LARVAL FISH AND ZOOPLANKTON COMMUNITY STRUCTURE

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ABSTRACT

The macrozooplankton samples from two CalCOFI cruises have been analysed for the abundance of most of the important species of zooplankton. The data show that there are large changes in the degree of numerical dominance from place to place and that the identity of the dominant species varies strongly from sample to sample. In all of these samples larval fish were rare to very rare as compared to other species. Many of these other species must be competitors of larval fish, and some are known predators. The picture that emerges from this study is that fish larvae live in an environment dominated by many different competitors and/or predators and that this biological environment is highly variable.

RESUMEN

Las muestras de macrozooplancton de dos cruceros CalCOFI han sido analizadas para determinar la abundancia de las especies más importantes del zooplancton. Los datos indican que existen grandes cambios de un lugar a otro en cuanto al dominio numérico, y que las especies dominantes varían notablemente en las muestras. En todas estas colectas las larvas de peces eran raras en comparación con la abundancia de otras especies. Muchas de estas especies deben de competir con las larvas de peces, y algunas se sabe que son predadoras. El cuadro que surge de este estudio es que las larvas de peces viven en un ambiente dominado por una gran variedad de competidores y/o predadores, y que este medio ambiente biológico es muy variable.

INTRODUCTION

Larval fish are planktonic and are part of a much larger community of macrozooplankton. In the California Current this community consists of many species of invertebrates of sizes similar to larval fish. Although detailed studies of the feeding habits of many of these species have not been done, we do know that some of them are herbivores, some carnivores, and many seem to be omnivorous feeders on small particles. Some of the copepod, euphausiid, and chætognath species are known to be capable of feeding on larval fishes, and some copepods can eat the same size fraction of food that larval fish seem to eat (Poulet 1978). This implies that there are many species of potential competitors and predators of larval fish. Not only are there many species of competitors and predators present, but their abundance may frequently be greater than that of the fish larvae. Thus the biotic environment of larval fish is very different than that of the adult.

Since recruitment to the adult stock of many fish seems to bear little relationship to the size of the stock that spawned the recruits (Cushing 1975; Lasker and Smith 1977), there must be a large and variable mortality during the pre-recruit stage of life. Much of this happens during the egg and planktonic larval stage. For example, Isaacs (1965) and Lasker and Smith (1977) have shown large temporal variations in mortality rates for both sardine and anchovy, and the rate for anchovy is as high as 99.1% for 1.5- to 9.8-day-old larvae, with a mean of 96% for the years 1953 to 1960. Changes in the percent survival in these early stages could result in large fluctuations in subsequent adult abundance. As Larkin (1978) has pointed out, "A major question in fisheries investigations is thus: What happens to the eggs and the newly hatched larvae?" This question might be rephrased as: What are the various sources of mortality, and are some more important than others? It seems evident that in most populations of organisms there are many sources of mortality, particularly for the younger stages. For example, in terrestrial systems unusual cold snaps or wet or dry periods can kill a lot of young. But these are relatively rare events, and the effects are generally quite evident. In the ocean such abrupt and large changes in circulation or temperature are uncommon (due probably to the high heat capacity of water), and rather few mass mortalities of pelagic organisms have been associated with such temperature anomalies that do occur. More commonly it is variation in the availability of food that is hypothesized to be the critical factor in influencing the variations in larval survival (Cushing 1975; Lasker and Smith 1977). Since larval fish apparently have a threshold level of food concentration below which they do not feed "efficiently," the patchiness of their food and the factors influencing patchiness are important (Lasker and Zweifel 1978). But many invertebrate zooplankters, particularly large copepods, also have threshold levels of food density below which their feeding rate declines (Frost 1974). This phenomenon, also observed in terrestrial vertebrates, is generally referred to as the "functional response" (Holling 1966), and describes the short-term feeding behavior of individuals. However, in the case of populations, there is also a "numerical response" in which the size of the population increases and reaches a plateau with increasing

density of food. This is not an instantaneous measure but rather has a time constant dependent on the population being considered. It is obviously this numerical response that is of importance when considering survival of populations or year classes of larval fish. It is further obvious that competition can occur with other species that also have numerical responses, which co-occur with fish larvae and depend on the same food resource. The nature of the numerical response will depend then not only on the amount of food available but also on the intensity of competition for that food. A related argument may be made when larval fishes themselves are the food resource and other species having numerical responses are the predators.

