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ARTICLE

Influence of Basin- and Local-Scale Environmental Conditions on Nearshore Production in the Northeast Pacific Ocean

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Abstract

Nearshore marine habitats are productive and vulnerable owing to their connections to pelagic and terrestrial landscapes. To understand how ocean basin- and local-scale conditions may influence nearshore species, we developed an annual index of nearshore production (spanning the period 1972–2010) from growth increments recorded in otoliths of representative pelagic-feeding (Black Rockfish *Sebastes melanops*) and benthic-feeding (Kelp Greenling *Hexagrammos decagrammus*) nearshore-resident fishes at nine sites in the California Current and Alaska Coastal Current systems. We explored the influence of basin- and local-scale conditions across all seasons at lags of up to 2 years to represent changes in prey quantity (1- or 2-year time lags) and quality (within-year relationships). Relationships linking fish growth to basin-scale (Pacific Decadal Oscillation, North Pacific Gyre Oscillation, and multivariate El Niño–Southern Oscillation index) and local-scale (sea surface temperature, sea surface height anomalies, upwelling index, photosynthetically active radiation, and freshwater discharge) environmental conditions varied by species and current system. Growth of Black Rockfish increased with cool basin-scale conditions in the California Current and warm local-scale conditions in the

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Alaska Coastal Current, consistent with existing hypotheses linking climate to pelagic production on continental shelves in the respective regions. Relationships for Kelp Greenlings in the California Current were complex, with faster growth related to within-year warm conditions and lagged-year cool conditions. These opposing, lag-dependent relationships may reflect differences in conditions that promote quantity versus quality of benthic invertebrate prey in the California Current. Thus, we hypothesize that benthic production is maximized by alternating cool and warm years, as benthic invertebrate recruitment is food limited during warm years while growth is temperature limited by cool years in the California Current. On the other hand, Kelp Greenlings grew faster during and subsequent to warm conditions at basin and local scales in the Alaska Coastal Current.

Understanding the fluctuations in marine fish and ecosystem production is a pressing research goal as scientists and policy-makers address climate change forecasts (Hollowed et al. 2011; Link et al. 2012). Commercial fishing records and stock assessment surveys provide a wealth of observational data that are needed to understand climatic drivers of fish production in continental shelf systems (Hare and Mantua 2000; Hollowed et al. 2001; Mueter et al. 2009; Noakes and Beamish 2009; Litzow and Mueter 2014), but these data sources are not available for every species or every system. Nearshore systems are economically important for local, small-scale commercial and recreational fishing, diving, and wildlife viewing. However, they seldom support large-scale commercial fisheries and thus tend to lack adequate catch, stock assessment, and recruitment data, which are needed to estimate production or to understand climatic drivers across a wide geographic area (Cooke and Cowx 2004, 2006; Agardy et al. 2005). Nearshore systems are very productive; they function as critical spawning and rearing habitat for commercial and noncommercial species, and they support high biodiversity (Kruse and Tyler 1989; Dean et al. 2000; Agardy et al. 2005; Laurel et al. 2007; Doyle et al. 2009). A lack of available data relating environmental conditions to productivity in nearshore systems is compounded by complex interactions of atmospheric, oceanographic, watershed, and human influences at the marine–terrestrial interface (Cloern and Jassby 2008). To provide insights about nearshore biological responses to basin- and local-scale conditions, we developed an annual index of nearshore production from the growth rates of two nearshore-resident fishes at nine sites in the California Current and Alaska Coastal Current. “Basin scale” refers to the Pacific Ocean basin, and “local scale” refers to conditions at sample sites and their adjacent areas (thousands to tens of thousands of square kilometers).

Relationships between basin-scale environmental indices and nearshore fish growth would imply strong linkages between global environmental dynamics and local biology. Basin-scale conditions could influence nearshore systems through their linkages to offshore or terrestrial systems, as basin indices correlate well with offshore sea surface temperature (SST), salinity, and upwelling (Di Lorenzo et al. 2008; Ainley and Hyrenbach 2010) and with terrestrial indicators such as freshwater discharge (Royer et al. 2001; Papineau 2001; Neal et al. 2002; Hickey et al. 2010). The Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), and El Niño–Southern Oscillation (ENSO) represent

both decadal (e.g., PDO and NPGO) and interannual (e.g., ENSO) scales of climate variability in the northeast Pacific Ocean basin (Hollowed et al. 2001) and are among the most consistent predictors of marine and terrestrial ecosystem production in the North Pacific Ocean and western United States, respectively (Neal et al. 2002; Mundy 2005; Spies 2007; Black 2009; Menge et al. 2009; Di Lorenzo et al. 2013; Sydeman et al. 2013). Interpretation of basin-scale relationships and their linkages to nearshore responses could be improved by a complementary analysis of organismal growth responses to local conditions.

Local-scale conditions (e.g., SST, upwelling, and freshwater discharge) influence nearshore fish growth through bottom-up shifts in prey availability and prey quality. At the lowest levels of the food web, local physical conditions control the rate of production for phytoplankton and other primary producers (e.g., kelp) by modifying the availability of the light and nutrients that are required for photosynthesis (Steneck et al. 2002; Cury et al. 2003). This energy is consumed first by herbivores and other primary consumers (e.g., detritivores consuming plant material) and is later transferred to predators by way of changes in the abundance and quality of their prey (Cury et al. 2003).

Time lags must be considered when linking predator production with environmental conditions through trophic interactions (sensu Post 2004), especially when predators are limited by the availability of prey that are at least 1 year old and when prey abundance is determined by conditions experienced early in life history (Miller and Sydeman 2004; Frederiksen et al. 2006). Analyses spanning multiple seasons at plausible biological time lags are helpful in identifying whether conditions that are present during a specific window of months or during the transition from one seasonal climate state to another are particularly important to biological function. For instance, variations in primary production, recruitment of benthic invertebrates, zooplankton abundance, rockfish *Sebastes* spp. growth, and seabird reproduction occur when the onset of upwelling in the California Current is delayed, whether or not normal upwelling conditions prevail later in the summer (Barth et al. 2007; Shanks and Roegner 2007; Black et al. 2011).

Black Rockfish *Sebastes melanops* and Kelp Greenling *Hexagrammos decagrammus* are common nearshore-resident fishes with similar geographic distributions that span the California Current and the Alaska Coastal Current. Individuals of both species occupy small (<1 km²) home

ranges, often in rocky reef habitats with canopy kelp (giant kelp *Macrocystis pyrifera* and bull kelp *Nereocystis luetkeana*; Freiwald 2009; Love 2011; Pirtle et al. 2012). Black Rockfish are pelagic-feeding generalists that target forage fishes, including Pacific Herring *Clupea pallasii*, Pacific Sand Lances *Ammodytes hexapterus*, and juvenile salmon *Oncorhynchus* spp., as well as invertebrates such as crab megalopae (Rosenthal 1983; Love et al. 2002; Love 2011; Sturdevant et al. 2012). Kelp Greenlings are benthic-feeding generalists that forage on a variety of benthic invertebrates, including amphipods, snails, sea cucumbers, decorator crabs, and brittle stars (Moulton 1977; Hines 1982; Rosenthal 1983; Love 2011).

We explored the influence of basin- and local-scale environmental indices across seasons and years on the growth of two nearshore fishes (Black Rockfish and Kelp Greenling) in the (1) California Current, which fluctuates seasonally between upwelling (summer) and downwelling (winter); and (2) Alaska Coastal Current, a predominantly downwelling system. A priori, we posited that fish growth would be related to basin- and local-scale indices (Figure 1), and we categorized relationships in terms of either “warm” water-column-stabilizing effects or “cool” water-column-destabilizing effects. More specifically, we hypothesized that nearshore pelagic Black Rockfish would benefit from cooler conditions in the California Current and from warmer conditions in the Alaska Coastal Current (Polovina et al. 1995; Gargett 1997; von Biela et al. 2015), whereas nearshore benthic Kelp Greenlings would benefit from warmer conditions in both of the current systems (Phillips 2005; Blanchette et al. 2006; von Biela et al. 2015). In our analysis, we examined the time lags for which basin- and local-scale indices were related to nearshore fish growth and production. Lagged relationships were intended to reflect changes in prey quantity through trophic interactions, while current-year relationships were taken to indicate changes in (1) the prey quality associated with feeding conditions, and (2) the quantity of age-0 prey. Lags of up to 2 years are considered to match the age-classes of the likely forage fish and invertebrate prey for both of our focal fish species (Hatch and Sanger 1991; Yang 1993; Van Pelt et al. 1997).

