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Temporal and Spatial Dynamics of a Tidepool Fish Assemblage in San Diego, California

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy in Oceanography

by

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ABSTRACT OF THE DISSERTATION

Temporal and Spatial Dynamics of a Tidepool Fish Assemblage
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by

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In a rocky intertidal tidepool habitat, factors like temperature, salinity, oxygen, and wave energy fluctuate tidally, daily, seasonally, and interannually. Unlike sessile organisms, motile organisms can adjust their location in response to environmental fluctuations; therefore, they may not fit into general intertidal ecological models based on sessile emergent communities. Fish populations were sampled at several sites in San Diego, California, from 1996 to 2000 to test effects of temporal environmental variability on habitat use, assemblage structure, and population dynamics of the major tidepool fishes of San Diego, California: *Clinocottus analis* (woolly sculpin), *Girella nigricans* (opaleye), *Gobiesox rhessodon* (California clingfish), *Hypsoblennius gilberti* (rockpool blenny), *Gibbonsia elegans* (spotted kelpfish), and *Paraclinus integripinnis* (reef finspot). These fishes were found to spatially and temporally partition tidepool habitat among species and ontogenetically within species.

Habitat use and assemblage structure were variable on the three temporal scales addressed in the study (diel, seasonal, and El Niño Southern Oscillation). Middle intertidal fishes used high and low intertidal pools differently depending on time of day. Fishes used higher tidepools during the fall, when sea level is seasonally highest. Recruitment and growth were seasonal and were the main influence on temporal variability in population growth rate of the assemblage dominant, *C. analis*.

Changes in population dynamics and assemblage structure were observed during the 1997-98 El Niño event. *C. analis* population size declined due to changes in early life-history (larval and juvenile) processes, including a drop in recruitment. *P. integripinnis* population size increased during the El Niño event. The combination of these two changes led to higher species evenness during El Niño. One species, *G. nigricans*, experienced a morphological shift (increases in dorsal spot number) associated with El Niño. Because the study spanned only one El Niño event, generalization to other ENSO events is not possible. However, as ENSO predictability increases, future studies will be able to test the generality of these results.

Rocky intertidal fishes of San Diego do not conform to the density-dependent, space-limitation model proposed for many rocky intertidal taxa that are sessile and emergent. Rather, community and population regulation appear forced by pre-recruitment processes, like many tropical reef fishes. Future studies targeting the larval stage will enable further identification of specific larval vital rates important in controlling population dynamics.

Chapter 1

Introduction to the Dissertation

Rocky intertidal tidepools are a unique habitat, both for their inhabitants and for ecologists studying spatial and temporal aspects of community organization. These pools buffer organisms from the harsh environmental fluctuations experienced by emergent areas of the intertidal zone, offering refuge from desiccation during low tide (Metaxas and Scheibling, 1993). However, relative to subtidal areas, tidepools are isolated and patchy islands of habitat (Wilson, *et al.*, 1992). Many environmental parameters vary on short time and small spatial scales, including temperature, salinity, oxygen, pH, and isolation time (Morris and Taylor, 1983; Jensen and Muller-Parker, 1994; Lennon, 1995). Temperature may increase in tidepools by 15°C or more and salinity by 3 ppt in several hours (Metaxas and Scheibling, 1993; Jensen and Muller-Parker, 1994). Oxygen content may decrease from ambient levels to hypoxic conditions during the period of a low tide (Congleton, 1980).

Tidepools provide habitat to two general types of organisms: sessile and motile. Because motility provides an organism with the ability to change habitats under certain conditions, controls of distribution, lifestyle, and population dynamics are likely to vastly differ between the two groups of organisms. Although sessile intertidal organisms have received much attention, there has been relatively less study of motile species (Gibson, 1982). Among the most motile taxa in tidepools are fishes, which include species belonging to three main groups: permanent residents, juveniles of predominantly subtidal species, and accidental or transient visitors (Thomson and Lehner, 1976; Gibson 1982; Moring, 1986; Moring, 1990).

Southern Californian tidepools support four major permanent re·:· ·nt fishes (Figure 1.1): the cottid *Clinocottus analis* (woolly sculpin), the blenniid *Hypsoblennius gilberti* (rockpool blenny), the gobiesocid *Gobiesox rhessodon* (California clingfish), and the clinid *Gibbonsia elegans* (spotted kelpfish). The system also supports juveniles of the girellid *Girella nigricans* (opaleye), which inhabit tidepools for up to the first two years of life (Norris, 1963; Stevens *et al.,* 1989). At certain times, a sixth species, *Paraclinus integripinnis* (reef finspot) also joins the assemblage (Figure 1.1).

The main purpose of this dissertation research was to characterize spatial and temporal patterns of habitat use, assemblage structure, and population dynamics of the major tidepool fishes. Because the environment of the habitat is highly variable on many temporal scales, three scales were examined in the study: (1) diel, (2) seasonal, and (3) El Niño Southern Oscillation (ENSO). Spatial scales examined included variation within-benches (scale of meters) and between rocky regions (scale of kilometers). Goals of the study were to (1) review the physical, geological, chemical, and biological forces that create rocky intertidal habitats and their tidepools, (2) test the hypothesis that members of the intertidal fish guild were distributed uniformly both in space and time, (3) determine whether the 1997-98 El Niño event induced changes in assemblage structure or habitat use, and (4) test the recruitment-limitation hypothesis and identify key life-history stages of the assemblage dominant, *C. analis* that determine population dynamics.

The first goal, the review of forces shaping rocky intertidal areas, was undertaken in order to better understand the setting and time frame in which tidepool fishes of southern California, and elsewhere worldwide, evolved. Results of this review are presented in Chapter 2.

The second goal of the study, to determine interspecific, intraspecific, spatial, and temporal patterns of habitat partitioning, is addressed in Chapters 3 and 4. Components include a determination of whether the five fishes are distributed randomly among intertidal pools or whether they partition the habitat based on characteristics of the tidepools both among and within species (Chapter 3). In addition, I tested effects of the time of day at which low tide occurred on tidepool use by the two upper intertidal species, *Clinocottus analis* and *Girella nigricans*. Because tidepools, especially high intertidal pools, and their residents experience vastly different conditions when isolated during the day versus at night, I hypothesized that fish would avoid them during inhospitable conditions. Chapter 4 presents a test of this hypothesis.

Not only are intertidal organisms subjected to tidal, daily, and seasonal environmental variability of their habitat, they are also subjected to interannual variability. Although often less severe than shorter-scale variability, interannual variability may also be important in structuring intertidal systems. The next dissertation component (Chapter 5) compares the magnitude of changes in composition in and habitat use by the rocky intertidal fish assemblage occurring on a seasonal scale to those occurring during an El Niño Southern Oscillation event (ENSO). In addition, climate effects potentially related to the El Niño event on a polymorphism in *Girella nigricans*, that of dorsal spot number, were tested (Chapter 6). Various manifestations of the 1997-98 El Niño event were expected to contribute to composition and habitat changes in the fish assemblage. These included factors that affected the rocky intertidal zone, such as an increases in rainfall, storm frequency, coastal water temperatures, and sea level, as well as factors influencing larval habitat, such as changes in coastal currents (Norton *et al.*, 1985; Lynn *et al.*, 1998).

The various scales of temporal environmental variation in rocky shore habitats (diel, seasonal, ENSO) were expected to play a role in the structuring of populations. The final thesis component (Chapter 7) examined how temporal variation shaped population dynamics of the assemblage dominant, *C. analis*. The main goals of this section were to determine whether *C. analis* populations are more highly controlled by pre-recruitment or post-recruitment processes using both cohort analyses and matrix population models and to determine whether the importance of specific population vital rates changed on seasonal or ENSO scales.

Together, these research components contribute to an understanding of how benthic fishes, specifically rocky intertidal benthic fishes, respond to various scales of environmental variation in their habitats. Although these questions have been addressed extensively for sessile intertidal organisms (Connell, 1985; Roughgarden et al., 1994; Dayton, 1971) and for subtidal reef fishes (Victor 1983 and 1986; Jones 1990; Forrester, 1990), this is one of the few studies that combine the extreme variability of the intertidal habitat with the ecology of motile fish species.

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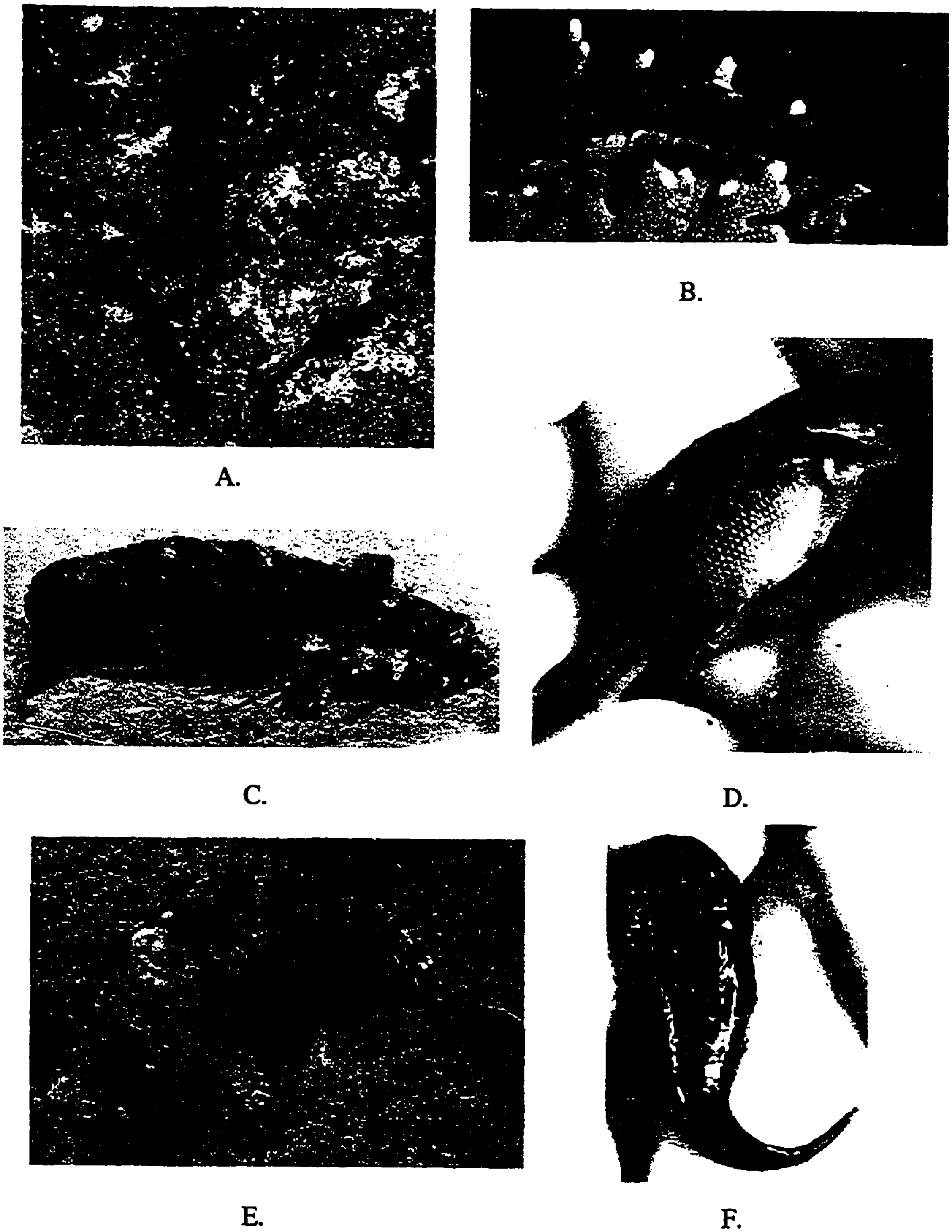

Figure 1.1: The six most common fishes of the San Diego rocky intertidal zone. A) *Clinocottus analis*, B) *Gibbonsia elegans*, C) *Paraclinus integripinnis*, D) *Girella nigricans*, E) *Hypsoblennius gilberti*, F) *Gobiesox rhessodon*.

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Chapter 2

The Relevance of Rocky Intertidal Geomorphology to Tidepool and Emergent Communities

Abstract

The location and characteristics of rocky intertidal areas are controlled by a suite of physical, chemical, and geological forces. Because many intertidal species require hard substrate, these forces are both directly and indirectly important to rocky intertidal biological communities. For example, factors involved in the distribution of rocky areas along the coast, including coastal shape, wave energy regimes, longshore sand transport patterns, and tectonics, are ultimately important to gene flow among isolated intertidal populations. Physical and chemical processes controlling features that develop within intertidal areas, like benches and tidepools, can ultimately determine organism abundance, species assemblage, and community structure. In this review, several non-biological processes that are important to intertidal organisms are put into an ecological context. These processes include forces responsible for along-shore distribution of rocky intertidal sites and within-shore development of hard-substrate features.

Introduction

Many rocky intertidal populations are limited by the amount of available hard substrate (Connell, 1985; Connolly and Roughgarden, 1999); therefore, factors pertaining to how rocky intertidal areas are distributed and constructed are important to rocky intertidal populations. For example, tidepool organisms are dependent on the presence of pits or crevices that will retain water during low tide. Certain rocky areas along a coastline may be more likely to have such features than others, a likelihood dictated by physical, chemical, and geological forces. As a result, these non-biological forces can be some of the most important factors that structure rocky intertidal biological communities. They range across wide spatial scales, from large-scale processes that affect entire coastlines, like tectonics, to small-scale processes that affect erosion in an individual tidepool. They also range across many temporal scales, including those greater than the time scale necessary for individual species' evolution (millions of years for processes like tectonics), time scales of about the same order of magnitude as the scale of species evolution (thousands of years, for processes like significant sea level change), and time scales within an individual organism's lifetime (days, for processes like episodic erosion of tidepool areas).

On large scales, physical factors affecting the distribution of rocky regions along the shore indirectly play a role in population genetics of rocky intertidal species. Genetic homogeneity of populations is maintained through exchange of planktonic larvae among rocky sites that may not be contiguous; therefore, the same physical factors that affect rocky site distribution also affect the distance a larva must travel, the probability of larval exchange, and most likely genetic relationships among distinct populations. The more isolated a rocky intertidal area, the greater the distance individual larvae and adults must travel in order to maintain genetic exchange (Yoshiyama, 1987; Hellberg, 1993). In populations for which recruitment is one of the most important life-history events, the distribution of rocky areas along the coast and thus point sources of larvae may determine population structure and dynamics.

Within a rocky intertidal area, geomorphologic features like tidepools and benches are determined by an additional set of physical, chemical, and geologic forces. Rocky intertidal organisms have adapted to use some of these features, and many studies have identified relationships between certain aspects of these geomorphologic features and certain ecological processes. For example, tidepool size determines species richness of fishes (Bennett and Griffiths, 1984). Rock type affects success of certain boring organisms (Evans, 1968) and settlement density of some sessile organisms (McGuinness and Underwood, 1986; Raimondi, 1988; James and Underwood, 1994). Differences between sites in such factors as species assemblage, density, and even growth and mortality may be explained by these non-biological parameters. Ecologists who study emergent intertidal and tidepool organisms and who wish to use them to construct general ecological models should consider if and how the geomorphologic settings of their systems restricts the ability to make generalizations. As Crowe and Underwood (1999) state, the application of models to new systems is made difficult without understanding the sources of differences between the systems. The purpose of this discussion is to identify the forces that control distribution of rocky intertidal areas and shape rocky intertidal outcrops, and discuss how these forces are relevant to community structure, species abundance, and other ecological attributes.

Formation and location of rocky intertidal habitats

During stillstands in sea level, broad marine terraces are cut into coastal features by prolonged wave activity focused consistently on a particular level of shoreline (Sunamura, 1992). The near horizontal terraces generally extend above mean lower low water to intersect with seacliffs (Rindell, 1991). Sandy horizontal beaches result when conditions permit sand to cover the shoreward-most portion of the terrace. Rocky beaches are present when sand does not accumulate. The amount of sand that will cover a specific coastal location is determined by several interacting factors, including the amount of wave energy reaching specific areas of the shore, shape of the shoreline, patterns of local longshore sand transport, tectonic history of the coast, and the composition of local cliffs and their erosion rates.

Wave energy and coastal shape

The amount of sand covering a particular intertidal section is largely dependent on the shape of the coastline and position along the coast. An initially straight coastline can be carved into headlands and coves by the scalloping action of waves, induced through several processes. Offshore obstacles tend to bend wave fronts toward shore, resulting in differential wave energy along the coast (Kaye, 1959). In higher energy areas, sand is washed away leaving underlying bedrock exposed, and in lower energy areas, sand can accumulate.

Differences in rock strength in areas along the coast also promote scalloping (Kaye, 1959; Trenhaile, 1987). Igneous, high-grade metamorphic, and some types of carbonate rock tend to resist weathering and become headlands, whereas shales or sandstones often give way to embayments (Trenhaile, 1987). Headlands tend to be devoid of sand because they focus wave energy. From the perspective of an onshore traveling wave front, water depth shallows sooner in front of headlands, and because waves travel more slowly in shallow water, they bend toward headlands and points on either side of these features. The waves from both sides converge, and wave height increases (Shepard and Grant, 1947). For the opposite reason, low energy areas such as embayments and coves tend to be covered with sand or mud as wave fronts are bent away from these areas.

Wave energy patterns can change on short temporal scales, potentially influencing life-history strategies within species. For example, the amount of sand covering part of the rocky bench and boulders of the Scripps Coastal Reserve in La Jolla changes seasonally, with a larger rocky area exposed in the winter (Rindell, 1991). Sand cover at this location has also changed on a decadal time scale. In 1977, the wave energy regime shifted from a predominantly northern-dominated one, driven by Pacific Northwest storms, to a southern-dominated wave energy regime, generated by southern subtropical cyclones (Rindell, 1991). As a result, since 1977, southern sand transport along this region of the San Diego coast has decreased, resulting in the exposure of rock outcrops and an increase in rocky substrate for benthic organisms (Rindell, 1991).

Longshore sand transport

The river of sand flowing along the coast, which generally supplies beaches with sediment, may be interrupted by several types of features (Herzer, 1979; Bergensen, 1989; Rindell, 1991). The first type of interruption is submarine canyons. Sand in the process of being transported along-shore may be intercepted by canyons and funneled down their slopes away from the coast (Herzer, 1979, Bergensen, 1989; Rindell, 1991). An example of such an interception in San Diego County, where the longshore current is from north to south, is found offshore of the La Jolla area. There, two branches of a large submarine canyon intersect the shore, the Scripps Canyon just north of Scripps Institution of Oceanography, and the La Jolla Canyon just north of La Jolla Point (Kuhn, 1980; Griggs and Savoy ,1985; Rindell, 1991). Partly because of the canyons, beaches just south of the two canyon branches are starved of sand, including the Dike Rock area north of Scripps and the coastline of La Jolla from La Jolla Point to False Point.

A second type of interception of or barrier to longshore sand transport is wave divergence zones (Rindell, 1991). These divergence zones may be created by obstacles, like canyon heads, that divert waves in opposite directions. In this case, the canyon head affects the transport of sand not by intercepting it, but by changing the wave energy regime.

Longshore sand transport may also be influenced by humans. In San Diego County, the longshore river of sand has been historically fed in part by sediment input from rivers and streams emptying out through coastal lagoons (U.S. Army Corps, 1985; Rindell, 1991). Because most of these streams have been dammed upstream to form reservoirs like Lake Hodges, which controls 88% of the San Dieguito River watershed in San Diego County (U. S. Army Corps, 1988), sediment input to the longshore current has likely been affected. Construction of jetties has also influenced longshore sand transport. An example is the jetty system at the mouth of San Diego's Mission Bay, which has interrupted the natural flow of sand from Mission Beach to Ocean Beach (U.S. Army Corps, 1985).

Tectonic history

General tectonics may explain the difference in abundance of rocky coastal habitat between, for example, the Atlantic and Pacific Coasts of the United States. The Pacific Coast is an active margin, experiencing uplift that pushes up rock material. During stillstands in sea level, waves cut into this uplifted rock, forming cliffs on the landward side of sea level, intertidal rock benches in the intertidal zone, and marine terraces below sea level. The Atlantic Coast is a passive margin and, with the exception of the northern portion which is still rebounding from glacial depression, is generally subsiding. Most of this coast, excluding parts of New England, is sand beach (Emery, 1946). Less cliff rock is available on the Atlantic Coast for the cutting of intertidal rock benches.

Cliff composition and erosion

The composition of local cliffs, determined by long-term geological processes beyond the scope of this review, affects the substrate of a beach and therefore what types of organisms will inhabit its intertidal area. Erosion of cliff bases by waves causes an undermining of the cliff, which then slumps (Emery and Kuhn, 1982). The slumped material can remain at the cliff base and form part of the rocky intertidal area. An example of this may be seen at False Point in southern La Jolla, California, one of the study sites used in the present dissertation research. Here, cobbles eroded from the conglomerate sandstone cliff face form the rocky intertidal base (Tway, 1991). In other areas, however, where the cliff consists of easily eroded elements, the slumped material may not remain as a semi-permanent part of the intertidal area. Instead, the smaller, softer rock fragments may be easily ground up and carried away by waves.

Creation and destruction of features in intertidal rock

Rocky intertidal benches

In the landward portion of the marine terrace cut by waves during stillstands in sea level, strong wave action often carves a horizontal platform or rock bench between the high tide and mean low tide levels (Wentworth, 1938 and 1939; Trenhaile, 1987; Sunamura, 1992). Depending on the original height of the cliff being cut, wave energy, rock strength, and tidal range, two types of platforms may be formed (Trenhaile, 1987; Sunamura, 1992). Type A platforms are continuously sloped from the subtidal zone to the cliff base, and are found cut into softer rock in regions of lower wave energy and greater tidal range. Type B platforms are more horizontal, with a near vertical step at their seaward edges. They are often located in higher wave energy, lower tidal range, and harder rock regimes. Bench width and elevation above mean sea level are negatively correlated with rock strength and positively correlated with wave energy, with benches absent in wave-protected areas (Kaye, 1959; Sunamura, 1992). Relationship between bench width and tidal range is unclear and requires further investigation. Despite the fact that bench width, slope, and other characteristics may have great effects on such diverse processes as coastal erosion and biological colonization, factors determining many bench characteristics are not well-studied (Trenhaile, 1987).

Although the mechanism of bench formation is still not entirely understood, it is clear that benches are remnants of sea cliffs and the result of stillstands or relatively slow changes in sea level (Hodgkin, 1970; Rindell, 1991; Sunamura, 1992). Two methods of bench formation have been suggested, one mainly physical and chemical and the second mainly biological and chemical. The first hypothesis suggests that on a vertical or sloping rock face, between the mean low and mean high tide lines, both rock solution and mechanical erosion carve out an indentation or "nip" (Wentworth, 1938; Kaye, 1959). Solution processes are invoked in this intertidal span because of its exposure to air. The surface water film on wet rock surfaces at night experiences a drop in temperature, increase in CO_2 content, lower pH, and undersaturation of calcium, thereby enabling the dissolution of the calcium carbonate rock surface (Emery, 1946; Revelle and Emery, 1957). Mechanical erosion in the vertical intertidal span is due both to cobbles pounded into the rock face by waves, and by the quick compression and expansion of air in rock cracks or joints caused by breaking waves (Shepard and Grant, 1947; Trenhaile, 1987). Several authors have suggested that the nip is created mainly by boring intertidal organisms (Hodgkin, 1970), but the chemical and mechanical erosion processes are better supported by other studies (Trenhaile, 1987; Sunamura, 1992). Regardless of mechanism, the nip can be carved deep into the rock face, leaving a near horizontal base at about the mean low tide level and a near horizontal overhang at the mean high tide level. Often the overhang is eroded away, leaving only the base of the nip, now a bench, near the mean low tide level (Kaye, 1959).

The second hypothesis in bench formation involves the chemical erosion of a cliff or cemented dune. Rainwater allows the dissolution of the top of the cliff or dune, which is continuously eroded until it reaches the intertidal level. There, encrusting coralline algal mats protect the rock from further erosion (Kaye, 1959). According to this hypothesis, bench height relative to mean tidal height would then be determined by the vertical distribution range of the coralline algal species of a region. Unlike the first hypothesis of bench formation, which involves bench formation at intermediate cliff height, this hypothesis invokes a top-down mechanism. Both processes may occur, with some areas and cliff types more likely to give rise to nip-derived "wave-cut benches" and others to "solution benches" (Wentworth, 1938 and 1939). Confusion over the identification of required conditions has lead to the use of contradictory terminology for these formations, including wave-cut platforms, wave-cut benches, solution benches, water-leveled terraces, and wave ramps (Sunamura, 1992).

The physics, chemistry, and geology that govern the formation of intertidal rock benches are extremely important to bench organisms. For example, many intertidal populations are space-limited (Connell, 1961; Dayton, 1971, Roughgarden *et al.*, 1984). Therefore, the width of the bench, which determines the amount of habitat available in the dimension perpendicular to the shore, must be directly related to population size. Benches tend to be wider in higher energy areas (Kaye, 1959; Sunamura, 1992), which may be one factor contributing to the increased population size or biomass of some species observed in high energy areas in several studies (e.g. McQuaid and Branch, 1985; McQuaid *et al.*, 1985; Ricciardi and Bourget, 1999). Also, many intertidal organisms have specific vertical zones, or ratios of emergence to immersion time, in which they are capable of living. Vertical zonation has been displayed for many organisms, including algae, invertebrates, and fishes (e.g. Connell, 1961; Dayton, 1971; McQuaid, 1985; Gibson, 1982; Bell, 1995). The height of the intertidal bench above mean sea level, then, must be directly related to species composition of bench life. Certain organisms may be more abundant in higher wave energy regimes not because they are physiologically better at withstanding wave abuse, but because the benches in these regions tend to be higher above mean sea level in the intertidal zone.

Creation of tidepools

Rocks of all types that are exposed in intertidal zones are shaped by several diverse forces. These forces are biological, chemical, and physical in nature, and differ slightly according to region (tropics versus temperate zones) and consistency of the rock (soft versus hard). The pits, crevices, scratches, and holes that are formed in rocky intertidal regions provide habitat to many plant and animal species. Those depressions that form in a horizontal surface, like an intertidal bench, retain water and present a unique environment for organisms that require submergence in water to survive, but that can withstand the environmental fluctuations of the intertidal zone (e.g. Wilson, *et al.*, 1992; Metaxas and Scheibling, 1993; Underwood and Skilleter, 1996).

The retention of water in scratches or depressions in intertidal rock surfaces at low tide plays a key role in the formation of tidepools. Immediately after an ebbing tide exposes a scratch or depression, its water has the same chemical characteristics as seawater and is saturated with calcium. The saturation status changes during the isolation of the depression. If the low tide occurs at night, the water in such depressions decreases in temperature. Plants and animals that inhabit the depression respire, producing CO_2. This CO_2 accumulates, forming carbonic acid which increases the alkalinity and decreases the pH of the water. Under these conditions, the calcium in the depression water combines with bicarbonate ion, resulting in its undersaturation with respect to calcium. The cementing material of the rock begins to dissolve, and the rock grains become loose. These are washed away by waves with the next tide or ingested by snails and other foragers feeding on endolithic algae (Emery, 1946; Revelle and Emery, 1957; Kaye, 1959; Sunamura, 1992). As this process continues, the depression widens and deepens, and may eventually coalesce with another depression. Emery (1946) estimated that a 5 cm deep depression in sandstone takes about 200 years to develop by dissolution processes.

During a daytime low tide, photosynthesis by algae in the depression will counterbalance the CO_2 produced by respiration and eventually cause a net decrease in CO_2 content. The pH increases, and combined with the increase in water temperature during the day, causes a precipitation of $CaCO_3$. This precipitate is either washed away by the incoming tide, or is deposited at the upper rim of the tidepool due to capillary action where it may reinforce the tidepool rim against erosion (Emery, 1946).

Another process was proposed in the 1950s as an alternative to the biochemical hypothesis outlined above. Ginsburg (1953) suggested that the dissolution of calcium carbonate in depressions in the rocky intertidal zone could only explain a small part of the creation and broadening of tidepools. Instead, he proposed that boring by species of cyanobacteria, algae, annelids, and arthropods; scraping by burrowing mollusks, echinoderms, and chitons (Figure 2.1); and grazing by gastropods would better explain the formation of tidepools. Borers and scrapers would act to weaken the rock, and grazers would serve to remove rock material.

The purely biological hypothesis of Ginsburg (1953) and the biochemical hypothesis are not mutually exclusive, and both processes are likely to play a role in the formation of tidepools. The shape of newly formed pits and pools in the spray zone suggests that solution processes are at work (Kaye, 1959). However, certain types of depressions are clearly attributable to the boring or scraping actions of organisms. Chitons, for example, dig pits into relatively soft rock such as sandstone (Figure 2.1). Individual pits, worked on by a succession of individual chitons, may be 20 to 30 years old (Tway, 1991). In five to six years, boring clams can excavate a hole in intertidal rock that measures up to 2.5 cm in diameter and 15 cm deep, with boring rate and extent inversely related to the hardness of the substrate (Evans, 1968). Echinoderms create basins more than 30 cm deep in Puerto Rican benches (Kaye, 1959). Although most boring is probably mechanical, pits may also be created by animals chemically through acid secretion as in several bivalve species (Hodgkin, 1970). Boring rocky intertidal organisms have been identified in many systems world-wide (Young, 1963; Trudgill, 1988), including sea urchins in Colombia (Schoppe, 1991); bivalves, sipunculans, and clionid sponges in the Gulf of California (Stearley and Ekdale, 1989); annelids in the United Kingdom (Trudgill, 1988); bivalves in Israel (Lewy, 1985); endolithic algae in Malaysia (Hodgkin, 1970); and fungi, cyanobacteria, and sea urchins in Senegal (Allouc *et al.*, 1996). Humans, too, are responsible for starting tidepools through such activities as carving graffiti in softer rock areas (Emery, 1941; Emery and Kuhn, 1980).

Once created, pits and depressions excavated by borers and scrapers become available to all intertidal organisms. Many non-boring species seek out these pits after the excavators have abandoned them, as well as crevices created through physical processes (Chapman and Underwood, 1994). The burrow-colonizers, through nighttime respiration, enhance biochemical solution of the pit walls and steadily increase the size of the pit. In this way, the actions of the original burrower can continue to have effects on the growth of the pool long after the burrow is abandoned and the burrower has moved on to another excavation.

Purely physical processes may also contribute to the formation of tidepools. In some areas, in which cobbly cliff material has slumped into the rocky intertidal, waves may work individual cobbles free from the cemented material, leaving pits that retain water during low tide. An example of this type of tidepool formation is found at the False Point dissertation site (Tway, 1991). In colder climates, ice may gouge out grooves and pits in intertidal rock platforms (Dionne, 1996). In all types of pits, whether formed by solution, boring animals, boulder excavation, or ice, cobbles introduced into the pits can abrade their walls when tossed about by waves during immersion. A specific wave energy regime is necessary, however, as waves must be strong enough to move the abrasives about within the depression, but not strong enough to wash them out (Sunamura, 1992). The pits gradually become deeper and trap more cobbles, increasing the rate of abrasive erosion (Kaye, 1959; Sunamura, 1992). This type of pit, called a pothole in the geology literature (Wentworth, 1944; Sunamura, 1992), can be distinguished from a basin formed purely from solution in that the pothole generally has smooth walls. An unabraded solution basin often has rough or fluted walls (Emery, 1946).

Characteristics of tidepools

Many organisms that inhabit tidepools select pools based on certain characteristics, such as pool surface area, pool depth, and intertidal height. These characteristics have been found to determine the density and distribution of many organisms that inhabit intertidal zones, but that must be immersed in water at all times. These include fishes (Nakamura, 1976b; Yoshiyama, 1981; Gibson, 1982; Prochazka and Griffiths, 1992; Davis, 2000); invertebrates (Underwood and Skilleter, 1996; Metaxas and Scheibling, 1994) and algae (Van Tamelen, 1996). For example, the number of fish per tidepool usually increases with tidepool surface area. A rocky intertidal platform with larger pools, therefore, would likely be inhabited by more fish than a platform with the same number of smaller pools. Several species of fish select for deeper tidepools (Nakamura, 1976a; Richkus, 1981; Davis, 2000); therefore, a platform with deep tidepools might house a different species assemblage than a platform with shallower pools.

Few studies have examined the distribution of tidepools with different shapes and sizes within intertidal benches, despite the fact that the forces behind tidepool distribution can indirectly determine the species composition of entire benches and thus entire rocky intertidal regions. Some authors, however, have suggested certain trends regarding dimensions and within-bench location of tidepools. Emery (1946) noted an increase in tidepool diameter with increased depth in a sandstone bench in La Jolla, California. Tidepool diameter tends to be greater than depth (Emery, 1946; Sunamura, 1992), rarely falling below 2/3 of the depth measurement (Trenhaile, 1987). Diameter and depth may reach an equilibrium ratio, as abrasion decreases due to the weakening of flow with pool depth. Weakening of this flow also permits accumulation of sediment (Trenhaile, 1987). The shape of the tidepool surface (the length and the width across the top) may also be constrained. Tidepools are usually circular, with a 1:1 ratio of length to width, unless two tidepools coalesce (Emery, 1946; Sunamura, 1992). A possible explanation of this circular shape is that abrasive forces act on all sides of the tidepool equally.

Emery (1946) also noted a seaward increase in diameter and depth in tidepools in La Jolla, with the largest, deepest tidepools occurring in the seaward-most portion of the sandstone bench. No direct explanation was offered for this relationship, although several authors have suggested that position within an intertidal bench is related to timing of tidepool evolution (Emery 1946; Kaye, 1959). Emery (1946) suggested that shoreward tidepools are in an "earlier stage of development" than seaward tidepools. Kaye (1959) also described a relationship between pool formation and height in the spray zone. As a pool moves from the upper spray zone to lower spray zone, a migration caused by several cycles of chemical dissolution of its floor, its bottom changes from round to flat, then back to round. At this stage, the pit would reach intertidal level and would move into the next phase, that of being ground out by cobbles in the surf. The correlation of pool size with intertidal height is consistent with an abrasion hypothesis. Pools lower in the intertidal zone would be immersed and therefore subjected to wave-induced abrasion for longer periods of time, resulting in larger, deeper tidepools.

Differences in size, shape, and formation mechanism of tidepools in various areas may be the cause of between-bench differences in tidepool community composition or species densities. For example, benches in which more tidepools were able to form may have more stable, diverse, trophically more complex communities than benches with relatively few pools, which could be considered patchier habitat. Intertidal benches in which tidepool formation processes lead to deeper tidepools might be more richly colonized by fishes that select for deep pools. Depth preference is also size-specific in some species, with larger individuals choosing deeper pools (Davis, 2000). Tidepool formation processes therefore may ultimately structure populations within and migrations from these benches. Although between-bench differences in abiotic factors like slope, rock type, and exposure have been addressed for a few emergent communities (e.g. McQuaid *et al.*, 1985; McGuinness and Underwood, 1986; Ricciardi and Bourget, 1999), equal attention has not been turned to direct effects of between-bench differences in tidepool habitat on tidepool communities.

In addition to direct influence by tidepool characteristics, tidepool communities may be indirectly influenced by abiotic characteristics of the emergent bench habitat. The prey of tidepool species or the epibionts used by tidepool species for cover, like macroalgae, may preferentially settle on specific types of substrate or intertidal benches. For example, polychaetes recruited more heavily to dark gray shale boulders than to light yellow sandstone boulders in Australia, influenced by both rock color and type (James and Underwood, 1994). Barnacle settlement and post-settlement survivorship was greater on granite than basalt boulders in a region of the Gulf of California (Raimondi, 1988). A green alga was more abundant on sandstone substrate, which retains more water at low tide, than shale on an Australian shore. Conversely, spirorbid worms were more abundant on shale substrate, which is more pitted and offers greater protection from abrasion, than sandstone (McGuinness and Underwood, 1986). Tidepool organisms that graze on these species or use them for cover may then be indirectly influenced by rock type.

Biological forces may also contribute to within-bench variation among tidepools in size and shape. Because intertidal organisms are distributed in vertical zones and because type of rock substrate may be heterogeneous within a rocky site, excavation of pits by borers and scrapers is not uniform throughout the intertidal zone. For example, one species of boring fungi in Senegal is most abundant in the upper intertidal zone, whereas a sea urchin species, and therefore its pits, are most abundant in the lower intertidal zone (Allouc *et al.*, 1996). This distribution difference most likely affects the distribution of differently-shaped pits in the intertidal zone of this region. Differences in rock type within the intertidal bench also leads to pit heterogeneity. For example, in the same Senegal system, one type of rock is bored by the sea urchin species at about 1 mm/yr, and the other at 0.4 mm/yr (Allouc *et al.*, 1996).

Several differences exist between tidepools at the two main sites used in the present dissertation, False Point and Ocean Beach, that may be related to tidepool formation mechanism. Ocean Beach is characterized by smooth sandstone benches, riddled with circular pools similar to potholes described by Emery (1946) and Wentworth (1944) (Figure 2.2). These potholes were most likely created by abrasion of solution pits in a substrate more erosive than that of False Point. False Point consists mostly of loose cobbles and boulders surrounding conglomerate sandstone outcrops (Figure 2.3A). Tidepools in the outcrops are probably originally formed as depressions left by the removal of boulders from the sandstone cement (Figure 2.3B, Tway, 1991). Possibly as a result of these formation differences, depth of the 50 Ocean Beach study tidepools, as measured in Davis (2000), was significantly greater than depth of the 55 False Point tidepools (Ocean Beach: 26±2 cm; False Point: 14±2 cm, *t*-test, t=5.9, $p<0.001$). Average ratio of diameter to depth of the False Point pools (3.1±0.3) was significantly larger than that of the Ocean Beach pools (1.6±0.1; t=4.6, $p<0.001$). Supporting the hypothesis that abrasion had a bigger effect on tidepool shape at Ocean Beach, the ratio of pool length to width ratios differed between the two sites. Pools at Ocean Beach are more circular, with length-to-width ratios closer to 1 than those at False Point (t=2.2, p=0.031).

Differences in pool size and shape between False Point and Ocean Beach could be the source of differences in the fish assemblage noted between the two sites (Davis, 2000). Although both sites were inhabited by the same suite of species, the smaller, deeper pools of Ocean Beach had higher densities of 4 of the 5 species (the sculpin, *Clinocottus analis;* the opaleye, *Girella nigricans*; the blenny *Hypsoblennius gilberti*; and the kelpfish, *Gibbonsia elegans*). False Point pools had slightly higher densities of the clingfish, *Gobiesox rhessodon* . At least for some of the species, these discrepancies are consistent with habitat affinities displayed by the species (Davis, 2000). Pool depth is an important habitat parameter for both opaleye and sculpin, which could explain why their densities are higher at the site with the deeper tidepools. Kelpfish, evolved to mimic pieces of kelp, were more abundant at Ocean Beach, the site with the higher algal cover (Davis, 2000), which in turn could be driven by differences between the sites in rock type, bench slope, or pool depth. Clingfish, which are found under rocks in the shallowest depressions in intertidal areas (Addessi, 1994; Davis, pers. obs.), may actually prefer shallower pools, explaining their higher abundance at False Point.

Destruction of tidepool habitat

Individual tidepools are often destroyed by chemical, physical, and biological processes similar to those by which they are created. Drainage channels from tidepools, formed by the biochemical dissolution of the rock surface, can eventually cut as deep as the tidepool, so that all water drains out during low tide. This waterless pit then provides the surface for the next level of tidepool formation, and the cycle continues (Kaye, 1959).

Mechanical erosion by waves can weaken the base of a tidepool on the edge of a platform, undermining it and eventually causing its collapse. Tidepool collapse has been observed in the soft sandstone of the Ocean Beach study site, especially during the storms of the 1997-98 El Niño event (Davis, pers. obs.). Tidepools can also be destroyed by extensive surface pitting and abrasion (Kaye, 1959). The continuous wetting and drying of the intertidal zone can lead to cracks in the rocks, which allow waves to remove large chunks of the bench (Trenhaile, 1987). In colder areas, frost weathering is important in the erosion of intertidal rock (Trenhaile and Mercan, 1984; Robinson and Jerwood, 1987).

Biological erosion of tidepool walls and intertidal benches can alter tidepool habitats. Boring and scraping organisms loosen rock surfaces and allow waves to tear off sections of bench rock. At the same time they act to create pits that become tidepools, their erosive action serves to gradually deplete the entire intertidal bench. For example, bioerosion rate of calcareous Gulf of California benches by sipunculans and bivalves was measured at 30 cm of downward erosion per 1,000 yrs (Stearley and Ekdale, 1989). Nocturnal respiration of tidepool organisms adds to the dissolution of calcium carbonate cement that supports the walls of their habitat (Shepard and Grant, 1947).

Episodic changes in sections of coastline can also cause the functional loss of intertidal benches and other platforms. The localized uplift of intertidal rocks and benches due to earthquakes has been identified in many tectonically active coastal regions (Plafker, 1965; Hull, 1987; Castilla, 1988; Plafker and Ward, 1992; Carver, 1994). During one earthquake in Alaska, coastal benches were uplifted by over 11 m, pushing not only the intertidal zone but a large band of the subtidal zone out of the marine realm (Plafker, 1965). Changes on a seasonal time scale may cause temporary loss of rocky intertidal habitat, such as the summer inundation of rocky intertidal areas with sand (Shepard, 1950; Norris, 1963; Rindell, 1991).

The steady erosion of rocky headlands and other rocky shores causes the large-scale loss of tidepool habitat. In La Jolla, California, for example, a sandstone bench that prior to 1940 projected more than 7 m from the base of the sea cliffs was almost completely eroded away by 1979 (Emery and Kuhn, 1980). In 1998, there is little evidence that the bench, and its tidepools, ever existed (Davis, pers. obs.). In other areas, both episodic sea cliff landslides and continuous abrasive and chemical erosion cause the loss of tidepool habitat. Anthropogenic activities that enhance the erosion of seacliffs; such as overwatering, drainage pipes, and construction (Emery and Kuhn, 1982) also have effects on the tidepool habitats below.

Rates of intertidal rock erosion are controlled by such factors as rocky type, bench angle, and biological colonization. Limestone and sandstone erodes faster than basalts and granites. Steep slopes erode faster than horizontal slopes (Trenhaile, 1987). Coralline and other epilithic algae are suspected to protect intertidal benches of eolianite (Kaye 1959) and limestone (Hodgkin, 1970) from erosion. Other intertidal organisms may act as a protective layer by outcompeting or preying upon borers and scrapers. Rock surface may also be protected from erosion by indurated limestone crusts, which form in the intertidal zone in tropical areas when aragonite precipitates in sediment or rock interstices (Kornicker, 1958).

Conclusion

The roles of geology, chemistry, biology, and physics in shaping rocky coastal habitats are perhaps overlooked by many ecologists studying rocky intertidal species (Trudgill, 1988). Although most forces that determine the location and construction of rocky intertidal areas operate on time scales that have no direct effect on individual organisms and individual populations, these forces can be important in the evolution of habitat use and life-history traits. In addition, some forces, such as episodic erosion and excavation of burrows, do operate within the lifespan of individual organisms and can affect short-term habitat use and community structure. Coastal geomorphology is directly and indirectly related to many aspects of rocky intertidal species and whole communities, including gene flow, distribution of habitat types and thus species assemblage, and potential distribution of prey and refuge species.

These relationships between geomorphologic processes and intertidal biological communities may change with time, especially during large shifts in sea level. For example, marine terrace and intertidal bench formation is generally associated with stillstands in sea level such as that which characterizes the planet at present (Boyd and Penland, 1984; Miller, 1994). As a result, the amount of horizontal substrate available for intertidal organisms, and therefore the degree of tidepool formation, is likely determined by the rate of sea level change. The ratio of vertical to horizontal bench space in the intertidal, in turn, most likely has great effects on the types of species present in the intertidal zone. During stillstands, horizontal rock benches and tidepools may be more abundant, and therefore the number of tidepool species may increase. During periods of rapid change in sea level when benches may not develop, the rocky intertidal zone would provide habitat predominantly to emergent species capable of inhabiting vertical space, a hypothesis that would be interesting to test using the fossil record. Because geomorphologic processes are linked to biological communities on many temporal as well as spatial scales, such processes should not be ignored in the study of rocky intertidal ecology.

