DIVERSITY AND ECOLOGICAL ROLES OF NONCOMMERCIAL FISHES IN CALIFORNIA MARINE HABITATS

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ABSTRACT

The marine fish fauna of California is highly diverse and consists of about 550 species of varied origin and complex distribution. Species richness is greatest in southern California and gradually declines northward in a pattern that is significantly correlated with increasing latitude and decreasing minimum surface temperature. Greater activity with regard to species range terminations occurs in southern California than in central and northern California and is consistent with the higher species richness in southern California waters.

Less than 3% of the species of this diverse fauna contributes significantly to the California commercial fish catch. Many noncommercial species, therefore, perform essential roles in the habitats occupied by economically important fishes. The noncommercial species may function as 1) predators or prey, thus as direct trophic links in the food chain of commercial species; 2) competitors of exploited species; or 3) fishes which otherwise, by their ecological position, affect community structure and indirectly influence economically important populations.

The fish communities and certain ecologically important species are briefly described for each of seven major habitats in California marine waters: 1) deep midwaters, 2) epipelagic zone, 3) coastal demersal region, 4) kelp beds/subtidal reefs, 5) rocky intertidal zone, 6) harbors, and 7) bays and estuaries. Bays and estuaries are emphasized in the concluding statements as important but diminished and altered habitats in need of preservation and wise management.

RESUMEN

La fauna de peces marinos de California es sumamente diversa y comprende unas 550 especies que proceden de varias regiones y que presentan una distribución compleja. La riqueza en especies es mayor en el sur de California y disminuye gradualmente hacia el norte siguiendo un patrón que se relaciona con la latitud y el descenso en la temperatura mínima de las aguas de superficie. En el sur de California se encuentran más límites de zonas de distribución de las especies que en el centro y norte de California, lo cual concuerda con el mayor número de especies que habitan las aguas del sur de California.

Menos del 3% de las especies de esta fauna diversa contribuyen a la captura comercial de los peces de California. Por lo tanto, muchas especies que carecen de valor comercial desempeñan un papel esencial en el hábitat ocupado por los peces de importancia económica. Las especies que no son comerciales pueden funcionar como 1) predadores o presas, así son eslabones tróficos directos en la cadena alimenticia de las especies comerciales; 2) competidores de las especies explotadas; ó 3) peces que, por su posición ecológica, afectan la estructura de la comunidad e influyen indirectamente en las poblaciones de importancia económica.

Se describe brevemente las comunidades de peces y ciertas especies de importancia ecológica para cada uno de los siete hábitats más importantes en las aguas oceánicas de California: 1) zona profunda mesopelágica, 2) zona epipelágica, 3) región demersal costera, 4) lechos de algas marinas/arrecifes sublitorales, 5) zona de entre mareas rocosa, 6) puertos, y 7) bahías y estuarios. En las conclusiones se señala que las bahías y estuarios son importantes, pero estos hábitats se alteran y por eso necesitan cuidados para conservarlos.

INTRODUCTION

A primary purpose of this paper is to focus attention on the diversity and complexity of the California marine fish fauna especially beyond the relatively small number of species that contribute to the commercial catch. Noncommercial forms have both direct and indirect relationships with economically important species. The "other" fishes may be predators or prey of exploited species, competitors of commercial species, or in other ways affect community structure and secondarily influence economically important populations. In this account, the fish communities are briefly described and the roles of ecologically important and interesting species emphasized in seven major marine habitats: 1) deep midwaters; 2) epipelagic zone; 3) coastal demersal region; 4) kelp beds/subtidal reefs; 5) rocky intertidal zone; 6) harbors; and 7) bays and estuaries.

DIVERSITY AND DISTRIBUTION PATTERNS OF CALIFORNIA MARINE FISHES

The fishes occurring off the coast of California comprise a rich fauna of varied origin and complex distribution. As recently shown by Horn and Allen (1978), diversity (number of species) is greatest in southern California gradually declining northward to Alaska in a pattern that is highly correlated with increasing latitude and decreasing minimum surface temperature. The steep decline in the number of California fishes occurring off Baja California and southward is apparently related (Horn and

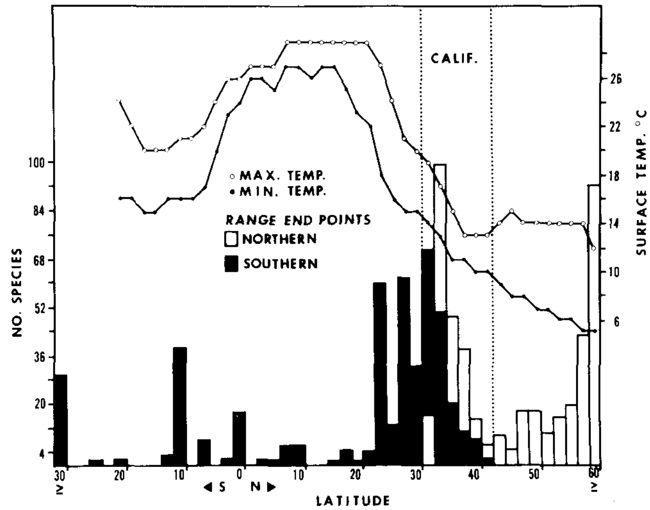

Figure 1. Frequency of northern and southern end points of geographic ranges of 499 California coastal fish species at each degree of latitude over the total distributional range (≥ 30°S to ≥ 60°N. The bars representing the number of northern and southern end points originate at the basal line. The bars for northern and southern values at 32°N are reversed in position relative to other latitudes because the open (northern) bar represents a smaller value than the black (southern) bar only at this latitude. Maximum and minimum surface temperatures are derived from monthly means for the 14-year period 1949-62. (All data from those compiled by Horn and Allen 1978.)

