

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

Jana L. D. Davis*

Scripps Institution of Oceanography, 9500 Gilman Drive 0208, San Diego, California 92093-0208, USA

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).

*E-mail: jana@ucsd.edu

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 blennioid *Hypsoblennius gilberti* (rockpool blenny), the gobioid *Gobiesox rhesodon* (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 spe-

cies 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 (Addressi 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 m². 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)	1.7 ± 0.1 ft (0.52 ± 0.03 m)
	OB	-0.2 to 3.7 ft (-0.06 to 1.13 m)	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 ($n = 35$, $r^2 = 0.71$, $p \ll 0.01$). 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 $\geq 20\%$ 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 rhesodon* 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. rhesodon* were divided into 2 size classes containing approximately equal numbers of individuals. The small size class of *G. nigricans* included fish <50 mm, and that for *G. rhesodon* 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 rhesodon* 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. rhesodon*; 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 rhesodon*

Species	Total number	No. in small size class	Size range	Mean size
November				
<i>C. analis</i>	197	7	31–138	62 \pm 1.4
<i>G. nigricans</i>	45	16	29–91	56 \pm 2.8
<i>H. gilberti</i>	30	2	27–128	74 \pm 4.5
<i>G. rhesodon</i>	119	49	11–52	33 \pm 0.7
<i>G. elegans</i>	13	0	51–120	88 \pm 5.8
February				
<i>C. analis</i>	168	31	23–113	59 \pm 1.5
<i>G. nigricans</i>	63	18	32–81	55 \pm 1.4
<i>H. gilberti</i>	19	2	26–120	79 \pm 5.4
<i>G. rhesodon</i>	63	26	22–49	35 \pm 0.8
<i>G. elegans</i>	11	1	31–120	92 \pm 7.8
May				
<i>C. analis</i>	301	150	13–109	47 \pm 1.6
<i>G. nigricans</i>	35	2	45–110	65 \pm 2.5
<i>H. gilberti</i>	15	0	74–109	91 \pm 2.3
<i>G. rhesodon</i>	49	22	27–47	34 \pm 0.7
<i>G. elegans</i>	15	3	41–122	83 \pm 8.0
August				
<i>C. analis</i>	319	96	23–126	52 \pm 1.0
<i>G. nigricans</i>	121	73	24–95	45 \pm 1.1
<i>H. gilberti</i>	42	9	22–126	64 \pm 3.9
<i>G. rhesodon</i>	60	21	16–46	35 \pm 1.0
<i>G. elegans</i>	8	1	46–111	79 \pm 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 rhesodon* 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 m². Significant differences in tidepool fish densities between FP and OB are designated by asterisks (*t*-tests: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.005$)