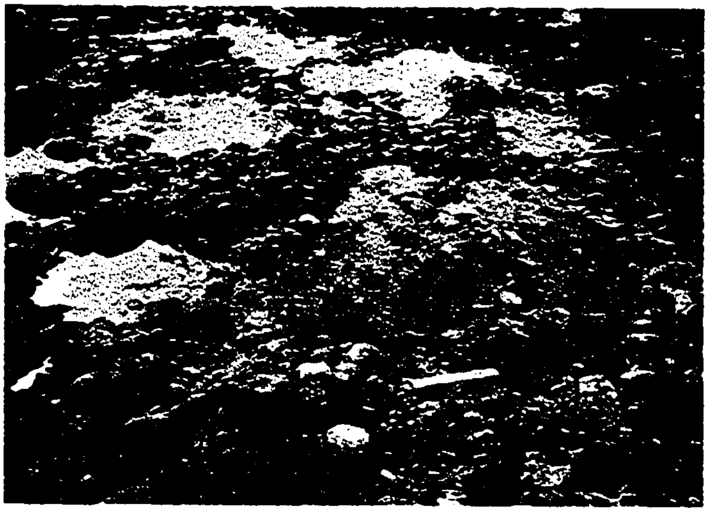
Figure 2.1: A biologically created pit in the sandstone cliffs of Ocean Beach, San Diego, California. The pit, occupied now by two crabs (*Pachygrapsus crassipes*) and one chiton (*Nuttilina fluxa*), was probably formed by one or more chitons.

A

B

Figure 2.2: The rocky intertidal bench at Ocean Beach, San Diego, California. (A) The bench itself, formed of smooth sandstone. (B) A typical cylindrical tidepool. The cylindrical shape is most likely the result of abrasion over a long period of time by the loose cobbles in the bottom of the tidepool.

A



B

Figure 2.3: The rocky intertidal bench at False Point, San Diego, California. (A) The conglomerate sandstone and loose boulders of the bench. (B) High intertidal tidepools at False Point, probably first formed by cobbles pried loose by waves from their conglomerate sandstone framework.

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Chapter 3

Spatial and seasonal patterns of habitat partitioning in a guild of southern California tidepool fishes

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ABSTRACT: Five species of fish, *Clinocottus analis, Girella nigricans, Hypsoblennius gilberti, Gobiesox rhessodon*, and *Gibbonsia elegans*, commonly occur in southern California's rocky intertidal zone. To examine the extent to which tidepool habitat is segregated by the 5 fishes, habitat partitioning patterns among and within the species were determined at 2 sites in San Diego. Fish density, species composition, and fish size were measured in 105 tidepools every 3 mo from November 1996 to August 1997. Hypotheses were tested pertaining to the segregation of habitat among different species and different size classes within species relative to the tidepool characteristics of intertidal height, surface area, depth, rugosity, and percent algal cover. A manipulative field experiment was conducted to further investigate these results. Tidepools were partitioned among and within fish species. Tidepool characteristics most important in partitioning were intertidal height, depth, and rugosity, with the order of importance of these characteristics different for each species. Habitat partitioning between size classes within species, although not as great as partitioning among species, was also based largely on tidepool intertidal height and rugosity. Although fish abundance changed seasonally, species' distribution patterns, with the exception of *C. analis*, were seasonally stable. The seasonal change in *C. analis* distribution was due to the arrival of new recruits rather than a seasonal change in adult habitat. The use of different types of tidepools by different species and by different size classes within species serves to limit contact among these groups, and therefore both direct and indirect competition, during low tide.

KEY WORDS: Fish · Rocky intertidal zone · *Clinocottus analis* · *Girella nigricans* · *Hypsoblennius gilberti* · *Gobiesox rhessodon* · *Gibbonsia elegans*

INTRODUCTION

Resource partitioning by co-occurring species serves to limit interspecific competition, whether the direct result of competition (Nakamura 1976a, Mayr & Berger 1992) or simply the result of differential evolutionary histories of the species involved (Andrewartha & Birch 1954, Brothers 1975). Partitioning can be manifested in several ways, including the segregation of prey based on type or size and the partitioning of habitat, both temporal and spatial (Ross 1986). Examples of the latter include partitioning of substratum type by fishes (Nakamura 1976a, Mayr & Berger 1992, Zander 1995) and substratum color by differently pigmented individuals of the intertidal fish *Apodichthys fucorum* (Burgess 1978). Vertical as well as horizontal space can be partitioned. For example, different zooplankters select different water column depths (Barange et al. 1991), and barnacles (Connell 1961a,b), other sessile organisms (Metaxas & Scheibling 1993), and fishes (Gibson 1972, Nakamura 1976b, Yoshiyama 1981, Bennett & Griffiths 1984) partition vertical zones of rocky intertidal habitats.

Tidepools within the rocky intertidal zone present an ideal workshop for studies of microhabitat segregation, exhibiting variation in many quantifiable habitat variables on the meter scale. These pools buffer organisms from the harsh environmental fluctuations experienced by the rest of the intertidal zone, offering refuge from emersion during low tide (Metaxas & Scheibling 1993). Relative to subtidal areas, however, tidepools are isolated and patchy islands of habitat (Wilson et al. 1992).

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Their water is subject to large thermal and chemical changes as well as variation in duration of exposure depending on the tide (Underwood & Skilleter 1996). Temperature may increase in tidepools by 15°C or more and salinity by 3 ppt in only a few hours (Metaxas & Scheibling 1993, Jensen & Muller-Parker 1994). Oxygen content may decrease from ambient levels to hypoxic conditions during the period of a low tide (Congleton 1980).

Several tidepool characteristics are important in determining the 'quality' of a particular tidepool as habitat. Tidepool size, intertidal height, and the amount of shade-providing cover determine the extent to which pool water temperature and chemistry deviate from that of ambient seawater during a low tide (Metaxas & Scheibling 1993). In addition, pool depth and amount of cover may be related to predation pressure by intertidal and aerial predators. Because of their mobility, intertidal organisms such as fishes may be able to select among pools to avoid physico-chemical fluctuations and predation. Different groups of fishes may have dissimilar refuge requirements, which may lead to differences in their intertidal distributions. Alternatively, 2 groups of fishes may have similar habitat requirements, but competition forces 1 group into a less preferred area of the intertidal.

Tidepool regions in general provide habitat for many types of fishes, including permanent residents, juveniles of predominantly subtidal species, and accidental or transient visitors (Thomson & Lehner 1976, Gibson 1982, Moring 1986, 1990). Intertidal rock pools of San Diego, California, support 4 major permanent residents: the cottid *Clinocottus analis* (woolly sculpin), the blenniid *Hypsoblennius gilberti* (rockpool blenny), the gobiesocid *Gobiesox rhessodon* (California clingfish), and the clinid *Gibbonsia elegans* (spotted kelpfish). The system also supports juveniles of the girellid *Girella nigricans* (opaleye), which inhabit tidepools for up to the first 2 yr of life (Norris 1963, Stevens et al. 1989). This paper presents research designed to: (1) investigate seasonal changes in species composition of fish assemblages in the San Diego rocky intertidal zone, (2) determine whether the 5 fishes are distributed randomly among intertidal pools, or whether their distributions are related to specific characteristics of the tidepools, (3) determine whether the 5 species have identical distributions relative to tidepool characteristics or whether habitat partitioning occurs, and (4) examine the intensity of size-based habitat partitioning within species. Multivariate analyses were employed to examine these issues using data on fish abundance, size, and distribution collected seasonally for 1 yr at 2 locations in San Diego. Further examination of fish habitat selection was accomplished by habitat manipulation experiments in the field.

METHODS

Field distributions. Fish were studied in 105 permanent tidepools at 2 sites along the coast of San Diego. Both sites are located in urban areas, frequently visited by humans. Such human traffic has been shown to have significant effects on density and distribution of invertebrates under rocks at 1 of these sites, False Point (Addessi 1994). The False Point (FP) study area, located south of Bird Rock in La Jolla, California, consists of 55 tidepools on and around 2 conglomerate sandstone outcrops. The study area south of the Ocean Beach Pier (OB) consists of 50 tidepools in a relatively flat shale and sandstone region measuring 200 m^2. Data were collected during November 1996 and February, May, and August 1997 at each of the 2 sites.

Pools in the 2 study areas were mapped in October and November of 1996, and 5 environmental variables of the pools were measured (Table 1). Length, the maximum distance across the top of the pool, and width,

Table 1. Characteristics of 55 tidepools at False Point (FP) and 50 at Ocean Beach (OB), San Diego, California, USA. Surface area, depth, and intertidal height were measured in October and November 1996. Rugosity and algal cover were estimated each season (November 1996 and February, May and August 1997). MLLW: mean lower low water

Characteristic	Site	Range	Mean ± 1 SE
Surface area	FP	0.1 to 13.5 m^2	1.5 ± 0.4 m^2
	OB	0.1 to 3.0 m^2	0.5 ± 0.1 m^2
Depth	FP	4 to 35 cm	14 ± 2 cm
	OB	3 to 69 cm	26 ± 2 cm
Intertidal height	FP	–0.1 to 3.1 ft (–0.03 to 0.94 m) above MLLW	1.7 ± 0.1 ft (0.52 ± 0.03 m)
	OB	–0.2 to 3.7 ft (–0.06 to 1.13 m) above MLLW	1.8 ± 0.2 ft (0.52 ± 0.03 m)
Rugosity	FP	1 to 5	2.5 ± 0.2 Nov, May 2.7 ± 0.2 Feb, Aug
	OB	1 to 5	2.6 ± 0.2 Nov, Feb 2.3 ± 0.2 May, Aug
Algal cover	FP	0 to 100%	38 ± 4% Nov, 34 ± 4% Feb 39 ± 4% May, 41 ± 4% Aug
	OB	0 to 90%	22 ± 4% Nov, 31 ± 5% Feb 26 ± 4% May, 32 ± 5% Aug

the distance perpendicular to the length axis at the midpoint of the pool, were measured to the nearest cm and multiplied to approximate surface area. Mean depth was determined by making approximately 10 haphazardly distributed measurements to the nearest 0.5 cm and averaging the values.

The intertidal height of each pool relative to the mean lower low water (MLLW) mark was obtained by measuring the time at which each pool was isolated by the ebbing tide in November 1996. As a high tide ebbs, pools higher in the intertidal zone are isolated first, followed by middle intertidal pools, then low pools. Pools are resubmerged on the flooding tide in the reverse order, so that high intertidal pools are emerged for the greatest amount of time. Intertidal height, therefore, is a proxy for emergence duration, or isolation, of a tidepool and can be determined from its isolation point. In the present study, the isolation point of a tidepool was determined to the nearest minute on a given day, then Harbor Master™ software was used to determine tidal height to the nearest 0.1 ft (0.03 m) above MLLW at that time. Isolation was defined as the last time at which there was a flux of water in (by wave, surge, or splash) or a flux of water out (by draining) of the pool. The effects of sea state on isolation times were unknown; therefore, 2 full days, 1 calm and 1 relatively rough, were devoted to this exercise at each site. Intertidal heights determined for these different sea states differed only by as much as 0.2 ft (0.06 m), so averages were used when discrepancies occurred.

Following Bennett & Griffiths (1984), a qualitative assessment was made of rugosity, which was defined as the amount of rocky substratum in a pool. Rugosity was categorized subjectively on a scale of 1 to 5 each time a pool was sampled, with category 1 pools containing little or no relief. This subjective method was validated by quantitative rugosity calculations of 35 tidepools at False Point. Quantitative rugosity measurements were made by placing a grid over the tidepool, using a random numbers table to choose 3 lengthwise transects, then measuring depth every 1.5 cm along the transect. Rugosity was calculated as the mean difference between adjacent 1.5 cm depth measurements. Quantitative and qualitative assessments were strongly correlated ($n = 35$, $r^2 = 0.71$, $p < 0.01$). As in Gibson (1972), Marsh et al. (1978), Bennett & Griffiths (1984), Prochazka & Griffiths (1992), Mahon & Mahon (1994), and Pfister (1995), a subjective method was also used to estimate algal cover each time a pool was sampled, in this case to the nearest 5%.

To collect all fish in a pool, the pool was drained by bailing or by siphoning with hoses guarded by 1 mm mesh. Because this sampling was repeated seasonally, neither quinaldine nor rotenone was used due to their adverse effects on biota. Every crevice was searched, and rocks were removed if necessary. On 1 occasion, when it was discovered that a crevice was too deep to be adequately searched, the pool was discarded from the study. All fish were identified to species and their total lengths measured to the nearest mm. The rocks were then replaced, the pool refilled, and the fish returned. Between 3 and 6 d were required to sample all pools within a site. Data were collected only during the day and only during tides lower than 1.0 ft (0.30 m) above MLLW. Three of the lowest pools at False Point were in regions of shifting rocks and boulders; if a pool was no longer present during subsequent seasonal sampling, a substitute pool with similar characteristics was located.

Hypotheses pertaining to inter- and intraspecific differences in fish distribution relative to the 5 tidepool characteristics (Table 1) were tested using both multiple regression and principal component analysis on SYSTAT (Macintosh version 5.2.1). Because the 5 environmental tidepool characteristics were often inter-correlated, residuals of these variables were used in the multiple regression analysis to achieve uncorrelated independent variables (Graham 1997). The 5 tidepool variables were hierarchically arranged based on the strength of simple regressions conducted between each variable and densities of each species. Each variable was then regressed against the others in the order they appeared on the list, and if the regression produced a p-value ≤ 0.25, the residual of the variable lower on the list was determined and substituted. This hierarchy of variables was held constant for data analyses of all 4 months, both sites and all species. Therefore, rugosity was regressed against intertidal height and if correlated was retained as residual rugosity. Then depth was regressed against intertidal height, and if correlated residual depth was regressed against residual rugosity. This process continued in such a manner that surface area, the last variable on the list, was regressed against 4 other variables. These 5 new environmental variables were regressed against average tidepool fish densities using backwards step-wise multiple regressions (Graham 1997). Factor variables with p-values ≥ 0.10 were removed from the regression models.

The limitations of this approach (e.g., the subjective ordering of environmental factors and the potential loss of much of the meaning of those factors towards the end of the list) prompted the use of principal component analysis, a statistical method designed to examine correlations and variability of non-independent factors (Manly 1986). Linear combinations of the 5 environmental factors (principal components, or PCs) were constructed to account for the variability between the factors for each month at each site. In all 8 analyses, only those PCs explaining ≥20% of the variability among the 5 environmental factors were retained. These included the first 3 PCs at False Point and the first 2 PCs at Ocean Beach. The tidepool PCs, by definition all orthogonal and therefore independent, were regressed against tidepool fish densities using backwards step-wise multiple regressions (Reyment & Joreskog 1993). Again, factor variables with p-values ≥ 0.10 were removed from the models.

Intraspecific differences in fish distribution were analyzed using both the set of uncorrelated, residual environmental variables and the set of tidepool PC values computed from the original environmental variables. *Clinocottus analis*, *Girella nigricans*, and *Gobiesox rhessodon* were divided into size classes, and the proportion of small individuals was calculated as the number of small individuals divided by the total number of individuals. This proportion was regressed against both the residual factors and the PCs. The 2 size classes of *C. analis*, <40 mm and ≥40 mm in total length, were loosely based on cohorts visible in the size-frequency histograms for each sampling month (J.L.D.D. unpubl. data). *G. nigricans* and *G. rhessodon* were divided into 2 size classes containing approximately equal numbers of individuals. The small size class ot *G. nigricans* included fish <50 mm, and that for *G. rhessodon* included fish <33 mm. *Hypsoblennius gilberti* and *Gibbonsia elegans* were not abundant enough for this analysis.

Experimental manipulation of the natural habitat. Tidepool rugosity was manipulated to determine the effects of both addition and depletion of rock structure on tidepool fish composition. Four groups of tidepools, 9 high-rugosity control pools, 9 high-rugosity experimental pools, 9 low-rugosity control pools, and 9 low-rugosity experimental pools, were established in the rocky section of shoreline from Bird Rock, La Jolla, to False Point. The pools were designated high-rugosity or low-rugosity based on subjective rugosity ratings discussed above. Surface area, depth, intertidal height, and subjective algal cover were also determined for each pool.

Following removal of all fishes, the experimental high-rugosity pools were transformed into low-rugosity pools by removing all loose rocks, and the experimental low-rugosity pools were made into structurally complex pools by adding a layer of loose rocks to cover the bottom. Structure of the control pools was left unchanged. All fish were then measured, identified, and returned to their original pools. Two days later, each pool was sampled again and fish species composition, abundance, and size data were collected. The experimental pools were sampled on January 8–9, 1998, and re-sampled on January 10–11. The control pools, because they were part of the 55-pool set described in the previous section, were not sampled and re-sampled until January 29 and January 31.

RESULTS

Community structure

Clinocottus analis was the most abundant species at both sites, making up 48, 52, 72, and 58% of the total fish collected at both sites combined in November, February, May, and August, respectively (Table 2). *Girella nigricans* comprised from 8 to 22% and *Gobiesox rhessodon* from 11 to 30% of the total number of fish collected per sampling month. *Hypsoblennius gilberti* comprised from 4 to 8% of the individuals, and *Gibbonsia elegans* from 2 to 4%. Between 324 (February) and 550 (August) individuals were collected during each sampling month. None of the individual species exhibited significant differences in abundance in all 105 tidepools among sampling periods (ANOVA, $F_{4,105} = 0.59$, p = 0.62 for *C. analis*; $F_{4,105} = 1.47$, p = 0.22 for *G. nigricans*; $F_{4,105} = 1.42$, p = 0.24 for *H. gilberti*; $F_{4,105} = 1.13$, p = 0.34 for *G. rhessodon*; and $F_{4,105} = 0.37$, p = 0.81 for *G. elegans*).

Tidepool densities of *Clinocottus analis* and *Girella nigricans* were greater at Ocean Beach than False Point during all 4 months (Table 3). Density of *Hypsoblennius gilberti* was higher in Ocean Beach during February and August (*t*-tests, p < 0.05). These density

Table 2. Number, size range, and mean total length (±1 SE) of intertidal fishes collected seasonally at False Point and Ocean Beach. Small size classes are <40 mm for *Clinocottus analis*, <50 mm for *Girella nigricans*, *Hypsoblennius gilberti*, and *Gibbonsia elegans*, and <33 mm for *Gobiesox rhessodon*

Species	Total number	No. in small size class	Size range	Mean size
November				
C. analis	197	7	31–138	62 ± 1.4
G. nigricans	45	16	29–91	56 ± 2.8
H. gilberti	30	2	27–128	74 ± 4.5
G. rhessodon	119	49	11–52	33 ± 0.7
G. elegans	13	0	51–120	88 ± 5.8
February				
C. analis	168	31	23–113	59 ± 1.5
G. nigricans	63	18	32–81	55 ± 1.4
H. gilberti	19	2	26–120	79 ± 5.4
G. rhessodon	63	26	22–49	35 ± 0.8
G. elegans	11	1	31–120	92 ± 7.8
May				
C. analis	301	150	13–109	47 ± 1.6
G. nigricans	35	2	45–110	65 ± 2.5
H. gilberti	15	0	74–109	91 ± 2.3
G. rhessodon	49	22	27–47	34 ± 0.7
G. elegans	15	3	41–122	83 ± 8.0
August				
C. analis	319	96	23–126	52 ± 1.0
G. nigricans	121	73	24–95	45 ± 1.1
H. gilberti	42	9	22–126	64 ± 3.9
G. rhessodon	60	21	16–46	35 ± 1.0
G. elegans	8	1	46–111	79 ± 11.0

differences do not represent an increase in the number of individuals collected per pool at Ocean Beach (t-tests, $p > 0.05$), but rather a similar number of individuals in pools with smaller surface area.

Clinocottus analis individuals ranged in size from 13 to 138 mm in total length. Maximum recruitment based on size data occurred from late April to August, with some recruitment as early as February (Table 2). *Girella nigricans* individuals ranged from 24 to 110 mm, with peak recruitment occurring during August. *Gobiesox rhessodon* ranged in size from 11 to 52 mm, with the largest number of small individuals occurring during November. *Hypsoblennius gilberti* and *G. elegans* never showed strong recruitment peaks, but greatest numbers of smaller individuals appeared during August and May, respectively (Table 2).

Table 3. Tidepool fish densities at False Point (FP) and Ocean Beach (OB). Densities (number of fish divided by pool surface area) were averaged for all pools containing at least 1 individual of a particular species (zero densities were excluded). All densities are presented in number of fish per m^2. Significant differences in tidepool fish densities between FP and OB are designated by asterisks (t-tests: $^*p \le 0.05$; $^{**}p \le 0.01$; $^{***}p \le 0.005$)

Species	Month	FP densities		OB densities		OB vs FP
		Range	Mean ± 1 SE	Range	Mean ± 1 SE	*t*-test
C. analis	Nov	0.7–5.8	2.5 ± 0.4	1.5–49.3	8.3 ± 2.2	*
	Feb	0.7–5.8	1.9 ± 0.3	1.3–27.7	6.3 ± 1.6	*
	May	0.5–17.6	4.2 ± 0.9	1.5–34.0	9.5 ± 1.9	**
	Aug	0.7–29.9	4.5 ± 1.2	1.3–67.0	12.5 ± 3.4	*
G. nigricans	Nov	0.1–1.4	0.7 ± 0.2	0.3–9.2	4.0 ± 0.9	***
	Feb	0.2–3.4	1.3 ± 0.4	2.9–3.9	3.3 ± 0.3	*
	May	0.4–1.8	1.1 ± 0.4	3.0–5.0	4.0 ± 0.6	**
	Aug	0.5–6.8	2.3 ± 0.5	0.8–15.0	5.3 ± 1.0	**
H. gilberti	Nov	0.6–1.6	1.2 ± 0.2	0.7–2.5	1.4 ± 0.3	
	Feb	0.1–1.1	0.6 ± 0.2	0.7–1.7	1.3 ± 0.2	*
	May	0.4–1.8	0.9 ± 0.4	0.3–2.5	1.2 ± 0.7	
	Aug	0.1–6.7	1.6 ± 0.8	1.5–6.8	4.1 ± 0.8	*
G. rhessodon	Nov	0.1–31.8	5.3 ± 2.2	1.6–9.3	4.9 ± 1.3	
	Feb	0.5–27.0	4.2 ± 2.0	0.8–1.6	1.1 ± 0.3	
	May	0.5–45.0	7.9 ± 4.8	0.7–3.2	1.8 ± 0.6	
	Aug	0.4–13.6	4.5 ± 1.3	2.4–4.7	3.3 ± 0.7	
G. elegans	Nov			0.9–5.7	2.8 ± 0.8	
	Feb			0.8–4.4	2.0 ± 0.6	
	May			0.8–3.7	1.9 ± 0.5	
	Aug			0.8–2.0	1.3 ± 0.4	

Effects of tidepool factors on fish distribution

In general, low intertidal pools that were large, deep, highly rugose and high in algal cover harbored larger numbers of fish than small, shallow, high intertidal pools with little rock or algal cover. However, importance of the tidepool characteristics varied among species. Tidepool densities of the 5 species were correlated with different pool environmental variables, (multiple regression analysis, Table 4), suggesting that each species selects a different type of tidepool in the intertidal zone.

Two fishes were commonly found in the upper and middle intertidal zones. *Clinocottus analis* occurred in pools over a wide intertidal height range, but had greatest densities in lower intertidal pools (Table 4). Density of this species was also usually positively correlated with rugosity. Unlike that of *C. analis*, *Girella nigricans* density was not correlated with intertidal height, and individuals were consistently absent from the lower intertidal zone. Tidepool depth and, to a lesser extent, rugosity were most important in models of *G. nigricans* density.

The other 3 species were not found in the middle or upper intertidal zones; they were restricted instead to the lower intertidal zone. Of the 5 environmental variables, intertidal height contributed most to models relating these variables to *Hypsoblennius gilberti*, *Gobiesox rhessodon*, and *Gibbonsia elegans* densities. However, satisfactory analysis of rugosity and algal cover was prohibited by the use of their residuals in multiple regression analysis. This transformation process, which was dependent on the subjective ordering of the 5 variables, masked the importance of lower-ordered variables. The use of uncorrelated tidepool PCs instead of variable residuals in multiple regression analysis alleviated this problem.

The contribution of the 5 variables to the first PC (PC1) at both sites indicated several consistent patterns across all 4 months (Table 5). At False Point, PC1 was a combination of lower tidal height, greater pool depth, increased surface area, increased rugosity, and low or negligible algal cover. In all months except May at Ocean Beach, PC1 was comprised of a similar combination of variables, except that the contribution of algal cover was positive. In May at Ocean Beach, this combination described PC2 (Table 5).

PC analysis revealed that tidepools with fish exhibited a different set of environmental properties than pools without fish (Figs. 1 & 2). Pools devoid of fish were characterized by higher intertidal height, a result consistent with the significant negative correlations of intertidal height with fish density for most of the 5 species (Table 4). Pools that contained fish had positive values of PC1 (or PC2 in May at Ocean

Table 4. Multiple regressions of fish species densities in tidepools at False Point (FP) and Ocean Beach (OB) against tidepool environmental factors (intertidal height, rugosity, depth, algal cover, and surface area). Tidepools were sampled seasonally from November 1996 to August 1997. Analyses were not performed if fewer than 4 tidepools contained individuals of a particular species. Overall regressions statistics are given along with probabilities and slopes for each significant factor. Degrees of freedom are 54 for FP and 49 for OB analyses

Species	Season/ site	Factor	Slope	p-value	Model *F*	Model p	Model R^2
C. analis	Nov/FP	Rugosity	+0.7	<0.001	10.4	<0.001	0.40
		Height	−2.3	0.002			
		Surface area	+2.0	0.009			
	Nov/OB	Rugosity	+1.8	0.031	4.4	0.009	0.24
		Height	−1.8	0.042			
		Algal cover	+11.8	0.060			
	Feb/FP	Rugosity	+0.4	<0.001	13.1	0.000	0.52
		Depth	+0.1	<0.001			
		Height	−0.4	0.008			
		Surface area	+0.1	0.035			
	Feb/OB	Height	−1.2	0.017	4.4	0.009	0.24
		Depth	+0.1	0.060			
		Rugosity	+1.1	0.063			
	May/FP	Height	−2.0	<0.001	9.2	<0.001	0.27
		Rugosity	+0.7	0.062			
	May/OB	Height	−2.6	<0.001	15.6	<0.001	0.25
	Aug/FP	Height	−2.1	0.006	8.3	0.006	0.14
	Aug/OB	Height	−3.7	0.002	7.7	0.001	0.25
		Algal cover	+14.7	0.047			
G. nigricans	Nov/FP	Depth	+0.05	0.001	11.8	0.001	0.20
	Nov/OB	Depth	+0.04	0.070	3.4	0.070	0.07
	Feb/FP	Depth	+0.05	0.001	10.4	0.000	0.52
		Rugosity	+0.2	0.002			
		Surface area	+0.05	0.031			
	Feb/OB	Rugosity	+0.2	0.031	5.0	0.031	0.10
	May/FP	Surface area	+0.05	0.013	5.7	0.006	0.23
		Depth	+0.01	0.034			
	Aug/FP	Depth	+0.08	0.024	4.4	0.017	0.15
		Rugosity	+0.3	0.069			
	Aug/OB	Rugosity	+1.0	0.011	5.3	0.008	0.18
		Depth	+0.06	0.063			
H. gilberti	Nov/FP	Height	−0.2	0.009	7.3	0.009	0.13
	Nov/OB	Surface area	+0.4	0.004	7.5	0.002	0.26
		Height	−0.1	0.019			
	Feb/FP	Height	−0.09	0.059	3.8	0.030	0.13
		Rugosity	+0.03	0.068			
	Feb/OB	Height	−0.1	0.003	9.9	<0.001	0.32
		Surface area	+0.3	0.004			
	AugFP	Height	−0.4	0.045	3.7	0.032	0.13
		Algal cover	−1.4	0.100			
	AugOB	Depth	+0.04	0.052	3.8	0.057	0.07
G. rhessodon	Nov/FP	Surface area	−3.5	<0.001	18.6	<0.001	0.28
	Nov/OB	Height	−0.6	0.004	8.3	0.001	0.28
		Rugosity	+0.5	0.013			
	Feb/FP	Height	−2.0	0.002	11.1	0.002	0.18
	May/FP	Height	−2.6	0.014	6.5	0.014	0.15
	May/OB	Rugosity	+0.2	0.013	4.8	0.005	0.25
		Surface area	+0.3	0.082			
		Height	−0.1	0.097			
	Aug/FP	Height	−1.6	<0.001	21.9	<0.001	0 47
		Algal cover	−5.0	<0.001			
G. elegans	Nov/OB	Height	−0.4	0.007	8.1	0.007	0.16
	Feb/OB	Height	−0.3	0.006	5.9	0.006	0.22
		Rugosity	−0.2	0.079			
	May/OB	Height	−0.2	0.003	9.5	<0.001	0.30
		Surface area	+0.5	0.008			

Table 5. Loadings of principal components (PCs) based on the tidepool environmental factors of intertidal height, depth, surface area, rugosity, and algal cover for sets of approximately 50 tidepools. Tidepools were sampled at 2 sites, False Point and Ocean Beach, seasonally from November 1996 to August 1997. Loadings for PCs that explain >20% of the variability among the tide pool environmental factors are listed

Season	Factor	False Point PC1	False Point PC2	False Point PC3	Ocean Beach PC1	Ocean Beach PC2
November	Height	−0.731	0.309	0.529	−0.818	0.443
	Depth	0.559	−0.025	0.659	0.305	0.746
	Surface area	0.607	0.186	0.434	0.363	0.452
	Rugosity	0.730	0.448	−0.357	0.380	0.687
	Algal cover	0.211	−0.944	0.072	0.799	−0.477
% variance explained		35.8	24.5	20.7	37.2	33.2
February	Height	−0.645	0.381	0.599	−0.851	0.363
	Depth	0.728	−0.023	0.491	0.230	0.778
	Surface area	0.681	0.087	0.528	0.455	0.575
	Rugosity	0.671	0.473	−0.498	0.603	0.391
	Algal cover	0.118	−0.966	0.028	0.783	−0.469
% variance explained		37.5	26.2	22.5	39.2	28.8
May	Height	−0.645	0.381	0.599	0.873	−0.317
	Depth	0.728	−0.023	0.491	0.381	0.673
	Surface area	0.681	0.087	0.528	0.010	0.767
	Rugosity	0.671	0.473	−0.498	0.177	0.676
	Algal cover	0.118	−0.966	0.028	−0.935	0.115
% variance explained		37.5	26.2	22.5	36.3	32.2
August	Height	−0.651	−0.330	0.645	−0.934	0.134
	Depth	0.693	−0.094	0.533	−0.100	0.772
	Surface area	0.654	0.100	0.561	0.289	0.707
	Rugosity	0.778	−0.412	−0.410	0.324	0.642
	Algal cover	−0.025	0.981	−0.063	0.894	−0.267
% variance explained		38.7	25.2	23.7	37.4	31.8

Beach). Densities of all 5 species were generally positively correlated with this linear combination of variables (Table 6).

Although densities of all 5 tidepool species were related in a similar way to PC1, interspecific differences in distribution were often revealed by PC2 or PC3 (Figs. 3 & 4). Pools with *Gobiesox rhessodon* present were generally characterized by increased rugosity and lower intertidal height, whereas pools with *Girella nigricans* were characterized instead by increased depth and surface area (Fig. 3). At False Point, pools with *G. nigricans* had higher values of PC3 than did pools with *G. rhessodon* ($t_{7,14}$ = 2.6, p = 0.02 for November; $t_{10,12}$ = 2.2, p = 0.04 for February; only 4 pools with *G. nigricans* in May; and $t_{17,10}$ = 1.9, p = 0.07 in August). In contrast to both of these species, *Clinocottus analis* had a more ubiquitous distribution throughout the range of tidepools; it was present in pools encompassing the range of both *G. nigricans* and *G. rhessodon* (examples shown in Fig. 4). Because *Hypsoblennius gilberti* and *Gibbonsia elegans* were present in relatively few pools per sampling season, they are not plotted in Figs. 3 & 4; however, their pools are similar to those of *G. rhessodon* and are found in the same regions of the plots.

Habitat partitioning by size

Clinocottus analis, *Girella nigricans*, and *Gobiesox rhessodon* exhibited similar size-based intraspecific patterns in intertidal distribution (Table 7). When small individuals were abundant, the proportion of small individuals generally increased in pools with declining values of PC1 or with declining values of those variables that contributed to PC1, such as depth, rugosity, and surface area (Table 7). Small (<40 mm) *C. analis* individuals were present only in May and August at Ocean Beach and from February to August at False Point. During May at False Point, the season and the site of highest small *C. analis* abundance, the proportion of small *C. analis* was greatest in shallow, small, low rugosity, low algal cover, high intertidal pools.

Girella nigricans size partitioning had some similarities to that of *Clinocottus analis*. Like *C. analis* in May, the proportion of small (<50 mm) *G. nigricans* was lowest in tidepools with high values of PC1 in 3 of 4 analyses (Table 7). During August at Ocean Beach, the period of highest recruitment, smaller *G. nigricans* individuals were found higher in the intertidal than larger individuals.

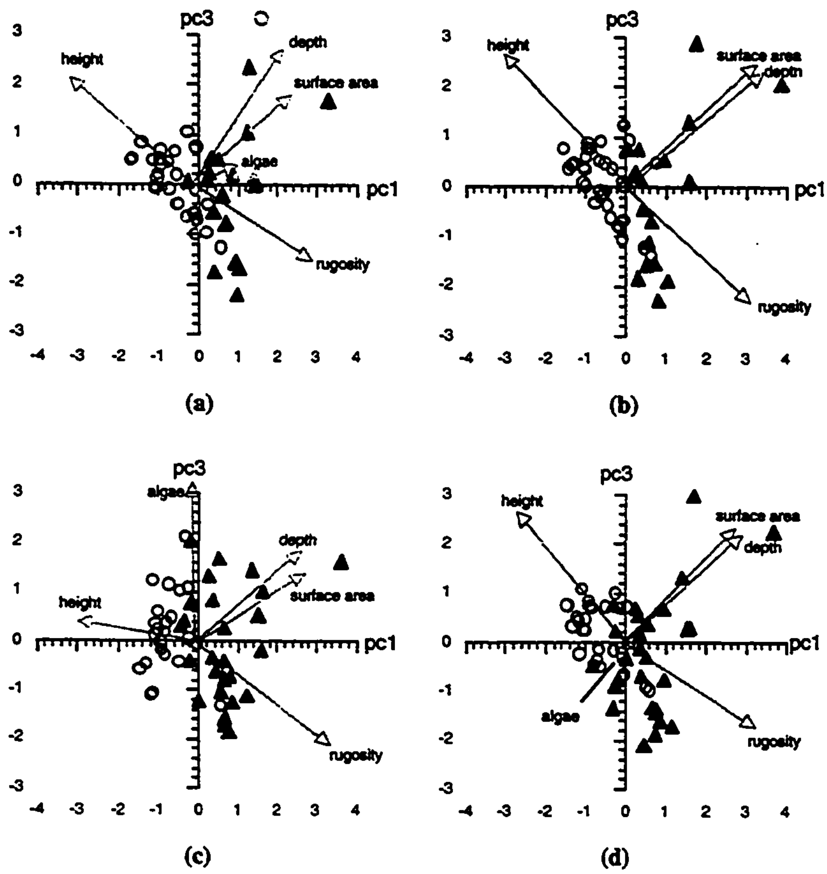

Fig. 1. Distribution of tidepools with fish (▲) versus tidepools without fish (O) at False Point in (a) November, (b) February, (c) May, and (d) August. Values of PC1 for each tidepool are plotted against values of PC3. PC3 was chosen for the *y*-axis instead of PC2 because component loadings of PC3 were more consistent across months, enabling better seasonal comparisons. Loading of the original variables on the PC axes are indicated by arrows

Gobiesox rhessodon also displayed size-related differences in density and proportion with respect to environmental factors (Table 7). Like that of *Clinocottus analis* and *Girella nigricans*, the proportion of small (<33 mm) *G. rhessodon* present in pools was negatively correlated with rugosity. In contrast to the pattern observed in several cases for the other 2 species, the proportion of small *G. rhessodon* decreased with intertidal height during February at False Point (Table 7). Analysis of *G. rhessodon* size patterns was not possible at Ocean Beach due to the relatively low abundance of this species at this site.

Seasonal patterns

Habitat distribution of fishes remained fairly constant in the rocky intertidal at False Point and Ocean Beach from November to August. At both sites, the distribution of tidepools that contained fish versus tidepools devoid of fish was seasonally consistent relative to PC1 and PC2 or PC3 (Figs. 1 & 2). Component loadings shifted in May at Ocean Beach (Fig. 2c), resulting in a rotation of the contributions of the 5 environmental factors relative to the PC axes. However, pool distributions shifted as well, such that the bulk of tidepools without fish retained a similar relationship to height and the other components.

The few seasonal changes in habitat distribution that did occur can be attributed to the arrival of new recruits from spring to fall. Abundance of *Clinocottus analis* almost doubled at the 2 sites from February to May, and the number of individuals <40 mm increased by almost 500% (Table 2). This abundance of smaller fish in May and August with potentially different habitat preferences might explain the lack of correlation of *C. analis* density with such factors as tidepool rugosity,

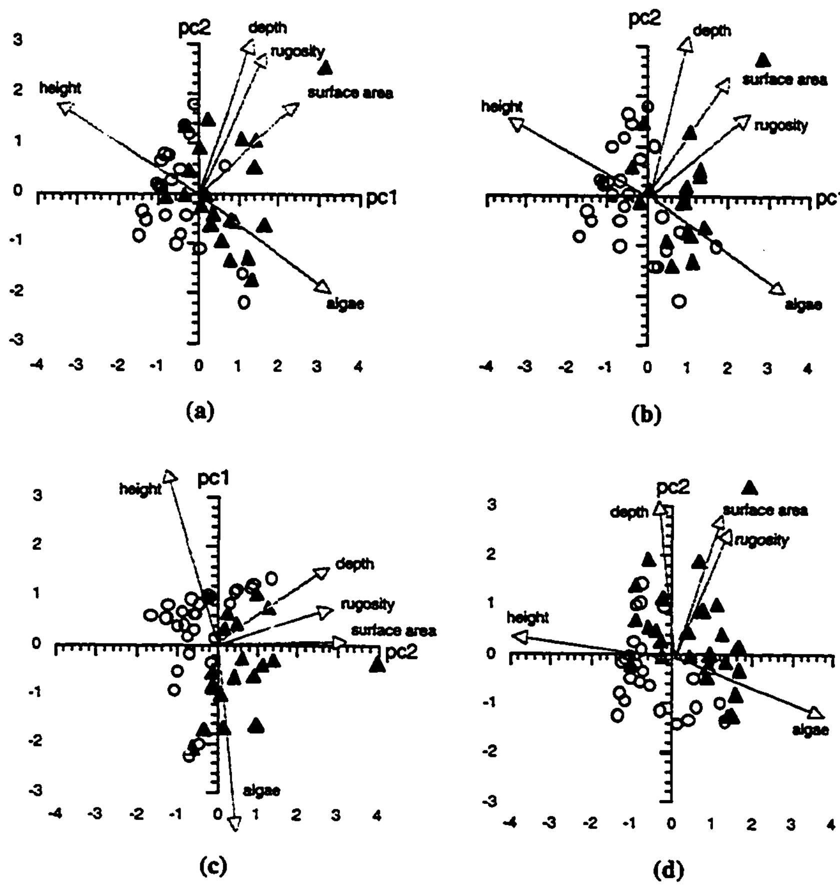

Fig. 2. Distribution of tidepools with fish (▲) versus tidepools without fish (O) at Ocean Beach in (a) November, (b) February, (c) May, and (d) August. Values of PC1 for each tidepool are plotted against values of PC2. Loading of the original variables on the PC axes are indicated by arrows. Axes for PC1 and PC2 are switched in (c) to keep variable loading quadrants as consistent as possible with (a), (b), and (d) (see text)

surface area, and depth in these months. When the smaller fish were less abundant (November and February), density of this species was always significantly correlated with rugosity and often with surface area and depth. Consistent with these broad seasonal changes in habitat are the results shown in Table 7, in which the proportion of smaller individuals present in a pool increased in smaller, less rugose pools.

The number of *Girella nigricans* individuals at the 2 sites increased by more than 3 times from May to August, the result of smaller individuals arriving in the intertidal zone. These individuals occupied pools up to 3.7 ft (1.13 m) above MLLW and account for the positive relationship between the proportion of small fish and intertidal height noted in August at Ocean Beach (Table 7). Despite this change in size composition of *G. nigricans*, overall density exhibited roughly similar relationships with the environmental factors across months (Table 4).

Habitat manipulation experiment

Experimental manipulation of rocky structure within tidepools led to changes in fish densities consistent with the observations described above. When highly rugose tidepools were depleted of their rocky structure, the total number of fish and the number of species in the pools decreased (paired *t*-tests: $t_8 = 5.4$, $p < 0.001$ and $t_8 = 5.2$, $p < 0.001$, respectively, Fig. 5c). The number of individuals of the 2 most abundant species, *Clinocottus analis* and *Gobiesox rhessodon*, also decreased ($t_8 = 2.5$, $p = 0.035$ and $t_8 = 5.3$, $p < 0.001$, respectively). The decline in *G. rhessodon* density over a period of 2 d (loss of 6.7 fish m^{-2}) was significantly greater than the decline in *C. analis* density over the same period (loss of 0.4 fish m^{-2}; $t_8 = 4.2$, $p = 0.003$). This suggests that *G. rhessodon* was more affected by loss of rocky structure over a period of 2 d than was *C. analis*. Tidepools with little structural

Table 6. Multiple regressions of fish species densities in tidepools at False Point (FP) and Ocean Beach (OB) against tidepool principal components (PCs) based on environmental parameters. Tidepools were sampled seasonally from November 1996 to August 1997. Only the first 3 PCs at FP and the first 2 at OB were included in the regression analysis. Analyses were not performed if fewer than 4 tidepools in a data set contained individuals of a particular species. Overall regression statistics are given as well as probabilities and slopes for each significant component

Species	Season/ site	PC	Slope	p-value	Model *F*	Model p	Model R^2
C. analis	Nov/FP	1	+0.7	<0.001	16.3	<0.001	0.25
	Nov/OB	1	+3.3	0.005	9.0	0.005	0.17
	Feb/FP	1	+0.8	<0.001	42.4	<0.001	0.45
	Feb/OB	1	+2.2	0.002	11.2	0.002	0.21
	May/FP	1	+1.5	0.002	10.6	0.002	0.18
	May/OB	1	−2.9	0.002	8.0	0.001	0.27
		2	+1.9	0.033			
	Aug/FP	1	+1.4	0.014	5.7	0.006	0.19
		3	−1.3	0.031			
	Aug/OB	1	+5.3	0.001	13.3	0.001	0.22
G. nigricans	Nov/FP	1	+0.1	0.006	8.1	0.006	0.15
	Nov/OB	No significant relationships					
	Feb/FP	1	+0.4	<0.001	21.8	<0.001	0.30
	Feb/OB	No significant relationships					
	May/FP	1	+0.2	0.001	13.1	0.001	0.21
	Aug/FP	1	+0.5	0.033	4.8	0.033	0.09
	Aug/OB	2	+1.2	0.005	8.6	0.005	0.15
H. gilberti	Nov/FP	1	+0.1	0.008	7.7	0.008	0.14
	Nov/OB	1	+0.3	<0.001	15.2	<0.001	0.26
	Feb/FP	1	+0.1	0.002	10.6	0.002	0.18
	Feb/OB	1	+0.2	0.001	13.8	0.001	0.24
	Aug/FP	3	−0.3	0.057	3.8	0.057	0.07
	Aug/OB	2	+0.5	0.068	3.5	0.068	0.07
G. rhessodon	Nov/FP	3	−2.3	<0.001	10.4	0.018	0.31
		1	+1.5	0.018			
	Nov/OB	1	+1.0	<0.001	14.9	<0.001	0.26
	Feb/FP	3	−1.5	0.005	6.2	0.004	0.20
		1	+0.9	0.059			
	May/FP	2	−1.5	0.085	3.1	0.085	0.06
	May/OB	2	+0.2	0.013	6.7	0.013	0.13
	Aug/FP	1	+0.8	0.016	6.2	0.016	0.11
G. elegans	Nov/OB	1	+0.4	0.016	6.2	0.016	0.13
	Feb/OB	1	+0.3	0.027	5.2	0.027	0.11
	May/OB	1	−0.2	0.023	5.6	0.023	0.11

tural relief exhibited changes in fauna when transformed into highly rugose habitats (Fig. 5a). Total fish density increased ($t_8 = 2.3$, p = 0.050) and *C. analis* density increased ($t_8 = 2.5$, p = 0.042) over the 2 d period. The increase in total number of species was not significant ($t_8 = 1.8$, p = 0.104). *G. rhessodon* density also did not increase significantly ($t_8 = 1.3$, p = 0.234). The 2 sets of control experiments indicated that there was no change in number of species, total number of fish, or number of individuals of either *C. analis* or *G. rhessodon* due to sampling pressure alone (Fig. 5b,d).

