

# Temporal variability in the environmental and geographic predictors of spatial-recruitment in nearshore rockfishes

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**ABSTRACT:** Geography and habitat availability may be key drivers underlying spatial patterns of larval supply and recruitment success of nearshore marine fishes, but they are poorly understood. We assessed spatial recruitment patterns of nearshore young-of-the-year Pacific rockfishes *Sebastes* spp. in kelp forest and eelgrass meadow habitats from 2004 to 2014 on the west coast of Vancouver Island, British Columbia. Our sites varied in habitat area, wave exposure, sea surface temperature, and distance from the open coast. We observed recruitment of several species of rockfish, including black rockfish *S. melanops*, bocaccio rockfish *S. paucispinis*, and a complex of copper, quillback, and brown rockfishes (*S. caurinus*, *S. maliger*, and *S. auriculatus*; CQB). For black rockfish, the species recruiting in highest abundances, we found that although the environmental variables that predicted recruitment were temporally variable, in some years recruitment was higher at sites with colder sea surface temperature, higher tidal velocity, higher fetch, and higher salinity. In contrast, CQB rockfish recruitment was consistently higher at sites with higher fetch but lower tidal velocity, and this relationship was stable through time. Interactions among environmental variables and habitat area explained the counterintuitive observation of higher recruitment in smaller eelgrass meadows but larger kelp forests. Moreover, sites in or on the boundary of a rockfish conservation area experienced the lowest recruitment during an exceptionally strong black rockfish recruitment event in 2006. These results suggest that temporal variability in the ability of environmental variables to predict the spatial distribution of young-of-the-year rockfishes should be considered in models of population connectivity.

**KEY WORDS:** Marine protected areas · Larval supply · Population replenishment · Spatial patterns · Rockfish Conservation Areas

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## INTRODUCTION

Knowledge of the processes underlying variation in the supply of individuals to local populations (i.e. replenishment and connectivity) is critical to understanding marine population dynamics (Roberts 1998, Fogarty & Botsford 2007, Botsford et al. 2009, Cowen

& Sponaugle 2009). Many marine fishes and invertebrates have complex life histories (Roughgarden et al. 1988) that include pelagic larvae or eggs that may last several months and be transported hundreds of kilometers (Shanks et al. 2003, Pineda et al. 2007). ‘Recruitment’ is commonly used to describe inter-annual variation in the number of pelagic larvae that

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have settled and persisted through an initial period on the benthos (Carr & Syms 2006).

In nearshore environments, dominant current regimes interact with local topography (i.e. headlands, islands, bays and reefs) to produce complex secondary flows that can aggregate and accumulate eggs and larvae, and therefore drive subsequent spatial patterns of recruitment (Wolanski & Hamner 1988, Woodson et al. 2012). Thus, not all locations within nearshore seascapes are equivalent with respect to the probability of receiving eggs and larvae (Gaines et al. 2003). Because recruitment influences rates of local population replenishment (Cowen 1985, Caley et al. 1996, Armsworth 2002, Cowen & Sponaugle 2009), understanding drivers of spatially variable recruitment is critical to models of population connectivity and marine protected area (MPA) design.

At intermediate scales (i.e. mesoscales, 10 to 100 km — the scale most relevant to MPA design) spatial patterns of recruitment may be influenced by rates of larval delivery to nearshore habitats, habitat type or availability, settlement preferences, and intrinsic (i.e. competition) or extrinsic (i.e. predation or prey availability) mechanisms that determine mortality rates and the strength of density dependence (Meekan et al. 1993, Hixon et al. 2002, Hixon & Jones 2005, Johnson 2006, 2007). Numerous studies of marine fishes have reported consistent spatial patterns of recruitment on mesoscales (Caselle & Warner 1996, Sponaugle & Cowen 1997, Tolimieri et al. 1998, Booth et al. 2000, Hamilton et al. 2006, White & Caselle 2008). Many of these studies have concluded that spatial consistency in recruitment at mesoscales is driven primarily by consistent oceanographic processes that determine larval delivery, rather than habitat or intrinsic/extrinsic mechanisms that determine mortality rates. For example, Hamilton et al. (2006) identified consistent spatial patterns of bluehead wrasse *Thalassoma bifasciatum* recruitment, which they attributed to predictable oceanographic processes along the windward to leeward shores, rather than to habitat selection or post-settlement mortality. In addition, spatial consistency in recruitment may be species dependent (i.e. Tolimieri et al. 1998, Schmitt & Holbrook 2002). Notably, however, not all recruitment studies have found consistent patterns of spatial recruitment (e.g. DiFranco et al. 2012).

Although most studies attribute the spatial distribution of recruits at mesoscales to oceanographic processes rather than post-settlement habitat selection (e.g. Booth 1992, Caselle & Warner 1996, Tolimieri et al. 1998), other studies have found that the density of habitat was a significant predictor of the spatial distri-

bution of recruits (e.g. Booth et al. 2000, Holbrook et al. 2000). The relative roles of oceanographic processes and habitat availability in determining the spatial pattern of recruitment may be further complicated when habitat structure interacts with and influences current flow rates on small spatial scales. Such is the case in giant kelp (*Macrocystis* and *Nereocystis* spp.) and eelgrass *Zostera* spp. habitats, which modify and reduce flow in their interior and vicinity, and flow is reduced more within larger kelp forests compared with smaller ones (Gaylord et al. 2007). While flow reduction in larger habitat areas could result in higher settlement rates, isolated habitats of smaller area may also aggregate settlers if it is the only suitable habitat in a large area (such as fish aggregation devices or oil rigs; e.g. Dempster & Kingsford 2004). Likewise, while larger habitats may support a higher total abundance of recruits, the relationship between habitat area and density of recruits per unit area may be more complicated as recruits can be diluted across large areas, resulting in lower density in larger habitats compared to smaller habitats. But ultimately, the relationship between habitat area and settlement will depend on many factors, such as area, location, larval entrainment, predator diversity or abundance, and movement of recruits throughout the habitat.

In this study, we investigate the relationships among habitat type, habitat area, and environmental variables in determining recruitment of young-of-the-year (YOY) rockfishes *Sebastes* spp. on mesoscales. Previously, we have documented large fluctuations in the inter-annual recruitment of black rockfish *Sebastes melanops*, including a year of extremely high recruitment in 2006. We found that overall annual recruitment was related to large-scale oceanographic processes, with recruitment being positively correlated with temperature during parturition and the strength of upwelling at settlement (Lotterhos & Markel 2012). This finding was consistent with the hypothesis that upwelling and the productivity associated with it are favorable to rockfish recruitment (Larson et al. 1994, Yoklavich et al. 1996, Bjorkstedt et al. 2002, Woodson et al. 2012, Wheeler et al. 2017).

Here, we examined patterns of recruitment for these annual cohorts on finer spatial scales, and extended our analysis to other YOY rockfishes. Settlement of these species occurs in shallow nearshore habitats including kelp forests, eelgrass meadows, and rocky and soft-bottom habitats (Love et al. 1991, 2002, Carr 1994, Johnson et al. 2001, Robinson et al. 2011). Dramatic population declines from Alaska to California over the past 4 decades (Parker et al. 2000, Williams et al. 2010) have made rockfishes key tar-

gets for protection by marine reserves and other forms of MPA networks in the USA and Canada (Yamanaka & Logan 2010, Lotterhos et al. 2014).