Species	Month	FP densities		OB densities		OB vs FP <i>t</i> -test
		Range	Mean \pm 1 SE	Range	Mean \pm 1 SE	
<i>C. analis</i>	Nov	0.7–5.8	2.5 \pm 0.4	1.5–49.3	8.3 \pm 2.2	•
	Feb	0.7–5.8	1.9 \pm 0.3	1.3–27.7	6.3 \pm 1.6	•
	May	0.5–17.6	4.2 \pm 0.9	1.5–34.0	9.5 \pm 1.9	**
	Aug	0.7–29.9	4.5 \pm 1.2	1.3–67.0	12.5 \pm 3.4	•
<i>G. nigricans</i>	Nov	0.1–1.4	0.7 \pm 0.2	0.3–9.2	4.0 \pm 0.9	***
	Feb	0.2–3.4	1.3 \pm 0.4	2.9–3.9	3.3 \pm 0.3	•
	May	0.4–1.8	1.1 \pm 0.4	3.0–5.0	4.0 \pm 0.6	**
	Aug	0.5–6.8	2.3 \pm 0.5	0.8–15.0	5.3 \pm 1.0	**
<i>H. gilberti</i>	Nov	0.6–1.6	1.2 \pm 0.2	0.7–2.5	1.4 \pm 0.3	
	Feb	0.1–1.1	0.6 \pm 0.2	0.7–1.7	1.3 \pm 0.2	•
	May	0.4–1.8	0.9 \pm 0.4	0.3–2.5	1.2 \pm 0.7	
	Aug	0.1–6.7	1.6 \pm 0.8	1.5–6.8	4.1 \pm 0.8	•
<i>G. rhesodon</i>	Nov	0.1–31.8	5.3 \pm 2.2	1.6–9.3	4.9 \pm 1.3	
	Feb	0.5–27.0	4.2 \pm 2.0	0.8–1.6	1.1 \pm 0.3	
	May	0.5–45.0	7.9 \pm 4.8	0.7–3.2	1.8 \pm 0.6	
	Aug	0.4–13.6	4.5 \pm 1.3	2.4–4.7	3.3 \pm 0.7	
<i>G. elegans</i>	Nov			0.9–5.7	2.8 \pm 0.8	
	Feb			0.8–4.4	2.0 \pm 0.6	
	May			0.8–3.7	1.9 \pm 0.5	
	Aug			0.8–2.0	1.3 \pm 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 rhesodon, 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 <i>F</i>	Model p	Model R ²	
<i>C. analis</i>	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				
	Feb/OB	Surface area	+0.1	0.035	4.4	0.009	0.24	
		Height	-1.2	0.017				
		Depth	+0.1	0.060				
	May/FP	Rugosity	+1.1	0.063	9.2	<0.001	0.27	
		Height	-2.0	<0.001				
	May/OB	Height	-2.6	<0.001	15.6	<0.001	0.25	
Height		-2.1	0.006					
Aug/FP	Height	-2.1	0.006	8.3	0.006	0.14		
	Height	-3.7	0.002					
Aug/OB	Height	-3.7	0.002	7.7	0.001	0.25		
	Algal cover	+14.7	0.047					
<i>G. nigricans</i>	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	
		Surface area	+0.05	0.013				
	May/FP	Depth	+0.01	0.034	5.7	0.006	0.23	
		Depth	+0.08	0.024				
	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				
	<i>H. gilberti</i>	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				
Aug/FP		Height	-0.4	0.045	3.7	0.032	0.13	
		Algal cover	-1.4	0.100				
Aug/OB	Depth	+0.04	0.052	3.8	0.057	0.07		
<i>G. rhessodon</i>	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					
<i>G. elegans</i>	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 tidepool environmental factors are listed

Season	Factor	False Point			Ocean Beach	
		PC1	PC2	PC3	PC1	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 rhesodon* 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. rhesodon* ($t_{7,14} = 2.6$, $p = 0.02$ 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. rhesodon* (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. rhesodon* and are found in the same regions of the plots.

Habitat partitioning by size

Clinocottus analis, *Girella nigricans*, and *Gobiesox rhesodon* 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.

