

# Contrasting effects of coastal upwelling on growth and recruitment of nearshore Pacific rockfishes (genus *Sebastes*)

Russell W. Markel and Jonathan B. Shurin

**Abstract:** Knowledge of processes underlying recruitment is critical for understanding marine population dynamics and their response to ocean climate. We investigated the relationship between coastal upwelling and early life history of black rockfish (*Sebastes melanops*), a midwater aggregating species, and CQB rockfishes (a solitary benthic species complex including *Sebastes caurinus*, *Sebastes maliger*, and *Sebastes auriculatus*), between two oceanographically distinct years on the west coast of Vancouver Island, Canada. We analysed otolith microstructure to determine parturition and settlement dates, pelagic durations, and pre- and postsettlement growth rates. High CQB rockfish recruitment in 2005 was associated with prolonged downwelling and warm ocean temperatures, late parturition dates, fast presettlement growth, short pelagic durations, and small size-at-settlement. In contrast, high black rockfish recruitment in 2006 was associated with strong upwelling and cool ocean temperatures, slow presettlement growth, and protracted pelagic durations. Presettlement growth of both rockfish complexes increased with high sea surface temperature, but was unrelated to chlorophyll *a* concentration. Our results indicate that the same oceanographic conditions give rise to fast presettlement growth and short pelagic durations for both groups, but that different factors lead to strong recruitment in each.

**Résumé :** La connaissance des processus qui sous-tendent le recrutement est d'importance cruciale pour la compréhension de la dynamique des populations marines et de leur réaction au climat océanique. Nous examinons le lien entre les remontées d'eau côtières et le début du cycle biologique des sébastes noirs (*Sebastes melanops*), une espèce de profondeur intermédiaire formant des groupements, et des sébastes « CQB » (un complexe d'espèces benthiques solitaires comprenant *Sebastes caurinus*, *Sebastes maliger* et *Sebastes auriculatus*) pour deux années aux conditions océaniques différentes, sur la côte ouest de l'île de Vancouver (Canada). Nous analysons la microstructure d'otolites afin de déterminer les dates de parturition et d'établissement, la durée des étapes pélagiques et les taux de croissance pré- et postétablissement. Un fort recrutement de sébastes CQB en 2005 est associé à une plongée d'eau prolongée et des températures océaniques élevées, des dates de parturition tardives, une croissance postétablissement rapide, des étapes pélagiques de courte durée et de faibles tailles au moment de l'établissement. En revanche, un fort recrutement de sébastes noirs en 2006 est associé à une forte remontée d'eau et de faibles températures océaniques, une croissance préétablissement lente et de longues étapes pélagiques. La croissance préétablissement des sébastes des deux complexes augmente parallèlement à la température de la surface de la mer, mais n'est pas reliée à la concentration de chlorophylle *a*. Nos résultats indiquent que les mêmes conditions océanographiques donnent lieu à une croissance préétablissement rapide et de courtes étapes pélagiques chez les deux groupes, mais qu'un fort recrutement dans ces deux complexes est le produit de facteurs différents. [Traduit par la Rédaction]

## Introduction

Variation in the frequency and magnitude of recruitment has strong effects on marine population sizes, persistence, and connectivity (Armstrong 2002; Caley et al. 1996; Cowen and Sponaugle 2009; Doherty and Williams 1988). Recruitment of marine fishes is often highly variable, with large cohorts separated by many years of weak or no recruitment (Houde 2009). Because many years can pass between years of high recruitment, recruitment events may be “stored” in adult populations with generation times that match or exceed intervals between episodic years of strong recruitment (Hjort 1914; Secor 2007). Warner and Chesson (1985) proposed the “storage effect” as a mechanism to explain species coexistence in systems where recruitment is limited by juvenile habitat (Sale 1977). The storage effect also promotes population resilience through interaction among overlapping generations by maintaining populations over long periods of unfavourable conditions for recruitment (Secor 2007). Thus, under-

standing processes underlying recruitment variability and year-class strength is critical to predicting population and community responses to exploitation, climate change, and conservation and management strategies.

Recruitment variation in space or time may be driven by reproduction, survival through the larval stage, or onshore advection and settlement of juveniles into benthic habitats (Pepin 1991). Most coastal fishes and invertebrates have complex life histories where recruitment in populations is decoupled from local production by widely dispersed pelagic eggs and larvae that experience high and variable mortality (Leggett and Deblois 1994; Pepin and Myers 1991; Roughgarden et al. 1988). Following pelagic stages lasting from days to several months and dispersal distances from tens to hundreds of kilometres (Shanks 2009), juveniles settle into benthic habitats and local adult populations (Roughgarden et al. 1985). Postsettlement density-dependent mortality may obscure the effects of larval recruitment variation on population numbers

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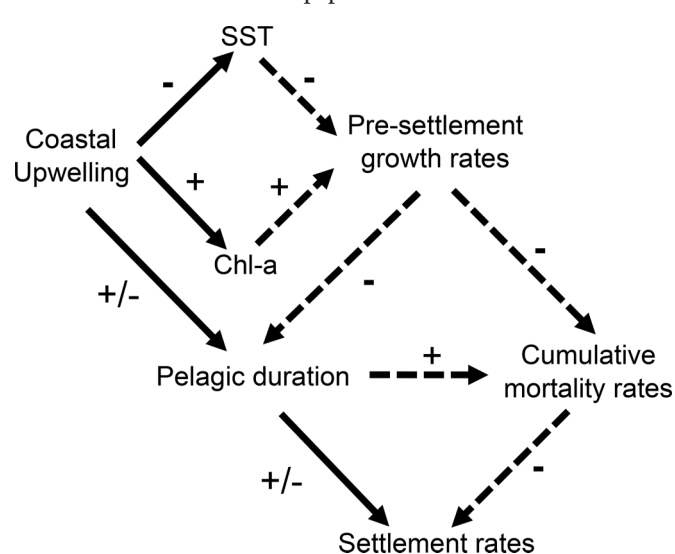
(Caley et al. 1996; Hixon and Webster 2002). Ocean conditions affecting larval mortality are major drivers of annual recruitment success (Doherty and Fowler 1994; Field and Ralston 2005; Houde 1989; Jenkins and King 2006; Pepin 1991). Infrequent spatial and temporal alignment of ocean conditions favoring larval growth and survival are likely to create narrow windows of reproductive opportunity and success (Agostini and Bakun 2002; Cury and Roy 1989; Cushing 1990; Hedgecock 1994; Lasker 1975).

Years of strong recruitment likely result from ocean conditions favoring high larval growth and (or) survival (e.g., Bergenius et al. 2002; Jenkins and King 2006) and (or) high rates of larval delivery (Bertness et al. 1992). Although adult body condition and larval production vary with ecosystem productivity (Lenarz and Echeverria 1986; Woodbury 1999), larval production and recruitment are often uncoupled in time (Carr and Syms 2006a). Larval fish mortality is size-dependent, decreasing rapidly with increasing body size. Factors promoting high growth rates may therefore also reduce mortality (Hare and Cowen 1997; Houde 1989; Otterlei et al. 1999; Pepin 1991). Survival through the larval stage is a function of daily mortality (i.e., losses to starvation and predation) and the number of days over which mortality accrues (Houde 2009; Leggett and Deblois 1994). Pelagic duration is therefore a major contributing factor to cumulative mortality and recruitment strength (Pepin and Myers 1991). The oceanographic processes affecting larval growth, pelagic duration, and onshore transport (i.e., delivery or retention; Selkoe et al. 2006; Warner and Cowen 2002) therefore shape the population dynamics of many marine species.

Rockfishes of the genus *Sebastes* (family Scorpaenidae) comprise one of most ecologically and economically important groups of marine fishes along the Pacific coast of North America (Love et al. 2002). Courtship and copulation generally occur in the fall, and females give birth to live young (i.e., parturition) during the winter and early spring. Adult females may release more than a million larvae that are approximately 3–7 mm long at parturition. Larvae develop into pelagic juveniles after 1–2 months (Love et al. 2002) and remain in the water column and offshore for additional weeks to months before moving to inshore settlement habitats and adult populations (Moser and Boehlert 1991). Following settlement, growth and condition are closely tied to population density and habitat availability (Markel and Shurin 2015). Extreme longevity (100–200 years in some species; Munk 2001), low reproductive rates, and stochastic recruitment make rockfishes vulnerable to over-exploitation (Leaman 1991; Parker et al. 2000; Williams et al. 2010). As a result, rockfish populations are increasingly the focus of protection by marine protected areas and catch restrictions (e.g., Haggarty et al. 2016a, 2016b; Yamanaka and Logan 2010). Because local population persistence depends on replenishment (Cowen and Sponaugle 2009), incorporating the processes that regulate the frequency, magnitude, and spatial scales of recruitment variability is key to designing effective marine protected area networks (Carr and Reed 1993; Gaines et al. 2003). As different rockfish year classes show uneven representation in fisheries (Laidig et al. 2007; Mason 1998; Mearns et al. 1980; Ralston and Howard 1995), the processes driving rockfish recruitment may determine population abundance and fisheries landings (but see Haggarty et al. 2017).

Recruitment variation of nearshore rockfishes in the northeastern Pacific coastal margin is associated with upwelling (Ainley et al. 1993; Caselle et al. 2010a; Ralston and Howard 1995). Upwelling occurs seasonally along eastern boundaries of ocean basins during spring and summer months when northerly winds push the low-density surface Ekman layer offshore and cause a drop in nearshore sea level. As a result, cold and nutrient-rich deepwater flows inshore and upwells into the euphotic zone where it fuels primary production (Cury and Roy 1989). Figure 1 summarizes the hypothesized relationships among upwelling, temperature, marine productivity, presettlement growth and mortality, and settle-

ment rates of rockfishes. Cross-shelf flows during upwelling may transport pelagic larvae offshore or onshore, depending on the depth of larvae relative to the thermocline (Mace and Morgan 2006; Shanks and Brink 2005). Coastal upwelling influences rockfish recruitment both by inhibiting or facilitating nearshore retention or onshore movement of larvae and pelagic juveniles and by regulating ocean temperature and primary productivity and therefore presettlement growth rates (Fig. 1). Larval growth and survival may be promoted by upwelling due to increased primary production or reduced due to low temperature. Caselle et al. (2010a) found that coastal upwelling was the best oceanographic predictor of delivery of pelagic juvenile rockfishes to nearshore adult habitats.



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However, evidence for the effects of upwelling on recruitment is mixed (Shanks and Brink 2005), and attempts to relate interannual recruitment variation to the timing and magnitude of upwelling have met with mixed success (Caselle et al. 2010a, 2010b; Laidig et al. 2007; Wilson et al. 2008). In a related study, Lotterhos and Markel (2012) examined relationships between coastal upwelling and black rockfish (*Sebastes melanops*) reproductive success and revealed contrasting effects on the abundance of recruits. Although both warmer ocean temperatures and the strength of upwelling were positively correlated with the abundance of recruits, warmer ocean temperatures were positively correlated with larval growth rates and the effective number of breeders, whereas upwelling was negatively correlated with the effective number of breeders. These results suggest that ocean temperature affects survival and recruitment via larval growth, while the strength of upwelling affects survival through oceanographic processes determining larval delivery. These patterns, however, may be limited to species of rockfishes with similar distribution of larvae in the water column (Lenarz et al. 1995).

