

Evidence of bottom-up limitations in nearshore marine systems based on otolith proxies of fish growth

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Abstract Fish otolith growth increments were used as indices of annual production at nine nearshore sites within the Alaska Coastal Current (downwelling region) and California Current (upwelling region) systems (~36–60°N). Black rockfish (*Sebastes melanops*) and kelp greenling (*Hexagrammos decagrammus*) were identified as useful indicators in pelagic and benthic nearshore food webs, respectively. To examine the support for bottom-up limitations, common oceanographic indices of production [sea surface temperature (SST), upwelling, and chlorophyll-*a* concentration] during summer (April–September) were compared to spatial and temporal differences in fish growth using linear mixed models. The relationship between pelagic black rockfish growth and SST was positive in the cooler Alaska Coastal Current and negative in the warmer California Current. These contrasting growth responses to SST among current systems are consistent with the optimal

stability window hypothesis in which pelagic production is maximized at intermediate levels of water column stability. Increased growth rates of black rockfish were associated with higher chlorophyll concentrations in the California Current only, but black rockfish growth was unrelated to the upwelling index in either current system. Benthic kelp greenling growth rates were positively associated with warmer temperatures and relaxation of downwelling (upwelling index near zero) in the Alaska Coastal Current, while none of the oceanographic indices were related to their growth in the California Current. Overall, our results are consistent with bottom-up forcing of nearshore marine ecosystems—light and nutrients constrain primary production in pelagic food webs, and temperature constrains benthic food webs.

Introduction

Nearshore temperate kelp forests (defined here to be within 1 km of shore) are among the world's most productive marine habitats, supporting a diversity of ecologically and economically important fish, bird, and mammal populations. Top-down competition and trophic cascades have long been identified as important for ecosystem functioning in these nearshore systems (Menge 2000), while bottom-up controls have received less attention, due in large part to abundant photosynthetic biomass from the combined production of benthic macroalgae and water column phytoplankton (Duggins et al. 1989; von Biela et al. submitted), both of which provide a robust foraging base for a variety of resident and nonresident species (Agardy et al. 2005). Indeed, bottom-up limitations may explain the high interannual and spatial variability in nearshore production (Harley et al. 2006; Cloern and Jassby 2008; Cavanaugh

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et al. 2011), but few hypotheses have been tested or developed to explain these patterns (Hoegh-Guldberg and Bruno 2010). Bottom-up processes operating offshore may also be important, for example by contributing to the onshore advection of nutrients or plankton (Steneck et al. 2002; Barth et al. 2007; McPhee-Shaw et al. 2011). Disentangling these processes and establishing climate–biology relationships are, however, limited by the availability of long-term biological datasets for nearshore resident species, especially at upper trophic levels.

In offshore pelagic systems, sea surface temperature (SST), upwelling, and chlorophyll concentrations are good predictors of marine production and biomass at higher trophic levels (Ware and Thomson 2005; Behrenfeld et al. 2006; Mueter et al. 2009; Demarcq 2009). Water column stability can be related to SST (Boyce et al. 2010), with cooler SST indicating stronger vertical mixing and availability of deep water nutrient sources (Sydeman and Allen 1999; Chavez and Messié 2009; Demarcq 2009; Black et al. 2011) and warmer SST reflecting seasonal increases in water column stability that support photosynthesis (Mueter et al. 2009; Strom et al. 2010; Boyce et al. 2010). Primary production may be maximized at intermediate levels of water column stability with sufficient mixing to replenish nutrients and enough stratification to retain phytoplankton in the photic zone (Sverdrup et al. 1942; Gargett 1997). Coastal upwelling indices are correlates for large-scale vertical mixing of deeper, nutrient-rich water that promotes production in nutrient-limited systems, or hinders production in light-limited systems that benefit from increased stratification (Barth et al. 2007; Demarcq 2009; Takahashi et al. 2012). Satellite-based chlorophyll-*a* indices approximate phytoplankton standing stock biomass available to aquatic food webs; higher values of chlorophyll-*a* have been associated with increased fish catches (Ware and Thomson 2005; Boyce et al. 2010).

In contrast to patterns found in pelagic systems, benthic production is associated with reduced upwelling and warmer temperatures, which is consistent across upwelling and downwelling regions (Phillips 2005; Blanchette et al. 2006). Warmer water present during downwelling or relaxed upwelling conditions may be associated with increases in invertebrate larval recruitment if onshore advection leads to delivery of zooplankton or detritus to the benthic invertebrate communities (Phillips 2005; Blanchette et al. 2006). Growth rates of benthic consumers have been linked to chlorophyll concentrations in some (Menge et al. 1997) but not all cases examined (Phillips 2005; Blanchette et al. 2006).

To understand oceanographic influences on nearshore systems, we developed a network of otolith growth records from multiple sites spanning two current systems with contrasting oceanography, and then we compared fish

growth response to spatial and temporal variation in SST, upwelling, and chlorophyll concentrations. Black rockfish (*Sebastes melanops*) and kelp greenling (*Hexagrammos decagrammus*) were identified for this study as useful indicator species feeding in pelagic and benthic nearshore food webs, respectively, because they are non-migratory, nearshore resident species with generalist diets that can be caught easily throughout a wide geographic range (Parker et al. 2007; Freiwald 2009; Love 2011; Green and Starr 2011). Black rockfish feed in the water column on forage fish including Pacific herring (*Clupea pallasii*), sand lance (*Ammodytes hexapterus*), and juvenile salmon (*Oncorhynchus* spp.) and invertebrates, such as crab megalopae (Love et al. 2002; Love 2011). Kelp greenling are benthic generalists, foraging on a variety of benthic invertebrates including snails, sea cucumbers, decorator crabs, and brittle stars (Moulton 1977; Love 2011). Both species are widely distributed from the Aleutian Islands to central California (Love 2011), spanning the Alaska Coastal Current and California Current and thus allowing comparisons between downwelling and upwelling current systems (Fig. 1).