METHODS

Nearshore production was indexed by using annual growth increments recorded in the otoliths of Black Rockfish and Kelp Greenlings that were collected at nine sites in the California Current and Alaska Coastal Current (Table 1; Figure 2). Study sites were characterized by rocky reef habitat and by the presence of macrophytes (kelp) and sea otters *Enhydra lutris*. A keystone predator in nearshore North Pacific systems, the sea otter is 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). Details of collections, otolith sectioning, otolith measuring, and crossdating procedures were described previously (von Biela et al. 2015). We

provide a brief summary here. Fish were collected by using a combination of hook-and-line sampling, trammel-netting, and spearfishing in shallow (<15 m) rocky reef habitats from 2009 to 2011. Otoliths were removed, sectioned, and mounted on slides to measure annual increment widths on high-resolution digital images that were captured with a digital camera (Leica DFC Model 425 or 450; 5-megapixel resolution) mounted on a stereomicroscope (Leica Model MZ6 or M60) under 20–40× magnification following the methods of Black et al. (2005). These polishing and photographing procedures were sufficient to clearly reveal growth increment structure in most of the samples; only otoliths with clearly defined growth increment boundaries were used in the study. Dendrochronology crossdating procedures were used to verify that all increments were assigned the correct calendar year of formation (Black et al. 2005) and to assess measurement error. If measurement error was high, visual crossdating and the statistical interseries correlation results from the software COFECHA (Grissino-Mayer 2001) were used to determine whether there was low synchrony among individuals, indicative of high error rates or weak environmental signals. Crossdating identifies missing or incorrectly added growth increments most easily in relatively old fish (age > 15 years), which have more years of data from which to assess coherence among individuals. Error rates in year assignments for younger fish were almost certainly low given their rapid growth rates and correspondingly wide increments, which are difficult to miss; although there are few cases in a short time series, conspicuously narrow (or wide) increments also corresponded among individuals collected from the same site. Only fish older than age 5 at capture were included in this study, and the measured increments spanned the subadult and adult growth history (i.e., increments represented age-1 growth and beyond). Annual growth increments spanned the period 1972–2010 for Black Rockfish and spanned 1994–2010 for Kelp Greenlings; however, the years 2000–2010 were best represented because younger fish only provided data from these more recent years (see von Biela et al. 2015 for the number of otolith increments plotted by growth year). The interseries correlations ranged from 0.37 to 0.70 (von Biela et al. 2015) and were comparable with those of other rockfish chronologies (Black et al. 2005, 2008, 2009), suggesting that increment growth boundaries were correctly delineated with minimal measurement error and good signal-to-noise ratios.

Growth was compared to basin-scale conditions and local conditions across seasons with time lags of up to 2 years. Seasons were defined as autumn (October–December), winter (January–March), spring (April–June), and summer (July–September) following Cummins and Masson (2014). The PDO, NPGO, and the multivariate ENSO index (MEI) were selected as indicators of basin-scale conditions. The PDO is the leading principal component of monthly SST, and the NPGO is the second dominant mode of sea surface height anomalies (SSHa) in the North Pacific Ocean (Mantua et al. 1997; Di Lorenzo et al. 2008). Positive values of PDO indicate

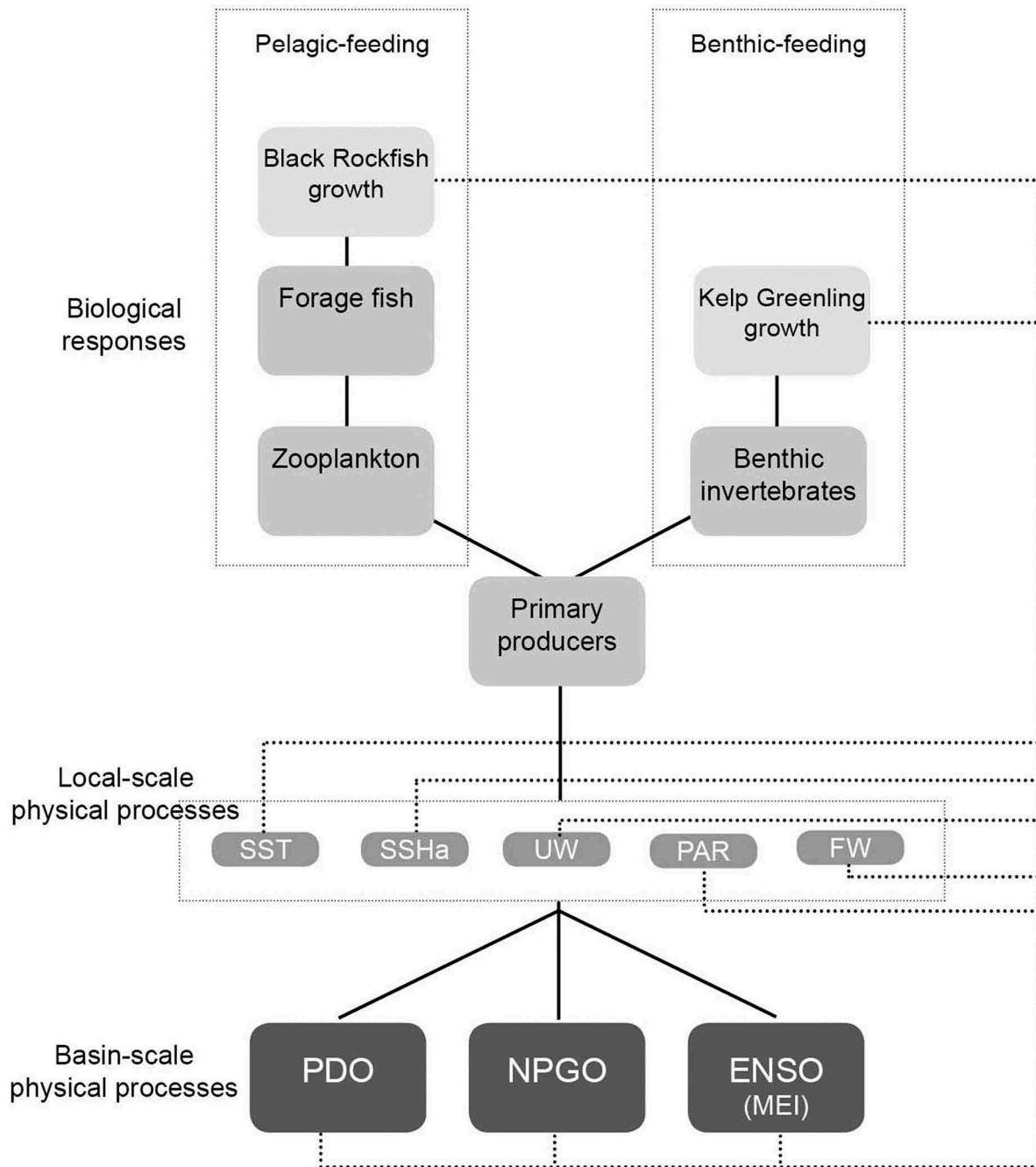


FIGURE 1. Conceptual diagram of food web responses to basin- and local-scale conditions in the northeast Pacific Ocean. Basin-scale variables are represented by the Pacific Decadal Oscillation (PDO), the North Pacific Gyre Oscillation (NPGO), and the El Niño–Southern Oscillation (ENSO), which is indexed by the multivariate ENSO index (MEI). Local-scale conditions are indicated by sea surface temperature (SST), sea surface height anomalies (SSHa), the Bakun upwelling index (UW), photosynthetically active radiation (PAR), and freshwater discharge (FW). Solid lines represent conceptual relationships, and dotted lines represent indirect relationships that are analyzed. Other relationships (e.g., direct effects of temperature on fish growth) are excluded for simplicity.

