ENVIRONMENTAL EFFECTS ON GROWTH OF EARLY LIFE HISTORY STAGES
OF ROCKFISHES (SEBASTES) OFF CENTRAL CALIFORNIA BASED ON
ANALYSIS OF OTOLITH GROWTH PATTERNS

By

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ABSTRACT

ENVIRONMENTAL EFFECTS ON GROWTH OF EARLY LIFE HISTORY STAGES OF ROCKFISHES (SEBASTES) OFF CENTRAL CALIFORNIA BASED ON ANALYSIS OF OTOLITH GROWTH PATTERNS

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Understanding the causes of recruitment variability in many marine fish populations is a long standing problem in fisheries research, and one that remains pressing due to the consequences of uncertainty in production models for effective management decisions. Recruitment often fluctuates greatly between years for species with a pelagic early life history (ELH) phase, and can appear independent of stock size. This phenomenon is believed to be a direct result of variable environmental conditions influencing the survival rates of marine fishes during ELH. Environmental influence on growth rate during early life may affect rates of survival through various mechanisms, and as such, examining environment-growth relationships may provide insight into the environmental effects on overall year class strength. In an effort to quantify the environmental influence on growth during the critical ELH stages, this study developed a daily growth rate time series from 1984-2004 for each of three species of winter-spawning rockfish using otolith
micro-increment analysis techniques. After removing the effects of ontogeny on daily growth rate, I was able to explain a large amount of variability in growth patterns with an autoregressive multiple regression model which included several environmental parameters. Models included a combination of sea surface temperature as well as a measure of ecosystem productivity, such as modified upwelling or solar illumination indices. Environmental variables in best-fit models were able to account for 5 – 33% of overall variability in growth rate, a significant improvement over previous research into environment-growth dynamics. This analysis represents a step forward in understanding one of many potential mechanisms that connect environmental conditions to recruitment variability for winter-spawning rockfishes, and provides a foundation for future research into the environmental effects on growth during early life history.
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INTRODUCTION

Recruitment is the process through which newly spawned individuals survive to join the adult population, and is central to the population dynamics of fishes. The strength of recruitment varies greatly from year to year in many marine species which exhibit a pelagic early life history stage, making simple stock-recruit relationships unreliable tools for predicting recruitment strength. Estimates of recruitment are necessary for fishery assessment models that are used to inform important management decisions, and error in such models has led to serious over-fishing in the past (Keyl and Wolff 2008). As a consequence, improving the understanding of the underlying causes of inter-annual recruitment variability is a central goal of fisheries oceanography (Houde 2008). It is a widely accepted notion that oceanographic conditions experienced by fish during early life strongly influences year-class strength (Cushing 1990, Houde 2008). The goal of this study is to provide insight into the environmental influence on larval growth rate, one potential mechanism linking oceanographic variability to survival through early life, for three species of rockfishes off central California.

Growth and Survival During Early Life

The number of fish that survive to recruitment is determined by the distribution, abundance, and quality of offspring and processes that effect their survival, especially during the egg and larval life history stages (Cushing 1990, Houde 2008, Lasker 1978).
Simple numerical experiments have illustrated how small changes in survival rates experienced by fish during early life history (ELH) can lead to order-of-magnitude differences in the numbers surviving to recruitment (Hjort 1914, Houde 1987). Density-dependent mortality in the subsequent juvenile stages may substantially reduce subsequent survival in exceptionally large year-classes (Ralston and Howard 1995, Adams and Howard 1996, Iles and Beverton 2000).

For a fish to survive the early life phase, it must avoid both starvation and predation, rates of which are virtually impossible to estimate in wild populations. Growth rate, however, is observable and it may be related to survival through two distinct, but complementary mechanisms (Andersen 1988): (1) higher growth rate during ELH is hypothesized to shorten the duration of developmental stages susceptible to high predation mortality (the ‘stage-duration’ hypothesis; Houde 1987), and (2) fish that grow to a larger size at a given age may gain survival advantages. The ‘bigger-is-better’ mechanism (Miller et al 1988, Letcher et al 1996, Fuiman 1994) suggests that larger fish are better able to develop food reserves that may give them a higher relative tolerance to starvation, and that larger fish are able to avoid predation more successfully. Although some mesocosm experiments have failed to find support for the ‘growth-mortality’ hypothesis (Fuiman 1989, Litvak and Leggett 1992, Fuiman et al 2005), field studies show that faster growing individuals do in fact have a higher survival probability in the majority of instances (Miller et al 1988, Cowen and Houde 1996, Meekan and Fortier 1996, Hare and Cowen 1997, Sogard 1997, Shima and Findlay 2002, Vigliola and Meekan 2002, Gagliano et al 2007).
Oceanographic Influence on Growth

The growth rate of fishes during ELH is highly influenced by their surrounding environment, which can affect their basal metabolic rate, available prey resources, and their ability to forage efficiently. Oceanographic processes shape the environment experienced by fish larvae directly and through complex bio-physical pathways (Figure 1, Checkley and Barth 2009, Doney et al. 2012). Metabolic processes in fish, as in other poikilotherms, is strongly dependent on temperature and underpins potentially strong relationships between fish growth rates and ocean temperature. Ecological conditions, and especially the foraging environment, reflect more complex ecosystem responses to physical processes. In general, favorable feeding conditions require an oceanographic forcing mechanism that enriches the environment, and one that concentrates the products of enrichment to allow efficient foraging (Bakun 1996).

Off central California, upwelling along the continental margin drives sometimes dramatic enrichment of coastal waters, often drawing nutrient-rich waters from several hundred meters depth to the surface (Bakun 1996, Wells et al 2007, Rykaczewski and Checkley 2008, Checkley and Barth 2009). Coastal upwelling occurs most strongly during the spring and summer months when winds blow predominantly from the north, causing offshore advection of the surface layer as a result of the Coriolis effect (Huyer 1983). Under typical conditions displaced surface water is replaced by colder, saltier, and more nutrient-rich water from beneath the thermocline, and the resulting supply of nutrients supports increased primary production in illuminated surface waters.
Figure 1. The various pathways through which oceanographic conditions influence otolith growth are outlined in this conceptual model. Parameters surrounded by dashed boxes were empirically measured, those surrounded by ovals were modeled from empirical measurements, and those surrounded by black boxes are known relationships where it is not possible to obtain a direct measurement. Arrows connecting parameters represent known bio-physical pathways; solid arrows represent positive relationships, short dashed arrows represent negative relationships, and arrows with long dashes represent a parabolic relationship.
Primary production fuelled by this enrichment propagates up the food web, beginning with increased production of herbivorous zooplankton such as copepods, whose eggs and larvae are key prey for larval fishes. The effectiveness of upwelling as a mechanism for supplying nutrients depends in part on vertical structure of the water column, and in particular the depth of the nutricline relative to the depth from which upwelled waters are drawn (Huyer 1983, Chavez et al 2002). Variability in this process is captured by variability in sea level: higher than normal sea level along the coast corresponds to a depressed (deeper) nutricline and reduced enrichment, while lower than normal sea level corresponds to shoaling nutriclines and more effective enrichment. Consequently, periods of positive sea level anomaly require stronger wind forcing to drive the same amount of nutrients to the surface, while the opposite is true during periods of negative sea level anomaly.

Concentration mechanisms make food more available to fish by creating and maintaining patches of zooplankton in which larval fish can forage efficiently—such patchiness is as or more important to fish survival than overall prey abundance (Letcher and Rice 1997). Stratification during breaks in strong upwelling winds can allow planktonic prey to accumulate at density gradients that form as vertical mixing weakens (Lasker 1975, 1978). Similarly, upwelling fronts can promote both enhanced production and concentration of plankton in convergent flow fields (Traganza et al. 1987, Franks 1992). Larval fish have been observed at such fronts at high abundances relative to nearby, non-frontal water masses (Bjorkstedt et al. 2002, Sadrozinski 2008), providing evidence that larval fish are often associated with these micro-habitats. Evidence that
pelagic juvenile rockfish are also associated with such fronts suggests that these may be important habitats for recruitment (Woodson et al. 2012, Sakuma et al. 2013).

Small-scale foraging efficiency is also believed to be important to fish feeding and growth. The amount of energy expended to obtain a particle of food is determined by a larvae’s ability to visually detect prey, which is highly influenced by how well the water column is illuminated (Fiksen et al. 1998, Fiksen and MacKenze 2002). Micro-scale turbulence, a function of wind stress and depth, or current speed and height above the seafloor, also plays a role in foraging efficiency by altering relative velocities of predators (larval fish) and their prey (MacKenzie and Leggett 1991, Dower et al 1997, MacKenzie 2000, Pitchford et al 2003, Galbraith et al 2004). As micro-scale turbulence increases, the encounter rate between larval fish and their prey increases, but is countered by a decline in capture success, leading to a dome-shaped relationship between foraging success and turbulence (MacKenzie et al. 1994, Fiksen et al 1998).

Variability in local environmental conditions is also influenced by larger-scale climatic processes, represented by several indices (DiLorenzo et al. 2013). The Pacific Decadal Oscillation (PDO), based on variability in sea surface temperature across the North Pacific (Mantua et al 1997), reflects variability in the strength and position of the Aleutian low sea level pressure system. Positive PDO is associated with a weakening of the California current, positive coastal sea level anomalies, and changes in the depth of upwelling cells along the coast (Chaak and DiLorenzo 2007). The North Pacific Gyre Oscillation (NPGO) is indexed as the second mode of sea surface height (SSH) throughout the Northeast Pacific (Di Lorenzo et al 2008), and represents changes in the
strength of gyre circulation driven by dipole sea level pressure anomalies in the northeast Pacific. The influence of these major climate modes on the California Current Ecosystem appears to shift from the PDO being dominant off Oregon and Washington (and north) and the NPGO being more important off central California and to the south (DiLorenzo et al. 2008). The El Niño Southern Oscillation (ENSO; Trenberth 1997) typically varies more rapidly than the PDO and NPGO (approximately 3-7 years, as compared to 8-20 years). El Niño events originate in the equatorial Pacific, and have both atmospheric and oceanic signals that typically lead to weakening of the California current, positive sea level anomalies, and decreased upwelling. The opposite is true during La Nina events. Feedbacks and synergies between these and other climate modes are only now becoming clear (Di Lorenzo et al. 2013).

**Estimating Daily Growth History**

Cohort-level survival is the consequence of the cumulative influences experienced by individuals over the course of early life history. Environmental conditions often fluctuate substantially over daily to weekly periods, suggesting that daily estimates of growth rate are necessary to resolve the environmental influence over fish growth during ELH. Otoliths, the inner ear bones of fishes, are frequently used as a tool to uncover past age and growth information in numerous species. Light and dark bands accrete to the otolith nucleus on a diel cycle (Panella 1971, Morales-Nin 2000), forming the daily micro-increments which are counted to age larval and juvenile fishes. Otolith micro-increment enumeration is generally considered a reliable measure of age (Campana and
Neilson 1985, Morales-Nin 2000), except in rare instances of extreme physiological stress (Mugiya and Uchimura 1989). The width of a given micro-increment, however, is highly variable and is believed to form in some proportion with somatic growth, thus being a good indicator of daily growth rate over the course of a fish’s life (Morales-Nin 2000).

