Persistent regional variation in populations of a tidepool fish

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Abstract

Understanding the factors that drive population dynamics is particularly challenging in systems that are connected via propagule dispersal because the rate of arrival of new individuals is both notoriously unpredictable and potentially critical in determining future dynamics. Furthermore, patterns of propagule recruitment can be fundamentally modified by post-recruitment interactions. We investigated how variation in both the recruitment of juveniles and local community structure affected the demography of an intertidal fish in two oceanographically distinct regions in Oregon. From 2001–2003, we observed persistently higher densities of adult tidepool fish *Clinocottus globiceps* (Girard) at Cape Foulweather, a stronger-upwelling region compared to Cape Perpetua, a weaker-upwelling region. In 2002, recruitment was roughly two times higher in the Cape Perpetua region. By the following spring, densities of adults were more than three times higher in the Cape Foulweather region, implicating intense post-recruitment mortality in the Cape Perpetua region as the cause of regional differences in adult densities. We manipulated, using a factorial experimental design, the presence and absence of dominant sessile organisms in tidepools at one site in each region in the spring of 2002 and explored whether differences in tidepool communities could be related to regional variation in fish abundance. Fish recruited disproportionately to pools with low cover of mussels in both regions. By the following spring, adults were more abundant in pools with mussels in one region and equally abundant in pools with or without mussels in the other region. Possible explanations for regional differences in *C. globiceps* populations include regional variation in the cover of intertidal invertebrates, in local biological interactions such as predation, or in coastal bathymetry that may be linked to variation in physical processes controlling recruitment and over-winter survival.
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1. Introduction

In recent years, ecologists have placed increasing emphasis on understanding how regional-scale processes impact local ecological communities (Holt, 1993; Menge, 2000b). The importance of regional-scale processes is especially true for many benthic marine animals with complex life histories in which larval stages may experience long-distance planktonic dispersal while adults are

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relatively sedentary (Roughgarden et al., 1988; Leis, 1991; McEdward, 1995; Eckert, 2003). Such communities are often termed 'open' because the rate of arrival of new individuals through settlement can be decoupled from local production during dispersal. Rates of settlement to local populations may be partly determined by regional oceanographic processes that underlie the survival and transport of larvae (Houde, 1987; Menge et al., 1997; Connolly and Roughgarden, 1999; Swearer et al., 1999). Following settlement, individuals are frequently subjected to a suite of intense post-settlement interactions that can alter patterns established at settlement (Hixon, 1991; Eggleston and Armstrong, 1995; Menge, 2000a; Hixon and Webster, 2002). Thus, the abundance of adults may be jointly determined by both patterns of settlement and post-settlement interactions (Connell, 1985; Jones, 1991; Caley et al., 1996; Menge, 2000a; Minchinton and Scheibling, 1991).

Determining the relative importance of settlement patterns and post-settlement processes for marine populations has become a key goal in ecology (Caley et al., 1996). The rocky intertidal zone has served as a model system in ecology, in which much progress has been made in measuring the contribution of both settlement and post-settlement processes in shaping ecological communities (Menge and Branch, 2001). For example, studies of barnacles have determined that the relative importance of recruitment, an estimate of the number of new individuals that enter a population, and post-recruitment interactions varies from site to site (Gaines and Roughgarden, 1985; Menge, 2000a). Similarly, previous studies of coral reef fish have demonstrated that the relative strength of recruitment and post-recruitment processes may be site dependent (Caselle, 1999) and that post-recruitment mortality may produce adult abundance patterns that do not reflect spatial variation in recruitment (Caselle et al., 2003). Because regional differences in circulation patterns may drive local recruitment patterns (Gaines and Roughgarden, 1985; Menge, 2000a), understanding between-site variation in ecological patterns may require a larger-scale perspective in which regional processes determine the intensity of local-scale interactions (Roughgarden et al., 1988).

Extensive work in intertidal systems in Oregon has highlighted how regional-scale processes can set the context of ecological interactions. Studies by Menge and colleagues have shown substantial variation in rocky intertidal communities between two regions of the Oregon Coast: Cape Perpetua (44°15′N, 124°07′W) and Cape Foulweather (approximately 80 km to the north; 44°50′N, 124°03′W, Fig. 1a, b) (Menge et al., 1997, 2002). Regional patterns may stem from fundamental differences

in coastal circulation caused by continental shelf bathymetry that is relatively narrow near Cape Foulweather and wide near Cape Perpetua (Kosro et al., 1997; Menge et al., 1997). Variation in circulation patterns (Fig. 1b) generates different intensities of upwelling (Barth and Wheeler, 2005; Kosro, 2005; Tapia et al., unpublished data) and thus the degree of retention or dilution of propagules, nutrients, and seston to intertidal communities. Judging from rates of recruitment of mussels and concentration of phytoplankton, retention is greater at Cape Perpetua, with weaker-upwelling, than at Cape Foulweather with stronger-upwelling (Menge et al., 1994; Menge, 2000a, 2002). Such variation in oceanographic subsidies has been identified as a likely candidate driving regional differences in the abundance, growth rates and composition of invertebrates and algae (Menge et al., 1997; Menge, 2004). Further, at Cape Perpetua mussel bed disturbance from winter storms and rate of recovery are greater than at Cape Foulweather (Guichard et al., 2003). A final difference between these sites is that massive sand incursions occur in late summer and early autumn at Cape Perpetua but not at Cape Foulweather (Menge et al., 1994), often burying and smothering mussels, barnacles and algae. These differing suites of processes are believed to underlie differences in community structure: Cape Perpetua communities tend to be dominated by sessile invertebrates, whereas macrophytes tend to dominate those at Cape Foulweather (Menge et al., 1994, 2002; Menge, 2000a).

Rocky intertidal communities are also home to a diverse suite of benthic fishes (Gibson and Yoshiyama, 1999), which are considerably less well studied. Many intertidal fishes have a planktonic phase in their life history (DeMartini, 1999; Pfister, 1999), and previous work has demonstrated effects of both recruitment and post-recruitment interactions on populations and communities of rocky intertidal fishes at Tatoosh Island on the outer coast of Washington state (Pfister, 1995, 1996, 1997, 1999).