Thus it seems that, on both observational and theoretical grounds, competition for a limiting resource (food) and predation rate of predators ought to be important factors influencing the survival rate of larval fish populations and the subsequent recruitment to the adult population. What do we know of the intensity of competition and predation of planktonic invertebrates with and on the young larvae of the anchovy, hake, and jack mackerel? Not much. That is, there are very few direct observations, at the population level, of these interactions. However, there are some data that bear on this question.

There are at least two CalCOFI cruises (5804 and 5810) where the species of copepods, euphausiids, thaliacians, chætognaths, pelagic molluscs, and larval fish have all been counted. From these data we can see how many of what kinds of things co-occur with larval fish, the degree to which they dominate (numerically) the fish, and the spatial constancy or coherence of the relationships. None of this information will demonstrate conclusively the importance or even the existence of competition or predation, but it can at least lead us to suspect that both could be occurring and that both could, on occasion, be quite intense.

SPECIES STRUCTURE

The number of species present and their relative abundance is what community ecologists call species structure. This may be illustrated by histograms of the rank order of species abundance. From these we can determine aspects of the position of fish larvae in the zooplankton community. Figures 1 and 2 are examples of such diagrams and are based on the zooplankton species counts from CalCOFI Cruise 5804. We selected these for presentation as rank order histograms because they represent the near- and offshore northern area, the central sector, and the near- and offshore southern sector of the system. There are several things about the ecology of larval fishes these histograms tell us. It is evident that, at the locales sampled, larval fish were *rare* species in the zooplankton community. Further, there are usually many other species of similar sized zooplankton present, some of which are known to be small particle feeders, others are carnivores capable of eating young fish.

If we visualize a larval fish moving randomly about in its immediate environment (say the volume of water of an average CalCOFI net tow), then the probability that it will contact one of these other species will depend on the abundance of that species and its degree of aggregation. The probability that the second individual it meets will be the same species as the first depends on the relative abundance of the two, and so forth for the whole community. It is clear that at Station 60.90 the chances of a larval fish (which were so rare in this sample they do not even appear on the histogram) meeting a *Eucalanus californicus* are very high indeed (Figure 1). Its biotic habitat is strongly dominated by a single species at Station 80.60, but this time it is *Calanus helgolandicus** (Figure 2). If either of these two species is capable of eating the same food as the fish and with anywhere near the same efficiency, then these must be severely competitive environments for the fish. There are also samples where larval fish are strongly outranked by known carnivores: Station 100.40 for example, where three species of chætognaths (*Sagitta*) and the copepod *Candacia* are much more abundant than fish (Figure 2).

In all of the Cruises 5804 and 5810 samples that were analyzed, larval fish were rare species in the community. That is, their biotic habitat was strongly dominated by species of potential competitors and predators. An impression of the areal extent of these relationships may be gotten by merely examining the plots of larval fish distribution and abundance and those of species of copepods, chætognaths, euphausiids, and so forth in the CalCOFI Atlas series. It is evident that on a broad scale large numbers of these invertebrates are present where larval fish are found (Figure 3). The temporal extent may also be examined in a cruder way (i.e. above the species level) by comparing larval fish patterns with those of the taxa Copepoda, Amphipoda, Chætognatha, etc., where there are time series data available (Fleminger et al. 1974).

CONSTANCY OF STRUCTURE

The histograms show very large differences in the degree of numerical dominance of species. That is, some rank order curves are very steep; others are more flattened. This can be interpreted to mean that when a larval fish is in a locale where dominance is strong it will very frequently encounter one or a few species over its ambit, but where dominance is not strong it will encounter a wide variety of species over the same ambit. The shape of these

*Calanus helgolandicus = C. pacificus in the California Current.

