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PREDATION IN THE PLANKTON REALM; MAINLY WITH REFERENCE TO FISH LARVAE

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RESUMEN

Se presentan y discuten los trabajos sobre depredación, en los organismos que sirven de alimento a los zooplanctontes carnívoros, incluyendo además información, que se encuentra dispersa en la literatura, sobre las dietas de los animales planctónicos carnívoros. Con esta revisión se establece la importancia que tiene el proceso de depredación en los mecanismos implicados en la supervivencia de larvas de peces.

Se recopilan los datos publicados y la información personal inédita, sobre la alimentación de las especies de los principales depredadores en el plancton; Medusas, Condróforos, Sifonóforos, Ctenóforos, Quetognatos, Copépodos, Eufáusidos, Anfípodos, Crustáceos, Decápodos, Poliquetos, Moluscos.

La información que existe sobre la dieta de los depredadores planctónicos indica, que estos animales tienen que ingerir alimento continuamente para subvenir a sus requisitos en proteinas, debido a su incapacidad de almacenar en el cuerpo sustancias de reserva. Esta particularidad se refleja en su comportamiento, alimentándose activa y continuamente. Estos voraces animales aparecen abundantes en los mares en todas las épocas del año, afectando el balance ecológico, y asimismo a las poblaciones de animales de importancia en las pesquerías.

La información publicada sobre especies planctónicas depredadoras y sus presas aparece recopilada en varias tablas.

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ABSTRACT

This discussion and presentation encompass published works on predation, food organisms of carnivorous plankton and pertinent dietary information included under different topics in the literature. The aim of this review is to elucidate predation and related subjects to better understand some of the mechanisms involved in the fish larvae survival.

Data are compiled on the feeding of main plankton predators; Medusae, Siphonophorae, Chondrophorae, Ctenophora, Chaetognatha, Copepoda, Euphausiidae, Amphipoda, Decapod Crustacea, Polychaeta, Cephalopoda, within the scope of the information published, together with personal unpublished data obtained along years of study.

The information on the dietary characteristics of most planktonic predators indicate that these carnivorous animals need to feed continuously to fulfill their requirements for protein intake, and their inability to store food reserves in their bodies, which is implied by their active feeding behavior. These voracious animals appear in large numbers in some years and areas, and this abundance affects the ecological balance of the environment, and subsequently the pupulations of animals of importance in the commercial fisheries.

Published information on predatory plankton species is compiled in tables.

INTRODUCTION

The marine fishes of commercial importance have an extremely high fecundity; mortality must, therefore, be correspondly high during certain life stages in order to give balance to the population. Joubin (1924) discussed this factor and stated, "mais tous ces petit poissons n'arrivent pas a leur état adult; leur destruction est intense et necessaire pour arriver à un equilibre entre la quantité de nourriture et le nombre de ceux qui la mangent".

Most mortality is believed to occur in the first few months of life (Gulland 1965, Lasker 1965, 1975, and May 1974); during the egg, larval, and juvenile stages. For example, in *Sardinops caerulea*, 99% mortality of the offspring occurs in a period from the egg to the pre-metamorphosed larval stage.

Many factors control the survival of eggs, larvae, and young fish, and it is widely accepted that abundance of eggs and strength of larval stages determine the size of the recruiting population (Ahlstrom, 1966). The magnitude of the recruiting fish stock is influenced by variables such as spawning (quality and quantity of eggs); the oceanic environment (mechanical effects related to disturbance of waves and currents); physical factors (temperature and light and currents which may transport the larvae into unfavourable environment); chemical factors (salinity, oxygen and pollutants); and biological factors such as food supply and predation. While the relations of most of these factors to abundance of fish generations have been independently analyzed, it would appear that combined analyses of the intrincate interaction of all the factors affecting the future of the fish generation are needed. Graham (1943) indicated, "wise administration of the Fisheries must work with the natural processes of the Sea".

An important part of the fishery investigations is the study of fluctuations in the relative strength of the different age groups (Hardy, 1956). "Identification of the mechanisms regarding recruitment will probably require the study of the entire larval and juvenil stages" (Hunter, 1979) in order to establish the difference between good and bad year classes (Baranenkova, 1961).

Research on the abundance of eggs and larvae began subsequent to Hensen's (1887) development of a method to estimate adult fish populations using calculations based on the number of eggs collected at sea. The abundance of the eggs spawned by several species of fish, together with measurements on the fecundity of females, enable investigators to estimate the total spawning stock. The number of eggs spawned will vary with the number of the adult fish on the grounds, but scarcity of one particular year class is not necessarily due to any decrease in the number of reproducing adults.

The survival of eggs, larvae, and juveniles, fluctuates throught the years; at times, a large adult population may give only a small number of recruits, and vice versa. Poulsen (1944) demonstrated a correlation between fluctuations in numbers of larvae and adult fish, that was based on larval generation; he believed that the frequency of a year class and its effects on the size stock (in this case cod) was already determined at the larval stage.

The analyses of factors involved in the life of fish indicate that the major causes of larval mortality are starvation - and predation, and that these interact with other environmental and biotic factors (Hunter 1976). Hunter (1979) states that in order to "identify mortality at sea, the incidence of starvation and predation must be estimated over the spawning range of the species and at all life stages, and these losses compared to estimated rates of mortality. "There is, however, disagreement as to which factor, starvation or predation is more influentia.

Until recently, more emphasis had been given to the lack of food as the main cause of larval mortality in many stocks of marine fish, because it was assumed that the rate of predatory mortality in the stock of fish larvae was mainly determined by the number of predators, with no consideration for their feeding capacity, and considering that the larvae were able to avoid the predators. Hempel (1965) further assumed that, "In many cases, years of high predator abundance are also years of rich food abundance for the fish larvae, and the food for the larvae is often also the main food for the planktonic predators".

The amount and quality of food available to the larvae does influence their survival, producing robust, healthy larvae; when food is scarce, larvae are weak, small, and more vulnerable to predation and sickness.

Losses by starvation are heavy, because larvae are small and require food of various qualities, sizes, and in specific quantities, at the various stages of the larval period (Lasker 1965). Murphy (1961) estimated the amount of food available for the calculated density of spawned larvae and found that food organisms for *Sardinops caerulea* appear to be "1 to 500 or 1 to 1500, or greater in 70 percent or 50% of the stations, respectively". He also calculated the distance each food item would be from the sardine larvae, and found it to be 5 cm to 3 cm or less.

Blaxter and Hempel (1963) have shown that larger sized eggs of *Clupea harengus* produce larger and healthier larvae which have a better chance of survival than those hatched from small eggs. However, feeding must be established before the yolk sac is absorbed, otherwise death of the larvae is unavoidable. In some cases, the survival capacity of larvae in laboratory experiments does not appear to be dependent on the size of the eggs, but rather on the availability of food (Ciechomski (1966) with larvae of Argentina anchovy). Apparently, both large size in normally constituted eggs, and suitable food are factors to be considered in the survival capacity of the larvae.

Although a number of publications deal with the planktonic food of fish larvae, the extent of mortality due to predation has not been thoroughly determined, even though this factor is widely accepted by marine biologists who consider that losses of larvae by predation may be high and related to the abundance and types of predators (Alvariño 1976b, 1977, 1979 and 1980b). While starvation cannot be clearly evidenced in the field, predation is a real phenomenon, observed by planktologists when analyzing the plankton material, because fish larvae, under various degrees of digestion, can be seen inside the predators' digestive tract.

In addition to these biotic factors, the mortality of fish larvae may also be affected by abiotic factors such as wave action and light intensity (Hempel and Weikert 1972, Pommeranz 1974). Wave action has for a long time been considered a cause of severe mortality of pelagic fish eggs (Rollefsen 1930, 1932; Devold 1935; Zaitsev 1968, and Pommeranz 1974). Ultraviolet light may be dangerous to pelagic eggs and larvae when they are close to the surface waters (Marinaro and Bernard 1966; Hunter, Taylor, and Moser 1979), and light also appears to be more harmful to demersal eggs which usually develop at low light intensities. In addition, "the vertical position of larvae in the sea in relation to their food, predators and time of day needs to be considered" (Hunter 1979), as does water temperature.

Temperature during incubation and during yolk sac stages affects duration of development and eventual survival of the larval stage (the most vulnerable period in the life cycle of fish), and also the metabolic activity of the fish.

All these factors, both biotic and abiotic, interact in different ways and degrees, on fish larvae, their prey species, and their predators. Some of these interactions are discussed in the following examples.

In the California region, the most outstanding ocean feature is the California Current System, which affects the temperature of the ocean in this region and the quality and abundance of its faunistic complex. From 1944 to 1956 temperatures in the oceanic region off California were lower than usual, and from 1957 to 1960 temperatures were higher than usual. Tempera tures from 1960 to 1964 were lower than those in the early fifties. From 1965 to present temperatures in this region could be considered high, on the average (with some yearly fluctuations) but not as high as for the late 1950's. Historical records (Murphy 1961) indicate that "warm years tend to be associated with good year classes and cold years with poor ones" for sardine. He examined the possibility that cold temperatures may increase larval mortality due to predators or/and that cold temperatures are associated with other factors affecting the sardine population. He also suggested that low temperatures might prolong the larval phase, lengthening the vulnerability of the larvae to predation.

Data I obtained during my studies of the plankton off California indicated that the abundance of predators (mainly chaetognaths) is greater during cold years than during warm years. In addition, they are of larger size, and their populations cover a larger area of the California Current Region. Low temperatures prolong the larval stage of the fish, increasing their vulnerability to the eventualities of the oceanic environment, including predation. During cold periods, the predatory organisms present are more abundant, of larger size, and are at their peak of predatory capacity. These predators not only feed on fish larvae, but also compete for food with the fish larvae and plankton consuming fish.

ZOOPLANKTON PREDATION

Fish larvae mortality by predation has been discussed by Lebour 1922, 1923 and 1925; Bigelow 1926; Murphy 1961; Fraser 1969; Hempel 1965; Dekhnick et al 1970, etc., and the analysis of the literature related to mortality of fish larvae indicates that predation may be responsible for a high toll. Indeed, Johannes (1978) in discussing strategies of reproduction in fishes, indicates that "predation appears to be more important than availability of food in influencing where, when and how many (Tropical marine) fishes spawn and where their eggs and larvae are distributed".

The younger growth stages of fish consitute part of the plankton realm. Although the study of changes in the plankton holds "important keys to a better understanding of success of failure in the fisheries" (Hardy 1956), little has been published on the feeding activity of the main predatory organisms of the plankton realm. What is known on the subject is scattered through the literature, in few lines included in works not dealing specifically with predation.

Murphy (1961) considers that "fish larvae will be subject to roughly the same rate of predation, as have other organisms in the plankton possesing the same general dimensions and behavioral characteristics". Predation therefore, can become an important factor in the study of fish populations, particularly of food. Murphy (1961) believes that "the intense predation typical of the plankton community is responsible for the rapid decline in numbers of sardine larvae, and variations in this rate of predation are primarily responsible for variations in the rate of survival. Medusae, Chondrophora, Siphonophorae, Ctenophora, Chaetognatha, pelagic Polychaeta, and other carnivorous zooplankters not only impose a heavy toll on the delicate fry of many fish species, but also compete with them for the same food. These voracious animals are present in great numbers in some years and areas, affecting the ecological balance of the micro-environment of the oceans.

The diagram (Fig. 1 in Alvariño 1976b) of plankton volumes and average number of Chaetognatha for 1954 and 1958 off California shows that large volumes of zooplankton correspond to low number of chaetognaths and vice versa. In addition, high volumes of zooplankton only in few cases coincide with good generations of anchovy larvae. (Note: plankton volume is a magnitude which does not provide proper biological information relative to the micro-environment. Different types of organisms are integrated in that volume, which are not accounted for and could be critical to the study. Volume of samples are numbers with no major biological significance, and should not be used to draw biological conclusions. The term "plankton" encompasses all the zoological invertebrate groups at any stage of development in the ocean, including the vertebrates, fish eggs and larvae. It is therefore necessary to know not only the amount, volume, or number for each of the plankton groups in the plankton sample, but also the abundance of each of the species integrated into the total volume of plankton).

Strasburg (1960) compared data on tuna larvae (*Katsuwonus pelamys* and *Thunnus albacares* combined) and invertebrate plankton volumes; and he found that large catches of tuna larvae coincided with small or moderate volumes of plankton, while poorest and richest catches of plankton contained few larvae. Large number of zooplankters coinciding with low numbers of fish larvae could indicate that predators were abundant in the plankton, and have been devouring tuna larvae. Small plankton volumes and high numbers of tuna larvae imply that plankton present served as food for the tuna larvae and that few or no predatory species were present. The consideration on this indicates that, it is not advisable to compare facies, such as fish larvae and plankton, as Strasburg has done, when one of the factors, plankton, includes many unidentified species. There is need to explain the abundance of each of the species included in the plankton volume being discussed.

Analysis of zooplankton and fish larvae collected at the low part of the Newport River Estuary, North Carolina (Thayer et al 1974), indicates both an increase in the zooplankton abundance prior to the seasonal immigration of larval fish into the estuary and a general decrease in zooplankton during the period of larval abundance. Copepods were dominant in most collections (comprising up to 81% of the zooplankton) and the rest included barnacle larvae, ostracods, cladocerans, crustacea larvae, and chaetognaths. These data demonstrate the inverse relation in abundance between fish larvae and their food; a decrease in one indicates an increase in the other. This inverse relation between number of larval fish and the volume of plankton was also noted by Ali Khan and Hempel (1974) in the collections from the Gulf of Aden. Studies by Harding and Talbot (1973) in the southern part of the North Sea showed that, in general, the abundance of eggs and larvae of *Pleuronectes platessa* (plaice) was inversely related to abundance of predators.

The copepods *Acartia*, *Centropages*, *Euterpina*, and *Temora* appeared to be the major food items of larval fish in the Newport River estuary, declining from a mean of 81% of the biomass in March to a mean of 48% during June-July for the years of survey, 1970-1972. Thayer et al (1974) thus stated, "Maximum densities of fish larvae coincided with the period of zooplankton decline". However, the diagrams included in the work do not show a sharp relation of those parameters for 1970 and 1971, and the situation of the plankton during part of 1972 is unknown as plankton data for this year only covered January to April. In 1970 the zooplankton peaked precisely in March-April, but in 1971 the peak occurred in May, after rising from a low value in February. Thayer et al (1974) found some discrepancies in their calculations due to the fact they only considered two factors, fish larvae and plankton as food, neglecting type of plankton, abundance of food items, and abundance and identification of plankton predators on fish larvae.

Studies on the distribution and survival of *Clupea pallasi* Vallenciennes (herring) larvae in the British Columbia waters (Stevenson 1962) indicate that predation, lack of food, and temperature were not considered mortality factors at inshore waters, the loss of larvae was due to seaward transport of the larvae by currents. However Stevenson did observe predation by Ctenophora, Medusae and Chaetognatha on herring larvae during the period of study, 1947 to 1951. Although the species of predators and their abundance were not determined; Stevenson considered only percentage of predators as evidenced in the actual sampling, with no information on the relation between number of individuals per predatory species and their predatory capacity, and co-occurrences with fish larvae. Lucas and Henderson (1936) discovered that good catches of herring were not usually taken where jellyfish abounded. Poulsen (1944) reviewed the results of a series of plankton observations and the occurrence of young cod in the Danish region for the period of 1932 to 1933, and found a correlation between the number of young cod in ring trawl catches in April and May and the kind of plankton in the same region, and Hunter (1984) analysed relation of cod larvae and predation.

Study of the vertical distribution of the larval and post-larval stages of fishes of commercial importance (Russel 1925) in the British Isles region, were related to their occurrence with other organisms, including both food and predators. The numerical abundance of the Chaetognatha *Sagitta elegans* and *S. setosa* in the Atlantic region off the English channel (Russel 1933) together with abundance of Copepoda, other Crustacea, Medusae, Siphonophorae, and Ctenophora in 1930 collections were compared with young fish data for the same collections (Russel 1935a). The analysis of these data indicates that abundance of young fish was coincident with rich food plankton, and low concentration of young fish coincided with great abundance of Medusae, Siphonophorae and Ctenophora. It was observed in the same set of data high concentration of *S. elegans* occurred in waters rich in *Calanus finmarchicus*, *Metridia lucens*, *Candacia armata*, *Anomalocera patersoni*, and zoeas; and low concentration of *S. elegans* and/or high abundance of *S. setosa* was coincident with high concentration of species of Medusae, Siphonophorae and Ctenophora.

Studies on changes in abundance of fish larvae off Plymouth, England, were related (Russell 1935b) to variations in environmental conditions, mainly temperature and availability of adequate food supply for the larvae (important factor in the success of the year class), and abundance of predatory planktonic organisms. The results showed absence of the normal peak of abundance of fish larvae from spring spawning fish, probably due to concurrence of large number of Ctenophora.

The bulk of the spawning population of fish from the Atlantic waters (Russell 1936) spread over the English Channel region and the plankton rich Atlantic water (identified by *S. elegans*) permitted high survival of young fish, while Channel waters characterized by *S. setosa* concurred with scarcity of young fish. *S. elegans* waters contain abundant food supply, while *S. setosa* waters included abundance of planktonic predators, which contributed to the depletion of the food supply. Russell in several of his papers, related the success of young fish population to the co-occurrence of rich waters, and their failure to the presence of poor waters and abundance of predatory animals.

Observations along series of years at Plymouth (Russell 1952) indicated that waters rich in phosphates increased the abundance of plankton and hence the survival of young fish populations. That is, abundant rich plankton will substain a high survival value for fish larvae. However, rich water could not necessarily lead always to a good survival rate, as happened in 1939 off Plymouth, when fertile waters were present and the peak of young fish was absent, but Ctenophores abundant.

Zooplankton from 40 locations in the Great Barrier Reef Lagoon, Australia, 3 miles east of Low Isles (Russell 1934) included numbers per station of protozoa, Medusae, Siphonophorae, Chaetognatha, Polychaeta, Ostracoda, Copepoda, Mysidacea, Amphipoda, Euphausiidae, Appendicularia, Thaliacea, Pteropoda, Heteropoda, fish larvae and eggs and larvae of Echinodermata, Crustacea, and Mollusca. Analyses of these data indicate that high concentration of Chaetognatha, Medusae and Siphonophorae coincided with low concentration of fish larvae, although apparently Copepoda appeared more or less consistently abundant in all stations. The percentage of predators (Medusae, Siphonophorae, Chaetognatha, Stomatopoda larvae, fish larvae) of the total zooplankton at the Great Barrier Region was 3.1% compared to 5.0% in The North Sea (Russell 1934).

Observations and experiments evidence that Chaetognatha, Siphonophorae, Medusae, Chondrophorae, Ctenophora and in less degree other zooplankters, feed voraciously on fish larvae (Lebour 1922, 1923, 1925), which are often found in the stomachs of individuals belonging to the mentioned planktonic groups. Bigelow (1926) explains that the organisms to be studied in relation to the survival of fish larvae are: "Medusae, Ctenophores, Sagitta and Crustacea that prey upon them, and so many species are plentiful in the Gulf of these groups are known to prey on fish larvae that they are almost certainly the most effective check on the survival of the countless myriads of young fish that are yearly produced in the Gulf. There is good reason, then to believe that the fluctuations known to occur from year to year in the stocks of herring, mackerel, haddock etc., which are reared in the Gulf, depend more on the abundance of the rapacious members of the planktonic community (and especially on the abundance of *Sagitta*, Medusae, *Pleurobrachia*, and *Euthemisto*) than on any other factor. If plankton studies need any defense from the standpoint of fisheries we need look no further".

Anchovy abundance off California coincided with abundance of Copepoda and Euphausiidae, and scarcity or absence of anchovy larvae with abundance of Chaetognatha (mainly those of high predatory potential and large size), Siphonophorae, Medusae (Alvariño 1980b), and scarcity of Copepoda and Euphausiidae.

Predation studies on fish larvae imply the species competition in the plankton, and the proper identification of the organisms which are potential food for the larvae; their quantities, food value, and predatory capacity.

Lebour (1922, 1923, 1925), Bigelow (1926), Fraser (1969) observations and analyses of food in species of Chaetognatha, Medusae, Chondrophorae, Ctenophora, Polychaeta, and other zooplankters, indicate that these transparent and delicate creatures are very voracious and are in a continuous feeding process.

Scarce attention has been dedicated to the predatory effect of a small predator *Noctiluca*, present in high aggregations in the oceans. The occurrence of dense patches of this dinoflagellate occurred at the spawning areas of Clupeidae and Engraulidae. It feeds on diatoms, dinoflagellates, protozoans, Cladocera, Nauplii and copepod eggs and juveniles, *Oikopleura* (Enomoto 1956), and the eggs of *Sardinia melanosticta* and *Engraulis japonica* (Enomoto 1956, Hattori 1962). *Noctiluca miliaris* (Syn, with *N. scintillans*) was observed feeding on *Acartia clausi* (Seguchi and Kato 1976) and *A. tonsa* eggs (Kimor 1979). Published information and observations of enormous aggregations of *Noctiluca* at the bays of Northwest Spain feeding on *Sardina pilchardus* eggs and copepods, and other zooplankters (personal observations) indicate a direct effect on the survival of fish, and indirectly as competitors for food with the fish larvae, by using the food available.