We integrated data collected from 2 recruitment habitats on the west coast of Vancouver Island, British Columbia: eelgrass *Zostera marina* meadows and kelp forests (*Macrocystis pyrifera*). Here, we define recruitment as the number of fish caught per unit effort in these 2 habitats. Because otolith data have shown that the recruits caught in our surveys had settled weeks earlier, the measure of recruitment in this study will reflect larval supply and post-settlement mortality and/or movement of fishes. In each habitat, we evaluated spatial consistency in YOY recruitment and the association between recruitment and environmental or geographic variables that may predict larval supply, post-settlement mortality, and/or the physiological preferences of the rockfishes. We also evaluated YOY recruitment inside and outside of a recently established rockfish conservation area (RCA) relative to other regions in the study area.

## MATERIALS AND METHODS

### Study species

Pacific rockfishes are among the most ecologically and economically important fishes on the west coast of North America (Love et al. 2002). Larvae typically remain in the water column for 30–150 d (Love et al. 2002) and the few available estimates of dispersal distances range from 10 to 120 km (Buonaccorsi et al. 2004, Miller & Shanks 2004, Lotterhos et al. 2014). In this study, we found the species recruiting in the highest abundances were black rockfish (*Sebastes melanops*, pelagic larval duration 57–99 d; Lotterhos & Markel 2012) and a complex that could have been any of copper (*S. caurinus*), quillback (*S. maliger*), and/or brown (*S. auriculatus*) rockfishes (hereafter CQB rockfishes, pelagic larval duration 36–73 d; Markel 2011). We also observed sporadic recruitment of endangered bocaccio rockfish (*Sebastes paucispinis*; COSEWIC 2013).

It is thought that years of good upwelling will enhance larval survival of species such as black rockfish that have a long larval duration, are found deeper, and need to feed for longer in the plankton, ultimately resulting in higher recruitment (Carr 1991, Love et al. 2002, Wilson et al. 2008, Caselle et al. 2010, Markel 2011, Lotterhos & Markel 2012). Previous otolith analysis revealed black rockfish settlement occurred in late spring—a few weeks before

juveniles were observed in visual surveys in near-shore habitats—suggesting that they settle into the benthos and either migrate onshore or are advected onshore as deep water moves onshore with upwelling (Moser & Boehlert 1991, Lotterhos & Markel 2012). In contrast, species such as copper, quillback, and brown rockfish have a relatively short larval duration and tend to stay closer to the surface as larvae. These species settle into the kelp canopy and eelgrass beds later in the summer in relation to warm water and relaxation of upwelling (Carr 1991, Love et al. 2002, Wilson et al. 2008, Caselle et al. 2010, Markel 2011, Robinson et al. 2011).

### Study system

This research was conducted in Barkley Sound (48° 50.0' N, 125° 22.0' W) on the southwest coast of Vancouver Island (Fig. 1), an island-studded sound that has a wide range of wave exposure and tidal velocities encompassing an area of approximately 500 km<sup>2</sup>. Our study sites were distributed across Barkley Sound in 5 regions (from west to east, Fig. 1): George Fraser Islands (GF), Loudoun Channel (LC), Broken Group Island (BGI), Deer Group Islands (DG), and Prasiola Point to Execution Rock (PE) (Fig. 1).

The oceanography of the fjord-like estuary of Barkley Sound has been studied for more than 65 yr (e.g. Tully 1948, Hodgins 1979, Stronach et al. 1993, Linder 2010). In general, the physical oceanography is mainly influenced in late winter to early summer by the discharge of freshwater into the sound from the largest river, the Somass, and many smaller rivers in the region. The freshwater discharge results in a relatively shallow (<2–3 m thick) pycnocline with a seaward surface salinity gradient difference ranging from 27 to 30 ppt (Hodgins 1979, Stronach et al. 1993, Linder 2010). Tidal inflows and outflows are thought to be mainly restricted to the relatively non-variable saltier intermediate depth layer (3–9 m) (Hodgins 1979, Stronach et al. 1993, Linder 2010). Ultimately, the majority of net water flow into and out of Barkley Sound is via the widest and deepest channel, Imperial Eagle (Hodgins 1979, Stronach et al. 1993, Linder 2010). Overall, variations in bathymetry and density (driven by salinity) gradients are the primary factors influencing water circulation in Barkley Sound.

Within the boundaries of the BGI is the Pacific Rim National Park and an RCA, one of 164 established on the British Columbia coast between 2004 and 2007 by Fisheries and Oceans Canada (Fig. 1; Yamanaka & Logan 2010). RCAs exclude all commercial and re-

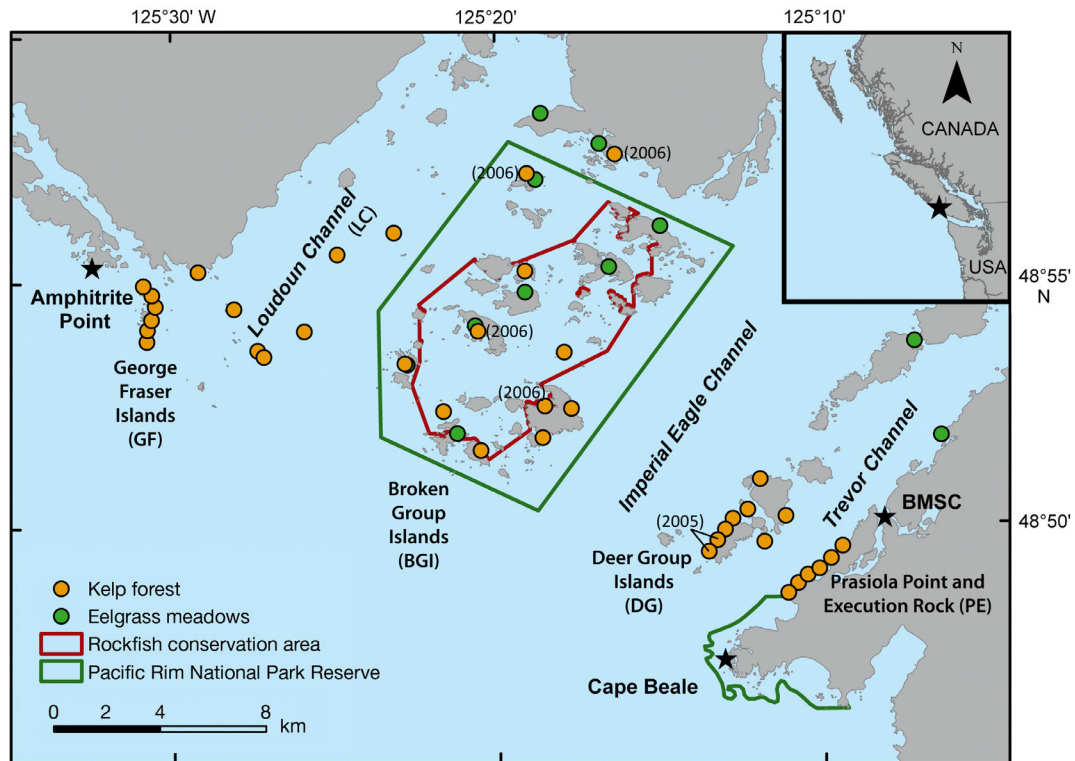


Fig. 1. Eelgrass (*Zostera marina*) and kelp forest (*Macrocystis pyrifera*) sampling locations throughout Barkley Sound. The BGI kelp forest sites were not monitored in 2005. Some DG and BGI kelp forest sites were only monitored in 2005 or 2006, respectively (indicated in parentheses beside the site). In 2010, only kelp forests in PE and DG were monitored

creational rockfish fishing, but they were not designed with knowledge of rockfish densities at different life-history stages. Instead, suitable habitat was first identified with a model that integrated benthic habitat complexity (measured as the second derivative of the depth) and commercial rockfish catch (catch-per-unit-effort density), and then ultimately determined following a stakeholder consultation process (Yamanaka & Logan 2010). Since rockfish have high site fidelity (Love et al. 1991, Byerly 2001, Nelson 2001, Parker et al. 2007, Freiwald 2012), spatial data on rockfish densities at different life history stages are particularly valuable for evaluating the efficacy of these areas.