Allen 1978) not only to changing oceanographic conditions but to competition with the large tropical fauna south of California that is greater than that with the small boreal fauna which occurs north of California. The distribution of range end points of California fishes (Figure 1) serves to emphasize the richness and multiple affinities (especially northern and southern) of the fauna and to illustrate the relationship of diversity to surface sea temperatures. Frequency of both northern and southern terminations of species ranges are bimodal in pattern with the proximal modes of each occurring in southern California. The high concentration of range terminations in southern California is to be expected since it is the region of greatest species richness. Increased diversity in southern California is probably related (Horn 1974) to environmental heterogeneity as expressed by the expansive borderland, the insular habitats adjacent to deep basins, and the converging water masses characteristic of the region.

Species with southern affinities tend to have northern range end points off southern California, and southern end points off Baja California or much farther south off Central or South America. Fishes with northern affinities most frequently have northern range end points at high latitudes off British Columbia or Alaska and southern end points off southern California and northern Baja California. Point Conception (34.5°N), a widely recognized faunal boundary, is a more effective barrier for southern species than for northern species. Oceanographic conditions, especially of temperature in the Point Conception area (Figure 1), are apparently more critical for southern species than for northern ones.

Miller and Lea (1972) listed 554 species as occurring off California. Of these, 439 are found in coastal waters (< ~ 120-m depth), 48 in meso- and bathypelagic zones (about 25% of the total midwater fauna), and 67 benthic forms found at depths greater than 120 m. Eleven families account for 256 species (46%) of Miller's and Lea's (1972) total list (Table 1). This group of families illustrates the multiple origins of the fauna since it includes families of temperate affinities (Cottidæ, Pleuronectidæ, Embiotocidæ, and Agonidæ), of tropical-subtropical relationships (Scombridæ, Carangidæ, Gobiidæ, Clinidæ, Carcharhinidæ, and of deep-water origin (Myctophidæ). Scorpænidæ is primarily a family of tropical affinity, although the subfamily Sebastinæ (containing the diverse genus *Sebastes*) has a temperate-boreal distribution.

COMPOSITION OF THE CALIFORNIA COMMERCIAL FISHERY

Only a small percentage of California species occur in the commercial catch. No more than about 120 species are among the annual landings and shipments in California (e.g. McAllister 1976). However, most of these species are rarely captured or otherwise contribute insignificantly to the total catch. The California commercial fishery is overwhelmingly dominated by pelagic wetfish (northern anchovy, *Engraulis mordax*, and jack mackerel, *Trachurus symmetricus*) and tunas (Table 2). The tunas, mainly yellowfin (*Thunnus albacares*) and skipjack (*Euthynnus pelamis*), are primarily caught in tropical waters outside of California (e.g. about 94% of the 1972 catch, Bell 1974). Trawl fisheries are relatively more important from Santa Barbara northward but con-

TABLE 1
The 11 Most Speciose Families of Fishes in California Waters.[1]

Family	Common name	Number of species
Scorpænidæ	Thornyheads, scorpionfishes, rockfishes	62
Cottidæ	Sculpins	42
Myctophidæ	Lanternfishes	32
Pleuronectidæ	Right-eye flounders	20
Embiotocidæ	Surfperches	19
Agonidæ	Poachers	17
Scombridæ	Mackerels and tunas	15
Carangidæ	Jacks and pompanos	13
Gobiidæ	Gobies	12
Clinidæ	Clinids	12
Carcharhinidæ	Requiem sharks	12
		256

[1]Based on Miller and Lea (1972).

tribute only a small percentage to the total California catch. In 1974 and 1975, only slightly more than 2% of the total fauna (about 13 species) made up 90% of all landings and shipments (Table 2). The significant point is that only a small fraction of a rich fauna contributes to the commercial fishery. This fact magnifies the importance of noncommercial species in terms of both their ecological influence on economically valuable fishes and their contribution to the structure of marine fish communities as a whole.

MAJOR MARINE HABITATS

Deep Midwaters

The midwater environment off California, especially southern California, provides a complex and heterogeneous habitat for deep-sea fishes. Three converging water masses, the California Current itself and a series of deep basins in the southern California borderland, result in a rich, dynamic midwater fauna. In general, the diversity of the mesopelagic and bathypelagic faunas increases with vertical expansion of their habitats offshore. Both resident and transient species occur and assort themselves by depth and basin.

The size of the deep-sea fauna is difficult to determine and somewhat artificial to consider because of the transitional and dynamic nature of the environment and its fish communities. According to estimates of Miller and Lea (1972), approximately 200 species comprise the fauna. Fitch and Lavenberg (1968) provided a list of 260 species, but their account included bottom-dwelling forms.

TABLE 2
Landings and Shipments of the Top 10 Commercial Fishery Species in California for 1974 and 1975.[1]

1974			1975		
Species	Millions of lbs.	% of Total	Species	Millions of lbs.	% of Total
Yellowfin tuna	263	28.0	North anchovy	317	32.4
Skipjack tuna	230	24.5	Yellowfin tuna	262	26.7
Northern anchovy	165	17.6	Skipjack tuna	121	12.3
Albacore	89	9.5	Albacore	58	5.9
Market squid	29	3.1	Jack mackerel	37	3.8
Jack mackerel	25	2.7	Pacific bonito	32	3.3
Rockfish	21	2.3	Rockfish	24	2.4
Dover sole	19	2.0	Market squid	24	2.4
Pacific bonito	19	2.0	Dover sole	23	2.3
Bluefin tuna	13	1.4	Bluefin tuna	18	1.8
		93.1%			93.3%

1974		SUMMARY	1975	
20.3%	(2 species)	Wetfish	36.2%	(2 species)
65.4%	(5 species)	Tunas	50.0%	(5 species)
2.3%	(~5 species)	Rockfish	2.4%	(~5 species)
2.0%	(1 species)	Flatfish	2.3%	(1 species)

~13 species (2.3% of total fauna) comprise 90% of catch

[1]Based on McAllister (1976) and Pinkas (1977).

