Annual and Spatial Variation of the Kelp Forest Fish Assemblage at San Nicolas Island, California

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Abstract - The kelp forest fishes of San Nicolas Island, California were studied from 1981-1986 to examine the causes of among-site and among-year variation in the fish assemblages. Fish counts and seven physical and biological variables were recorded at six sites around the island every spring and fall. Over the study period, a total of 45 fish species from 18 families were recorded, though members of nine families dominated at all sites. Among-site variation was considerable with two sites on the south side of the island having two to four times as many non-schooling fishes as the other four sites. Three variables, based on stepwise multiple regression techniques, were important predictors of site-specific fish abundance: 1) vertical relief; 2) sand cover and 3) understory algal cover. The total number of fishes varied interannually by a factor of three. Due to recruitment occurring each spring, there was a strong seasonal component to the variation in fish abundance. The extent of seasonal and interannual variation of fish abundance is an indication of the variable nature of recruitment to this area. Over the 6 yr period, there were three distinct groupings of fish assemblages corresponding to pre- (Fall 1981 - Fall 1982), during (Spring 1983 - Spring 1984) and post-El Niño (Fall 1984 - Fall 1986) sampling dates. During the El Niño sampling period, there was considerable recruitment of southern affinity fish species, increasing both the abundance and diversity of the fish assemblages. Large-scale oceanographic processes, coupled with site-specific features of the reef habitat, produce a moderately diverse, though relatively abundant fish fauna at San Nicolas Island.

Introduction

The kelp forests along the west coast of North America provide some of the richest habitat for fishes in this region (Quast 1968; Feder *et al.* 1974; Ebeling *et al.* 1980a, b). Within this habitat, the diversity and abundance of the fish assemblages may be strongly influenced by the various physical and biological components of the kelp forest community (Ebeling *et al.* 1980a). It generally has been accepted that rocky reefs with high physical relief will support more fishes than one with little relief (Quast 1968; Miller & Geibel 1973; Ebeling *et al.* 1980a) and that an area with kelp, particularly canopy forming species, will support more fishes than one without kelp (Quast 1968; Miller & Geibel 1973; Larson & DeMartini 1984; Ebeling & Laur 1988; Laur & Ebeling 1988; Bodkin 1988). Additionally, latitudinal changes in species composition occur, changing from the colder, temperate water fauna north of Pt. Conception, to a warm water fauna in southern California and off Baja California, Mexico (see Miller & Geibel 1973; Quast 1968).

Around the California Islands, kelp forests are a dominant habitat. The structural nature of these kelp forests vary around the islands, resulting in among-site variation in the abundance of fishes (*e.g.*, Santa Cruz Island, Ebeling *et al.* 1980a). Small-scale differences among islands with respect to species composition may be as large as large scale latitudinal differences that reflect the major current patterns. Such processes may be particularly important in a transition area such as San Nicolas Island. The proximity of San Nicolas Island to both the southward flowing California Current and the outer edge of the northward flow of the Southern California Eddy subjects this island to occasional shifts in water mass influence (Cowen 1985), thereby adding a significant influence on the interannual variability of the kelp forest fish assemblage.

The purpose of this study is to separate the causes of among-site from among-year variation in the fish assemblages around San Nicolas Island. Studies have been done on the fish assemblages associated with kelp forests on the inner California Islands and mainland (Quast 1968; Hobson & Chess 1978; Ebeling *et al.* 1980a, b; Stephens *et al.* 1983; Larson & DeMartini 1984) but this is the first such study of one of the outer California Islands.

Site description

This study was done at six kelp forest sites around San Nicolas Island, California (Fig. 1). The sites were chosen to be representative of the available kelp forested habitat of the island. One site was located on the north side of the island (NAVFAC), one on the southeast (EDAYTONA), two on the south (WDUTCH and EDUTCH) and two on the west end (WEU and WEK). The WDUTCH site also was used as an experimental site where California sheephead densities were altered during 1980-1982 (Cowen 1983). No other species were manipulated during this study. Brief descriptions of each site follow.