### Recruitment surveys

We analyzed 2 datasets that assessed spatial and interannual patterns of rockfish recruitment throughout Barkley Sound in an overlapping time period. The first study was conducted in *Zostera marina* eelgrass meadows (hereafter *Zostera*) from 2004 to 2014 (Robinson et al. 2011, Robinson & Yakimishyn 2013) and the second was conducted from 2005 to 2010 in

*Macrocystis pyrifera* kelp forests (hereafter *Macrocystis*). Because of the placement of standard monitoring units for recruitment of fishes (SMURFs) in kelp habitat (see 'Kelp forests' below), both SMURF and eelgrass surveys represent a snapshot measure of fish density in the habitat at any point in time; that is, an integrated measure including larval delivery, post-settlement mortality, and movement or habitat selection.

YOY rockfishes collected in each survey were weighed, measured (total length, TL), and identified on the basis of size, body shape, and pigment patterns (Matarese et al. 1989, Kendall 1991). Copper (*S. caurinus*), quillback (*S. maliger*), and brown (*S. auriculatus*) rockfishes were grouped as 'CQB complex' rockfishes because of difficulty distinguishing early post-settlement juveniles in the field.

### Eelgrass meadows

Eight to 12 eelgrass meadows accessible during low tides were sampled by Parks Canada within the BGI each July between 2004 and 2014. Meadows ranged in size from 50 to 19 000 m<sup>2</sup> and were repre-

sentative of eelgrass meadows located in the BGI. At each meadow, 2 or 3 beach seine sets were completed using a 9.2 m long seine having a 3.1 m drop in the center tapering to 1.1 m at the wings with 4.0 mm black stretch mesh. Seining was conducted during a 2 h window before and after the early morning lowest low tide (tidal height <0.6 m Canadian chart datum). The sampled area of each eelgrass meadow after 3 beach seines was approximately 300 m<sup>2</sup>. Rockfish recruitment in eelgrass meadows is reported as the number of rockfish per set (Robinson et al. 2011).

### Kelp forests

Rockfish recruitment was surveyed in *Macrocystis* kelp forests between 2005 and 2010. *Macrocystis* forests in this region are typically found on the leeward side of outer coast islands and headlands on rocky bottoms in areas of moderate wave exposure; kelp forest size was measured in 2006 and 2008 and ranged in size from 10 to 27 000 m<sup>2</sup> (including *Nereocystis* spp.). To assess rockfish recruitment in kelp forest habitats, we employed SMURFS at the seaward edge of, and in physical contact with *Macrocystis* forests (Ammann 2004). This design differs from other SMURF datasets, where SMURFs were deployed in minimal habitat in order to obtain an aggregated measure of settlement (Ammann 2004)—in this study, SMURFs measure a snapshot of recruit density in the kelp forest. We deployed 1 SMURF at each of 6 sites nested within 5 zones throughout Barkley Sound at a depth of 2 m (Fig. 1). SMURFs were monitored between 2005 and 2010, but not all sites were monitored in all years. In 2005 only 4 SMURFs were deployed per region and sites within the BGI were not included in this sampling. In 2006, some of the sites in the BGI were different than the sites monitored from 2007 to 2009. In 2010, only DG and PE were monitored (see Fig. 1).

Kelp forest locations were sampled approximately every 14 d between June and August. Snorkelers used a benthic ichthyofaunal net for coral/kelp environments (BINCKE; Anderson & Carr 1998) to capture all fish occupying SMURFs on each sampling date. Rockfish recruitment in kelp forests is reported as the number of rockfish per SMURF. Previous analysis of fish otoliths revealed that black rockfish caught in SMURFs throughout the summer came from the same cohort that settled in early April, indicating that fish settled and then swam into SMURFs (Lotterhos & Markel 2012, Kashef et al. 2014).

### Temporal and spatial patterns of recruitment

Because a direct comparison in the magnitude of recruitment between habitats is not meaningful due to gear type differences, eelgrass and kelp forest habitats were analyzed separately for all analyses. To test for differences among years in kelp forests, we modeled recruitment as a function of the fixed effects of region and year and their interaction, with a linear mixed effects model including random effects of site and sampling date. For eelgrass meadows, all sites were within the same region and so we tested for the fixed effect of year, with the random effects of site and sampling date. Since a Poisson model was deemed inappropriate because data were overdispersed, we attempted to use negative binomial generalized linear models to fit the data, but many of these models did not converge. We found that a  $\log_{10}(x+1)$  transformation of fish recruitment provided a reasonable distribution of residuals. We included year as a fixed factor because the annual abundance of YOY is largely determined by oceanographic conditions and chance events during parturition and settlement (Caselle et al. 2010, Lotterhos & Markel 2012). We used ANOVA to summarize the main effects from the mixed model and used likelihood ratio tests to test for significance of main effects. We tested the coefficients of the linear mixed effects model for significance using Kenward–Roger approximation to obtain approximate degrees of freedom and the *t*-distribution to obtain *p*-values with the R package *pbrtest* (Halekoh & Højsgaard 2014). We used the autocorrelation function (*acf*) in R to check for autocorrelation in the residuals. The autocorrelation is based on the residuals of the model for sites ranked according to their proximity to each other by water distance within a region in the sound. When spatial autocorrelation was not properly accounted for (e.g. by not including sites as random effects), covariance in the residuals was observed because nearby sites had similar residuals. Finally, pairwise comparisons were made using a Tukey honest significant differences (HSD) test based on least squared means. All statistical analyses were performed in R (R Core Team 2015).

### Predictors of spatial recruitment

For each species in each habitat, we tested the hypothesis that annual mean recruitment to a site was a function of year (fixed effect), environmental characteristics (covariates), and habitat area (covari-

ate). For each site we measured the following environmental or geographic variables, which are explained in more detail below: distance to open water (km), cumulative fetch (a measure of wave exposure in km), tidal velocity ( $\text{m s}^{-1}$ ), sea surface temperature (SST,  $^{\circ}\text{C}$ ), and habitat area. In eelgrass meadows, salinity (ppm) was additionally measured. Because all these variables were all highly correlated with each other, we used a principal components analysis (PCA) in each habitat to quantify the environment and habitat characteristics at each site. We hypothesized that juvenile density of black rockfish would be higher at sites that were (1) closer to the open water with high fetch (because these would be the first sites larvae would encounter) and had (2) higher tidal velocity (because these sites would experience more exchange with offshore water), (3) colder SST (because larval transport is associated with colder, upwelled water, and because SST is negatively correlated with kelp forest productivity; Konotchick et al. 2012), (4) larger habitat size (because larger kelp forests and eelgrass beds may reduce water flow to allow for settlement), and (5) higher salinity (Robinson et al. 2011). For CQB rockfish, the hypotheses are the same but the relationship with temperature would be harder to predict because although recruitment is associated with warmer waters (Wilson et al. 2008), the production of the giant kelp they settle into decreases with warming temperatures (Konotchick et al. 2012).