We considered hypotheses that examine bottom-up limits on nearshore production under the assumptions that pelagic nearshore food webs are nutrient limited in the California Current and light limited in the Alaska Coastal Current at the level of primary production, and benthic nearshore food webs are limited by temperature effects on benthic invertebrates or primary production. Specifically, we examined the following bottom-up hypotheses for the pelagic nearshore using black rockfish: (H₁) Fish growth is positively associated with cooler summer temperatures in the California Current and warmer summer temperatures in the Alaska Coastal Current; (H₂) fish growth is positively associated with upwelling in the California Current system, and fish growth is negatively associated with downwelling in the Alaska Coastal Current system; and (H₃) fish growth in both current systems is positively associated with local summer chlorophyll concentrations. Benthic nearshore (i.e., kelp greenling) hypotheses are that: (H₄) Fish growth is positively associated with warmer temperatures in both systems; (H₅) fish growth is positively associated with relaxation of upwelling in the California Current and downwelling in the Alaska Current systems; and (H₆) fish growth is positively associated with local increases in summer chlorophyll concentrations. As these hypotheses involve conditions in the current year of growth and our focal species tend to consume prey ≥ 1 year old, our analyses assume that changing conditions likely influence nearshore fish by controlling the quality, rather than the abundance, of their prey. The condition of key prey groups (forage fish and invertebrates) is already known to respond quickly (within the year) to environmental conditions (Asthorsson and Gislason 1998; Robards et al. 2002; Phillips

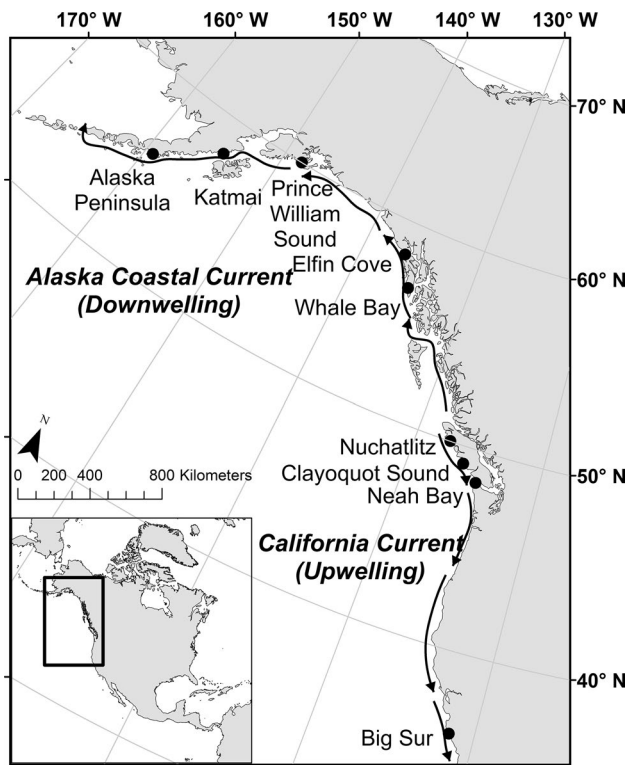


Fig. 1 Nearshore fish collection sites (solid dots) and generalized nearshore current flow in summer (arrows) in the Alaska Coastal Current and California Current

2005; Blanchette et al. 2006; MacFarlane 2010; Takahashi et al. 2012).

Materials and methods

Nearshore production was indexed using the annual growth increments recorded in black rockfish and kelp greenling otoliths collected at nine sites in the California Current and Alaska Coastal Current (Table 1; Fig. 1). All fish were captured within study site boundaries determined a priori based on habitat characteristics. Study sites were characterized by rocky reef habitat, and the presence of macrophytes (kelp), and sea otters (*Enhydra lutris*), a keystone predator in nearshore systems known to increase community diversity and kelp production via top-down control of major kelp grazers such as sea urchins (*Strongylocentrotus* spp.; Steneck et al. 2002). Fish were captured using trammel nets, spearfishing, and hook and line sampling in shallow nearshore waters (<5 m depth).

Otoliths were embedded in epoxy and sectioned through the nucleus on a transverse plane using a low-speed wafering saw to allow for measurements of annual growth increments on a thin section approximately 0.5 mm thick (Black et al. 2008). Measurements of each annual growth

Table 1 Collection sites, code, dates, and sample sizes for black rockfish and kelp greenling otoliths

Site	Site code	Black rock-fish	Kelp greenling	Collection dates	Site area (km ²)	Buffered site area (km ²)
Paul Island, Alaska Peninsula, Southwest Alaska	APEN	35	0	July 2009	4137	53,554
Katmai National Park and Preserve, Alaska Peninsula, Southcentral Alaska	KATM	39	50	July 2010	1698	20,823
Western Prince William Sound, Southcentral Alaska	WPWS	40	84	June and August 2010	1910	32,187
Elfin Cove, northern Chichagof Island, Southeast Alaska	ELFI	45	43	May 2011	1171	18,758
Whale Bay, southern Baranof Island, Southeast Alaska	WHAL	44	41	May and June 2011	1516	24,313
Nuchatlitz, west Vancouver Island	NUCH	45	61	May, June and September 2010	1062	16,959
Clayoquot Sound, west Vancouver Island	CLAY	47	43	May 2010 and July 2011	3344	23,622
Neah Bay, Olympic Peninsula, Washington	WASH	50	50	Throughout 2010 and 2011	3650	28,976
Big Sur, central California	BIGS	28	18	September 2010	2616	14,528

The buffered site area includes a 100-km buffer around the site used to calculate mean sea surface temperature

increment, delineated from the interior edge of an opaque zone to the outer edge of the next translucent zone, were taken along a line perpendicular to the axis of growth on a high-resolution image captured with a digital camera (Leica DFC 425 or 450) mounted on a stereomicroscope (Leica MZ6 or M60) under 20–40 \times magnification using ImagePro Plus 7.0 software (Media Cybernetics, Rockville, MD, USA) following Black et al. (2005). The first growth increment was not included given that it represents age-0 growth when habitat and diet differ from later ages (Love et al. 2002; Love 2011) nor was the last increment used given that it is incomplete at the time of capture. The calendar year of each increment formation was assigned by working backward from the year of capture at the outermost growth increment.