The north side site, NAVFAC, is a fairly low relief area transected with many sand channels. Some of the low flat reef is covered with dense stands of *Laminaria* and *Eisenia*. This site is typical of much of the north side of the island. EDAYTONA is relatively low relief interspersed with high relief rocky outcrops. Like the NAVFAC site, the low relief portions of EDAYTONA occasionally are influenced by sand cover. Both WDUTCH and EDUTCH have extensive vertical relief and deep crevices with depths ranging from 6-18 m these two sites are separate lobes of a single large reef system as described in Cowen (1983). The west end sites, WEU and WEK are areas of low to moderate relief They are located immediately adjacent to each other, originally chosen as a kelp free, urchin dominated area (WEU) and a nearby kelp forested area (WEK). During the time of this ongoing study, the extent of kelp coverage and urchin domination differed between the sites (Harrold & Reed 1985).

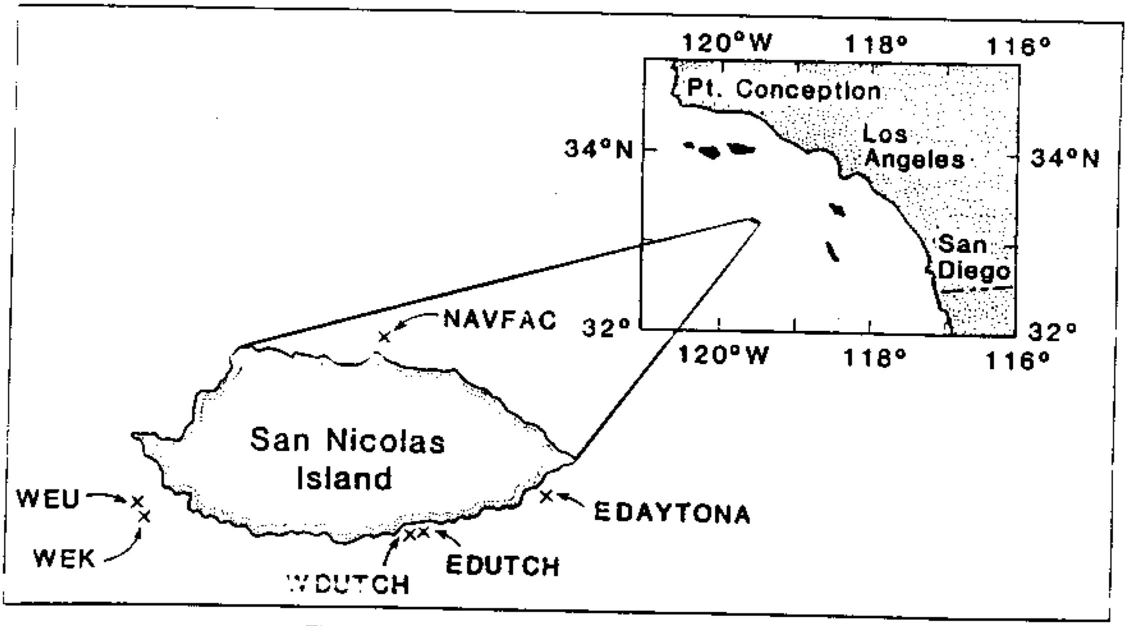

Figure 1. Map of San Nicolas Island showing study sites.

Methods

All fish species were identified and enumerated along belt transects swum by a diver who recorded all observations on an underwater tape recorder. This method minimizes bias in allowing the diver to maintain continual observation of the fish by eliminating the need to look down at a slate while writing. Transects were taken in both midwater and benthic habitats. The midwater transects were 5x50 m; the diver swam about 2-3 m off the bottom and counted all fish that were not sitting on the bottom as well as those fish typically schooling up to about 6 m off the bottom. This transect would be roughly equivalent to the bottom transects of Ebeling & co-authors (1980a, b). The benthic transects were 2x50 m. In these transects the diver carefully counted all benthic fish species, many of which live in and about the benthic algae. These transects were considerably slower than the midwater transects, hence their width was narrower. Typically, the diver would attach a 50 m tape at a point along a centrally located permanent transect and immediately start swimming out counting the midwater fishes on the way out. Once the diver came to the end of the tape, he would then count the benthic fishes on the way in. This method allowed the more mobile midwater fishes to be counted on their initial encounter with the diver, thereby minimizing bias associated with the divers presence.

Five midwater and five benthic transects were counted at each site during the fall and spring sampling periods from 1981-1986, with the following exceptions. The permanent transect at EDAYTONA could not be located in the fall of 1983, probably due to extensive sand coverage. Only NAVFAC and EDUTCH were sampled in the spring of 1984 due to weather conditions. In all, 610 transects were counted during the 5 1/2 yr of this study.