Though otolith size and fish size are highly correlated in most situations (Geffen 1982, McGurk 1984, Secor and Dean 1987, Secor et al 1989, Strelcheck et al 2003), there are instances where otolith growth and somatic growth can become decoupled, such that otolith size or increment width may not serve as a simple indicator of size or growth rate. Under starvation conditions, somatic growth declines or ceases while daily increment deposition continues (except in the most extreme cases), leading to an increase in otolith size relative to fish length (Secor et al 1989). However, this is likely to be a moot concern in field-based studies of early life history, as poor nutrition typically leads to elevated mortality in larval and juvenile fishes. Consequently, daily otolith growth from juvenile fishes is often considered a robust proxy for somatic growth during the larval life history stage, and will be treated as such for the purposes of this study.

Winter-Spawning Rockfishes

Winter-spawning rockfishes are species for which understanding the consequences of environmental variability during early life has potentially great value for fishery management. Rockfishes comprise a set of species that have historically been (and remain) important targets of recreational and commercial fisheries (Mason 2004).
Intense fishing pressure throughout the mid- to late 20th century contributed to severe population declines for many species, some of which may take decades to recover under current restrictive management plans (Punt and Ralston 2007). The most recent stock assessments indicate that significant increases in (age 4+) biomass have occurred in yellowtail, widow, and chilipepper rockfish in recent years, though estimated biomass for widow rockfish remains below the statutory definition for designating stocks as “overfished” (Wallace and Lai 2004, Field 2007, He et al 2009). Rockfishes exhibit a life history that is prone to overfishing; they are generally slow-growing, long-lived species that reproduce relatively later in life.

Off central California, many commercially important species of rockfishes release live larvae (i.e., undergo parturition) into the plankton during the winter-spring transition into upwelling season (Wyllie-Echeverria 1987, Love et al 2002). This period of time is typically marked by highly variable periods of upwelling and downwelling, including winter storms and calms. Flexion occurs after several weeks’ development, with a corresponding increase in swimming capability, visual acuity, and other capabilities typical of teleost ontogeny. After individuals develop adult characteristics (~45-60 days), they remain in the upper water column for several months as pelagic juveniles before settling into benthic habitats. The mechanisms through which fish return to the nearshore environment are not well understood, but may fish may rely on shoreward currents at depth (Larson et al. 1994) or fronts to prevent offshore advection (Woodson et al. 2012). Larval and juvenile rockfish are thought to be opportunistic feeders, preying upon various life history stages of calanoid copepods, sub-adult euphausiids, and other available

**Research Question and Context**

In this study, I investigate responses in daily growth rates of larval and juvenile rockfish, as recorded in their otoliths, to environmental conditions off central California. To do so, I substantially extend an existing data set of individuals’ daily otolith growth trajectories for three species of winter-spawning rockfishes captured during NOAA mid-water trawl surveys off central California. The historic data set included fish captured from 1984 to 1989, and the present analysis added data for these species from 1990 to 2008. I fit models that explain observed growth patterns as a function of environmental conditions based on a conceptual understanding of how ecosystem responses to physical forcing impinge on growth of rockfish larvae (Figure 1). The overarching goal is to advance our understanding of the relationship between ocean conditions and larval fish growth over short time scales. Fish included in this study were captured as pelagic juveniles, and as such, provide insight into the environment-growth relationships experienced by fish that survived the larval life history phase. This study represents a small portion of a larger research question, intended on relating oceanographic conditions to overall recruitment strength.
MATERIALS AND METHODS

Otolith Archive: Collection and Preparation

Otoliths of pelagic juvenile rockfishes were obtained from the Fisheries Ecology Division of NOAA Fisheries’ Southwest Fisheries Science Center from an archived collection developed as part of the Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) (Wyllie Echeverria et al 1990, Sakuma et al 2006, Ralston et al 2013, Sakuma et al 2013). Between 1983 and 2004, the RREAS consisted of three trawl samples each of several stations off the central California coast between Monterey Bay and Point Reyes (36°30’ and 38°20’ N, Figure 2). Stations were grouped in lines or clusters that could be sampled in a single night, and were designed to span cross-shelf variability in pelagic habitats over a range of bottom depths and bathymetric structure. Sampling was typically conducted from early May to mid-June in each year. In 2005, the RREAS was extended south to the U.S./Mexico Border (32°45’N) and north to Cape Mendocino (40°00’N).

Pelagic juvenile rockfishes were collected using a mid-water trawl with an approximate mouth opening of 26 square meters, fitted with mesh of diminishing width, and culminating in a cod-end lined with 9.5 mm stretch mesh. The trawl was rapidly deployed, fished at 30 m (headrope depth) for 15 minutes at speeds ranging from 3.6-5.6 km per hour, and rapidly retrieved. Upon retrieval of each trawl, pelagic juvenile rockfishes were immediately sorted, preserved in chilled seawater, identified to species,
enumerated, and frozen at -80°C for transport and storage. Upon return to the laboratory, individuals’ at-sea species identifications were confirmed and standard lengths measured.

For abundant species, a subset of individuals was selected for otolith extraction. Individuals were selected non-randomly, being retained as encountered during sample processing to fill a series of size-classes (at 0.1 mm or 0.5 mm intervals) and were non-uniformly distributed across the sampling region or the timing of collection. For each selected individual, the sagittal otoliths were extracted, washed, dried, and mounted on a microscope slide using clear nail polish or crystal-bond mounting material. Each slide was labeled by species, haul number, and total length for future reference. For further detail of the survey sampling procedure, see Wyllie-Echeverria et al (1990). The otoliths used in this study were collected in accordance with the policies and practices of Humboldt State University’s Institutional Animal Care and Use Committee (IACUC Protocol No. 07/08.ML.86.E).
Figure 2. Map of the central California study region with capture locations from the Rockfish Recruitment and Ecosystem Assessment Survey (RREAS). Nighttime mid-water trawl stations where fish were captured between the years of 1986 and 2003 are represented by filled circles, while capture locations from 2004 to present are represented by open circles.
Otolith Increment Analysis

I analyzed otoliths collected between 1990 and 2008, adhering closely to (and building upon) previously developed methods (Woodbury and Ralston 1991, Laidig et al 1991). I observed each otolith from every pair at 400x magnification, selected the clearest of the two, and polished the otolith surface with 5-micron aluminum oxide lapping film (3M Corp.) until the initial area to be read was thin enough to reveal daily growth micro-increments clearly at 400x magnification. Otoliths that were mounted convex-side down were read from the edge in towards the nucleus; otoliths that were mounted convex side up were read from the nucleus out.

Otolith increment analysis was performed at 1000x under an oil-immersion objective lens, using a polarized light source and a differential inter-phase contrast (DIC) filter to heighten contrast in the image. I measured each daily increment along the axis of maximum growth on the post-rostral side of each otolith between the outer margin and the extrusion check mark (figure 3). The post-rostral axis was chosen both for consistency with previous methods and because it is the longest axis, hence has the widest increments, thus reducing the contribution of measurement error to each observation.

Each set of increments was brought into focus and the field of view photographed with a microscope-mounted digital camera (Infinity 2, Lumenera Corp., 2.0 megapixel resolution). I measured increments immediately on each photograph using the measurement function of the image analysis software, which was capable of resolving
increment widths to the nearest 0.01 µm (Infinity Analyze, Lumenera Corp., ver. 5.03), and which I regularly calibrated to the objective lens using a stage micrometer. I then shifted the field of view to span the next set of otolith increments, taking great care to maintain some overlap between fields of view and to align increments using visible landmarks in the otolith microstructure. Each sequential field of view was processed in a similar fashion and archived to produce a series of images representing a complete cross-section of the post-rostral axis. Because otolith thickness varies along the axis, it was often necessary to stop and carefully re-polish and reposition an otolith several times to maintain consistent increment clarity throughout the process. Throughout the polishing-reading process, care was taken to avoid spurious counting of increments viewable at multiple depths through thin sections. This occurred most frequently near the outer otolith margin, and in these regions I focused the field of view slightly above the otolith surface to ensure I counted the leading edge of each increment.
Figure 3. Image of a yellowtail rockfish otolith taken at 200x magnification with three axes. Post-rostral (PR) axis extends from the nucleus in the center of the otolith towards the outer margin, and is the preferred axis for measuring growth increments. The rostral (R) and anti-rostral axes are noted for reference, but are not used for growth analysis.
In some specimens, short series of increments proved difficult to resolve along the preferred axis, apparently due to natural variability in otolith microstructure. To estimate otolith growth over these intervals, I measured the distance between the last clear increment and the next clear increment along the preferred axis, measured increments along a nearby axis (typically < 15 degrees off the post-rostral axis), and expanded the relative widths of the off-axis increments to fill the gap along the post-rostral axis. Comparisons based on several unaffected otoliths confirmed that increment widths are proportional across growth axes separated by small angles (results not shown).

Individuals’ ages were estimated from the count of increments between parturition and capture, assuming that increment formation occurs daily (see Laidig et al 1991). Individuals’ birth dates were estimated by subtracting their estimated age from the known date of capture. On many otoliths, parturition (age 0) is indicated by a clear ‘check mark’—a distinct first ring surrounding the nearly spherical nucleus—formed during the first day of growth after parturition. Such checks, when present, are clearly distinguishable from any faint pre-extrusion rings that may also be present (Woodbury and Ralston 1991, Laidig et al 1991). For otoliths which lacked clear extrusion checks, I estimated the location of the age-0 increment based on published reports of mean otolith diameters at parturition for each species (Laidig and Ralston 1995). Specifically, I measured a straight-line distance from the center of the primordium along the post-rostral axis until I reached the estimated diameter and assigned day’0’ to the inner margin of the increment that overlapped that point. Any possible consequences of error in estimating
the extrusion check would be limited to a modest shift in the age assignment, and would leave increment date assignments unaffected.

**Historical Otolith Data**

Data developed in the present study were compiled with existing data developed by Keith Sakuma and Tom Laidig (SWFSC) based on analysis of otoliths collected between 1984 and 1989 (inclusive). Historical otolith increment data were collected using methods similar to those described above, with a few noteworthy exceptions. First, increment widths in the earlier data are reported as average measurements made across non-overlapping pairs of increments, not as individual increments. The earlier data also estimate increment widths across blurry regions by dividing the measured distance between resolvable increments by the corresponding count of increments taken elsewhere on the otolith. Rather than repeating average increment widths, I developed a method to estimate individual increments across obstructed regions that retained growth variability. Last, the historical data do not include measurements from otoliths that lacked clear extrusion checks, whereas I include data from such otoliths due to the limited number of otoliths available in collections from the 1990’s and 2000’s.