warm coastal SSTs throughout the northeast Pacific Ocean, weaker upwelling and decreased precipitation in the California Current, and stronger downwelling and increased precipitation in the Alaska Coastal Current (Mantua et al. 1997; Royer 2005). Positive values of NPGO indicate enhanced transport

of the North Pacific Current as well as increased transport of the Alaska Coastal Current and California Current (Di Lorenzo et al. 2008). Increased transport of the California Current is associated with stronger upwelling, higher sea surface salinity and nutrient concentrations, weaker thermoclines,

TABLE 1. Collection sites, collection dates, and sample sizes for Black Rockfish and Kelp Greenlings from which otoliths were obtained; the areas of the marine study sites, buffered study sites, and associated watersheds are also presented. The buffered site area includes a 100-km buffer around the site and was used to calculate mean sea surface temperature.

| Site | Collection dates | Black Rockfish <i>n</i> | Kelp Greenling <i>n</i> | Site area (km ²) | Buffered site area (km ²) | Watershed area (km ²) |
|---|--------------------------|-------------------------|-------------------------|------------------------------|---------------------------------------|-----------------------------------|
| Paul Island, Alaska Peninsula, southwest Alaska | Jul 2009 | 35 | 0 | 4,137 | 53,554 | 2,100 |
| Katmai National Park and Preserve, Alaska Peninsula, south-central Alaska | Jul 2010 | 39 | 50 | 1,698 | 20,823 | 1,476 |
| Western Prince William Sound, south-central Alaska | Jun, Aug 2010 | 40 | 84 | 1,910 | 32,187 | 1,033 |
| Elfin Cove, northern Chichagof Island, Southeast Alaska | May 2011 | 45 | 43 | 1,171 | 18,758 | 1,841 |
| Whale Bay, southern Baranof Island, Southeast Alaska | May, Jun 2011 | 44 | 41 | 1,516 | 24,313 | 1,399 |
| Nuchatlitz, west Vancouver Island, British Columbia | May, Jun, Sep 2010 | 45 | 61 | 1,062 | 16,959 | 1,478 |
| Clayoquot Sound, west Vancouver Island | May 2010, Jul 2011 | 47 | 43 | 3,344 | 23,622 | 3,924 |
| Neah Bay, Olympic Peninsula, Washington | Throughout 2010 and 2011 | 50 | 50 | 3,650 | 28,976 | 4,705 |
| Big Sur, central California | Sep 2010 | 28 | 18 | 2,616 | 14,528 | 876 |

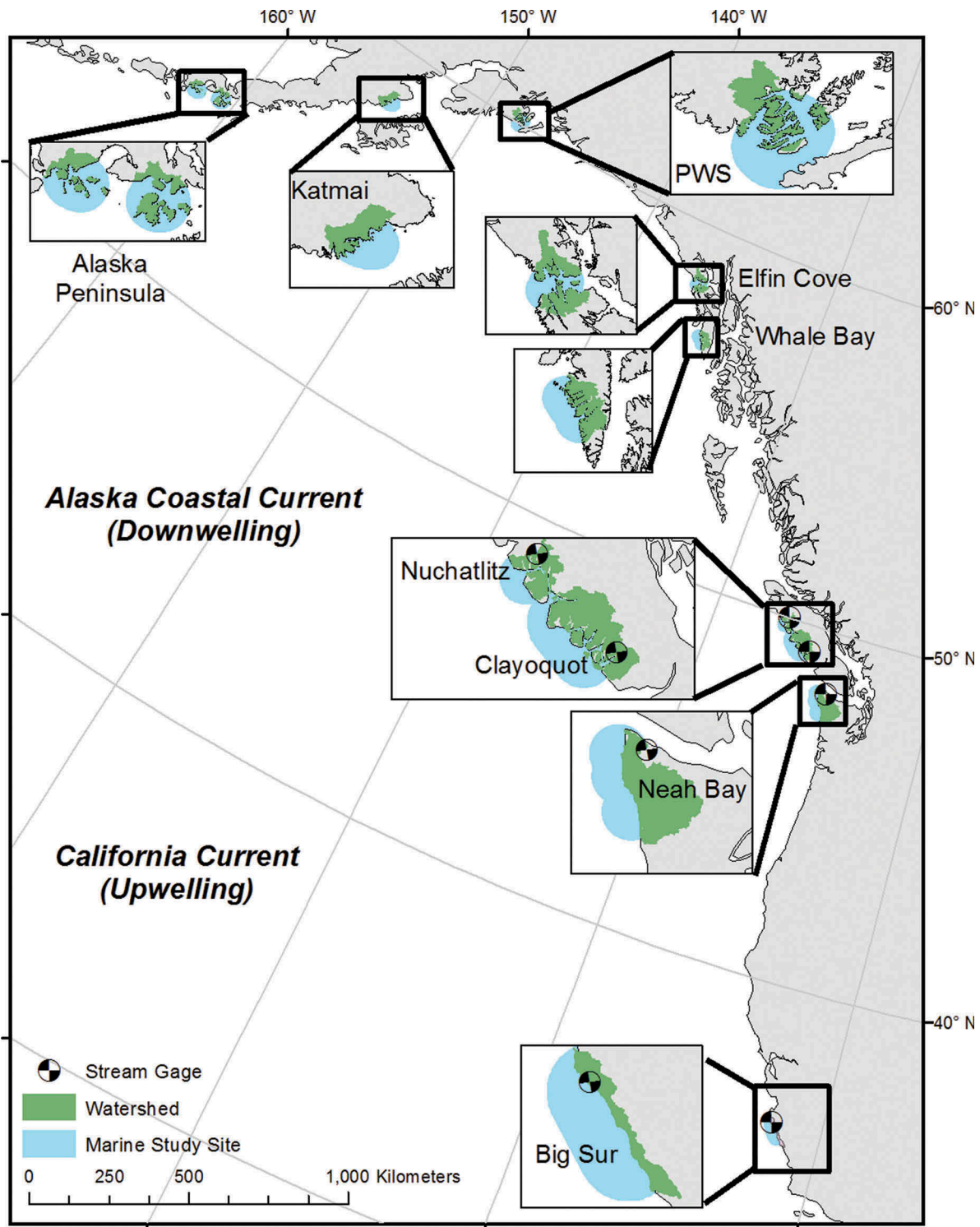


FIGURE 2. Map of nearshore fish collection sites (blue), associated watersheds (green), and stream gauge locations (black-and-white circles; California Current sites only) along the Pacific coast (PWS = Prince William Sound). The blue-shaded area represents the largest possible extent of a study site, but fish were only captured in depths less than 15 m and therefore were generally closer to shore than indicated here.

decreased stability of the water column, and cool conditions in the California Current (Di Lorenzo et al. 2008, 2009). Increased transport of the Alaska Coastal Current is associated

with an intensified Subarctic Gyre, which draws warm waters from the south into the Gulf of Alaska (Di Lorenzo et al. 2008; Danielson et al. 2011). The MEI is the leading principal

component of six variables over the tropical Pacific: sea level pressure, meridional and zonal wind components, cloudiness, surface air temperature, and SST (Wolter and Timlin 1998). Positive MEI values are associated with ENSO conditions, including a warmer, fresher, more stable water column with low nutrient concentrations in the eastern Pacific Ocean (Wolter and Timlin 1998). The three basin-scale indices interact with ENSOs centered over the eastern Pacific, thereby modifying the Aleutian low-pressure system and PDO, whereas ENSOs that are centered over the central Pacific modify the North Pacific Oscillation and the NPGO (Di Lorenzo et al. 2013). Monthly values for the PDO, NPGO, and MEI were obtained from the Joint Institute for the Study of the Atmosphere and Ocean at the University of Washington, Seattle (jisao.washington.edu/pdo); monthly NPGO values were from the Department of Ocean Climate and Ecosystem Science at Georgia Tech University, Atlanta (www.o3d.org/npgo); and monthly MEI values were from the National Oceanic and Atmospheric Administration's Earth System Research Laboratory (www.esrl.noaa.gov/psd/enso/mei).