Among site and among sampling period comparisons were made only within a given sampling period or site, respectively. This eliminated any confounding variation across years and sites. Diversity was calculated as the Shannon-Weaver Index, H', as:

$$H' = -\sum_{j+1}^{S} n_j/N \log n_j/N,$$

where n_j is the number of individuals in species j, S is the total number of species, and N is the total number of individuals. To measure similarity of the fish assemblages among sites and among sampling periods, the similarity index, I, was calculated as follows:

$$I = 1.0 - [0.5(\sum_{j+1}^{S} | p_{ij} - p_{ik} |)],$$

where p_{ij}, is the proportionate abundance of species i in sample j (see Ebeling *et al.* 1980b). Clusters of similar samples were computed from matrices of I using the nearest neighbor linkage method (Sneath & Sokal 1973). Among site and seasonal differences in the mean density and number of species of fish was tested for with a two-way analysis of variance. Fish densities were $\log_{10}$ transformed.

The relationship of the within-site and among-site variation in the abundance and diversity of fishes to seven different physical and biological variables was examined with multiple regression techniques. These variables were: 1) abundance of *Macrocystis pyifera* plants; 2) understory canopy plant cover (*i.e.*, *Laminaria* and *Eisenia*); 3) encrusting algae cover; 4) encrusting invertebrate cover; 5) sand; 6) bare substrate and 7) vertical relief Measurement of most of these variables was done within 10 m of a permanent 50 m transect at each site. As such, some finer scale variation of fish abundance to these variables may have been missed since the fish transects extended as much as 50 m from the permanent transects. The first variable, *M. pyrifera* abundance, was estimated from counts along five 2x10 m transects perpendicular to each permanent transect. The next five variables were estimated as percent cover from ten 1 m^2 point contact quadrats along the permanent transect in each

Table 1. Relative abundance of all species of fishes from semiannual benthic and midwater transects sampled from 1981-1986 at six sites around San Nicolas Island, California. Values are percent of mean number of individuals.

Family and Species	NAVFAC	WEU	WEK	WDUTCH	EDUTCH	EDAYTONA
Serranidae						
Paralabrax clathratus	2.09	1.06	0.85	0.45	0.96	1.89
Kyphosidae						
Girella nigricans	0.48	0.90	1.53	2.48	2.91	2.06
Medialuna californiensis	0.12	0.47	0.49	1.82	1.55	1.13
Embiotocidae						
Brachyistius frenatus	0.10	0.47	0.24	0.66	0.17	0.22
Damalichthys vacca	0.14	0.50	0.31	0.58	0.68	0.40
Embiotoca jacksoni	0.70	3.96	3.38	2.42	1.86	3.26
E. lateralis	0.04	1.12	0.82	1.63	1.68	0.99
Hypsurus caryi	0.21	0.40	0.25	0.36	0.32	0.18
Phanerodon furcatus	0.00	0.00	0.03	0.00	0.03	0.00
Rhacochilus toxotes	0.04	0.00	0.00	0.28	0.22	0.11
Pomacentridae						
Chromis punctipinnis	15.50	23.80	17.90	23.80	40.20	28.70
Hypsypops rubicundus	0.28	0.15	0.07	0.44	0.13	1.21
Labridae						
Halichoeres semicinctus	0.03	0.01	0.02	0.02	0.00	0.00
Oxyjulis californica	70.20	52.40	58.00	26.10	11.70	33.10
Semicossyphus pulcher	1.72	2.06	1.87	3.20	3.32	4.08
Clinidae						
Gibbonsia spp.	0.39	0.35	0.37	0.61	0.14	0.20
Heterostichus rostratus	0.06	0.03	0.02	0.03	0.00	0.04
Neoclinus stephansae	0.07	0.00	0.00	0.00	0.00	0.00
Gobiidae						
Coryphopterus nicholsii	4.59	0.45	0.29	3.71	5.39	8.29
Lythrypnus dalli	0.00	0.00	0.00	0.09	0.02	0.00
L. zebra	0.00	0.00	0.00	0.04	0.00	0.00
Scorpaenidae						
Scorpaena guttata	0.02	0.00	0.00	0.02	0.00	0.04
Sebastes atrovirens	0.92	2.30	2.15	8.09	10.3	3.89
S. auriculatus	0.02	0.03	0.04	0.04	0.02	0.04
S. carnatus	0.07	0.07	0.29	0.27	0.24	0.08
S. caurinus/S. vexillaris	0.00	0.00	0.00	0.04	0.00	0.00
S. chrysomelas	0.12	0.17	0.29	0.53	0.77	0.52
S. miniatus	0.00	0.03	0.14	0.00	0.00	0.00
S. mystinus	0.05	2.19	1.70	1.22	1.12	0.33
S. rastrelliger	0.02	0.33	0.08	0.52	0.11	0.24
S. serranoides	0.69	1.04	2.71	4.57	4.92	2.81
S. serriceps	0.00	0.03	0.08	0.11	0.24	0.08
Hexagrammidae						
Oxylebius pictus	0.49	4.69	4.86	7.67	9.11	4.54
Cottidae						
Artedius corallinus	0.20	0.66	0.54	0.17	1.14	0.24
Leiocottus hirundo	0.12	0.07	0.00	0.02	0.15	0.24
Orthonopias triacis	0.35	0.07	0.33	0.11	0.42	0.72
Scorpaenichthys marmoratus	0.05	0.00	0.12	0.19	0.02	0.08
Brachiostegidae						
Caulolatilus princeps	0.02	0.00	0.00	0.01	0.01	0.05
Gasterosteridae						
Aulorhynchus flavidus	0.00	0.00	0.02	0.37	0.00	0.00
Carangidae						
Trachurus symmetricus	0.00	0.00	0.00	7.37	0.00	0.00
Pleuronectidae						
Pleuronichthys coenosus	0.02	0.00	0.08	0.00	0.02	0.04
Squatinidae						
Squatina californica	0.02	0.00	0.00	0.00	0.00	0.08
Scyliorhinidae						
Cephaloscyllium ventriosum	0.00	0.00	0.08	0.02	0.02	0.00
Torpedinidae						
Torpedo californica	0.04	0.06	0.04	0.02	0.02	0.11
Myliobatidae						
Myliobatus californica	0.02	0.04	0.02	0.00	0.00	0.00

