THE RELATION BETWEEN THE DISTRIBUTION OF ZOOPLANKTON PREDATORS AND ANCHOVY LARVAE

ANGELES ALVARIÑO
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, CA 92038

ABSTRACT

Monthly CalCOFI cruises of 1954, 1956, and 1958 were analyzed for abundance of populations of species of Chætognatha, Siphonophoræ, Chondrophoræ, Medusæ, and Ctenophora. Data were also noted on other abundant zooplankters in the samples (copepods, euphausiids, decapod larvae, pteropods, heteropods, polychætes, salps, doliolids, and pyrosomes). Information was grouped into three categories of abundance of anchovy larvae per standard haul (more than 241 anchovy larvae, from 1 to 240, and absence of larvae). In general, concentration of predators was inversely related to aggregations of anchovy larvae. Absence of anchovy larvae coincided with prochordates, decapod larvae, pteropods, heteropods, and polychætes, and abundance of anchovy larvae concurred with abundance of copepods and/or euphausiids. This habitat can be designated "anchovy water."

Gut content analysis indicated that predatory pressure on fish larvae was weaker when there was abundance of other food animals, e.g. copepods and euphausiids in the waters, as shown by the plankton collections.

RESUMEN

Las poblaciones de especies de Quetognatos, Sifonóforos, Condróforos, Medusas y Ctenóforos han sido analizadas en las colecciones de plancton obtenidas durante los cruceros mensuales de CalCOFI en 1954, 1956 y 1958. Conjuntamente se anotaron datos sobre la abundancia de otros zooplanctones presentes en esas muestras de plancton (Copépodos, Eufáusidos, larvas de Decápodos, Pterópodos, Heterópodos, Poliquetos, Salpas, Doliolos y Pirosomas). La información obtenida sobre la abundancia de las especies correspondientes, se ha agrupado en tres categorías, en relación con la cantidad de larvas de anchoa en cada arrastre (más de 241 larvas, desde 1 hasta 240, y ausencia de larvas). En general, la concentración de depredadores y larvas de anchoa aparecía en relación inversa. Se observó con frecuencia, que en las zonas de surgencia no aparecían larvas de anchoa. La ausencia de larvas de anchoa coincidía con la presencia de Procordados, larvas de Decápodos, Pterópodos, Heterópodos, y Poliquetos, y la abundancia de larvas de anchoa concurría con gran cantidad de Copépodos y Eufáusidos. Este hábitat podría denominarse "agua de anchoa."

Los análisis del contenido estomacal de los depredadores y las correspondientes muestras de plancton han demostrado que cuando abundaban en el plancton copépodos y eufáusidos, los depredadores ingerían menos larvas de peces.

INTRODUCTION

Mortality of pelagic marine fish larvae can result from a variety of causes, both biotic and abiotic. Among the more important biotic causes are starvation, predation, parasites, and disease; among the abiotic causes are storms, currents, ultraviolet radiation, temperature, salinity, oxygen, and pollution. It was the consensus of participants in a Colloquium on Larval Fish Mortality Studies, held in La Jolla during January of 1975, "that the major causes of larval mortality are starvation and predation, and that these may interact" (Hunter 1976). It was noted in the report that most research emphasis had been placed on starvation and relatively little work existed on predation. Observations on predation of invertebrate plankton organisms on fish larvae appear in Lebour (1922, 1923, 1925), Bigelow (1926), Fraser (1969), Dekhnik et al. (1970), and others, as discussed in Alvariño (1976, 1977).

Several recent laboratory studies have dealt with invertebrate predation on newly hatched larvae of the northern anchovy: copepods as predators (Lillelund and Lasker 1971) or the euphausiid *Euphausia pacifica* in Theilacker and Lasker (1974). These predators are most effective on the relatively passive yolk-sac larvae of the anchovy and less so on actively swimming larger anchovy larvae. The principal planktonic predators on large anchovy appear to be Chætognatha, Siphonophoræ, Chondrophoræ, Medusæ, and Ctenophora. Predation by these zooplankters has been observed frequently by planktologists, who find fish larvae in various stages of digestion inside the guts of these predators. Despite such observations, no one has attempted a thorough analysis of such predation on fish larvae.

It is the purpose of this contribution to study the relation between occurrence and abundance of anchovy larvae (*Engraulis mordax*) to the other elements in the plankton, with emphasis on potential predators, and also to characterize the assemblages of plankters in relation to anchovy larva abundance. The monthly CalCOFI collections made off California and Baja California in 1954, 1956, and 1958 were selected for this study. These three

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years were respectively, slightly colder, colder, and warmer than the long-term average for the California Current region. One reason for reanalyzing field collections of plankton rather than doing experimental studies in the laboratory on Chætognatha, Siphonophoræ, Chondrophopæ, Medusæ, and Ctenophora as predators is that these organisms are difficult subjects for experiments. They lack the capacity for food reserve storage, for example, hence must feed continuously to avoid starvation. The reason for limiting the study to anchovy larvae while ignoring occurrence and abundance of anchovy eggs is that the eggs are less exposed to predation by these predators, which respond primarily to movement.

METHODS

The plankton collections analyzed were from the monthly cruises of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) for 1954, 1956, and 1958. The area covered was the California Current region off California and Baja California, with usual coverage between San Francisco, off central California, to Cape San Lazaro, off southern Baja California (CalCOFI lines 60 to 137). The plankton was collected with a bridled net, 1 m in diameter at the mouth, about 5 m in length, constructed of heavy-duty bolting grit gauze of 50xxx mesh. The nets were equipped with flow meters to measure the volume of water strained during each tow. The hauls were made obliquely from about 140 m to the surface, depth of water permitting.

The total plankton sample was analyzed for the five groups of predators: Chætognatha, Siphonophoræ, Chondrophoræ, Medusæ, and Ctenophora. It should be pointed out that Ctenophora are often destroyed by preservation, hence the numbers recorded are underestimates of their true abundance in the collections. In all five groups, specimens present in each sample were identifed to species and counted by species. Only occasionally, when a species occurred in large numbers, were counts made on an aliquot of the total sample. Numbers of each species were standardized to the number in 1,000 m^3 of water strained. In addition, the size of each specimen in mm was recorded, together with stage of sexual maturity and/or stage of life cycle. Also, the number of specimens with food in the stomachs was noted, and partially digested organisms were identified. It is supposed that many of these predators fill their guts while in the plankton net, hence presumed newly ingested organisms were not considered. Table 5, which is not included in this report, but is available from the author upon request, detailed the assemblages of plankton at selected locations in the anchovy larvae realm, with absence of anchovy and highest concentration of anchovy larvae, for the monthly cruises of 1954, 1956, 1958. Also in this Table appear for each selected station the abundance of each of the species of Chætognatha, Siphonophoræ, Medusæ, Ctenophora; the presence of copopods, euphausiids, pteropods, heteropods, decapoda larvae, polychætes, tunicates; and information on the volume of water strained per haul.