Nearshore rockfishes can be subdivided into “midwater aggregating” and “solitary benthic” complexes, composed of species

representing primarily two subgenera that differ remarkably in their morphology, ecology, and evolutionary histories (Hyde and Vetter 2007). Species within the subgenus *Sebastes* are midwater aggregating species (e.g., *Sebastes flavidus*, *S. melanops*, *Sebastes mystinus*, *Sebastes serranoides*), generally associated with shallow semipelagic habitats, are darkly or drably coloured, and have elongated bodies with greatly reduced head spines. In contrast, subgenus *Pteropodus* is composed of solitary benthic species (e.g., *Sebastes carnatus*, *Sebastes caurinus*, *Sebastes chrysomelas*, *Sebastes maliger*, *Sebastes nebulosus*, *Sebastes rastrelliger*) that are generally associated with shallow high-relief habitats, have deep bodies, often with distinct coloration patterns, and strong head spination. Lenarz et al. (1995) and Carr and Syms (2006) observed that during El Niño years (1992–1993 and 1997–1998), high recruitment of solitary benthic rockfishes corresponded to above average ocean temperatures and weak upwelling that favoured onshore advection. In contrast, midwater aggregating rockfishes recruited heavily during a La Niña event in 1999 that was associated with strong upwelling and cold ocean temperatures.

Our objective was to understand how ocean climate variability affects early life history stages and recruitment of nearshore Pacific rockfishes off the west coast of Vancouver Island, Canada. We measured recruitment over 6 years (2005–2010) that included two exceptionally strong recruitment events. CQB complex recruitment (a species complex of solitary-benthic rockfishes including copper (*S. caurinus*), quillback (*S. maliger*), and brown (*Sebastes auriculatus*) rockfishes with juveniles that cannot be distinguished morphologically) was high in 2005. In contrast, black rockfish (*S. melanops*), a midwater aggregating species, was high in 2006. These recruitment events provided the opportunity to investigate how the timing and magnitude of coastal upwelling differentially affect early life history attributes and recruitment success of rockfishes with contrasting life history strategies. We compared oceanographic conditions between 2005 and 2006 with juvenile rockfish life history parameters using otolith microstructure analysis to determine parturition and settlement dates, pelagic durations, and pre- and postsettlement growth rates. We assessed the effects of upwelling intensity, ocean temperature, and primary productivity on these early life history attributes and corresponding recruitment success. Our goal was to determine whether the conditions that favor growth of pelagic larvae increase settlement and recruitment into the nearshore habitat and whether these effects vary among solitary benthic and midwater aggregating rockfish complexes.

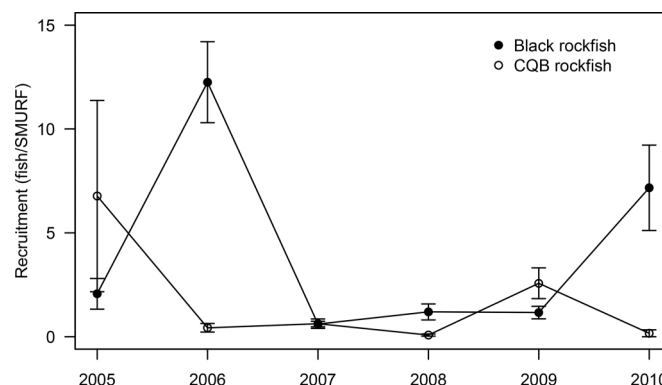
## Methods

### Study system

This study was conducted in Barkley Sound (48°50.0'N, 125°22.0'W) on the southwest coast of Vancouver Island, British Columbia, at the northern-most boundary of the California Current Large Marine Ecosystem. This region shows seasonal transitions between upwelling-favourable northwest winds (spring–summer) and downwelling-favourable southerly winds (fall–winter) characteristic of the California Current System (Shanks and Eckert 2005). The Vancouver Island Coastal Current (VICC) is a narrow current (5–25 km) driven primarily by buoyancy flux from coastal runoff exiting the Strait of Georgia via the Strait of Juan de Fuca (Hickey et al. 1991). Following the spring transition, the VICC continues in a reduced band flowing northward towards Brooks Peninsula (Hickey et al. 1991; Thomson and Ware 1996).

We used standard monitoring units for the recruitment of fishes (SMURFs; Ammann 2004) to assess rockfish recruitment between 2005 and 2010. We deployed SMURFs at the seaward edge of kelp forests (*Macrocystis pyrifera*), where they were moored horizontally 1.5 m below the surface. We used a Benthic Ichthyofaunal Net for Coral/Kelp Environments (BINCKE; Anderson and Carr 1998) and snorkeling equipment to collect all fish within SMURFs

**Fig. 2.** Annual recruitment (rockfish per standard monitoring unit for the recruitment of fishes (SMURF; mean  $\pm$  SE) in August between 2005 and 2010. The number of SMURFs deployed varied annually: 2005 ( $n = 16$ ), 2006–2009 ( $n = 30$ ), 2010 ( $n = 6$ ).



on each sampling date. All young-of-the-year (YOY) rockfishes were identified, weighed, and measured (total length). Copper (*S. caurinus*), quillback (*S. maliger*), and brown (*S. auriculatus*) rockfishes were grouped as “CQB” rockfishes because of difficulty distinguishing early postsettlement juveniles. Beginning in 2010, we reduced our sampling program whereby recruitment estimates and collection of postsettlement rockfishes for otolith analyses took place only in August. We therefore report the average number of rockfish per SMURF in August between 2005 and 2010 (Fig. 2). Full details of sampling sites and locations are described in Markel et al. (2017).

### Age and parturition date determination

We used otolith microstructure analysis to determine parturition dates, settlement dates, and pelagic durations of juvenile black and CQB complex rockfishes collected by SMURFs in 2005 and 2006. Deposition of daily increments by juvenile rockfishes has been validated for early postsettlement rockfishes (Kokita and Omori 1999; Laidig et al. 1991; Plaza et al. 2001; Woodbury and Ralston 1991; Yoklavich and Boehlert 1987). We did not conduct additional validation experiments and assumed for both groups that each increment represents 1 day of growth and that the total number of increments corresponds to the number of days between parturition and capture (i.e., age). To ensure representation of all sizes and ages, we pooled black and CQB rockfishes collected in 2005 and 2006 over all sampling dates and randomly selected individuals from 10 mm size classes. We mounted right sagittal otoliths on glass slides in clear Crystalbond 509 thermoplastic epoxy with the sulcus facing downward and the antirostral end angled downward ~30–40 degrees from horizontal. We measured otolith lengths (the longest distance across the sagittae) using a digital image of the entire otolith. All digital images were obtained using a JVC 3-CCD camera mounted on a dissecting microscope or an inverted transmission light microscope. We used the digital imagery software Auto-Montage Pro (version 5.03, Syncroscopy, Beacon House, Cambridge) for image capture and otolith microstructure measurements.

We exposed daily growth increments using 30 and 3  $\mu\text{m}$  lap-ping paper and viewed them at 40 $\times$ –1000 $\times$  magnification. We did not use otoliths if the primordium or large sections of increments were not visible. Dark checks at the edge of the nuclear radius of numerous *Sebastes* species have been identified as extrusion or parturition checks (Laidig and Ralston 1995; Miller and Shanks 2004; Plaza et al. 2001; Ralston et al. 1996). Consistent with these studies, we found checks at median nuclear radii of 11.77  $\mu\text{m}$  for *S. melanops* and 12.55  $\mu\text{m}$  for CQB rockfishes. When visible we measured increment widths from the primordium to parturition checks and subsequently between each increment along a



straight line to the most distal portion of the antistroal end. In most cases parturition checks were not observed and increments closest to the primordium were not visible. Instead, we started counts and measurements where increments first became continuously visible to a maximum distance of 25  $\mu\text{m}$  from the core. If increments were not continuously visible beyond 25  $\mu\text{m}$  from the core, these otoliths were rejected from our analyses. We estimated the number of increments between the first measurement and the nuclear radius at parturition by subtracting the median radii of parturition checks (above) and dividing the difference by the mean width of the first five increments measured. Sample micrographs of a black rockfish otolith at 100 $\times$ , 200 $\times$ , 400 $\times$ , and 1000 $\times$  magnification are shown in the online Supplemental material, Fig. S1<sup>1</sup>.

### Settlement date determination

Settlement marks on the otoliths of early postsettlement rockfishes have been identified and validated previously (Amdur 1991; Gallagher 2007; Pasten et al. 2003). We determined settlement dates using the transition-centered method (Pasten et al. 2003; Wilson and McCormick 1997, 1999). This method uses longitudinal profiles of daily increment width to identify a distinct transition from slow and consistent presettlement growth to fast and variable postsettlement growth associated with settlement of reef fishes. In addition, we constructed longitudinal profiles of increment width variance calculated over 5-day intervals and plotted these as 5-day moving averages. We used both types of plots to identify settlement age and date by the increment immediately preceding a distinct transition to persistently rapid and variable growth. To visualize these relationships for each species and year, we centered increment width and variance profiles on designated settlement increments and plotted resulting mean increment widths and variances for the 20 days (increments) preceding and following settlement. We determined settlement dates twice independently using the longitudinal profiles of growth and the moving window and averaged the two readings. We determined pelagic duration by subtracting parturition dates from settlement dates.

Finally, we compared the timing of parturition and settlements in 2005 and 2006 with the timing of specific oceanographic events. We focused these comparisons on time periods when the majority of parturition and settlements occurred each year by using the first and third quartiles of parturition and settlement date distributions to define parturition and settlement intervals for each rockfish group and year.

### Annual and interannual oceanographic variability

We obtained daily upwelling index estimates of Ekman transport ( $\text{m}^3 \cdot \text{s}^{-1} \cdot 100 \text{ m}^{-1}$  of coastline) for position 48°N, 125°W from the Pacific Fisheries Environmental Lab (<http://www.pfeg.noaa.gov>). Upwelling index values are modeled from recorded wind direction, velocity, and duration. Positive values indicate upwelling-favourable winds and offshore transport of the shallow low-density Ekman layer, and negative values indicate downwelling-favourable winds and onshore transport of the Ekman layer. We obtained daily sea surface temperature (SST) data collected from Amphitrite Point Lighthouse, located at the northwest corner of Barkley Sound, from Fisheries and Oceans Canada (<http://www.pac.dfo-mpo.gc.ca>). We obtained satellite-derived estimates of daily chlorophyll concentrations ( $\text{mg} \cdot \text{m}^{-3}$ ) from Aqua MODIS sensors (<https://seadas.gsfc.nasa.gov/>). We used the SeaDAS Level 3 browser to sample an 11  $\times$  11 matrix of 4 km  $\times$  4 km pixels (1936 km<sup>2</sup>) situated at the entrance to Barkley Sound and centered at 48.649°N, 125.559°W. Owing to cloud cover, data were not available for all days or for all pixels on each day. We derived daily estimates by

averaging across pixels on each day and using an 11-day moving average (the shortest interval that gave continuous values) to smooth trends and minimize data gaps.

We compared the average ocean conditions experienced by black and CQB rockfish cohorts in 2005 and 2006 during their pelagic phases. To control for observed differences in pelagic duration, we limited analyses to the first 40 and 60 days of the pelagic durations of individual CQB and black rockfishes, respectively. We selected these intervals based on observed pelagic durations for black and CQB rockfishes to maximize interval length and sample sizes. We aligned intervals of all individuals and calculated daily averages of upwelling index values, SST, and chlorophyll *a* concentrations.