Newly hatched and young fish have little chance against all these enemies, as they are an important food supply for the above mentioned zooplankters. Compiled information on the general diet of most of the important planktonic groups indicate that these carnivorous zooplankters need to feed continuously to fulfill their need for high protein intake and inability to store food reserves in their bodies.

PREDATION BY COELENTERATES

Coelenterates are active predatory carnivores, considered by Bigelow (1926) to be the most destructive of the small and delicate animals in the oceans. Duvault (1965) and Alvariño (1976a,b) indicated that they feed exclusively on living animals, primarily small invertebrates and fish larvae.

The basic feeding behavior of Colenterates (Medusae, Chondrophorae, Siphonophorae) in the plankton, and in some extent also in the Ctenophora, rely on some poisonous mechanisms. They have developed a unique system which produces venom to inject into the body of the prey or any item coming close to or in contact with them. The nematocyst, cnidocyst, or nettlecells are filled with a toxin which is discharged by coiled tubes into the victim. In small animals the poison produces a paralyzing effect which becomes lethal. The toxin may even kill humans and other large animals.

MEDUSAE

Medusae are beautiful, delicate animals, both in form and color. Mayer (1917) explained that, "No class in the animal kingdom exhibits a more surprising variety of forms than do the jellyfish and their close allies the Siphonophorae". Medusae present multitude of shades of colors and hues, ranging from dark purple to red, to brown, with many crystal clear specimens; the tonality or color is not specific in many cases. The coloration in some medusae may be a protection against ultraviolet rays light (Ries and Ries 1924).

Medusae are of interest to study in relation to faunistics, ecology, indicators of ocean currents, predation, and in modern pharmacological studies related to medical research. Medusae (Hydro-and Scyphomedusae) are exclusively carnivores, and their growth rate and size reached at maturity is related with the quality and quantity of food available.

The Medusae detect and localize the potential prey with the aid of the statocyst, sensing the vibrations produced by moving water. They prey on actively swimming animals, such as Copepoda, other Crustacea and their larvae, and the larvae of fish and other groups. The victim is paralyzed by the tentacles of the Medusae with the poison produced in the stinging cells; the prey is later ingested in the Medusa's stomach. Medusae may inject 3 cc poison by a single discharge.

Medusae are considered important in the destruction of eggs and larvae of cod (Mayer 1917) and other fish. They may be the primary enemies of young fish (Joubin 1924). However, while fish may become entangled, trapped, and poison within the tentacles, the larvae and young of some species of fish are known to aggregate under the umbrella of large Scyphomedusae, living together in an apparent biological association. The offspring of some fish may be protected under the canopy of the Medusae's umbrella from the attacks of other animals, while themselves avoiding the proximity of the Medusae. The smooth vibrations produced during swimming by various fish larvae and young fish may not excite the nematocysts of the medusae and no releasing reaction occurs. In underwater observations on association of Scyphomedusae (110 mm diameter) *Acromitus flagellatus* Stiasny and young fish 10.6 to 30.0 mm long *Seleroides leptolepis* (Carangidae), Jones (1960) noted that "the fish kept themselves close to the medusa but not in actual contact with it. Their movements were so well synchronized that it would appear that the fish, which were never seen to turn round or make any special attempt to check the position of the jellyfish, could anticipate the direction in which and the distance to which the later would move". Similar observations were made for the Medusae *Mastigias papua* L. Agassiz and the fish *Caranx kalla;* in both cases, the fish appear swimming slightly ahead of the medusae.

It has been implied that Medusae's poison does not affect some species of fish, which become immune to the medusae's -

toxin; but there is not enough available evidence to totally prove this matter. Some of the fish and larvae do in fact get poisoned and devoured by the medusae, but other remain alive, sheltered, and protected up to the time close to adulthood. This biological association could be considered a case of mutualism, which supplies a source of fresh, live food for the medusae, and protection for some of the young fish surviving through the most critical period of their life history.

I have observed large number of Scyphomedusae off Plymouth (England), Vigo (Spain), Callao (Peru), San Diego (California, United States), appearing in areas concurrently with concentrations of Clupeidae, Engraulidae, Trachuridae, Merluccius, Gadidae, etc. The young of some species of fish tend to swim towards the shelter of any floating object at sea, and large Scyphomedusae offer an ideal canopy shelter. Young fish may also be lured by the swift gliding tentacles of the Medusae, and they swim towards them. Some become trapped and are devoured, while other continue to enjoy shelter and protection until they have grown to the stage where they can independently move out as recruits of the adult population.

These associations have been widely observed. Osterbol (1885) noted young mackerel and young cod sheltered under the Scyphomedusae umbrella, and observed that occasionally the medusae "snatch a fish, which therefore has to pay with its life for the protection that still other comrades are enjoying". - Mayer (1898) found two species (a Clupeididae and a Butterfish) accompanying the Scyphomedusae *Chrysaora (Dactylometra) quinquecirrha*. Damas (1909a,b) noted that *Cyanea lamarcki* in the North Sea appeared often associated with young pollak (*Gadus pollachius*), poor cod (*G. minutus*) and pouting (*G. luscus*). Underwater observations have also showed young *G. merlangus* (whiting) swimming and moving around and above *C. lamarcki's* umbrella (Rees 1966). In fact, the vertical distribution of *C. lamarcki* (as *C. capillata*) appears to be correlated with the vertical distribution of whiting. In the English Channel off Plymouth, whiting 12-22 mm long appear to associate with medusae of all sizes, while those of more than 25 mm were associated with medusae 100 mm or more in diameter (Russell 1928). - Young *Trachurus trachurus* 11-15 mm in length also appeared associated with *C. lamarcki* (as *C. capillata*) in the Plymouth area (Russell 1930 a,b).

Nagabushanam (1959) mentioned three young *Gadus morhua* gathered under the Scyphomedusae, one of which had ingested

Hyperia (Amphipoda considered associated or ectoparasite of Medusae) and to *G. luscus* larvae 33-45 mm long. *Rhizostoma* sp. swimming against the tide together with an aggregation of *T. trachurus* were observed by Browne (1900), Phillips (1971) found the medusae *Stomolophus meleagris* associated with various young fish (*Trachurus*, *Peprilus*, *Poronotis* and *Chloroscombrus*). *Poronotis burti* were found in association with *Cyanea capillata* and *Stomolophus meleagris*. *Chloroscombrus chrysurus*, *Peprilus paru*, *Trachurus trachurus*, *Monocanthis hispidus*, appeared associated with *Chrysaora*, and *Stomolophus meleagris* with *Cyanea capillata versicolor*. *Cyanea capillata* is often found sheltering young whiting (*Gadus merlangus*), the mackerel (*T. trachurus*), young cod (*Gadus callarias* or *G. morhua*), and haddock (*G. aeglefinus*).

Beebe and Tee-Van (1928) described the high number of young fish (*Chloroscombrus* (*scomber*) *chrysurus*) or bumber, 12.5 to 47 mm long and 22 mm *Peprilus paru* (harvest fish) captured under the medusae *Chiropsalmus*, *Tamoya haplonema*, and *Cyanea* of about 100 cm diameter in the Port-au-Prince Bay. Lowles (1877) and Romanes (1877a,b) found young fish occasionally associated with *Aurelia aurita*, swarms of one to two-year old *Gadus merlangus* appeared under the Scyphomedusae, and large numbers of *A. aurita* were concurrent with dense aggregations of this Gadoid.

Mansueti (1963) reported *Peprilus alepidotus* (harvest fish) and *Poronotus triacanthus* (butterfish) in association with *Chrysaora quinquecirrha* from July to October in Chesapeake Bay. Small pieces of the medusae tentacles and oral lappets were obtained from the stomach content of *Peprilus*, and nematocysts could be observed on *P. alepidotus*. These fish, when placed in an aquarium, developed infectious spots on the body, swam in an erratic manner, displayed loss of equilibrium, and finally died. All signs of fish being poisoned. Other *P. alepidotus* not associated with scyphomedusae did not show any of those symptoms, and remained alive por a long period of time in the aquarium. My observations of *Gadidae Merluccius* and *Trachurus* larvae with *Cyanea* and *Chrysaora* indicated that the fish were not very active and a high proportion of them were under the effect of the toxins from the Medusae. Experiments carried by Dahl (1961) provide the conclusion that "young fish initially use medusae for shelter, thus reflecting simple thigmotaxis". The fish may later be stung by the host and, "if the fish touches places with no stinging cells, there is an accidental association".

These associations may be influential in the brood dissemination of the offspring of fish (Damas 1909 a,b). In the material I have studied from the English Channel, *Trachurus trachurus* and *Gadus merlangus* larvae appeared associated with *Cyanea lamrcki* a medusae inhabiting mainly the coastal regions. These medusae may also be carried far offshore and transported to other latitudes by currents, carrying with them the associated fish fry.

Considering the huge quantities of Medusae and their size range, from a few millimeters to about 1000 mm or more in diameter, and their world wide oceanic distribution and particulary great concentrations in the fishing regions, these animals may play an important role in the recruitment of fish and in relation to the commercial fisheries. Mayer (1910) in his Medusae of the World listed 737 species of Medusae, primarily marine, and Kramp (1961) mentions more than 800. The published literature shows direct observation of 65 of these species of Medusae, eating fish larvae and young fish, and/or planktonic animals. These observations are compiled in Table 1, and indicate that fish larvae are the preferred food items. Lebour (1922) explained that the Medusae she observed would feed exclusively on fish larvae when those were available in any quantity.

In 1768 Slabber observed a medusae feeding on fish and in 1778 published this observation of the medusae he named *Medusa cymbaloides* (probably *Phialidium hemisphaericum*) devouring a young fish. Slabber*s brief comments appear in Gudger (1937): "As soon as I had caught it, I placed it under the microscope and found that it had caught a very small fish for its prey, which could still be seen outside of the body...(the fish) was only lively when I looked at it, and one could see plainly that it was being drawn in. Thus drawn in was completed in two hours time, and then the whole creature..." Slabber had already realized that the millions of medusae in the North Sea might consume a great amount of fish, which would effect the number of fish later available for commercial fishing. K. Nair (1947) analyzed the Medusae and fisheries of the Travancore coast, India, and found that large concentrations of Medusae during certain seasons affected the fisheries destroying fish eggs and larvae as well as other organisms which constitute the food of small fish. In addition, studies of the zooplankton on the Bombay region (Bal and Pradhan 1952) show that a minimum number of fish larvae and post larval stages coincide with high numbers of hydromedusae.

Phialidium hemisphaericum (probably the first medusae observed feeding on fish larvae by Slabber in 1768, devour almost exclusively young fish (Lebour 1922), which constitute its whole diet when available in quantity. Bigelow (1926) discussed the great abundance of *P. hemisphaericum* which, together with *Aurelia aurita*, he considered the two most abundant Medusae of the coastal and open waters of the Gulf of Maine. They are proven eaters of fish, euphausiids, copepods, appendicularian and various larvae, and "must take heavy toll of the little fish that cross their paths". Gudger (1937) reported that "at the high of the herring spawning season in the vicinity of the Bay of Fundy, it was found that *Phialidium* formed an important enemy of the fry"; of the 356 herring larvae collected in one station, 16 were in the stomach of *Phialidium* and other 53 were partially digested.

Orton (1922) described in detail the feeding process and characteristics of Medusae. The analysis of the food pouches in *Aurelia* showed that the Medusae devour various kinds of planktonic organisms as well as some of the young fish taking shelter under its umbrella. A typical meal for *Aurelia aurita* from early ephyra into large adult state includes 16 small fish (*Cottus or Blennius*), which were eaten (Lebour 1922) in less than 30 minutes, and if fish were not available, amphipods, zoeas, other crustaceans, and medusae were eaten. Gudger (1937) reported that Fish in 1924 indicated that *A. aurita* fed on winter flounder larvae in the New England region and that in Waquoit Bay "where both animals breed in abundance, *Aurelia aurita* proved of very vital importance in depleting the flounder stock".

Russell (1970) indicates that "in view of their size and abundance the Scyphomedusae must play a large part in the economy of the sea as predators and competitors of fish". Hela (1951) commented on the inverse relation found on the abundance of sprat and herring larvae with the abundance of *Aurelia aurita* off Finland, and Lebour (1922) observed a similar relation for the British Isles, where huge concentrations of *A. aurita* coincided with nil catches of fish.

Yasuda (1970) calculated the biomass patches of the medusae *Aurelia aurita* in Urazolo Bay, Japan, in the range of 1.4 to 9.2 tons. These medusae are mainly abundant in the upper 10 m; their distribution is thus closely related with the epipelagic fish larvae and the abundance of the medusae will reduce drastically that of the larvae. Studies on the ecology of zooplankton (Neale and Bayly 1974) in the Patterson, Yabarra, Maribyrnong, and Werribee River estuaries in Victoria, Australia, on fish eggs and larvae, copepods, crustacea larvae, mollusks, echinoderms, inmature *Aurelia* sp. medusae and *Australomedusa baylii* Russell in the Werribee area coincided, in one case, with no fish eggs or larvae.

Cyanea capillata is another medusae which effects commercial fisheries. It reaches a large size, more than 1 m in diameter, and has numerous tentacles which spread through the waters while moves by jet propulsion produced by rhythmic pulsations of the umbrella. It engulfs enormous quantities of zooplankters as it glides through the water. Russel (1970) stated that, "a Northeast coast fisherman told me that he had heard that *Cyanea* preyed on planktonic lobster and that a poor lobster fishery might result four years after a year of great abundance of these hellyfish. This seems to me quite possible".

Russell (1931), and Lucas and Henderson (1936) have suggested that the abundance of *Gadus merlangus* may be correlated with the abundance of large *Cyanea* in the North Sea. Lucas and Henderson (1936) examined the reports of fishermen on the incidence of several species of Medusae with catches of *Clupea harengus* and concluded that "large catches of herring were related to low abundance of medusae, including *Cyanea capillata*". They also indicated instances of medusae occurring in certain areas of herring fishery, coincident with nil or extremely poor catches of herring. In all cases, the herring were taken outside the zone where these medusae were present. The information compiled by Lucas and Henderson (1936) indicates a definite inverse relation between low quantities of herring and abundance of medusae.

To further investigate this relation, Russell (1938) added the average monthly catches of Medusae for 1920-1937, and the total young fish (excluding Clupeidae). The numerical data show that values for 1931, 1932, 1934, and 1935 included low numbers of medusae coinciding with high numbers of young fish. Similar results, although in a different order of magnitude for the fish, were found for 1936 and 1937. However, the number of Clupeidae larvae was not included in the listings, so it is not possible to obtain a clear picture of the situation; the number of Clupeidae larvae could be an important factor in the final determination of the relation of fish larvae and Medusae. It is possible that in 1930, year of highest amount of Medusae and no of lowest amount of fish larvae (excluding Clupeidae), the medusae could be feeding on herring or sardine, and thus the abundance of medusae would not affect the abundance of larvae of other species of fish.

Liriope tetraphylla is the most abundant medusae in the warm and temperate oceanic regions. A voracious predator, it captures prey up to three times its own size (McCrady; 853; Fraser 1969). Candeias (1931) stated that in June 1926 huge quantities of *L. tetraphylla* coincided at Olhae, off Algarves coast, Portugal, with total lack of *Sardina pilchardus*, in a region where this Clupeidae is abundant. Compiled information on the co-occurrence of anchovy larvae and zooplankton predators off California and Baja California for 1954, 1956, 1958 (Alvariño 1979, 1980 b) show that abundance of Medusae coincided with low number of absence of anchovy larvae.

Observations by Nagabushanam (1959) on the associations of young *G. merlangus* with the Scyphomedusae *Rhizostoma pulmo* (as *R. octopus*) indicated that 14 of 59 *G. merlangus* were in semi-digested stage, and he concluded that "they might have got into the stomach accidentally through rupture of the gastrointestinal membrane". Another circumstance to consider is the regurgitation of food occurring in animals when disturbed by the trawling strain of the collecting nets, and the destruction of soft large medusae during the trawling operation.

Fraser (1969) detailed the feeding behavior of *Cyanea capillata* and roughly estimated the food consumption to provide an indication on the amount of food needed. He estimated that a small medusae 50 mm in diameter can capture 80 fish larvae in six and a half hours (indication of the importance of this feeding activity on recruitment of commercial fish stocks). Fraser (1969) observed the active voracity of *C. capillata* on the Amphipoda (*Gammarellus homarus*, *Calliopius laeviusculus*, *Parathemisto gaudichaudi*) Euphausiidae, Brachyuran zoeas, *Mytilus edulis*; 10.032 gr of *Temora*, and fish larvae; a 30 mm *C. capillata* consumed in 17 days, 500 specimens of *Temora*, 6 flat fish larvae, 12.5 to 15 mm in length, 3.34 gr of *Mytilus* meat; a 45 cm *Cyanea* weighting 6 Kg would require 3570 gr of wet weight food, about 166x 10^4 *Calanus*, which is equivalent to 15.000 fish larvae.

Fraser (1969) also notes that one *Melicertum costatum* consumed 36 fish larvae, 6 copepoda (*Temora*), and one piece of the medusae *Staurophora* in a period of 4 days. One *Leuckartiara nobilis* 17 mm in diameter consumed in 26 days, 22 fish larvae (yolk sac and post-yolk sac stages), 222 copepods (mostly *Temora*), 4 Amphipoda, 0.875 gr *Mytilus edulis*, 4 *Aglantha*, 1 *Sarsia*, 1 *Clione*, and pieces of *Staurophora*. *L. nobilis* uses its coiling and twisting tentacles to entangle fish larvae, copepods and large food items such as *Sarsia* and *Clione limacina* 25 mm long. Lebour (1922) observed a *L. octona* which ate young squid larger than itself, the squid "completely filled its (the medusae's) stomach and took several days to digest". The same specimen three days later caught two young *Cottus bubalis* at the same time it was catching another fish larvae with its tentacles. This species is highly voracious swallowing food larger than itself, and is "a dangerous species to keep in an aquarium, as it will eat almost anything and apparently is not much eaten by other animals "(Lebour 1923).

Staurophora mertensi the most abundant medusae in Logy Bay, ranges from 15 to 164 mm (90 to 120 mm is the most common size range). Fraser (1969) observed that the smallest specimen caught 8 post yolk sac fish larvae, which digested within 45 minutes, and in 4 days consumed 13 fish larvae, 47 copepods, 2 amphipods, and 0.1 gr *Mytilus*. Another specimen consumed within two weeks, 21 fish larvae. 200 copepods, 2 amphipoda, 2 zoeas, and 0.29 gr *Mytilus*.

Fraser (1969) observed a small 5 mm *Boungainvillia superciliaris* catch 80 fish larvae in 6.5 hours, and noted a 10 mm diameter *Laodicea undulata* eat 5 fish larvae (inmediately post yolk sac) and 21 copepods, mainly *Temora*, within a 6-day period. He also saw small 7 mm diameter specimens of *L. undulata* from Logy Bay, constantly wiping the tentacles on the lips of the mouth to remove detritus, ciliates, and minute oil globules from *Coscinodiscus* (abundant in the plankton). This medusae swallowed, within a few minutes, *pandalid* larvae, euphausiid calyptopis, and *Calanus*.

Another medusae, *Tamoya haplonema* was observed feeding on small fish (Beebe 1928), and 4 *Chloroscombrus* (*Scombrus*) *chrysurus* fish, which had been killed with the powerful toxic nematocyst of the tentacles, were being draw into the mouth; at the same time, other fish had been trapped and were dying in convulsion in the water.

Chrysaora quinquecirrha also prefer fish as food; one specimen collected in the Travancore coastal waters of India, contained 239 fish larvae and young fish within the stomach (K. Nair 1947). I have observed *Chrysaora quinquecirrha* with *Trachurus trachurus* young invading the cavities of the medusae, which was already damaged and dying; and the fish took advantage of the situation seeking shelter and possibly also obtaining food.

Chiropsalmus quadrumanus is a Cubomedusae considered to be dangerous to humans as well as fish. Fish and Cobb (1954) believe it to be responsible for killing some swimmers.

There is a marker food selection and difference in catching ability in three large coelenterates, *Velella* and *Porpita* (Chondrophorae), and *Physalia* (Siphonophorae). These coelenterates appear in large dense patches at the surface of the oceans consuming fish eggs, larvae and young, and the eggs and various stages of the life cycle of other animals in the plankton inhabiting the surface waters of the oceanic domain. The food preferences of these two orders (Chondrophorae and Siphonophorae) are listed in Table II.