During the analysis of the collections of the three years, it was observed that approximately 36% of the chætognaths had food in their stomachs, and all specimens of the two largest species, *Sagitta hexaptera* and *S. scrippsae*, contained food in many collections. Some chætognath stomachs contained prey not present in the corresponding plankton samples.

Data also were taken on the relative abundance of the various constituent groups in each sample. The groups included, in addition to the five groups of predators discussed above, were copepods, euphausiids, decapod larvae, pteropods, heteropods, polychætes, salps, doliolids, and pyrosomes. The determinations were based on dominance of a group or groups in the collections analyzed.

Although initially it was proposed to analyze all samples taken during the three years, 1954, 1956, and 1968, this soon proved to be too large a task. Instead, emphasis was placed on the areas that contained anchovy larvae in some abundance, in order to determine areal and temporal coverages that would bear most directly on the problem of predator-anchovy interactions. The collections used in the following analyses were 849 for 1954, 316 for 1956, and 899 for 1958.

Anchovy abundance was divided into three categories on the basis of abundance in the tows: high, low, and zero. The standard haul values of anchovy larvae in the high category corresponded to 241 larvae or more per haul. The standard haul value is the estimated number of anchovy larvae under 10 m^2 of sea surface. The count of low abundance included all positive hauls with counts lower than 241 larvae per standard haul. Inasmuch as the average CalCOFI haul sampled to about 140 m depth, the actual volume of water involved under 10 m^2 of sea surface is approximately 1,400 m^3. Although the number of anchovy larvae is not ordinarily expressed as the number in 1,000 m^3 water strained, the unit of volume used for zooplankters would be about 10/14 that of anchovy larvae on the average, or approximately 172 larvae or more for the high category of anchovy larvae abundance.

KINDS AND ABUNDANCE OF PREDATORY SPECIES IN THE FIVE CATEGORIES BEING STUDIED

A list of the species encountered by category, number of individuals taken and number of positive hauls (occurrences) of each species by year, and information on size and depth distribution of each species is contained in Table 1. The information included in this table, such as the kinds and abundance of the species of chætognaths,

TABLE 1

Abundance of Predatory Species (Frequency, in Parentheses) with Information on Size and Depth Distribution.

	Total number (and frequency)			∼Maximum size			
Species	1954 (849 hauls)	1956 (316 hauls)	1958 (899 hauls)	(mm)	Nect.	cm complete animal	Depth distribution
Eukrohnia bathypelagic, Alvariño 1962		34(1)		23			Upper 100 m during upwelling
E. hamata (Möbius) 1875		43(1)		43			Upper 100m during upwelling
Krohnitta pacifica (Aida) 1897	464(20)		943(40)	8			Upper 100 m
K. subtilis (Grassi) 1881	5402(144)	2186(29)	5735(242)	16			Upper 100 m to surface
Pterosagitta draco (Krohn) 1895	5189(175)	1761(43)	13531(350)	10			Upper 100 m to surface
Sagitta bedoti Beraneck 1895	528(5)		2797(12)	15			Upper 100 m to surface
S. bierii Alvariño 1961	785319(712)	235853(210)	481090(700)	17			Upper 100 m to surface
S. bipunctata Quoy and Gaimard 1827	10870(244)	2969(43)	32665(384)	18.5			Upper 100 m to surface
S. decipiens Fowler 1905	3446(12)	3184(35)	1744(46)	16			Upper 100 m during upwelling
S. enflata Grassi 1881	366890(511)	43618(135)	831089(794)	25-30			Upper 100 m to surface
S. euneritica Alvariño 1961	2052102(616)	592934(284)	983727(485)	15.5			Upper 100 m to surface
S. hexaptera d'Orbigny 1834	10941(422)	2599(157)	14009(477)	40-60			Upper 100 m to surface
S. maxima (Conant) 1896		184(12)		>90			Upper 100 m during upwelling
S. minima Grassi 1881	250862(625)	44374(217)	300710(662)	10			Upper 100 m to surface
S. neglecta Aida 1897	606(12)		466(13)	8			Upper 100m to surface
S. pacifica Tokioka 1940	8664(84)	3137(26)	25187(256)	14			Upper 100 m to surface
S. pseudoserratodentata Tokioka 1936	40940(248)	6301(36)	92194(420)	10			Upper 100 m to surface
S. pulchra Doncaster 1903			23(1)	24			Upper 100 m to surface
S. regularis Aida 1897	1996(22)		5065(54)	6			Upper 100 m to surface
S. robusta Doncaster 1903	179(6)		1539(24)	12			Upper 100 m to surface
S. scrippsae Alvariño 1962	52289(443)	13903(169)	11192(169)	60			Upper 100 m to surface
S. zetesios Fowler 1905		24(1)		43			Upper 100 m during upwelling
Agalma okeni Eschscholtz 1825	25(5)	37(13)	58(18)		20	>100	Surface and depth
Nanomia cara Agassiz 1865		5(1)			>51	>100	Surface and depth
Stephanomia bijuga (Delle Chiaje) 1841	552(59)	1157(101)	210(43)		15	>100	Surface and depth
Bargmannia elongata Totton 1954		82(5)	11(1)		30	>100	Surface and depth
Physophora hydrostatica Forskal 1775		56(15)	19(6)		8	12	Surface and depth
Erenna richardi Bedot 1904			3(1)		40	>100	Surface and depth
Epibula ritteriana Haeckel 1888	15(2)	3(1)				6	Surface
Rosacea cymbiformis 1841 Chiaje	6(2)	11(2)	3(1)		350	many	Surface and depth
R. plicata Quoy and Gaimard 1827	6(2)	12(2)			200	many	Surface and depth
Nectodroma dubia Quoy and Gaimard 1834	3(1)	88(4)	6(2)		85	many	Upper 100 m
N. reticulata Bigelow 1911		2(1)			55	many	Upper 100 m
Nectopyramis thetis Bigelow 1911			3(1)		40	many	Upper 100 m and depth
Lilyopsis rosea Chun			6(2)		120	many	Upper 100 m and depth
Amphicaryon acaule Chun 1888	6(2)	9(2)			>15	many	Upper 100 m and depth
A. ernesti Totton 1954	18(4)	9(1)	6(1)		>15	many	Upper 100 m and depth
Hippopodius hippopus Forskal 1776	3(1)	20(6)	18(6)		19	many	Surface and depth
Vogtia kuruae Alvariño 1967		3(1)			20	many	Surface and depth
V. spinosa Kefferstein and Ehlers 1861		40(2)			20	many	Surface and depth
Chelophyes appendiculata Eschscholtz 1829	15819(145)	7079(160)	14628(154)		10	2	Upper 100 m to surface
C. contorta (Lens and Riemsdijk) 1908	83(3)	7(1)	2622(20)		7	14	Upper 100 m to surface
Dimophyes arctica Chun 1897		23(2)			13		Upper 100 m to surface
Diphyes bojani (Eschscholtz) 1829		12(3)	562(150		15	3	Upper 100 m to surface
D. dispar Chamisso and Eysenhardt 1821	19802(89)	614(9)	150(6)		20	4	Upper 100 m to surface
Diphyopsis mitra Huxley 1859	79(3)	105(5)	2243(22)		10	2	Upper 100 m to surface
Muggiaea atlantica Cunningham 1892	25117(123)	29565(165)	11495(95)		7		Surface
Eudoxia macra Totton 1954	916(8)	366(12)	808(12)		4		Surface
Eudoxoides spiralis Bigelow 1911	1008(15)	617(12)	16690(64)		7		Upper 100 m to surface
Sphaeronectes sp.	29(2)	135(6)	155(8)		8		Upper 100 m to surface
Lensia campanella Moser 1925			279(4)		6	1	Upper 100 m to surface
L. challengeri Totton 1954	14366(69)	17862(99)	7236(77)		9	1.7	Upper 100 m to surface
L. conoidea Kefferstein and Ehlers 1861	53(3)	495(30)	267(12)		20	4	Upper 100 m and depth
L. grimaldii Leloup 1933		4(1)			7	1.3	Upper 100 m
L. hotspur Totton 1954	1273(11)	855(35)	1711(31)		5	0.9	Upper 100 m to surface
L. meteori Leloup 1934			14(1)		5		Upper 100 m
L. multicristata Moser 1925	61(4)	730(36)	498(23)		17	3.5	Upper 100 m and depth
L. subtilis Chun 1886			115(3)		12	2.2	Surface
L. subtiloides (Lens and Van Riemsdijk) 1908			31(2)		5	1	Surface
Chuniphyes multidentata Lens and van Riemsdijk 1908	2(1)	4(1)	37(2)		40	7.6	Upper 100 m and depth
Sulculeolaria biloba Sars 1846		12(2)	29(2)		20	4	Surface and depth
S. chuni Lens and van Riemsdijk 1908	34(1)	3(1)	113(4)		8	1.5	Upper 100 m

