

Interannual and regional variability in settlement of groundfishes to protected and fished nearshore waters of Oregon, USA

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ABSTRACT: For most benthic marine organisms, settlement of pelagic offspring to bottom-associated habitats is a necessary step in the replenishment of adult populations. Quantifying spatial and temporal variation in settlement is therefore important to fully understand population dynamics, inform fisheries management targets, and design effective spatial management strategies. Data on nearshore patterns of fish settlement are lacking for the northern California Current System (CCS), which is characterized by complex oceanographic currents and a seasonal, intermittent upwelling regime. Thus, to quantify spatial and temporal patterns of fish settlement in the northern CCS in relation to oceanographic conditions, we measured settlement of 5 fish taxa to 2 regions of the Oregon coast over 5 settlement seasons (late spring to early fall, 2012–2016). Temporal patterns of settlement reflected taxon-specific degrees of episodic settlement, with *cabezon* *Scorpaenichthys marmoratus* exhibiting the most uniform settlement across each season, and *splitnose* *Sebastes diploproa* and *redbanded* *S. babcocki* rockfishes exhibiting the most episodic settlement. Fish settlement tended to be greater during short periods of downwelling (upwelling relaxation events) for all but the largest fish taxa. Within settlement season, variation in size-at-settlement tracked taxon-specific temporal patterns of arrival but was unrelated to water temperature. Differences in fish settlement between small marine reserves and nearby unprotected areas was region- and taxon-specific, highlighting the fact that size and habitat heterogeneity should be considered in the design of marine reserves. These findings provide a deeper understanding of settlement patterns across the mosaic of environmental variability in eastern boundary currents such as the CCS.

KEY WORDS: Fish settlement · California Current System · Nearshore habitats · Marine reserves

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INTRODUCTION

Many marine organisms undergo an early pelagic stage before recruiting to benthic populations to complete their lifecycle. In these cases, settlement of late-stage larvae or pelagic juveniles to bottom-associated structures (e.g. reefs, vegetation canopy, intertidal substrates) is a necessary precursor to recruitment to the population (Roughgarden et al. 1988,

Doherty & Fowler 1994). Here we use the term ‘settlement’ to describe when pelagic juveniles are first observed in association with a near-benthic structure and the term ‘recruitment’ to denote the subsequent process of newly settled juveniles entering a benthic population. Examination of the processes involved in the movement or settlement of pelagic stages to the benthos should enhance our understanding of recruitment and population dynamics (King & McFar-

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lane 2003). Such data can also be valuable for applied management of populations. For example, most studies evaluating the effects of marine reserves are based on changes in the abundance of the adult population (Lester et al. 2009). These changes may be the result of reduced adult mortality due to management, but may also arise from changes in the number of new individuals entering the population. Settlement of young is rarely constant among years in the ocean due to high interannual variation in early-life survival and stochastic oceanographic processes that alter the dispersal pathways of offspring (Wilson 2001, Ralston et al. 2013, Shulzitski et al. 2016). For instance, settlement timing of most coral-reef fishes is synchronized with the lunar phase. However, oceanographic features, such as the passage of mesoscale eddies, and biological factors, such as pre-settlement condition of the fishes, superimposes additional noise on this synchrony (D'Alessandro et al. 2007, Rankin & Sponaugle 2014, Shulzitski et al. 2015).

In the California Current System (CCS), an eastern boundary current flowing along the US west coast from British Columbia to Baja California, complex oceanographic processes such as cycles in upwelling strength and seasonal shifts in alongshore currents (Huyer 1983, Lynn & Simpson 1987, Checkley & Barth 2009) exacerbate the challenges of identifying proximate sources of settlement variation (e.g. Shanks & Eckert 2005, Caselle et al. 2010b). Examination of nearshore fish settlement in such complex systems requires high-frequency monitoring programs across multiple years and locations (White & Caselle 2008, Wilson et al. 2008, Shanks 2009, Caselle et al. 2010a, Jones & Mulligan 2014). Such studies have shown that fish settlement to nearshore habitats of the central and southern CCS is highly variable across time and space (10s to 100s of km; Caselle et al. 2010a, Jones & Mulligan 2014, Markel et al. 2017), largely due to changes in upwelling strength, alongshore currents, and oceanographic conditions that affect larval transport and pre-settlement mortality (Petersen et al. 2010, Wheeler et al. 2017). For species like rockfishes *Sebastes* spp., which are viviparous and have a relatively high fecundity, differences in mortality rates during the pelagic stage amplify variability in the number of individuals that survive to settlement (Winemiller & Rose 1992, Love et al. 2002, Ralston et al. 2013). Adults are long-lived and the quality of offspring varies with age: older females release larger clutches of high-condition larvae that are more likely to survive than those from younger females (Sogard et al. 2008).

Variable settlement of offspring to coastal habitats along the CCS is a consequence of interactions between alongshore currents and coastline morphology (e.g. prominent headlands creating retention zones), latitudinal differences in physical parameters that may alter the growth and development of the fish (i.e. water temperature and day length), and variation in upwelling strength or regime (Boehlert 1981, Lenarz et al. 1995, Wing et al. 1998, Shanks & Eckert 2005, Checkley & Barth 2009). In particular, strong alongshore winds south of Cape Mendocino, northern California, USA, are predominantly equatorward (upwelling-favorable), with a relatively weak inversion between Cape Mendocino and Point Conception (southern California) in winter. There is a more drastic inversion of alongshore winds north from Cape Mendocino, with stronger northward (downwelling-favorable) winds in winter and southward winds in summer (Huyer 1983). Here, wind-stress relaxation events reverse the upwelling-driven offshore transport more frequently than in lower latitudes, resulting in 2–6 d cycles of downwelling that have been associated with increased settlement of intertidal organisms (Dudas et al. 2009).

Although recruitment of nearshore fishes to coastal benthic populations has been examined throughout the CCS (West et al. 1994, Carr & Syms 2006, Gallagher & Heppell 2010, Dauble et al. 2012, Markel et al. 2017), settlement has only been systematically monitored and described along the California coast (Wilson et al. 2008, Caselle et al. 2010a, Jones & Mulligan 2014). To examine how patterns of juvenile fish settlement vary along the Oregon coast, we analyzed spatial and temporal variability in fish settlement to nearshore, rocky-reef habitats in 2 regions (separated by >200 km) over 5 annual recruitment seasons (2012–2016). Settlement was examined relative to oceanographic conditions and compared between protected marine reserve sites and non-reserve sites within each region to inform our understanding of settlement within these managed areas.