DISCUSSION

The 5 most abundant fishes in the San Diego rocky intertidal, *Clinocottus analis, Girella nigricans, Gobiesox rhessodon, Hypsoblennius gilberti,* and *Gibbonsia elegans,* were not distributed uniformly in tidepool habitats. Instead, each species occupied a subset of available tidepools. The cues used by fish to choose microhabitats and cues used at certain stages to promote intraspecific shifts in microhabitats are unknown (Gibson 1982). However, several processes related to environmental characteristics of tidepools are likely to be important. Larger, deeper tidepools at False Point and Ocean Beach remain more thermally and chemically stable during isolation from the subtidal zone than smaller, shallower pools at identical intertidal heights (J.L.D.D. unpubl. data). These larger pools may also shelter fish from predation by birds. Although pools lower in the intertidal zone do not undergo the same thermal and chemical changes as higher pools, they are isolated for shorter durations and thus expose

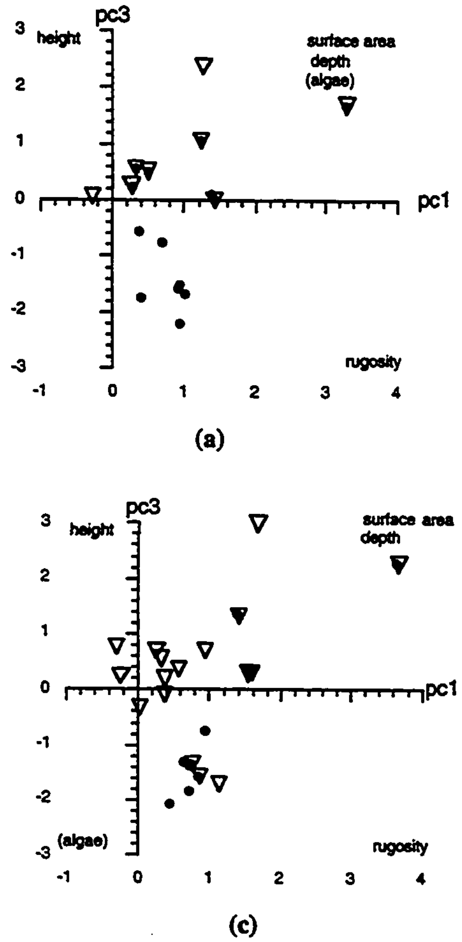

Fig. 3. Distribution of tidepools with *Girella nigricans* (▼) and *Gobiesox rhessodon* (●) at False Point in (a) November, (b) February, and (c) August. Values of PC1 are plotted against values of PC3, as in Fig. 1. Variable loadings are not plotted again, but their quadrants are noted

inhabitants to subtidal risks, such as predation by larger coastal fishes, for greater periods of time. Structural refuge provided by rocks or algae might counter such risks, offering protection from predation in both the high and the low intertidal. Prey distribution, not studied here, is also likely to be important in determining tidepool distributions of rocky intertidal fishes (Ross 1986).

Interspecific similarities in microhabitat distribution

Bigger, deeper tidepools with rock or algal cover generally had more individuals of all fish species than smaller, shallower, bare rock substratum pools. PC analyses indicated that the linear combination of variables explaining the greatest amount of environmental variability was generally one of negative intertidal height, positive depth, positive surface area, and positive rugosity during all 4 sampling months at both sites (except for May at Ocean Beach, in which this linear combination was PC2). This calculation of PCs was made for the tidepools at each site independent of fish densities and distributions; it simply represents an index that accounts for the greatest amount of environmental variability among tidepools. Densities of all 5 fish species were positively correlated with this PC, suggesting that fish detected or cued in to this same environmental variability when choosing habitats in the intertidal zone. Fish of all 5 species appeared to be finding pools that maximize the value of this index, which is composed of factors that all tend to be related to tidepool physico-chemical stability and lower risk of intertidal predation. This relationship between PC1 and stability or predation has no ecological basis; the creation of tidepools by erosion or chance deposition of boulders is unlikely to be controlled by factors that would tend to maximize or minimize thermal or chemical stability or predation. The fact that the variability is similar at the 2 sites suggests that it may be a general

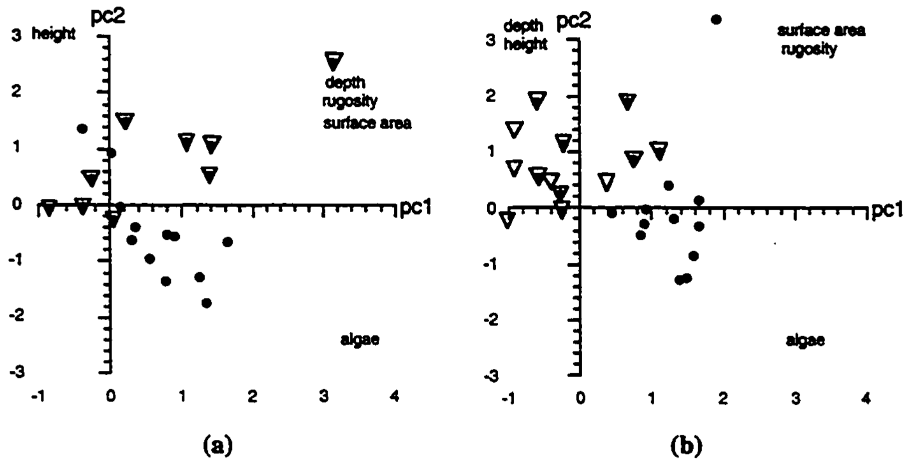

Fig. 4. Distribution of tidepools with *Girella nigricans* (▼) and *Clinocottus analis* (●) at Ocean Beach (a) November and (b) August. Variable loadings are not plotted again, but their quadrants are noted. *C. analis* appears in pools over a wider range of PC values

Table 7. Intraspecific size-based partitioning in (a) *Clinocottus analis*, (b) *Girella nigricans* and (c) *Gobiesox rhessodon* at False Point (FP) and Ocean Beach (OB) from November 1996 to August 1997. Multiple regressions of the proportion of small (<40 mm for *C. analis*, <50 mm for *G. nigricans*, and <33 mm for *G. rhessodon*) fish per tidepool were conducted against the 5 tidepool environmental factors (intertidal height, depth, rugosity, algal cover, and surface area) and against the principal components (PCs). Analyses were not conducted if fewer than 4 pools per data set contained small fish. Analyses were conducted only using pools that had fish of the species in question (zero density pools were omitted). All relationships of environmental factors or PCs and the proportion of large fish are inverse to those presented here

Season/	Model using environmental factors						Model using PCs					
site	Factor	Slope	p-value	Model F	Model p	Model R^2	PC	Slope	p-value	Model F	Model p	Model R^2
(a) *Clinocottus analis*												
Feb/FP	Rugosity	−0.2	0.039	5.2	0.039	0.27	No significant relationships					
May/FP	Depth	−0.01	0.001	10.2	<0.001	0.73	1	−0.2	<0.001	20.0	<0.001	0.47
	Rugosity	−0.1	0.001									
	Algal cover	−0.7	0.002									
	Height	+0.1	0.023									
	Surface area	−0.02	0.024									
May/OB	Height	−0.2	0.012	8.1	0.012	0.34	No significant relationships					
Aug/FP	Rugosity	−0.2	0.006	8.4	0.002	0.44	1	−0.3	0.003	11.3	0.003	0.34
	Surface area	−0.05	0.016									
Aug/OB	Height	+0.2	0.029	5.7	0.029	0.25	No significant relationships					
(b) *Girella nigricans*												
Nov/FP	Algal cover	+0.5	0.002	27.6	0.002	0.92	1	−0.3	0.001	22.3	0.003	0.90
	Depth	−0.1	0.011				3	+0.02	0.020			
Feb/FP	Rugosity	−0.4	0.036	3.7	0.089	0.55	No significant relationships					
	Algal cover	+1.4	0.085									
Aug/FP	No significant relationships						1	−0.2	0.026	6.2	0.026	0.31
Aug/OB	Height	+0.2	0.043	9.0	0.006	0.64	2	+0.4	0.002	10.8	0.003	0.68
	Surface area	+0.2	0.052				1	−0.3	0.014			
(c) *Gobiesox rhessodon*												
Nov/FP	No significant relationships						No significant relationships					
Feb/FP	Height	−0.3	0.099	7.3	0.016	0.65	2	−0.4	0.054	4.9	0.054	0.35
	Rugosity	−0.2	0.100									
May/FP	Rugosity	−0.3	0.040	6.4	0.040	0.48	No significant relationships					
Aug/FP	Rugosity	−0.3	0.002	20.9	0.002	0.72	No significant relationships					

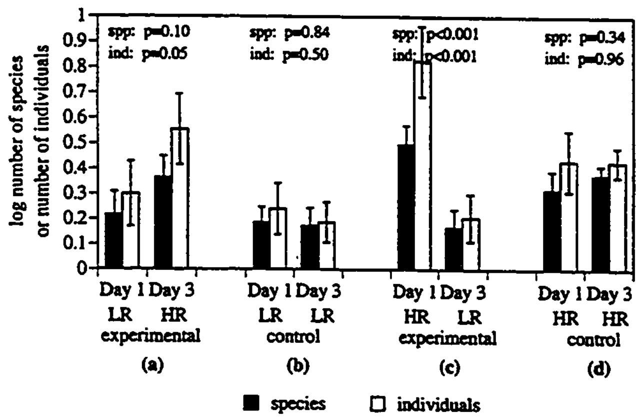

Fig. 5. Number of species and number of individual fish per pool (mean ± 1 SE) before (Day 1) and after (Day 3) (a) the addition of rocky structure in tidepools and (c) the removal of rocky structure in tidepools. LR = low-rugosity; HR = high-rugosity. Control data show (b) low-rugosity pools and (d) high-rugosity pools sampled 2 d apart. p-values are given for paired t-test comparisons of number of species and number of individuals between Day 1 and Day 3 (n = 9). Experiments were conducted during winter 1997 at False Point

feature of many southern California rocky intertidal sites. Such a generality would be useful in the evolution of cue use in fish of these systems.

Interspecific differences in microhabitat distribution

Although all 5 species inhabit tidepools with high values of PC1, their habitats differ in certain respects. The hierarchical importance of the tidepool characteristics of intertidal height, size, depth, rugosity, and algal cover differs among species. Pool depth most strongly influenced the distribution of *Girella nigricans*, rugosity and height were most important to *Clinocottus analis*, and height alone was most important to *Gobiesox rhessodon*, *Hypsoblennius gilberti*, and *Gibbonsia elegans*. Differences in relative importance of characteristics among species most likely result from differences in behavior, physiology and life history of these species. For example, the 3 low intertidal species, *G. rhessodon*, *H. gilberti*, and *G. elegans*, may not be physiologically capable of tolerating the large temperature, salinity, and oxygen fluctuations of the upper intertidal zone. They also may be less successful at avoiding intertidal predators, such as birds, than subtidal predators, such as larger fishes, and therefore may choose lower pools as refuge from intertidal predation. In contrast, *G. nigricans* may be present in the middle and upper intertidal in order to avoid predation by subtidal fishes or other predators. The wide intertidal height range measured for *C. analis*, consistent with measurements by Wells (1986) in Los Angeles, California, suggests that this species faces different physiological constraints and predation risks than the 3 lower intertidal species. *C. analis* may choose highly rugose pools instead of lower pools as a refuge, allowing it to occupy a wider height range in the intertidal.

Tidal height zonation is the best documented manifestation of habitat partitioning among intertidal fish species (Gibson 1972, Bennett & Griffiths 1984). The green morph of *Apodichthys fucorum* in central California lives higher in the intertidal zone than the red morph (Burgess 1978). *Oligocottus snyderi* in British Columbia selects lower intertidal pools than *O. maculosus*, possibly as a result of temperature-tolerance differences between the species (Nakamura 1976b). Vertical zonation has been observed among subtidal gobiids, blennioids (Zander 1995), and cottids (Norton 1991) as well.

In the present study, tidepool depth also served as a segregator of species, important to *Girella nigricans* and relatively unimportant to the others. The importance of pool depth in multiple regression models for *G. nigricans* was consistent with observations that this species tends to be found in deeper pools (Norris 1963). Unlike the other 4 relatively cryptic species, *G. nigricans* is a more water-column-oriented, visible resident of tidepools. It may select deeper pools as refuge from visually foraging bird predators. Although *Clinocottus analis* was shown to prefer deeper pools to shallower ones in the laboratory (Richkus 1981), depth was not the most important tidepool characteristic to this species in the field. Interspecific differences in the importance of tidepool depth to cottids were also shown by Nakamura (1976a). The tidepool cottid *Oligocottus maculosus* was shown to inhabit shallower pools, those under 90 cm deep, while its congener *O. snyderi* showed no depth preference (Nakamura 1976a).

In the present system, rugosity was important to some species (*Clinocottus analis*, *Girella nigricans*, and *Gobiesox rhessodon*) but not to others (*Hypsoblennius gilberti* and *Gibbonsia elegans*). Difference in response to this variable indicates that rugosity may play a role in interspecific habitat partitioning. Algal cover was less important in species density models; however, the use of residuals limited effective analyses of algal cover as a factor determining fish distribution, as discussed above.

Relationships between fish densities and percent cover of both rock and algae in pools have been demonstrated in other studies. *Clinocottus analis* was found to select experimental pools with the greatest amount of structure (Richkus 1981). Tidepool rock cover was not described as important to any particular species, but was significantly correlated with abundance (Bennett & Griffiths 1984) and mass (Prochazka & Griffiths 1992) of South African tidepool fishes. Abundance of several of these South African species was also positively correlated with algal cover (Prochazka & Griffiths 1992). Similar relationships between fish distribution and algal cover were noted for tidepool clinids (Marsh et al. 1978), the blenniid *Coryphoblennius galerita* (Nieder 1993), and the cottid *Oligocottus snyderi* (Green 1971). However, in a later study, Nakamura (1976a) found that, although *O. snyderi* chose habitats with vegetative cover in the laboratory, it did not occupy pools with high algae cover in the high intertidal zone, suggesting interaction between intertidal height and algal cover in microhabitat selection.

The habitat partitioning patterns displayed by the overall fish guild and by individual species in the present study were consistent between sites, despite the fact that Ocean Beach pools were on average smaller and deeper. At both sites, pools devoid of fish were high in the intertidal, shallow, small, and had low rugosity. Tidepool characteristics of greatest importance for each species were the same at both sites. These between-site similarities suggest that, despite variation in the type or shape of tidepools that constitute different rocky sections of the San Diego coast, tidepool fishes may partition the available habitat in a similar manner.

The biggest difference between the 2 sites was the higher abundance of *Gibbonsia elegans* at Ocean Beach. Results from the study do not provide an explanation for this difference. Because relatively few individuals were found, even at Ocean Beach, it is possible that sample sizes were too small to adequately measure habitat patterns of *G. elegans*. Also possible is that *G. elegans* abundance may be determined by a factor not measured in the present study that differs between sites. The 2 sites differ in rock type and pool shape; Ocean Beach pools are relatively small, deep circular holes cut in a flat shale bench. False Point pools are larger but shallower indentations in and around conglomerate sandstone outcrops.

Size-specific differences in microhabitat distribution

Although the intertidal fishes at False Point and Ocean Beach generally selected lower, bigger, deeper pools with high levels of rock cover, the affinity for these characteristics may be a function of fish size for several species. Proportions of both small *Clinocottus analis* and small *Gobiesox rhessodon* increased with decreasing rugosity. Often, very small (<30 mm) *C. analis* individuals were spotted in extremely bare pools. Distributions of these small cottids may be driven by competition with, or predation by, a species present in the highly rugose areas of the intertidal, by prey preferences, or by lack of aerial predation risk at such small size.

Other environmental factors contribute to intraspecific partitioning of available tidepools by fish of different size classes. New recruits of *Girella nigricans* and *Clinocottus analis* were found higher in the intertidal zone at Ocean Beach in August. It is unknown whether these species selectively settle in the higher intertidal, whether they settle uniformly but experience selective mortality, or whether they settle low in the intertidal but are pushed higher by competition with adults. However, selective settlement is supported by the life-history strategy of *G. nigricans*. After 1 or 2 yr (Norris 1963) or at about 75 mm (Stevens et al. 1989), these fish move from the intertidal to subtidal habitats, a migration that would explain the relationship between intertidal height and fish size during its intertidal phase.

Although densities of *Clinocottus analis* and *Girella nigricans* were generally positively correlated with values of PC1 in the current study, fish size was negatively correlated with PC1. Smaller fish tended to be more abundant in higher, shallower, smaller, less rugose pools, pools with negative values of PC1. Other studies have noted similar trends for these 2 species (Norris 1963, Richkus 1981, Yoshiyama 1981). Like *C. analis* and *G. nigricans*, other intertidal fishes also display an increased association with substrate as fish size increases (Setran & Behrens 1993). Such ontogenetic shifts may be the manifestation of new threats posed by aerial predators as the fish grow beyond a size threshold. Mahon & Mahon (1994) also suggested size-based shifts in habitat due to increased predation pressure, having found that mean fish size of several Caribbean species increased with increasing pool size. In the present system, *C. analis* and *G. nigricans* adults may find refuge from predators in deeper, larger, more structurally complex pools in the lower intertidal.

Several theories have been presented to explain size-based partitioning in rocky intertidal systems. Prochazka & Griffiths (1992) found that smaller fish in South African tidepools are found higher in the intertidal, and suggested that the pattern is a result of territoriality by adults occupying lower, 'better' pools. Nieder (1993) also invoked an intraspecific competition hypothesis to explain why larger tidepools harbor lower densities and larger individuals. Large pools are better buffered from the elements during emergence than small pools and therefore might be favorable. Because territoriality is common in intertidal fishes (Horn & Gibson 1988, Mayr & Berger 1992), and because larger fish tend to be more successful in territorial skirmishes (Mayr & Berger 1992), larger fish should be found in the most favorable pools. Levels of both interspecific and intraspecific territoriality within and among the species of the present study are not yet described, so Nieder's (1993) and Prochazka & Griffith's (1992) hypotheses have yet to be tested for this system.

Seasonal differences in microhabitat distribution

Several processes might be expected to cause seasonal changes in habitat partitioning patterns of intertidal fishes. The first is temperature change, which might make certain microhabitats unsuitable at certain times of the year, such as the upper intertidal in the summer. In the present study, the summer temperature increase did not induce large-scale migration of upper intertidal fish to lower intertidal pools. Because lowest low tides in southern California occur at night or in the early morning during the summer, the full potential for extreme values of physico-chemical properties in most tidepools is not realized, perhaps allowing fish to remain in the upper intertidal during most summer low tides. These fish may abandon high pools on some occasions, for example, when neap low tides occur during the day (J.L.D.D. unpubl. data), but their ability to home to specific pools (Williams 1957, Stephens et al. 1970, Valle 1989, Yoshiyama et al. 1992) perhaps enables them to return to the upper intertidal when low tide shifts back to the early morning. These short-term migrations, therefore, are not seasonal in duration, and all summer data used in the present study were collected during early morning low tides.

A second process that might lead to seasonal changes in habitat partitioning patterns is the arrival of recruits of both permanent intertidal residents and nursery species. Resident species' distribution patterns might change as a result of ontogenetic habitat preferences or competition with recruits of other species. As in several other studies (Beckley 1985, Moring 1986, 1990), fish abundance in the present study was greatest in the spring and summer. However, unlike the above studies, no additional fish species recruited to the rocky intertidal zone during these seasons. Instead, the increase in total number of fish was attributed only to the recruitment of permanent residents. These peaks in recruitment generally did not induce large changes in habitat partitioning among the species. Only in the case of *Clinocottus analis* did the seasonal arrival of young fish change the species' distribution. Distribution patterns of the other species, however, were not greatly affected by arrival of juveniles. This stability suggests that size-based intraspecific habitat differences may be of smaller magnitude than interspecific habitat differences for those species.

CONCLUSIONS

Despite the suggestion that systems with low species richness have low levels of microhabitat segregation (Prochazka & Griffiths 1992), results from this paper indicate that rocky intertidal pools are partitioned among and within species by the relatively species-poor San Diego rocky intertidal fish community. This community only contains 5 common species, compared with the 14 species of the Southern African west coast rocky intertidal (Prochazka & Griffiths 1992), 20 species in northern California (Moring 1986), 26 species in Wellington, New Zealand (Willis & Roberts 1996), and 63 species in Barbados (Mahon & Mahon 1994). In the present study, the 5 species partitioned tidepools similarly at 2 sites based mainly on pool intertidal height, rugosity, and depth. The order of importance of these factors was different for each species, but was temporally stable for all species except *Clinocottus analis*. The seasonal change in this species was due to the arrival of new recruits with different habitat requirements and not to movement by adults. Different habitat requirements of new recruits, demonstrated by several species, reflect intraspecific size-based partitioning. Each species occupied a height or pool depth range in the intertidal; individuals of different sizes were segregated within this range. Mechanisms of both interspecific and intraspecific partitioning by fishes remain unknown (Gibson 1982, Prochazka & Griffiths 1992). However, its demonstration in this species-poor fish guild may direct future hypothesis testing of these mechanisms.

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Chapter 4

Diel Changes in Habitat Use by Two Tidepool Fishes in Relation to Temperature

Abstract

I examined the effects of low-tide timing on tidepool use by two southern California fishes, *Clinocottus analis* and *Girella nigricans.* Abundance of these fishes in middle and upper intertidal pools was higher when low tides occurred at night or in the early morning than in the afternoon. Mean fish size was also higher during nighttime low tides than daytime low tides. Tidepools higher in the intertidal zone generally displayed greater differences in fish abundance between early morning and afternoon low tides than lower pools. In addition, these upper tidepools reached higher temperatures during afternoon low tides than lower tidepools, often exceeding the preferred and lethal maximum temperatures reported for the two study species. Diel vertical habitat shifts by middle and upper tidepool fishes indicate that their partitioning of rocky intertidal habitat occurs on short-term temporal as well as spatial scales.

Introduction

Vertical gradients in environmental variables in rocky intertidal habitats, such as emergence time and wave exposure, have resulted in vertical specialization of many organisms (Connell, 1961a,b; Dayton, 1971). This physical variation, combined with terrestrial and subtidal predation risk, leads to microhabitat-specific risks and benefits that are usually fixed for sessile animals and algae. However, motile organisms may have the ability to shift their vertical position in response to temporally variable environmental cues. Such plasticity enables motile organisms to take advantage of zones that are habitable only during certain tidal, diel, lunar, or seasonal periods and that exclude competitors or predators. Motility also enables a species to accommodate ontogenetic differences in risks and resource requirements, by permitting different size or age classes to select different parts of the habitat. Sessile organisms do not have this advantage.

Several studies describe low-tide vertical zonation patterns among fishes (see Yoshiyama, 1981; Gibson, 1982; Zander *et al.*, 1999) and relate these to temperature (Nakamura, 1976b), but combined effects of diel and tidal cycles on shifts in zonation patterns within species have not been examined in the field. The interaction between time of day and time of low tide results in variation of the diel timing of tidepool emergence, and therefore leads to a complicated pattern of variation in tidepool physico-chemical characteristics, especially temperature (Lennon, 1995). Temperature may be the most important determinant of an intertidal organism's vertical distribution (Jensen and Muller-Parker, 1994) and has been shown to affect height distribution of a cottid, *Oligocottus snyderi,* in the laboratory (Nakamura, 1976a). Further consequences of diel shifts in low tide timing include limitation or facilitation of predation by terrestrial, aerial, and subtidal aquatic predators to intertidal prey. For example, an intertidal organism that is preyed upon by a diurnally foraging non-aquatic predator might be forced to remain in refuge habitat during daytime low tides, but might be able to inhabit a wide area during nighttime low tides.

My objective was to evaluate the influence of daily timing of low tides on abundance and size structure of fishes in southern California tidepools. *Clinocottus analis,* the woolly sculpin (Cottidae), is a permanent tidepool resident and the most abundant fish in those habitats (Davis, 2000). *Girella nigricans*, opaleye (Girellidae), is a nursery resident, moving after 1-2 years of its juvenile phase to the subtidal zone where it spends its adult life (Norris, 1963; Stevens *et al.*, 1989). Both of these species demonstrate site fidelity and homing ability, with individuals repeatedly occupying the same pool or set of pools during consecutive low tides and returning to a home range when displaced (Williams, 1957; Richkus, 1978; Valle, 1989). Familiarity with local topography may provide fish with the ability to choose among tidepools with different characteristics, such as intertidal height, depending on environmental cues.

I tested the following null hypotheses: 1) the abundance of fish in middle and upper intertidal pools at low tide is similar when low tides occur nocturnally versus diurnally, 2) the size of fish occupying pools is independent of the time of low tide, and 3) diel variation in tidepool fish abundance with time of day is not correlated with factors that affect thermal and chemical stability, such as pool intertidal height. Relationships between fish abundance or size and thermal stability were examined as mechanisms leading to variation in diel habitat use.

Methods

I tested the above hypotheses at three sites in San Diego, California, USA: False Point, Ocean Beach, and Dike Rock (Scripps Coastal Reserve) (Figure 4.1). *Clinocottus analis* and *Girella nigricans* were the two most abundant intertidal fishes at these sites during the spring and summer, found up to 100 cm above mean lower low water (MLLW). *Gobiesox rhessodon* (Gobiesocidae) was also common, but only below 30 cm MLLW. *Hypsoblennius gilberti* (Blennidae), *Gibbonsia elegans* (Clinidae), and *Paraclinus integripinnis* (Labrisomidae) also contributed to total fish abundance in the lower intertidal zone. The tidal regime along the San Diego coast is mixed semidiurnal, with two unequal low tides per day.

Temperature variation in tidepools

Bottom and surface tidepool temperatures were measured in 17 pools at False Point on May 2, 1997 (1315-1430 h), 16 pools at Ocean Beach on May 3 (1240-1420 h), and 21 pools at Ocean Beach on May 4 (1430-1600 h). Temperature was measured to the nearest 0.1 C using a YSI® 30 portable conductivity, salinity, and temperature meter. Bottom measurements were taken at the deepest point in the tidepool, where most fishes reside, and surface measurements were taken at the point directly above the deepest area.

In December 1997, temperature in each tidepool was measured multiple times, at intervals of 60 ± 5 min, over the course of an afternoon. Temperatures were measured at False Point in 45 pools from 1300 h to 1615 h on Dec. 13, and in 36 pools from 1230 h to 1600 h on Dec. 14. Temperatures were standardized to 40 min periods based on temperature curves constructed for each tidepool. Although December temperature data were collected in a different season than the fish data, they were included in the study to provide more information about temperature trends in tidepools.

Backwards step-wise multiple regression analysis was used to test the relationship between pool temperature and pool intertidal height, depth, and surface area, which were measured in a concurrent study (Davis, 2000). In these regression analyses, the residuals of depth and surface area after removing intertidal height were used due to the correlations of these factors with height ($r^2 > 0.25$). Factors with p-values greater than 0.10 were removed from the models.

Because temperature in tidepools varies spatially and temporally, temperature in the Dike Rock tidepool was approximated by using average hourly air temperature for the sampling periods July 19 to August 4 and September 8 to September 19. Tidepools reach maximum temperatures generally at the same time as air temperatures, rarely lagging more than 1 or 2 h (Morris and Taylor, 1983). Air temperatures were obtained from sensors located on the Scripps Pier 500 m south of Dike Rock (http://cdip.ucsd.edu/

wc/scripps.html). Duration of tidepool exposure, light conditions during exposure, and time of exposure were determined for the tidepool at Dike Rock using Harbor Master™ software.

Distribution of fishes at low tide

During spring and summer 1997 and spring 1998, I censused fish abundance and size in 10-15 tidepools during paired morning (0500 h to 0800 h) and midday-afternoon (1100 h to 1600 h) low tides within a 10-day period at False Point and Ocean Beach (Table 4.1). I collected all fish in each tidepool after water was siphoned or bailed out of the pools and rocks were removed to facilitate detection of fishes. Fishes were removed, identified to species, and returned after restoring rocks and water to the pools. In all sampling periods except the first at False Point, fish total length (TL) was measured in mm prior to release.

During the study, six comparisons of early morning *versus* afternoon low tide censuses from False Point and Ocean Beach were made (Table 4.1). The first, second, and third False Point comparisons (FP1, FP2, and FP3) were based on middle and upper intertidal tidepools ranging from 33.5 to 70.1 cm MLLW. Pools at these intertidal height levels are isolated from the subtidal zone for a total of about 22-41%, or about 150-280 hours, of a lunar month (Figure 4.2). To test the effect of intertidal height on diel patterns of tidepool fish abundance, I made three additional comparisons including pools lower in the intertidal zone: False Point 4 (FP4), which included pools from 3.0 to 70.1 cm MLLW, Ocean Beach 1 (OB1), which included pools from 0.0 to 76.2 cm MLLW, and Ocean Beach 2 (OB2), which included pools from -6.1 to 67.1 cm MLLW. The range of isolation times of tidepools in FP4, OB1, and OB2 was about 7-41% of a lunar month.

I log-transformed total number of fish, number of *C. analis,* and number of *G. nigricans* per pool for statistical analysis. Morning low tide values (abundance and size) were compared with afternoon low tide values using paired *t* -tests. Mean size of *C. analis* and *G. nigricans* were computed for each pool at False Point for FP2, FP3, and FP4. Due to the relatively low abundance of *G. nigricans* at Ocean Beach during early May of 1997, comparisons were only made for *C. analis*. Paired *t*-tests were used to compare average fish size per pool during morning and afternoon low tides.

Temporal scale of variation in low tide distribution

I tested hypotheses that fish abundance and fish size are greatest during early morning tides and are negatively correlated with temperature for *G. nigricans* in the largest permanent tidepool at Dike Rock. The pool, located at 51.8 cm MLLW, measures approximately 5 m by 1.5 m and is 40 cm deep at the deepest point, depending on shifting sand. On 22 occasions during almost every tide low enough to expose the pool from July 19 to August 4, 1997, a 40 cm minnow trap with 2 mm mesh and openings of 2.8 cm was deployed for 60 min. During each deployment, the trap was baited with canned cat food and placed in the same location in the same orientation in the tidepool. All opaleye caught in the minnow trap were measured to the nearest mm and released back into the pool. This exercise was repeated from September 8 to September 19, 1997, using two minnow traps. The second trap, with 6 mm mesh and 4 cm openings, was added to account for increased fish size in September.

Minnow traps were used at Dike Rock but not False Point or Ocean Beach because the Dike Rock pool is much larger than those of the other two sites. Traps did not capture enough individuals for analysis at False Point and Ocean Beach, and the Dike Rock pool was too large to drain. Minnow traps also offered an opportunity for repeated daily sampling over a period of weeks, enabling a more detailed examination of the relationship between fish use of tidepools and timing of low tide.

Results

Tidepool temperature and physical correlates

Tidepools reached maximum temperatures between 1350 h and 1450 h. At this peak hour, pools during May and December were from 2 to 8° C and from 0 to 2° C warmer, respectively, than the surface waters of the subtidal zone (Figure 4.3). Within these ranges, the magnitude of temperature difference between a tidepool and the surface waters of the subtidal zone depended on the characteristics of the pool, especially intertidal height and depth.

Tidepool intertidal height, depth, and surface area were correlated with temperature, with the strength of relationships changing over the course of pool isolation. Of the three parameters, height was the best predictor of temperature at False Point in December, 1997 (Table 4.2). Bottom and surface temperatures were positively correlated with height for the duration of measurement; however, these relationships weakened over time. Until about 1440 h, depth also was a predictor of temperature, with shallower pools reaching higher temperatures than deeper pools (Figure 4.3). After the pools reached maximum temperatures, a significant positive correlation developed between tidepool surface area and temperature (Table 4.2), indicating that larger pools were slower to lose heat. Similar relationships were noted at False Point and Ocean Beach in May, 1997. Midday bottom temperatures, measured from 0.5 to 2.5 h after isolation, were positively correlated with intertidal height and negatively correlated with pool depth (Table 4.2). Although bottom temperatures in May were 8 to 11 C higher than those in

December (Figure 4.3), relationships between pool parameters and temperature are expected to be similar across seasons.

Temporal changes in high intertidal fish abundance

Abundance of fishes in middle and upper intertidal pools was dependent on the time of day the pools were isolated. During the first three False Point study periods, middle and upper intertidal tidepools isolated by afternoon low tides had significantly fewer fishes (total number of individuals) and fewer *C. analis* individuals than the same set of pools isolated by morning low tides (Figure 4.4). *Girella nigricans* abundance showed the same pattern during the second and third False Point periods (FP2 and FP3). Abundance of *G. nigricans* was not analyzed for the first period (FP1) because it was present in only two pools in the early morning and no pools in the afternoon.

Abundance of *G. nigricans* at Dike Rock in July and August 1997 displayed a pattern similar to that described for *C. analis*. Abundance was greater during low tides that isolated the pool during the hours of darkness (2000 h to 0600 h) than during daylight hours ($t_{8,12}$=4.1, $p<0.001$). This difference was not observed in September 1997 ($t_{10,5}$=0.1, p=0.954) (Figure 4.5). Average air temperature was lowest just before dawn and greatest from 1400 to 1500 h during both the July/August and September sampling periods. *Girella nigricans* abundance in the Dike Rock tidepool was significantly correlated with average air temperature during the July/August sampling period at the time of pool isolation (n=21, r^2= 0.45, $p<0.001$) and the time at low tide (n=21, r^2=0.49, $p<0.001$). These abundance relationships did not persist in September (temperature at isolation: n=17, r^2=0.01, p=0.69; temperature at low tide: n=17, $r^2<0.01$, p=0.90).

Spatial patterns of abundance - high and low intertidal pools

The effect of low tide timing on fish abundance was related to intertidal height in two of the three False Point/Ocean Beach study periods that included low intertidal pools. In those two periods (FP4 and OB1), the log-transformed difference in fish abundance between morning and afternoon was positively correlated with intertidal height ($n = 12$, $r^2 = 0.58$, $p = 0.004$ for FP4; $n = 11$, $r^2 = 0.37$, $p = 0.026$ for OB1). The relationship was not significant in OB2 ($n = 13$, $r^2 = 0.03$, $p = 0.611$). In FP4 and OB1, the difference in fish abundance between morning and afternoon had greatest values in upper intertidal pools and negative values in the lowest pools. As in FP1-3, the six middle and upper pools of FP4 had significantly lower numbers of total fish ($t_5 = 2.9$, $p = 0.035$) and *C. analis* ($t_5 = 4.5$, $p = 0.007$) during the afternoon low tides than during the early morning low tides. In contrast, the six lowest intertidal pools did not have different numbers of total fish ($t_5 = 1.8$, $p = 0.138$) or *C. analis* ($t_5 = 0.3$, $p = 0.801$) when the low tide occurred in the afternoon compared with the morning. *Girella nigricans* was not abundant enough to be included in this analysis.

Temporal patterns in fish size

Fishes of different sizes respond differently to changes in timing of low tide. In middle and upper intertidal pools (FP2 and FP3), mean size of *C. analis* per pool was greater when low tides occurred during the early morning than the afternoon (Figure 4.6). In study periods that included low intertidal pools (FP4, OB1, OB2), fish size was greater during morning low tides, but the differences were not significant at the α=0.05 level. *Girella nigricans* size was not different between morning and afternoon low tides, but low numbers of *G. nigricans* found in the sampled pools during the afternoon tides

(Figure 4.6) reduced the power of statistical tests. *Girella nigricans* was not found in enough pools for comparison at Ocean Beach.

Girella nigricans collected at Dike Rock ranged from 25 to 67 mm total length during the July/August sampling period and from 31 to 89 mm during the September sampling period. Mean size of trapped *G. nigricans* was significantly greater when the study area was isolated at night than during daylight hours in both July/August and September ($t_{8,12}$=4.9, p<0.001 and $t_{10,5}$=3.1, p=0.008, respectively, Figure 4.7). To identify differences in response by different size classes of fish, abundance patterns were analyzed separately for two size classes: large fish (≥45 mm TL) and small fish (<45 mm TL). During both sampling periods, the mean number of large individuals trapped when the pool was isolated at night was greater than the mean number trapped after daylight isolations (night: 10.3 ± 2.0, day: 0.4 ± 0.2 , $t_{8,12}$ = 3.51, p=0.002 for July/August, and night: 12.5± 1.1, day: 6.5 ± 2.2 , $t_{10,5}$=2.11, p=0.052 for September). Results for small fish were not consistent between sampling periods. In July/August, mean numbers of small fish trapped after daylight and nighttime isolations were not different ($t_{8,12}$ = 1.42, p = 0.169). In September, the number of small fish trapped after daylight isolations was greater than the number trapped after nighttime isolations (day: 11.3± 1.8, night: 6.9± 0.8, $t_{10,5}$ = 2.36, p = 0.032). The opposite diel pattern of small and large fish in September caused the lack of relationship, described above, between total abundance and time of day.

Fish size at Dike Rock was negatively correlated with average air temperature in both July/August and September. Correlations between mean fish size and temperature both at low tide (July/August: n=21, r^2=0.19, p=.051; September: n=17, r^2=0.43, p=0.004) and at the time of pool isolation (July/August: n=21, r^2=0.60, p<0.001; September: n=17, r^2=0.36, p=0.011) were significant (Figure 4.7).

Discussion

In the present study, vertical distribution of middle and upper intertidal fishes shifted depending on timing of low tide and life stage. *Clinocottus analis* and *G. nigricans* were more likely to occupy middle and upper intertidal pools during nighttime low tides and less likely to occupy these areas during daytime low tides. The strength of the diel influence on tidepool occupation depended on intertidal height. Lowest pools were occupied by more fishes when low tide was in the afternoon than the early morning. These results suggest that although certain habitat regions are available during all parts of the day, at times their suitability decreases, rendering them effectively unavailable at these times.

As a tide starts to ebb, a motile tidepool organism has the option of becoming isolated in a high intertidal tidepool, resulting in lengthy emergence time, becoming isolated in a lower intertidal pool with shorter emergence time, or remaining in areas contiguous with the subtidal zone. To this organism, low-tide habitat suitability may be a function of the trade-off between risks and benefits associated with tidepool isolation and subtidal immersion. Isolation offers protection from subtidal competitors and from subtidal predators, such as the cottid *Scorpaenichthys marmoratus* (Yoshiyama, 1981; Wyttenbach and Senn, 1993). However, isolation also exposes fishes to the potential of heat-related physiological stress (Zander *et al.*, 1999), subjects fishes to predation by intertidal predators such as birds (Yoshiyama, 1981; Pierce and Pierson, 1990; Horn *et al.*, 1999), and restricts foraging area (Wyttenbach and Senn, 1993; Zander *et al.*, 1999). Immersion offers protection from intertidal predators, protection from physiological stress, and access to forage areas outside the tidepool, but exposes intertidal fishes to competition with subtidal species and subtidal predation. Appropriate balance of these trade-offs would lead to an optimal emergence time, achieved by occupying an optimal intertidal height. However, these low-tide risks and benefits likely change on a diel cycle. For example, potential of heat-related physiological stress decreases at night, perhaps making high pools riskier than lower pools during daytime isolation. Through allocation of time spent among habitats that vary temporally in certain risks and benefits, an organism can influence its survival or condition (Brown, 1992).

Results of the present study are consistent with the hypothesis that the diel cycle of temperature-related physiological stress risk plays a role in diel vertical habitat shifts by fishes. In the laboratory, the cottid *Oligocottus snyderi* occupied 'lower tidepools' (basins that were isolated by an experimental tide for shorter periods of time) during a high temperature regime (23.5° C) than a cold regime (11.5-13.5°C) (Nakamura, 1976a). This result and those of the present study suggest that fishes occupy upper intertidal pools during cool hours and remain in lower pools during periods when temperature becomes stressful. In the present study, May afternoon bottom temperatures of middle and upper intertidal pools often exceeded the lethal maximum temperature of *C. analis* (26-27°C; Graham, 1970), and the preferred temperature (25.6-26.5°C) of unacclimated *G. nigricans* collected from field sites of differing thermal regimes (Douderoff, 1938; Norris, 1963). The highest tidepool bottom temperatures measured in the present study were only a few °C less than the upper lethal temperature of 60-92 mm SL *G. nigricans* (31-33° C; Douderoff, 1942), and temperature of the Dike Rock study pool can often reach 35°C in the summer (Norris, 1963; Davis, unpubl. data). High temperatures may be physiologically disadvantageous to *G. nigricans*; individuals in the laboratory grew almost twice as fast at 17.6 ± 1°C than at 27.5°C (Norris, 1963). Other physical and chemical properties that change in tidepools on a diel cycle may also be important physiologically, such as the decrease of oxygen solubility in seawater during the day, increase in pH, and increase in salinity (Morris and Taylor, 1983; Horn *et al.*, 1999).

The risk of intertidal predation may also change on a diel cycle, influencing the balance of isolation and immersion trade-offs. Diurnal nonaquatic predators, especially birds, significantly impact intertidal invertebrate communities (Marsh, 1986; Wootton, 1995), and have also been suggested to affect the spatial distribution of intertidal fishes (Yoshiyama, 1981; Pierce and Pierson, 1990). Several bird species, including herons (*Aredea herodias*), egrets (*Leucophys thulus*), and willets *Catoptrophorus semipalmatus*), have been observed to feed during low tide on tidepool cottids and other fishes along the coast from southern California to Washington (Yoshiyama, 1981; Pierce and Pierson, 1990; Davis, pers. obs.). Intertidal fish may abandon high intertidal areas before daytime low tides in order to limit exposure to these visual diurnal predators. During daytime low tides, should the predation risk in isolated high intertidal pools exceed the risk of predation by subtidal predators in immersed low intertidal areas, fish may, by moving lower and thus decreasing emergence time, optimize the ratio of intertidal to subtidal predation exposure in order to minimize total predation risk. During nighttime low tides, a higher ratio of intertidal predation exposure (isolation) to subtidal predation exposure (immersion) may be optimal.

In the present study, lower average fish size during daytime than nighttime low tides suggests that the balance of trade-offs between isolation in tidepools and immersion in subtidal conditions is a function of ontogeny as well as time of day. In laboratory experiments, temperature preference of *G. nigricans* was stage- and size-specific (Norris, 1963). Newly settled fish (usually <30 mm SL) preferred temperatures of 28°C, while older fish (30 to 80 mm SL) chose temperatures of 26°C (Norris, 1963). Optimum temperature for growth decreases with size in may fish species (Brett, 1979; Pedersen and Jobling, 1989), and although this trend has not been demonstrated for the two study species, Norris (1963) hypothesized that temperature selection in young *G. nigricans* serves to guide them to areas where growth rate is greatest. In the present study, fish size at Dike Rock was inversely related to temperature, suggesting that ontogenetic differences in physiology plays a role in vertical habitat selection.

Size-based susceptibility in avian predation may also contribute to ontogenetic differences in diel patterns of tidepool occupation. In the Puget Sound, Washington, herons selectively preyed on tidepool sculpins larger than 45 mm TL (Pierce and Pierson, 1990). In southern California as well, larger fishes may be more visible and thus more susceptible to bird predation. As a result, larger fishes in southern California would minimize predation risk by minimizing emergence time during the day.