Table 2. Summary table of mean total number, standard deviation and range of fish per hectare for each site at San Nicolas Island during 1981-1986. Midwater and benthic transects combined. See text for schooling species.

	Total Numbers				Total Numbers Without Schooling Species				
Site	$\bar{x}$	SD	Range	n	$\bar{x}$	SD	Range	$\bar{x}$ # Spp	$\bar{x}$ H'
NAVFAC	907.3	751.88	169-2745	55	113.3	34.30	78-204	12	0.88
WEU	627.4	349.45	234-1522	50	140.1	48.22	76-224	16	1.23
WEK	577.2	424.83	1286-1624	40	122.2	58.05	60-274	14	1.17
WDUTCH	1163.1	355.53	685-1891	50	407.4	94.25	267-588	18	1.48
EDUTCH	885.3	291.38	323-1294	55	359.2	89.98	284-606	16	1.51
DAYTONA	490.6	378.14	112-1168	45	159.7	64.90	79-288	15	1.35

site. Vertical relief was subjectively scored for each site (0 for no relief; 5 for extensive vertical relief and crevices).

Results

A total of 45 species in 18 families were recorded over all sites from 1981-1986, though members of nine families predominated and not all species were observed at any one site (Table 1). The total number of fishes per hectare ranged from a low estimate of 112 to a high of 2,745 individuals (Table 2). Typically, over 90% of these were of two common, resident schooling species: señorita (*Oxyjulis californica*) and blacksmith (*Chromis punctipinnis*). These two species, which often form large schools of 100s to 1000s of individuals, are patchy in occurrence and thereby contribute substantial variability to these estimates. Therefore, all statistical analyses excluded señorita and blacksmith, as well as jack mackerel (*Trachurus symmetricus*), another schooling, though non-resident, species that was encountered rarely but in very large numbers.

Among-site Variation: There was considerable among-site variation in the total number of fishes without the three schooling species (Table 3). The two sites on the south side, WDUTCH and EDUTCH, had two to four times as many fishes as the remaining sites (Table 2). These two sites also tended to have higher diversity, though only slightly. The dominant species were painted greenling (*Oxylebius pictus*), black-eyed goby (*Coryphopterus nicholsii*), California sheephead (*Semicossyphus pulcher*), kelp bass (*Paralabrax clathratus*), opaleye (*Girella nigricans*), halfmoon, (*Medialuna californiensis*), kelp rockfish (*Sebastes atrovirens*), olive rockfish, (*S. serranoides*), blue rockfish (*S. mystinus*), black perch (*Embiotoca jacksoni*) and striped seaperch (*E. lateralis*) though the relative importance of these species also varied among sites.

