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Distribution Patterns of Rocky Subtidal Fishes Around the California Islands

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Abstract – Relative abundances of 60 shallow-water, rocky-habitat fishes around the eight California Islands were assessed during 309 reconnaissance scuba-diving surveys conducted from 1978 to 1986. Most fishes with southern or northern biogeographic range affinities showed clear southeast to northwest trends of decreasing or increasing abundances, respectively, among the islands. Four island groups based on southern vs. northern species abundances were evident: 1) Santa Catalina and San Clemente (warm); 2) Anacapa, Santa Barbara, and Santa Cruz (warm intermediate) 3) San Nicolas and Santa Rosa (cold intermediate) and 4) San Miguel (cold). Island groupings by satellite sea surface temperatures generally were similar. These island-wide ichthyofaunal and temperature patterns correspond with generalized hydrographic conditions in the Southern California Bight, confirming the concept of the California Islands as an important transition area between northern and southern biogeographic provinces.

Introduction

The shallow-water ichthyofauna south of Pt. Conception is quite diverse, owing to the variety of mainland and island habitats available and to this region's transitional location between northern (cold-temperate) and southern (warm-temperate) biogeographic provinces (Horn & Allen 1978; Horn 1980; Allen 1985). The California Islands are centrally located within this major transition region and contain the most pristine marine habitats remaining in southern California (Murray *et al.* 1980; Seapy & Littler 1980). However, most nearshore fish studies have taken place along mainland shores (Allen 1985). Except for various observations (*e.g.*, Hewatt 1946; Limbaugh 1955) and isolated studies (*e.g.*, Hobson & Chess 1976; Ebeling *et al.* 1980a,b), little is known about the composition of subtidal fish assemblages around the eight islands.

This study is part of a long-term effort by the Channel Islands Research Program to characterize the subtidal flora and fauna of the California Islands. My objective here is to describe subtidal fish abundances at the eight islands. Specifically, I compare the relative abundance patterns of 60 rocky-habitat taxa with respect to their biogeographic affinities and water temperature.

Methods

Three-hundred and nine reconnaissance scuba-diving surveys of shallow-water (0-18 m depth) rocky habitats around the eight California Islands were conducted for nine years (1978-86) during 73 cruises sponsored by the Channel Islands Research Program or the Channel Islands National Park (Fig. 1). Nearly all of the surveys (93%) were conducted from June to November. Representative sites around each island were explored, although weather conditions restricted surveys at highly-exposed sites. Typically, 2-3 dives were made at each site by 4-8 divers. Search efforts varied from 4-49 person-dives per survey ($\bar{x}$=13), with 86% of the surveys consisting of 6-20 person-dives. Diver pairs searched haphazardly throughout each survey site, recording all species of fishes observed and estimating their abundances. Afterwards, a concensus was reached among the divers for each species regarding its level of abundance relative to the range of abundance typically exhibited by