Each series of growth increments from a given location was cross-dated to ensure accuracy in year assignment following methods of Black et al. (2005). Cross-dating is principally a visual procedure, but was statistically verified using the computer program COFECHA (<http://web.utk.edu/~grissino/software.htm>). In COFECHA, long-term trends, including age-related growth declines, were removed and the growth pattern of each individual was correlated with the average of all others. A low correlation is an indicator that an error may have occurred. In such cases, the sample was visually re-inspected to identify any missed or falsely added increments. At no time was cross-dating ‘forced’ on any individual; changes were made to measurements only if there was clear visual evidence that an error had been made. Interseries correlations of black rockfish and kelp greenling otolith growth records were compared to those of other chronologies (Black et al. 2005, 2008, 2009) to ensure a similar degree of synchrony among individuals, as well as accurate age assignments and growth increment delineation, before otolith growth records were interpreted as an index of fish growth and ecosystem production.

The annual periodicity of increment formation, and thus accuracy of black rockfish age assignments, is supported by anomalous oxygen stable isotope values in otoliths associated with the 1983 El Niño event (Piner et al. 2005) and bomb radiocarbon dating (K. Munk, Alaska Dep. of Fish and Game, pers. comm.). Kelp greenling otolith yearly increment deposition was validated with oxytetracycline marks in the otoliths of captive fish (S. Hoobler, Calif. Dep. of Fish and Wildlife, pers. comm.). Using otolith growth increments as proxies for fish growth is supported by strong positive correlations between otolith and somatic size in black rockfish (Munk 2012) and kelp greenling (this study; fork length in mm vs. otolith radius measured from the focus to the ventral proximal edge on the longest axis in microns of 50 randomly selected individuals; slope = 2.4; $r^2 = 0.75$, $P < 0.05$). To establish a series of growth increments from an individual for cross-dating, only fish aged

5 years and older at capture were included in this study (age range 5–40 years old) and the increments measured spanned the subadult and adult growth history (increments representing age-1 growth and beyond).

Monthly SST and chlorophyll-*a* data, gridded over 4-km resolution, and monthly coastal upwelling indices were used to predict annual growth. Monthly mean values were averaged over a 6-month productive summer period, defined here as April–September following the definition of Menge and Menge (2013). Summer averages were chosen to integrate growth conditions during formation of the opaque zone, the larger component of an annual increment in otoliths of northern hemisphere fish (Beckman and Wilson 1995). Monthly SST averages were extracted from AVHRR Pathfinder version 5.0 satellite SST data for each site from 1982 to the year prior to collection (<http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/user-guide.html>). For SST, the study site area included a 100-km buffer (buffered site area in Table 1) to increase the number of grid cells sampled (878–4079 pixels) and site area (range 14,000–60,000 km²). In all cases, the spatial extent of an SST calculation was truncated at the 200 m isobath. We made no attempt to interpolate missing data, which represented 13 % of pixels in an average month. At all sites, chlorophyll-*a* concentrations (mg/m³) were available from MODIS-Aqua satellite data with 4-km resolution from 2003 to the year prior to collection (May 2012 release, <http://oceancolor.gsfc.nasa.gov/>). For chlorophyll analyses, study sites did not include a 100-km buffer because the possibility of patchy chlorophyll distributions makes localized data more desirable, even at the expense of reducing the number of grid cells sampled (62–279 pixels). On average, 12 % of pixels had missing chlorophyll data. Upwelling indices were obtained from the Pacific Fisheries Environmental Laboratory (<http://www.pfeg.noaa.gov/>) for the latitude and longitude closest to each study area and for all years with increment growth data. When an entire month of data for an environmental variable was missing, the site and year were dropped from the analysis.

Hypotheses relating annual growth to summer conditions were tested using linear mixed models to account for intrinsic (age or size) and extrinsic (environmental) growth components using the ‘nlme’ package in the statistical program R (Weisberg et al. 2010; Morrongiello et al. 2011; R Development Core Team 2013). All models included age during increment formation as an intrinsic component to account for faster growth when fish are young (Morrongiello et al. 2011). Annual otolith increment widths and age were log-transformed prior to analysis to achieve homoscedasticity and a linear relationship between these two variables. Growth intercepts (increment width at age-0) for individual fish were included as random effects nested

within a random site effect, in addition to an overall model intercept across all sites. Black rockfish models also included random slope terms for the fixed age effect that modified the effect of age on growth for individual fish nested within sites, essentially fitting an individual growth trajectory to each fish and site. In doing so, the model varied the relationship between age and increment width around the site-specific mean slope. Models predicting kelp greenling annual growth increments did not converge when random slopes were included for each individual, so only random intercepts were included. Random intercepts and slopes provided a mean of detrending age-related growth for each individual, similar to techniques that have traditionally been used in dendrochronology studies. Inclusion of site as a random intercept and slope effect allowed for local site-specific deviations from the overall model intercept and slope. Models independently considered the extrinsic influence of SST, upwelling, or chlorophyll concentration as fixed effects. Only one extrinsic influence was considered at a time so that all available data could be used, rather than truncating all models to data with the shortest time series.