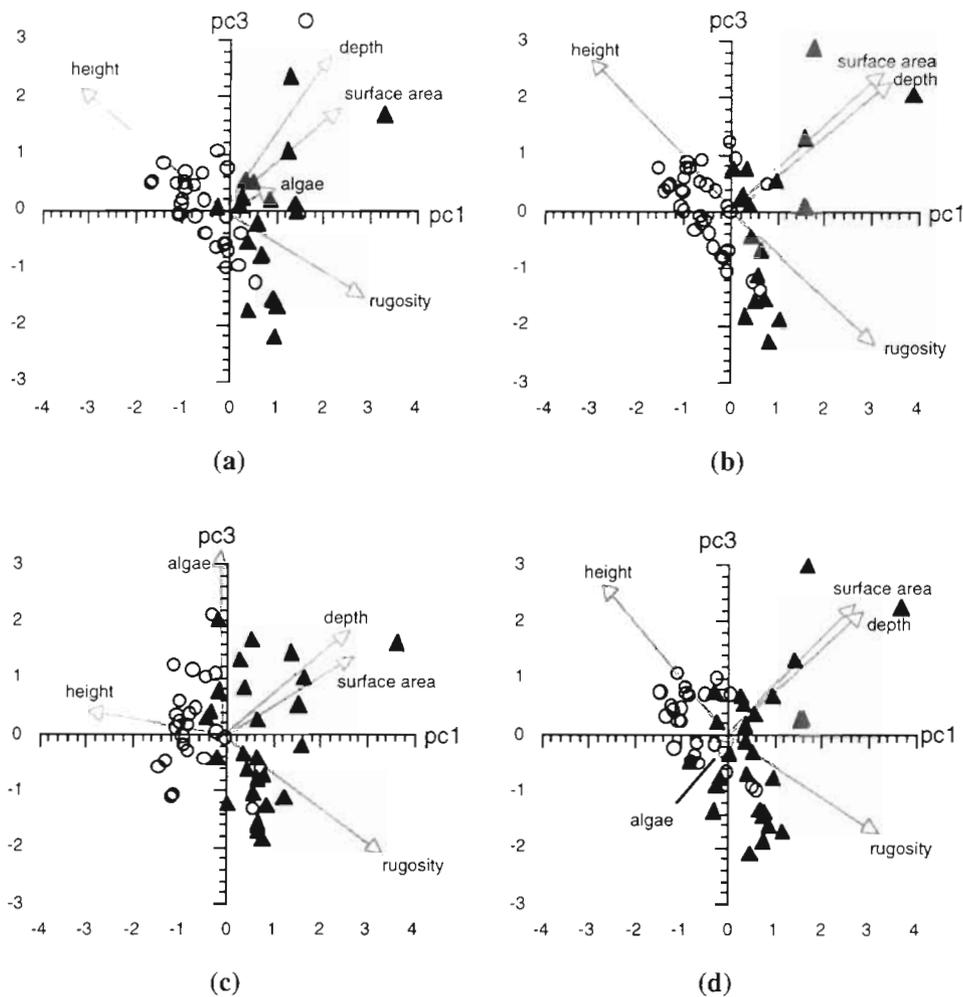


Fig. 1. Distribution of tidepools with fish (▲) versus tidepools without fish (○) at False Point in (a) November, (b) February, (c) May, and (d) August. Values of PC1 for each tidepool are plotted against values of PC3. PC3 was chosen for the y-axis instead of PC2 because component loadings of PC3 were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

Gobiesox rhesodon 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. rhesodon* 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. rhesodon* decreased with intertidal height during February at False Point (Table 7). Analysis of *G. rhesodon* 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,