TABLE 1 (CONTINUED)
Abundance of Predatory Species (Frequency, in Parentheses) with Information on Size and Depth Distribution.[1]

	Total number (and frequency)			~ Maximum size			
Species	1954 (849 hauls)	1956 (316 hauls)	1958 (899 hauls)	(mm)	Nect.	cm complete animal	Depth distribution
S. monoica Chun 1888	94(1)	45(6)	94(7)		10	2	Surface and depth
S. quadrivalvis Blainville 1834	86(4)	65(7)	796(29)		20	3.7	Upper 100 m to surface
Abyla bicarinata Moser 1925		6(2)			10	2	Upper 100 m
A. brownia Sears 1953		41(2)					Upper 100 m to surface
A. haeckeli Lens and van Riemsdijk 1908		9(2)	53(7)		9	1.8	Upper 100 m to surface
Abylopsis eschscholtzi Huxley 1859			26(3)		8	1.3	Upper 100 m to surface
A. tetragona Otto 1823	165(3)	3(1)	3(1)		20	4.3	Upper 100 m to surface
Bassia bassensis Quoy and Gaimard 1834		92(2)	88(2)		7	1.3	Upper 100 m to surface
Velella velella Linne 1758		4(2)				10.4	Surface
					µm (height ×width)		
Euphysora furcata Kramp 1948	6(1)		13(3)		8×6.5		Surface
Annatiara affinis (Hartlaub) 1913		3(1)			23		Upper 100 m during upwelling
Leuckartiara octona (Fleming) 1823			82(4)		20		Upper 100 m to surface
L. zacae Bigelow 1940	840(32)	326(36)	806(22)		21×18		Upper 100 m to surface
Octotiara russelli Kramp 1953		3(1)			7		Surface
Bythotiara murrayi Gunther 1903		3(1)			20		Upper 100 m during upwelling
Calycopsis nematophora Bigelow 1913		2(1)			30		Upper 100 m to surface
C. simulans (Bigelow) 1903			52(1)		30×22		Upper 100 m to surface
Sibogita geometrica Maas 1905	7(1)				38×20		Upper 100 m
Melicertum georgicum Agassiz 1862			7300(1)		20		Upper 100 m to surface
Mitrocoma discoidea Torrey 1909	10(1)				45		Surface
Obelia spp.	6(1)	147(3)			6		Upper 100 m to surface
Phialidium gregarium (L. Agassiz) 1862	97(2)				12		Surface
Eirene hexanemalis (Goette) 1886			3(1)		18		Surface
Phialopsis diegensis Torrey 1909	655(13)	78(12)	153(8)		10×30		Upper 100 m
Gossea brachymera Bigelow 1909			21(3)		20		Surface
Liriope tetraphylla (Chamisso and Eysenhardt) 1821	39853(119)	16035(148)	21548(99)		30		Upper 100 m to surface
Aglaura hemistoma Pèron and Lesueur 1809	3892(14)	3157(11)	33144(58)		6×4		Upper 100 m to surface
Colobonema sericeum Vanhoffen 1902			11(1)		45×35		Upper 100 m and deep waters
Rhopalonema velatum Gegenbaur 1856	5709(57)	2883(60)	9913(78)		10		Upper 100 m to surface
Aegina citrea Eschscholtz 1829	134(50	1032(17)	82(3)		50		Surface and deep water
Aeginura beebei Bigelow 1940			3(1)		18×100		Upper 100 m
A. grimaldii Maas 1904	186(5)	329(9)	225(9)		45		Upper 100 m and deep water
Solmundella bitentaculata (Quoy and (Gaimard) 1822		240(4)	9(1)		12		Upper 100 m to surface
Pegantha clara R.P. Bigelow 1909		14(2)	6(1)		25×55		Upper 100 m
P. laevis H.B. Bigelow 1909		3(1)			40		Upper 100 m
Solmaris corona (Keferstein and Ehlers)1861	8(2)	108(8)			>15		Upper 100 m and surface
S. rhodoloma (Brandt) 1838	13800(1)				7		Surface
Cunina globosa Eschscholtz 1829		6(1)			18		Surface
C. tenella (Bigelow) 1909		3(1)			7		Surface
Atolla wyvillei Haeckel 1880			6(2)		150		Upper 100 m during upwelling
Atorella vanhoeffeni Bigelow 1909		7(2)			7		Upper 100 m during upwelling
Periphylla periphylla (Pèron and Lesueur) 1809	3(1)		4(1)		200		Upper 100 m during upwelling
Pelagia colorata Russell 1964		2(1)			450		Surface
Bolinopsis sp.		10(2)	116(1)		122		Surface
Pleurobrachia sp.	182(2)	765(2)	121(1)	30, tentacles 20 times longer			Surface
Mertensia ovuum (Fabricius) 1780		3(1)		55, tentacles 5 times longer			Surface
Beroe sp.	1397(55)	443(44)	632(29)		>90		Surface

