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THE RELATION BETWEEN THE DISTRIBUTION OF ZOOPLANKTON PREDATORS AND ANCHOVY LARVAE

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The plankton collections analyzed for this study correspond to the monthly California Cooperative Oceanic Fisheries Investigation (CalCOFI) cruises of 1954, 1956, 1958. These years were selected because they were respectively "slightly colder", "colder", and "warmer" than the long-term average for the California Current. The total plankton was analyzed for species of Chaetognatha, Siphonophorae, Chondrophorae, Medusae and Ctenophora. Predation by these zooplankters has been observed frequently by planktologists, who find larvae in various stages of digestion in the guts of these predators, which are more effective on actively swimming large fish larvae than on relatively passive yolk-sac larvae.

Data on the distribution and abundance of larvae of the northern anchovy (*Engraulis mordax*) were compared with concentrations of predator species. Anchovy eggs were not included in the analysis due to the feeding characteristics of the predatory zooplankters, which respond primarily to movement or chemical agents, stimuli that are not provided by eggs.

While analyzing collections for the five groups of invertebrate predators, information was also taken on other zooplankton groups which occurred abundantly in the collections; Copepods, Euphausiids, Decapod larvae, Pteropods, Heteropods, Polychaetes, Salps, Doliolids and Pyrosomes.

METHODS

For each collection, individuals of the five predator groups were identified to species and the number of individuals were counted for the total sample. Counts from each sample were standardized to the number per 1000 m^3 of water strained. Other observations taken simultaneously included stage of sexual maturity, phase of life cycle, and occurrence of food in the stomach. Partially digested organisms in stomachs which evidenced feeding previous to collection, were identified.

Altogether more than 2000 plankton samples were analyzed. The CalCOFI collections were usually obtained with a net, 1 m in diameter at its mouth, hauled obliquely from 140 m depth, or less in shallow waters, to the surface. The CalCOFI collections were grouped into three categories with respect to abundance of anchovy larvae per standard haul; anchovy rich (more than 241 larvae), anchovy poor (1–240 larvae), and anchovy lacking (zero anchovy larvae per standard haul).

KINDS AND ABUNDANCE OF PREDATORY SPECIES

Altogether 22 species of Chaetognatha, 48 Siphonophorae, 34 Medusae, 3 Ctenophora, and 1 Chondrophorae were recorded. Variations in the composition of species of all groups were observed in the 3 years. Tropical species were taken mainly in 1958, the warmer than average year. The highest variability occurred in the Medusae, which usually show erratic distribution in time and space. Agalmid Siphonophorae are among the most successful predators, as they move swiftly through the waters acting as living nets capturing other plankters. *Stephanomia bijuga*, the most abundant agalmid in the CalCOFI collections, could be one of the primary predators on fish larvae. Ctenophores, except Beroë, were infrequently taken. These organisms are often destroyed by preservation, hence the numbers recorded are underestimations of their true abundance in the collections. Ctenophores float at or near the surface, and their predatory activity would be limited to this zone.

Yearly abundance of Chaetognatha,

Siphonophorae and Medusae were compared for the three categories of anchovy larvae abundance [high, low, and zero (Fig. 1)]. Chaetognatha were abundant in all three types of hauls. It should be noted that the two most abundant chaetognaths, *S. euneritica* and *S. bierii* are not considered important as predators on fish larvae, whereas, as discussed below, the three species of chaetognaths considered to be prime predators occurred less frequently and usually in less abundance in anchovy rich hauls. In 1956 samples there was little difference in abundance in all three groups of predators in the three categories of anchovy hauls. In 1954 and 1958 Siphonophorae were less abundant in anchovy rich hauls. A striking inverse relation between abundance of Medusae and abundance of anchovy larvae is evidenced in the 1954 and 1958 collections.