Models were formulated to allow the relationships between annual otolith growth increments ($\mu\text{m y}^{-1}$) and summer SST, upwelling, or chlorophyll to vary by current system. The width of an annual increment in year t , at site k , for individual i is y_{tki} and was estimated as:

$$y_{tki} = (\alpha + a_k + a'_{i(k)}) + (\beta + b_k + b'_{i(k)})X_{ti} + \gamma_c \text{SST}_{tk} + \varepsilon_{tki}, \quad (1)$$

where α is the fixed intercept and a_k and $a'_{i(k)}$ are the random deviations in the intercept for each site, k , and individual, i , nested within sites, respectively. Similarly, the decline in growth with age (X_{ti}) is described by a fixed slope, β , a random site deviation, b_k , and an individual deviation, $b'_{i(k)}$. The growth response to SST (SST_{tk}) in year t differed by current system as a fixed effect (γ_c). The variance–covariance structure of the random effects is given by:

$$\mathbf{b}_k = \begin{bmatrix} a_k \\ b_k \end{bmatrix} \sim N(0, \boldsymbol{\Psi}_1) \quad \mathbf{b}_{i(k)} = \begin{bmatrix} a'_{i(k)} \\ b'_{i(k)} \end{bmatrix} \sim N(0, \boldsymbol{\Psi}_2),$$

where \mathbf{b}_k is the site-level random effects vector, assumed to be independent for different k , $\mathbf{b}_{i(k)}$ is the individual within site-level random effects vector, assumed to be independent for different i , k and independent of the \mathbf{b}_k , and $\boldsymbol{\Psi}_1$ and $\boldsymbol{\Psi}_2$ are unstructured 2×2 variance–covariance matrices. The errors ε_{tki} are assumed to be first-order autocorrelated within individuals and independent of the random effects, such that:

$$\varepsilon_{tki} = \phi \cdot \varepsilon_{t-1,ki} + v_t \quad \text{and} \quad v_t \sim N(0, \sigma_v^2),$$

where ϕ is the first-order autoregressive coefficient and v_t is a normally distributed variable with mean 0 and variance σ_v^2 . Autocorrelation was included to capture time series patterns in growth anomalies that could not be explained by the selected covariates. Upwelling, UW_{tk} , or chlorophyll concentrations, Chla_{tk} , were considered in lieu of SST by substituting these terms for SST_{tk} in Eq (1).

The kelp greenling global model without random slope effects for age was:

$$y_{tki} = (\alpha + a_k + a'_{i(k)}) + \beta X_{ti} + \gamma_c \text{SST}_{tk} + \varepsilon_{tki}. \quad (2)$$

As with black rockfish, UW_{tk} and Chla_{tk} were substituted for SST_{tk} when appropriate, to test their effects on growth increments.

Models were initially fitted using maximum likelihood for model comparisons, with the best model refitted using restricted maximum likelihood to obtain unbiased coefficients (Pinheiro and Bates 2000). Nested model formulations with and without each environmental effect were compared using the Akaike information criterion to determine the best fit (Burnham and Anderson 2001). Individual coefficients were evaluated using a statistical significance level of $P < 0.05$ and depicted using output from the ‘effects’ package in R (R Development Core Team 2013). Multicollinearity among SST, upwelling, and chlorophyll was examined within each site using linear regression.

Results

Black rockfish from the Alaska Coastal Current were often 20–30 years old and yielded records spanning the 1980s through the 2000s, while black rockfish from the California Current and kelp greenling from both current systems were generally ≤ 10 years old and provided annual otolith growth increments primarily during 2000–2010 (Fig. 2). For both species, growth increment sample sizes were largest in the 2000s. Correlations between individual time series of detrended annual growth increments and the average of all others (the series intercorrelation, as provided by COFECHA) ranged from 0.37 to 0.70 (Table 2).

Mixed models supported hypotheses relating SST to black rockfish and kelp greenling growth. Inclusion of current-specific SST effects improved models of annual black rockfish and kelp greenling growth compared to SST models with either a single linear effect applied to both current systems or no effect (Table 3). Pelagic black rockfish growth was faster with warmer SST in the Alaska Coastal Current (Fig. 3a, $P = 0.0003$ for SST coefficient) and cooler SST in the California Current (Fig. 3b, $P = 0.01$ for SST coefficient). Kelp greenling growth increased with warmer SST in the Alaska Coastal Current (Fig. 4a,

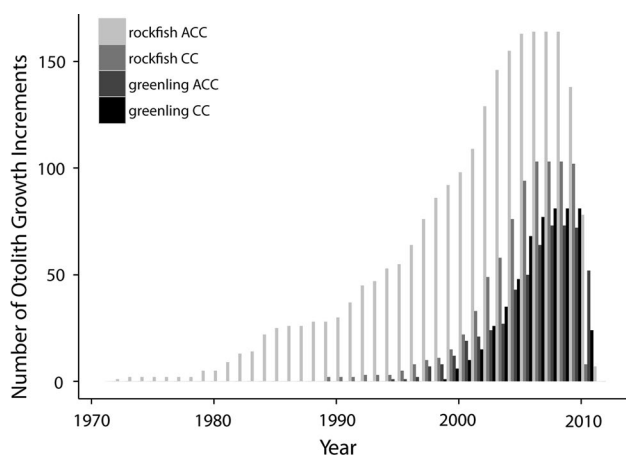


Fig. 2 Annual otolith growth increment sample sizes by growth year for black rockfish and kelp greenling captured in the Alaska Coastal Current (ACC) and California Current (CC). All growth increments were from individuals at least 5 years old and measured increments spanned the subadult and adult growth history (increments representing age-1 growth and beyond). Black rockfish are longer lived than kelp greenling and provided longer data records, particularly in the ACC. Sea surface temperature analyses included increments during 1982–2009, upwelling analyses included all increments, and chlorophyll analyses included increments during 2003–2011

$P = 0.0004$) and had a similar, albeit statistically nonsignificant, relationships with SST in the California Current (Fig. 4b, $P = 0.1$).