Similarity in diel patterns of tidepool occupation between *Clinocottus analis* and *G. nigricans*, two phylogenetically, ecologically, and behaviorally different species (Graham, 1970; Norris, 1963), suggests that upper-intertidal fishes may share a general strategy. The hypotheses that explain the pattern described above (physiological forces and predation avoidance) are not mutually exclusive. Both may lead to increased nighttime densities of larger fish in high pools, and smaller individuals may avoid this microhabitat at night due to intraspecific competition with the larger fish. Intraspecific aggression has been observed in *C. analis*, especially in larger fish (Yoshiyama, 1981), in ohter tidepool cottids (Pfister, 1995), and in *G. nigricans* in the laboratory (Davis, pers. obs.). Both *C. analis* and *G. nigricans* extend farther north in California and south into Baja California, areas with different temperature regimes than San Diego. Replication of this study at other latitudes would determine whether this strategy of diel habitat shifts is shared by populations in both cooler and warmer areas. If shifts occur to relieve thermal stress, more pronounced shifts might be expected south of San Diego and reduced shifts expected to the north.

The avoidance of the middle and upper intertidal zone by fishes during daytime low tides, as well as differential habitat use patterns by different size classes, has potential to cause sampling bias in rocky intertidal systems. Often, as is the case in

California, lowest low tides occur in the afternoon during one season (winter, in California) and in the early morning in the opposite season (summer, in California). Seasonal declines observed in fish populations when afternoon spring tides prevail could simply reflect a redistribution of fishes to lower pools that are more difficult to sample. Results also indicate that fishes select habitat in response to factors that change on daily and tidal cycles, and that fishes may have to assess both diurnal and tidal rhythms at the same time. Homing studies of rocky intertidal fish species indicate spatial complexity in tidepool use by fishes. The discovery of diel patterns in tidepool use implies temporal complexity as well.

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Table 4.1: Sample size and dates of tidepool fish abundance comparisons between early morning and afternoon low tides. Four paired comparisons were made at False Point (FP1, FP2, FP3, and FP4) and two at Ocean Beach (OB1 and OB2), San Diego, California. Number of pools and mean intertidal height of pools (cm above mean lower low water) are listed for each paired comparison. Sampling dates and the times of low tide on those dates are also given.

Data set	No. pools	mean height (cm)	early morning low tides		afternoon low tides	
			date(s)	time(s)	date(s)	time(s)
FP1	15	48.8	Apr. 26-28, 1997	0631-0836	May 1-2, 1997	1159-1249
FP2	13	51.8	Jun. 10, 1997	0747	May 31, 1997	1212
FP3	10	54.9	Jul. 21, 1997	0443	Jul. 20, 1997	1520
FP4	12	39.6	Apr. 27-30, 1998	0446-0727	May 3-5, 1998	1057-1241
OB1	11	30.5	May 10, 1997	0648	May 3, 1997	1334
OB2	13	27.4	Apr. 29, 1998	0636	Apr. 23, 1998	1354

Table 4.2: Multiple linear regressions of tidepool temperatures with pool intertidal height, surface area, and depth at False Point (FP) and Ocean Beach (OB). Temperatures were measured once during the afternoons of May 2-4, 1997, and multiple times throughout the afternoons of December 13 -14, 1997. Number of tidepools sampled were 17 on May 2 at FP, 16 on May 3 at OB, 21 on May 4 at OB, 45 on December 13 at FP, and 36 on December 14 at FP. Afternoon low tides were lower than 30 cm below MLLW on all sampling days. Temperatures were measured at both the surface and the bottom at the deepest point in the pool. NS indicates no relationship ($p > 0.10$).

		Height		Depth		Surface Area		model values		
Time	location	slope	p-value	slope	p-value	slope	p-value	R^2	F	p
False Point - 5/2/97										
1315-	bottom	+1.44	0.016	-13.94	0.002	+0.20	0.013	0.65	8.0	0.003
1430	surface	----	NS	-5.32	0.083	----	NS	0.19	3.5	0.083
Ocean Beach - 5/3/97										
1240-	bottom	+0.38	0.050	-0.03	0.064	----	NS	0.41	4.5	0.033
1420	surface	----	NS	----	NS	----	NS	----	----	NS
Ocean Beach - 5/4/97										
1430-	bottom	+0.31	0.032	-0.03	0.057	----	NS	0.38	4.8	0.023
1600	surface	+0.55	0.092	----	NS	----	NS	0.16	3.2	0.092
False Point - 12/13/97										
1320	bottom	+0.66	<0.001	-5.58	0.002	----	NS	0.39	13.2	<0.001
	surface	+0.58	<0.001	-4.89	0.003	----	NS	0.37	12.1	<0.001
1400	bottom	+0.57	0.001	-4.05	0.017	----	NS	0.32	9.64	<0.001
	surface	+0.55	0.002	-3.26	0.062	----	NS	0.26	7.5	0.002
1440	bottom	+0.40	0.011	----	NS	+0.07	0.075	0.20	5.2	0.009
	surface	+0.47	0.005	----	NS	+0.08	0.038	0.24	6.7	0.003
1520	bottom	+0.32	0.033	----	NS	+0.07	0.045	0.18	4.6	0.016
	surface	+0.44	0.005	----	NS	+0.09	0.014	0.27	7.7	0.001

table 2, cont'd.

False Point - 12/14/97

1320	bottom	+0.61	<0.001	-3.49	0.007	----	NS	0.53	16.1	<0.001
	surface	+0.61	<0.001	-2.85	0.018	----	NS	0.52	15.7	<0.001
1400	bottom	+0.50	0.001	-3.01	0.035	+0.06	0.068	0.42	7.6	0.001
	surface	+0.46	0.001	-3.02	0.036	----	NS	0.35	8.5	0.001
1440	bottom	+0.39	0.005	----	NS	+0.06	0.071	0.28	6.3	0.005
	surface	+0.36	0.007	----	NS	+0.05	0.083	0.27	5.8	0.007
1520	bottom	+0.36	0.005	----	NS	+0.06	0.055	0.29	6.6	0.004
	surface	+0.37	0.002	----	NS	+0.06	0.029	0.34	8.3	0.001
1600	bottom	+0.26	0.033	----	NS	+0.08	0.010	0.28	6.2	0.005
	surface	+0.33	0.005	----	NS	+0.08	0.006	0.35	8.7	0.001

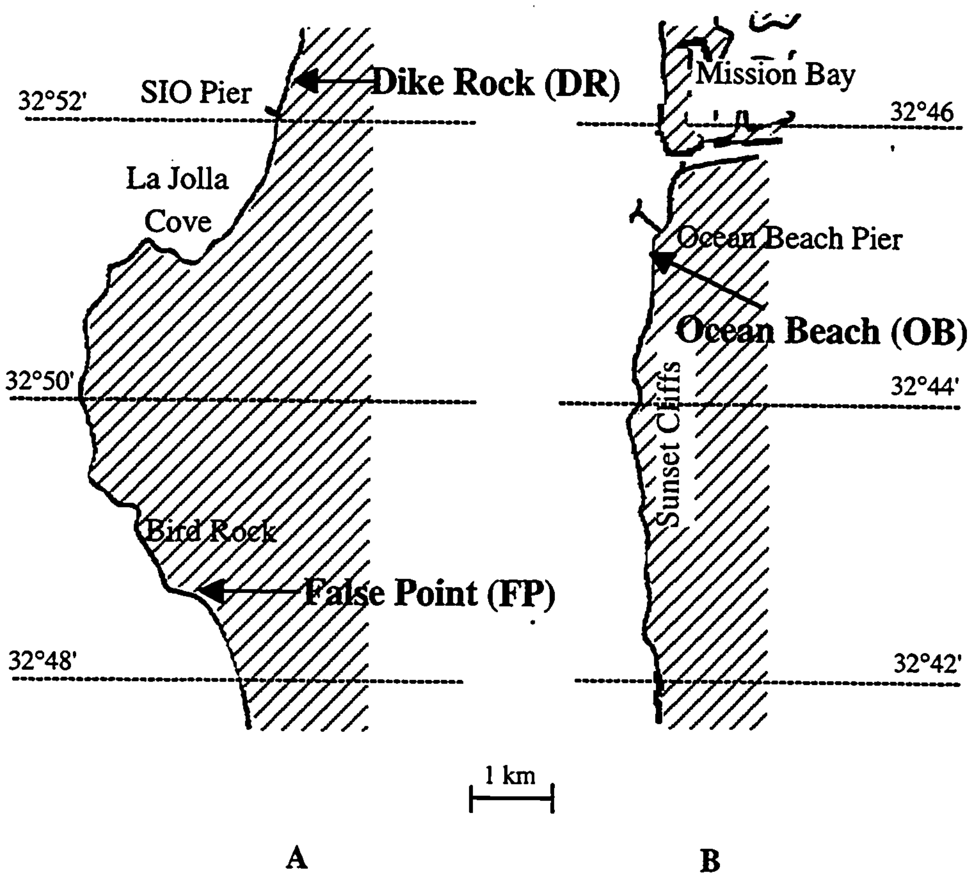


Figure 4.1: Map of the San Diego, California, coastline showing the three study sites: (A) section containing Dike Rock (DR) and False Point (FP); (B) section containing Ocean Beach (OB).

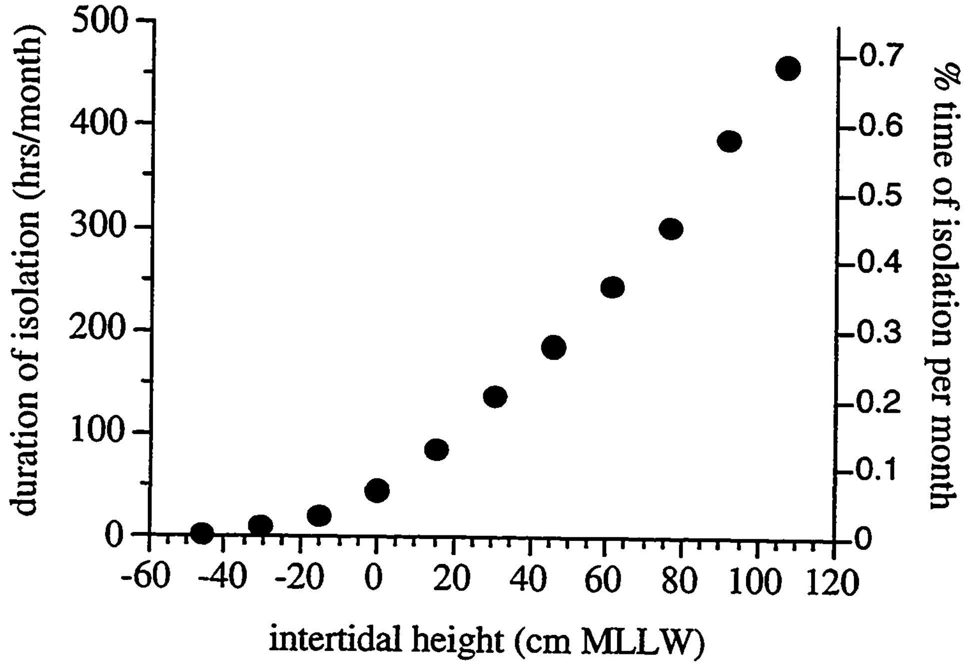


Figure 4.2: Relationship between the intertidal height of a tidepool and the duration of its isolation from subtidal conditions during a spring lunar month. Isolation duration was calculated for 11 intertidal height levels for the period of May 1-28, 1998, using HarborMaster™ software.

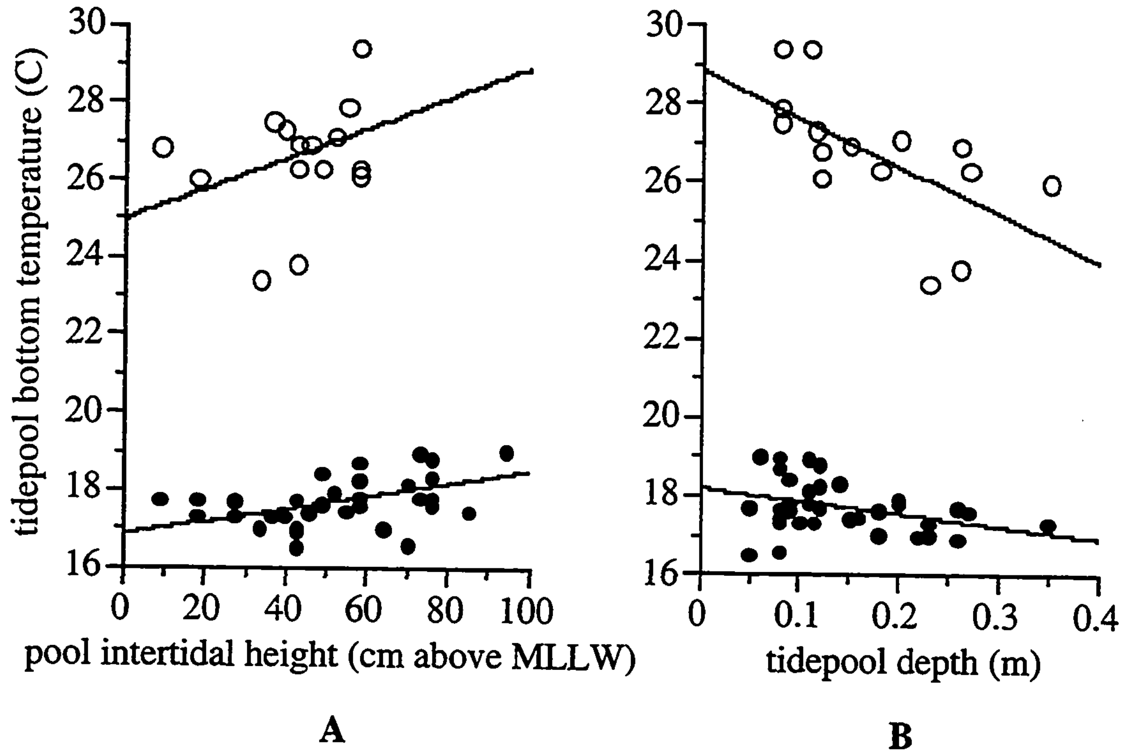


Figure 4.3: Tidepool bottom temperatures versus (a) pool intertidal height and (b) pool depth at False Point, San Diego, during two seasons. Open circles are temperatures from 1315 h to 1430 h on May 2, 1997. Black circles are temperatures at 1400 h on Dec. 14, 1997. Linear regressions between tidepool intertidal height and temperature (r^2=0.13, p=0.016 for May; r^2=0.27, p=0.001 for December) and tidepool depth and temperature (r^2=0.38, p=0.002 for May; r^2=0.12, p=0.035 for December) are plotted (see Table 4.2 for full multiple regression models). Surface water temperature at 1330 h in the subtidal region immediately offshore was on 21.0 C on May 2, 1997 and 16.9 C on December 14, 1997.

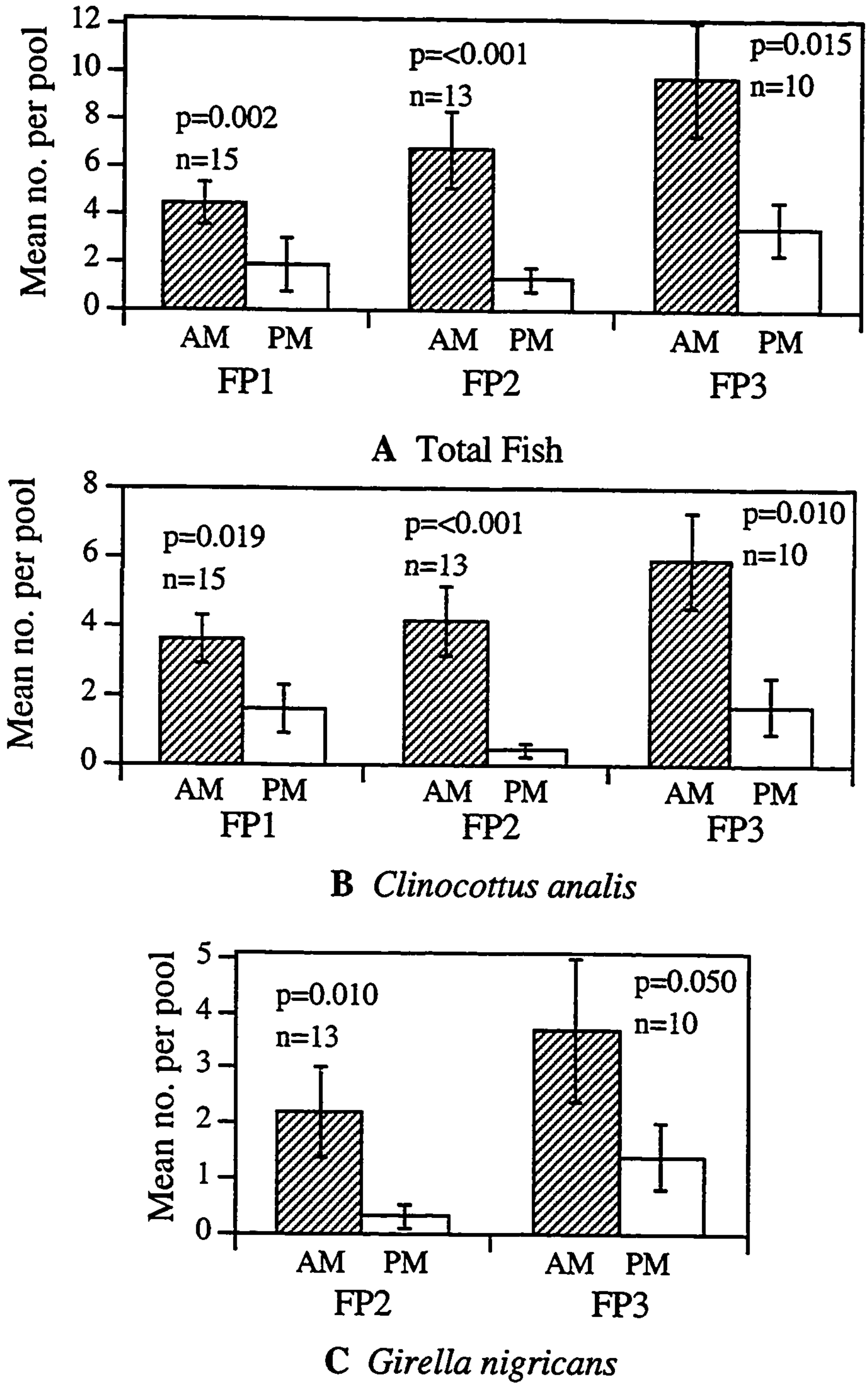
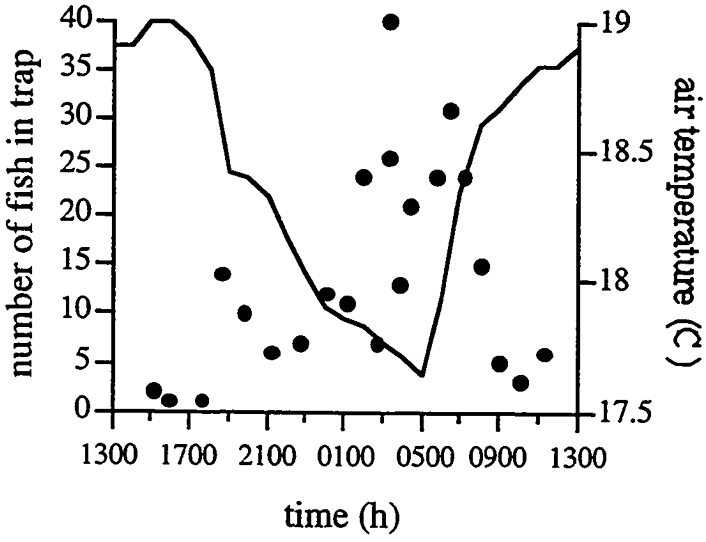
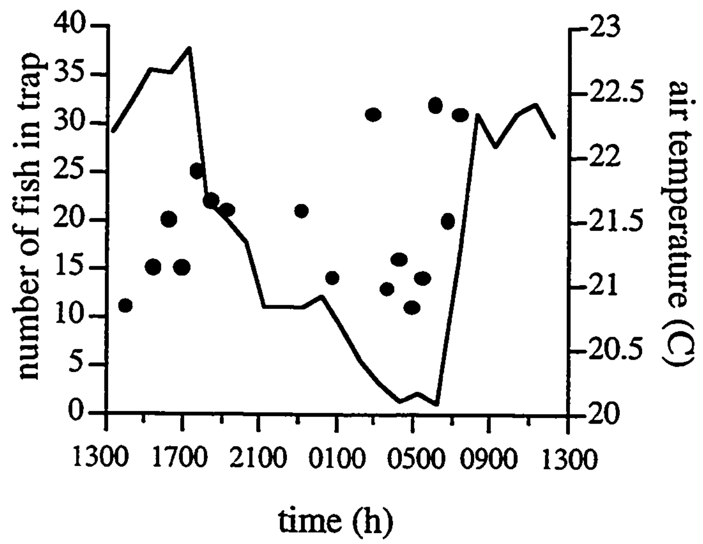


Figure 4.4: Number of total fish, *C. analis*, and *G. nigricans* in middle and upper intertidal pools when low tide was in early morning (AM) *versus* afternoon (PM). Results of paired *t*-tests are presented for three comparisons made at False Point (FP1, FP2, and FP3). Number of tidepools censused (n) and p-values (p) are listed.

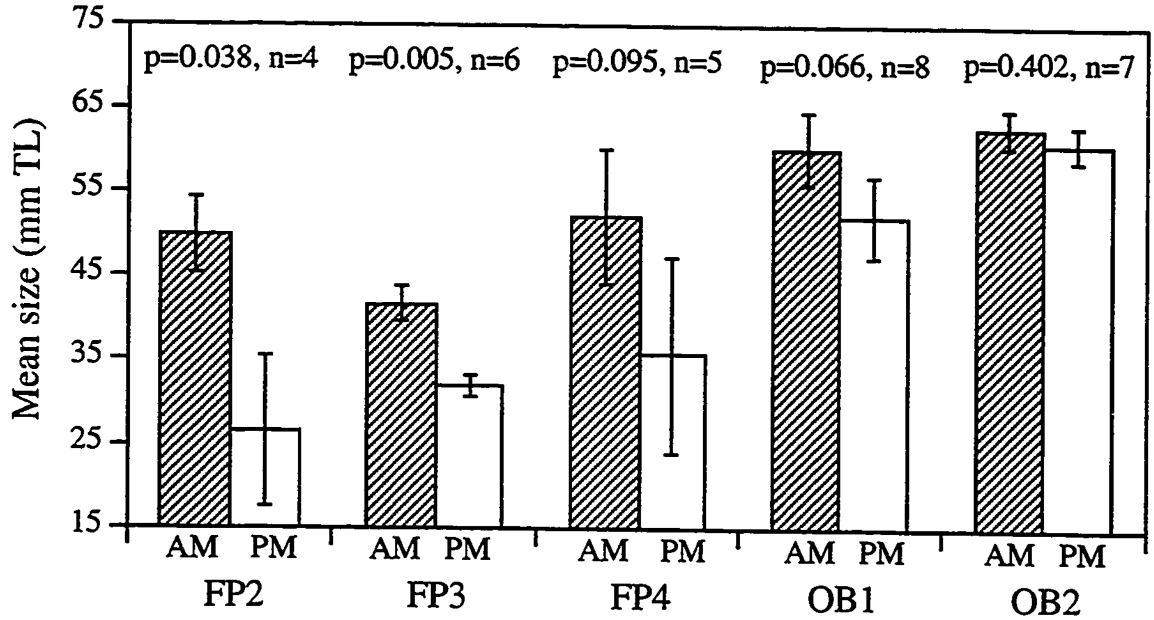


A July/August

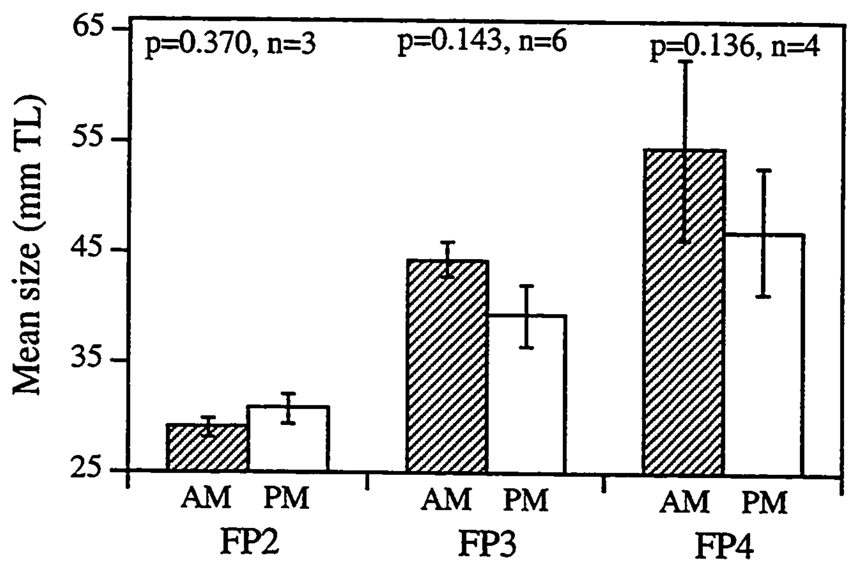


B September

Figure 4.5: Number of *G. nigricans* trapped at Dike Rock relative to the time of day of low tide in (a) late July to early August, and (b) September. Mean hourly air temperature at Dike Rock for the sampling periods is also plotted. Fish abundance was negatively correlated with mean air temperature at the time of pool isolation in July/August ($n=21$, $r^2=0.45$, $p<0.001$) but not in September ($n=17$, $r^2=0.01$, $p=0.69$).



A *Clinocottus analis*



B *Girella nigricans*

Figure 4.6: Mean size (± 1 SE) of *C.analis* and *G.nigricans* collected in all tidepools at low tide in early morning (AM) *versus* afternoon (PM). Five comparisons between morning and afternoon censuses were made, 3 at False Point (FP2, FP3, FP4) and 2 at Ocean Beach (OB1, OB2), San Diego, using paired *t*-tests. P-values (p) and the number of tidepools containing fish in both the morning and afternoon (n) are given.

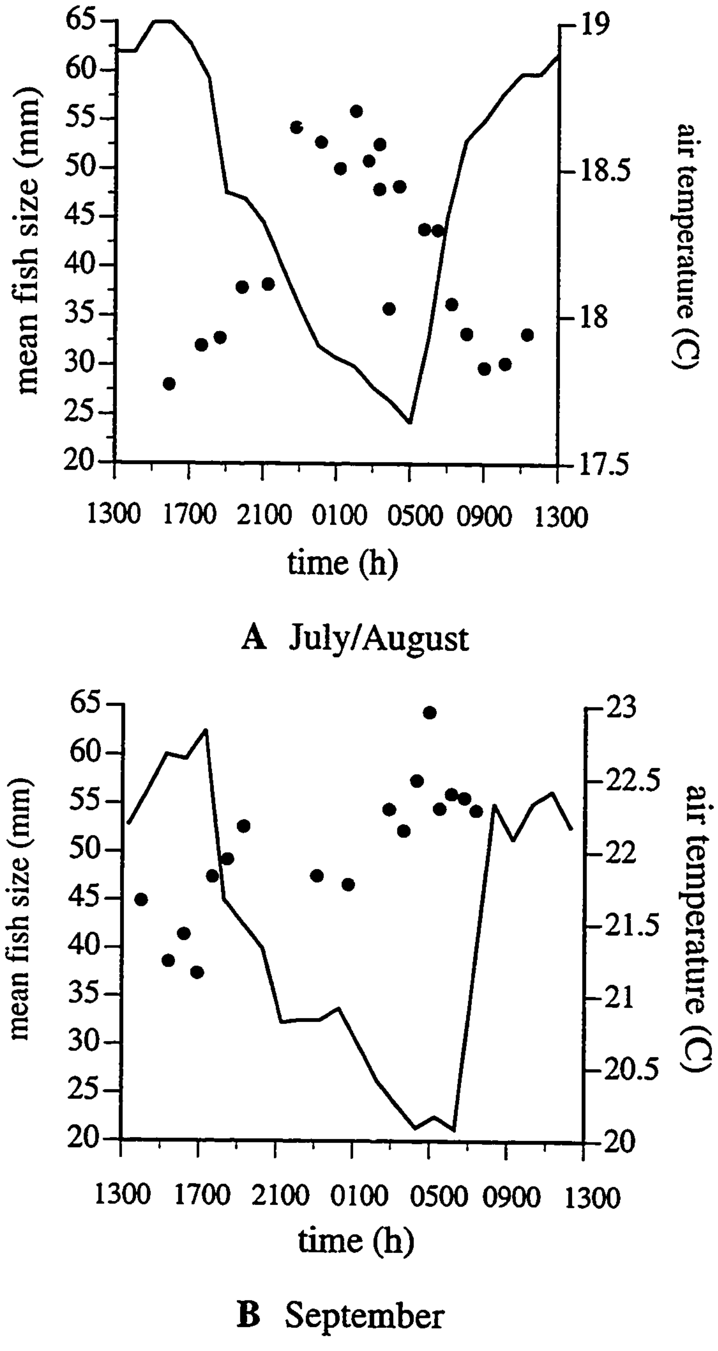


Figure 4.7: Mean size of *G. nigricans* trapped at Dike Rock in (a) late July to early August, and (b) September relative to the time of day of low tide. Mean hourly air temperature at Dike Rock for the sampling periods is also plotted. Mean fish size was negatively correlated with mean air temperature at the time of pool isolation in July/August ($n=21$, $r^2=0.060$, $p<0.001$) and September ($n=17$, $r^2=0.36$, $p=0.011$)

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Chapter 5

Changes in a tidepool fish assemblage on two scales of environmental variation: Seasonal and El Niño Southern Oscillation

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Abstract

Intertidal organisms are influenced by the tidal, daily, and seasonal environmental variability of their habitat. Interannual variability, although often less severe than shorter-scale variability, may also be important in structuring intertidal systems. This study compares the magnitude of changes in a rocky intertidal fish guild occurring on a seasonal scale with those occurring during an El Niño Southern Oscillation (ENSO). I examined tidepool fish assemblage structure and habitat use in two southern California sites approximately every 3 months from 1996 to 2000, a period including non-ENSO conditions, the 1997–1998 El Niño, and the 1998–1999 La Niña. During each sampling period, I censused fish abundance in 105 tidepools of differing intertidal height, depth, and surface area. Several aspects of habitat use varied seasonally for the four most common species: *Clinocottus analis* (woolly sculpin), *Girella nigricans* (opaleye), *Gobiesox rhessodon* (California clingfish), and *Hypsoblennius gilberti* (notchbrow blenny). All four species migrated vertically within the intertidal zone on a seasonal scale, corresponding to seasonal changes in sea level. The assemblage dominant, *C. analis*, occupied tidepools of different sizes depending on season. Although seasonality in habitat use suggests an influence of environmental variability on seasonal scales, fish habitat was generally not altered by temperature and sea level changes imposed by the El Niño. Species assemblage, however, differed among climate conditions. *C. analis* declined in abundance during the El Niño because of lack of recruitment but increased immediately after its conclusion. *Paraclinus integripinnis* (reef finspot), usually rare, was more abundant during the El Niño. Effect of the El Niño on the other four species was not detected. Assemblage changes suggest that although intertidal fishes regularly experience large tidal, daily, and seasonal environmental fluctuations, interannual changes in environmental factors, even when relatively small in magnitude, can perturb the system. Perturbations in the present system, however, did not persist beyond the end of the El Niño event as they often do in lower-latitude nearshore areas.

Coastal habitats such as the rocky intertidal zone are characterized by dynamic environmental conditions. Properties such as wave action, temperature, and water chemistry have large ranges, cycling on tidal, daily, seasonal, and interannual time scales (Metaxis and Schiebling 1993; Barry et al. 1995). Environmental variation on each scale has potential to affect intertidal populations and assemblage structure. For example, tidal and daily cycles may affect individual feeding and habitat use patterns on the centimeter-to-meter scale (Gibson 1999). Interannual cycles may affect abundance and distribution of populations on the scale of kilometers (Barry et al. 1995).

Seasonal cycles in environmental factors are important on a range of spatial scales and drive many rocky intertidal population and community processes. For example, seasonal storms may lead to increased mortality of intertidal algae (Gunnill 1985). Seasonal fluctuations in temperature may structure fish, invertebrate, and algal reproductive and recruitment cycles, and therefore cycles of population size and size structure of individuals (Chen and Chen 1992; Schoschina et al. 1996; Pfister 1999). Changes in sea level on a seasonal scale might be expected to impose cycles of vertical migration in mobile intertidal organisms. Seasonal changes in population size and size structure of one species may have community-level implications, affecting predator, prey, and other associated species. For example, seasonal cycles in algal composition of an Asian rocky shore resulted in seasonal diet switching by, and ultimately seasonal growth and reproductive cycles of, an herbivorous crab (Kennish et al. 1996).

Episodic climatic events such as the El Niño Southern Oscillation (ENSO) also have potential to affect communities and to interfere with community fluctuations that occur on seasonal and other temporal cycles. Intertidal communities may be sensitive to ENSO-induced environmental changes in part because the intertidal habitat marks the intersection of terrestrial and marine environments and therefore is exposed to environmental changes in both realms. Many intertidal species occupy a wide range of habitats throughout their lifetimes, sometimes ranging from tens or hundreds of kilometers offshore during a planktonic larval phase to the nearly terrestrial splash zone. A change in environmental conditions in any of those areas could, by influencing individual populations, affect entire intertidal systems

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(Sanford 1999). Although intertidal organisms are adapted to fluctuating environments, some may exist close to their upper or lower tolerances of environmental factors, and changes in climate could cause an extension of the environmental range beyond tolerable conditions (Tomanek and Somero 1999).

In southern California, signals of El Niño span the gradient from marine to terrestrial, including increases in air temperature, ocean temperature, sea level, storm activity, rainfall, and terrestrial runoff; decreases in coastal upwelling and nearshore productivity; and changes in nearshore currents (McGowan 1984; Norton et al. 1985; Glynn 1990). Fewer generalizations can be made about La Niña events, the phase of the ENSO opposite to El Niño, but they tend to be characterized by decreases in temperature, sea level, and rainfall and increases in upwelling and productivity (Philander 1990). Almost all characteristic ENSO signals have been identified as agents of ecological change to intertidal communities. An increase in water temperature can change the role of keystone predators in structuring communities (Sanford 1999) and can alter community composition by increasing survivorship of warm-tolerant species and decreasing survivorship of cold-water species (Arntz and Tarazona 1990). A decrease in offshore transport of surface waters during El Niño, a result of upwelling relaxation, can cause assemblage changes by enabling onshore advection of typically offshore species (Brodeur et al. 1985; Arntz and Tarazona 1990). Increases in storm activity during El Niño can cause mortality of certain species (Dayton and Tegner 1984; Gunnill 1985), leaving habitat open for colonization by other species.

The purposes of this study were to identify the extent to which assemblage structure of a midlatitude (San Diego, California) intertidal fish guild changed during the 1997–1998 El Niño event, to measure seasonal patterns in fish habitat use, and to determine the extent to which the ENSO event interfered with seasonal habitat use patterns. Because the study included only one El Niño event and did not include climatic replication, results cannot be generalized to all El Niño events. Instead, the study's goals are to determine changes that occurred in the fish assemblage during the 1997–1998 event only and to compare these results with those of other El Niño studies set in similar habitat types. As ENSO prediction improves, facilitating the planning of future ENSO studies, results and broad hypotheses generated by studies of single El Niño events can be compared and tested.

I addressed four questions in the present study: (1) Did assemblage structure change during El Niño? Species that are members of warm-water families were expected to increase in abundance, and cold-water family members were expected to decrease in abundance during El Niño. (2) Did intertidal fishes exhibit seasonal patterns in use of tidepools as a function of intertidal height, depth, and surface area? Seasonal cycles of sea level and temperature were expected to drive seasonal patterns of habitat use. (3) Did intertidal fishes change pool use patterns over vertical tidal scales during the El Niño period? Higher temperatures of middle and upper intertidal tidepools were expected to cause a redistribution of middle and upper intertidal fishes to lower pools. Higher sea level, which temporarily forced subtidal conditions onto low intertidal habitat, was expected to cause low intertidal fishes to move to higher pools to conserve the amount of time they spent isolated from the subtidal zone. As a result of these two processes, the horizontal band of available intertidal fish habitat was expected to narrow. (4) Was fish use of pool depth and surface area altered during El Niño? Increased air and water temperatures during El Niño were expected to induce fishes to relocate to bigger, deeper tidepools, which do not heat up as much during daytime low tides (Davis unpubl. data).

Methods

I measured fish abundance in one set of 55 tidepools from November 1996 to August 1999 and a second set of 50 tidepools from November 1996 to March 2000. The first set was located in the conglomerate sandstone outcrops of False Point (FP), and the second was located in a flat shale bench in Ocean Beach (OB), San Diego, California. Censuses were taken during all four seasons on a quarterly schedule, with sampling dates during November, February, May, and August. Two deviations from this schedule occurred during the study period. First, several additional sampling periods were added (June 1998, October 1998, and March 1999 at both sites and March 2000 at OB). Second, 1999 spring sampling at OB was conducted in June instead of May.

Tidepool fish abundance, species composition, and fish size were measured by collecting all fish in each pool. Pools were drained by bailing or by siphoning using hoses with mesh-covered openings. Rocks were removed, and crevices were searched for fish. All fish were identified to species and their total lengths (TL) measured to the nearest millimeter. The rocks were then replaced, the pool refilled, and the fish returned. Data were collected only during the day and only during tides lower than 30 cm above mean lower low water (MLLW). Three of the lowest pools at FP were in regions of shifting rocks and boulders; if a pool was no longer present during subsequent seasonal sampling, a substitute pool with similar characteristics was located.

El Niño signals—To characterize the ENSO conditions at the time of fish sampling, sea level and temperature data measured at the Scripps Pier, La Jolla, California, 7 km north of FP and 15 km north of OB, were used. Scripps Pier sea level values were obtained from the University of Hawaii's Sea Level Center data server (ftp://ilikai.soest.hawaii.edu/rqds/pacific). Sea level relative to a fixed reference point on shore was measured in millimeters at hourly intervals, from which monthly means were computed. Using data from January 1966 through December 1996, mean values were calculated for each month of the year to determine seasonal sea level fluctuations. Monthly sea level anomaly was calculated as the difference between a monthly sea level mean (1966–1996) and the mean sea level for the entire period of 1966–1996. Sea level anomalies for the months during the study period were calculated as the difference between the value for a particular study period month and the mean value for that month during the 1966–1996 period (Fig. 1).

Scripps Pier water temperatures were obtained from the

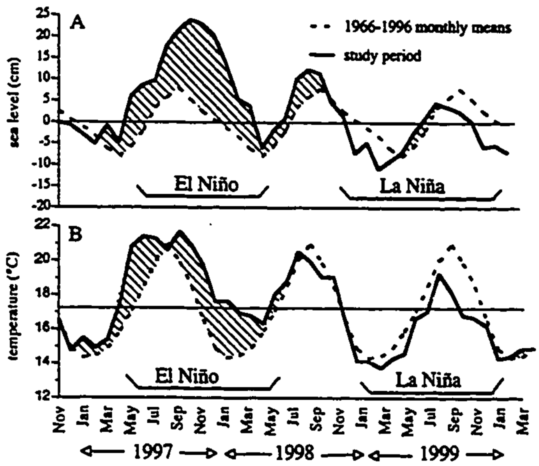

Fig. 1. (A) Sea level and (B) water temperature at the Scripps Pier, San Diego. The solid line in (A) represents monthly sea level over the course of the study (November 1996 to March 2000), calculated as the difference in sea level from the long-term 1966–1996 mean. The solid line in (B) represents mean monthly water temperature over the course of the study. The dashed lines in (A) and (B), representing mean sea level anomalies (relative to a fixed point on shore) and mean water temperature for each calendar month from 1966 to 1996, are included to denote normal seasonality in the two parameters. Mean values for the 1966–1996 period (0 cm in [A] and 17.2°C in [B]) are marked with thin lines.

Scripps Institution of Oceanography data servers (http://www.opsd.nos.noaa.gov and ftp://nemo.ucsd.edu/pub/shore). Mean monthly water temperatures were calculated by averaging hourly values. Months in which fish were sampled were divided into the categories of El Niño, "normal," or La Niña, defined by extended positive or negative sea level and temperature anomalies or lack thereof (Fig. 1).

Patterns in species composition—To assess changes in species composition of the San Diego rocky intertidal zone during ENSO conditions, the total number of individuals of each fish species collected during each sampling period was tallied. Data from the two sampling sites were analyzed separately but were combined across all tidepools at a site. A modification of the Simpson's species diversity index was calculated using the equation described by Rosenzweig (1995):

$$-\ln(SI) = \sum [(n^2 - n)/(N^2 - N)],$$

where n is the number of individuals present of a particular species and N is the total number of individuals present. This index was chosen as a measure of species evenness because it incorporates information on species' proportional abundances and focuses on dominance patterns rather than richness (Magurran 1988); richness in the present system is not highly variable. Species evenness ($-\ln[SI]$), as well as abundance of the six most common fish species, were compared among El Niño, normal, and La Niña months using analyses of variance (ANOVAs). Normality of the data was determined using Lilliefors test of residuals. When Lilliefors $P > 0.05$, abundance values were log-transformed to meet the ANOVA assumption of normality.

Habitat use—Surface area, depth, and intertidal height of all study tidepools were measured in fall 1996. Surface area was approximated as the product of length, the maximum distance measured in centimeters across the top of the pool, and width, the distance perpendicular to the length axis at the midpoint of the pool. Tidepool depth was approximated as the average of 10 haphazardly distributed depth measurements to the nearest 0.5 cm. With the exception of the three lowest pools at FP, these parameters were not remeasured over the course of the study. On the basis of calculated rates of tidepool erosion (Emery 1946), changes in depth or surface area during a 3-year period were most likely negligible and within measurement error of the methods used to measure these parameters.

The intertidal height value of each pool relative to MLLW was obtained in November 1996 (Davis 2000). Time to the nearest minute of each tidepool's isolation point by the ebbing tide was noted, then Harbor Master® software was used to determine tidal height to the nearest 3 cm above MLLW at that time. Isolation point was defined as the time at which water ceased to enter (by wave, surge, or splash) or drain from the pool. Two days in November 1996, one calm and one relatively rough, were devoted to this exercise at each site. Intertidal heights determined for these different sea states differed only by as much as 6 cm, so averages were used when discrepancies occurred.

Seasonal and ENSO changes in the types of tidepools occupied by the four most common species, *C. analis, G. rhessodon, G. nigricans,* and *H. gilberti,* were evaluated separately for the two sites. Within a particular month, the average of each habitat parameter (intertidal height, surface area, and depth) was computed for all pools at a site containing individuals of a particular species. Monthly values were not calculated for sampling periods in which a species was found in fewer than four pools at a site.

To determine whether habitat use had a seasonal component, I regressed average intertidal height of each species against monthly sea level and average tidepool depth and surface area of each species against monthly water temperature. Because habitat use might be expected to lag the environmental signal, sea level and temperature were offset by −2, −1, and 0 months to explore the best and most consistent regression fit for all species. To determine climate effect on habitat use, I used ANOVAs to compare values of habitat parameters among El Niño, normal, and La Niña periods. Normality of the data was established using Lilliefors test ($P > 0.05$).

Results

Seasonal, El Niño, and La Niña environmental anomalies—Using sea level and water temperature anomalies measured in La Jolla, I identified seasonal environmental cycles and ENSO conditions. The mean seasonal range in sea level (1966–1996) measured in La Jolla was 16 cm, with values highest in September and lowest in April (Fig. 1). From about April/May of 1997 to about April 1998, sea levels were higher than normal. The largest anomaly during this El Niño period was measured in November of 1997, when sea level was 18.3 cm higher than the November average from 1966–1996. This El Niño sea level anomaly (18.3 cm) was larger than the normal seasonal range (16 cm).