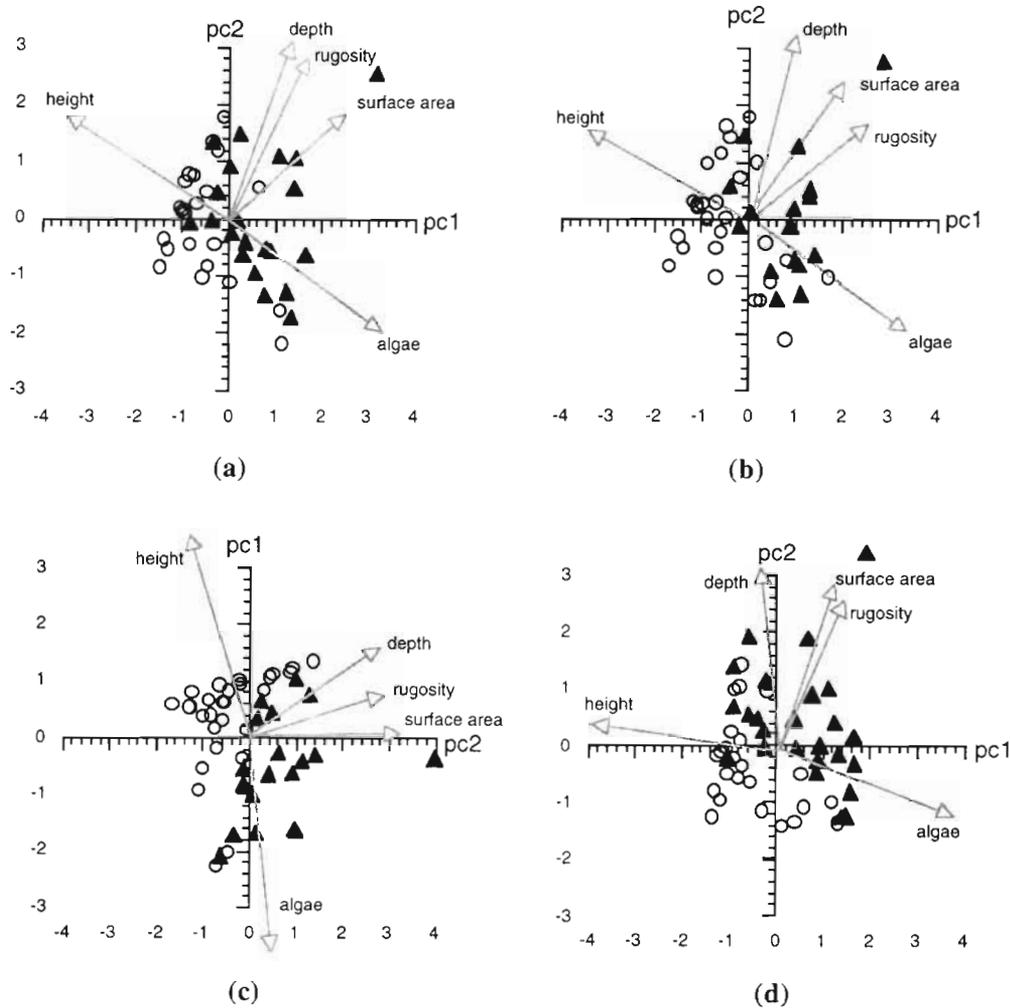


Fig. 2. Distribution of tidepools with fish (▲) versus tidepools without fish (○) at Ocean Beach in (a) November, (b) February, (c) May, and (d) August. Values of PC1 for each tidepool are plotted against values of PC2. Loading of the original variables on the PC axes are indicated by arrows. Axes for 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: $t_8 = 5.4$, $p \leq 0.001$ and $t_8 = 5.2$, $p \leq 0.001$, respectively, Fig. 5c). The number of individuals of the 2 most abundant species, *Clinocottus analis* and *Gobiesox rhesodon*, also decreased ($t_8 = 2.5$, $p = 0.035$ and $t_8 = 5.3$, $p \leq 0.001$, respectively). The decline in *G. rhesodon* 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. rhesodon* 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	
<i>C. analis</i>	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	
<i>G. nigricans</i>	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	
<i>H. gilberti</i>	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	
<i>G. rhesodon</i>	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	
<i>G. elegans</i>	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. rhesodon* 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. rhesodon* due to sampling pressure alone (Fig. 5b,d).

DISCUSSION

The 5 most abundant fishes in the San Diego rocky intertidal, *Clinocottus analis*, *Girella nigricans*, *Gob-*

iesox rhesodon, *Hypsoblennius gilberti*, and *Gibsonia 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