Here we address the issue of how recruitment and abundance of rocky intertidal fishes vary both locally and in relation to large-scale oceanographic variation. Specifically, we conducted studies at replicate sites in two regions along the Oregon coast, Cape Foulweather and Cape Perpetua (Fig. 1a, b), to examine whether previously observed regional variation in intertidal algal and invertebrate communities extended to populations of a highly abundant intertidal fish, the mosshead sculpin (*Clinocottus globiceps*). We hypothesized that *C. globiceps* populations at Cape Perpetua would be more abundant and would experience increased recruitment and growth relative to populations at Cape Foulweather
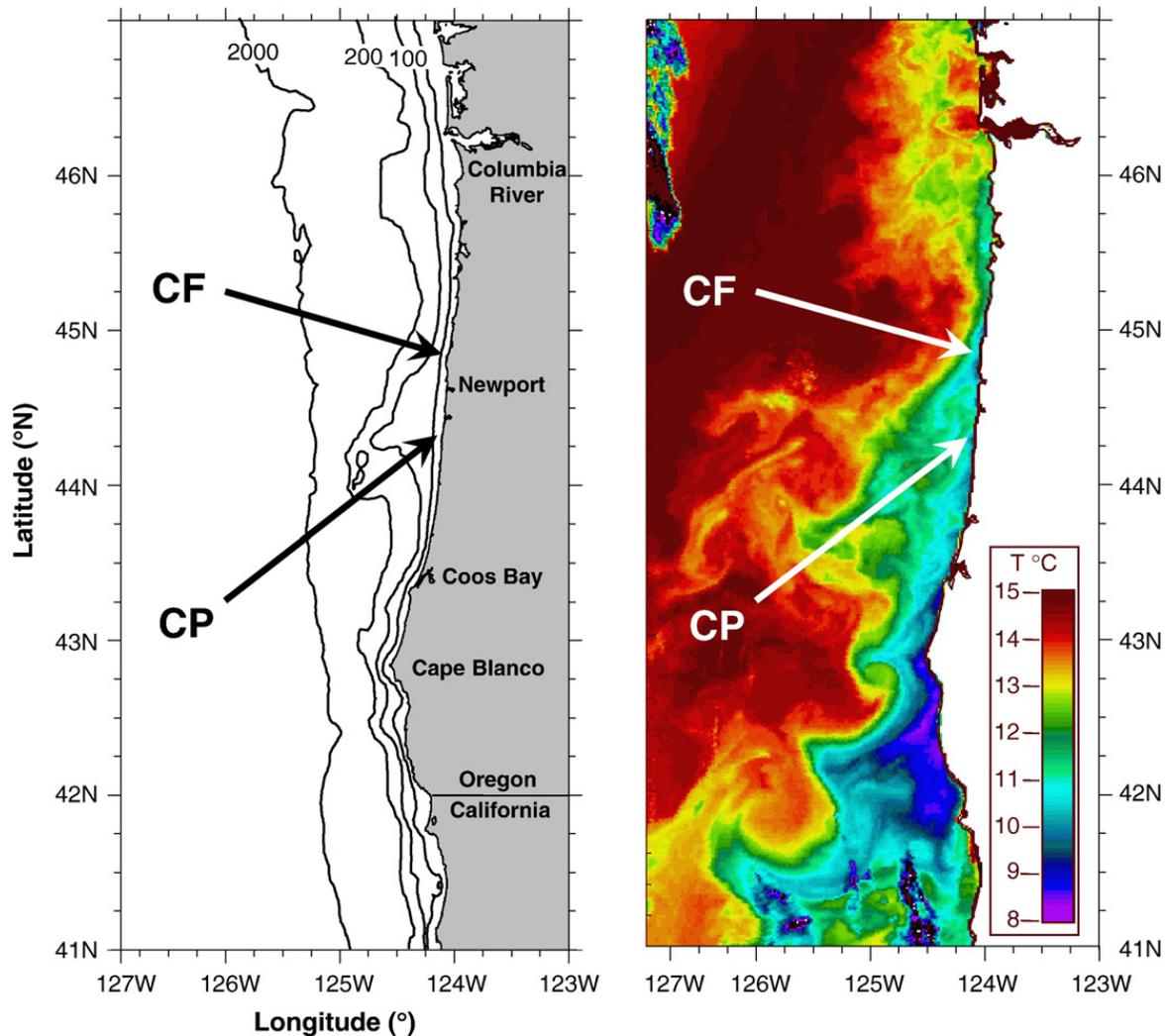
Fig. 1. The coastal bathymetry (a) and sea surface temperatures (b) along the Oregon coast, with reference to the two study regions, Cape Foulweather (CF) and Cape Perpetua (CP).

(i.e., similar to filter-feeding invertebrate populations at each cape). We asked three specific questions: (1) Does the abundance of *C. globiceps* vary between regions? (2) Does regional variation in *C. globiceps* result from differences in the cover of dominant algae and invertebrates? (3) Are regional differences in *C. globiceps* populations the result of regional variation in recruitment or post-recruitment processes? To answer these questions, we used a two-tiered approach combining observations of regional differences in *C. globiceps* populations and a targeted experiment to address mechanisms that might underlie regional patterns.

2. Methods

2.1. Study species

Sculpins, family Cottidae, are abundant members of rocky intertidal communities along the U.S. West Coast (Gibson and Yoshiyama, 1999). In Oregon, sculpins comprise roughly 99% of the fish captured in mid-zone tidepools, of which roughly two-thirds are mosshead sculpins, *C. globiceps* (Webster, unpublished data). *C. globiceps* are fast growing (Chadwick, 1976; Mgaya, 1995), highly productive (Mgaya, 1992) and have planktonic larvae that recruit to tidepools throughout the spring and summer (Grossman, 1982; Pfister, 1997, 1999). Like many intertidal fishes, *C. globiceps* have highly catholic diets that include both plant and animal material, although, in some areas, they have been shown to selectively forage on sea anemones and various algal species (Yoshiyama, 1980; Grossman, 1986; Norton and Cook, 1999, Osborne-Gowey, personal observations). At low tide, *C. globiceps* seek refuge in tidepools where, due to strong site fidelity and homing behavior (Green, 1971; Yoshiyama et al., 1992), they can be repeatedly captured over periods of many months (Pfister, 1996, 1997).