MATERIALS AND METHODS

Field sampling

Juvenile fishes were collected from 2 nearshore regions of the northern CCS: northern and southern Oregon (233 km apart; Fig. 1). These regions were selected to compare settlement of larvae and pelagic juveniles above and below the biogeographic break at Cape Blanco, and to complement long-term eco-

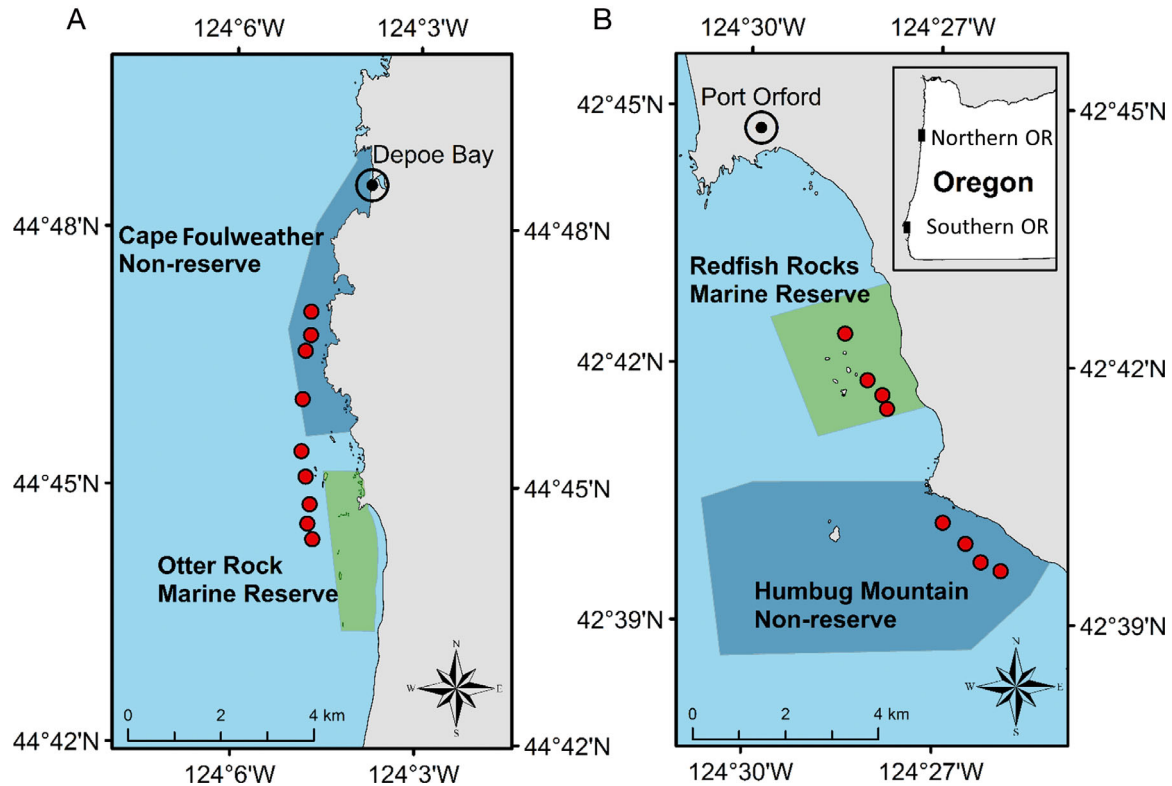


Fig. 1. Sampling locations in 2 nearshore regions: (A) northern (2012–2016) and (B) southern (2014–2016; Oregon (upper right inset), USA). Within each region, newly settled pelagic juveniles were sampled in replicate standardized monitoring units for the recruitment of fishes (SMURFs) grouped at either a marine reserve (green) or an unprotected comparison area (dark blue). For Otter Rock Marine Reserve, SMURFs were located outside of the reserve to align with the 15 m bottom depth. Red points indicate all locations where SMURFs were deployed between 2012 and 2016. In 2012–2013, one SMURF was located between the marine reserve and the non-reserve and was removed from the analysis that compared settlement between reserve and non-reserve

logical monitoring currently underway in Oregon's marine reserves (established between 2012 and 2016). Newly settled juvenile fishes were collected using standardized monitoring units for the recruitment of fishes (SMURFs; Ammann 2004). These collectors consist of black polyvinyl chloride mesh folded inside a long (100 × 35 cm) cylinder of garden fencing, forming a 3-D structure that simulates natural settlement substrates such as a kelp canopy. In each region, up to 8 replicate SMURFs were deployed 1 m below the surface by attaching them to a mooring anchored in sandy substrates at a bottom depth of ~15 m, 390–1200 m from shore. The distance between SMURFs was >300 m, and the deployment locations were selected at a conservative distance offshore of underwater boulders and kelp canopy to ensure direct pelagic settlement of fishes to SMURFs as opposed to movement from other surrounding substrates. To evaluate potential differences in fish arrival to protected and unprotected sites, in each region, half of the SMURFs were deployed at a mar-

ine reserve site and the other half at a nearby (<3 km) non-reserve site selected as a comparison area to the reserve based on similar depths, relief, and habitats. In one location (Otter Rock), the outer limit of the marine reserve is <15 m and has some rocky reefs; thus we had to deploy the moorings outside of the reserve, but in direct proximity to it, in sand patches with no settlement habitats between these and the reserve borders. We note that juveniles that settle to SMURFs have just completed their pelagic stage and arrived to these nearshore habitats. Thus, we assume they have not experienced any effects of the reserve yet (regardless of whether the SMURFs are inside or at the periphery of the reserve). Instead, settlement to SMURFs is a relative measure of new fishes arriving to these habitats. For logistical reasons, the specific position of several SMURFs at the northern Oregon region was modified during the first 2 yr of the study. Similarly, some SMURFs were occasionally lost, especially during the first year, which affected the number of replicates for each site. New fish set-

tlers were collected every 2 wk during the summer settlement season (Love 2011), which started in April–June (weather-dependent) and extended through September of 2012–2016 in northern Oregon and 2014–2016 in southern Oregon. Earlier studies have demonstrated that the presence of fishes in SMURFs coincides with subsequent recruitment of juvenile fishes to the benthic habitat (Ammann 2004, White & Caselle 2008, Markel et al. 2017). These studies showed that most fish taxa experience little to no loss from SMURFs over a 2 wk deployment interval. In light of this finding, and because we did not observe adult rockfishes (potential predators) surrounding our SMURFs, we assume that loss of settlers in our study is comparable to that of previous studies. To retrieve SMURF samples, 2 snorkelers used a butterfly-style net (BINCKE; Anderson & Carr 1998) to enclose each SMURF and bring it to the vessel. Collected fish were euthanized with 2 mM tricaine methanesulfonate (MS-222) buffered in 6 mM sodium peroxide, placed on ice, and transported to the lab for further processing.