**Estimating Age-Independent Growth**

For the analysis, I focused on otolith growth between day 5 and 50. Excluding earlier increments reduced the contribution of disproportionately high measurement error associated with measurements of the early (<5 day), narrow increments (Pepin et al. 2001,
personal observation). Excluding later increments eliminated potential biases in increment width measurements associated with morphological changes in otolith structure, including the emergence of secondary growth nuclei that may distort daily growth measurements (Neilson 1992, figure 4).

Otolith growth increments (OI) were log-transformed to standardize variance in residuals at size. Growth trajectories were aligned by calendar date to assign each increment an age (A) and date (D; day since 1/1/1970). For each species, I fit a 2-way analysis of variance (ANOVA) model

Equation 1.  
\[ \log(\text{OI}) = \gamma_A + \gamma_D + \varepsilon \]

to estimate age-specific coefficients ($\gamma_A$) that together describe the mean ontogenetic growth pattern across all fish in the sample (regardless of year), and date-specific coefficients ($\gamma_D$) that represent mean age-independent mean growth rates across all fish alive (and between 5d and 50 d old) on each day (Equation 1). The error term, $\varepsilon$, is an independent, normally distributed random variable. Based on Ralston’s (1995) conclusion that age-time interactions were not significant in pelagic juvenile rockfish otolith growth patterns, I did not include an interaction term in the ANOVA.

In contrast to Ralston’s (1995) approach, I assumed that ontogeny and development as a function of individuals’ age were consistent across years, and fit a single ANOVA to the entire data set, rather than to individual year classes. By fitting a single, consistent age-growth relationship across years, I have assumed that departures
from this mean age-growth relationship, whether at intra- or inter-annual scales, are related to environmental conditions experienced during early life.
Figure 4. Image of a yellowtail rockfish otolith at 400x magnification. Arrows denote the origin of secondary growth along the post-rostral axis (right) and an alternate axis (left), which may indicate the larval-juvenile transition.
Environmental Time Series

Based on our conceptual model (figure 1), I obtained time series of several environmental variables that represent conditions likely to influence the growth rates of larval rockfish, taking care to select data at scales relevant to fish captured in the ‘core region’ of the survey off central California (figure 5). Although the location of capture for each fish is known, individuals’ locations throughout early life are not known, and may have included excursions further offshore or elsewhere along the coast prior to being captured as pelagic juveniles in the core region. CalCOFI research surveys, which targeted fish larvae and plankton earlier in the season, provided evidence that the majority of rockfish larvae were captured within 1-degree of shore, though the distribution of larvae extends much further offshore (Ahlstrom et al. 1978).

Several of the environmental time series are assumed to have ‘immediate’ and relatively short-lived effects on growth. Sea surface temperature, which I treat as a proxy for temperature throughout the upper water column, is modeled as having a direct influence on growth rate. Effects of turbulence and illumination are also assumed to have immediate consequences through effects on foraging efficiency (Dower et al. 1997, Fiksen et al. 1998, MacKenzie 2000). These time series were smoothed with a 3-day running mean to reduce noise and in an attempt to better match temporal scales of variability in the environmental time series to that observed in the environmental component extracted from the otolith growth data.
Growth responses to upwelling and sea level are expected to reflect lagged ecosystem responses to cumulative forcing, as both the physical response to the onset of forcing (e.g., Austin and Barth 2002, Austin and Lentz 2002) and the ecosystem response to enrichment takes some time to develop (e.g., Botsford et al. 2003, 2006). Therefore, to convert upwelling and sea level into proxy indices of prey availability, we first filtered each time series with an 8-day moving average to reflect cumulative enrichment, and then shifted each time series to precede the otolith growth time series by 12 days to reflect the propagation time necessary to convert nutrients to phytoplankton to zooplankton. These transformations were selected a priori on the basis of dynamics reported in the literature and were not fitted as part of the model estimation. No attempt was made to account for spatial pattern in prey distributions.

Missing values in time series data are a common, yet potentially problematic phenomenon since models generally require a complete time series of explanatory data. I evaluated the presence of missing daily values and replaced them with estimates using one of two methods. For all environmental time series, gaps of less than 10-days were replaced using cubic-spline interpolation (‘spline’ function, package ‘zoo’ ver. 1.7-10, R ver. 2.12). Missing values lasting more than 20 days were replaced with appropriate climatological values. Where time series from multiple locations were merged to create one regional time series, missing values were replaced using the methods described above prior to merging. I also identified the presence of large data gaps that occurred coincidently with growth data.
Figure 5. Map of central California study region with environmental data sources. The black and grey circle represents the sea level height measurement location. Offshore circles represent NOAA data collection buoys. Grey diamonds indicate the locations where upwelling index was estimated. The innermost box (solid line) represents the area over which the first regional sea surface temperature time series (rSST1) and solar illumination time series were calculated. The slightly larger box (solid line) shows the region over which the second regional sea surface temperature (rSST2) time series was calculated, and the largest box (dashed line) represents the third regional sea surface temperature (rSST3) time series area.
Regional sea surface temperature (rSST)

Three indices of mean regional SST (°C) were extracted from daily fields of optimally interpolated sea surface temperature (OISST, ver. 2), available from NOAA’s National Climatic Data Center, Climate Data Record Program (http://www.ncdc.noaa.gov/cdr/; see Reynolds et al 2007). Each rSST time series represented mean SST over areas of different extent:

- rSST$_1$ spans the “core region” (roughly 36°30’ to 38°20’ N) of the RREAS between Point Reyes and Monterey Bay and extends 1° offshore of the coastline (roughly 160 km) to capture the dynamics of upwelling centers off Point Reyes and north of Monterey Bay while excluding warmer regions to the south;
- rSST$_2$ has the same latitudinal extent as rSST$_1$, but extends 1.5° offshore of the coast to capture a wider range of cross-shelf variability; and
- rSST$_3$ extends as far offshore as rSST$_2$ but extends one degree of latitude further to the north and south to include conditions along a broader range of potential larval source locations.

Upwelling index (UI)

Daily indices of upwelling intensity ($m^3/s/100m$ coastline) calculated along the coastline at 36.125°N and 39.125°N were obtained from NOAA, Pacific Fisheries Environmental Laboratory (http://www.pfeg.noaa.gov). These indices spanned the northern and southernmost edges of the core study region, and I calculated the mean of
the two normalized time series to represent regional conditions. Details of the methods used to calculate upwelling index can be found in Schwing et al (1996).

**Coastal sea level anomaly (SLa)**

Daily sea level measurements (mm) were obtained from station #551A (San Francisco; 37° 48.4’N, 122° 27.9’W) from The Joint Archive for Sea Level (JASL) at The University of Hawaii [http://ilikai.soest.hawaii.edu/uhslc/data.html](http://ilikai.soest.hawaii.edu/uhslc/data.html), for the period from 11/1/1973 to 12/31/2008. Daily sea level was calculated from hourly data by JASL using a two-stage filter in which the dominant tidal components and the remaining high frequency variability were removed prior to calculating a daily mean. I converted daily sea level measurements to sea level anomaly (SLa) by subtracting the time series mean. Preliminary analysis indicated that it was not necessary to account for a secular trend from the sea level time series prior to calculating SLa.

**Solar illumination index (IL)**

Indices of downward solar radiation flux (Watts/m²) at the ocean surface were extracted from daily interpolated values available from NOAA’s Earth Systems Research Laboratory, Physical Sciences Division [http://www.esrl.noaa.gov/psd/](http://www.esrl.noaa.gov/psd/). IL is interpolated at 0.25° grid resolution, and daily mean values were calculated over the area roughly spanning 36°30’ to 38°20’ N, and 1° offshore of central California.
Wind speed (WS) and micro-scale turbulence ($\xi$)

Wind speed data (knts, converted to m/s for analysis) was obtained from NOAA, National Data Buoy Center (http://www.ndbc.noaa.gov) for buoy numbers 46012 (Half Moon Bay; 37.363° N, 122.881° W), 46042 (Monterey; 36.785° N, 122.469° W), and 46013 (Bodega Bay, 38.242° N, 123.301° W). I calculated the daily average of the wind-speed time series from the three buoys as an index of regional wind speeds. From the regional index, I developed an approximate index of turbulence in the surface mixed layer as the cube function of wind speed.

Modeling Environmental-Otolith Growth

I assumed that the date-specific growth coefficients ($\gamma_D$) are influenced by environmental conditions, and developed models to estimate the relationship between environmental conditions (based on our conceptual model) and the $\gamma_D$, herein referred to as scaled otolith growth (SOG) in the text. I fit an autoregressive multiple-regression model (Equation 2) in which SOG is a function of all combinations of $n$ non-correlated environmental time series variables $E_n(t)$. The model includes first-order autocorrelation $\Phi$ in the residual $\gamma_D(t) - \hat{\gamma}_D(t - 1)$, where $\hat{\gamma}_D(t - 1)$ is predicted SOG at time $t - 1$. The model residual $\epsilon(t)$ is an independent, normally distributed random variable.

**Equation 2.** $\gamma_D(t) = \alpha + \sum_1^n \beta_n E_n(t) + \Phi(\gamma_D(t - 1) - \hat{\gamma}_D(t - 1)) + \epsilon(t)$
To avoid issues associated with multi-collinearity, candidate models only included combinations of environmental parameters with correlation coefficients of absolute value less than 0.5 (Pearson’s product moment correlation test, ‘cor’ function, R ver. 3.01). Coefficients (β) were estimated by fitting (Equation 2) a linear mixed effects model without a fixed effect (package ‘nlme’, R ver. 3.01). This model assumes that environmental conditions have a linear effect on SOG, an assumption I checked through examination of bi-variate relationships between SOG and individual environmental time series. Contributions of daily estimates of $\gamma_D$ to model fits were weighted by $1/ SE_{\gamma_D}^2$ to account for greater uncertainty in estimates of $\gamma_D$ from the very beginning and end of each SOG time series, when fewer individuals contributed to each estimate. Estimates of first-order autocorrelation from an AR(1) model applied to each SOG time series (typically 0.91-0.93) were used as a starting value for estimating the autocorrelation coefficient $\Phi$.

The best-fit model was selected using a multi-faceted approach. I used Akaike’s Information Criterion (AIC; Burnham and Anderson 2002) scores as a coarse guide to model selection, calculating the ΔAIC for each candidate model and omitting those models that substantially deviated from the lowest overall AIC score. However, the percent variance assigned to the autocorrelation term is included in the calculation of AIC scores, so that a good AIC score may not necessarily mean that a model represents a better explanation of otolith growth in response to environmental conditions. To estimate goodness-of-fit, I used generalized $R^2$ (Equation 3, Nash and Sutcliff 1970, Nagelkerke 1991), where $y_i$ is the observed value of observation $i$, $\bar{y}$ is the mean of the $y_i$, $n$ is the
number of observations, and $\epsilon_i$ is the model residual. I calculated a generalized $R^2$ to assess the amount of variance explained by only the environmental variables ($R^2_{\text{ENV}}$) as well as in the full autoregressive model ($R^2_{\text{FULL}}$).