The mean (1966–1996) seasonal water temperature range measured in La Jolla was 6.6°C, with values highest in August and lowest in January. Water temperature at the Scripps Pier was anomalously high from about May 1997 to May 1998, staying above 20°C for six consecutive months. Monthly temperature usually averages above 20°C for only three summer months. The greatest El Niño temperature anomaly occurred in January of 1998, when water temperature was 3.3°C higher than the long-term January mean. This value is half that of the normal seasonal range during the 1966 to 1996 period (6.6°C).

The El Niño sea level and water temperature signals differed in two major ways. First, the El Niño sea level anomaly was greater than the seasonal sea level range, whereas the El Niño water temperature anomaly was less than the seasonal water temperature range. Second, the El Niño had its greatest influence on sea level during the fall, the season of highest sea level, and as a result intensified seasonal sea level differences. The El Niño had its greatest influence on water temperature during the winter, the season of lowest water temperature, and therefore served to dampen seasonal water temperature differences.

The La Niña period following the 1997–1998 El Niño did not produce signals as strong as those of the El Niño. Sea level was lower than normal from November 1998 to April 1999 and again from August 1999 through January 2000, with a maximum deviation from normal conditions (1966 to 1996) of 10 cm. Water temperature was lower than normal from about August 1998 through January 2000, but by an average of less than 1°C.

In this study, the El Niño period has been defined as June 1997 through May 1998. Fish data collected in August 1997, November 1997, February 1998, and May 1998 were considered to fall within the El Niño period. Data collected from February to November 1999 were considered to fall within the La Niña period. Data collected during the first period of the study (November 1996 to May 1997), during the period between El Niño and La Niña (June 1998 to November 1998), and after La Niña (February and March 2000) were considered data from normal conditions.

Species composition—Fifteen fish species were found in the tidepools of FP and OB during the study period. Six species were common, found at each site in six or more sampling months, including *C. analis,* (woolly sculpin), juvenile *G. nigricans* (opaleye), *G. rhessodon* (California clingfish), *H. gilberti* (notchbrow blenny), *Gibbonsia elegans* (spotted kelpfish), and *Paraclinus integripinnis* (reef finspot). The other nine species were represented by fewer than 25 individuals throughout the study period and were collected in four or fewer sampling months. These included *Atherinops affinis,* (topsmelt), juvenile *Hermosilla azurea* (zebraperch), juvenile *Paralabrax clathratus* (kelp bass), *Hypsoblennius jenkinsi* (mussel blenny), *G. metzi* (striped

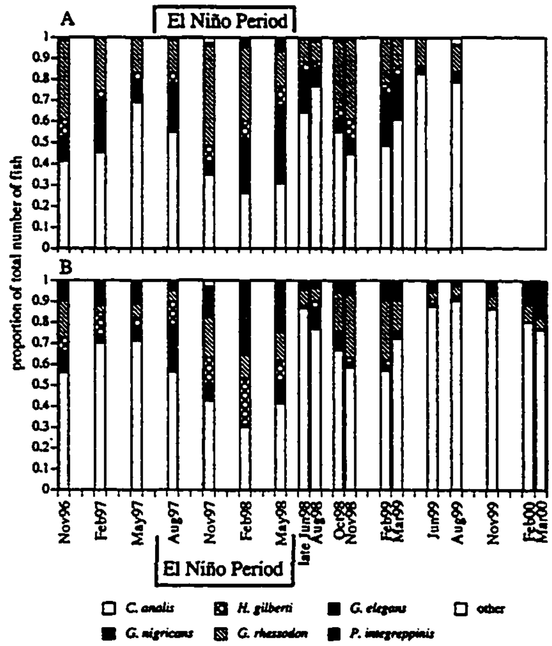

Fig. 2. Proportional species composition of intertidal fishes at (A) FP from November 1996 to August 1999 and (B) OB from November 1996 to March 2000.

kelpfish), juvenile *Hypsypops rubicundus* (garabaldi), juvenile *Micrometris minimus* (dwarf surfperch), *Scorpaenichthys marmoratus* (cabezon), and juvenile *Sebastes rastrelliger* (grass rockfish).

Before the El Niño event, *C. analis* was the assemblage dominant, constituting from about 40–70% of the total number of fishes present at the two sites (Fig. 2). At FP, *G. rhessodon* and *G. nigricans* were the second and third most abundant species, making up about 20–40% and 10–25% of the total assemblage, respectively (Fig. 2A). At OB, that component of the assemblage not attributable to *C. analis* was more evenly divided among *G. rhessodon, G. nigricans, H. gilberti,* and *G. elegans* (Fig. 2B).

Several changes in the species assemblage occurred during the 1997–1998 El Niño. The number of individuals of the usually dominant *C. analis* was significantly different among El Niño, normal, and La Niña months, lower during the El Niño period than during the other two periods (Table 1, Fig. 3). The decrease in numbers of *C. analis* was mainly attributable to low numbers of larvae recruiting from the plankton to FP (Fig. 4) and OB. Recruitment occurred during the non-El Niño winter and spring periods of 1997 and 1999; however, during the winter and spring of 1998 (El Niño), recruitment was low. In 1998, recruitment began in June, indicated by the recovery of the populations at this time (Fig. 3), after the environmental influence of the El Niño had dissipated but before the La Niña phase began.

P. integripinnis, absent or rare before the El Niño, in-

Table 1. Comparison of species evenness and tidepool fish abundance among climate periods at False Point (FP) and Ocean Beach (OB). Mean values of −ln (Simpson's index) and mean abundance of each species (mean number individuals per site) are presented for El Niño months (August 1997 to May 1998; $n=4$), normal months (November 1996 to May 1997, June 1998 to November 1998, February 2000 to March 2000; $n=7$ for FP and 9 for OB), and La Niña months (February 1999 to November 1999; $n=4$ for FP and 5 for OB). ANOVAs were used to compare evenness and abundance among El Niño, normal, and La Niña periods (df=14 for FP, df=17 for OB). When ANOVA model P values were < 0.10, Fisher's least significant difference test was used to compare pairs of climate periods. Significant post hoc comparison results ($P<0.05$) are listed below (EN = El Niño, norm = normal, LN = La Niña).

Variable	El Niño mean	Normal mean	La Niña mean	*F* statistic	*P* value	Post hoc comparisons
Species evenness						
FP	1.17	0.88	0.68	3.97	0.047	EN>LN
OB	1.34	0.62	0.47	15.77	<0.001	EN>norm, EN>LN
C. analis						
FP	106.8	223.7	449.3	3.62	0.059	LN>EN
OB	61.8	142.1	150.0	4.43	0.031	LN>EN
P. integripinnis						
FP	3.8	1.0	0.0	3.51	0.063	EN>LN
OB	10.0	3.8	3.4	3.90	0.043	EN>norm, EN>LN
H. gilberti						
FP	18.3	18.7	13.0	1.15	0.350	
OB	17.0	5.0	2.2	18.72	<0.001	EN>norm, EN>LN
G. nigricans						
FP	55.3	44.3	55.5	0.18	0.841	
OB	17.5	9.9	3.4	0.88	0.436	
G. rhessodon						
FP	73.5	84.6	87.0	0.13	0.884	
OB	16.5	26.4	21.8	0.10	0.906	
G. elegans						
FP	3.3	1.6	2.0	1.65	0.232	
OB	11.0	11.7	10.0	0.13	0.877	

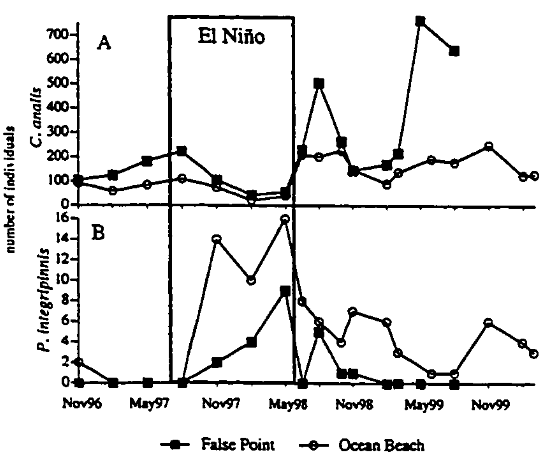

Fig. 3. Abundance of *C. analis* and *P. integripinnis* from November 1996 to March 2000 in all 55 pools at FP and 50 pools at OB. The boundaries of the El Niño period, estimated from sea level and sea surface temperature anomalies, are marked with vertical lines. At both sites, number of *C. analis* individuals was lower and number of *P. integripinnis* individuals was higher during the 1997–1998 El Niño (*see Table 1*).

creased in abundance at both sites during the El Niño period and declined as the El Niño waned in June 1998 (Table 1; Fig. 3). This species did not appear at the onset of the El Niño, but first increased in November 1997. *H. gilberti* was more abundant during El Niño than during La Niña or normal months at OB, but not at FP (Table 1; Fig. 5). Abundance of *G. nigricans*, *G. rhessodon*, and *G. elegans* did not change at either site during El Niño or La Niña (Table 1; Fig. 5).

Mainly as a result of the decrease in abundance of the assemblage dominant, *C. analis*, species evenness increased significantly during the El Niño. Because the other major species did not also decrease in number, *C. analis*'s decrease resulted in the decline of its relative contribution to the assemblage. Contribution by this species dropped to lows of 26% at FP and 30% at OB during February 1998, one of the most anomalously warm months of the El Niño (Fig. 2). This drop, along with the increase in abundance of the rare *P. integripinnis*, led to higher species evenness during El Niño months than during normal or La Niña months at both sites (Table 1).

Habitat use—The four most common species, *C. analis*, *G. nigricans*, *G. rhessodon*, and *H. gilberti*, displayed seasonal patterns of tidepool use with respect to intertidal

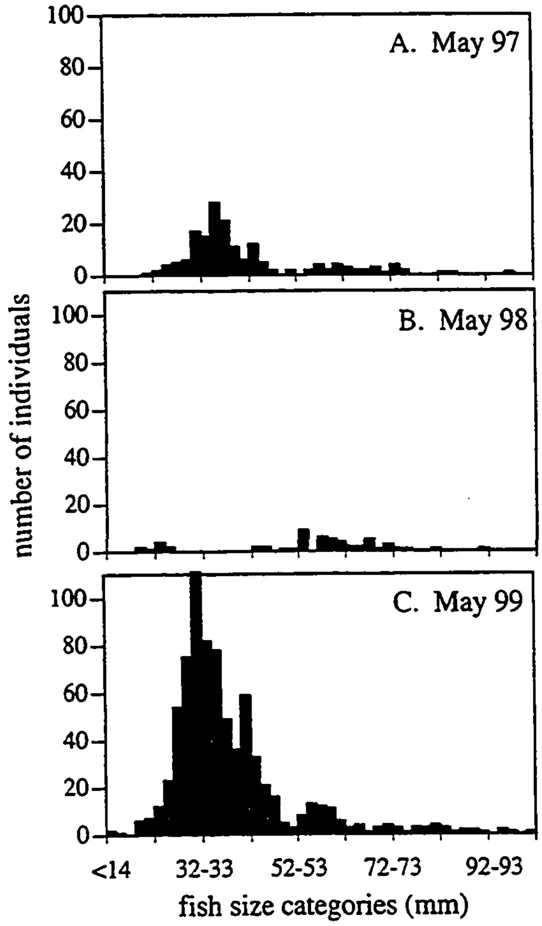

Fig. 4. Size-frequency histograms portraying population structure of *C. analis* at FP in (A) May 1997, before El Niño; (B) May 1998, during El Niño; and (C) May 1999, during La Niña. Histograms are constructed with 2-mm-size bins. In the histograms of May of 1997 and 1999, the smallest-sized cohorts are the result of recruitment from late March to April. The next largest cohorts are the survivors of January–February recruitment events. In 1998, no winter recruitment was measured, and few recruits appeared by May.

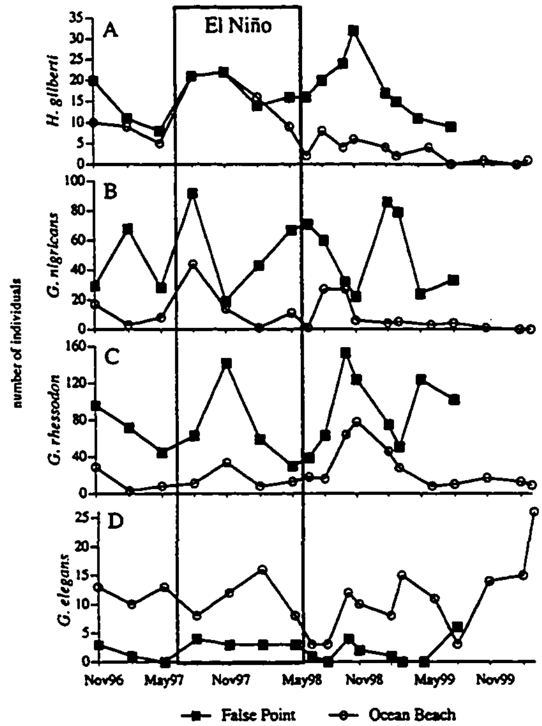

Fig. 5. Abundance of *H. gilberti, G. elegans, G. nigricans,* and *G. rhessodon* from November 1996 to March 2000 in 55 pools at FP and 50 pools at OB. Number of *H. gilberti* individuals increased at OB during the 1997–1998 El Niño. None of the other species changed significantly in abundance during El Niño (*see Table 1*).

height. All four species moved vertically in the intertidal zone within at least one of the study sites. When sea level reached its seasonal maximum in the fall, the average intertidal height (relative to the MLLW mark of November 1996) of pools occupied by members of these species increased (Fig. 6). Of offsets in mean sea level by −2, −1, and 0 months, an offset in sea level by −1 month provided the best regression fit for pool height of all species, suggesting that the fishes' tidal height response lagged sea level changes by 1 ± 0.5 months. Relationships were significant for *C. analis* and *G. rhessodon* at FP, *G. nigricans* at both sites, and *H. gilberti* at OB (Table 2). Low abundance of *G. rhessodon* at OB and *H. gilberti* at both sites may explain the lack of consistency between sites for these species.

The magnitude of seasonal vertical shifts by the fishes generally matched the magnitude of seasonal sea level anomalies during non-El Niño periods, but not sea level anomalies of the 1997–1998 El Niño. For example, fall 1998, a period of normal sea level conditions, brought an increase in sea level of 17 cm from the previous May, an increase matched by intertidal height shifts of all fish populations except *C. analis*. Average intertidal height of *G. nigricans, H. gilberti, G. rhessodon* at FP, and *C. analis* increased by 15–20, 15–17, 12, and 4–8 cm, respectively, from May to November 1998 (Fig. 6). In contrast, sea level during the El Niño fall of 1997 rose 30 cm from the previous May, almost double the magnitude of normal years (Fig. 1). However, *G. nigricans* at FP, *H. gilberti, G. rhessodon* at FP, and *C. analis* rose only 18, 13–18, 16, and 12–15 cm, respectively. Only *G. nigricans* at OB matched the 30-cm magnitude of sea level rise, increasing in mean height by 40 cm. However, the maximum intertidal height occupied by this species during the 1997 El Niño fall was similar to that

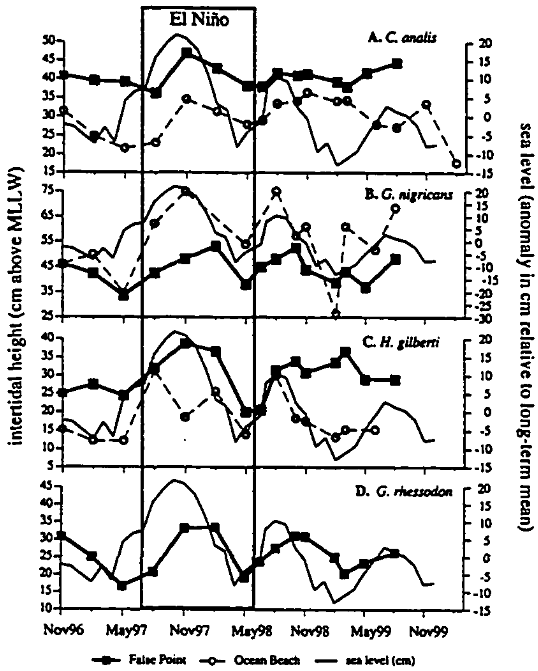

Fig. 6. Mean intertidal height of pools containing fishes (relative to intertidal heights measured in November 1996) and mean monthly sea level anomaly from November 1996 to March 2000. Both sea level and intertidal height of fishes fluctuated seasonally, with fish height values lagging sea level changes by approximately 1 month (*see Table* 2). These relationships were significant for *C. analis* at FP, *G. nigricans* at FP and OB, *G. rhessodon* at FP, and *H. gilberti* at OB. A monthly intertidal height value for a species was not included in the analyses if individuals of the species were present in fewer than four pools.

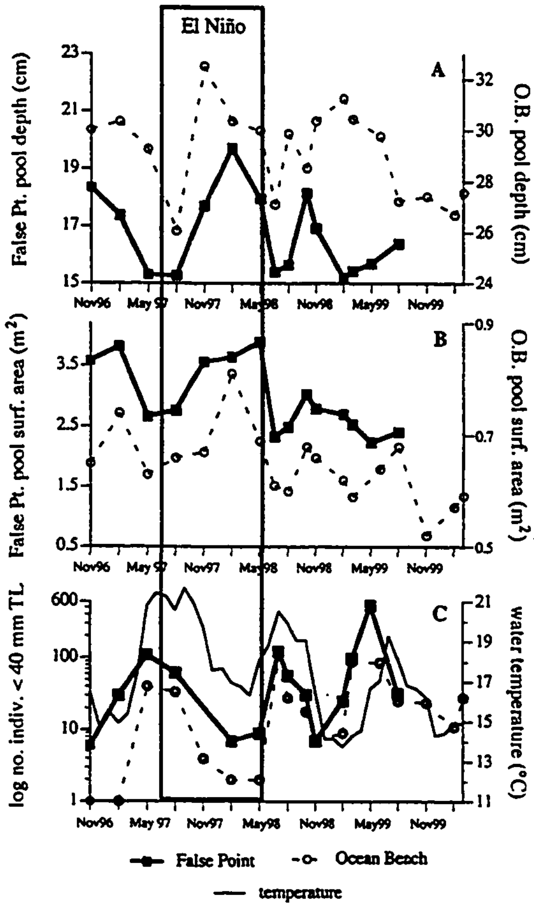

Fig. 7. Seasonal fluctuations of depth and surface area of pools occupied by *C. analis* from November 1996 to March 2000 relative to temperature and the number of small individuals. (A) Mean tidepool depth and (B) mean pool surface area at FP and OB. (C) Number of individuals <40 mm TL at FP and OB, and water temperature at the Scripps Institution of Oceanography Pier. Tidepool depth and surface area were not correlated with temperature (except depth at OB), but were correlated with the number of small individuals present in the population (*see text*).

Table 2. Linear regressions between intertidal height of fishes and sea level (lagged by 1 month). Sea level values were calculated as deviations from the long-term mean (1996 to 1999). Intertidal height values for each species during each sampling period were calculated by averaging the intertidal height of all pools containing individuals of the species in question. Intertidal height values were not included in the analysis for sampling periods in which a species was found in fewer than three pools at a site.

Species	Site	Slope	n	r^2	P
C. analis	False Point	+0.17	15	0.36	0.018
	Ocean Beach	+0.19	17	0.10	0.207
G. nigricans	False Point	+0.44	15	0.55	0.002
	Ocean Beach	+0.88	12	0.37	0.036
H. gilberti	False Point	+0.26	13	0.19	0.106
	Ocean Beach	+0.38	11	0.35	0.033
G. rhessodon	False Point	+0.42	15	0.57	0.001
	Ocean Beach	−0.09	17	0.05	0.411

occupied during fall 1998 (Fig. 6). *G. rhessodon* at OB and *G. elegans* were not abundant enough for similar analysis.

Use of pool depth and surface area by one species, *C. analis*, had seasonal components (Fig. 7). Average depth and surface area of pools occupied by this species tended to be lowest during spring and summer. Although pool depth and surface area were not correlated with Scripps Pier water temperature ($P > 0.05$, with the exception of depth at OB: $n = 18$, $r^2 = 0.24$, $P = 0.035$), both parameters were positively correlated with the number of small individuals (<40 mm TL) present in the populations (Fig. 7). Average pool surface area was negatively correlated with the log-transformed

Table 3. Effects of climate period (El Niño, normal, and La Niña) on tidepool intertidal height, depth, and surface area of fishes. F statistics, P values, and r^2 are presented for ANOVAs for each species at False Point (FP) and Ocean Beach (OB); df = 14 for all species at FP, 17 for *C. analis* and *G. rhessodon* at OB, and 13 for *G. nigricans* and *H. gilberti* at OB.

	False Point			Ocean Beach		
Variable	F	P	r^2	F	P	r^2
C. analis						
Intertidal height	0.14	0.871	0.02	0.70	0.513	0.09
Depth	2.25	0.148	0.27	0.39	0.739	0.04
Surface area	4.39	0.037	0.42	3.31	0.065	0.31
G. nigricans						
Intertidal height	0.41	0.674	0.06	1.13	0.370	0.20
Depth	5.31	0.022	0.47	0.07	0.932	0.01
Surface area	2.90	0.094	0.33	0.68	0.530	0.12
H. gilberti						
Intertidal height	1.08	0.370	0.15	1.44	0.283	0.22
Depth	13.34	0.001	0.69	10.86	0.003	0.69
Surface area	4.16	0.043	0.41	7.62	0.010	0.60
G. rhessodon						
Intertidal height	0.01	0.990	<0.01	3.40	0.061	0.31
Depth	3.86	0.051	0.39	0.02	0.981	0.01
Surface area	0.31	0.736	0.05	0.37	0.700	0.05

number of small fish (FP: n = 15, r^2 = 0.52, P = 0.002; OB: n = 18, r^2 = 0.33, P = 0.013), as was average tidepool depth (FP: n = 15, r^2 = 0.17, P = 0.005; OB: n = 18, r^2 = 0.24, P = 0.061). *C. analis* exhibits ontogenetic habitat shifts (Davis 2000); therefore, seasonal trends in habitat use may be driven by the seasonal influx of smaller individuals. Unlike *C. analis*, use of pool depth and surface area by *G. nigricans*, *H. gilberti*, and *G. rhessodon* did not have a seasonal pattern. Neither average depth nor surface area for these species was correlated with water temperature (regression analysis: $P \gg 0.05$).

Despite El Niño-induced changes in water temperature, air temperature, and sea level that might be expected to alter habitat use and interfere with seasonal relationships to the tidepool parameters, the El Niño did not disrupt most of the fishes' use of tidepool intertidal height, depth, or surface area. Average intertidal height was not different for any species when compared among El Niño, normal, and La Niña months (Table 3). Use of pool size was different between climate periods only for *C. analis*, which occupied larger pools during the El Niño at both sites, and for *H. gilberti*, which occupied larger and deeper pools during the La Niña (Table 3, Fig. 8). *C. analis*'s occupation of larger tidepools during the El Niño was not simply due to the lack of young fish, which are found in smaller pools (Davis in press), and presence of mainly large fish during the El Niño. Average size of tidepools occupied by large *C. analis* (≥40 mm TL) was significantly greater during the El Niño as well (t-tests, FP: t_{14} = 2.91, P = 0.012; OB: t_{17} = 2.48, P = 0.025), suggesting that individuals had changed pools.

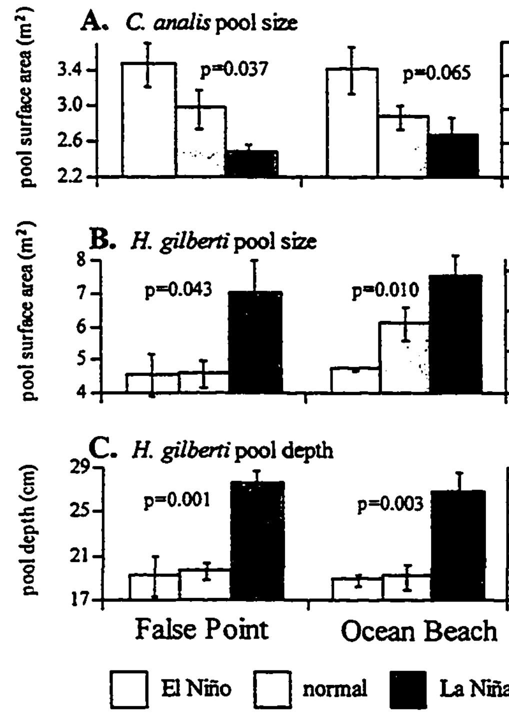

Fig. 8. Habitat differences among El Niño, normal, and La Niña periods. (A) Tidepool surface area of *C. analis*, (B) tidepool surface area of *H. gilberti*, and (C) tidepool depth of *H. gilberti*.

Discussion

Several aspects of the San Diego rocky intertidal fish assemblage changed with season and during the 1997–1998 El Niño event, and several aspects did not change on those scales. Use of some habitat parameters was observed to have a seasonal component, suggesting that environmental fluctuations are directly or indirectly important to habitat use. However, with the exception of *C. analis*'s and *H. gilberti*'s use of tidepool size, environmental changes associated with the El Niño event did not affect species' habitat patterns. Although habitat use was not greatly altered during the El Niño, changes in assemblage structure were observed during this period. Because the study spanned only one El Niño and therefore no replication was possible, these changes cannot be directly attributed to El Niño-induced environmental forces. However, the changes are consistent with those observed and predicted by studies of other El Niño events (Arntz and Tarazona 1990). Assemblage changes in the present study were not long-ranging; the assemblage returned to pre-El Niño conditions almost immediately after the El Niño period.

Species assemblage—Two main changes occurred within the rocky intertidal fish assemblage during the 1997–1998 El Niño: a decrease in abundance of *C. analis*, the assemblage dominant, and an increase in *P. Integripinnis* abundance. The latter attained levels only approaching those of *G. elegans*, one of the least common assemblage members, and therefore most likely had little effect on the community. Results are consistent with those of two California intertidal algal studies, in that some species changed in abundance during an El Niño, but the majority did not (Gunnill 1985; Murray and Horn 1989).

It has not been established which of the various El Niño signals contributed to the changes observed in intertidal fish assemblage. Other works have attributed El Niño assemblage changes to increases in water temperature, which can lead directly to mortality of certain dominant species and the release of resources to other species, can lead indirectly to mortality by allowing warm-tolerant species to better compete, or can prompt certain dominant species to migrate poleward, freeing resources for use by other species (Arntz and Tarazona 1990; Urban 1994; Palomarez-Garcia and Gomez-Gutierrez 1996). As in the present study, species evenness in Peruvian rocky intertidal systems increased during the 1982–1983 El Niño because of the mortality of dominant mytilid species and the release of space to less common species (Arntz and Tarazona 1990). In nonintertidal assemblages as well, El Niño-induced temperature change has been partially implicated in the replacement of dominants by warmer-water species, including Peruvian nearshore fishes (Santander and Zuzunaga 1984; Arntz and Tarazona 1990), copepods in a Mexican bay (Palomarez-Garcia and Gomez-Gutierrez 1996), soft-sediment bivalves (Arntz et al. 1987; Urban 1994), and zooplankton off Oregon (Peterson 1999).

In the present study, species composition shifts were consistent with temperature-regime affinities and ancestry. *C. analis*, which declined in abundance during the El Niño period, is a member of the cold-temperate Cottidae (Graham 1970). San Diego (32.8°N) falls within the southern third of the species' latitudinal range (from 28.5°N to 40°N), and its family's center of distribution is in the north Pacific (Graham 1970; Miller and Lea 1972). Ancestral temperature affinities may explain the maintenance of extremely high abundance during 1999, a La Niña period. However, post-El Niño population size began to recover during normal conditions, before the La Niña phase began.

The other five common species all belong to warm-temperate or tropical to warm-temperate families. *P. integripinnis*, which increased in abundance at both sites during the El Niño, is a member of the tropical to warm-temperate Labrisomidae (Stepien et al. 1993). *H. gilberti*, which increased at OB during El Niño and declined during La Niña, is a member of the tropical to warm-temperate Blenniidae (Stepien et al. 1993). *G. nigricans*, *G. elegans*, and *G. rhessodon*, unchanged in abundance at both sites, belong to the warm-temperate Girellidae, warm-temperate Clinidae, and tropical to warm-temperate Gobiesocidae, respectively (Briggs 1955; Johnson and Fritzsche 1989; Stepien et al. 1993; Nelson 1994).

The decrease in *C. analis* population size during the El Niño in the present study (Fig. 3), due mainly to a decrease in the number of new recruits (Fig. 2), may have been caused by events during the planktonic larval phase. Females carried eggs throughout the El Niño period (Davis, unpubl.). Unless spawning behavior was affected, the instigation of the population decrease occurred between the egg phase and recruitment. Coastal waters were warmer, possibly serving to increase metabolic rates, food requirements, and therefore starvation potential of *C. analis* larvae. Recruitment also may have been diminished because larvae were not transported to intertidal settling areas. Although recruitment of some nearshore species is enhanced during El Niño events because of relaxation of upwelling, which normally induces offshore advection of surface water and larvae (Brodeur et al. 1985; Ebert et al. 1994; Connolly and Roughgarden 1999), El Niño conditions can negatively affect recruitment of other species (Dayton and Tegner 1984; Gunnill 1985; Milligan et al. 1999). The recruitment mechanism of *C. analis* larvae, which are epibenthic (Barnett et al. 1989; Feeney 1992), may be the onshore transport of bottom waters from features like internal tidal bores, similar to the mechanism for barnacle larvae (Pineda 1991, 1994). During El Niño periods, deepening of the thermocline (McGowan 1985; Philander 1990) may prevent bores, which depend on stratification (Pineda 1994), from reaching the shore.

The mechanisms causing *P. integripinnis* to increase in abundance also may be related to temperature or transport. Temperature changes may have induced migration from lower latitude regions, as San Diego (32.8°N) is near the northernmost extent of its along-shore distribution (Almejas Bay [24.5°N] to Santa Cruz Island [34°N], Miller and Lea 1972). Fish may have also colonized the study pools from subtidal or low intertidal areas below the study area, induced by the sea level increase associated with El Niño. Finally, transport of new recruits to the study area from Baja California may have increased. During the El Niño event, the northward California Countercurrent increased in velocity, transporting more water (Norton et al. 1985; Lynn et al. 1998), and perhaps *P. integripinnis* larvae, from the south.

Assemblage shifts occurring during El Niño did not persist after the El Niño period. Instead, the assemblage returned quickly to pre-El Niño conditions. Arntz and Tarazona (1990) describe low-latitude South American intertidal and nearshore communities that were severely perturbed by the 1982–1983 El Niño and had not returned to normal several years after the El Niño. Three explanations could account for the lack of similar ENSO-induced severe changes in north Pacific rocky intertidal communities. First, the effects of El Niño (and La Niña) may be diminished at these latitudes (Paine 1986). Second, natural variability may mask or make more difficult measurements of ENSO-induced changes in these systems (Paine 1986; Murray and Horn 1989). Third, El Niño environmental signals may counterbalance each other in rocky intertidal pools. For example, the rise in sea level, which increases submergence time of tidepools, may counter the temperature effects of warmer El Niño air and water. All three mechanisms may dampen rocky intertidal community change in higher latitudes.

Habitat use—Motile intertidal organisms, unlike their sessile counterparts, are able to alter their habitats in response to seasonal and climatic changes. Seasonal changes in intertidal height were probably the result of migration by individuals, and not the result of seasonal input of recruits with different intertidal height preferences. Although some species show ontogenetic differences in intertidal microhabitat (Nakamura 1976; Yoshiyama 1981; Prochazka and Griffiths 1992; Davis 2000), timing prevents the acceptance of recruitment as an explanation of seasonal vertical shifts. Heaviest recruitment of *C. analis* and *G. nigricans* juveniles, which tend to settle in pools higher than those occupied by older fish, occurs in late spring, when sea level is low, and in midsummer, when sea level is close to its annual mean, respectively (Davis 2000). However, average intertidal height of both species was greatest in the fall when sea level is highest, not during recruitment season.

Few intertidal studies have examined vertical habitat changes and their potential relationship to ENSO-induced or seasonal changes in sea level (Zander et al. 1999). Paine (1986) measured the upper limits of one species of algae and two species of mussels, and concluded that none responded to changes in sea level associated with El Niño. Two studies have reported seasonal vertical habitat shifts for intertidal fishes. Along the New England coast, *Pholis gunnellus* abandoned the intertidal zone during winter, possibly to avoid freezing temperatures (Sawyer 1967). In central California, *Xererpes fucorum* was found highest in the intertidal zone in summer and lowest in spring, possibly due to springtime downshore spawning migration (Burgess 1978). Neither temperature nor spawning migration explains shifts observed in the present system, as winter temperature is not extreme and spawning occurs from fall through spring (Davis unpubl.). Instead, individuals may migrate vertically on a seasonal cycle, matching sea level changes, to keep constant the amount of time spent isolated from the subtidal zone and its predators. Shifts in intertidal height may not be in direct response to sea level changes, but may be an innate seasonal response. During the El Niño fall of 1997, when the sea level anomaly was greatest, none of the species occurred higher in the intertidal zone than during the previous or subsequent fall.

Unlike seasonal intertidal height shifts by fishes, seasonal changes in tidepool depth and surface area for *C. analis* were apparently not directly related to adult selection for specific environmental conditions, but to the number of small *C. analis* present in the population during each sampling month. Small individuals are often more abundant in smaller, shallower tidepools than larger individuals (Richkus 1981; Davis 2000), thereby influencing the average depth and surface area values during months when they are prevalent.

The shift to larger tidepools during the El Niño event by *C. analis* cannot be explained by a lack of small fish during this period; large fish exhibited an increase in average pool size when analyzed alone. Although individuals may have moved to larger tidepools during the warm El Niño period to combat the temperature increase, they would have been expected to move to deeper tidepools as well, since tidepool depth is more important in preventing daytime rises in tidepool temperature than is surface area (Davis unpubl.). Alternatively, differences in pool size for both *C. analis* and *H. gilberti* among climate periods may simply have been a function of tidepool occupancy probability. During the El Niño, there were fewer *C. analis* and fewer pools contained *C. analis* individuals. During most of the La Niña period, especially at OB, there were fewer *H. gilberti*. Because average pool surface area was calculated on the basis of presence or absence of fish, the chance that a pool lost all of its fish and was therefore excluded from the calculation was greater for a smaller pool, which had fewer fish initially, than a larger pool. Finally, it is possible that when fewer fish are present, a larger proportion of them may be found in optimal habitats, which may be larger pools.

Conclusions—Expectations of answers to the four questions addressed in this study were partially met. Family affinities of the study species ranged from cold-temperate (*C. analis*) to warm-temperate (*G. nigricans* and *G. elegans*) to tropical/warm-temperate (*P. integripinnis*, *H. gilberti*, and *G. rhessodon*). During the El Niño, the cold-temperate family member decreased in abundance. Neither of the two warm-temperate family members changed in abundance. Of the tropical/warm-temperate family members, one increased at both sites, one increased at only one site, and one did not change. The changes that occurred were consistent with expectations, but not all predicted changes occurred.

Expectations of seasonality and ENSO-scale changes in fish habitat use were also partially met. Seasonal patterns in all four common species' use of intertidal height were identified, and seasonal use of pool depth and surface area was observed for *C. analis*. However, few habitat changes occurred as a result of the El Niño event. Upper intertidal fishes did not move lower and lower intertidal fishes did not move higher in the intertidal zone as predicted. The prediction that fishes would move to deeper, larger tidepools during El Niño to avoid warming was supported only by *C. analis*, whose distribution shifted to larger tidepools.

The greatest influence of ENSO events on intertidal organisms may not take place in the intertidal zone at all, but may be concentrated in the relatively short offshore, planktonic larval stage. Such offshore disturbances, whether affecting larval survivorship or larval transport, result in differences in recruitment, as was observed for *C. analis*. Events affecting larval stages outside of the intertidal realm have potential to affect species dominance patterns and structure of the entire intertidal assemblage. The use of rocky intertidal organisms to study seasonal- and ENSO-scale climate variation may enhance understanding of climate-related changes in various oceanographic realms.

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Chapter 6

Spot pattern of *Girella nigricans*, the California opaleye: variation among cohorts and climate periods

Abstract

Girella nigricans (California opaleye) exhibits variability in dorso-lateral spot pattern. Southern California opaleye usually have one pair of white spots; however, fish with additional spots are frequently observed. Additional spots are thought to result from gene flow with the six-spotted Gulf of California *Girella simplicidens*. In the present study, the proportion of fish with extra spots was compared among and within nine *G. nigricans* cohorts settling from 1997 to 1999. This proportion was variable among the nine cohorts. When analyzed by climate regime, cohorts settling during the 1997-98 El Niño event had significantly higher proportions of multi-spotted fish than "normal" and La Niña cohorts. Within five of nine cohorts, the proportion of fish with additional spots significantly increased through time during the study, suggesting that survivorship of multi-spotted fish was greater than that of two-spotted fish during the juvenile stage. The easily identifiable spot polymorphism of *Girella nigricans* provides a useful tool by which to study hybridization between two marine fishes and track changes in gene flow and gene expression over time.

Introduction

The distribution of nearshore marine populations is often partly determined by abiotic factors. Gradients in temperature, for example, are important on several spatial scales, from meter-scale intertidal zonation (Nakamura 1976) to latitudinal distribution on the kilometer-scale (Morris 1960). Changes in temperature on different temporal scales can affect species' distributions as well. The daily temperature cycle plays a role in meter-scale cross-shore movements of fish (Gibson et al. 1998), seasonal temperature changes force vertical habitat shifts in motile intertidal species (Zander et al. 1999), and temperature variation on scales longer than a year shapes alongshore distribution of nearshore populations (Barry et al. 1995). Over a 60-year period during which water temperature increased by 0.75°C, Barry et al. (1995) found increases in abundance of southern species and decreases in northern species at a California rocky intertidal site, suggestive of range shifts to the north.

Interannual temperature cycles on scales shorter than 60 years, such as that driven by the El Niño Southern Oscillation (ENSO), may also influence species ranges. During warm El Niño events, a rise in water temperature results in shifts of many species to higher latitudes (Arntz and Tarazona 1990). A similar range shift might be expected for hybrid zones where reproductive isolation of species is incomplete. One such zone occurs in Baja California in the region of overlap between *Girella nigricans* (California opaleye) and *Girella simplicidens* (Gulf opaleye). *Girella nigricans* occurs mainly from Cabo San Lucas, Baja California to San Francisco and has one pair of lateral white spots flanking its dorsal fin (Thomson et al. 1979). *Girella simplicidens* occurs in the Gulf of California to Cabo San Lucas and has three or four pairs of white spots (Thomson et al. 1979; Robins et al. 1991). Although listed as separate species based on dentition, body shape, and spot number, this status may not be warranted morphologically or genetically (Orton and Buth 1984), and genetic exchange between the two groups produces individuals with three, four, and five spots in various lateral arrangements (see Orton et al. 1987).

The forces driving hybridization between marine fish species are poorly understood (Rao and Lakshmi 1999). Reports of marine fish hybrids are much rarer than those of freshwater fish hybrids, due to both a lower tendency of marine fish to hybridize as well as mistaken classification of hybrids as distinct species (Hubbs 1955; Rao and Lakshmi 1999). Possible conditions favorable to marine hybridization include outnumbering of one closely related species by another, intergradation in the parental species' habitats, and environmental disturbances (Rao and Lakshmi 1999). The relative contribution of these conditions to specific hybridization cases, like that of *G. nigricans* and *G. simplicidens*, have not been adequately addressed (Rao and Lakshmi 1999). Questions pertaining to the location of the *G. nigricans-G. simplicidens* hybrid zone, the validity of species-level distinction, the frequency of interbreeding, the fertility of the hybrid offspring, and hybrid variability among others, remain and warrant further study.

One *Girella* hybrid study has addressed the relationship between latitude and the number of three-, four-, five-, and six-spotted fish (referred to hereafter as "multi-spotted") within the *G. nigricans* range (Orton et al. 1987). Lower proportions of multi-spotted fish were found at three southern California sites than at Miller's Landing, Baja California. The presence of such a gradient was attributed to a higher level of genetic exchange between *G. nigricans* and *G. simplicidens* at southern latitudes closer to *G. simplicidens'* range (Orton et al. 1987). If El Niño and other warm water events cause species' ranges to shift to higher latitudes, this gradient of multi-spotted opaleye abundance might also be expected to shift to higher latitudes. At fixed points in California, which are north of the peak region of genetic exchange between the two *Girella* groups, such a range shift might be observed as local increases in the proportion of multi-spotted individuals.

The purpose of the present study was to address the temporal variability in opaleye spot pattern in San Diego, California. Specific goals were to (1) test whether the frequency of spot patterns varied among cohorts recruiting at different times, (2) determine whether spot pattern differed among climate regimes in which the cohorts settled (El Niño, "normal," or La Niña), and (3) determine whether the proportion of multi-spotted individuals within a cohort changed over time, indicating differential survivorship.

Methods

Opaleye and their spot patterns were sampled at two sites in San Diego, California, USA: False Point, in La Jolla (117.3°W, 32.8°N), and Dike Rock, 500 m north of the SIO Pier in the Scripps Coastal Reserve (117.3°W, 32.9°N). After a two- to three-month planktonic larval stage, opaleye generally occupy tidepools for one or two years or until they reach 75 mm total length (Norris 1963; Stevens et al. 1989). Juvenile opaleye are most frequently found in middle to high intertidal pools from 30 - 90 cm above mean lower low water (MLLW) in San Diego (Davis 2000b). After their intertidal stage, they abandon the intertidal zone in favor of subtidal areas.

Opaleye at False Point were collected from a set of 55 tidepools ranging from 6 cm below MLLW to 107 cm above MLLW. Each tidepool was bailed or siphoned to permit collection of all fish present. Rocks were removed, and each pool was thoroughly searched. Opaleye were collected, their total lengths (TL) and standard lengths (SL) were measured in mm, and the number of spots on each side was recorded. The pool was then refilled, and the fishes were returned. About 4 to 8 days were needed to sample all 55 tidepools. Data were collected during 12 sampling periods: May 1997, August 1997, November 1997, February 1998, May 1998, June 1998, August 1998, October 1998, November 1998, February 1999, March 1999, and August 1999. In August 1999, spot patterns were measured only for opaleye collected from the largest False Point tidepool.

At Dike Rock, opaleye spot pattern was scored in one large tidepool (52 cm above MLLW) from May through October of three years: 1997, 1998, and 1999. This study pool, used by Norris (1963) for behavioral observations of opaleye, is the largest permanent tidepool in the reserve, measuring 4.5 m long, 1.5 m wide, and about 40 cm maximum depth. Opaleye in the pool were collected with minnow traps one to three times per week on average during each May-to-October period, a period that included most opaleye recruitment and therefore highest abundances. From May 25 - August 4, 1997, one 40 cm minnow trap with 2 mm mesh and openings of 2.8 cm was deployed for 60 min on each sampling day. On all dates after August 4, 1997, a second trap, with 6 mm mesh and 4 cm openings, was added. The traps were baited with canned cat food and placed in fixed locations in the tidepool. All opaleye collected were measured (TL and SL), their spot pattern was identified, and they were released back into the pool.

Minnow traps were used only at Dike Rock because its pool, much larger than the False Point pools, harbored more opaleye than the False Point pools. At False Point, traps did not capture enough individuals for analysis. In addition, traps were easier to use than the method of draining pools, permitting more frequent sampling at Dike Rock.

Opaleye cohorts were identified from size-frequency histograms and from the arrival of prejuveniles to the study areas. Prejuveniles, characterized by silvery sides, green dorsal surfaces, and the absence of spots, transform into juveniles within a few days of settlement (Stevens et al. 1989). During this transformation period, they turn an olive color and attain their characteristic spots, which are fixed in number during an individual's lifetime (Orton et al. 1987). In general, prejuveniles supplying each cohort identified in the study arrived over an approximately two-week period, followed by a period of absence of prejuveniles. Each cohort was identified at or within a month of settlement, with the exception of one cohort that settled during winter 1998 at Dike Rock, a period when fish were not sampled at this site. Settlement period for this winter cohort was estimated based on the mean size of its fish (64 mm TL) when sampling began in May 1998. For all summer cohorts at Dike Rock, settlement period was determined by the arrival of prejuveniles. Settlement period for each False Point cohort was estimated from periodic (approximately every 2-3 months) size-frequency histograms and when possible, the presence of prejuveniles. Cohorts were followed through time at False Point until they left the intertidal zone and followed at Dike Rock either until they left the intertidal zone or until the end of October of their settlement year.

