

AN ABSTRACT OF THE THESIS OF

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Abstract approved:

Su Sponaugle

Most benthic marine organisms have a bipartite life with an early pelagic stage that enables dispersal of offspring, connecting spatially separated populations, and a late stage where individuals reside in a benthic habitat. Settlement of pelagic offspring to bottom associated substrates is the process that connects the two life history phases. Thus, settlement is fundamental to the recruitment of individuals to the adult benthic population. Together with collaborators, in my first data chapter (Chapter 2) I evaluated patterns and processes of temperate fish dispersal and settlement to nearshore habitats of central and southern Oregon (northwest U.S.) over 6 yrs, and related these patterns to oceanographic conditions. Our results revealed that settlement of the five focal taxa peaked at different times of the sampling season and exhibited varying degrees of episodic timing. Settlement of most species tended to peak during upwelling relaxation events, although most trends were statistically insignificant. Size-at-settlement varied among taxa and within taxa over time, but in no case did we find a significant correlation between size and water temperature, likely due to multiple factors (growth rate, pelagic duration) contributing to size-at-settlement. Settlement of splitnose rockfish (*Sebastes diploproa*) was the most episodic of all the taxa analyzed in this study.

Chapter 3 reports on the results of a genetic kinship analysis conducted on individuals of a very large pulse of splitnose rockfish that settled during a single sampling event in 2013. Our results revealed that at least 11.6% of the settlers were siblings, indicating that they remained aggregated throughout their 4-6 mo dispersal phase. This is the first demonstration of such long term aggregation by early stages in a complex oceanographic environment and has major implications for our understanding of the dispersal process. Together, the two data chapters in this thesis provide new information on settlement patterns and processes for fishes along the coast of Oregon. The settlement data are important to monitoring efforts in local marine reserves and enable comparisons over large spatial scales with similar studies conducted along the California coast. Our demonstration that offspring can remain aggregated throughout their entire dispersal phase reveals an underestimated layer of complexity in larval dispersal, building fundamental knowledge towards a more complete understanding of marine dispersal and its influence on population genetics and population regulation.

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Patterns and Processes of Fish Dispersal and Settlement along the Oregon Coast

by
Daniel Ottmann Riera

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Daniel Ottmann Riera, Author

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CONTRIBUTION OF AUTHORS

Chapter 2. Kirsten Grorud-Colvert and Su Sponaugle conceived and designed the study. Brittany Huntington supplied resources. Daniel Ottmann, Kirsten Grorud-Colvert, and Brittany Huntington acquired field data. Daniel Ottmann conducted the statistical analyses. Daniel Ottmann wrote the chapter with guidance and editorial assistance of Su Sponaugle and Kristen Grorud-Colvert.

Chapter 3. Kirsten Grorud-Colvert and Su Sponaugle conceived and designed the study. Brittany Huntington and Michael Banks supplied resources. Daniel Ottmann, Kirsten Grorud-Colvert, and Brittany Huntington acquired field data. Daniel Ottmann and Nicholas Sard designed the genetic approach and conducted laboratory and statistical analyses. Daniel Ottmann, Kirsten Grorud-Colvert, and Su Sponaugle wrote the manuscript. All authors discussed the results and commented on the manuscript.

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PATTERNS AND PROCESSES OF FISH DISPERSAL AND SETTLEMENT
ALONG THE OREGON COAST

CHAPTER 1: GENERAL INTRODUCTION

Marine organisms experience the highest rates of mortality early in their life cycle, when small individuals are particularly vulnerable to predation (Houde & Hoyt 1987). Processes affecting the success of these early stages have long been recognized as critical factors in the reproductive success of marine populations (Hjort 1914, Houde 2009). Thus, quantifying these processes is a key to understanding natural fluctuations in the abundance of adult populations (Lindgren et al. 2013). Data on early life processes can be used to refine management strategies operating over multiple spatial and temporal scales to enhance extractive practices while protecting populations from overharvest (King & McFarlane 2003). For benthic marine organisms, settlement of pelagic stages to bottom-associated substrates is a necessary component of their lifecycle. Spatial and temporal patterns in the number of individuals that settle successfully depends on species-specific characteristics, survival rates throughout the pelagic stage, and current patterns affecting dispersal pathways (Roughgarden et al. 1988).

In the California Current System (CCS) in the northeast Pacific Ocean, settlement patterns of benthic fishes to nearshore habitats has been examined along the coast of California, revealing that settlement is highly variable across time and space (Wilson et al. 2008, Caselle et al. 2010, Jones & Mulligan 2014). These patterns vary latitudinally along the CCS, but settlement to nearshore habitats has not

been systematically examined north of California. In the second chapter of this thesis, my collaborators and I extend this knowledge to broader spatial scales by evaluating patterns of fish settlement to nearshore habitats along the Oregon coast. Presence of young fish in artificial settlement substrates sampled every two weeks was used to estimate fish settlement to nearshore habitats (Ammann 2004, White & Caselle 2008). We measured settlement over five settlement seasons from 2011-2016 and related these patterns to upwelling strength and water temperature. We focused on five common species or species complexes and compared settlement patterns between two regions, southern and central Oregon, and within each region, between reserves and non-reserve areas. Finally, we compared our results to settlement of similar species elsewhere along the CCS to evaluate differences in settlement timing and magnitude of the focal taxa.

For benthic marine organisms, the frequency, distribution, and magnitude of settlement depend on pre-settlement processes occurring during the dispersive stage. Long distance dispersal occurs mainly via early pelagic life stages, enabling offspring to colonize new spaces and maintain ecological connectivity among geographically separated subpopulations (Marsh et al. 2001, Cowen et al. 2006). However, given the minute sizes of offspring and the immense size of the ocean, knowledge of the exact dispersal pathways of larvae and pelagic juveniles remains elusive, as continuous *in situ* tracking of these early life stages is not yet possible. Thanks to advances in biophysical model simulations of larval dispersal, new genetic techniques, and chemical and microstructural analysis of hard body structures, progress has been made in evaluating potential dispersal distances of larvae and the capacity for

offspring to return to their natal location (reviewed in Cowen & Sponaugle 2009, Shanks 2009). However, actual dispersal pathways and fine-scale dispersal processes, such as interactions among larvae of the same species, are largely unknown. In the third chapter of this thesis, my collaborators and I evaluated the degree to which early pelagic stages can remain cohesive throughout their dispersal stage. We conducted a kinship analysis on a large pulse of splitnose rockfish (*Sebastes diploproa*) that settled together in close proximity in 2013. Adult splitnose rockfish typically live at depths of 100-350 m, and release pre-hatched larvae into the pelagic environment (Love et al. 2002). These larvae disperse for up to 1 yr in the CCS before settling to a benthic habitat. Given the highly diffusive environment of the CCS (Drake et al. 2011), detecting siblings within a large recruitment pulse would point to cohesive dispersal of larvae throughout the entire pelagic stage (Awise & Shapiro 1986). Together, these two data chapters contribute new information on dispersal and settlement of young fish within the CCS that furthers our understanding of processes underlying population replenishment of important fish species.

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CHAPTER 2: PATTERNS OF FISH SETTLEMENT ALONG THE OREGON COAST

Abstract

For benthic marine organisms, settlement of pelagic offspring to bottom-associated habitats is a necessary precursor for the completion of their life cycle and recruitment to the adult population. Thus, quantifying spatial and temporal variation of settlement is important to fully understand population dynamics, set appropriate fisheries management targets, and design spatial management strategies such as marine reserves that protect essential fish habitats. In the northern California Current System (CCS), dominated by complex oceanographic currents and a seasonal and intermittent upwelling regime, information about nearshore patterns of fish settlement is lacking. To compare fish settlement patterns from this region with the highly variable patterns observed along the upwelling dominated system of southern and central California, we tracked juvenile fish settlement over five settlement seasons in central and southern Oregon. We found species-specific temporal patterns of settlement, which reflected variable degrees of episodic settlement, similar to patterns observed in the central and southern CCS. With the exception of the species complex settling at the largest size, we found that fish settlement tended to be greater during short periods of downwelling in upwelling relaxation events. Within-season variation in size tracked species-specific temporal patterns, but size-at-settlement was not related to water temperature. Further analyses, including additional sampling years that encompass complete cycles of environmental anomalies and a better understanding of fish age and growth via otolith microstructure analysis, are needed

to understand the mechanisms driving similar settlement patterns across the mosaic of environmental variability created by large-scale boundary currents.

Introduction

Many marine organisms undergo an early pelagic stage before recruiting to benthic environments 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 rock) is a necessary precursor to recruitment to the population (Roughgarden et al. 1988, Doherty & Fowler 1994). Thus, understanding settlement processes enables a more nuanced insight into the recruitment of juveniles to the adult population (King & McFarlane 2003). For example, most studies evaluating the effectivity of marine reserves are based on changes in the abundance of the adult population (Lester et al. 2009). However, these changes can result from reduced mortality of the adults as well as from changes in the number of new individuals entering the system (Doherty & Fowler 1994). Measuring the settlement patterns of new individuals can contribute to our understanding of the dynamics of local populations, but identifying such patterns is frequently obscured by high interannual variation in early-life mortality and stochastic oceanographic processes that alter the dispersal pathways of competent offspring (Roughgarden et al. 1988, Ralston et al. 2013, Shulzitski et al. 2016). For instance, settlement timing of most coral-reef species is synchronized with the lunar phase (Robertson 1992), yet oceanographic features such as the passage of mesoscale eddies, and pre-settlement condition of these fishes, superimposes additional noise on this signal (D'Alessandro et al. 2007, Rankin & Sponaugle 2014).

In the California Current System (CCS), characterized by a western boundary current flowing along the U.S. west coast from British Columbia to Baja California, complex oceanographic processes such as cycles in upwelling strength or seasonal shifts in alongshore currents (Huyer 1983, Lynn & Simpson 1987, Checkley & Barth 2009) exacerbate the challenges of identifying consistent settlement patterns (e.g. Shanks & Eckert 2005, Caselle et al. 2010b). Elucidating settlement patterns of pelagic juvenile fish 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), particularly because oceanographic patterns can vary from predominantly upwelling to intermittent upwelling within regions (Menge & Menge 2013). 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, Markel 2011, Jones & Mulligan 2014), 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. 2016).

Settlement of offspring to coastal habitats in the CCS likely differs along the coast because oceanographic patterns and processes change latitudinally (Shanks & Eckert 2005, Checkley & Barth 2009). For instance, alongshore winds south of Cape Mendocino, northern California, are persistent, equatorward and upwelling-favorable; but in higher latitudes, alongshore winds change seasonally from northward, downwelling-favorable winds in winter, to equatorward, upwelling-favorable winds in summer (Huyer 1983). Here, seasonal upwelling typically undergoes 2-6 d cycles

of upwelling-relaxation events where increased recruitment of intertidal organisms has been associated with downwelling periods (Dudas et al. 2009). Additionally, the strong alongshore, coastal upwelling jet that flows equatorward along the Oregon coast separates from the shore at Cape Blanco, southern Oregon, creating a biogeographic boundary and advecting cold, upwelled water farther offshore. Compared to other regions of the central and southern CCS, the contrasting oceanographic processes off the Oregon coast may lead to different settlement patterns of local fish species.

While recruitment of nearshore fish to coastal habitats has been examined throughout the CCS (West et al. 1994, Carr & Syms 2006, Gallagher & Heppell 2010, Markel 2011, Dauble et al. 2012), settlement, the first step of recruitment, 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 spanning 233 km along the Oregon coast for 5 yrs (2012-16) and investigated how these patterns relate to oceanographic conditions.

Methods

Field sampling

Samples were collected from two sites within each of two nearshore regions of central and southern Oregon (233 km apart; Fig. 2.1). These sites were chosen to compare settlement of larvae and pelagic juveniles above and below the

biogeographic break at Cape Blanco, and to augment marine reserve monitoring currently underway in Oregon. 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 x 35 cm) cylinder of garden fencing. This 3-D structure simulates natural settlement substrates such as kelp canopy. In each region, up to eight replicate SMURFs were deployed 1 m below the surface at locations where the depth was ~15 m and the distance to the shore ranged from 390-1,200 m. Half of the SMURFs were set at a marine reserve site and the other half were set at a nearby (< 3 km) non-reserve site chosen as a comparison area due to similar depth, relief, and habitat. Due to logistical issues, the specific position of several SMURFs in central Oregon was modified during the first 3 yrs of the study. Similarly, some SMURFs were occasionally lost, especially during the first 2 yrs, which affected the number of replicates for each site. New fish settlers were collected every 2 wks from April/June through September of 2011-16 in central Oregon and 2014-16 in southern Oregon. This is the time of year when most pelagic juveniles settle to coastal habitats along the CCS (Love 2011). Earlier studies demonstrated that presence of fish in SMURFs coincided with subsequent recruitment of juvenile fishes to the benthic habitat, and that most of our fish taxa experience little to no loss from SMURFs over a 2-wk deployment interval (Ammann 2004, White & Caselle 2008, Markel 2011). Therefore, we use the term ‘settlement’ to refer to the presence of juvenile fishes in SMURFs (Caselle et al. 2010a). To retrieve SMURF samples, two snorkelers used butterfly-style nets (Anderson & Carr 1998) to enclose each SMURF and bring it to

the vessel. Collected fish were euthanized with tricaine methanesulfonate (MS-222), 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 sufficient to distinguish juveniles of some rockfishes. We grouped these species into two complexes: OYTB, which included olive (*Sebastes serranoides*), yellowtail (*S. flavidus*), and black (*S. melanops*) rockfish; and QGBC, which included quillback (*S. maliger*), gopher (*S. carnatus*), black-and-yellow (*S. chrysomelas*), copper (*S. caurinus*), and china (*S. nebulosus*) rockfishes. We used these species complexes to be consistent with previous research conducted off California (Wilson et al. 2008, Caselle et al. 2010a), but we note that “K” was substituted for “Q” in our QGBC complex because we collected quillback rockfish but not kelp rockfish (*S. atrovirens*). To confirm the presence of species within these complexes, we sent 107 samples that included different morphotypes of each complex to be genetically identified at the National Oceanic and Atmospheric Administration (NOAA) Southwest Fisheries Science Center in Santa Cruz (CA) (Pearse et al. 2007). Results confirmed the presence of all the QGBC species in both regions, including gopher and black-and-yellow rockfishes, which had never been described at such northern latitudes (Love 2011). For the OYTB complex, genetic results confirmed the presence of only yellowtail and black rockfishes. Elsewhere along the CCS, juvenile

yellowtail and black rockfishes arrive to nearshore habitats during overlapping times of the year (mid spring and summer) at sizes that range from 2.5 – 6.3 cm in SL (Love et al. 2002, Love 2011). The species grouped in the QGBC complex typically settle at smaller sizes (1.5 – 3.5 cm) and arrive to nearshore habitats at overlapping times from spring to fall. Hereafter we refer to OYTB and QGBC as ‘taxa’ and report their settlement patterns as such.

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 2.1). These models included offsets for the number of SMURFs and days per sampling interval to account for variable number of replicates and length of each sampling interval. An offset is a model variable with a known coefficient (i.e., number of days or number of SMURFs) that adjusts the expected value (i.e., fish count) with the effect of omitted variables (i.e., length of the sampling interval or sampling effort). Therefore, our model outputs can be interpreted as the variation in settlement rate, where settlement rate is the number of fish per SMURF per day (Zuur et al. 2013). Analyses focused on five taxa that comprised over 98% of the samples collected in this study: cabezon (*Scorpaenichthys marmoratus*), OYTB, QGBC, splitnose rockfish (*S. diploproa*), and tiger rockfish (*S. nigrocinctus*). We further restricted our analyses to the 2012-16 sampling seasons because low and uneven sampling in 2011 resulted in insufficient statistical power. To reduce zero-inflated data, we excluded the months when

settlement was very low or absent across all years of the study (see Fig. 2.2). Thus, the analyses focused on the days prior to July 1 for OYTB, the days after June 1 for QGBC, and the days after July 1 for splitnose and tiger rockfishes. Because cabezon settled throughout all the sampled months, they were analyzed for the entire season. To evaluate settlement variation within the recruitment season, we used the midpoint of each deployment period instead of the actual sampling date.

To evaluate differences among SMURF locations within region, we applied an initial GAMM with random effects to account for interannual and within season variation. Fish settlement was not affected by the mooring location within region (central OR: $\chi^2_8 = 10.76$, $P = 0.22$; southern OR: $\chi^2_7 = 5.82$, $P = 0.56$); so, hereafter we analyzed the data using SMURFs within region or sites as replicates. To evaluate annual differences in settlement of each species for each region separately we applied a second GLMM with only one random effect to account for within season variation. To examine regional differences in settlement patterns for each species we applied a third GLMM that included annual and within season variation as random effects. We applied a fourth GLMM to evaluate differences in settlement of each species between the marine reserves and their comparison non-reserve areas (sites). We accounted for annual and within season variation in each region separately by including the same two random effects.

Effect of upwelling strength and water temperature on fish settlement. To evaluate upwelling strength at our respective central and southern Oregon sites, we obtained Bakun index values of daily upwelling at 45°N, 125°W (central 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 Fleet Numerical Meteorology and Oceanography Center six-hourly surface pressure analysis. Positive values indicate offshore transport in units of cubic meters per second along each 100 m of coastline.

In situ water temperature at ~3 m depth was recorded at each SMURF mooring from 2014 to 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 applying the Pearson coefficient of correlation. We then calculated the mean settlement rate (No. fish SMURF⁻¹ day⁻¹) for each region separately, and examined the relationship between settlement rate of each species and mean Bakun index and mean water temperature over each sampling interval. Water temperature values were lagged one day after Bakun index values to account for the lag observed between these two variables (see Results). These correlations were calculated separately for 2014-16, and for the three years combined.

Fish size and effect of water temperature. To evaluate interannual differences in the size at which each taxa settled to the SMURFs, we applied a generalized additive model (GAM; Zuur 2012) with a normal distribution and a smoothing parameter for the within season variation in fish length (Table 2.1). Because growth of poikilotherms is typically related to temperature, we examined region-specific SL of settlers with regional water temperature. To examine this relationship, we obtained daily offshore sea surface temperature (SST) data for 2012-

16 from the NOAA National Data Buoy Center at the Stations #46050 and #46015, located 35 and 20 km offshore of our central and southern Oregon sites, respectively. For each region, we regressed the mean SL of the fish collected in each sampling event against the mean water temperature of the previous 90 d.