Probably well over one-half of California deep midwater species occurs off southern California.

The three numerically most abundant deep-sea pelagic fish families in southern California waters are Myctophidæ, Gonostomatidæ, and Bathylagidæ. The species most frequently encountered are two myctophids, *Stenobrachius leucopsarus* and *Triphotorus mexicanus*, (Paxton 1967; Ebeling et al. 1970) and a bathylagid, *Leuroglossus stilbius* (Ebeling et al. 1970). Based on larval abundance in the California Current (Table 3), these species and a fourth, the gonostomatid *Vinciguerria lucetia*, are the most common deepwater fishes.

The great abundance of the above three families is illustrated by their high ranking among families contributing to larval numbers in the upper 150 m of the California Current (Table 4). According to Ahlstrom et al. (1976), myctophids, on the average, make up 50% of all fish larvae in any oceanic plankton and may have the greatest

TABLE 3
Most Abundant Species of Larvae of the Three Principal Families of Deep-Sea Pelagic Fishes in California Current Region off California and Baja California 1955-1960.[1]

Family and species	Mean % contribution to deep-sea total
Myctophidæ	
Triphoturus mexicanus	14.5
Stenobrachius leucopsarus	10.1
Gonostomatidæ	
Vinciguerria lucetia	31.9
Bathylagidæ	
Leuroglossus stilbius	15.2

[1]Based on Ahlstrom (1969).

TABLE 4
Mean Percentage Contribution of Principal Fish Families to Larval Abundance in California Current Region off California and Baja California 1955-1960.[1]

Family	Mean % contribution
Engraulidæ	41.6
Gadidæ	12.9
Myctophidæ[2]	11.2
Gonostomatidæ[2]	10.8
Scorpænidæ	5.9
Bathylagidæ[2]	5.0
Bothidæ	3.1
Clupeidæ	2.6
Carangidæ	2.2
Scombridæ	0.4
Pleuronectidæ	0.4

[1]Based on Ahlstrom (1969).
[2]Deep-sea pelagic families.

biomass of any vertebrate family. Although such statements of the prodigious abundance of lanternfishes frequently generate ideas for harvesting these fishes, their small size and diffuse distribution tend to weaken the prospects for widespread commercial exploitation.

Lanternfishes apparently play very important ecological roles in pelagic food webs off California. The proximity of the deep-sea basins to coastal and epipelagic waters increases the probability of interaction of these abundant fishes with a variety of other organisms in the region. Ahlstron (1969) emphasized the forage role of myctophids and gonostomatids and recognized them as a vital link between the zooplankton community and the larger vertebrate predators including both economically and æsthetically important species (Figure 2). These small midwater fishes, especially the lanternfishes, appear to occupy a position in the trophic structure of offshore, basin waters similar to that of northern anchovy in more inshore, shallower waters.

Epipelagic Zone

The epipelagic fish fauna may include at any given time a mixture of species from a variety of habitats including deep midwaters, inshore bottom-associated habitats, as well as offshore surface layers. Trophic interactions in this environment are possible among a diverse array of species from dissimilar habitats. Horn (1974) provided a list of 80 species in 30 families, all of which are epipelagic to a certain degree in southern California waters. The list could be expanded since, for example, the carcharhinid sharks were not included. The present account focuses on two truly epipelagic species that occupy important but different trophic positions in California waters: 1) Pacific saury, *Cololabis saira*, a low-level carnivore and forage species, and 2) blue shark, *Prionace glauca*, a high-level carnivore.

Pacific saury is a cold temperate scomberesocid fish of the eastern North Pacific that occurs (Frey 1971) in greatest concentrations at distances of 40 to 120 miles (64 to 193 km) offshore. Although the species has been fished commercially by the Japanese in the eastern North Pacific (Frey 1971) and has been the subject of exploratory research as a potential resource (Smith and Ahlstrom 1970), its primary ecological importance lies in its utilization as forage by a variety of offshore predators (Figure 3). Immature sauries are a major food item of albacore (Frey 1971). George Hunt (personal communication, see also Hunt and Butler this volume) has noted that western gulls switch to alternate prey including Pacific saury when northern anchovy are apparently in low numbers and that as much as 50% of the diet of western gull chicks may be Pacific saury during certain years. Saury feed on large copepods, amphipods, euphausiids, and common fish larvae such as those of northern anchovy; thus, like the deeper living myctophids, they form a trophic link between zooplankton and higher level carnivores. Energy transfer both to and from Pacific saury includes commercially important fish species.

The blue shark is probably the most abundant of the larger noncommercial shark species in California waters. It is frequently observed at the surface and during diving activities especially around the Channel Islands. Pelagic longlining operations in the eastern North Pacific (Kato 1969; M.H. Horn unpublished data) have caught blue sharks on 30-50% of the hooks, a very high catch rate for any species with this type of gear. This shark is a voracious, primarily nocturnal, carnivore known to feed on a variety of abundant invertebrates and fishes (Figure 4). The diet includes the commercially important market squid (*Loligo opalescens*) and the two most important species in the pelagic wetfish industry, northern anthovy and jack mackerel. Another food item, pelagic red crab (*Pleuroncodes planipes*), is also significant prey of tunas off California and Baja California (e.g. Blackburn 1969; Pinkas et al. 1971). In a recent study, Tricas (1977)

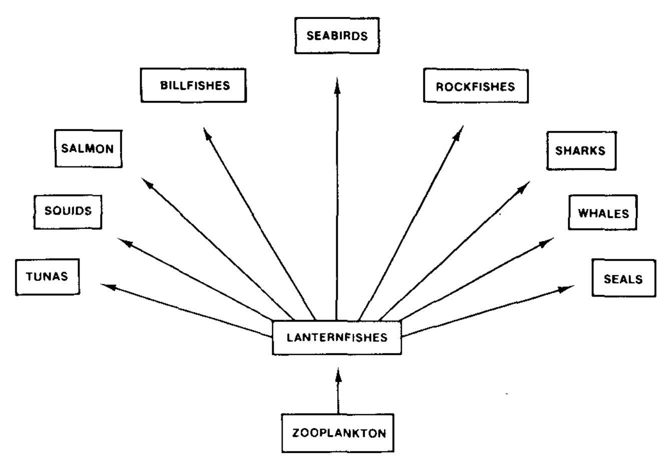

Figure 2. Prey and some known predators of lanternfishes (Myctophidæ) in California waters.