[1] Size and depth distribution from Alvariño unpublished and published information.

siphonophores, chondrophores, medusæ, and ctenophores in the California Current is not available elsewhere.

Chaetognatha

Altogether 22 species of Chætognatha were observed in the collections analyzed. Not all of the species were taken in a given year; rather, 17 species were found in 1954 collections, 16 in 1956, and 18 in 1958. Only 12 species were taken in all three years. The species occurring in greatest abundance were *Sagitta euneritica* (maximum size 15.5 mm), *S. bierii* (maximum size 17 mm), and *S. enflata* (maximum size 25-30 mm). Of these, *S. enflata* is the most voracious predator of fish larvae. The size of chætognaths obtained ranged from 6 to more than

90 mm in length. The predatory potential of an individual chætognath is roughly proportional to its size; the predatory potential of the species is related to both size and abundance.

Siphonophorae

During the three years, 48 species of siphonophores were observed, with the largest complement of species; 40 taken in 1956, 37 in 1958, and only 26 in 1954. Specimens of siphonophores ranged in size from 5 mm total length for nectophores of some species of Diphyidæ in the polygastric phase, to several meters in total length in various species of Agalmidæ and related families. Undoubtedly, the siphonophores in the family Agalmidæ are among the most successful predators inasmuch as they can move swiftly through the waters and can act as living nets in capturing other plankters. The only commonly occurring agalmid in CalCOFI collections was *Stephanomia bijuga*; this could be one of the primary predators on fish larvae. Several siphonophores in the family Diphyidæ are common to abundant, including *Chelophyes appendiculata, Muggiaea atlantica, Lensia challengeri, L. hotspur,* and *Diphyes dispar.* The latter species was commonly taken only in 1954; among diphyid siphonophores it is a relatively large species, consequently it has the potential to be an effective predator on fish larvae. *M. atlantica*, the most abundant diphyid, particularly in inshore waters, is a small species that would be an effective predator only on small anchovy larvae. *C. appendiculata*, also among the most common diphyid siphonophores, is large, hence perhaps a more effective predator on fish larvae.

Chondrophorae

Only a single species was observed, *Velella velella,* and this only in two hauls made in 1956.

Medusae

The total number of species of Medusæ taken during the three years was 34, with 15 species in 1954, 20 in 1956, and 19 in 1958. The distribution of Medusæ is more erratic than that of Chætognatha or Siphonophoræ. Only seven species were common to the three years; of these the most abundant species, both with regard to abundance and to frequency of occurrence, were *Liriope tetraphylla* and *Rhopalonema velatum*.

Ctenophora

Ctenophores except *Beroë* sp. were infrequently taken. Although there were 128 occurrences of *Beroë* sp. recorded during the three years, there were only five occurrences of *Pleurobrachia* sp., three of *Bolinopsis* sp., and one of *Mertensia ovum*. Even so, the number of specimens of *Pleurobrachia* or *Bolinopsis* in the samples in which they did occur could be quite large (i.e. over 100 individuals per sample). Most ctenophores occur at or near the surface; hence, their predation would be limited to this zone. *Beroë* is known to feed on other Ctenophora, but the other ctenphores are known to be voracious predators on zooplankton including fish larvae (Chun 1880; Kamshilov 1960; Kamshilov et al. 1958; Horridge 1965; Lebour 1922, 1923; Mayer 1912; Miller 1974; Swanberg 1974). As mentioned earlier, Ctenophora tend to fragment and disintegrate on preservation and could easily be overlooked.

ABUNDANCE OF THREE GROUPS OF PREDATORS IN RELATION TO ABUNDANCE OF ANCHOVY LARVAE

Variations in the composition of species of all groups were observed in all years. Tropical species were taken in 1958, the year with warmer than average temperatures. The highest variability occurred in the Medusæ, which show erratic distribution both in time and space.

Information on the abundance of Chætognatha, Siphonophoræ, and Medusæ is summarized for 3-month intervals for the three years, 1954, 1956, and 1958, in Table 2. Yearly abundance values are summarized in Table 3 and illustrated in Figure 1.

Monthly average abundance of plankton predators are compared to the monthly percentage concentration of anchovy larvae (from Ahlstrom 1967) for all three years in Figure 2.

Chaetognatha

Little or no relation appeared between abundance of anchovy larvae and abundance of chætognaths. This applies both for abundance of total chætognaths versus anchovy larvae and for *Sagitta enflata*, a common species known to be a prime predator on fish larvae. The only prime predator species to show an inverse abundance relation with anchovy larvae, i.e. fewer present when anchovy larvae were abundant, was *Sagitta hexaptera*. However, it should be noted that the two most abundant chætognaths, *S. euneritica* and *S. bierii* are not considered important predators on fish larvae, because of their size, and the abundance is mainly made up of young specimens, too small to feed on anchovy larvae.