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 10.2 (ESRI 2014) and R package ‘ggplot2’ v2.0.0 (Wickham 2009).

Results

Patterns of fish settlement. In total, 7,804 fishes (Table S2.1) were collected over the 6 yrs of the study. The five focal taxa exhibited contrasting settlement patterns across the season (Fig. 2.2). 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 little settling afterwards. Settlement of QGBC peaked between June and August for most years, but there were additional early and late-season settlement pulses in 2016. Both splitnose and tiger rockfish tended to settle later in the season, starting in July and peaking in September.

With the exception of cabezon, settlement of all the other sampled taxa was highly variable across years and included years when settlement rate was close to zero (occasionally zero) and years when settlement was several orders of magnitude greater (Fig. 2.3). Settlement rates were not significantly different between regions for OYTB, QGBC and splitnose rockfish. However, cabezon had higher overall

settlement in southern Oregon than in central Oregon, while tiger rockfish had the opposite pattern (Fig. S2.1). Within each region, OYTB exhibited greater settlement to marine reserves than to their unprotected comparison areas (Fig. 2.4). Cabezon exhibited the opposite trend, but only in southern Oregon, with greater settlement in the unprotected area than in the marine reserve. Settlement of the remaining taxa did not differ significantly between reserves and non-reserve areas.

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 S2.2; central OR: $r = -0.53$, $P < 0.001$; southern OR: $r = -0.55$, $P < 0.001$). These correlations were stronger when upwelling strength was compared to water temperature of the following day (central OR: $r = -0.67$, $P < 0.001$; southern OR: $r = -0.66$, $P < 0.001$), indicating that there was a one-day lag between changes in upwelling strength and changes in the nearshore water temperature. There were very few significant correlations between fish settlement in 2014-16 and environmental parameters (Table 2.2; Fig S2.3). However, consideration of taxon-specific settlement over all three years generally resulted in negative correlations with upwelling strength and positive correlations with water temperature.

Fish size and effect of water temperature. Interannual differences in mean SL were significant ($P < 0.05$) for cabezon and tiger rockfish in central Oregon, and for QGBC in southern Oregon (Fig. 2.5). The mean length of the settlers varied over the season, but each taxon showed different trends (Fig. 2.6). For cabezon, the largest individuals tended to settle around June, while later settlers tended to be smaller. Excluding the months of lowest settlement, the average length of settling OYTB and

QGBC increased by 0.11 mm d^{-1} and 0.09 mm d^{-1} , respectively, as the season progressed. The splitnose rockfish size distribution over the season exhibited a sinusoidal pattern that was particularly apparent in southern Oregon in 2015 (Fig. S2.4), while tiger rockfish did not exhibit a particularly distinct pattern. Average monthly temperatures were generally higher off central Oregon than off southern Oregon, likely driven by stronger upwelling in southern Oregon advecting colder water to the surface (Fig. S2.5; Huyer 1983). However, there was no significant relationship between 90-d averaged water temperature and the mean SL of the settlers, regardless of the region ($P > 0.05$ for all species; Fig. S2.6).

Discussion

Patterns of fish settlement. Settlement of juvenile rockfish taxa along the Oregon coast was highly variable over the 6 yrs 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, Caselle et al. 2010b, Jones & Mulligan 2014), density of post-settlement recruits (White & Caselle 2008, Gallagher & Heppell 2010, Markel 2011, Dauble et al. 2012, Wheeler et al. 2016), 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, sea surface temperature, and alongshore currents (Bjorkstedt et

al. 2002, Ralston et al. 2013, Wheeler et al. 2016). In our study, we found that interannual settlement of young cabezon was less variable than rockfish, especially in central Oregon, suggesting that annual egg production and larval survival of cabezon is less variable among years.

Within years, cabezon and rockfish reproduction tends to peak later at higher latitudes than at lower latitudes (Love et al. 2002, Cope & Key 2009, Laidig 2010). However, settlement peaks of our taxa were fairly synchronized between central and southern Oregon, likely because our two sampling regions were only 233 km apart. Settlement of cabezon peaked between late April and June which is consistent with the settlement peaks in central California (Wilson et al. 2008). Similarly, settlement peaks of OYTB also coincided with the same months (May – June) as along the California coast (Ammann 2004, Wilson et al. 2008, Caselle et al. 2010a, Jones & Mulligan 2014; J. Caselle, University of California, Santa Barbara, California; unpubl. data). However, the settlement of QGBC tended to peak about one month later along Oregon (June – August) than the KGBC complex (“K” standing for kelp rockfish) along southern and central California (Wilson et al. 2008; J. Caselle, unpubl. data). These comparisons suggest that although there was some lag in the settlement peaks across the spatial range of several focal species, this difference in timing was less pronounced than would be expected based on previous studies (2-3 mo; Love et al. 2002, Cope & Key 2009). Such unexpectedly early settlement may be driven by anomalous warm water temperature in the northeast Pacific in 2013-16 (Bond et al. 2015, Hu et al. 2016). Unfortunately, we could not test this hypothesis as we found no distinct settlement peaks in our time series prior to 2013. Adding

subsequent years to our ongoing time series will further elucidate links between settlement patterns and multiannual oceanographic patterns, such as this temperature anomaly.

Along Oregon, the settlement magnitude per sampling interval of OYTB and QGBC was similar to that observed in central California, with as many as ~ 3 and ~ 2.5 fish SMURF⁻¹ day⁻¹, respectively (Wilson et al. 2008). However, the greatest settlement peaks of cabezon along Oregon were as high as ~ 1 fish SMURF⁻¹ day⁻¹ (Wilson et al. 2008), approximately twice as high as the largest pulses observed in central California.

Comparing regional patterns of settlement, we found that settlement of juvenile cabezon was significantly greater to southern Oregon than to central Oregon, while settlement of tiger rockfish exhibited the opposite pattern. For cabezon, this difference may be driven by a greater population density around Cape Blanco than in central 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 species except cabezon in southern Oregon (lower in reserve) and OYTB in both regions (higher in reserve). Significant settlement differences between reserves and non-reserves can result from several processes: (i) variable local currents leading to differential arrival of settlers, (ii) contrasting predation pressure on pelagic juveniles before settlement to SMURFs, and/or (iii) different settling behavior driven by habitat suitability cues such as sound (Doherty et al. 2004, Leis et al. 2011, McCarroll et al. 2014). However, none of these drivers is consistent with our observations. (i) Local coastal morphology and nearshore bathymetry can create particular current patterns at

scales of a few km (McCarroll et al. 2014), presumably driving similar settlement patterns for different fish taxa. However, we found that cabezon and OYTB had an opposite settlement pattern in central Oregon, and OYTB was the only species exhibiting a significant difference in settlement between the reserve and non-reserve area in southern Oregon. Thus, our data are not consistent with the hypothesis that settlement differences between the reserves and non-reserves are driven by local currents. *(ii)* Fish surveys have shown that there is no substantial difference in the density of fish predators between the reserve and non-reserve in either of our study regions (Huntington et al. 2015). Consequently, differential piscivory rates on juveniles as they settle to the SMURFs is unlikely to drive the differences in settlement observed in our study. *(iii)* In southern Oregon, the marine reserve has a greater proportion of rock and boulder substrates than the non-reserve, but in central Oregon, the proportion of rocky substrates is reversed between the reserve and the non-reserve (Huntington et al. 2015). Because we found that OYTB settled in higher numbers to the marine reserve than to the non-reserve in both central and southern Oregon, and that cabezon settlement differences were only significant for southern Oregon, there is no evidence that substrate quality cues significantly altered fish settlement behavior. Species-specific behavior in response to habitat cues or to adult population remains the most plausible driver of the observed differences; however, given settlement of these taxa is highly variable over time, more than 5 yrs of data (only 3 yrs in southern Oregon) is needed to clarify differences at these small spatial scales.

Understanding settlement differences between reserves and non-reserves provides valuable information for our understanding of how reserves function (Grorud-Colvert & Sponaugle 2009). Although site fidelity of young recruits has rarely been examined in the CCS, evidence indicates that cabezon and a number of other rockfishes (including fishes inside the Oregon marine reserves) exhibit strong homing behavior to a specific area (e.g. Matthews 1990, Mireles et al. 2012; T. Calvanese, Oregon State University; unpubl. data). Thus, quantifying settlement of new fishes to reserves can help provide an annual baseline to which the number of new recruits can be compared. Such data can help us better understand fluctuations in year-class abundances of fishes, and evaluate how protection of piscivores affects survival of newly recruited fish.

Effect of upwelling strength and water temperature on fish settlement.

Because coastal upwelling fronts along the CCS are highly productive, higher growth rates and survival of larvae and pelagic juvenile rockfishes have been associated with high primary productivity (Bjorkstedt et al. 2002, Wheeler et al. 2016). Previous studies examining the relationship between upwelling strength and annual settlement of pelagic juveniles revealed contrasting patterns depending on the region of study. For instance, interannual settlement of both OYTB and KGBC was found to be positively related to upwelling strength in regions south of Point Conception and north of Cape Mendocino (Caselle et al. 2010a, Jones & Mulligan 2014), but only settlement of KGBC was positively related to upwelling strength off central California (Caselle et al. 2010a, Wheeler et al. 2016). 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 2011).

Within season, short (2-6-d) events of upwelling-relaxation that reverse offshore transport of surface waters have been associated with warmer nearshore water and recruitment pulses of intertidal organisms (Dudas et al. 2009). For our study region, we found that variation in water temperature was lagged by 1 d with respect to upwelling (as reflected in the Bakun index), suggesting that changes in offshore transport of surface waters is equally lagged. Unlike off Oregon, where surface water is downwelled during relaxation periods, water off California is persistently upwelled, with the intensity only weakening during relaxation periods. Despite the prevailing upwelling regime off central California, settlement of KGBC appears to be higher during periods of relaxation and warm water events, while OYTB settlement peaks during episodes of strong upwelling and cold water (A. Amman, as cited in Caselle et al. 2010b). We found that settlement of pelagic juveniles of all focal taxa except OYTB in southern Oregon was generally correlated with periods of downwelling and relatively warmer water. Because OYTB settlers were generally larger, with stronger swimming capacities than most other species analyzed in this study (Kashef et al. 2014), it is plausible that pelagic OYTB are able to counteract the offshore advective currents occurring during upwelling events. Overall, we found no significant correlation between the timing of settlement and local environmental parameters for the focal species. We note that our power to identify significant relationships is reduced due to the long sampling interval (~15 d).

Both upwelling strength and water temperature frequently fluctuated during the sampling interval, reducing our ability to detect relaxation events.

Fish size and effect of water temperature. Although we found significant interannual differences in the sizes of settling cabezon and OYTB in central Oregon and QGBC in southern Oregon, in no case did we find a direct relationship between settler size (SL) and water temperature, despite the fact that higher water temperatures generally result in faster growth of fish (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 have a full understanding of how growth and age-at-settlement resulted in the size distribution observed in our study (Sponaugle 2010). For OYTB and QGBC, the mean size-at-settlement increased as the season progressed, suggesting that these settlers were part of the same seasonal cohort arriving at different times during the sampling season. Occasional early settlers of QGBC were larger than expected, suggesting that early settlers of this complex may be a different species from the mid- and late-season settlers. We found that the mean SL of the OYTB and QGBC settlers increased by 0.11 mm d^{-1} and 0.09 mm d^{-1} , respectively, as the season progressed, which is generally slower than the expected growth rate of the species in these complexes ($0.2 - 0.7 \text{ mm d}^{-1}$; Boehlert & Yoklavich 1983, Woodbury & Ralston 1991, Gallagher & Heppell 2010, Markel 2011). The difference between the size of our settlers and the size expected based on their growth rates suggests that fast-growing OYTB and QGBC juveniles settle earlier than slow-growing juveniles, which achieve larger sizes at settlement overall due to a longer period (pelagic duration) of growth.

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 cabezon settled over 5 mo, there are clearly multiple reproductive events within the same year. Therefore, the most plausible hypothesis for decreasing lengths of cabezon settlers over the sampling season is that the larvae that hatched later in the year either grew more slowly as a result of poor growing conditions (e.g., food availability) or settled at younger ages than the larvae that hatched earlier in the year.

Within season, the size distribution of splitnose rockfish was the most variable. Interestingly, there was also variation within the same year and between both sampling regions. For instance, in 2015, splitnose rockfish size increased linearly in central Oregon, but followed a sinusoidal shape in southern Oregon (Fig. S2.4). As with cabezon, existence of multiple reproductive events within year or different pelagic growth rates could explain why the length distribution of splitnose settlers increases and decreases within the sampling season. However, splitnose rockfish can have a very long (up to 1 yr) pelagic duration, and the observed length of fluctuations during 2015 occurred over a relatively short (2.5 mo) period of time. If all of the offspring from a reproductive season were mixed together, we would expect the mean size of the settlers to increase across the sampling season as observed in OYTB and QGBC. However, the sinusoidal shape observed over such a short period (relative to the dispersal period) suggests that the multiple cohorts may have experienced relatively little mixing during their pelagic stage, which is consistent with recent evidence that larval splitnose rockfish can remain cohesive over long time

periods (Ottmann et al. 2016). For tiger rockfish, relatively little is known about its life history, but pelagic juveniles can display gregarious behavior to floating debris similar to splitnose rockfish (Love et al. 2002). However, tiger rockfish sizes remained more uniform, increasing only slightly over time. Without otolith microstructure data it is not possible to distinguish whether these were separate cohorts.

This was the first effort to systematically monitor nearshore fish settlement fish north of California along the CCS. Consistent with previous research, our findings show that settlement of competent pelagic juveniles along the Oregon coast is highly variable among years, but within year, settlement peaks of most taxa often coincided with short (2-6-d) episodes of downwelling and warm water. OYTB was the only taxa that was not influenced by short cycles of upwelling strength, possibly due to stronger swimming capacities of the larger pelagic juveniles at time of settlement. We found that the timing and magnitude of settlement was relatively similar to that along central and southern California, despite the different upwelling regimes between California (persistent year-round, but stronger during the spring and summer) and Oregon (seasonal, with intermittent periods of downwelling). Continued monitoring of fish settlement will provide us with a better understanding of the variation that is driven by interannual fluctuations in oceanographic processes along the CCS, such as the Pacific Decadal Oscillation or El Niño events. A deeper understanding of biological processes, including variable patterns of settlement and its effect on population dynamics, will contribute to more sustainable management and more effective design of marine reserves (Green et al. 2015). Combining

settlement data with monitoring data of post-settlement individuals may help refine measurements of post-settlement mortality, and quantify the most 'essential' fish habitats (Pikitch et al. 2004). Protecting specific habitats that are necessary for the completion of the life cycle of marine fishes can boost the replenishment of their populations with minimal disruption from fishing activities, supporting sustainable fisheries.

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Table 2.1. Models used in the analysis of settlement patterns of pelagic juvenile fish along the Oregon coast.

M1.	$N_{iyd} = \beta_0 + \beta_1 \times LS_{iyd} + \text{offset}(I_{iyd}) + a_y \sim N(0, \sigma^2_{year}) + b_d \sim N(0, \sigma^2_{day}) + \mathcal{E}_{iyd} \sim N(0, \sigma^2)$
M2.	$N_{id} = \beta_0 + \beta_1 \times Y_{id} + \text{offset}(I_{id}) + \text{offset}(NS_{id}) + b_d \sim N(0, \sigma^2_{day}) + \mathcal{E}_{id} \sim N(0, \sigma^2)$
M3.	$N_{iyd} = \beta_0 + \beta_1 \times R_{iyd} + \text{offset}(I_{iyd}) + \text{offset}(NS_{iyd}) + a_y \sim N(0, \sigma^2_{year}) + b_d \sim N(0, \sigma^2_{day}) + \mathcal{E}_{iyd} \sim N(0, \sigma^2)$
M4.	$N_{iyd} = \beta_0 + \beta_1 \times S_{iyd} + \text{offset}(I_{iyd}) + \text{offset}(NS_{iyd}) + a_y \sim N(0, \sigma^2_{year}) + b_d \sim N(0, \sigma^2_{day}) + \mathcal{E}_{iyd} \sim N(0, \sigma^2)$
M5.	$L_i = \beta_0 + \beta_1 \times Y_i + f(D_i) + \mathcal{E}_i \sim N(0, \sigma^2)$

N: Number of settlers

LS: Location of the 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 season effect (day of the year)

\mathcal{E} : 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 (central Oregon vs southern Oregon)

S: Site (marine reserve vs non-reserve area)

L: Mean standard length of the fishes collected per sampling interval

f(D): Smoother for the within season (day of the year) variability in fish length

Table 2.2. Pearson correlation coefficients between settlement rate and mean Bakun index of upwelling (BI), *in situ* mean water temperature T(C°).

Region	Year	Cabezon		OYTB		QGBC		Splitnose		Tiger	
		BI	T(C°)	BI	T(C°)	BI	T(C°)	BI	T(C°)	BI	T(C°)
Central 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
	2016	0.30	-0.19	0.13	0.02	-0.64	0.47	-0.56	0.50	-0.56	0.50
	2014-16	-0.09	0.09	-0.04	0.27	-0.15	0.34	-0.39*	0.44	-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*
	2014-16	-0.27	0.05	0.05	-0.24	-0.36	0.37	-0.27	0.44	-0.23	0.22

BI source: NOAA-PFEL; 45°N, 125°W and 42°N, 125°W. Settlement rate = No. fish SMURF⁻¹ day⁻¹. Environmental parameters were averaged for each sampling interval, with a 1-d lag for water temperature. Species complex: OYTB = olive, yellowtail, and black rockfishes; QGBC = quillback, gopher, black-and-yellow, copper, and china rockfishes. Statistical significance: $P < 0.05^*$; $P < 0.01^{**}$.