SIPHONOPHORAE *Nectocarmen antonioi* **Alvariño 1983**

TABLE 1. OBSERVATIONS ON THE FOOD OF MEDUSAE

Order: Family Species	Food	Author
ANTHOMEDUSAE: Corynidae		
Dipurena binicella Rees 1977	*Artemia*; epibenthic plankton	Rees, 1977
Sarsia tubulosa (M.Sars) 1835	*Hyperia* (Amphipoda)	Linko, 1900
	Acartia clausi, *Calanus finmarchicus*, *Temora longicornis* (Copepoda), and other Crustacea.	Lebour, 1922
	Copepoda, Decapod larvae	Lebour, 1923
	Small crustaceans	Fraser, 1969
	Clupea harengus (herring) larvae	Sveshnikov, 1963
	Clupea pallasi (herring) larvae	Arai and Hay, 1982
Sarsia gemmifera Forbes 1848	*Calanus finmarchicus* (Copepoda)	Lebour, 1922
Sarsia prolifera Forbes 1949	*Labrus* sp. (larvae and juveniles); *Centropages typicus*, *C. finmarchicus* (Copepoda); Crustacea larvae; Annelid larvae; *Oikopleura* (Appendicularia)	Lebour, 1922
	Copepoda; Decapod larvae; other Crustacea	Lebour, 1923
Sarsia princeps (Haeckel) 1879	Copepoda	Fraser, 1969
: Tubulariidae		
Hybocodon prolifer L. Agassiz 1862	Eggs and larvae of Clupeidae and Ammodytidae; *Calanus*, *Acartia*,	
	Pseudocalanus, *Temora* (Copepoda): Chaetognatha	Lebour, 1922
	Young *Sepia* (Cephalopoda)	McIntosh, 1926
Steenstrupia nutans (M.Sars) 1835	Fish eggs and larvae; *Temora longicornis*, *Corycaeus anglicus* (Copepoda); *Porcellanidae* larvae; *Gebia* larvae; Chaetognatha.	Lebour, 1922,1923
:Zancleidae		
Zanclea costata Gegenbaur 1856	Copepoda, Nauplii, and other zooplankters	Russell and Rees, 1936
:Cladonematidae		
Cladonema radiatum Dujardin 1843	Copepoda	Browne, 1900
C. californicum Hyman 1947	*Artemia*; fauna associated with *Zostera marina*	Rees, 1979
Eleutheria dichotoma Quatrefages 1842	*Harpacticus fulvus* (Tigriopus Copepoda)	Drzewina and Bohn, 1911, 1912, 1913
	Tigriopus, Copepoda	Fraser, 1969
:Rathkeidae		
Rathkea octopunctata (M.Sars) 1835	*Sardina pilchardus* larvae; *Pseudocalanus elongatus* (Copepoda): Crab zoea; *Poecilochaetus* larvae; other Crustacea larvae; *Oikopleura*	Lebour, 1922

Table 1. Cont.

Order: Family Species	Food	Author
	Herring and Sprat, Clupeidae larvae; Copepoda; Crustacea larvae; *Phialidium* and other Medusae, *Gebia* larvae; Chaetognatha; *Oikopleura* (Appendicularia)	Labour, 1923
	Synchaeta sp. (Rotifera)	Hollodway, 1947
	Fish larvae, even before the medusae were liberated from the hydroid	Fraser, 1969
Bougainvillidae		
Bougainvillia superciliaris (L. Agassiz) 1849	Copepoda; Chaetognatha	Hartlaub, 1897
	Fish larvae; Copepoda	Fraser, 1969
B. britannica (Forbes) 1841	*Ammodytes tobianus* larvae	Lebour, 1923
B. multitentaculata Foerster 1923	*Clupea pallasi* (herring) larvae	Arai and Hay, 198
Nemopsis bachei L. Agassiz 1849	Crustacea larvae; Dinoflagellates, and other plankters	Phillips et al, 1969
: Pandeidae		
Amphinema dinema (Péron and Lésueur) 1809	Copepoda; Chaetognatha	Hartlaub, 1897
	C. finmarchicus (Copepoda); Chaetognatha; *Cosmetira pilosella*, *Phialidium* sp. (Medusae); *Oikopleura* (Appendicularia)	Lebour, 1922
	Copepoda; Chaetognatha; 7 mm *Eutima gracilis* (Medusae)	Lebour, 1923
	fish larvae; Copepoda; Amphipoda; Medusae; Siphonophorae	Fraser, 1969
Leuckartiara octona (Fleming) 1823	*Nanomia cara* (Siphonophorae)	Mayer, 1910
	Cottus bubalis, *Blennius pholis* larvae; squids and other zooplankters	Lebour, 1922
	Gadus merlangus, *Cottus* sp., *Callionymus* sp. larvae; *Calanus*, *Acartia*, *Anomalocera* (Copepoda); *Podon* (Cladocera): *Poecilochaetus* larvae; *Gebia* larvae; Decapoda larvae, and other Crustacea	Lebour, 1923
	Ctenophora; other Medusae; Siphonophorae	Fraser, 1969
L. nobilis Hartlaub, 1913	Fish larvae; *Temora* (Copepoda); Amphipoda; *Clione limacina* (Pteropoda); *Sarsia*, *Aglantha* (Medusae)	Fraser, 1969
L. zacae Bigelow, 1949	Fish larvae	Alvariño (unpublished data)
Stomotoca atra L. Agassiz 1862	*Eperetmus typicus*, *Proboscidactyla flavicirrata*, *Aurelia aurita* (Medusae); *Pleurobrachia* (Ctenophora)	Arai and Jacobs 1980

Table 1. Cont.

Order: Family Species	Food	Author
	Clupea pallasi (herring) larvae	Arai and Hay, 1982
: Calycopsidae		
Bythotiara stilbosa Mills and Rees, 1979	*Artemia*	Mills and Rees, 1979
LEPTOMEDUSAE: Melicertidae		
Melicertum octocostatum (M.Sars) 1853	*Polydora* (Polychaeta); Copepoda	Russell, 1953
	Larvae and young fish; *Temora* (Copepoda); *Staurophora* (Medusae)	Fraser, 1969
: Laodiceidae		
Laodicea undulata (Forbes and Goodsir) 1853	*Calanus* (Copepoda)	Lebour, 1922
	Blennius pholis larvae; Copepoda	Lebour, 1923
	Fish larvae; *Calanus*, *Temora* (Copepoda); Calyptopis Euphausiidae; *Pandalidae* larvae; other larvae	Fraser, 1969
Staurophora mertensi Brandt 1838	Copepoda; Annelida; Medusae	L. Agassiz 1849
	Calanus (Copepoda)	Bigelow, 1926
	Fish larvae; Copepoda; Amphipoda; other Crustacea and larvae; Mollusca	Fraser, 1969
:Mitrocomidae		
Cosmetira pilosella Forves 1848	*Lepadogaster gouani* larvae; *Caliqus rapax* (Copepoda); Crustacea larvae; Chaetognatha	Lebour, 1922
	Cottus, *Callionymus*, *Labrus* larvae; Copepoda; *Pleurobrachia* (Ctenophora); Chaetognatha	Lebour, 1923
Tiaropsis multicirrata (M.Sars) 1835	*Euphysa*, *Sarsia* (Medusae); other small animals	L. Agassiz, 1849
:Campanulariidae		
Obelia spp.	Fish larvae; Copepoda; Cladocera; Amphipoda; Ctenophora; Chaetognatha; *Oikopleura* (Appendicularia)	Lebour, 1922
	Gadus merlangus, *Callionymus* sp. larvae; *Acartia*, *Paracalanus parvus*; *Pseudocalanus*, *C. finmarchicus* (Copepoda): *Gebia* larvae; Crustacea zoeas; *Podon*, *Evadne* (Cladocera); *Tomopteris helgolandica* and Annelida larvae; *Hybocodon*, *Obelia*, *Steenstrupia* (Medusae); *Oikopleura* (Appendicularia)	Lebour, 1923
Phialidium hemisphaericum (Linne) 1767	Fish larvae	Slabber, 1778
	Cottus bubalis, *Ammodytes tobianus*, *Agonus cataphractus*, *Solea vulgaris*, *Labrus bergylta*, *Gadus merlangus*, *G. minutus*, *Blennius pholis* larvae, and	

Table 1. Cont.

Order: Family Species	Food	Author
	Clupea pallasi (herring) larvae	Arai and Hay, 1982
: Calycopsidae		
Bythoriara stilbosa Mills and Rees, 1979	*Artemia*	Mills and Rees, 1979
LEPTOMEDUSAE: Melicertidae		
Melicertum octocostatum (M.Sars) 1853	*Polydora* (Polychaeta); Copepoda	Russell, 1953
	Larvae and young fish; *Temora* (Copepoda); *Staurophora* (Medusae)	Fraser, 1969
: Laodiceidae		
Laodicea undulata (Forbes and Goodsir) 1853	*Calanus* (Copepoda)	Lebour, 1922
	Blennius pholis larvae; Copepoda	Lebour, 1923
	Fish larvae; *Calanus*, *Temora* (Copepoda); Calyptopis Euphausiidae; *Pandalidae* larvae; other larvae	Fraser, 1969
Staurophora mertensi Brandt 1838	Copepoda; Annelida; Medusae	L. Agassiz 1849
	Calanus (Copepoda)	Bigelow, 1926
	Fish larvae; Copepoda; Amphipoda; other Crustacea and larvae; Mollusca	Fraser, 1969
:Mitrocomidae		
Cosmetira pilosella Forves 1848	*Lepadogaster gouani* larvae; *Caliqus rapax* (Copepoda); Crustacea larvae; Chaetognatha	Lebour, 1922
	Cottus, *Callionymus*, *Labrus* larvae; Copepoda; *Pleurobrachia* (Ctenophora); Chaetognatha	Lebour, 1923
Tiaropsis multicirrata (M.Sars) 1835	*Euphysa*, *Sarsia* (Medusae); other small animals	L. Agassiz, 1849
:Campanulariidae		
Obelia spp.	Fish larvae; Copepoda; Cladocera; Amphipoda; Ctenophora; Chaetognatha; *Oikopleura* (Appendicularia)	Lebour, 1922
	Gadus merlangus, *Callionymus* sp. larvae; *Acartia*, *Paracalanus parvus*; *Pseudocalanus*, *C. finmarchicus* (Copepoda): *Gebia* larvae; Crustacea zoeas; *Podon*, *Evadne* (Cladocera); *Tomopteris helgolandica* and Annelida larvae; *Hybocodon*, *Obelia*, *Steenstrupia* (Medusae); *Oikopleura* (Appendicularia)	Lebour, 1923
Phialidium hemisphacricum (Linne) 1767	Fish larvae	Slabber, 1778
	Cottus bubalis, *Ammodytes tobianus*, *Agonus cataphractus*, *Solea vulgaris*, *Labrus bergylta*, *Gadus merlangus*, *G. minutus*, *Blennius pholis* larvae, and	

Table 1. Cont.

Order: Family Species	Food	Author
	eggs of *Onos* and *Gobius*; *Acartia clausi*, *C. finmarchicus*, *Temora longicornis*, *Pseudocalanus elongatus* (Copepoda); nauplii of Cirripedia; *Pandalus*, *Porcellana* larvae; *Carcinus maenas* zoeas, *Gebia* larvae and other Crustacea; *Hypolite* and *Spionid* larvae (Polychaeta); *Obelia*, *Cosmetira pilosella*, *Phialidium* (Medusae); *Muggiaea* (Siphonophorae), Chaetognatha; *Oikopleura* (Appendicularia)	Lebour, 1922
	Cottus, *Onos*, *Labrus*, *Clupea harengus* larvae; *Pseudocalanus*, *Centropages typicus*, *Calanus* (Copepoda); *Gebia* *Porcellana* larvae, crab zoeas (Crustacea); *Rathkea*, *Obelia*, *Amphinema* (Medusae); Chaetognatha; *Oikopleura* (Appendicularia)	Lebour, 1923
	Fish larvae; Euphausiidae; Copepoda; Onvertebrate larvae; Appendicularia	Bigelow, 1926
	Herring and other fish larvae	Fish, 1932 (i Gudger, 1937)
	Preference of fish larvae over Copepoda	Fraser, 1969
Phialidium gregarium (L.Agassiz) 1862	Herbivorous zooplankters	Huntley and Hobson, 1978
	Clupea pallasi (herring) larvae	Arai and Hay, 1982
:Eutimidae		
Eutima gracilis (Forbes and Goodsir) 1853	*Gebia* larvae	Lebour, 1922
	Fish larvae; Copopoda; *Obelia* Medusae); Chaetognatha	Lebour, 1923
	Other Medusae	Fraser, 1969
Tima formosa L. Agassiz 1862	Ammodytidae larvae and young	Fish 1924 (in Gudger, 1937)
Eutonina indicans (Romanes 1876	*Sarsia*, *Aurelia aurita* (Medusae); *Pleurobrachia* (Ctenophora)	Arai and Jacobs, 1980
	Clupea pallasi (herring) larvae	Arai and Hay, 1982
Aequoreidae		
Aequorea sp.	*Lepadogaster*, *Blennius pholis*, pipefish larvae and young; *Palaemon* and other Crustacea larvae; *Pleaurobrachia* (Ctenophora)	Lebour, 1923
	Eggs and fish larvae	Lee, 1966
	Bolinopsis (Ctenophora); *Salpa cylindrica* and other salps (Tunicates)	Hamner et al, 1975
Aequorea victoria (Murbach and Shearer) 1902	*Artemia salina*, other Crustacea; *Sarsia*, *Phialidium gregarium*, *Aurelia*	

Table 1, Cont.

Order: Family Species	Food	Author
	(Medusae); *Pleurobrachia* (Ctenophora)	Arai, 1980 Arai and Jacobs, 1980
	Clupea pallasi (herring) larvae	Arai and Hay, 1982
LIMNOMEDUSAE: Olindidae		
Aglauropsis aeora Mills, Rees and Hand, 1976	*Artemia*	Mills, Rees and Hand, 1976
Gosea corynectes (Gosse) 1853	Crab zoeas (Crustacea)	Russell, 1953
Craspedacusta sowerbyi Lankester 1880	Gold fish	Schmitt, 1939
	Young fish	Kramp, 1950
	Daphnia and other Crustacea; Rotifera; Protozoa	Rusell, 1953
Gonionemus vertens A. Agassiz 1862	Young fish	C.W. Hargitt, 1905 a, b Perkins (in Gudger, 1937)
	Siphonophorae; Ctenophora; other Medusae	Fraser, 1969
:Proboscidactylidae		
Proboscidactyla stellata (Forbes) 1846	Chaetognatha	Lebour, 1923
P. flavicirrata Brandt 1853	Small Cyclopoid and Copepoda nauplii; *Artemia*; Cladocera Trocophora larvae; crab zoea; eggs	Spencer, 1975 Rees, 1979
TRACHYMEDUSAE: Geryonia		
Liriope tetraphylla (Chamisso and Eysenhardt) 1821	Fish larvae and young fish	McCrady, 1858
	Fish larvae	Fraser, 1969
:Ptychogastriidae		
Tesserogastria musculosa Beyer 1959	Harpacticoid Copepoda; small Crustacea	Hesthagen, 1971
:Rhopalonematidae		
Aglantha digitale (O. F. Muller) 1776	*Calanus finmarchicus* (Copepoda)	Lebour, 1922
	Oithona similis, *Oncaea borealis* and other Copepoda; *Polydora* larvae; Gastropod larvae; Lamellibranch larvae; eggs of invertebrates; *Noctiluca* (Dinoflagellate)	Smedstad, 1972
PTEROMEDUSAE		
Tetraplatia volitans Busch 1851	Crustacea; Annelid larvae; Chaetognatha	Dantan, 1925

Table 1, Cont.

Order: Family Species	Food	Author
	Copepoda; young Euphausiidae; Chaetognatha	Hand, 1955
STAUROMEDUSAE: Eleutherocarpidae		
Kishinouyea corbini Larson 1980	Small shrimps; *Hippolyte* and Gammparids; Amphipoda	Larson, 1980
CUBOMEDUSAE: Carybdeidae		
Carybdea marsupialis (Linnaeus) 1758	Young fish	Conant, 1897
	Larval and young fish, *Acartia* (Copepoda); Stomatopod larvae; Isopoda; *Ceratonereis* (Polychaeta): Chaetognatha	Berger, 1900; Larson, 1976
Carybdea alata Reynaud, 1830	Mysidacea; crab megalopa; Polychaeta	Larson, 1976
C. rastoni Haacke 1886	Fish larvae and juveniles; Mysidacea; Polychaeta	Uchida, 1929 Ishida, 1936 Gladfelter, 1973 Larson, 1976
Tamoya haplonema Müller, 1859	*Chloroscombrus chrysurus* larvae	Beebe, 1928
Tripedalia cystophora Conant 1897	*Oithona* (Copepoda)	Larson, 1976
:Chirodropidae		
Chiropsalmus quadrumanus (Müller) 1859	Young fish	Hyman, 1940
	Squilla, *Lucifer* spp., other Crustacea larvae; crab zoeas; Amphipoda	Phillips and BURKE, 1970
	Fish larvae; Amphipoda; Cumaçea; Stomatopoda; *Lucifer*, crabs and other Crustacea larvae	Phillips et al. 1969 Larson, 1976
Ch. quadrigatus Haeckel 1880		
Chironex fleckeri Southcott 1956	Fish; Caridean and other Crustacea	Barnes, 1966
CORONATAE: Linuchidae		
Linuche unguiculata (Schwartz) 1788	Young fish	Beebe, 1928
:Periphyllidae		
Periphylla periphylla (Perón and Lésueur) 1809	Young Myctophidae fish	Clarke and Herring 1969
SEMAEOSTOMEAE: Pelagidae		
Chrysaora sp.	Fish larvae; Copepoda; *Tomopteris* (Polychaeta); *Leuckartiara* (Medusae); *Beroë* (Ctenophora); Siphonophorae; Chaetognatha	Delap, 1901

Table 1, Cont.

Order: Family Species	Food	Author
	Fish larvae	Lebour, 1922
	Ctenophora	McNamara, 1955
	Fish egg and larvae	Lee, 1966
Chrysaora hysoscella (Linnaeus) 1766	Coelenterata	Delap, 1901
	Cottus, *Blennius*, *Gobius*, *Lepidogaster* larvae; Copepoda; Decapoda larvae; *Phialidium*, *Cosmetira*, *Amphinema*, *Obelia*, *Aurelia* (Medusae); *Pleurobrachia* (Ctenophora); *Tomopteris* (Polychaeta); Chaetognatha	Lebour, 1923
	Fish larvae; Copepoda; Amphipoda; Siphonophorae; other Medusae; Ctenophora	Fraser, 1969
Ch. quinquecirrha (Desor) 1848	Clupeidae young fish	A. Agassiz, 1865
	Larvae and young fish	K. Nair, 1947
	Peprilus triacanthus young fish	Mansueti, 1963
	Shrimp Crustacea; *Mnemiopsis leidyi* (Ctenophora); Polychaeta	Cargo and Schultz 1966, 1967
	Cyprinodon variegatus, *Mugil cephalus*, *Oligoplites saurus* larvae and juveniles; small Crustacea and larvae; *Mnemiopsis mccradyi* (Ctenophora)	Phillips et 1969
	Mnemiopsis leidyi, *Beroë ovata* (Ctenophora)	Miller, 1974
	Mnemiopsis leidyi (Ctenophora)	Burrell and van Engel, 1976
Small *Pelagidae*	Fish eggs	Oesterbol, 1885
Pelagia sp.	*Obelia* and other Hydromedusae; *Thalia democratica* (Tunicata)	Delap, 1907
:Cyaneidae		
Cyanea capillata (Linnaeus) 1758	Young fish; *Nereids* Annelida	Gaede,1816
	Young fish and larvae	C. W. Hargitt, 1902 1905 a, 1905 b Bartels, 1910
	Copepoda; Medusa planula; Echinoderm larvae	C. W. and G. T. Hargitt, 1910
	Copepoda and other zooplankters	Bigelow, 1926
	Crustacea; Hydromedusae; Ctenophora	Hagmeir, 1933
	Obelia (Medusae)	Russell, 1953
	Ctenophora	Cargo and Schultz 1967
	Fish larvae; *Temora* (Copepoda); *Parathemisto gaudichaude* (Amphipoda); *Gammarellus homarus*, *Calliopius laevisculus* (Crustacea); Brachyura zoeas; *Mytilus* (Mollusca)	Fraser, 1969

Table 1, Cont.