Equation 3. $$R^2 = 1 - \frac{\sum_{i=1}^{n} \epsilon_i^2}{\sum_{i=1}^{n} (y_i - \hat{y}_i)^2}$$

After selecting best-fit model for each species, model robustness was evaluated using a simple jack-knife procedure. Data from each year was excluded in turn from the analysis, the best-fit model re-fit to the reduced data set, and the resulting model used to predict growth time series for the excluded year. Normalized root mean square error (RMSE) was calculated for the model predictions and observations over the excluded time period, and compared to RMSE from the original model predictions and observations over the same time period. Large changes in RMSE were expected to provide insight into years that may have significant leverage over the global model predictions.
RESULTS

Summary of Otolith Collection

This study includes data for 344 widow rockfish, 410 yellowtail rockfish, and 345 chilipepper otoliths spanning a period of 24 years. Of these, I measured growth increments in otoliths from 186 widow rockfish (*Sebastes entomelas*), 130 yellowtail rockfish (*Sebastes flavidus*), and 93 chilipepper (*Sebastes goodei*), all of which had been captured since 1990, and combined these data with growth increment data for the same three species captured in the late 1980s (Table 1; Ralston 1995). However, after examining the spatial variability of the environmental time series along with changes in fish latitude at capture by year (figure 6), I retroactively omitted growth data occurring after the 2005 cruise expansion. The drastic increase in spatial variance at the time of capture may have resulted in a meaningless “average” growth response, which was evident in decreased model performance when these data were included (results not shown). In the end, a total of 315 widow rockfish, 396 yellowtail rockfish, and 320 chilipepper rockfish were analyzed over a period of 20 years to generate the following results.
Table 1. Total number of otoliths analyzed by each year and species, excluding those which were damaged or otherwise excluded from the dataset. However, otoliths captured after 2004 were retroactively omitted from the model.

<table>
<thead>
<tr>
<th>Year</th>
<th>S. entomelas</th>
<th>S. flavidus</th>
<th>S. goodei</th>
<th>Source</th>
</tr>
</thead>
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<tr>
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<td>-</td>
<td>51</td>
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Figure 6. Latitude of capture (°N) for all individual rockfishes captured between 1984 and 2008. Chilipepper (S. goodei) rockfish are represented by diamonds, widow (S. entomelas) rockfish are represented by asterisks, and grey triangles represent yellowtail (S. flavidus) rockfishes. The Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) expanded its’ geographic scope in 2005.
Age- and Date-Specific Otolith Growth Rates

The two-way ANOVA showed that Age and Date had significant effects (both p-values< 0.0001) on otolith growth rates for all three species, and in combination explained 83-87% of the variability in otolith growth (Table 2). The unbalanced design of the ANOVA precluded rigorously partitioning variance explained between Age and Date, but did not affect estimates of marginal means. However, separate one-way ANOVAs for Age and Date suggest that Age explains approximately twice as much variability in growth as does Date (results not shown). All three species exhibited a similar ontogenetic growth pattern, in which, growth rates increased steeply between ages 5 d to 20 d, slowed between ages 20 d to 40 d, and again accelerated after age 40 d (Figures 7-9).
Table 2. Two-way Analysis of Variance (ANOVA) tables for the daily otolith growth rates of chilipepper, widow, and yellowtail rockfishes, where fish age (Age) and unique day of year (Day) were evaluated as explanatory factors.

<table>
<thead>
<tr>
<th></th>
<th>D.F.</th>
<th>S.S.</th>
<th>F Value</th>
<th>Pr (&lt;F)</th>
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<tr>
<td>Residuals</td>
<td>15750</td>
<td>897</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| **Widow** |      |       |         |         |
| Age       | 45   | 5263  | 1868.85 | <0.0001 |
| Day       | 1408 | 273   | 3.096   | <0.0001 |
| Residuals | 13450| 841.7 |         |         |

| **Chilipepper** |      |       |         |         |
| Age             | 45   | 3108.3| 1285.256| <0.0001 |
| Day             | 1385 | 277.8 | 3.732   | <0.0001 |
| Residuals       | 12373| 841.7 |         |         |
Figure 7. Estimated coefficients for growth rate at each age between days five and fifty (approximate larval duration) obtained from a 2-way analysis of variance (ANOVA) of chilipepper rockfish increment width as a function of age and day of year. The solid lines are the estimated coefficients, while the dashed lines represent two times the standard error of the estimate for each age and species combination.
Figure 8. Estimated coefficients for growth rate at each age between days five and fifty (approximate larval duration) obtained from a 2-way analysis of variance (ANOVA) of yellowtail rockfish increment width as a function of age and day of year. The solid lines are the estimated coefficients, while the dashed lines represent two times the standard error of the estimate for each age and species combination.
Figure 9. Estimated coefficients for growth rate at each age between days five and fifty (approximate larval duration) obtained from a 2-way analysis of variance (ANOVA) of widow rockfish increment width as a function of age and day of year. The solid lines are the estimated coefficients, while the dashed lines represent two times the standard error of the estimate for each age and species combination.
Growth Comparisons Among Species

Scaled otolith growth (SOG) was highly variable across years within a species, but was highly correlated among species on both intra- and inter-annual scales. Chilipepper and widow rockfish exhibited the highest degree of coherency, with a correlation coefficient of 0.86 across the entire time series. Yellowtail and widow rockfish shared a correlation of 0.75, while chilipepper and yellowtail rockfish also exhibited a strong correlation of 0.62 across all years. Inter-annual scale correlation in scaled otolith growth among species is further demonstrated by covariance in time series plots of annual average SOG (figure 10). Higher than average SOG occurred for each of the three species in 1986, 1992, and 2006, while lower than average annual SOG was observed in 1985 and 1988.

However, SOG time series are also strongly correlated within many of the years examined (table 3), and often exhibit very similar patterns in growth (figure 11). In 1985 for example, SOG had very little slope throughout the season, but exhibited a relatively high degree of variability and a few more subtle, shared trends among species. In February of that year, all species exhibited constant growth rate that began to decline in March. The only notable deviation that year occurred when chilipepper and widow SOG began to increase in April, while yellowtail SOG continued to decline. In 1986, all three species exhibited a sharp decline in SOG at the beginning of March and again in mid to late May, followed by a slight increase later in the season. In contrast, SOG for all three species increased very quickly throughout the season in 2001, with a slight decline in late
May/early June. Certain cases of poor correlation between species may have resulted from a clear offset related to the timing on exposure to the same conditions (e.g. chiliespepper & yellowtail 1989, chiliespepper & widow 1985). In general, yellowtail and widow rockfish SOG time series were the least well correlated with one another.
Figure 10. Average, normalized annual age de-trended growth rates for Chilipepper, Widow, and Yellowtail rockfishes from 1984-2008.
Table 3. Pairwise species comparisons of intra-annual correlations (\(\hat{\rho}\)) in \(\gamma_D\), maximum cross-correlations (\(\hat{\rho}^*\)) and relevant lag, and correlations across years in mean(\(\gamma_D\)). All calculations based on periods of overlapping estimates of \(\gamma_D\) that satisfy a precision threshold of \(\text{SE}(\gamma_D)/\gamma_D < 0.15\).

<table>
<thead>
<tr>
<th>Year</th>
<th>(\hat{\rho})</th>
<th>n(days)</th>
<th>(\hat{\rho}^*)</th>
<th>lag</th>
<th>(\hat{\rho})</th>
<th>n(days)</th>
<th>(\hat{\rho}^*)</th>
<th>lag</th>
<th>(\hat{\rho})</th>
<th>n(days)</th>
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<td>0.43</td>
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<td></td>
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<td>87</td>
<td>0.31</td>
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<tr>
<td>1993</td>
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<td>70</td>
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<tr>
<td>2001</td>
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<td>89</td>
<td>0.75</td>
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<td>0.35</td>
<td>5</td>
<td>0.48</td>
<td>38</td>
<td>0.48</td>
<td>0</td>
</tr>
</tbody>
</table>

Interannual 0.616 0.863 0.753
Figure 11. Comparison of estimated coefficients for Date ($\gamma_D$) from a 2-way ANOVA for selected years. Coefficients represent environmentally-driven otolith growth, or scaled otolith growth (SOG) in the model. Solid lines represent estimates, while dashed lines represent two standard errors about the estimates. Results are graphically provided for three selected years (1985, 1986, and 2001) to highlight contrast in the data within and between years.
Summary of Environmental Time Series

Regional sea surface temperature (rSST)

In general, the three SST time series exhibited similar patterns. All showed warmer-than-average conditions during 1983, 1992, and 1998, while 1989, 1991, and 1999 were much colder than average (figure 12). However, there were some key differences between the time series that resulted from their spatial coverage. The rSST₁ time series was the most variable among the three and also included the coldest values as a direct result of its greater dominance by upwelling zones along the coast. The rSST₂ time series generally followed the same pattern as rSST₁, but was slightly warmer due to broader inclusion of (typically) warmer surface waters further offshore. The difference in temperature was most pronounced during intense periods of near-shore upwelling (figure 13). The rSST₃ time series was generally warmer and muted some of the variability in temperature due to coastal upwelling by including regions further to the north and south of major upwelling hotspots, in addition to offshore.
Figure 12. Image plot of the second regional optimally interpolated sea surface temperature (rSST$_2$) time series. Day of year is given on the x-axis, and year is given on the y-axis. The z-axis represents sea surface temperature values (°C) using a heat color-scale ranging from dark blue (lowest SST) to dark red (highest SST).
Figure 13. Time series of normalized upwelling (black dashed line), plotted from January through June, the period where winter spawning rockfish exist in the plankton as either larvae or pelagic juveniles. Values for 1984 are given for illustrative purposes. All three (normalized) regional optimally interpolated sea surface temperature (rSST) time series are also plotted in black (rSST1), blue (rSST2), and red (rSST3).
Upwelling index (UW_{1,8})

The integrated upwelling index smoothed over high-frequency variability in daily mean upwelling time series and reduced the overall variance in the data, but captured the lingering effects of periods of sustained upwelling or downwelling (figure 14).