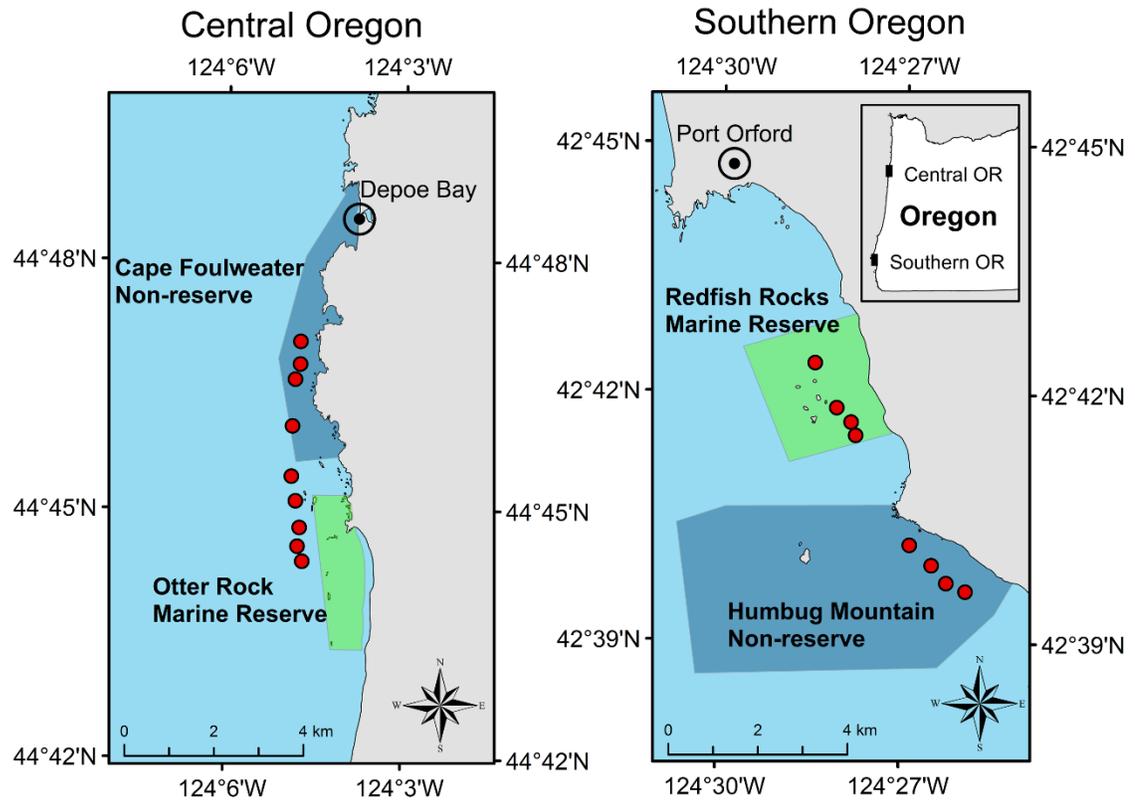


Fig 2.1. Sampling locations in two nearshore regions: central (2011-16) and southern (2014-16) Oregon. Within each region, newly settled pelagic juveniles were sampled in replicate SMURFs grouped at either a marine reserve (green) or an unprotected comparison area (dark-blue). For Otter Rock Marine Reserve, SMURFs were located outside of the reserve to align with the 15-m bottom depth. Red points indicate all the locations where SMURFs were deployed between 2012 and 2016. In 2012-13, one SMURF was located between the marine reserve and the non-reserve. To compare settlement between the reserve and the non-reserve, this SMURF was removed from the analysis.

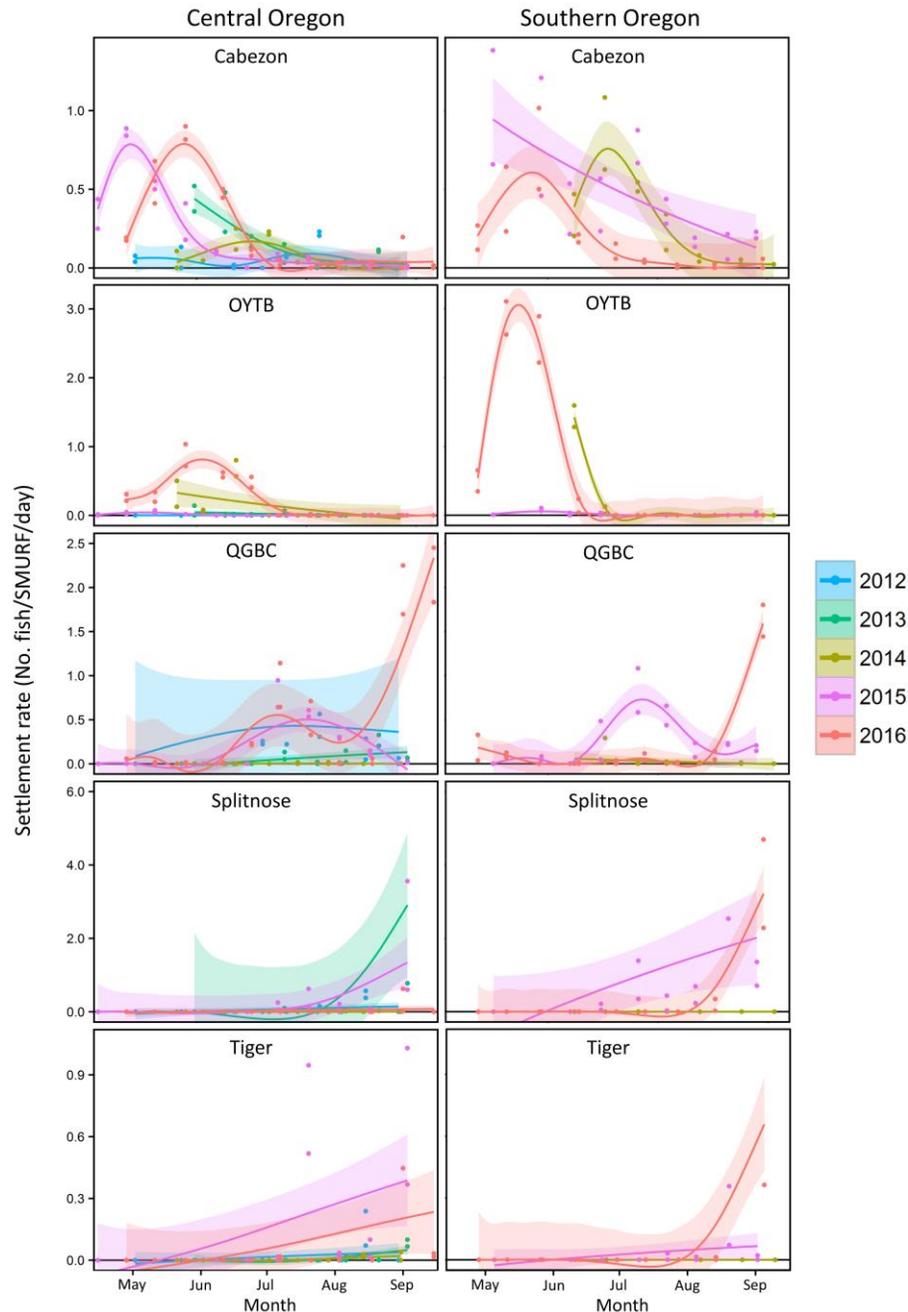


Fig. 2.2. Settlement of five fish species or species complexes to central and southern Oregon nearshore habitats during spring and summer seasons of 2012-16. Settlement peaked at the beginning of the season for cabezon (*Scorpaenichthys marmoratus*) and OYTB, mid-to-late season for QGBC, and late season for splitnose (*Sebastes diploproa*) and tiger (*S. nigrocinctus*) rockfishes. Settlement rate (number of fish per SMURF per day) was averaged over all the replicate SMURFs within each site (two sites per region). Only data from 2014-16 were available for southern Oregon. Shading indicates the 95% CI. Note different scales for the y-axis. Species complexes: OYTB = olive, yellowtail, and black rockfishes; QGBC = quillback, gopher, black-and-yellow, copper, and china rockfishes.

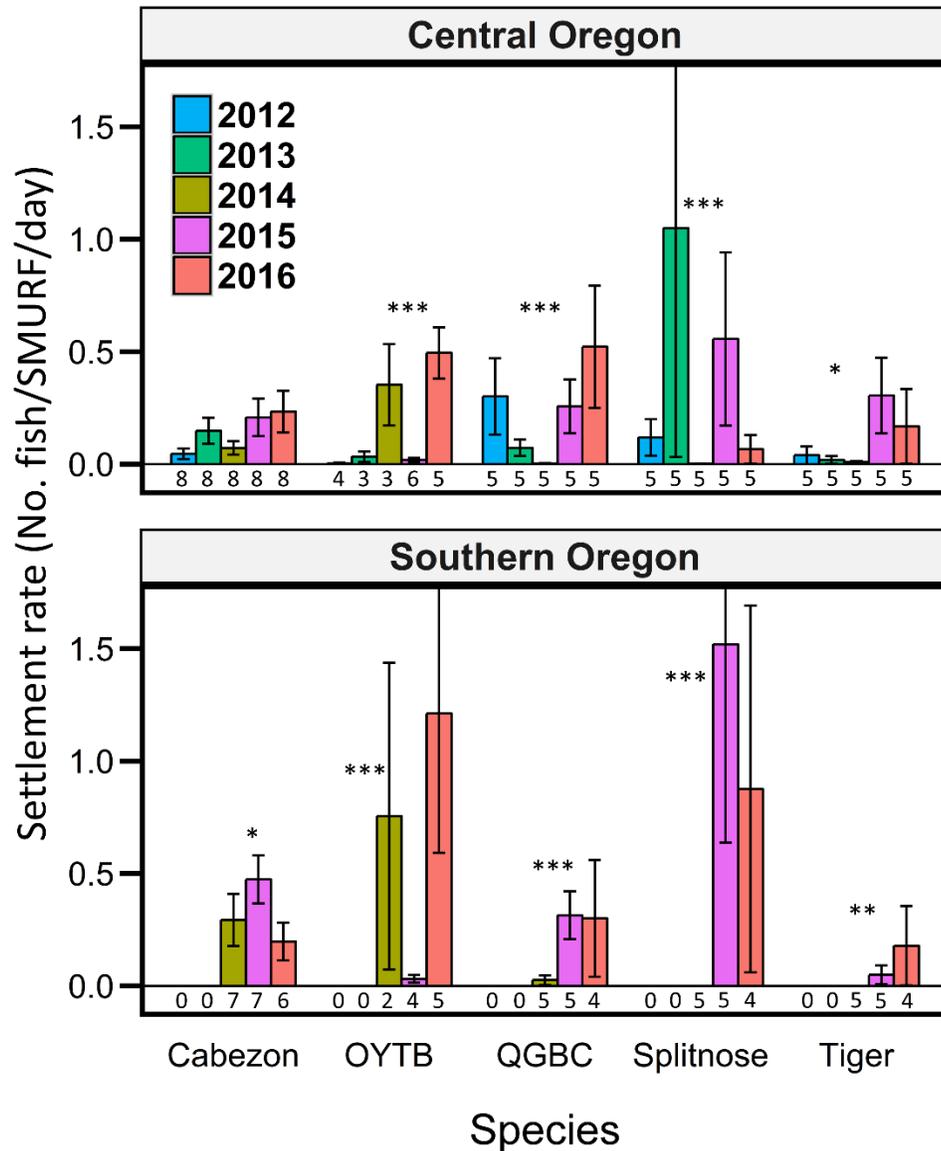


Fig. 2.3. Settlement of five fish species or species complexes to central and southern Oregon. Settlement rate (number of fish per SMURF per day) was averaged over all the replicate SMURFs within each region. Settlement varied significantly among years for all species, and differed by region. Only data from 2014-16 were available for southern Oregon. Error bars indicate standard error (number of collections under bars). Species complexes: OYTB = olive, yellowtail, and black rockfishes; QGBC = quillback, gopher, black-and-yellow, copper, and china rockfishes. Statistical significance: $P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$.

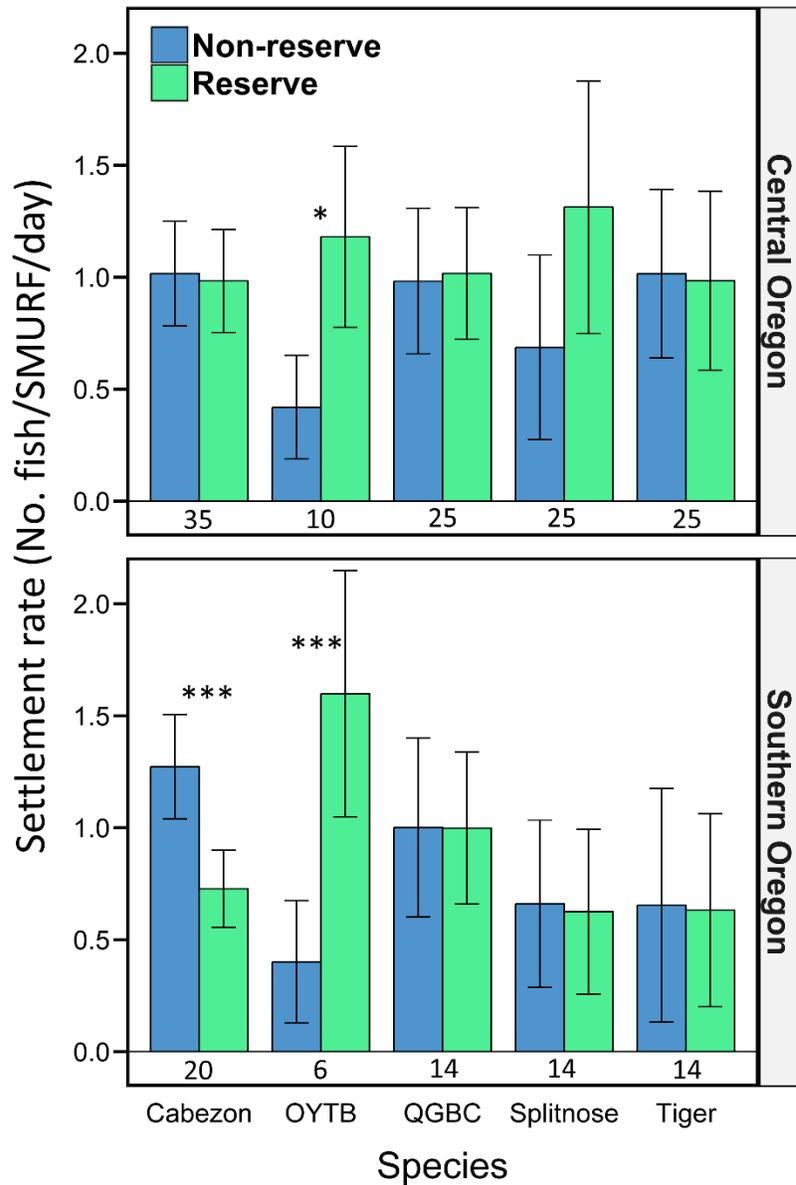


Fig. 2.4. Settlement of five fish species or species complexes to marine reserves (green) and non-reserve (blue) in central and southern Oregon. Settlement rate (number of fish per SMURF per day) was averaged over all the replicate SMURFs within site and normalized by the annual mean settlement from each region (2012-16 in central Oregon and 2014-16 in southern Oregon). Error bars indicate standard error (number of collections under bars). Species complexes: OYTB = olive, yellowtail, and black rockfishes; QGBC = quillback, gopher, black-and-yellow, copper, and china rockfishes. Statistical significance: $P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$.

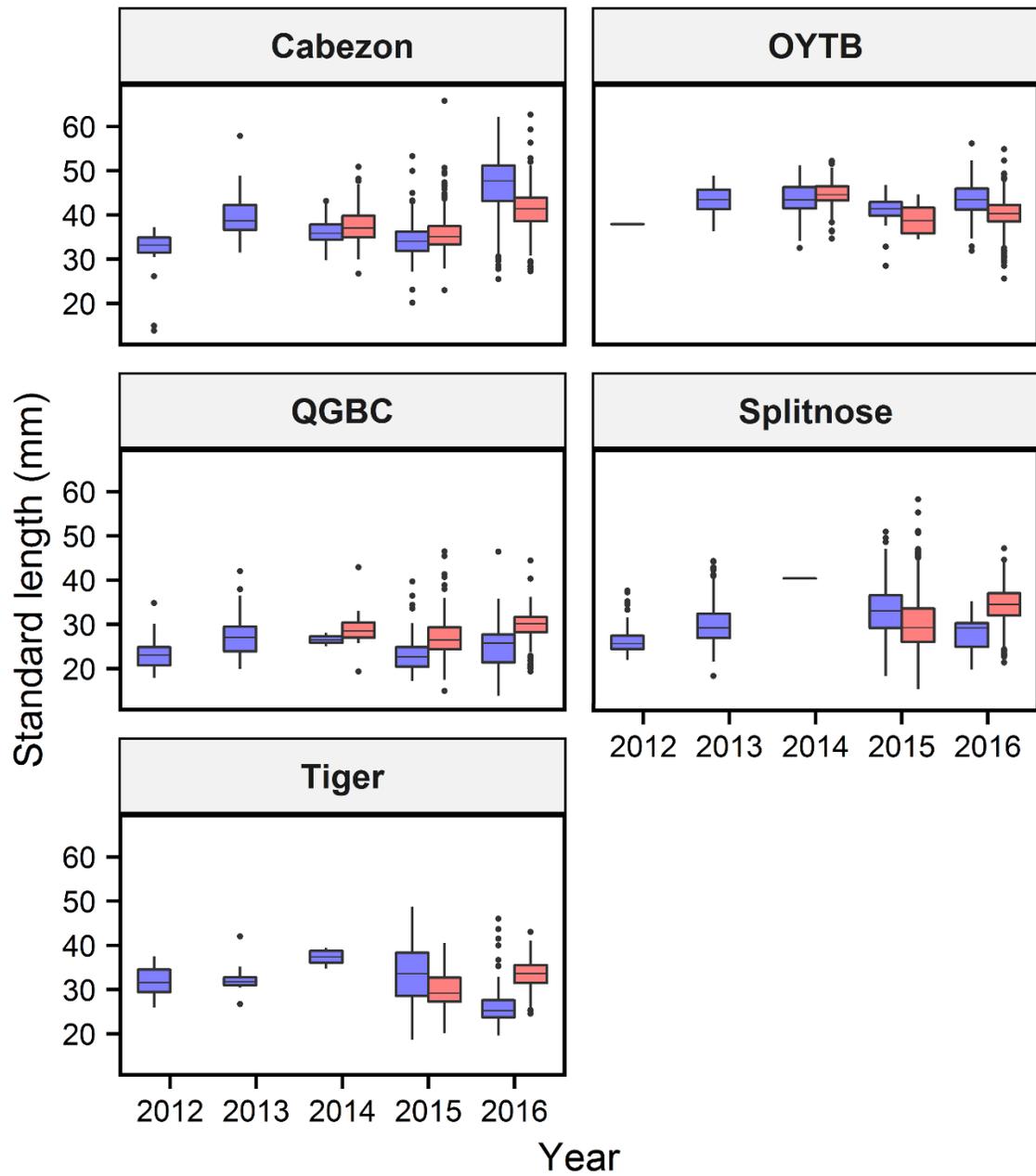


Fig. 2.5. Annual standard length variation of cabezon (*Scorpaenichthys marmoratus*), OYTB = olive, yellowtail, and black rockfishes, QGBC = quillback, gopher, black-and-yellow, copper, and china rockfishes, splitnose rockfish (*Sebastes diploproa*), and tiger rockfish settling to central (2012-16; blue) and southern (2014-16; red) Oregon. Interannual differences in mean length were significant at a $P < 0.05$ for cabezon and tiger rockfish in central Oregon and for QGBC in southern Oregon.