We measured distance to the open water by drawing a line perpendicular to the entrance of Barkley Sound (demarcated as a line between Cape Beale and Amphitrite Point, Fig. 1), inshore to each kelp and eelgrass location. Fetch is an estimate of the exposure of a site to ocean swell that is integrated over time. We estimated fetch for each location by extending and measuring radiating lines every 10 deg to the nearest landmass using the navigational software Nobletech (v.4.1). Where lines extended into the offshore region, we assigned a maximum distance of 185 km (100 nautical miles; results were not sensitive to this assignment). Fetch was recorded as the summed length of all lines for each location (Ekebom et al. 2002, Lessard & Campbell 2007). We assigned all eelgrass and kelp forest locations single values of tidal velocity using the modeled estimates produced by Stronach et al. (1993). SST was measured on each sampling date (May–August), and then averaged to provide an average value for each location. Salinity (ppm) was only measured in eelgrass meadows on each sampling date, and was also averaged over all years to provide an average value for

each location. Habitat area ( $\text{m}^2$ ) for eelgrass meadows (*Zostera*) and kelp forests (*Macrocystis* and *Nereocystis*) was measured by GPS and log transformed for analysis. Kelp forest area was measured in 2006 and 2008, and was averaged for analysis.

We used linear models to test: (1) whether recruitment was related to environmental or geographic variables and (2) whether the relationship, if one existed, was consistent through time (e.g. no interaction with year of sampling). Mean recruitment to each site was calculated over all years and was  $\log_{10}(x+1)$  transformed for this analysis. The environmental variables, geographic variables, and habitat area were all highly correlated and summarized with a PCA. For each species (black or CQB) in each habitat, we used an ANCOVA with log mean annual recruitment to a site as the response variable and with the explanatory variables of: year of sampling as a fixed effect, the first 2 components of the PCA (which explained the majority of the variance in the environmental and habitat variables, see Results) as covariates, and the interactions of  $\text{PC1} \times \text{year}$  and  $\text{PC2} \times \text{year}$ . We used model selection based on Akaike's information criterion (AIC) to drop non-significant terms from the model. We also used the *acf* in R to check for autocorrelation in the residuals.

### Consistency in spatial patterns of recruitment

To assess whether the rank order of location-specific recruitment was consistent between years, we used Spearman's rank correlation. For eelgrass or kelp forest sites, we calculated the correlation between all pair-wise combinations of black rockfish mean annual recruitment (2005–2010). We limited this analysis to black rockfish (because CQB complex rockfish recruitment was weak and variable after 2005) and to the years 2005–2010 when both eelgrass meadows and kelp forest sites were monitored. Sample sizes differed somewhat between years because of slight annual differences in the sites that were sampled, as described above. We controlled for false discovery rate in each family of tests with the Benjamini & Hochberg (1995) method.

## RESULTS

### Temporal and spatial variation in recruitment

Rockfish recruitment varied widely over the course of the study between years and species. Black rock-

fish recruitment was exceptionally high in kelp and eelgrass habitats in 2006 (Fig. 2). CQB complex rockfish recruitment was exceptionally high in 2005 in kelp forests (Fig. 2B). We observed YOY bocaccio in only 2 years of surveys, 2006 and 2010 (higher numbers were observed in 2006, which coincided with the highest recruitment year of black rockfish).

### Kelp

In kelp forest habitats, the best model for recruitment of both black and CQB YOY included the main effects of year and region and their interaction. For black rockfish, a year  $\times$  region interaction ( $F = 2.75$ ,  $df = 16$ ,  $p < 0.001$ ) was caused by significantly higher recruitment to all regions in 2006—except for the BGI, which encompasses the RCA—than most other years (Fig. 3A). For CQB YOY rockfish, a significant region  $\times$  year interaction ( $F = 29.38$ ,  $df = 16$ ,  $p < 0.001$ ) was driven by higher CQB recruitment to Loudoun Channel than all other regions in 2005 and to all regions in all other years (Fig. 3B). This single, spatially localized recruitment event was responsible for the above average recruitment of CQB to kelp in 2005 (Fig. 2B).

### Eelgrass

In eelgrass habitats, which were all located within the same region (BGI), the main effect of year was

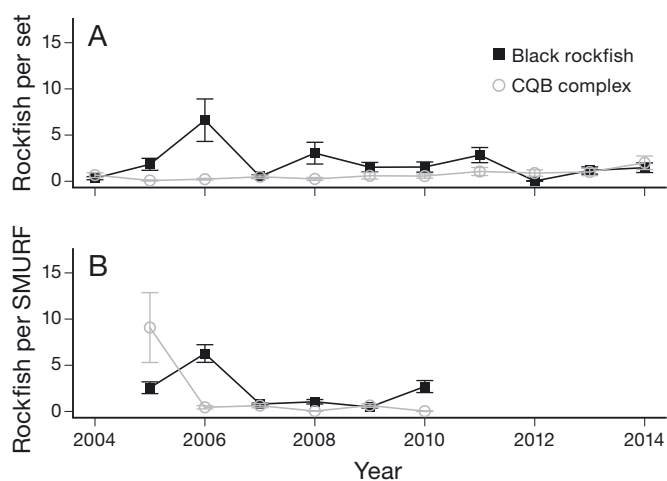


Fig. 2. Annual recruitment of CQB complex (*Sebastes caurinus*, *S. maliger*, *S. auriculatus*) and black (*S. melanops*) rockfishes in: (A) eelgrass meadows (2004–2014), mean number of rockfish per set; and (B) kelp forests (2005–2010), mean number of rockfish per SMURF (standard monitoring units for recruitment of fishes). Error bars:  $\pm$ SE

significant for both the black ( $F = 8.86$ ,  $df = 10$ ,  $p < 0.001$ ) and CQB models ( $F = 3.27$ ,  $df = 10$ ,  $p < 0.001$ ). For black rockfish, recruitment in 2006 was significantly higher in all other years except for 2008, and recruitment in 2004 and 2012 was significantly lower than in many other years (Fig. 2A; R Markdown output in the Supplement at [www.int-res.com/articles/suppl/m574p097\\_supp.pdf](http://www.int-res.com/articles/suppl/m574p097_supp.pdf)). For CQB rockfish, recruitment in 2014 was significantly higher than in many other years (Fig. 2A and the Supplement).