2.2. Regional monitoring

We monitored tidepool fishes at five wave-exposed, rocky intertidal sites, two at Cape Foulweather (Boiler Bay and Fogarty Creek), and three at Cape Perpetua (Yachats Beach, Strawberry Hill, and Gull Haven). In 2000, we monitored only two of the sites, Strawberry Hill and Fogarty Creek, while all five sites were monitored in 2001 and 2002. The temporal extent of monitoring varied among years, but typically began in the spring and continued through the summer or into fall (Fig. 2), except in 2003 when each site was sampled only once in spring. We did not sample during winter months due primarily to dangerous field conditions caused by high waves during nocturnal low tides.

At each site, we located tidepools within mussel beds. The primary criterion for selection was that they were isolated such that movement between pools was prevented at low tide, although movement among pools was possible during high tide. The number of pools varied among sites, ranging from 5 to 9, and some pools originally monitored were subsequently eliminated from monitoring when they were no longer isolated due to large shifts in mussel beds. Pools ranged in volume from 14 to 280 L with an average of 78.8 L (SE=9.23). We drained tidepools during each sampling period using siphons and manual bilge pumps. As pools were draining, we added a small amount of clove oil to each pool to anesthetize and immobilize fishes (Munday and Wilson, 1997; Wagner et al., 2003). Once pools were drained, we captured anesthetized fishes and transferred them to buckets filled with clove oil-free seawater to allow recovery from anesthesia. We flushed and filled each pool, after a thorough search, with fresh seawater to remove residual clove oil.
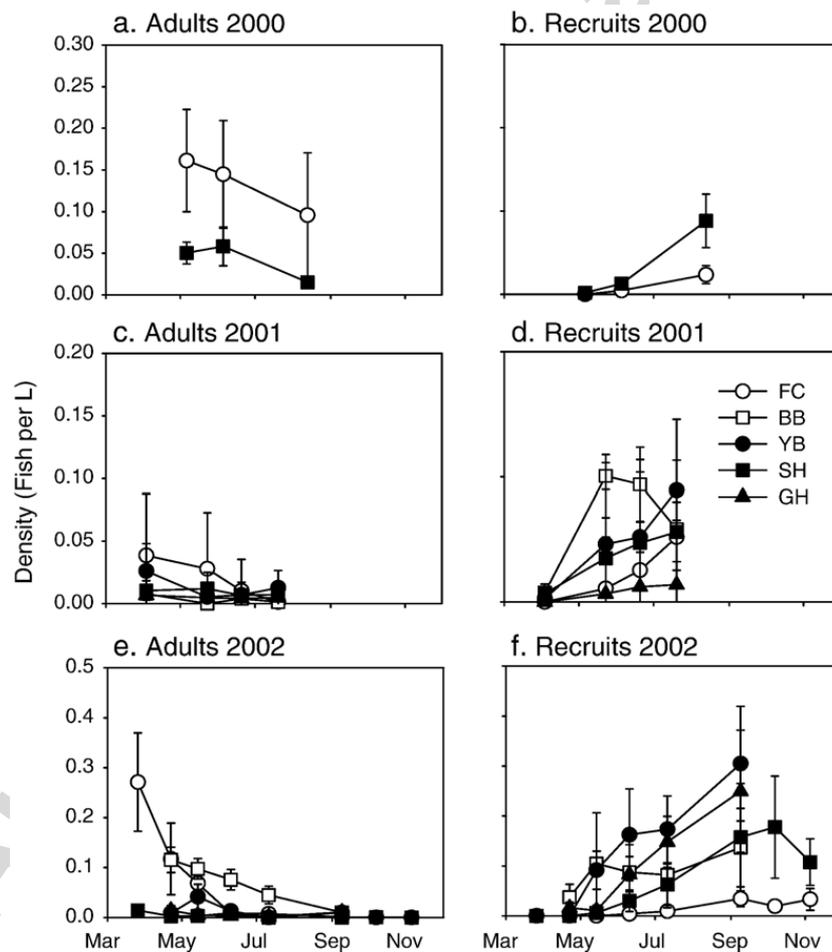

Fig. 2. Temporal dynamics of adult (a, c, e) and recruit (b, d, f) *Clinocottus globiceps*. Recruits were defined as young-of-year fish. Data points represent the average (±SE) density in replicate pools at each site on each sampling date. Fish density is scaled separately for each year to emphasize spatial and monthly patterns. Two sites were sampled in 2000, Fogarty Creek (FC) and Strawberry Hill (SH), while all five sites were sampled in 2001 and 2002. Regions are denoted by filled (Cape Perpetua) and open (Cape Foulweather) symbols, and sites are arranged in latitudinal order in the legend with the most northerly site (FC) at the top. In 2002, Strawberry Hill and Fogarty Creek were sampled in March, October and November, while Boiler Bay (BB), Yachats Beach (YB), and Gull Haven (GH) were not.

We identified the captured fish to species (Lamb and Edgell, 1986), measured (mm Standard Length, SL), tagged, and released them back to the pool from which they were captured. We defined recruits as all young-of-year fish found in pools in the summer and fall, and therefore recruit density was equivalent to the total density of juvenile fish in each pool, since maturation occurs the year following settlement (Pfister, 1997; Webster, personal observations). We defined adults as all individuals that did not settle that year, and therefore were either reproductively mature or nearing maturity. The size cut-off used to distinguish between recruits and adults changed throughout the season as new recruits and older fish grew. At all times, length frequency distributions were bimodal (Webster, unpublished data), so the nadir between modes was used as the size cut-off to help distinguish between recruits and adults.

We also measured the volume of each pool at low tide and used this size to calculate the density (fish per L) of fish in each pool, which standardizes density among pools of varying sizes and shapes and incorporates measures of both pool area and depth. By using volume to calculate fish densities, we accounted simultaneously for differences among pools in benthic substratum, which is likely associated with habitat availability, and in pool depth, which is likely associated with predator avoidance as well as physical conditions at low tide.