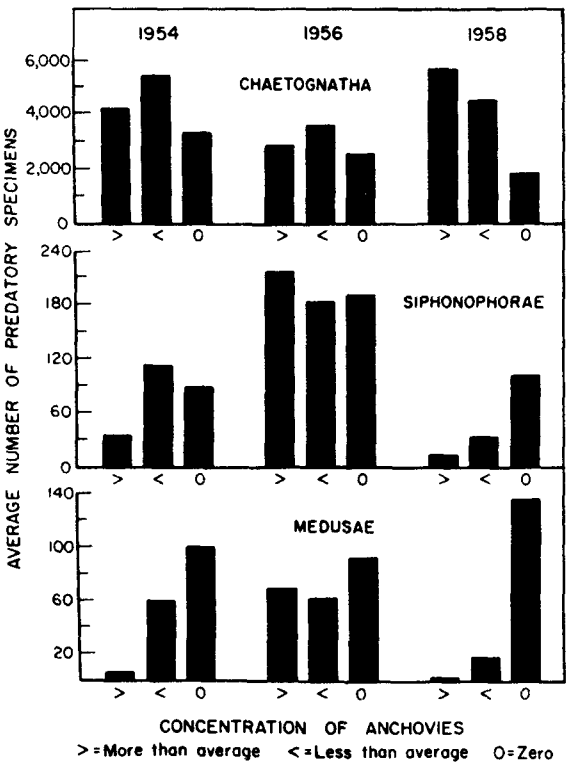

Figure 1. Yearly abundance of predators (Chaetognatha, Siphonophorae, Medusae) and concentration of anchovy larvae (high = more than 241 larvae per standard haul; low = 1–240 anchovy larvae per standard haul; zero = absence of anchovy larvae).

The predatory potential of an individual is roughly proportional to its size, and the predatory potential of the species is related to both size and abundance.

Based on these criteria, a selection was made from among the three principal groups of species considered to be primary candidates as effective predators on fish larvae. Those selected for separate study were the chaetognaths *Sagitta enflata*, *S. hexaptera*, *S. scrippsae*; the Siphonophorae *Chelophyes appendiculata*, *Diphyes dispar*, *Stephanomia bijuga*; and the Medusae *Liriope tetraphylla*, *Rhopalonema velatum*, *Aglaura hemistoma*. In each species recurrence and abundance were analyzed for anchovy rich and anchovy lacking hauls for each of the 3 years. Altogether these nine species, during 3 years result in 27 comparisons. In 24 of these the predator species occurred in greatest or major abundance in hauls lacking anchovy larvae, and in all 27 the frequency of occurrence of predator species was higher in hauls lacking anchovy larvae than in those with large aggregations of larvae (Table 1).

RELATION OF UPWELLING AND ANCHOVY LARVAE

Sagitta decipiens (mesopelagic chaetognath) can be used as an indicator of upwelling (Alvariño, 1965; Nair, 1977; Nair and Rao, 1973). Upwelling based on *S. decipiens* was most intense in 1956, intermediate in 1958, and low in 1954, which agrees with Bakun (1973) and Wyllie (1966). *S. decipiens* occurred in 2.8% of

Table 1. Most abundant large species of predators, and highest and zero concentration of anchovy larvae during 1954, 1956, 1958.

Abundance of anchovy larvae:	1954				1956				1958			
	High		Zero		High		Zero		High		Zero	
Species abundance: Species	% occur.	Aver. occup.	% occur.	Aver. occup.	% occur.	Aver. occup.	% occur.	Aver. occup.	% occur.	Aver. occup.	% occur.	Aver. occup.
Sagitta enflata	56	491.3	73	1 093.7	43	191.8	47	121.6	74	271.6	82	308.4
S. hexaptera	22	5.5	55	16.1	27	1.8	53	62.0	26	15.5	52	42.2
S. scrippsae	33	48.1	52	19.2	20	3.2	33	17.4	16	6.5	27	9.9
Stephanomia bijuga	7	0.2	27	0.8	13	1.2	22	2.0	11	0.2	27	1.8
Chelophyes appendiculata	33	10.0	76	89.3	17	5.0	47	7.6	32	2.6	67	46.2
Diphyes dispar	22	14.7	48	44.1	0	0	0	0	0	0	3	0.4
Liriope tetraphylla	22	20.9	64	253.6	37	96.5	42	41.8	21	6.8	58	89.4
Rhopalonema velatum	7	0.6	46	30.3	7	0.3	28	4.1	5	0.3	33	18.2
Aglaura hemistoma	0	0	12	40.2	0	0	3	1.1	5	0.2	18	51.7