Sample processing

Fishes were identified to species and their standard length (SL) measured to the nearest mm with calipers. Species identification was based on meristic characteristics (Anderson 1983, Matarese et al. 1989, Moser 1996); however, meristics are not always sufficient for the conclusive identification of some rockfish juveniles (Caselle et al. 2010a, Woodson et al. 2012, Jones & Mulligan 2014, Markel et al. 2017, E. Anderson & J. C. Garza unpubl. data). We conservatively grouped these species into 3 complexes: OYTB, which included olive *Sebastes serranoides*, yellowtail *S. flavidus*, and black *S. melanops* rockfishes; QGBCC, which included quillback *S. maliger*, gopher *S. carnatus*, black-and-yellow *S. chrysomelas*, copper *S. caurinus*, and china *S. nebulosus* rockfishes; and SR, which included splitnose *S. diploproa* and redbanded *S. babcocki* rockfishes. We used the OYTB and QGBCC complexes to facilitate comparisons with previous research conducted off of California that used similar groupings (KGBC; Wilson et al. 2008, Caselle et al. 2010a), but we note that our QGBCC complex includes china and quillback rockfishes, and omits kelp rockfish *S. atrovirens* to accommodate regional variation in species occurrence. To confirm the presence of species within these complexes, we sent 598 (7.7%) samples of what appeared to be different morphotypes of each com-

plex to be genetically identified at the NOAA Southwest Fisheries Science Center in Santa Cruz, California. A combination of microsatellite (Pearse et al. 2007), mtDNA, and restriction site-associated DNA (RAD) sequencing techniques were employed for this purpose. Aspects of species' life histories are consistent with these morphological groupings. Elsewhere along the CCS, juvenile olive, yellowtail, and black rockfishes settle to similar substrates (kelp mats, eelgrass, boulders, and oil platforms) during overlapping times of the year (mid spring and summer) at sizes that range from 2.5 to 6.3 cm SL (Love et al. 2002, Love 2011). The species grouped in the QGBCC complex typically settle to kelp canopy at smaller sizes (1.5–3.5 cm SL) and arrive to nearshore habitats at overlapping times from spring to fall (with copper rockfish possibly settling earlier in the season than the other species of the complex; Anderson 1983). Larval release by OYTB species generally occurs earlier in winter than for the QGBCC species. Splitnose and redbanded rockfish juveniles display rafting behavior to drifting kelp during their pelagic stage. Although splitnose rockfish has a particularly long (up to 1 yr) pelagic stage and may settle almost year-round, most juveniles settle in late summer in Oregon, overlapping with the settlement time of redbanded rockfish. In fact, throughout the study, no SR settlers appeared before June 15. Given the ecological similarities among the species in these 3 complexes, and limited resources available for genetic identification, we report the settlement patterns of rockfish complexes.

Data analysis

Patterns of fish settlement

To analyze spatial and temporal patterns of juvenile fish settlement, we applied generalized linear mixed effects models (GLMMs; Zuur et al. 2013) with a negative binomial distribution (Table 1). These models included offsets for the number of SMURFs and days per sampling interval to account for a variable number of replicates and length of each sampling interval. The offsets are model variables with a known coefficient (slope) of 1 that adjusts the observed fish count with the effect of the sampling effort (sampling days and number of SMURFs), so observed fish count is evaluated at an effort unit of 1 SMURF and 1 d (Zuur et al. 2013). Therefore, our model outputs can be interpreted as the variation in settlement rate, where settlement rate is the number

Table 1. Models used in analysis of settlement patterns of pelagic juvenile fish along the Oregon coast. N : number of settlers; LS : location of the standardized monitoring unit for the recruitment of fishes (SMURF) within region; $offset(I)$: offset for the variable length of the sampling interval (days); $a_y \sim N(0, \sigma^2_{year})$: random effect of year; $b_d \sim N(0, \sigma^2_{day})$: random within-settlement season effect (day of the year); ϵ : error; β_0 : intercept; β_1 : slope of the subsequent explanatory variable; Y : year; $offset(NS)$: offset for the variable number of SMURFs; R : region (northern vs. southern Oregon); S : site (marine reserve vs. non-reserve area); L : mean standard length of each fish collection (Model M5a) or standard length of each individual fish (Model M5b); $f(D)$: smoother for the within-settlement season (day of the year) variability in fish length

Model	Equation
M1	$N_{iyd} = \beta_0 + \beta_1 \times LS_{iyd} + offset(I_{iyd}) + a_y \sim N(0, \sigma^2_{year}) + b_d \sim N(0, \sigma^2_{day}) + \epsilon_{iyd} \sim N(0, \sigma^2)$
M2	$N_{id} = \beta_0 + \beta_1 \times Y_{id} + offset(I_{id}) + offset(NS_{id}) + b_d \sim N(0, \sigma^2_{day}) + \epsilon_{id} \sim N(0, \sigma^2)$
M3	$N_{iyd} = \beta_0 + \beta_1 \times R_{iyd} + offset(I_{iyd}) + offset(NS_{iyd}) + a_y \sim N(0, \sigma^2_{year}) + b_d \sim N(0, \sigma^2_{day}) + \epsilon_{iyd} \sim N(0, \sigma^2)$
M4	$N_{iyd} = \beta_0 + \beta_1 \times S_{iyd} + offset(I_{iyd}) + offset(NS_{iyd}) + a_y \sim N(0, \sigma^2_{year}) + b_d \sim N(0, \sigma^2_{day}) + \epsilon_{iyd} \sim N(0, \sigma^2)$
M5a,b	$L_i = \beta_0 + \beta_1 \times Y_i + f(D_i) + \epsilon_i \sim N(0, \sigma^2)$

of fish $SMURF^{-1} d^{-1}$. Our analyses focused on 5 taxa that comprised over 98 % of the samples collected in this study: cabezon *Scorpaenichthys marmoratus*, OYTB, QGBCC, SR, and tiger rockfish *Sebastes nigrocinctus*. To reduce zero-inflated data, we narrowed settlement windows for each taxon by excluding months when settlement was very low or absent across all years of the study (see Fig. 2). The data windows included days prior to July 1 for OYTB, after June 1 for QGBCC, and after July 1 for SR and tiger rockfishes. Because cabezon settled throughout all of the sampled months, settlement for this species was analyzed over the entire settlement season (April to September). The timing of each settlement pulse was considered to be the midpoint of each ~15 d deployment period.

To evaluate differences among SMURF locations within region, we applied an initial GLMM with random effects to account for interannual and within-settlement season variation. This model did not include an offset for the number of SMURFs, as it evaluated the individual performance of each sampling location. Fish settlement was not affected by the mooring location within region (northern Oregon: $\chi^2_8 = 10.76$, $p = 0.22$; southern Oregon: $\chi^2_7 = 5.82$, $p = 0.56$), so thereafter we assumed each SMURF was independent from other SMURFs and we analyzed the data using SMURFs within region or sites as replicates. To evaluate annual differences in settlement of each taxon for each region separately, we applied a second GLMM with only 1 random effect to account for within-settlement season variation. To examine regional differences in settlement patterns for each taxon, we applied a third GLMM using data from 2014–2016 that included annual and within-settlement season variation as random effects. For each region separately, we applied a fourth GLMM to evaluate differences in settlement of each taxon

between the marine reserves and their comparison non-reserve areas (sites), accounting for annual and within-settlement season variation by including the same 2 random effects.