We tagged individuals with either elastomer or alphanumeric tags (Northwest Marine Technology). Elastomer is a silicone-based material that is pigmented and injected subcutaneously. Because elastomer solidifies after injection, it makes a permanent tag (Buckley et al., 1994; Beukers et al., 1995). Alphanumeric tags are small silicone rectangles with a letter and a two-digit number that, once injected subcutaneously with a wide-gauge needle, can be read through transparent skin. All tags were placed on the ventral surface of sculpins because in this area sculpins are typically only lightly pigmented, permitting the visual identification of tagged individuals. Whenever possible, we marked individual sculpins with unique tags by using different tag location and color combinations for elastomer tags, and unique letter–number combinations for alphanumeric tags. Because of the large needle size required to inject alphanumeric tags, fish greater than ∼40 mm SL were tagged with alphanumeric tags, while those less than ∼40 mm SL were tagged with elastomer.

The purpose of tagging fish was twofold. First, we tagged fish to monitor differences in growth for recaptured fish among sites in 2002. Second, by tagging and recapturing individuals, we were able to distinguish between recruits (young-of-year fish) and adults from previous years for recaptured fish. In late spring and early summer, recruits and adults can be easily distinguished based on their size, resulting in a strikingly bimodal length frequency histogram (Webster, unpublished data). As recruits rapidly grow over the summer and fall, they approach the size of adults from previous years, although these large recruits are not yet reproductively mature. By tagging all the fish we captured, we were able to accurately differentiate between large recruits and older adults for recaptured fish, even in late summer and fall when the size of large recruits approached the size of small adults.

2.2.1. Adult abundance

Based on the natural history of intertidal sculpins and field observations, we focused on adult abundances in the spring. In particular, because *C. globiceps* is reproductive in the winter and spring (Pfister, 1997; Webster, personal observations), densities of adults in spring are likely to estimate the reproductive population. Thus we treated spring densities as a critical endpoint that summarizes the potential reproductive success of fish populations in each year. We examined regional differences over four years, from 2000 to 2003. Spring measurements were made in either April or May in all cases except three sites that were measured in June of 2003 (Boiler Bay, Yachats Beach, and Gull Haven).

By not sampling every site in the same month every year, we may have inadvertently introduced bias because the populations of adult sculpins generally decrease over the summer. Bias would be expected to be most severe if the timing of sample collection varied predictably among regions (e.g., if Cape Perpetua populations were always sampled later in the year than Cape Foulweather samples). However, when sites were sampled at two separate times within a year (i.e., in 2003), sites from each region were sampled during both sampling periods. This sampling scheme decreased the potential for spurious conclusions that might arise from bias, since variation among sites within each region was non-significant and small relative to variation between regions (see Results Section). Bias could also exist among years such that the timing of sampling could affect the overall abundance of adult sculpins (e.g., sites sampled earlier in the year could appear to have a greater adult abundance of sculpins). An examination of the temporal trends in sculpin abundance (Fig. 2), however, shows that this type of bias was unlikely to be present in our analyses. Large year-to-year differences in adult abundance were evident well into the summer (i.e., well beyond the spring comparison), indicating that among-

year biases due to the times of sampling were likely small in comparison to natural among-year variation.

Because only two sites were monitored in the spring of 2000, we compared adult densities in this year with a simple *t*-test of differences between sites. We used comparable data from 5 sites in 2001–2003 to calculate a factorial nested ANOVA (Sokal and Rohlf, 1995; Zar, 1999) that included terms for Year, Region, Year * Region interaction, Site (Region), and Pool (Site, Region). Adult densities were $\ln(x+0.01)$ transformed to normalize heterogeneous variances on the linear scale. Year and region were considered fixed effects, while Site (Region), and Pool (Site, Region) were considered random.

2.2.2. Peak recruitment

We focused on densities during the fall because this season represents the time at which the maximum number of recruits was observed in pools, providing an estimate of the magnitude of yearly recruitment. The upward trajectory of recruit densities at the end of our sampling season in 2000 and 2001 (Fig. 2) suggests that our monitoring did not accurately measure maximum recruitment in those years. Therefore, we have limited our analyses of regional differences in recruitment to data from 2002 only. Peak recruitment was defined as the density of young-of-year *C. globiceps* in pools in September, when data were available for all 5 sites. These data were analyzed using a nested ANOVA with terms for Region and Site (Region). Recruit densities were $\ln(x+0.01)$ transformed to normalize heterogeneous variances on the linear scale. Region was considered a fixed effect, while Site (Region) was considered random.

2.2.3. Growth

We compared growth rates of fish (in terms of change in standard length) by computing the daily growth of individuals, both adults and recruits, recaptured in consecutive months between sampling dates from April to October in 2002 (final minus initial length divided by the number of days). To compare growth rates of fish that vary in size, we first examined whether there was an allometric relationship between size and growth rate by calculating a linear regression between initial length and daily growth. We found no such relationship (Linear regression $p=0.47$), consistent with the findings of Pfister (1997), suggesting that growth measured as linear elongation was independent of size. Because different pools had different recapture rates and numbers of individuals, not all pools had growth data in each interval. When an individual pool had multiple

recaptures in a single interval, we calculated the average growth as the response. Averaging within pools was aimed at eliminating any non-independence between fish in a given pool. We used growth data from 5 sites in 2002 in a factorial nested ANOVA that included terms for Month, Region, Month * Region interaction, Site (Region), and Pool (Site, Region). Month and Region were considered fixed effects, while Site (Region), and Pool (Site, Region) were considered random.