Local-scale environmental indices included SST, SSHa, photosynthetically active radiation (PAR), the Bakun upwelling index, and freshwater discharge. These environmental variables were selected because they are either used to derive (i.e., SST and SSHa) or track basin-scale conditions and are useful for predicting biological responses (Mantua et al. 1997; Papineau 2001; Royer et al. 2001; Neal et al. 2002; Di Lorenzo et al. 2008; Ainley and Hyrenbach 2010; Hickey et al. 2010). The SST measures the heat near the surface of the ocean. Winds, currents, and the heat content of the water column all influence SSHa, with lower values indicating offshore water movement during periods of upwelling and reduced heat content as heat causes water column expansion (Wolf et al. 2009). We used PAR as a measure of the energy available for photosynthesis at the ocean's surface within the waveband used by primary producers (400–700 nm). Coastal upwelling indices are derived from wind stress, with positive values indicating upwelling and negative values indicating downwelling. In the California Current, upwelling index values are generally positive such that increasing values are associated with more upwelling and cooler, less-stable conditions. In the Alaska Coastal Current, upwelling index values are typically negative so that relatively high (near zero) values are associated with the relaxation of downwelling and a lack of vertical mixing that promotes stability and “warm” conditions. Freshwater discharge is an estimate of the freshwater input to the marine study sites, and high rates of discharge are associated with greater water column stability (Royer et al. 2001). Warmer, more stable conditions were assumed to be associated with higher SST, SSHa, PAR, and freshwater discharge in both current systems; increased upwelling (i.e., relaxed downwelling) in the Alaska Coastal Current; and decreased upwelling (i.e., relaxed upwelling) in the California Current. Categorization of the relationships for

each environmental variable in terms of warm and cool effects recognizes that (1) environmental variables act in concert, and (2) there is an inherent lack of independence among environmental indices.

An index of primary production could not be included for two reasons. First, the time series of phytoplankton data was too short for an analysis with lagged relationships. Second, recent evidence from stable isotopes in Black Rockfish and Kelp Greenlings suggests that a substantial proportion of energy is provided by kelp and other macroalgae (von Biela et al., *in press*), but systematic long-term data sets on production and standing stocks of macrophytes across the study region do not exist. Our analysis assumes that the physical environment controls the total amount of primary production available, but we do not differentiate or make specific assumptions about phytoplankton and kelp production patterns.

Gridded environmental data (SST, SSHa, and PAR) were averaged over an area spanning a 100-km buffer around each study site to increase the number of grid cells sampled (buffered site area in Table 1; range = 14,000–60,000 km²). In all cases, the spatial extent of calculations was truncated at the 200-m isobath. Monthly SST averages for each site from 1982 to the year prior to fish collection were extracted from satellite SST data via AVHRR (Advanced Very High Resolution Radiometer) Pathfinder software (version 5.0; www.nodc.noaa.gov/SatelliteData/pathfinder4km/userguide.html). Monthly SSHa values were obtained via satellite altimetry measurements from the AVISO (Archiving, Validation, and Interpretation of Satellite Oceanographic Data) product (coastwatch.pfeg.noaa.gov/erddap/griddap) for each site from 1993 to the year prior to fish collection. Monthly PAR averages were obtained from the MODIS (Moderate Resolution Imaging Spectroradiometer) Terra satellites (ocean.data.sci.gsfc.nasa.gov/MODIST/Mapped/Monthly/4km/par) from 2000 to the year prior to fish collection. In the northern part of our study range, seasonally low light conditions prevented PAR detection by satellites and resulted in a data gap for November–January. Therefore, there are no models for autumn PAR, and the PAR values for the winter season were averaged over February and March only. Monthly averaged upwelling indices for a location offshore of each study site were obtained from the National Marine Fisheries Service's Pacific Fisheries Environmental Laboratory (PFEL; www.pfeg.noaa.gov; latitude and longitude rounded to the nearest 0.5° and at least 1° offshore following the recommendations of PFEL) for all years with increment growth data.

Freshwater discharge was considered as an additional local-scale variable representing a terrestrial influence on water column stratification and was estimated using either a spatially explicit discharge model for sites in the Alaska Coastal Current (Hill et al. 2015; except the Alaska Peninsula site, which is beyond the domain of the discharge model) or stream

gauge data for sites in the California Current. In each case, the watershed for a given study site was delineated by identifying all of the coastal pour points in the marine study site and associated watersheds via use of a digital elevation model (2-arc-seconds' resolution; data available at ned.usgs.gov for U.S. sites and gdex.cr.usgs.gov/gdex for Canadian sites) following established methods for defining hydrography (Jenson and Domingue 1988). When the discharge model was used to estimate monthly freshwater discharge, the mean monthly discharge from a study watershed was extracted from the model (Hill et al. 2015) for the years 1980–2010.

When stream gauge data were used to estimate freshwater discharge, monthly values were obtained from stream gauges within the watershed corresponding to the study site (Figure 2). If no streams in the study watershed were gauged, discharge from the nearest gauge with adequate data was obtained. Because gauged watersheds are much smaller than the study watersheds, discharge values were scaled to estimate the total discharge from the larger study watershed. Scaled discharge values were calculated by multiplying the area of the study watershed by the measured discharge per unit area of the gauged watershed. The stream gauges used to estimate freshwater discharge for sites in the California Current were located in Big Creek (U.S. Geological Survey [USGS] 11143000; within the Big Sur [California] study watershed, 1951–2010), the Hoko River (USGS 12043300; adjacent to the Neah Bay study watershed, 1996–2010), Tofino Creek (Water Survey of Canada 08HB086; within the Clayoquot Sound [British Columbia] study watershed, 1996–2010), and the Zeballos River (Water Survey of Canada 08HE006; within the Nuchatlitz [British Columbia] study watershed, 1972–2010). The combination of modeled discharge and scaled gauge estimates provided the best possible approach for estimating discharge at each study site. Sites in Alaska were covered by a spatially explicit discharge model but no river gauges, and sites in the California Current system were associated with gauged watersheds but were not included in a spatially explicit discharge model. This approach provided some indication for the potential of freshwater discharge to stratify the nearshore water column across years and sites, although a direct measure of stratification would have been preferred if available.

Models were formulated to (1) allow the relationships between annual otolith increment width and each basin- or local-scale indicator to vary between current systems, and (2) recognize that growth increment width is related to the fish's age during increment formation and that these relationships may vary across sites and across individual fish. All models included the age at increment formation to account for the faster growth of younger fish (Morrongiello et al. 2011). Annual otolith increment widths and ages were log transformed prior to analysis to achieve homoscedasticity and a linear relationship between these two variables. In addition to an overall growth intercept (increment width at age 0) across all sites, increment widths were allowed to vary across individual fish by including random intercepts that were specific to

each individual fish, nested within random site-specific intercepts. We included a within-individual, autocorrelated error structure for growth increment width to account for any biological processes that might result in growth rates from the previous year being related to the current year's growth or to accommodate any remaining autocorrelated measurement error. Because the measurements within an individual are successive, overestimating the width of a given growth increment results in underestimation of the next growth increment's width (Morrongiello et al. 2015). Black Rockfish models also included a random slope term in addition to the age effect that modifies the slope describing the decline in growth increment width as fish age by allowing the rate of decline to be faster or slower for each individual—essentially fitting an individual growth trajectory to each fish, as modified by environmental effects that are shared among all individuals. However, models for predicting Kelp Greenling annual growth increments did not converge when random slopes were included for each individual; this is likely due to the younger ages and shorter within-individual growth records, which resulted in less data for fitting slopes to each individual. Therefore, Kelp Greenling models included random intercepts—but not random slope terms—for each individual. The random intercepts allowed for some individuals to have overall wider or narrower growth increments; however, the absence of a random slope term for age equates to the assumption that all individuals grow at the same rate after environmental influences on growth are taken into account. Only one environmental index was considered at a time, and the indices were scaled (mean = 0; SD = 1) prior to analysis so that model coefficients would be comparable across analyses, such that coefficients of larger magnitude indicated stronger relationships.

