SPATIOTEMPORAL VARIABILITY OF ROCKFISH RECRUITMENT ON CALIFORNIA'S NORTH COAST IN RELATION TO HABITAT AVAILABILITY

By

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ABSTRACT

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Characterizing primary drivers of temporal and spatial variability in recruitment is imperative to understanding the role of pre- and post-settlement processes influencing marine population dynamics. On benthic reefs, the quality and quantity of suitable settlement habitat can alter post-settlement density-dependent mortality rates and increase chances of survival. The north coast of California has experienced highly unusual oceanographic conditions in recent years, leading to severe loss of highly productive kelp forests and potentially deleterious ecosystem consequences. In the present thesis, I aimed to determine the effects of canopy-forming bull kelp (*Nereocystis*) and alternative complex habitats on the recruitment of several kelp-associating species of rockfish (genus *Sebastes*), an ecologically and economically important demersal fish on nearshore rocky reefs. Zero-altered mixed models were employed to analyze the presence and abundance of rockfish recruits seen in two datasets of differing spatiotemporal scales. “Coarse-scale” annual surveys were conducted across 430 km of northern California coastline for five years as part of a long-term Marine Protected Area monitoring effort. To better resolve seasonal recruitment patterns, a “fine-scale” study was also designed, which consisted of one year of monthly surveys concentrated over 10 km in Mendocino County. Rates of settlement, habitat availability, and spatiotemporal factors were explored as effects on rockfish recruitment rates. Model results confirm previously-documented high interannual variability in recruitment but also suggest that rockfish young-of-the-year primarily use complex habitats other than bull kelp as shelter during recruitment. The probability of presence of new recruits was strongly associated with timing of settlement and latitude, indicating that large-scale oceanographic effects likely play a role in predicting the distribution of rockfish. Recruit density was positively related to the abundance of understory algae and negatively correlated with low relief and bull kelp density. Although reliance on surface kelp canopy has been documented elsewhere, rockfish recruit habitat preferences had not been previously described in northern California, and understanding the strength of habitat associations during a period of severe kelp decline will help to anticipate how rockfish populations might respond to environmental variation. While this study spanned a time of unusual oceanographic conditions, my results suggest that young-of-the-year may still be able to find suitable refuge in understory algae and high-relief reefs for survival.

ACKNOWLEDGEMENTS

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For my princess potcake.
Thanks for loving the ocean as much as I do.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

INTRODUCTION

Temporal and spatial variability in recruitment rates are major determinants of the distribution, size, and dynamics of marine populations (Hjort 1926, Roughgarden et al. 1988, Doherty & Williams 1988, Caley et al. 1996). Characterizing drivers of recruitment variability has been a primary focus and concern in ecology and fisheries management, as cohort strength and subsequent population biomass is often determined during this critical period (Hjort 1914, Houde 1987, Bailey & Houde 1989, Cushing 1990, Warner et al. 2000). For many demersal marine species with a pelagic larval stage, recruitment success is linked to pre- and post-settlement processes – the relative impacts of which are often scale-dependent and interannually variable (Bradford & Cabana 1997, White & Caselle 2008, Markel et al. 2017).

The early life history (ELH) stages of marine fish and invertebrates experience high natural mortality rates during pre- and post-settlement phases (Bailey & Houde 1989, Almany & Webster 2006). Although definitions vary (Hixon & Webster 2002), for the present study “settlement” is defined as fish exiting the neritic zone and transitioning to benthic habitat and “recruitment” as the appearance of recently settled fish onto a reef (sensu Keough & Downes 1982). Before recruiting into benthic populations, the survival of larvae depends on the environmental conditions in the pelagic zone. Oceanographic variability affects pre-settlement mortality and the abundance of successful settlers by altering prey availability and larval growth, survival, and transport to nearshore habitats (Ainley et al. 1993, Cowen 2002, Caselle et al. 2010a, Ralston et al. 2013). While larval supply is influenced by large-scale oceanographic features, the ultimate success of new recruits is heavily dependent upon post-settlement processes experienced on the reef surface. Ecological dynamics, such as intra- and interspecific competition (Robertson 1996, Almany 2003, Bonin et al. 2009) and predation (Taylor 1984) can drive variability in mortality rates in the benthic habitat (Hixon & Carr 1997, Hobson et al. 2001), modulating recruitment. Habitat availability affects the strength of density-dependence in these dynamics and thus determines the intensity with which post-settlement processes modify recruitment (Sale 1991, Johnson 2006, Beukers & Jones 1997, Hixon & Jones 2005, Haggarty et al. 2017).

The quality and quantity of habitat available to demersal organisms impacts both the abundance of recruits to local populations and the subsequent survivorship of juveniles (Sale et al. 1984, Carr 1994). In both tropical and temperate ecosystems, the extent of optimal habitat is a primary driver of ELH success, from cuing settlement behavior to providing adequate nursery cover (Carr & Syms 2006, Caddy 2007, Grorud-Colvert & Sponaugle 2009). High quality, complex habitat can provide a refuge for juveniles from density-dependent predation (Forrester & Steele 2004, Johnson 2007) and increase prey availability (Allen & Griffiths 1981, Lough et al. 1989), leading to faster growth rates (Calvert 2005) and higher rates of survival (Shima 2001, Wilson 2004). Additionally, the quantity of ideal settlement habitat may be important to juvenile success, as shown by seasonal variability in macroalgae abundances (Horinouchi 2007, Wilson et al. 2017) and artificial reef manipulations (Campbell et al. 2011) affecting the number of new recruits seen on a reef. Active habitat selection may de-couple pre-settlement effects on recruitment, such as climate variability and subsequent larval supply, from post settlement survivorship (Gibson 1994, Pineda et al. 2010). As habitat availability from settlement to ontogenetic migration affects overall population size and structure (Sale 1980, Wellington 1992, Haggarty et al. 2017), hypotheses on recruitment have long considered the importance of habitat on population distributions. Understanding habitat requirements of early life history stages and how benthic habitat availability affects recruitment is thus important for understanding population dynamics and informing effective management.

Rockfish (genus *Sebastes*) are an ecologically important group of marine fishes found in the northeastern Pacific, inhabiting a diversity of rocky habitats from deep seamounts to subtidal reefs to intertidal pools (Love et al. 2002). Many species of rockfish are also economically important and a major target of recreational and commercial fisheries on the northern California coast (Moser et al. 2000). Throughout their life cycle, both deep- and shallow-water dwelling species rely on habitat provided by kelp forest and rocky reefs during settlement, recruitment, and subsequent juvenile growth and survival (Bodkin 1986, Carr 1991, Steele & Anderson 2006). Management efforts of highly targeted species have strived to understand drivers of population dynamics (Butler et al. 2003, Tolimieri & Levin 2005), but much remains unknown regarding population responses to nearshore recruitment and habitat availability. Although recruitment variability and post-settlement mortality linked with habitat availability may cause population bottlenecks (Doherty & Fowler 1994, Doherty et al.

2004, Haggarty et al. 2017), these processes in rockfish populations in northern California’s coastal ecosystems are not well understood.

Rockfish are viviparous and release pelagic larvae during winter and spring parturition. Larvae spend roughly 1-4 months in the open ocean, developing into pelagic juveniles before recruiting to coastal reefs in late spring and summer (Love et al. 2002). Most shallow-dwelling rockfish species exhibit a distinct annual recruitment season (MacGregor 1970), and thus all young-of-the-year (YOY) are considered new recruits in this study. Many rockfish species depend primarily on nearshore kelp forests during recruitment, several of which are grouped into two complexes based on their life histories and similar appearance as recruits. The OYB group, consisting of olive, yellowtail and black rockfish (*Sebastes serranoides, S. flavidus,* and *S. melanops,* respectively), typically recruit directly to benthic rocky substrate in April to September after winter parturition and a relatively long pelagic larval duration (PLD; Miller & Geibel 1973, Willie-Echeverria 1987). In contrast, KGBC recruits, including kelp, gopher, black-and-yellow, and copper rockfish (*S. atrovirens, S. carnatus, S. chrysomelas,* and *S. caurinus,* respectively), settle into the surface canopy of kelp forests following early- to mid-spring parturition and a shorter PLD (Larson 1980, Love et al. 2002).

Most research describing kelp as important recruitment habitat has previously focused on giant kelp (*Macrocystis pyrifera)* (Anderson 1983, Carr 1989), and relatively few studies have investigated the importance of bull kelp (*Nereocystis luetkeana;* herein referred to as *Nereocystis),* which is the dominant canopy-forming species north of San Francisco. Giant kelp is a perennial species with blades running along the entire length of the stipe (Rosenthal et al. 1974). In contrast, bull kelp is an annual species, producing ephemeral forests, and each individual consists of a bare stipe and a surface terminal blade cluster (Springer et al. 2007). Albeit lacking, existing research has found correlations between KGBC recruitment rates and bull kelp abundances (Bodkin 1986; Haldorson & Richards 1987, Calvert 2005). The timing of KGBC parturition and settlement varies latitudinally across their range, potentially coinciding with the annual development of mature bull kelp beds (Matthews 1990). Thus, the dependence of rockfish recruitment on bull kelp merits further investigation in northern California.

Complex rocky reef and understory algae may also be important settlement habitat for KGBC rockfish (Matthews 1990, Anderson 1994). In Puget Sound, West et al. (1994) discovered YOY rockfish selected low-relief habitats on artificial reefs, while Dean (2000) found a stronger association between juvenile rockfish and reef geomorphology than with kelp in Prince William Sound. Furthermore, the understory algae *Agarum fimbriatum* creates complex sub-canopy cover and was utilized by copper rockfish in the Strait of Georgia as bull kelp decreased in abundance (Haldorson & Richards 1987). These studies suggest that, in regions with low surface kelp canopy cover, substratum relief and understory algae may play an important role in the distribution and abundance of new recruits (Matthews 1990, Jones 1992). On the northern coast of California (hereafter referred to as the “north coast”), where bull kelp contributes less to the physical subsurface structure compared to giant kelp (Shaffer 2000), smaller subcanopy-forming “understory” species such as *Pterygophora californicum* and *Laminaria setchelii (*herein referred to as *Pterygophora and Laminara*, respectively*)* may potentially influence successful rockfish recruitment and subsequent survival. However, habitat affinities and substrate preferences of juvenile rockfish remain undescribed for the north coast region of California.

California’s north coast is a harsh environment, often limiting field operations. As such, much of the dynamics of reef fish recruitment and the subsequent impact on populations have gone unstudied. Very little research has investigated north coast rockfish recruitment patterns, and limited studies have focused on the timing of settlement and influences of environmental variability. Jones and Mulligan (2014) described species composition and settlement timing of YOY rockfish in Trinidad Bay, Humboldt County and documented a predominance of black and copper rockfish. Laidig et al. (2007) conducted a more extensive study on recruitment patterns over 20 years in Mendocino County, linking yearly abundances to sea surface anomalies and variability in temperature during the larval stage. Northern California ecosystems have also experienced unusual oceanographic conditions for the last six years. An unprecedented marine heatwave, followed by a simultaneous El Niño event, brought sea surface temperature anomalies of ~3°C during 2014-2016 (Di Lorenzo & Mantua 2016) and caused shifts in species’ geographical distributions, deaths of temperature-sensitive individuals, and a severe loss of bull kelp on the north coast (Leising et al. 2015, Rogers-Bennett & Catton 2019, Sanford et al. 2019). Expanding the breadth of recruitment research on habitat preferences in northern California can help managers to identify coast-wide stock level phenomena and increase understanding of population responses to recent ecosystem changes.

Accordingly, the present study addresses two questions: 1) What are the effects of variation in bull kelp abundance on north coast rockfish recruitment? And; 2) Do sub-canopy algae and rocky relief serve as alternate habitats for recruitment? Insights gained on the importance of habitat on rockfish recruitment could be applied to management strategies and future studies aiming at understanding impacts of ecosystem changes.