Inclusion of upwelling or chlorophyll concentration did not consistently improve models of black rockfish and kelp greenling growth. Upwelling was related to the growth of kelp greenling, but not black rockfish (Table 3; Fig. 3c, $P = 1.0$; and 3d, $P = 0.08$). Relaxed downwelling was associated with improved kelp greenling growth in the Alaska Coastal Current (Fig. 4c, $P = 0.0003$), but no relationship was observed between upwelling and kelp greenling growth in the California Current (Fig. 4d, $P = 0.3$). Chlorophyll concentrations improved annual growth predictions for black rockfish, but not kelp greenling (Table 3). Black rockfish grew faster during years of higher summer chlorophyll concentration in the California Current (Fig. 3f, $P = 0.006$); a similar trend was present in the Alaska Coastal Current (Fig. 3e, $P = 0.07$). Kelp greenling growth was not related to chlorophyll in the California (Fig. 4e, $P = 0.3$) or Alaska Coastal Currents (Fig. 4f, $P = 0.4$). Multicollinearity was weak among environmental variables at each site (Table 4).

Discussion

Our results support the presence of bottom-up limitations on production in nearshore kelp forests. The

Table 2 Interseries correlations (measure of common signal strength in each time series) for growth increments of black rockfish and kelp greenling captured at sites in the northeast Pacific Ocean

Site	Black rockfish	Kelp greenling
APEN	0.54 ($n = 26$)	n/a
KATM	0.41 ($n = 35$)	0.67 ($n = 6$)
WPWS	0.37 ($n = 36$)	0.70 ($n = 9$)
ELFI	0.41 ($n = 35$)	0.47 ($n = 23$)
WHAL	0.41 ($n = 26$)	0.45 ($n = 28$)
NUCH	0.41 ($n = 28$)	0.51 ($n = 23$)
CLAY	0.49 ($n = 37$)	0.57 ($n = 14$)
WASH	0.49 ($n = 29$)	0.51 ($n = 31$)
BIGS	0.58 ($n = 11$)	0.50 ($n = 9$)

Sample size (n) refers to the number of fish that were ≥ 5 years old and could be cross-dated

climate–growth patterns observed across current systems and species are consistent with nearshore pelagic food webs limited by a combination of nutrients and light at the level of primary producers and nearshore benthic food webs limited by temperature effects on their benthic invertebrate prey. Pelagic black rockfish growth increased with SST in the Alaska Coastal Current, consistent with light-limited bottom-up production, and decreased with SST in the California Current, consistent with nutrient-limited bottom-up production (Gargett 1997). Positive chlorophyll–growth relationships further suggested the likelihood of bottom-up limits in the nearshore pelagic food webs of black rockfish (Ware and Thomson 2005). Benthic kelp greenling growth increased during conditions that are known to be favorable for the condition of the benthic invertebrates they consume, including warmer SST and relaxed downwelling (Phillips 2005; Blanchette et al. 2006; Menge and Menge 2013). Lagged environmental effects on prey quantity owing to trophic interactions within these nearshore pelagic and benthic food webs are also likely, but it was beyond the scope of our study to model the numerous temporal lags associated with a variety of life histories and trophic levels among the species comprising kelp greenling and black rockfish diets.

Sea surface temperature

Overall, SST was the most consistent predictor of growth across nearshore pelagic and benthic food webs and current systems in our study. It should be noted, however, that longer data records were available for SST (28 years) and upwelling (39 years), compared to chlorophyll concentrations (8 years) and the difference in time series length could have influenced the general finding that SST was the most consistent predictor of growth.

Table 3 Model selection results for predicting black rockfish and kelp greenling growth using sea surface temperature (SST; Apr–Sep), upwelling (UW; Apr–Sep), and chlorophyll concentrations (Chla; Apr–Sep)

Species	Model group	Model	<i>df</i>	<i>n</i>	Δ AIC	
Black rockfish	SST	Age + current * SST	13	2991	0	
		Age + current	11	2991	14.3	
		Age	10	2991	15.0	
		Age + SST	11	2991	15.6	
	UW	Age + current	11	3129	0	
		Age	10	3129	0.5	
		Age + current * UW	13	3129	1.0	
		Age + UW	11	3129	2.5	
	Chla	Age + current * Chla	13	1826	0	
		Age + Chla	11	1826	3.0	
		Age + current	11	1826	8.6	
		Age	10	1826	9.4	
	Kelp greenling	SST	Age + current * SST	9	987	0
			Age + SST	7	987	1.4
			Age + current	7	987	10.3
			Age	6	987	24.6
UW		Age + current * UW	9	1102	0	
		Age + current	7	1102	9.2	
		Age + UW	7	1102	20.7	
		Age	6	1102	23.2	
Chla		Age + current	7	949	0	
		Age + current * Chla	9	949	2.3	
		Age	6	949	14.2	
		Age + Chla	7	949	15.4	