Effect of upwelling strength and water temperature on fish settlement

To evaluate upwelling strength at our respective northern and southern Oregon sites, we obtained Bakun index values of daily upwelling at 45° N, 125° W (northern Oregon) and 42° N, 125° W (southern Oregon) from the NOAA Pacific Fisheries Environmental Laboratory. This index represents daily averages of wind-driven cross-shore transports computed from the Fleet Numerical Meteorology and Oceanography Center (www.usno.navy.mil/FNMOC). Positive values indicate offshore transport in units of $m^3 s^{-1}$ along each 100 m of coastline.

In situ water temperature at ~3 m depth was recorded at each SMURF mooring from 2014–2016 with HOBO® Water Temp Pro v2 and Odyssey® Conductivity & Temperature Logger sensors. Temperature was recorded hourly and averaged to obtain the mean daily average for each region. We examined the relationship between water temperature and Bakun index of upwelling by calculating a Pearson correlation coefficient. We then calculated the mean settlement rate (no. of fish $SMURF^{-1} d^{-1}$) for each region separately, and examined the relationship between settlement rate of each taxon and mean Bakun index and mean water temperature (separately) over each sampling interval. Water temperature values lagged Bakun index values by 1 d (see ‘Results’) so the data were offset to account for this lag. Correlations were calculated separately for 2014–2016, and for the 3 years combined.

Relationship between fish size and water temperature

To evaluate temporal differences in the size at which each taxon settled to the SMURFs, we applied 2 generalized additive models (GAM; Zuur 2012) with a normal distribution that included a discrete variable for year and a smoothing parameter for within-settlement season variation in fish length (Table 1, Models M5a,b). The interannual variation in size-at-settlement was analyzed for each study region separately, using the average length of each fish collection to avoid data redundancy. To analyze within-settlement season variation, we combined the data from both regions and used individual fish measurements as data points. Because growth of poikilotherms is typically related to temperature, we examined the relationship between region-specific SL of settlers and regional water temperature. We obtained daily offshore sea surface temperature (SST) data for 2012–2016 from the NOAA National Data Buoy Center at Stns #46050 and #46015, located 35 and 20 km offshore of our northern and southern Oregon sites. For each region, we regressed the mean SL of the fish collected in each sampling event against the mean water temperature during the previous 90 d, which is the shortest pelagic larval duration of our analyzed taxa.

All analyses were conducted in R v3.2.1 (R Core Team 2015) using packages 'plyr' v1.8.3 (Wickham 2011), 'lme4' v1.1-10 (Bates et al. 2015), 'mgcv' v1.8-6 (Wood 2001), and 'zoo' v1.7-13 (Zeileis & Grothendieck 2005). Figures were created using ARCGIS v10.2 (Esri 2014) and R package 'ggplot2' v2.0.0 (Wickham 2009).

RESULTS

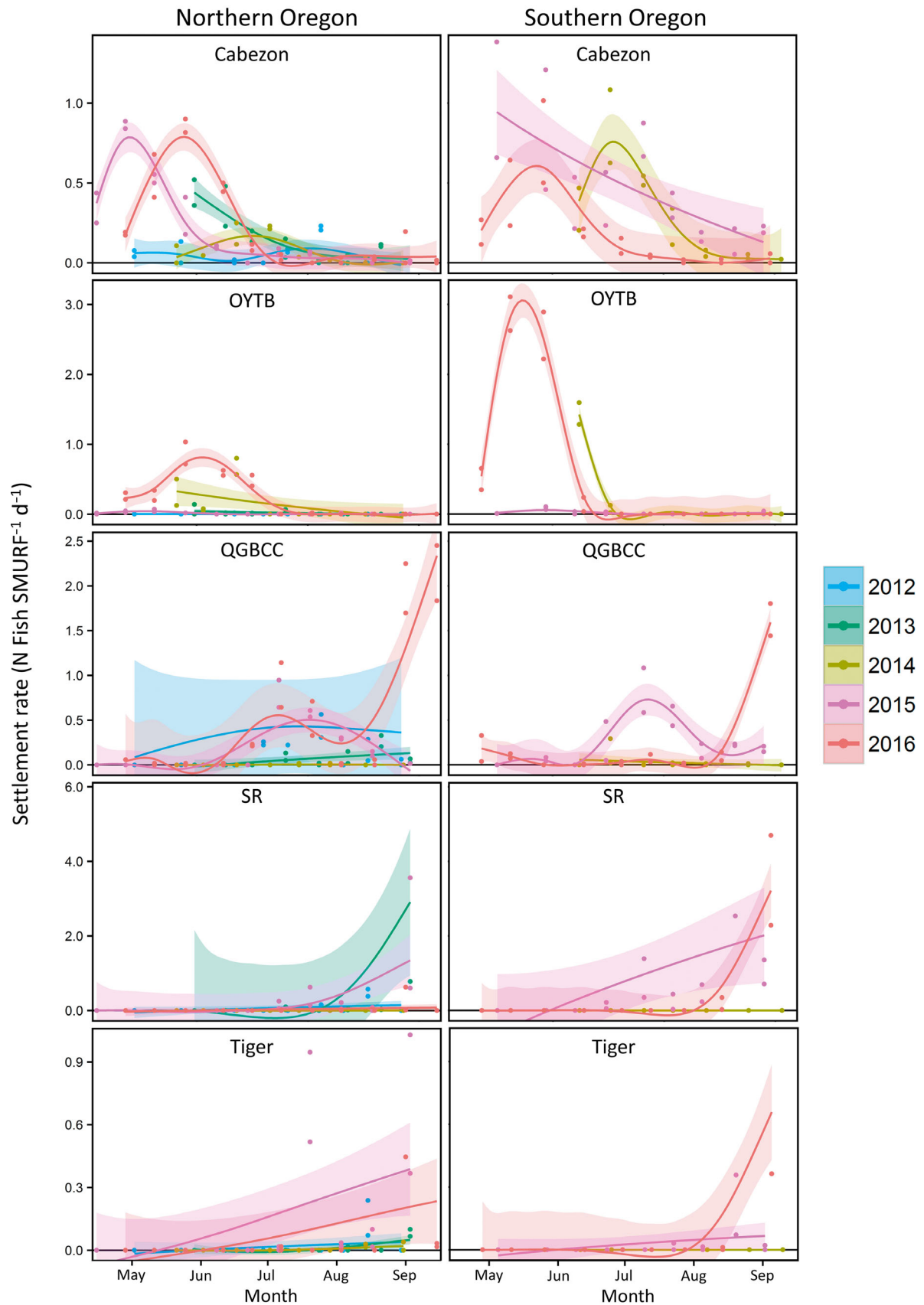
Patterns of fish settlement

In total, 7768 fishes (Table S1 in the Supplement at www.int-res.com/articles/suppl/m598p131_supp.pdf) were collected over the 5 yr of the study. Within complexes, different species had different