METHODS

To investigate how the abundance of bull kelp and the availability of alternate habitats affect rockfish recruitment, I analyzed data from two studies: 1) “Coarse-scale” data - from annual surveys associated with Marine Protected Areas (MPAs) along a 430 km stretch of the north coast, yielding habitat resolution at the level of targeted isobaths, and 2) “Fine-scale” data - from monthly surveys conducted along a geographically narrower range of 10 km of Mendocino County coast, specifically designed to investigate patterns at transect-level resolution across sites with that vary in bull kelp abundance.

Coarse-scale annual MPA surveys

Annual surveys were conducted as part of a MPA monitoring program, the subtidal portion of a state-funded project established to assess the efficacy of MPAs implemented under California’s Marine Life Protection Act (MLPA). Continuing the work of the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) from the past 20 years, the project was expanded into the North Coast Study Region (NCSR) to: 1) establish a baseline characterization of species populations in 2014-15, after the 2012 establishment of the northern California MPAs (OPC 2019), and 2) subsequently monitor in 2017-2019. Biological data were collected via self-contained underwater breathing apparatus (SCUBA) in MPAs and at associated reference sites, with a focus on no-take reserves. The variation in rockfish recruitment and levels of bull kelp and other habitat metrics across sites surveyed allowed me to evaluate the relationships between rockfish recruitment and these habitat variables.

MPA SCUBA surveys were conducted annually by Humboldt State University (HSU) at 10 study sites in northern California, spanning from the Oregon/California border, to southern Mendocino County (Figure 1). To monitor appropriate reef habitat, small research vessels (19 and 22 ft Boston whalers) were used to complete all diving operations. Within each study site, 2-3 fixed replicate “cells” were established, containing contiguous rocky reef from shore to approximately 20 m in depth (Figure 2a). On the north coast, the majority of hard substrate and bull kelp forest habitat is within this depth range. Cells varied in distance from one another (300 m – 3 km), dependent on the expanse of the site’s along-shore reef, and extended offshore up to 1.5 km, dependent upon the distance of the 20 m isobath from the shoreline. Random transects were stratified across fixed depth zones within each cell to capture zonation patterns across the offshore extent of the reef (Figure 2b).

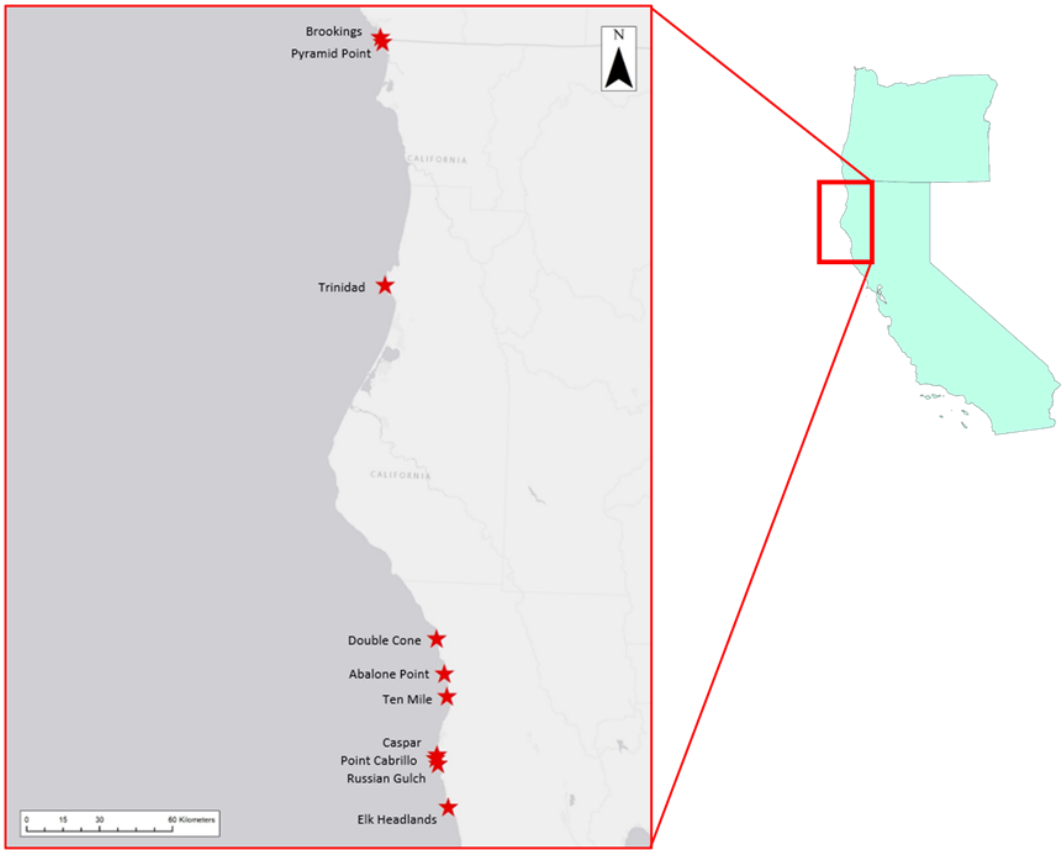

Figure 1. North Coast MPA and reference study sites, stretching along the coast from Brookings, OR, to Elk Headlands, CA.

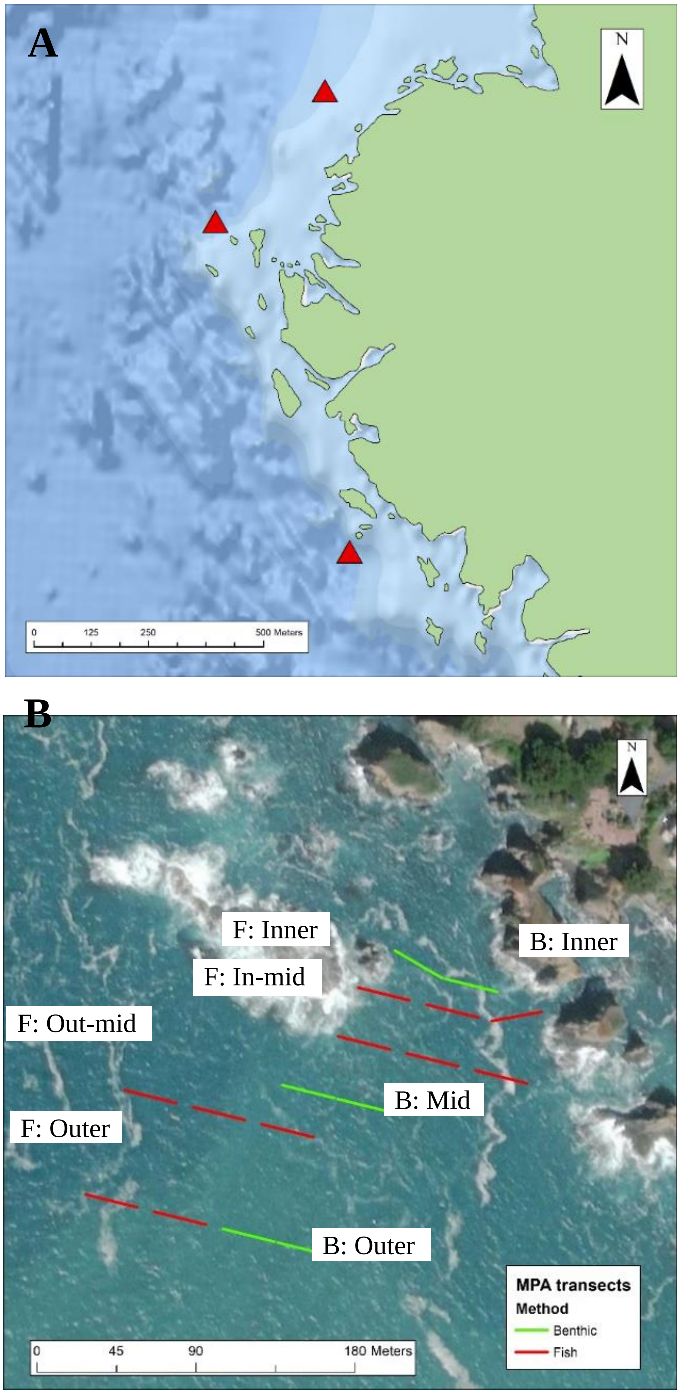

Figure 2. A. Experimental design at Point Cabrillo, showing 2-3 replicate cells across along-shore reef extent. B. Surveys transects at a single Caspar cell, showing fish

transects (“F”) at four depths and benthic (“B;” swath & UPC) transects at three depths following isobaths positioned parallel to shore.

Three types of benthic visual surveys were conducted to estimate the density of rockfish recruits and to characterize the abundance of habitat variables along transects: fish, swath, and uniform point contact (UPC). Following PISCO protocols (http://www.piscoweb.org/kelp-forest-study), the abundance of rockfish recruits was visually recorded along replicated 30 m long x 2 m wide x 2 m tall fish transects. All conspicuous fish species were identified and enumerated, and total length was visually estimated to the nearest 1 cm. For accuracy in counting and sizing, surveys were only conducted when visibility was $\geq$ 3 m. Three fish transects were performed at each of four depth zones – 5, 10, 15, and 20 m (“inner,” “in-mid,” “out-mid,” “outer,” respectively) – totaling twelve per cell (Figure 2b).

Counts of stipitate macroalgae (*Pterygophora* (stipe length > 30 cm), *Laminaria* (> 30 cm), and *Nereocystis* (> 1 m)) were recorded along 30 m long x 2 m wide swath transects. Along the same swath transect, the UPC method was used to quantify substrate and relief directly beneath the tape at every meter along the length of the tape (30 UPC points per transect). Substrate type was recorded as one of four categories based on grain size (sand, cobble, boulder, and bedrock). Vertical relief, measured as the greatest change in reef height within a 1 x 0.5 m box surrounding a UPC point, was also binned into four categories: 0-10 cm, 10 cm-1 m, 1-2 m, and >2 m. Within each cell, two swath/UPC transects were performed at each of three depth zones – 4, 12, and 18 m (“inner,” “mid,” “outer,” respectively) – for a total of six transects per cell.

Fine-scale monthly surveys

Annual surveys do not document temporal variation in larval delivery and juvenile recruitment over the summer settlement season. Therefore, to assess temporal and spatial variability in rockfish recruitment patterns in relation to habitat availability and larval delivery, I conducted monthly surveys in 2019 during peak settlement season (July – September) at selected study sites located between Noyo Harbor and Russian Gulch State Marine Conservation Area (SMCA) in Mendocino County CA (Figure 3a). I chose three sites to conduct fish, swath, and UPC surveys; these sites represented different bull kelp densities spanning the range of current kelp density in the region, designated as high (Russian Gulch), mid (Jefferson), and low (Point Cabrillo) density treatment levels. Within each site, I established two cells which were spaced an average of 600 m apart (similar to the spatial scale of the MPA study) and paired so that each site had a “kelp” and a “no kelp” cell treatment, to assess the effects of bull kelp presence and abundance on rockfish recruitment (Figure 3b). To control for the effects of benthic habitat structure, cells were located using visual assessments of multibeam bathymetric digital elevation models (DEMs) created by the California Seafloor Mapping project (CSMP 2010) and selected to contain similar relief and rocky cover. A “kelp” cell was defined by the presence of inshore kelp beds, determined by previous kelp bed extent documented by California Department of Fish and Wildlife aerial surveys (CDFW 2020) and extensive scouting. Both cells spanned the reef from 4 m to 20 m in depth and extended offshore a maximum of 500 m.