### Pre- and postsettlement growth rates

We compared daily growth rates of black and CQB rockfishes between 2005 and 2006 by testing for differences in slopes of length-at-age relationships using simple linear regression and ANCOVA. In addition, we constructed longitudinal profiles of average pre- and postsettlement daily increment width. For each annual cohort and rockfish group, we centered individual longitudinal profiles on increments corresponding to settlement dates and then calculated mean increment width for each increment (day) preceding and following settlement. Finally, we used individual longitudinal profiles of otolith increment width to model individual length-at-age profiles from parturition to collection. This approach allowed us to fit growth models representing each cohort and to estimate the body lengths of individual rockfish at the time of settlement (i.e., size-at-settlement).

We used the Modified-Fry back-calculation model to estimate body length for each incremental increase in otolith radius (Vigliola et al. 2000; Wilson et al. 2009). This model (eq. 1) assumes nonlinearity between otolith and somatic growth and constrains an allometric body length – otolith radius function through a biologically meaningful intercept as

$$(1) \quad L_i = a + \exp \left\{ \ln(L_{op} - a) + [\ln(L_{cpt} - a) - \ln(L_{op} - a)] \times \frac{[\ln(R_i) - \ln(R_{op})]}{[\ln(R_{cpt}) - \ln(R_{op})]} \right\}$$

where  $L_i$  is the length of the *i*th fish at capture in millimetres,  $L_{op}$  is mean fish body length at first increment (parturition),  $R_i$  is otolith radius,  $R_{op}$  is mean otolith radius at first increment (parturition), and  $R_{cpt}$  is otolith radius at capture, and where  $a = L_{op} - bR_{op}^c$ . The parameters  $b$  and  $c$  were obtained by fitting a nonlinear regression (eq. 2) to the relationship between fish length and otolith radius:

$$(2) \quad L_{cpt} = L_{op} - bR_{op}^c + bR_{cpt}^c$$

where  $L_{cpt}$  is fish body length at capture,  $b$  is the slope of the  $L$ - $R$  relationship, and  $c$  is the coefficient of allometry. We constructed individual length-at-age profiles by plotting modeled estimates of body length for each daily growth increment from parturition to capture. To represent average growth profiles of each cohort, we fit a single growth model to the individual growth profiles comprising each cohort. We compared von Bertalanffy, logistic, Gompertz, and Schnute-Richards growth models using Akaike's information criterion (AIC) and found that the logistic growth model most closely represented the sigmoidal growth trajectories of juvenile rockfishes in this study.

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2019-0179>.

$$(3) \quad L_i = \frac{a}{1 + b \times \exp(-c \times \text{age})}$$

where  $L_i$  is fish length,  $a$  is the asymptotic fish length,  $b$  is the inflection point, age is in days since parturition, and  $c$  is a relative growth coefficient (Bates and Watts 1988).

### Data analyses

All analyses were performed using R (R Core Development Team 2011). We fit logistic growth models to modeled length-at-age profiles of annual black and CQB rockfish cohorts using non-linear least squares approximation (R package “nls”). To test for interannual differences in parturition dates, settlement dates, pelagic durations, and size-at-settlement, we used Student's  $t$  tests.

We used simple linear regression to assess the effects of SST ( $^{\circ}\text{C}$ ) and chlorophyll  $a$  ( $\text{mg}\cdot\text{m}^{-3}$ ) on presettlement growth rates ( $\mu\text{m}\cdot\text{day}^{-1}$ ) of individuals and the effects of growth rates (i.e., developmental rates and swimming abilities) and upwelling (i.e., onshore-offshore transport) on pelagic duration. Because increment width increases with body and otolith length, and because pelagic durations vary widely among individuals, we restricted analyses to growth profiles corresponding to 5–40 and 5–60 days following parturition for CQB and black rockfishes, respectively. We calculated mean upwelling index, SST, and chlorophyll concentrations over dates corresponding to individual growth profiles.

We estimated the independent effects of these explanatory variables on growth rates and pelagic durations using hierarchical variance partitioning (R package “hier.part”). Hierarchical partitioning is a form of multiple regression that determines the contribution of each predictor to the total explained variance of a regression model, both independently and in conjunction with the other predictors, for all possible candidate regression models. Hierarchical partitioning alleviates the problems of multicollinearity associated with traditional multiple regression approaches (Mac Nally 2002; Mac Nally and Walsh 2004).

## Results

### Interannual recruitment variability

Black rockfish recruitment varied around 10-fold among years, with strongest recruitment events occurring in 2006 and 2010. High CQB rockfish recruitment occurred in 2005 and, to a lesser extent, in 2009 (Fig. 2).

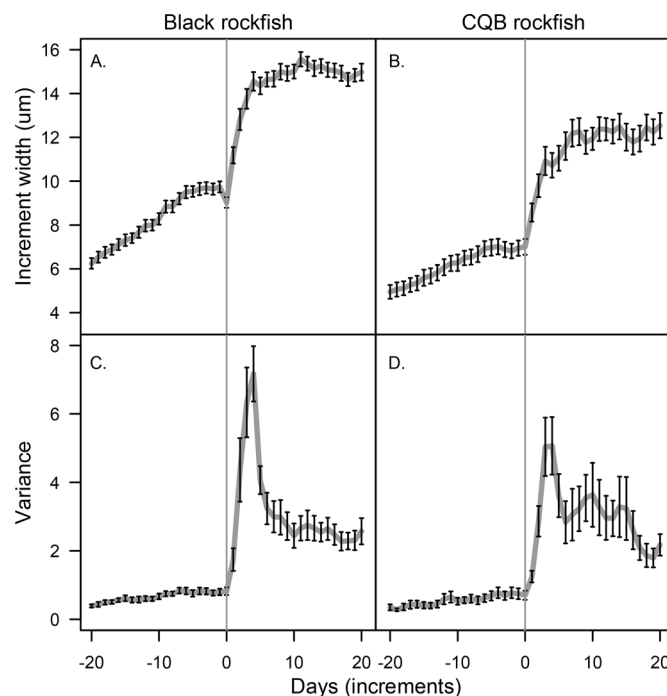
### Parturition, settlement, and pelagic duration

Longitudinal profiles of otolith daily increment width and variance were effective for identifying settlement dates of both black and CQB rockfishes (Fig. 3). Presettlement growth was clearly differentiated from postsettlement growth by an abrupt transition from small and invariable to large and variable increment widths. Black rockfish parturition and settlement dates did not differ between the year with weak (2005) and strong (2006) recruitment, but pelagic durations were on average 9 days shorter, and settlement dates 12 days earlier, in 2005 (Table 1A). Back-calculated estimates of black rockfish size-at-settlement did not differ between years. CQB rockfish parturition dates were on average 28 days later in 2005 than in 2006, while pelagic durations were 12 days shorter, and settlement dates 15 days later, in 2005 than in 2006. CQB rockfishes were significantly smaller at settlement in 2005 than in 2006 (Table 1B).

### Cohort-specific oceanographic conditions

Oceanographic conditions experienced by pelagic larvae and juveniles of black and CQB rockfishes differed markedly between 2005 and 2006. Presettlement black rockfish in 2005 experienced downwelling conditions (i.e., negative upwelling index values), warm temperatures, and low primary productivity (Figs. 4A, 4C,

**Fig. 3.** Comparison of black rockfish ( $n = 68$ ) and CQB rockfish ( $n = 42$ ) otolith daily growth increment width and variance (mean  $\pm$  SE) corresponding to the 20 days preceding and following increments designated as the day on which settlement occurred.



**Table 1.** Comparison of early life history attributes of black and CQB rockfishes between 2005 and 2006.

(A) Black rockfish				
	2005 ( $n = 27$ )	2006 ( $n = 40$ )	$T$ value	$P > T$
Parturition date	17 Feb. $\pm$ 2.5 days	20 Feb. $\pm$ 1.8 days	0.78	0.4404
Settlement date	25 Apr. $\pm$ 3 days	7 May $\pm$ 1.8 days	3.25	0.0022
Pelagic duration	67 $\pm$ 1.7 days	76 $\pm$ 1.4 days	4.04	0.0002
Size-at-settlement	19.85 $\pm$ 0.73 mm	19.95 $\pm$ 0.54 mm	0.11	0.9117
(B) CQB rockfish				
	2005 ( $n = 20$ )	2006 ( $n = 19$ )	$T$ value	$P > T$
Parturition	16 Apr. $\pm$ 4.7 days	19 Mar. $\pm$ 3.7 days	5.70	<0.0001
Settlement	6 June $\pm$ 3.4 days	22 May $\pm$ 4 days	2.89	0.0065
Pelagic duration	51 $\pm$ 2.6 days	63 $\pm$ 2.7 days	3.37	0.0018
Size-at-settlement	11.83 $\pm$ 0.9 mm	14.09 $\pm$ 0.90 mm	2.17	0.0355

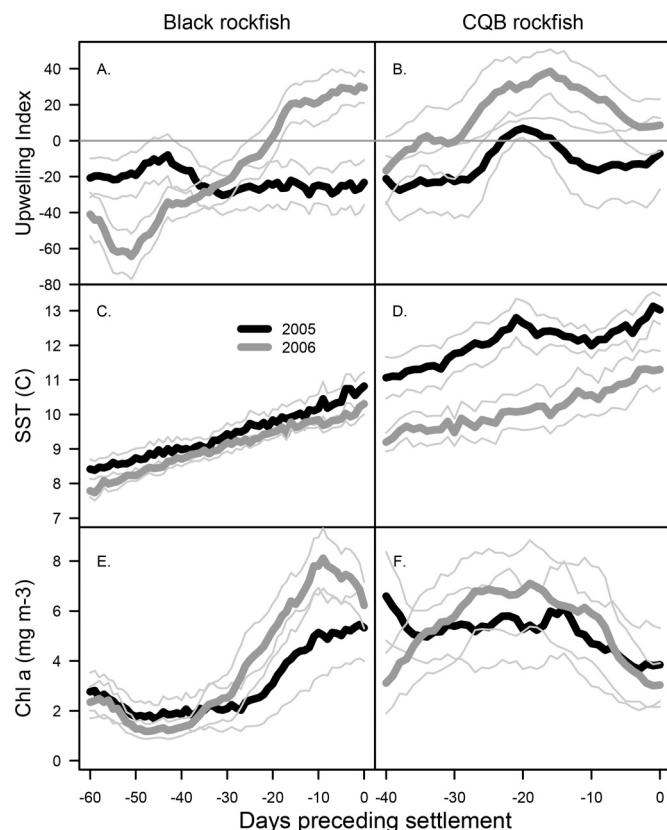
4E). Upwelling increased in 2006 beginning ~50 days prior to black rockfish settlement, becoming positive ~20 days prior to settlement. Strong upwelling began in mid-April of 2006 and resulted in elevated chlorophyll  $a$  levels.

CQB rockfishes also experienced markedly different oceanographic conditions between 2005 and 2006 both due to parturition dates that occurred later than black rockfish in both years and because parturition dates occurred a month later in 2005 than in 2006. In 2005, presettlement CQB rockfishes experienced unusually warm and downwelling-favourable ocean conditions during the 40 days prior to settlement. In contrast, pelagic larvae and juveniles in 2006 experienced strong upwelling and cool ocean temperatures (Figs. 4B, 4D, 4F).