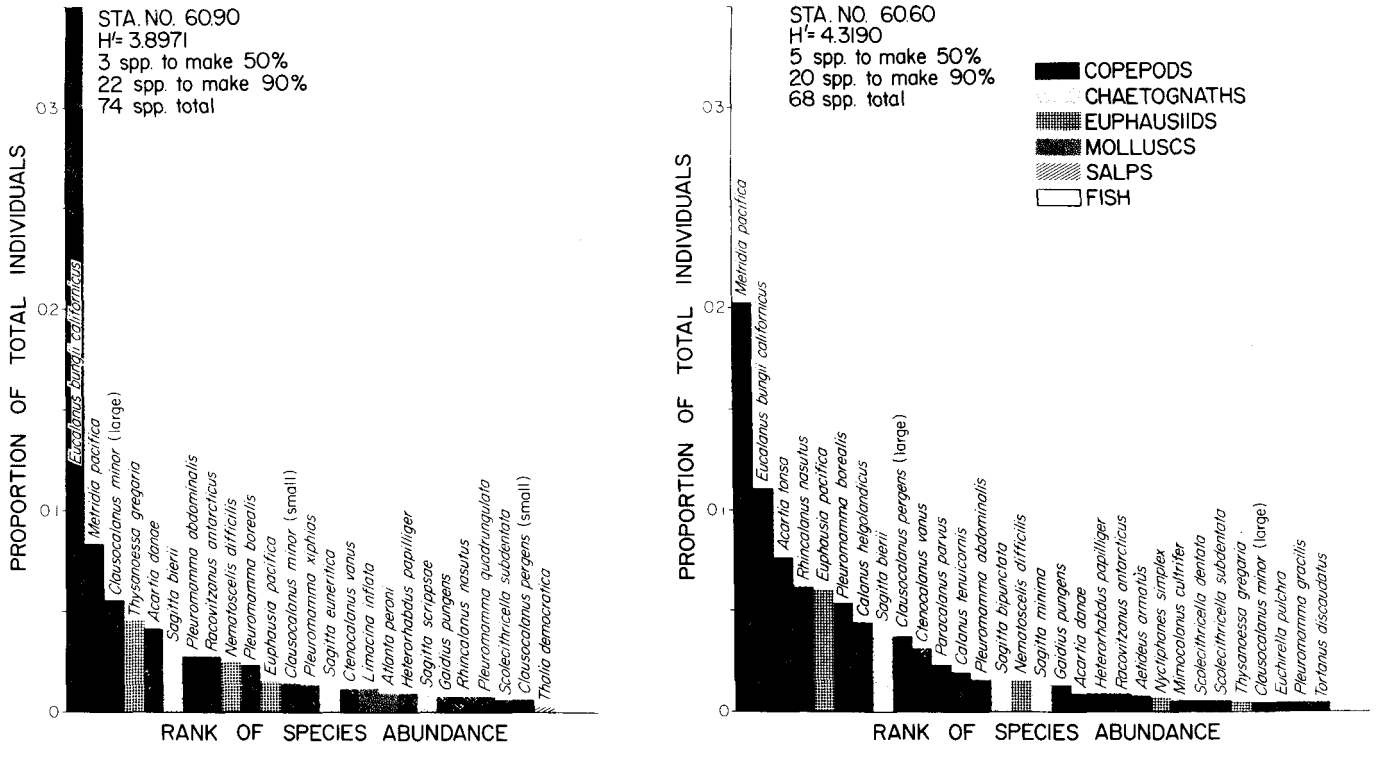


Figure 1. The rank order of abundance of zooplankton species caught by a 1-m-diameter net of 505 μm mesh size. Only the taxa shown in the key were counted to species. The category "molluscs" includes Thecosomata, Gymnosomata, Heteropoda, and larval Cephalopoda. The category "salps" includes only the orders Salpida and Doliolida. "*H*" is the Shannon diversity measure as defined in the text. Not all of the rare species are shown on the histograms. The stations are from line 60 off San Francisco.

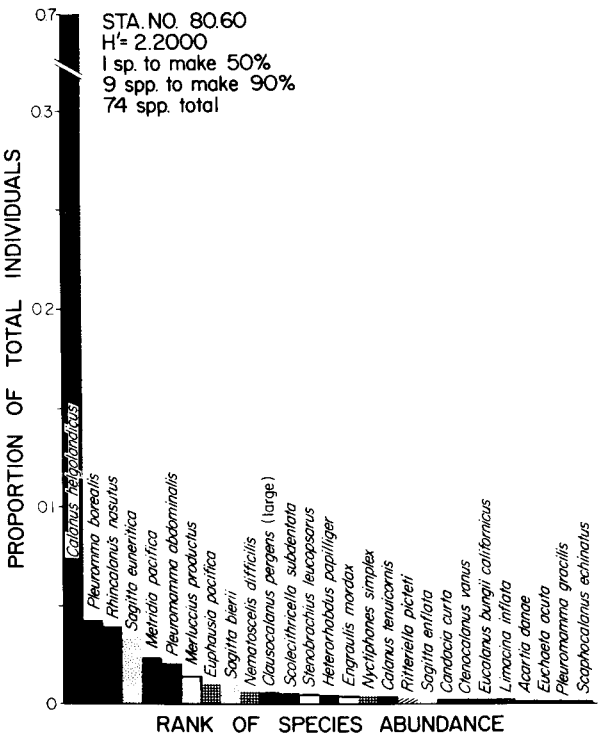
curves can be quantitatively expressed by the diversity index $H' = -\sum_{i=1}^{s} p_i \log_2 p_i$ (where p_i is the proportion of the sample that belongs to the ith species). This index has an unusually large range in the California Current as compared, for example, to the North Pacific Central Gyre (Figure 5; McGowan 1977).