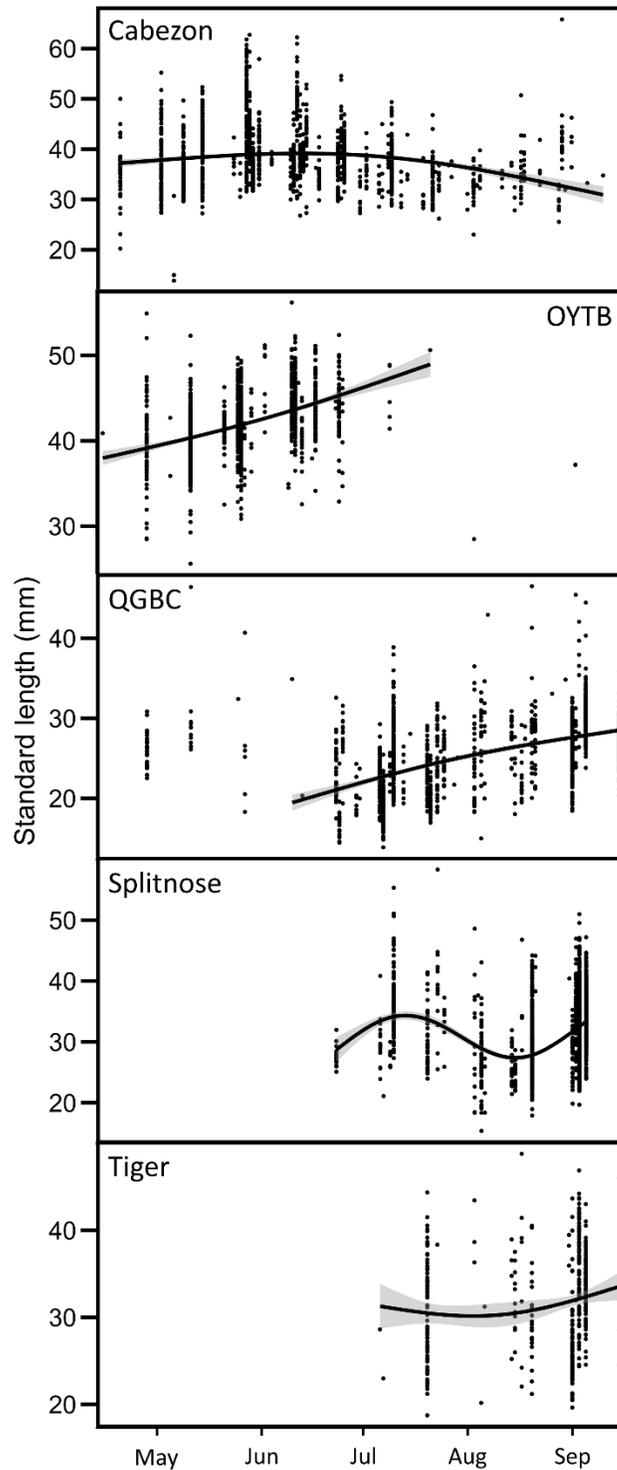


Fig. 2.6. Standard length of five fish species or species complexes collected from 2012-16. (a) Cabezon (*Scorpaenichthys marmoratus*); (b) OYTB = olive, yellowtail, and black rockfishes; (c) QGBC = quillback, gopher, black-and-yellow, copper, and china rockfishes; (d) splitnose rockfish (*Sebastes diploproa*), (e) tiger rockfish (*S. nigrocinctus*). Regression curves from OYTB and QHBC exclude juveniles that settled in atypical times of the season. Shading indicates the 95% CI.

CHAPTER 3: LONG-TERM AGGREGATION OF LARVAL FISH SIBLINGS DURING DISPERSAL ALONG AN OPEN COAST

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Abstract:

Pelagic dispersal of most benthic marine organisms is a fundamental driver of population distribution and persistence and is thought to lead to highly mixed populations. However, the mechanisms driving dispersal pathways of larvae along open coastlines are largely unknown. To examine the degree to which early stages can remain spatially coherent during dispersal, we measured genetic relatedness within a large pulse of newly recruited splitnose rockfish (*Sebastes diploproa*), a live-bearing fish whose offspring settle along the U.S. Pacific Northwest coast after spending up to a year in the pelagic environment. A total of 11.6% of the recruits in a single recruitment pulse were siblings, providing the first evidence for persistent aggregation throughout a long dispersal period. Such protracted aggregation has profound implications for our understanding of larval dispersal, population connectivity, and gene flow within demersal marine populations.

Introduction

Dispersal of offspring from parental sources to distant destinations benefits natural populations by reducing density-dependent mortality and inbreeding, as well as enhancing population persistence in a changing environment (Levin et al. 2003).

These benefits are widely accepted for terrestrial species, where diverse taxa have developed strategies to enhance dispersal, especially of the young (Levin et al. 2003, Bowler & Benton 2005). Similarly, the early stages of demersal marine taxa are often pelagic, a strategy that connects local populations over a range of ecologically relevant scales (Cowen & Sponaugle 2009). The pelagic habitats experienced by these early life stages are highly dynamic, especially along open coasts with complex current systems. Thus the prevailing thought has been that dispersal of offspring of most marine organisms is highly diffusive and dominated by ocean currents (Roberts 1997). However, recent studies have shown that behavior of pelagic larvae can reduce dispersal distances (Swearer et al. 1999, Cowen et al. 2006, Shanks 2009), to the extreme case where larvae of some species can recruit to their natal reef after spending days in the pelagic environment (Jones et al. 1999, Almany et al. 2007). Such retentive patterns typically involve vertical migration of larvae to depths with reduced or recirculating currents, larval navigation, and habitat selection at settlement (Leis 2006).

Although it is currently not possible to test these mechanisms directly via continuous *in situ* tracking of larvae, modern molecular techniques can provide critical information to indirectly test fine-scale dispersal hypotheses. For instance, parentage analysis has proven useful to determine starting and ending positions of larvae with relatively short dispersal periods (Planes et al. 2009). However, disentangling the mechanisms that drive dispersal patterns across larger spatial and temporal scales has been more elusive. Evidence of sibling co-recruitment (when siblings are detected simultaneously as newly settled recruits in the same local

habitat) has only been found in species inhabiting relatively retentive systems (semi-enclosed bays, estuaries, and coral reef lagoons), or in species with relatively short (11-36 d) pelagic larval durations (Planes et al. 2002, Selkoe et al. 2006, Veliz et al. 2006, Bernardi et al. 2012, St-Onge et al. 2015). In some of these examples, high rates of retention near the natal habitat inherently increase the abundance of related individuals at a particular location.

Alternatively, sibling co-recruitment after dispersal may result from aggregation of siblings throughout the entire pelagic stage. While protracted larval aggregation has been suggested as a possible mechanism, clear distinction between this and other processes (larval retention, natal homing), requires the examination of species that occur in open, oceanographically dynamic (i.e. non-retentive) systems, that have relatively long pelagic larval durations (i.e. time to diffuse), and that settle to a site distinct from the natal location (i.e. natal homing does not occur). We tested the hypothesis that persistent larval aggregation occurs in splitnose rockfish (*Sebastes diploproa*) by genetically identifying the occurrence of siblings among members of a large co-recruiting pulse. Rockfishes comprise a highly diverse genus with many live-bearing demersal species that are targeted by commercial and recreational fisheries. While adult splitnose inhabit deep water (commonly 100-350 m), pelagic juveniles frequently settle to shallow (< 20 m) nearshore habitats after dispersing for up to a year in the pelagic ocean (Boehlert 1977). Given the oceanographically dynamic system that splitnose rockfish inhabit (i.e. the California Current), co-recruiting siblings in this species would indicate that individuals remained cohesive throughout their larval period.

Materials and Methods

Study System. Oceanographic conditions off the Oregon Coast in the US Pacific Northwest are characterized by an offshore, southward-flowing current (California Current), and an inshore, northward-flowing current (California Undercurrent) that has seasonal flow inversions in the top 50 m of water (Lynn & Simpson 1987). Seasonal wind-driven upwelling occurs throughout spring and summer, with intermittent periods of relaxation that are often accompanied by an inshore flow of surface currents, and large recruitment events of intertidal and nearshore organisms (Roughgarden et al. 1988, Barth et al. 2007, Caselle et al. 2010). We obtained Bakun index values of daily upwelling at 45 °N, 125°W from the Pacific Fisheries Environmental Laboratory division of the National Oceanic and Atmospheric Administration (NOAA-PFEL). This index represents daily averages of wind-driven cross-shore transports computed from Fleet Numerical Meteorology and Oceanography Center six-hourly surface pressure analysis. Positive values indicate offshore transport in units of cubic meters per second along each 100 m of coastline.

Study Species. Splitnose rockfish (*Sebastes diploproa*) occur from Alaska to Baja California, and adults are most abundant at depths of 100-350 m. They live up to 103 yrs, have a relatively late (6-10 yrs) age of maturity, and females can produce up to 255,000 eggs per brood (Love et al. 2002). Like other rockfish species, female splitnose are live-bearing: eggs hatch in the maternal ovary several days prior to extrusion, and larvae are capable of swimming upon release (Kashef et al. 2014). Females can store sperm from multiple males for several months before fertilizing the eggs, thereby releasing offspring with multiple paternity (Hyde et al. 2008). Larvae

and early juveniles can remain in the pelagic environment for up to one year before settling to a benthic habitat at a size of 30-50 mm (Love et al. 2002). Pelagic juveniles frequently aggregate to drifting kelp mats (Mitchell & Hunter 1970) and the transition to benthic habitats occurs later in northern than southern latitudes, peaking in May-June in Southern California, and in August-September in Oregon and Washington. The long pelagic duration of benthic species like splitnose rockfish is thought to enable larvae and pelagic juveniles to disperse large distances from the parental source (Shanks 2009). The reproductive output of the splitnose population is estimated to be ~10 billion larvae per year, and there is no evidence of spatial population structure, likely due to their long pelagic larval duration and longevity (Gertseva et al. 2009).

Recruits. We collected newly settled splitnose rockfish recruits near Depoe Bay, central Oregon, using Standardized Monitoring Units for the Recruitment of Fishes (SMURFs; Ammann 2004). These collectors are made of black polyvinyl chloride (PVC) mesh folded inside garden fencing that is shaped in a long cylinder (100 x 30 cm). This creates a three-dimensional structure that simulates natural recruitment substrates such as a kelp canopy. We deployed seven replicate collectors at 1 m below the surface at sites where the depth was ~15 m. Collectors were located 390-1,170 m offshore and were 425-1,315 m apart (Fig. 3.1). From April 20 to September 11, 2013, we collected newly recruited fish approximately every two weeks using hinged butterfly-style nets to enclose each SMURF and collect the recruited fishes. Collected fish were euthanized with MS-222, measured with calipers to the nearest mm, and stored at -80°C. An exceptionally large (n = 538) pulse of

splitnose recruits was collected on September 11 (Fig. 3.2). A fin-clip of each recruit was stored in 95% ethanol for the kinship analysis. Based on a size-at-age regression of juvenile splitnose rockfish (Boehlert 1981), these recruits ranged in age from 120 to 180 days.

Reference Population. Unbiased measures of genetic relatedness (r) require a reference population of unrelated and non-inbred individuals (Queller & Goodnight 1989, Wang 2014). This assumption is violated when the focus population (i.e., fish recruits of the same cohort) is used as a reference population (Wang 2014).

Therefore, we used adult splitnose from nine different locations off the Oregon Coast as a reference population (Fig. S3.1). Tissue samples from 144 adult splitnose rockfish were collected during the 2015 NOAA West Coast Groundfish Bottom Trawl Survey in Aberdeen net trawls (15 minutes at $\sim 2.2 \text{ nm hr}^{-1}$) at depths of 117-225 m and stored in 95% ethanol.

Microsatellite Genotyping. We genetically analyzed 513 splitnose recruits and 95 individuals from the reference population. The remaining 25 recruit samples were suspected of cross-contamination in the lab processing and therefore removed from the analysis. The 95 reference population samples represent all nine sampling locations (Fig. S3.1). Within location, samples were randomly selected for the analysis. DNA was extracted following a standard silica-based method for all samples (Ivanova et al. 2006).

We optimized PCR conditions of 35 microsatellite markers isolated from congeneric species and screened the loci using 16 of our splitnose recruits. We successfully amplified 24 markers that had multiple alleles per locus. We then

selected the 20 most polymorphic markers (Table S3.1) to genotype all the remaining samples. PCR products were visualized using an ABI 3730xl DNA Analyzer, and alleles were sized using GENEMAPPER SOFTWARE 5 (Applied Biosystems®).

We adopted a conservative approach and removed all of the recruit samples that had any missing loci, leaving 491 (96%) fully genotyped recruits (at 20 loci) to conduct the kinship analysis. One sample from the reference population that was missing > 10 loci was also removed, leaving 94 total samples (99%). We re-genotyped 95 (19%) randomly selected recruits, and calculated the genotyping error rate by dividing the number of discordant alleles by the total number of scored alleles. The genotyping error rate across all 20 loci was $2\% \pm 2\%$ (mean \pm SD; Table S3.1). Hardy-Weinberg proportions (HWP) and linkage disequilibrium (LD) were tested independently for the recruit and reference samples using GENEPOP 4.2 (Raymond & Rousset 1995). Significance ($P < 0.05$) of HWP and LD was tested after Bonferroni-adjustments (Guo & Thompson 1992). We evaluated the effect of the sample size affecting the power to detect departures from HWP by applying a paired t-test on the coefficient of inbreeding (F_{IS}). The mean F_{IS} was not significantly different between the reference population and the recruits ($t_{19} = -1.22$, $P = 0.24$), indicating that the power to detect loci out of HWP is greater in the recruits. However, F_{IS} was positive in both cases, indicating that both recruits and reference population have deficient heterozygosity. Presence of null alleles is frequently associated with this condition. Using MICRO-CHECKER (Van Oosterhout et al. 2004) we found presence of null alleles in nine loci of the recruits and three loci of the reference population (Table S3.1). Thus, presence of null alleles may contribute to

a deficiency of heterozygosity in the recruits. However, null alleles alone are unlikely to account for similar deficiencies in the reference population. To test if the deficiency of heterozygosity in the reference population was due to a Wahlund effect, adult genotypes were grouped into northern ($n = 46$) and southern ($n = 48$) sample sites, respective to 44°N (Fig. S3.2), and we calculated the index of fixation (F_{ST}) between the groups using FSTAT v2.9.3.2 (Goudet 1995). After 1,000 permutations we found evidence of small but significant amount of genetic differentiation ($F_{\text{ST}} = 0.002$, $P = 0.042$) that, along with the presence of null alleles, likely contributes to the heterozygote deficiency.

Data Analysis. Pairwise relatedness was measured with the Triadic IBD estimator of relatedness using COANCESTRY 1.0.1.5 (Wang 2007, 2011), which applies a maximum likelihood method that estimates pairwise relatedness using the genotype of a third individual as a control. This estimator measures relatedness effectively (Wang 2007, Santure et al. 2010, St-Onge et al. 2015, Taylor 2015), and is robust to minor error rates, null alleles, deviation of HWP, and LD, as well as small amounts of genetic structure (Wang 2007). Allele frequencies of the adult population were used as reference in COANCESTRY (Wang 2014). The number of missing alleles in the reference population relative to the recruits ranged from 0 to 15 (Table S3.1). This was expected because the sample size of the reference population was smaller than the sample size of the recruits (Leberg 2002). Thus we assigned a low (≤ 0.005) frequency value to all missing alleles in the reference population. Although this approach might introduce marginal bias for r estimates, it is likely a conservative

bias since most of the assigned frequencies were higher than those observed in the recruits, thus underestimating r (Wang 2007).