The proportion of multi-spotted opaleye (P_M) per weekly period was calculated as:

$$P_M = N_M/(N_T - N_{PJ})$$

where N_M is the number of fish with more than two spots collected during a 7-day period, N_T is the number of total fish collected, and N_{PJ} is the number of prejuveniles (fish with undeveloped spots). P_M was calculated over a weekly period instead of daily because the percentage of multi-spotted fish was generally on the order of 5-10%, and on some occasions fewer than 10 fish were caught per day. Therefore, daily data were combined on weekly intervals to avoid zero values and artificially high values driven by low sample size. At False Point, spot proportions were calculated for each cohort using N_M, N_T, and N_{PJ} summed across all 55 study pools. No pool was sampled more than once, but because from three to six days were needed to sample all 55 pools, it is possible that fish moved between pools from day to day resulting in some fish being resampled. At Dike Rock, P_M was calculated for all fish within a cohort caught within a 7-day period. Because data were always collected from the same pool, it is likely that many of the same fish were caught day after day. However, the frequency of recaptures was not expected to be different for two-spotted and multi-spotted fish at either site. Therefore, although the data are not independent, they are not expected to be biased with regard to the hypotheses. For statistical analyses, these values were subjected to arcsin square root transformation.

To determine whether cohorts settling during different climate periods ("normal," El Niño, or La Niña) had different P_M values, each cohort was assigned to a climate period based on temperature and sea level data measured at Scripps Pier. According to temperature and sea level anomalies, the El Niño period began in late summer 1997 and continued through about May of 1998. The La Niña period was in its early stages in August 1998 and continued through the end of the study (Lynn et al. 1998).

To address the question of whether the cohorts had significantly different values of P_M, a one-way analysis of variance (ANOVA) was used to test the difference in average weekly spot proportions among all nine cohorts. Normality of the data was examined using Lilliefors test of residuals ($p>0.05$). ANOVAs were also used to test whether P_M was different among cohorts within each of the three climate periods. To determine whether spot proportion was different among climate periods, an ANOVA was used with average weekly spot proportion for each cohort within a climate period as replicates. A nested ANOVA with cohort nested within climate period would have provided the most appropriate test to address these questions. However, because different numbers of cohorts were measured during the three climate periods, a nested design was not possible.

To address the question of whether spot proportion changed within cohorts over time, regression analysis was used. In these models, weekly P_M was the dependent variable and time served as the independent variable. To determine whether the proportion of three-spotted fish (P_3) was greater than the proportion of four-spotted fish (P_4) within cohorts, a paired t-test was used.

Results

During the study, 4012 spot number and configuration scores were taken on post-prejuvenile *Girella*: 1569 at Dike Rock in 1997, 1335 at Dike Rock in 1998, 493 at Dike

Rock in 1999, and 615 at False Point from May 1997 to August 1999. As in Orton et al. (1987), most individuals were two-spotted. Of the multi-spotted fish captures, there were 203 scores of three-spotted fish, 118 scores of four-spotted fish, 7 scores of five-spotted fish, and 2 scores of six-spotted fish

From opaleye size frequencies at the two sites, nine cohorts were identified throughout the study period: three at False Point and six at Dike Rock (Table 6.1). At False Point, cohorts settled in summer 1997, winter 1998, and summer 1998. The summer 1997 cohort was actually produced by two recruitment events, one occurring in late June 1997 and one in late July. However, although they were distinct during August 1997, they were not identifiable in subsequent sampling months and therefore were combined into one cohort for analysis.

At Dike Rock, two cohorts settled in summer 1997 (Figure 6.1), three were identified from summer 1998, and one cohort settled in summer 1999. One 1998 cohort was greater than 60 mm TL in May of that year, and therefore it likely settled at about the same time as the winter 1998 False Point cohort. The other two 1998 cohorts settled during the summer. Although cohorts that appeared at the same time at the two sites were possibly part of a large scale "meta-cohort," they were considered separate cohorts in the present study. Because some cohorts settled at different times than others, and because cohorts probably abandon their tidepool nursery areas at different times, not all cohorts were followed over the same size ranges (Table 6.1).

The proportion of multi-spotted fish (P_M) varied among the nine cohorts (ANOVA: $F_{8,72}$=5.12, p<<0.001) (Figure 6.2). However, within the El Niño and La Niña climate periods, P_M was not significantly variable among cohorts (ANOVA: El Niño, $F_{1,11}$=2.18, p=0.168; La Niña, $F_{2,23}$=0.50, p=0.612). P_M of the four normal cohorts was variable ($F_{3,38}$=6.42, p=0.001); however, for the "normal" cohort that settled during the period between El Niño and La Niña (June 1998), El Niño conditions prevailed during most of its larval stage. Without this cohort, which had a relatively high average weekly P_M (11.8%), the pre-El Niño cohorts did not exhibit variation in weekly P_M ($F_{2, 25}$=1.34, p=0.281).

Mean weekly proportion of multi-spotted fish in a cohort was significantly different among climate periods (normal, El Niño, and La Niña) (ANOVA: $F_{2, 6}$=6.47, p=0.032; Figure 6.2). Cohorts recruiting during the El Niño period had higher mean values of P_M (mean of mean P_M =20.4%) than those recruiting during the normal periods (6.7%) (a posteriori Fisher's LSD; p=0.009) and the La Niña period (7.8%) (a posteriori Fisher's LSD; p=0.013). Spot proportions of the normal and La Niña cohorts were not significantly different from each other (p=0.886).

P_M tended to increase over time within cohorts (Figure 6.3). This increase was significant in 5 cohorts: 1997 summer 1, 1997 summer 2, 1998 winter, and 1998 summer 1 cohorts at Dike Rock, and the summer 1998 cohort at False Point (Table 6.2). Within cohorts, the proportion of three-spotted fish was greater than the proportion of four-spotted fish (Table 6.3). Two-spotted fish were most abundant, followed by three-spotted fish, then by four-spotted fish.

Discussion

Hundreds of three- and four-spotted and several five-spotted *Girella* individuals were observed in San Diego from 1997 to 1999. However, only two *Girella* individuals with six spots, individuals that may have been genetically "pure" *G. simplicidens,* were observed. The rarity of juvenile *G. simplicidens* suggests that adult *G. simplicidens* were not common in the San Diego area. Therefore, multi-spotted fish in the present study were probably not the result of *G. nigricans-G. simplicidens* hybridization occurring within the San Diego region. Instead, high numbers of fish with three and four spots suggests either that 1) hybrid larvae were transported north, or 2) alleles or series of alleles coding for extra spots were present in San Diego populations. The present study does not permit rejection of either hypothesis; however, results of the present study do indicate that processes controlling presence of multiple-spotted fish are variable over time. The frequency of multi-spotted fish varied temporally, both among cohorts and within cohorts. Cohorts recruiting during the El Niño period had higher spot-proportions than those recruiting during non-El Niño periods. Within cohorts, regardless of climate period, the proportion of multi-spotted fish increased over time.

Among-cohort variability

Increases in the proportion of multi-spotted *Girella* (P_M) among cohorts recruiting during the El Niño period could have resulted from several processes. Environmental disturbance tends to promote marine fish hybridization (Rao and Lakshmi 1999), and the 1997-98 El Niño event may have served as a natural disturbance inducing more interbreeding of *G. nigricans* and *G. simplicidens* in the southern hybrid zone. Northward transport of hybrid larvae to San Diego might have increased during El Niño due to changes in currents. Opaleye larvae are neustonic, usually found up to 110 km from shore (Stevens et al. 1989), and are subjected to surface transport by the southward offshore California Current and the northward inshore California Countercurrent. During the 1997-98 El Niño event, the California Current moved offshore and the California Countercurrent increased in velocity (Norton et al. 1985; Lynn et al. 1998). As a result, the inshore band of northward transport widened, encompassing a greater width of the cross-shore opaleye larval distribution, and the northward transport of anomalously warm water increased (Lynn et al. 1998), presumably along with associated larvae. Hybrid larvae transported north may also have experienced increased survivorship. If hybrids are intermediate between *G. nigricans* and *G. simplicidens* in temperature-related characters, as they are in spot number, then opaleye with a southern, warm-water *G. simplicidens* ancestor might survive better in warmer El Niño years than colder years.

The multi-spotted fish collected in San Diego may not be hybrid offspring, but instead may reflect a polymorphism for spot number within the San Diego population. In this case, the variable P_M among cohorts may have resulted from temperature-sensitive expression of genes controlling spot number. Although spot number is not a plastic trait after post-settlement development (Orton et al. 1987), conditions during the larval stage may dictate the number of spots that are to develop. Alternatively, larvae with additional-spot alleles may experience different survivorship during different environmental conditions, leading to recruiting cohorts with different spot proportions. If fish with additional spots are characterized by other southern traits, such as higher warm-water affinity, then anomalously warm El Niño events might lead to cohorts with higher P_M. However, in the present study, the response of spot proportion to temperature was not consistent in two ways. First, the two El Niño cohorts recruited during the winter of 1998, which although anomalously warm, was still cooler than the usual summer season of recruitment. The fact that these El Niño cohorts were in addition the only two winter cohorts also complicates the comparison among these and the summer-recruiting normal and La Niña cohorts. Second, La Niña temperature was about 1-2°C cooler than long-term (1966-1994) average temperatures (Davis 2000a), but spot proportions of fish recruiting during early (summer 1998) and late (summer 1999) La Niña conditions were not lower than "normal" period spot proportions (Figure 6.2).

<u>Within-cohort variability</u>

The within-cohort variability of P_M observed in the present study is opposite to that expected based on Orton et al. (1987)'s examination of fish size and spot proportion. In the present study, the proportion of multi-spotted fish within most cohorts increased over time as fish grew larger (Figure 6.3). At one of Orton et al. (1987)'s sites, the proportion of multi-spotted fish was lower in 1-3 year-old fish (> 60 mm SL or > about 75 mm TL) than in young-of-the-year fish (30-60 mm SL or about 37-75 mm TL), suggesting that survivorship of fish with extra spots was lower than that of two-spotted fish.

Results of the present study were not consistent with this suggestion. Two explanations may account for the discrepancy. First, Orton et al. (1987) studied fish from 30-120+ mm SL (about 37-150+ mm TL), and grouped 30-60 mm SL (about 37-75 mm TL) fish for size comparisons. In the present study, most cohorts were not followed beyond 75 mm TL, so the two studies examined slightly different ranges of *G. nigricans'* life history. The proportion of multi-spotted fish may increase during opaleye's intertidal phase (< 75 mm TL, Stevens et al. 1989), as indicated by the present study, then decrease after the intertidal phase, as suggested by Orton et al. (1987). Second, in Orton et al. (1987), large and small fish were collected at the same time, so comparisons were made across cohorts. The present study shows that different cohorts can have significantly different proportions of multi-spotted fish. As a result, across-cohort comparisons may not adequately address survivorship or selection issues. Therefore, variability in spot proportion among size classes at a particular time in Orton et al. (1987) might not have been the result of differences in survivorship of multi-spotted fish as a cohort aged, but may reflect variability among cohorts.

The increased frequency of multi-spotted fish over time in most of the cohorts in the present study indicates that within the size range of 30 to 75 mm TL, over the course of several months, the survivorship of multi-spotted fish is higher than that of two-spotted fish. Intertidal opaleye generally occupy middle and upper tidepool habitats (Davis 2000b), which can reach temperatures during spring and summer daytime low tides that are above their preferred temperature of 27-28°C (Norris 1963) and close to their lethal maximum temperature (Douderoff 1942). If the presence of additional spots is associated with warm-water adaptations, multi-spotted fish might cope with high temperatures better than two-spotted fish during the intertidal life-history phase. Survivorship of multi-spotted fish in size classes larger than 75 mm TL might then decrease after this intertidal phase during the colder subtidal phase, perhaps explaining why Orton et al. (1987) observed lower proportions of multi-spotted fish in larger size classes.

Conclusion

The presence of a visible, easily measured hybrid intermediate trait potentially associated with temperature affinity, like dorsal spot pattern in *G. nigricans*, provides an ideal tool with which to measure effects of climate change on gene flow and genetic expression within populations. Further studies are needed to explicitly address selection and survivorship questions. Genetic analysis could establish whether *G. nigricans* and *G. simplicidens* are distinct species and also whether spot number is associated with other warm-water southern or cold-water northern traits. If these are two species, collections over a latitudinal range in southern Baja and the Gulf of California could establish whether stabile hybrid *Girella* populations exist, where the boundaries of the *Girella* hybrid zone are, and the extent to which the two species share genetic information. Tagging studies in which individuals are followed through time would address survivorship questions based on fewer assumptions than cohort analysis. Such information would contribute both to the understanding of influences on hybridization in marine fishes and the sensitivity of hybridization to climate change. Management plans of *Girella* recreational and commercial fisheries would also benefit from information about species identities and hybridization.

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Table 6.1: Settlement and size of the nine study cohorts: Cohorts are identified by site (DR=Dike Rock and FP=False Point) and are named by season of settlement (sum=summer, win=winter), the last two digits of the year in which they settled, and their order if more than one cohort settled during a season (1=first to settle, 2=second to settle). Dates of settlement and climate type at time of settlement (NORM=normal, EN=El Niño, and LN=La Niña) are listed. The time period over which each cohort was followed and average total length (mm) of fishes at the start and end of that time period are presented.

Site	Cohort	Settlement	Climate type	Sampling dates start	end	Avg. fish size start	end
DR	sum 97 1	mid—end-Jun 97	NORM	Jun 8 97	Oct 14 97	28.0	81.1
DR	sum 97 2	mid—end-Jul 97	NORM	Jul 9 97	Oct 18 97	30.0	48.4
FP	sum 97	Jun—Jul 97	NORM	Jun 20 97	May 15 98	28.8	78.0
DR	win 98	Jan or Feb 98	EN	May 25 98	Nov 6 98	64.4	94.0
FP	win 98	Feb 98	EN	Feb 15 98	May 2 99	33.7	88.0
DR	sum 98 1	mid—end-Jun 98	NORM	Jun 8 98	Nov 6 98	29.8	60.3
DR	sum 98 2	mid—end-Aug 98	LN	Aug 19 98	Nov 6 98	24.8	46.2
FP	sum 98	Aug 98	LN	Aug 1 98	Aug 20 99	32.0	74.6
DR	sum 99	mid-Jul—Aug 99	LN	Jul 11 99	Oct 26 99	30.6	49.8

Table 6.2: Regression analyses of the number of multi-spotted fish within a cohort versus time. Cohorts are identified and named as in Table 6.1. The number of total spot measurements of fish within each cohort, as well as the number of weeks for which spot data were taken, are listed.

Site	Cohort	No. measurements	No. weeks	slope	r^2	p-value
DR	sum 97 1	841	11	$+8.0 \times 10^{-3}$	0.43	0.028
DR	sum 97 2	728	12	$+4.1 \times 10^{-3}$	0.32	0.055
FP	sum 97	196	5	-0.3×10^{-3}	0.04	0.749
DR	win 98	176	8	$+27.4 \times 10^{-3}$	0.70	0.010
FP	win 98	179	5	$+4.4 \times 10^{-3}$	0.26	0.380
DR	sum 98 1	938	14	$+11.0 \times 10^{-3}$	0.641	<0.001
DR	sum 98 2	221	9	$+8.8 \times 10^{-3}$	0.27	0.156
FP	sum 98	240	6	$+1.7 \times 10^{-3}$	0.80	0.016
DR	sum 99	493	11	$+5.9 \times 10^{-3}$	0.26	0.111

Table 6.3: Comparison of the proportion of opaleye with three spots (P_3) and four spots (P_4) in each cohort. Cohorts are identified as in Table 6.1. A paired *t*-test indicates that P_3 is greater than P_4 within cohorts ($n=9$, $t=2.40$, $p=0.034$).

Site	Cohort	P_3	P_4
DR	sum 97 1	0.045	0.024
DR	sum 97 2	0.044	0.031
FP	sum 97	0.038	0.006
DR	win 98	0.060	0.089
FP	win 98	0.165	0.096
DR	sum 98 1	0.065	0.053
DR	sum 98 2	0.057	0.021
FP	sum 98	0.035	0.029
DR	sum 99	0.061	0.030

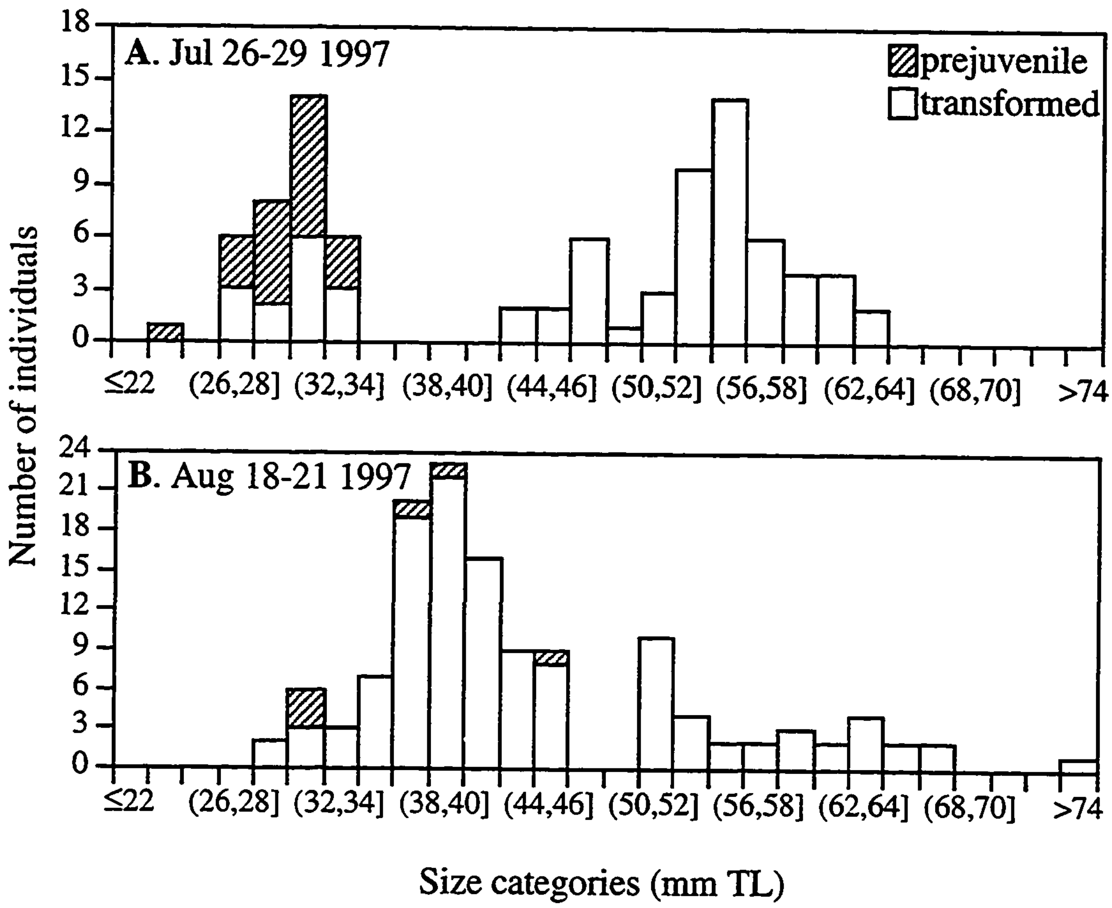

Figure 6.1: An example of opaleye cohorts distinguishable by size-frequency histograms. Two cohorts settled at Dike Rock during the summer of 1997. The two cohorts A) from July 26 to July 29, 1997, at the end of the settlement period for the smallest cohort, and B) from August 18 to August 21, after three weeks of growth. A few prejuveniles were still contributing to the younger cohort, but most juveniles had already settled.

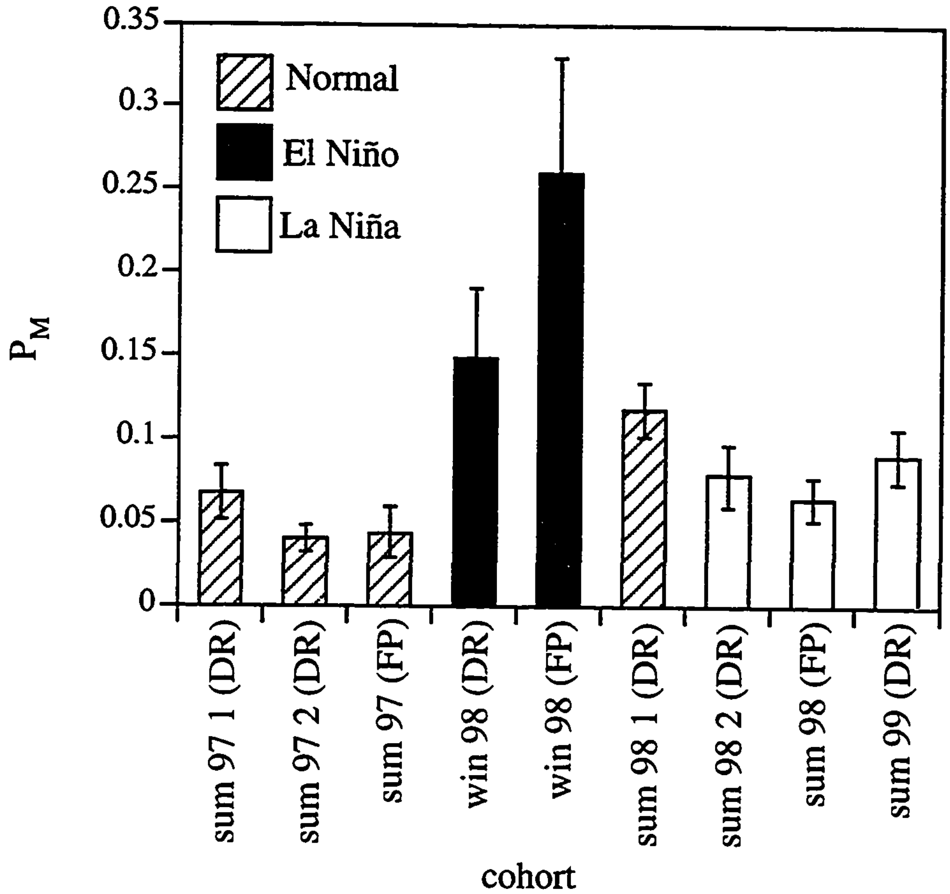

Figure 6.2: Average weekly proportion of multi spotted opaleye (P_M) ± 1 SE (back-transformed) among nine opaleye cohorts sampled at Dike Rock (DR) and False Point (FP) during normal, El Niño, and La Niña climate periods. Cohorts are named by season, year, order of settlement, and site as in Table 6.1.

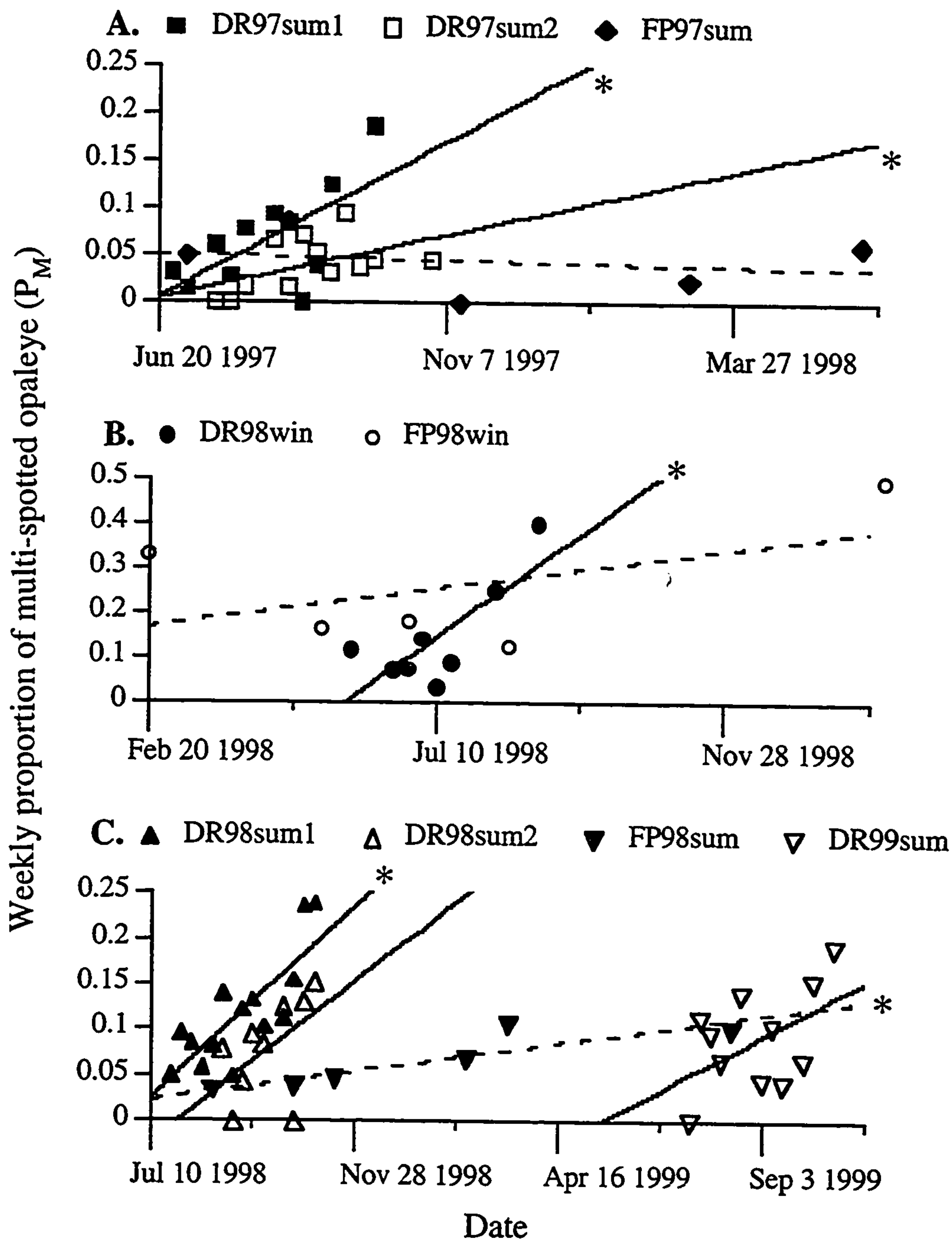

Figure 6.3: Weekly proportions of multi-spotted opaleye (P_M) over time of each of the nine False Point (FP) and Dike Rock (DR) cohorts. Cohorts are named as in Table 6.1. A) Cohorts that settled in the summer of 1997; B) cohorts that recruited in the winter of 1998; C) cohorts that recruited in summer 1998 and summer 1999. Dotted lines and solid lines indicate regression lines for cohorts from FP and DR, respectively. Asterisks indicate regression lines with slopes significantly different from zero. See Table 6.2 for r^2 and p-values.

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Chapter 7

Importance of pre-recruitment life-history stages to population dynamics of the woolly sculpin, *Clinocottus analis*.

Abstract

Sessile intertidal organisms have been traditionally thought of as space-limited, with population sizes controlled by post-recruitment processes. Motile intertidal organisms may be able to avoid some of the density-dependent post-recruitment mortality forces, and as a result, their population sizes may be less dependent on post-recruitment events and more directly linked to pre-recruitment processes. The goal of the present study was to determine the relative contribution of recruitment and post-recruitment processes in shaping population structure of *Clinocottus analis*, a southern Californian intertidal sculpin, from 1996 to 2000. In addition, elasticity and decomposition analyses of population matrices were used to determine which vital rates (growth, survivorship, and fertility) contributed most to theoretical and actual changes in population growth rate (λ).

Recruitment pulses persisted in the population for a relatively long time (up to a year) and were not obscured by post-recruitment, density-dependent mortality. These recruitment pulses were not correlated with spawning biomass, suggesting that some process during the egg or larval phase of development was important in determining the magnitude of recruitment, and ultimately, population size. Analyses indicate that those vital rates with high elasticity to which λ is theoretically most sensitive are not necessarily those that are responsible for observed temporal differences in λ. λ was generally most sensitive to potential changes in juvenile growth and adult survivorship during the 3-4 year period. However, fertility and recruitment as well as growth drove seasonal

differences in λ. Two main processes contributed to decreased population size during the 1997-98 El Niño event: a decrease in batch fecundity of older adults and a decrease in recruitment. Decomposition analyses indicate that juvenile survivorship also may have contributed to differences in λ between El Niño and non-El Niño periods. In general, results of the study emphasize the importance of pre-recruitment and other early life-history events in structuring *C. analis* populations on both seasonal and longer-term (ENSO) scales. These results contrast to those discussed for many sessile intertidal organisms traditionally considered substrate-limited, but they are consistent with recent findings for some recruitment-limited sessile species and for tropical reef fishes.

Introduction

The debate about the processes controlling population size, structure, and dynamics in marine systems is still an active one (Underwood and Denley, 1984; Victor, 1986; Forrester, 1990; Jones, 1990; Raimondi, 1990; Caley et al., 1996; Pfister 1996). For coastal marine species, it was long believed that recruits were too abundant to ever be population-limiting or regulating, and that population size was determined by post-recruitment processes such as predation, competition, facilitation, or disturbance (Underwood and Denley, 1984; Connell, 1985; Victor, 1986; Forrester, 1990; Raimondi, 1990; Caley et al., 1996). Since the 1980s, however, varying degrees of recruitment regulation have been recognized for some coastal populations (Forrester, 1990; Jones, 1990). Larval supply and settlement have been identified as the most important processes determining population structure of some sessile intertidal invertebrates (Raimondi, 1991) and several reef fishes (Victor 1983 and 1986; Forrester 1990) as well as overall structure of nearshore hard-bottom communities (Gaines and Roughgarden, 1985).

Although one set of processes occurring during recruitment or post-recruitment may dominate, an either-or scenario is unrealistic (Underwood and Denley 1984; Caley et al., 1996). Populations are most likely affected by both, and the most appropriate goal is to determine the relative contribution of each of these processes. According to Caley et al. (1996), no matter how important post-recruitment processes are, recruitment probably influences population size and structure to some extent. The most common case may be one in which both processes are important, but density-dependent mortality does not eliminate the signals of strong recruitment pulses. Only if all new recruits over a threshold population size died would the effects of recruitment pulses, and therefore a degree of recruitment-regulation, be eliminated (Caley et al., 1996).

Factors affecting which processes dominate, recruitment or post-recruitment, include the absolute magnitude of the processes as well as certain life-history parameters of the population. In a short-lived population, recruitment pulses persist for a relatively longer proportion of the organism's lifespan (Lo et al., 1995; Caley, 1996). In a long-lived population, individuals recruiting in pulses can pile up in the adult stage, obscuring the history of recruitment. In addition, longer post-recruitment duration subjects a population to a longer period of post-recruitment mortality.

Although these issues have been addressed for sessile intertidal organisms (Roughgarden et al., 1984; Connell, 1985) and reef fishes (Victor, 1983; Victor 1986; Doherty and Fowler, 1984; Jones, 1990; Forrester, 1990), only a few studies have reported on this issue for intertidal fishes (Pfister 1996, 1998), which face many of the same habitat limitations as sessile intertidal organisms but have the advantage of motility. This motility advantage may be important enough to cause differences in population controls of fishes from those of sessile organisms, which are often more limited by space for adults and less limited by recruitment (Roughgarden et al., 1984). For example, a motile fish may be able to escape some sources of mortality, such as density-dependent predation on clusters of individuals (Bertness et al., 1999), by controlling their post-settlement distribution.

The purpose of this study was to address the relative importance of pre-and post-recruitment processes for the southern Californian woolly sculpin, *Clinocottus analis,* and to compare its population dynamics to those described for sessile intertidal invertebrates and hard-substrate benthic fishes, especially the North Pacific tidepool sculpins of Pfister (1996, 1997, 1998). Differences between the latter study and the present sculpin system were expected for several reasons. First, fewer species of fish occupy southern California tidepools (Davis, 2000b) than more northern tidepools (Moring, 1986). Although total number of individuals may not differ, interspecific competition for space by adult fish may be less severe in southern California, lessening the importance of density-dependent, post-recruitment events. Second, the southern California system experiences less severe seasonality in factors like temperature, which may broaden the time window of events like growth, spawning, and recruitment. If recruitment is spaced out more evenly throughout the year, competition among young-of-the-year recruits for resources like food may decrease, diminishing density-dependent juvenile mortality.

Several questions pertaining to the *C. analis* system were addressed in order to accomplish the study's main goal. First, did recruitment occur in pulses? If so, for how long did recruitment pulses persist in the population and were they obscured by density-dependent mortality?

Second, could size of recruitment pulses be predicted by adult biomass? Several processes can erase relationships between spawning biomass and recruitment, including variable egg-to-larval-phase mortality (Hjort, 1914; Lasker 1981) and input of recruits from non-local sources outside the population (Caley et al., 1996).

Third, to which vital rates was population growth rate potentially and actually sensitive? Whether recruitment or post-recruitment processes exert most control on population size and structure, it has been suggested that the demographically most important processes, those to which population growth rate are most sensitive, are the least variable processes. Pfister (1998) argues that, because a population's probability of extinction is sensitive to variations in population growth rate, natural selection should lead to systems in which population growth rate varies as little as possible. As a result, population growth rate should not be sensitive to life-history processes that are the most variable. One of the goals of the study was to test the relationship between vital rate variability and vital rate importance.

Fourth, how did variation on temporal scales of season and El Niño Southern Oscillation (ENSO) influence population dynamics? Factors that affect the types of processes controlling population size and structure may not be temporally stable (Fox and Gurevitch, 2000). For example, adult survivorship may be density-dependent only during some parts of the year, perhaps when food is limited. Adult survivorship may differ during different climate regimes, such as those that are associated with the El Niño Southern Oscillation (ENSO). In such a case, the relative importance of recruitment versus post-recruitment processes could change depending on climate. *C. analis* population size is known to have declined during the 1997-98 ENSO (Davis, 2000a). In the current study, I test the hypothesis that pre-recruitment events are the sources of the ENSO variation in population size.

Several of the above goals are addressed using elasticity and decomposition analyses of matrix population models. These analyses have been successfully applied to other taxa to determine prospective (potential) effects and retrospective (observed) effects of vital rate changes (Levin and Huggett, 1990; Levin et al., 1996; Horvitz et al., 1997). In the present study, prospective and retrospective analyses were used to test the hypothesis that, similar to tidepool sculpins in the North Pacific (Pfister 1996), population growth rate was most sensitive to variation in early adult survivorship. Retrospective analysis was also used to test the hypothesis that pre-recruitment vital rates were the cause of differences in population growth rate between El Niño and non-El Niño conditions.

Methods

Study Sites and Species

Populations of *C. analis* were studied at two sites in San Diego, California, USA: False Point (FP) and Ocean Beach (OB). This species inhabits the rocky intertidal zone during its entire life history except for a planktonic larval stage of approximately two months (Wells, 1986) during which larvae can be found close to shore near rocky intertidal regions (Feeney, 1992). At a size of 12 to 25 mm, larvae return from the plankton and settle in tidepools. They mature within a few months, at a size of 50-60 mm total length (TL) (Williams, 1957; Wells, 1974; Davis, unpubl. data) and can live up to 7 or 8 years (Wells, 1986).

C. analis can be found at intertidal heights over 1 m above mean lower low water (MLLW) (Miller and Lea, 1972; Davis, pers. obs); however, its maximum intertidal abundance is in the intertidal zone within 30 to 90 cm above MLLW (Davis, 2000b). Habitat shifts ontogenetically; individuals move to increasingly larger, deeper, lower intertidal tidepools with more rock cover as they grow (Davis, 2000b). Despite such habitat shifts, fish exhibit strong homing behavior and maintain a home range of tidepools to which they return or in which they stay during consecutive low tides (Williams, 1957; Richkus, 1978; Yoshiyama et al., 1992).

The strong homing tendencies of *C. analis* permitted the resampling of the population at FP and OB in fixed sets of tidepools over time. FP is located at the southern edge of La Jolla and consists of tidepools distributed within and around conglomerate sandstone outcrops. At this site, 55 tidepools were chosen and mapped in October of 1996. The 50 tidepools of OB, located 7.5 km south of FP in a flat shale bench near the Ocean Beach pier, were chosen and mapped in November of 1996. Pools at the two sites ranged from -6 cm below to 113 cm above MLLW, from 4 cm to 45 cm deep, and from 0.23 to 13.65 m^2 in surface area (Davis, 2000b).

Data collection

Fish censuses were taken in the 55 FP tidepools from November 1996 to August, 1999 and in the 50 OB tidepools from November 1996 to August 2000. The quarterly census schedule included sampling dates during November, February, May, and August of each year, with the exception that 1999 spring sampling at OB occurred in June instead of May. In addition to regular seasonal sampling, all pools at FP and OB were also sampled in June 1998, October 1998, and March 1998; and all OB pools were sampled in March 2000 and July 2000. A subset of the 55 FP pools were sampled in October 1996, June 1997, October 1997, January 1998, January 1999, April 1999, and July 1999. These additional sampling months, although not used in population matrix models, were added in order to keep closer track of cohorts.

Sculpin abundance and size were measured by collecting all fish in each pool. Pools were drained by bailing or by siphoning using hoses with mesh-covered openings. Rocks were removed, and crevices were searched for fish. Total lengths (TL) of all fish were measured to the nearest mm. From February 1998 to March 1999 and August 1999 to August 2000, the gender of mature fish was also identified. After measurement, rocks were replaced, the pool refilled, and the fish returned. Three to six days were required to sample all pools within a site. Data were collected only during the day and only during tides lower than 31 cm above MLLW. Three of the lowest pools at False Point were in regions of shifting rocks and boulders; if a pool was no longer present during subsequent seasonal sampling, a substitute pool with similar characteristics was located.

Assumptions of the study are that (1) the 105 study tidepools provide habitat for the entire juvenile to adult life cycle, (2) the size range of their inhabitants at any one time reflects the size range of the entire population, and (3) any immigration of juveniles or adults to the study area is offset by equal emigration of the same size classes out of the study area. Because ontogenetic habitat shifts occur (Davis, 2000b), tidepool selection could affect estimated population structure. For example, the largest *C. analis* inhabit the largest, lowest intertidal pools (Davis, 2000a). Should a study pool set include more large pools, this study would report a greater proportion of large fish. Effort was made in this study to chose pools that were a representative sample of all available pools at a site. Because *C. analis* has such strong homing tendencies (Williams, 1957; Richkus, 1978; Yoshiyama et al., 1992), and because other studies of tidepool sculpins have reported little migration, even when accounting for emigration and immigration (Pfister, 1996), lack of emigration and immigration measurements probably did not produce much bias.

Cohort survivorship

C. analis recruits in pulses, like most temperate coastal species (Pfister 1997), allowing identification and tracking of cohorts from size-frequency histograms constructed with field data. Using histograms only from census periods in which all pools at a site were sampled, the number of individuals within each cohort was counted. Monthly survivorship (S) of a cohort (i) during a period from time t to time (t+1) was calculated as:

$$S_i = (n_i(t) / n_i(t+1))^{(1/T)}, \tag{1}$$

where $n_i(t)$ is the number of fish in the cohort at time t, $n_i(t+1)$ is the number of fish in the cohort surviving to time $t+1$, and T is the number of months between censuses. Least squares regression was used to determine whether survivorship of individuals within a cohort was related to the average size of all fish within a cohort.

Batch fecundity

Batch fecundity of 9, 7, 7, and 8 females collected from a site 0.5 km north of FP was measured in January 1998, April 1998, January 1999, and April 1999, respectively. Batch fecundity was defined as the number of hydrated eggs ready to be spawned carried by a female at any one time. Attempts were made to collect females spanning the entire adult size range available during each of the four sampling periods. Ovaries from each female were separated and weighed wet. The number of hydrated eggs within the larger ovary was counted, then the ratio of number of hydrated eggs in the larger ovary to ovary weight was used to estimate the total number of hydrated eggs per female. One female in January 1998 and two in April 1999 did not carry hydrated eggs and therefore were omitted from the analysis.

Regressions between female ovary-free wet weight (g) and number of hydrated eggs were calculated for the four periods in which egg data were collected. Analysis of covariance (ANCOVA) was used to determine whether the relationship between female weight and egg number differed with time. Although relationships did differ among time periods, data for all females were pooled to obtain one regression equation with an r^2 of 0.93:

$$O = 18.54\ e^{0.037\ TL}, \tag{2}$$

where O is the number of eggs carried by a female and TL is the total length of the female. This equation was then used to calculate the number of eggs potentially produced by the sculpin population during each census period. Ideally, separate equations would have been used for each census period; however, fecundity data were not collected during each census. Instead of using separate equations for some of the censuses and the average regression equation for the rest, I chose to use the average equation for all censuses. Use of the average regression equation generally did not produce egg number estimates for a particular census period that differed by more than 10% from the separate regression equation for that census period. For example, when applied to the February 1998 FP census, the average equation yielded an estimate of 8716 eggs and the January 1998 equation yielded an estimate of 7969 eggs, a 9% difference. The average equation applied to February 1999 FP data resulted in an estimate of 29,328 eggs, 5% lower than the January 1998 regression estimate of 30,891.

For census periods in which gender information was recorded, the number of eggs produced by each female was calculated. For months in which gender data were not collected, the number of eggs produced by each individual was calculated as if female, then multiplied by 0.58 to account for the fact that on average 58 ± 10% (mean ± SD) of all fish were female during periods when gender information was collected. Egg estimates were not corrected in these months for differences in size between the sexes. Males were significantly larger than females in 3 of 8 censuses at FP and 9 of 14 censuses at OB, with females larger than males only once, in August 2000 at OB (*t*-tests, $p < 0.05$). Therefore, assumptions that some of the largest fish were female probably produced slight overestimates of egg number.

Population abundance statistics

Linear regression analysis was used to determine whether cohort size at time (t+1) could be predicted from cohort size or mass at a previous time *t*. In the first of two such analyses, the correlation between adult biomass at time *t* and the number of new recruits at time t+1 was tested. Because *C. analis* has a one-month egg stage followed by a two-month larval stage (Hubbs, 1966; Wells, 1986), three months was deemed an appropriate time step. Adult biomass was calculated using a weight-TL regression calculated from 34 fish collected between January 1998 and April 1999 (r^2=0.97):

$$\text{weight} = 0.284\, e^{0.037\, \text{TL}} \tag{3}$$

Recruitment in the present study, as in other studies (Caley et al., 1996), was defined as the number of new juveniles settling between censuses separated by 3 months. Therefore, the likelihood of some post-settlement, pre-census mortality as a potential bias must be acknowledged. The second analysis was intended to examine whether the number of individuals in a cohort at time *t* was correlated with the number of individuals in that cohort at time (t+ 3 mo), or whether processes occurring during those initial three months, such as non-local recruitment or temporally variable larval mortality, obscured the expected relationship.

Matrix population models

Population growth rates were calculated for *C. analis* populations using 3-month time increments at both FP and OB. Staged-based population matrix models were generated following Caswell (1989). Models were constructed with three stages based on fish size: juvenile (new recruits to 55 mm TL); adult 1, or A1 (56 to 75 mm TL); and adult 2, or A2 (> 75 mm TL) (Figure 7.1). The division between juvenile and A1 stages was based on the onset of female maturity determined by gonad analyses described above and from Wells (1986). The division between A1 and A2 stages was arbitrary.

Separate matrices were constructed for all seasons, during which fish populations were censused at time t and time t+1. The 3-month time step was chosen to represent the time between spawning and larval recruitment (1-month egg phase and 2-month larval phase). Each matrix corresponded to one of 4 periods: (a) November-February, (b) February-May, (c)May-August, and (d) August-November, with the addition of a late-June-to-early-October matrix in 1998. In total, 12 seasonal matrices were constructed using data from November 1996 to August 1999 at FP, and 16 matrices were constructed using data from November 1996 to August 2000 at OB.