Similarity in species composition among all sites was low within each sampling period and over all sampling periods (Table 4). Cluster analysis indicated three distinct site pairs (Fig. 2). These groupings may be expected in part due to the proximity of some sites to others (*e.g.*, WDUTCH and EDUTCH), but the groupings also reflect differences that may be due to physical attributes of each site such as the extent of vertical relief and sand cover (see below). Certain species were more common at particular sites. For example, two rockfish species were either more abundant or only found at the two west-end sites (blue rockfish and vermilion rockfish, *S. miniatus*, respectively), while the black-eyed goby was very common at all sites except the two west-end sites. In addition, several species were relatively abundant at all sites except NAVFAC (*i.e.*, olive rockfish, striped seaperch and painted greenling).

Stepwise multiple regression analysis identified: A) three variables as being important in predicting the abundance of fishes: vertical relief, sand cover and understory algae and B) two variables for predicting the number of

Table 3. Two-way analysis of variance of total fish counts (without schooling species) and number of species. Samples were classified by site and season (spring and fall). Fish counts were $\log_{10}$ transformed.

	Fish Counts			Species Counts	
Source	df	MS	F	MS	F
Site	5	2.71	28.52***	21.31	7.15***
Season	1	0.80	8.43**	23.74	7.96**
Site x Season	5	0.04	0.44	1.49	0.50
Error	35	0.09		2.98	

Significant at: **p<0.01; ***p<0.001

species: vertical relief and sand cover (Table 5). Of these measured variables, vertical relief accounted for most of the variability (70% and 35% for fish density and number of species, respectively). For fish abundance, the addition of sand cover only explained an additional 4% of the variance, whereas sand cover accounted for an additional 10% of the variance for predicting the number of species.

Interannual Variation: Within each site, the total number of fishes varied roughly threefold during this study (Table 2). Our impression was that this variation was primarily due to large variations in the influx of juvenile fishes, although growth stages were not distinguished in the counts. Though there was considerable interannual variation in the magnitude of the influx of juvenile fishes, these were annual events and thereby also contributed to a significant seasonal signal (Table 3). Although the total number of species varied seasonally (Table 3), species composition remained fairly constant with the few exceptions discussed below. Several species, namely: rock wrasse (*Halichoeres semicinctus*); blue-banded goby (*Lythrypnus dalli*), and zebra goby (*L. zebra*) were absent from all sites until a large recruitment occurred in the summer of 1983, (*i.e.*, concomitant with the 1982-1983 El Niño). The two goby species disappeared within three sampling periods (*i.e.*, by Fall 1984), while the rock wrasse persisted to at least the fall 1985 sampling. Other species that had strong recruitment during 1983 include the kelp bass, California sheephead and garibaldi (*Hypsypops rubicundus*). Both señorita and blacksmith had strong recruitments that were more regular than the above species.

Table 4. Mean and standard deviation of similarity values (*I*) within sites (for all sampling periods) and among sites (within each sampling period).

Among Periods, Within Sites						
Site	NAVFAC	WEU	WEK	WDUTCH	EDUTCH	EDAYTONA
Mean Similarity	0.51	0.60	0.60	0.65	0.63	0.30
SD	0.13	0.16	0.09	0.09	0.15	0.20
Total Mean	0.56					
SD	0.17					
n	291					

Among Sites, Within Periods										
Sampling Period	F81	S82	F82	S83	F83	F84	S85	F85	S86	F86
Mean Similarity	0.52	0.63	0.54	0.56	0.46	0.52	0.51	0.54	0.56	0.49
SD	0.14	0.08	0.14	0.17	0.21	0.18	0.07	0.17	0.12	0.15
Total Mean		0.54								
SD	0.15									
n	145									