Testing the estimator performance on simulated data is a critical process to predict true relatedness based on measures of r (Blouin et al. 1996, Wang 2007, Taylor 2015). We therefore tested our analytical power by measuring r in simulated datasets comprised of individuals with defined relationships. A dataset of 1,000 half-sibling pairs and 1,000 full-sibling pairs (sharing one and both parents, respectively) was employed to calculate the expected r estimates among individuals and provide criteria that could be used to distinguish related individuals from unrelated individuals. To predict the number of expected false positive siblings at a given r threshold, we calculated r in 100 datasets comprised of $n = 491$ unrelated individuals (120,295 pairwise comparisons) and averaged the number of false pairs falling above alternate thresholds. The number of simulated unrelated fish was selected to match the sample size of analyzed recruits. We additionally simulated 1,000 first order cousin pairs to estimate the number of false positive siblings that might be attributed to cousin relationship. All of these simulations were conducted with COANCESTRY using the allele frequencies of the 491 completely genotyped splitnose recruits. We found that $r = 0.35$ was an optimal cutoff that minimized the number of false positive pairs (unrelated individuals with an $r \geq 0.35$) while still preserving power to identify true sibling pairs (Fig. S3.2). The 100 simulations of $n = 491$ unrelated individuals yielded $\sim 6 \pm 2$ (mean \pm SD) false positive pairs, which is a low proportion (4.6×10^{-5}) considering the 120,295 possible pairwise comparisons of each dataset. Using the same threshold ($r \geq 0.35$) at least 16% of the simulated half-siblings and 90% of the

simulated full-siblings were detected, while less than 1% of the simulated cousin pairs fell above the threshold. Thus, we concluded that most of the pairs observed above a cutoff of $r = 0.35$ are likely to be siblings and not cousins. A lower r cutoff ($r = 0.3$) resulted in a higher proportion of false positives (36 ± 7 ; mean \pm SD), hampering the discrimination of real siblings from false positives. A higher r cutoff ($r = 0.4$) reduced the detection of real siblings (5% half-siblings; 78% full-siblings), resulting in an increased number of false negatives. We performed a similar power analysis with six other commonly used r estimators implemented in COANCESTRY (Wang 2011) and found that the Triadic IBD estimator was the most precise and conservative. We tested the performance of COLONY (Wang & Santure 2009) and ML-Relate (Kalinowski et al. 2006) on simulated data as alternative methods of sibling identification. COLONY produced ~750 false positive siblings and only identified 37% of the 1,000 simulated full-sibling pairs correctly; 58% were incorrectly identified as half-siblings, and the remaining 5% were classified as unrelated. ML-Relate performed slightly better, detecting 88% and 85% of 1,000 simulated full- and half-sibling pairs, but producing 15 false full-sibling pairs and ~6,300 false half-sibling pairs. Consistent with these results, only 27 of the 695 sibling pairs identified by COLONY among the recruits coincided with the siblings identified with the Triadic IBD estimator, while all of the 74 sibling pairs identified by the Triadic IBD estimator were found within the 9,198 sibling pairs identified with ML-Relate (Fig S3.3). Based on these simulations, using the Triadic IBD estimator appeared to be the most conservative approach.

As a consequence of siblings sharing common parents, a relatively small effective number of breeders would be expected in a recruitment cohort containing siblings. Using LDNE v2.0 (Waples & Do 2008), a program that estimates the effective population size based on linkage disequilibrium information, we estimated the effective number of breeders for the entire sample collection ($n = 491$), the putative siblings ($n = 57$), and the collection minus the putative siblings ($n = 434$). The effective number of breeders is expected to be larger in the 434-recruit group than in the entire collection because we removed most of the linkage disequilibrium signature induced by siblings sharing common parents.

All analyses were performed in R v3.2.1 (R Core Team 2015) using packages ‘plyr’ v1.8.3 (Wickham 2011) and ‘reshape2’ v1.4.1 (Wickham 2007). Figures were created using ARCGIS 10.2 (ESRI 2014), and R packages ‘ggplot2’ v2.0.0 (Wickham 2009) and ‘venneuler’ v1.1-0 (Wilkinson 2012). The network visualization was created with R package ‘igraph’ v1.0.1 (Csardi & Nepusz 2006), which distributes each node (i.e., fish) maximizing the occupied space of the figure while minimizing crossing-over of connected nodes.

Microsatellite genotype data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.b7m47>.

Results

In 2013 we collected newly settled splitnose rockfishes recruiting to a nearshore habitat in central Oregon (Fig. 3.1) after a period of low recruitment from May to August (0-7 fish per sampling interval; Fig. 3.2). A pulse of 538 recruits settled to mid-water collectors during a 15-d sampling interval (August 20-September 11). This

pulse coincided with a strong upwelling relaxation event that triggered an onshore-north flow of surface waters. The spatial pattern of recruitment to our seven collectors during this pulse was highly patchy, spanning a range from 1 to 239 (mean = 79; median = 28) fish per collector (Fig. 3.1).

Measurements of pairwise levels of relatedness (r ; (Wang 2007) showed that this recruitment pulse contained multiple sibling pairs. We genotyped all of the 538 recruits and an additional 95 adults collected off the Oregon Coast (used as reference population; Fig. S3.1) by applying a large panel (20 loci) of polymorphic microsatellite markers. Only 491 fully genotyped recruits and 94 adults genotyped at 10 or more loci were used for the analysis (see explanation in Methods). The genotypes yielded 23 ± 12 (mean \pm SD) alleles per locus in the recruit samples and 17 ± 8 (mean \pm SD) in the reference population (Table S3.1), providing powerful means to detect siblings. Deviation from Hardy Weinberg proportions (HWP) and linkage disequilibrium (LD) is expected in samples containing a high proportion of related individuals (Allendorf & Phelps 1981). Indeed, independent tests showed that the recruits had 15 (75%) loci out of HWP, 31 (16%) pairs of loci in LD, as opposed to one (5%) locus out of HWP, and one (0.5%) pair of loci in LD in the reference population. We note that the analytical power driven by the different sample sizes of the recruits and reference population likely contributes to these differences, but the estimator of r used in this analysis is remarkably robust to departures of HWP and LD (Wang 2007). Thus, neither of these factors is expected to substantially affect our estimates of r .

Based on a power analysis consisting of r measurements of simulated data, we found an optimal and conservative $r = 0.35$ threshold to discriminate siblings from cousins and unrelated pairs (Fig. S3.2). The simulations predicted 6 ± 2 (mean \pm SD) false positive pairs (unrelated pairs with an $r \geq 0.35$), yet r estimates among our recruits yielded 74 pairs of related individuals (Fig. 3.3). We note that 74 pairs of siblings is a conservative estimate given the proportion of expected false negatives (related pairs with an $r < 0.35$; 84% half-siblings, 10% full-siblings; Fig. S3.2). Thus the real number of sibling pairs is probably greater. Among the 57 different fish that comprised the 74 related pairs, 35 were clumped into a large ‘family’ of half- and full-siblings, while the remaining 22 formed independent sibling pairs. The effective number of breeders for all 491 recruits was estimated to be 153 (95% CI: 146-159), which is relatively small, as expected for a cohort containing individuals that share common parents. Furthermore, the effective number of breeders was estimated to be smaller (35, 95% CI: 33-38) when using only the 57 related recruits (i.e. sharing common parents), and larger (651, 95% CI: 577-744) when using only the remaining 434 individuals. Related recruits were identified at all but one of the collectors (dark blue collector in Fig. 3.1) where only one recruit was collected, suggesting that co-recruiting siblings arrived within a water mass extending over at least 4 km.

Discussion

Sibling co-recruitment. The finding of at least 57 (11.6%) siblings in a single pulse of co-recruiting individuals is the first documentation of high relatedness among recruits of a species with a long pelagic period spent along an open coast. Given that larvae were released by adults residing in deep waters ≥ 20 km away from

the nearshore area where the recruits were collected, such a high co-occurrence of siblings cannot be attributed to offspring returning to a natal location. Three possible explanations remain: (i) related larvae diverged after being released into the water column and somehow regrouped shortly before settling to a suitable habitat as juveniles. This scenario is unlikely because once separated, particles in such a dynamic environment have a very low probability of re-encountering each other at the end of a long (120-180 d) period (Drake et al. 2011). (ii) Due to maternal effects, large splitnose females may produce more eggs and higher condition larvae than smaller and younger females, contributing a greater proportion of the total recruitment (Berkeley et al. 2004). Although maternal effects have not yet been demonstrated in splitnose rockfish, other rockfish species show variable degrees of maternal effects (Sogard et al. 2008). However, we found that ~7% of co-recruiting splitnose comprised a single 'family' that shared common parents. Considering that the splitnose population produces ~10 billion larvae, maternal advantage alone is highly unlikely to account for the large contribution of so few parents (Waples 2016). The remaining alternative is that (iii) offspring sharing at least one parent experienced greater pelagic survival relative to offspring of other parents and remained aggregated throughout the entire dispersal period. The first part of alternative (iii) relates to the hypothesis of sweepstakes reproductive success (Hedgecock & Pudovkin 2011), whereby a small fraction of the adult population contributes disproportionately to recruits due to differential survival of offspring in variable oceanographic conditions. Consequentially, the likelihood of detecting co-recruiting siblings at a given location are greater under sweepstakes reproductive success than if all the adults contribute

equally to the genetic pool of the recruits. However, likelihood of detecting co-recruiting siblings diminishes in species with long pelagic stages unless larvae and pelagic juveniles remain aggregated during dispersal. If dispersal is diffusive, differences in larval survival will be homogenized because larvae released simultaneously will randomly diffuse to high- and low-quality habitats regardless of their original location. Thus, the genetic signal of sweepstakes reproductive success will be diluted. Furthermore, models of larval dispersal (Drake et al. 2011) show that passive larvae dispersing over 4-6 mo. experience high rates of mixing over scales of hundreds of kilometers, which would further dilute the genetic signal of sweepstakes reproductive success (Broquet et al. 2013, Eldon et al. 2016). Because the splitnose recruits in this study spent ≥ 4 mo. in an oceanographically dynamic environment, co-recruitment of such a large proportion (11.6%) of siblings is only expected if they dispersed together.

Sibling Aggregation Throughout Dispersal. It is generally assumed that eggs and early larvae diffuse at the onset of dispersal, and that larvae may only actively aggregate with conspecifics as their swimming capabilities improve. Our results challenge this hypothesis by suggesting that larval behavior, starting at the onset of dispersal and continuing throughout the pelagic juvenile stage, can counteract early diffusive forces and maintain patch cohesiveness throughout the entire pelagic stage. Elsewhere in regions with currents that favor larval retention, larvae of fish species with relatively short pelagic larval durations can share common dispersal paths for up to 30 d prior to settlement (Ben-Tzvi et al. 2012, Shima & Swearer 2016). However, large scale current movement along the Oregon Coast

makes the finding of larval aggregation striking and surprising. Recruitment to our collectors was spatially patchy, and siblings from the same family settled to multiple collectors, indicating that they formed loose cohesive patches with other related and unrelated pelagic juveniles in the same water mass. Larval and pelagic juvenile fish likely co-occurred offshore in this water mass until the upwelling relaxation event transported them nearshore (Roughgarden et al. 1988) in patches that encountered our collectors.

Most surprising is the finding that siblings maintained this cohesiveness for 4-6 months, despite the potentially immense diffusion and advective mixing that larvae and pelagic juveniles experience in the open ocean. Although previous studies have found evidence of siblings among recruits and post-recruits of species with shorter dispersal phases (Planes et al. 2002, Selkoe et al. 2006, Veliz et al. 2006, Bernardi et al. 2012, St-Onge et al. 2015), or suggested larval aggregation over time periods up to 30 d before settlement (Ben-Tzvi et al. 2012, Shima & Swearer 2016), no study has demonstrated that larvae can remain cohesive for extended periods of time (120-180 d) in an open, dynamic system. Such long-term cohesive dispersal may underlie unexpected levels of relatedness found within adult subpopulations of some benthic organisms with high dispersal potential such as the California spiny lobster, *Panulirus interruptus* (Iacchei et al. 2013). However, the extent to which aggregation during dispersal is a widespread trait among marine organisms will remain an intriguing question until studies of this kind are conducted with other species that have long dispersal phases.

Our results reinforce the shifting paradigm that larval dispersal is not driven purely by the physical forces in the marine environment, but is rather a product of biophysical interactions (Cowen et al. 2006, Leis 2006). Potential physical mechanisms fostering cohesion of larval and pelagic juvenile patches over extensive time periods include coherent physical features such as mesoscale eddies and current filaments (Sponaugle et al. 2005, Harrison et al. 2013). However, along the open coast of Oregon, these physical features are not present over sufficient spatial or temporal scales to sustain the cohesiveness observed in this study. For species such as splitnose rockfish, long-term cohesive dispersal may be enhanced by larval and pelagic juvenile aggregation to floating debris, such as kelp mats. Furthermore, as live bearers, splitnose rockfish release larvae capable of early swimming behaviors that may enhance their capacity to remain cohesive. Interactions among group members both early and later in larval life may play a role – evidence suggests that successful larval/pelagic juvenile navigation to nearshore settlement sites may be enhanced by remaining in small groups (Irisson et al. 2015).

Implications for Larval Ecology, Management, and Conservation. Our ongoing understanding of larval behavior during dispersal in the ocean, including the aggregation of related individuals, underscores knowledge gaps that are key to understand for effective conservation and management of marine species. In recent years, efforts have focused on quantifying population connectivity of structured populations (Cowen & Sponaugle 2009), often with the goal of designing networks of marine reserves (Planes et al. 2009, Gaines et al. 2010, Green et al. 2015) or developing more effective fisheries management of stocks across genetic or

geopolitical boundaries (Richardson et al. 2016). Yet these approaches seldom consider the impact of fine-scale processes that are influenced by stochastic and patchy dispersal, such as high spatial coherence in the genetic structure of recruits. Such genetic patchiness can translate into cascading effects on local genetic diversity and population regulation (Johnson et al. 2016, Selwyn et al. 2016). By demonstrating that larval aggregation can shape dispersal processes to a greater degree than previously thought, our results highlight the need to better understand the fine-scale physical and biological processes occurring in the pelagic ocean that affect the growth, survival, and dispersal of larvae. Successful recruitment of young individuals is critical to the population dynamics of most marine species and thus also to their effective management and conservation.

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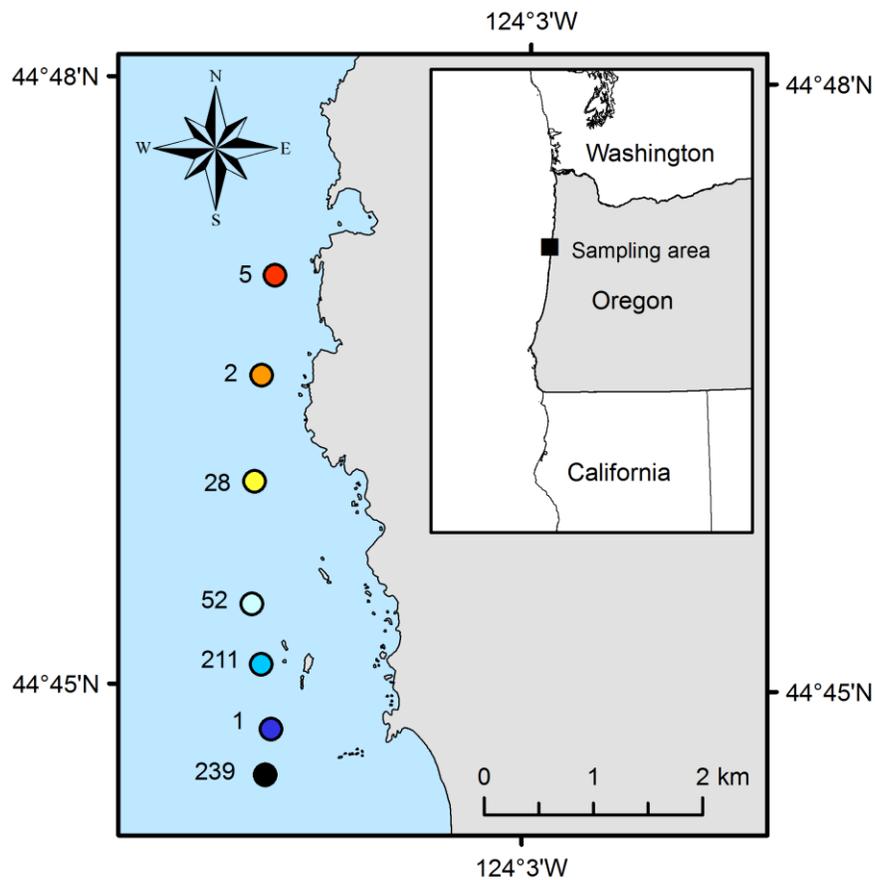


Figure 3.1. Sampling locations of fish recruits. Recruits were sampled using seven collectors (colored circles) that were located 425-1,315 m apart in a nearshore rocky reef habitat along the Oregon Coast. Values indicate number of splitnose rockfish (*Sebastes diploproa*) collected in September 2013 after a 15-d sampling interval.

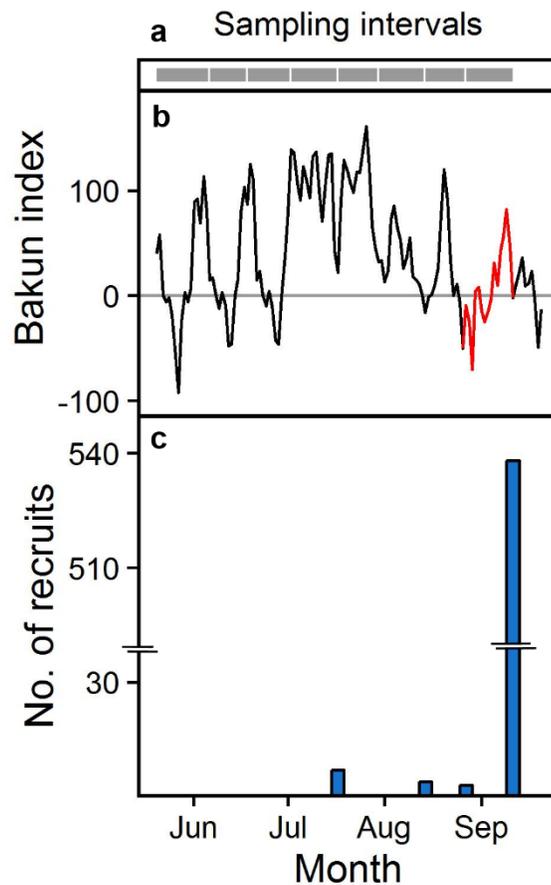


Figure 3.2. Upwelling strength and number of collected recruits. Fish collectors were sampled approximately every two weeks from May 20 through September 11, 2013. (a) The sampling region was characterized by upwelling (Bakun index > 0) interrupted by relaxation periods (Bakun index < 0) associated with onshore flow of surface currents. A strong relaxation event coincided with the sampling interval (red) when (b) 538 splitnose rockfish (*Sebastes diploproa*) recruited to the collectors. Daily Bakun index source: NOAA-PFEL; 45°N, 125°W.