Matrices were structured as:

$$\mathbf{n}(t+1) = \mathbf{An}(t)\,, \tag{4}$$

or

$$\begin{pmatrix} J(t+1) \\ A1(t+1) \\ A2(t+1) \end{pmatrix} = \begin{pmatrix} P1 & F2 & F3 \\ G1 & P2 & 0 \\ 0 & G2 & P3 \end{pmatrix} \times \begin{pmatrix} J(t) \\ A1(t) \\ A2(t) \end{pmatrix} \tag{5}$$

such that:

$$J(t+1) = (P1 * J(t)) + (F2 * A1(t)) + (F3 * A2(t)), \tag{6}$$

$$A1(t+1) = (G1 * J(t)) + (P2 * A1(t)), \tag{7}$$

and

$$A2(t+1) = (G2 * A1(t)) + (P3 * A2(t)), \tag{8}$$

where J, A1, and A2 are the number of juveniles, adult 1s, and adult 2s at a particular time, G_i represents the probability of surviving and growing from stage i to stage i+1 in the 3-month time interval, P_i is the probability of surviving but staying in the same stage during the 3-month time interval, and F_i is the contribution by adults in stage *i* at time *t* to the juvenile stage at time *t*+1. Survivorship (P1, P2, and P3) and growth (G1 and G2) matrix entries were calculated from the field data described above. Sites were analyzed separately, but data for *C. analis* individuals from all pools within each site were combined. Sculpin cohorts were generally easy to follow through time. Individual growth over a three-month time interval, or the fraction of individuals in a stage at time *t* advancing to the next stage at time *t*+1, was calculated by comparing size frequency histograms at times *t* and *t*+1. The proportion of individuals advancing from stage *i* to stage *i*+1 over a three-month period (G_i) is defined as:

$$G_i = g_i / n_i(t) \ , \tag{9}$$

where g_i is the number of advancing individuals, and $n_i(t)$ is the number of individuals in stage *i* at time *t*..

P1, P2, and P3 values, or the proportion of individuals that survived the 3-month period but did not grow to the next stage, were also determined by comparing size frequency histograms at times *t* and *t*+1. Survivorship (P_i) values were calculated as:

$$P_i = (n_i(t+1) - g_i) / n_i(t) \tag{10}$$

where $n_i(t+1)$ is the number of individuals in stage *i* that survived in the three-month period. In the equation for P3, g = 0 because there was no higher stage into which individuals could grow; individuals either remained A2 adults or died.

Fertility matrix entries (F1 and F2) were calculated using the number of new recruits at time *t*+1 and the number of eggs produced per time period described above. F2 and F3 entries were calculated to incorporate egg production as well as survivorship to the juvenile stage at the next time step, three months later:

$$F2 = S_e * O_{A1} * A1^{-1} \quad (11)$$

$$F3 = S_e * O_{A2} * A2^{-1} \quad (12)$$

where O_{A1} and O_{A2} are the number of eggs produced by all A1 and A2 females present at time t, respectively, determined from the average regression between egg number and female size from January 1998-April 1999, and S_e is the probability of one egg surviving and becoming a new recruit after a 3-mo period. S_e was calculated as:

$$S_e = R(t+1) \;/\; (O_{A1} + O_{A2}), \quad (13)$$

where, $R(t+1)$ is the number juveniles recruiting to the population after 3 mo. To construct these equations, I assume that egg viability does not depend on adult stage, and that adult 1 and adult 2 eggs have the same probability of survivorship. Because *C. analis* has not been observed to guard its eggs (Wells, 1974), this assumption may be realistic. Therefore:

$$F2 = (R(t+1) \;/\; (O_{A1} + O_{A2})) * O_{A1} * A1^{-1} \quad (14)$$

$$F3 = (R(t+1) \;/\; (O_{A1} + O_{A2})) * O_{A2} * A2^{-1} \quad (15)$$

Of all the matrix elements, F2 and F3 terms are most sensitive to measurement error because they depend on a relatively large number of parameters and several assumptions. Estimates of fertility matrix entries (F_i) assume closed populations, an assumption that is probably not valid for most coastal populations. For most populations, the source of most recruits is believed to be non-local, and therefore local adult fecundity can be decoupled from magnitude of recruitment (Caley et al., 1996). I did not account for non-local recruitment for two reasons. First, evidence suggests that *C. analis* and other cottid larvae, while planktonic, are not transported like passive particles but remain close to their parent source, partly because they remain close to the bottom for much of the larval phase (Feeney, 1992). Second, the two study sites show very similarly-timed population events and very similar population structure over time (Davis, 2000a). Therefore, even if San Diego's *C. analis* populations do exchange larvae among sites, so that one population's recruits may not be derived from its own adults, local fecundity and recruitment magnitude are not decoupled. The ratio of eggs to juveniles in the entire metapopulation and within each subpopulation are likely to be similar.

As indicated by equations (14) and (15), each fertility matrix entry (F_i) reflects several components: the number of eggs produced by each individual at time t and the number of new recruits that appear at time t+1. F_i is relatively sensitive to measurement error of several of its components and insensitive to measurement error of others. F_i is insensitive to measurement error in spawning that is proportional across A1 and A2. For example, if all adults spawned more than once at the beginning of a 3-month period, doubling O_{A1} and O_{A2}, then estimates of egg-larval survivorship (S_e) would decrease, but F2 and F3 terms would not change. Therefore, although spawning frequency is unknown (Wells, 1986), this error does not affect estimates of F_i and population growth rates. If, however, A1s spawned more frequently than A2s, or if size at maturity decreased, then O_{A1} would increase, O_{A2} would remain the same, and F_i values would change. For the same reason, F_i equations are very slightly sensitive to which female size-egg number regression equation is used to calculate batch fecundity. For example, the average regression equation applied to the February 1998 FP data produces an F2 of

0.50 and an F3 of 1.61, whereas the winter 1998 egg number regression produces an F2 of 0.51 and an F3 of 1.58. Finally, F_i equations can also be sensitive to measurements of the number of new recruits at time t+1, the term $R(t+1)$. If the assumption of coupled fecundity-recruitment is invalid, if the egg-larval period is prolonged for greater than 3 months, or if the number of new recruits is miscounted, then F_i would be inaccurate.

Analysis of population matrices

Population growth rates (λ) were calculated using Matlab to determine the eigenvalue structure of each seasonal matrix. Elasticity analysis, a prospective analysis, was used to assess the sensitivity of λ to hypothetical proportional changes in the 7 matrix elements (P1, P2, P3, G1, G2, F2, and F3) (Caswell, 1989; Horvitz et al., 1997). Elasticity (E) of the matrix element (a_{ij}) was defined as a proportional version of sensitivity (S) of that matrix element (a_{ij}) (de Kroon et al., 1986):

$$E_{ij} = (a_{ij} / \lambda) * S_{ij}, \qquad (16)$$

where λ is the first eigenvalue of the matrix. S_{ij} was calculated as:

$$S_{ij} = (v_i\, w_j) / \langle \mathbf{w},\mathbf{v} \rangle. \qquad (17)$$

Here, **w** is the first right eigenvector of the matrix, **v** is the first left eigenvector, $\langle \mathbf{w}, \mathbf{v} \rangle$ is the scalar product of those vectors, w_j is the jth element of the right eigenvector, and v_i is the ith element of the right eigenvector.

Retrospective decomposition analyses were used to determine which matrix elements were responsible for differences in λ among time periods (Caswell, 1989). In the first of these analyses, differences in λ between each quarterly matrix and the average matrix for the entire study period were "decomposed" into contributions by each of the seven matrix elements. Contribution (C) of a matrix element (a_{ij}) to quarterly differences in λ was calculated as:

$$Ca_{ij} = (a_{ij}^{(k)} - a_{ij}^{(\cdot)}) * S_{ij} \mid_{(A^{(k)}+A^{(\cdot)})/2} \qquad (18)$$

where $a_{ij}^{(k)}$ is the value of matrix element a_{ij} of the *k*th quarterly matrix, $a_{ij}^{(\cdot)}$ is the average a_{ij} calculated over then entire study period, and S_{ij} is the sensitivity of λ to element a_{ij} evaluated using an average matrix. This average matrix is the average of the *k*th quarterly matrix and the average matrix of the entire study period. Ca_{ij}, then, is simply the product of the deviation of a_{ij} from the average a_{ij} for the entire period and the sensitivity of λ to average a_{ij} (Caswell, 1989).

In the second analysis, causes of differences in λ between the El Niño and non-El Niño periods were sought. Prior to decomposition, seasonal matrices for the full El Niño period, which spanned from August 1997 to May 1998 (Davis, 2000) were combined into one matrix. This matrix was compared to August-May matrices of subsequent years. Consecutive August-November ($\mathbf{A}_{AN}$), November-February ($\mathbf{A}_{NF}$), and February-May ($\mathbf{A}_{FM}$) matrices were combined into one August-May matrix ($\mathbf{A}_{AM}$) using the formula (Caswell, 1989):

$$\mathbf{A}_{AM} = \mathbf{A}_{FM} * \mathbf{A}_{NF} * \mathbf{A}_{AN}. \qquad (19)$$

This combination yielded two matrices at each site: August-May 1997-98 and August-May 1998-99. August-May 1999-2000 at OB was not included in order to facilitate comparisons between the two sites.

Seasonality of population parameters

Seasonality was tested in the seven matrix entries (F2, F3, P1, G1, P2, G2, and P3), total juvenile survivorship (P1 + G1), total adult survivorship (P2 + G2), total growth of juveniles, total growth of adult 1 fish, and elasticity and contribution of the seven population parameters. Total growth of juveniles and adults was defined as the proportion of surviving fish that grew to the next stage:

$$\text{Total Growth}_i = G_i \,/\, (P_i + G_i). \tag{19}$$

The seasonal cycle was characterized using daylight values. Daylight was treated as a proxy for a host of seasonal environmental changes, including temperature and sea level (Davis, 2000a). Months were ranked in order of least to most daylight on a scale of 1 (December) to 12 (June). Each sculpin sampling period was then assigned a light value which was the average light rank of all months within the period. For example, any November to February sampling period had a light value of 2.5, the average of November (3), December (1), January (2), and February (4).

Because population parameters might follow a seasonal pattern offset from the light cycle, 12 lags of one-month intervals were applied to the light values, from 0 to -11 months. Regression analysis revealed, for those parameters that had a seasonal component, which lag provided the best fit, as defined by the highest positive correlation coefficient (r). Because elasticity values, P_i, G_i, total juvenile and adult survivorship, and total growth terms have boundaries of 0 and 1, they were arcsin-square root-transformed prior to regression analysis. F2 and F3 values were log-transformed.

Density-dependence of population parameters

The density-dependence of total juvenile survivorship (P1 + G1), total A1 survivorship (P2 + G2), total A2 survivorship (P3), total juvenile growth (G1/ (P1+G1)), total adult 1 growth (G2/ (P2+G2)), population growth rate (λ), and the elasticity and decomposition values of the seven population parameters (F2, F3, P1, G1, P2, G2, P3) was tested. Simple linear regression analysis was used to test relationships between each parameter and total population size at time *t*. Before total juvenile growth and total adult 1 growth were regressed against number of fish, these ratios were checked for correlation with mean juvenile and mean adult size, respectively. One might expect a lower ratio even with equal individual growth rates simply if the individuals were smaller and farther away from the next stage boundary.

Results

Predicting cohort size and density-dependence

Clinocottus analis recruitment peaks of varying magnitudes were observed in all four seasons at FP and OB. Adult biomass at time *t* was not correlated with the number of new recruits at time *t*+1, 3 mo later, indicating that within the range of observed adult population sizes, no density-dependent recruitment variation was observed (Figure 7.2). Decoupling between spawning biomass and recruitment likely occurred in the egg or larval stage of development.

The signal of recruitment peaks was detectable in the population for up to 1 year, after which cohorts were no longer separable in the censuses and were no longer represented by more than a few individuals (Figure 7.3). The number of fish in a cohort when its fish averaged 30 mm TL was correlated with the number of fish in the cohort 3 , 6 , and 9 months later at FP and 3, 6, and 12 months later at OB. These results, when coupled with the lack of relationship between adult biomass and recruitment (Figure 7.2), suggest that processes occurring in the egg or larval stage determine cohort size for at least the first year.

A positive relationship between the number of fish in a cohort at times t and t+1 does not necessarily rule out density-dependent controls of mortality. In the case of density-dependent mortality, one would expect either a significant positive or negative correlation between cohort size and the proportion of fish surviving after a certain period of time. However, no such correlation was observed in the *C. analis* population at either site (Figure 7.4), suggesting that the processes acting to reduce cohort size after recruitment were not density-dependent. Further supporting the hypothesis of density-independence, total survivorship of juveniles (P1+G1) and adults (P2+G2) over a 3-month time interval were not correlated with number of fish present at either site (Table 7.1). Juvenile survivorship, although not correlated with fish abundance, was correlated with fish size. Juvenile survivorship decreased with increasing fish size at both FP and OB (Figure 7.5). However, there was no relationship between size and survivorship within the adult size range ($p>>0.05$).

One post-recruitment process, juvenile growth, was found to be density-dependent. Total juvenile growth (G1/ (P1+G1)) was negatively correlated with number of fish at both FP and OB; juveniles grew more slowly when more fish were present in the population (Figure 7.6). This relationship suggests that growth was negatively density-dependent, but is also consistent with the hypothesis that factors enhancing recruitment might also create poor growth conditions in the intertidal zone. Total adult 1 growth (G2/ (P2+G2) was not density-dependent at either site (Table 7.1).

<u>Population dynamics of C. analis</u>

Seasonal population growth rates (λ per 3-mo period) varied from 0.4 to 3.6 at FP, and from 0.3 to 2.1 at OB (Figure 7.7). Elasticity analyses suggested that λ should be most sensitive to changes in G1, which represents survival and growth of juveniles to the adult 1 stage, and P2, which represents survival of adult 1 fish but lack of growth out of the adult 1 stage. This was true at both study sites (Fig 7.8A-D, Table 7.2). Therefore, λ seems to be sensitive to the number of adult 1 fish that accumulate in the population. λ was most sensitive to potential change in G1 during 5 of 12 3-month intervals at FP and 9 of 16 intervals at OB, and was most sensitive to potential change in P2 4 and 5 times at FP and OB, respectively (Table 7.2). Elasticity of P_i tended to be highest during August through February, and elasticity of G_i tended to dominate during the opposite time of year. λ was never most sensitive to potential change in F_i, which includes both adult fertility and recruitment (equations 14 and 15). Because there are 7 matrix elements, if they vary randomly, each element should have highest elasticity by chance on 1.7 occasions at FP and 2.3 occasions at OB.

Decomposition analysis indicated that those life-history elements to which λ was theoretically most sensitive were not necessarily those elements responsible for seasonal changes in λ during the study period (Figure 7.8E-H, Table 7.2). F2, the production of new recruits by adult 1 fish, overwhelmingly contributed to differences in λ among seasons. At FP and OB, F2 had highest absolute contribution values in 9 of 12 analyses and 6 of 15 analyses, respectively (Table 7.2). G1 had highest absolute contribution values in an additional 5 of the 15 OB analyses. Although λ was often sensitive to P2, the survivorship but lack of growth of adult 1 fish, it did not contribute much to temporal variation in λ. Instead, F2 and G1 were primarily responsible for differences among the 3-month seasonal matrices, suggesting that these elements have strong seasonality.

Seasonality

Sculpin population dynamics were highly seasonal, although the various vital rates were not synchronized. Some, like F3 (production of new recruits by adult 2 fish), were maximal in May (Fig 7.9A,D). Others, like total juvenile growth, peaked in March (Fig 7.9B,E). Some, like adult 2 survival (P3), were not significantly seasonal at all (Fig 7.9C,F).

Seasonality in λ was driven by seasonal peaks in growth and fertility/recruitment terms. In general, growth (G_i) and fertility/recruitment terms (F_i) peaked from early spring to summer (Table 7.3). P_i terms, which indicate survival but lack of growth, were generally maximal in fall. As a result, total growth ($G_i/(G_i+P_i)$) was highest in late spring-summer. Total juvenile, A1, and A2 survivorship were not seasonal at either site.

Elasticity and contribution of matrix elements tended to peak during the same season as their associated matrix elements. However, λ's sensitivity is not always driven by seasonal changes in a life-history element. For example adult 2 survivorship (P3) was not significantly seasonal (Figure 7.9C,F); however, λ became more sensitive to potential changes in P3 in the fall. In contrast, λ's sensitivity to potential changes in G2 (survivorship and growth of adult 1 fish) was not seasonal, despite the fact that both G2 and G2's contribution to temporal differences in λ peaked in spring/summer (Table 7.3).

1997-98 El Niño event

C. analis population size was significantly lower during the El Niño period than during non-El Niño periods at both OB and FP (Davis, 2000a). Quarterly population growth rate of *C. analis* (λ per 3 month-period) was lower during the 3 quarters during the El Niño period (0.73 ± 0.23 at FP and 0.63 ± 0.20 at OB than before or after (1.34 ± 0.27 at FP and 1.17 ± 0.14 at OB, Figure 7.7). However, due to the small sample size

(El Niño n=3) and the temporal variability in λ, these differences were not significant (t_{10}=1.39, p=0.194 for FP and t_{14}=1.78, p=0.097 for OB).

The decline in number of *C. analis* during the El Niño period was due to a drop in recruitment, and not to abnormally high mortality in the number of juveniles and adults already present in the population. The number of recruits ≤ 39 mm TL per 3 month period was lower during the El Niño event than during non-El Niño sampling periods (t_{13}=2.13, p=0.053 for FP and t_{19}=1.97, p=0.064 for OB) (Figure 7.10A). The average number of recruits during the El Niño event was 20±14 at FP and 11±8 at OB, about 20% of that during non-El Niño periods (96±48 at FP and 47±13 at OB).

The variation in number of recruits can be attributed in part to differences in batch fecundity during El Niño and non-El Niño periods (Figure 7.11). Batch fecundity-female weight relationships during the El Niño period (January and April 1998) were significantly different than those during the post-El Niño period (January and April 1999, Student's *t*: = 4.06, p<0.001), but regression slopes were not different between the two seasons, January and April, within each climate period. Slopes of the El Niño and post-El Niño regression lines differed in such a way that batch fecundity of large fish was most greatly influenced by climate period, whereas fecundity of smaller fish was similar between climate periods. For example, a 60 mm TL female was estimated to produce 161 and 170 eggs per batch during the El Niño and post-El Niño period, respectively, whereas a 100 mm female produced 654 eggs during the El Niño period and 920 eggs during the post-El Niño period.

Although batch fecundity decreased during the El Niño period (Figure 7.11), it probably did not account for the total El Niño reduction in recruitment, which was about 20% of non-El Niño recruitment levels (Figure 7.10A). Other factors, such as lower larval survivorship, lower egg survivorship, or decreased spawning success, most likely contributed as well. Values of F2, which included both fertility of adult 1 fish and recruitment of their larvae, were lower during El Niño periods at both sites. Again, however, because of small El Niño sample sizes, the differences were not quite significant at the α=0.05 level (*t*-tests with unequal variances: at FP, El Niño F2= 0.21± 0.17, non-El Niño F2=2.99±1.59, $t_{9.9}$=2.2, p=0.052; at OB, El Niño F2=0.34± 0.32, non-El Niño F2=1.73±0.62, $t_{5.2}$=2.0, p=0.097).

The decline in recruitment translated after an approximately 3-month lag into a drop in abundance of adults in the population (Figure 7.10B). However, the number of adults was not immediately reduced by mortality during the El Niño event, and there were no significant differences in juvenile survivorship (P1+G1), A1 survivorship (P2+G2), or A2 survivorship (P3) between El Niño and non-El Niño periods (*t*-tests, p>0.05).

Because the number of new recruits decreased during the El Niño event but the number of adults did not, it was hypothesized that matrix elements related to recruitment and fertility (F2 and F3) would prove to have contributed most greatly to differences in λ between El Niño and non-El Niño time periods. At OB, the lower F3 and F2 of the El Niño period did contribute most greatly, in a negative direction, to the decrease in λ during the El Niño event (Figure 7.12). At FP, however, P1, contributed most negatively to decreases in λ during the El Niño event, followed by F2.

Discussion

Recruitment limitation and density dependence

Results of the present study contribute to the debate about the extent to which intertidal populations are limited by recruitment versus by post-recruitment events. In a population limited not by recruitment but by such factors as availability of space or food for juveniles or adults, the number of recruits over a certain threshold has little effect on the total number of individuals that can be supported in the population (Roughgarden, 1985). For example, if a rocky outcrop has space for only 100 adult *C analis,* it is insignificant to the population whether 1000 or 2000 new recruits settle out of the plankton. Mortality between settlement and adulthood would depend on the density of individuals in the cohort. On the other hand, if recruitment to the outcrop is on the order of tens of individuals, so that potentially all recruits could survive through adulthood, then the number of recruits will likely be more important in determining the number of juveniles and adults in the population. Mortality between settlement and adulthood might then have no relationship to the density of individuals in the population.

The *C. analis* populations at False Point and Ocean Beach, San Diego, appear to exhibit the latter, recruitment limitation. Density-dependent mortality was not demonstrated at any life history stage (Figure 7.3), unlike the tidepool sculpins of Pfister (1996) in Washington State and unlike many sessile rocky intertidal invertebrates (Connell, 1985). Also unlike the Washington State sculpins, whose recruitment pulses were detectable in the population for only a few months (Pfister 1996), recruitment pulses of *C. analis* were evident in cohorts for at least a year, past the time to maturity, for as long as cohorts were discernible by the study methods. Other studies of hard-bottom nearshore fishes present results spanning the gradient from long-term persistence of recruitment pulses (Victor, 1983, 1986; Doherty and Fowler, 1994) to dampening of recruitment pulses within a few months, before adulthood is reached (Pfister, 1996). Persistence of recruitment pulses and density-dependent mortality are not mutually exclusive, however, and most studies of benthic fishes show that mortality is at least to some degree density-dependent (Forrester, 1990; Jones, 1990).

Identification of factors controlling the size of recruitment pulses is beyond the scope of this work. However, one possible mechanism, that of direct, proportional development of recruiting cohorts from adult spawners, can be eliminated. As in many fish populations, spawning biomass of *C. analis* was not related to recruitment (Lasker, 1981). The stock-recruitment problem has made prediction of population size very difficult (Roughgarden et al., 1984) confounding management efforts of fisheries and habitats. If the number of fish at time (t+1) cannot be predicted using adult biomass and other information at time *t*, it becomes hard to set and defend quotas (Rothschild, 2000).

The factor causing a decoupling of recruitment and spawning biomass in *C. analis* is likely similar to that suggested by Hjort (1914) to decouple spawner-recruitment relationships in most fish populations: differential larval mortality (Hjort, 1914; Lasker, 1981). Assuming closed populations or presence of a metapopulation as discussed above, other factors include temporal variability in mating or settlement success. Batch fecundity did not differ enough temporally to account for the magnitude of recruitment variation observed, but spawning frequency may have varied temporally. It is also possible that the populations are open, and that recruitment and spawning biomass were decoupled because separate populations varied significantly in larval production within the range of larval transport between populations. However, because False Point and Ocean Beach, two sites 7.5 km apart, did not differ in spawning biomass at a given time, and because *C. analis* larvae have been suggested to have limited dispersal (Feeney, 1992), recruitment-biomass decoupling probably occurred at some point between spawning and settlement. Because recruitment pulses persisted in the population for at least a year, those processes occurring between egg and settlement that determined the size of the recruiting pulse had effects on the population far beyond the recruitment stage. These processes effectively controlled the cohort size for the rest of its existence. These results reaffirm the importance of larval ecology to benthic adult population structure (Ekman, 1996).

As survivorship of all three stages (juvenile, adult 1 fish, and adult 2 fish) appeared to be both density-independent and non-seasonal, the question remains as to what factors were controlling or influencing survivorship. For juveniles, at least, fish size played a role, with survivorship decreasing as juvenile size increased. This result supports a small-size refuge hypothesis and perhaps explains why fish increasingly use structural refuge as they grow from settlement size to adult size (Davis, unpubl. data). One would expect an increase in survivorship with adult size, as fish in the 55 mm range, now perhaps large enough to appeal to bird predators, begin to use refugia. However, adult survivorship was not correlated with fish size. Factors controlling adult survivorship remain a question.

Elasticity and decomposition

Dominance of the contribution of the F2 term to seasonal differences in λ (Table 7.3) is consistent with the suggestion that a post-spawning, pre-settlement process controls population size. The F2 term includes both fertility of the adult 1 female as well as the survivorship of her offspring through the larval stage until recruitment 3 months later. Differences in F2 among time periods therefore reflect differences in egg and larval processes among time periods, again assuming closed or metapopulations. The fact that λ was not overwhelmingly sensitive to changes in F2 reaffirms the importance of its variation. Because contribution is a combination of λ's sensitivity to a parameter and its variation (equation 18), F2 therefore must have varied quite a bit to generate such differences in λ over time.

One might have suspected that P2 and P3 terms, which represent survivorship of but lack of growth by adults, would also have contributed highly to temporal differences in λ. Similar to other studies of nearshore fishes, in which λ was most sensitive to potential variation in early adult survivorship (Pfister, 1996; Lo et al., 1995), elasticity of λ was often greatest to the P2 and P3 terms at both sites (Table 7.2). However, despite λ's sensitivity to P2 and P3, changes in these terms did not account for quarterly differences in λ observed over time. This discrepancy illustrates the importance of distinguishing between those life-history traits that actually contribute to differences in λ (retrospective analyses) and those to which λ is sensitive (prospective analyses). Population growth rate's sensitivity to a life-history parameter does not necessary translate into importance of that life-history parameter to changes or differences in λ (Horvitz et al., 1997).

Elasticity results are consistent with Pfister's (1999) hypothesis that those matrix elements to which λ is most sensitive should vary least. Although the relationship was not significant between coefficients of variation (CV) of the matrix elements, calculated from each seasonal matrix over the entire study period, and mean elasticities of the matrix elements, also calculated over the entire study period, the trend does not contradict Pfister's (1999) prediction (Figure 7.13). Those elements with the lowest CVs at FP (G1 and P3) and OB (G1 and P2) had the lowest mean elasticities. The relationships were not significant because those elements with the highest CVs (F2 and F3) did not have the lowest elasticities. Pfister (1998) reported that in 17 matrix population model studies, fertility elasticity was never higher than growth or survivorship elasticities. F2 and F3 in the present system did occasionally have high elasticity values, especially in the winter and spring (Table 7.2).

Temporal aspects of population dynamics

Prior to the study, abundance variation on two temporal scales, seasonal and ENSO, was observed for *C. analis* at FP and OB (Davis, 2000a). Results from the present study indicate that, despite the mild winters of San Diego relative to more northern latitudes, and despite the year-round nature of *C. analis* recruitment (Figure 7.12), certain factors do force seasonality on *C. analis* population dynamics. Those factors most highly seasonal were growth and fertility/ recruitment (F_i). However, because batch fecundity did not differ seasonally (between January and April), the driving force behind seasonality of F_i was probably larval survivorship. Perhaps unsurprisingly, G_i and F_i terms both contributed highly to temporal differences in λ. High contribution of very seasonal terms (Tables 7.2 and 7.3) reaffirms the importance of the seasonal cycle to *C. analis* population dynamics. Juvenile and adult survivorship were not seasonal and were inconsequential to changes in λ. These results place the southern Californian *C. analis* system between the highly seasonal north Pacific intertidal cottids and other temperate fishes (Victor, 1983; Pfister, 1997) and the relatively non-seasonal tropical reef fishes (Victor, 1986).

Longer temporal scales have been shown to be important for nearshore populations. Population structure of many nearshore organisms has been shown to be affected by warm-water El Niño events (Arntz and Tarazona, 1990). At the two sites in the present study, *C. analis* abundance decreased during the 1997-98 El Niño period (Davis, 2000a). This decrease resulted not from differences in mortality of individuals after settlement, but from events occurring between spawning and recruitment. Although part of the decrease may have been due to a decrease in adult fecundity, especially that of Adult 2 fish, recruitment declines were much greater. Therefore, the importance of very early life-history-stage events, most likely processes occurring in the planktonic larval stage, is again indicated.

Consistent with the hypothesis that events occurring in the larval stage led to lower λ between El Niño and non-EL Niño periods, decomposition analyses indicate that F3 and F2 contributed most greatly to climate period differences in λ at OB. The different result for the FP population, which implicated P1 as the biggest contributor to climate differences in λ, is not consistent with predictions that terms incorporating recruitment (F2 and F3) would have highest decomposition values. However, this result does emphasize importance of relatively early, pre-maturity, life-history (juvenile) stages.

Conclusions

Clinocottus analis cohort and population sizes in southern California appear to be shaped more by pre-recruitment events than by density-dependent post-recruitment processes. Processes occurring during either the egg or larval stage determine the size of recruiting cohorts, which in turn determines the number of adults that mature and persist in the population. As a result, variability in these early life history stages was the source of quarterly differences in population growth rate (λ), despite the fact that λ was not very sensitive to potential changes in egg and larval vital rates. Direct measurements of larval stage duration, growth, and survivorship in their planktonic habitat are necessary in order to further specify which of these specific larval vital rates are most important in structuring population size.

Combined with similar information about other rocky intertidal species, both motile and sessile, these results may contribute to general ecological models about what types of populations are likely to be most severely limited by pre- versus post-recruitment processes. Because different types of species have different adaptations to the harsh conditions of the rocky intertidal zone, one may not necessarily expect each to be limited during the same life-history stage by the same processes. Although the *C. analis* system may initially serve as a general model for other motile intertidal species, studies of other intertidal fish species and other taxa are required to determine if and how life-history differences translate into differences among species in the controls of population dynamics. In addition, further study of *C. analis* during an additional El Niño event would allow ecological generalization pertaining to climate effects on population dynamics.

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Table 7.1: Density dependence of *Clinocottus analis* growth and survivorship at False Point (n=12 quarterly time periods) and Ocean Beach (n=16 quarterly time periods). Correlation coefficients (r) and p-values of regression analysis are presented.

Vital rate	False Point r	False Point p	Ocean Beach r	Ocean Beach p
P1	**+0.59**	**0.020**	**+0.50**	**0.050**
G1	**-0.72**	**0.009**	+0.02	0.944
Total Juv survivorship (P1+G1)	-0.02	0.956	+0.25	0.342
Juvenile growth [G1/(P1+G1)]	**-0.86**	**0.002**	**-0.48**	**0.062**
P2	-0.32	0.314	+ 0.16	0.559
G2	+0.54	0.072	-0.29	0.280
Total A1 survivorship (P2+G2)	-0.06	0.846	-0.19	0.492
A1 growth [G2/(P2+G2)]	+0.27	0.399	- 0.19	0.493
A2 survivorship (P3)	+0.14	0.662	+0.01	0.990

Table 7.2: Terms to which λ was most sensitive (highest elasticity) for each quarterly matrix and terms most responsible for differences in λ between each quarterly matrix and the average (highest contribution). The term with the highest elasticity value and the term with the highest absolute value of contribution for each seasonal analysis are listed. If the second highest term was within 10% of the highest term, it is also listed. In the case of contribution, the sign indicates whether the term contributed positively or negatively to differences in λ.

Time	False Point elasticity	False Point contribution	Ocean Beach elasticity	Ocean Beach contribution
Nov-Feb 97	P2	-F2	P2	-F2
Nov-Feb 98	P3	-F2	P2	-F2, -G1
Nov-Feb 99	P2	-F2	P2	-F2
Nov-Feb 00			P2	-F2
Feb-May 97	G1, F2	-F2,+G1	G1	+G1
Feb-May 98	P2	-F2	G1, F2	-G1, +G2
Feb-May 99	G1, F2	+F2	G1, F2	-G1
Feb-May 00			G1, F2	+P3
May-Aug 97	G1	+G1, +G2	G1	-P2
May-Aug 98	G1	+F2, +F3	G1, F3	-G1
May-Aug 99	P3	-F3, -G1	P2, G1	+P1, -F2
May-Aug 00			G1, F2	-P2,+F2
Aug-Nov 97	P3	-F2	P1	-F2, -F3
Aug-Nov 98	P2	-F2, -G1	P3	+P3
Aug-Nov 99			G1	+G1

Table 7.3: Seasonality of matrix elements, growth and survivorship (surv), elasticity (elast) and contribution (contr) as determined by cross-correlation analysis. Eleven monthly lags were applied to monthly daylight ranks prior to regression with vital rates. Listed here are the light lags providing the highest r^2 with each vital rate, as well as the month during which the vital rate peaked. For example, a significant lag of 0 translates to a vital rate peak in June, the month with the most daylight. NS=not seasonal.

	False Point				Ocean Beach			
vital rate	peak month	peak lag	p	r^2	peak month	peak lag	p	r^2
G1	Mar	-9	0.066	0.299	NS	0	0.828	0.008
Juv growth	Mar	-9	0.007	0.534	NS	-10	0.167	0.132
G1 elast	Apr	-10	0.012	0.482	Jun	0	<0.001	0.600
F2 elast	Apr	-10	0.009	0.475	NS	-11	0.106	0.176
F3 contr	NS	-11	0.121	0.224	May	-11	0.008	0.407
F3	May	-11	0.012	0.482	Jun	0	0.013	0.364
F2	May	-11	0.033	0.380	Jun	0	0.002	0.507
λ	May	-11	0.054	0.323	NS	0	0.102	0.179
F2 contr	Jun	0	0.031	0.388	Jun	0	0.005	0.443
A1 growth	Jun	0	<0.001	0.712	Jun	0	0.001	0.543
F3 elast	Jul	-1	0.060	0.311	Jun	0	0.024	0.313
G2 contr	Jul	-1	0.003	0.599	Apr	-10	0.036	0.278
G2	Jul	-1	0.005	0.567	May	-11	0.042	0.264
P1 contr	Aug	-2	0.061	0.308	NS	-3	0.402	0.051
P1	Sep	-3	0.041	0.354	NS	-4	0.177	0.126
P1 elast	Sep	-3	0.034	0.377	NS	-3	0.224	0.104
P2	Dec	-6	0.003	0.610	Dec	-6	0.034	0.284
P2 elast	Dec	-6	0.009	0.513	Dec	-6	<0.001	0.738
P2 contr	Dec	-6	0.026	0.404	Dec	-6	0.051	0.246
J surv	NS	-10	0.792	0.007	NS	-9	0.498	0.033
A1 surv	NS	-6	0.153	0.193	NS	-8	0.260	0.089
P3 (A2 surv)	NS	-5	0.160	0.188	NS	-6	0.551	0.026
P3 elast	NS	-4	0.062	0.306	NS	-3	0.690	0.012
P3 contr	NS	-5	0.373	0.080	NS	-6	0.608	0.019
G2 elast	NS	-1	0.080	0.275	NS	-11	0.347	0.063
G1 contr	NS	-9	0.121	0.223	NS	-4	0.698	0.011

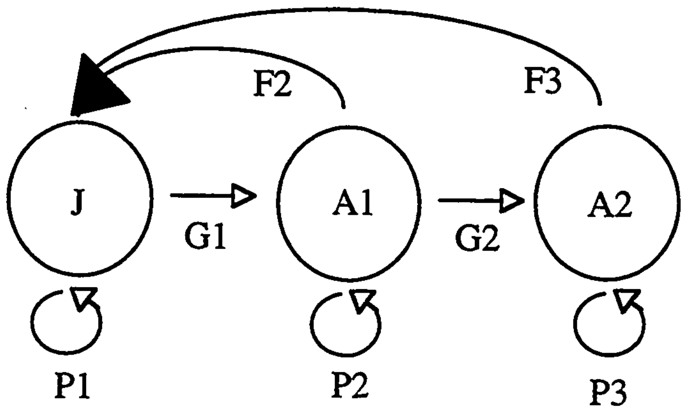

Figure 7.1: Life cycle diagram used to construct stage-based population matrix models for *Clinocottus analis.*

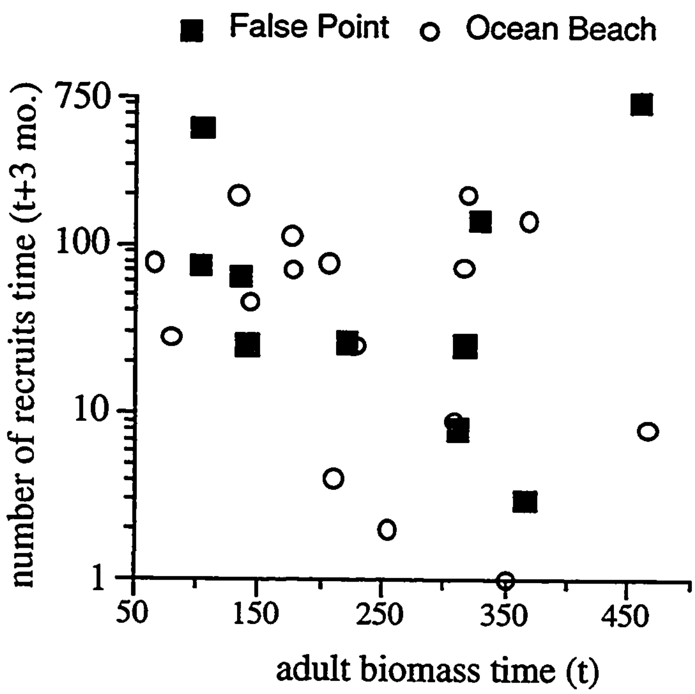

Figure 7.2: Lack of relationship between adult biomass at time *t* and number of new recruits at time *t*+1 in 2 southern California populations of *Clinocottus analis* (r^2=0.07, p=0.773 at False Point and r^2=0.05, p=0.471 at Ocean Beach)

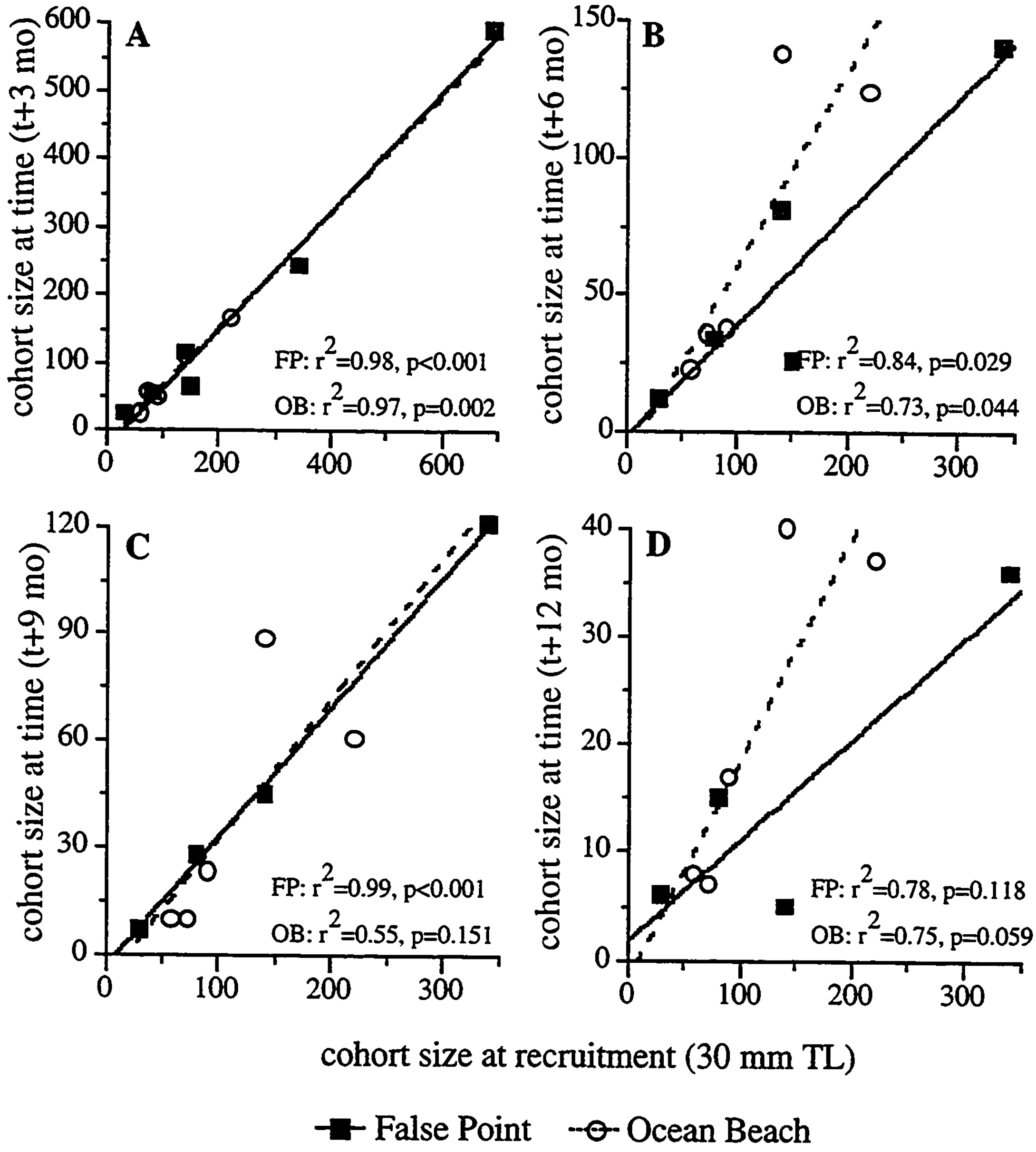

Figure 7.3: Number of *C. analis* in a cohort when mean fish size is 30 mm versus number in the cohort: (A) 3 months later (B) 6 months later, (C) 9 months later, and (D) 12 months later. The largest cohort visible in (A) does not appear in plots (B)-(D) because the study ended 4 months after its recruitment. Several other cohorts similarly disappear from the plots.

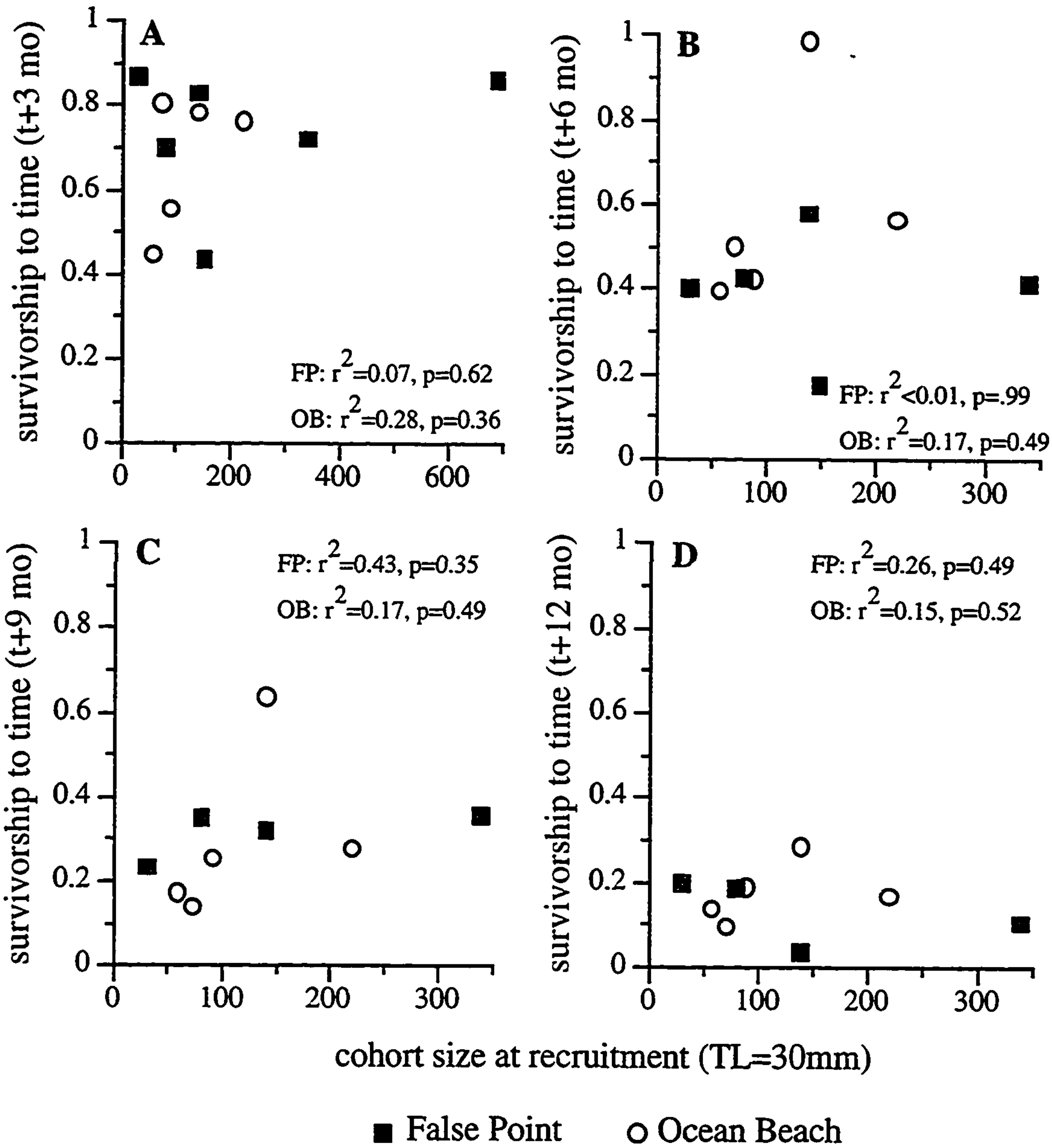

Figure 7.4: Density-independence of *C. analis* survivorship. Survivorship of fish in a cohort over (A) 3 months, (B) 6 months, (C) 9 months, and (D) 12 months was not related to the number of fish that recruited to the cohort.