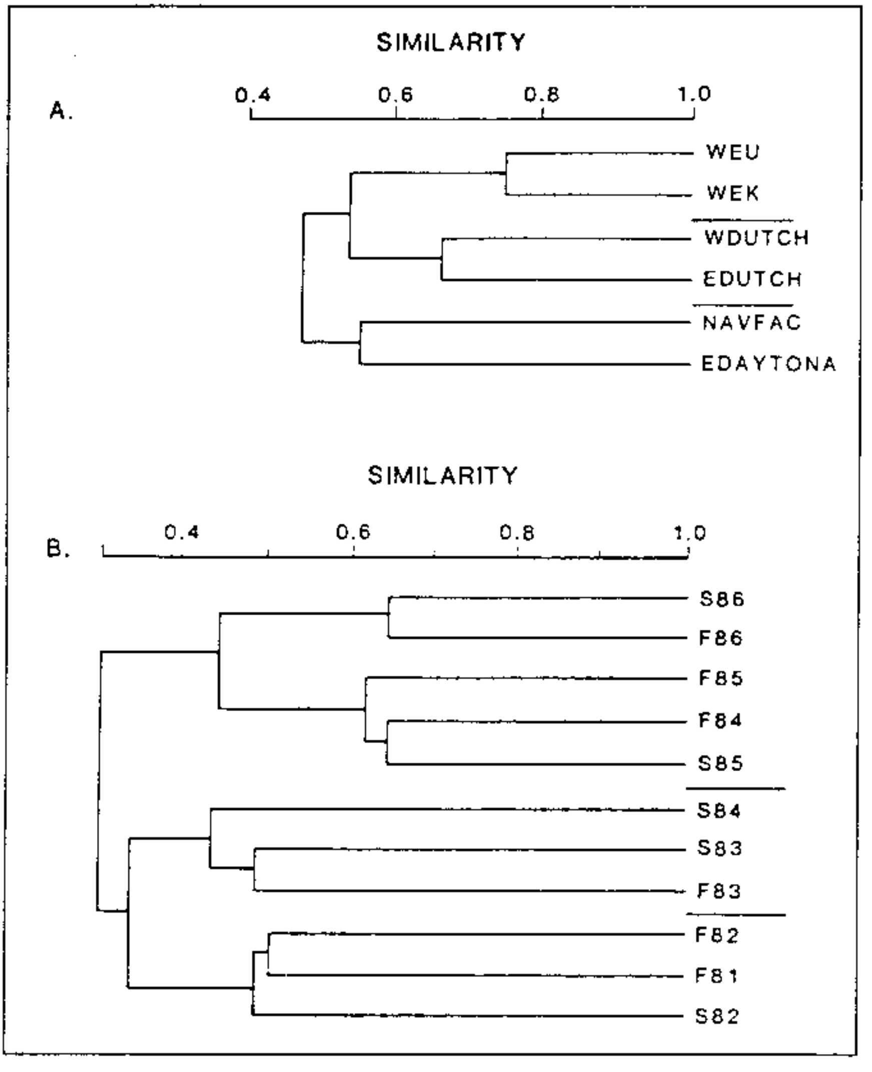

Figure 2. Clustering of fishes counted in both midwater and benthic transects. A) By site (over all sampling periods). B) By sampling date (within site comparions).

Between season (within site) similarity averaged about the same value as that among sites (Table 4). EDAYTONA was the most variable of the sites over time. There were three distinct groupings of sampling periods as determined by cluster analysis (Fig. 2). These groups correspond to pre- (Fall 1981 - Fall 1982), during (Spring 1983 - Spring 1984) and post-El Niño (Fall 1984 - Fall 1986) sampling dates. During the El Niño event a variety of species recruited (see above), some of which only persisted for about one year. Others (*e.g.*, California sheephead) recruited in large numbers during the El Niño event but persisted for the remainder of the study, thereby increasing the overall abundance from that of pre-El Niño levels.

Thus recruitment of species during the 1982-1983 El Niño event was strongest for those species that have a southern affinity relative to those that range well north of Pt. Conception (Fig. 3). The northern species did

Table 5. *Multiple regression analysis of fish density or number of species as dependent variables and Macrocystis pyrifera* abundance, understory algae, benthic algae, encrusting invertebrates, bare substrate, sand cover and vertical relief as predictor variables. Stepwise regression techniques identified the listed predictor variables as providing the best fit. The stepwise *r*-squared values represent the combined value progressively from top to bottom for each dependent variable.