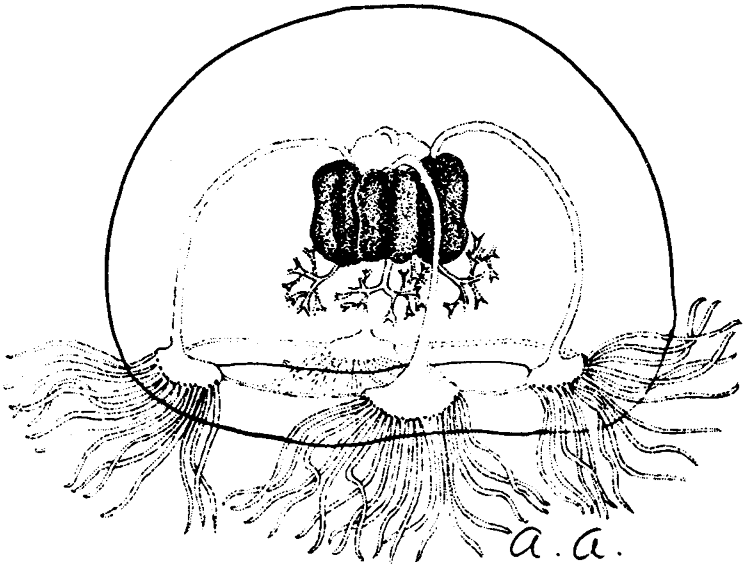
Order: Family Species	Food	Author
	Ctenophora	Phillips et at. 1969
	Artemia and small plankton	Cargo, 1975
C. lamarcki Perón and Lésueur 1809	Fish eggs; Copepoda; *Pleurobrachia*, *Beroë*, *Bolina* (Ctenophora); *Obelia*, *Phialidium*, *Cosmetira*, *Laodicea*, *Steenstrupia* (Medusae)	Delap, 1905
C. purpurea Kishinouye 1910	Young fish	K. Nair, 1947
:Ulmaridae		
Aurelia aurita (Linnaeus) 1758	Sea scorpio young fish	Fabricius, 1780
	Young fish	Spallanzani, 1793 C. W. Hargitt, 1905 a, 1905 b
	Copepoda; Ctenophora; *Obelia*, *Phialidium* (Medusae); Pteropoda	Delap, 1907
	Ammodytes tobianus, *Cottus bubalis*, *Agonus cataphractus*, *Solea vulgaris*, *Gobius minutus*, *Blennius pholis*, *Nerophis lumbriciformis* larvae; Amphipoda; crab zoeas; Decapoda and Mollusca larvae	Lebour, 1922
	Young fish; *Calanus*, *Harpacticoid* (Copepoda); *Balanus* and other Cirripedia larvae; Crustacea larvae; Oyster larvae; *Crepidula* larvae; Gastropoda larvae; young Polychaeta; Nematoda; *Epicarium* larvae; *Polydora*; Ascidian; Tintinnidae; Rotifera; Diatomacea	Orton, 1922
	Cottus bubalis, *Gadus pollachius*, *Syngnatus acus*, Flat fish, Clupeidae larvae; *Acartia clausi*, *Centropages typicus*, Harpacticoids (Copepoda); Decapoda larvae; Mollusca larvae; *Rathkea octopunctata*, *Phialidium* sp. (Medusae)	Lebour, 1923
	Fish larvae; Copepoda; Euphausiidae; other invertebrate larvae; Appendicularia	Bigelow, 1926
	Fish larvae	Fish, 1926 (in Gudger, 1937)
	Plaice larvae; Copepoda	Southward, 1955
	Nereids; Gammarids; *Balanus balanoides* larvae; spiders, Insects; *Corophium*	Hüsing, 1956
Aurelia aurita (Linnaus) 1758	*Coscinodiscus jonesianus*, *C. janischii*, *Thalassionema nitzschoides*, *Cyclotella caspia*, *Rhizosolenia calcaravis*, *Melosira sulcata* (Diatoms); *Ceratium furca*, *Prorocentrum micans*, *Peridinium steinii* (Dinoflagellates); *Ebria tripartita*, *Pontosphaera huxley* (Cocolitophorida); *Anomalocera*	

Table 1, Cont.

Order: Family Species	Food	Author
	patersoni, *Paracalanus parvus*, *Oithona nana* (Copepoda); *Sagitta setosa* (Chaetognatha); Decapod Crustacea larvae; Cirripedia Cypris; *Oikopleura dioica* (Appendicularia)	Milhailov, 1962
	Fish eggs and larvae; *Tigriopus* (Copepoda); Crustacea larvae; *Noctiluca;* Ciliates; Diatomacea	Lee, 1966
	Calanus glacialis, *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia longiremis*, *Oithona similis*, *Oncaea borealis*, *Cyclopina* sp., *Harpacticus uniremis*, *Microsetella norvegica*, *Tisbe furcata* (Copepoda); *Balanus balanoides* nauplii and cypris (Cirripedia); Gastropoda and Bivalvia larvae; *Podon leuckarti*, *Evadne nordmanni* (Cladocera; *Sagitta elegans* (Chaetognatha); *Ophiopluteus* and Bipinnaria larvae (Echinodermata); Polychaeta larvae; *Beroë cucumis*, *Bolinopsis infundibulum* (Ctenophora); *Obelia* sp., *Rathkea octopunctata*, *Coryne tubulosa*, *Bougainvillia superciliaris* (Medusae); *Oikopleura vanhoffeni*, *Fritillaria borealis* (Appendicularia); *Tintinopsis campanula*, *Parafavella gigantea*, *Helicostomella subulata* (Tintinoidea)	Longinova and Perzova, 1967
	Ammodytes, *Gadus callarias*, *G. minutus* larvae; Copepoda; Amphipoda; Decapoda larvae; other medusae; *Mytilus* (Mollusca)	Fraser, 1969
Aurelia aurita (Linnaeus) 1758	*Artemia*	Cargo, 1975
	Fish larvae; Copepoda	Möller, 1979
	Obelia sp., *Rathkea octopunctata*, *Laodicea*, *Phialidium*, *Sarsia* (Medusae); *Pleurobrachia* (Ctenophora)	Arai and Jacobs, 1980
	Clupea harengus, *Cottus* larvae; Hydromedusae, *Aurelia* ephyra; Copepoda; Cladocera; Amphipoda; Cumacea	Möller, 1980
	Clupea harengus (herring) larvae	Moeller, 1982, 1983 Bailey and Bathy 1983
RHIZOSTOMEAE: Cassiopeidae		
Cassiopea frondosa (Pallas) 1774	Young fish; Crustacea; Mollusca	H.G. Smith, 1936
:Catostylidae		
Cambrionella orsini (Vanhoffen) 1888	Young fish	K. Nair, 1947

Table 1, Cont.

Order: Family Species	Food	Author
:Rhizostomatidae		
Rhizostoma octopus (Linnaeus) 1758	Larvae and young fish; Copepoda; Isopoda; other Crustacea and their larvae; Polychaeta larvae; Chaetognatha	Hamann, 1881
:Stomolophidae		
Stomolophus maleagris L. Agassiz 1862	Small plankton	Phillips et al., 1969



MEDUSAE: *Bougainvillia principis* **(Steenstrup) 1850**

CHONDROPHORAE

The Order Chondrophorae includes organisms inhabiting the- Uppermost oceanic layers at the air-water interface. These vo racious animals feed on fish eggs and larvae, and the larvae - and adults of other zooplanketers. Data on the food of Chondrophorae include only two genera, *Porpita* and *Valella*.

Porpita, with no sail or propulsion mechanism, drifts with the waters, and relies largely on the muscular movements of its dactilozoids (Mackie 1959) to capture the food. It can detect vibrations in the waters (Horridge 1966), and is thus able to grab actively swimming animals. Large *Porpita* catch food by the medusae-bearing appendages (Bieri 1970) and the central - oral chamber ingests most of the food in the small ones. *Porpita* shows great ability to catch active copepods and a *Porpita* 5.5 mm in diameter is able to eat adult *Pontellid* copepods as big as itself.

Porpita catching large, fully mature carnivorous copepods (Bieri 1970) could be an example of a predator attempting to attack *Porpita* but being eaten themselves. *Porpita* would in - this case be a secondary carnivore. Analysis of the food of - *Porpitas* washed up on the beaches of Shirahama, Japan, in November 1965 (Bieri 1970) consisted of carnivorous Calanoid cope - pods (90% of the diet), together with crab megalopas, fish larvae and fish eggs (10%), as well as Gastropoda veligers, Lucifer, Larvaceans, Medusae, and Nematodes.

The wind-driven *Velella* sails through the water, offering minimum resistence to movement because it has no tentacles; the dactilozoids are of oval cross section with nematocyst bands on their narrow edges. *Velella* feeding is mainly passive; the animal drifts along the waters at the vein of the blowing wind, and captures zooplankters and eggs of fish and other animals inhabiting the uppermost layers of the ocean in the *Velella's* sailing path.

Velella do not appear to catch motile organisms such as - fish larvae, copepods and nauplii, as effectively as the weak swimming zooplankters, larvaceans or the non motile eggs of fish and invertebrates, although comparatively large and active organisms, such as fish larvae and adult Euphausiidae are - - occasionally caught. In studying the post-larval food of *Velella lata* obtained off San Diego, California Bieri (1961) found that in 99 specimens collected on May 1950, fish eggs, mostly of *Trachurus symmetricus* (jack mackerel) made up 48% of the total food count, and euphausiid eggs 7%; in 36 specimens collected in March 1954, euphausiid eggs made up 78% of the food - - items, and fish eggs 3%. Huxley (1858) found Copepoda remains in the gastrozoids of *Velella lata* Chamisso and Eysenhardy 1821. Lebour (1947) observed the stomachs of *Velella* from Valencia, Ireland, filled with Harpacticoid copepods, and Totton (1954) observed Copepoda and crustacea remains. From the data available, it appears that fish eggs and euphausiid eggs make up a large portion of *Velella's* diet. Variations in the food type observed correspond to the populations which *Velella* encounters, while through a region. If the prey animals escape, *Velella* cannot purse them.

Velella is a recognized conspicuous carnivorous feeder, - eating any organism ranging in size from 0.2 mm to 10 mm or more. The amount of food intake increases with the size of *Velella;* Bieri (1961) noted that the amount of Calanoid copepods caught by *Velella* increases with the size of the *Velella* when these are greater than 30 mm in length. In these cases, *Velella* appeared with digested and semidigested animals in the gastrozoids and siphons; fish egg and larvae, primarily *Engraulis mordax* (northern anchovy) and *Cololabis saira* (saury), Chaetognatha and - their eggs, barnacle nauplii (probably of *Lepas*) Siphonophorae, Crustacea Decapoda larvae, Mysids, Copepoda (eggs, larvae and adults), Euphausiidae (eggs, larvae and adults), Pteropoda, AmPhipoda, Cladocera, *Emerita* larvae and the Diatom *Coscinodiscus*. The seasonal occurrence of *Velella* off California (Bieri 1961) is closely related with the spring spawning of *Merluccius productus*, *Cololabis saira*, *Sardinops Caerulea*, and *Trachurus symmetricus*. I have observed large quantities of *Velella* in the Peru Current region off Peru, in 1968, feeding on *Engraulis ringens* (anchovy) eggs and larvae, Copepoda, and other fish larvae.

SIPHONOPHORAE

Relatively little has been published on the feeding habits of siphonophores. They are planktonic animals which are difficult to maintain in the laboratory due to the large size of some species, and their general excitability and autotomy; yet, under adequate conditions, they have been maintained in laboratory aquaria for some weeks, feeding, growing, reaching sexual maturity, and reproducing. Under these conditions, their feeding and excitable behavior have been closely observed, and they have been found to be rapacious predators (Alvariño 1967a).

Siphonophores occur primarily in temperature and warm oceanic waters, where they feed on fish larvae and young fish, as well as competing for food with young and adult fish and other pelagic animals. Siphonophores possess anatomical structures ideally suited for "fishing" purposes; their tentacles containing poisonous nematocysts, glide through the waters like fishing lines, luring even with mimicry (Purcell 1980) the fish into a deadly trap. Siphonophores swim swiftly and their transparent bodies are not easily detected by their victims. Observations on the searching action of the gastrozoids indicate their activity is due to tactic and chemical excitability - (Mackie and Boag 1963); nematocysts are located in the tentacles, tentilla, and also around the oral region.

Siphonophorae ingest countless number of Copepoda and - other zooplankters (Bigelow 1926), but feed primarily on fish larvae when available. Analysis of zooplankton of the Bombay region during 1944 to 1947 showed (Bal and Pradhan 1952) that the highest number of siphonophores coincided with a minimum of fish larvae and post larval stages, and high numbers of hydromedusae and siphonophores in 1947 coincided with the lowest number of fish larvae. Unfortunately, published observations on the food of siphonophores include only a few of the approximately 140 species in the group.

The Cystonectae *Epibulia ritteriana* Haeckel 1888 is a surface-floating organism which is seldom captured by plankton hauls, primarily because this stratum is almost never sampled by plankton tows (Alvariño 1972). Therefore, the scarcity of *E. ritteriana* is probably only apparent. Thus cystonect feeds voraciously on epiplanktonic animals, primarily those inhabiting the uppermost layers of the oceans, Clupeidae, Engraulidae and other fish larvae and animals eventually reaching the - neuston or pleustonic epiplanktonic domain. The tentacles of this Cystonectae may reach 80 to 200 mm or more when fully extended through the waters like fishing lines, with the gastrozoids actively searching for food. I have observed *E. ritteriana* with remains of Clupeidae and the eyes of Myctophid inside the gastrozoids. Some authors indicate photophores on *E. ritteriana* siphons and gastrozoids, while others disagreed on this. I observed that photophores inside the gastrozoids of *E. ritteriana* belong to the Myctophids the siphonophore has been feeding on.

The Cystonectae *Physalia physalis* (Portuguese-Man-of-War), catches fish (larvae, young and adults) swimming or floating near the surface of the oceans (Gudger 1942). This siphonophore has long, delicate, and almost transparent tentacles 8-10 meters long. These tentacles are covered with deadly neeling poisonous cells and cnidoblasts, which sting and poison young fish; the prey is later drawn and digested by the gastrozoids. Mackie and Boag (1963) observed that *Physalia* shortens its tentacles by coiling and contracting them to 12-15 cm in lenght during their feeding, an observation which was further corroborated by Bieri (1970).

The feeding behaviour of *P. physalis* has been described in detail by Wilson (1947) from specimens maintained in a tank in the Marine Laboratory at Plymouth, England, and found *Physalia* feed on young and small fish. This Cystonectae first would sting the fish with the poisonous dactylozoids and then the gastrozoids would actively cover the fish and ingest it.

Totton (1960) indicated that *P. physalis* is apparently - very successful in avoiding being devoured, except in the juvenile stage, and that surface swimming fish (Trachuridae, Exocetidae and others) become entagled by the tentacles of *Physalia*, obtaining more food than can digest.

Physalia physalis inhabit warm waters, and during some seasons and years they appear in great abundance; this happens in the Portuguese coastal areas; reaching northward to the British Isles. They are found similary along the Atlantic coasts of North America.

Physonectae siphonophores feed on small fish and crustaceans (Hardy 1956). Observations on *Nanomia cara* specimens - kept alive (Mackie and Boag 1963) for 36 days at Friday Harbor show that they swim by contractions of the nectophores; and changes in the vertical displacements are controlled by adjustment of the volume of CO inside the pneumatophore. When the specimens were fed with small crustaceans (*Artemia* nauplii, *Tigriopus*, etc.) and pieces of fresh meat, it was observed that their need for food was indicated by the state of expansion of palpons; and also, when the palpons were filled with a milky fluid, no food was necessary. Siphonophores react to stimulation by a sudden swimming action at the speed of 8 cm per second, with a contraction of the nectophores 4 times per second, at 16°C temperature. Barham (1966) observed a mixed population of Physonectes, mainly *Stephanomia bijuga* extending above the

Myctophids layers, their migratory descent to deep layers was - more rapid in the physonectes than in the Mytophids.

The feeding behavior of several other physonectae have described *Physophora hydrostatica* by Hardy (1956), with upward - jerks-like contraction of elastic fibers made by the tentacles in order to carry small crustaceans to the mouth of gastrozoid. *Ph. hydrostatica* may appear to be quietly floating, while all its tentacles are extended like fishing lines. At other times it will swim actively, with tentacles and tentilla contracted, offering the least resistance to movements, as it swiftly moves towards a more adequate field of feeding operations.

Stephanomia bijuga was observed by Barham (1963) motion - less in a "feeding position with the tentacles stretched out in all directions. "These active predatory animals create a living net formed by living fishing lines, apreading across the world oceans. They are able to sink to deep layers expelling gas from the Pneumatophore, reduce their body area by contraction of the stem, tentacles and tentilles, and perform rapid movements, swimming to the upper oceanic layers by "expansion of the gas within the pneumatophore". Berril (1930) described the behavior of *S. bijuga,* explaining that "unless disturbed" the specimens remain perfectly motionless in an inclined position, with the pneumatophore and nectosome part of the stem in a vertical position, and the scyphosoma part of the stem falling out "at an angle of about forty five degrees". In this manner the tentacles and tentille hang separately and are - - spaced to form an efficient trap, drifting with the current and catching small active zooplankters. For example, the Physonect *Stephanomia rubra* reach 150 cm of total length and the extended tentacles up to 750 cm. Contact of any small organism with a filament or tentacle triggers the instantaneous discharge of dactylozoids, and contraction of the tentacles, and a searching activity of the associated gastrozoids. Gastrozoids of *Forskalia edwardsi* were observed to contain fish of more than 25 mm in length (Leuckart 1853) which were digested up to the skelton.

Duvault (1965) studied the feeding reaction in siphonophore Calcycophorae, which paralize their prey by the discharge of nematocysts, followed by contraction of the tentacles and dilatation of the mouth of gastrozoids. These animals move through the water in an ondulatory fashion (Hardy 1956) powered by the jet propulsion of the swimming bells; and in time of danger the scyphosoma is quickly retracted into the shelter of the hydroecium of the nectophore. Observations on the small Calcycophorae *Muggiaea atlantica* conducted at Friday Harbor (Mackie and - Boag 1963) revealed that, the specialized type of swimming and spreading behavior of the tentacles is quite different from that occurring in the Physonectes. The nectophore performs rapid movements in spiral loop fashion; the tentacles are thus spread - out simultaneously in a centrifugal sequence, in the manner of the bullfighter "veronica". It is a technique of combing the water in swirls, by which a good number of victims are captured by the siphonophore and the prey are transferred from the tentacles to the mouth of adjacent gastrozoids. I have observed the small *Muggiaea atlantica* with the tentacles spread reaching 25 mm long.

Parasites which appear in siphonophores may be related to the prey they are feeding on. Dollfus (1963) cited observations by T. Studer (1878) on a Tetraphyllidear like protocercoid observed in the float cavity of the Physonectae *Agalma* sp., and Totton (1954) described a specimen of *Hippopodius hippopus* from Villefranche-sur-Mer, with 50 *Trichocercous* cercaria (with eyes) probably the larval stage (*Cercaria setigera* Monticelly) of the trematode *Lepocraedium album* Stossich. These parasites made tubular tunnels into the mesoglea of *H. hippopus*, lost their tail, and *H. hippopus* may obtained the parasites by feeding on fish.

TABLE II. OBSERVATIONS ON THE FOOD OF COELENTERATES

ORDER/SUBORDER: Family Species	Food	Author
CHONDROPHORAE: Porpitidae		
Porpita sp.	Eggs, larvae and juvenile fish; carnivorous *Calanoid* Copepoda; Medusae; *Lucifer;* Gastropoda larvae; Nematoda	Bieri, 1970
: Velellidae		
Velella sp.	Harpacticoid Copepoda	Lebour, 1947
	Fish eggs; small Crustacea larvae	Bieri, 1970
Velella lata Chamisso and Eysenhardt 1821	Copepoda	Huxley, 1858
	Calanoid Copepoda	Totton, 1954
	Fish eggs and larvae; larval and adult Copepoda; Euphausiidae; Amphipoda; Cladocera; *Barnacle* nauplii, and other Crustacea larvae; Chaetognatha; Diatomacea	Bieri, 1961
	Angraulis ringens larvae and eggs	Alvariño (Unpublished data)
SIPHONOPHORAE		
Suborder CYSTONECTIDAE: Epibulidae		
Epibulia ritteriana Haeckel 1888	Young fish	Alvariño, 1972
	Engraulidae, Clupeidae, Myctophidae, Scomberesocidae larvae and young fish	Alvariño (unpublished data)
: Rhizophysidae		
Bathyphysa sibogae Lens and van Riemsdijk 1908	Associated Hyperid Amphipoda *Schizoscelus ornatus*, *Thyropus edwardsii*	Biggs and Harbison 1976
	Fish larvae	Purcell, 1981a
Rhizophysa filiformis (Forskal) 1775	Small fish; Alcyopid Polychaeta	Biggs, 1977
R. eysenhardti Gegenbaur 1859	Fish larvae	Purcell, 1981a
: Physalidae		
Physalia physalis Linn 1858	Herring, flying fish and other	Lesson, 1843; Quatrefages, 1854 Bigelow, 1891
	Centronotus ingerfish	Bennet (Gudger 1942)
	Young fish	Gudger, 1942
	Ctenolabrus rupestris	Wilson, 1947

TABLE II. Cont.

ORDER/SUBORDER: Family Species	Food	Author
	young and small fish	Totton, 1960; Mackie and Boag, 1963; Bieri, 1970
Suborder PHYSONECTAE: Agalmidae		
Nanomia cara Agassiz 1865	*Artemia* nauplii; *Tigriopus* (Copepoda)	Mackie and Boag, 1963
	Euphausiidae	Rogers, Biggs and Cooper, 1978.
Agalma okeni Eschscholtz 1825	*Acartia*, *Pleuromamma* (Copepoda) *Leander tenuicornis*, crab megalopa, *Artemia* and other Crustacea	Biggs, 1976
	Parathemisto (Amphipoda)	Biggs, 1977
	Crab megalopa, large Copepoda; Euphausiids	Purcell, 1980
Agalma elegans Sars 1846	Megalopa larvae	Biggs, 1977
Stephanomia bijuga (Chiaje) 1841	Mysidacea	Biggs, 1977
	Euphausiidae	Alvariño (unpublished data)
Stephanomia rubra Vogt 1852	Copepoda	Alvariño (unpublished data)
:Athorybiidae		
Athorybia rosacea Forskal 1775	Small fish; *Lucifer typis* (Sergestidae); Hyperidae Amphipoda; *Candacia*, *Corycaeus* (Copepoda); Polychaeta	Biggs, 1977
	Fish larvae; Shrimp larvae; Chaetognatha	Purcell, 1980
: Physophoridae		
Physophora hydrostatica Forskal 1775	Crustacea	Hardy, 1956
: Forskaliidae		
Forskalia edwardsi Kölliker 1853	Young fish Stomatopod larvae	Leuckart, 1853 Biggs, 1977
Forskalia tholoides Haeckel 1888	Small fish; *Anchylomera blossevillei*, *Hemityphis rapax* (Amphipoda); *Candacia* (Copepoda); Polychaeta; Heteropoda	Biggs, 1977
Suborder CALYCOPHORAE: Prayidae		
Rosacea cymbiformis (Chiaje) 1822	*Corycaeus*, *Candacia* (Copepoda)	

TABLE II. Cont.