2.3. Tidepool community experiment

To determine whether the presence or absence of upright algae and mussels affected the population or community dynamics of tidepool fishes, we conducted an experiment at two sites: Strawberry Hill in the Cape Perpetua region and Fogarty Creek in the Cape Foulweather region. We began by identifying 20 tidepools at each site that contained both mussels and upright algae. We focused our efforts on upright algae because they, in contrast to crustose algae, might provide shelter for fishes and their prey. We measured percent cover of algae and mussels for each tidepool using a 10 cm × 10 cm mesh grid that was carefully placed into drained tidepools. For each pool, we first estimated the percent cover by upright algae and mussels (*Mytilus californianus* and *M. trossulus*) within each 10 cm × 10 cm square of the grid for the entire pool. The cover of algae and mussels were then summed for all grid squares to calculate the total area covered by either algae or mussels in each pool. We then calculated the total substrate area of the pool by counting the total number of squares of the mesh grid that covered the bottom of the pool. Total percent cover of algae and mussels was thus the total area covered by either mussels or algae divided by the total substrate area of the pool. In March 2002, prior to any experimental manipulation, mussel cover in tidepools did not differ between sites at Strawberry Hill and Fogarty Creek (SH=60.3%, FC=61.3%; *t*-test $p=0.90$), while algal cover was higher at Fogarty Creek than Strawberry Hill (SH=9.8%, FC=26.1%; *t*-test $p=0.004$). At each site, all pools were located between the upper and lower tidal limits of mussel beds, and pools ranged in size from 21 to 336 L. On average, experimental pools at Strawberry Hill were larger than pools at Fogarty Creek (average volume in liters: SH=109.2, FC=62.4; *t*-test $p=0.038$).

Five pools at each site were assigned randomly to each of four orthogonal treatments: (1) algae and mussels present (control), (2) algae present and mussels removed, (3) algae removed and mussels present, and (4) both algae and mussels removed. Experimental pools were selected across a common range of pool sizes

as similarly isolated pools in the same tidal height (the mid-zone, or mussel zone) at each site. Because each pool initially contained both mussels and algae, experimental manipulations were achieved by removing either or both of these types of organisms with metal scrapers, pry bars and wire brushes. Experimental manipulations were conducted in April 2002. Prior to experimental manipulations, we captured, measured, and tagged (as described above) all fishes in each pool. Following the establishment of experimental treatments, we censused fishes monthly until November 2002 and then again in March 2003. Treatments were maintained monthly from April through November by removing algae and mussels that appeared in manipulated pools. This method worked particularly well for mussels because they are slow to return to pools. Algal growth, however, was often high between monthly removals. For example, across both sites average algal cover was 11.5% in algal-removal pools after a month of growth in October, compared to 34.9% in pools where algae were unmanipulated. Thus algal-removal treatments persistently reduced cover, but did not completely remove algae.

After November 2002, we did not maintain experimental treatments, which raises the question of whether or not our experimental treatments persisted until our final census in March 2003. Algal treatments were unlikely to have persisted because the cover of intertidal algae decreases substantially in winter months (Dayton, 1975; van Tamelen, 1996; Nielsen, 2001). The net result would be conditions similar to algal-removal in all pools. Thus any effect of algae on the density of adults by the spring of 2003 would have had to be the result of patterns established during the summer and fall of 2002. In contrast, mussel treatments were largely intact in spring 2003 indicating that any effect of mussels on spring 2003 adult abundance could be due to interactions in the previous winter, fall, or summer.

We analyzed results from the experiment using three-way factorial ANOVAs with terms for Site, Algae, and Mussels, as well as interactions among all three parameters, and modeled each term as a fixed effect (Sokal and Rohlf, 1995; Zar, 1999). Our analyses focus on two responses: (1) peak recruitment, and (2) reproductive adult abundance in spring. In each case, pools were considered the experimental units, for a total sample size of 40. The responses were measured as recruit and adult density per pool volume, respectively. We used $\ln(x + 0.01)$ transformations for both recruit and adult density to meet assumptions of constant variance. For significant effects ($p < 0.05$), we calculated estimates and 95% confidence intervals derived from ANOVA parameter estimates.

2.3.1. Peak recruitment

We defined peak recruitment as the density of all young-of-year *C. globiceps* in pools, averaged across the months of September, October and November 2002. Because peak values did not occur for all sites in the same month, we averaged across these three months, which included the maximum value for all site/treatment combinations. Recruitment values were $\ln(x + 0.01)$ transformed to correct for non-constant variance.

2.3.2. Adult abundance

We examined whether pools under different experimental treatments at each of the sites had different adult abundances in the spring. The response in this analysis was the density of all adult *C. globiceps* in pools in April 2003, one year after the establishment of experimental treatments. Adult abundance values were $\ln(x + 0.01)$ transformed to correct for non-constant variance.

3. Results

3.1. Regional monitoring

3.1.1. Adult abundance

We observed higher densities of adult *C. globiceps* at sites in the Cape Foulweather region consistently over 4 years (Figs. 2, 3). While spring adult densities appeared to be higher at Fogarty Creek (Cape Foulweather) than Strawberry Hill (Cape Perpetua) in 2000, differences were not significant (*t*-test $p = 0.19$) due to high between-pool variability at Fogarty Creek. From
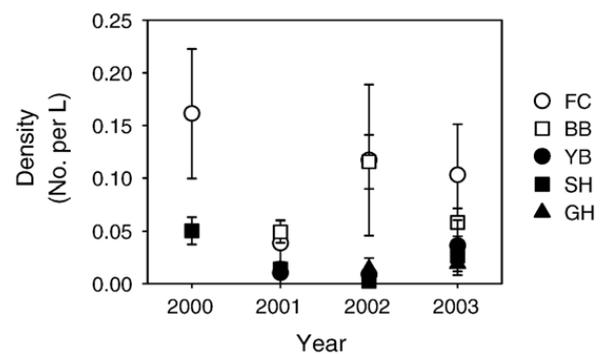