### Oceanographic conditions during parturition and settlement intervals

Black rockfish parturitions occurred in mid- to late February in both 2005 (10 to 23 February) and 2006 (12 February to 1 March),

**Fig. 4.** Cohort-specific oceanographic conditions experienced by presettlement black rockfish (2005:  $n = 27$ ; 2006,  $n = 39$ ) and CQB rockfishes (2005:  $n = 22$ ; 2006,  $n = 19$ ). Thick lines represent daily averages of oceanographic metrics corresponding to the 60 days (black rockfish) and 40 days (CQB rockfishes) prior to settlement of individuals comprising each cohort. Thin lines represent 95% confidence intervals around daily means.



during short periods of high upwelling, low SST, and high chlorophyll *a* concentrations (Figs. 5A, 5C, 5E). Black rockfish settlement in 2005 (17 April to 9 May) and 2006 (27 April to 14 May) corresponded to periods of strong upwelling. High black rockfish settlement in 2006 occurred through late April and early May during the peak and declining phase of an exceptionally strong upwelling event.

CQB rockfish parturitions (9 to 29 April) and settlements (24 May to 18 June) in 2005 occurred at the end of periods of exceptionally low upwelling and increasing SST and chlorophyll *a* levels (Figs. 5B, 5D, 5F). In 2006, CQB parturitions (11 to 30 March) occurred nearly a month earlier than in 2005 and immediately before upwelling increased in early April and remained above average until mid-May when settlement occurred (16 to 29 May).

### Pre- and postsettlement growth

We used the positive correlation between otolith length and body length for both species (Supplemental Fig. S2<sup>1</sup>) to model individual length-at-age profiles using the Modified-Fry back-calculation model (Supplemental Fig. S3<sup>1</sup>). Logistic growth models fitted to back-calculated length-at-age profiles indicate that black rockfish presettlement growth rates were initially slightly higher in 2005 than in 2006; however, in 2005 postsettlement growth slowed at ~150 days, after which 2006 growth rates were faster (Fig. 6A). Fitted growth models for CQB rockfishes show faster pre- and postsettlement growth in 2005 compared with 2006 (Fig. 6B). Length-at-age relationships closely mirrored the modeled comparison of pre- and postsettlement growth. Black rockfish growth was

slightly higher in 2006 (Fig. 6C; ANCOVA, length  $\times$  year,  $F = 6.49$ ,  $P = 0.0123$ ), and CQB rockfish length-at-age was markedly higher in 2005 (Fig. 6D; ANCOVA, length  $\times$  year,  $F = 8.19$ ,  $P = 0.0067$ ).

Comparison of average daily increment width profiles reinforced these patterns. Black rockfish grew faster presettlement in 2005 than in 2006, but postsettlement growth was faster in 2006 (Fig. 7A). Black rockfish size-at-settlement was similar in 2005 and 2006, despite the trend towards higher presettlement growth in 2005 (Fig. 7A; Table 1). CQB rockfish presettlement increments were consistently wider in 2005 than in 2006, and this trend continued postsettlement (Fig. 7B). Higher CQB rockfish growth rates (logistic models, length-at-age, and increment width-at-age) in 2005 corresponded to significantly smaller sizes-at-settlement (Fig. 7B; Table 1).

### Ocean conditions, growth rates, and pelagic duration

We found strong and consistent relationships between black (Fig. 8) and CQB (Fig. 9) rockfish presettlement growth rates, pelagic duration, SST, and upwelling. Growth rates increased significantly with increasing SST (black rockfish,  $R^2 = 0.2369$ ,  $F_{[1,54]} = 16.76$ ,  $P = 0.00014$ ; CQB rockfishes,  $R^2 = 0.3377$ ,  $F_{[1,36]} = 18.36$ ,  $P = 0.00013$ ), but not chlorophyll concentrations (black rockfish,  $R^2 < 0$ ,  $F_{[1,54]} < 0$ ,  $P = 0.9950$ ; CQB rockfishes,  $R^2 = 0.0555$ ,  $F_{[1,36]} = 2.11$ ,  $P = 0.1547$ ). Pelagic durations decreased with increasing growth rates (black rockfish,  $R^2 = 0.2993$ ,  $F_{[1,54]} = 23.07$ ,  $P < 0.0001$ ; CQB rockfishes,  $R^2 = 0.2506$ ,  $F_{[1,36]} = 12.04$ ,  $P = 0.0014$ ) and increased with upwelling experienced during the 30 days prior to settlement (black rockfish,  $R^2 = 0.1996$ ,  $F_{[1,54]} = 13.47$ ,  $P = 0.0006$ ; CQB rockfishes,  $R^2 = 0.1784$ ,  $F_{[1,36]} = 7.82$ ,  $P = 0.0082$ ). Hierarchical variance partitioning showed that growth rates of black and CQB rockfishes were primarily associated with the independent effects of SST (black rockfish = 87.7%; CQB rockfishes = 89.8%) but not chlorophyll *a* levels (black rockfish = 12.3%; CQB rockfishes = 10.2%). Pelagic durations of rockfishes were strongly affected by the independent effects of presettlement growth rates (black rockfish = 45.4%; CQB rockfishes 61.2%) and the magnitude of upwelling prior to settlement (black rockfish = 54.6%; CQB rockfishes = 38.8%).

### Discussion

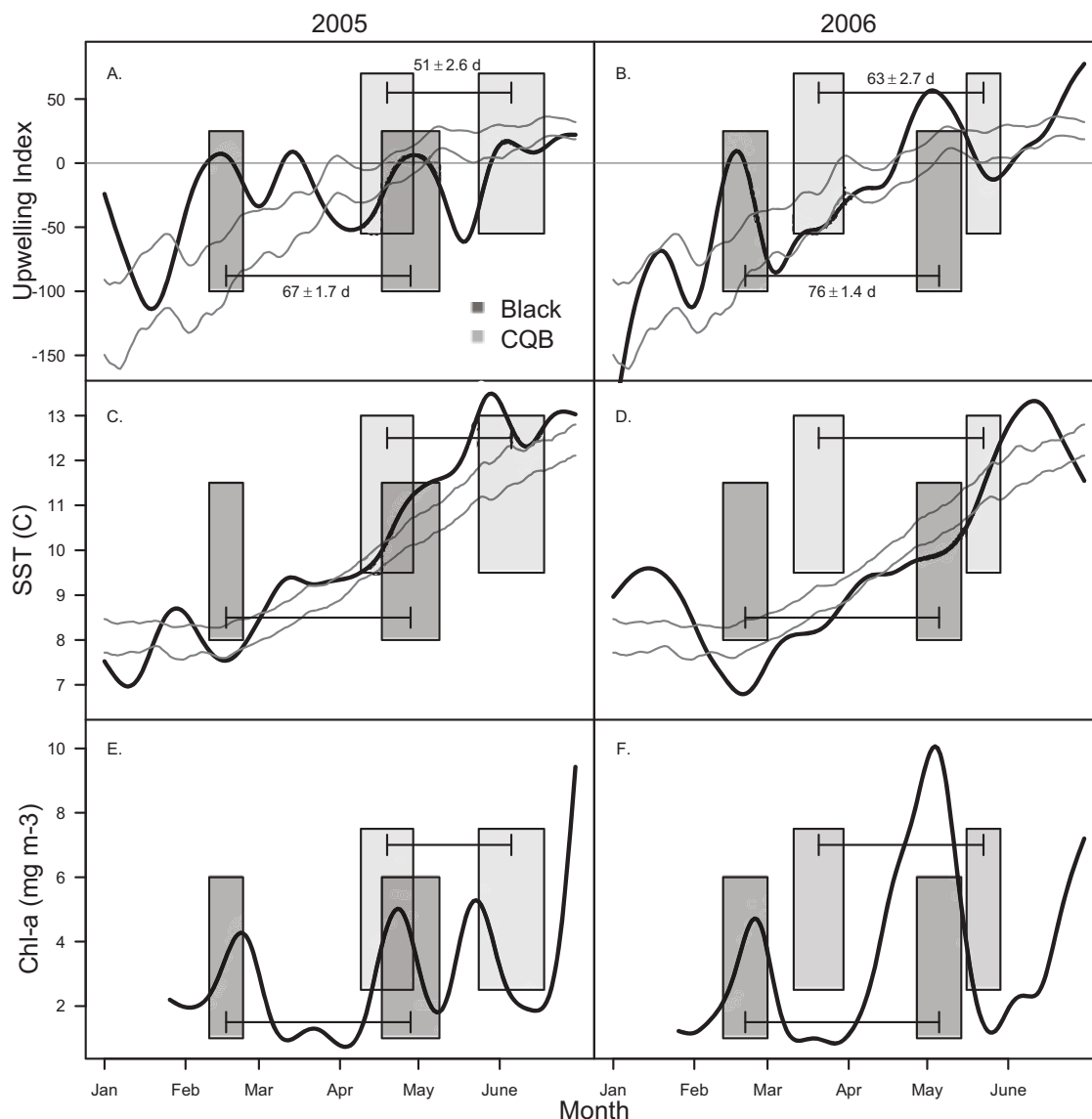
Our research reveals distinct responses of midwater aggregating black rockfish and solitary benthic CQB rockfish growth and recruitment to seasonal and interannual climate variation and its effect on upwelling, temperature, and marine productivity. Both complexes showed large interannual variability in early life history attributes (i.e., parturition and settlement dates, growth rates, and pelagic durations) corresponding closely, but in different ways, to specific upwelling events. Black rockfish reproduce earlier in the year than CQB rockfishes, and upwelling had nearly opposite effects on recruitment, although both showed faster growth during times of warmer SST. High CQB rockfish recruitment was associated with prolonged downwelling-favorable winds, warm ocean temperatures, late parturition dates, high growth rates, and short pelagic durations. In contrast, strong black rockfish recruitment was associated with strong upwelling, cool ocean temperatures, slow growth rates, and long pelagic durations. These results provide evidence that high larval growth rates and reduced pelagic durations are not preconditions necessary for strong black rockfish recruitment success. Rather, oceanographic processes facilitating onshore delivery of late-stage pelagic juveniles may be the primary determinant of black rockfish recruitment success.

### Contrasting oceanographic conditions in 2005 and 2006

Oceanographic conditions differed remarkably between 2005 and 2006 on the west coast of Vancouver Island and throughout the northern California Current Large Marine Ecosystem (CCLME). In 2005 the spring transition to upwelling-favourable winds that



**Fig. 5.** Black and CQB rockfish parturition and settlement intervals (defined as the first and third quartiles of date distributions) and mean pelagic durations in 2005 and 2006 in relation to upwelling index values and sea surface temperatures (7-day moving averages) and chlorophyll *a* levels (11-day moving averages). Thin gray lines represent 95% confidence intervals around daily mean values between 1977 and 2010.