ORDER/SUBORDER: Family Species	Food	Author
	Gastropoda veliger	Biggs, 1977
	Fish larvae; crab zoea and megalopa larvae; *Lucifer* and other Segestids; Polychaeta; *Creseis* sp. (Pteropoda); Atlanta sp. (Heteropoda); clam veligers and Gastropod veligers; juvenile shrimps; Mysids; *Sagitta enflata* (Chaetognatha); *Labidocera acutifrons*, *Pontellopsis lubbochi*, *Candacia curta*, *Oncaeca venusta*, *Oncaea media*, *Acrocalanus longicornis*, *Eucalanus attenuatus*, *Labidocera acuta*, *Paracalanus parvus*, *Scolecith danae*, *Temora discaudata*, *Corycaeus catus*, *Corycaeus* sp., *Farranula gibbula*, *Oithona plumifera*, *Clytemnestra rostrata* (Copepoda)	Purcell, 1981b
Stephanophyes superba Chun 1891	*Candacia* (Copepoda); Euphausiidae	Biggs, 1977
: Diphyidae		
Sphaeronectes gracilis (Claus) 1873	Copepoda	Purcell and Kreme 1983
Sulculeolaria monoica Chun 1888	*Candacia* (Copepoda)	Biggs, 1977
Muggiaea atlantica Cunningham 1892	Clupeidae larvae; small Copepoda	Alvariño 1979. 1980a, 1980b
Chelophyes appendiculata Eschscholtz 1829		
Diphyes dispar Chamisso and Eysenhardt 1821		
Diphyes chamissonis Huxley 1859		
Eudoxoides spiralis Bigelow 1911	Fish larvae; Copepoda	Alvariño (unpublished data)

PREDATION BY CTENOPHORA

Ctenophora are beautiful delicate marine animals commonly named comb-jellies, comb-bearers or sea walnutts. They have a gelatinous crystal clear or translucent appearance, of soft bluish or pinkish tonality with iridescent shine. They are generally spherical, ovoidal, or pearshaped organisms, except for the band-like *Venus* girdle specimens.

Ctenophora propel themselves through the water by beating strokes of their iridescent comb-like plates (comb rows or ribs), while the tentacles, in tentaculate species, are smoothyl trailed. These tentacles are retractile and are enclosed in the tentacle sheath or pocket at each side of the body. The tentacles are covered with filamentous lateral branches, which contain pinna with colloblasts or glue cells which secret an adhesive matter (Gudger 1943). These tentacles, when extended may stretch out to 20 cm or more.

Small crustaceans, young fish and other prey are continously caught on the adhesive cells of the tentacles, which contract and protrude actively during prey capture. The prey usually - dies immediately after touched by these cells, possibly due to a poisonous substance (Hyman 1940; Ralph and Kaberry 1950); a toxin extracted from the Ctenophora was observed to kill "small invertebrates and when injected into frogs, rabbits, toads and dogs elicits excesive skin secretion, muscular weakness, paralysis and death" (Hyman 1940). However, Lebour (1922) watched a *Pleurobrachia* attack and entangle a pipe-fish, which struggle for half an hour until succeeding in getting free, and no detection of any poisoning effect was observed.

The general accounts on the Ctenophora feeding behavior (Hardy 1956) indicates that they devour fish larvae, small crustaceans and other zooplankters (see Table III). They are considered by Bigelow (1926) to be of importance in the "natural economy of the plankton community". He reports that they are at times extremely abundant in the Gulf of Maine, and that - "they are among the most voracious of pelagic animals". Wherever Ctenophores swarm practically vacuum clean the waters and hardly any zooplankter can coexist with them. Ctenophores, excluding probably *Beroë*, can seriously affect the fisheries by predation on the planktonic stages of the animals of commercial importance, and all of them, including *Beroë*, are competitors for food with the meroplanktonic animals of commercial importance. More details of Ctenophora feeding behavior are given in

Harbison et al (1978).

Ctenophores occur some times in great numbers and may then seriously reduce the population of zooplankters upon which they prey, including fish eggs and larvae, crustacean and other zooplankters on which the fish depend for food. Bal and Prodham (1952) studies on the zooplankton of Bombay indicated that high number of Ctenophora coincided with a minimum number of fish larvae and young fish in that region. A peak of fish larvae occurred off Plymouth, England in the first fortnight of May 1930, but a low number of young fish, excluding Clupeidae, was found in the second fortnight of the same month (Russell 1930 a, b, 1935 a, b,). This coincided with high concentrations of medusae, siphonophores, and the Ctenophora *Pleurobrachia pileus*. During June, July, August and September of the same year, the numbers of Medusae, Siphonophorae and Ctenophora were high, - while the concentrations of fish larvae remained unusually low. The fish larvae catches for 1929 (Russell 1935a) were well below the average for the years 1930 to 1934, and during the hatching time in 1929 were present great quantities of ctenophores *Beroë cucumis*, *Belinopsis infundibulum*, *Pleurobrachia pileus*, and the Agalmidae siphonophore *Stephanomia bijuga* Russell's data indicate that the exceptional abundance of predator populations was responsible for the absence of the peak abundance of fish larvae normally occurring in the area.

Studies on plankton and herring in the Barents Sea (Mantenfel 1941) indicate that ctenophores feed actively on plankton which undoubtedly affects the survival and growth of the herring of the region. Swarming Ctenophora observed at the herring hatching grounds off Yorkshire, England, are discussed by Hardy (1956). "At such times these ctenophores must levy a very heavy toll upon young herring, and variations in their numbers from year to year must play a part in determining whether some broods of herring are more successful than other. It is possible that this may be one of the factors leading to the - well known fluctuations in the relative strength of different age-groups in a herring population".

Bigelow (1926) stated; "There is reason to believe that *Pleurobrachia* is a serious enemy of the successful reproduction of sundry fishes (e.g. cod and haddock) by feeding on their - buoyant eggs, few of which can escape destruction in localities where ctenophores are numerous". Mayer (1912) stated that "In cold northern waters where Ctenophora occur in vaste swarms, they constitute a serious menace to the cod fisheries by devouring pelagic eggs and young fish". Lebour (1922, 1923, 1925) - analyzed the food of ctenophores and found they feed on practical every type of plankton, including fish, and observed up to several fish per ctenophora stomach.

Plankton studies in the Gulf of Aden (Ali Khan and Hempel 1974) showed fish larvae in the digestive tract of Ctenophorae. In addition, Bigelow (1926) considered ctenophores to be serious enemies of gadoids and flat fish hatching at nursery - areas of the German Bank and the Banks of the North Atlantic extending to the Southwest of Cape Sable.

Russell (1931) in discussing the part played by crustaceans in the economy of the seas, stated that "the inmense swarms of plankton predators specially the Ctenophores, must play havoc among the copepod population and serve as serious competitors to the fish themselves, at times even depleting the supply. This is specially noticeable at times when ctenophores predominate in the catches, as on such occasions the remaining animal plankton appears exceptionally poor". Copepods in particular are exterminated in the centers of abundance of *Pleurobrachia*, though in their own turn they may swarm nearby; and it is common to find ctenophores packed with copepods or euphausiids and larval fish ingested and partially digested (Bigelow 1926). Bishop (1968) observed that Ctenophora feed selectively on Copepoda, eating *Pseudocalanus minutus* at greater rate than *Epilabidocera amphitritis* Ctenophores also have serious effects on the survival of shellfish larvae and spat production of oysters. *Pleurobrachia* is considered a serious - enemy of the oyster in Washington, due to the large amounts of larvae consumed by this ctenophore (Kincaid 1915), Nelson (1925) indicated that the abundance of the ctenophore *Mnemyopsis leidyi* appeared inversely related to the abundance of *Teredo*, *Bankia*, and the setting of *Ostrea* during 1921 to 1923 in Barnegat Bay and adjacent waters; the abundance of oysters setting in this region, Mulloca River and nearby regions correlated with the absence or scarcity of *M. leidyi*.

Feeding mechanism differ among the Ctenophora. The Tentaculata, represented by *Pleurobrachia*, spread their tentacles and feed on everything available in the waters. The Nuda Ctenophora, represented by *Beroë*, however, feed by engulfing and swalling food items by rapid suction, preying on larger organisms than the Tentaculata, which include also species of Tentaculata Ctenophora, thus limiting their populations.

Pleurobrachia is an inhabitant of the uppermost layers of the ocean, being found mainly along the upper 30-0m or 50-0m strata (Bigelow 1926). It is a voracious feeder; Lebour (1923) observed one 4mm-long *P. pileus* catch and partially digest a 10 mm-long *Gobius ruthenparry*. Fraser (1970) indicates that crustaceans are the dominant food, making up 80-97% of the total. The maximum amount found in a 13 mm-long *Pleurobrachia* included 1 *Calanus*, 1 *Centropages*, 44 *Acartia*, 4 *Evadne*, 2 *Podon* and 1 cyprid larvae of *Balanus*. Differences in the food found in *Plaurobrachia* stomachs will reflect the composition of the plankton of the area rather than differences in the selective diet of the Ctenophora. Kuhl (1932) described *Pleurobrachia* catching food in the aquarium: "The most usual prey-catching attitude is a stationary position with mouth upwards and the tentacles up to 20 cm long, with their lateral filaments extended like nets". Their hunting activity are displays of swimming in spirals "loop-the loop" turns, covering large spaces through the waters.

Studies on the distribution of *Clupea pallasi* larvae in British Columbia, Canada, from 1947 to 1952 (Stevenson 1962) describe predation caused by *Pleurobrachia* sp., together with numerous medusae and chaetognaths (with no determination of the respective species), indicating that "45% of the larvae in the sample had been or were being devoured by the Ctenophores". These ctenophores were so numerous in Mayne Bay that during - both day and night they appeared to form a false thick bottom at about 4 m depth, where they were observed preying heavily on fish larvae.

Large concentrations of *Pleurobrachia* at the northern part of Moray Firth, Scotland, concurred with absence of herring larvae, abundant at the adjacent regions where ctenophores were not present (Fraser, 1970). Swarms of *Pleurobrachia pileus* may be responsible of larval fish mortality, even if the larvae are not eaten by the ctenophores, which by consuming the food could affect the survival of the larvae, the adult herring and other plankton feeding animals of commercial importance Fraser (1970) explained that 1965 was a peak year for *P. pileus* in Scottish waters, when more than 47,000 were obtained in the northern North Sea; 6, 162 of these were examined for food content. The monthly average of those with food ranged from 4 to 60% with an annual average of 26%. During 1966, the monthly average resulted 4 to 40%, with 21.5% of yearly average, in 1967 the amount of ctenophores with food ranged from 0 to 58% and 19%, respectively, for monthly and annual average; during 1968 the feeding animals ranged from 0 to 10% monthly, and 27% for the year.

Bigelow and Leslie (1930) indicated that the plankton off Monterey (California) in 1928 presented high number of Copepoda and other planktonic organisms in various stations, but that "without exception they were relatively scarce wherever *Pleurobrachia* were plentiful". Kincaid (1915) indicated that the species feeds on Oyter larvae, and Lebour (1922) reported it eats *Calanus*, *Porcellana* larvae, and Chaetognatha.

The feeding behavior of other Cyppidae Ctenophora has been noted. *Mertensia ovum* has been observed by Bigelow (1909) entirely engulfing "a young sculpin (*Acanthias groelandicus* Fabricius) no less than 21 mm long, the victim being doubled up so to fit into the digestive cavity of the captor". *Hormiphora palmata*, a 40 mm long ctenophore with tentacles reaching 200 mm long when fully extended, excrets mucus which expands in a spider net pattern; it has been seen to catch and wrap specimens of the medusa *Sarsia* in this manner (Fukuchi, Yoshida and Hara 1971).

The Non-Tentaculata *Beroë* sp. are large and more voracious than the other ctenophores (Bigelow 1926). Lebour (1922) stated that when *Beroë* and *Pleurobrachia* are present together, the former feeds on the latter. *Beroë* has a rapid digestive activity devouring *Pleurobrachia* and *Bolinopsis* (Bigelow 1926), and it always less abundant than either of the latter, which reflects on the equilibrium found in their respective populations.

Studies on the sensorial mechanisms of *Beroë cucumis* and *B. ovata* by Horridge (1965b) showed that juice of pulverized *Pleurobrachia* applied to the lips of *Beroë* caused a strong feeding response, and when *C. cucumis*, *B. ovata*, and *Pleurobrachia* co-occur, the long tentacles of *Pleurobrachia* are caught by the current at the side of *Beroë* which rapidly engulf and swallow the *Pleurobrachia*.

Beroë could accidentally digest crustaceans or fish, but when remnants of those organisms are found in *Beroë* may come from the food in the prey consumed by the ctenophores (Kamshilov 1960b). Mantenfel (1941 considered that *Beroë* probably fed on herring in the Barents Sea. Kamshilov (1960 a,b), indicated that a 35 mm-long *Beroë* swallowed and digested 31 *Bolinopsis* about 20 mm-long, and that it also fed on *Pleurobrachia*. However, Phillips et al (1969) described *Peprilus alepidotus* (harvest fish) as commensal with *Beroe ovata*, and Matthews and

Shoemaker (1952) observed the fish *Palinurichthy* sp., *Syngnathus*, *Hemicaranx amblyrhynchus*, and *Chloroscombrus* (*Scomber*) *chrysurus*, swimming in and out of *Beroe* in the Mississippi Sound near Biloxi, Mississippi.

Beroë usually inhabit the deeper layers, to about 100 m - depth, avoiding the surface waters where there is danger of the "destructive wave action" (Bigelow 1926).

The swimming activity increases in both *Beroë* and *Bolinopsis* in the presence of the prey (Swanberg 1974) or the swarms of prey animals.

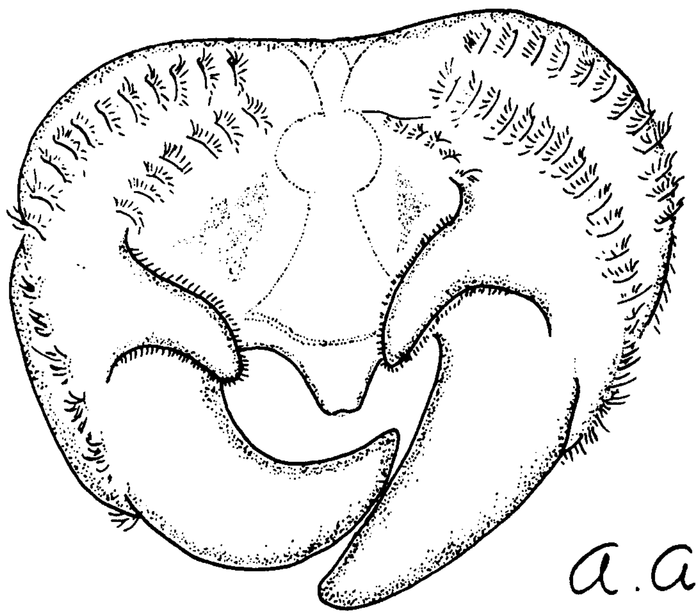
Bolinopsis infundibulum move through the water with "their large paired peristomieae (oral) lobes expanded like trawl-doors, and these were observed came together occasionally to enclose quantities of water containing food organisms (Nagabushanam - 1959). *Bolinopsis* are extremely voracious, and calculations by Kamshilov (1960b) indicated that 2 *Bolinopsis* can eliminate in one month a population of *Calanus* at a concentration of 300 per m^3. A 23 mm-long *B. infundibulum* was observed to capture 18 small copepods of various species and 15 cladocerans, all of which was digested in 58 minutes; 2.5-3 mm specimens digested one *Calanus* per hour and 10 to 11 in two hours. They will also take capelin larvae although it will take several hours to digest (Kamshilov 1960b, Kamshilov et al 1958).

Bolinopsis infundibulum appeared in the plunger jars and aquarium tanks at Plymouth (Lebour 1922, 1925) containing *Lophius piscatorius* (anglers) larvae, together with copepods, on which the larvae had been actively feeding; but although it was thought that *B. infundibulum* would prey on copepods and the anglers larvae would be safe, this was not the case. *B. infundibulum* caught and devoured the fish larvae. Lebour (1925) described 4 to 30 mm *B. infundibulum* grabbing the larvae with - their tentacles. Although the fish struggled, the lobes of the ctenophore would close on the prey, engulfing it within its mouth; it was then conveyed to the stomach to be promptly digested.

Predatory behavior has also been described for the ctenophores *Leucothea multicornis* and *Mnemyopsis* sp. The activity of the pulsations of the oral lobes and tentacles of *L. multicornis* were observed to increase with the presence of prey organisms (Horridge 1965a). The gathering of bunches of plankton performed by this species were typical (carying them to the mouth). Plankton animals were not attached to the finger-like protrusions scattered over the body of the ctenophore but only on the tentacles and oral lobes. The fingers dart out and - strike the passing zooplankton, which immediately become partially paralyzed. It appears that some powerful poison is present at the tip of the fingers, probably produced by the large glandular cell. The fingers (Horridge 1965a) are extremely sensitive to vibrations, and a 100 µm at 10 c/s vibration 5 mm - away from the tip of the finger is detected. A disturbance of this degree may be produced by a copepod or other zooplankter, with the finger extending about 5 mm to reach the prey.

The feeding mechanism of *Mnemyopsis leidyi* was described by Main (1928). Nelson (1925) observed these animals in Barnegat Bay during several years and seasons and found that at summer temperature (more than 20°C), the rate of digestion of food and ejection of residues are so rapid that it is necessary to examine the specimens just at the time of capture, as the stomoderm empties in 20 to 30 minutes. *M. leidyi* 5 to 70 mm in polar length from Solomon, Maryland, were observed to feed on *Acartia tonsa*, consuming 472 copepods per hour, but the rate of feeding changed in relation with the concentration of copepods and the size of the ctenophore, the large specimens consuming more food (Bishop 1967). However, *M. leidyi*, the most abundant zooplankter in the estuaries of the mid-Atlantic United States, itself experiences a reduction in its biomass in spring with the occurrence of the Medusae *Chrysaora quinquecirrha* and the Nuda ctenophore *Beroë ovata* which feed actively on *M. leidyi* (Miller 1974). *M. mccradyi* appears to be one of the most important bioeconomic plankton species in the Mississippi Sound, inhabiting the surface waters in concentrations of 10-100 individuals per m^2, and feeds on microplankton, resulting in a drastic reduction on the zooplankton abundance with the increase in numbers of *M. mccradyi* (Phillips et al 1969).

Reported accounts and observations on the food of ctenophores show that they are carnivores and may produce serious devastation of zooplankters. However, Ctenophora appear in patchy distribution and are mainly abundant in close to shore waters where productivity is usually extremely high, because of the occurrence of larvae of benthic and coastal Crustacea, Mollusca, Annelids, etc. Ctenophora may, in this context, act as a regulatory agent of those populations, while other zooplankton populations survive in the more offshore locations, away from the activity of dense populations of ctenophores. However, the Cte nophora populations themselves may be limited by predation of some species of Ctenophora on other species of the same group.



CTENOPHORA: *Ocyropsis maculata* **(Rang) 1828**

TABLE III. OBSERVATIONS ON THE FOOD OF CTENOPHORA

Order: Family Species	Food	Author
CYDIPPIDAE: Mertensiidae		
Mertensia ovum (Fabricius) 1780	*Acanthias groenladicus* (young Sculpin fish), and other zooplankters	Bigelow, 1909
	Fish larvae	Mayer, 1912
Lampea pancerina (Chun) 1880	Salps (Tunicata)	Harbison et al. 1978
: Pleurobrachiidae		
Pleurobrachia sp.	Oyster larvae	Kincaid, 1915
	Calanus (Copepoda); *Porcellana* larvae and other Crustacea; Chaetognatha	Lebour, 1922
	Shellfish and other Mollusca larvae	Nelson, 1925
	Eggs and fish larvae; Copepoda; Euphausiidae; small Crustacea; Coelenterata; Chaetognatha	Bigelow, 1926
	Copepoda	Bigelow and Leslie, 1930
	Young fish	Hardy, 1956
	Capelin larvae; *Calanus* (Copepoda); Euphausiidae; other Crustacea; other Ctenophora	Kamshilov, 1959
	Eggs and larvae of cod, Mackerel, haddock and other fish; Copepoda; Euphausiidae; Decapoda larvae; Chaetognatha	Fraser, 1962
	Clupea pallasi larvae	Stevenson, 1962
Pleurobrachia bachei L. Agassiz 1860	*Pseudocalanus minutus* copepodites and adults (Copepoda); nauplii larvae	Bishop, 1968
	Labidocera trispinosa, *Acartia tonsa*, *Calanus helgolandicus*, *Corycaeus* (Copepoda); *Artemia salina*; Cladocera; Chaetognatha; other zooplankters	Hirota, 1972
	Labidocera trispinosa, *Corycaeus anglicus*, *Oncaea*, *Paracalanus parvus*, *Euterpina acutifrons*, *Acartia tonsa*, *Rhincalanus nasutus*, Copepod eggs and nauplii; *Evadne nordmanni*, *E. spinifera* (Cladocera)	Hirota, 1974
Pleurobrachia globosa Moser 1903	Fish eggs and larvae; Copepoda; Chaetognatha	Nagabhushanam and Jothinayagam, 1977
Pleurobrachia pileus (Fabricius) 1780	Any planktonic organism	Bigelow, 1915

TABLE III. Cont.