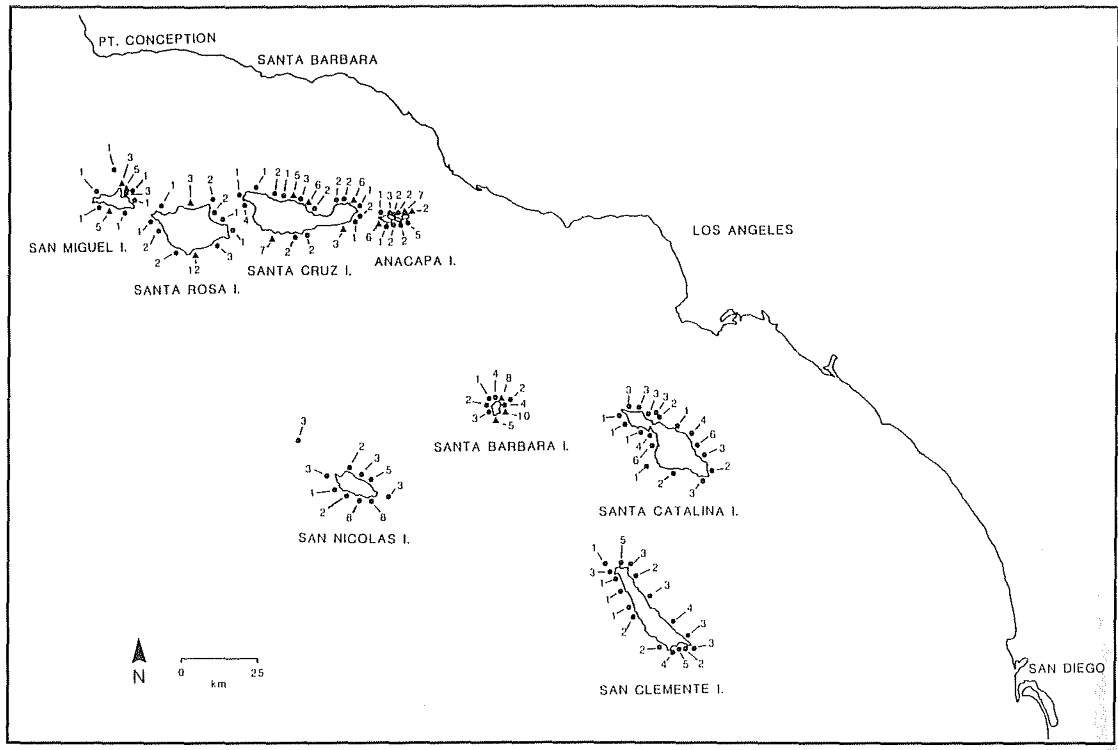

Figure 1. Location of the 105 California Island regions surveyed during the period 1978-1986. The number of different surveys (different sites or different years at same site) per area is indicated. Triangles represent areas that include Channel Islands National Park monitoring sites.

the species. The purpose is not to compare actual abundances of different species, but to evaluate changes in relative abundance levels for each species among the California Islands. The relative abundance levels were expressed as 0: (absent); 1 (rare); 2 (present); 3 (common); 4 (abundant) or X (species seen but abundance level not determined). While the relative abundance ranks represent different actual abundances for each species, overall the relationship between the categories approximates a logarithmic (base 3) progression. Table 1 provides examples of this log base 3 relationship for fishes whose actual range of abundance typically is low (*e.g.*, *Myliobatis californica*), medium (*e.g.*, *Hypsypops rubicundus*) and high (*e.g.*, *Oxyjulis californica*). For all taxa, the actual abundance ranges upon which relative abundance levels were based remained essentially the same throughout the study.

Efforts were made to survey representative sites (characterized by rock or mixed rock and sand habitats) within all major island regions. Prominant geographical and geological features were used to define 105 regions for the eight islands (Fig. 1). These regions range from small, isolated offshore rocks (*e.g.*, Begg Rock) to relatively uniform coastal stretches up to 7 km in length (*e.g.*, northeast San Clemente Island). The mean length is 2.5 km. Weather and other logistical factors resulted in more surveys in some regions than in others. In order to minimize survey effort bias, data for all survey sites located within each region were combined by averaging the relative abundance values for each fish species. Since relative abundance levels represent a log base 3 scale, values were linearized by taking the antilog base 3, averaged, and then transformed back by taking their log base 3.

Table 1. Representative examples of the logarithmic (base 3) relationship of estimated fish abundances categorized in relative abundance terms as rare (1), present (2), common (3) or abundant (4). Actual abundance estimates (shown as abundance ranges) represent the approximate number of fishes seen by a slowly swimming diver searching for all species haphazardly for 30 min. Means for each abundance range for the four relative abundance categories demonstrate the log base 3 progression.

	Relative Abundance			
Example Species	Rare 1	Present 2	Common 3	Abundant 4
Myliobatis californica				
Abundance Range	1	2-4	5-13	14-40
Mean No. Individuals	1	3	9	27
Hypsypops rubicundus				
Abundance Range	1-3	4-9	10-27	28-81
Mean No. Individuals	2	6	18	54
Oxyjulis californica				
Abundance Range	1-22	23-67	68-202	203-607
Mean No. Individuals	15	45	135	405

Of 124 fish taxa observed, 60 fishes typical of rock or rock/sand habitats were chosen for comparative analysis. The others were primarily sand dwellers or were rare, cryptic, or difficult to identify in the field. The 60 species were divided into three geographic affinity categories (southern, northern, intermediate) based on their latitudinal ranges as given in Eschmeyer & co-workers (1983). Twenty-one species with southern affinities are common in warm-temperate waters south of Pt. Conception and generally range as far south as southern Baja California to the Gulf of California (Table 2). Twenty-three species with northern affinities are common in cold-temperate waters north of Pt. Conception (Table 3). They typically range as far north as northern California to British Columbia, and are rare south of southern California except in deeper water or upwelling areas. Sixteen species with intermediate affinities range both north and south of Pt. Conception, with either widespread or transitional latitudinal distributions (Table 4). The three categories are similar to those used by Horn & Allen (1978) for fishes and Seapy & Littler (1980) for invertebrates. Average relative abundances for each species and each geographic affinity group per island were calculated in the same manner as described above.