Upwelling was generally stronger from 1999-2003 and relatively weaker in the early to mid-1990s, particularly during the spring transition period (figure 15).
Figure 12. Time series plot upwelling index (m$^3$/sec/100m coastline) for 1983. Postive values indicate offshore advection and negative values indicate onshore advection (i.e. downwelling). Raw upwelling index is plotted in dashed grey. The solid blue line represents the 8d running mean of the daily time series as a proxy for integrated ocean responses to forcing.
Figure 13. Image plot of upwelling index (UI) filtered with an 8-day running mean. Day of year is given on the x-axis, and year is given on the y-axis. The z-axis represents UI values ($m^3/sec/100m$ coastline) using a heat color-scale ranging from dark blue (highest downwelling volume) to dark red (highest upwelling volume).
Coastal sea level anomaly (SLa)

Figure 14. Image plot of sea level anomaly (SLa) filtered with an 8-day running mean. Day of year is given on the x-axis, and year is given on the y-axis. The z-axis represents SLa values (mm) using a heat color-scale ranging from dark blue (most negative anomaly) to dark red (most positive anomaly).
Solar illumination index

Solar illumination index (figure 17) is dominated by a strong seasonal component, peaking in the early summer and reaching an annual minimum in December/January. However, there are clear inter-annual variations within a season that are short in duration and likely associated with storm events. There is some variation in the onset of the more highly illuminated season (i.e. spring/summer). The early 2000’s in particular appear to be cloudier relatively later into the season.
Figure 15. Image plot of daily mean solar illumination index (IL). Day of year is given on the x-axis, and year is given on the y-axis. The z-axis represents IL values using a heat color-scale ranging from red (lowest illumination) to light yellow (highest illumination).
Wind speed (WS) and micro-scale turbulence (ξ)

Environmental time series of wind speed and micro-scale turbulence were compromised by an exceedingly large amount of missing data. As a consequence, much of the data was interpolated over periods of time where growth data occurred, likely misrepresenting actual conditions. The majority of wind data was missing in 1987, 1994, 1997, and 2002 for all three data buoys.

Environment-Otolith Growth Relationships

Strong correlations (|\(\hat{\rho}\)| > 0.5) were detected between time series of Illumination index (IL) and integrated, lagged upwelling index (UW\(_{1.8}\)), and between sea level anomaly (SLa) and regionally averaged sea surface temperature (rSST). Moderate correlations (0.3 < |\(\hat{\rho}\)| < 0.5) were detected between time series of UW\(_{1.8}\) and turbulence (ξ), and between UW\(_{1.8}\) and SLa. These correlations precluded modeling certain combinations of environmental parameters (table 4), and in turn led to nine candidate models for each of the three species.
Table 4. Pearson’s product-moment correlation matrix for all environmental variables examined in the model. Strong correlations (bold) are considered to be between 0.5 and 1 (absolute value), and medium correlations (italic) are considered to be between 0.3 and 0.5 (absolute value).

<table>
<thead>
<tr>
<th></th>
<th>UW_{I,8}</th>
<th>ξ</th>
<th>SLa</th>
<th>rSST_{2}</th>
</tr>
</thead>
<tbody>
<tr>
<td>SI</td>
<td>0.647</td>
<td>0.163</td>
<td>-0.174</td>
<td>0.095</td>
</tr>
<tr>
<td>UW_{I,8}</td>
<td>0.334</td>
<td>0.420</td>
<td>-0.078</td>
<td></td>
</tr>
<tr>
<td>ξ</td>
<td></td>
<td></td>
<td>-0.138</td>
<td>-0.194</td>
</tr>
<tr>
<td>SLa</td>
<td></td>
<td></td>
<td></td>
<td>0.600</td>
</tr>
</tbody>
</table>
Nine candidate models were fit to chilipepper SOG data, and are ranked in order of AIC score from lowest to highest (Table 5). The model with the lowest AIC score included $rSST_2$ and $IL$ time series as predictors. Both parameters collectively explained approximately 33% of the overall variance in chilipepper SOG based on generalized $R^2$ (figure 19). The autocorrelation coefficient ($\Phi$) was 0.7638 (Table 6), which was the lowest of any of the models tested. The model which included $rSST_2$ and $UW_{I,8}$ was also a strong candidate model by AIC ($\Delta$AIC = 2.18). However, $rSST_2$ and $UW_{I,8}$ together explained only 25% of the variability in chilipepper SOG according to generalized $R^2$ (Table 5).

Seven of the nine candidate models tested included only one environmental time series and although none were strong candidate models, the results provide insight into the level of influence each parameter has individually on chilipepper SOG. All parameters had statistically significant effects, with the exception of turbulence ($\xi$). Of the three sea surface temperature time series, $rSST_2$ had the lowest AIC score and was included in the multivariate models; $rSST_3$ performed nearly as well. Modeled individually, $rSST_2$ explained approximately 9% of the variability in growth. In all candidate models, when start-values were provided the effects of autocorrelation were able to explain between 96-97% of the variability in growth rate.
Table 5. List of candidate models used to assess environment-growth relationships for chilipepper rockfish, where $\gamma_D$ represents scaled otolith growth, $\alpha$ is the model intercept, $\beta_1$ and $\beta_2$ are the estimated environmental time series coefficients, $rSST_x$ are the three regionally averaged sea surface temperature time series, $IL$ is the index of illumination, $UW_{1,8}$ is an integrated/lagged index of coastal upwelling, $SLa$ is a time series of sea level anomaly, and $\xi$ is a time series of regional turbulence. Models are ranked low to high using AIC score, and goodness-of-fit is represented by generalized $R^2$ for each model including the effects of autocorrelation ($R^2$ FULL) and only the effects of the environmental variables ($R^2$ ENV).

<table>
<thead>
<tr>
<th>Rank</th>
<th>Model Description</th>
<th>$\Delta$AIC</th>
<th>$R^2$ FULL</th>
<th>$R^2$ ENV</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$\gamma_D(t) = \alpha + \beta_1 rSST_2(t) + \beta_2 IL(t) + \epsilon(t, t-1)$</td>
<td>0</td>
<td>0.96</td>
<td>0.33</td>
</tr>
<tr>
<td>2</td>
<td>$\gamma_D(t) = \alpha + \beta_1 rSST_2(t) + \beta_2 UW_{1,8}(t) + \epsilon(t, t-1)$</td>
<td>2.18</td>
<td>0.97</td>
<td>0.25</td>
</tr>
<tr>
<td>3</td>
<td>$\gamma_D(t) = \alpha + \beta_1 rSST_2(t) + \epsilon(t, t-1)$</td>
<td>57.91</td>
<td>0.97</td>
<td>0.09</td>
</tr>
<tr>
<td>4</td>
<td>$\gamma_D(t) = \alpha + \beta_1 IL(t) + \epsilon(t, t-1)$</td>
<td>62.12</td>
<td>0.96</td>
<td>0.27</td>
</tr>
<tr>
<td>5</td>
<td>$\gamma_D(t) = \alpha + \beta_1 rSST_3(t) + \epsilon(t, t-1)$</td>
<td>63.91</td>
<td>0.98</td>
<td>0.16</td>
</tr>
<tr>
<td>6</td>
<td>$\gamma_D(t) = \alpha + \beta_1 rSST_1(t) + \epsilon(t, t-1)$</td>
<td>74.19</td>
<td>0.97</td>
<td>0.05</td>
</tr>
<tr>
<td>7</td>
<td>$\gamma_D(t) = \alpha + \beta_1 UW_{1,8}(t) + \epsilon(t, t-1)$</td>
<td>81.22</td>
<td>0.97</td>
<td>0.06</td>
</tr>
<tr>
<td>8</td>
<td>$\gamma_D(t) = \alpha + \beta_1 SLa(t) + \epsilon(t, t-1)$</td>
<td>117.53</td>
<td>0.98</td>
<td>-0.27</td>
</tr>
<tr>
<td>9</td>
<td>$\gamma_D(t) = \alpha + \beta_1 \xi(t) + \epsilon(t, t-1)$</td>
<td>132.34</td>
<td>0.97</td>
<td>-0.01</td>
</tr>
</tbody>
</table>
Table 6. Coefficient estimates, associated standard errors (SE), degrees of freedom (DF), t-value, and p-value, for the two highest ranked models describing chilipepper rockfish scaled otolith growth. The coefficients $rSST_2$, $IL$, and $UWI_{1.8}$ represent regional sea surface temperature, illumination index, and integrated/lagged coastal upwelling index time series, respectively.

<table>
<thead>
<tr>
<th>Coefficient</th>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
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<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-0.0624</td>
<td>0.1291</td>
<td>1127</td>
</tr>
<tr>
<td>$rSST_2$</td>
<td>0.0986</td>
<td>0.0102</td>
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<tr>
<td>$SI$</td>
<td>0.0017</td>
<td>0.0001</td>
<td>1127</td>
</tr>
<tr>
<td>$\Phi$</td>
<td>0.7638</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>Model 2</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>0.2141</td>
<td>0.1340</td>
<td>1127</td>
</tr>
<tr>
<td>$rSST_2$</td>
<td>0.0989</td>
<td>0.0108</td>
<td>1127</td>
</tr>
<tr>
<td>$UWI_{1.8}$</td>
<td>0.0013</td>
<td>0.0002</td>
<td>1127</td>
</tr>
<tr>
<td>$\Phi$</td>
<td>0.7976</td>
<td>-</td>
<td>-</td>
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</table>
Figure 16. Observed scaled otolith growth (SOG) time series, by year, for chilipepper rockfish (solid blue lines), with associated uncertainty (2 standard errors, blue dashed lines). Predictions are plotted in solid black lines and are generated from the highest ranked model for chilipepper (model 1).
Based on root mean square error (RMSE), model fits were better for some years than others. The three best-predicted years were 1985, 1986, and 2001, while the model predicted the 2003 growth data least well (Table 7). In general, model fits were weakly sensitive to the presence or absence of a given year’s data (Table 7). Surprisingly, year-specific RMSE was slightly reduced for two years, 1985 and 1997, which may reflect a poor fit to observations during a part of each of these years (Figure 19).
Table 7. Root mean square error (RMSE (model)) by year for model predictions of the highest ranked model explaining environment-growth relationships for chilepepper rockfish. A jack-knifed root mean square error (RMSE (jack-knife)) represents RMSE for each years’ predictions generated by a model fit to the data in the absence of that year.

<table>
<thead>
<tr>
<th>Year</th>
<th>N</th>
<th>RMSE (model)</th>
<th>RMSE (jack-knife)</th>
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<td>1984</td>
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<td>0.17</td>
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<tr>
<td>1985</td>
<td>38</td>
<td>0.12</td>
<td>0.12</td>
</tr>
<tr>
<td>1986</td>
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<td>1987</td>
<td>86</td>
<td>0.16</td>
<td>0.18</td>
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<td>1988</td>
<td>75</td>
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<tr>
<td>1989</td>
<td>17</td>
<td>0.16</td>
<td>0.18</td>
</tr>
<tr>
<td>1997</td>
<td>17</td>
<td>0.16</td>
<td>0.16</td>
</tr>
<tr>
<td>2001</td>
<td>31</td>
<td>0.14</td>
<td>0.14</td>
</tr>
<tr>
<td>2003</td>
<td>11</td>
<td>0.18</td>
<td>0.19</td>
</tr>
<tr>
<td>2004</td>
<td>9</td>
<td>0.17</td>
<td>0.18</td>
</tr>
</tbody>
</table>
Of the nine candidate models used to assess the environmental influence on widow rockfish SOG, the model with the lowest AIC score included $rSST_1$ and $IL$ (table 8). Collectively, these two parameters had explained approximately 5% of the overall variance in widow SOG based on a generalized $R^2$ calculation (table 8). In this model, the autocorrelation coefficient was 0.77 (table 9). Visually, however, the model predictions appeared to track the data relatively better than the 5% explained variability would suggest (figure 20), being driven largely by the effects of autocorrelation. A model relating SOG to $IL$ only was not a strong candidate per AIC ($\Delta AIC = 5.16$) yet explained slightly more of the variance in SOG (8%) due to the environmental term(s) according to the generalized $R^2$ while the autocorrelation coefficient remained virtually identical (table 9).