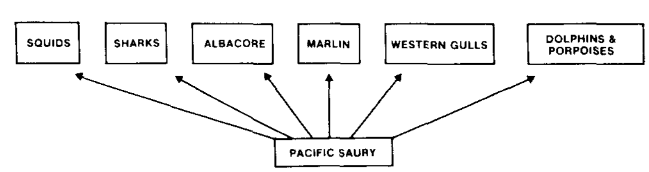

Figure 3. Some known predators of Pacific saury (*Cololabis saira*) in California waters.

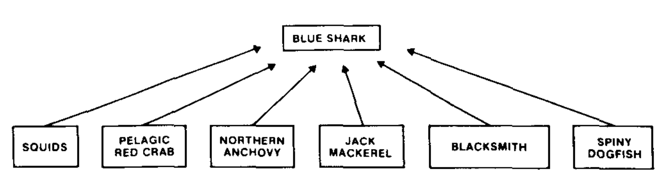

Figure 4. Some known prey of blue shark (*Prionace glauca*) in California waters.

found *Histioteuthis heteropsis* to be the dominant pelagic cephalopod in the diet, whereas the market squid represented the major portion of onshore squid prey, especially during winter inshore spawning of the squid. Northern anchovy was the principal fish prey item through the year of the Tricas (1977) study. Sciarrotta and Nelson (1977) suggested that evening-twilight onshore movements of blue shark in March to early June were due to nearshore abundance of squid and reduced availability of prey offshore. Conversely, the offshore pattern of late June to October may be a result of reduced squid populations nearshore and increased populations of jack mackerel and northern anchovy offshore. Blue sharks move over long distances (Tricas 1977; Sciarrotta and Nelson 1977) and do not maintain local populations (Tricas 1977).

Coastal Demersal Region

Trawl Surveys

Trawl studies conducted over the past several years, especially those by the Southern California Coastal Water Research Project (SCCWRP), of the fish populations associated with the bottom in the shelf waters of southern California have provided a variable but recurrent list of the abundant species in this habitat zone out to approximately 100-m depth. In terms of numbers of species, the list (Table 5) is dominated by flatfishes (Bothidæ, Cynoglossidæ, Pleuronectidæ) and rockfishes (Scorpænidæ). Of the 26 species that accounted for 95% of the catch in the SCCWRP trawls off Orange County (Table 5), only a few (e.g. Dover sole, English sole, northern anchovy) are of commercial importance. The ranking, therefore, identifies abundant, noncommercial species that presumably play significant roles in community structure and undoubtedly interact with economically important species.

Speckled sanddab, the most abundant fish in the Orange County surveys, is a small (< 170 mm TL) flatfish extremely numerous on sandy bottoms. Its diet includes larval and post-larval northern anchovy (Feder et al. 1974), and the fish is most likely an important forage item for larger species. Pacific sanddab, the second most abundant species in the SCCWRP trawls, is a larger (< 406 mm TL), longer lived species that is of some commercial importance in central and northern California and is also caught in the sport fishery. Because of its abundance and small size, it should, however, be considered as a significant forage species as well. According to Feder et al. (1974), the pelagic young are fed upon by tunas and other pelagic fishes and the adults by fishes from a variety of habitats. Both speckled and Pacific sanddabs occur in the diets of seabirds off California (Baltz and Morejohn 1977).

Little is known of the life history and ecology of several of the most abundant trawl-caught species. Fishes in this category include yellowchin sculpin, roughback sculpin, shortspine combfish, longspine combfish, and calico rockfish. The last species is a small rockfish that has had high recruitment in the past four or five years, particularly in 1975 (A.J. Mearns, abstract, 1978 CalCOFI meeting). Variation in the Orange County trawl catches was shown (Mearns 1977) to be largely due to fluctuations in recruitment of juvenile rockfishes (especially calico, stripetail, half-banded, and splitnose), which, in turn, were related to changing oceanographic conditions.

TABLE 5
Total Numbers of the 26 Fish Species that Accounted for 95% of the Catch in 32 Quarterly Trawl Surveys by SCCWRP off Orange County 1969-1977.[1]