General sea surface temperatures for the waters surrounding the eight California Islands were obtained from satellite data compiled by the National Weather Service (Washington, DC) in the form of semi-monthly means for 1° latitude-longitude blocks. Temperatures for islands near block borders were calculated by averaging the values from adjacent blocks.

Results

Most of the fish species with northern or southern affinities showed characteristic trends in relative abundance among the eight California Islands (Tables 2-3). The island series (southern to northern affinities) that best fits these overall trends is the following: Santa Catalina (SCA), San Clemente (SCL), Anacapa (ANA), Santa Barbara (SBA), Santa Cruz (SCR), San Nicolas (SNI), Santa Rosa (SRO) and San Miguel (SMI). Thirteen of the 21 southern fishes showed greater than fourfold decrease in mean relative abundance from SCA to SMI (a decrease of > 1.26 in relative abundance level), with generally declining intermediate values for the other islands (>> trend in Table 2). These are good

Table 2. Mean relative abundances of fishes with southern biogeographic affinities at the eight California Islands. Fishes are listed in order of decreasing abundance at SCA. See text for explanation of trends.

	SCA	SCL	ANA	SBA	SCR	SNI	SRO	SMI	TREND
Chromes punctipinnis	3.3	2.7	2.7	2.4	2.5	2.5	1.8	1.4	>>
Lythrypnus dalli	3.0	2.3	1.1	0.6	2.2	0.2	0.2	0.1	>>
Alloclinus holderi	2.9	2.7	2.7	2.7	2.1	0.3	0.3	0	>>
Hypsypops rubicundus	2.9	2.7	2.3	2.4	1.9	1.2	0.6	0	>>
Semicossyphus pulcher	2.8	3.3	2.6	2.8	2.8	3.4	2.5	1.8	=
Paralabrax clathratus	2.8	2.8	2.9	2.5	2.6	2.3	2.1	1.0	>>
Halichoeres semicinctus	2.7	2.2	1.9	1.9	1.9	0.3	0.9	0	>>
Medialuna californiensis	2.6	2.2	2.5	2.3	2.1	2.0	1.8	1.2	>>
Girella nigricans	2.5	2.2	2.2	2.2	2.2	2.3	2.0	0.6	>>
Gymnothorax mordax	2.4	1.6	0.7	1.5	0.6	0	0	0	>>
Heterodontus francisci	2.1	1.5	0.7	1.0	1.2	0	0.7	0	>>
Scorpaena guttata	1.9	2.0	1.0	1.8	1.1	0.4	0.3	0.2	>>
Lythrypnus zebra	1.6	1.5	1.0	1.4	1.5	0.4	0.2	0.2	>>
Anisotremus davidsonii	1.4	0.3	0.1	0.8	0.4	1.2	0	0	>>
Leiocottus hirundo	0.7	0.6	1.1	1.6	1.2	1.1	1.2	0.4	=
Cephaloscyllium ventriosum	0.7	0.3	0.7	0	1.0	0.5	1.5	0.9	=
Hermosilla azurea	0.6	0.4	<0.1	0.3	0	0	0	0	>
Xenistius californiensis	0.5	0.1	0	0	0	0	0	0	>
Paralabrax nebulifer	0.5	<0.1	0.1	0	0.3	0	0	0	>
Cheilotrema saturnum	0.4	0	0	0	0	0	0	0	>
Stereolepis gigas	0	0	0.1	0.1	0	0	0.2	0	=

indicator species for warm-water conditions, such as are found at SCA or SCL. Four southern-affinity fishes were found in low numbers at the more southerly or easterly islands and were absent at the more northerly or westerly islands (> trend). Four other species displayed either a uniform pattern or no clear trend among the islands (= trend). No

Table 3. Mean relative abundances of fishes with northern biogeographic affinities at the eight California Islands. Fishes are listed in order of decreasing abundance at SMI. See text for explanation of trends.