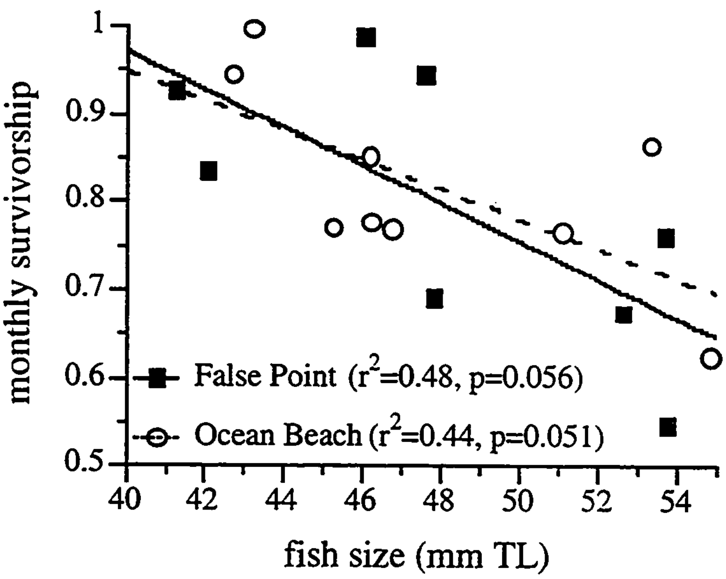

Figure 7.5: Survivorship of *C. analis* cohorts during the juvenile stage as a function of fish size. Size was computed as the mean of the mean size of all fish in the cohort at time *t* and the mean size of all fish in the cohort at time *t*+1. Survivorship is measured in monthly units.

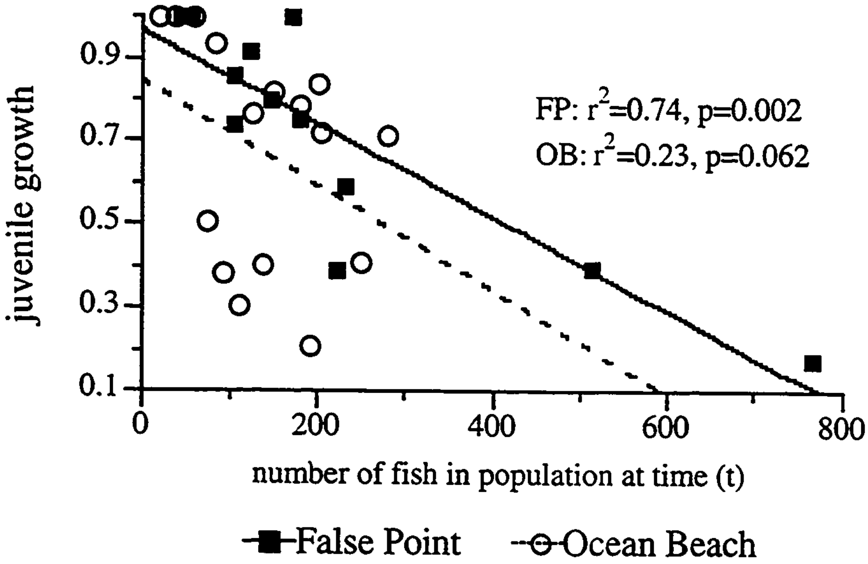

Figure 7.6: Negative density-dependence of *C. analis* juvenile growth at two sites in southern California, False Point and Ocean Beach. Juvenile growth (G1/(G1+P1)) was measured from time *t* to time *t*+1 and regressed against the number of fish present in the population at time *t*.

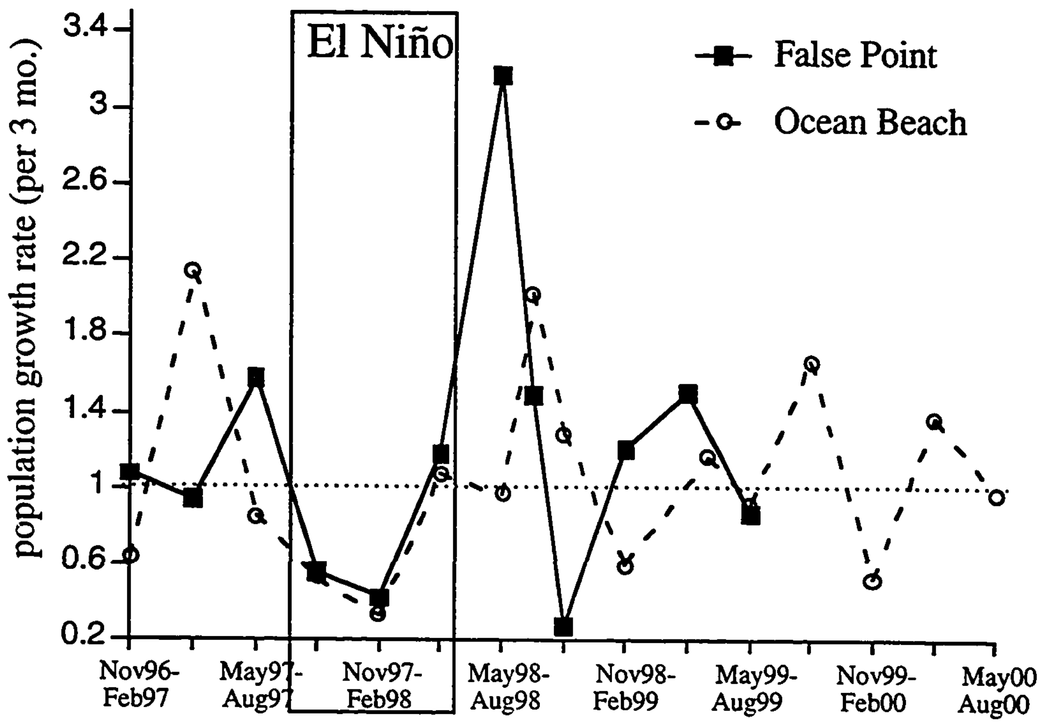

Figure 7.7: Population growth rate (λ) of *C. analis* from November 1996 to August 1999 at False Point and from November 1996 to August 2000 at Ocean Beach.

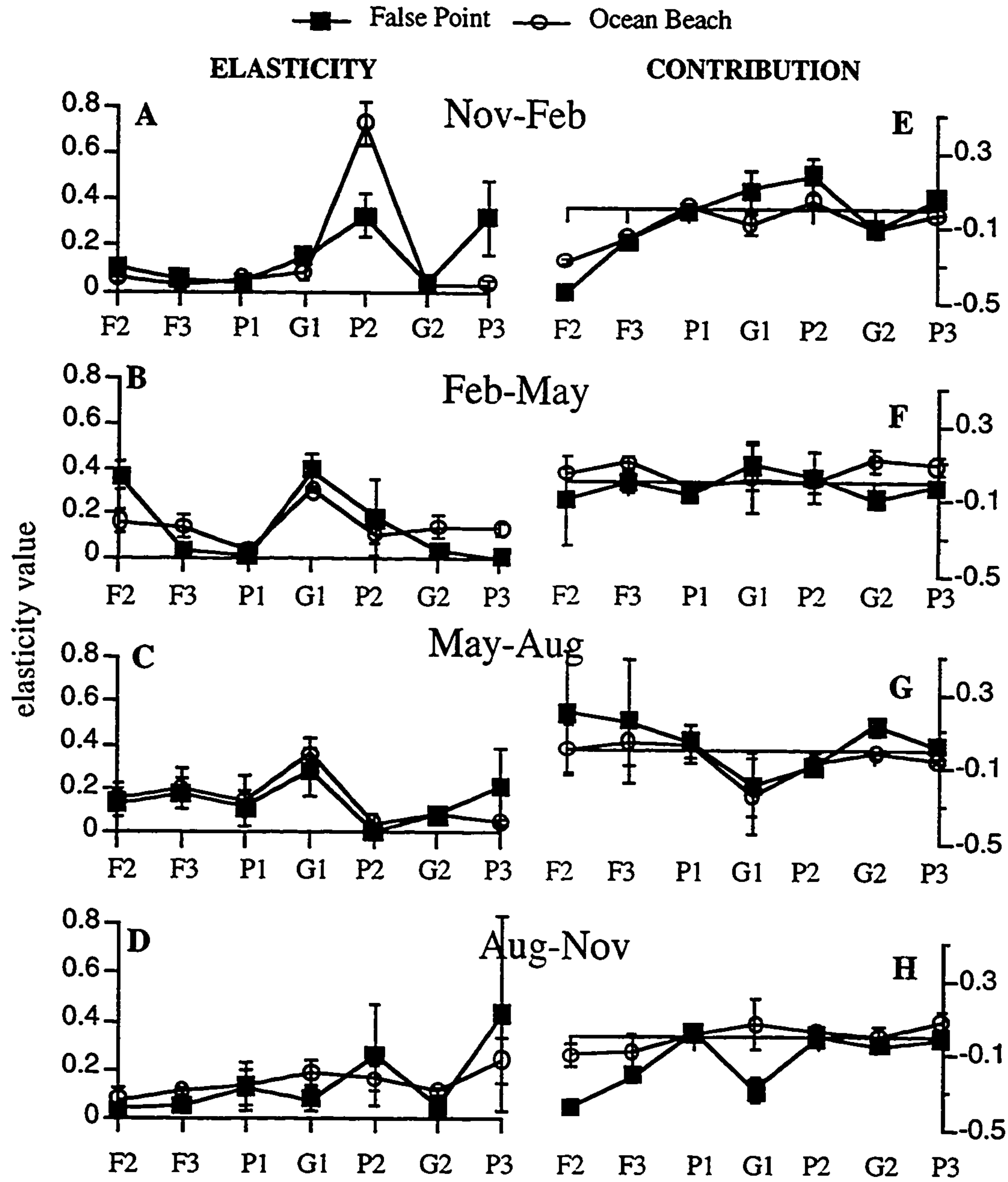

Figure 7.8: Elasticity and contribution of each *C. analis* matrix element (mean ± SE) averaged for all years within a season at False Point and Ocean Beach.

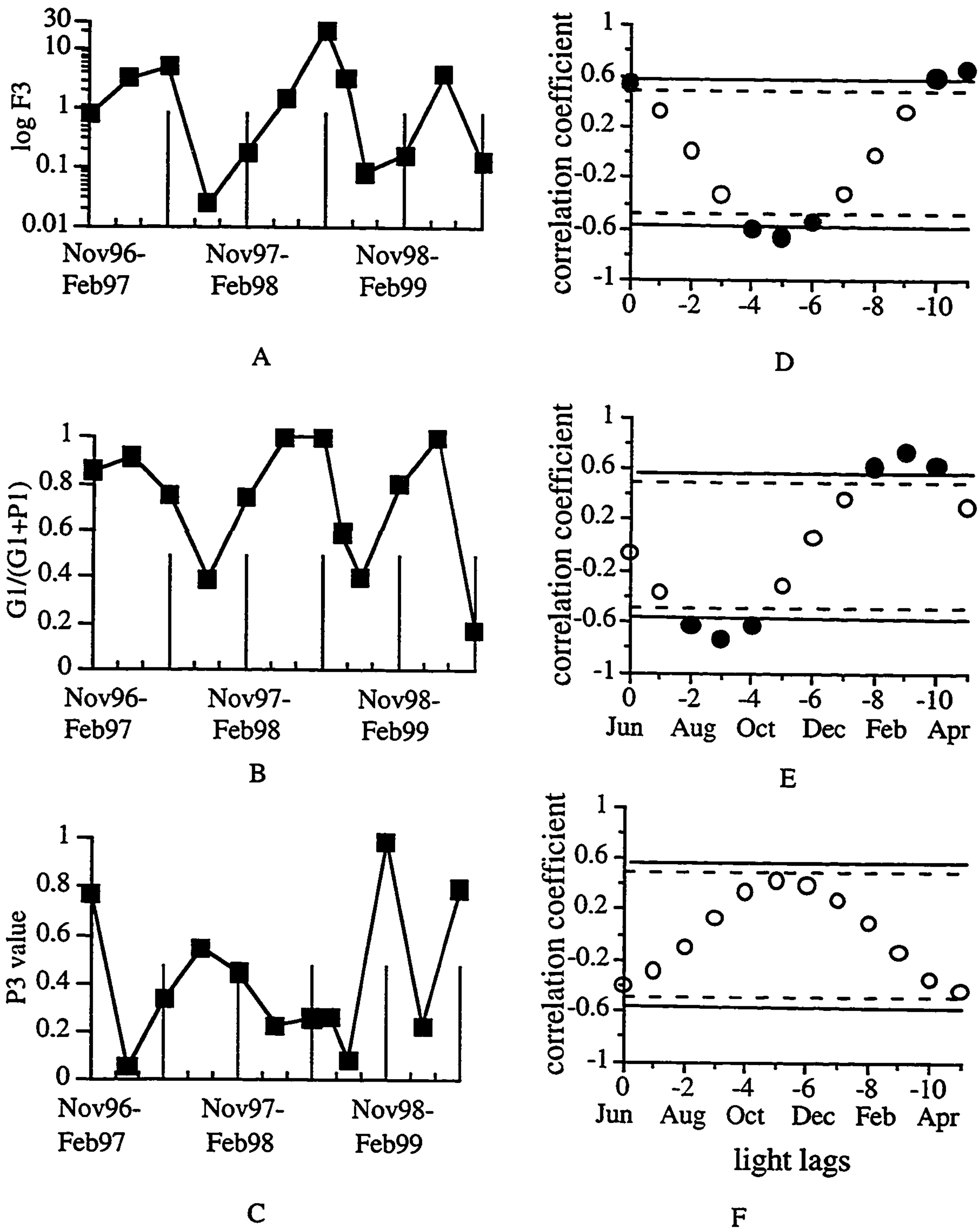

Figure 7.9: Seasonality of *C. analis* vital rates at False Point as determined by cross-correlation analysis. (A) F3, (B) juvenile growth (G1/(G1+P1)), and (C) P3 over time from November 1996 to August 1999. (D-F) Correlation coefficients of regressions between each vital rate and 11 lags of monthly daylight. Black circles indicate lags that resulted in significant regressions ($p<0.05$). Gray circles indicate lags that returned p-values between 0.05 and 0.10.

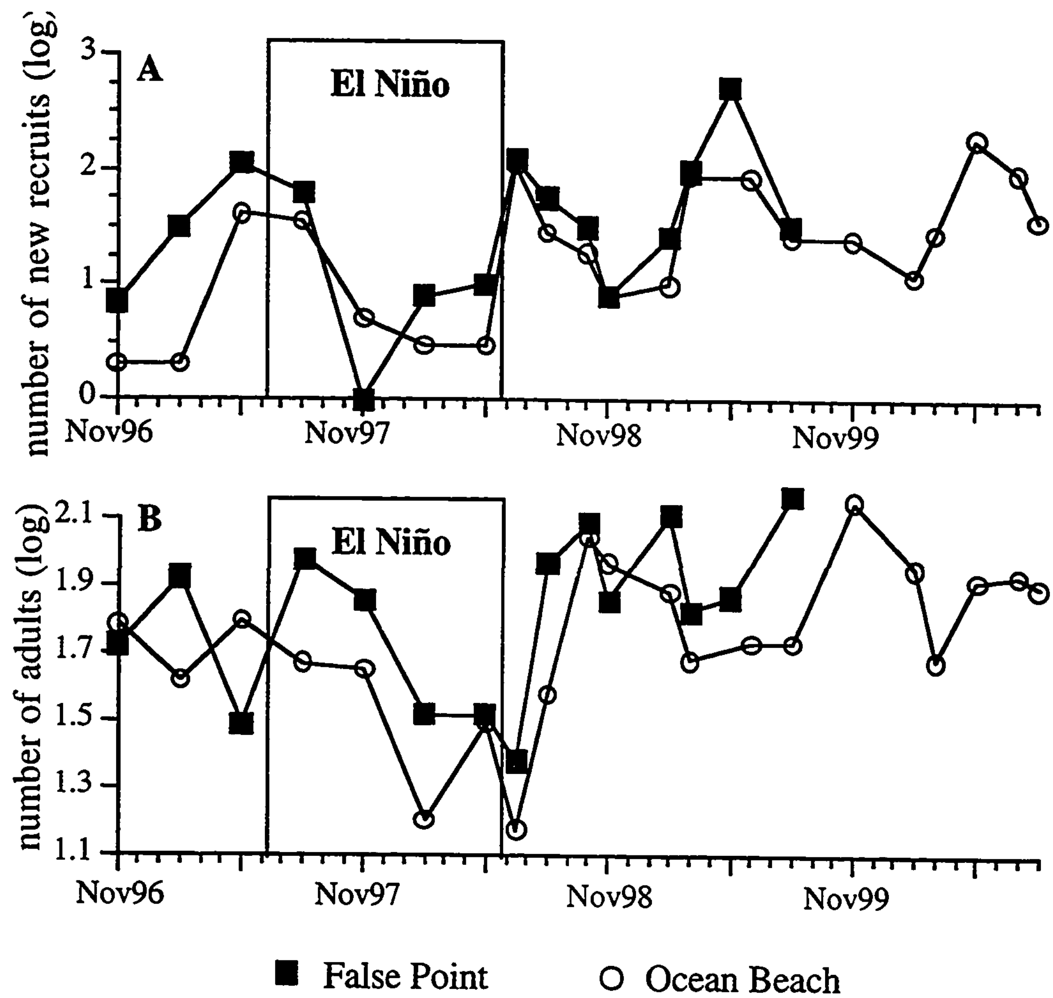

Figure 7.10: Number of *C. analis* (A) recruits (≤ 39 mm TL) and (B) adults (≥ 55 mm TL) over time at False Point and Ocean Beach.

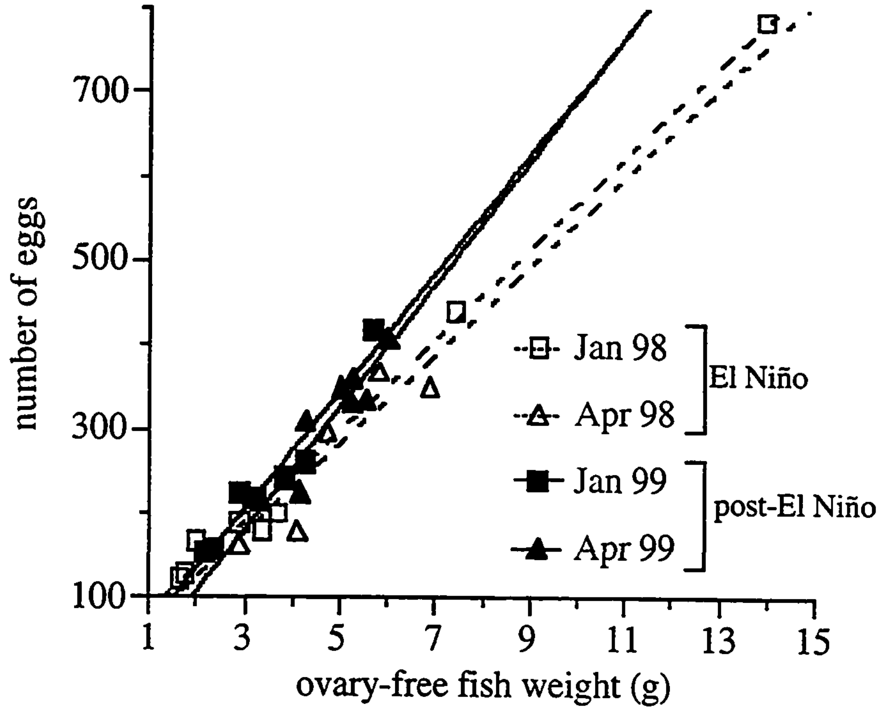

Figure 7.11: Number of *C. analis* eggs per female versus female wet weight (ovary-free) in four time periods: January 1998 (El Niño), April 1998 (El Niño), January 1999 (post-El Niño), and April 1999 (post-El Niño). Regression equations are: Jan 98: y=54x+27, r^2=0.99; Apr 98: y=53x+18, r^2=0.82; Jan 99: y=71x-7, r^2=0.94; Apr 99: y=73x-40, r^2=0.75.

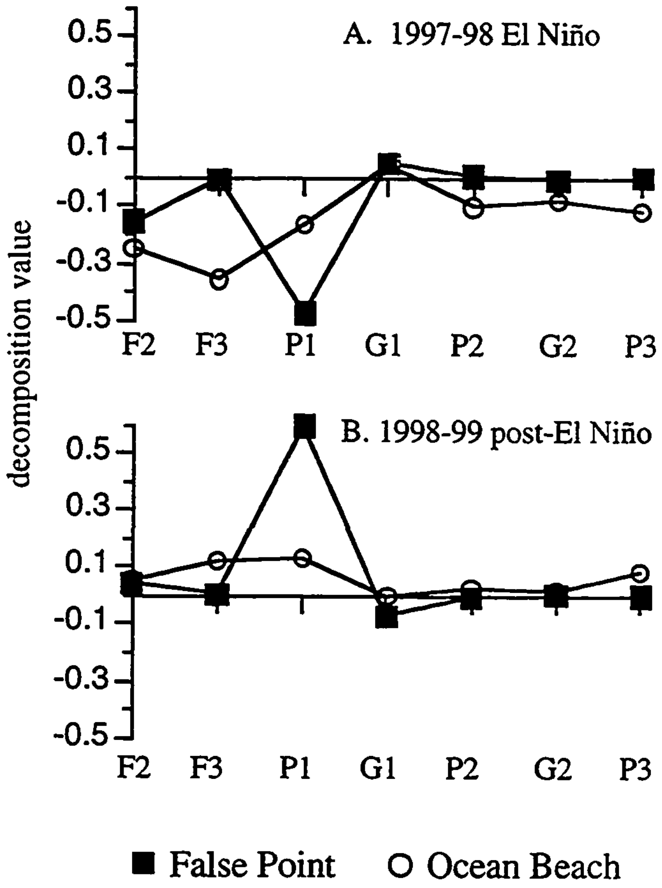

Figure 7.12: Contribution of the seven *C. analis* matrix elements to differences in λ between (A) the August 1997-May 1998 El Niño period and (B) the August 1998 - May 1999 non-El Niño period at False Point and Ocean Beach). Population growth rates during these periods were (A) 0.29 at FP and 0.32 at OB and (B) 1.40 at FP and 1.53 at OB.

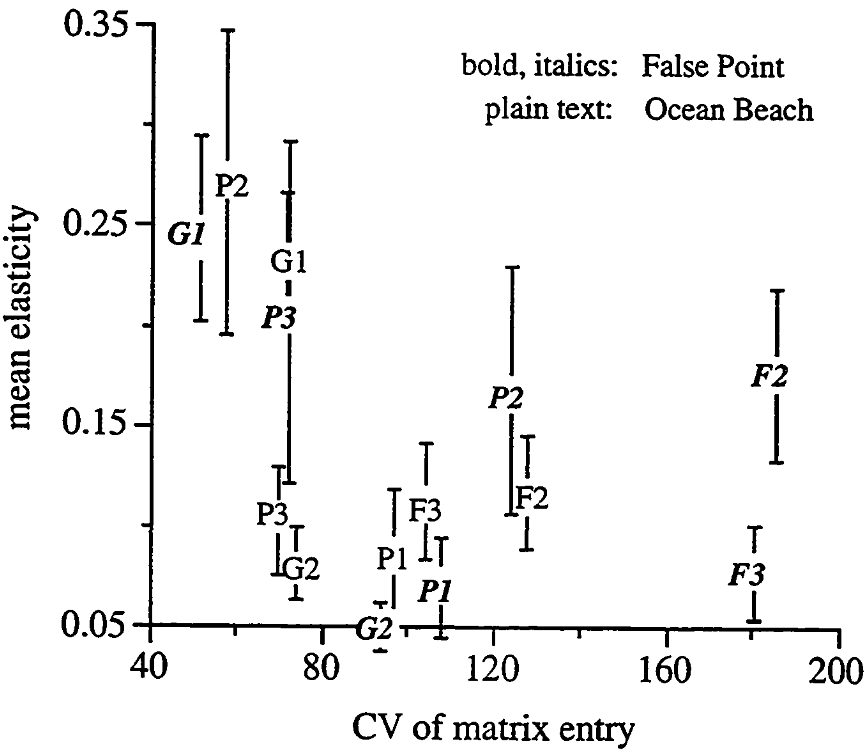

Figure 7.13: Mean elasticities of the *C. analis* matrix elements and their coefficients of variation during the study period. At False Point, $r^2 = 0.131$ and $p = 0.434$. At Ocean Beach, $r^2 = 0.307$, $p=0.197$

Appendix 7.1: Stage-based population matrix entries for *Clinocottus analis*. Matrix entries are presented for each quarterly matrix from November 1996 to August 1999 at False Point (FP) and to August 2000 at Ocean Beach (OB), San Diego, California.

Site	Quarter	Matrix entry P1	F2	F3	G1	P2	G2	P3
FP	Nov96-Feb97	0.13	0.23	0.77	0.73	0.79	0.06	0.77
	Feb97-May97	0.06	1.16	3.29	0.65	0	0.03	0.05
	May97-Aug97	0.20	2.21	5.07	0.59	0	0.37	0.33
	Aug97-Nov97	0.34	0.01	0.02	0.22	0.35	0.17	0.55
	Aug97-Nov97	0.11	0.09	0.18	0.33	0.25	0	0.44
	Nov97-Feb98	0	0.55	1.48	0.81	0.80	0.01	0.23
	Feb98-May98	0	14.8	21.5	0.51	0	0.26	0.26
	May98-Aug98	0.38	2.27	3.33	0.55	0	0.26	0.26
	Jun98-Oct98	0.17	0.03	0.08	0.11	0.22	0.06	0.08
	Aug98-Nov98	0.17	0.03	0.08	0.11	0.22	0.06	0.08
	Nov98-Feb99	0.20	0.39	0.16	0.79	0.83	0.16	0.99
	Feb99-May99	0	5.77	3.90	0.35	0.07	0.17	0.22
	May99-Aug99	0.72	0.04	0.13	0.15	0	0.54	0.79
OB	Nov96-Feb97	0.39	0.01	0.03	0.24	0.62	0.01	0.40
	Feb97-May97	0	1.31	3.35	1.13	0.70	0.43	1.10
	May97-Aug97	0.03	0.9	1.65	0.41	0.00	0.28	0.26
	Aug97-Nov97	0.41	0.02	0.03	0.18	0.39	0.41	0.35
	Nov97-Feb98	0.16	0.03	0.07	0.16	0.31	0	0.19
	Feb98-May98	0	0.51	4.92	1	0.44	0.56	1.00
	May98-Aug98	0	6.75	6.16	0.13	0.00	0.13	0.13
	Jun98-Oct98	0.21	4.95	6.23	0.55	0.38	0.15	0.30
	Aug98-Nov98	0.09	0.76	4.15	0.43	0.39	0.13	1.00
	Nov98-Feb99	0.1	0.08	0.24	0.46	0.46	0.11	0.25
	Feb99-May99	0.29	2.73	0.67	0.19	0.48	0.28	0.76
	May99-Aug99	0.72	0.34	0.76	0.19	0.50	0.13	0.14
	Aug99-Nov99	0.22	1.17	2.82	0.78	0.57	0.25	0.89
	Nov99-Feb00	0.27	0.05	0.13	0.19	0.47	0.04	0.36
	Feb00-May00	0.14	2.35	1.5	0.44	0.25	0.24	0.96
	May00-Aug00	0.13	1.97	1.82	0.31	0.00	0.26	0.18

Appendix 7.2: Elasticities of the 7 matrix entries of each *C. analis* quarterly stage-based population matrix. Matrices were constructed for each quarterly period from November 1996 to August 1999 at False Point (FP) and to August 2000 at Ocean Beach (OB), San Diego, California.

Site	Quarter	Matrix entry						
		P1	F2	F3	G1	P2	G2	P3
FP	Nov96-Feb97	0.02	0.10	0.06	0.16	0.45	0.06	0.15
	Feb97-May97	0.03	0.42	0.04	0.46	0	0.04	0
	May97-Aug97	0.05	0.23	0.15	0.38	0	0.15	0.04
	Aug97-Nov97	0.04	0	0.03	0.03	0.05	0.03	0.82
	Nov97-Feb98	0.04	0.05	0.05	0.11	0.14	0	0.65
	Feb98-May98	0	0.24	0.01	0.24	0.51	0.01	0
	May98-Aug98	0	0.17	0.30	0.40	0	0.02	0.03
	Jun98-Oct98	0.13	0.29	0.09	0.38	0	0.09	0.02
	Aug98-Nov98	0.20	0.06	0.06	0.12	0.47	0.06	0.03
	Nov98-Feb99	0.04	0.14	0.04	0.18	0.39	0.04	0.18
	Feb99-May99	0	0.43	0.04	0.47	0.02	0.04	0.01
	May99-Aug99	0.27	0	0.05	0.06	0	0.05	0.57
OB	Nov96-Feb97	0.02	0.01	0	0.02	0.94	0	0
	Feb97-May97	0	0.14	0.15	0.28	0.14	0.14	0.15
	May97-Aug97	0.01	0.2	0.17	0.37	0	0.17	0.08
	Aug97-Nov97	0.32	0.02	0.08	0.09	0.26	0.08	0.15
	Nov97-Feb98	0.06	0.07	0	0.07	0.8	0	0
	Feb98-May98	0	0.02	0.17	2.41	0.13	0.19	0.36
	May98-Aug98	0	0	0.46	0.49	0	0	0.07
	Jun98-Oct98	0.05	0.37	0.04	0.41	0.09	0.04	0.01
	Aug98-Nov98	0.01	0.05	0.13	0.18	0.08	0.13	0.43
	Nov98-Feb99	0.03	0.09	0.07	0.16	0.52	0.07	0.05
	Feb99-May99	0.09	0.25	0.04	0.29	0.2	0.04	0.08
	May99-Aug99	0.5	0.1	0.04	0.14	0.17	0.04	0.01
	Aug99-Nov99	0.04	0.16	0.12	0.28	0.14	0.12	0.14
	Nov99-Feb00	0.08	0.05	0.03	0.08	0.66	0.03	0.07
	Feb00-May00	0.03	0.23	0.08	0.31	0.07	0.08	0.19
	May00-Aug00	0.06	0.31	0.1	0.4	0	0.09	0.02

Appendix 7.3: Contribution values of the 7 matrix entries obtained through decomposition analysis of each *C. analis* quarterly stage-based population matrix. Matrices were constructed for each quarterly period from November 1996 to August 1999 at False Point (FP) and to August 2000 at Ocean Beach (OB), San Diego, California. Decomposition analysis revealed the contribution of a term at time *t* to differences between the matrix of time *t* and the average matrix for the entire period.

		Matrix entry						
Site	Quarter	P1	F2	F3	G1	P2	G2	P3
FP	Nov96-Feb97	-0.02	-0.53	-0.10	+0.19	+0.26	-0.12	+0.05
	Feb97-May97	-0.06	-0.26	0	+0.17	-0.12	-0.14	-0.04
	May97-Aug97	0	-0.01	+0.07	+0.14	-0.11	+0.14	-0.01
	Aug97-Nov97	+0.06	-0.39	-0.16	-0.22	+0.03	0	+0.03
	Nov97-Feb98	-0.03	-0.46	-0.13	-0.11	-0.02	-0.14	0
	Feb98-May98	-0.07	-0.49	-0.05	+0.25	+0.30	-0.15	-0.01
	May98-Aug98	-0.09	+0.86	+0.51	-0.41	-0.08	+0.05	-0.04
	Jun98-Oct98	+0.09	0	0	+0.09	-0.11	+0.06	-0.02
	Aug98-Nov98	-0.01	-0.42	-0.11	-0.35	-0.03	-0.08	-0.05
	Nov98-Feb99	0	-0.45	-0.15	+0.23	+0.27	-0.02	+0.10
	Feb99-May99	-0.08	+0.45	+0.01	-0.17	-0.09	0	-0.02
	May99-Aug99	+0.22	-0.27	-0.22	-0.31	-0.08	+0.18	+0.11
OB	Nov96-Feb97	+0.07	-0.35	-0.12	-0.13	+0.12	-0.13	-0.02
	Feb97-May97	-0.06	-0.04	+0.09	+0.47	+0.14	+0.15	+0.15
	May97-Aug97	-0.06	-0.10	-0.04	0	-0.15	+0.04	-0.06
	Aug97-Nov97	+0.08	-0.25	-0.21	-0.21	+0.01	+0.08	-0.04
	Nov97-Feb98	-0.01	-0.31	-0.12	-0.20	-0.03	-0.13	-0.05
	Feb98-May98	-0.07	-0.08	+0.16	+0.82	+0.02	+0.16	+0.15
	May98-Aug98	-0.08	+0.38	+0.18	-0.71	-0.11	-0.04	-0.11
	Jun98-Oct98	+0.01	+0.54	+0.10	+0.17	0	-0.04	-0.02
	Aug98-Nov98	-0.03	-0.11	+0.11	+0.01	+0.01	-0.07	+0.16
	Nov98-Feb99	-0.03	-0.36	-0.14	+0.03	+0.04	-0.06	-0.04
	Feb99-May99	+0.03	+0.14	-0.07	-0.28	+0.04	+0.04	+0.06
	May99-Aug99	+0.24	-0.24	-0.07	-0.21	+0.05	-0.04	-0.05
	Aug99-Nov99	+0.01	-0.06	+0.04	+0.27	+0.08	+0.03	+0.08
	Nov99-Feb00	+0.03	-0.30	-0.13	-0.18	+0.05	-0.10	-0.03
	Feb00-May00	-0.02	+0.11	-0.03	+0.02	-0.05	+0.02	+0.13
	May00-Aug00	-0.02	+0.10	-0.01	-0.08	-0.21	+0.03	-0.04

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Chapter 8

Conclusions

Results of the research presented in this dissertation contribute to theoretical population and community ecology, recruitment and population modeling, and ecosystem conservation. From a purely theoretical standpoint, the way in which co-occurring organisms share a habitat is critical to understanding the organization of their community. The southern California rocky intertidal fish guild can be used as a model for other mobile intertidal species assemblages, including fish in other systems and motile invertebrates. The present study will also contribute to life-history-based population and recruitment models, which can be generalized to address the relevance of life history in the poorly understood transition from planktonic to benthic mode of life in other types of organisms. The 1997-8 El Niño event serves as a natural habitat fluctuation to model effects of climatic change on community structure and habitat use. These models will also aid in the conservation of the rocky intertidal, an area frequented by human visitors, yet threatened by human activity (Addessi, 1994).

Ecological results of the study

Despite the suggestion that systems with low species richness have low levels of microhabitat segregation (Prochazka and Griffiths, 1992), results from this dissertation indicate that rocky intertidal pools are partitioned among and within species by the relatively species-poor San Diegan rocky intertidal fish community. Tidepool use, spatially different among and within species, also changes temporally. Habitat use, especially vertical zonation, varied seasonally in the four most abundant assemblage members. Vertical zonation was also dynamic on a diel scale for the two middle and upper intertidal fishes, *Clinocottus analis* and *Girella nigricans*. This flexibility in the vertical zonation of intertidal fishes emphasizes a key difference between intertidal fishes and sessile intertidal invertebrates, which have served as model for hard-bottom intertidal species in the bulk of the rocky intertidal community ecology work (e.g. Dayton, 1971; Paine, 1974; Underwood and Denley, 1984; Connell, 1985; Roughgarden and Isawa, 1986). New recruits of motile species like fishes have the ability to shift to alternate habitats if conditions at the spot of settlement become inhospitable. Although newly settled juveniles of some sessile species also have this ability just after settlement (Mullineaux and Garland, 1993), individuals belonging to motile species retain this ability to shift habitats throughout their lives. Results of the present dissertation suggest that intertidal fishes take advantage of this motility to change habitats in response to factors that change on tidal, daily, seasonal, and in a few cases, possibly ENSO scales. Changes also occur ontogenetically, with older fish occupying different habitats than juveniles. A sessile individual, if confronted by inhospitable conditions, which abound in the environmentally harsh and dynamic intertidal zone, dies.

This fundamental difference between sessile and motile intertidal organisms stresses the need for studies of fishes and other motile species to fully understand the rocky intertidal habitat, its limitations, and its evolutionary pressures. For example, the advantage of motility could generate significant differences between population controls of motile and sessile species. Studies of sessile species played a large role in the paradigm that intertidal and other nearshore hard-bottom populations are space-limited, limited by post-recruitment density-dependent factors (Underwood and Denley, 1984; Forrester, 1990; Caley, 1996). More recent studies indicate that some nearshore populations of motile individuals, like reef fish, are not limited by adult resources at all, but are limited by supply of new recruits to the adult habitat (Victor 1983; Forrester, 1990; Jones 1990, but see Pfister, 1996). The present research suggests that for rocky intertidal fish as well, magnitude of recruitment is important to overall intertidal fish populations.

Identification of the importance of recruitment points to an important conclusion of this dissertation work; the larval stage of intertidal fish species is extremely important. Controls on the size of recruiting *C. analis* cohorts, which most likely occur while the planktonic larvae are out of the rocky intertidal zone, also control the size of that cohort through adulthood. During the 1997-98 El Niño event, the observed decrease in population size was the result of recruitment failure. Immediately after the 1997-98 El Niño, very large cohorts recruited to False Point and Ocean Beach, again emphasizing the importance of recruitment, this time in the post-El Niño population recovery.

Implications of the study

Research results contribute to the growing evidence that climate change has significant influence on biological communities. Although the rocky intertidal environment is extremely dynamic and variable on short time scales, results of the present research indicate that relatively less severe but longer-term climatic shifts, such as those that occur on the scale of the El Niño Southern Oscillation, can impact rocky intertidal communities. Although future studies spanning at least another ENSO event are necessary to identify causal mechanisms, the 1997-98 El Niño event appeared to influence structure of the San Diego tidepool fish assemblage, vertical distribution of the four most abundant assemblage members, population dynamics of the assemblage dominant, and spot polymorphism of a second assemblage member. This event may be viewed as a preview to global climate change, both anthropogenically-induced and natural. Although the mechanisms underlying ENSO events and global warming may be different, they may induce similar environmental changes in rocky intertidal and nearshore coastal habitats, including increased temperature, increased sea level, and changes in nearshore currents. Studies of both ENSO changes (e.g. Arntz and Tarazona, 1990; Sanford 1999) and decadal regime shifts (e.g. Barry et al., 1995; Holbrook et al., 1997) in nearshore communities should be kept in mind as future researchers tackle the study of ecological effects of global warming and other climate change.

Understanding how co-occurring species share a habitat and how their distributions change over time can also aid conservation efforts. The coastline of southern California is highly developed, with promise of even more development. As global human population increases, rocky coastlines of other areas are also poised for increased development. Unlike the San Diegan coastal sage habitat which is directly removed to make way for development, there is no reason that the rocky intertidal system cannot co-exist with human development just inshore. However, studies of distribution of intertidal plants and animals should be used in the planning of developments and nearshore construction projects in order to minimize impacts. For example, many storm drains in San Diego, including several at the Ocean Beach and False Point study sites of this dissertation, open up directly into the high intertidal zone. During winter months, especially during El Niño events, these drains empty large quantities of fresh water into the intertidal area. This water follows natural drainage patterns and finds its way into tidepools at low tide, displacing seawater. During several of the 1997-98 El Niño storms, salinity of some of the upper intertidal pools directly in the path of the storm drain outflow at Ocean Beach was < 20 ppt (Davis, pers. obs.). Other physico-chemical effects pertaining to the quality of the storm drain water no doubt occur as well. Because these tidepools can be isolated from the flushing actions of subtidal conditions for as much as 12 hours per day during neap tides, such drastic changes in physico-chemical conditions have the potential to wreak havoc on the pool's inhabitants. Results of this dissertation indicate that these high tidepools directly impacted by storm drain runoff, although lacking the plush algal mats of the lower intertidal zone and perhaps appearing barren, are important habitats for *C. analis* and *G. nigricans* juveniles. A simple solution to this problem would be to lengthen storm drains to open up past the low intertidal zone, where their effects would be more quickly diluted by the ocean.

Another area in which results of the present research and similar studies may be used by development planners is in the construction of seawalls. Often seawalls are built in the middle and high intertidal zones well within the vertical tidal range of many animals. For example, at Ocean Beach, a seawall is built into the sandstone platform at about 3.5-4.0 ft above mean lower low water (MLLW). Both *C. analis* and *G. nigricans* occupied the highest pools at that site, just below the seawall, and no doubt would have occupied those even higher pools lost to construction of the seawall. Results of this dissertation suggest that these high pools provide a nursery habitat to youngest *C. analis* and *G. nigricans* juveniles. Wherever possible, developers may be encouraged to consider habitat requirements of those species displaced by such features as seawalls.

Results of the present study may also be useful to those engaged in protecting the rocky intertidal zone from too much well-intentioned interest. The rocky intertidal sections of San Diego are popular destinations for tourists and provide valuable natural classrooms for educators. For example, the rocky intertidal reserve at Cabrillo National Monument at Point Loma, San Diego, receives 100,000 tidepool visitors a year (B. Becker, pers. comm.). The University of California's Scripps Coastal Reserve can be visited by as many as 500 people in a day, many of them belonging to school groups (Davis, pers. obs.). The attention thus bestowed on the rocky intertidal zone can lead to severe trampling problems and declines in abundance of plants, invertebrates, and even fishes (Addessi, 1994). Cabrillo National Monument recently established a no-visitation zone within the park partly to protect some of its inhabitants and partly in order to study effects of trampling. Information of the present dissertation, especially that pertaining to habitat partitioning among species, may be useful to other reserve managers interested in protecting either certain species or certain habitats from trampling. For example, if a reserve manager chooses to protect declining *G. rhessodon* populations, which use shallow, low tidepools, he or she may designate a different area of tidepools as "no access" than if he or she were attempting to protect *G. nigricans*, which uses big, deep, high tidepools.

Future research

Several avenues of future research can be identified as important upon consideration of the dissertation results. Future studies of El Niño events, described above, will serve to test the generality of the El Niño results presented here. Direct study of the larval stage of *C. analis* and other species will reveal which larval vital rates contribute to recruitment failure, when it occurs, and which most greatly control recruiting cohort size. Manipulative experiments may be attempted to further test density-dependence hypotheses for *C. analis* and other species. Information gleaned in the pursuit of these theoretical ecological goals can be applied to conservation of the urban rocky intertidal zone. With further study of anthropogenic effects on this habitat, we may be able to establish a way to confidently protect its inhabitants alongside increasing urbanization.

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