Siphonophorae

During two of the three years, 1954 and 1958, lowest abundance of siphonophores occurred in hauls with high abundance (> 241/haul) of anchovy larvae. The inverse relation was most marked in the warmest year, 1958, when only 12 siphonophores/1,000 m^3 on the average were taken in hauls with anchovy larvae counts exceeding 241 larvae/standard haul, 33 siphonophores/haul on the average for low abundance of anchovy larvae (1 to 241/standard haul), and 101 siphonophores in hauls with 0 anchovy larvae.

However, in 1956, siphonophores were more abun-

TABLE 2

Part I. Abundance of Chaetognatha, Siphonophorae, and Medusae in Hauls with High Number of Anchovy Larvae (i.e. > 241 Larvae per Standard Haul) in 1954, 1956, 1958.

Cruises	Predators Number hauls	Chaetognatha Number species	Chaetognatha Total count	Chaetognatha Average count	Siphonophorae Number species	Siphonophorae Total count	Siphonophorae Average count	Medusae Number species	Medusae Total count	Medusae Average count	Average all categories
5401-5403	41	12	139,906	3,412	8	2,024	49	3	175	4	3,465
5404-5406	22	11	116,767	5,308	4	319	14	3	56	3	5,378
5407	3	4	24,304	8,101	2	28	9	3	153	51	8,161
5412	3	5	12,522	4,174	1	25	8	0	0	0	4,182
Yearly total	69	13	293,499	4,254	9	2,396	35	4	384	6	4,295
5601-5603	15	12	35,869	2,391	11	2,093	140	5	930	62	2,593
5604-5606	18	7	66,909	3,717	8	5,042	280	4	872	48	4,045
5607-5608	8	7	15,228	1,904	4	1,741	218	1	1,035	129	2,251
5610-5612	–	–			–			–			–
Yearly total	41	12	118,006	2,878	15	8,876	216	6	2,837	69	3,163
5801-5803	53	15	149,975	2,830	8	652	12	7	151	3	2,845
5804-5806	48	13	409,398	8,529	8	536	11	4	103	2	8,542
5807	4	7	35,522	8,888	2	31	8	0	0	0	8,896
5810-5812	–	–			–			–			–
Yearly total	105	16	594,895	5,666	12	1,219	12	9	254	2	5,680

Part 2. Abundance of Chaetognatha, Siphonophorae, and Medusae in Hauls with Low Concentration of Anchovy Larvae (i.e. 1 to 241 Specimens per Standard Haul) in 1954, 1956, 1958.

Cruises	Predators Number hauls	Chaetognatha Number species	Chaetognatha Total count	Chaetognatha Average count	Siphonophorae Number species	Siphonophorae Total count	Siphonophorae Average count	Medusae Number species	Medusae Total count	Medusae Average count	Average all categories
5401-5403	91	14	206,977	2,274	10	14,525	159	4	986	10	2,443
5404-5406	135	14	741,944	5,495	16	18,025	133	8	11,622	86	5,714
5407-5409	74	13	745,777	10,078	8	3,508	47	8	4,761	64	10,189
5410-5412	34	13	110,430	3,259	8	1,693	49	5	2,721	80	3,388
Yearly total	334	16	1,805,128	5,405	23	37,751	113	12	20,090	60	5,578
5601-5603	57	14	253,326	4,444	17	8,321	146	9	1,482	26	4,616
5604-5606	39	9	115,795	2,969	10	6,381	163	5	3,220	82	3,214
5607-5608	20	12	60,705	3,035	12	6,642	332	6	2,128	106	3,475
5610-5612	10	10	25,121	2,512	10	1,664	166	2	968	96	2,774
Yearly total	126	14	454,947	3,611	24	23,008	183	11	7,798	62	3,856
5801-5803	116	13	474,664	4,091	20	3,883	33	8	1,755	15	4,139
5804-5806	143	16	682,198	4,770	17	5,390	37	8	2,774	19	4,826
5807	26	10	126,351	4,859	6	214	8	2	634	24	4,891
5810-5812	13	15	33,753	2,596	3	312	24	3	303	23	2,643
Yearly totaL	298	17	1,316,966	4,419	25	9,799	33	11	5,466	18	4,470

Part 3. Abundance of Chaetognatha, Siphonophorae, and Medusae in Hauls with Absence of Anchovy Larvae in 1954, 1956, 1958.

Cruises	Predators Number hauls	Chaetognatha Number species	Chaetognatha Total count	Chaetognatha Average count	Siphonophorae Number species	Siphonophorae Total count	Siphonophorae Average count	Medusae Number species	Medusae Total count	Medusae Average count	Average all categories
5401-5403	94	17	238,679	2,539	13	9,075	97	4	2,490	26	2,662
5404-5406	210	15	592,525	2,822	16	17,253	82	6	19,512	93	2,997
5407-5408	75	13	449,014	5,986	9	6,760	90	7	5,076	68	6,144
5410-5412	67	16	217,842	3,251	10	6,386	95	6	17,654	263	3,609
Yearly total	446	17	1,498,060	3,359	21	39,474	89	10	44,732	100	3,548
5601-5603	46	12	113,954	2,477	28	5,606	122	8	5,389	117	2,716
5604-5606	44	14	75,215	1,709	20	11,939	271	11	4,570	104	2,084
5607-5609	26	13	131,240	5,048	15	9,049	348	9	1,632	63	5,459
5610-5612	33	13	59,742	1,810	18	1,805	55	9	2,155	65	1,930
Yearly total	149	15	380,151	2,551	37	28,399	191	17	13,746	92	2,834
5801-5803	129	18	241,677	1,873	22	11,374	88	10	4,186	32	1,993
5804-5806	211	16	436,361	2,068	29	30,844	146	11	42,592	201	2,415
5807	55	12	80,724	1,467	15	3,734	67	5	8,899	161	1,695
5810	101	16	133,053	1,317	12	4,116	40	4	11,984	118	1,475
Yearly total	496	18	891,815	1,798	32	50,068	101	14	67,661	136	2,035

dant in all types of hauls than in the other two years and were equally abundant in hauls with > 241 anchovy, < 241 anchovy larvae, and 0 anchovy larvae.