	SCA	SCL	ANA	SBA	SCR	SNI	SRO	**SMI**	TREND
Sebastes mystinus	0.1	0.1	0.3	0	1.8	2.3	2.2	2.9	<<
Oxylebius pictus	0.6	1.1	2.0	2.0	2.3	2.7	2.6	2.7	<<
Coryphopterus nicholsii	2.6	2.2	2.6	2.5	2.7	2.5	2.2	2.6	=
Embiotoca lateralis	0	0.2	1.2	1.6	1.9	2.3	2.2	2.5	<<
Sebastes caurinus	0.1	0	0.6	0.4	0.9	1.5	1.8	2.5	<<
Sebastes chrysomelas	0.1	0.4	1.2	1.8	1.9	1.9	1.8	2.4	<<
Damalichthys vacca	1.2	1.0	1.9	1.9	2.0	2.2	2.5	2.3	<
Artedius corallinus	0.1	0.1	0.4	0.4	0.3	1.8	1.9	2.2	<<
Scorpaenichthys marmoratus	0.5	0.1	0.4	0.8	1.1	1.2	1.9	2.2	<<
Sebastes serranoides	0.3	0.7	1.5	1.6	1.7	2.3	1.9	2.1	<<
Sebastes carnatus	0.1	0.1	0.2	1.5	1.4	1.3	1.5	2.0	<<
Aulorhynchus flavidus	0	0	0	0	0.1	0	0.4	1.7	<<
Brachyistius frenatus	1.7	2.2	2.4	2.0	1.9	2.3	1.8	1.6	=
Hypsurus caryi	<0.1	0.5	1.4	1.1	0.8	2.2	2.0	1.5	<<
Sebastes rastrelliger	0.9	0.6	0.1	1.4	1.4	1.3	1.4	1.5	<
Pleuronichthys coenosus	1.3	1.0	1.3	1.4	1.3	1.2	1.4	1.4	=
Ophiodon elongatus	0	0	0	0	0	0	0.1	1.1	<
Sebastes miniatus	0	0	0	<0.1	<0.1	0.2	0.5	0.9	<
Sebastes melanops	0	0	0	0	<0.1	0	0.1	0.8	<
Hexagrammos decagrammus	0	0	0	0	0	0	0	0.8	<
Cymatogaster aggregate	1.1	0.2	1.1	0.8	1.3	0.8	1.3	0.6	=
Sebastes paucispinis	<0.1	0	0.1	0	0.1	0.6	0.5	0.5	<
Torpedo californica	0.1	0	0.5	<0.1	0.2	0.1	0.2	0.1	=

Table 4. Mean relative abundances of fishes with intermediate (widespread or transitional) biogeographic affinities at the eight California Islands. Fishes are listed in order of decreasing abundance at SCR. See text for explanation of trends.

	SCA	SCL	ANA	SBA	**SCR**	SNI	SRO	SMI	TREND
Oxyjulis californica	2.7	2.7	2.6	2.5	2.6	3.1	2.7	2.4	=
Embiotoca jacksoni	2.6	2.2	2.6	2.2	2.6	2.7	2.5	2.0	=
Sebastes atrovirens	1.2	1.9	2.1	2.0	2.3	2.6	2.2	2.6	<<
Trachurus symmetricus	0.3	0.8	2.0	1.3	2.1	0.8	1.6	0.4	=
Gibbonsia spp.	1.8	1.1	1.8	2.2	2.0	1.7	1.9	2.1	=
Heterostichus rostratus	1.8	1.9	2.0	2.0	1.9	1.3	1.8	0.8	=
Atherinidae	1.6	1.4	2.2	2.0	1.8	1.4	1.5	0.7	=
Sebastes serriceps	2.0	1.8	1.3	1.8	1.8	1.3	1.6	1.3	=
Rhacochilus toxotes	1.2	0.5	0.9	1.9	1.8	1.4	1.4	1.1	=
Phanerodon spp.	0.9	0.6	0.7	0	1.8	0.7	1.3	0.8	=
Neoclinus stephensae	0	0	0.2	0	1.3	0.7	1.7	1.0	<
Myliobatis californica	1.7	1.5	1.2	1.8	1.2	0.9	1.0	1.2	=
Squatina californica	1.0	0.5	1.0	0.5	1.2	0.5	1.6	0.8	=
Orthonopias triacis	0.1	0.4	0.7	1.5	1.0	2.0	1.8	2.3	<<
Caulolatilus princeps	0.6	0.4	0.2	1.3	0.9	1.5	0.7	0.4	=
Rathbunella hypoplecta	0	0	0	0	0.4	0	0.8	0.2	<

southern species showed a positive trend in the island series from SCA to SMI.