Common name, scientific name	Number of individuals	% of total catch
Speckled sanddab, *Citharichthys stigmaeus*	19,083	16.8
Pacific sanddab, *Citharichthys sordidus*	15.418	13.5
Yellowchin sculpin, *Icelinus quadriseriatus*	12,232	10.7
Dover sole, *Microstomus pacificus*	7,361	6.5
Stripetail rockfish, *Sebastes saxicola*	6,852	6.0
White croaker, *Genyonemus lineatus*	6,090	5.3
California tonguefish, *Symphurus atricauda*	5,503	4.8
Plainfin midshipman, *Porichthys myriaster*	4,354	3.8
Calico rockfish, *Sebastes dallii*	4,028	3.5
Halfbanded rockfish, *Sebastes semicinctus*	4,009	3.5
Pink surfperch, *Zalembius rosaceus*	3,322	2.9
Slender sole, *Lyopsetta exilis*	2,606	2.2
English sole, *Parophrys vetulus*	2,086	1.8
Blackbelly eelpout, *Lycodopsis pacifica*	1,961	1.7
Rex sole, *Glyptocephalus zachirus*	1,605	1.4
Northern anchovy, *Engraulis mordax*	1,566	1.4
Roughback sculpin, *Chitonotus pugetensis*	1,562	1.4
Queenfish, *Seriphus politus*	1,545	1.4
Longspine combfish, *Zaniolepis latipinna*	1,536	1.4
Splitnose rockfish, *Sebastes diploproa*	1,491	1.3
Shiner surfperch, *Cymatogaster aggregata*	986	0.9
Hornyhead turbot, *Pleuronichthys verticalis*	846	0.7
Blacktip poacher, *Xeneretmus latifrons*	779	0.7
Shortspine combfish, *Zaniolepis frenata*	632	0.6
Bigmouth sole, *Hippoglossina stomata*	491	0.4
White surfperch, *Phanerodon furcatus*	387	0.3
	108,331	95.2

[1]Based on Mearns (1977).

Deep Demersal Habitat

The demersal fish fauna at depths greater than 200 m off California is poorly known. The information that is available has come mainly from photographs taken with deep-sea cameras and a small number of recorded trawls (Fitch 1966; Allen and Mearns 1977), all taken at depths of less than 700 m. Allen and Mearns (1977) found that, although individual fishes found at depths greater than 200 m weighed five times as much as fishes taken in shallow waters, fish abundance, biomass, and numbers of species were reduced at the greater depths. The most frequently occurring species in their deep trawls were Dover sole, sablefish (*Anoplopoma fimbria*), longspine thornyhead (*Sebastolobus altivelis*), shortspine thornyhead (*S. alascanus*) and splitnose rockfish. Sablefish have recently become the subject of an increasingly large trap fishery in southern California, particularly off San Clemente Island. The deep bottom fauna is undoubtedly important in the vertical transfer of nutrients and energy and deserves greater attention in future studies involving offshore fish communities.

Rockfish Ecology

Members of the family Scorpaenidae form one of the most diverse groups of fishes in the eastern North Pacific. The great majority of species are in the genus *Sebastes*, which is represented by about 58 species in California waters. Rockfishes occupy a variety of habitats and depth ranges and are significant components of California sport and commercial landings. The diversity and importance of the group provided the impetus for the brief but separate account here.

Since rockfishes are ovoviviparous and produce large broods, as many as one million of more young (Moser 1967), they release enormous numbers of larvae into coastal waters. Rockfish ranked fifth in mean abundance of all fish larvae collected in the California Current for the period 1950-1975 (see Ahlstrom, Moser, and Sandknop, CalCOFI stations (shore to station 90) over the 26-year period 1950-1975 (see Ahlstrom, Moser, and Sandknop, abstract, 1978 CalCOFI meeting). These abundant young comprise a forage resource of certainly significant but as yet undetermined proportions. Rockfish larvae and juveniles are at least known to serve as prey for several fishes of high economic importance including rockfishes themselves and for a number of seabirds (Figure 5).

Although the overall abundance of rockfish larvae based on CalCOFI surveys has been increasing in recent years (Ahlstrom, Moser, and Sandknop, abstract, 1978 CalCOFI meeting), there is evidence that the rockfish resource is being overexploited or at least is under heavy fishing pressure. Although as many as 40 species are taken by the sport and commercial fisheries, a very small number of species comprise a large portion of the rockfish catch in either case. In the commercial fishery, two species, bocaccio (*Sebastes paucispinis*) and chilipepper (*S. goodei*), make up well over 50% of the catch in southern and central California, whereas in northern California the diversity of the catch increases with fewer chilipepper taken and the significant addition of another scorpaenid, shortspine thornyhead (H.G. Moser and W.H. Lenarz, personal communication).

In the California partyboat fishery over the period 1966-1975, the total catch remained relatively stable, but the contribution of rockfishes to this total increased from 30% to more than 70% (Figure 6). As with the commercial fishery, only a few species make up the large proportion of the catch and most of these are the same species that figure heavily in the commercial catch. In southern California, bocaccio, chilipepper, and olive rockfish (*Sebastes serranoides*) are the species of major importance, whereas in central and northern California the principal sport species are blue (*S. melanops*) and yellowtail (*S. flavidus*) rockfish (H.G. Moser and W.H. Lenarz, personal communication).

The trend toward fishing in deeper waters, especially in southern California, by both commercial fishers and partyboats, is indicative of the degree of exploitation of the shallow-water populations of the few sought-after rockfish species. Evidence exists that fishing pressure, especially by partyboats, has reduced the populations in local inshore areas of at least two species. Off Santa Barbara, adults of olive rockfish have essentially been eliminated on certain reefs (Love 1978). It has become necessary to fish for this species on the outer, deeper banks. Similarly, Miller and Geibel (1973) reported that blue rockfish have been reduced in numbers and individual fish size by partyboat and skiff fisheries within 16 km of all major ports in the Monterey area.

Rockfishes are vulnerable to overexploitation because

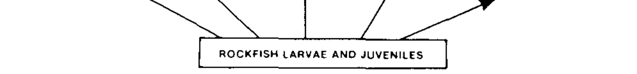

Figure 5. Some known predators of rockfish (Scorpænidæ) larvae and juveniles in California waters.