All seven parameters tested individually had statistically significant effects, with the exception of turbulence ($\xi$). Out of the three sea surface temperature time series, $rSST_1$ had the lowest AIC score and was consequently selected for the multivariate models, though none of the $rSST$ time series performed particularly well. Modeled individually, $rSST_1$ explained virtually none of the variability in growth based on the adjusted $R^2$ approximation, and the $rSST_1$ coefficient estimate in the best-fit model (table 8) was very small and negative, counter to what would have been theoretically expected. However, the model explained the majority of variation in growth (94-95%) when the autocorrelation term was included (table 8).
Table 8. List of candidate models used to assess environment-growth relationships for widow rockfish, where \( \gamma_D \) represents scaled otolith growth, \( \alpha \) is the model intercept, \( \beta_1 \) and \( \beta_2 \) are the estimated environmental time series coefficients, \( rSST_x \) are the three regionally averaged sea surface temperature time series, \( IL \) is the index of illumination, \( UWI_8 \) is an integrated/lagged index of coastal upwelling, \( SLa \) is a time series of sea level anomaly, \( \xi \) is a time series of regional turbulence, and \( \Phi \) is the auto-correlated error term. Models are ranked low to high using AIC score, and goodness-of-fit is represented by generalized \( R^2 \) for each model including the effects of autocorrelation (\( R^2 \) FULL) and only the effects of the environmental variables (\( R^2 \) ENV).

<table>
<thead>
<tr>
<th>Rank</th>
<th>Model Description</th>
<th>( \Delta \text{AIC} )</th>
<th>( R^2 \text{ FULL} )</th>
<th>( R^2 \text{ ENV} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>( \gamma_D(t) = \alpha + \beta_1 rSST_1(t) + \beta_2 IL(t) + \epsilon(t, t-1) )</td>
<td>0</td>
<td>0.95</td>
<td>0.05</td>
</tr>
<tr>
<td>2</td>
<td>( \gamma_D(t) = \alpha + \beta_1 IL(t) + \epsilon(t, t-1) )</td>
<td>5.16</td>
<td>0.95</td>
<td>0.08</td>
</tr>
<tr>
<td>3</td>
<td>( \gamma_D(t) = \alpha + \beta_1 SLa(t) + \epsilon(t, t-1) )</td>
<td>44.02</td>
<td>0.95</td>
<td>-0.77</td>
</tr>
<tr>
<td>4</td>
<td>( \gamma_D(t) = \alpha + \beta_1 UWI_8(t) + \epsilon(t, t-1) )</td>
<td>130.30</td>
<td>0.94</td>
<td>-0.17</td>
</tr>
<tr>
<td>5</td>
<td>( \gamma_D(t) = \alpha + \beta_1 rSST_1(t) + \beta_2 UWI_8(t) + \epsilon(t, t-1) )</td>
<td>139.19</td>
<td>0.94</td>
<td>-0.17</td>
</tr>
<tr>
<td>6</td>
<td>( \gamma_D(t) = \alpha + \beta_1 rSST_1(t) + \epsilon(t, t-1) )</td>
<td>404.23</td>
<td>0.94</td>
<td>-0.25</td>
</tr>
<tr>
<td>7</td>
<td>( \gamma_D(t) = \alpha + \beta_1 rSST_3(t) + \epsilon(t, t-1) )</td>
<td>411.51</td>
<td>0.95</td>
<td>-0.15</td>
</tr>
<tr>
<td>8</td>
<td>( \gamma_D(t) = \alpha + \beta_1 rSST_2(t) + \epsilon(t, t-1) )</td>
<td>434.98</td>
<td>0.95</td>
<td>-0.15</td>
</tr>
<tr>
<td>9</td>
<td>( \gamma_D(t) = \alpha + \beta_1 \xi(t) + \epsilon(t, t-1) )</td>
<td>435.21</td>
<td>0.95</td>
<td>-0.08</td>
</tr>
</tbody>
</table>
Table 9. Coefficient estimates, associated standard errors (SE), degrees of freedom (DF), t-value, and p-value, for the two highest ranked models describing widow rockfish scaled otolith growth. The coefficients $rSST_t$ and $IL$ represent regional sea surface temperature and illumination index time series, respectively.

<table>
<thead>
<tr>
<th>Coefficient</th>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Model 1</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>1.3587</td>
<td>0.1403</td>
<td>1267</td>
</tr>
<tr>
<td>$rSST_t$</td>
<td>-0.0424</td>
<td>0.0112</td>
<td>1267</td>
</tr>
<tr>
<td>$IL$</td>
<td>0.0032</td>
<td>0.0001</td>
<td>1267</td>
</tr>
<tr>
<td>$\Phi$</td>
<td>0.7727</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Model 2</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>0.8397</td>
<td>0.0311</td>
<td>1268</td>
</tr>
<tr>
<td>$IL$</td>
<td>0.0033</td>
<td>0.0001</td>
<td>1268</td>
</tr>
<tr>
<td>$\Phi$</td>
<td>0.7731</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 17. Observed scaled otolith growth (SOG) time series, by year, for widow rockfish (solid blue lines), with associated uncertainty (2 standard errors, blue dashed lines). Predictions are plotted in solid black lines and are generated from the highest ranked model for widow (model 1).
RMSE estimates for each year suggest that the best-fit model for widow rockfish fit the data relatively consistently over time, with the exception of 1994 and 1995, which had notably poorer fits than the other years (table 10). Plots of observed vs. predicted data for these years (figure 20) shows that predicted growth was generally much lower than observed. However, predictions from 1986, 1989, 1993, and 2001 were well matched to observations during periods where $\gamma_D$ had relatively high precision (table 10) as can be seen in comparisons of year-specific observations and predictions (Figure 20). There were no years that appeared to have substantial leverage over the fit of the best model (Table 10). However, RMSE declined for two years (1990 and 1994) when year specific data was omitted from the analysis. The original model fit was relatively poor in 1994, and the original model fit poorly to part of 1990 (late in the season).
Table 10. Root mean square error (RMSE (model)) by year for model predictions of the highest ranked model explaining environment-growth relationships for widow rockfish. A jack-knifed root mean square error (RMSE (jack-knife)) represents RMSE for each years’ predictions generated by a model fit to the data in the absence of that year.

<table>
<thead>
<tr>
<th>Year</th>
<th>N</th>
<th>RMSE (model)</th>
<th>RMSE (jack-knife)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1985</td>
<td>25</td>
<td>0.18</td>
<td>0.19</td>
</tr>
<tr>
<td>1986</td>
<td>10</td>
<td>0.13</td>
<td>0.13</td>
</tr>
<tr>
<td>1987</td>
<td>49</td>
<td>0.19</td>
<td>0.21</td>
</tr>
<tr>
<td>1988</td>
<td>50</td>
<td>0.15</td>
<td>0.17</td>
</tr>
<tr>
<td>1989</td>
<td>24</td>
<td>0.15</td>
<td>0.15</td>
</tr>
<tr>
<td>1990</td>
<td>29</td>
<td>0.16</td>
<td>0.16</td>
</tr>
<tr>
<td>1991</td>
<td>30</td>
<td>0.14</td>
<td>0.14</td>
</tr>
<tr>
<td>1993</td>
<td>26</td>
<td>0.17</td>
<td>0.18</td>
</tr>
<tr>
<td>1994</td>
<td>10</td>
<td>0.25</td>
<td>0.25</td>
</tr>
<tr>
<td>1995</td>
<td>11</td>
<td>0.32</td>
<td>0.32</td>
</tr>
<tr>
<td>2001</td>
<td>29</td>
<td>0.09</td>
<td>0.09</td>
</tr>
<tr>
<td>2004</td>
<td>12</td>
<td>0.13</td>
<td>0.13</td>
</tr>
</tbody>
</table>
Yellowtail

Of the nine candidate models fit to yellowtail SOG data, the highest ranked model included time series of $r_{SST}^2$ and $IL$, which and collectively explained 35% of the overall variance in yellowtail SOG based on the generalized $R^2$ (table 11, figure 21). The autocorrelation coefficient was 0.71, among the lowest of any model estimated for any of the three species (table 12). The model that included $r_{SST}^2$ and $UW_{I,8}$ (model 2) explained 30% of variance due to both the environmental terms, but the AIC score was over 26 units higher. Plots of predictions from model 2 are also presented (figure 22), and appear to track variability in SOG slightly less well based on a visual comparison. When modeled as individual parameters, $UW_{I,8}, SLa,$ and $\xi$ did not appear to explain any of the variability in SOG based on generalized $R^2$. Out of the three sea surface temperature time series, $r_{SST}^2$ had the lowest AIC score and was consequently selected for the multivariate models, performing much better than the other two $r_{SST}$ time series (table 11).
Table 11. List of candidate models used to assess environment-growth relationships for yellowtail rockfish, where $\gamma_D$ represents scaled otolith growth, $\alpha$ is the model intercept, $\beta_1$ and $\beta_2$ are the estimated environmental time series coefficients, $r_{SST_x}$ are the three regionally averaged sea surface temperature time series, $IL$ is the index of illumination, $UWI_8$ is an integrated/lagged index of coastal upwelling, $SLa$ is a time series of sea level anomaly, $\xi$ is a time series of regional turbulence, and $\Phi$ is the auto-correlated error term. Models are ranked low to high using AIC score, and goodness-of-fit is represented by generalized $R^2$ for each model including the effects of autocorrelation ($R^2$ FULL) and only the effects of the environmental variables ($R^2$ ENV).