Similar trends though in the opposite direction were evident for northern-affinity species (Table 3). Eleven of the 23 northern fishes showed greater than fourfold decrease in mean relative abundance from SMI to SCA, again with intermediate values for the other six islands (= trend). These are good indicator species for cold-water conditions such as are found at SMI. Seven other northern species revealed similar trends but of lesser magnitude (< trend). The remaining five species were distributed fairly evenly throughout the islands trend). No northern species showed a positive trend in the series from SMI to SCA.

Intermediate fishes, whose geographic ranges did not fit into distinct northern or southern patterns, mostly did not show increasing or decreasing trends among the islands (Table 4). Two exceptions (*Sebastes atrovirens* and *Orthonopias triacis*) displayed trends indicative of northern indicator species. Two others (*Neoclinus stephensae* and *Rathbunella hypoplecta*) exhibited similar but less obvious patterns. Three of the intermediate fish taxa (*Gibbonsia* spp., Atherinidae, *Phanerodon* spp.) may represent more than one species.

Island biogeographic patterns can be clarified by averaging the relative abundances for all northern, southern, and intermediate fishes respectively (Fig. 2). Using the same island order as above, fishes with northern affinities show progressive increases in relative abundance from SCA to SMI. Fishes with southern affinities reflect the opposite trend, while intermediate fishes have no obvious pattern. Considering northern and southern fishes together, four island groupings become evident. Warm-water fishes predominate at SCA and SCL. ANA, SBA, and SCR have warm-intermediate fish faunas. SNI and SRO have cold-intermediate ichthyofaunas. Finally, cold-water fishes are best represented at SMI. These groupings can be summarized by comparing the combined relative abundances of southern vs. northern species among the eight islands. Here I define a relative abundance index of southern species as equal to the summed relative abundances of southern species divided by the summed relative abundances of both southern and northern species. Summations were performed on antilog base 3 transformed data as described above for the means. The resultant relative abundance indices are shown in Fig. 3, together with the island groupings.

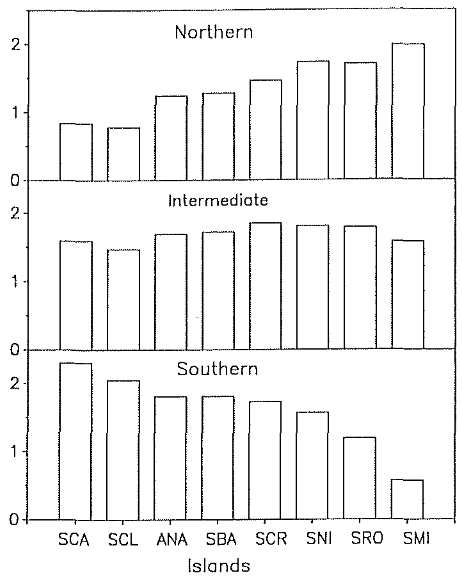

Figure 2. Mean relative abundances of fishes with northern, intermediate, and southern biogeographic affinities at the eight California Islands.

Specific water temperature regimes to which subtidal fishes at the various islands are exposed are not completely known. However, sea surface temperature data from satellite infrared photographs likely reflect general temperature relationships (Bernstein *et al.* 1977). Mean monthly sea surface temperatures for 1981-1986 reveal characteristic island trends (Fig. 4). Most islands have distinct temperature regimes, the exceptions being the pairs SCA/SCL and ANA/SNI. Island sea surface temperature differences are most pronounced during the period April-October. Ordering the islands from warmest to coldest temperature regimes results in the following series: SCA, SCL, SBA, SNI, ANA, SCR, SRO and SMI. Three island groupings are evident, as indicated by mean annual sea surface temperatures (Fig. 3). SCA, SCL and SBA are the warmest islands. SNI, ANA and SCR are intermediate. SRO and SMI have the coldest sea surface temperatures. Island groupings by temperature are slightly different from groupings by relative abundance of southern vs. northern species (Fig. 3). Overall, there is an obvious southeast to northwest trend of decreasing abundance of southern species associated with decreasing water temperatures.

Discussion

Fish Surveys: Fish abundance is difficult to measure, primarily because fishes are mobile and have varied behavior patterns. Nondestructive sampling techniques require numerous replicates to obtain a precise, although not necessarily accurate, census of one habitat (Sale & Douglas 1961; Davis & Anderson, 1989). Tremendous quantitative sampling efforts would be needed to survey adequately the complex mosaic of habitats typically present within a coastal section. Given the practical limitations of time, personnel and funds, reconnaissance surveys employing relative abundance estimates permit reasonable overall characterization of heterogeneous nearshore regions as long as the estimation criteria are standardized. Relative abundance rankings provide a level of information intermediate between presence/absence and actual counts that is adequate for identifying major patterns.