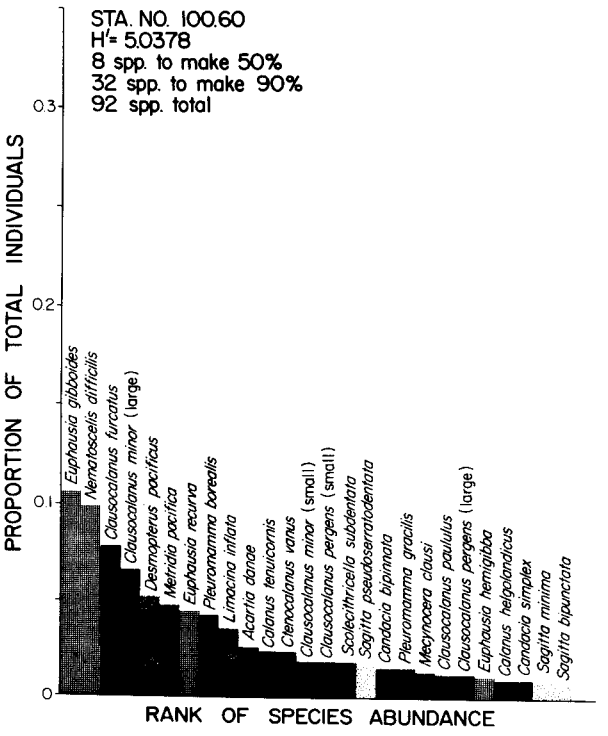
Another aspect of community species structure that seems highly variable in the California Current is that of constancy of rank order of macrozooplankton species. The histograms (Figures 1 and 2) show that the rank order of species changes dramatically from sample to sample. This may be expressed quantitatively by use of the Whittaker percent similarity index. This index expresses the degree to which one sample resembles another with respect to species proportions and is most strongly influenced by dominants. Figure 4 shows a series of these at two locales in the California Current and one in the Central Gyre. Again, we see that species proportions may vary widely on this scale of sampling in the California Current. Total macrozooplankton biomass and phytoplankton biomass also seem to be highly variable in both time and space as compared to the North Pacific Central Gyre (Figure 5). Thus the biotic habitat of larval fish in the California Current is much more variable than that of larvae in the Central Gyre.