One of the siphonophores that is probably an effective predator on fish larvae is the diphyid *Chelophyes appendiculata*. This species had a striking inverse relation to abundance of anchovy in all three years. Another diphyid species, *Diphyes dispar*, was commonly taken only in

TABLE 3
Yearly Abundance of Chaetognatha, Siphonophorae, and Medusae in the Three Categories of Anchovy Hauls: High, Low, and Zero Abundance.

Anchovy abundance	Number hauls	Chaetognatha Number species	Chaetognatha Total specimens	Chaetognatha Average count/haul	Siphonophorae Number species	Siphonophorae Total specimens	Siphonophorae Average count/haul	Medusae Number species	Medusae Total specimens	Medusae Average count/haul	Average count 3 plankters
1954											
High, > 241	69	13	293,499	4,254	9	2,396	35	4	384	6	4,295
Low, < 241	334	16	1,805,128	5,405	23	37,751	113	12	20,090	60	5,578
Zero anchovy	446	17	1,498,060	3,359	21	39,474	89	10	44,732	100	3,548
1956											
High, >241	41	12	118,006	2,878	15	8,876	216	6	2,837	69	3,163
Low, < 241	126	14	454,947	3,611	24	23,008	183	11	7,798	62	3,856
Zero anchovy	149	15	380,151	2,551	37	28,399	191	17	13,746	92	2,834
1958											
High, > 241	105	16	594,895	5,666	12	1,219	12	9	254	2	5,680
Low, < 241	298	17	1,316,966	4,419	25	9,799	33	11	5,463	18	4,470
Zero Anchovy	496	18	891,815	1,798	32	50,068	101	14	67,661	136	2,035

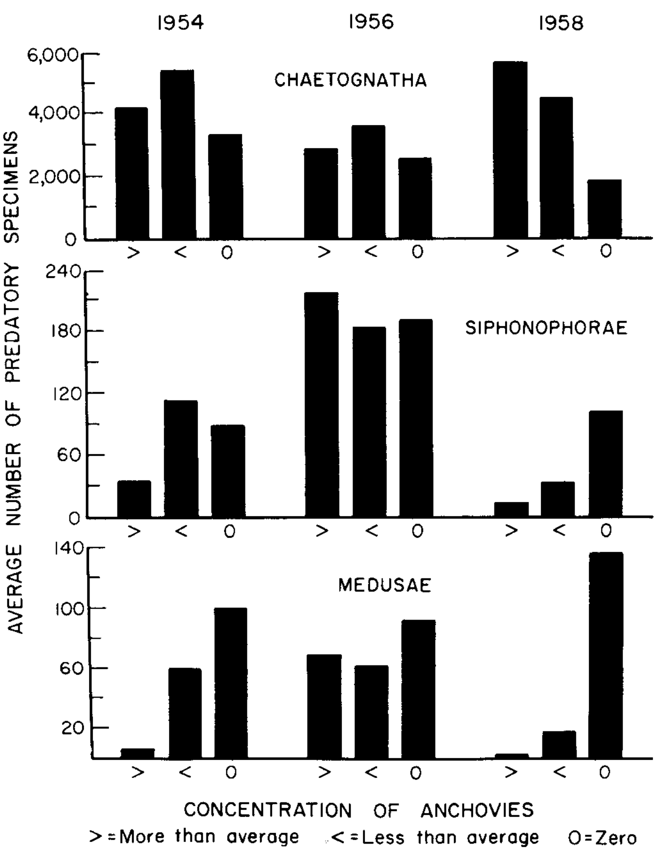


Figure 1. Yearly abundance of predators (Chætognatha, Siphonophoræ, Medusæ) and concentration of anchovy larvæ (high = more than 241 larvæ per standard haul, low = less than 241 anchovy larvæ per standard haul, zero = absence of anchovy larvæ).

1954; in fact, 96.3% of the total specimens of this species were obtained during this year, 3% in 1956, and less than 1% in 1958. In the 1954 collections, there was also a marked inverse relation between abundance of this species and of anchovy larvae. The agalmid, *Stephanomia bijuga*, was the only one in this family taken in any abundance; it was least common in hauls containing high counts of anchovy larvae.

Medusae

During 1954 and 1958, abundance of medusæ showed a striking inverse relation with abundance of anchovy larvae. However, as also shown above for siphonophores, this relation breaks down in 1956. In this year, one species of medusæ, *Liriope tetraphylla*, contributed 85% of the specimens of medusæ in hauls with high anchovy counts, 74% in hauls with low anchovy counts, and 67% in zero count hauls. This is a moderately large species attaining a width across the umbrella of 30 mm, hence undoubtedly an effective predator on fish larvae.

RELATION OF UPWELLING AND ANCHOVY LARVAE

Sagitta decipiens has been used as an indicator of upwelling (Alvariño 1965; Nair 1977; Nair and Rao 1973; and others). During the three years studied, *S. decipiens* was taken in 93 of 2064 hauls, or in 4.5% of the hauls. During 1954 it was taken in only 12 hauls, or in 1.4%; in 1956 it was taken in 35 hauls or in 11.1% of the hauls; in 1958 it was taken in 46 hauls or in 5.1% of the hauls.

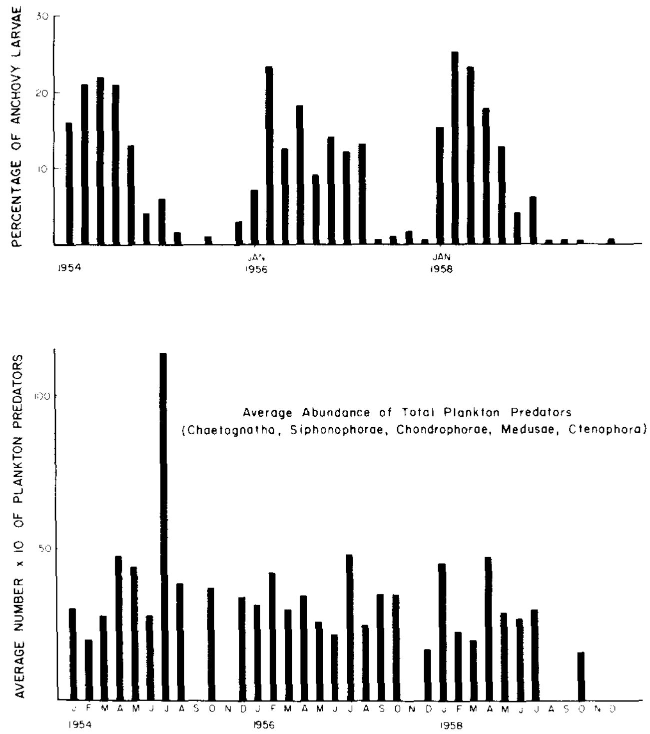


Figure 2. Monthly average of abundance of plankton predators, compared with Ahlstrom (1967) monthly percentages of anchovy larvæ for 1954, 1956, and 1958.