<table>
<thead>
<tr>
<th>Rank</th>
<th>Model Description</th>
<th>$\Delta$AIC</th>
<th>$R^2$ FULL</th>
<th>$R^2$ ENV</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$\gamma_D(t) = \alpha + \beta_1 r_{SST_2}(t) + \beta_2 IL(t) + \epsilon(t, t-1)$</td>
<td>0</td>
<td>0.94</td>
<td>0.30</td>
</tr>
<tr>
<td>2</td>
<td>$\gamma_D(t) = \alpha + \beta_1 r_{SST_2}(t) + \beta_2 UWI_8(t) + \epsilon(t, t-1)$</td>
<td>26.06</td>
<td>0.93</td>
<td>0.30</td>
</tr>
<tr>
<td>3</td>
<td>$\gamma_D(t) = \alpha + \beta_1 r_{SST_2}(t) + \epsilon(t, t-1)$</td>
<td>46.65</td>
<td>0.94</td>
<td>0.16</td>
</tr>
<tr>
<td>4</td>
<td>$\gamma_D(t) = \alpha + \beta_1 IL(t) + \epsilon(t, t-1)$</td>
<td>49.13</td>
<td>0.93</td>
<td>0.08</td>
</tr>
<tr>
<td>5</td>
<td>$\gamma_D(t) = \alpha + \beta_1 r_{SST_3}(t) + \epsilon(t, t-1)$</td>
<td>61.72</td>
<td>0.93</td>
<td>0.23</td>
</tr>
<tr>
<td>6</td>
<td>$\gamma_D(t) = \alpha + \beta_1 r_{SST_1}(t) + \epsilon(t, t-1)$</td>
<td>67.37</td>
<td>0.94</td>
<td>0.09</td>
</tr>
<tr>
<td>7</td>
<td>$\gamma_D(t) = \alpha + \beta_1 UWI_8(t) + \epsilon(t, t-1)$</td>
<td>100.17</td>
<td>0.93</td>
<td>-0.03</td>
</tr>
<tr>
<td>8</td>
<td>$\gamma_D(t) = \alpha + \beta_1 SLa(t) + \epsilon(t, t-1)$</td>
<td>120.54</td>
<td>0.93</td>
<td>-0.16</td>
</tr>
<tr>
<td>9</td>
<td>$\gamma_D(t) = \alpha + \beta_1 \xi(t) + \epsilon(t, t-1)$</td>
<td>127.69</td>
<td>0.93</td>
<td>-0.13</td>
</tr>
</tbody>
</table>
Table 12. Coefficient estimates, associated standard errors (SE), degrees of freedom (DF), t-value, and p-value, for the two highest ranked models describing yellowtail rockfish scaled otolith growth. The coefficients $rSST_2$, $IL$, and $UW_{1,8}$ represent regional sea surface temperature, illumination index, and integrated/lagged coastal upwelling index time series, respectively.

<table>
<thead>
<tr>
<th>Coefficient</th>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Model 1</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>0.2308</td>
<td>0.1397</td>
<td>1499</td>
</tr>
<tr>
<td>$rSST_2$</td>
<td>0.0883</td>
<td>0.0113</td>
<td>1499</td>
</tr>
<tr>
<td>$IL$</td>
<td>0.0012</td>
<td>0.0001</td>
<td>1499</td>
</tr>
<tr>
<td>$\Phi$</td>
<td>0.7066</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>Model 2</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>0.2071</td>
<td>0.1386</td>
<td>1499</td>
</tr>
<tr>
<td>$rSST_2$</td>
<td>0.1063</td>
<td>0.0111</td>
<td>1499</td>
</tr>
<tr>
<td>$UW_{1,8}$</td>
<td>0.0010</td>
<td>0.0001</td>
<td>1499</td>
</tr>
<tr>
<td>$\Phi$</td>
<td>0.6913</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure 18. Observed scaled otolith growth (SOG) time series, by year, for yellowtail rockfish (solid blue lines), with associated uncertainty (2 standard errors, blue dashed lines). Predictions are plotted in solid black lines and are generated from the highest ranked model for yellowtail (model 1).
Figure 22. Observed scaled otolith growth (SOG) time series, by year, for yellowtail rockfish (solid blue lines), with associated uncertainty (2 standard errors, blue dashed lines). Predictions are plotted in solid black lines and are generated from the second highest ranked model for yellowtail (model 2), which included rSST$_2$ and IL.
The fit of the best-fit model for yellowtail rockfish appears to have been poor for 1989, 1992, and 1995 relative to other years, as indicated by sensitivity of years-specific RMSE to exclusion of these years’ data. Based on plots of observed and predicted time series, it appears that 1989 was consistently overestimated, while both 1992 and 1995 were consistently underestimated throughout the growing season (figure 21). The remaining years fit relatively well, with model fits exhibiting little sensitivity to inclusion or exclusion of data from particular years (table 13). RMSE declined for 1992 when data for that year were excluded from the fit, suggesting that the fit of the global model to 1992 was relatively poor.
Table 13. Root mean square error (RMSE (model)) by year for model predictions of the highest ranked model explaining environment-growth relationships for yellowtail rockfish. A jack-knifed root mean square error (RMSE (jack-knife)) represents RMSE for each years’ predictions generated by a model fit to the data in the absence of that year.

<table>
<thead>
<tr>
<th>Year</th>
<th>N</th>
<th>RMSE (model)</th>
<th>RMSE (jack-knife)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1984</td>
<td>51</td>
<td>0.16</td>
<td>0.17</td>
</tr>
<tr>
<td>1985</td>
<td>19</td>
<td>0.13</td>
<td>0.14</td>
</tr>
<tr>
<td>1986</td>
<td>50</td>
<td>0.15</td>
<td>0.16</td>
</tr>
<tr>
<td>1987</td>
<td>84</td>
<td>0.17</td>
<td>0.17</td>
</tr>
<tr>
<td>1988</td>
<td>54</td>
<td>0.16</td>
<td>0.16</td>
</tr>
<tr>
<td>1989</td>
<td>22</td>
<td>0.25</td>
<td>0.27</td>
</tr>
<tr>
<td>1990</td>
<td>23</td>
<td>0.15</td>
<td>0.15</td>
</tr>
<tr>
<td>1991</td>
<td>30</td>
<td>0.20</td>
<td>0.21</td>
</tr>
<tr>
<td>1992</td>
<td>6</td>
<td>0.23</td>
<td>0.23</td>
</tr>
<tr>
<td>1993</td>
<td>20</td>
<td>0.18</td>
<td>0.18</td>
</tr>
<tr>
<td>1994</td>
<td>4</td>
<td>0.20</td>
<td>0.20</td>
</tr>
<tr>
<td>1995</td>
<td>6</td>
<td>0.24</td>
<td>0.24</td>
</tr>
<tr>
<td>2001</td>
<td>25</td>
<td>0.15</td>
<td>0.15</td>
</tr>
<tr>
<td>2004</td>
<td>2</td>
<td>0.18</td>
<td>0.19</td>
</tr>
</tbody>
</table>
DISCUSSION

Based on analysis of otolith growth increments during ELHS for three species of rockfish off central California, I was able to explain more variability in daily otolith growth patterns in terms of linear functions of several indices of environmental conditions than reported in previous research (Ralston 1995). Importantly, several of the patterns described here appear to be robust across a data set that spans several decades, and do not require estimation of unexplained random year-effects. This analysis represents a step forward in understanding mechanisms that connect environmental conditions to recruitment variability for winter-spawning rockfishes, in that it provides strong evidence that environmental conditions affect larval growth. Best-fit models included only one or two environmental terms and generally predicted growth data well, successfully capturing unique seasonal patterns in growth for each species. Environmental variables in best-fit models were able to account for up to 32% of the variability in SOG for chilipepper, 30% for yellowtail rockfish, and 5% for widow rockfish. As anticipated, a significant portion of the overall error was attributed to the autocorrelated error term (φ), which ranged from 0.71 – 0.77 for the three best-fitting models.
Comparison to Previous Larval Rockfish Environment-Growth Analysis

This study builds upon and extends Ralston’s (1995) previous analysis of environment-growth relationships based on data from the late 1980s that have been included in the data analyzed here. In both studies, initial analysis of otolith increment data yielded very similar age-growth relationships (see below). However, relative to the previous work, the present study appears to have attributed substantially more variability in growth to environmental conditions—nearly doubling the amount of variability explained—as a result of several differences in the modeling approach taken. Some differences are likely to have had relatively modest effects, as for example my decision to assume a consistent ontogenetic growth pattern across all years, rather than estimating age-growth relationships separately for each cohort. Other differences were more substantial, including the decision to structure the models to estimate ‘global’ environment-growth relationships across the entire data set rather than including a random year effect to account for unexplained inter-annual variability. I also chose to focus on estimating linear (as opposed to quadratic) relationships between environmental conditions and growth, as well as the use of a conceptual model that connect environmental parameters to otolith growth in ways that account for mechanisms that likely involve integrated or lagged effects (Figure 1). As a consequence of these differences, I found evidence for several strong, linear environment-growth relationships that differ substantially from the weak quadratic relationships between growth and environmental conditions reported in Ralston (1995).
Accounting for Ontogenetic Effects on Growth

Ontogenetic patterns in otolith growth were similar among species, and are consistent with the piece-wise linear growth model developed by Laidig et al. (1991) for shortbelly rockfish (*Sebastes jordani*) and the patterns reported by Ralston (1995) for the species studied here. ANOVA-based estimation of ontogenetic growth patterns yielded an age-growth relationship that was somewhat more complex than simple Gompertz or logistic models commonly used to describe growth of fish during early life (Laidig et al. 1991, Otterlei et al. 1999), and may have captured the effect of substantial developmental changes related to flexion or other ontogenetic milestones (Zweifel and Lasker 1976). Furthermore, this flexible approach minimized the potential for bias stemming from selection of a particular growth model, which is especially true during early larval stages, when growth would be systematically over- or underestimated as a function of age when using Gompertz-based models (Laidig et al. 1991).

Environmental Effects on Larval Growth

In general, the results were consistent with our expectations regarding environment-growth relationships as summarized in the conceptual model. Correlations between growth of each species and coincident environmental conditions (e.g., temperature) suggest substantial environmental influence through control of metabolic activity. Correlations with integrated-lagged indices of ecosystem enrichment were less strong but provide evidence that productivity affects growth as well. The best-fit model for
yellowtail rockfish included additive linear effects of sea surface temperature and upwelling, while growth of chilipepper rockfish was best explained by sea surface temperature and an index of illumination. Growth of widow rockfish was best explained by a combination of SST and illumination, but growth variability for widow was the least well explained of the three species overall. In the following paragraphs, I provide an overview and interpretation of the results from my analysis in light of our conceptual model (figure 1) and previous findings, as they were modeled individually to present a relative sense of how each variable relates to growth.

Temperature

Otolith growth rates in all three species showed an increasing, linear response to regional sea surface temperature (rSST) consistent with several previous field-based studies which also found linear temperature-growth relationships in larval fishes (Dower et al 2002, Meekan et al 2003, Green and Fisher 2004). Previous work has also identified parabolic relationships between the effects of temperature and larval growth (Boehlert 1981, Ralston 1995, Otterlei et al 1999, Baumann et al 2003, Buckley et al 2004, Baumann et al 2006, Takasuka and Aoki 2006). Laboratory experiments have shown that larval fish grow linearly with temperature when food is not a limiting factor (Otterlei et al 1999, Buckley et al 2004), a pattern also reported for juvenile black rockfish (*Sebastes melanops*) (Yoklavich and Boehlert 1984). However, it is also possible that linear responses may be observed when the range of observed temperatures does not exceed the optimum temperature above which growth rates decline. In this case,
it remains unlikely that fish larvae who have experienced highly stressful temperature conditions would have survived to be captured in the field.