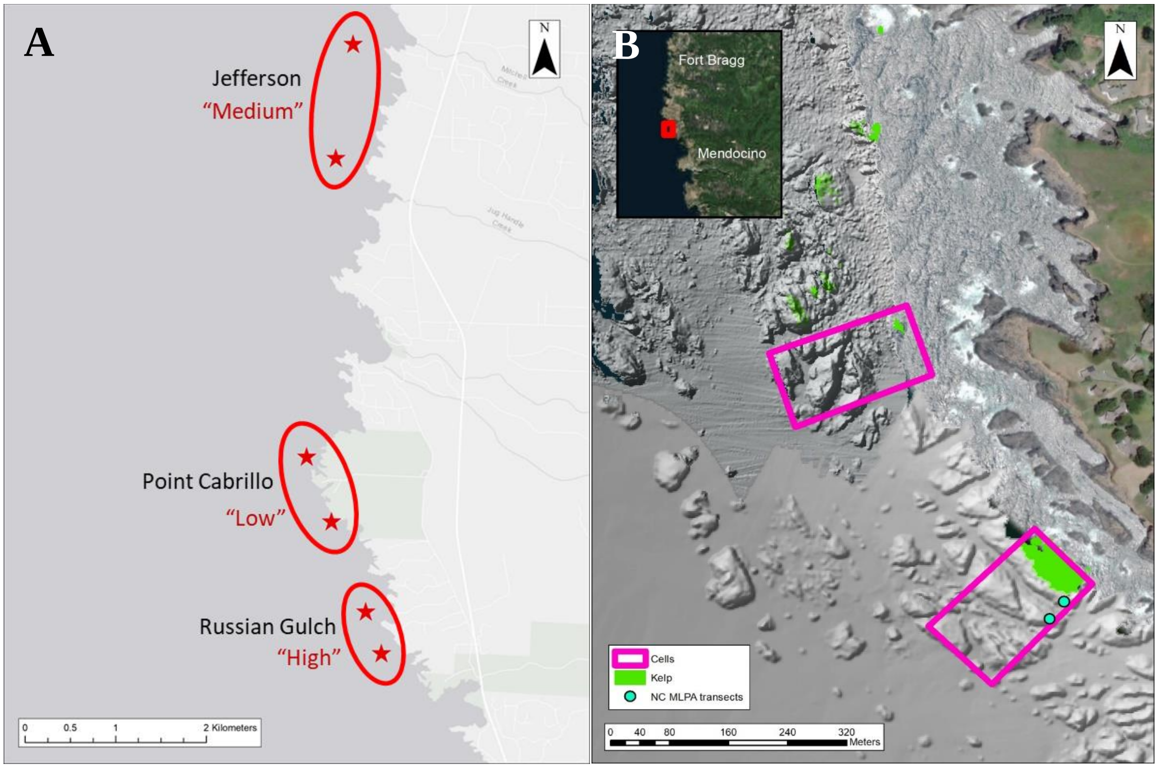

Figure 3. A. Three sites used for fine-scale surveys, representing variation in bull kelp densities. Two cells, denoted by red stars, were established at each site. B. Cell locations at Russian Gulch, determined from aerial kelp survey data (CDFW 2020); each site contained a "kelp" and a "non-kelp" treatment cell.

Within each cell, transects were established similarly to the MPA fish transects, with three transects at each of four depth zones – 5, 10, 15, and 20 m. However, in contrast, swath and UPC surveys were conducted along the same transect as the fish surveys to measure habitat characteristics directly associated with rockfish recruit abundances. Substrate type and vertical relief were measured at every meter using the same metrics as the MPA methods, but because most UPC points were recorded within a single category (10 cm-1 m) in MPA surveys (Jenkinson & Craig 2017), I subdivided the relief categories. Therefore, I defined two new bins for relief as 10-50 cm and 50 cm-1 m. Algae counts were limited to *Nereocystis*, *Pterygophora*, and *Laminaria*, using the same size cutoffs as MPA surveys.

Settlement

To investigate differences in larval delivery along the study region, I installed Standardized Monitoring Units for the Recruitment of Fishes (SMURFs; Ammann 2004) at all three fine-scale study sites. Mimicking the complex structure of a kelp canopy, SMURFs are an established method for estimating the settlement of competent pelagic juveniles in species attracted to kelp habitats (Steele et al. 2002, Caselle et al. 2010b). SMURFs can track larval delivery rates independent of the availability and quality of settlement habitat by serving as a refuge for a small fish and these traps are effective in collecting YOY rockfish along the Pacific coast (Wilson et al. 2008, Haggarty et al. 2017). Following the design of Ammann (2004), I built each SMURF using a 1.2 x 1 m piece of green garden fencing (2.54 cm mesh), wrapped lengthwise to form a hollow frame. Filling this frame, three 1.5 x 1.2 m pieces of black construction fencing were randomly folded and arranged to maximize complexity. A small lead weight (~1 kg) was placed inside one end to assist in vertical positioning in the water column (Figure 4). Two long-line clips, tied to the SMURF with paracord encased in PVC tubing, were used to secure the trap to 19 mm rope. Each SMURF was moored by a 45 kg steel anchor and buoyed by two crab floats. Steel chain attached to the anchor and a subsurface buoy provided additional support against large swell events. Temperature loggers (Onset HOBO pendant #UA-002-64) were installed along each SMURF line, at both the surface and the anchor depth, to document temperature variation and identify coastal fronts and upwelling events.

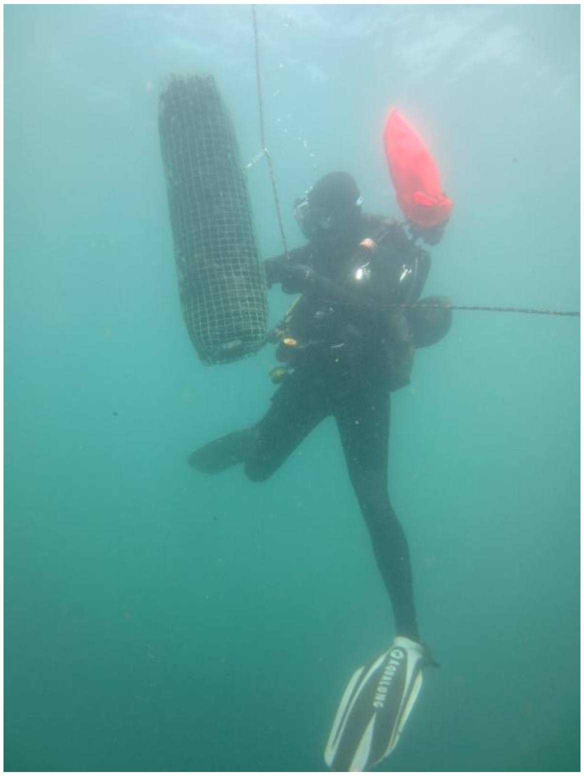

Figure 4. The author installs a SMURF. Traps sat just beneath the surface and were collected by a free diver every two weeks.

One SMURF was installed in each of the six sampled cells. To test for spatial variability among traps within a cell, an additional SMURF was positioned 100 m away within cells at Jefferson and Russian Gulch. SMURFs were placed 50-150 m offshore of bull kelp beds in “kelp” cells and in similar depth and distance-from-shore in “non-kelp” cells following Caselle et al. (2010b). As bull kelp grows in a thin band along the shore, SMURFs were typically deployed 100-300 m offshore and in 15 m of depth. Units were located 3 m below the surface, a position proven to target KGBC recruits (Ammann 2004).

SMURFs were sampled every two weeks – an interval shown to efficiently and adequately resolve recruitment patterns (Steele et al. 2002) - between June and September. Fish were collected using a Benthic Ichthyofauna Net for Coral/Kelp Environments (BINCKE; Anderson & Carr 1998). The BINCKE net was constructed using a folding 1 X 1 m PVC frame and 1.5 mm mesh netting. After unclipping the trap, a free diver wrapped the net around the SMURF and brought it to the surface. There, it was transferred to the support vessel, and the SMURF was shaken and rinsed with fresh seawater. Fish caught in the net were transferred immediately to an aerated seawater container for processing. Individuals caught were identified to species or species group, measured to the nearest mm (total length), and photographed. Fin clips were collected from all rockfish were taken for future genetic analysis. Most fish were returned to their site of collection but several individuals were retained and transported in coolers to HSU’s Telonicher Marine Laboratory for a grow-out study (IACUC permit #1819.M.3-A).

Data management

Fish from diver surveys were pooled into four functional groups for analyses: KGBC, OYB, “predator,” and “other.” Following Johnson (2007), recruits were defined as fish measuring $\leq$ 9 cm in length, and predators were classified from known feeding habits of groundfish species (Lea et al. 1999, Hobson et al. 2001, Beaudreau & Essington 2007). Substrate and relief point counts were calculated by category as a percentage of total points per transect (e.g., number of bedrock UPC points / 30 points total). Algae counts for each transect were converted to densities by dividing counts by the 60 m^2 of substrate surveyed. An “understory” algae category was created by combining densities of functionally-similar *Pterygophora* and *Laminaria* stipes, and used in analysis. As I hypothesized that the abundance of bull kelp within a given cell - rather than a specific depth zone - was contributing to the probability of KGBC presence, bull kelp densities were also averaged across all transects within a cell, to serve as a cell-level variable, “*Nereocystis*_cell.”

Observations for fine-scale surveys were used at transect-level resolution in analysis. However, because fish and swath/UPC benthic transects were not co-located in the coarse-scale study (Figure 2b), data manipulation was required to compare habitat associations with fish abundances. First, all fish counts, environmental features, and habitat features were averaged across transects within each depth zone in each cell, resulting in four depth zone averages for fish transects and three for swath/UPC transects. Second, habitat characteristics (substrate, relief, and algae densities) at each of the four fish depth zones were assumed to be represented by the nearby reef; swath/UPC values were averaged and inferred as outlined in Table 1.

To incorporate the SMURF data into the analysis for fine-scale surveys, counts per collection period were standardized by number of days fished. The standardized counts for the two biweekly collections prior to each SCUBA survey (i.e. spanning approximately one month) were then averaged to calculate a SMURF count per collection for each cell, which was used across all transects during a survey period. Mean surface temperatures from the two weeks prior to each SMURF collection, using a one-day lag (Wilson et al. 2008), were calculated to compare with settlement rates in SMURFs.

Table 1. Pooled coarse-scale swath/UPC transects for calculation of inferred habitat characteristics along fish transects. Swath/UPC transects measured substrate, relief, and algae data, while fish densities and environmental factors were taken from fish transects. Refer to Figure 2b for a layout of survey design.

Swath/UPC depth-zone		**Fish depth-zone**
Inner	➡	Inner
Mean (Inner + Mid)	➡	In-mid
Mean (Mid + Outer)	➡	Out-mid
Outer	➡	Outer

Statistical analyses

Statistical models were developed to predict the number of KGBC recruits surveyed on the reef for each dataset using explanatory habitat metrics (*Nereocystis* density, understory algae density, substrate, and relief), spatial variables (depth, latitude, site, and cell) and temporal factors (day-of-year and year). In the fine-scale study, biweekly settlement into SMURFs was also included as an explanatory variable. As the data contained a large number of zeros, I used zero-inflated models to predict the effects of habitat and spatio-temporal factors on recruitment. Additionally, random effects were incorporated to account for the lack of spatial and temporal independence among observations. Site and cell random effects were intended to capture location-specific effects not otherwise represented by fixed spatial measures, and including year was appropriate due to the highly interannually variable, but spatially-coherent, nature of rockfish recruitment (Field & Ralston 2005, Solinger 2019). Due to the complexity of zero-inflated mixed models I used a Bayesian approach, in which the posterior distributions of model parameters are estimated from prior distributions and likelihoods (Appendix A Equation 1, Zuur & Ieno 2016; see Appendix A for full details).

I compared several zero-inflated Generalized Linear Mixed Models (GLMMs) to estimate the effects of predictors on KGBC recruitment in each dataset, accounting for spatial and temporal nesting via random effects in a hierarchical design. After considering ecological applicability and assessing goodness-of-fit through out-of-sample model validations, I determined that a zero-altered Poisson (ZAP) GLMM adequately reduced overdispersion and outperformed zero-inflated Poisson and zero-altered Negative Binomial models and was thus chosen for the final analysis. Zero-altered Poisson models, used for count data, consist of two components. KGBC recruitment data are first modeled as presence/absence using a binomial model, then non-zero observations are modeled with a zero-truncated Poisson model (Neelon et al. 2010). The ZAP model estimates two main quantities, a probability that the species is present (π) and, if present, the mean abundance of the species (μ). (Appendix A Equation 2).