## Predictors of spatial recruitment

### PCA results

In both the principal component analyses used to summarize the environmental variables for the kelp and eelgrass habitats, the first 2 principal components explained the majority of the variance (83% in kelp and 86% in eelgrass; Fig. 4). For both habitat types, habitat area positively loaded onto PC1, but the direction of loading of environmental variables onto PC1 differed (Fig. 4). In kelp, PC1-kelp was positively correlated with area, fetch, and tidal velocity, but negatively correlated with SST and distance from the mouth of the sound (Fig. 4A). In eelgrass, PC1-eelgrass was positively correlated with area, SST, and distance from the mouth of the sound, and negatively correlated with tidal velocity, fetch, and salinity (Fig. 4B). Thus, the kelp and eelgrass PC1 axes were both positively correlated with habitat area, but the conditions positively correlated with kelp forest size were negatively correlated with eelgrass bed size (Fig. 4).

**Black recruitment model.** In kelp forest habitats, the best model for mean black YOY annual abundance in kelp forests explained 55% of the variance ( $F = 19.14$  on 9 and 123  $df$ ,  $p < 0.001$ , adjusted  $R^2 = 0.55$ ). The model included the significant main effect of year ( $F = 39.63$ ,  $df = 4$ ,  $p < 0.001$ ), the covariate of PC1-kelp ( $F = 3.53$ ,  $df = 1$ ,  $p = 0.06$ ), and a significant year  $\times$  PC1-kelp interaction ( $F = 2.55$ ,  $df = 4$ ,  $p = 0.04$ ). To explore this interaction, we used individual linear models for each year, which revealed that PC1-kelp was significantly positively related to recruitment only in 2006, which was the year of highest recruitment of black rockfish (Fig. 4C, dark bars). In this year of highest recruitment, black YOY abundance increased with fetch, tidal velocity, and lower SST.

In eelgrass habitats, the best model for mean black YOY annual abundance in eelgrass beds included the significant main effect of year ( $F = 5.47$ ,  $df = 10$ ,  $p < 0.001$ ), the covariate of PC1-eelgrass ( $F = 105.40$ ,

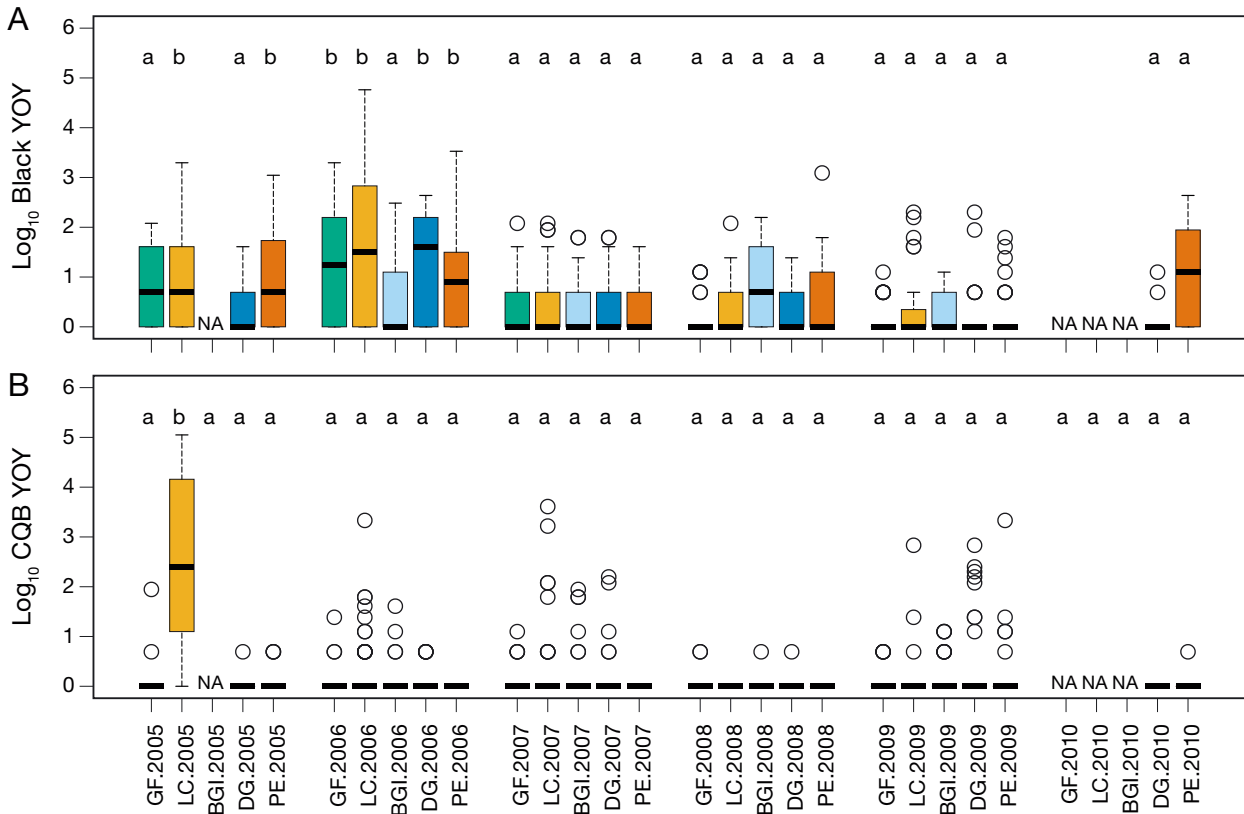


Fig. 3. Comparison of (A) black (*Sebastes melanops*) and (B) CQB (*Sebastes caurinus*, *S. maliger*, *S. auriculatus*) young-of-the-year (YOY) abundance in kelp forests across regions in Barkley Sound as measured by SMURFs. In A, letters denote whether sites are significantly different from the large recruitment event of black rockfish in Loudoun Channel in 2006. In B, letters denote whether sites are significantly different from the large recruitment event of CQB rockfish in Loudoun Channel in 2005. GF: George Fraser Islands; LC: Loudoun Channel; BGI: Broken Group Islands (encompass the Rockfish Conservation Area); DG: Deer Group Islands; PE: Prasiola Point to Execution Rock. Boxplot delimitations: thick horizontal line represents the median; box limits represent the 25% and 75% quantiles; whiskers represent data range excluding outliers; circles represent outliers as determined by the R function boxplot. NA: not sampled in that year

df = 1, p < 0.001), the covariate of PC2-eelgrass ( $F = 9.19$ , df = 1, p = 0.003), and a significant year × PC1-eelgrass interaction ( $F = 4.98$ , df = 10, p < 0.001). Individual linear models for each year revealed that PC1-eelgrass significantly explained recruitment in 6 of the 10 yr, including the year (2006) of highest recruitment (Fig. 4D, dark bars). The relationship between black YOY abundance with PC1-eelgrass was analogous to that with the kelp forests, in that abundance increased with fetch, tidal velocity, and lower SST.

Overall, the analysis for black YOY suggests that recruitment to both kelp forest and eelgrass habitats was higher at sites with higher fetch, higher tidal velocity, and lower SST (see Fig. 5), but also that this relationship was temporally variable. These conclusions qualitatively held for a subset of kelp forest sites located only within the BGI that overlapped spatially with the eelgrass bed sampling extent (not shown, see the Supplement).