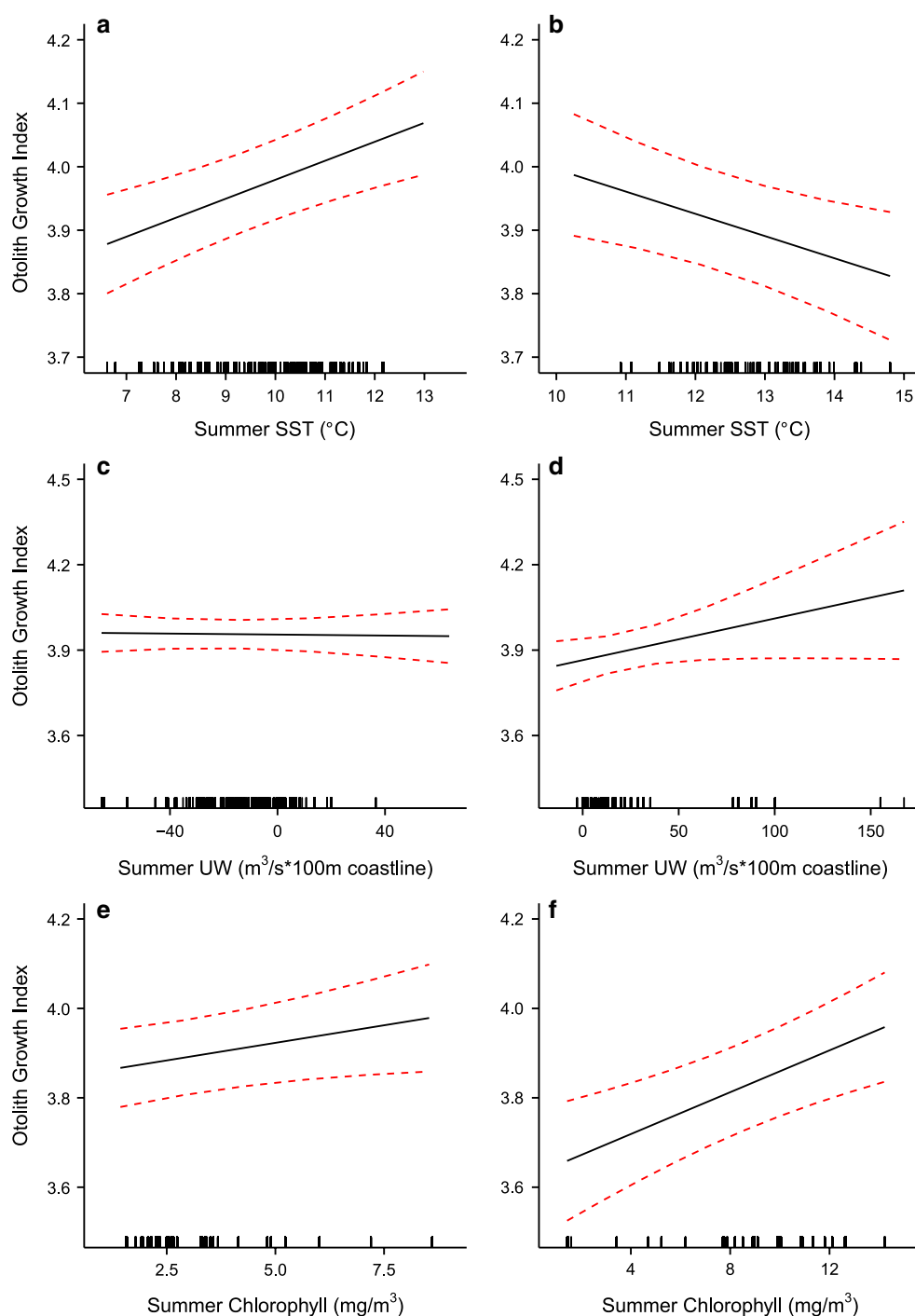
Models in bold provided the best fit for each model group as judged by AIC values. The degrees of freedom (*df*) and sample size (*n*), or unique number of growth increments, are also reported for each model

Our findings that pelagic black rockfish growth is positively related to SST in the Alaska Coastal Current and negatively related to SST in the California Current are consistent with the optimal stability window hypothesis. The optimal stability window hypothesis suggests that production peaks with intermediate water column stability, which allows some mixing for nutrient replenishment but enough stratification to keep plankton in the photic zone (Gargett 1997). Nearshore primary producers (phytoplankton and macrophytes) may also maximize production at intermediate water column stabilities as they too acquire nutrients from deep water sources through mixing and cross-shelf exchange mechanisms (Steneck et al. 2002; Ladd et al. 2005) and can be light limited by turbidity (Steneck et al. 2002; Etherington et al. 2007). Opposite SST–production relationships in the Alaska Coastal Current and California Current have been repeatedly observed in other studies including pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*Oncorhynchus keta*), and sockeye salmon (*Oncorhynchus nerka*) survival rates as well as Chinook salmon (*Oncorhynchus tshawytscha*) and yelloweye rockfish (*Sebastes ruberrimus*) growth rates, which all improve during warm conditions in the Alaska Coastal Current and cool conditions in the California Current (Mueter et al. 2002; Wells et al.

2008; Black et al. 2008). Under the optimal stability window hypothesis, increased production during warm conditions is indicative of light limitation eased through increased stratification, while increased production during cool conditions is indicative of nutrient limitations eased through mixing.

Sea surface temperature was used as a proxy for water column stability in this study for both the Alaska Coastal Current and California Current in lieu of a more direct measure of stability such as mixed layer depth (Thomas et al. 2012). In the California Current, seawater density and stratification are primarily controlled by temperature. Cooler SSTs indicate reduced stratification and increased availability of nutrients, which stimulate primary production (Chavez and Messié 2009). In the Alaska Coastal Current, stratification is primarily controlled by salinity, and salinity is linked to temperature during the spring and summer. Warm air temperatures stimulate freshwater discharge and formation of a fresh surface layer in addition to enhancing stratification through solar heating. In combination, these processes result in a synchronous surface salinity minimum and surface temperature maximum in August associated with strong water column stratification (Royer 2005). Moreover, years of warmer SST are characterized by increased freshwater input and stronger water

Fig. 3 Mean growth response of nearshore pelagic-feeding black rockfish to sea surface temperature (SST; monthly average Apr–Sep; **a, b**), upwelling (UW; monthly average Apr–Sep; **c, d**), and chlorophyll-*a* (monthly average Apr–Sep; **e, f**) in the Alaska Coastal Current (*left column*) and California Current (*right column*). Dashed lines denote 95 % confidence intervals, and tick marks along the *x*-axis denote observations. Model selection criteria and coefficients ($P < 0.05$) suggest that inclusion of SST and chlorophyll improve predictions of annual rockfish growth (significant effects in panels **a, b**, and **f**), whereas inclusion of the upwelling index did not improve the fit



column stability in the Alaska Coastal Current (Brickley and Thomas 2004).

A direct temperature relationship could explain the positive SST–growth relationship in the Alaska Coastal Current, but not the negative SST–growth relationship in the California Current. Experimental studies with juvenile black rockfish suggest that optimal temperatures for growth are near 18 °C (Boehlert and Yoklavich 1983), indicating that temperatures sufficiently warm to adversely influence

growth are well beyond the range of SST observed in this study (average summer temperatures ~8–15 °C). Thus, negative SST–growth relationship observed in the California Current supports an optimal stability window across these two ocean domains of the northeast Pacific.