For both datasets, covariates likely to influence either model component were identified based on prior ecological knowledge and subsequently selected to avoid collinearity. To avoid overparameterization, the maximum number of covariates in each model component was constrained based on the sample size of each dataset. Following Som et al. (2017), to explore inclusion of potential fixed covariates, the Widely Applicable Information Criterion (WAIC; Vehtari et al. 2017) was applied separately to each model component variation to calculate a measure of goodness-of-fit from the average likelihood of the data given the parameter estimates. WAIC scores were compared once Markov Chain Monte Carlo (MCMC) chains showed adequate mixing, which was confirmed visually with trace plots and quantitatively using $\hat{R}$ statistic values (Gelman et al. 2014). Variables were only included if WAIC scores provided strong evidence for its addition (ΔWAIC < 10).

Once the optimal set of variables for the presence and abundance model components were individually identified, I compiled the final model for each dataset. I ran three simultaneous MCMC chains and retained 6000 samples per chain after a burnin period of 200,000 iterations and a thinning rate of 150. Goodness-of-fit was assessed for the final model using a Bayesian *p* value with a chi-squared discrepancy measure (Kery & Schaub 2014). Bayesian *p* values provide a numerical summary quantifying the proportion of times a chosen discrepancy measure for the simulated datasets is greater than the discrepancy measure computed for the actual dataset. Well-fitting models have a Bayesian *p* value near 0.5 whereas values close to 0 or 1 suggest a questionable fit of the model (Gelman et al. 2013). All models were run using the statistical software program R (v3.6.3; R Core Team 2017), utilizing the R2jags package (v0.5-7; Su & Yajima 2015) to call up the Bayesian programming language JAGS ("Just Another Gibbs Sampler;" Plummer 2013).

Finally, importance of covariates in the final models were evaluated based on the posterior distribution of their estimations. Covariates were identified as statistically "important," and therefore subject to interpretation, based on the probability that regression coefficients were non-zero, determined by calculating the lower and upper limits of 95% Bayesian credible intervals using the 0.025 and 0.975 quantiles of posterior distribution values. If the regression parameter's credible interval did not span zero, the covariate was considered an important predictor of KGBC presence (binomial component) or abundance (Poisson component). Covariates with credible interval limits spanning zero were reported as a probability that the covariate influences presence or abundance.

Coarse-scale data analysis

Initial exploration of the coarse-scale data indicated collinearity between metrics of both substrate and relief. Thus, just one of each of these categories was considered in each model component: boulder and 10 cm-1 m. These specific variables were chosen based on previous studies documenting benthic preferences of newly recruited KGBC (Carr 1991, West et al. 1994). Densities of kelp and understory algae, depth, and latitude were also included as linear fixed covariates in the theoretical full ZAP GLMM defined in Table 2 (Appendix B Equation 3). The temporal variable day-of-year was incorporated as a quadratic term, to account for an observed peak in recruitment during the settlement season. Interaction terms between habitat metrics and depth were included because I postulated that the availability of boulders, mid-range relief, or bull kelp would influence any depth effect (and vice versa) on rockfish presence or abundance.

Table 2. Designations and descriptions of covariates considered in the full ZAP GLMM for abundance and presence components in data analyses. All covariates were considered continuous variables, except for *Kelp_treatment* and *Site*, indicated by “*.” Italics random effects. Note: *Site* was used as a fixed effect in fine-scale analysis, but as a random effect in coarse-scale analysis.

Covariate	**Definition**	**Coarse-scale**		**Fine-scale**	
		Abundance	Presence	Abundance	Presence
Boulder	Percentage of UPC points designated as boulder	X		X	

Covariate	**Definition**	**Coarse-scale**		**Fine-scale**	
		Abundance	Presence	Abundance	Presence
Relief 10 cm – 1 m	Percentage of UPC points, 10 cm – 1 m	X			
Relief 50 cm – 1 m	Percentage of UPC points, 50 cm – 1 m			X	
Nereocystis	Density of stipes per m^2 at depth-zone (coarse-scale) or transect (fine-scale)	X		X	
*Nereocystis*_cell	Density of bull kelp in each cell, per m^2		X		X
Understory	Density of *Pterygophora* and *Laminaria* stipes > 30 cm, per m^2	X	X	X	X
Latitude	Latitude of study site, decimal degrees	X	X		
Depth	Depth of fish transects, taken by diver	X	X	X	X
Depth x Boulder	Interaction between depth and percentage of boulder habitat	X			
Depth x Relief 10 cm - 1 m	Interaction between depth and percentage of relief, 10 cm-1 m	X			
Depth X *Nereocystis*_cell	Interaction term between depth of transect and bull kelp density at each cell		X		
SMURF	Number of KGBC found in each SMURF, standardized by collection period			X	X
Kelp_treatment*	Kelp within paired cells at fine-scale sites: “kelp” or “no kelp”			X	X
Day of year^2	Day of year of survey	X	X	X	X
Year	*Year of survey*	*X*	*X*		
Cell	*Replicate cells within sites*	*X*	*X*	*X*	*X*
*Site**	Study site	*X*	*X*	X	X

Cell was confirmed as a spatial random effect for inclusion in the model after finding significant across-cell variance in KGBC counts (ANOVA, $F_{1,24} = 1.75$, $p = 0.018$). Although YOY rockfish are unlikely to be migrating between cells within a site, the random effect of site was also included, for two reasons: 1) No information is available on larval delivery throughout the 2014-2019 study period, and 2) Large scale oceanographic influences that drive environmental and recruitment variability were not evaluated in the present study. Thus, within my nested study design, potential co-varying pre-settlement effects may have occurred across the 400 km study area. Lastly, as strong interannual variability in rockfish recruitment has been previously documented (Field & Ralston 2005), year was incorporated as a random effect.

Because there is no previous knowledge of rockfish recruit habitat associations on the north coast, diffuse normal priors were used for each of the regression parameters in the count (β) and binary (γ) portions of the full coarse-scale model ($\beta \sim N(0, 100)$ & $\gamma \sim N(0, 100)$, respectively). Priors for all random effects were also derived from uninformative normal distributions, following $N(0, \sigma^2)$, while $\sigma \sim Unif(0.1, 10)$. All continuous covariates were standardized for use in JAGS.

Fine-scale data analysis

Fine-scale monthly survey data contained a large number of zero observations with of YOY KGBC. Therefore, a ZAP GLMM was used to capture the high percentage of zeros and to incorporate multiple random effects. Collinearity between metrics of substrate and relief led to the inclusion of just one of each variable in both the count and binary model components. For substrate, boulder was chosen, but for relief, 50 cm – 1 m was used. The theoretical, initial ZAP GLMM with all covariates, including habitat metrics, settlement into SMURFs, and spatial and temporal factors, is shown in Table 2 and Appendix B Equation 4. The random effect of cell was included, as a nested component. However, in contrast to coarse-scale data analysis, site was used as a fixed effect in the full model because there was an insufficient number of site levels (3) to treat it as a random effect.

Diffuse normal priors were used for each of the regression parameters ($\beta \sim N(0, 100)$ & $\gamma \sim N(0, 100)$, respectively) and random effects of cell ($\sim N(0, \sigma^2)$) in both components of the fine-scale data. However, to improve the mixing of MCMC chains during calculations (Zuur & Ieno 2016), the standard deviation parameter σ for each random effect was taken from a half-Cauchy distribution, such that $\sigma \sim$ half-Cauchy(A) for $A = 25$ (Marley & Wand 2010).

RESULTS

Coarse-scale surveys

A total of 295 depth zone-level observations were made from 25 cells in 10 study sites between 2014-2019; no data were collected in 2016. Each site was sampled an average of 3.3 times over the study period. KGBC rockfish recruitment showed strong interannual variation, with peak abundances in 2015 when densities were almost 600x all other years combined when pooled by site (Figure 5).

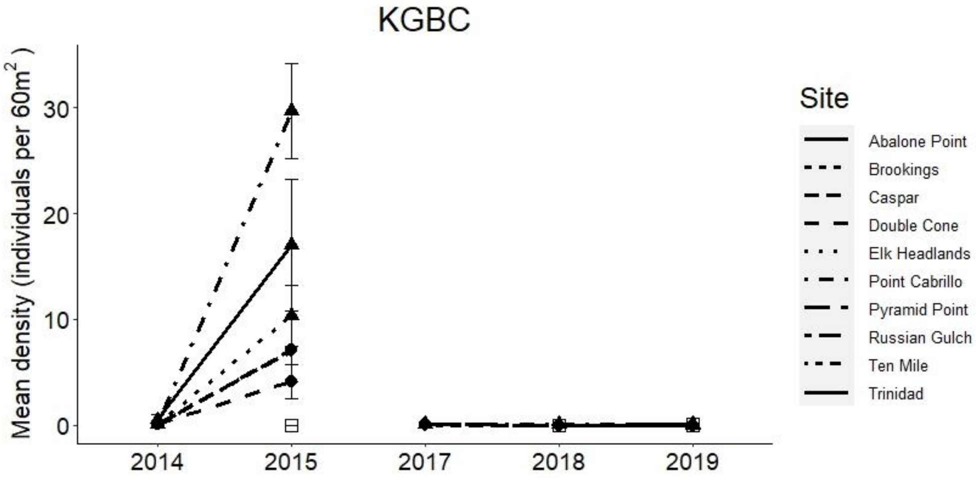

Figure 5. Mean density ± SE of YOY KGBC counted on transects during annual MPA surveys, 2014-2019. No data was collected in 2016.

KGBC recruits were also spatially variable, but not statistically significantly different between all cells or sites (Figure 6). Of the 295 observations, 84% included a zero count of KGBC, justifying the use of the Zero-Altered Poisson Generalized Linear Mixed Model (ZAP GLMM).

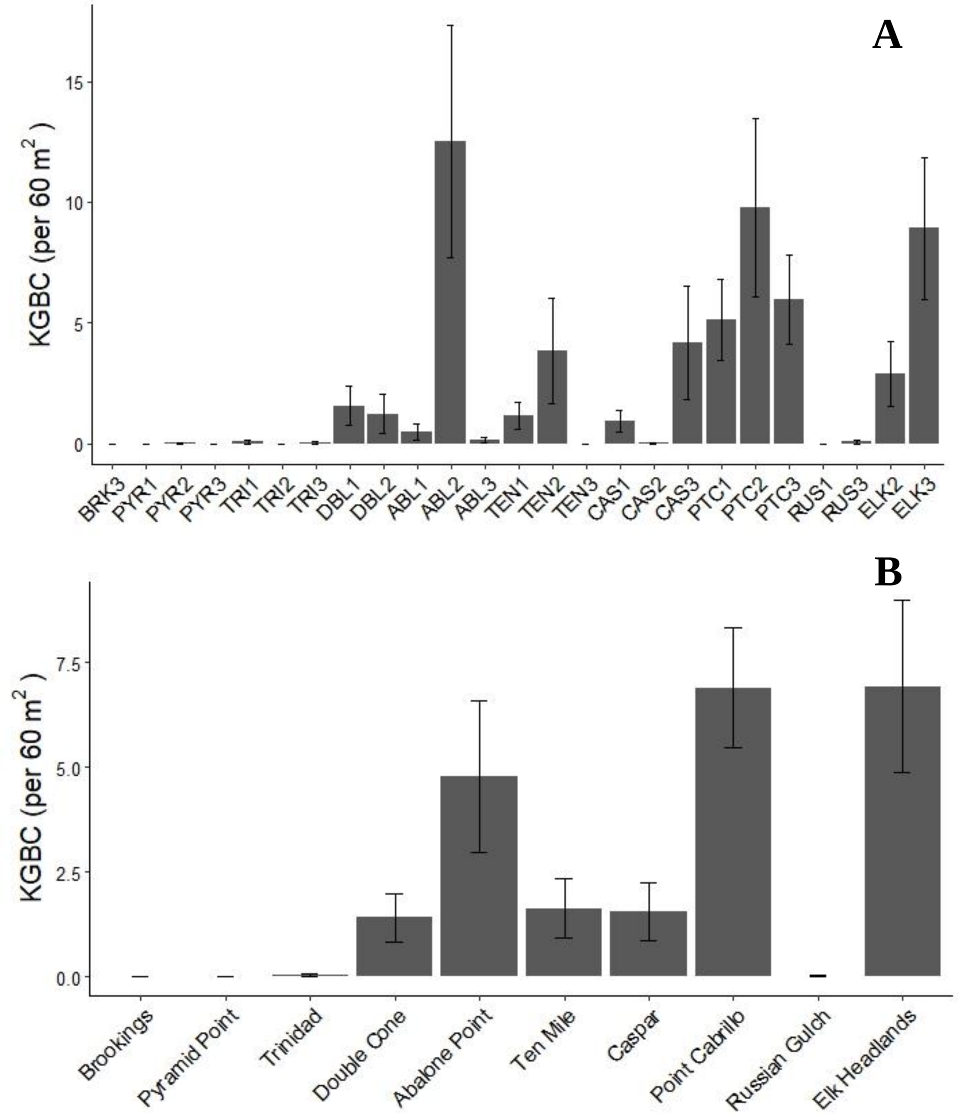

Figure 6. Barplots showing the mean densities ±SE of KGBC by: A. cell (e.g., BRK3 = Brookings cell 3) and B. site, across sampling years combined. Locations are listed from north (left) to south (right).