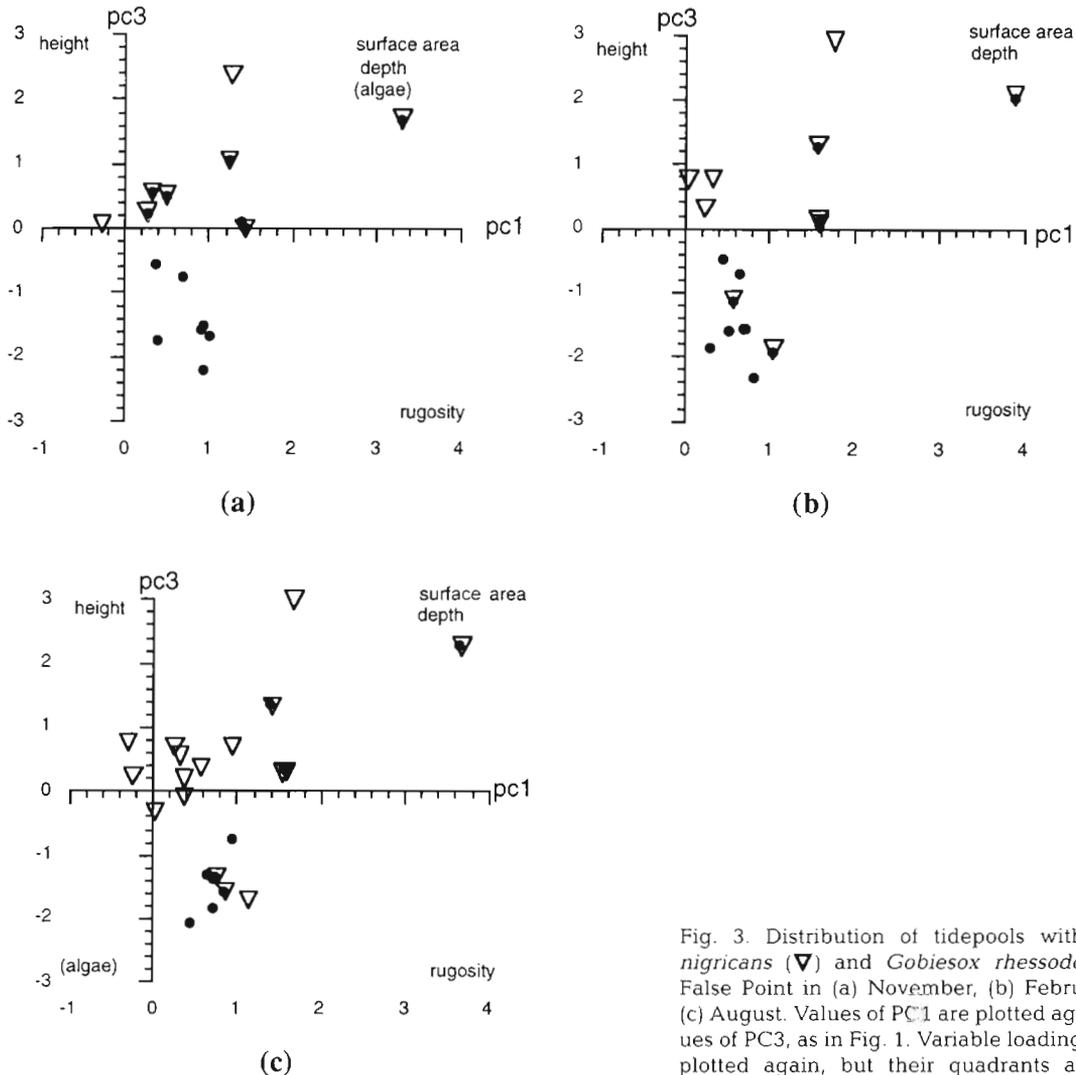


Fig. 3. Distribution of tidepools with *Girella nigricans* (∇) and *Gobiesox rhesodon* (\bullet) at False Point in (a) November, (b) February, and (c) August. Values of PC1 are plotted against values of PC3, as in Fig. 1. Variable loadings are not plotted again, but their quadrants are noted

