). An improvement to model fit scaled to the "south shelf" is expected if model predictions reflect natural larval distributions. Although the geographic origins of larvae used in this study are unknown, the comparison of model fit among spatial regions improves our understanding of the scale at which oceanographic processes can have a measurable effect on larval growth. An analysis that compares indices scaled over a broader range of spatial scales, such as local, regional and basin scales, is needed to adequately determine the explicit scale at which oceanographic processes affect growth.

Identifying how biological and environmental processes act on individual larvae is an important step in understanding variation in larval condition and recruitment. Here, we establish a link between parturition date, food supply, larval growth, recent settlement, and juvenile recruitment (year-class-strength) through intra- and interannual comparisons of larval traits. Annual growth and age at metamorphosis

reflects differences in NPP. Average growth was higher in 2010 when NPP experienced by individuals was higher overall and occurred earlier in the year. The benefits to growth from higher productivity appear to be consistent through space and time, as the relationship between NPP and pre-metamorphic growth was similar across years and spatial regions. Although we were not able to directly compare adjusted mean age at metamorphosis, we detected higher variance in age in 2011 when more fish were older. Hence, larvae in 2010 may have been competent to metamorphose at a younger age presumably due to faster growth and favorable feeding conditions (Pechenik 2006). In addition, poor feeding conditions in 2011 may have resulted in slower growth, delayed metamorphosis, and thus, older fish at metamorphosis. The negative effects of environmental conditions on growth and delayed metamorphosis may also explain lower recruitment in 2011. Given the variability in age at metamorphosis, a longer time series is needed to fully evaluate interannual patterns for this trait.

There is ample evidence that even small changes in larval condition can influence juvenile survival (Bergenius et al. 2002; Jenkins and King 2006; Johnson 2008) and recruitment (Jenkins and King 2006; Kristiansen et al. 2011; Payne et al. 2013). Overall, CPUE of both recent settlers and juveniles was almost an order of magnitude higher in 2010 relative to 2011, which is consistent with measured and reported differences in productivity and the abundance of pelagic juvenile rockfishes (Bjorkstedt et al. 2010, 2011, 2012; Jones and Mulligan 2014). The “extraordinarily successful” breeding season for most seabirds in the Gulf of the Farallones in 2010 was attributed to notably high productivity and abundance of pelagic juvenile rockfishes (Bjorkstedt et al. 2011). Similarly, reduced breeding success in 2011 relative to 2010 was attributed to poor ocean conditions and lower abundance of juvenile rockfishes in the same region (Warzybok and Bradley 2011). High levels of NPP were detected 1 month earlier in 2010, which overlaps with the pelagic larval duration for the majority of individuals collected. In addition, no recently settled fishes were collected in 2012 from April through June when productivity was lower and bloomed later in the season relative to 2010 and 2011. Weaker and delayed NPP likely contributed to higher larval mortality, further suggesting that the overlap of pelagic larval durations with productivity plays an important role in driving larval growth and survival. Together, these results provide evidence that the food supply experienced by individual larvae affects larval growth rates and variable survival within and among years.

The strength and timing of seasonal productivity is likely a principal factor determining year-class strength for many marine fishes and invertebrates (Cushing 1990; Morgan 2001; Beaugrand et al. 2003; Durant et al. 2005; Burrow et al. 2011; Toupoint et al. 2012; Platt et al. 2003; Siddon et al. 2013). Planktotrophic larvae of species with similar life histories and movement will experience comparable environmental conditions, highlighting the potential for similar patterns in growth

and survival that were observed in this study. Although this study was limited to the analysis of rockfishes in the subgenus *Pteropodus*, annual recruitment for many rockfishes is synchronous (Caselle et al. 2010aa,b; Ralston et al. 2013). Year-class strength and subsequent adult recruitment of dungeness crab is related to upwelling strength and the timing of the spring transition (Shanks 2013), indicating that the magnitude and timing of upwelling-driven productivity experienced by larvae affects survival and population replenishment. In combination with our results, these findings suggest match-mismatch dynamics likely play an important role in upwelling systems.

This study takes an important step toward understanding the mechanisms driving larval growth, recent settlement, and year-class strength of fish populations by linking environmental conditions experienced by individuals to larval traits. Despite this contribution, our ability to relate larval growth and abundance to the timing of spring production is restricted by having only 2 yr of available data for the 3 yr in which recent settlement of rockfishes were monitored. A multi-year study is needed to establish whether the relationship between productivity and larval growth is consistent across years and oceanographic regimes (El Niño Southern Oscillation and the North Pacific Gyre Oscillation) and to better evaluate the interannual component of match-mismatch dynamics. Moreover, oceanographic conditions acting over longer time-scales may change the relative importance of the factors that influence growth (Lenarz et al. 1995; Hollowed et al. 2001; Bailey et al. 2005; Shanks 2013). In addition, our approach does not account for many other potentially influential factors. For example, we were unable to measure parental investment directly, as initial growth is affected by environmental conditions experienced early in development. We recommend future studies also consider onshore transport mechanisms, which must be present for settlement to occur even during favorable feeding conditions. Long-term studies in combination with focused evaluation of larval traits are needed to fully elucidate the complex interactions driving larval condition, survival, and subsequent recruitment.

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Conflict of Interest

None declared.

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