Coarse-scale modeling

For the final model, $\hat{R}$ values for all parameters were <1.1, indicating that all three MCMC chains had converged to the same posterior space. This mixing was also confirmed by trace plots, which showed no signs of requiring further burn-ins or thinning. The number of fixed covariates was constrained to a maximum of six for each model component, due to the low number of positive observations (N=47). Adhering to these constraints, WAIC selection indicated the best covariate combinations (Table 3). ΔWAIC for the second-best models were equal to 147.6 and 1.8 for the count and presence portions, respectively. Parameter estimates for retained covariates in the final model are shown in Table 4 (and see Appendix B Equation 5). The Bayesian *p* value for the best model was 0.416.

Table 3. Fixed covariates in the top three best models (ranked 1-3) for coarse-scale abundance (“Abun”) and presence (“Pres”) model components. Competing model variations were compared and selected for using ΔWAIC.

	Abun			**Pres**		
Covariate	**1**	**2**	**3**	**1**	**2**	**3**
Boulder	X		X			
Relief, 10 cm – 1 m	X	X	X			
Nereocystis	X	X	X			
*Nereocystis*_cell					X	
Understory	X	X	X			X
Latitude				X	X	X
Depth	X	X				
Depth x Boulder	X					
Depth x Relief, 10 cm - 1 m						
Depth X *Nereocystis*_cell						
Day of year				X	X	X
Day of year^2				X	X	X
ΔWAIC	**0**	**147.6**	**156.8**	**0**	**1.8**	**2.1**

Table 4. Posterior means and 95% lower and upper credible interval limits for the parameters included in the final coarse-scale model. Parameter posterior densities are separated into predictors for the presence (A) and abundance (B) components of the ZAP GLMM.

A

Parameter	**Mean**	**2.5%**	**97.5%**
Presence			
Day of year	18.6	8.61	31.0
Day of year ^{2}	-21.1	-34.2	-10.5
Latitude	-3.66	-7.93	-1.27
σ_{Year}	4.88	0.25	9.74
σ_{Cell}	1.99	0.96	3.64
σ_{Site}	5.00	0.25	9.72

B

Parameter	**Mean**	**2.5%**	**97.5%**
Abundance			
Boulder	0.23	0.07	0.39
Relief 10 cm -1 m	-0.37	-0.61	-0.13
Nereocystis	-3.38	-5.65	-1.08
Understory	0.78	0.26	1.27
Depth	0.29	0.14	0.43
Boulder * Depth	-0.42	-0.49	-0.34
σ_{Year}	5.41	1.60	9.71
σ_{Cell}	1.04	0.63	1.72
σ_{Site}	0.47	0.03	1.63

Posterior distribution estimates indicate that both the presence and abundance of KGBC recruits were associated with temporal factors and habitat features. The probability of observing a KGBC YOY was estimated to be dependent on seasonal timing and latitude: more rockfish settled mid- to late-summer and were more likely to be found at southern sites (Figures 7 & 8a). Bull kelp, understory algae, and depth did not show a strong relationship with KGBC presence to be selected for the best binomial model (Table 4: Presence).

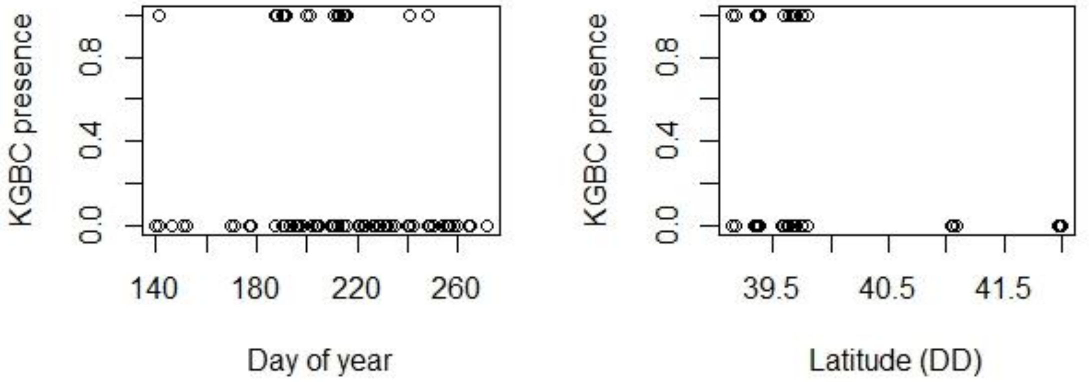

Figure 7. Relationship between KGBC presence and day of year (A) and latitude (B) during coarse-scale annual surveys.

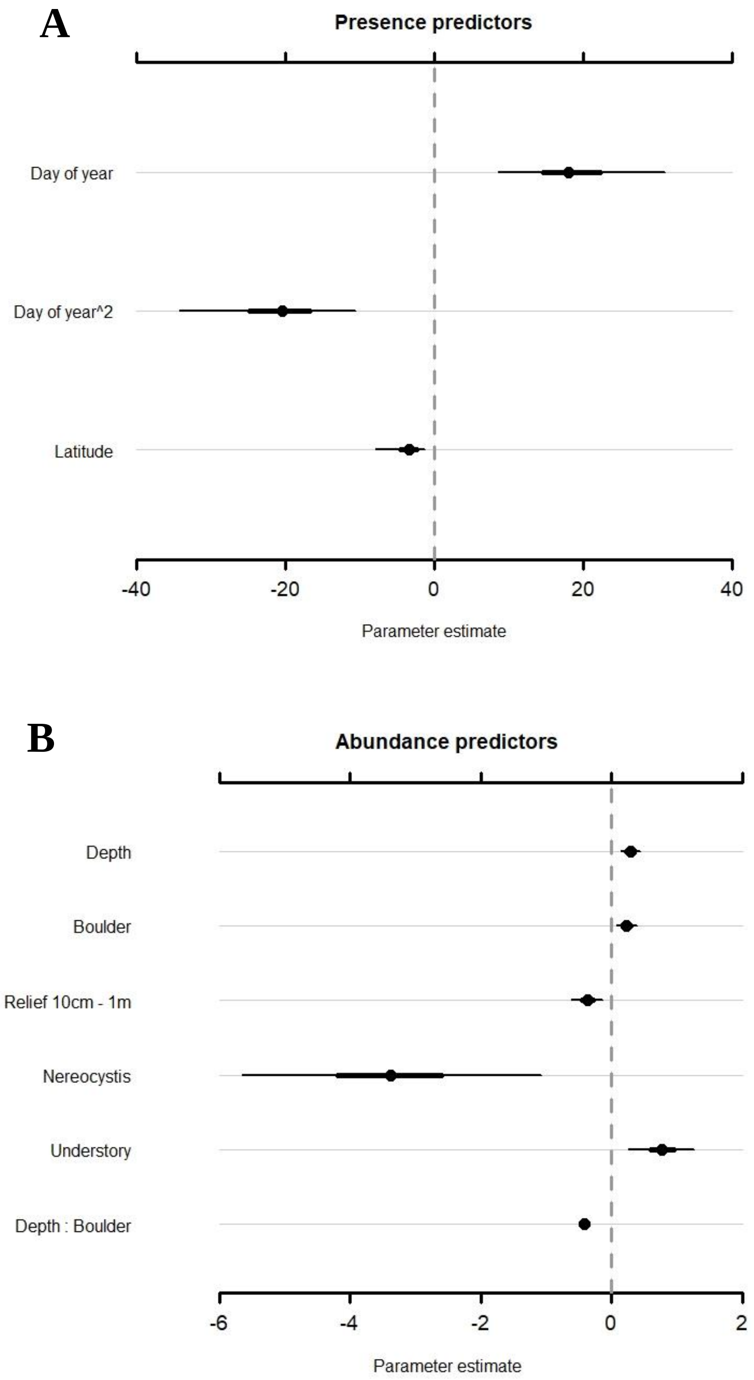

Figure 8. Effects of variables included in the final coarse-scale model on the presence (A) and abundance (B) of KGBC recruits. Points represent posterior medians. Thick lines

represent 50% credible intervals while thin lines represent 95% credible intervals. A posterior distribution spanning directly across the dashed line (“0”) indicated no likely predictive value of the covariate.

When present, KGBC density increased with a higher percentage of boulder habitat and density of understory algae (Figure 8b; Table 4: Abundance). Higher KGBC abundances were also associated with deeper depths. However, the negative interaction term between depth and substrate revealed that the effect of depth on abundance declined with increasing availability of boulder habitat. Interestingly, recruit abundance declined with increases in low-relief habitat and bull kelp (*Nereocystis*) cover, however, there was a limited number of observation with bull kelp densities greater than zero (Figure 9).

The spatial random effects estimates show that KGBC recruit abundances varied across cells, sites, and years. The posterior distributions showed evidence for similar magnitudes of effects on presence by site and year, and the inclusion off all three random variables accounted for variation in both ZAP GLMM components.

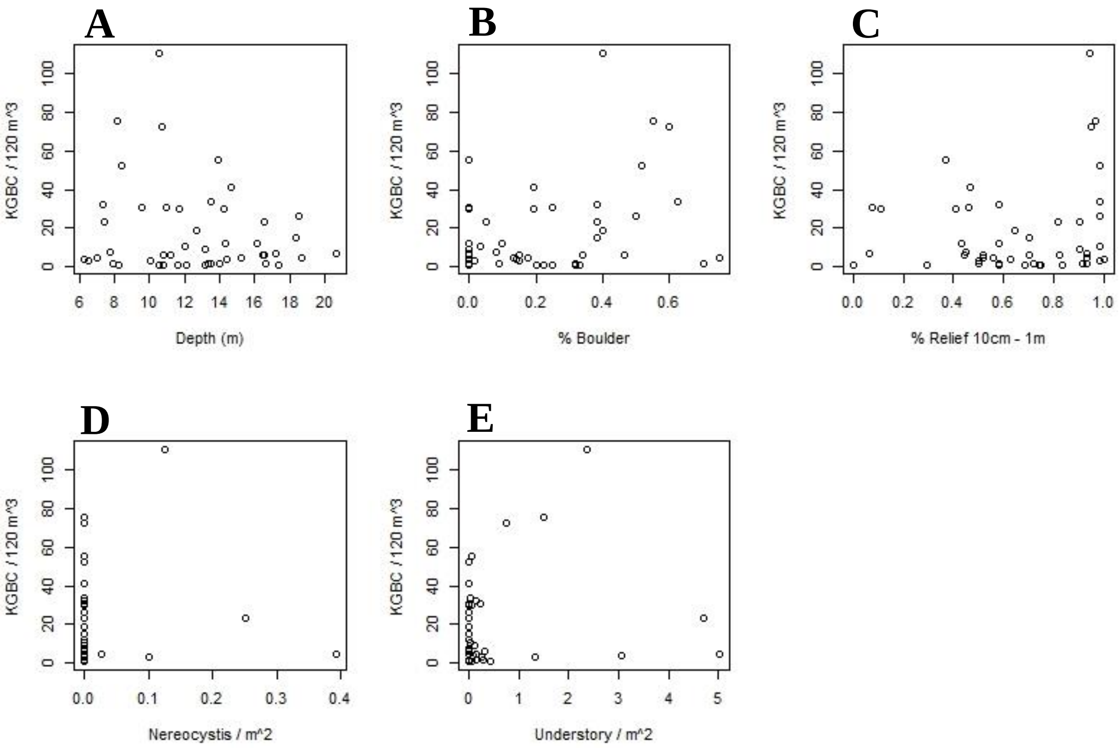

Figure 9. KGBC density from coarse-scale annual surveys plotted against each of five covariates: Depth (A), Boulder (B), Relief (C), *Nereocystis* (D) and Understory (E).