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

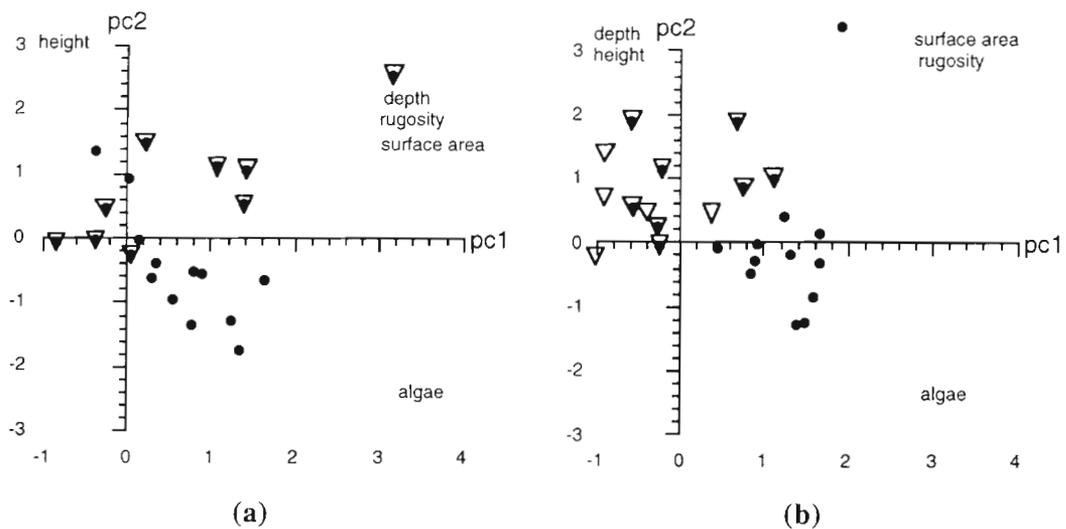


Fig. 4. Distribution of tidepools with *Girella nigricans* (▼) and *Clinocottus analis* (●) at Ocean Beach (a) November and (b) August. Variable loadings are not plotted again, but their quadrants are noted. *C. analis* appears in pools over a wider range of PC values

Table 7. Intraspecific size-based partitioning in (a) *Clinocottus analis*, (b) *Girella nigricans* and (c) *Gobiesox rhesodon* 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. rhesodon*) 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/ site	Model using environmental factors						Model using PCs					
	Factor	Slope	p-value	Model F	Model p	Model R ²	PC	Slope	p-value	Model F	Model p	Model R ²
(a) <i>Clinocottus analis</i>												
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) <i>Girella nigricans</i>												
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									
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									
(c) <i>Gobiesox rhesodon</i>												
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					

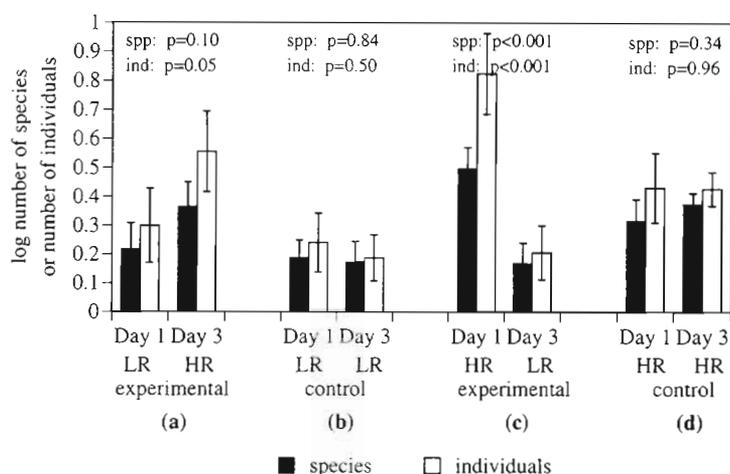


Fig. 5. Number of species and number of individual fish per pool (mean \pm 1 SE) before (Day 1) and after (Day 3) (a) the addition of rocky structure in tidepools and (c) the removal of rocky structure in tidepools. LR = low-rugosity; HR = high-rugosity. Control data show (b) low-rugosity pools and (d) 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 rhesodon*, *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. rhesodon*, *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 rhesodon*) 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 blennioid *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.

Acknowledgements. I would like to thank Lisa Levin for her ideas and support during the course of this project. I would also like to thank Lisa Levin and Robin Gibson for their invaluable comments on various drafts of the manuscript. Thanks to David Checkley, Paul Dayton, Paul Smith, Trevor Price, Clinton Wynant, and 2 anonymous reviewers for their suggestions and advice. Field assistance by Andrew Juhl and Nicole Dederick and statistical advice from Michael Graham are greatly appreciated. Thanks also to the Department of Defense for graduate funding from a National Defense Science and Engineering Graduate Fellowship. Funding for the project was provided in part by grants from Sigma Xi, the PADI Foundation, Sigma Delta Epsilon Graduate Women in Science, and the Mildred Mathias Foundation.