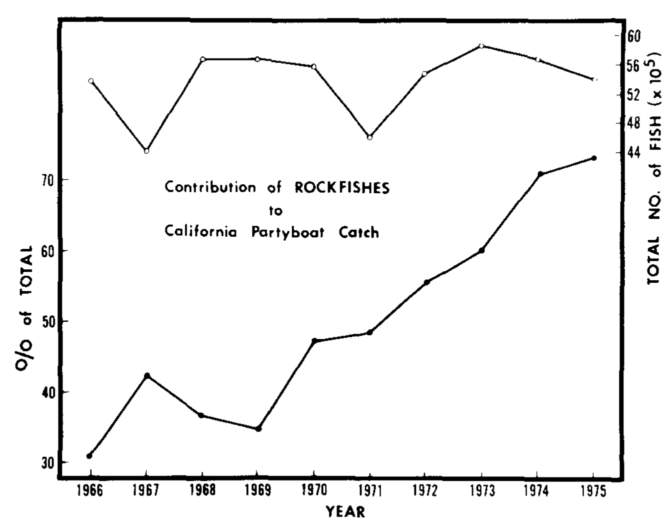

Figure 6. Percent contribution (●) of rockfishes (Scorpænidæ) to the annual partyboat catch (O) in California for the years 1966 to 1975 (based on Pinkas 1977).

they grow rather slowly (bocaccio is an exception), mature only after several years of age, and often have limited movements. If the species are schooling or aggregating forms over reefs and kelp beds, they are especially subject to excess fishing pressure by the sport fishery.

These and other considerations have led Miller and Geibel (1973) to recommend the establishment of subtidal reef preserves to allow proper management of rockfish and other reef-dwelling populations. These areas would be closed to sport and commercial fishing and would provide source regions from which recruits could repopulate adjacent exploited areas. Bag limits are of questionable value, because once caught the species may not be recognized or it may die even if released due to injury on ascent. Closed seasons likewise do not provide the full answer since under intense fishing pressure mature adults of low vagility would be removed during open season and therefore unavailable to spawn during closed season. I concur with Miller and Geibel's (1973) recommendation of the designation of subtidal preserves as perhaps one of the few effective procedures available for managing vulnerable reef species.

The potential of rockfishes as a resource of increased importance in the future is apparently not great. Many of the species not presently utilized are either too small in size or too deep living for efficient exploitation. A few species currently being studied, however, do seem to have the appropriate population characteristics to withstand greater exploitation. These include blackgill rockfish (*Sebastes melanostomus*; Moser and Ahlstrom 1978), calico rockfish (previously mentioned as having high recruitment in recent years) and, in central and northern California, stripetail rockfish and shortbelly rockfish (*S. jordani*). This last species is a midwater schooling fish found to be of high abundance in the San Francisco Bay region (W.H. Lenarz, personal communication).

In summary, rockfishes are a diverse group of particular ecological and economic importance. Much more research is needed on their life history and population biology so that the population sizes of individual species can be accurately estimated and predicted.

Kelp Beds/Subtidal Reefs

The above discussion of rockfishes associated with rocky substrates leads to this account of kelp beds and subtidal reefs which occur as distinct habitats in California coastal waters. Kelp stands and adjacent rocky outcrops provide a heterogeneous environment that serves as a source of food, shelter, and attraction for fishes (Quast 1968a). A total of 57 species were listed by Quast (1968a) as being associated with kelp beds in southern California; kelp bass (*Paralabrax clathratus*), California sheephead (*Pimelometopon pulchrum*), and blacksmith (*Chromis punctipinnis*) were the most frequently encountered species. Even larger numbers of species have been recorded in other studies. Miller and Geibel (1973) identified 67 species over a five-year period in kelp beds from San Simeon to Monterey in central California, and Feder et al. (1974) listed 111 species that were observed by diving in kelp bed-rocky bottom habitats in southern California.

Quast (1968b) determined that the mean standing crop of resident kelp bed fishes was 313 pounds/acre (351 kg/ha), an estimate close to median values for lakes and coral reefs. Miller and Geibel (1973) obtained higher estimates (706-1120 kg/ha) for fishes of central California kelp beds using techniques difficult to compare with those of Quast (1968b). Increased standardization of sampling procedures are required to obtain comparable values.

In terms of habitat complexity and species richness, kelp beds and associated areas form the temperate counterpart of coral reefs in the tropics, although overall diversity is greater in the latter environment. The diel behavior of kelp bed fishes follows the same basic patterns as tropical reef species but the kelp bed community appears (Ebeling and Bray 1976) to be more loosely programmed in terms of specialized day-night activities. Less large-scale replacement of fishes between discrete areas or vertical zones occurs at dusk, even though Hobson and Chess (1976) have shown that there are generalized planktivores feeding at night in open shallow waters seaward of kelp beds off Santa Catalina Island.

Interestingly, Ebeling and Bray (1976) have observed that kelp bed fishes belonging to primarily tropical families, especially Labridæ and Pomacentridæ, tend to show the same specialized pattern of nocturnal shelter-seeking as do their close tropical relatives. Perhaps this behavoir stems from the historic threat of crepuscular/nocturnal predation in tropical regions (Hobson 1972). Alternatively, Ebeling and Bray (1976) suggested that crepuscular and nocturnal predation by, for example, Pacific electric ray (*Torpedo californica*), is important in kelp beds but that the fishes derived from tropical families compete more successfully against temperate species for shelter.

The predatory role of the Pacific electric ray, a unique species associated with kelp beds, has not been fully appreciated. According to recent observations off Santa Barbara by Bray and Hixon (1978), this species is an important nocturnal predator of temperate reef fishes. The ray apparently forages exclusively on fishes and uses powerful electric discharges to immobilize a variety of prey species (Figure 7). Off Santa Barbara, the primary dietary item was northern anchovy (thus a direct link with this predator and an important commercial species), although kelp bass and demersal fishes of the sand-mud community were also taken. Bray and Hixon (1978) concluded that Pacific electric ray may be a major predator of temperate reef fishes that descend from the water column at night and become quiescent within about 1 m above the bottom.