Fine-scale surveys

Due to logistical constraints, monthly surveys were completed in 2019 at all three sites in July and August, but only Point Cabrillo in September. Over the course of the study period, 168 transects were surveyed. Site and cell locations established before mature bull kelp bed formation were consistent with kelp abundances that developed over the summer at all density treatment levels (Table 5). Surveys also contained a high percentage of transects (93%) with zero KGBC.

Table 5. *Nereocystis* densities per 100 m^2 along fine-scale benthic transects at three sites used in the fine-scale study. Densities are represented by mid-summer counts (August) once kelp beds reached maturity, but across-site density patterns remained consistent for the duration of the summer. Although no stipes were seen in the low kelp treatment cell at Point Cabrillo, a small bed formed within 20 m of survey location.

Site	**Kelp treatment**	**No-kelp treatment**
Russian Gulch (high)	17.22	0
Jefferson (mid)	3.89	0
Point Cabrillo (low)	0	0

SMURFs were deployed an average of 16 days between each collection. Replicate traps installed within cells showed a non-significant difference in number of KGBC at both Jefferson (ANOVA; $F_{1,4}$ = 3.2, p = 0.148) and Russian Gulch ($F_{1,5}$ = 1.084, p = 0.322), and counts were subsequently averaged. One replicate SMURF, located in Jefferson, was lost in early September due to a large storm event; counts from the one remaining trap within the cell were used thereafter.

The number and species of fish caught in the SMURFs varied throughout the summer. In early June, cabezon (*Scorpaenichthys marmoratus*) and OYB rockfish dominated collections through early August, with snailfish and clingfish caught in late August to September. KGBC were found in the traps only in mid-September 2019 (Figure 10). Neither the abundances of KGBC nor total fish combined revealed a significant difference in settlement between sites (ANOVA: $F_{2,39}$ = 0.135, p = 0.874; $F_{2,39}$

= 1.081, *p* = 0.349, respectively), and KGBC in SMURFs did not vary significantly between “kelp” and “no-kelp” cells (ANOVA: $F_{1,40}$=2.335, *p* = 0.134).

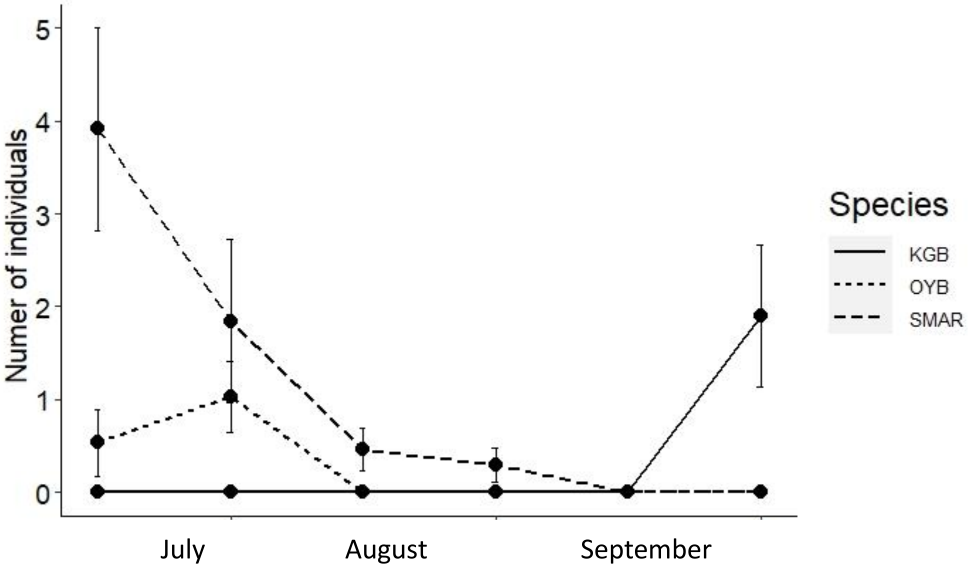

Figure 10. Mean number of individual fishes (± SE) settling into the SMURFs over the 2019 fine-scale study season. Values represent biweekly collection abundances standardized by number of days fished (fish/collection period; see text for more details) for KGBC and OYB rockfish groups, and cabezon (SMAR).

Fine-scale modeling

The final fine-scale ZAP GLMM was evaluated after $\hat{R}$ values for all parameters were <1.1 and visual examination of trace plots confirmed proper mixing. As only 12 transects contained non-zero KGBC counts, the number of fixed covariates was constrained to a maximum of two for each model component. Given these constraints, WAIC selection indicated the best covariate combinations and ΔWAIC values for the second-best models were 0.7 and 1.7 for the count and presence portions, respectively (Table 6). With a Bayesian *p* value of 0.278, the set of covariates in the best fit model are shown in Table 7 (Appendix B Equation 6).

Table 6. Fixed covariates included in the top five fine-scale abundance (“Abun”) and presence (“Pres”) model components, ranked 1-5. Competing model variations were compared using ΔWAIC.

	Abun					**Pres**				
Covariate	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Boulder		X								
Relief 50 cm – 1 m			X							
Nereocystis				X						
*Nereocystis*_cell									X	
Understory					X					
Depth	X									
SMURF	X	X	X	X	X		X			X
Kelp_treatment								X		
Day of year						X	X	X	X	
ΔWAIC	**0**	**0.7**	**8.2**	**18.1**	**18.3**	**0**	**1.7**	**1.7**	**1.9**	**3.5**

Table 7. Posterior means and 95% lower and upper credible interval limits for each of the parameters included in the optimal fine-scale model. Parameter posterior densities are separated into predictors for the presence (A) and abundance (B) components of the ZAP GLMM.

A

Parameter	**Mean**	**2.5%**	**97.5%**
Presence			
Day of year	0.82	0.21	1.50
σ_{Cell}	0.47	0.01	1.68

B

Parameter	**Mean**	**2.5%**	**97.5%**
Abundance			
Depth	2.10	1.07	3.38
KGBC in SMURF	4.70	1.43	10.1
σ_{Cell}	12.8	4.01	29.0

Most of the habitat covariates tested did not remain in any of the top final models explaining KGBC presence or abundance (Table 6). As indicated by the posterior distributions of the regression parameters, presence on the reef was primarily explained by day-of-year that surveys were conducted: the majority of recruits showed up in late summer (Figure 11a; Table 7: Presence). Once present, density of new KGBC recruits showed a positive relationship with both depth and settlement into SMURFs (Figure 11b; Table 7: Abundance), but boulder was also included in the second-best model. Posterior estimates of the random effect of cell indicate high spatial variation in KGBC recruit abundance, although these associations were stronger in the Poisson distribution.

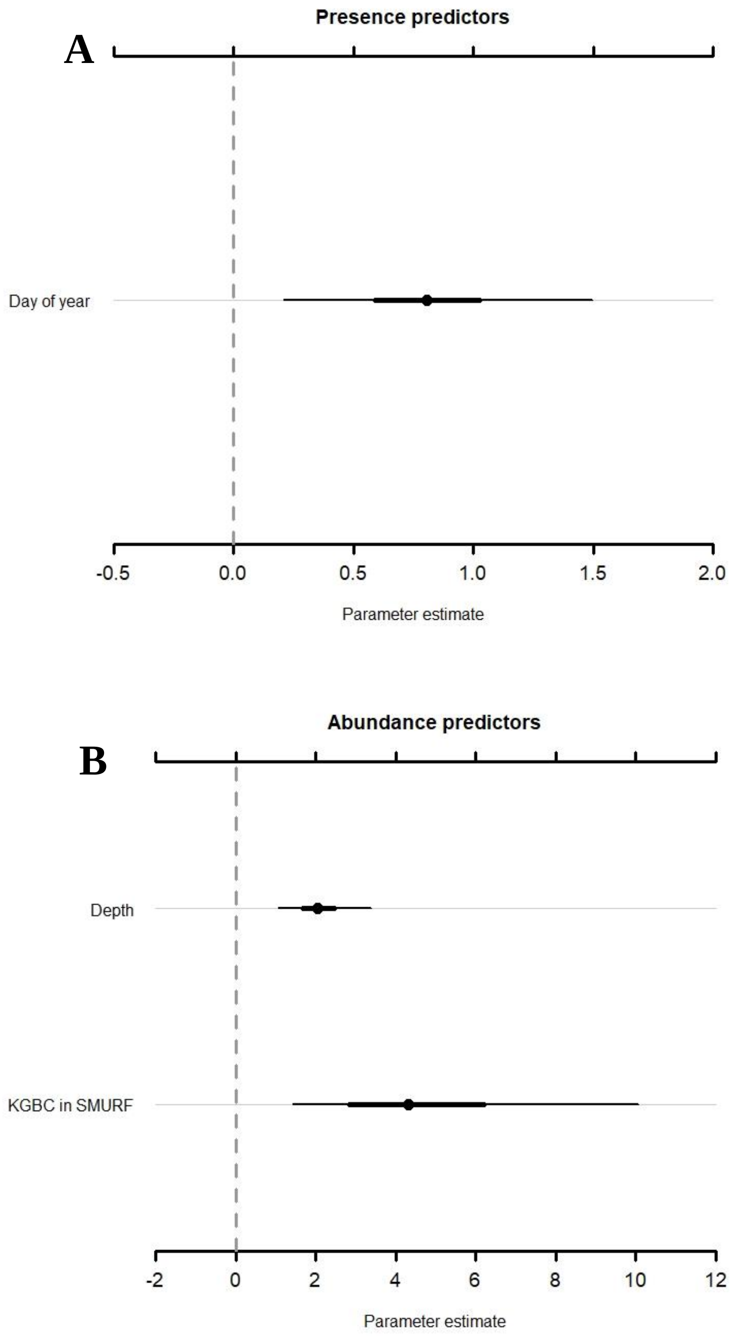

Figure 11. Effects of variables included in the final fine-scale model on the presence (A) and abundance (B) of KGBC recruits. Points represent posterior medians. Thick lines

represent 50% credible intervals while thin lines represent 95% credible intervals. A posterior distribution spanning directly across the dashed line (“0”) would indicate no likely effect of the covariate.

DISCUSSION

In contrast to previous studies of rockfish recruitment patterns documenting habitat preferences, I found that variability in KGBC recruitment showed a stronger relationship with the availability of understory algae and relief than with surface canopy-forming bull kelp. However, the present study was conducted during a period of unusually warm oceanographic conditions and severe kelp loss, resulting from an unprecedented marine heatwave and El Niño event (Di Lorenzo & Mantua 2016). Habitat associations and recruitment patterns described below thus may be unique to the study period and could help to gain insight on population responses to future ecosystem changes.