Order: Family Species	Food	Author
	Labrus and other fish larvae; *Calanus finmarchicus*, *Centropages typicus* (Copepoda); *Porcellana* and *Gebia* larvae, crab zoea and other Crustacea larvae; Chaetognatha	Lebour, 1922
	Young *Cottus* and *Labrus*, *Syngnatus* (pipe-fish), *Gobius rutherparry*, plaice eggs and herring larvae; *Calanus*, *Temora*, *Pseudocalanus* (Copepoda); *Gebia* and other Crustacea larvae; Euphausiidae; Mysidacea; Cumacea; Chaetognatha; *Oikopleura* (Appendicularia); other Ctenophora	Leobour, 1923
	Fish larvae; Copepoda; Chaetognatha	Alvariño, 1956a 1956b
Pleurobrachia pileus (Fabricius) 1780	*Oithona nana*, *O. similis*, *Acartia clausi*, *Paracalanus parvus*, *Pseudocalanus elongatus*, *Calanus helgolandicus*, *Centropages Kroyeri*, (Copepoda), *Evadne spinifera*, *E. tergestina*, *Podon* (Cladocera); Crustacea larvae; Lamellibranch larvae; Polychaeta; Chaetognatha; *Oikopleura dioica* (Appendicularia)	Lazareva, 1962
	Eggs and fish larvae; eggs, nauplii and adult *Calanus* and other Copepoda; Euphausiidae; Amphipoda; Mysidacea; *Evadne*, *Podon* (Cladocera); Cumacea; Decapoda and Cirripedia larvae; Lamellibranch and Echinodermata larvae; *Oikopleura*, *Thaliacea* (Tunicata); Phytoplankton	Fraser, 1970
	Calanus plumchrus (Copepoda)	Lee, 1974
Hermiphora palmata Chun 1898	*Sarsia* (Medusae)	Fukuchi, Yoshida and Hara, 1971
Lampetia (*Hormiphora*) sp.	Salps (Tunicata)	Hamner et al, 1975
LOBATA: Bolinidae		
Bolinopsis sp.	Clupeidae, other fish larvae, and other zooplankters	Mantenfel, 1941
	Copepoda	Fraser, 1962
Bolinopsis infundibulum (O.F. Müller) 1776	Microplankton	Lebour, 1923
	Lophius piscatorius and other fish larvae	Lebour, 1925
	Various zooplankters	Alvariño, 1956a
	Pseudocalanus elongatus, *Acartia clausi*, *Temora longicornis* (Copepoda) *Evadne nordmanni*, *Podon intermedius* (Cladocera); nauplii larvae	Nagabushnam, 1959
Bolinopsis infundibulum (O.F. Müller) 1776	*Gadus capellanus* larvae,	

TABLE III. Cont.

Order: Family Species	Food	Author
	Calanus (Copepoda)	Kamshilov, 1960b; Kamshilov et al, 1958
	Pseudocalanus elongatus, *Centropages hamatus*, *Temora longicornis*, *Oithona similis*, *Oncaea borealis*, *Microsetella norvegica*, *Acartia longiremis* (Copepoda); *Evadne nordmanni*, *Podon leuckarti* (Cladocera); Cirripedia nauplii; *Synchaeta* (Rotatoria); *Tintinopsis*, *Campanula*, *Helicostomella subulata* (Tintinnoidea)	Loginova and Perzov 1967
Bolinopsis vitrea L. Agassiz 1882	Copepoda; Ostracoda	Swanberg, 1974
Leucothea multicornis Fewkes 1882	Various zooplankters	Horridge, 1965a
Mnemyopsis leidyi A. Agassiz 1865	Copepoda; *Oyster* and other Mollusca larvae (*Teredo*, *Bankia*); detritus	Nelson, 1925
	Acartia Tonsa (Copepoda)	Bishop, 1967
	Entomostracea	Miller, 1974
	Fish eggs and larvae; Copepoda; Cladocera; Mysidacea; Amphipoda; Cumacea; Brachyuran and Cirripedia larvae; Annelida; Mollusca	Burrell and van Engel, 1976
	Acartia tonsa (Copepoda)	Kremer, 1979
Mnemyopsis mccradyi Mayer 1900	Microplankton	Phillips et al, 1969
	Copepoda; *Barnacle* nauplii; Mollusca Veliger larvae	Baker and Reeve, 1974
Eurhamphaea vexilligera Gegenbaur 1856	Copepoda	Harbison et al, 1978
Ocyropsis chrystallina Rang 1828 *O. maculata* (Lesson) 1843	Small fish; Copepoda; *Hyperid* Amphipoda; Euphausiidae; Beroë	Harbison et al, 1978
CESTIDA		
Cestus veneris Lésueur 1813	Copepoda	Harbison et al, 1978
BEROIDA: Beroidae		
Beroë sp.	Other Ctenophora, and zooplankters	Chun, 1880
	Pleurobrachia, *Bolinopsis*	Bigelow, 1926; Kamshilov, 1960a

TABLE III. Cont.

Order: Family Species	Food	Author
	Herring larvae and juveniles; other zooplankters	Mantenfel, 1941
Beroë cucumis Fabricius 1780	*Pleurobrachia*	Mayer, 1912
	Calanus finmarchicus, *Centropages typicus*, *Pseudocalanus elongatus* (Copepoda); *Podon intermedius* (Cladocera), other Crustacea; *Pleurobrachia pileus*	Lebour, 1922
	Calanus (Copepoda); other crustacea; *Pleurobrachia*, *Bolina*; *Coscinodiscus* (Diatomacea)	Lebour, 1923
	Pleurobrachia	Horridge, 1965b
	Bolinopsis vitrea, *Eurhamphaea vexilligera*, *Ocyropsis maculata*, and other zooplankters	Swanberg, 1974
Beroë ovata Chamisso and Eysenhardt, 1821	*Pleurobrachia*	Horridge, 1965b
	Mnemyopsis leidyi	Miller, 1974; Burrell and van Engel, 1976
	Bolinopsis vitrea, *Cestus veneris*, *Ocyropsis chrystallina*, *O. maculata*, *Leucothea multicornis*	Swanberg, 1974

PREDATION BY CHAETOGNATHA

Plankton indicator species such as Chaetognatha are useful in fisheries research to identify the characteristics of rich or poor water regions, which in turn affect fish populations (Russell 1939). Plankton conditions may thus operate in two ways; influencing the survival of recently hatched fish producing a strong parental population and causing the alteration of the routes of migration of fish.

Such an example is the rich plankton *Sagitta elegans* waters and poor plankton content of the *S. setosa* waters, a well-documented fact in the work of many years by Russell and others at the Marine Laboratory in Plymouth, England; similar studies have been carried out in Scotland by Fraser (1952, 1961). Russell (1939) noted that the highest percentage of *S. setosa* occurring in 1938 coincided with the lowest amount of spring fish larvae (Clupeidae not included). However, the lack of data on the fish larvae for other seasons, and the exclusion of the Clupeidae larvae, may in some cases, alter the results to some degree.

Chaetognatha feed on Copepoda, other Chaetognatha, Ostracoda, Medusae, Salps and the larvae of other marine animals (Oye 1918). The food of the chaetognaths is concidered heterogenous (Della Croce 1963), including cannibalism, and representants of every group in the plankton: diatoms, ciliates, Tintinnids (Protozoa, Medusae (Coelenterates), Crustacea, Copepoda, Amphipoda, Cladocera, larval stages of Crustacea, Mollusca Pteropoda and Heteropoda, Chaetognatha, Tunicata, fish eggs and larvae. A listing of food of chaetognaths is given in Table IV.

Analysis of the intestinal content of Chaetognatha from the Northeast of Amazon estuary included cuticle of copepods and fragments of Dinoflagellates, diatoms and radiolarians (Barth 1963). Rakusa-Suszczewski (1969) indicated that in summer *S. elegans* from the North Sea was feeding on *Pseudocalanus elongatus* and *Calanus finmarchicus* showing a preference for the former, even when *C. finmarchicus* was the most abundant species in the region. The selection by *S. elegans* of *P. elongatus* contributed to the decrease of this species in the waters and to the greater relative abundance of *C. finmarchicus*. Analyses of food content of few individuals of *S. elegans* from the Baltic Sea (Rozanska 1971) indicated 2 to 12% with food in their guts, and an increase of intake of food during daylight, while feeding mainly on copepods. Studies of the Chaetognatha population of Southeastern Australia (Thomson 1947) show that they feed mainly on Copepoda, fish larvae and other chaetognaths, and are considered to play an important part in the food cycle of the pelagic communities because of their role as competitors and prey. Chaetognatha eat larvae of fish and of small crustacea (Johnson and Snook 1927), young fish (Graham et al 1954); fish larvae, copepods ciliates and cannibalism was more outstanding in *Sagitta enflata*, *S. hexaptera* and *S. hispida* (Suarez-Caabro 1955 and author's data); preying also on fish larvae, copepods, euphausiids, cladocerans, amphipods other crustacea and the larvae of other animals of commercial importance (Alvariño 1962, 1965, 1974). The prey in the digestive tract of chaetognaths from the Agulhas Current region (Stone 1969), *S. enflata*, *P. draco*, *S. bipunctata*, *S. serratodentata*, *S. hexaptera*, *S. robusta*, *S. lyra*, *S. friderici*, *S. ferox*, *S. minima*, *S. regularis*, *S. decipiens*, *S. bedoti*, *K. subtilis*, *S. planctonis*, included Copepoda and other Chaetognatha, and were not found eating fish larvae, in a region where Clupeidae and *Merluccius* fish populations are abundant. In the Agulhas Current region it is expected that the large specimens of Chaetognatha would be devouring a good amount of fish larvae.

The food organisms found in the digestive tract of chaetognaths from the Hilutangan Channel, Philippines, in January 1972 (Jumao-as and Westernhagen 1975) included 401 Copepoda (74.8%), 105 Chaetognatha (19.6%), 7 Foraminifera (1.3%), 6 Echinoid larvae (1.1%), 6 Decapod larvae (1.1%), 4 fish larvae (0.8%), 3 Tunicata (0.6%), 1 Polychaeta larvae (0.2%), 1 Isopoda (0.2%) and 1 veliger larvae (0.2%). The species observed were *S. enflata* (the most abundant and showing highest degree of cannibalism), *S. neglecta*, *S. robusta*, *S. regularis*, *Krohnitta pacifica*, *S. bedoti*, *S. decipiens*, *S. pulchra*, *S. ferox*, *K. subtilis*, *S. pacifica* (as *S. serratodentata*), *P. draco*, *S. hexaptera*. Jumao-as and Westernhagen (1975) did not find considerable variations in dietary composition with season and standing crop of the plankton communities.

The stomach content of the Chaetognatha collected in the Arabian Sea during the International Indian Ocean Expedition (Nair and Rao 1973) included fish larvae, Polychaeta larvae, Ostracoda, other chaetognaths, Copepoda (*Centropages*, *Eucalanus*, *Corycaeus*, *Oithona*, *Lucicutia*, *Oncaea*) and rarely *Harpacticoid* copepods.

Several authors have given accounts of their observations on the effects of chaetognath populations on fish larvae. The consistent presence of fish larvae in the gut of Chaetognatha (Lebour 1922, 1923) indicates these animals prey on young fish, mainly *Clupea harengus*, in the North Atlantic. Similar situations (Bigelow 1926) show that chaetognaths should be a serious menace to the stock of various fish in the Gulf of Maine region. Corbin (1947) published data on *Scomber scombrus* and *Sardina pilchardus* larvae, together with information on co-occurring abundance of Chaetognatha *S. setosa*, *S. elegans*, *S. tasmanica* (as *S. serratodentata*), *S. lyra* and the Siphonophore *Muggiaea atlantica*. The data show that, the presence of *S. scombrus* larvae coincided with no or few Chaetognatha or Siphonophorae, and high concentrations of these chaetognaths occurred with few or absence of *S. scombrus*. Similar observations were made for chaetognaths off California (Alvariño 1979, 1980b) primarily between *S. enflata*, *S. hexaptera* and *S. scrippsae*, and *Engraulis mordax* larvae.

Zooplankton studies off Bombay during 1944 to 1947 (Bal and Pradham 1952) indicated that highest number of *Sagitta* coincided with lowest amount of fish larvae. In 1945 the high number of chaetognaths did not correspond to a low number of fish larvae; however, a high concentration of copepods occurred, which may have affected the results, as was also demonstrated in Alvariño (1980b). The quantitative distribution of chaetognaths (Furnestin 1960) *S. setosa*, *S. enflata*, *S. serratodentata*, *S. bipunctata*, and *Engraulis encrasicholus* larvae, indicated that highest concentrations of chaetognaths coincided with low numbers of anchovy larvae and vice-versa. Studies on the distribution of Chaetognatha at Coringa Bay, India (Rao 1962) also include data on plankton; and when Chaetognatha, Ctenophora (*Pleurobrachia*) and Medusae were abundant, no or few fish larvae were observed, and vice-versa.

Ecological survey studies of the Scottish fishery and the changes in the plankton during the period 1949 to 1959 (Williams 1961) include data on Copepoda, Chaetognatha, Euphausiidae, young fish and eggs obtained with the Hardy Plankton Recorder; although the data are presented in annual averages, it can be found that in more than 50% of the yearly periods, high concentrations of large chaetognaths coincided with low averages of fish larvae. Plankton collections obtained at Eddystone, off England during several months of 1958, 1959, 1960 showed (Southward 1962) that highest concentration of *S. elegans* and *S. setosa* coincided with no Clupeidae larvae, and highest number of these larvae or any other fish occurred with scattered specimens of *S. setosa* and/or *S. elegans*, and high concentrations of the medusae *Liriope tetraphylla* and the siphonophore *Muggiaea atlantica* and moderate amount of chaetognaths, coincided with no fish larvae.

The distributional characteristics of the plankton in the oceanic fishing grounds of salmon in the North Pacific (Tsuruta 1963) showed in 80% of cases that, high concentration of *S. elegans* or medusae concurred with absence of Pleuronectidae and Gadidae fish larvae. In the tuna fishing grounds of the Marshall, Gilbert and Phoenix Islands, the abundance of *S. bipunctata* coincided with scarcity or absence of fish; and in waters around Bikini Atoll, high concentration of any of the chaetognaths (mainly *S. pacifica*, *S. hexaptera*, *S. enflata*, *Pterosagitta draco*) coincided with lowest occurrence of fish larvae. In the tuna fishing grounds of the Indian Ocean, off Nias Islands, concentrations of any of *S. bipunctata*, *S. pacifica*, *S. enflata*, *S. regularis* species coincided also with scarcity or absence of fish larvae (Tsuruta 1963).

Systematic list of zooplankters (Lakkis 1971) at surface waters off Lebanon during 1969 show, that lowest quantities of fish larvae coincided with large amounts of Medusae, Chaetognatha, and Ctenophora, and highest concentrations of fish larvae and eggs with high numbers of Copepoda and Cladocera.

Observations on the feeding of *S. elegans* from the northwest North Sea (Wimpenny 1937) indicate they eat Copepoda, mainly *Calanus finmarchicus*. The number of individuals containing food was greatest in June and July, with an average of 30.5% for the whole year. Analyses of the diagrams from Wimpenny (1937) for *S. elegans*, *S. setosa*, *C. finmarchicus*, show that for 1934, high concentrations of *C. finmarchicus* coincided with no *S. elegans* and *S. setosa*, and vice-versa, and that the distribution of the copepods agreed with concentrations of phytoplankton they were feeding on; thus an inverse relation was found for the proportion of food in the stomachs of chaetognaths and the density of the zooplankton populations, which appeared more abundant in regions rich in phytoplankton, where copepods will be grazing. Studies of zooplankton in the northwest north Sea (Bainbridge and Forsyth 1972) correlat the relation of zooplankton with physical changes in the environment and in the herring stock in an attempt to understand the dramatic changes observed in this fishery, which diminished progressively until its virtual disappearance. The study of the plankton showed the presence of lar ge quantities of *Sagitta* (no specific data) and *Tomopteris*, with a positive relation with the total number of Copepoda, principal food of herring. Thus the fluctuations in the abundance of *Calanus* and *Spiratella* (main food organisms of herring) and abundance of plankton predators could have caused the numbers of fish larvae to decrease drastically.

In St. Margaret's Bay, Canada, the *Sagitta elegans* biomass was found to be negatively related (Sameoto 1975) with zooplankton biomass (*Pseudocalanus*, *Temora*), while the Cladocerans *Podon* and *Evadne* and the copepod *Eurytemora* were positively correlated to either *S. elegans* number or biomass. It was implied that the animals may be reacting to one another or to environmental factors to which they respond positively or negatively, although the negative correlations observed may have been produced by a predatory/prey activity.

Mechanical waves contitute the most efficient transmission in the waters, and the vibrations produced by prey, enemies, etc., are registered by the aquatic animals. Water vibrations elicit an escape reaction, unless the vibrations are of the frequency range and amplitude adequate for the animals to make an accurate movement towards the prey to catch it. The nervous system of the chaetognaths includes some mechanisms of integration which discriminate the characteristics signal of the typical prey, its distance and dart direction (Horridge and Boulton 1967). The eyes of the chaetognaths are of a particular structure with at least five lenses pointing in different directions.

The animals are transparent, and they can see down through their own body (Hardy 1956). Eakin and Westfall (1964) indicated that since Chaetognatha inhabit the subsurface oceanic waters where light is weak and diffuse, the small lenticular bodies within the eye might be useful for a sufficient perception of the light to stimulate the photoreceptor tubules; they even tempt to speculate that the conical body in the photoreceptors cell might have wave guide effects or that it might act as a resonator in the manner of a laser. The accuracy of vision in Chaetognatha is unknown in regard to determination of the location and distance of the prey, and because of their indiscriminating feeding at daylight and night, it is assumed that they might detect the victim by a vibration sense, located in the ciliar tuffs and bristtles scattered over their body, and the corona ciliata which may function also as chemoreceptor.

Because Chaetognatha feed both in the dark and in light, it may be that capture of prey is unaffected by the presence or absence of light, suggesting that they may have another mechanism besides the visual detection, such is the perception of the prey by vibrations produced or chemicals released (Scheuer 1977). *Spadella cephaloptera* (benthic chaetognath) fed well in daytime, and *Sagitta* species dart directly towards a moving prey in the light, rather than relying on chance contact for food (Reeve 1964). *Spadella cephaloptera* under laboratory conditions was able to make accurate feeding movement towards any source of vibrations are 9 to 20 c/s with an amplitude of 100 to 500 µm at the distance of 1 to 3 mm (Horridge and Boulton 1967). It was then observed that *S. cephaloptera* attacks only with a small range frequency (9 to 20 c/s), and that is also sensitive to the amplitude of the vibration of 100 to 500 µm at a distance of 1 to 3mm. The responses fall off above 20 c/s or below 9 c/s for a vibration of constant amplitude.

Spadella were observed to grab the prey (Parry 1944) only when it is above or behind its head, which may indicate the tactile or other sensitivity receptor role of the corona ciliata. The food organisms appear in the gut of chaetognaths, with the heads toward the anus of the chaetognaths, which indicates Chaetognatha attack head on. Hardy (1956) explained the behavior of Chaetognatha in the ocean, resting motionless until a prey organism swimms by and suddenly at "lightning speed" the chaetognath dart forward, in the appropriate direction, propelled by the violent up and down flapping of the tail, striking with - speed and accuracy, capturing the prey with the rapid grab of the hooks and teeth. In this manner, chaetognaths are able to cover in a flash by their dart swimming 5 or 6 times their own length.

Experiments on *Spadella* showed that their actual feeding - response can be triggered by a source of vibration of approximate correct combinations of amplitude, frequency, and location. General vibration is ineffective (Horridge and Boulton 1967) because strong stimuli excessively close to the ciliary organs produce an escape movement response. This indicates the nervous system of chaetognaths must include some mechanism (Horridge and Boulton 1967) to identify the characteristic signals of a typical prey, its distance, and location. Chaetognatha probably use both their sensory mechanism, vibration and chemical sensitivity, and the eyes, to capture food. Their unimpaired feeding ability in the dark indicates that chaetognaths may well rely to a large extent on the numerous tangoreceptors covering their body and the corona ciliata, and under light conditions by using also the eyes perception. In this manner they alternate use of both methods of sensory perception to capture food, under dark and light conditions.

S. elegans and *S. setosa* were observed by Rakusa-Suszczewski (1969) feeding more actively at night (in agreement with Pearre 1973 for *S. elegans* from Bedford Basin, Nova Scotia), and a relation was found between the frequency of food species in the gut content of the predators and its frequency in the biotope, and large species were able to grab larger food individuals, being possible to obtain the size range of food depending on the size of the predators. However, continuous daily studies by Mironov (1960) on the food of *S. setosa* from the Bay of Sevastopol indicated that "apparently the intensity of feeding is not linked with any particular time of day", but rather is related to the availability of food.

To try to determine the daily food ration of *Sagitta*, Mironov (1960) assumed that the longer period of time necessary to digest food (Copepoda and other Crustacea), the more probable it is that individuals with full intestines will be found more frequently than individuals with empty intestines. Conversely, the shorter the digestive time (fish larvae prey), the more often are found individuals with empty digestive tracts. The fact that many chaetognaths are found with no food in the digestive tract indicates that may be a long period between evacuation of remains of previous meal and intake. No or few individual with empty intestines would be observed if feeding follows immediately evacuation of remains of previous meal. Availability of food, length of digestion time, and regurgitation of food by animals under the stress of capture are factors which must be considered.