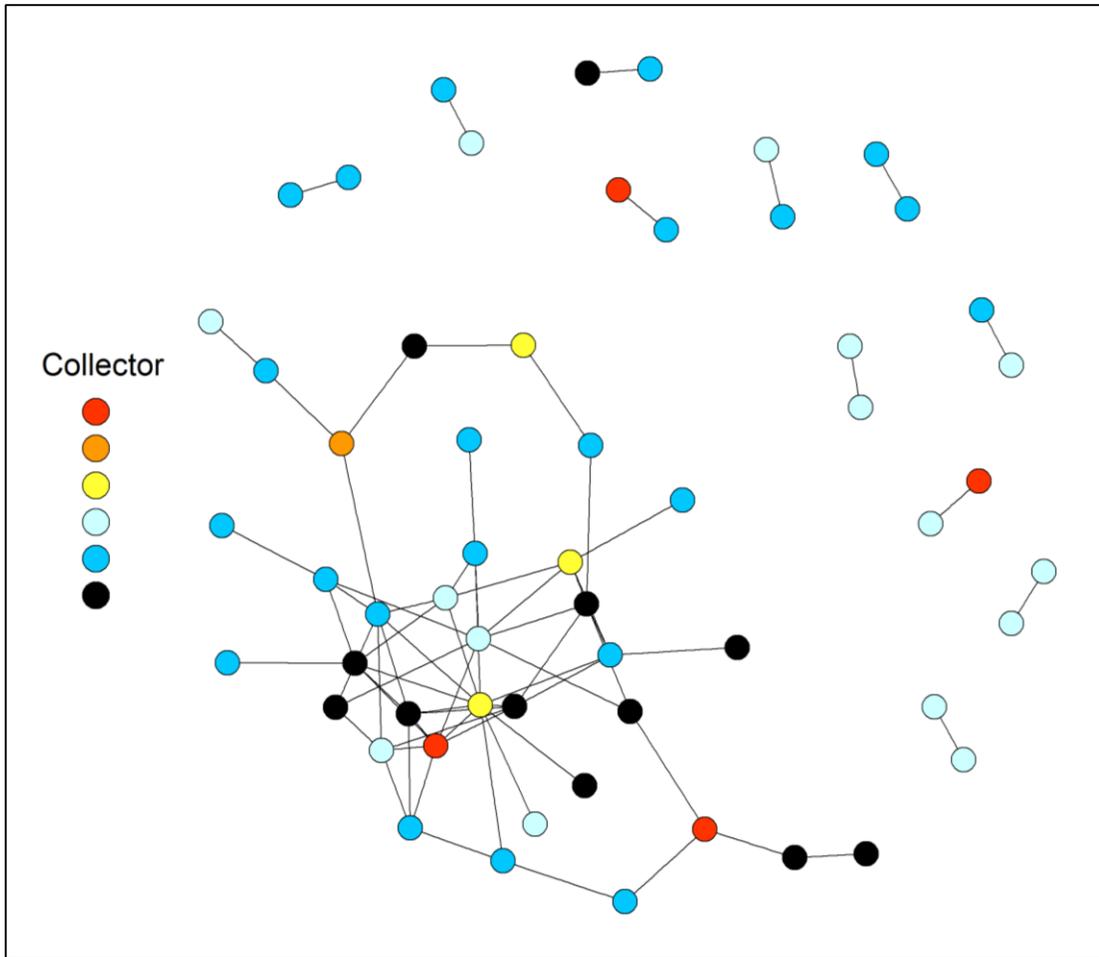


Figure 3.3. Recruitment of related splitnose rockfish (*Sebastes diploproa*) to a series of nearshore collectors along the Oregon Coast. Relatedness (r) was determined by analysis of 20 polymorphic microsatellites. Out of 491 recruits, 120,295 pairwise comparisons yielded 57 related individuals (circles), of which 35 were grouped into a single ‘family’ of half- and full-siblings (bottom-left web) and 22 formed independent sibling pairs. Collection location of each fish is color-coded to correspond with collector locations in Fig. 1. Related pairs ($r > 0.35$; $n = 74$) are indicated by connected circles. Arrangement and length of connecting lines are optimized for display purposes only. Some missing connections are expected due to false negative sibling relationships.

CHAPTER 4: GENERAL CONCLUSIONS

Dispersal and settlement of early life stages are fundamental processes in the lifecycle of most benthic marine organisms, but little is known about the mechanisms underlying such processes in temperate fishes with relatively long pelagic larval durations. To contribute to a better understanding of how dispersal and settlement occur, my collaborators and I conducted observational and hypothesis-driven studies to evaluate patterns and processes of fish dispersal and settlement in a temperate system. In the first data chapter (Chapter 2), we analyzed 6 yrs of fish settlement monitoring data (estimated as the presence of competent pelagic juvenile fish in midwater artificial settlement substrates) from along the Oregon coast. The analysis of this time series, including two regions located 233 km apart along the Oregon coast, revealed distinct species-specific spatial and temporal patterns of benthic fish settlement. The focal species or species complexes exhibited settlement peaks that occurred at different times of the sampling season and varied in the degree of episodic settlement. Evaluation of settlement patterns in the context of oceanographic conditions demonstrated that, with the exception of the fish taxa that settled at the largest sizes (black [*Sebastes melanops*] and yellowtail [*S. flavidus*] rockfishes), settlement was roughly and positively correlated with periods of downwelling and high water temperature (although only few of these correlations were significant). This finding suggests that fish taxa settling at larger sizes may have sufficiently strong swimming capabilities to counteract the offshore advective currents occurring during upwelling events. We also found that although the size of most taxa varied across the settlement season, size was not significantly related to water temperature.

However, because settlement size reflects both daily growth and duration of the pelagic phase, analysis of otolith microstructure is necessary to fully examine how temperature interacts with age and growth (Sponaugle 2010).

Comparing our results over broader spatial scales, we found that the within-season settlement peaks of our focal taxa occurred at similar times as in other regions along the California Current System (CCS; Wilson et al. 2008, Caselle et al. 2010, Jones & Mulligan 2014). This finding was unexpected because reproduction of most benthic species along the CCS occurs progressively later at higher latitudes (Love 2011). This surprising timing may be due to the presence of anomalous warm water temperatures in the northeast Pacific during 2013-16 (Hu et al. 2016), advancing the reproductive phenology of fish at higher latitudes. Cross-comparison of settlement magnitude revealed that while settlement magnitude of our two rockfish complexes along the Oregon coast were similar to those in central California, settlement of cabezon along Oregon's coast could be as much as twice the magnitude of cabezon settlement to central California (Wilson et al. 2008). We have no data on underlying causes: this difference may be driven by different abundances of the adult population of cabezon, or by differential survival of pelagic offspring. Further monitoring of fish settlement along the Oregon coast, combined with cross-regional comparison within the CCS, will likely reveal a wider effect that major oceanographic processes, such as the El Niño Southern Oscillation, Pacific Decadal Oscillation, North Pacific Gyre Oscillation, or anomalous alterations of water temperature have on settlement.

The settlement patterns reported in Chapter 2 are the product of adult reproduction and dispersal processes of offspring during their pelagic phase.

Knowing which species settle where, when, and in what numbers informs hypothesis testing regarding processes occurring during dispersal. For instance, the episodic arrival of a very large pulse of splitnose rockfish (*S. diploproa*) in 2013 led us to test whether there is cohesive dispersal of siblings over protracted periods of time, a topic that has been previously theorized (e.g. Broquet et al. 2013, Eldon et al. 2016), but never demonstrated empirically.

In Chapter 3, the hypothesis of whether larvae and pelagic juvenile splitnose rockfish disperse together was tested using a microsatellite genetic approach to analyze kinship. Our results revealed that a relatively large (11.6%) proportion of the individuals arriving to a site along the Oregon coast were full- or half-siblings. The occurrence of these siblings is only possible if fish remained aggregated throughout their long (4-6 mo) pelagic duration. This finding is the first evidence of such aggregation over a long period in an oceanographically dynamic area and therefore has fundamental implications for our understanding of larval dispersal. Biophysical modeling efforts often include an element of fish behavior as either simple vertical migration or directional swimming at the time of settlement (Werner et al. 2007). These findings highlight an underestimated layer of complexity in the dispersal process. At this stage, it is not clear how pervasive this process is among other marine organisms, but previous studies have found that older individuals at the same benthic location can be more closely related than expected based on a diffusive pattern of dispersal (e.g. Planes et al. 2002, Veliz et al. 2006, Iacchei et al. 2013). Thus, it is possible that such cohesive dispersal of siblings is common among a number of taxa with different pelagic larval durations.

Results of this thesis provide the first data on nearshore fish settlement for the Oregon coast and demonstrate the importance of individual behavior (i.e., cohesive dispersal), species-specific responses to ocean conditions (i.e., taxon-specific temporal patterns of settlement), frequency of cohorts in a given year (i.e., species-specific size frequency distributions in a sampling season), and regional differences in settlement magnitude (i.e., central vs. southern Oregon and Oregon vs. California). This information can be used to refine stock-recruitment models to improve management of fisheries. While these settlement data have not yet been compared to annual recruitment to the adult populations, such settlement records can potentially be used as an indicator of population replenishment. We urge consideration of these data to explore the inclusion of settlement information in stock assessments of groundfish (Cope & Key 2009). Results of these studies also have the potential to improve marine reserve management. Combined with the monitoring of new post-settlement individuals, these data can contribute to measurements of post-settlement mortality rates, thereby quantifying the degree to which habitats are ‘essential’ to the survival of juveniles (Pikitch et al. 2004). Several commercially and recreationally valuable fishes of the CCS live at depths >50 m, but their offspring settle to nearshore habitats before undergoing an ontogenetic migration to deeper waters (Love 2011). Although cross-shelf protected corridors would be ideal spatial management tools to promote the completion of their life cycles (Mumby 2006, Pendoley et al. 2014), protection of the settlement habitat may be sufficient to substantially reduce post-settlement mortality at this critical stage. Continued monitoring of settlement to the reserves will

reveal whether changes in the density of resident adult populations result from protection or from fluctuations in the settlement intensity.

This research would benefit from further study in a few key areas: (1) Some of our sampling seasons began as late as June or were completed as early as the first week of September, limiting the power of some analyses, and excluding the detection of settlement early and late in the season. Although weather conditions are the primary factor limiting sampling efforts from October to March, where possible, efforts should be made to maximize the length of the sampling season. (2) The assumption that there is no substantial loss of fishes from the SMURFs over a 2-wk sampling interval was tested in central California, where greater water visibility may affect piscivory and vertical migration of new settlers differently than in Oregon (Ammann 2004). Thus, it may be useful to test this assumption for fishes settling to the Oregon coast. (3) A 2-wk sampling interval is sufficiently frequent to describe seasonal and interannual variation of settlement; however, this interval is too long to effectively resolve settlement processes occurring at shorter frequencies, such as those in association with cycles of upwelling-relaxation events (2-6 d; Dudas et al. 2009). Reducing the sampling interval to 1 wk would enhance resolution, but would clearly entail higher costs. (4) Although the genetic kinship analysis employed a panel of 20 polymorphic microsatellite markers, there was still some overlap in the coefficient of relatedness among full-siblings, half-siblings, and unrelated fish. Future genetic studies should consider including additional markers.

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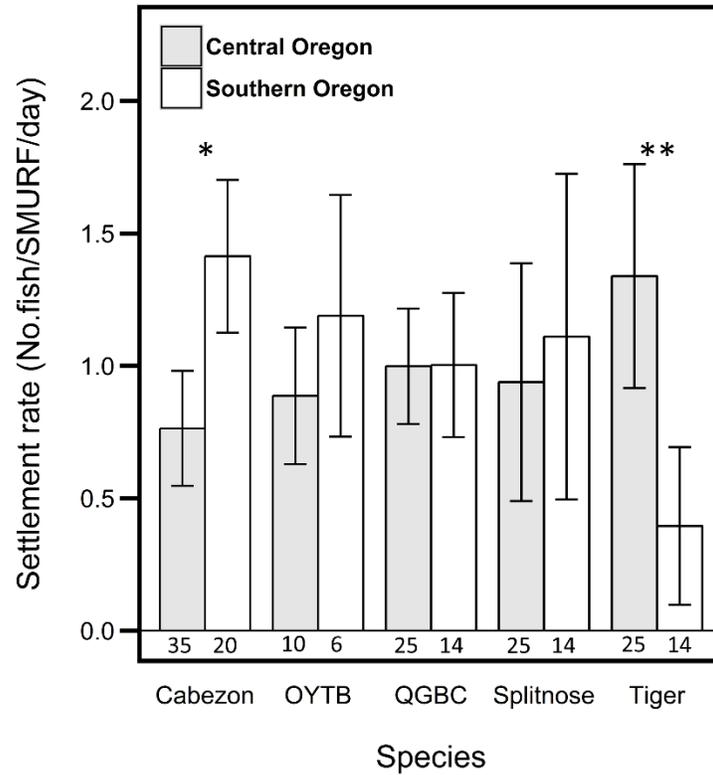
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APPENDIX A – CHAPTER 2 SUPPLEMENTARY TABLES AND FIGURES

Table S2.1. Fish recruits collected between 2011 and 2016 in central and southern Oregon using SMURFs. Boccacio (*Sebastes paucispinus*), splitnose (*S. diploproa*) and tiger (*S. nigrocinctus*) rockfishes, kelp greenling (*Hexagrammos decagrammus*), slimy snailfish (*Liparis mucosus*). Species complex: OYTB = olive, yellowtail and black rockfish; QGBC = quillback, gopher, black-and-yellow, copper, and china rockfish. UnID contains rockfishes, snailfishes (*Liparis* spp.), and gobies (*Gobiesox* spp.) that could not be identified to species or species complex.

	2011	2012	2013	2014	2015	2016	
Central Oregon	<i>Scorpaenichthys marmoratus</i>	25	24	127	65	241	267
	OYTB	1	1	16	125	13	279
	QGBC	4	116	52	2	203	668
	<i>Sebastes diploproa</i>	1	32	552	1	364	37
	<i>Sebastes nigrocinctus</i>	1	11	10	6	188	97
	<i>Sebastes paucispinus</i>	0	0	0	0	1	1
	<i>Hexagrammos decagrammus</i>	1	0	3	0	1	2
	<i>Liparis mucosus</i>	3	6	1	1	0	1
	UnID	0	5	4	2	2	8
	Total	36	195	765	202	1,013	1,360
Southern Oregon	<i>Scorpaenichthys marmoratus</i>			232	606	220	
	OYTB			191	16	722	
	QGBC			18	256	305	
	<i>Sebastes diploproa</i>			0	878	542	
	<i>Sebastes nigrocinctus</i>			0	27	110	
	<i>Sebastes paucispinus</i>			0	18	1	
	<i>Hexagrammos decagrammus</i>			10	27	23	
	<i>Liparis mucosus</i>			1	6	1	
	UnID			1	3	19	
Total			453	1,837	1,943		



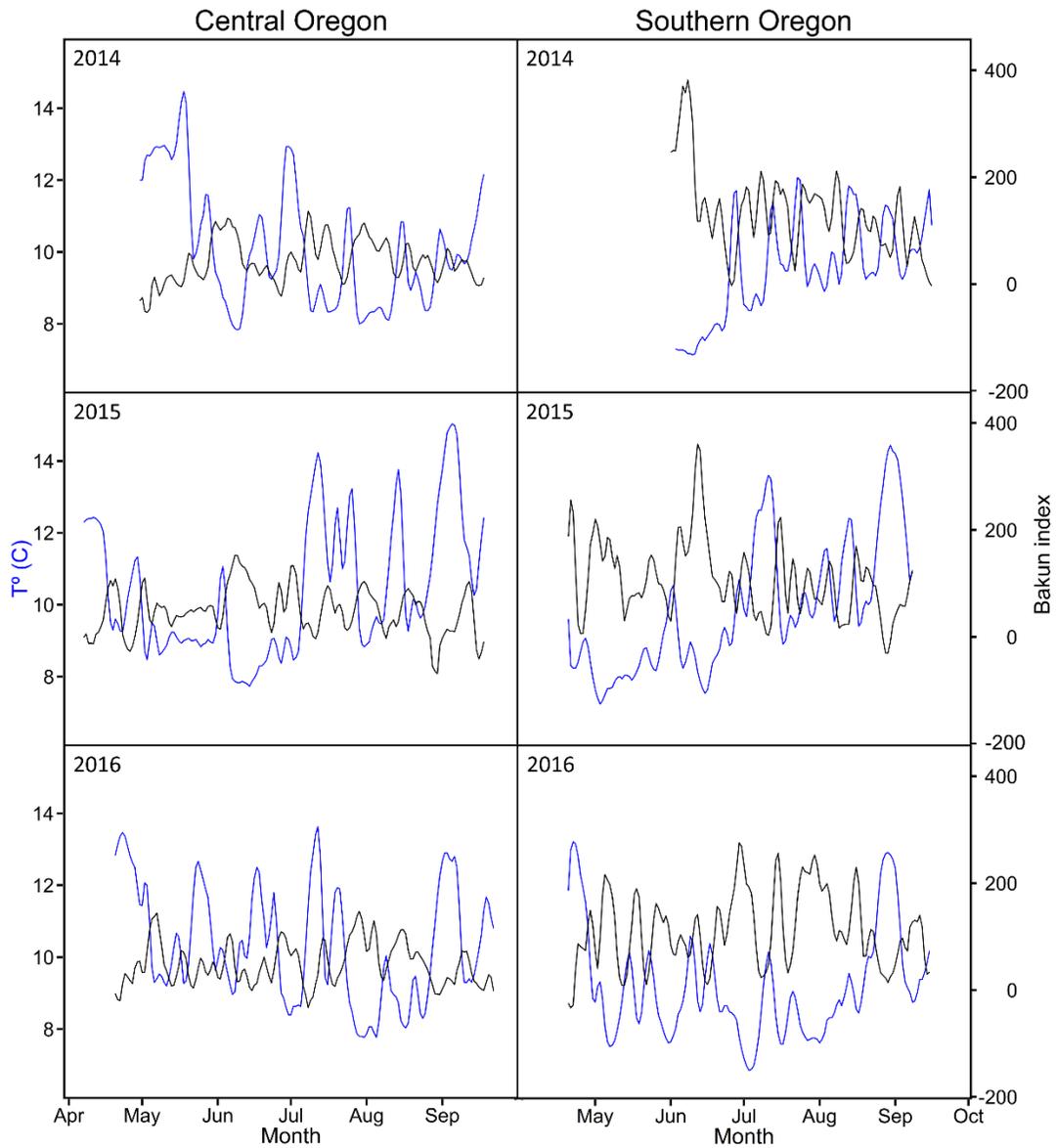


Fig. S2.2. Bakun index of upwelling (black) and *in situ* water temperature (blue) at central and southern Oregon during the 2014-16 sampling seasons. Daily Bakun index source: NOAA-PFEL; 45°N, 125°W and 42°N, 125°W.