LITERATURE CITED

- Addressi L (1994) Human disturbance and long-term changes on a rocky intertidal community. *Ecol Appl* 4:786-797
Andrewartha HG, Birch LC (1954) The distribution and abundance of animals. University of Chicago Press, Chicago

- Barange M, Gibbons MJ, Carola M (1991) Diet and feeding of *Euphausia hanseni* and *Nematoscelis megalops* (Euphausia) in the northern Benguela current: ecological significance of vertical space partitioning. *Mar Ecol Prog Ser* 73: 173–182
- Beckley LE (1985) Tide-pool fishes: recolonization after experimental elimination. *J Exp Mar Biol Ecol* 85:287–296
- Bennett BA, Griffiths CL (1984) Factors affecting the distribution, abundance, and diversity of rock-pool fishes on the Cape Peninsula, South Africa. *S Afr J Zool* 19:97–104
- Brothers EB (1975) The comparative ecology and behavior of three sympatric California gobies. PhD thesis, University of California at San Diego
- Burgess TJ (1978) The comparative ecology of two sympatric polychromatic populations of *Xerxerpes fucorum* Jordan and Gilbert (Pisces: Pholididae) from the rocky intertidal zone of Central California. *J Exp Mar Biol Ecol* 35:43–58
- Congleton JL (1980) Observations on the responses of some southern California tidepool fishes to nocturnal hypoxic stress. *Comp Biochem Physiol Part A* 66:719–722
- Connell JH (1961a) The influence of interspecific competition and other factors on the distribution of the barnacle *Balanus balanoides*. *Ecol Monogr* 31:61–104
- Connell JH (1961b) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–723
- Gibson RN (1972) The vertical distribution and feeding relationships of intertidal fish on the Atlantic coast of France. *J Anim Ecol* 41:189–207
- Gibson RN (1982) Recent studies on the biology of intertidal fishes. *Oceanogr Mar Biol Annu Rev* 20:363–414
- Graham MH (1997) Factors determining the upper limit of giant kelp, *Macrocystis pyrifera* Agardh, along the Monterey Peninsula, central California, USA. *J Exp Mar Biol Ecol* 218:127–149
- Green JM (1971) Local distribution of *Oligocottus maculosus* Girard and other tidepool cottids of the West coast of Vancouver Island, British Columbia. *Can J Zool* 49:1111–1128
- Horn MH, Gibson RN (1988) Intertidal fishes. *Sci Am* 258(1): 64–71
- Jensen SL, Muller-Parker G (1994) Inorganic nutrient fluxes in anemone-dominated tide pools. *Pac Sci* 48:32–43
- Mahon R, Mahon SD (1994) Structure and resilience of a tidepool fish assemblage at Barbados. *Environ Biol Fishes* 41: 171–190
- Manly BFJ (1986) *Multivariate statistical methods: a primer*. Chapman and Hall, London
- Marsh B, Crowe TM, Siegfried WR (1978) Species richness and abundance of clinid fish (Teleostei: Clinidae) in intertidal rock pools. *Zool Afr* 13:283–291
- Mayr M, Berger A (1992) Territoriality and microhabitat selection in two intertidal New Zealand fish. *J Fish Biol* 40: 243–256
- Metaxas A, Scheibling RE (1993) Community structure and organization of tidepools. *Mar Ecol Prog Ser* 98:187–198
- Moring JR (1986) Seasonal presence of tidepool fish species in a rocky intertidal zone of northern California, USA. *Hydrobiologia* 134:21–27
- Moring JR (1990) Seasonal absence of fishes in tidepools of a boreal environment (Maine, USA). *Hydrobiologia* 194: 163–168
- Nakamura R (1976a) Experimental assessment of factors influencing microhabitat selection by the two tidepool fishes *Oligocottus maculosus* and *O. snyderi*. *Mar Biol* 37: 97–104
- Nakamura R (1976b) Temperature and the vertical distribution of two tidepool fishes. *Copeia* 1976:143–152