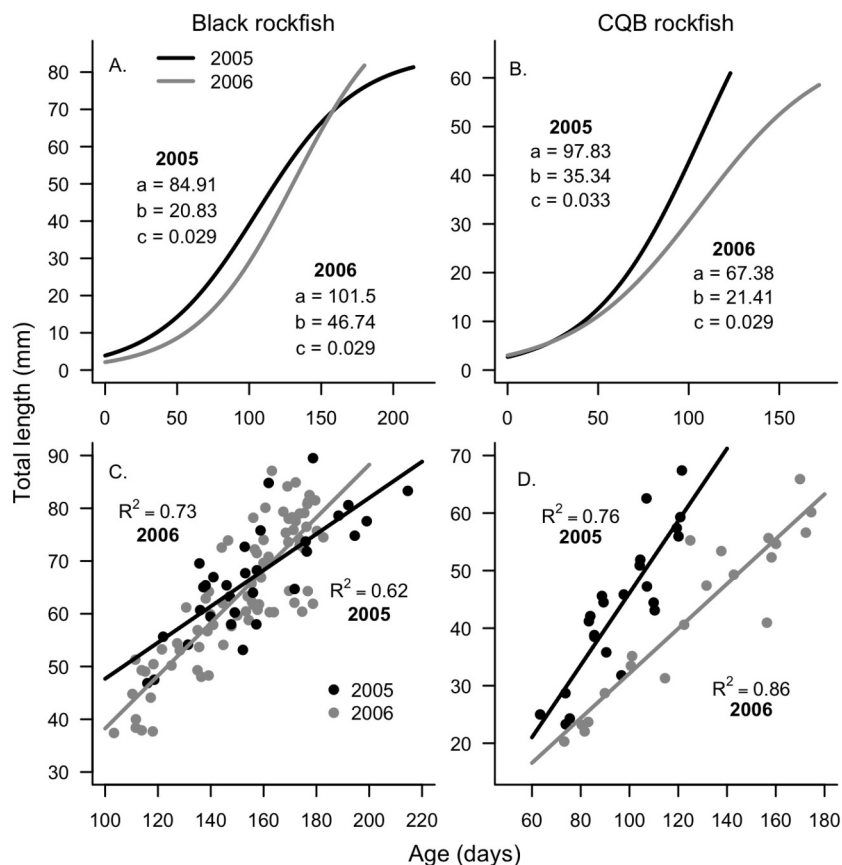
normally occurs in mid-April was delayed by 2–3 months resulting from atmospheric blocking of the jet stream (Schwing et al. 2006). Prolonged downwelling-favourable winds resulted in vertically stable ocean conditions, unusually warm sea surface temperatures (Kosro et al. 2006), and low primary productivity (Thomas and Brickley 2006). Poleward and onshore displacement of numerous taxa were detected, reflecting the lack of cross-shelf offshore Ekman transport that usually occurs at this time of year with the seasonal onset of upwelling (Brodeur et al. 2006). Ecosystem-level effects associated with this event included altered zooplankton community composition (Mackas et al. 2006), recruitment failures of intertidal invertebrates (Barth et al. 2007), seabird breeding failure (Sydeman et al. 2006), and changes in marine mammal foraging behaviour (Newell and Cowles 2006; Weise et al. 2006). In contrast, in 2006 the west coast of Vancouver Island experienced above average upwelling-favourable winds through the spring and summer (DFO 2007). In the same year, intense and prolonged upwelling off the coast of Oregon resulted in the oxygen minimum zone being pulled up onto the continental shelf and causing a large-scale anoxia event that resulted in

mass mortalities of benthic invertebrates and displacement of demersal fishes (Chan et al. 2008). Thus, upwelling dynamics in 2005 and 2006 likely represent opposite ends of a continuum of oceanographic variability occurring throughout the CCLME and their corresponding effects on nearshore Pacific rockfish recruitment dynamics. Our results show that the two complexes of rockfish showed contrasting responses to these opposite extremes in the range of oceanographic conditions experienced off Vancouver Island.

#### Effects of upwelling on growth

By regulating nearshore ocean temperatures and primary productivity, variable coastal upwelling may affect presettlement growth and size-dependent vulnerability to predation, pelagic durations, and cumulative mortality rates of pelagic larvae and juveniles. Larval growth and development rates increase with ocean temperature and are highest near larval thermal tolerance maxima (Houde 1989, 2009; Neuheimer et al. 2011; Pepin 1991). In turn, high developmental rates associated with increasing growth rates can reduce pelagic duration by decreasing the age at which meta-

**Fig. 6.** Growth rates of black and CQB rockfishes in 2005 and 2006. Growth curves (A and B) are logistic growth models fitted to back-calculated growth trajectories of individuals comprising each cohort. Length-at-age relationships (C and D) represent length (total length) and age (days) at capture.



morphosis occurs and larval competency is reached (Francis 1994). In contrast, coastal upwelling lowers SST and provides nutrients that fuel primary productivity and may enhance the resources available to developing juvenile rockfishes. Therefore, the effects of upwelling on larval growth and mortality depend on whether larval growth is more constrained by ocean temperature or productivity. Upwelling may generate conditions of high productivity and prey abundance where growth is temperature-limited, while downwelling corresponds to warm temperatures but low resource availability.

We found higher presettlement growth rates in both black and CQB rockfishes during the warm ocean temperatures of 2005. Furthermore, growth rates varied strongly with SST but not with chlorophyll *a*, and pelagic durations of both groups were inversely related to growth rates. The highest growth rates and shortest pelagic durations were associated with the warm ocean conditions of 2005. High growth rates and short pelagic durations of CQB rockfishes were also associated with significantly smaller body sizes (total length) at settlement in 2005. These results support the hypothesis that intense upwelling and low ocean temperatures led to low presettlement growth rates, increased pelagic durations, and, by extension, high cumulative mortality rates during the pelagic stage in 2006. Although years of high CQB rockfish recruitment coincide with higher presettlement growth, black rockfish demonstrated the opposite pattern; the highest black rockfish recruitment we observed was associated with slow presettlement growth rates and protracted pelagic durations. These contrasting relationships indicate that black and CQB rockfish life histories differ fundamentally with respect to the relative importance of processes affecting larval growth and mortality versus those affecting larval transport and delivery.

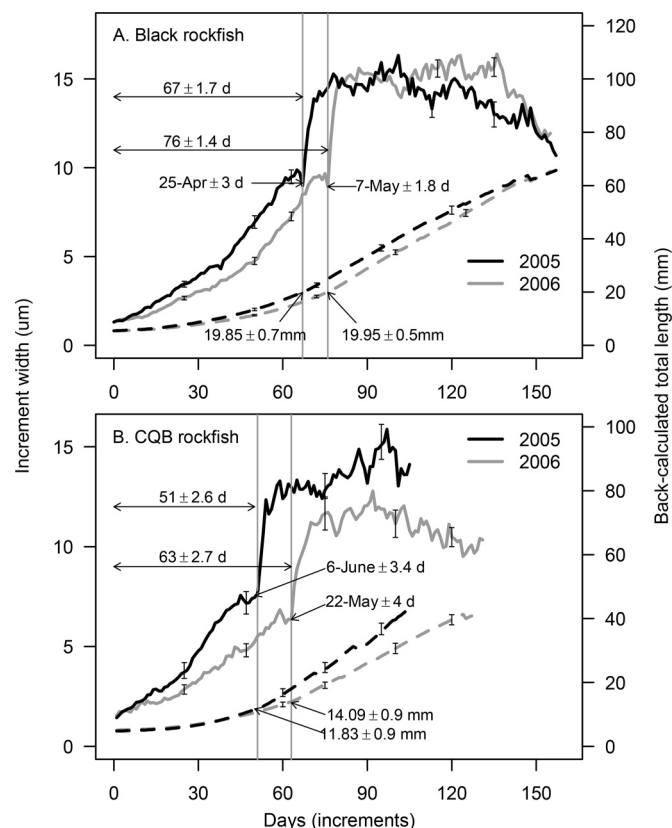
#### Parturition and settlement in relation to upwelling events

Coastal upwelling may affect pelagic duration and mortality rates of rockfishes if cross-shelf flows inhibit or facilitate movement of pelagic juveniles to adult habitats. We found that CQB rockfish parturition and settlement intervals in 2005 and 2006 were associated with downwelling-favourable winds (i.e., onshore advection of the surface layer). Short pelagic durations and high recruitment in 2005 occurred when upwelling intensity remained low throughout the pelagic stage. Long pelagic durations and low recruitment in 2006 occurred when upwelling intensity remained above average throughout the pelagic duration. Thus, these patterns support the "upwelling-relaxation" hypothesis (Cury and Roy 1989; Farrell et al. 1991; Roughgarden et al. 1988; Shanks and Brink 2005) and suggest that downwelling and onshore advection of the surface layer reduce pelagic durations and facilitate near-shore retention or onshore movement of CQB rockfish larvae and pelagic juveniles. Parturition and settlement intervals associated with downwelling events also suggest that CQB rockfish larvae and pelagic juveniles occupy shallow surface layers above the thermocline (Shanks and Brink 2005).

In contrast with CQB rockfishes, black rockfish parturition and settlement intervals in 2005 and 2006 were associated with periods of above average upwelling. Black rockfish parturition intervals in 2005 and 2006 occurred in mid-February and corresponded closely to short but strong upwelling events that resulted in a rapid decrease in SST and increase in chlorophyll *a*. The extent to which these events contributed to recruitment in these years is unknown. One possibility is that high primary productivity coinciding with spawning may have increased very early larval growth and survival rates (Cury and Roy 1989). Most black rockfish settlement in 2006 occurred during the peak and declining phase of a



**Fig. 7.** Longitudinal growth profiles of black and CQB rockfishes based on mean otolith daily growth increment width (solid lines, left y axis) and back-calculated (Modified-Fry model) length-at-age (dashed lines, right y axis). Daily means ( $\pm$ SE) were calculated by centering individual growth profiles on settlement increments per day (vertical lines). Settlement dates and pelagic durations are set to annual means of each cohort.



strong upwelling event. In contrast with CQB rockfishes, this pattern suggests that black rockfish pelagic juveniles may occupy deepwater layers below the thermocline (Shanks and Brink 2005). Hierarchical variance partitioning revealed that although pre-settlement growth rates of both complexes contribute substantially and independently to variable pelagic durations, the independent effects of upwelling intensity experienced in the 30 days prior to settlement was higher for black rockfish than for CQB rockfishes (55% and 39%, respectively). These results indicate that ocean conditions favourable for high larval growth rates and survival are not necessary for high settlement and recruitment rates of black rockfish. Rather, exceptional oceanographic events favoring onshore movement of pelagic juveniles, in this case strong upwelling, may be primary determinants of black rockfish recruitment. Consistent with these findings, Lotterhos and Markel (2012) found that high black rockfish recruitment in 2006 was associated with a low effective number of breeders (i.e., low allelic richness and high reproductive variance), also indicating the pre-eminent role of transportation processes and resulting narrow windows of opportunity favouring the success of relatively few breeding individuals (i.e., high reproductive variance). However, persistently poor ocean conditions for larval production, growth, and survival are expected to underlie chronically low rockfish recruitment success, regardless of flow regimes that may inhibit or facilitate larval delivery (Caselle et al. 2010a; Cury and Roy 1989; Laidig et al. 2007). Our results highlight the importance of episodic oceanographic events for spatial and temporal

patterns of recruitment success that differ among species or complexes.