Sampling variables in this study include those associated with search effort, oceanographic conditions at the site, types of habitats and biotic communities, and times of surveys. Although search efforts (person-dives per survey) varied, several divers were able to adequately characterize the main fish assemblage. Additional divers provided progressively diminishing amounts of new information. Searcher experience varied as well, but the fishes chosen for analysis were relatively conspicuous and identifiable. On all cruises, the author was the primary surveyer, with supplemental input from the other divers.

Oceanographic variables at survey sites included temperature, surge, current, turbidity and depth; however, surveys with inadequate data due to extreme conditions (*e.g.*, poor visibility) were eliminated. The entire depth

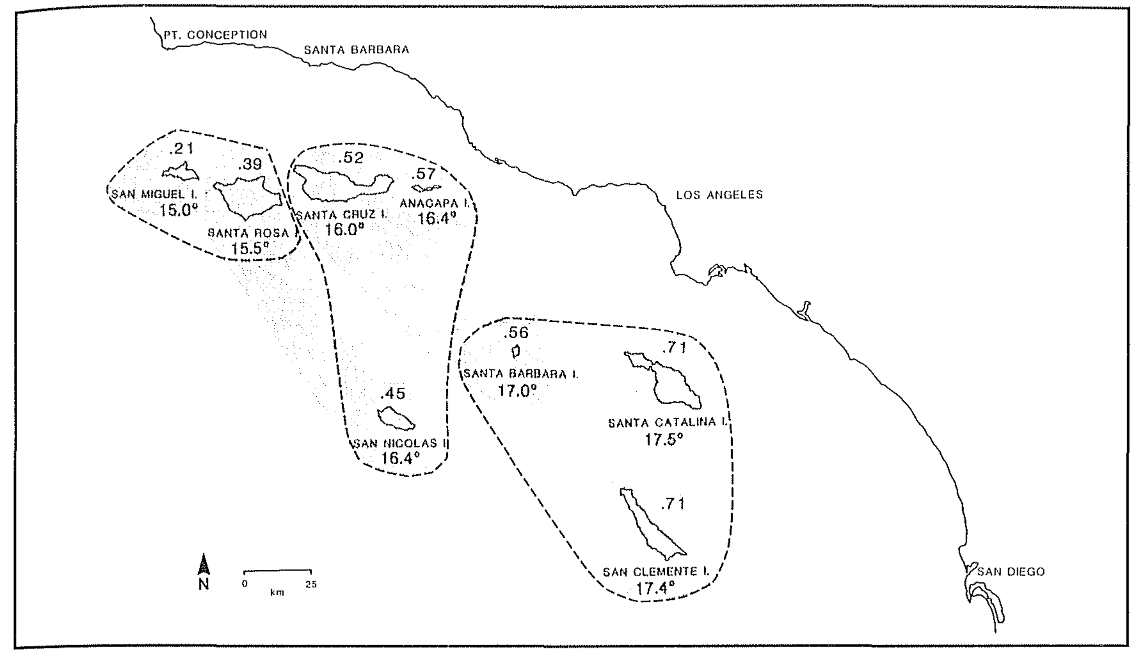

Figure 3. Island groupings by proportion of southern vs. northern fish species relative abundances (shaded areas) and by sea surface temperatures (areas enclosed by dashed lines). The relative abundance index of southern species and mean sea surface temperature for 1981-1986 are shown above and below each island respectively. See text for details.

range of 0-18 m was explored at each site wherever possible.

Fish species composition is known to vary with structural habitat and biotic community types (Ebeling *et al.* 1980a). In this study rock and rock/sand habitats varied in substratum, slope, and relief both within and among station areas. Associated communities varied as well, especially with regard to algal cover. Extremes ranged from dense *Macrocystis pyrifera* forests to "barren" reefs overgrazed by sea urchins. Within sampling areas, abundance estimates for the various habitats and communities were pooled to reflect the overall character of the site. Numerous sites were combined for the whole island comparisons (Fig. 1), thereby minimizing the influence of individual site differences.