Dependent Variable	Predictor Variables	Coefficient	SE	Standard Coefficient	*t*	Stepwise *r*-squared
Fish Density	Constant	4.133	0.242	0.0	17.07***	
	Vertical Relief	0.393	0.042	0.772	9.27***	0.697
	Sand Cover	0.008	0.004	0.161	2.07*	0.733
	Under Algae	-0.005	0.003	-0.151	1.78	0.751
			ANOVA			
	Source	SS	df	MS	F	
	Regression	13.77	3	4.59	43.233***	
	Redidual	4.57	43	0.11		
Number of Species (s)	Constant	12.361	0.738	0.0	16.74***	
	Vertical Relief	0.019	0.210	0.6	5.42***	0.355
	Sand Cover	0.065	0.051	-0.325	2.94**	0.461
			ANOVA			
	Source	SS	df	MS	F	
	Regression	116.45	2	58.22	18.78***	
	Residual	136.41	44	3.1		

Significant at: *p < 0.05; ** p < 0.01; *** p < 0.001

not show any trend throughout the study, whereas the southern species showed a significant increase during the El Niño (1983) which resulted in nearly a doubling in abundance of those species. Following the increase there is a slight drop in numbers, probably representing a decline due to mortality without a replenishment by further recruitment events.

Discussion

Overall, the fish assemblages at San Nicolas Island varied as much among sites in a given year as they did among years at a given site. Most of the among site variability was due to the extent of vertical relief: the areas with the greatest vertical relief supported the greatest numbers of fishes. The amount of sand cover was of secondary importance overall: sand areas supported fewer species and total number of fish than other habitat types. Several species typically associated with sand or the reef-sand interface (*e.g.*, black-eye goby and angel shark) were either more abundant or only found at NAVFAC and EDAYTONA, probably as a result of the relatively extensive sand channels intersecting the reefs at these two sites.

The lack of a significant kelp effect was probably due to the fact that each site had substantial kelp coverage, and thus all sites had sufficient threshold cover to supply necessary resources. The lack of a significant effect due to benthic invertebrate coverage or benthic algal coverage may have been due to insufficient sample size or areal representation. Fish abundance is estimated along a transect that typically is pulled taut to simulate a flat bottom. However, the associated invertebrate and algal coverage is estimated as a standardized, per meter quantity or as percent coverage. As such, the additional biomass associated with a high relief area is not accounted for. Over a 50 m horizontal distance (*i.e.*, a standard transect distance) the actual

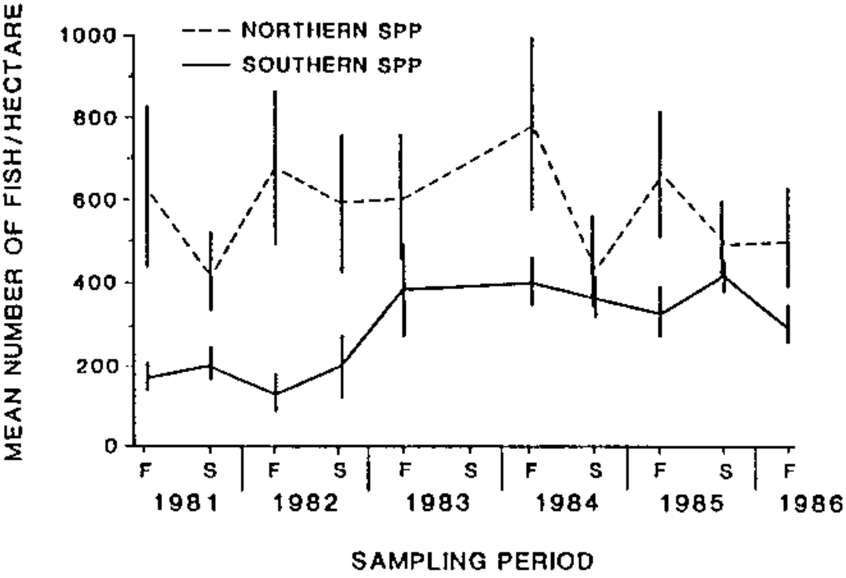

Figure 3. Mean (95% CI) number of 9 northern and 6 southern affinity fishes/ha by sampling period (all sites combined). Northern affinity fishes (*i.e.*, those species whose range extends well north of Pt. Conception) include: grass rockfish; vermilion rockfish; striped seaperch; rubberlip seaperch; pile perch; rainbow seaperch; kelp perch; white seaperch and painted greenling. Southern affinity species (primarily tropical derivatives) include: California sheephead; rock wrasse; bluebanded and zebra gobies; garibaldi and kelp bass.

distance covered along the bottom in a high relief area may easily exceed two times the distance along the same horizontal distance on a low relief reef. Though vertical relief is a good predictor of among-site fish abundance, we anticipate that estimates of total surface area would be better, especially when total benthic invertebrate and algal biomass is incorporated into the calculations. The productivity of the area also has a large effect on the growth and, therefore, size of the fishes. For example, California sheephead at San Nicolas Island weigh as much as an order of magnitude more than California sheephead found off Baja California (Cowen 1986).