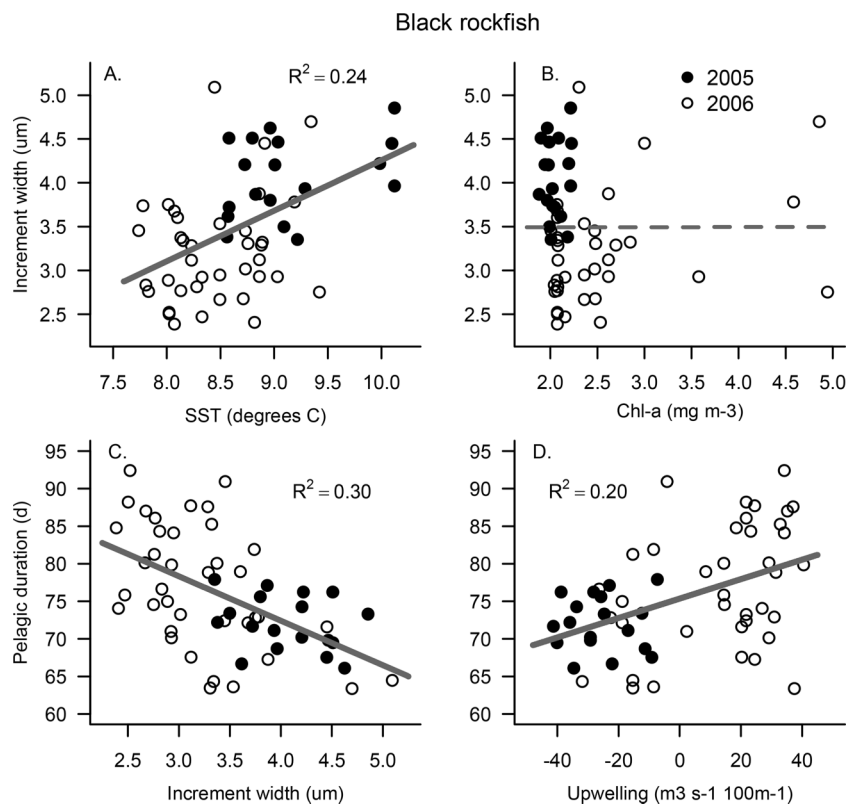
### Contrasting black and CQB rockfish life histories

Synchronous recruitment among different species across large spatial scales suggests that suites of oceanographic variables favor taxa with similar early life histories (Field and Ralston 2005; Sponaugle and Cowen 1997). Our data add to a growing number reporting distinct recruitment patterns of midwater aggregating and solitary benthic complexes of nearshore rockfishes (Carr and Syms 2006b; Lenarz et al. 1995). Both complexes showed faster postsettlement growth in the year when they experienced strong recruitment. The species in our study are members of two diverse groups containing many species belonging to the genus *Sebastes*; therefore, the contrast between the two life history strategies may be relevant to a broader suite of species. We note that in their phylogenetic reconstruction of the genus *Sebastes*, Hyde and Vetter (2007) propose that elongate body plans and semipelagic lifestyles of midwater aggregating species are derived characteristics closely associated with pronounced increases in upwelling and primary productivity in the western Pacific Ocean approximately 9 million years ago.

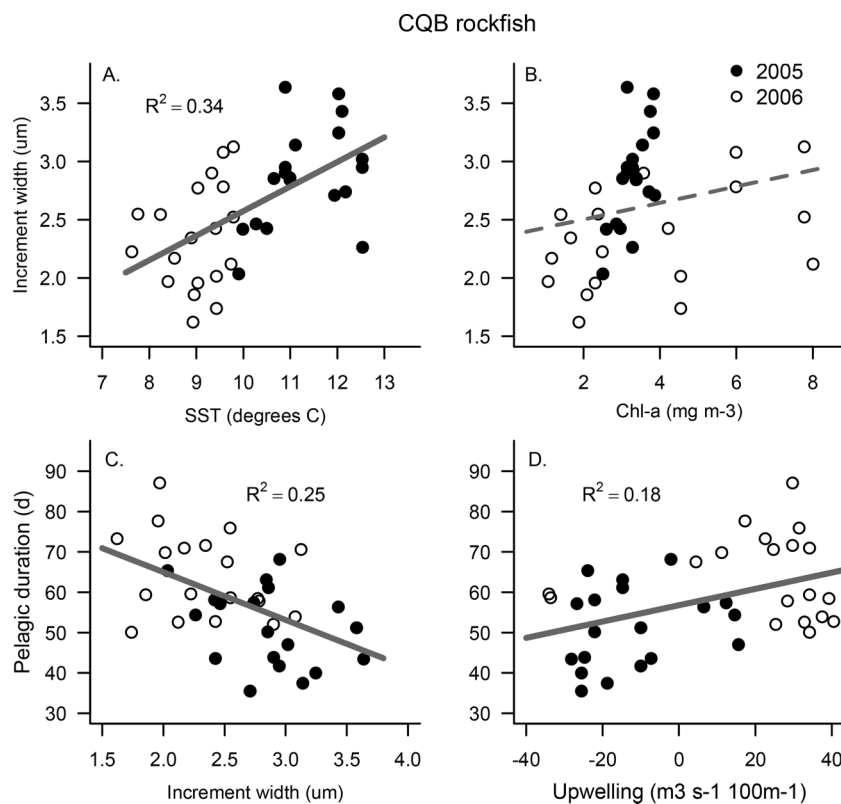
Our study supports evidence that solitary benthic and midwater aggregating rockfishes exhibit distinct responses to coastal upwelling. One possible explanation for the differential recruitment success of midwater aggregating and solitary benthic species during upwelling versus downwelling, respectively, is the differential use of deep versus shallow depth strata by pelagic stages. Recent studies have demonstrated that the effects of coastal upwelling on the pelagic stages of marine organisms are taxon-specific and depend strongly on their vertical location in the water column relative to the thermocline (Mace and Morgan 2006; Shanks and Brink 2005). Lenarz et al. (1995) investigated this hypothesis and found that larvae of solitary benthic species were more abundant higher in the water column than midwater aggregating species and therefore more likely to benefit from onshore advection of surface waters during downwelling events. Conversely, midwater aggregating rockfish larvae were more abundant in deep water and therefore more likely to benefit from onshore advection during upwelling. Although the west coast of Vancouver Island is an active upwelling zone and conforms to the general patterns off-shore advection of surface layers and concomitant onshore flow of cold and nutrient-rich deep layers (Ware and Thomson 2005), we have no information about how upwelling events affect the environment in the deeper pelagic habitat of presettlement black rockfish.

Black rockfish use of deepwater habitat also implies tolerance, if not preference, for low ocean temperatures (Neuheimer et al. 2011). Black rockfish and other midwater aggregating species spawn in the early winter (January–March) and have pelagic durations lasting 2–4 months. CQB rockfishes and other solitary benthic species spawn in early spring (March–May) and have pelagic durations of 1–2 months. We found that both black and CQB rockfish presettlement growth rates increased, and pelagic durations decreased, with increasing ocean temperature. Therefore, as a result of their earlier parturition and protracted pelagic durations, black rockfish larvae experience colder ocean temperatures and are likely to be more vulnerable to slow growth and high pelagic mortality. However, the fact that high recruitment success of black rockfish did not coincide with high larval growth rates or short pelagic durations in 2006 indicates that favourable transportation processes were more important determinants of successful recruitment (Lotterhos and Markel 2012). The difference in pelagic juvenile body sizes of black and CQB rockfishes likely mitigates vulnerability to predation and processes affecting onshore movement. The smallest early postsettlement black rockfish that we collected in Barkley Sound were ~35–40 mm total length, whereas CQB rockfishes are 20–25 mm total length.

**Fig. 8.** Effects of sea surface temperature (SST), chlorophyll *a* (Chl-*a*), and upwelling (Upwelling Index) on black rockfish presettlement growth (A and B) and pelagic duration (C and D). Values of growth, SST, and Chl-*a* are averages for the 60 days following parturition. Values of upwelling are averages for the 30 days prior to settlement.



**Fig. 9.** Effects of sea surface temperature (SST), chlorophyll *a* (Chl-*a*), and upwelling (Upwelling Index) on CQB rockfish presettlement growth (A and B) and pelagic duration (C and D). Values of growth, SST, and Chl-*a* are averages for the 40 days following parturition. Values of upwelling are averages for the 30 days prior to settlement.



Because large body sizes are associated with enhanced swimming and foraging abilities (Green and Fisher 2004; Pepin 1991), black rockfish larvae and pelagic juveniles may compensate metabolically for low ocean temperatures by increasing prey intake rates.

## Conclusions

The ecological and economic importance of Pacific rockfishes has fuelled extensive research to understand relationships among physical oceanographic processes, recruitment success, and year-class strength (Bjorkstedt et al. 2002; Caselle et al. 2010a, 2010b; Laidig et al. 2007; Lotterhos and Markel 2012). Our study adds to a growing understanding of the contrasting ways in which midwater aggregating and solitary benthic rockfishes are affected by upwelling. The distinct early life history attributes of midwater aggregating and solitary benthic rockfishes suggest that these groups may differ in terms of dispersal and population connectivity. Pelagic duration and recruitment success are fundamental determinants of population connectivity and persistence (Cowen and Sponaugle 2009). The long pelagic durations and higher recruitment success of black rockfish and other midwater aggregating species (Carr and Syms 2006) suggests relatively high potential for connectivity within regional metapopulations. In contrast, short pelagic durations and low recruitment rates of CQB rockfishes may indicate lower connectivity and threaten persistence of solitary benthic rockfish populations and lead to slower responses to protection by marine protected areas (Fogarty and Botsford 2007; Lipcius et al. 2008). Our study also shows that species responses to climate variability depend greatly on life history traits, suggesting that ongoing climate change will produce winners and losers among marine taxa (Harley et al. 2006).