The log-transformed width of an annual increment in year t at site k for individual i ($y_{t ki}$) was estimated as

$$y_{t ki} = \left[\alpha + a_k + a'_{i(k)} \right] + \left[\beta + b_k + b'_{i(k)} \right] X_{ti} + \gamma_c \text{EI}_{t k L} + \varepsilon_{t ki},$$

where α is the fixed intercept; a_k is the random deviation in the intercept for each site k ; and $a'_{i(k)}$ is the random deviation in the intercept for each site k and each individual i nested within sites. The log-transformed age of individual i in year t (X_{ti}) is included to capture the decline in growth with age and is described by a fixed slope β , a random site deviation b_k , and an individual deviation $b'_{i(k)}$. The growth response to each environmental index ($\text{EI}_{t k L}$) in year t at site k with lag L differs between current systems as a fixed effect (γ_c). For basin-scale indicators, the environmental index ($\text{EI}_{t k}$) is not site specific. The variance-covariance structure of the random effects was given by

$$b_k = \begin{bmatrix} a_k \\ b_k \end{bmatrix} \sim N(0, \Psi_1), b_{i(k)} = \begin{bmatrix} a'_{i(k)} \\ b'_{i(k)} \end{bmatrix} \sim N(0, \Psi_2),$$

where b_k is the site-level random effects vector, which is assumed to be independent for different sites k ; $b_{i(k)}$ is the individual-within-site-level random effects vector, which is assumed to be independent for different individuals i and sites k and independent of b_k ; and Ψ_1 and Ψ_2 are unstructured 2×2 variance–covariance matrices. If a model did not converge with this random effects structure, a simplifying assumption was imposed whereby the individual-level random intercepts and slopes were assumed to be independent in a diagonal 2×2 variance–covariance matrix. Independence of the random slopes and intercepts is unlikely, but this assumption was less restrictive than eliminating the random slopes for the few instances (~10%) in which these models failed to converge. The errors ε_{tki} were assumed to be first-order autocorrelated within individuals and independent of the random effects such that

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

where ϕ is the first-order autoregressive coefficient; and v_t is a normally distributed variable with a mean of 0 and a variance of σ_v^2 . The Kelp Greenling model without random slope effects was

$$y_{tki} = \left(\alpha + a_k + a'_{i(k)} \right) + \beta X_{ti} + \gamma_c EI_{tkL} + \varepsilon_{tki}.$$

Model diagnostics were examined by reviewing plots of the observed and expected growth increment widths for individual fish and the residuals across years and collection sites to assess fit. Models were initially fitted using maximum likelihood for model comparisons, and the best model was refitted by using restricted maximum likelihood to obtain unbiased coefficients (Pinheiro and Bates 2000). Nested model formulations with and without each environmental effect were compared by using Akaike's information criterion (AIC) to determine the best fit (Burnham and Anderson 2002). Basin- and local-scale effects were considered significant if the AIC value decreased by 2.0 units or more relative to the same model without the basin- or local-scale effect and if the coefficient describing the effect was statistically significant ($P < 0.05$). All statistical analyses were conducted by using the package nlme (Pinheiro and Bates 2000) in R version 3.1.2 (R Development Core Team 2013). Otolith growth indices were not converted to changes in somatic size for any analysis because otolith indices likely reflect overall body condition rather than simply changes in length (Black et al. 2013).

RESULTS

Black Rockfish and Kelp Greenling growth across the California Current system and Alaska Coastal Current system appeared to be related to conditions indexed by basin- and

local-scale environmental variables based on improvements in model AIC values (Tables 2, 3; Supplemental Tables S.1–S.4 available separately online). The best single growth model for Black Rockfish included the spring PDO from 2 years prior (AIC difference for the null model [ΔAIC_{null}] ~ 41; Table S.1). The best growth model for Kelp Greenlings included the PDO from the prior winter (ΔAIC_{null} ~ 26; Table S.3). For both Black Rockfish and Kelp Greenlings, AIC scores indicated that basin-scale models including the PDO outperformed those that contained the MEI, which in turn outperformed those that included the NPGO (Tables S.1, S.3).

Local-scale environmental variables were related to the growth of Black Rockfish and Kelp Greenlings in both current systems (Tables 2, 3). Among the Black Rockfish growth models, the best models included the SST for the current summer (ΔAIC_{null} ~ 23; Table S.2), freshwater discharge for the current winter (ΔAIC_{null} ~ 20), the upwelling index for the current autumn (ΔAIC_{null} ~ 19), PAR for the previous spring (ΔAIC_{null} ~ 17), or SSHa for the previous spring (ΔAIC_{null} ~ 11; Table S.2). Among the Kelp Greenling growth models, the best models included the upwelling index for the current winter (ΔAIC_{null} ~ 29), PAR for the summer 2 years prior (ΔAIC_{null} ~ 25), SST for the current summer (ΔAIC_{null} ~ 20), SSHa for the current summer (ΔAIC_{null} ~ 20), or freshwater discharge for the winter 2 years prior (ΔAIC_{null} = 6.5; Table S.4). Model diagnostics provided no evidence that model assumptions were violated. Seasonal SST had little to no overlap between current systems (Alaska Coastal Current sites versus California Current sites) in the fall (5–10°C versus 10–15°C), winter (2–7°C versus 7–14°C), or spring (2–10°C versus 8–14°C). However, considerable overlap occurred in the summer (9–15°C versus 12–17°C), with warm years at Alaska Coastal Current sites overlapping the SST range from cool and average years at the California Current sites.

Black Rockfish in the California Current

Current-specific coefficients indicated that cool conditions at the basin scale were generally associated with faster Black Rockfish growth in the California Current (17 of 18 significant coefficients; Table 2; Supplemental Figure S.1). Specifically, Black Rockfish growth was inversely related to the PDO and MEI and was positively related to the NPGO with and without lags (Table 2). Among local-scale conditions, improved Black Rockfish growth was more commonly associated with cooler conditions (15 of 23 significant coefficients; Table 2; Figure S.2) that were primarily lagged (11 of 15 cool local-scale relationships). Growth was inversely related to SST; growth relationships with SSHa, the upwelling index, and freshwater discharge were mostly inverse, while relationships with PAR were mostly positive. Compared to the consistent association of cool basin-scale conditions with increased growth, the relationships with local-scale conditions were more variable.

TABLE 2. Relationships between Black Rockfish growth and environmental indices at the basin scale (PDO = Pacific Decadal Oscillation; NPGO = North Pacific Gyre Oscillation; MEI = multivariate El Niño–Southern Oscillation index) and local scale (SST = sea surface temperature; SSHa = sea surface height anomalies; UW = Bakun upwelling index; PAR = photosynthetically active radiation; FW = freshwater discharge). Growth rates are based on the annual growth increment width in otoliths. Environmental indices are represented for each season (Aut = autumn; Win = winter; Spr = spring; Sum = summer) in the year of growth and up to 2 years prior (L1 = 1-year lag; L2 = 2-year lag). Blank cells indicate nonsignificant relationships from mixed models. An effect was considered significant if (1) the Akaike’s information criterion value for the model was at least 2.0 units lower than that of the same model without the environmental effect and (2) the coefficient describing the effect was statistically significant ($P < 0.05$). The sign of the coefficient is noted in each cell as either positive (Pos) or negative (Neg). Light-blue and dark-blue cells indicate relationships between cool conditions and increased fish growth ($P < 0.05$ and $P < 0.01$, respectively). Pink and red cells indicate relationships between warm conditions and increased fish growth ($P < 0.05$ and $P < 0.01$, respectively).