Kelp greenling growth increased with temperature, suggesting that warmer temperatures result in increased growth rates of kelp greenling through direct effects on fish metabolism or increases in the quality of their benthic

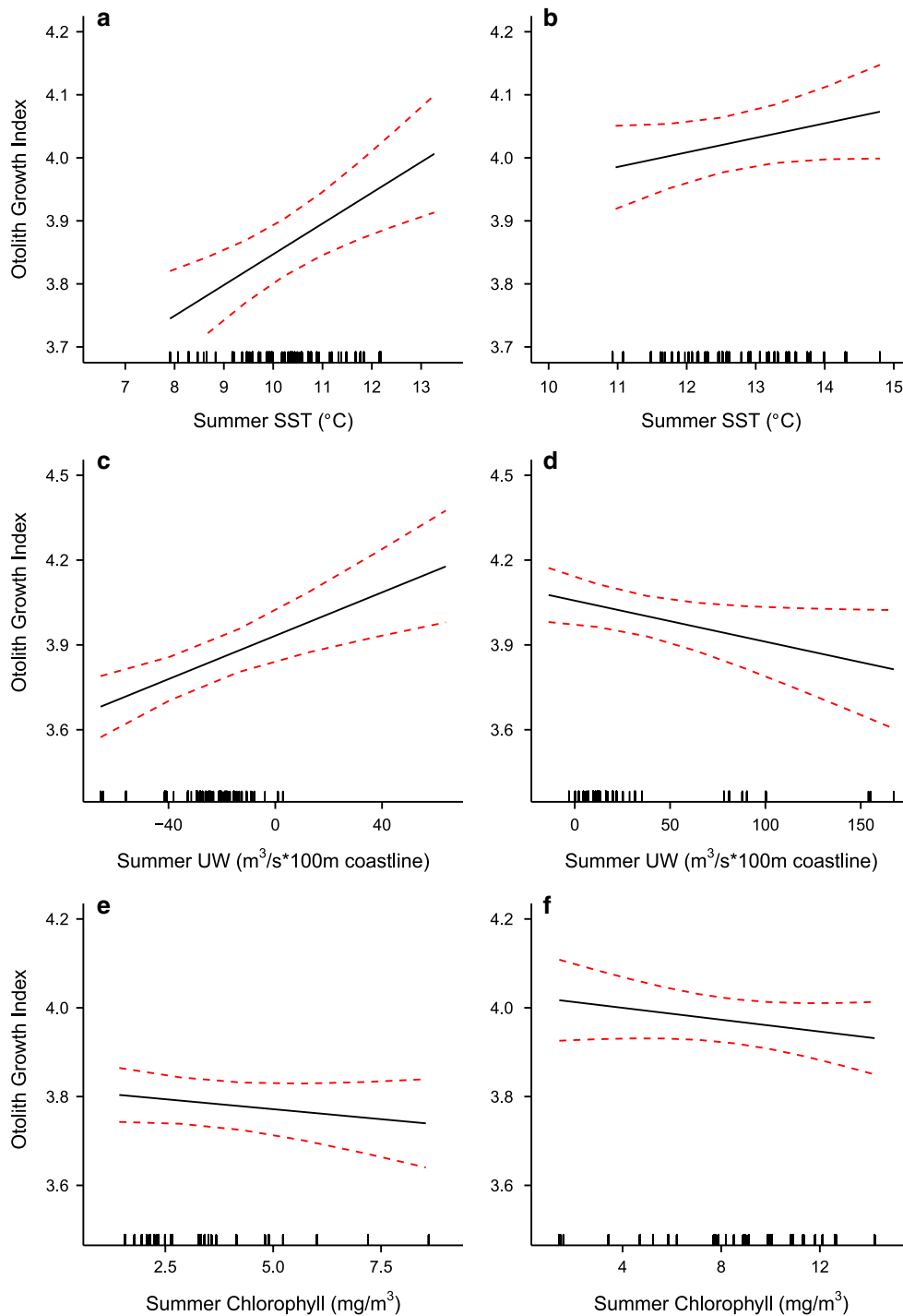


Fig. 4 Mean growth response of nearshore benthic-feeding kelp greenling to sea surface temperature (SST; monthly average Apr–Sep; **a**, **b**), upwelling (UW; monthly average Apr–Sep; **c**, **d**), and chlorophyll-*a* (monthly average Apr–Sep; **e**, **f**) in the Alaska Coastal Current (*left column*) and California Current (*right column*). *Dashed*

lines denote 95 % confidence intervals, and *tick marks* along the *x*-axis denote observations. Model selection criteria and coefficients ($P < 0.05$) suggest that SST and upwelling effects improved predictions of annual greenling growth (significant effects in panels **a** and **c**), whereas inclusion of chlorophyll did not improve the fit

invertebrate prey. A direct temperature effect is neither supported nor refuted by existing literature as optimal temperatures for growth in kelp greenling have not been

studied. We cannot rule out the possibility that the positive SST–growth relationship observed here is the result of a direct temperature effect across suboptimal temperatures.