Fig. 3. Densities of adult *Clinocottus globiceps* during the spring from 2000–2003. Data points represent the average (±SE) density of adults in replicate pools at each site in either April or May, except for Boiler Bay (BB), Yachats Beach (YB), and Gull Haven (GH), which were sampled in June 2003. Two sites were sampled in 2000, Fogarty Creek (FC) and Strawberry Hill (SH), while all five sites were sampled in 2001 and 2002. Regions are denoted by filled (Cape Perpetua) and open (Cape Foulweather) symbols, and sites are arranged in latitudinal order in the legend with the most northerly site (FC) at the top.
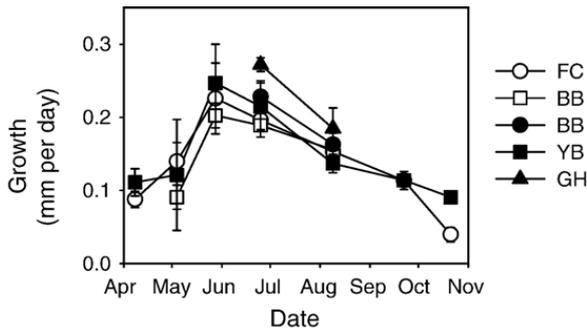
Fig. 4. Growth rates of *Clinocottus globiceps* in 2002. Data points represent the average (±SE) growth of fish in replicate pools. Regions are denoted by filled (Cape Perpetua) and open (Cape Foulweather) symbols, and sites are arranged in latitudinal order in the legend with the most northerly site Fogarty Creek (FC) at the top. In 2002, Strawberry Hill (SH) and FC were sampled in April, October and November, while Boiler Bay (BB), Yachats Beach (YB), and Gull Haven (GH) were not. Dates on the *X*-axis are midpoints between when a fish was captured and when it was recaptured. Only fish that were captured on two consecutive sampling dates were used in growth calculations.

2001 to 2003, adult densities were consistently higher in the Cape Foulweather region, although regional patterns varied among years as evidenced by an interaction between Year and Region (ANOVA $p = 0.0004$). Due to this interaction, we have estimated the effect of Region separately for each of the three years using ANOVA

parameter estimates: at Cape Foulweather, adult fish were 1.62 times (95% CI: 1.04 to 2.54 times; $p = 0.03$), 5.98 times (95% CI: 3.82 to 9.35 times; $p < 0.0001$), and 2.61 times (95% CI: 1.68 to 4.04 times; $p < 0.0001$) more abundant than at Cape Perpetua in 2001, 2002 and 2003, respectively. We observed no effect of Site (Region), indicating that sites within regions tended to remain similar to each other despite large interannual variation in regional patterns. Strong variation among Pools (Site, Region) indicates that not all pools responded similarly at each site ($p < 0.0001$).

3.1.2. Peak recruitment

The density of young-of-year *C. globiceps* in fall 2002 differed between Regions ($p = 0.041$), but not among sites within regions. Peak recruitment was 3.52 times (95% CI: 1.03 to 11.99) higher, overall, at Cape Perpetua than at Cape Foulweather. The non-significant Site (Region) term suggests that the processes that drive the magnitude of recruitment were operating similarly within regions.

3.1.3. Growth

Growth rates varied considerably from month to month, reaching a peak during mid summer months, while in spring and fall, growth rates were much lower (Fig. 4). Based on ANOVA results, growth varied among Months ($p < 0.0001$), but we observed no
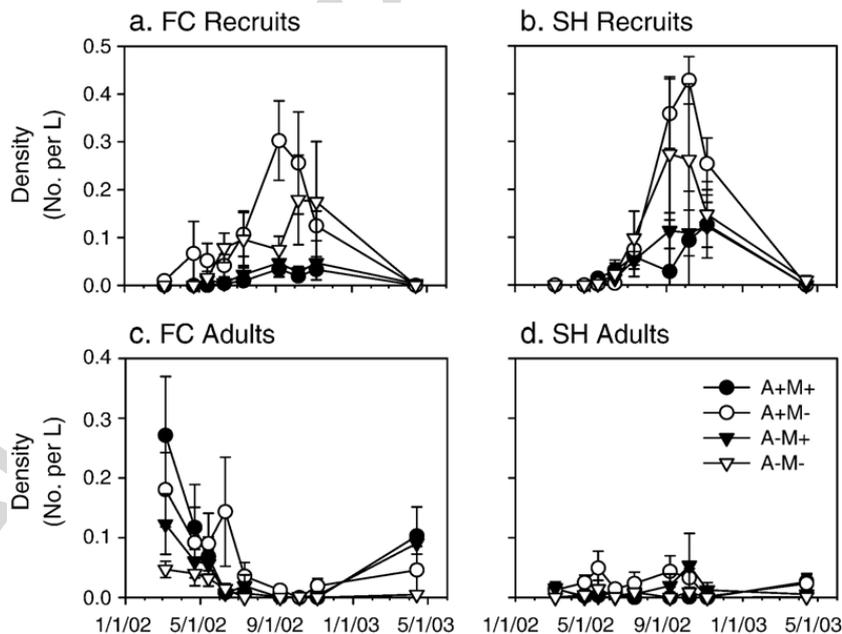

Fig. 5. Densities of recruit (a, b) and adult (c, d) *Clinocottus globiceps* in tidepools where the presence and absence of algae and mussels were experimentally manipulated. Data points represent the average (±SE) density in 5 replicate pools at each site on each sampling date. Replicate experiments were conducted at two sites, Fogarty Creek (FC) in the Cape Foulweather region (a, c), and Strawberry Hill (SH) in the Cape Perpetua region (b, d). Symbols in the legend indicate each of the four experimental treatments that cross-factored the presence (+) and absence (−) of both algae (A) and mussels (M).

apparent differences between Regions, no Month * Region interaction, and no effect of Site (Region). As with adult abundance, growth differed among Pools (Site, Region), indicating that not all pools within sites responded similarly ($p=0.050$).

3.2. Tidepool community experiment

At the beginning of the experiment in April 2002, adult densities were much higher at Fogarty Creek than Strawberry Hill (Fig. 5c, d). Adult densities at Fogarty Creek steadily declined over the summer, while densities remained low during this entire period at Strawberry Hill. By September, adult densities were similar at both sites. Recruit densities peaked in the fall from September to November (Fig. 5a, b).

3.2.1. Peak recruitment

Based on the results of the three-way ANOVA, only the presence of mussels ($p=0.0002$) and sites ($p=0.0085$) affected the recruitment of *C. globiceps*. The presence of algae and all combinations of interactions between mussels, algae, and sites were non-significant (Fig. 6a, b). Recruitment was 3.01 times (95% CI: 1.76 to 5.11 times) higher in the absence of mussels, and 2.08 times (95% CI: 1.21 to 3.53 times) higher at Strawberry Hill than Fogarty Creek.