Copepoda are more frequently found in the gut of chaetognaths due to a variety of factors; for example, need to capture more individuals of this group than fish larvae to fulfil the nutritional requirements; the exoskeleton of Copepoda lasts a far longer time under attack by the digestion process and remains longer in the digestive tract before expelled; and Copepoda constitute the most abundant zooplankters and are therefore always available.

In the digestive tract of Chaetognatha I observed fish larvae at advanced stages of development more often than yolk sac larvae. In fact, yolk sac larvae are very rarely seen in the stomachs of chaetognaths. Either the yolk sac larvae are rapidly digested by the Chaetognatha reducing the chances to observe them, or Chaetognatha more efficiently detect the vibrations produced by the swimming of well developed larvae than those by the yolk sac larvae. The feeding behavior of Chaetognatha described by Newbury (1972) to catch food organisms appears closely related to the activity of the prey. *Sagitta hispida* consumed actively swimming *Artemia* but not their eggs swirling in the waters, and also fed on living plankton while ignoring dead organisms. These observations indicate that chaetognaths locate and attack the prey when the latter is actively swimming, producing vibrations and turbulence in the waters. Such is, the vibration produced by the continuous filter-feeding Copepoda, which fit within the range of vibration to which Chaetognatha respond. Chaetognatha may select specific copepods by the frequency of the vibrations produced. There is an evident need for more experimental work on the vibration rate registered by each species of chaetognath under various environmental conditions, and the vibration ranges produced by the organisms considered food of Chaetognatha, to properly understand their feeding behavior and feeding pattern, and to elucidate the part played by sensorial organs in the feeding behavior.

Kotori (1969) estimated that the maximum consumption of food is always lower than the amount of existing food organisms (and it must be or they will starve), and that Chaetognatha may consume 8.1 to 70 % (average 23.5 %) of the standing crop of food organisms in the waters they inhabit. Mironov (1960) calculated that *S. setosa* consumed daily about 0.5 % of the mean available plankton biomass. These estimations will fluctuate drastically with the number of chaetognaths, species, the dominant stage of development, type of food, and condition of the populations.

Laboratory experiments show that *Sagitta hispida* has a maximum rate of ingestion (Reeve 1964) which will not exceed with the availability of food, and field observations by Nagasawa and Marumo (1972) on *S. nagae* indicated the food contained ratio was "affected neither by food density nor by the copepod number per *Sagitta*". Indeed, laboratory observations on the feeding behavior of chaetognaths indicate they are adapted to use and encounter concentrations of food organisms which are patchily rather than uniformly distributed and at low density (Reeve et al 1975).

Revee (1964) observed the feeding behavior of *S. hipida* during long periods (tropical Atlantic species) maintaining one specimen per each 50 ml jar in the laboratory. *Artemia* nauplii were offered as food to each jar to measure the feeding capabilities of *S. hispida*. It was found that they capture more than an average 2 *Artemia* per hour, but if starved will take several in a few minutes. Feeding rates increased with the size of the and selection of food increased with age. *S. hispida* ingested up to 64 %, and 37.6 % for *S. nagae* (Nagasawa and Marumo 1972) own dry weight of food per day, and herbivores in a natural community reached a maximum of only 30 % (Riley and Bumpus 1946).

One to two day-old *S. hispida* appeared to be able to recognize and deal with food as does the adult (Reeve and Walter 1972), feeding on copepod nauplii and copepodites of *Acartia tonsa* and *Oithona nana*. They did not take Rotifera or ciliates, perhaps due to their large size or because they did not produce the type of vibrations which stimulate the sensory apparatus of the chaetognath. The size of food ingested is related to the maximum expansion of the mouth of the chaetognath.

The food passed in 8 seconds to the end of the gut immediately following ingestion, and if several prey organisms are ingested in rapid succession, they are lined up, one in front of the other, occupying the whole length of the gut, In this manner it appears (Cosper and Reeve 1975) that an adult *S. hispida* could capture enough food at one time to satisfy its optimal nutritional requirements for a 24-hour period. Data on the duration of digestion in various Chaetognatha is presented in Table V.

Sagitta hispida can live without food for at least 7 days using body protein as energy source (Reeve 1964). Lee (1974) explained that the protein does not have an energy storage function and low levels of neutral lipids are associated with plankton with constant feeding requirements such as Chaetognatha, Ctenophora, both low in neutral lipids; thus species of those groups can starve within 48 hours if they do not eat.

Chaetognaths do not store food reserves and their high - need of proteins results in a high active predatory capacity. Data on digestive efficiency (Cosper and Reeve 1975) of these carnivores, for instance, *S. hispida*, suggest that a 400 µg dry weight adult ingests a maximum of about 9 % of its own weight in food per day, or 37 µg dry wight, feeding on copepods, and will be most efficient preying on fish larvae.

The estimations of Sameoto (1972) on the K-cal consumed by *S. elegans* was higher than the estimated Copepoda production for the period, therefore suggesting that *S. elegans* may have another source of food which was not recorded in the samples analyzed. The food was probably fish larvae, which is digested rapidly after ingestion and thus offer few chances to be observed in the gut of the chaetognaths collected.

Studies on feeding behavior of *S. elegans*, the only chaetognath taken in the waters near the southeast coast of Newfoundland (Fraser 1969) suggest that after sorting the collections in the laboratory within an hour after capture, most of individuals were dead and of those still alive, only 5% survived overnight; no feeding was observed in these dying plankters. At Plymouth I also observed the jars with alive plankton - brought daily to the laboratory. The species included, *S. elegans* and *S. setosa* could be seen darting about actively catching fish larvae and copepods; however, their activity diminished progressively with the physical deterioration of the body which apparently impaired the normal physiology of the animal, until they died. Similary I observed the same results with *S. euneritica* and *S.enflata* collected off Scripps Pier and off San Diego, California. The vacuolar collarette-like tissue covering totally the body appears to be affected, the animal cannot regenerate this tissue, the anatomical damage is not reversible, and the specimens endure a progressive deterioration until death. The best method to collect chaetognaths alive is with a bucket, in this manner they are caught together with a good amount of water, and the body of these animals is not mechanically damaged or suffers any other kind of injury.

In most cases, the above mentioned Chaetognatha were not in a normal, healthy condition when observed in the laboratory and the animals were growing progressively weaker and consequently their physiologic functions would not be performed at a proper rate. Further more, digestion of Crustacea would be more laborious than digestion of soft body zooplankters such as Chaetognatha or fish larvae, as the digestive activity necessary to break down the external teguments to reach the digestive parts of the body of the animals is greater for the crustaceans than for the soft body prey. This should be kept in mind when comparying laboratory results to the feeding and predation processes in the oceans, and when making assumptions about the impact of predation on fisheries.

TABLE IV. OBSERVATIONS ON THE FOOD OF CHAETOGNATHA

Species	Food	Author
Spadella cephaloptera Bush 1851	Copepoda	Parry, 1944
	Artemia	Horridge and Boulton, 1967
Spadella gaetanoi Alvariño 1978	Copepoda; Invertebrate larvae	Alvariño, 1978
Eukrohnia fowleri Ritter-Zahony 1909	Copepoda; Euphausiidae	Furnestin, 1959; Alvariño (unpublished data)
	Copepoda; Radiolaria	Tchindonova, 1959
	Calanus pacificus, *Lucicutia bicornuta* (Copepoda)	Terazaki et al, 1977
Eukrohnia hamata (Möbius) 1875	Copepoda, mainly *Euchaeta* sp.	Tokioka, 1939
	Copepoda; Ostracoda; Chaetognatha; Radiolaria	Tchindonova, 1959
	Diatomacea, probably obtained with the gulp of water swalled with the prey	Alvariño, 1965
	Herring larvae	Lee, 1966
	Oithona similis, *Metridia pacifica*, *Oncaea borealis*, *Calanus plumchrus* (Copepoda)	Sullivan, 1980
Pterosagitta draco (Krohn) 1853	*Oncaea*, *Corycella*, *Microsetella* (Copepoda); *Sagitta serratodentata* (Chaetognatha)	Stone, 1969
	Oncaea and other Copepoda; Chaetognatha; Tunicata	Newbury, 1978
Sagitta sp.	Fish larvae; *Pseudocalanus*, *Calanus* and other Copepoda; Chaetognatha	Lebour, 1922
	Young fish; Crustacea; Chaetognatha	Bigelow, 1926
	Fish larvae; Copepoda; Crustacea larvae; Salps (Tunicata)	Massuti Oliver, 1954
	Fish larvae; small Crustacea	Hardy, 1956
	Young fish, Copepoda; Chaetognatha	Nicol, 1960
Sagitta bedoti Béraneck 1895	Fish larvae; Copepoda; Crustacea larvae; other zooplankters	Alvariño (unpubished data)
Sagitta bierii Alvariño 1961	Fish larvae; Copepoda; Crustacea larvae; Euphausiidae; Medusae; Chaetognatha	Alvariño (unpublished data)
Sagitta bipunctata (probably *S. elegans* Verrill 1873)	Herring larvae; *Pseudocalanus elongatus*, *Acartia clausi*, *Temora*	

TABLE IV. Cont.

Species	Food	Author
	longicornis, *Centropages*, *Calanus finmarchicus*, *Corycaeus anglicus* (Copepoda); *Gebia* larvae; Chaetognatha	Lebour, 1922, 1923 *
Sagitta bipunctata Quoy and Gaimard 1827	*Corycella concinus*, *Oncaea* (Copepoda)	Stone, 1969
S. bipunctata (probably *S. friderici* Ritter-Zahony 1911)	Fish larvae; *Paracalanus*; *Clausocalanus*, *Calocalanus*, *Centropages*, *Oithona*, *Oncaea*, *Temora*, *Microsetella*, *Euterpina* (Copepoda); *Evadne*, *Podon*, *Penilia* (Cladocera); Ostracoda; eggs, veliger larvae; Chaetognatha; Dinoflagellates; Diatomacea	Pearre, 1974
Sagitta bruuni Alvariño 1967	Fish larvae; Copepoda; Crustacea larvae; Mollusca larvae; Chaetognatha	Alvariño (unpublished data)
Sagitta crassa Tokioka 1938	*Acartia clausi*, *A. erythraea*, *Calanus*, *Tortanus*, *Centropages*, *Paracalanus* (Copepoda)	Murakami, 1959
	Tigriopus japonicus (Copepoda)	Takano, 1971
Sagitta elegans Verrill 1873	*Clupea harengus* larvae	Lebour, 1923
	young fish; Copepoda	Bigelow, 1926; Kuhlmann, 1977
	Calanus finmarchicus (Copepoda)	Wimpenny, 1937
	Fish larvae; *Calanus plumchrus* (Copepoda)	Lee, 1966, 1974
	Nauplii, small Copepoda	McLaren, 1966
	Eggs and fish larvae; *Metridia lucens*, *Centropages typicus*, *Calanus finmarchicus*, *Pseudocalanus elongatus*, *Paracalanus parbus*, *Temora longicornis*, *Centropages hamatus*, *Acartia clausi*, *Corycaeus anglicus*, *Oithona* sp., *Microsetella norvegica*, *Euterpina acutifrons* (Copepoda); *Podon intermedius*, *P. leuckarti* (Cladocera); Cirripedia larvae; Euphausiidae; Chaetognatha	Rakuza-Suszczenski, 1969
	Copepoda	Rozanska, 1971; Sameoto, 1972; King, 1979
	Acartia, *Pseudocalanus*, *Oithona*, *Eurytemora*, *Tortanus*	

TABLE IV. Cont.

Species	Food	Author
Sagitta elegans Verrill 1873 (Cont.)	(Copepoda); Nauplii; Polychaeta; Chaetognatha; *Podon leuckarti*, *Evadne nordmanni* (Cladocera); Tintinnidae; Rotifera	Pearre, 1973, 1981
	Calanus cristatus, *Oithona similis*, *Metridia pacifica*, *Calanus plumchrus* (Copepoda); Chaetognatha	Sullivan, 1980
	Fish larvae; Copepoda; Euphausiidae; Crustacea larvae; Medusae; Chaetognatha	Alvariño (unpublished data)
Sagitta enflata Grassi 1881	Chaetognatha	Grey, 1930
	Copepoda; Chaetognatha	Furnestin, 1953, 1957
	Fish larvae; Copepoda; Chaetognatha	Suárez-Caabro, 1955
	Fish larve; *Corycaeus*, *Calanus* (Copepoda); *Lucifer*, other Crustacea; Chaetognatha; *Thalia democratica* and other Tunicata	Furnestin, 1957
	Decapod larvae	Wickstead, 1965
	Stephanopyxis palmeriana (Diatomacea)	Almeida Prado, 1968
	Oncaea, *Corycella*, *Eucalanus*, *Corycaeus* (Copepoda)	Stone, 1969
	Chaetognatha	Venter, 1969
	Fish larvae; *Paracalanus*, *Clausocalanus*, *Ctenocalanus*, *Calocalanus*, *Centropages*, *Oithona*, *Oncaea*, *Corycaeus*, *Microsetella*, *Euterpina*, *Temora* (Copepoda); *Evadne*, *Podon*, *Penilla* (Cladocera); other Crustacea; Chaetognatha; Dinoflagellates	Pearre, 1974
	Fish larvae; *Paracalanus*, *Clausocalanus*, *Ctenocalanus*, *Calocalanus*, *Centropages*, *Temora*, *Cadacia*, *Mecynocera* *Acartia*, *Oithona*, *Oncaea*, *Corycaeus*, *Corycella*, *Microsetella*, *Euterpina*, *Sappirina*, *Copelia* (Copepoda); *Evadne*, *Podon*, *Penilla* (Cladocera); Arthropod eggs; Chaetognatha; Appendicularia; Dinoflagellata; Diatomacea	Pearre, 1976
	Copepoda; Chaetognatha; *Oikopleura* (Appendicularia); Cillata	Szyper, 1978

TABLE IV. Cont.

Species	Food	Author
Sagitta enflata Grassi 1881	*Corus julis*, *Serranus hepatus*, *Cepola macrophthalma* fish larvae	Regner, 1980
	Fish larvae; Copepoda; Euphausiidae larvae; Hydromedusae; Siphonophorae; Chaetognatha	Alvariño (unpublished data)
Sagitta euneritica Alvariño 1961	Eggs and larvae of *Engraulis mordax*; *Artemia salina*	V.R. Nair, 1976
	Sardinops caerulea, *Engraulis mordax* larvae; Copepoda; Crustacea larvae; Hydromedusae; Chaetognatha	Alvariño (unpublished data)
Sagitta euxina Moltchanoff 1909	*Calanus helgolandicus* (Copepoda); Cladocera; Crustacea larvae; Chaetognatha	Elian, 1960
	Eggs and fish larvae; Copepoda; Mollusca larvae; Polychaeta; Chaetognatha; Appendicularia	Mironov, 1960
Sagitta ferox Doncaster 1903	Diatomaceas	Nagasawa (in Nagasawa and Marumo 1976)
	Fish larvae; Copepoda; Euphausiidae; Crustacea larvae; Medusae; Siphonophorae	Alvariño (unpublished data)
Sagitta friderici Ritter-Zahony 1911	*Calanus*, *Corycaeus* (Copepoda); *Hyperia* (Amphipoda)	Furnestin, 1957
	Fish larvae	Heydorn, 1959
	Fish-larvae; Copepoda; Cladocera; Amphipoda; Hydromedusae; Appendicularia	Almeida Prado, 1968
	Undinula, *Corycella*, *Corycaeus*, *Centropages* (Copopoda)	Stone, 1969
	Copepoda	Venter, 1969
	Fish larvae; *Paracalanus*, *Clausocalanus*, *Centropages*, *Candancia*, *Oithona*, *Oncaea*, *Corycaeus*, *Microsetella*, *Euterpina* (Copepoda); *Evadne*, *Podon* (Cladocera); Arthropod eggs, Chaetognatha; Appendicularia; Dinoflagellata	Pearre, 1976
	Fish larvae; Copepoda; Medusae	Alvariño (unpublished data)
Sagitta gazellae Ritter-Zahony 1909	*Calanus propinguos*, *Rhincalanus gigas*, *Pleuromamma robusta*, *Metridia gerlachi*, *Calanus* sp., (Copopoda); *Tysanoessa* sp., *T. macrura*, *T. vicina* (Euphausiidae);	

TABLE IV. Cont.

Species	Food	Author
Sagitta gazellae Ritter-Zahony 1909	Amphipoda; *Primo macropa* and other Crustacea; Chaetognatha	David, 1955
	Copepoda; Euphausiidae; Crustacea larvae	Alvariño (unpublished data)
Sagitta hexaptera d'Orbigny 1843	Fish larvae; Copepoda; Chaetognatha	Suárez-Caabro, 1955
	Candacia aethiopica and other Copepoda	Furnestin, 1957
	Oncaea, *Eucalanus*, *Corycella* (Copepoda), Ostracoda; Chaetognatha	Stone, 1969
	Sardina pilchardus, *Engraulis encrasicholus*, *Sardinops caerulea*, *Engraulis mordax*, and other fish larvae, Copepoda; Euphausiidae; Amphipoda; other Crustacea; Hydromedusae; Siphonophorae; Chaetognatha	Alvariño (unpublished data)
Sagitta hispida Conant 1895	Fish larvae; Copepoda; Chaetognatha	Suárez-Caabro, 1955
	Fish larvae; Copepoda; *Lucifer* and other Crustacea; Medusae; Siphonophorae; Chaetognatha; Appendicularia	Furnestin, 1957
	Artemia nauplii; other *S. hispida* (under laboratory conditions)	Reeve, 1964
	Fish larvae; *Corycaeus giesbrechti* (Copepoda); *Penilia avirostris* (Cladocera); Amphipoda; *Liriope tetraphylla* (Medusae); Chaetognatha; Appendicularia	Almeida Prado, 1968
	Acartia tonsa, *Oithona nana* (Copepoda); Chaetognatha	Reeve and Walter, 1972
	Copepoda	Reeve et al, 1975
	Copepoda; Chaetognatha	Alvariño (unpublished data)
Sagitta lyra Krohn 1853	Copepoda; Ostracoda	Tchindonova, 1959
	Oncaea (Copepoda)	Stone, 1969
	Copepoda	Venter, 1969
	Fish larvae; Copepoda; Euphausiidae; Amphipoda; Crustacea larvae; Medusae;	

TABLE IV. Cont.

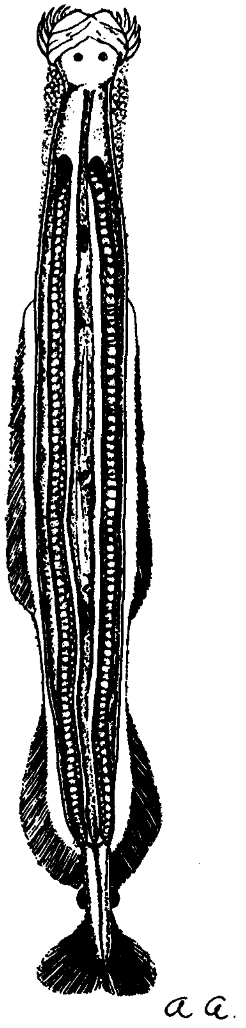
Species	Food	Author
	Siphonophorae; Chaetognatha	Alvariño (unpublished data)
Sagitta macrocephala Fowler 1905	Chaetognatha	Tchindonova, 1959
	Calanus pacificus, *Lucicutia bicornuta* (Copepoda)	Terazaki et al, 1977
	Copepoda	Alvariño (unpublished data)
Sagitta maxima (Conant) 1896	*Euchaeta* (Copepoda); Amphipoda; *Tomopteris* (Polychaeta); Chaetognatha	Bigelow, 1926
	Fish larvae	Lee, 1966
	Fish larvae; Copepoda; Euphausiidae; Crustacea larvae	Alvariño (unpublished data)
Sagitta minima Grassi 1881	Copepoda	Venter, 1969
	Paracalanus, *Clausocalanus*, *Ctenocalanus*, *Calocalanus*, *Oithona*, *Centropages*, *Oncaea*, *Corycaeus*, *Microsetella*, *Euterpina* (Copepoda); *Evadne*, *penilia* (Cladocera); Crustacea larvae; veliger larvae; invertebrate eggs; Chaetognatha	Pearre, 1974, 1976
	Small Copepoda; Invertebrate larvae	Alvariño (unpublished data)
Sagitta nagae Alvariño 1967	*Candacia pinnata*, *Calanus pacificus*, *Pareuchaeta russelli* (Copepoda)	Nagasawa and Marumo, 1972
	Calanus pacificus, *Corycaeus affinis*, *C. dahli*, *C. dubius*, *Clausocalanus arcuicornis*, *Paracalanus parvus*, *Ctenocalanus vanus* (copepoda)	Nagasawa and Marumo, 1976
	Fish larvae; Copepoda; Crustacea larvae; Hydromedusae; Mollusca larvae	Alvariño (unpublished data)
Sagitta pacifica Tokioka 1940	Copepoda; Hydromedusae; Chaetognatha	Alvariño (unpublished data)
Sagitta pulchra Doncaster 1903	Fish larvae; Copepoda; Crustacea larvae; Polychaeta larvae	Alvariño (unpublished data)
Sagitta robusta Doncaster 1903	*Corycella*, *Oncaea*, *Microsetella*, *Candacia*, *Corycaeus* (Copepoda)	Stone, 1969

TABLE IV. Cont.