overlapping morphological traits, and specimens that we initially grouped into similar morphotypes were not consistently identified as the same species using genetics. Genetic results confirmed the presence of all species within the SR and QGBCC complexes in both our sampling regions. We genetically identified 3 gopher and 1 black-and-yellow rockfishes in northern Oregon (these species had never been reported north of Cape Blanco; Love 2011), and 4 gopher and 2 black-and-yellow rockfishes in southern Oregon. However, we do not know exactly how many of these were collected throughout our study series, as due to funding constraints, only a subset of the samples was genetically identified. There is a lack of published information on the early life history and settlement of china and quillback rockfishes (Love 2011, but see Markel et al. 2017), which makes these collections particularly novel. For the OYTB complex, genetic results confirmed the presence of only yellowtail and black rockfishes. However, the presence of olive rockfish in our samples cannot be discounted because adults are reported off southern Oregon. The 5 focal fish taxa exhibited different settlement patterns across the settlement season (Fig. 2). Cabezon settled throughout the season, but peaked between late April and late June. The highest settlement of OYTB occurred between May and early June, with very low numbers settling afterwards. Settlement of QGBCC peaked between June and August for most years, but there were additional early and late-season settlement pulses in 2016. In years where SR and tiger rockfish were abundant, these species tended to settle later in the settlement season, starting in July and increasing towards September, possibly peaking beyond our sampling season.

With the exception of cabezon, settlement of most sampled taxa was highly variable across years (GLMM, $p < 0.05$), with annual means ranging from 0 to 1.5 fish SMURF⁻¹ d⁻¹ in some taxa (Fig. 3). Settlement rates did not differ significantly between the 2 regions for OYTB, QGBCC, and SR (GLMM, $p > 0.05$). However, cabezon had a significantly higher settlement rate in southern Oregon than in northern

Fig. 2. Settlement of 5 fish taxa to northern (left panels; 2012–2016) and southern Oregon (right panels; 2014–2016) nearshore habitats during the settlement season (spring and summer). Settlement rate was averaged over all replicate SMURFs within each site (2 sites per region). Shading indicates 95% CI. Note different scales for y-axes. From top to bottom: cabezon *Scorpaenichthys marmoratus*; species complex OYTB (olive *Sebastes serranoides*, yellowtail *S. flavidus*, and black *S. melanops* rockfishes); species complex QGBCC (quillback *Sebastes maliger*, gopher *S. carnatus*, black-and-yellow *S. chrysomelas*, copper *S. caurinus*, and china *S. nebulosus* rockfishes); species complex SR (splitnose *Sebastes diploproa* and redbanded *S. babcocki* rockfishes); and tiger rockfish *Sebastes nigrocinctus*



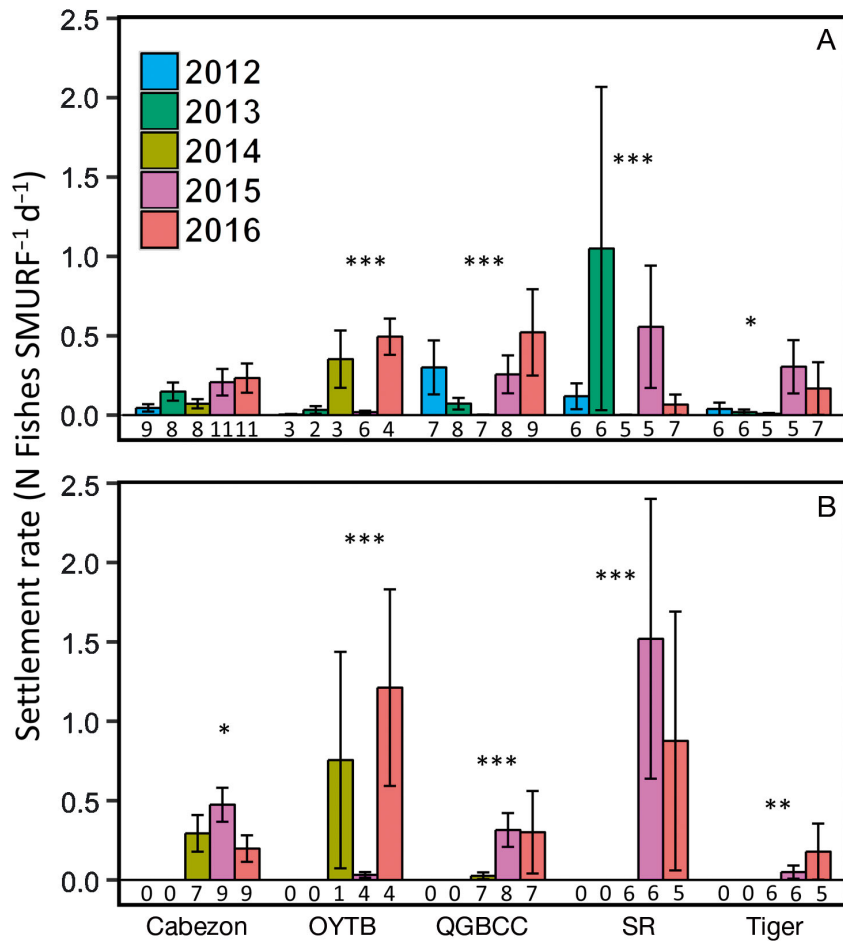


Fig. 3. Annual settlement of 5 fish taxa to (A) northern (2012–2016) and (B) southern (2014–2016) Oregon. Settlement rate was averaged over all replicate SMURFs within each region per year. Error bars indicate standard error. Number of sampling collections shown under bars. See Fig. 2 for definitions of species complexes. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Oregon, while tiger rockfish had the opposite pattern (Fig. S1 in the Supplement; GLMM, $p < 0.05$). Within each region, OYTB exhibited greater settlement to marine reserves than to unprotected comparison areas (Fig. 4; GLMM, $p < 0.05$). Cabezon exhibited the opposite trend, but only in southern Oregon, with greater settlement to the unprotected area than to the marine reserve. Settlement of the remaining taxa did not differ significantly between reserves and non-reserve areas (GLMM, $p > 0.05$).

Effect of upwelling strength and water temperature on fish settlement

Daily upwelling strength was negatively correlated with *in situ* water temperature in both regions (Fig. S2 in the Supplement; Pearson coefficient of

correlation: northern Oregon: $r = -0.53$, $p < 0.001$, southern Oregon: $r = -0.55$, $p < 0.001$). These correlations were stronger when upwelling strength was compared to water temperature the following day (northern Oregon: $r = -0.67$, $p < 0.001$, southern Oregon: $r = -0.66$, $p < 0.001$), indicating that there was a 1 d lag between changes in upwelling strength and changes in nearshore water temperatures. Because the 15 d sampling intervals could encompass multiple cycles of upwelling–relaxation, there were very few significant correlations between fish settlement and these environmental parameters (Table 2; Fig. S3 in the Supplement). Despite the lack of statistical significance, it is worth noting that these correlations tended to be negative with upwelling strength and positive with water temperature, with the only exception being OYTB in southern Oregon.