**CQB recruitment model.** In kelp forest habitats, the best model for mean CQB YOY annual abundance in kelp forests explained 21% of the variance ( $F = 4.42$  on 10 and 122 df, p < 0.001, adjusted  $R^2 = 0.21$ ). The model included the significant covariate of PC2-kelp ( $F = 5.78$ , df = 1, p = 0.018), the significant main effect of year ( $F = 4.46$ , df = 4, p = 0.002), a significant year × PC1-kelp interaction ( $F = 4.38$ , df = 4, p = 0.002), and the covariate of PC1-kelp ( $F = 3.13$ , df = 1, p = 0.08). Individual linear models for each year revealed that PC1 had an unusually large slope in 2005, which was the year of highest CQB recruitment (Fig. 4C light bars; the Supplement). Most of the variation in CQB recruitment, however, was explained by PC2-kelp, which indicated that CQB abundance was higher at sites with higher fetch and lower tidal velocity (Fig. 4E).

In eelgrass habitats, the best model for CQB recruitment to eelgrass beds explained 23% of the variance ( $F = 2.404$  on 22 and 83 df, p = 0.002, adjusted



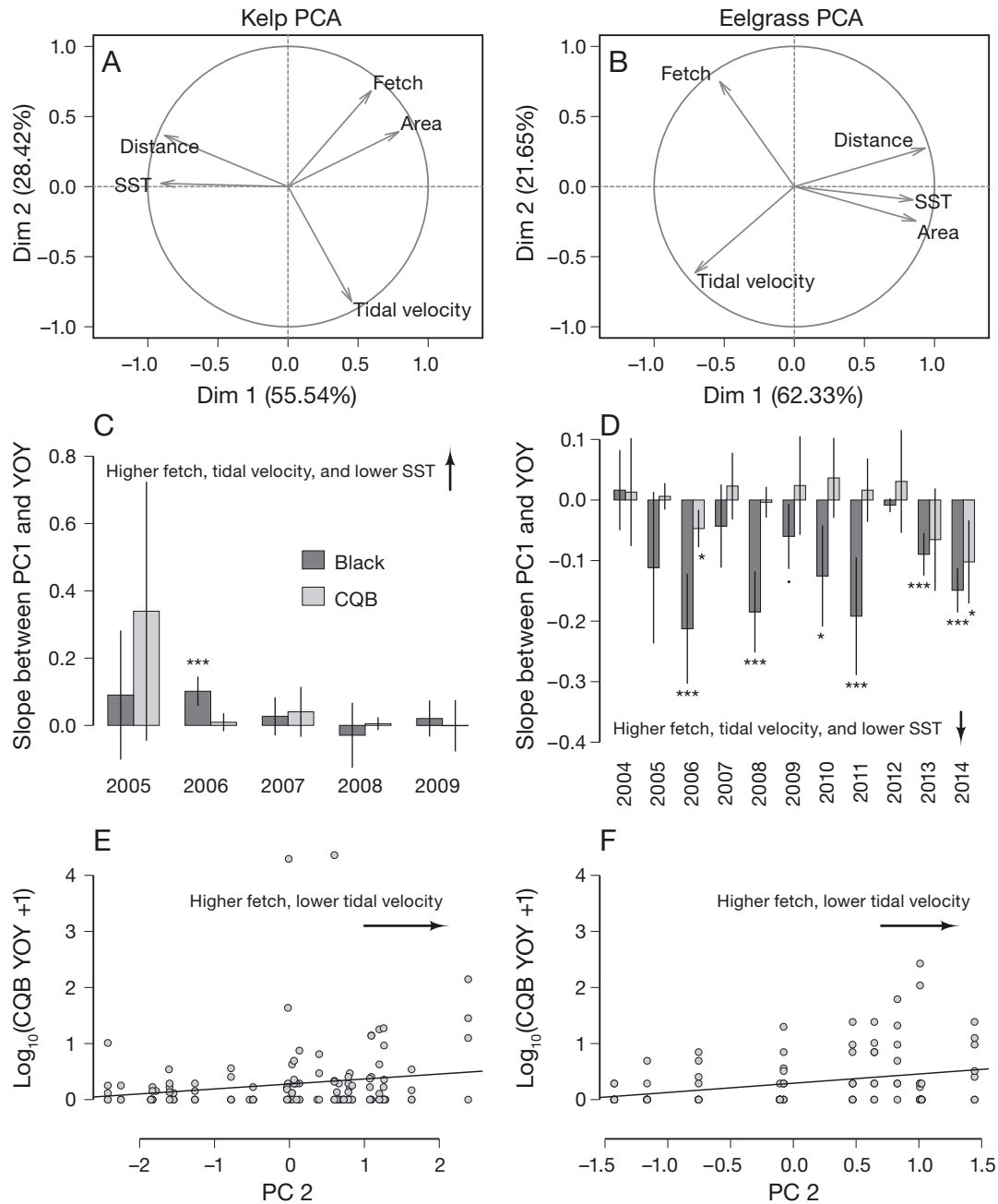


Fig. 4. Summary of analysis between rockfish recruitment and geographic variables. (A,B) Results of a principal components analysis for 5 geographic variables measured in (A) kelp forests and (B) eelgrass beds. (C,D) PC1  $\times$  year interaction as variation in the magnitude of the slope between PC1 and rockfish recruitment to (C) SMURFs and (D) eelgrass beds across each year of sampling; asterisks represent statistical significance based on linear models (\*\* $p < 0.001$ ; \* $p < 0.01$ , \* $p < 0.05$ ,  $p < 0.1$ ). The arrows represent the direction of the slope by which recruitment increases with fetch and tidal velocity, but decreases with SST (the directions of the arrows are different in C and D because of the opposite loadings shown in A and B). (E,F) The relationship between PC2 and CQB (*Sebastes caurinus*, *S. maliger*, *S. auriculatus*) recruitment to (E) SMURFs and (F) eelgrass beds; there was no significant PC2  $\times$  year interaction (see 'Results'), so the data include annual mean abundance of fish at all sites. SST: sea surface temperature

$R^2 = 0.23$ ). The best model included a significant effect of PC2-eelgrass ( $F = 11.54$ ,  $df = 1$ ,  $p = 0.001$ ), a significant year  $\times$  PC1-eelgrass interaction ( $F = 2.176$ ,  $df = 10$ ,  $p = 0.027$ ), the main effect of year ( $F = 1.81$ ,  $df$

$= 10$ ,  $p = 0.07$ ), and PC1-eelgrass ( $F = 1.48$ ,  $df = 1$ ,  $p = 0.22$ ). Contrasts and individual linear models for each year revealed that the year  $\times$  PC1-eelgrass interaction was caused by a significant relationship between

CQB recruitment and PC1-eelgrass in 2 of the 11 yr (Fig. 4D, light bars). Similar to what was observed in kelp forests, the majority of the variation in CQB recruitment was explained by PC2-eelgrass, which indicated that CQB abundance was larger at sites with higher fetch and lower tidal velocity (Fig. 4F).

Overall, the analysis for CQB YOY suggests that, in contrast to black YOY, recruitment to both kelp forest and eelgrass habitats was higher at sites with higher fetch and lower tidal velocity, and that this relationship was temporally stable over time. In some years, the abundance of CQB recruits was secondarily related to fetch, tidal velocity, and SST, but this relationship was temporally variable. Similar to what was found for the black YOY model, these conclusions qualitatively held for a subset of kelp forest sites located only within the BGI that overlapped spatially with the eelgrass bed sampling extent (see the Supplement).