| Scale | Index | 2 years prior | | | | | | 1 year prior | | | | | | Current year | | | | | |
|-------|-------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-----|-----|-----|-----|--------------|-----|-----|-----|--|--|
| | | Aut _{L2} | Win _{L2} | Spr _{L2} | Sum _{L2} | Aut _{L1} | Win _{L1} | Spr _{L1} | Sum _{L1} | Aut | Win | Spr | Sum | Aut | Win | Spr | Sum | | |
| Basin | PDO | | Neg | Neg | Neg | | | | | | | | | | | | | | |
| | NPGO | | Pos | Pos | Pos | | | | | | | | | | | | | | |
| | MEI | | Neg | Neg | Neg | | | | | | | | | | | | | | |
| | SST | | | Neg | Neg | | | | | | | | | | | | | | |
| | SSHa | | Neg | Neg | Neg | | | | | | | | | | | | | | |
| | UW | | Neg | Pos | Pos | | | | | | | | | | | | | | |
| | PAR | | | | Pos | | | | | | | | | | | | | | |
| Local | PDO | | | | | | | | | | | | | | | | | | |
| | NPGO | | | | | | | | | | | | | | | | | | |
| | MEI | | | | | | | | | | | | | | | | | | |
| | SST | | | | | | | | | | | | | | | | | | |
| | SSHa | | | | | | | | | | | | | | | | | | |
| | UW | | | | | | | | | | | | | | | | | | |
| | PAR | | | | | | | | | | | | | | | | | | |
| Basin | PDO | | | | | | | | | | | | | | | | | | |
| | NPGO | | | | | | | | | | | | | | | | | | |
| | MEI | | | | | | | | | | | | | | | | | | |
| | SST | | | | | | | | | | | | | | | | | | |
| | SSHa | | | | | | | | | | | | | | | | | | |
| | UW | | | | | | | | | | | | | | | | | | |
| | PAR | | | | | | | | | | | | | | | | | | |
| Local | PDO | | | | | | | | | | | | | | | | | | |
| | NPGO | | | | | | | | | | | | | | | | | | |
| | MEI | | | | | | | | | | | | | | | | | | |
| | SST | | | | | | | | | | | | | | | | | | |
| | SSHa | | | | | | | | | | | | | | | | | | |
| | UW | | | | | | | | | | | | | | | | | | |
| | PAR | | | | | | | | | | | | | | | | | | |

California Current

Alaska Coastal Current

Black Rockfish in the Alaska Coastal Current

Results for Black Rockfish growth in the Alaska Coastal Current generally suggested that warm basin-scale conditions were associated with faster growth (7 of 9 coefficients; Table 2; Figure S.1). Growth was positively related to the NPGO, whereas both positive and negative relationships were observed for the PDO and MEI. At the local scale, Black Rockfish growth increased prior to and during warm conditions (19 of 24 significant coefficients; Table 2; Figure S.2). Specifically, Black Rockfish growth in the Alaska Coastal Current was positively related to SST and primarily showed positive relationships with the upwelling index, PAR, and freshwater discharge. The relationships between Black Rockfish growth and SSHa were particularly inconsistent, with an equal number of positive and negative relations (Table 2).

Kelp Greenlings in the California Current

Kelp Greenling growth models from the California Current generally indicated a complex relationship wherein faster growth was associated with recent warm conditions and prior cool conditions (Table 3). Among basin-scale conditions, the PDO and MEI during the prior year were negatively related to growth (3 of 3 significant coefficients), while conditions in the current year were positively related to growth (3 of 3 significant coefficients; Figure S.1). Among the local-scale conditions, increased growth was associated with prior cooler conditions (12 of 15 significant coefficients) and warm conditions in the summer of the current year (Table 3; Figure S.2). In all of the significant relationships except those for the current summer, Kelp Greenling growth was negatively related to SST, SSHa, and discharge and was positively related to the upwelling index. With regard to the current summer, the relationships with SST and SSHa were positive, and the relationship with the upwelling index was negative.

Kelp Greenlings in the Alaska Coastal Current

For Kelp Greenlings in the Alaska Coastal Current, models at both the basin and local scales suggested that warm conditions improved growth. Growth was positively related to the PDO with and without time lags, negatively related to the NPGO without time lags, and positively related to the MEI with and without time lags. Current-specific coefficients from Kelp Greenling growth models generally indicated that growth increased during and after warm conditions in the Alaska Coastal Current (13 of 17 significant coefficients; Table 3; Figure S.1). Among local-scale associations, all 18 significant coefficients indicated that warm conditions were associated with increased growth (Figure S.2). Growth was positively related to SST, SSHa, upwelling index, PAR, and discharge.

DISCUSSION

Growth rates of Black Rockfish and Kelp Greenlings in nearshore habitats of the California Current and Alaska Coastal Current were related to basin- and local-scale indices of environmental conditions. In general, pelagic-feeding Black Rockfish grew faster during cool basin-scale conditions in the California Current and warm local-scale conditions in the Alaska Coastal Current. The results of this study generally support the notion that California Current pelagic production is bottom-up limited by nutrients and that Alaska Coastal Current production is bottom-up limited by light, as water column stability is generally higher than optimal in the California Current and lower than optimal in the Alaska Coastal Current (Gargett 1997).

Benthic-feeding Kelp Greenlings grew faster during and subsequent to warm basin- and local-scale conditions in the Alaska Coastal Current. In the California Current, the Kelp Greenling growth response to environmental conditions was complex, with both warm and cool conditions relating to increases in growth at different time lags. Thus, we suggest that benthic production is highest (1) during warm years in the Alaska Coastal Current, and (2) when cool and warm years alternate in the California Current.

Otolith chronologies likely indicate biologically relevant species and ecosystem conditions. At the species level, otolith size correlates with somatic size (Campana 1990) and suggests that chronologies are related to interannual differences in somatic size and condition. In a recent study, Black et al. (2013) found that annual body mass indices (weight/length) of Yellowfin Sole *Limanda aspera* were well correlated with prior otolith growth at the population level. At the ecosystem level, otolith chronologies of Yelloweye Rockfish *Sebastes ruberrimus* and Splitnose Rockfish *Sebastes diploproa* were observed to be synchronous with bivalve and tree-ring chronologies (Black 2009) as well as seabird reproductive success (Black et al. 2011), implying that otolith growth does reflect broad ecosystem conditions. Climatic events are particularly useful for identifying links between otoliths and biological responses at the species and ecosystem levels. For example, the 1983 El Niño was associated with very narrow otolith growth increments (Black 2009), reduced levels of visceral fat (Lenarz and Wyllie Echeverria 1986), and recruitment failures (Lenarz et al. 1995) in several rockfish species as well as a general reduction in ecosystem production (Lenarz et al. 1995).

Black Rockfish in the California Current

Basin- and local-scale conditions were correlated with the growth of Black Rockfish in the California Current and generally suggested that cooler conditions were favorable for growth, both with and without time lags. Growth of California Current rockfish was related to the PDO at the basin scale and to SST, SSHa, and freshwater discharge at the local scale. In the California Current, cooler conditions

were previously linked to increases in pelagic production, including rockfish growth (Lenarz et al. 1995; Black 2009), rockfish condition (Lenarz and Wyllie Echeverria 1986), salmon catch (Hare et al. 1999), reproductive success of the common murre *Uria aalge* (Gladics et al. 2015) and Cassin's auklet *Ptychoramphus aleuticus* (Sydeman et al. 2009; Wolf et al. 2009), forage fish abundance (Sydeman et al. 2013), zooplankton biomass and species composition (Peterson and Schwing 2003; Keister et al. 2011; Di Lorenzo et al. 2013), and chlorophyll-*a* concentrations (Harris et al. 2009; Boyce et al. 2010). These previous results are consistent with our findings.

For Black Rockfish, cooler conditions in the California Current may reflect increases in prey quality and abundance or favorable shifts in prey species composition or distribution. Cooler conditions and decreased water column stability associated with coastal upwelling indicate greater vertical mixing and nutrient availability to primary producers in the California Current (Chavez and Messié 2009; Demarcq 2009). Increases in nutrient availability cause bottom-up increases in phytoplankton and zooplankton abundances and subsequent increases in forage fish consumption (Peterson and Schwing 2003; Harris et al. 2009; Boyce et al. 2010; Keister et al. 2011), condition (Astthorsson and Gislason 1998; Robards et al. 2002; Takahashi et al. 2012), and abundance (Hedd et al. 2006; Thayer et al. 2008; Sydeman et al. 2013). Furthermore, cooler conditions can prompt favorable shifts in prey composition (Hedd et al. 2006; Mackas et al. 2007; Thayer et al. 2008; Keister et al. 2011; Gladics et al. 2015). For example, during cool conditions, Pacific Sand Lances and Northern Anchovy *Engraulis mordax* dominate seabird diets, with commensurate increases in seabird breeding success, whereas in warm years, rockfishes and Pacific Herring are more common in seabird diets and breeding success is lower (Hedd et al. 2006; Thayer et al. 2008; Gladics et al. 2015). Because Black Rockfish also consume these same forage fish species (Moulton 1977; Love 2011), the increased availability of Pacific Sand Lances and Northern Anchovy may confer similar benefits to the condition and growth of Black Rockfish. Moreover, a shift to a forage fish community dominated by Pacific Sand Lances, which tend to be more closely associated with nearshore waters than other forage fish (e.g., Pacific Herring; Gladics et al. 2015), likely results in greater spatial overlap between Black Rockfish and their prey.