The high temporal variation in YOY recruitment seen is similar to other research documenting frequency of occurrence. When grouping all *Sebastes* species together, Bodkin (1986) recorded YOY on 26% of transects, while I observed KGBC recruits in 18% and 8% of coarse- and fine-scale datasets, respectively. Annual abundances have also been shown to vary significantly: Laidig et al. (2007) noted annual abundance indices for yellowtail rockfish recruits varied from 162 fish/min to 0.03 fish/min on roving surveys across their 21-year study period, and Markel (2011) recorded a single year pulse in SMURFs of the CQB complex (*Sebastes caurinus, S. maliger, S. auriculatus*) followed by three subsequent years of near-zero recruitment. Although both the probability of presence and KGBC densities seem unusually low in my study, it is not out of the norm for studies of similar scope and is consistent with the high recruitment variability commonly observed in rockfishes.

In contrast to my results, previous studies of rockfish recruitment patterns indicate that bull kelp and low relief substrate are important habitats for the recruitment of YOY rockfishes (Matthews 1990). I found that the abundance of bull kelp did not predict the abundance of new KGBC recruits at either monthly or annual time scales. Rather, my models revealed that observations with greater densities of bull kelp exhibited fewer KGBC recruits on the reef. Abundances in SMURFs were also not significantly correlated with kelp density. These results are in contrast to Haldorson and Richards (1987) and personal observations (Belak, pers. obs,), in which rockfish juveniles were ultilize bull kelp surface canopy as a settlement habitat before migrating to the reef below. At both spatiotemporal scales, bull kelp at the cell level was included in the second-best binomial component modeling presence, indicating that the likelihood of occurrence may depend on inshore kelp; however, these relationships were weak and not statistically important. The negative association between bull kelp and recruitment suggests that, regardless of their association with the kelp canopy, juveniles reaching the bottom may select sheltered benthic habitat away from mature bull kelp stipes.

Unlike the giant kelp *Macrocystis pyrifera*, bull kelp lacks blades along the length of the stipe to the bottom (Abbott & Hollenberg 1976). As a result, the terminating bull kelp blades create an intricate surface canopy, but habitat complexity is reduced throughout the water column. Giant kelp is a perennial species, with individuals surviving on average three to four years (Rosenthal et al. 1974), whereas bull kelp is an annual species, producing ephemeral forests (Springer et al. 2007). Additionally, as this study was conducted during a period of rapid kelp decline (Rogers-Bennett & Catton 2019), my low number of non-zero bull kelp observations suggests that bull kelp was not available for rockfish to associate with. For these reasons, the benthic association of rockfish with bull kelp may be weaker than with giant kelp. Instead, rockfish may experience lower mortality in the persistent shelter and complex subcanopy offered by benthic substrate and understory algae.

Although previous work has linked KGBC recruitment to low relief habitats (West et al. 1994), the present study found a negative correlation between low relief and abundance on rocky habitats. This result, along with personal observations, suggest that recruits instead prefer habitats with higher relief on the north coast. Seasonal and ontogenetic migrations to high-relief microhabitats have been previously documented (Matthews 1990, Carr 1991), but immediately post-settlement it has been hypothesized that YOY prefer low-relief areas with smaller holes that provide refugia from predation (West 1994). In Monterey Bay, Carr (1991) found that during the summer, YOY *S.caurinus* and *S. carnatus* predominately occurred in low rock and sand before shifting to crevices in high-relief habitat after the onset of fall storms. Studies in Puget Sound demonstrated that KGBC recruits preferentially chose low- over high-relief cobble on artificial reefs (West 1994), and Matthews (1990) documented summer use of low-relief habitat. As the present results indicate that recruits exhibit an affinity for high relief during the summer on the north coast, relationships with relief may be geographically specific. Associations may potentially be tied to habitat availability and the frequency of storm events as previous studies were located in relatively protected locations. At exposed, offshore sites in southeastern Alaska, Carlson and Straty (1981) observed high abundances of juvenile rockfish taking shelter in cracks on high-relief rocky pinnacles. In northern California, where the majority of the coastline is exposed to high energy swells, my results indicate that newly-settled rockfish recruits may instead seek refuge in crevices within higher relief reef rather than ephemeral bull kelp canopy and stipes. Indeed, many KGBC were observed in these microhabitats during the present study.

While the presence of KGBC recruits was not strongly related to the understory algae *Pterygophora* and *Laminaria*, densities of these algae were positively associated with strength of annual recruitment. Despite the paucity of research describing understory preference by newly-settled rockfish, understory algae density has been shown to increase abundances of other, more benthic-associated fishes (Siddon et al. 2008). However, this association often occurred in the presence of bull kelp canopy. Danner et al. (1994) found juvenile rockfish congregating on artificial reefs with bull kelp and *Pterygophora* but attributed this trend to the presence of bull kelp, but Carr (1989) also documented differences in species composition of reefs with and without giant kelp, suggesting variable macroalgae preferences by taxa. After investigating seasonal kelp dynamics following storms, Dayton and Tegner (1984) postulated that the stability of understory patches may provide a stable, long-term recruitment habitat. In spite of a lack of prior evidence for rockfish using understory algae, its structural complexity and persistence likely contributes to its use as a nursery habitat (Carr 1994).

In investigating substratum use by juvenile rockfish, prior studies have primarily focused on either relief categories or general substrate types (i.e. rock vs. sand). While these two are inevitably linked, the present thesis aimed to distinguish specific substrate preferences. I found that the density of KGBC recruits on the reef increased with boulder habitat, and Tissot et al. (2007) found a similar positive association between juvenile rockfish and large boulders off Heceta Bank, OR. However, the negative interaction between depth and boulders shows that this relationship weakens with increasing depth; I attributed this to the lack of available boulder habitat in the 15 – 20 m depth zones. Rockfish recruits were found across all depths and are likely using the rocky substrate accessible to them nearby. At shallower depths, as boulders are sized at 10 cm-1 m, higher boulder cover increases the amount of interstitial spaces within a reef, providing increased refuge from predators. In contrast, bedrock habitat (> 1 m) spans a wide range of reef types, from low-lying relief in the shallows (thus often containing fewer crevices for shelter) to steep vertical walls at depth. Rockfish recruits found along these deeper surveys were frequently found utilizing cracks in bedrock.

The lack of strong associations between recruitment and habitat covariates in the fine-scale study may be a consequence of the low number of non-zero observations. A high frequency of zeros required that the abundance analyses be based on a small fraction of the dataset, and I had to restrict the models to avoid over-parameterization. However, while the abundance model component with SMURF settlement and depth yielded the lowest WAIC score, the model including boulder habitat was a close candidate. This suggests that the availability of preferred substrate may play a role in successful recruitment, although a longer study period would be required to make specific conclusions on habitat use. 2019 was a relatively weak recruitment year and all juvenile rockfish seen may have come from a single recruitment pulse.

Results from both datasets suggest strong variability in the presence and density of KGBC recruits over time. The annual five-year study period revealed high interannual variability in KGBC recruitment, exhibiting a peak in 2015, when newly settled juveniles were observed on 64% of transects, compared to an average of 1% across all other years. Although not a focus of the present study, OYB juveniles (*Sebastes serranoides, S. flavidus, S. melanops*) also showed a strong peak in recruitment in 2014 with mostly zeros in all other years. Previous studies have documented high interannual variation in rockfish recruitment across the northeast Pacific (reviewed by Carr & Syms 2006). These fluctuations have largely been linked to broad climatic oscillations (Norton 1987; Ralston & Howard 1995) with recruitment of KGBC increasing during El Niño events (Lenarz et al. 1995, Carr & Syms 2006). The present study period spanned one summer of strong El Niño conditions (2015) and saw a high recruitment pulse during that year. Patterns in interannual variability were ubiquitous across all ten study sites, corroborating prior evidence that coast-wide, rather than site-specific, processes are the primary drivers of recruitment (Field & Ralston 2005, White & Caselle 2008, Solinger 2019).

Throughout all surveys, KGBC presence also exhibited high variability throughout the summer settlement season. Day-of-year was an important variable, with the probability of KGBC occurrence showing either a linear or quadratic relationship with time and indicating that KGBC YOY were more likely to be present mid- to late-summer. The timing of settlement in rockfish is species-dependent and strongly linked with time of parturition and subsequent larval duration (Love et al. 2002). For kelp-associating reef fish, the seasonality of early life history strategies might be partially determined by the timing of kelp growth and formation of mature surface canopies (Carr 1991), potentially evolved as a match-mismatch mechanism allowing greater survival (Cushing 1990). The late settlement of KGBC in SMURFs coinciding with the late maturation of bull kelp in 2019 - adult bull kelp appeared in late-July and the first KGBC pulse was not documented until mid-September (Belak, pers obs) – supports the observations made by Haldorson & Richards (1987) that YOY rockfish use the surface canopy for settlement.

Random spatial effects were also important components in the models. In the monthly dataset, the relative importance of the random effect of cell varied between predicting presence versus density. When considering recruit presence, KGBC recruitment differed among cells, though at a lower level of variation than the fixed effect of day-of-year. In contrast, density of KGBC on the reef exhibited greater variation among cells in comparison with fixed effects. Annual surveys showed that site was more important than cell as a distinct random effect, explaining substantially more variability in the presence model component. These findings suggest that, at coast-wide scales, the probability of the presence of KGBC is greater explained by variability across sites, rather than cells, along the coast, and captured by unresolved variability associated with factors and processes at large spatial scales (100s of km) rather than at local scales (100s of m). Although beyond the scope of this study, Field and Ralston (2005) concluded that physical forcing on even larger scales (1000s of km) may be important in controlling recruitment for winter-spawning rockfish.

Combined sampling with SMURFs and at adjacent reefs provided insight on pre- and post-settlement processes to assess their potential roles in rockfish recruitment. Larval supply, as measured by settlement into the SMURFs, showed a strong association with YOY abundance on the reef, whether adjacent to a kelp forest or not. This suggests that factors (e.g. shelter availability) and processes (e.g. predation) on the seafloor do not substantially modify patterns of larval supply. The positive relationship between settlement and recruitment across a range of kelp densities contrasted previous studies. White and Caselle (2008) showed that both larval delivery rates and kelp abundance influenced recruitment; at low kelp densities, recruitment was close to zero regardless of larval delivery but at higher kelp densities the relationship between recruitment and larval delivery became increasingly positive. However, Steele et al. (2002) found that neither larval supply nor kelp abundances predicted kelp bass recruitment, instead they recorded a correlation between cohorts, suggesting undocumented consistency in recruitment determinants. Cohort strength is likely determined by pelagic prey availability and growth rates during the larval stage (Ralston et al. 2013). As my monthly surveys only spanned one summer, to make conclusions regarding the relative importance of pre- versus post-settlement processes, settlement data across a broader time scale is necessary to assess interannual variation.

The scale at which variability in environmental processes and habitat factors act on recruitment have been previously shown high variation in space and time (Bradford &

Cabana 1997, White & Caselle 2008), and the results from my study suggest similar trends. Although I did not directly investigate the role of spatial scale in recruitment variability, the importance of site and latitude suggests that large-scale climate influences likely drive recruitment across broad geographical scales, corroborating previous studies (Field & Ralston 2005, Solinger 2019). However, fluctuations in relevant spatial scale may vary depending on large-scale climate variability (Edwards 2004) and investigating scale specifically would require data across the large scales of environmental disturbances. In describing rockfish recruitment patterns off Vancouver Island, Markel et al. (2017) found strong interactions among environmental variables and habitat availability, suggesting that temporal variability in the ability of environmental factors to predict spatial distributions of recruits should be considered in models of population connectivity. At the scales investigated in this study, I would have expected to see a greater influence of habitat availability on recruitment success acting on a local scale (100s of m), especially in times of low recruitment (Caley et al. 1996, White & Caselle 2008). However, oceanographic processes driving environmental variability and larval delivery likely played a larger role than habitat at both the local and regional (100s of km) scales, suggesting that at a local scale, suitable habitat was not a constraint on recruitment.