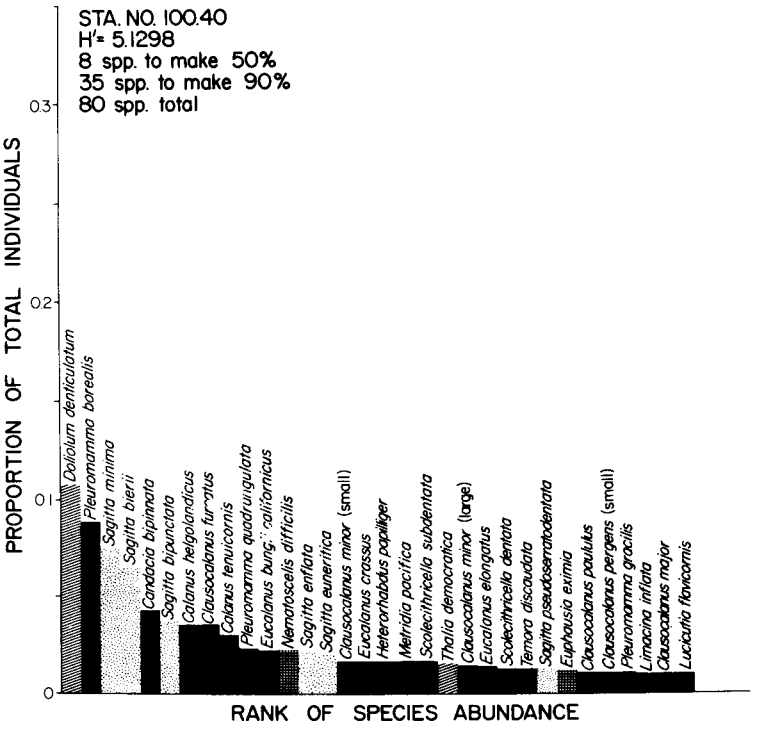
DISCUSSION

The picture of the biotic habitat of California Current fish larvae that emerges from this analysis is one of extreme variability or heterogeneity. In some places, part of any one population of larvae may be heavily dominated by one or two species of potential competitors; in other places, there may be many competitors, none of which are particularly dominant. In still other places, another part of the population is experiencing a habitat where potential predators are far more abundant than are the larval fish.

This apparent heterogeneity of biotic habitat may to some degree be a product of our sampling scheme. That is, the relatively long oblique net tows may be integrating the plankton in such a way that many species which do not actually occur very close together in the ocean are caught together in the same tow. But larval fish also integrate the environment by simply swimming around in some sort of a daily ambit. Therefore, while the instantaneous habitat may not look like what is caught in a net tow, the integrated habitat over a larva's two or three day ambit may resemble what we see in a net tow quite well. There is an additional problem in interpreting these data because of the spacing of the CalCOFI tows. The average distance between stations is large (several tens of kilometers), and the community structure and its constancy


STA. NO. 80.60
H'= 2.2000
1 sp. to make 50%
9 spp. to make 90%
74 spp. total
PROPORTION OF TOTAL INDIVIDUALS
0.7
0.3
0.2
0.1
0
Calanus helgolandicus
Pleuromamma borealis
Rhincalanus nasutus
Sagitta euneritica
Metridia pacifica
Pleuromamma abdominalis
Meriuccius productus
Euphausia pacifica
Sagitta bierii
Nematoscelis difficilis
Clausocalanus pergens (large)
Scolecithricella subdentata
Stenobrachius leucopsarus
Heterorhabdus papilliger
Engraulis mordax
Nyctiphanes simplex
Calanus tenuicornis
Ritterella picteti
Sagitta enflata
Candacia curta
Ctenocalanus vanus
Eucalanus bungii californicus
Limacina inflata
Acartia danae
Euchaeta acuta
Pleuromamma gracilis
Scaphocalanus echinatus
RANK OF SPECIES ABUNDANCE


STA. NO. 100.60
H'= 5.0378
8 spp. to make 50%
32 spp. to make 90%
92 spp. total
PROPORTION OF TOTAL INDIVIDUALS
0.3
0.2
0.1
0
Euphausia gibboides
Nematoscelis difficilis
Clausocalanus furcatus
Clausocalanus minor (large)
Desmopterus pacificus
Metridia pacifica
Euphausia recurva
Pleuromamma borealis
Limacina inflata
Acartia danae
Calanus tenuicornis
Ctenocalanus vanus
Clausocalanus minor (small)
Clausocalanus pergens (small)
Scolecithricella subdentata
Sagitta pseudoserratodentata
Candacia bipinnata
Pleuromamma gracilis
Mecynocera clausi
Clausocalanus paululus
Clausocalanus pergens (large)
Euphausia hemigibba
Calanus helgolandicus
Candacia simplex
Sagitta minima
Sagitta bipunctata
RANK OF SPECIES ABUNDANCE


STA. NO. 100.40
H'= 5.1298
8 spp. to make 50%
35 spp. to make 90%
80 spp. total
PROPORTION OF TOTAL INDIVIDUALS
0.3
0.2
0.1
0
Doliolum denticulatum
Pleuromamma borealis
Sagitta minima
Sagitta bierii
Candacia bipinnata
Sagitta bipunctata
Calanus helgolandicus
Clausocalanus furcatus
Calanus tenuicornis
Pleuromamma quadrungulata
Eucalanus bungii californicus
Nematoscelis difficilis
Sagitta enflata
Sagitta euneritica
Clausocalanus minor (small)
Eucalanus crassus
Heterorhabdus papilliger
Metridia pacifica
Scolecithricella subdentata
Thalia democratica
Clausocalanus minor (large)
Eucalanus elongatus
Scolecithricella dentata
Temora discaudata
Sagitta pseudoserratodentata
Euphausia eximia
Clausocalanus paululus
Clausocalanus pergens (small)
Pleuromamma gracilis
Limacina inflata
Clausocalanus major
Lucicutia flavicornis
RANK OF SPECIES ABUNDANCE