Hence, based on *S. decipiens* as an indicator of upwelling, this phenomenon was most intense in 1956, intermediate in 1958, and low in 1954, which agrees with Bakun (1973) and Wyllie (1966). Occurrences are probably preferable to actual counts of specimens because of the influence on counts of few large hauls. In fact, 36.2% of the total specimens taken in all three years were obtained at a single station in April of 1954. This may have been an indication of intense upwelling at that station, but it certainly biases results based on counts. Based on numbers taken, the average abundance per haul was 10.0 in 1956, 4.1 in 1954, and 1.9 in 1958. However, for stations other than that in 5404, the average count per haul was 0.5 specimens for 1954.

Sagitta decipiens occurred in 2.8% of the hauls with large concentrations of anchovy larvae, in 4.35 % of the hauls with low counts of anchovy larvae, and in 4.95% of the hauls with zero anchovy abundance. This could be interpreted as an indication that large concentrations of anchovy larvae occur infrequently in upwelling areas.

Based on occurrence by quarters (seasons) of the year, there were 3.6% positive hauls in winter, 4.5% in spring, 4.1% in summer, and 6.1% in the fall. Occurrences in 1956 contributed substantially to the fall total, inasmuch as 11 of 43 hauls taken in these months in 1956 contained *Sagitta decipiens* (i.e. it occurred in over 25% of the hauls). This appears to be the period of most widespread upwelling encountered during the three years. During 1958, upwelling as indicated by the occurrences of *S. decipiens* was most widespread during the spring months.

RELATION OF PLANKTON ASSEMBLAGES TO ANCHOVY LARVAE

To obtain information on the plankton assemblages associated with high and zero abundance of anchovy larvae, several stations with high and zero abundances of anchovy larvae were selected from each monthly cruise within the main anchovy spawning areas. The number of stations thus chosen from 1954 survey cruises was 27 with high anchovy abundance and 33 with zero anchovy abundance; for 1956 the number of corresponding stations was 30 and 36, and for 1958, it was 19 and 33.

During 1954, 14 of the 27 stations with high concentrations of anchovy larvae were dominated by copepods, 11 by copepods and euphausiids, and 2 by euphausiids and pteropods. In contrast, 17 of the 33 stations with zero abundance of anchovy larvae contained predominantly salps; 4 stations were dominated by salps and doliolids; 4 others were mostly decapod larvae; 1 each were dominated by pteropods, by heteropods, by polychætes, by euphausiids, and by euphausiids and decapods; and the other 3 had a mixture of constituent organisms.

During 1956, 22 of the 30 collections from stations with high abundance of anchovy larvae were dominated by copepods, 5 by copepods and euphausiids, 2 by euphausiids, and 1 by copepods, euphausiids, and pteropods. The selected stations from 1956 that lacked anchovy larvae had 23 of 36 composed mostly by pyrosomes; 1 had a mixture of pyrosomes and salps; 3 contained mainly salps; 4 were dominated by megalopa larvae; 2 included mostly pyrosomes and the euphausiid *Euphausia pacifica*, and 1 had salps with *E. pacifica*; and 2 had a mixture of constituents. Pyrosomes were markedly more abundant in 1956 than in the other two years.

During 1958, 16 of the 19 collections from stations with high counts of anchovy larvae were dominated by copepods, and 1 each with copepods and euphausiids, with copepods and pteropods, and with a mixture of constituents. The dominant constituents of the 33 stations that lacked anchovy larvae were salps in 16, megalopa larvae in 2, doliolids in 1, doliolids and salps in 1, pteropods in 1, copepods in 1, and a miscellaneous array of constituents without a dominant group in 11.

The dominant plankton constituents in hauls with large concentrations of anchovy larvae were markedly different from the constituents in hauls with zero anchovy larvae (Figure 3). In the former, the dominant constituents in most hauls were copepods, followed by euphausiids alone or copepods and euphausiids, and less frequently with pteropods together with euphausiids and/or copepods.

Areas in which these constituents dominate could be called "anchovy water." Hauls from areas lacking anchovy had only an occasional sample with copepods or euphausiids as the dominant constituent, and the majority of the samples were dominated by jelly-like organisms, by salps, or salps and doliolids in 1954 and 1958 and by pyrosomes in 1956. In "anchovy water," the organisms needed for food for anchovy larvae, particularly copepods, were abundant. In areas lacking anchovy larvae, organisms needed for food by anchovy larvae were scarce.

Most Abundant Large Predators and High and Zero Concentration of Anchovy Larvae

Invertebrate predators in the three main groups (Chætognatha, Siphonophoræ, and Medusæ) were present in many of the hauls containing large numbers of anchovy larvae, as well as in the hauls lacking anchovy larvae during these three years, 1954, 1956, and 1958. In fact, two species, the chætognath, *Sagitta euneritica*, and the siphonophore, *Muggiaea atlantica*, occurred in larger numbers in anchovy-rich hauls than in hauls lacking anchovy larvae. Both species are small in size. Abundance of *S. euneritica* is usually contributed by young specimens, not observed to prey on anchovy larvae.

The species considered to have the highest potential as predators because of size and abundance are the chætognaths, *Sagitta enflata*, *S. hexaptera*, and *S. scrippsae*; the siphonophores, *Stephanomia bijuga, Chelophyes appendiculata*, and *Diphyes dispar*; and the medusæ *Liriope tetraphylla*, *Rhopalonema velatum*, and *Aglaura hemistoma*, (Table 4). These species are present in fewer of the anchovy-rich hauls in all instances and occur in lesser abundance in most comparisons (i.e. 18 out of 21).