Understanding the strength of habitat associations for newly recruited rockfish will inform fisheries management and help to anticipate how rockfish populations might respond to a changing kelp forest ecosystem. In the past five years, California kelp ecosystems have seen significant declines of nearshore biomass associated with anomalously warm waters coupled with a die-off of local urchin predators. These changes have led to a 90% loss in bull kelp surface canopy in Mendocino and Sonoma counties relative to historical values (Di Lorenzo & Mantua 2016, Harvell et al. 2019, Rogers-Bennett & Catton 2019). Recently, patchy *Nereocystis* beds have been limited to a thin band nearshore (Cavanaugh 2019) following a phase shift from abundant kelp forests to urchin "barrens," areas dominated by urchins and coralline algae (Rogers-Bennett & Catton 2019). With lower structural complexity and primary productivity than kelp forests (Steneck et al. 2002, Graham 2004, Christie et al. 2009), urchin barrens may not be able to support the habitat requirements of organisms like juvenile rockfish. Although the present study was conducted entirely during this unusual time of drastic kelp decline, I found that KGBC YOY were not strongly dependent on bull kelp and may instead be using high relief habitat and understory algae as refuge. My results suggest that at low bull kelp densities through current phase shifts to urchin barrens, some rockfish recruits have still been able to find habitat to survive.

Based on my results I suggest the following changes to enhance future studies. As both datasets and previous studies have documented, rockfish recruitment is highly variable annually and settlement occurs in distinct pulses over the summer. As White and Caselle (2008) conclude, if the bulk of kelp-associated species arrive after annual benthic surveys, severe underestimates of the total number of new recruits occurs. To accurately capture both within- and across-year variability in recruitment, monthly surveys should be repeated over the span of multiple years. Second, increasing the temporal resolution of recruitment data would allow further investigation into the role of large-scale environmental fluctuations. Temperature, sea surface anomalies, and upwelling indices have previously been linked to KGBC recruit abundance (Laidig et al. 2007; Caselle et al. 2010b). While these factors were not evaluated directly in this study, the 2015 KGBC pulse may have partially been a result of a delayed spring upwelling period experienced by larvae, bringing nutrient-rich waters to the surface and leading to increased growth rates and survival (PSEMP Marine Waters Workgroup 2015). These measures of oceanographic regimes affect the likelihood of larval survival (Tolimieri & Levin 2005, Ralston et al. 2013) and gaining insight into the impact of environmental variability on rockfish larval supply and settlement will help to understand the relative roles of pre-and post-settlement processes.

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APPENDIX A

Appendix A. Detailed description of Bayesian methodology and zero-altered models.

Recently, Bayesian statistical methods have been increasing in popularity across the field of ecology. In contrast to frequentist methodology, models combine new observations with previous information to estimate parameters (θ) in accordance with Bayes’ probability theorem.

$$P(\theta \mid data) = \frac{P(data \mid \theta)\ x\ P(\theta)}{P(data)} \qquad (1)$$

where the term $P(\theta \mid data)$ is the posterior distribution of a parameter θ given the data and is the final result of the model. $P(data \mid \theta)$, in turn, is the likelihood of the data given the parameter(s) θ, and $P(\theta)$ is the prior of θ; the knowledge available for θ *a priori*, whether informative or not. Lastly, $P(data)$ is the probability of the data, used as a scaling factor so that the distribution on the left adds up to 1. (Zuur & Ieno 2016). The probability that a parameter has a certain value is calculated from a specific data set, rather than the reversed, classical approach, and is often more intuitive.

The posterior statistical distribution is computed for each parameter using Markov Chain Monte Carlo (MCMC) techniques. MCMC tools fit a model by starting with either informative or diffuse priors, generating random samples through repetitive iterations to calculate the best fit of parameters given the data (Zuur et al 2009). By formally incorporating external knowledge into analyses, Bayesian statistics can greatly increase the precision of the estimates and in fact may be the only estimable method in complicated cases (McCarthy & Masters 2005, Kery 2010).

Ecological datasets involving animal counts often contain a high number of zeros, known as zero-inflation. Standard model distributions are likely to either neglect or heavily weigh the high frequency of zeros, and models based on zero-inflation provide better estimates. Among those modeling count data, Zero-Inflated Poisson (ZIP), Zero-Inflated Negative Binomial (ZINB), and Zero-Altered Poisson (ZAP; also known as “hurdle”) models are most commonly applied (Lambert 1992, Greene 1994, Rose et al 2006). Data is modeled in two components: a count component (μ_{ij}) and a binary zero-inflation component (π_{ij}; Equation 2). I accounted for spatial nesting via random effects and compared several zero-inflated Generalized Linear Mixed Models (GLMMs) to model each dataset in the present study. After assessing fit through initial model validations, a ZAP GLMM accounted for overdispersion and outperformed the other models for both coarse- and fine-scale data. ZAP GLMMs are defined as:

$$log(\mu_{ij}) = x'_{ij}\beta + a_i$$

$$logit(\pi_{ij}) = z'_{ij}\gamma + b_i$$

$$P\left(Y_{ij} = y_{ij} \,\middle|\, \beta, \gamma\right) = \begin{cases} (1 - \pi_{ij}) & y_{ij} = 0\,; \\ \pi_{ij} \text{ x } f_{TruncPoisson}(Y \mid \beta) & y_{ij} = 0 \end{cases} \qquad (2)$$

In the above model, the dependent variable y_{ij} represents the response of the *j*th measurement within the *i*th subject, accounting for nested data. The binary parameter π_{ij} is the probability of a positive observation, while μ_{ij} is the mean of the positive counts as modeled using a Poisson distribution. β and γ are the regression parameters for covariates within each model component, while *a* and *b* are random effects, to account for spatial nesting. The two-part model allows for differing sets of covariate, denoted by *x'* and *z'*.

APPENDIX B

Appendix B. Model equations.

Theoretical full models

A theoretical full coarse-scale model with all covariates considered is defined as follows, for an observation made within the *j*th cell and *i*th site. To avoid overparameterization, the number of fixed covariates included was constrained and evaluated using WAIC. See Table 3 in the main text for definitions of variables (*DOY* = Day of year). Random components *a*, *b*, and *c* correspond to effects of *Site*, *Cell*, and *Year*, respectively.

$$KGBC_{ij} \sim ZAP\left(\mu_{ij}, \pi_{ij}\right)$$

$$E\left(KGBC_{ij}\right) = \pi_{ij} \text{ x } \frac{\mu_{ij}}{1-e^{-\mu_{ij}}} \tag{3}$$

$$\begin{aligned} log\left(\mu_{ij}\right) = {} & \beta_1 + \beta_2 Boulder_{ij} + \beta_3 Depth_{ij} + \beta_4 Relief_{10.1_{ij}} + \beta_5 Boulder_{ij} \\ & * Depth_{ij} + \beta_6 Relief_{10.1_{ij}} * Depth_{ij} + \beta_7 Nereocystis_{ij} \\ & + \beta_8 Understory_{ij} + \beta_9 {DOY_{ij}}^2 + \beta_{10} Latitude_{ij} + a_{1ij} + b_{1j} + c_{1ij} \end{aligned}$$

$$\begin{aligned} logit\left(\pi_{ij}\right) = {} & \gamma_1 + \gamma_2 Nereocystis\_cell_{ij} + \gamma_3 Depth_{ij} + \gamma_4 Nereocystis\_cell_{ij} \\ & * Depth_{ij} + \gamma_5 Understory_{ij} + \gamma_6 DOY_{ij} + \gamma_7 {DOY_{ij}}^2 + a_{2ij} + b_{2j} \\ & + c_{2ij} \end{aligned}$$

$$a_{1ij} \sim N(0, \sigma^2_{1,Site})$$

$$a_{2ij} \sim N(0, \sigma^2_{2,Site})$$

$$b_{1j} \sim N(0, \sigma^2_{1,Cell})$$

$$b_{2j} \sim N(0, \sigma^2_{2,Cell})$$

$$c_{1ij} \sim N(0, \sigma^2_{1,Year})$$

$$c_{2ij} \sim N(0, \sigma^2_{2,Year})$$

A theoretical full fine-scale model with all covariates considered is defined as follows, for an observation made within the *j*th cell and *i*th site. To avoid overparameterization, the number of fixed covariates included was constrained and evaluated using WAIC. See Table 3 in the main text for definitions of variables (*DOY* = Day of year). Random component *a* corresponds with the effect of *Cell*.

$$KGBC_{ij} \sim ZAP(\mu_{ij}, \pi_{ij})$$

$$E(KGBC_{ij}) = \pi_{ij} \text{ x } \frac{\mu_{ij}}{1-e^{-\mu_{ij}}} \tag{4}$$

$$\begin{aligned} log\ (\mu_{ij}) = {} & \beta_1 + \beta_2 Boulder_{ij} + \beta_3 Relief\_50.1_{ij} + \beta_4 Nereocystis_{ij} \\ & + \beta_5 Understory_{ij} + \beta_6 Depth_{ij} + \beta_8 DOY_{ij} + \beta_9 SMURF_{ij} + \beta_{11} Site_{ij} \\ & + a_{1j} \end{aligned}$$

$$\begin{aligned} logit(\pi_{hij}) = {} & \gamma_1 + \gamma_4 Nereocystis\_cell_{ij} + \gamma_5 Understory_{ij} + \gamma_8 DOY_{ij} + \gamma_9 SMURF_{ij} \\ & + \gamma_{10} Site_{ij} + a_{2j} \end{aligned}$$

$$a_{1j} \sim N(0, \sigma^2_{1,Cell})$$

$$a_{2j} \sim N(0, \sigma^2_{2,Cell})$$

Final best models

The final best model for coarse-scale data, selected using WAIC techniques, was defined as follows. See Table in main text for ΔWAIC scores of competing models for each component.

$$KGBC_{ij} \sim ZAP(\mu_{ij}, \pi_{ij})$$

$$E(KGBC_{ij}) = \pi_{ij} \text{ x } \frac{\mu_{ij}}{1-e^{-\mu_{ij}}} \tag{5}$$

$$\begin{aligned} log\,(\mu_{ij}) = {} & \beta_1 + \beta_2 Boulder_{ij} + \beta_3 Depth_{ij} \\ & + \beta_4 Boulder_{ij} * Depth_{ij} + \beta_5 Relief_{10.1_{ij}} + \beta_6 Nereocystis_{ij} \\ & + \beta_7 Understory_{ij} + a_{1ij} + b_{1j} + c_{1ij} \end{aligned}$$

$$logit(\pi_{ij}) = \gamma_1 + \gamma_2 Latitude_{ij} + \gamma_3 DOY_{ij} + \gamma_4 {DOY_{ij}}^2 + a_{2ij} + b_{2j} + c_{2ij}$$

$$a_{1ij} \sim N(0, \sigma^2_{1,Site})$$

$$a_{2ij} \sim N(0, \sigma^2_{2,Site})$$

$$b_{1j} \sim N(0, \sigma^2_{1,Cell})$$

$$b_{2j} \sim N(0, \sigma^2_{2,Cell})$$

$$c_{1ij} \sim N(0, \sigma^2_{1,Year})$$

$$c_{2ij} \sim N(0, \sigma^2_{2,Year})$$

The final best model for fine-scale data, selected using WAIC techniques, was defined as follows. See Table in main text for ΔWAIC scores of competing models for each component.

$$KGBC_{ij} \sim ZAP(\mu_{ij}, \pi_{ij})$$

$$E(KGBC_{ij}) = \pi_{ij} \text{ x } \frac{\mu_{ij}}{1-e^{-\mu_{ij}}} \tag{6}$$

$$log\,(\mu_{ij}) = \beta_1 + \beta_2 Depth_{ij} + \beta_3 SMURF_{ij} + a_{1j}$$

$$logit(\pi_{ij}) = \gamma_1 + \gamma_2 DOY_{ij} + a_{2j}$$

$$a_{1j} \sim N(0, \sigma^2_{1,Cell})$$

$$a_{2j} \sim N(0, \sigma^2_{2,Cell})$$