Relationship between fish size and water temperature

Interannual differences in mean SL were significant (GAM, $p < 0.05$) for cabezon and tiger rockfish in northern Oregon, and for QGBCC in southern Oregon (Fig. S4 in the Supplement). The mean length of the

settlers varied significantly over the season for all species (GAM, $p < 0.01$), but each taxon exhibited different trends (Fig. 5). For cabezon, the largest individuals tended to settle in June, while later settlers tended to be smaller. Excluding some outliers (QGBCC settling before June and OYTB settling after mid-July), the average length of settling OYTB and QGBCC increased by 0.11 mm d^{-1} and 0.09 mm d^{-1} , respectively, as the season progressed. QGBCC size at settlement prior to June follows a similar growing trend. The size distribution of SR exhibited a sinusoidal pattern over the settlement season, while tiger rockfish did not exhibit a distinct pattern. Average monthly temperatures were generally higher off northern Oregon than off southern Oregon, likely driven by stronger upwelling in southern Oregon advecting colder water to the surface (Fig. S5 in the Supplement; Huyer 1983). How-

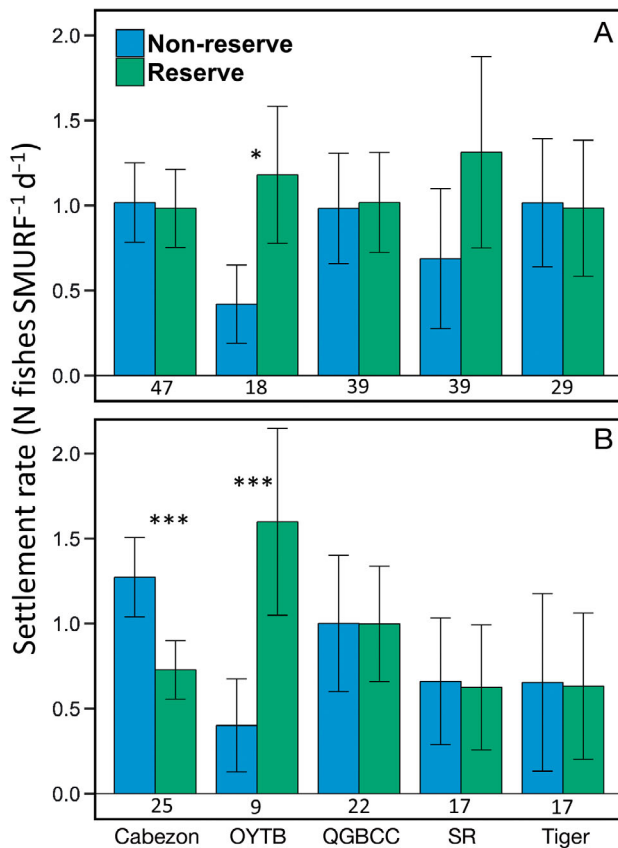


Fig. 4. Settlement rate of OYTB was greater in marine reserves of both regions (A, northern; B, southern Oregon), while settlement of cabezon *Scorpaenichthys marmoratus* was greater in the non-reserve (blue) of southern Oregon. Only data from 2014–2016 were available for southern Oregon. Settlement rate was averaged over all replicate SMURFs within site and normalized by annual mean settlement from each region to account for the year random effect. Error bars indicate standard error. Number of sampling collections shown under bars. See Fig. 2 for definitions of species complexes. * $p < 0.05$, *** $p < 0.001$

DISCUSSION

Patterns of fish settlement

Settlement of juvenile rockfishes along the Oregon coast was highly variable over the 5 yr of the study. This interannual variability is consistent with previous studies conducted along the CCS that evaluated annual reproductive success at different life stages, including the abundance of pelagic juveniles (Ralston et al. 2013, Sakuma et al. 2013), settlement of competent juveniles to nearshore habitats (Wilson et al. 2008, Caselle et al. 2010a,b, Jones & Mulligan 2014), density of post-settlement recruits (White & Caselle 2008, Gallagher & Heppell 2010, Dauble et al. 2012, Markel et al. 2017, Wheeler et al. 2017), and year-class fluctuations of the adult populations (Bradburn et al. 2011). Such variability is typically associated with interannual and regional differences in production and survival of larvae and pelagic juveniles, resulting from shifts in primary productivity, SST, alongshore currents, and persistence of ocean fronts (Bjorkstedt et al. 2002, Woodson et al. 2012,

ever, there was no significant relationship between the 90 d averaged water temperature and the mean SL of the settlers, regardless of the region (Pearson coefficient of correlation, $p > 0.05$ for all taxa; Fig. S6 in the Supplement).

Table 2. Pearson correlation coefficients between settlement rate (no. of fish SMURF⁻¹ d⁻¹) and mean Bakun index of upwelling (BI), *in situ* mean water temperature (T, °C). BI source: NOAA Pacific Fisheries Environmental Laboratory, for 45° N, 125° W (northern Oregon) and 42° N, 125° W (southern Oregon). Environmental parameters were averaged for each sampling interval, with a 1 d lag for water temperature. See Fig. 2 for definitions of species complexes **Bold**: significant values (* $p < 0.05$, ** $p < 0.01$). na: not applicable

Region	Cabezon		OYTB		QGBCC		SR		Tiger	
Year	BI	T (°C)	BI	T (°C)	BI	T (°C)	BI	T (°C)	BI	T (°C)
Northern Oregon										
2014	0.52	0.11	-0.45	0.15	0.42	-0.47	-0.43	-0.04	-0.42	-0.21
2015	-0.69	0.36	-0.60	0.09	-0.05	0.25	-0.98**	0.36	-0.65	0.82 ^a
2016	0.30	-0.19	0.13	0.02	-0.64 ^a	0.47	-0.56	0.50	-0.56	0.50
2014–2016	-0.09	0.09	-0.04	0.27	-0.15	0.34	-0.39*	0.44 ^a	-0.31	0.65*
Southern Oregon										
2014	-0.98	0.73	na	na	-0.35	-0.09	na	na	na	na
2015	-0.50	0.05	0.19	-0.19	-0.32	0.27	0.23	0.22	0.34	0.05
2016	-0.04	-0.21	-0.04	0.21	-0.52	0.86**	-0.71	0.96*	-0.70	0.95*
2014–2016	-0.27	0.05	0.05	-0.24	-0.36	0.37 ^a	-0.27	0.44 ^a	-0.23	0.22