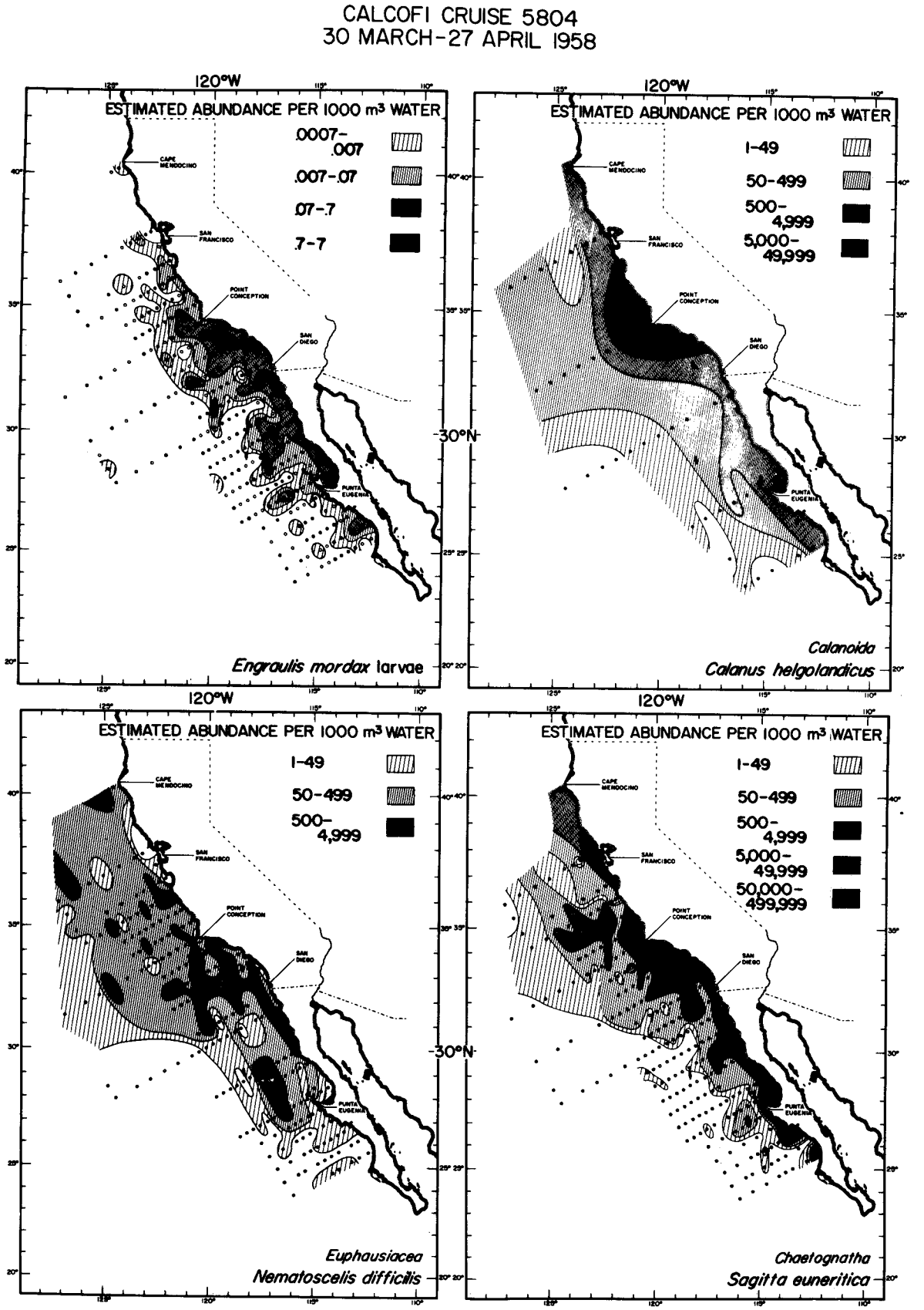


Figure 3. Contoured charts of the estimated abundance of the anchovy (*Engraulis mordax*) and three species of macrozooplankton. All estimates came from the same samples. (*Calanus helgolandicus* = *C. Pacificus*; from CalCOFI Atlases Nos. 2, 3, 5, and 9).