Table 4 Correlation strength among sea surface temperature (SST; Apr–Sep; 1982–2009), upwelling (UW; Apr–Sep; 1982–2011), and chlorophyll-*a* concentrations (Chla; Apr–Sep; 2003–2011) at each site in the Alaska Coastal Current (ACC) and California Current (CC) as indicated by the coefficient of determination (r^2) from linear regression

Site	SST versus Chla	SST versus UW	UW versus Chla
APEN	0.33	−0.02	−0.01
KATM	0.27	−0.01	0.13
WPWS	−0.51	0.00	−0.25
ELFI	0.04	0.05	0.28
WHAL	0.02	0.05	0.02
ACC average	0.03	0.01	0.03
NUCH	−0.01	−0.07	0.10
CLAY	0.00	−0.09	0.24
WASH	0.07	−0.19	0.20
BIGS	0.18	−0.12	−0.15
CC average	0.06	−0.12	0.10

Negative values denote inverse correlations

Beyond a direct effect, temperature may have an indirect influence through lower trophic levels. Studies have demonstrated that warmer temperatures promote increased benthic invertebrate production at small spatial scales (10 and 100 s of km). In both the Channel Islands and off Point Conception, California, warmer areas have higher invertebrate densities, faster invertebrate growth rates, and individuals that allocate more energy to reproductive tissues despite lower availability and quality of food for filter-feeding invertebrates as compared to cooler areas (Phillips 2005; Blanchette et al. 2006; Phillips 2007). It is interesting to note that kelp greenling growth was consistently faster in warmer California Current waters (summer average 11–15 °C) compared to cooler Alaska Coastal Current waters (summer average 8–13 °C) (Fig. 4). This difference may reflect a more productive benthic invertebrate community in the warmer California Current if the positive relationship between temperature and kelp greenling growth reflects differences in prey quality, or it may reflect a positive effect of temperature on growth if food availability is not limiting in either system.

Upwelling and chlorophyll

Black rockfish growth was related to chlorophyll concentrations, but not to the upwelling index. The positive relationship between chlorophyll and rockfish growth suggests that bottom-up processes limit pelagic-feeding nearshore fish growth rates and provide a potential mechanism underlying positive relationships between fisheries catch data and chlorophyll concentrations (Ware and Thomson 2005; Chassot et al. 2007). In places or years of higher

chlorophyll concentrations, black rockfish may consume higher quality prey due to within-year increases in the size or energy content of an individual prey item, such as a forage fish (Robards et al. 2002; Takahashi et al. 2012). Black rockfish growth was not related to the upwelling index despite the finding that cooler, presumably upwelled waters were associated with increased growth. The coarse spatial resolution of the upwelling index compared to SST could account for this inconsistency. Upwelling indices reflect large-scale atmospheric pressure systems >1000 km wide that minimize local influences (e.g., bathymetry and coast-line shape) on mass transport that can prevail at smaller scales in nearshore systems (Ladd et al. 2005; Broitman and Kinlan 2006).

Inclusion of the upwelling index improved models of kelp greenling growth in the Alaska Coastal Current, suggesting that persistence of downwelling into the spring and summer months reduced kelp greenling growth in agreement with our hypothesis. Relaxation of downwelling during spring in the Alaska Coastal Current system allows deep nutrient-rich waters to move onto the shelf at depth and is associated with the start of the spring bloom by enhancing water column stability at the surface (Childers et al. 2005; Henson 2007). Increased availability of macronutrients to nearshore surface waters and increased water column stability are likely to enhance primary production by increasing nitrate availability (Stabeno et al. 2004) and confining plankton in the photic zone (Henson 2007). The relationship between relaxed downwelling and production is consistent with growth rates of benthic mussels in a downwelling system (Menge and Menge 2013).

The hypothesis relating kelp greenling growth to chlorophyll was not supported, suggesting that benthic invertebrate prey quality was not limited by primary production from phytoplankton throughout the summer. Chlorophyll concentrations are not always predictors of benthic mussel and barnacle growth (Phillips 2005, 2007; Blanchette et al. 2006) and support the possibility of alternative hypotheses. Terrestrial and macroalgae sources of carbon may supplement or displace phytoplankton production (Foley 2009; Tallis 2009) and drive interannual differences in nearshore fish growth (Schoch and Chenelot 2004; Miller et al. 2011). Indeed, carbon stable isotope values from kelp greenling muscle tissue indicate high (>50 %) proportions of kelp-derived carbon (von Biela et al. submitted). The positive SST–growth relationships could indicate that feeding and digestion rates of benthic invertebrates across our study range are limited by temperature, so that even a relatively low level of primary production is able to satiate invertebrates at current temperatures (Phillips 2005; Blanchette et al. 2007). Finally, the community dynamics of benthic invertebrates are complex, with conditions that promote growth (i.e., prey quality) occurring on shorter timescales

(within a year) and differing from conditions that promote recruitment (i.e., prey quantity) on longer timescales (>1 year).

Upwelling events and their associated chlorophyll blooms operate on shorter timescales (days) than the 6-month averages considered in this study and may explain why upwelling and chlorophyll were not consistent predictors of annual production. Short-term variability in wind stress with periods of several days can cause upwelling, even during a month when the mean wind stress is not favorable for upwelling (Huyer 1983). Timing of upwelling and chlorophyll blooms can be critical to seasonally occurring processes such as reproduction, recruitment processes, and juvenile and adult growth (Barth et al. 2007; Brander 2010; Black et al. 2011; Takahashi et al. 2012). Still, it can be difficult to identify environmental variables that adequately capture the specific timing or duration of critical processes that matter most to reproduction, growth, or survival.

Conclusions

We uncovered bottom-up relationships in nearshore pelagic food webs that are consistent with mechanisms identified from offshore (continental shelf) pelagic food webs, including the influence of water column stability (indicated by SST) and primary production (indicated by chlorophyll) on fish growth. In benthic nearshore food webs, our results are consistent with temperature limitation acting directly on fish or indirectly through their prey (i.e., benthic invertebrates). These climate–growth relationships agree with the expectation that warming climate and shoaling thermoclines will reduce production in low-latitude pelagic systems that are already nutrient limited (Behrenfeld et al. 2006), increase production in high-latitude pelagic systems (Mueter et al. 2009), and add the prediction that limited warming will also increase nearshore benthic production in the California Current and Alaska Coastal Current systems. Moreover, otolith growth indices can be explicitly incorporated in stock assessment models under an ecosystem-based approach to management as either an indication of species biomass (Morrongiello et al. 2012) or as an indication of habitat. For instance, the otolith growth index of a nearshore resident fish could prove useful in models of other commercial fish species that have critical early life history stages in nearshore systems (Agardy et al. 2005; Laurel et al. 2007; Echave et al. 2012; Johnson et al. 2012).

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