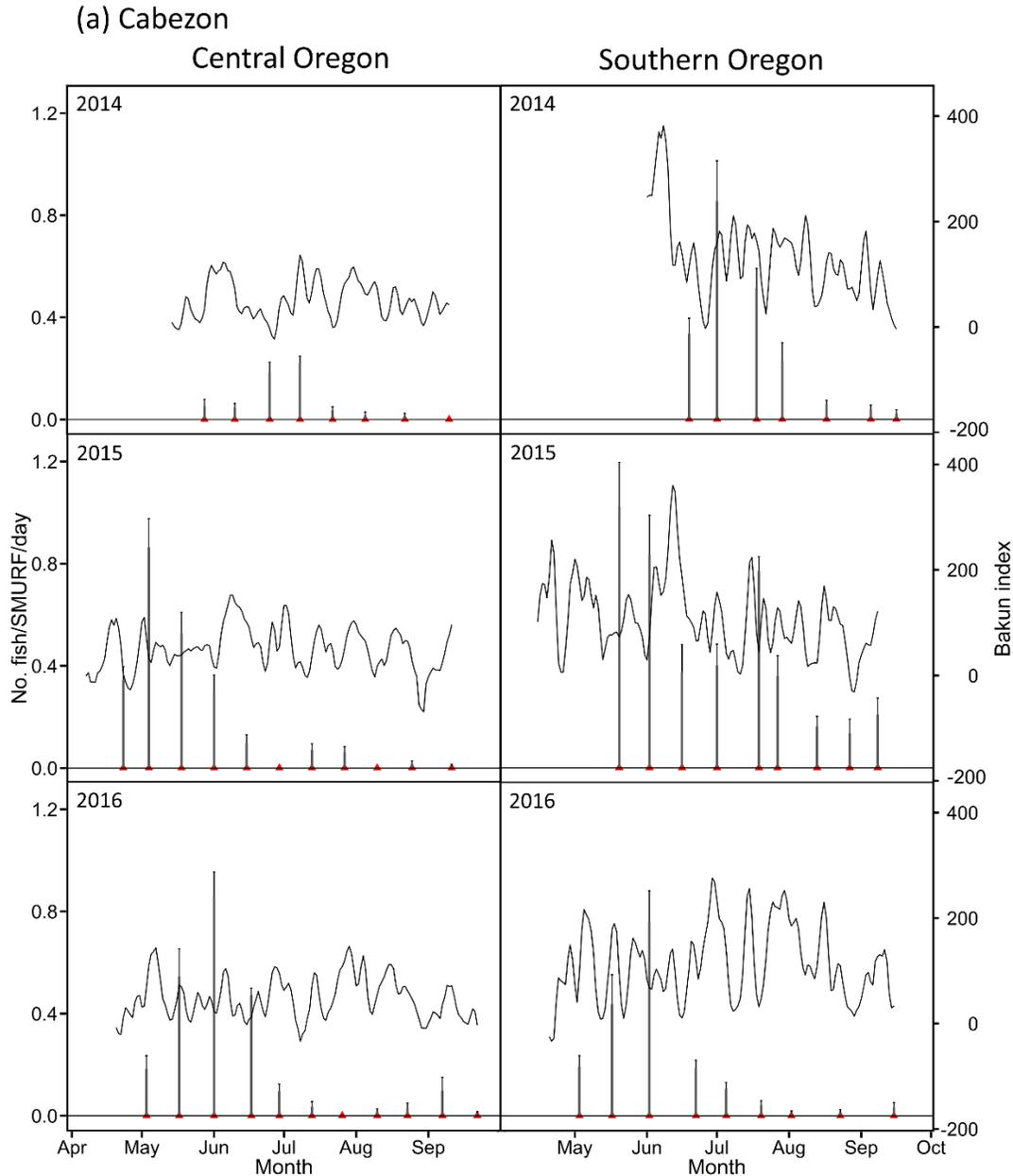
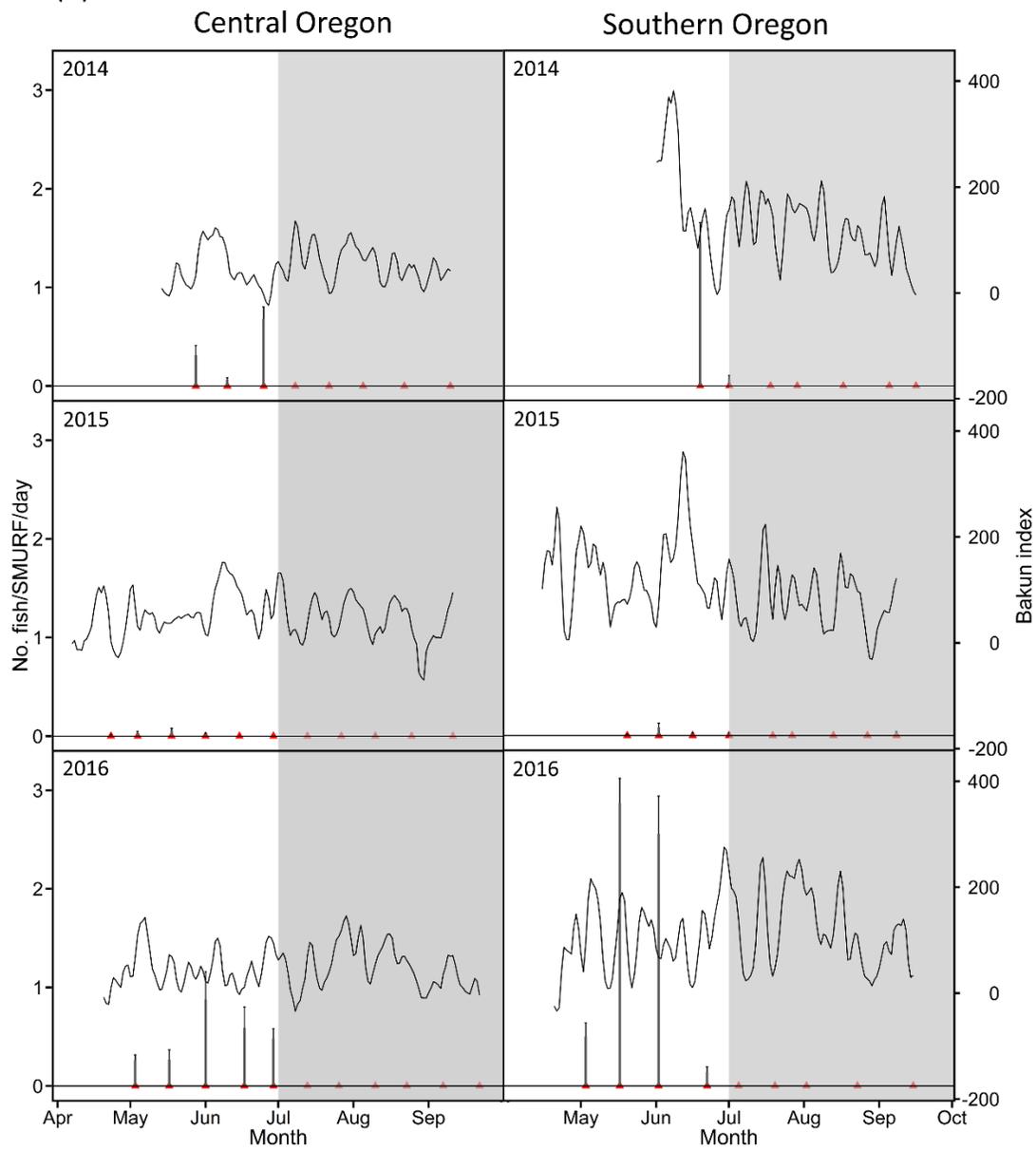
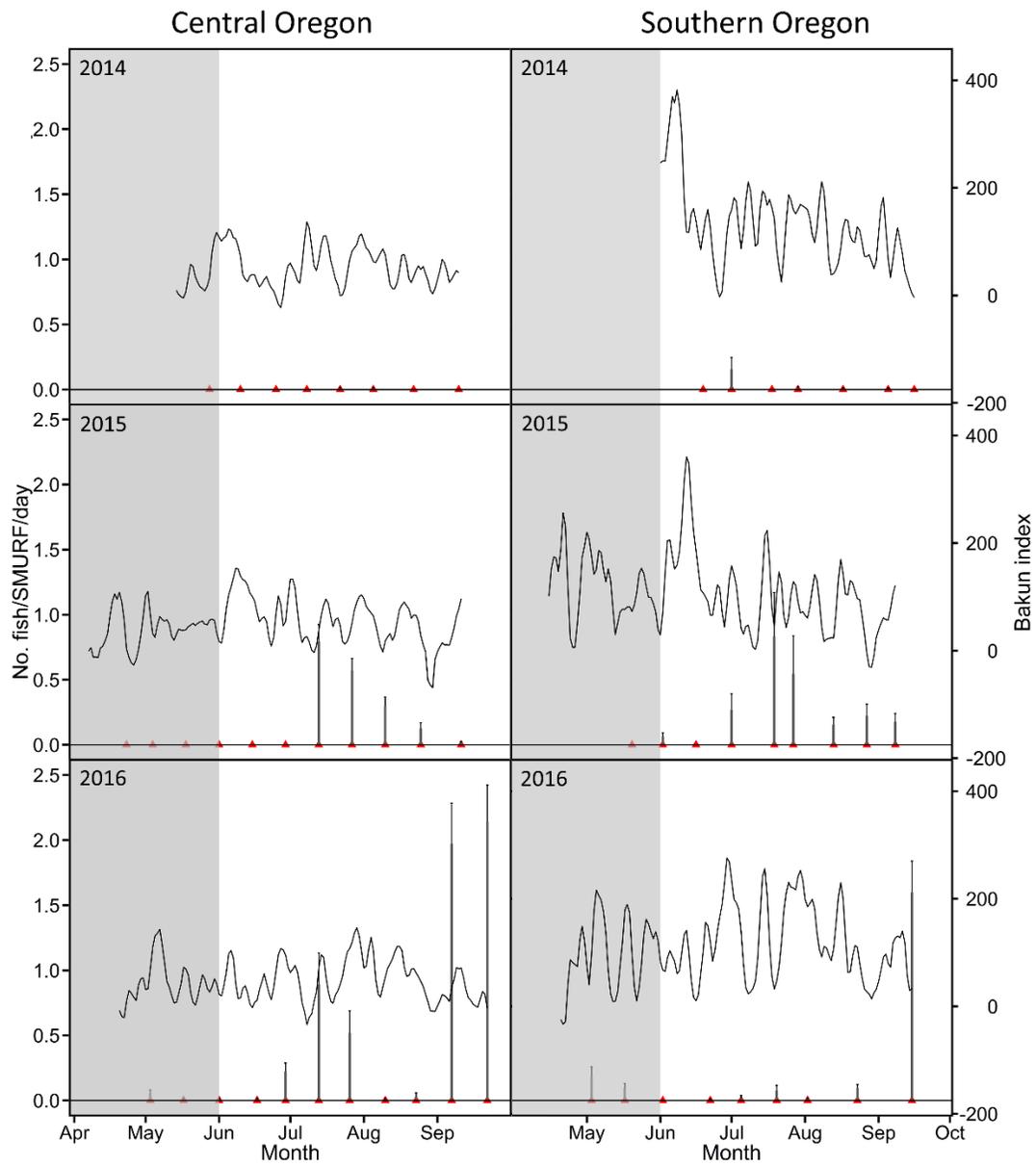


Fig. S2.3. Bakun index of upwelling and settlement rate (number of fish per SMURF per day) of five fish species or species complexes to central and southern Oregon during the 2014-16 sampling seasons. (a) cabezon (*Scorpaenichthys marmoratus*), (b) OYTB = olive, yellowtail, and black rockfishes, (c) QGBC = quillback, gopher, black-and-yellow, copper, and china rockfishes, (c) splitnose rockfish (*Sebastes diploproa*), (d) tiger rockfish (*S. nigrocinctus*). Shaded area indicates periods of infrequent settlement. Settlement rate (number of fish per SMURF per day) was averaged over all the replicate SMURFs within each region. Error bars indicate standard error ($n = 8$). Daily Bakun index source: NOAA-PFEL; 45°N, 125°W and 42°N, 125°W.

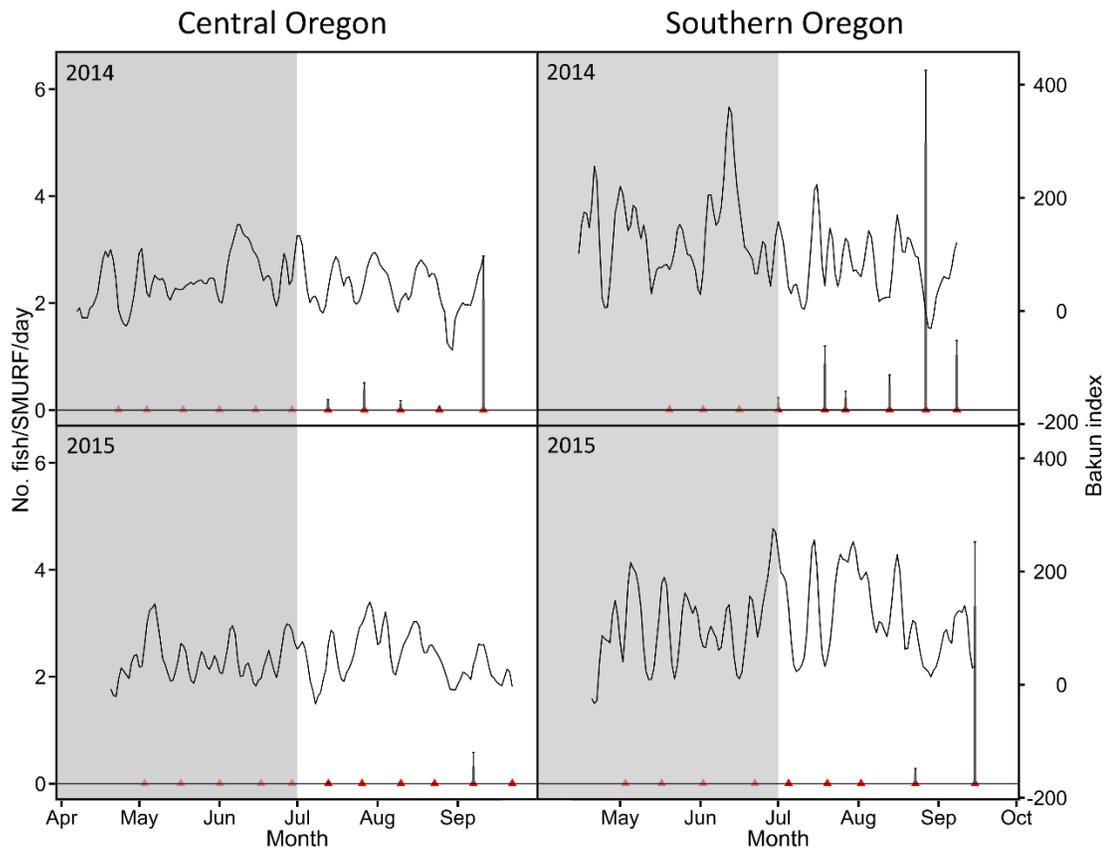
(b) OYTB



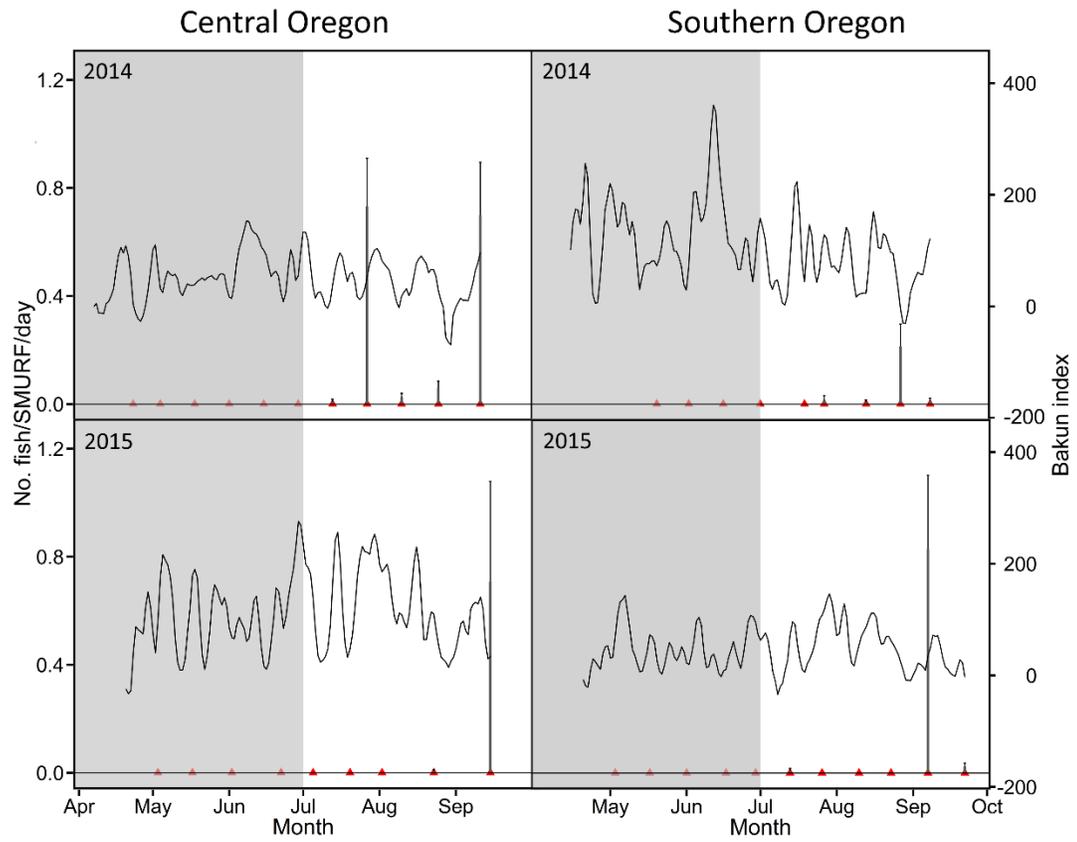
(c) QGBC



(d) Splitnose rockfish



(e) Tiger rockfish



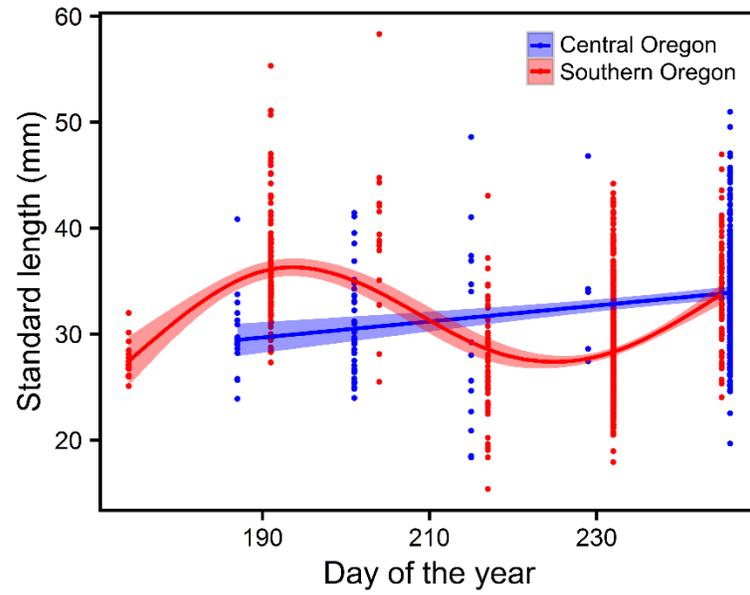


Fig. S2.4. Seasonal variation in standard length of splitnose rockfish (*Sebastes diploproa*) settling to the Oregon coast in 2015. Shading indicates the 95% CI.