3.2.2. Adult abundance

Results of the three-way ANOVA indicate that spring density of adult *C. globiceps* varied between sites ($p=0.0106$) and with the presence of mussels ($p=0.0068$) (Fig. 6c, d). However, because adult abundance depended on context (Mussels * Site interaction $p=0.0413$), we calculated the effect of mussels separately for each site. Overall, the abundance of adult sculpins in spring 2003 was 2.17 times (95% CI: 1.21 to 3.89 times) higher at Fogarty Creek than at Strawberry Hill (Fig. 5c, d). This difference represents a reversal of patterns observed the previous fall (2002), in which recruits were more abundant at Strawberry Hill (Fig. 5a, b). At Fogarty Creek, where adults were more abundant, mussels had a strong effect on adult density ($p=0.0012$), whereby adults were 4.21 times (95% CI: 1.84 to 9.51) higher in pools with mussels relative to those without. No effect of mussels on adult abundance was observed at Strawberry Hill, where adult densities were very low overall. There was no effect of algae in the spring of 2003 ($p=0.14$) nor were there any interactions between algae and sites or mussels ($p>0.25$ for all). The lack of an effect of algae in spring was not surprising given that algae had no effect during the previous summer and fall, and algal treatments likely deteriorated during winter months (Dayton, 1975; van Tamelen, 1996; Nielsen, 2001).
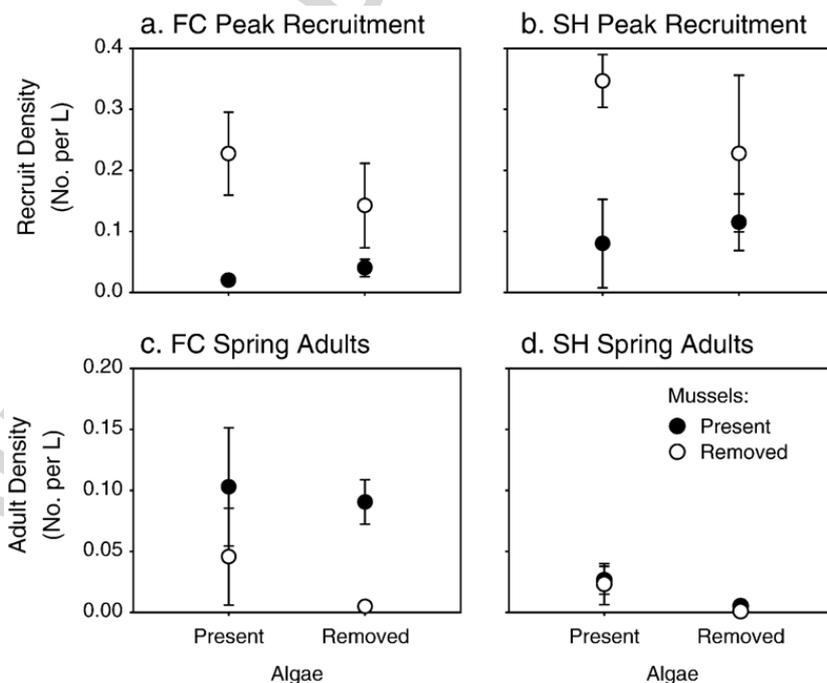

Fig. 6. Effects of the presence and absence of algae and mussels on the density of *Clinocottus globiceps* recruits in the fall of 2002 (a, b) and adults in the spring of 2003 (c, d). Data points represent the average (±SE) density in 5 replicate pools in each treatment at each site. Replicate experiments were conducted at two sites, Fogarty Creek (FC) in the Cape Foulweather region (a, c), and Strawberry Hill (SH) in the Cape Perpetua region (b, d).

4. Discussion

4.1. Regional monitoring

We observed large between-region differences in adult populations of *C. globiceps* on the Oregon Coast. From 2001 through 2003, the density of adults in the spring was higher at sites at Cape Foulweather than at Cape Perpetua. Although the magnitude of regional differences varied from year-to-year, the sign of the response did not, suggesting that the underlying processes responsible for higher adult densities in the Cape Foulweather region persisted for at least three years. Furthermore, the lack of among-site differences within each region argues for regional-scale coherence in the dynamics of *C. globiceps*.

In fall 2002, recruit densities at Cape Perpetua were 3× greater than at Cape Foulweather. Regional differences in recruitment could have been caused by the same mechanism that has been implicated in higher recruitment and growth of invertebrates in Cape Perpetua relative to Cape Foulweather (Menge et al., 1997): a relatively wide continental shelf near Cape Perpetua may lead to a circulation gyre that retains propagules and phytoplankton whereas a narrow shelf at Cape Foulweather can result in greater advection (Kosro et al., 1997; Kosro 2005). Differential recruitment, however, does not appear to be the cause of regional variation in adult sculpin populations in 2003 because patterns of adult abundance the following spring were the opposite: adult densities were ~3× greater at Cape Foulweather than at Cape Perpetua. Thus, a chronically low density of adult sculpins in the spring at Cape Perpetua appears to be the result of intense over-winter losses. In a similar study of the same species along the Washington coast, Pfister (1996) also observed that recruitment tended not to be a strong predictor of subsequent adult abundance, and that the population growth rate depended largely on post-recruitment survivorship. Together, these results suggest that in rocky pools along the Pacific Northwest of the U.S., abundances of adult *C. globiceps* may not be limited by recruitment, but are instead more generally predicted by post-recruitment processes.