### Consistency in spatial patterns of recruitment across years

Mean recruitment across years varied significantly among the sites surveyed throughout Barkley Sound

(Fig. 5). We tested for spatial consistency in the ranking of recruitment among sites in each habitat. Kelp forest sites did not have a significant correlation in any pairwise comparison (Fig. 6, upper diagonal). Eelgrass sites had several significantly positive pairwise comparisons, even after correction for multiple tests (Fig. 6, lower diagonal). The consistency of recruitment in eelgrass was largely driven by 2 sites near the mouth of the sound that had consistently high recruitment, and a few sites at the most inner part of the sound that had consistently low recruitment (Fig. 5).

### DISCUSSION

The dynamics in marine metapopulations are influenced by both, large-scale oceanographic processes that determine the survival and distribution of pelagic larvae and small-scale processes that affect post-settlement growth and survival (Roughgarden et al. 1988). Previously, it has been shown that consistency in year class strength (e.g. 2006 for black rockfish and 2005 for CQB) could be explained by large-scale oceanographic factors (Field & Ralston 2005, Wilson et al. 2008, Lotterhos & Markel 2012). Here, we found

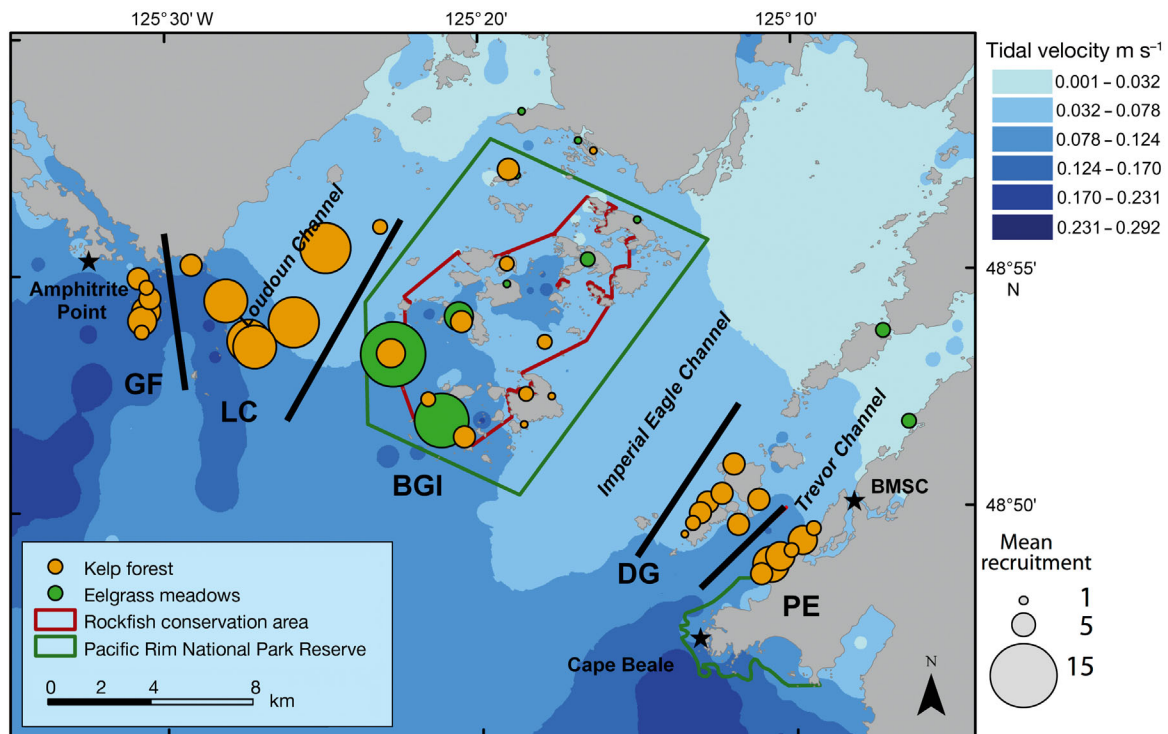


Fig. 5. Mean black rockfish (*Sebastes melanops*) recruitment (number per set or SMURF) at eelgrass meadow and kelp forest locations between 2005 and 2010. Bubble sizes indicate mean recruitment ranging from 0 (smallest) to 13 (largest). Black bars delineate regions with replicate kelp forest sites: George Fraser Islands (GF), Loudoun Channel (LC), Broken Group Islands (BGI), Deer Group Islands (DG), and Prasiola Point to Execution Rock (PE)

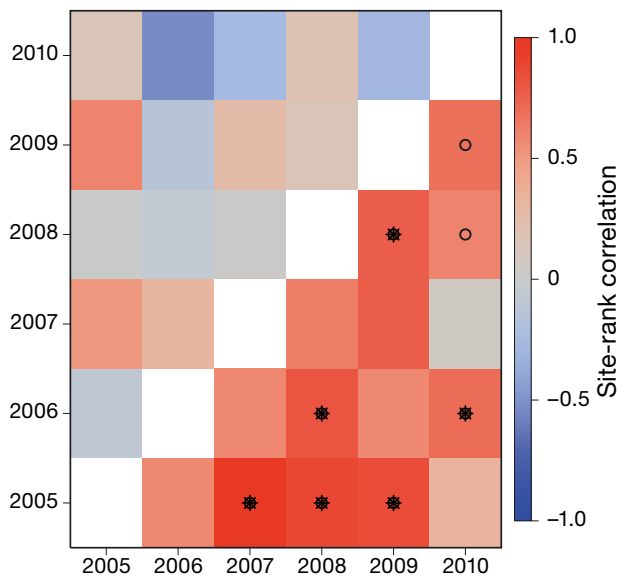


Fig. 6. Results from analysis of Spearman's rank correlation in recruitment of black rockfish to sites among years. Rank correlations for kelp forest sites are shown above the diagonal and rank correlations for eelgrass sites are shown below the diagonal. Circles indicate statistical significance before correction for multiple tests, asterisks indicate significant correlation before and after Benjamini–Hochberg correction

that in some years the distribution of recruitment events in space at the mesoscale is apparently due to environmental and geographic (and perhaps biological) factors. For black rockfish, we found that recruitment to both kelp forest and eelgrass sites could be explained in some years by environmental factors such as tidal velocity and SST, and geographic factors such as distance to the open coast and fetch. For CQB rockfish, we found that recruitment to both kelp forest and eelgrass sites could be consistently explained by tidal velocity and fetch. While it is likely that these environmental variables are indicators of larval supply to the study sites, they may also reflect physiological preferences or post-settlement mortality of recent settlers.

#### Temporal variation in recruitment

Over the years of this study, we observed substantial temporal variation in recruitment to eelgrass and kelp forest habitats for black rockfish and CQB rockfishes. The years 2005 and 2006, which showed opposing patterns in terms of recruitment for each species in kelp forests, were also characterized by anomalous oceanographic conditions. In 2005, a 1 mo delay in the spring transition to upwelling-favorable

winds resulted in warmer water with lower nutrient levels and lower primary productivity (Barth et al. 2007). These conditions were considered to be unfavorable to the recruitment of rocky intertidal invertebrates, which experienced unprecedented low recruitment in that year (Barth et al. 2007), as well as unfavorable to black rockfish recruitment in southern California (Wilson et al. 2008). These conditions, however, appeared to be favorable to CQB larvae, which typically have later birthdates and settlement dates than black rockfish (Markel 2011). In eelgrass meadows, 2014 had significantly higher recruitment of CQB than many other years; May 2014 marked the beginning of an El Niño event. El Niños are characterized by elevated temperatures, onshore and poleward advection, lower salinities, and reduced or delayed upwelling (Lenarz et al. 1995). CQB rockfishes have shorter larval durations than black rockfish, and may benefit from downwelling or relaxation events that retain larvae near suitable settlement habitat (Carr 1991, Love et al. 2002, Wilson et al. 2008, Caselle et al. 2010, Markel 2011).