Among local-scale relationships, there are also indications that warm conditions in the current year are associated with improved rockfish growth. Most of these relationships last only one season, suggesting the possibility that they are spurious. However, the pattern is evident in multiple indicators (SSHa, upwelling index, and PAR), lending some credibility to possible mechanistic linkages. Negative relationships between growth and upwelling are particularly unexpected given the previously established linkages between cool, nutrient-rich surface waters and higher production (e.g., Barth et al.

2007; Chavez and Messié 2009; Black et al. 2011). The unexpected growth–upwelling relationship could be related to the development of nearshore fronts that prevent planktonic food resources from reaching nearshore food webs (Shanks and McCulloch 2003). Nearshore fronts have been observed along the Oregon coast during periods of upwelling-favorable winds and result in lower nearshore concentrations of chlorophyll and diatoms (Shanks and McCulloch 2003).

Seasons that are the most informative for predicting Black Rockfish growth in the California Current are the winter and spring for basin conditions and spring for local conditions. Winter conditions might highlight the importance of preconditioning the water column for production (Polovina et al. 1995; Gargett 1997; Logerwell and Mantua 2003; Black et al. 2011). Spring conditions and the timing of the spring transition are known to be important for nutrient replenishment (Lynn et al. 2003), high levels of primary production (Hayward and Venrick 1998), and a sensitive phase for several marine animal populations in terms of recruitment, growth, and reproduction (Barth et al. 2007; Shanks and Roegner 2007).

Black Rockfish in the Alaska Coastal Current

Local-scale indices were generally stronger than basin-scale indices as predictors of Black Rockfish growth in the Alaska Coastal Current. Several studies focused on the Gulf of Alaska have indicated strong regional- and local-scale variation in oceanography (Stabeno et al. 2004; Ladd et al. 2005), primary production (Waite and Mueter 2013), ichthyoplankton assemblages (Doyle et al. 2002), fish survival (Mueter et al. 2002), and fish growth rates (Hurst and Abookire 2006), suggesting that production is more closely related to local-scale conditions than to basin-scale conditions. Basin-scale environment–growth relationships are inconsistent in their direction and are less persistent across seasons than local-scale relationships, indicating a higher likelihood of spurious relationships. Among local-scale indices, conditions that were associated with warm, more stable water columns (warmer SST, relaxed downwelling, increased PAR, and increased freshwater discharge) were related to increases in Black Rockfish growth, which is in contrast to the results for Black Rockfish in the California Current, where cooler conditions were associated with favorable growth. Warm conditions in the Gulf of Alaska have previously been found to be associated with increases in salmon survival rates (Mueter et al. 2002), salmon growth (Wells et al. 2008), and Yelloweye Rockfish growth (Black et al. 2008). The most informative season was the summer of the growth year, although relationships with 1–2-year lags were also common.

Black Rockfish results for the Alaska Coastal Current (positive influences of SST, relaxed downwelling, PAR, and freshwater discharge) were consistent with the light-limited production system in the Gulf of Alaska's nearshore pelagic food web (Gargett 1997; Brickley and Thomas 2004;

Henson 2007), but our findings do not necessarily rule out the possibility of nutrient limitation. Light limitation of phytoplankton in the Gulf of Alaska is thought to be common, as the phytoplankton must be able to cope with high light conditions, which are possible during the extended day lengths in summer, but are not necessarily common due to frequent cloud cover (Strom et al. 2010). In addition, spring blooms closely follow the onset of water column stratification (Henson 2007), which restricts phytoplankton to the photic zone, where light availability is greatest. The primary driver of stratification in the Alaska Coastal Current is freshwater discharge (Royer et al. 2001), with increases in freshwater stabilizing the water column. Because the Alaska Coastal Current is a buoyancy-driven current, increased discharge also results in accelerated flow and the possibility of a greater quantity of warm, nutrient-rich waters from the south (Royer et al. 2001). Relaxed downwelling indicates both the stabilization of the water column near the surface and the onshore movement of nutrient-rich water onto the Gulf of Alaska shelf at depth (Childers et al. 2005; Ladd et al. 2005; Weingartner et al. 2009).

Light availability, freshwater discharge, and relaxed downwelling have all been related to increased production in the Gulf of Alaska. A recent examination of interannual variation in chlorophyll-*a* concentration—a measure of phytoplankton standing stock and perhaps a metric of primary production—similarly suggested that increases in light (i.e., PAR) and relaxed downwelling improved pelagic primary production across the Gulf of Alaska shelf (Waite and Mueter 2013). Freshwater discharge has been positively related to primary production (Childers et al. 2005), secondary production of zooplankton (Coyle and Pinchuk 2003, using salinity), abundance of larval fishes (Doyle et al. 2009), and the survival of Pink Salmon *O. gorbuscha* (Mueter et al. 2005).

There are examples of studies in which increased freshwater discharge was associated with decreased primary production (Waite and Mueter 2013) and decreased abundance and recruitment of larval fishes (Doyle et al. 2009; Coffin and Mueter 2016). Conditions that promote recruitment likely differ among fish species because life history strategies vary, with some species being dependent upon retention and others being dependent upon transport. The mechanism relating high discharge to low larval recruitment may involve the inhibition of larval transport to favorable habitat (Coffin and Mueter 2016) or a negative influence of high sediment loads on fragile larvae (Doyle et al. 2009) rather than unfavorable foraging conditions. Even in our study, where most of the relationships with freshwater were positive, we identified a strong negative relationship between freshwater discharge and Black Rockfish growth with a time lag of 2 years. This lagged relationship could simply be spurious or could potentially reflect complex dynamics, such as a negative influence of high freshwater discharge on the recruitment and abundance of the forage fishes that are consumed by Black Rockfish. Overall, the

relationships between Black Rockfish growth and discharge suggest that freshwater discharge during winter plays an influential role in Gulf of Alaska nearshore production.

Just as in the California Current, increased primary production likely benefits Black Rockfish in the Alaska Current by increasing the quality and quantity of their prey. Of the potential prey species, reductions in Pacific Herring and greenlings and increases in Pacific Sand Lances and salmon were associated with warm conditions (Anderson and Piatt 1999; Hare et al. 1999; Litzow et al. 2002). Pacific Sand Lances are among the most energy-dense nearshore forage fishes available to Black Rockfish, and their abundance is strongly and positively related to interannual and spatial variation in summer SST within Gulf of Alaska nearshore habitats (Litzow et al. 2002). In another study, variation in Pacific Sand Lance growth was positively related to SST across years and primary production across sites (Robards et al. 2002). Thus, favorable influences of warmer temperature and increased primary production on Pacific Sand Lance abundance and condition may link local-scale conditions to Black Rockfish growth.

Kelp Greenlings in the California Current

Growth of Kelp Greenlings in the California Current was related to basin- and local-scale indicators. Faster growth was associated with (1) warm conditions under short or no time lags but (2) cool conditions under longer time lags. This was the case for relationships between growth and two basin-scale indicators: the PDO and MEI (in both cases, positive values represent warmer conditions). Similarly, warm local-scale conditions (warmer SST, increased SSHa, and reduced upwelling) were associated with increases in Kelp Greenling growth without time lags, whereas cool conditions (cooler SST, reduced SSHa, and increased upwelling) were associated with a lagged increase in growth. Few of these relationships were persistent across more than one season, but the consistent pattern across multiple indices suggested that the relationships were indicative of an underlying mechanism.