Rocky Intertidal Zone

An important landward extension of subtidal reefs is the rocky intertidal zone, a productive and heterogeneous habitat that is particularly well developed on the California coast and offshore islands. A wide variety of fishes occupy the intertidal environment either on a permanent or a periodic basis. Rocky shores with associated tidepools are generally considered to be important habitats for the juveniles of a number of commercial and noncommercial species. Reduced predation in these habitats, as compared to subtidal areas, is frequently cited (e.g. Barton in press) as a major factor in the occupation of the intertidal zone by young fishes; however, solid support of this hypothesis is yet to be obtained.

Although the eastern North Pacific including California has one of the most highly diverse intertidal fish faunas in the world, relatively little research has been conducted on community structure and composition. It is possible, however, to identify the fish families that contribute the greatest number of species to the zone. The results of a two-year survey of intertidal fishes at Diablo Cove, 35.2°N (Burge and Schultz 1973) is indicative of species composition for central California shores. In this study 54 species were encountered in the intertidal zone, with Cottidæ (10 species), Scorpænidæ (8 species), Embiotocidæ (8 species), and Stichæidæ (6 species) being the principal families in terms of richness of species. Intertidal habitats are particularly important for the juveniles of scorpænids and embiotocids, whereas many of the cottids and stichæids occur as adults and spawn in the intertidal zone.

Rocky intertidal habitats offer a number of interesting and important problems for ichthyological research. Among these are the following: 1) Several species (>5) of cottids co-occur in tidepools in central California. Increased knowledge of their life histories and mechanisms of coexistence would be a significant contribution to the understanding of community structure, resilience, and recruitment of tidepool fishes. Yoshiyama (1977) recently completed a study of competition in rocky intertidal fishes, especially cottids, on the central California coast and proposed that exploitative competition was a major factor responsible for the vertical stratification of species in the intertidal zone. 2) A wide range of color patterns exist within individual species of several families (e.g. Clinidæ, Cottidæ, Pholidæ). Burgess (1978) proposed that for the rockweed gunnel (Philidæ: *Xererpes fucorum*) multiple color phases allow expanded utilization of available resources within the intertidal zone. Ecological significance of color variations in other species awaits clarification. 3) Among the best examples of temperate herbivorous fishes are certain stichæids which occur in the intertidal zone. These fishes become progressively dependent upon a plant diet with age (Montgomery 1977; Horn et al., in preparation). 4) Plainfin midshipman (*Porichthys notatus*), one of the most abundant demersal fishes in trawl surveys off southern California (Table 5), spawns, among other sites, in the intertidal zone of central and northern California. This species is an example of a California marine fish of high abundance and broad habitat whose ecological role, although probably significant, has not been elucidated. According to Fitch and Lavenberg (1971), plainfin midshipman eat primarily small shrimp-like crustaceans and fishes (mostly northern anchovies) and are in turn fed upon by numerous large predators including rockfishes, lingcod (*Ophidion elongatus*), and sea lions. Attention to certain morphological and physiological attributes (e.g. luminescence, sound production) has overshadowed study of the ecological importance of this species and its shallower water congener, specklefin midshipman (*P. myriaster*).

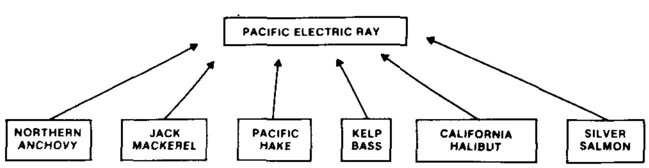

Figure 7. Some known prey of Pacific electric eel (*Torpedo californica*) in California waters.

Harbors

Harbors are artificial habitats formed by breakwaters that slow the movement of water and affect other changes making them in some ways similar to natural semi-enclosed bays and estuaries. These habitats are frequently characterized by calm, nutrient-rich waters and a variety of substrates. The protected rocky environment on the leeward side of a breakwater becomes an important and distinct habitat for shallow, subtidal fishes. King Harbor and Los Angeles/Long Beach Harbor are two such habitats that in recent years have been shown to support diverse and abundant fish faunas.

The number of fish species known to inhabit or visit Los Angeles/Long Beach Harbor has been more than doubled by recent investigations. Chamberlain (1974) compiled a list of 126 species in 48 families for this harbor complex. Based on trawl samples, Stephens et al. (1974) found that the fish density (one fish/8.9 m^2) in Los Angeles/Long Beach Harbor was the highest recorded for local waters and that diversity and richness approximated values recorded for similar depths outside the harbor (i.e. San Pedro Bay). The ten most abundant species in the trawls were 1) white croaker, 2) northern anchovy, 3) California tonguefish, 4) speckled sanddab, 5) queenfish,

6) shiner surfperch, 7) white surfperch, 8) specklefin midshipman (*Porichthys myriaster*), 9) bay goby (*Lepidogobius lepidus*), and 10) vermilion rockfish (*Sebastes miniatus*). White croaker, especially juveniles, and northern anchovy made up 69% of the catch. The abundance of these two species probably reflects a nutrient enrichment in the harbor. Stephens et al. (1974) were able to recognize three areas of distribution within the harbor: 1) an area rich in flatfishes, 2) one of high white croaker abundance, and 3) an area identified by the presence of rockfishes.

The King Harbor fish fauna has been shown (Stephens 1978) to be extremely diverse and abundant, especially in the vicinity of the breakwater. More than 90 species have been recorded in this harbor. Based on diver surveys, considerable seasonal variation existed in both abundance and species richness, but in general the community was dominated by speckled sanddab, shiner surfperch, and white surfperch. Two species abundant in Los Angeles/Long Beach Harbor but absent in the King Harbor surveys were white croaker and California tonguefish. The former species is known to avoid divers, and the latter has never been recorded in King Harbor. Stephens (1978) attributed much of the faunal richness in King Harbor to the thermal diversity and substrate heterogeneity characterizing the harbor.