The species showing the greatest difference between anchovy-rich and anchovy-lacking stations are *Sagitta hexaptera, Chelophyes appendiculata, Rhopalonema velatum,* and *Aglaura hemistoma*. *S. hexaptera* occurred twice as often in hauls lacking anchovy larvae as in anchovy-rich hauls, and for the other three species the disproportion between occurrences and numbers in anchovy-lacking versus anchovy-rich hauls is even more marked. The siphonophore, *Stephanomia bijuga*, also occurred most frequently and in large numbers in hauls lacking anchovy rather than in anchovy-rich hauls in all three years.

Although the medusa, *Liriope tertaphylla*, and markedly more abundant in hauls lacking anchovy larvae in 1954 and 1958 than in anchovy-rich hauls, it was present in about the same percentage of hauls of the two categories in 1956 and was more abundant on the average in anchovy-rich hauls during that year. As noted previously, the siphonophore *Diphyes dispar* was commonly taken during 1954, when it occurred more frequently and in larger numbers in collections lacking anchovy larvae. The other two chætognaths were taken in greater abundance in anchovy-rich hauls than in hauls lacking anchovy larvae in one of the three years, in 1956 for *Sagitta enflata* and in 1954 of *S. scrippsae*, but even for these the frequency of occurrences was higher in hauls lacking anchovy larvae in all three years.

SUMMARY

In summary, the numbers and kinds of plankton carnivores, potential predators on fish larvae, have been studied for five groups, Chætognatha, Siphonophoræ, Chondrophoræ, Medusæ, and Ctenophora, for three CalCOFI years, 1954, 1956, and 1958. Altogether, 22 species of Chætognatha, 48 species of Siphonophoræ, 1 Chondrophoræ, 34 Medusæ, and 5 Ctenophora were recorded. For each of these species, abundance and number of occurrences are given in Table 1 for each of the years.

Collections studied could be grouped into three categories with respect to anchovy larvae: anchovy rich (more than 241 larvae per standard haul), anchovy poor (1 to

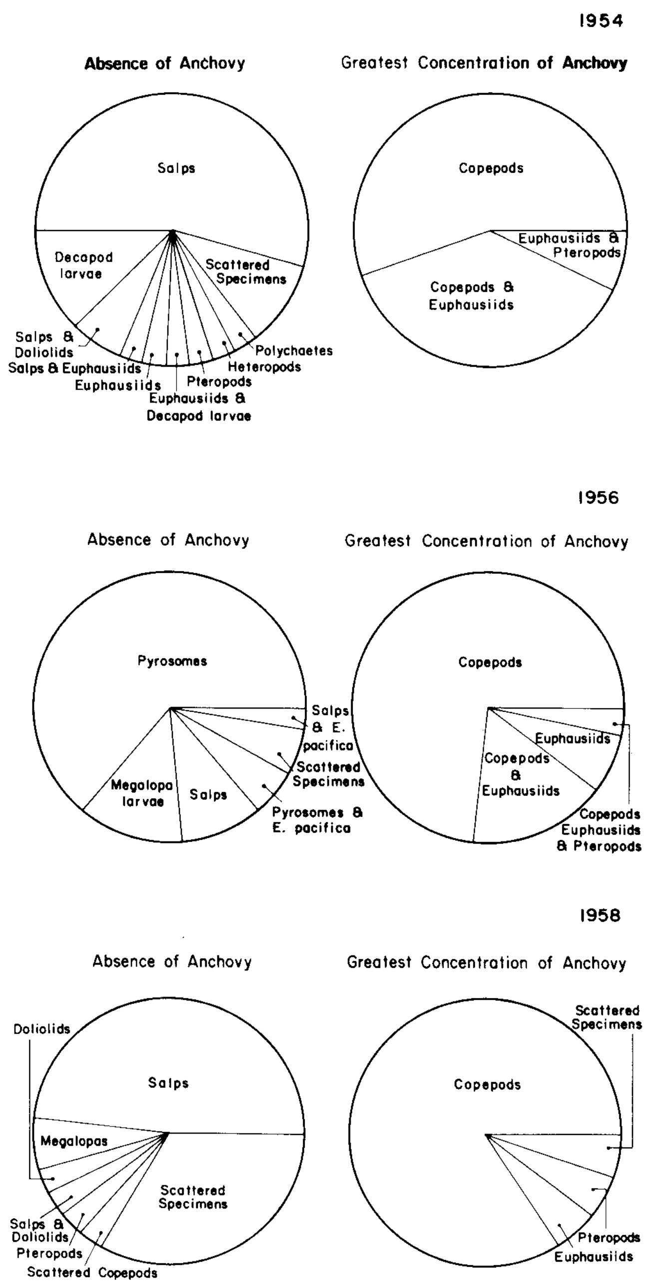
TABLE 4
Most Abundant Large Species of Predators Occurring with the Highest and with Zero Concentrations of Anchovy Larvae.

Anchovy larvae abundance	1954				1956				1958			
	High		Zero		High		Zero		High		Zero	
Sps. abundance Species	% occur.	Aver.[1] occup.	% occur.	Aver.[1] occup.	% occur.	Aver.[1] occup.	% occur.	Aver.[1] occup.	% occur.	Aver.[1] occup.	% occur.	Aver.[1] 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

[1]Average from all localities occupied, including those where species were present and absent.

240 larvae per standard haul), and anchovy lacking (zero anchovy larvae per standard haul). An inverse relation between abundance of anchovy larvae and abundance of predators was found for most siphonophores and medusæ, but the relation numerically is less well defined for chætognaths.

An unanticipated finding was that anchovy larvae occur in abundance primarily in hauls dominated by Copepoda and/or Euphausiidæ and never in hauls dominated by pelagic prochordates (salps or pyrosomes). The habitat of the former association can be characterized as "anchovy water."



In the introduction it was pointed out that the major causes of larval mortality are starvation and predation and that these may interact. This investigation, which studied the distribution and abundance of predatory and other planktonic organisms in relation to abundance of anchovy larvae, helps to confirm that statement.

One of the characteristics of "anchovy water" is the presence of potential food for anchovy larvae in some abundance. Another characteristic is that potential predators among chætognaths, siphonophores, and medusæ occur usually in lesser abundance than in hauls lacking anchovy larvae. In anchovy waters these potential predators have a greater range of prey to feed upon and, as evidenced by gut contents, prey primarily on copepods.

The best way to reduce mortality from starvation is for the anchovy larvae to be in waters with an adequate food supply. The best way to reduce mortality from predation is for anchovy larvae to be in waters where potential predators are in reduced abundance. This favorable combination of factors has been shown for "anchovy water."

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