PERCENT SIMILARITY

	A2 1326	A4 1230	A5 1230	A6 1230	A7 1255	A8 1305	A9 1250
A1 1425	72.80	66.81	63.18	69.47	68.69	64.42	64.98
A2 1326		71.63	67.75	71.19	75.94	64.64	68.05
A4 1230			69.00	70.52	62.81	66.46	67.82
A5 1230				71.49	68.78	66.58	64.46
A6 1230					77.94	70.68	77.13
A7 1255						72.88	75.21
A8 1305							69.78

$\bar{X}$ = 69.7 D
$\bar{X}$ = 70.0 N

PSI
CALIFORNIA CURRENT

	.80	.60	.70	.80	.90	1.00
.80		79.4	39.6	19.3	14.7	
.60			57.7	32.5	12.0	
.70				41.9	26.8	
.80					43.3	
.90						
1.00						

POINT CONCEPTION

$\bar{X}$ = 37.2
Md = 36.0

	1.00	.60	.70	.80	.90	1.00
1.00		61.9	43.3	41.4	48.8	
.60			33.3	24.7	40.4	
.70				65.9	44.7	
.80					49.0	
.90						
1.00						

ENSENADA

$\bar{X}$ = 45.3
Md = 44.0

Figure 4. The percent similarity index (Whittaker and Fairbanks 1958) compares the degree to which one sample resembles another with respect to species proportions. The upper matrix is from a set of stations (A1 through A9) taken in the North Pacific Central Gyre. The lower matrix is from two sets of stations taken in the California Current. The mean PSI from the Gyre is much higher than those from the California Current (from McGowan 1977).

INDEX OF DISPERSION
BIOMASS

		$S^2/\bar{X}$	n
CHLOROPHYLL			
CAL. CURRENT	10 m	0.3	18
	20 m	0.9	18
GYRE	25 m	0.012	18
	75 m	0.013	18
ZOOPLANKTON			
CAL. CURRENT	north	1300.8	69
	central	73.3	78
	south	16.3	75
GYRE		3.6	52

DIVERSITY

GYRE	CAL. CURRENT
H': 4.5 - 4.9	H': 1.8 - 5.1

Figure 5. A comparison of the variability of phytoplankton (as estimated by chlorophyll concentration) and zooplankton biomass in the California Current and the North Pacific Central Gyre. In both cases the index of dispersion is orders of magnitude higher in the California Current. The diversity measures from copepod species counts in the Gyre show a much narrower range than do similar data from the California Current.

could be quite different on much smaller scales. But larval fish populations occur on very large scales, much larger than the station spacing, so it seems almost certain that the heterogeneity of the entire population's biotic habitat is great.

If competition for food or predation are important in larval survivorship, then this should be demonstrated directly, and such studies probably must be done on small spatial and short temporal scales. But populations grow or decline on large spatial scales. If availability of food, competition, and predation are important regulators of entire larval fish populations, then these factors must also exert their influence on large time-space scales. Somehow the results of small-scale studies must be extrapolated to the population scale. Alternatively, such studies might be done simultaneously in several locales scattered throughout the range of the larval population so that the spatial coherence of the interaction can be estimated.

It would be very useful for planning such studies if we could detect some overall trends in time and space in the co-occurrence of larval fish with dominant species of invertebrates. But relatively few zooplankton samples have been analyzed with this degree of completeness and, in view of the large variability in the community structure, it seems unlikely to be a very easy matter to detect trends or consistent patterns of co-occurrence. This carries with it the corollary that it will be very difficult to select appropriate species of zooplankters to study in terms of their competitive abilities with fish larvae. Since there seem to be many of these and the "important" ones seem to change from place to place, which one should be selected for study? The same argument may be made for predators.

There are, however, some trends that are apparent, and

these give us some additional insight on the biotic habitat of larval fish. There is an areal pattern in diversity. Figure 6 shows a contoured plot of this index and it is evident that north of Point Conception there is a large, offshore tongue of low diversity that appears to be intruding from the north. In the central sector, the Southern California Bight region, diversity is high. From Punta Eugenia to the south there is another tongue of low diversity, nearshore and apparently intruding from the south. Cruise 5810 shows a similar pattern. The "intrusions" are consistent with what we know of the gross circulation of the system. The magnitude of the diversity index, H', is sensitive to both degree of dominance and number of species present and, in our data, is very well correlated with number of species (Figure 7). From this diversity map and the two aspects of diversity (dominance and number of species), we can see that in the north, fish tend to live in a habitat with relatively few other species but where dominance by one or a few species is strong. In the central sector, the fish are exposed to a habitat where there are relatively many species present but where dominance is much less pronounced.