^a $p < 0.1$

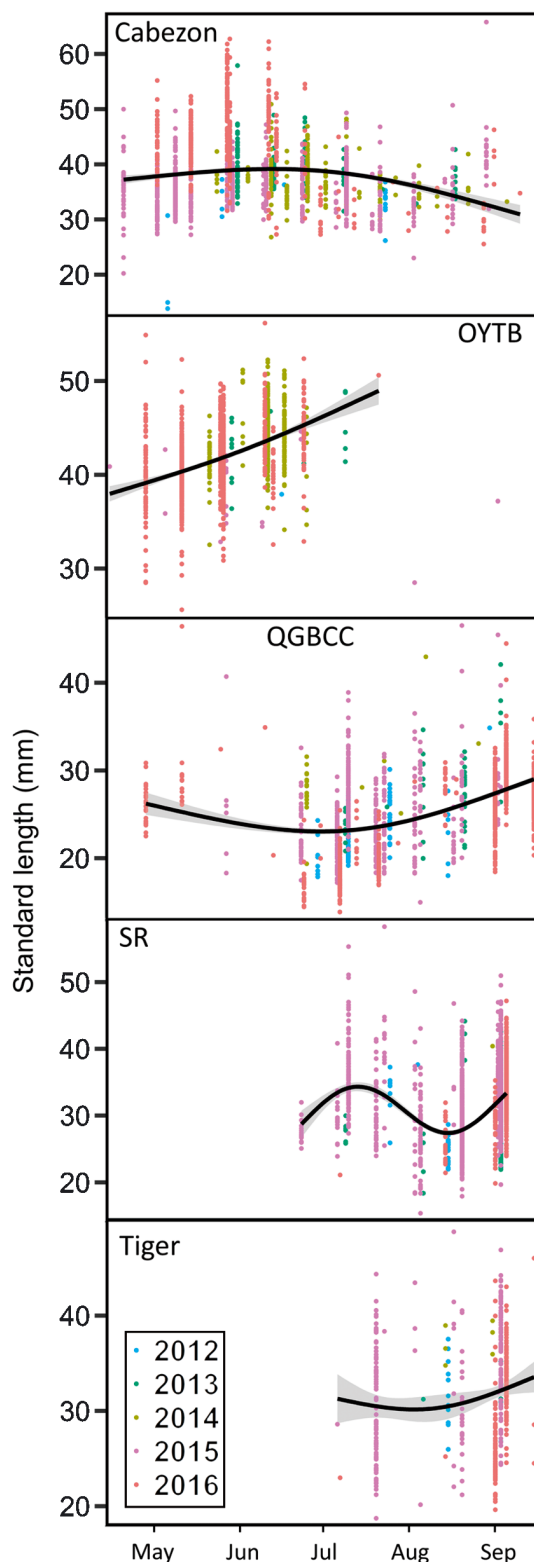


Fig. 5. Standard length of 5 fish taxa collected 2012–2016 varied as the season progressed. See Fig. 2 for definitions of species complexes. Regression curve for OYTB excludes 2 outliers. Shading indicates 95 % CI. Note different scales for y-axes

Ralston et al. 2013, Wheeler et al. 2017). In our study, we found that interannual settlement of cabezon was less variable than rockfish, especially in northern Oregon, suggesting that annual egg production and larval survival of cabezon is also less variable among years. These results are consistent with the life-history strategy of rockfishes (higher fecundity, lower early larval survival, and later age at maturity) compared to cabezon (Winemiller & Rose 1992).

As in previous studies, settlement peaks ranged over a 2 mo window among years. Despite this year-to-year variation, settlement peaks of our 5 focal taxa were generally synchronized between northern and southern Oregon (Fig. 2) and roughly aligned with previously published data from the central CCS. Settlement peaks of cabezon occurred between late April and June, consistent with settlement peaks in central California (Wilson et al. 2008). Similarly, settlement pulses of OYTB also occurred in the same months (May–June) along the California coast (Ammann 2004, Wilson et al. 2008, Caselle et al. 2010a, Jones & Mulligan 2014). Pulses of QGBCC settlement to Oregon also ranged over similar months (June–August) as KGBC, gopher, black-and-yellow, and copper rockfishes along southern and central California (Anderson 1983, Wilson et al. 2008). This latitudinal settlement synchrony is not consistent with other species along the CCS, such as the blue rockfish *Sebastes mystinus* (Laidig 2010), where settlement tends to occur later towards more northern latitudes. In general, previous studies of fish reproduction have shown that fish phenology frequently is shifted later at northern latitudes (Love et al. 2002, Cope & Key 2009). However, the overall synchrony observed during our 5 yr settlement time series indicates that fish settlement along the Oregon coast occurs earlier than expected. This early settlement may have been driven by anomalously warm water temperature in the northeast Pacific in 2013–2016, which coincided with an El Niño event (Bond et al. 2015, Hu et al. 2017). Previous work has demonstrated that this warm anomaly drove changes in the community of phyto- and zooplankton, potentially impacting higher trophic levels of the food web (Peterson et al. 2017). Unfortunately, there are no published studies evaluating seasonal patterns of settlement elsewhere along the CCS that coincides with our study period. By itself, our time series is not sufficiently long to test whether fish settlement timing along the Oregon coast has been influenced by this warm water anomaly. Further, this warm water anomaly has masked any potential settlement differences derived from the El Niño that may otherwise

have been apparent in our dataset. Additional sampling years in Oregon and upcoming studies of settlement timing elsewhere along the CCS may help elucidate links between settlement and such large-scale oceanographic processes. For instance, a multi-decadal study revealed that, compared to previous years, pelagic juvenile rockfishes were abundant in central California during the 2015–2016 El Niño event but were low in southern and northern California (McClatchie 2016).

Regional differences in settlement rates among taxa in our study may reflect spatial structure of the adult populations. Higher cabezon settlement rates observed in southern Oregon may be driven by the generally higher adult population density around Cape Blanco compared to northern Oregon (Cope & Key 2009). At a finer spatial scale, we found that settlement to marine reserves was similar to the nearby (<3 km) non-reserve areas for all taxa except cabezon in southern Oregon (lower in the reserve) and OYTB in both regions (higher in the reserve). Different predation pressure on pelagic juveniles before settlement to SMURFs may lead to differences in settlement magnitude between reserves and non-reserves, but this is unlikely to be the case here as adult fish surveys have revealed no significant difference in the density of piscivorous fishes between these newly established reserves and their non-reserve comparison areas (Huntington et al. 2015). Previous studies have shown that alongshore hydrodynamics interacting with coastal topography can affect the supply of competent settlers (Jenkins et al. 1997, Markel et al. 2017). **In upwelling zones, higher settlement of invertebrates on the lee of small headlands may be due to the formation of a retention zone, where lower portions of the water column are recirculated** (Mace & Morgan 2006). The local topography surrounding the 2 reserves in our study may create a similarly retentive zone during upwelling compared to the non-reserve comparison areas (Fig. 1). Such recirculation may contribute to the observed pattern of higher settlement of OYTB to the marine reserves, as this group includes species that occur deeper in the water column than the other rockfish species. In contrast, species that occur higher in the water column such as cabezon (Doyle 1992) exhibited no consistent difference in settlement magnitude between marine reserves and non-reserves. Settlement variation across space may also be influenced by settlement cues (reviewed in Pawlik 1992, Leis et al. 2011). The proportion of rock and boulder substrates differ between the reserve and non-reserve sites in both regions (Huntington et al.