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## References

- Agostini, V.N., and Bakun, A. 2002. 'Ocean triads' in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engraulis encrasicolus*). *Fish. Oceanogr.* **11**: 129–142. doi:10.1046/j.1365-2419.2002.00201.x.
- Ainley, D.G., Sydeman, W.J., Parrish, R.H., and Lenarz, W.H. 1993. Ocean factors influencing distribution of young rockfish (*Sebastes*) in central California: a predator's perspective. *Calif. Coop. Ocean. Fish. Investig. Rep.* **34**: 133–139.
- Amdur, J.R. 1991. The validation of a settlement mark on the otoliths of the blue rockfish *Sebastes mystinus*. M.Sc., San Francisco State University, San Francisco, Calif.
- Ammann, A.J. 2004. SMURFs: standard monitoring units for the recruitment of temperate reef fishes. *J. Exp. Mar. Biol. Ecol.* **299**: 135–154. doi:10.1016/j.jembe.2003.08.014.
- Anderson, T.W., and Carr, M.H. 1998. BINCKE: a highly efficient net for collecting reef fishes. *Environ. Biol. Fishes*, **51**: 111–115. doi:10.1023/A:1007355408723.
- Armstrong, P.R. 2002. Recruitment limitation, population regulation, and larval connectivity in reef fish metapopulations. *Ecology*, **83**: 1092–1104. doi:10.1890/0012-9658(2002)083[1092:RLPRAI]2.0.CO;2.
- Barth, J.A., Menge, B.A., Lubchenco, J., Chan, F., Bane, J.M., Kirincich, A.R., et al. 2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. *Proc. Natl. Acad. Sci. U.S.A.* **104**: 3719–3724. doi:10.1073/pnas.0700462104.
- Bates, D., and Watts, D. 1988. Nonlinear regression analysis and its applications. John Wiley & Sons, Inc.
- Berggren, M.A.J., Meekan, M.G., Robertson, D.R., and McCormick, M.I. 2002. Larval growth predicts the recruitment success of a coral reef fish. *Oecologia*, **131**: 521–525. doi:10.1007/s00442-002-0918-4.
- Bertness, M.D., Gaines, S.D., Stephens, E.G., and Yund, P.O. 1992. Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). *J. Exp. Mar. Biol. Ecol.* **156**: 199–215. doi:10.1016/0022-0981(92)90246-7.
- Bjorkstedt, E.P., Rosenfeld, L.K., Grantham, B.A., Shkedy, Y., and Roughgarden, J. 2002. Distributions of larval rockfishes *Sebastes* spp. across nearshore fronts in a coastal upwelling region. *Mar. Ecol. Progr. Ser.* **242**: 215–228. doi:10.3354/meps242215.
- Brodeur, R.D., Ralston, S., Emmett, R.L., Trudel, M., Auth, T.D., and Phillips, A.J. 2006. Anomalous pelagic nekton abundance, distribution, and apparent recruitment in the northern California Current in 2004 and 2005. *Geophys. Res. Lett.* **33**. doi:10.1029/2006GL026614.
- Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., and Menge, B.A. 1996. Recruitment and the local dynamics of open marine populations. *Annu. Rev. Ecol. Syst.* **27**: 477–500. doi:10.1146/annurev.ecolsys.27.1.477.
- Carr, M.H., and Reed, D.C. 1993. Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. *Can. J. Fish. Aquat. Sci.* **50**(9): 2019–2028. doi:10.1139/f93-226.
- Carr, M.H., and Syms, C. 2006a. Chapter 15: Recruitment. In *The ecology of marine fishes*. Edited by L.G. Allen, D.J. Pondella II, and M.H. Horn. University of California Press, Berkeley, Calif. pp. 411–427.
- Carr, M.H., and Syms, C. 2006b. Recruitment. In *The ecology of marine fishes*. Edited by L.G. Allen, D.J. Pondella II, and M.H. Horn. University of California Press, Berkeley, Calif. pp. 411–427.
- Caselle, J.E., Carr, M.H., Malone, D.P., Wilson, J.R., and Wendt, D.E. 2010a. Can we predict interannual and regional variation in delivery of pelagic juveniles to nearshore populations of rockfishes (Genus *Sebastes*) using simple proxies of ocean conditions? *CalCOFI Rep.* **51**: 91–105.
- Caselle, J.E., Kinlan, B.P., and Warner, R.R. 2010b. Temporal and spatial scales of influence on nearshore fish settlement in the southern California Bight. *Bull. Mar. Sci.* **86**: 355–385.
- Chan, F., Barth, J.A., Lubchenco, J., Kirincich, A., Weeks, H., Peterson, W.T., and Menge, B.A. 2008. Emergence of anoxia in the California current large marine ecosystem. *Science*, **319**: 920. doi:10.1126/science.1149016.
- Cowen, R.K., and Sponaugle, S. 2009. Larval dispersal and marine population connectivity. *Annu. Rev. Mar. Sci.* **1**: 443–466. doi:10.1146/annurev.marine.010908.163757.
- Cury, P., and Roy, C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.* **46**(4): 670–680. doi:10.1139/f89-086.
- Cushing, D.H. 1990. Plankton production and year-class strength in fish populations — an update of the match mismatch hypothesis. *Adv. Mar. Biol.* **26**: 249–293. doi:10.1016/S0065-2881(08)60202-3.
- DFO. 2007. State of the Pacific Ocean 2006. Ocean Status Report.
- Doherty, P., and Fowler, T. 1994. An empirical test of recruitment limitation in a coral reef fish. *Science*, **263**: 935–939. doi:10.1126/science.263.5149.935.
- Doherty, P.J., and Williams, D.M. 1988. The replenishment of coral-reef fish populations. *Oceanogr. Mar. Biol.* **26**: 487–551.
- Farrell, T.M., Bracher, D., and Roughgarden, J. 1991. Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnol. Oceanogr.* **36**: 279–288. doi:10.4319/lo.1991.36.2.0279.
- Field, J.C., and Ralston, S. 2005. Spatial variability in rockfish (*Sebastes* spp.) recruitment events in the California Current System. *Can. J. Fish. Aquat. Sci.* **62**(10): 2199–2210. doi:10.1139/f05-134.
- Fogarty, M.J., and Botsford, L.W. 2007. Population connectivity and spatial management of marine fisheries. *Oceanography*, **20**: 112–123. doi:10.5670/oceanog.2007.34.
- Francis, M.P. 1994. Duration of larval and spawning periods in *Pagrus auratus* (Sparidae) determined from otolith daily increments. *Environ. Biol. Fishes*, **39**: 137–152. doi:10.1007/BF00004931.
- Gaines, S.D., Gaylord, B., and Largier, J.L. 2003. Avoiding current oversights in marine reserve design. *Ecol. Appl.* **13**(sp1): 32–46. doi:10.1890/1051-0761(2003)013[0032:ACOIMR]2.0.CO;2.
- Gallagher, M.B. 2007. Growth rates and species composition of juvenile rockfish (*Sebastes* spp.) in Oregon's nearshore and estuarine habitats. M.Sc., Oregon State University.
- Green, B.S., and Fisher, R. 2004. Temperature influences swimming speed, growth and larval duration in coral reef fish larvae. *J. Exp. Mar. Biol. Ecol.* **299**: 115–132. doi:10.1016/j.jembe.2003.09.001.
- Haggarty, D.R., Martell, S.J.D., and Shurin, J.B. 2016a. Lack of recreational fishing compliance may compromise effectiveness of Rockfish Conservation Areas in British Columbia. *Can. J. Fish. Aquat. Sci.* **73**(10): 1587–1598. doi:10.1139/cjfas-2015-0205.
- Haggarty, D.R., Shurin, J.B., and Yamanaka, K.L. 2016b. Assessing population recovery inside British Columbia's Rockfish Conservation Areas with a remotely operated vehicle. *Fish. Res.* **183**: 165–179. doi:10.1016/j.fishres.2016.06.001.
- Haggarty, D.R., Lotterhos, K.E., and Shurin, J.B. 2017. Young-of-the-year recruitment does not predict the abundance of older age classes in black rockfish in Barkley Sound, British Columbia, Canada. *Mar. Ecol. Progr. Ser.* **574**: 113–126. doi:10.3354/meps12202.
- Hare, J.A., and Cowen, R.K. 1997. Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). *Ecology*, **78**: 2415–2431. doi:10.1890/0012-9658(1997)078[2415:SGDASO]2.0.CO;2.
- Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B.,