The extent of seasonal and interannual variation of fish abundance is an indication of the variable nature of recruitment to this area. Some species recruited annually although their numbers varied (*e.g.*, blacksmith and señorita). Other species recruited much more irregularly (*e.g.*, California sheephead, bluebanded and zebra gobies and rock wrasse). Following the initial increase in numbers after recruitment, there was an annual, as well as longer term, decline in fish numbers. Such a decline is presumably due to mortality of many of the juvenile fishes, as well as to losses due to emigration. However, these latter losses are probably balanced by equal increases due to immigration from adjacent reefs. Stephens & co-authors (1986) also attributed temporal fluctuations in abundance of temperate reef fishes to a combination of recruitment success and physical factors affecting emmigration.

Of particular significance to this study was the timing of the 1982-1983 El Niño. During this event, the northward flowing portion of the Southern California Eddy was particularly strong and it extended both farther west and north (around Pt. Conception) than during normal years (Cowen 1985). The result of such a change in flow pattern was an anomalously high recruitment of fish species with primarily southern affinities (Fig. 3), several of which had not previously been seen at San Nicolas Island. The importance of such events in supplying recruits and, hence, influencing the species composition of a given fish assemblage depends on the frequency of occurrence of the events, the duration of the event and the longevity of the species, in other words, the ability of the species to persist until the next recruitment event (Stephens & Zerba 1981; Cowen 1985).

A variety of species, primarily of southern affinity, were noticeably absent at San Nicolas Island, even though they are common elsewhere in the Southern California Bight (Quast 1968; Ebeling *et al.* 1980a, b; Stephens & Zerba 1981; Stephens *et al.* 1983; Larson & DeMartini 1984). These include various sciaenids, but especially black croaker (*Cheilotrema saturnum*), barred sand bass (*Paralabrax nebulifer*), combtooth blennies (*Hypsoblennius spp.*), horn shark (*Heterodontus francisci*) and California moray (*Gymnothorax mordax*). The absence of these species contribute to the generally lower species diversity at San Nicolas compared to the mainland sites to the east and south. The rockfish species at San Nicolas Island were similar to those found at Santa Cruz Island, Santa Barbara and Palos Verdes (Ebeling *et al.* 1980a,b; Stephens *et al.* 1983), but were more speciose compared to rockfish assemblages occurring further south at San Onofre and off the San Diego coast (Quast 1968; Rosenthal *et al.* 1974; Larson & DeMartini 1984). Except for a noticeable lack of lingcod (*Ophiodon elongatus*) most of the common central California fishes found off Monterey (Miller & Geibel 1973; Bodkin 1986) were present at San Nicolas Island.

The zoogeography of the entire California Island region is heavily influenced by variation in the timing and intensity of current patterns, which results in interannual variation in the transport of larvae to these various sites (Cowen 1985). The more removed the site is from the "typical" current path, the less commonly recruitment of the southern species will occur. As seen in this study and others around the Southern California Bight, the southern species are more completely represented at the inner islands and along the mainland. A similar pattern is found for invertebrates (Efford 1970; Seapy & Littler 1980) and intertidal algae (Murray *et al.* 1980; Murray & Littler 1981). As a result, the overall diversity will be reduced at the outer island sites (*e.g.*, San Nicolas Island).

In summary, the combined influence of the oceanic regime on recruitment and the suitability of habitat at San Nicolas Island acts to produce a moderately diverse, though relatively abundant and large fish fauna. Once the fishes arrive at the reef the suitability of the habitat is important to their survival. Choat & co-authors (1988) report similar results to the present study in their analysis of a 12 yr time-series of reef fish abundance in northern New Zealand. In their study, interannual variation in fish abundance was primarily driven by oceanic processes, whereas the among-site variability appeared to result from habitat selectivity by juvenile fishes at settlement. In both studies, however, it is still not clear what the relative importance these factors play (*e.g.*, role of oceanographic processes in affecting supply of larvae vs. survival of juveniles) in determining population size and diversity. Further work is needed that examines both the relationship between oceanographic processes and recruitment success, which will require additional long time-series records, as well as site-specific requirements of juvenile fishes.

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