For both widow and yellowtail rockfish, growth variability was better explained by regional sea surface temperature indices that extended further offshore (rSST2 and rSST3), indicating that larvae may have been located offshore of the colder, near-shore upwelling zone, or that the additional variability captured in these time series was a proxy for conditions not considered in this analysis (e.g., frontal structure). Widow rockfish growth, however, was explained poorly by all rSST time series, producing negative $R^2$ values indicates. In contrast, the best-fitting rSST time series was able to explain as 9% and 11% of growth variability for chilipepper and yellowtail rockfishes, respectively. Results from mid-water trawls conducted at different depths off central California suggest that widow rockfish larvae may occur at greater depths on average than either yellowtail or chilipepper (Lenarz et al 1991), which might undermine the validity of sea surface temperature as a proxy for the temperature that larval widow rockfish actually encountered. If widow rockfish tend to remain at depth, the range of temperatures that they encounter may be substantially narrower than the range encountered by species that tend to inhabit shallower depths.

**Upwelling**

Otolith growth rates also showed positive, linear responses to an index of upwelling that accounted for typical response times of the ocean to wind forcing and the lag in biological response to enrichment. This upwelling term was able to account for
approximately 5% of the variability in growth for chilipepper rockfish, yet generated negative $R^2$ values in models fit to yellowtail and widow rockfish growth data. This finding appears consistent with the generally tenuous relationships between measures of upwelling and rockfish growth (Ralston 1995) and abundance (Laidig et al 2007, Ralston et al 2013). The anticipated improvement in explanatory power attributed to upwelling was not fully realized despite theoretical improvements into how I brought upwelling into the model. Growth is not likely to respond immediately to upwelling (save through possible effects on temperature), as the ecological response to upwelling takes at least several days to develop (Barber et al 1971). Thus, I integrated and lagged the time series so to better represent the ecosystem response to upwelling (i.e., zooplankton production) that potentially contributes to variability in growth. The treatment of the upwelling time series remains an oversimplification of reality and does not address the benefits derived from upwelling variability, suggesting future research into upwelling-growth dynamics is still warranted.

Sea level anomaly

Sea level anomaly was included in the conceptual model because of its link to thermocline depth (e.g. Huyer 1987), potential modulation of how effectively upwelling winds inject nutrients into the system (Chavez et al 2002, Doney et al 2012), and connections to basin- and regional-scale climate indices of productivity, yet I found no support for the effects of sea level on growth rate, at least over short time scales. In contrast, monthly mean sea level during key times of the year (spring) has been linked to
recruitment strength in several species (Ralston et al 2013, Schirripa and Colbert 2006), and is presumed to reflect local responses to larger-scale climate forcing. Low frequency changes in coastal sea level typically reflect basin-scale processes such as PDO, NPGO, and ENSO, which may have limited our ability to detect effects on shorter (daily) time scales. Or alternatively, a better approach in the future may involve directly structuring the modulating effects of sea level on the upwelling time series itself, thereby creating an “effective” measure of upwelling. We briefly examined such an approach that in the end did not prove any more informative than the upwelling time series alone. However, there remains a strong theoretical basis for exploring such a functional relationship in the future.

Additionally, the surviving rockfish that constitute our sample may not have been exposed to enough contrast in sea level data to have had a detectable influence. The effects of sea level are most pronounced in strong El Niño years, where sea level is anomalously high, such as those that effected the 1983, 1992, and 1998 year classes. We have very few, if any, observations from these years as a result of low overall survival and consequently are not able to capture a strongly negative effect of sea level anomaly. Negative SLa typically corresponds to periods of greater enrichment, yet our analysis includes data from the 1989 and 2001 La Nina years and no significant effect was detected. El Niño years, and associated positive sea levels, may have disproportionately greater consequences on ocean productivity than their counterpart, perhaps further limiting our ability to detect a relationship between SLa and growth using a linear model.
Illumination

Illumination was found to have a consistently positive effect on otolith growth in all three species, explaining 27% of variability in growth for chilipepper, 8% for widow, and 8% yellowtail rockfish in a uni-variate analysis of each species. This pattern may capture the direct benefits of increasing light levels for larval fishes foraging success, in that greater illumination increases the range over which prey can be detected visually (Fiksen et al 1998, Fiksen and MacKenzie 2002). Light may also drive primary production when nutrients are not limiting, and in that case would likely correspond to larval prey production similarly to the integrated and lagged upwelling-based enrichment index. It is also possible that the illumination index serves as a proxy for the broader coincidence of several conditions beneficial to growth in rockfish early life history. In the study region, periods of higher light levels during the winter and early spring are an indicator of clear skies and weaker, and often northerly, upwelling-favorable winds. In contrast, lower illumination are more likely to indicate periods of stormy conditions, or at least periods of limited light for phytoplankton. The Pearson’s correlation test showed a high correlation coefficient (0.65) between upwelling and illumination, further suggesting that illumination may functionally serve as a proxy index of biological production.

Micro-scale turbulence

I did not find a significant relationship between otolith growth rates and a wind-based index of micro-scale turbulence for any of the three rockfish species studied. The lack of
observed relationship was almost certainly the result of poor quality wind data, though previous research into the effects of turbulence on larval fish feeding, growth, and survival has presented conflicting results (Maillet and Checkley 1991, Gallego et al. 1996, MacKenzie 2000, Dower et al. 2002). Laboratory studies with controlled feeding environments have noted a clear non-linear trend with micro-scale turbulence (i.e. particle movement) and foraging efficiency (MacKenzie et al. 1994, Fiksen and MacKenzie 2002), yet results from field studies were generally more equivocal (Mackenzie 2000, Reiss et al. 2002). It may be possible that field study results, including the present results, may be confounded by the dual effect of turbulence as an enrichment mechanism and as a non-linear influence on foraging efficiency. The relationship to foraging efficiency is also tightly linked to fish size—being stronger for young, small larvae that are poor swimmers—and may have been blurred by the decomposition of age- and date- effects on otolith growth.

**Goodness-of-Fit**

In general, many of the environmental variables were able to contribute to explained growth variability, as measured by generalized $R^2$ of models predicted without the effects of the auto-regression term. However, there were certain cases where models including certain variables generating strongly negative $R^2$ values, indicating exceedingly poor fits. In particular, models fit to widow rockfish generated negative $R^2$ values for all candidate models except those containing Illumination. Considering the strong theoretical basis for the environment-growth relationships tested, this result demonstrates
either that a major bias exists in the environmental data selected or that the model form chosen was incorrect. No apparent nonlinear relationship was detected between growth and environmental data, yet a more thorough analysis into the relationship form, as well as the interaction among environmental variables, would likely benefit future modeling efforts.

**Autoregressive Errors**

The autoregressive error term contributed significantly to observed variability in SOG. This is not entirely surprising, as individual fish are likely to continue along a growth trajectory for a variety of reasons, including the buffering effects of accumulated energy reserves on growth and continued foraging activity. However, the autocorrelation term may also have captured systematic biases between predicted and observed values under certain circumstances. There are instances where the predicted values consistently under- or over-estimate the observations within a portion of a given year. For example, in contrast to the very strong fit to chilipepper rockfish SOG in 1986 (figure 19), the model consistently overestimated SOG for much of 1987 until later in the time series for that year when it began closely tracking the observations.

Similar patterns can be observed in several years for each species, but in the majority of the cases where departures occur, the predicted values appear to generally track higher-frequency patterns in the observed data, but at values either consistently higher or lower than predicted. These cases may represent bias between our regional indices of environmental conditions and the local conditions experienced by the subset of fish
contributing to the mean $\gamma$ for a period of time. If so, abrupt changes in this offset may reflect a shift in the fish that contribute to estimates of $\gamma$ over the course of the season. Future work based on hind-cast trajectories and conditions may help to resolve these dynamics.

Potential Sources of Bias

Our analysis is potentially confounded by the fact that our samples are drawn entirely from individuals who survived the larval stages where mortality is most variable (Ralston and Howard 1995), which greatly limits our ability to resolve growth patterns experienced by the entire cohort. The sample bias likely resulted in over-estimating average growth rates at the population level, and thus limits our ability to detect any relationship between growth and recruitment. Moreover, in years with poor survival (and presumably poor average growth), few (if any) samples are available. Those that are available most likely represent survivors drawn from that small fraction of the cohort exposed to the best of otherwise marginal ocean conditions, perhaps by encountering those limited areas where production of prey sufficed to support growth under higher than normal temperatures. In such cases, mean environmental conditions may be less representative of conditions encountered by survivors. In contrast, samples are typically more abundant during highly productive (often cooler) years in which favorable conditions are widespread in space and time. In these cases, the expected trade-off between available prey (enrichment) and thermal controls on growth may more strongly influence our observations.
The otoliths contained in our data-set were also non-randomly sampled across the region, but were rather selected to uniformly span the size range of all of the fish captured by the REAAS for the entire year. I excluded from my analysis all data obtained after 2004 in an effort to reduce the geographic scope of the samples to the region off of central California. Even so, fish were still non-uniformly distributed within the sample, both between and within years. The potential concern is that, in years where fish distribution was limited to a narrow region, that regionally averaged conditions used in the model would not be reflective of the mean growth response in our sample. In addition, the data was non-uniformly distributed across time within a year, leading to the potential of merging two distinct cohorts. Furthermore, it is also possible that variation in sample size between years may have an impact in the accuracy of the data in years where few otoliths were collected, though this does not appear to have a large impact based on jack-knife analysis results.

Summary and Future Directions

Despite the several caveats outlined above, the results from this work appear to be robust and make a strong case for significant environmental influences on growth rates of larval and juvenile rockfishes off central California. Linear relationships with temperature and indicators of productivity are plausible and consistent with expected responses. Our ability to resolve these relationships was likely improved over previous work by insight taken from our conceptual model, which allowed us to frame more mechanistic hypotheses and identify relevant environmental parameters a priori, to avoid
correlations among environmental variables, and to identify potentially contradictory
effects of inherent trade-off between temperature and enrichment inherent to upwelling
regions.

Otolith growth patterns showed remarkable coherence among the three species at
intra- and inter-annual time scales, which suggests that the results of the present study
may represent dynamics affecting a broad range of winter-spawning rockfishes.
Likewise, differences in the level of explanatory power of certain environmental
parameters among species can be used to identify areas where future work is warranted.
Future research into the three dimensional spatial variation of fish larvae would be
beneficial, as would how environmental indicators vary and evolve in a three-
dimensional context. In this light, future work making use of individual-based models
(IBMs) capable of capturing the relationships resolved in this study as well as potentially
size-dependent environmental effects, as may be the case with the effects of micro-scale
turbulence on foraging success, and realistic circulation-ecosystem models are likely to
yield substantial insight to recruitment variability by resolving full-cohort dynamics. The
present study contributes directly to this effort by providing insight into environment-
growth relationships, at least for survivors, to which the upper range of simulated larval
growth trajectories can be tuned. Moreover, the underlying data set provides a rich
resource of information for future analyses using techniques that model data at the
individual level, rather than mean responses within a cohort.
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