Either emigration or mortality could potentially explain over-winter losses at Cape Perpetua. However, we believe emigration between sites to be an unlikely explanation because suitable rocky intertidal habitats along the Oregon coast are often separated by kilometers of sandy habitat, reducing the possibility of among-site movement by small sculpins. Furthermore, similar responses at all sites within the Cape Perpetua region suggest that over-winter losses occurred region-wide and are thus not the result of movement among sites. Vertical movement within sites could explain high losses from mid-zone pools at Cape Perpetua if adults tended to occupy either high or low zone pools at Cape Perpetua, while occupying mid-zone pools at Cape Foulweather. However, in the course of extensive sampling, we have observed that adult *C. globiceps* are most common in mid-zone pools at all sites, which is generally consistent with previous studies (Pfister, 1997; Zander et al., 1999). Because post-recruitment movement is unlikely to explain regional differences in adult abundances, we conclude that local-scale post-recruitment mortality during winter months was higher at Cape Perpetua than at Cape Foulweather, resulting in the between-region differences we observed.

Growth rates of *C. globiceps* varied considerably from month to month, but not between regions or among sites. The strong seasonal component of growth was similar to that observed in sculpins in Washington (Pfister, 1997). Pfister (1997) observed that the timing of recruitment partly determined subsequent growth and survival of sculpins, raising the possibility that between-region differences in sculpin densities in Oregon were the result of differences in either the timing of recruitment or growth rates. Similar to Chadwick (1976), however, we observed a comparable growth and synchronous recruitment between regions indicating that regional variation in adult densities cannot be explained by differences in the timing of recruitment or growth rates.

4.2. Tidepool community experiment

The tidepool experiment indicated that while algae had no effect on recruitment, young-of-year fish were three times more abundant in −mussel pools than in +mussel pools. Despite differences in the overall density of recruits, the multiplicative increase in recruitment with the removal of mussels was similar between regions. This effect suggests that recruits either prefer pools without mussels and recruited or immigrated disproportionately to these pools, or that mortality rates are higher in pools with mussels. The strong effect of mussels on recruitment of sculpins contrasts with the generally weak effects of conspecifics and congeners on previously observed recruitment patterns (Pfister, 1995), suggesting that *C. globiceps* may actively seek out particular habitats during settlement independent of resident fishes.

In spring 2003, adults were more abundant in pools with mussels at Fogarty Creek, suggesting a possible

ontogenetic shift in habitat preferences. Ontogenetic habitat shifts appear to be a widespread phenomenon in many fishes (Wootton, 1998) including intertidal fishes (Zander et al., 1999). The absence of a similar relationship at Strawberry Hill may have been the result of the overall scarcity of adult fish in the spring, making such a trend difficult to detect. Our observation of higher densities of adults in pools with mussels is consistent with patterns observed by Pfister (1995) where the overall density of C. globiceps had a positive relationship with mussels.

The presence of mussels in tidepools played an important role in both the recruitment and potentially the subsequent adult abundance of C. globiceps in pools. Frequent oxygen depletion in tidepools by way of biological respiration is well documented (Congleton, 1980; Truchot and Duhamel-Jouve, 1980; Morris, Taylor, 1983). Yoshiyama et al. (1995) documented increasing aerial emergence of several species of sculpins as oxygen levels in tidepools declined and suggested that it was a survival mechanism to avoid inhospitable environmental conditions. While our study does not identify the underlying mechanism(s), we propose two hypotheses for the effect of mussels on recruitment of C. globiceps. First, increased recruitment to pools without mussels could result if recruits actively avoid or experience higher mortality in pools with mussels because of hypoxic conditions or elevated (Bracken, 2004; Bracken and Nielsen, 2004), and potentially toxic (Evans et al., 1999), concentrations of nitrogenous wastes during isolation at low tide. If nitrogenous wastes do play a role in differential recruitment, the observation of higher adult densities in pools with mussels in spring 2003 suggests that adults are either unaffected or have developed a physiological tolerance to the elevated concentrations of nitrogenous wastes, as Yoshiyama et al. (1995) documented for hypoxia.

Alternatively, increased recruitment to pools without mussels could reflect ontogenetic habitat shifts. Newly settled C. globiceps can be highly abundant in tidepools that lie above the mussel zone in the intertidal (Webster, personal observations). If the absence of mussels is an important settlement cue, we may have inadvertently created pools that more closely resembled high-zone pools by removing mussels from pools in the mid-zone, thereby artificially increasing recruitment. An ontogenetic habitat shift from high-zone pools (and mussel-free pools in the mid-zone) to mid-zone pools with mussels could then have resulted in relatively high densities of adults in pools with mussels in spring 2003 at Fogarty Creek. One possible advantage to such a strategy is the avoidance of potential intraspecific competition between recruits and adults through the ontogenetic partitioning of habitat based upon tidal height or the presence of mussels in tide pools.

5. Conclusions

Variation in densities of recruit and adult populations of C. globiceps from two distinct regions on the Oregon coast was apparently the result of processes operating on regional scales in ways that led to differences in adult densities that persisted for at least 3 years. Cape Foulweather had persistently larger adult populations compared to Cape Perpetua, despite having equal or lower recruitment. Thus, our results indicate that regional variation in adult abundances was not a result of differential recruitment, but rather intense post-recruitment losses during winter months that were higher at Cape Perpetua relative to Cape Foulweather. Over-winter mortality rates could be linked to regional variation in oceanography (Kosro et al., 1997; Menge et al., 1997), the intensity of species interactions (e.g., with mussels or as yet unidentified predators such as raccoons, mink or other nocturnally active species; Menge, Richmond, and Noble, personal observations) or in physical conditions in tidepools.

Marine ecologists are increasingly recognizing that understanding local-scale processes requires an understanding of larger-scale phenomena (Holt, 1993; Menge, 2000b; Menge et al., 2003, 2004; Navarrete et al., 2005). In benthic systems, the effect of regional-scale processes on local communities can result from regional oceanographic circulation patterns that partly determine the rate of key subsidies, including propagules, planktonic food, and nutrients (Gaines and Roughgarden, 1985; Menge et al., 1997, 2003). Previous observations of regional variation in algae and invertebrates in this and other marine systems (Menge et al., 1997, 1999, 2002, 2003; Menge, 2000b) imply that the impacts of regional-scale processes acting through local-scale interactions on the structure of communities can be pervasive and far-reaching. In this study, the suggestion of a link between regional oceanographic processes, invertebrate community structure, and the local population dynamics of a tidepool fish furthers the idea that local marine populations must be considered within the context of regional-scale processes.

Acknowledgements

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