2015); thus it is possible that there are species-specific behaviors in response to subtle habitat differences that lead to contrasting settlement patterns of cabezon and OYTB between the reserve and non-reserve sites. More data are needed to consider local-scale retention structures and habitat heterogeneity when designing marine reserves. Such data may be useful for achieving marine reserve goals since most existing reserves around the world are generally small (Oregon's reserves range from 3 to 36.5 km²), and thus rarely encompass all ecologically important habitats (Lester et al. 2009).

Understanding settlement differences between reserves and non-reserves provides valuable information for our understanding of how reserves function (Gronrud-Colvert & Sponaugle 2009), both at reserve implementation and through time. Although site fidelity (i.e. fish remaining in the same area) of young recruits has rarely been examined in the CCS, evidence indicates that adult cabezon and a number of other rockfishes (including fishes inside Oregon marine reserves) are sedentary within a specific home range (e.g. Matthews 1990, Mireles et al. 2012, Calvanese 2016). Newly settled juveniles of these species may display a similar site fidelity behavior as that observed in adults. In these cases, quantifying settlement of fishes to reserves can help provide an annual baseline to which subsequent years of settlement data can be compared. Such data will eventually help us better understand fluctuations in year-class strength of fishes, and evaluate how protection of piscivorous fishes affects survival of newly recruited fish (Hobson et al. 2001).

Effect of upwelling strength and water temperature on fish settlement

Higher growth rates and survival of larval and pelagic juvenile rockfishes have been associated with high primary productivity in coastal upwelling fronts along the CCS (Bjorkstedt et al. 2002, Wheeler et al. 2017). Previous studies examining the relationship between upwelling strength and annual settlement of pelagic juveniles have revealed contrasting patterns depending on the region of study. For instance, interannual settlement of both OYTB and KGBC was positively related to upwelling strength in regions south of Point Conception and north of Cape Mendocino (Caselle et al. 2010a, Jones & Mulligan 2014), but settlement of only KGBC was positively related to upwelling strength off central California (Caselle et al. 2010a, Wheeler et al. 2017). At higher

latitudes (i.e. Canada), settlement of black rockfish appears to be associated with strong upwelling, and weak upwelling favors settlement of quillback and copper rockfishes (Markel et al. 2017).

For other marine organisms, short (2–6 d) downwelling (upwelling relaxation) events along the Oregon coast that reverse offshore transport of surface waters during the settlement season have been associated with warmer nearshore water and recruitment pulses of intertidal organisms to the Oregon coast (Dudas et al. 2009). Water off most of the California coast is almost persistently upwelled—during the relaxation periods, the upwelling intensity weakens, and only occasionally reverses. Compared to Oregon, downwelling episodes along central California are less frequent (Huyer 1983), yet settlement of KGBC to that coast is higher during periods of relaxation and warm water events, while OYTB settlement peaks during episodes of strong upwelling and cold water (A. Ammann, as cited in Caselle et al. 2010b). In our study, multiple cycles of upwelling–relaxation within each sampling interval hindered our ability to detect statistical significance between settlement magnitude and oceanographic events. However, although not significant for any taxon, settlement of all taxa except OYTB tended to be higher during downwelling and warm water temperatures over the 3 yr period (2014–2016). Because OYTB settlers were generally larger, with stronger swimming capacities than most other taxa analyzed in this study (Kashef et al. 2014), it is possible that pelagic OYTB are able to counteract offshore advection during upwelling. They also occur deeper in the water column where onshore transport of water can weaken or reverse during upwelling events (Lenarz et al. 1995).

Relationship between fish size and water temperature

There was no significant relationship between settler size (SL) and water temperature for any focal taxon, despite the fact that for most fishes, higher water temperatures generally result in faster growth (Houde 1989). This is likely because settler size is a function of both growth rate and stage duration; thus otolith microstructure analysis is needed to fully resolve the relationship between temperature, age, growth, and size (Sponaugle 2010). The largest cabezon arrived to SMURFs in June, followed by subsequently smaller settlers as the season progressed. Because the pelagic duration of cabezon is 3–4 mo

(O’Connell 1953), and they settled over a 5 mo period, we clearly sampled juvenile cabezon from multiple spawning events within the same year. Therefore, the most plausible hypotheses for decreasing lengths of cabezon settlers over the sampling season are that the larvae that hatched later in the year either grew more slowly because of poor growing conditions (e.g. food availability) or settled at younger ages than larvae that hatched earlier in the year.

For OYTB and QGBCC, mean size-at-settlement increased significantly as the season progressed, suggesting that these settlers may have been part of the same annual cohort that arrived to settle at different times during the sampling season. However, we cannot exclude a temporal shift in the timing of settlement of individual species within this complex. Early settlers of QGBCC in 2016 were larger than expected based on the regression curve, suggesting that early settlers of this complex are likely a different species (possibly copper rockfish; Anderson 1983) than the mid- and late-season settlers.

Within individual settlement seasons, the size distribution of SR was the most variable. Such variability could be driven by one of the SR species settling at a different size or time of the year. Indeed, genetically identified redbanded juveniles (~12%) were significantly larger than genetically identified splitnose juveniles (~88%) that settled simultaneously (August 27–September 11, 2013) to northern Oregon (D. Ottmann et al. unpubl. data).

This study is the first time-series effort to systematically measure nearshore fish settlement in the northern CCS. Our findings for Oregon are consistent with previous research conducted elsewhere in this system in showing that settlement of competent pelagic juvenile fishes is highly variable among years. However, within-season settlement peaks of most taxa tended to coincide with short (2–6 d) episodes of downwelling and warm surface waters. The overall timing of settlement during our study period was roughly similar to that reported previously for central and southern California, despite the different upwelling regimes between California and Oregon. Such similarity contrasts the previously described delay (Love 2011) of the reproductive phenology in higher latitudes of the CCS and may be driven by abnormally warm water temperatures (Hu et al. 2017) that existed during the study period. However, simultaneous settlement measurements in both geographical areas would be necessary to directly compare the degree to which there is a settlement delay along the CCS. Continued long-term monitoring of

fish settlement is necessary to estimate the contribution of interannual fluctuations in large-scale oceanographic processes, such as the Pacific Decadal Oscillation or El Niño events, as well as management influences on fish settlement (Green et al. 2015). Combining settlement data with the monitoring data of post-settlement individuals may help refine measurements of post-settlement mortality and identify the habitats most essential to sustaining healthy fish stocks.

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