The data for these diversity maps came from only two

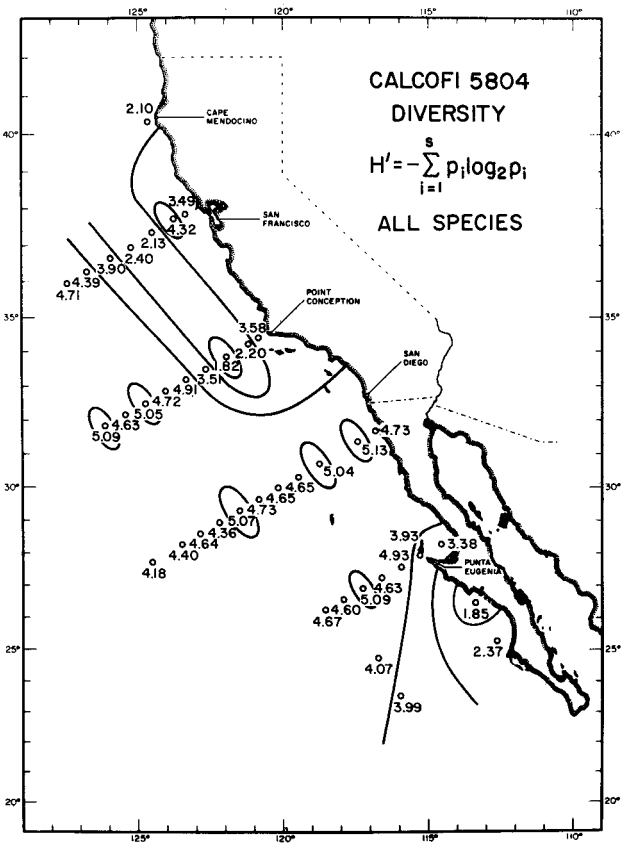


Figure 6. A contoured map of diversity measures. In the northern part of the California Current, diversity is low offshore. In the central sector, it is generally high. In the south, it is low nearshore.

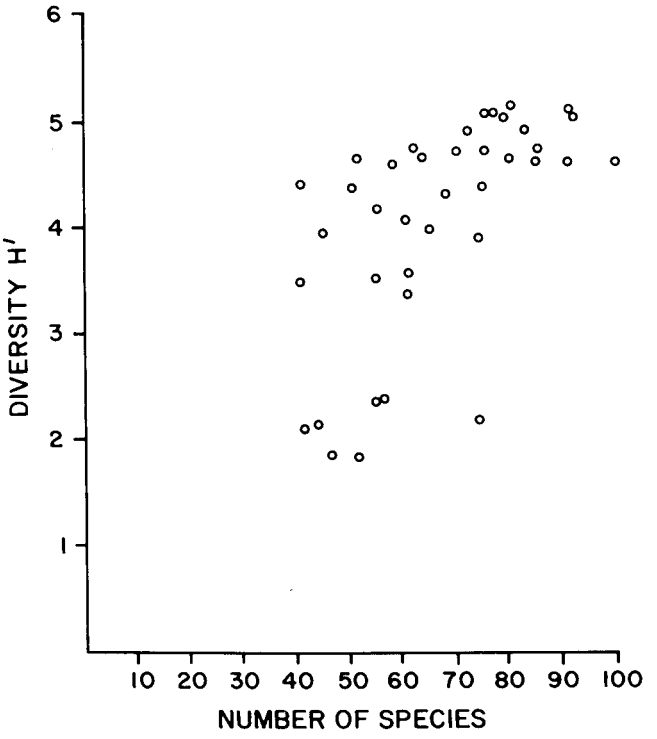


Figure 7. Diversity index (H') as a function of number of species of macrozooplankton $r_d = 0.7$ ($P < .001$).

cruises taken in a year when there was an anomalously warm California Current. Therefore, the diversity trend we see could also be anomolous and not representative of the system in general. But in addition to being consistent with the circulation, the generality of these maps is implied by long-term studies of biogeography and intuitive impressions one gains from perusal of the CalCOFI zooplankton species atlases. It would be of practical and theoretical interest to see if larval fish mortality was in any way correlated with this simple pattern.

ACKNOWLEDGMENTS

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