Survey dates varied seasonally (mostly within the period June-November) as well as annually (from 1978-1986). Seasonal and annual variations in nearshore fish species assemblages may be less important than site, habitat, and community-associated differences (Ebeling *et al.* 1980b). I observed some increases in abundance of southern fishes at the colder-water islands in the years following the 1982-1983 El Niño oceanographic anomaly. However, averaging data throughout the nine-year period likely reduced temporal biases and reflected broad-scale trends. Long-term phenomena, such as the general seawater warming trend which has occurred since 1976 (Norton *et al.* 1985), may have more important direct (*e.g.*, physiological) or indirect (*e.g.*, loss of kelp beds) effects on the ichthyofauna than individual year differences.

Island Patterns: The complex oceanographic circulation patterns occurring within the Southern California Bight have been extensively studied (see review by Hickey 1979). Through time, each of the eight California Islands is exposed to differing influences from the southerly-flowing colder waters of the California Current and the

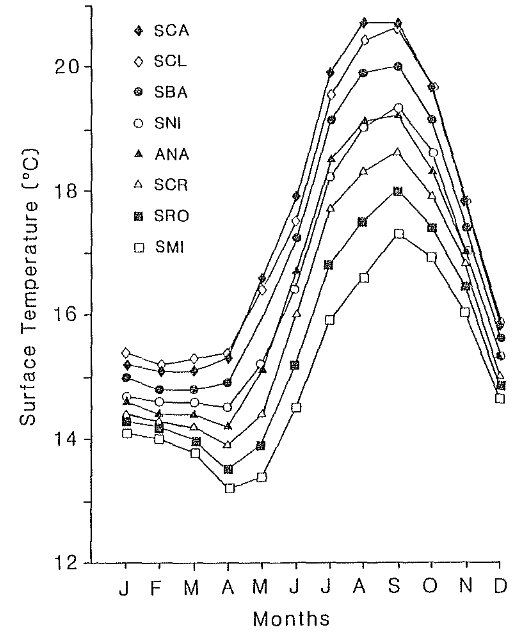

Figure 4. Mean monthly sea surface temperatures at the eight Channel Islands for the period 1981-1986. Data were taken from National Weather Service (Washington, D.C.) semi-monthly ocean temperature analyses.

northerly-flowing warmer waters of the Southern California Eddy. Neushul & co-workers (1967) proposed that the marine flora and fauna of the islands should reflect the oceanographic conditions to which they have been exposed, thus the overall affinities of each island could be characterized by the proportion of northern and southern biotic elements.

The relative abundance patterns for most southern and northern fishes in this study show obvious (and opposite) islandwide trends (Tables 2-4; Figs. 2-3) that are consistent with the above concept. Typically, the cold California Current flows south past Pt. Conception bathing SMI and to a lesser extent SRI and the western portion of SCI. Further south, SNI is far enough offshore also to receive these colder waters. On the other hand, the southeastern islands, SCA and SCL, are most influenced by the warm Southern California Eddy. Continuing north, this warm water affects SBI, ANA and the eastern parts of SCR. Thus island ichthyofaunal patterns correspond with generalized hydrographic conditions (Fig. 3).

The island groupings identified here for fishes are similar to those described for benthic biota by Neushul & co-workers (1967), for intertidal algae by Murray & co-workers (1980), and for intertidal macroinvertebrates by Seapy & Littler (1980). All the studies agree that SCA and SCL have the greatest southern affinities; SMI, SNI and SRO the greatest northern affinities; and SBA, ANA and SCR intermediate affinities. Relatively minor discrepencies in the level of southern vs. northern affinities between individual islands (especially the intermediate islands) exist among the four studies. These differences might be related to the fact that the intertidal studies (Murray *et al.* 1980; Seapy & Littler 1980) were based on only one or two sites per island, or that intertidal species are subject to slightly different oceanographic conditions than their subtidal counterparts.

Island groupings by fish species composition generally correlate with surface water temperature patterns; however, SNI and SBI were warmer and ANA colder than expected (Fig. 4). Comparison of satellite data with surface temperatures recorded during the survey cruises revealed good agreement for SCA, SCL and SRO, but satellite temperatures consistently were higher for SNI, SMI and SBA, and often were lower for ANA and SCR. These discrepancies may explain the differences in temperature vs. species composition island groupings (Fig. 3), and likely are due to the large size of the 1° latitude-longitude temperature blocks. Also, it is not known how sea surface temperature patterns are related to complex nearshore subsurface temperature profiles, although there is some evidence that open ocean surface and water-column thermocline temperature distributions can be correlated (Bernstein *et al.* 1977).