While upwelling was delayed in 2005, upwelling was higher than average in 2006 during settlement of black rockfish (Lotterhos & Markel 2012). Upwelling conditions may be favorable to black rockfish larvae, which have a longer pelagic larval duration (Carr 1991, Love et al. 2002, Wilson et al. 2008, Caselle et al. 2010, Markel 2011) and have been found to be associated with upwelling fronts (Larson et al. 1994, Sakuma & Ralston 1995, Yoklavich et al. 1996, Bjorkstedt et al. 2002). Although black YOY achieved very high densities in 2006, this cohort had low genetic diversity and high number of sibships compared to the other years (Lotterhos & Markel 2012). These data suggest that 2006 was a 'sweepstakes' year for black rockfish – a strong recruitment year apparently attributable to the high larval production of a limited number of adults.

#### Spatial variation in recruitment

Consistent with other research, we generally found that the spatial variability in recruitment was largely determined by geography and environmental variables driven by physical processes (Jenkins et al. 1997). For black rockfish, we found that recruitment was positively correlated with habitat area in kelp, but negatively correlated with habitat area in eelgrass. These contrasting patterns can be explained by the environmental variables that likely affect the successful establishment of kelp forest and eelgrass

meadows. In Barkley Sound, larger kelp forests are found in more exposed rocky areas of colder SST, higher tidal velocity, and higher fetch, while larger eelgrass meadows are found in more protected bays characterized by warmer temperatures, lower tidal velocity, and lower salinity. In both kelp forests and eelgrass meadows, however, we found that recruit intensity of black rockfish varied in a predictable manner with environmental variables. Sites with high fetch and high tidal velocity near the mouth of the Sound are likely to be among the first places larvae encounter (Jenkins et al. 1997). These sites are additionally characterized by low SST, lending support to the hypothesis that black rockfish are deeper in the water column, are associated with upwelling plumes, and settle in the benthos (Carr 1991, Love et al. 2002, Wilson et al. 2008, Caselle et al. 2010, Markel 2011, Lotterhos & Markel 2012). In California, regions with a high probability of ocean fronts experience higher overall settlement, lower variability in settler abundance, and higher YOY rockfish recruitment (Woodson et al. 2012).

Although CQB recruitment was weak and variable, our analysis did find that CQB recruitment was higher at sites with higher fetch (similar to black rockfish) but lower at sites with higher tidal velocity (in contrast to black rockfish). CQB larvae have a shorter pelagic larvae duration, are expected to be found higher in the water column, and are expected to experience more retention than black rockfish. Thus, while exposed sites (as measured by fetch) may receive more CQB larvae or fetch may indicate favorable habitat, tidal exchange may have a less important role in delivery of CQB larvae to the nearshore environment (Carr 1991, Love et al. 2002, Wilson et al. 2008, Caselle et al. 2010, Markel 2011, Lotterhos & Markel 2012).

Our results are consistent with the 'settle-and-stay' hypothesis, arguing that larvae are likely to settle in the first place they encounter, and that habitat location and the availability of competent larvae are the primary determinants of juvenile fish abundance (Bell et al. 1988). However, because environmental variables that correlate with recruitment also correlate with other biological variables including habitat area, habitat area may play a direct or indirect role in explaining our findings. Higher recruitment to larger habitat patches, as was observed in kelp forests, could be explained by direct effects of habitat on reducing flow and entraining larvae (Gaylord et al. 2007), or by indirect effects of habitat complexity by providing refuge from predators (Johnson 2006, 2007). Higher YOY abundance in smaller habitat patches, as was ob-

served in eelgrass, could also be explained by lower abundance of competitors or predators, as would be predicted by basic species diversity–area curves.

We observed consistent spatial rankings in recruitment to eelgrass beds, but not to kelp forest habitats. This may be explained by more consistent larval delivery to eelgrass sites than to kelp forest sites, or higher interannual variation in habitat characteristics in kelp compared to eelgrass. At our eelgrass sites, high persistence and stability of fish assemblages has been observed in meadows over time (Robinson & Yakimishyn 2013). In contrast, kelp forest biomass is known to fluctuate in biomass from year to year depending on winter storms, recruitment, and sea-urchin grazing rates (Dayton et al. 1992, Cavanaugh et al. 2013). Alternatively, other post-settlement processes such as predation or intraspecific competition from older year classes immigrating into kelp forest sites could obscure consistent spatial rankings in kelp forests (Caley et al. 1996, Hobson et al. 2001, Hixon & Webster 2002, Samhuri et al. 2009, Hixon et al. 2012).

While larval supply and habitat characteristics can explain the observed patterns, the physiological tolerance of rockfishes may also play an important role in the recruitment patterns observed in this study. Our results have corroborated those of others who have found salinity to be an important predictor of black rockfish recruitment (Robinson et al. 2011), and juvenile black rockfish may not be able to tolerate low levels of salinity at some of the interior eelgrass sites close to river outlets. In contrast, copper rockfish are found at the head or river inlets, and they may be able to tolerate lower salinity levels than black rockfish (Dick et al. 2014). CQB rockfish were found at lower salinity sites in eelgrass meadows in our study. Recruitment of both black and CQB YOY declined with temperature, however. Warmer sites may incur higher metabolic rates, requiring increased foraging to acquire energy and incurring higher risk of predation.

#### **Implications for the design of rockfish conservation areas**

In Barkley Sound, an RCA is located within the BGI Unit of the Pacific Rim National Park Reserve. Black rockfish recruitment was significantly lower at kelp forests inside the BGI in 2006 during the year of highest recruitment. Rockfishes have high site fidelity and prefer high-relief, exposed rocky reefs (home range sizes for CQB complex are 30–1500 m<sup>2</sup>,

Matthews 1990; and for black rockfish 0.55 km<sup>2</sup>, Parker et al. 2007). If YOY recruits have high site fidelity until they become reproductive, then recruitment patterns observed in this study may have important implications for the efficacy of the RCA in Barkley Sound. However, a companion study found that the annual year class strength may be obscured due to over-winter mortality in the first year (Haggarty et al. 2017 this volume). If post-recruitment processes significantly decouple the spatiotemporal relationship between strong recruitments and subsequent adult abundance, this may call into question the logic of designing reserves around recruitment hotspots (see also Gerber et al. 2003, White & Samhuri 2011).

## CONCLUSIONS

Not all locations within nearshore habitats are equivalent with respect to the probability of receiving eggs and larvae (Gaines et al. 2003). Our results contribute to a growing understanding of the characteristics of areas likely to experience relatively high or low fish recruitment, and may be applicable to other species. Environment and geography can interact with characteristics of habitat, including habitat size, to influence observed recruitment, and habitat characteristics can play a multitude of roles in mediating or exacerbating post-settlement processes.

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