- Thornber, C.S., et al. 2006. The impacts of climate change in coastal marine systems. *Ecol. Lett.* **9**: 228–241. doi:10.1111/j.1461-0248.2005.00871.x.
- Hedgecock, D. 1994. Does variance in reproductive success limit effective population sizes of marine organisms? In *Genetics and evolution of aquatic organisms*. Chapman & Hall, London. pp. 122–134.
- Hickey, B.M., Thomson, R.E., Yih, H., and Leblond, P.H. 1991. Velocity and temperature fluctuations in a buoyancy-driven current off Vancouver Island. *J. Geophys. Res. Oceans*, **96**: 10507–10538. doi:10.1029/90JC02578.
- Hixon, M.A., and Webster, M.S. 2002. Density dependence in reef fish populations. In *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Edited by P.F. Sale. Academic Press, San Diego, Calif. pp. 303–325.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. Proc.-v. Reun. Cons. Int. Explor. Mer*, **20**: 1–228.
- Houde, E.D. 1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fish. Bull.* **87**: 471–495.
- Houde, E.D. 2009. Chapter 3. Recruitment variability. In *Reproductive biology of fishes: implications for assessment and management*. Edited by T. Jakobsen, M. Fogarty, B. Megrey, and E. Moksness. Wiley-Blackwell. pp. 91–171.
- Hyde, J.R., and Vetter, R.D. 2007. The origin, evolution, and diversification of rockfishes of the genus *Sebastes* (Cuvier). *Mol. Phylogenet. Evol.* **44**: 790–811. doi:10.1016/j.ympev.2006.12.026.
- Jenkins, G.P., and King, D. 2006. Variation in larval growth can predict the recruitment of a temperate, seagrass-associated fish. *Oecologia*, **147**: 641–649. doi:10.1007/s00442-005-0336-5.
- Kokita, T., and Omori, M. 1999. Long distance dispersal of larval and juvenile rockfish, *Sebastes thompsoni*, with drifting seaweed in the Tohoku area, Northwest Pacific, estimated by analysis of otolith microstructure. *Bull. Mar. Sci.* **65**: 105–118.
- Kosro, P.M., Peterson, W.T., Hickey, B.M., Shearman, R.K., and Pierce, S.D. 2006. Physical versus biological spring transition: 2005. *Geophys. Res. Lett.* **33**. doi:10.1029/2006GL027072.
- Laidig, T.E., and Ralston, S. 1995. The potential use of otolith characters in identifying larval rockfish (*Sebastes* spp.). *Fish. Bull.* **93**: 166–171.
- Laidig, T.E., Ralston, S., and Bence, J.R. 1991. Dynamics of growth in the early life-history of shortbelly rockfish *Sebastes jordani*. *Fish. Bull.* **89**: 611–621.
- Laidig, T.E., Chess, J.R., and Howard, D.F. 2007. Relationship between abundance of juvenile rockfishes (*Sebastes* spp.) and environmental variables documented off northern California and potential mechanisms for the covariation. *Fish. Bull.* **105**: 39–48.
- Lasker, R. 1975. Field criteria for survival of anchovy larvae: relation between inshore chlorophyll maximum layers and successful 1st feeding. *Fish. Bull.* **73**: 453–462.
- Leaman, B.M. 1991. Reproductive styles and life history variables relative to exploitation and management of *Sebastes* stocks. *Environ. Biol. Fishes*, **30**: 253–271. doi:10.1007/BF02296893.
- Leggett, W.C., and DeBlois, E. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? *Neth. J. Sea Res.* **32**: 119–134. doi:10.1016/0077-7579(94)90036-1.
- Lenarz, W.H., and Echeverria, T.W. 1986. Comparison of visceral fat and gonadal fat volumes of yellowtail rockfish, *Sebastes flavidus*, during a normal year and a year of El-Nino conditions. *Fish. Bull.* **84**: 743–745.
- Lenarz, W.H., Ventresca, D.A., Graham, W.M., Schwing, F.B., and Chavez, F. 1995. Explorations of El Nino events and associated biological population dynamics off central California. *Calif. Coop. Ocean. Fish. Investig. Rep.* **36**: 106–119.
- Lipcius, R.N., Eggleston, D.B., Schreiber, S.J., Seitz, R.D., Shen, J., Sisson, M., et al. 2008. Importance of metapopulation connectivity to restocking and restoration of marine species. *Rev. Fish. Sci.* **16**: 101–110. doi:10.1080/10641260701812574.
- Lotterhos, K.E., and Markel, R.W. 2012. Oceanographic drivers of offspring abundance may increase or decrease reproductive variance in a temperate marine fish. *Mol. Ecol.* **21**: 5009–5026. doi:10.1111/j.1365-294X.2012.12002.x.
- Love, M.S., Yoklavich, M.M., and Thorsteinson, L. 2002. The rockfishes of the Northeast Pacific. University of California Press, Berkeley, Calif.
- Mac Nally, R. 2002. Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. *Biodivers. Conserv.* **11**: 1397–1401. doi:10.1023/A:1016250716679.
- Mac Nally, R., and Walsh, C.J. 2004. Hierarchical partitioning public-domain software. *Biodivers. Conserv.* **13**: 659–660. doi:10.1023/B:BIOC.0000009515.11717.0b.
- Mace, A.J., and Morgan, S.G. 2006. Biological and physical coupling in the lee of a small headland: contrasting transport mechanisms for crab larvae in an upwelling region. *Mar. Ecol. Progr. Ser.* **324**: 185–196. doi:10.3354/meps324185.
- Mackas, D.L., Peterson, W.T., Ohman, M.D., and Lavaniegos, B.E. 2006. Zooplankton anomalies in the California Current system before and during the warm ocean conditions of 2005. *Geophys. Res. Lett.* **33**. doi:10.1029/2006GL027930.
- Markel, R.W., and Shurin, J.B. 2015. Indirect effects of sea otters on rockfish (*Sebastes* spp.) in giant kelp forests. *Ecology*, **96**: 2877–2890. doi:10.1890/14-0492.1.
- Markel, R.W., Lotterhos, K.E., and Robinson, C.L.K. 2017. Temporal variability in the environmental and geographic predictors of spatial-recruitment in near-shore rockfishes. *Mar. Ecol. Progr. Ser.* **574**: 97–111. doi:10.3354/meps12120.
- Mason, J. 1998. Declining rockfish lengths in the Monterey Bay, California, recreational fishery, 1959–94. *Mar. Fish. Rev.* **60**: 15–28.
- Mearns, A.J., Allen, M.J., Moore, M.D., and Sherwood, M.J. 1980. Distribution, abundance, and recruitment of soft bottom rockfishes (Scorpaenidae: *Sebastes*) on the southern California mainland shelf. *Calif. Coop. Ocean. Fish. Investig. Rep.* **21**: 180–190.
- Miller, J.A., and Shanks, A.L. 2004. Evidence for limited larval dispersal in black rockfish (*Sebastes melanops*): implications for population structure and marine-reserve design. *Can. J. Fish. Aquat. Sci.* **61**(9): 1723–1735. doi:10.1139/f04-111.
- Moser, H.G., and Boehlert, G.W. 1991. Ecology of pelagic larvae and juveniles of the genus *Sebastes*. *Environ. Biol. Fishes*, **30**: 203–224. doi:10.1007/BF02296890.
- Munk, K.M. 2001. Maximum ages of groundfishes in waters off Alaska and British Columbia and considerations of age determination. *Alaska Fishery Research Bulletin* **8**.
- Neuheimer, A.B., Thresher, R.E., Lyle, J.M., and Semmens, J.M. 2011. Tolerance limit for fish growth exceeded by warming waters. *Nat. Clim. Change*, **1**: 110–113. doi:10.1038/nclimate1084.
- Newell, C.L., and Cowles, T.J. 2006. Unusual gray whale *Eschrichtius robustus* feeding in the summer of 2005 off the central Oregon Coast. *Geophys. Res. Lett.* **33**. doi:10.1029/2006GL027189.
- Otterlei, E., Nyhammer, G., Folkvord, A., and Stefansson, S.O. 1999. Temperature- and size-dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua*): a comparative study of Norwegian coastal cod and northeast Arctic cod. *Can. J. Fish. Aquat. Sci.* **56**(11): 2099–2111. doi:10.1139/f99-168.
- Parker, S.J., Berkeley, S.A., Golden, J.T., Gunderson, D.R., Heifetz, J., Hixon, M.A., et al. 2000. Management of Pacific rockfish. *Fisheries*, **25**: 22–30. doi:10.1577/1548-8446(2000)025<0022:MOPR>2.0.CO;2.
- Pasten, G.P., Katayama, S., and Omori, M. 2003. Timing of parturition, planktonic duration, and settlement patterns of the black rockfish, *Sebastes inermis*. *Environ. Biol. Fishes*, **68**: 229–239. doi:10.1023/A:1027388215711.
- Pepin, P. 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. *Can. J. Fish. Aquat. Sci.* **48**(3): 503–518. doi:10.1139/f91-065.
- Pepin, P., and Myers, R.A. 1991. Significance of egg and larval size to recruitment variability of temperate marine fish. *Can. J. Fish. Aquat. Sci.* **48**(10): 1820–1828. doi:10.1139/f91-215.
- Plaza, G., Katayama, S., and Omori, M. 2001. Otolith microstructure of the black rockfish, *Sebastes inermis*. *Mar. Biol.* **139**: 797–805. doi:10.1007/s002270100620.
- Ralston, S., and Howard, D.F. 1995. On the development of year-class strength and cohort variability in 2 northern California rockfishes. *Fish. Bull.* **93**: 710–720.
- Ralston, S., Brothers, E.B., Roberts, D.A., and Sakuma, K.M. 1996. Accuracy of age estimates for larval *Sebastes jordani*. *Fish. Bull.* **94**: 89–97.
- R Core Development Team. 2011. R: a language and environment for statistical computing. Vienna, Austria.
- Roughgarden, J., Iwasa, Y., and Baxter, C. 1985. Demographic theory for an open marine population with space-limited recruitment. *Ecology*, **66**: 54–67. doi:10.2307/1941306.
- Roughgarden, J., Gaines, S., and Possingham, H. 1988. Recruitment dynamics in complex life cycles. *Science*, **241**: 1460–1466. doi:10.1126/science.11538249.
- Sale, P.F. 1977. Maintenance of high diversity in coral reef fish communities. *Am. Nat.* **111**: 337–359. doi:10.1086/283164.
- Schwing, F.B., Bond, N.A., Bograd, S.J., Mitchell, T., Alexander, M.A., and Mantua, N. 2006. Delayed coastal upwelling along the US West Coast in 2005: a historical perspective. *Geophys. Res. Lett.* **33**. doi:10.1029/2006GL026911.
- Secor, D.H. 2007. The year-class phenomenon and the storage effect in marine fishes. *J. Sea Res.* **57**: 91–103. doi:10.1016/j.seares.2006.09.004.
- Selkoe, K.A., Gaines, S.D., Caselle, J.E., and Warner, R.R. 2006. Current shifts and kin aggregation explain genetic patchiness in fish recruits. *Ecology*, **87**: 3082–3094. doi:10.1890/0012-9658(2006)87[3082:CSAKAE]2.0.CO;2.
- Shanks, A.L. 2009. Pelagic larval duration and dispersal distance revisited. *Biol. Bull.* **216**: 373–385. doi:10.1086/BBLv216n3p373.
- Shanks, A.L., and Brink, L. 2005. Upwelling, downwelling, and cross-shelf transport of bivalve larvae: test of a hypothesis. *Mar. Ecol. Progr. Ser.* **302**: 1–12. doi:10.3354/meps302001.
- Shanks, A.L., and Eckert, G.L. 2005. Population persistence of California Current fishes and benthic crustaceans: a marine drift paradox. *Ecol. Monogr.* **75**: 505–524. doi:10.1890/05-0309.
- Sponaugle, S., and Cowen, R.K. 1997. Early life history traits and recruitment patterns of Caribbean wrasses (Labridae). *Ecol. Monogr.* **67**: 177–202. doi:10.1890/0012-9615(1997)067[0177:ELHTAR]2.0.CO;2.
- Sydemann, W.J., Bradley, R.W., Plazybok, P., Abraham, C.L., Jahncke, J., Hyrenbach, K.D., et al. 2006. Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: Unusual atmospheric blocking? *Geophys. Res. Lett.* **33**. doi:10.1029/2006GL026736.
- Thomas, A.C., and Brickley, P. 2006. Satellite measurements of chlorophyll distribution during spring 2005 in the California Current. *Geophys. Res. Lett.* **33**. doi:10.1029/2006GL026588.
- Thomson, R.E., and Ware, D.M. 1996. A current velocity index of ocean variability. *J. Geophys. Res. Oceans*, **101**: 14297–14310. doi:10.1029/96JC01055.
- Vigliola, L., Harmelin-Vivien, M., and Meekan, M.G. 2000. Comparison of techniques of back-calculation of growth and settlement marks from the otoliths

- of three species of *Diplodus* from the Mediterranean Sea. *Can. J. Fish. Aquat. Sci.* **57**(6): 1291–1299. doi:[10.1139/f00-055](https://doi.org/10.1139/f00-055).
- Ware, D.M., and Thomson, R.E. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. *Science*, **308**: 1280–1284. doi:[10.1126/science.1109049](https://doi.org/10.1126/science.1109049).
- Warner, R.R., and Chesson, P.L. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *Am. Nat.* **125**: 769–787. doi:[10.1086/284379](https://doi.org/10.1086/284379).
- Warner, R.R., and Cowen, R.K. 2002. Local retention of production in marine populations: evidence, mechanisms, and consequences. *Bull. Mar. Sci.* **70**: 245–249.
- Weise, M.J., Costa, D.P., and Kudela, R.M. 2006. Movement and diving behavior of male California sea lion (*Zalophus californianus*) during anomalous oceanographic conditions of 2005 compared to those of 2004. *Geophys. Res. Lett.* **33**. doi:[10.1029/2006GL027113](https://doi.org/10.1029/2006GL027113).
- Williams, G.D., Levin, P.S., and Palsson, W.A. 2010. Rockfish in Puget Sound: An ecological history of exploitation. *Mar. Pol.* **34**: 1010–1020. doi:[10.1016/j.marpol.2010.02.008](https://doi.org/10.1016/j.marpol.2010.02.008).
- Wilson, D.T., and McCormick, M.I. 1997. Spatial and temporal validation of settlement-marks in the otoliths of tropical reef fishes. *Mar. Ecol. Progr. Ser.* **153**: 259–271. doi:[10.3354/meps153259](https://doi.org/10.3354/meps153259).
- Wilson, D.T., and McCormick, M.I. 1999. Microstructure of settlement-marks in the otoliths of tropical reef fishes. *Mar. Biol.* **134**: 29–41. doi:[10.1007/s002270050522](https://doi.org/10.1007/s002270050522).
- Wilson, J.R., Broitman, B.R., Caselle, J.E., and Wendt, D.E. 2008. Recruitment of coastal fishes and oceanographic variability in central California. *Estuar. Coast. Shelf Sci.* **79**: 483–490. doi:[10.1016/j.ecss.2008.05.001](https://doi.org/10.1016/j.ecss.2008.05.001).
- Wilson, J.A., Vigliola, L., and Meekan, M.G. 2009. The back-calculation of size and growth from otoliths: validation and comparison of models at an individual level. *J. Exp. Mar. Biol. Ecol.* **368**: 9–21. doi:[10.1016/j.jembe.2008.09.005](https://doi.org/10.1016/j.jembe.2008.09.005).
- Woodbury, D. 1999. Reduction of growth in otoliths of widow and yellowtail rockfish (*Sebastes entomelas* and *S. flavidus*) during the 1983 El Nino. *Fish. Bull.* **97**: 680–689.
- Woodbury, D., and Ralston, S. 1991. Interannual variation in growth-rates and back-calculated birth-date distributions of pelagic juvenile rockfishes (*Sebastes* spp.) of the central California coast. *Fish. Bull.* **89**: 523–533.
- Yamanaka, K.L., and Logan, G. 2010. Developing British Columbia's inshore rockfish conservation strategy. *Mar. Coast. Fish. Dyn. Manage. Ecosyst. Sci.* **2**: 28–46. doi:[10.1577/C08-036.1](https://doi.org/10.1577/C08-036.1).
- Yoklavich, M.M., and Boehlert, G.W. 1987. Daily growth increments in otoliths of juvenile black rockfish, *Sebastes melanops*: an evaluation of autoradiography as a new method of validation. *Fish. Bull.* **85**: 826–832.