Relationships between cool or warm conditions and increased Kelp Greenling growth at different time lags could indicate that certain conditions lead to more abundant prey, whereas another set of conditions results in higher-quality prey. Benthic invertebrates are important prey for Kelp Greenlings (Moulton 1977; Rosenthal 1983), and previous work linking environment to benthic invertebrate production has led to hypotheses about both food- and temperature-limited production. Food-limited recruitment (Menge et al. 2009) and growth (Menge et al. 1997; Bracken et al. 2012) in mussels along the Oregon coast was associated with cool upwelling conditions that promoted an increase in phytoplankton abundance, which in turn benefited benthic filter feeders. Indeed, the duration of the pelagic larval stage in many benthic species is short and confined to the productive upwelling season (Shanks and Eckert 2005), suggesting that high

availability of planktonic food is important for successful recruitment.

On the other hand, there is also evidence of temperature-limited growth in benthic invertebrates within the California Current, as faster mussel growth was observed in warmer SSTs despite reduced food availability near Point Conception (central California; Phillips 2005, 2007), Santa Cruz Island (Channel Islands, California; Blanchette et al. 2006), and the Strait of Juan de Fuca (Strom 2004). Warm temperatures increase the rates of filter feeding, providing a plausible mechanism linking temperature to increases in growth (Phillips 2005). Both food availability and temperature were related to mussel growth rates in Oregon, with the direct (i.e., thermal) effects of temperature outweighing the indirect effect of food limitation, suggesting that temperature limitations on physiological rates are more common than food limitation (Menge et al. 2008).

At the rocky reef sites from which our samples were collected, the growth and condition of adult benthic invertebrates might not be limited by phytoplankton if kelp is the primary food resource (Duggins et al. 1989; Tallis 2009). Indeed, we found that kelp was an important carbon source for benthic Kelp Greenlings and that the presumed pathway for kelp-derived carbon was via the Kelp Greenlings' benthic invertebrate prey (von Biela et al., *in press*). Because benthic invertebrates are consumed during the adult life stage of Kelp Greenlings, the implication that kelp-based carbon is an important energy source for benthic invertebrates does not rule out the possibility that recruitment of juvenile Kelp Greenlings is phytoplankton limited (i.e., food limited).

The observed complex growth response to environmental conditions would be expected if the recruitment of benthic invertebrates is phytoplankton limited during warm years while adult growth and reproduction are temperature limited during cold years. A pattern in which intermittent conditions result in maximum growth and production is common in the literature. Indeed, several authors have coined names for such hypotheses, including the "optimal environmental window" (Cury and Roy 1989) to explain variable relationships between upwelling intensity and fish recruitment, the "optimal stability window" to explain the opposite response of salmon production to SST in current systems with different conditions (Gargett 1997), and the "intermittent upwelling hypothesis" to explain spatial variability in intertidal production across a gradient from persistent upwelling to persistent downwelling (Menge and Menge 2013). These hypotheses differ in temporal and spatial scales, but none is concerned with time scales greater than a year. Here, we expand these existing ideas and suggest that a series of years with intermittently cool and warm conditions may result in greater benthic production relative to blocks of back-to-back warm years or back-to-back cold years. Still, our understanding of benthic invertebrate production is based on information from only a few species of mussels, barnacles, and clams, which may or may

not be representative of the benthic invertebrate community as a whole; further research is needed to evaluate this interpretation.

Kelp Greenlings in the Alaska Coastal Current

Basin- and local-scale relationships indicated that warmer conditions and greater stability of the water column (positive PDO, positive MEI, warm SST, increased SSHa, relaxed downwelling, increased PAR, and increased freshwater discharge) were associated with increases in Kelp Greenling growth. Negative relationships between current-year NPGO and growth were the exception to the generally observed positive relationships between temperature and growth. Relationships with the PDO and SST were the most consistent predictors of growth. Environment-growth relationships were most common with 2-year lags or during the current summer of fish growth. Again, a mechanism involving the Kelp Greenlings' prey may be responsible, as warmer conditions are associated with increased abundance (Blanchard et al. 2010), growth (Neuparth et al. 2002; Black et al. 2009; Stoner et al. 2010; Helser et al. 2012), development (Shirley et al. 1987; Hoegh-Guldberg and Pearse 1995), and reproduction (Hines 1982; Neuparth et al. 2002) of benthic invertebrates.

Warmer temperatures generally increase rates of growth, development, and reproduction in benthic invertebrates until thermal tolerance limits are reached or until metabolic demands exceed food availability (Byrne 2011). For high-latitude systems like the Gulf of Alaska, colder years are associated with a prolonged duration of larval stages, potentially resulting in increased mortality and cohort failure (Fisher 2006). By necessity, rocky nearshore benthic invertebrates are thermal generalists (Byrne 2011) and are more likely to respond positively to increased temperatures because their thermal tolerance is quite high. Therefore, we hypothesize that the positive relationship between temperature and Kelp Greenling growth may reflect increases in the abundance and quality of their benthic invertebrate prey during warmer conditions, which could be accompanied by increases in the primary production of phytoplankton and kelp. Additional studies linking benthic invertebrate and kelp production to environmental conditions in the Alaska Coastal Current will be needed to test this hypothesis.

Summary and Conclusions

Our results are consistent with the previous understanding of environmental influences on marine production and contribute to an improved understanding of how basin- and local-scale conditions may influence nearshore production in the future. Nearshore pelagic-feeding Black Rockfish generally benefit from cool conditions in the California Current and warm conditions in the Alaska Coastal Current, consistent with findings for continental shelf ecosystems that have been extensively studied. Basin-scale indicators are much better

predictors of growth for pelagic-feeding Black Rockfish in the California Current, whereas local-scale indices are more informative for examining the growth of Black Rockfish in the Alaska Coastal Current. These patterns may indicate stronger or more coherent ties to basin-scale conditions in the California Current and more local heterogeneity in the Alaska Coastal Current.

Findings for the Kelp Greenling, a benthic-feeding species, are more nuanced and provide information for further hypothesis refinement and opportunities for hypothesis testing in future studies. Mixed relationships between the growth of Kelp Greenlings and environmental conditions at different time lags in the California Current could indicate that cooler conditions promote more benthic productivity and a greater abundance of benthic prey, whereas warmer conditions promote increases in prey quality. The veracity of this interpretation could reconcile long-disputed biophysical relationships in benthic production associated with the California Current, which contrast temperature (Phillips 2005, 2007; Blanchette et al. 2007) and food limitation (Menge et al. 1997, 2009; Menge and Menge 2013); our interpretation follows a number of hypotheses that point to the benefits of intermittently cool and warm conditions at shorter, within-season time scales (Cury and Roy 1989; Gargett 1997; Menge and Menge 2013).

Relationships between conditions and production differed between the pelagic and benthic trophic pathways, indicating that the anticipated responses to climate may vary between different components of an ecosystem. Although back-to-back years of cool conditions in the California Current may benefit pelagic nearshore species, it appears that benthic nearshore species are likely to profit from periods of high-frequency interannual variability in which cool and warm years alternate. Therefore, consideration of food-web-dependent mechanisms will improve our understanding and anticipation of ecosystem responses to climate change.

Nearshore systems are particularly vulnerable to changing environmental conditions due to their shallow depths and their location at the marine-terrestrial interface, which invokes variability from environmental drivers associated with both habitats (Agardy et al. 2005; Harley et al. 2006; Okey et al. 2014). Nearshore waters are expected to warm at rates up to twice those of offshore waters due to the rapid warming of discharged freshwater (Okey et al. 2014), although eastern-boundary upwelling systems like the California Current may experience cooler conditions due to the strengthening of upwelling (Sydeman et al. 2014). Overall, the relationships between environmental conditions and nearshore production indexed using otolith growth increments generally agree with the view that warming will have a negative influence at lower latitudes of a species' range first, while production at higher latitudes of the species' range may initially increase (Henson 2007; Boyce et al. 2010). Still, caution must be exercised when applying these relationships to future scenarios, as unexpected patterns may arise given the nonstationary nature of biophysical relationships (Schmidt et al. 2014). Moreover, the food webs considered here are likely to be altered due to a combination

of (1) increasing frequency of storms that diminish kelp forest canopies (Byrnes et al. 2011), (2) increasing kelp production driven by rising CO₂ concentrations (Koch et al. 2013), (3) increasing mortality of benthic invertebrate larvae due to ocean acidification (Byrne 2011), and (4) changes in direct and indirect species interactions as the ranges of individual fish species shift (Ainsworth et al. 2011), among other possibilities.

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