- Nieder J (1993) Distribution of juvenile blennies (Pisces, Blenniidae) in small tide-pools: result of low-tide lottery or strategic habitat selection? *Bonn Zool Beitr* 44:133–140
- Norris KS (1963) The functions of temperature in the ecology of the percid fish *Girella nigricans* (Ayres). *Ecol Monogr* 33:23–61
- Norton SF (1991) Habitat use and community structure in an assemblage of cottid fishes. *Ecology* 72:2181–2192
- Pfister CA (1995) Estimating competition coefficients from census data: a test with field manipulations of tidepool fishes. *Am Nat* 146(2):271–291
- Prochazka K, Griffiths CL (1992) The intertidal fish fauna of the west coast of South Africa—species, community, and biogeographic patterns. *S Afr J Zool* 27:115–120
- Reyment R, Joreskog KG (1993) *Applied factor analysis in the natural science*. Cambridge University Press, Cambridge
- Richkus WA (1981) Laboratory studies of intraspecific behavioral interactions and factors influencing tidepool selection of the woolly sculpin *Clinocottus analis*. *Cal Fish Game* 67: 187–195
- Ross ST (1986) Resource partitioning in fish assemblages: a review of field studies. *Copeia* 1986:352–388
- Setran AC, Behrens DW (1993) Transitional ecological requirements for early juveniles of two sympatric stichaeid fishes, *Cebidichthys violaceus* and *Xiphister mucosus*. *Environ Biol Fishes* 37:381–395
- Stephens JS, Johnson RK, Key GS, McCosker JE (1970) The comparative ecology of three sympatric species of California blennies of the genus *Hypsoblennius* Gill (Teleostomi, Blenniidae). *Ecol Monogr* 40:213–233
- Stevens EG, Watson W, Moser HG (1989) Development and distribution of larvae and pelagic juveniles of three kyphosid fishes (*Girella nigricans*, *Medialuna californiensis*, and *Hermosilla azurea*) off California and Baja California. *Fish Bull* 87:745–768
- Thomson DA, Lehner CE (1976) Resilience of a rocky intertidal fish community in a physically unstable environment. *J Mar Ecol Biol Ecol* 22:1–29
- Underwood AJ, Skilleter GA (1996) Effects of patch-size on the structure of assemblages in rock pools. *J Exp Mar Biol Ecol* 197:63–90
- Valle CF (1989) The homing behavior and intertidal movements of the opaleye, *Girella nigricans*. MSc thesis, California State University at Long Beach
- Wells AW (1986) Aspects of the ecology and life-history of the woolly sculpin, *Clinocottus analis*, from southern California. *Cal Fish Game* 72(4):213–226
- Williams GC (1957) Homing behavior of California rocky shore fishes. *Univ Cal Publ Zool* 59:249–284
- Willis TJ, Roberts CD (1996) Recolonization and recruitment of fishes to intertidal rockpools at Wellington, New Zealand. *Environ Biol Fishes* 47:329–343
- Wilson JB, James RE, Newman JE, Myers JE (1992) Rockpool algae: species composition determined by chance? *Oecologia* 91:150–152
- Yoshiyama RM (1981) Distribution and abundance patterns of rocky intertidal fishes in central California. *Environ Biol Fishes* 6(3–4):315–332
- Yoshiyama RM, Philippart MT, Moore JR, Coon CC, Schalk LL, Valpey CJ, Tosques I (1992) Homing behavior and site fidelity in intertidal sculpins (Pisces: Cottidae). *J Exp Mar Biol Ecol* 160:115–130
- Zander CD (1995) The distribution and feeding ecology of small-size epibenthic fish in the coastal Mediterranean Sea. In: Eleftheriou A, Ansell AD, Smith CJ (eds) *Biology and ecology of shallow coastal waters*. 28th European Marine Biology Symposium. Olsen and Olsen, Fredensborg, p 367–376