Water temperature is not necessarily the sole explanation for northern and southern ichthyofaunal distribution patterns. In the Southern California Bight, temperature, currents, and recruitment phenomena are all related (Hickey 1979). Warm currents carry the larvae of southern species northward to differing degrees seasonally and annually. For example, patterns of recruitment of a southern fish (*Semicossyphus pulcher*) at San Nicolas Island can be related to year-to-year variations in the northward flow of the Southern California Eddy (Cowen 1985). Cold currents can do the same for southern transport of larvae of northern species. Other physical processes, such as upwelling, wind patterns and climatic anomalies (*e.g.*, El Niño) affect larval dispersal. In addition, the nearshore environment may experience localized hydrographic conditions related to coastline configuration and bottom topography. A host of biological factors interact in complex ways with physical events, resulting in recruitment schemes that may be unique for each species. These include location and density of reproductive adults, timing of egg or larval release, length of larval life, larval swimming and settlement behavior, competition, predation and adult life span. Further studies are needed to distinguish the various physical and biological factors that determine fish distribution patterns around the California Channel Islands.

Acknowledgments

I thank the many volunteers of the Channel Islands Research Program who helped in the underwater surveys. J. Chomeau and the crew of the *R/V Cormorant* provided expert topside assistance. Staff of the USC Catalina Marine Science Center provided shoreside support. I am grateful to G. Davis and other Channel Islands National Park personnel for the opportunity to participate in Kelp Forest Monitoring Program cruises. I also thank J. Coyer for helpful comments on the manuscript and C. Vandenberg for assistance in its preparation. This work was sponsored by The Tatman Foundation. Additional support was provided by the Channel Islands National Park.

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Contribution No. 120 from the Catalina Marine Science Center.

The Effect of Food Density and Dispersion on Patch Selection by Foraging Black Surfperch

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Abstract. – Response to patterns of food density and dispersion was examined in young-of-year black surfperch (*Embiotoca jacksoni* Agassiz). Field studies of foraging revealed that the density of invertebrate prey on a substrate type was positively correlated with preference (selectivity). Forager responses to prey dispersion patterns varied with prey density. In both the field and the laboratory, when choosing among types of substrates containing equal mean prey but differing in variability, young-of-year black surfperch showed a declining preference for the more variable type as prey density increased. Laboratory experiments revealed that the surfperch employed a simple feeding mechanism involving random visits to patches, a higher probability of initiation of feeding on food-rich than food-poor patches, and few bites taken per patch, regardless of food level.

Introduction

An issue of great importance in predicting which patches will be chosen by a forager regards how characteristics of the feeding patches other than food density impact selection. For example, variation in physical structure among patches can alter the harvesting of food or provide differing degrees of protection to the forager from its predators (Stein 1979; Savino & Stein 1982; Cerri 1983; Schmitt & Holbrook 1985; Holbrook & Schmitt 1988a). The presence or density of predators can greatly reduce the value of an otherwise acceptable food patch (Milinski & Heller 1978; Sih 1980; Cerri & Fraser 1983; Werner *et al.* 1983a, 1983b; Schmitt & Holbrook 1985; Holbrook & Schmitt 1988b). One goal of field investigations of foraging behavior is to understand how these various constraints, in conjunction with underlying patterns of food distribution, influence patch choice.

Most studies of patch selection have concentrated on food density as the criterion influencing the behavior of foragers. Usually, the average density of food items is compared among types of patches. An additional way in which patch types might differ from one another is in the dispersion of food items. Two patch types that have the same average food level can have very different distributions of food items among patches. Since search time or other components of foraging behavior could be affected by the degree of prey dispersion, the relative value to a forager of patches that are similar in prey density but not in prey dispersion might be quite different.

Natural environments are often characterized by patch types with different spatial distributions of prey. Yet few studies have attempted to measure response of foragers to food dispersion patterns (Weissburg 1986), despite some theoretical interest (Oster & Wilson 1978; Real 1980; Caraco 1980, 1983; Weissburg 1986). In this paper, I explore response to patterns of food density and dispersion by young-of-year black surfperch (*Embiotoca jacksoni Agassiz*). Individuals feed on crustaceans harvested from the surfaces of foliose algae and other benthic substrates in reef environments. Although the size structure and species composition of prey are similar among species of algae used by juvenile black surfperch for feeding (Schmitt & Holbrook 1984b), the species of algae differ substantially in mean densities of prey they contain (Schmitt & Holbrook 1985). The species of algae (patch