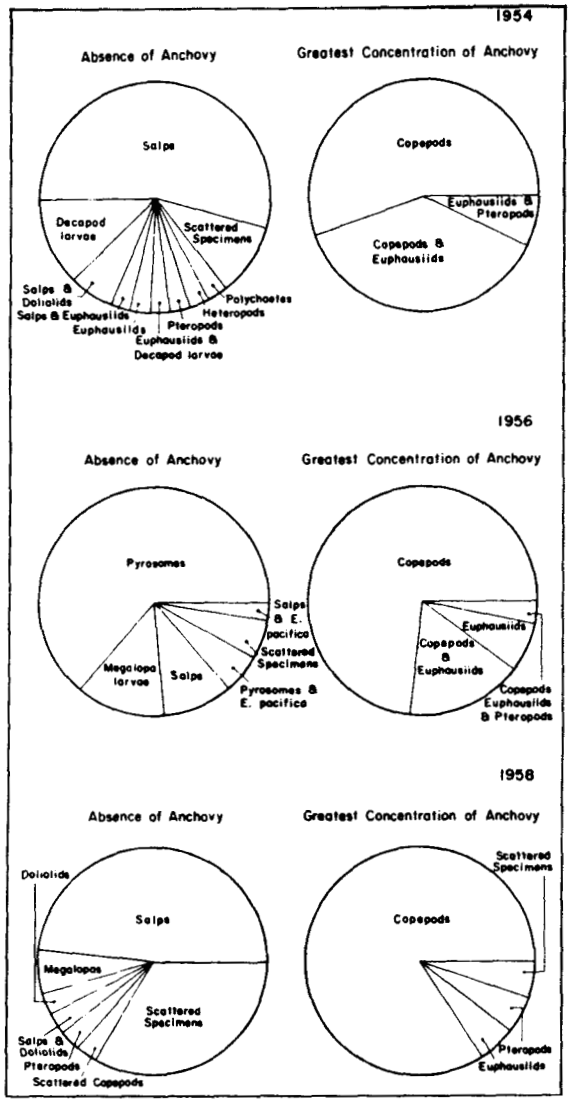

Figure 2. Relative abundance of various additional zooplankters at locations with highest concentration and absence of anchovy larvae, for 1954, 1956, 1958.

hauls with large concentration of anchovy larvae and in 4.95% of hauls with zero anchovy abundance. This could be interpreted as an indication that large concentrations of anchovy larvae occur infrequently in upwelling areas.

RELATION OF PLANKTON ASSEMBLAGES TO ANCHOVY LARVAE

During the 3 years Copepods were the dominant zooplankton group in samples rich in anchovy larvae. They dominated in almost 80% of those collections and in the remainder the dominant groups were Euphausiids and Pteropods.

In contrast, these groups were not dominant in hauls from localities with no anchovy larvae. In 1954 and 1958 the absence of anchovy larvae coincided in about 60% of the samples with dominance of Salps, and in other instances with Doliolids, Decapod larvae, Polychaetes, Pteropods and Euphausiids. In 1956 the dominant group in hauls lacking anchovy larvae were Pyrosomes, in more than 63% of hauls; while Megalops, Salps, and *Euphausia pacifica* dominated in other locations. The contrast in the major additional plankton constituents between anchovy rich and anchovy lacking hauls is striking (Fig. 2). This unanticipated finding indicates that anchovy larvae occur in abundance primarily in hauls dominated by Copepoda and/or Euphausiids, and never in hauls dominated by pelagic Prochordates. The former habitat can be characterized as "anchovy water". This fact also illustrates that predatory pressure of zooplankters is weaker when there is abundance of Copepods, which was also evidenced by the gut content analysis of those zooplankters.

In a recent colloquium dealing with larval fish mortality studies, it was concluded that "major causes of larval mortality are starvation and predation, and these may interact" (Hunter, 1976). Obviously, mortality from starvation is reduced when anchovy larvae are situated in waters with an adequate food supply, and mortality from predation is reduced when potential predators are in reduced abundance. This favourable combination of factors has been shown for "anchovy water".

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