Stephens (1978) stated that because of the limited amount of natural bay-estuarine habitat, especially in southern Califoria, the numerous harbors of the region supplement or replace the few estuaries as nursery areas for juvenile fishes. Although a large percentage (perhaps 75%) of the coastal wetlands and estuarine habitats in southern California have been obliterated as a result of human activities, the remaining bay-estuarine areas provide the principal habitat for several fish species and the setting for a unique fish community (see below).

Bays and Estuaries

According to data compiled by Horn and Allen (1976), almost one-half (224 species) of the California coastal fish fauna has been recorded from the major bays and estuaries in California. Horn and Allen (1976) showed that the number of species in each of these habitats was positively correlated with area and mouth width of the bay or estuary. This finding becomes important with the realization that these habitats are being continually altered including reduced in size by human activity.

Natural bays and estuaries in California do function in the classic sense of serving as spawning and nursery areas for coastal fishes, including those of economic importance such as northern anchovy and California halibut (*Paralichthys californicus*) (e.g. Allen 1976; White 1977—Newport Bay). A frequently overlooked characteristic of bays and estuaries, however, is that they support unique fish assemblages. Thus, to obliterate an estuary eliminates a unique community of fishes in a given area. In addition to seasonally occuring coastal species, the bay-estuarine community is primarily composed of a set of abundant, low trophic-level fishes that together form a distinct assemblage of species. Based on larval surveys, the principal species, other than gobies, in northern California are members of the Clupeidæ, Cottidæ, and Osmeridæ, whereas in southern California the main species, other than gobies, are representatives of the Engraulidæ, Blenniidæ, and Atherinidæ (White 1977; White and Horn in preparation). Various species of surfperches (Embiotocidæ) are also important members of bay-estuarine communities. Gobies (Gobiidæ) are among the most abundant bay-estuarine fishes and are well represented in all such California habitats. The focus below is on the abundant members of the Gobiidæ and their apparent ecological importance in bays and estuaries.

The most important goby species in California bays and estuaries are 1) arrow goby (*Clevelandia ios*), 2) longjaw mudsucker (*Gillichthys mirabilis*), 3) cheekspot goby (*Ilypnus gilberti*), 4) shadow goby (*Quietula ycauda*), and 5) bay goby (*Lepidogobius lepidus*). The larvae of one or more of these species are the most consistently abundant of all California fishes in bay-estuarine ichthyoplankton samples (White and Horn in preparation). The adults also appear to be highly abundant (Brothers 1975; MacDonald 1975), but the difficulty of adequately sampling them (Horn and Allen, in press) has resulted in an underestimation of their numbers and their role in the structure of bay-estuarine communities. A primary indication of their ecological importance, however, has come from the occurrence of these species in the diets of predatory fishes and birds.

MacDonald (1975) listed 12 species of fishes as predators of arrow goby, the most abundant and widespread bay-estuarine goby, in Anaheim Bay. These predators included California halibut, walleye surfperch (*Hyperprosopon argenteum*), California corbina (*Menticirrhus undulatus*), white croaker, staghorn sculpin (*Leptocottus armatus*), specklefin midshipman, and round stingray (*Urolophus halleri*). For some of these and other species identified, arrow goby was probably only an incidental prey item. Haaker (1975), however, showed that gobies were the most frequently occurring item in stomachs of California halibut in Anaheim Bay. Thus, gobies serve as forage for a fish of sport and commercial importance when the fish, especially in the juvenile stage, enters bays and estuaries.

Brothers (1975) commonly observed shorebirds probing invertebrate burrows in Mission Bay, possibly to feed on arrow gobies, and found that several species of shorebirds readily ate anesthetized gobies left on mud and sand flats. Other, primarily anecdotal, evidence (Brothers

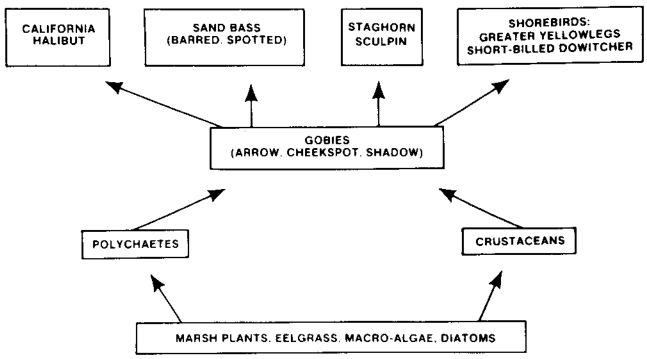

Figure 8. Trophic interactions involving gobies (Gobiidæ) in California estuarine habitats.

1975) indicates that gobies are important food for shorebirds.

Although little quantitative data are available to establish the importance of gobies in the bay-estuarine trophic structure, Brothers (1975) was sufficiently impressed with goby abundance to postulate a significant position in the food web for them. These fishes make available the high production of eelgrass (*Zostera marina*), green algae (e.g. *Ulva* sp.), diatoms, and marsh plants to higher level carnivores (Figure 8). By consuming large numbers of small crustaceans and worms that directly or indirectly feed on plants or plant detritus, gobies serve to channel substantial amounts of energy to the large predators in the ecosystem. Goby larvae may be equally important in the planktonic segment of the bay-estuarine food web.

Bays and estuaries serve as breeding and nursery areas for a wide array of coastal fishes, provide habitat for unique assemblages of fishes, and support large populations of small fishes that are important forage for high-level consumers in the ecosystem. For these ecological reasons, which directly relate to fishery considerations, natural bays and estuaries are worthy of preservation and wise management. The steps taken by the State of California to establish Upper Newport Bay as an ecological reserve should be repeated for other such habitats in California.

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