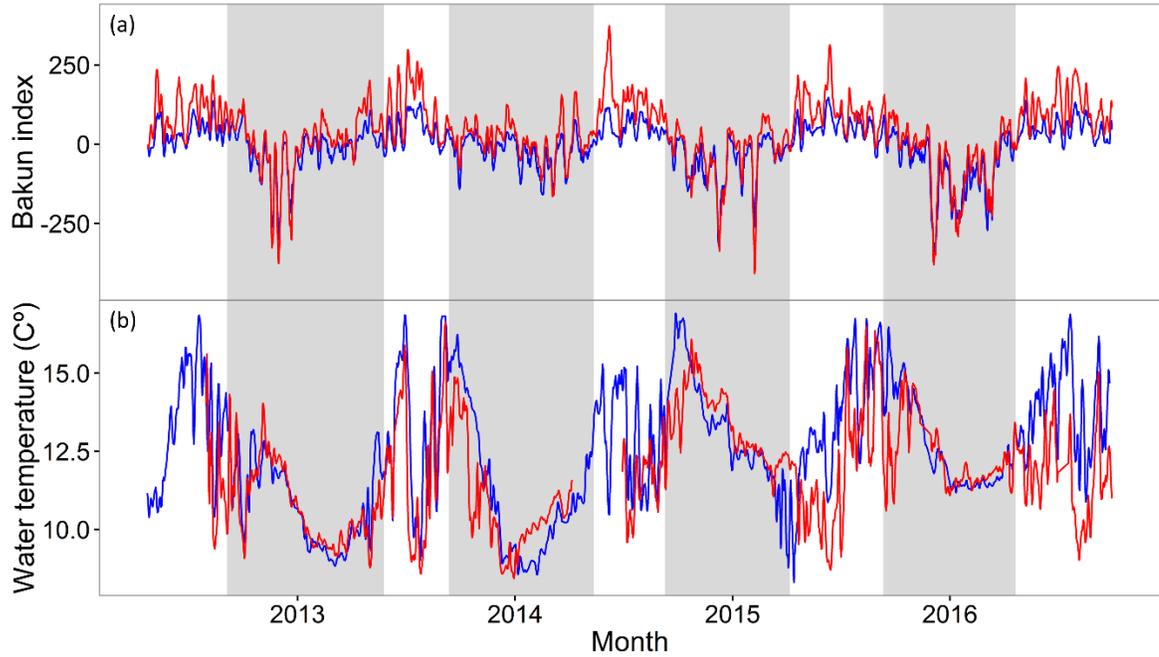


Fig. S2.5. Temporal fluctuations of (a) Bakun index of upwelling and (b) offshore water temperature at central (blue) and southern (red) Oregon through 2012-16. Daily Bakun index source: NOAA-PFEL; 45°N, 125°W and 42°N, 125°W. Water temperature source: NOAA-NDBC, Stations #46050 and #46015.

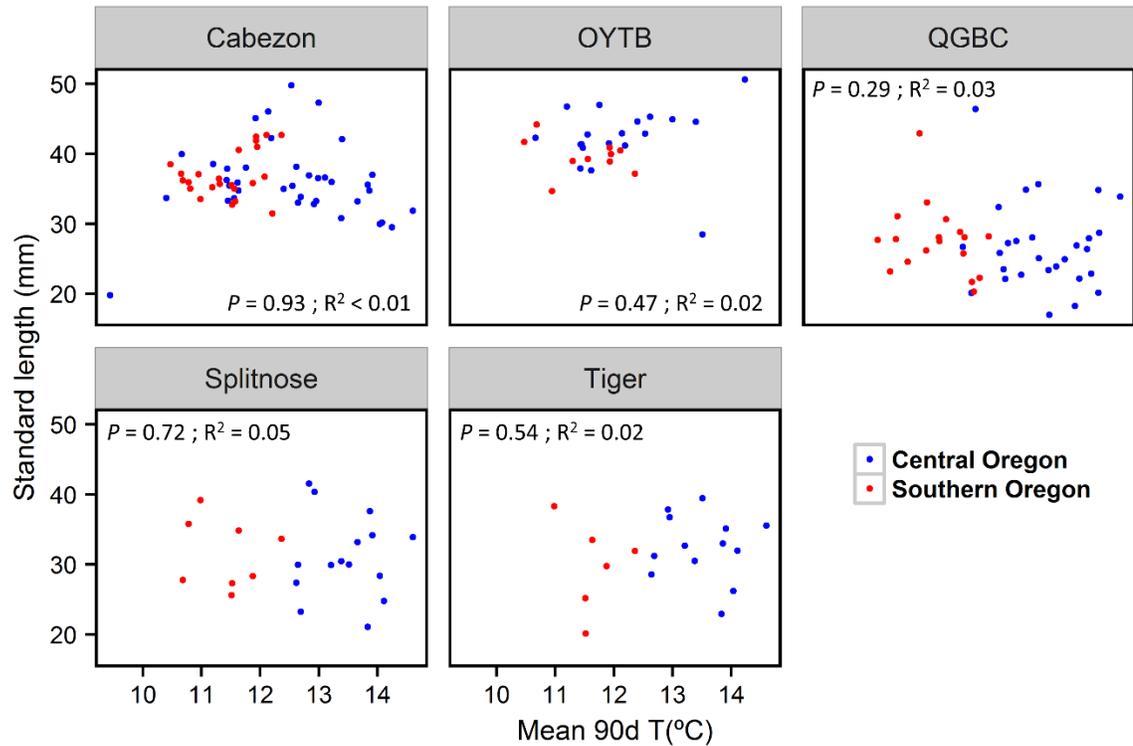


Fig. S2.6. Mean standard length of five fish species or species complexes versus the mean water temperature over 90 d prior to sampling during 2012-16. Standard length was not significantly related to water temperature, regardless of the region (color) where the samples were collected. Species complexes: OYTB = olive, yellowtail, and black rockfishes; QGBC = quillback, gopher, black-and-yellow, copper, and china rockfishes. Temperature source: NOAA-NDBC, Stations #46050 and #46015.

APPENDIX B – CHAPTER 3 SUPPLEMENTARY TABLES AND FIGURES

Table S3.1. Genotyping summary for splitnose rockfish (*S. diploproa*): 491 recruits and 94 adults from the reference population.

Locus	Recruit genotypes (n = 491)			Reference genotypes (n = 94)			E	Source
	A	H _E	H _O	A	H _E	H _O		
<i>Sal1</i>	34	0.95	0.90*	30	0.95	0.96	0.01	(Sekino et al. 2000)
<i>Sal2</i>	15	0.85	0.79*	12	0.84	0.79	0.03	
<i>Sal3</i>	11	0.61	0.60	08	0.58	0.59	0.02	
<i>Seb31</i>	24	0.82	0.79	21	0.85	0.82	0.03	(Roques et al. 1999)
<i>Seb33</i>	43	0.95	0.83*	28	0.96	0.86	0.05	
<i>Seb45</i>	16	0.87	0.86*	12	0.85	0.85	0.00	
<i>Sma10</i>	29	0.87	0.77*	20	0.84	0.84	0.07	(Wimberger et al. 1999)
<i>Sma11</i>	19	0.87	0.79*	19	0.86	0.80	0.01	
<i>Sma2</i>	07	0.55	0.47*	05	0.51	0.49	0.01	
<i>Sma3</i>	18	0.68	0.58*	14	0.61	0.60	0.00	
<i>Sma4</i>	24	0.84	0.84*	16	0.86	0.87	0.01	
<i>Spi10</i>	17	0.84	0.84	14	0.85	0.82	0.00	(Gomez-Uchida et al. 2003)
<i>Spi14</i>	17	0.84	0.70*	12	0.87	0.77	0.01	
<i>Spi18</i>	54	0.92	0.92*	30	0.89	0.89	0.02	
<i>Spi4</i>	30	0.75	0.75	17	0.71	0.73	0.03	
<i>Spi6</i>	31	0.85	0.71*	19	0.86	0.68*	0.05	
<i>Sra15.8</i>	16	0.73	0.69*	08	0.54	0.47	0.02	(Buonaccorsi et al. 2002)
<i>Sra7.2</i>	26	0.87	0.87*	23	0.88	0.87	0.02	
<i>Sra7.25</i>	30	0.90	0.88*	24	0.9	0.88	0.04	
<i>Sra7.7</i>	08	0.52	0.49	06	0.59	0.62	0.02	
Average	22.7	0.78	0.72	16.9	0.79	0.76	0.02	

(A) Number of alleles, (H_E) expected heterozygosity, (H_O) observed heterozygosity, (E) genotyping error rate.

* Significant deviations from Hardy-Weinberg proportions (Bonferroni adjusted Markov Chain (Guo & Thompson 1992) $P < 0.05$).

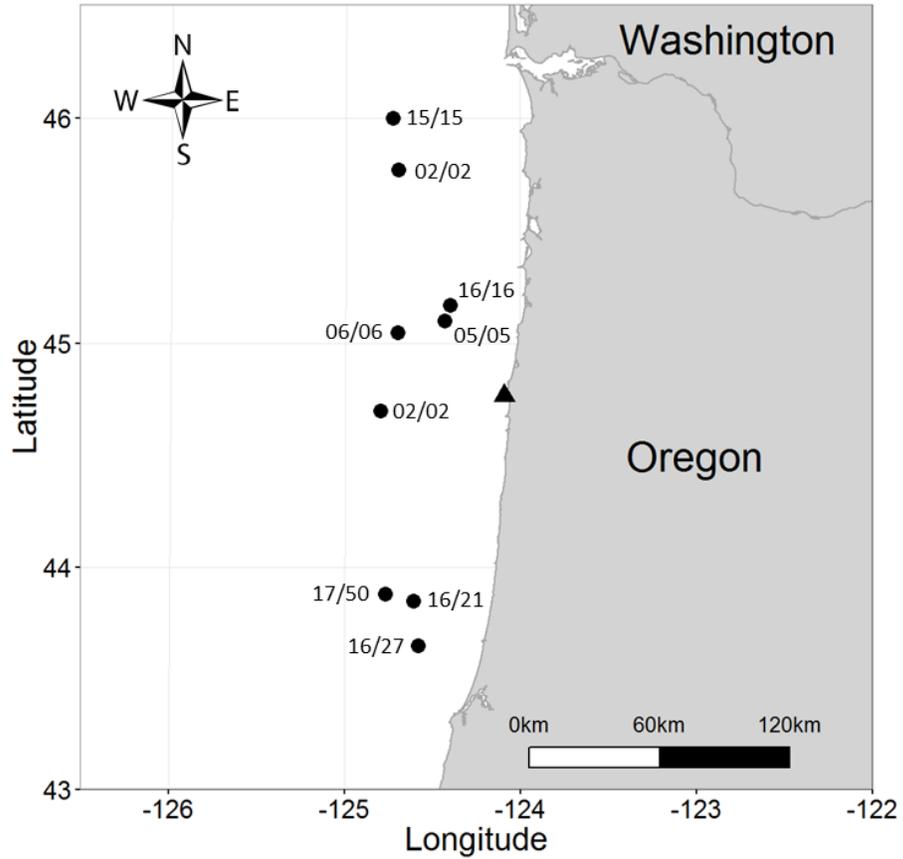


Figure S3.1. Sampling locations (circles) of 144 adult splitnose rockfish (*Sebastes diploproa*) used as the reference population. Sampling depth ranged between 117 and 225 m. Values indicate the number of fish genotyped/collected at each location. Sampling location of splitnose recruits indicated by the black triangle.

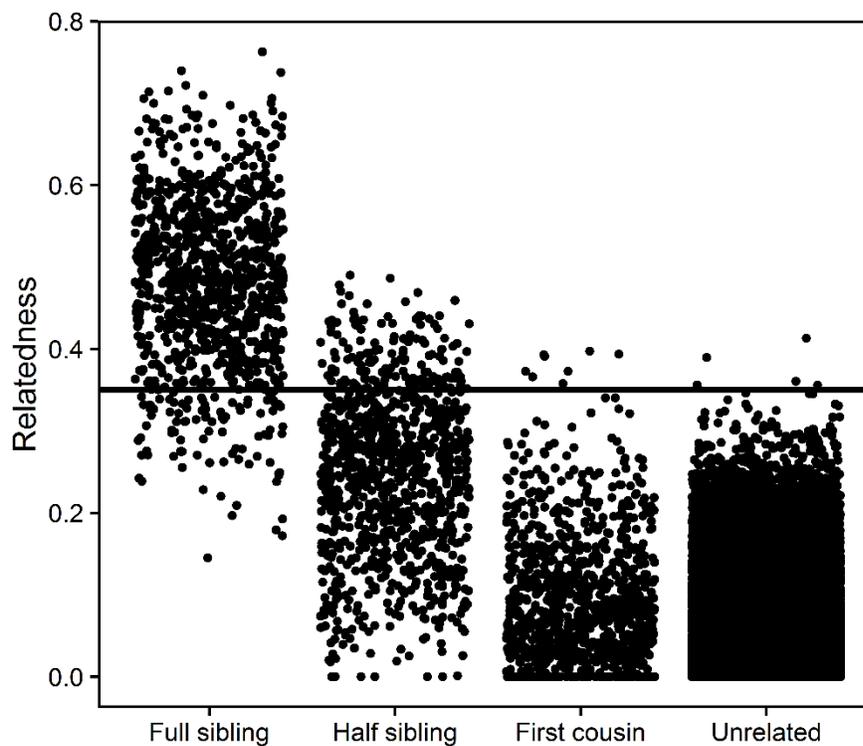


Figure S3.2. Relatedness estimates (r) of simulated half-sibling, full-sibling, first cousin, and unrelated pairs using the Triadic IBD estimator of relatedness (Wang 2007). 90 % of the 1,000 full-sibling pairs, 16% of the 1,000 full-sibling pairs, and 0.8% of the 1,000 first cousin pairs had an $r \geq 0.35$ (horizontal line). On average, $\sim 6 \pm 2$ (mean \pm SD) of the 120,295 pairwise comparisons generated by each one of the 491 unrelated individuals had an $r \geq 0.35$ (only one of the 100 simulated dataset outputs is shown).

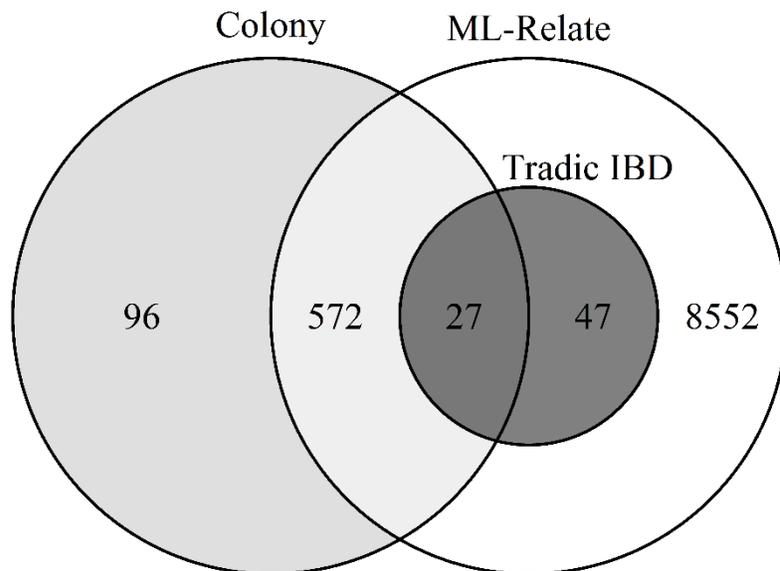


Figure S3.3. Number of siblings identified among 491 co-recruiting splitnose rockfish using Colony (light gray-filled circle; 695 pairs), ML-relate (white-filled circle; 9,198 pairs), and the Triadic IBD estimator of relatedness (dark gray-filled circle; 74 pairs). Circles are not drawn to scale and values indicate number of sibling pairs. Coinciding sibling pairs identified by multiple approaches are indicated by overlapping circles. There is relatively little overlap among the sibling pairs identified using Colony and the Triadic IBD estimator. A power analysis based on simulated data indicated that the Triadic IBD estimator performed best.

APPENDIX REFERENCES

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