Species	Food	Author
	Fish larvae; Copepoda; Crustacea larvae; Euphausiidae	Alvariño (unpublished data)
Sagitta scrippsae Alvariño 1962	Fish larvae; Copepoda; Euphausiidae; Medusae; Chaetognatha	Alvariño (unpublished data)
Sagitta serratodentata Krohn 1853	*Calanus* (Copepoda)	Furnestin, 1957
	Undinula, *Corycella*, *Centropages* (Copepoda)	Stone, 1969
	Copepoda; Medusae; Chaetognatha	Alvariño (unpublished data)
Sagitta setosa Müller 1847	*Calanus finmarchicus* (Copepoda); Diatomacea	Wimpenny, 1937
	Clupea harengus larvae; Copepoda	Parry, 1944
	Fish larvae; *Paracalanus*, *Acartia*, *Oithona*, *Centropages*, (Copepoda); Cladocera; Ostracoda; Crustacea larvae; Polychaeta larvae; Chaetognatha; Appendicularia	Mironov, 1960
	Clupea harengus eggs and larvae; *Isias clavides*, *Calanus finmarchicus*, *Pseudocalanus elongatus*, *Temora longicornis*, *Centropages anglicus*, *Microsetella norvegica*, (Copepoda); *Podon intermedius*, *P. leuckarti* (Cladocera); *Themisto abyssorum* (Amphipoda); Appendicularia	Rakusa-Suszczensk 1969
	Fish larvae; *Pseudocalanus elongatus* and other Copepoda	Kuhlmann, 1977
	Sardina pilchardus larvae; Copepoda; microplankton	Alvariño (unpublished data)
Sagitta tasmanica Thomson 1947	Copepoda	Venter, 1969
	Fish larvae; Copepoda; Amphipoda; Euphausiidae; Medusae	Alvariño (unpublished data)
Sagitta tokiokai Alvariño 1967	Copepoda; Euphausiidae	Alvariño (unpublished data)
Sagitta zetesios Fowler 1905	*Calanus pacificus*, *Pareuchaeta russelli*, *Eucalanus subtenuis*, *Euchaeta concinna* (Copepoda); *Conchoecia elegans* (Ostracoda); *S. nagae*, *S. zetesios* (Chaetognatha)	Terazaki (in Nagasawa and Marumo 1976)
	Calanus cristatus, *C. pacificus*,	

TABLE IV. Cont.

Species	Food	Author
Sagitta zetesios Fowler 1905 (Cont.)	*Calanus plumchrus*, *Undinula vulgaris*, *Eucalanus ngii*, *E. crassus*, *E. subtenuis*, *Rhincalanus cornutus*, *R. nasutus*, *Clausocalanus arcuicornis*, *Aetideus armatus*, *Gaetanus Armiger*, *Euchaeta concinna*, *Pareuchaeta russelli*, *P. scaphula*, *P. rubra*, *Scaphocalanus echinatus*, *Scolecithrix danae*, *S. nicobarica*, *Scolecithricella valida*, *Pleuromamma abdominalis*, *Heterorhabdus pacificus*, *Candacia bipinnata*, *Oncaea conifera* (Copepoda); *Sagitta nagae*, *S. lyra*, *S. decipiens*, *S. macrocephala*, *S. zetesios* (Chaetognatha); *Conchoecia elegans* (Ostracoda)	Terazaki and Marumo, 1982



CHAETOGNATHA: ***Sagitta scrippsae*** **Alvariño 1962**

OTHER ZOOPLANKTON PREDATORS ON FISH LARVAE AND SOME ZOOPLANKTER COMPETITORS FOR FOOD WITH FISH LARVAE.

COPEPODS

Revision of studies conducted by various biologists (as reviewed in Russell 1931) regarding food of fish, shows the importance of free-swimming copepods in the economy of living marine organisms. All fishes of commercial importance feed on Copepoda at some time of their life cycle, and certainly at least during their early stages of development. Pelagic species, such as sardine, anchovy, herring, and mackerel, (probably the most successful of fish populations) feed directly on Copepoda. Therefore, Copepoda constitute the main connection in the complicate web between the diatoms and the carnivores. Indeed, the abundance of copepods concurred with highest concentration of anchovy larvae (Alvariño 1979, 1980b) in the California region.

Copepods are distributed into three categories of feeding characteristics (Esterly 1916; Lebour 1922, 1923; Wickstead 1962) based on examination of the stomach content and structure of mouth parts. These include diatom feeders, omnivores, and carnivores. The observed foods of Copepoda and other predatory Crustacea, Mollusca, and Annelida in the plankton realm are listed in Table VI.

Several marine copepods have been observe to fatally injure, capture or ingest young fish and fish larvae during laboratory experiments. Species of Copepoda common in the surface waters of the California Current, *Labidocera jollae*, *L. trispinosa*, and *Pontellopsis occidentalis*, appear to show some predation on fish larvae (Lillelund and Lasker 1971). These copepods may detect and react to vibrations produced by the larvae tail beat by capturing and biting the larvae. Young anchovy larvae are more vulnerable to predation by these copepods, but when the swimming ability of the anchovy increases with age, the copepods are less effective fish larvae feeders or attackers. *P. occidentalis* was able to kill anchovy up to three and a half day-old (Lillelund and Lasker 1971), and the authors explain that "although capture and ingestion of fish larvae was a common fact under laboratory conditions, it is rare to find a copepod with a captured fish larvae in Formalin-preserved plankton". The copepod *Labidocera trispinosa* occurs in the upper 10 m of the California Current, strata which are also occupied by the larvae of *Engraulis mordax*, *Sardinops caerulea*, *Scomber japonicus*, *Trachurus symmetricus*, and *Cololabis saira*, but a quantitative relation between these copepods and the fish larvae has not been analyzed in nature. During experiments by Lillelund and Lasker (1971) the additional *Artemia* larvae included as an alternate prey decreased the feeding of *L. trispinosa* on the fish larvae. The laboratory observations indicate "that marine copepods may be effective predators on larval fish, at least in the sense that a predator need not devour its prey but is equally effective if it injures it mortally".

Experiments rearing fish larvae of *Blennius ocellaris* show (Garstand 1900) they were devoured by Harpacticoid copepods, mainly *Idia furcata*, which had entered the aquarium system; the rapacity of these copepods indicate they attacked healthy 25 mm long young *Gobius minutus* and fed indiscriminately on live, moribund, and dead *Blennius* larvae. The omnivorous copepod *Temora longicornis*, *Centropages typicus*, *Calanus finmarchicus*, and *Labidocera wollastoni* were fed on a mixed diet of copepods and diatoms (Lebour 1922), and the carnivorous *Anomalocera patersoni* fed on other copepods and fish larvae (Lebour 1923). Examination of digestive content of carnivorous Copepoda, *Labidocera*, *Anomalocera*, *Centropages*, *Euchaeta*, and *Candacia* showed they feed mainly on other copepods (Gould 1966). The copepod *Candacia bradyi* commonly found in the Singapore region (Wickstead 1959) was observed eating *Sagitta enflata* (the most abundant Chaetognatha in that region); however, no data have been published on its feeding on fish larvae, which would probably take place if they are abundant in the locations inhabited by *C. bradyi*. Females of the carnivorous copepods *Candacia aethiopica* have been observed (Wickstead 1965) sizing Myctophid fish larvae.

The study by Samyshev (1973) of the phytophagous, predatory and euryphagous copepods from the Gulf of Guinea, indicates that predatory copepods reach the 80 % of the total copepods - biomass in the 500-299 m layers, 35 % at the 200-100m, and 40 % at 100-0 m depth, and considers that the relation of phytophagous copepods to predators in the upper 100 m layer at the zone of divergence could be dependent on the rate of upwelling in the Equatorial region. The carnivorous copepods in the region included, *Oncaea* sp., *Oithona* sp, *Euchaeta marina*, *E. paraconcinna*, *E. hebes*, *Euchaeta* sp., *Paraeuchaeta* sp., *Microsetella gracilis*, *M. rosea*, *Corycaeus* sp., *Euchaeta marina* considered one of the most predatory of copepods, but no information was provided on the prey consumed. Deep sea adult copepods from the Sargasso Sea, *Euchaeta media*, *E. norvegica*, *E. tumidula*, *Euchaeta* sp., *Heterorhabdus abyssalis*, *H. compactus*, *H. norvegi* *ca, Euaugaptilus* sp., contained only crustacea remains in their guts (Harding 1974). The digestive tracts of *Pseudochirella polyspina* and *Scaphocalanus magnus* (from the slope waters off Nova Scotia) contained remains of Euphausiids and Copepoda.

EUPHAUSIIDS

Some species of Euphausiidae are omnivorous or carnivorous. The euphausid *Meganyctiphanes norvegica* was observed by Holt and Tattersall (1905) to feed upon fish larvae, Decapoda larvae, and Heteropoda. Euphausiids of the Gulf of Maine feed chiefly on phytoplankton, but *M. norvegica* were observed clasping bits of herring refuse from the packing factories (Bigelow 1926) and feeding on young fish and copepods; specimens were also found with masses of the diatom *Rhizosolenia* in their stomachs. *M. - norvegica* from Loch Fyne fed on *Calanus finmarchicus, Paraeuchaeta norvegica,* eucaridean species, other euphausiids, dinoflagellates, diatoms, fern sporangia, detritus, algae, and dipteran eggs. Cannibalism occurred when the proportion of euphausiids to other organisms in the plankton was high (Fisher and Goldie 1959).

Laboratory studies by Theilacker and Lasker (1973) on *Euphausia pacifica* and *Engraulis mordax* larvae, the most abundant Euphausiidae and Clupeidae, respectively, in the California Current region, appear to indicate that "the average number of anchovy larvae, juvenile euphausiids can process in a day catching, eating, digesting, and excreting is 10 or less. Increasing the prey concentration above this number had no effect on feeding in the volumes tested". The authors indicate that the results "suggest a constant feeding rate with food not a limiting factor". Theilacker and Lasker (1973) observed that the amount of feeding was not affected by the addition of more prey items and that increased larval activity decreased the ability of *E. pacifica* to capture anchovy larvae. *E. pacifica* exhibited a 60 % successful catch rate when dealing with one day (newly hatched) and 2 day-old larvae, but the capture rate diminished to 17 % for the three day-old larvae, and to 11 % for 4 day-old larvae. *E. pacifica* ingested few eggs in the laboratory, possibly due to either the eggs being unavailable to the euphausiids (eggs float at the surface of waters) or produce no vibrations in the water, which would atract euphausiids. Thailacker and Lasker (1973) calculated that the number of fish larvae

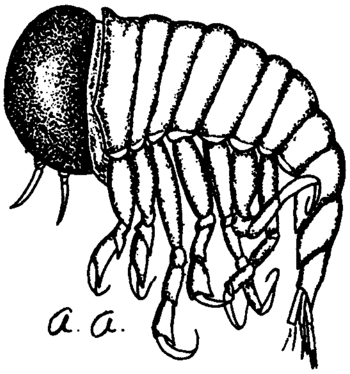
E. pacifica could consume daily per m^2 surface was 2.847, regardless of the presence of other zooplankters.

Chlorophyll pigments have been found in considerable amounts in the stomachs of such omnivorous or carnivorous euphausiid species as *Nematoscelis gracilis*, *N. microps*, *N. tenella*, *N. atlantica*, *N. difficilis* and *Euphausia pacifica*. Work on these findings will indicate these pigments may have some physiological role in the metabolism of euphausiids, or are totally removed from the system during defecation.

AMPHIPODS

The Amphipoda *Euthemisto* sp. prey upon small planktonic animals in the Gulf of Maine (Bigelow 1926); although it was not observed feeding on young fish, their stomachs have been found to be packed with copepods (mainly *Calanus* and *Temora*), pieces of other crustaceans, and fish eggs.

The observed food in Copepoda and other predatory Crustacea are listed in Table V.



AMPHIPODA: *Hyperoche medusarum* **Krøyer 1838**

TABLE V. OBSERVATIONS ON THE FOOD OF PELAGIC CRUSTACEA

CLASS: ORDER Species	Food	Author
CRUSTACEA: COPEPODA		
Acanthocyclops vernalis (Robertson and Gannon) 1981	*Notropis hudsoni* fish larvae	Harting, Jude and Evans, 1982
Acartia clausi Giesbrecht 1889 Sulcanus conflictus Nicholls 1944	*Gladioferens imparipes* and other Copepoda	Hodgkin and Rippindale 1971; Rippindale and Hodgkin, 1974
Acartia tonsa Dana 1849	*Scottolana canadiensis*, *Oithona colcarva*, *Eurythemora affinis*, *Acartia tonsa* nauplii (Copepoda)	Lonsdale et al, 1979.
Anomalocera pattersoni Templeton 1837	Copepoda, fish larvae	Lebour, 1922, 1925
Anomalocera sp. *Candacia* sp. *Centropages* sp. *Euchaeta* sp. *Labidocera* sp.	Copepoda	Gould, 1966
Calanus finmarchicus (Gunnerus) 1765 *Centropages typicus* Kroyer 1849 *Labidocera wollastoni* Giesbrecht 1892 *Temora longicornis* (Müller) 1792	Copepoda	Lebour, 1922
Calanus pacificus Brodsky 1948	Copepoda nauplii and copepodites; Phytoplankton	Landry, 1981
Candacia sp.	Sardine post-larvae	Karlovack, 1967
Candacia bradyi Scott 1904	Copepoda; Chaetognatha; other zooplankters	Wickstead, 1959
Candacia aethiopica Dana 1849	Fish larvae	Wickstead, 1965
Candacia columbiae Campbell 1929	Medusae; Crustacea	Gould, 1966
Corycaeus flaccus Giersbrecht 1891	Post larval fish *Electrona rissoi*	Regner, 1980
Cyclops bicuspidatus Thomasi-*Diacyclops thomasi* (Robertson and Gannon) 1981	*Morone saxalis* (striped bass), *M. americana* (white perch) larvae	Smith and Kernehan, 1981
	Alosa pseudoharengus and *Notropis hudsoni* fish larvae	Harting, Jude and Evans, 1982
Euaugaptilus sp.	Crustacea	Harding, 1974
Euchaeta elongata Esterly 1913	*Aetideus divergen*, *Pseudocalanus spp.*,	

TABLE V. Cont.

CLASS: ORDER Species	Food	Author
	Paracalanus parvus, *Oithona similis* (Copepoda); *Artemia* nauplii	Yen, 1982
	Merluccius productus (hake) eggs and larvae	Bailey and Yen, 1983
Euchaeta media Giesbrecht 1888	*Calanus*; other Crustacea	Brooks, 1970
Euchaeta norvegica Boeck 1872	*Acartia tonsa*, *Centropages hepatus* (Copepoda)	Conover, 1960
Euchaeta tonsa Giesbrecht 1895	*Calonus* nauplii, *Eucalanus* copepodites	Brooks, 1970
Idya furcata=*Tisbe furcata* (Baird) 1837	Fish larvae	Garstand, 1900
Labidocera jollae Esterly 1906 *Labodocera trispinosa* Esterly 1905 *Pontellopsis occidentalis* Esterly 1906	Fish larvae	Lillelund and Lasker, 1965
Labidocera trispinosa Esterly 1905	*Labidocera* nauplii, *Acartia tonsa*, *Paracalanus*, *Calanus* sp. (Copepoda)	Landry, 1978
Oithona nana Giesbrech 1892	Copepoda nauplii	Lampitt, 1978
Pleuromamma quadrangulata (Dahl) 1893	*Rhincalanus* nauplii	Brooks, 1970
Pseudochirella polyspina Brodsky 1950		
Scaphocalanus magnus (T. Scott) 1894	Euphausiidae	Harding, 1974
Sapphirina angusta Dana 1849	*Thalia democratica* (Tunicata)	Heron, 1973
Temora stylifera (Dana) 1849	*Gobius* sp. fish larvae	Regner, 1980
Tortanus discaudatus Thompson and Scott) 1897	*Calanus pacificus* (Copepoda)	Ambler and Frost, 1974
: EUPHAUSIIDAE		
Bentheuphausia amblyops G.O. Sars 1885	Copepoda; Medusae; Chaetognatha; Radiolaria; Tintinnidae; Phytoplankton	Tchindonova, 1959
Euphausia pacifica Hansen 1911	Eggs and fish larvae	Theilacker and Laske 1973
Megancyctiphanes norvegica (M. Sars) 1857	Young fish; Copepoda; Euphausiidae; Decapoda larvae; Heteropoda	Holt and Tattersal, 1905
	Fish; Copepoda; Diatomacea	Bigelow, 1926
	Calanus finmarchicus, *Euchaeta*	

TABLE V. Cont.

CLASS: ORDER Species	Food	Author
	norvegica, *Pseudocalanus elongatus*, *Acartia clausi*, *Oithona helgolandica* (Copepoda); Dinoflagellata; Silicoflagellata; Diatomacea	Macdonald, 1927
	Copepoda; other Crustacea; Dinoflagellata; Diatomacea; detritus	Fisher and Goldie, 1959
	Artemia salina (under laboratory conditions)	Heyrand, 1979
	Copepoda; *Chaetoceros atlanticus*; Phytoplankton	Sameoto, 1980
Nematobrachion sp.	Copepoda	Nemoto, 1972
Nematobrachion boopis (Colman) 1896	Copepoda	Roger, 1973
Nematobrachion sexpinosus Hansen 1911	Fish larvae; *Pleuromamma*, *Oithona* (Copepoda); Euphausiidae; Decapoda Crustacea; Chaetognatha	Hu, 1978
Thysanopoda aequalis Hansen 1905	Fish larvae; *Pleuromamma*, *Oithona* (Copepoda); Euphausiidae; Decapoda Crustacea; Chaetognatha	Hu, 1978
Thysanopoda cornuta Illig 1905	Copepoda; Medusae; Chaetognatha; Radiolaria	Tchindonova, 1959
	Fish larvae; Copepoda; Euphausiidae; Amphipoda; Decapod larvae; other Crustacea; Mysidacea; Chaetognatha; Radiolaria	Nemoto, 1977
Thysanopoda cristata G.O. Sars 1885	Copepoda	Roger, 1973
Thysanopoda egregia Hansen 1905	*Cyclothone* and other fish larvae; Copepoda; Euphausiidae; Mysidacea; Chaetognatha; pelagic Cephalopoda; Radiolaria	Nemoto, 1977
Thysanopoda monocantha Ortman 1893	Juvenile fish	Roger, 1973
	Fish larvae; *Pleuromamma*, *Oithona* (Copepoda); Euphausiidae; Decapod Crustacea; Chaetognatha	Hu, 1978
Thysanopoda orientalis Hansen 1910		
Thysanopoda pectinata Ortman 1893		
Thysanopoda tricuspidata Milne-Edwards 1837	Juvenile fish	Roger, 1973
Thysanopoda spinicaudata Brinton 1953	Fish larvae; Chaetognatha	Nemoto, 1977
Thysanoessa inermis (Krøyer) 1846	Copepoda; *Chaetoceros*	

TABLE V. Cont.

CLASS: ORDER Species	Food	Author
Thysanoessa inermis (Krøyer) 1846 (Cont.)	*atlanticus*; Plytoplankton	Sameoto, 1980
Thysanoessa raschii (M. Sars) 1840	Copepoda	Sameoto, 1980
:MYSIDACEA		
Mysidopsis bigelowi Tattersall 1926 *Neomyopsis americana* (S.I. Smith) 1873	*Acartia tonsa*, *Centropages* sp. *Pseudocalanus coronatus*, *Paracalanus crassirostris*, *Oithona colcarra* (Copepoda)	Fulton, 1982
Mysidopsis didelphys Norman 1906	Copepoda	Mauchline, 1970
Mysidopsis gibbosa G.O. Sars 1885	Copepoda; Dinoflagellata	Mauchline, 1970
Neomysis mercedis (Holmes)	*Eurithemora hirundoides*, (Harpacticoid Copepoda)	Siegfried and Kopache, 1980
:ISOPODA		
Rocinela belliceps pugettensis	Juvenile Pacific Salmon	Novotny and Mahnken, 1971
:CLADOCERA		
Podon intermedius Lilljeborg 1901	*Gobius* fish larvae	Regner, 1980
:OSTRACODA		
Conchoecia alata Müller 1906	Crustacea; Tintinnida; Radiolaria, Coccolithophorida; Foraminifera; Silicoflagellates; Diatomacea	Tchindonova, 1959
Conchoecia ametra Müller 1906	Crustacea, Tintinnida; Radiolaria, Coccolithophorida	Tchindonova, 1959
Conchoecia atlantica (Lubbock) 1865 *Conchoecia rhynchena* Müller 1906 *Conchoecia secernenda* Vavra 1906	Crustacea	Angel, 1970,1972
Conchoecia bispinosa Claus 1890 *Conchoecia echinata* Müller 1906	Crustacia; Diatomacea	Iles, 1961
Conchoecia borealis Sars 1865 *Conchoecia elegans* Sars 1865 *Conchoecia obtusata* Sars 1865	Crustacea	Elofson, 1941
Conchoecia skogsbergi Iles 1953	Coccolithophora; Foraminifera; Silicoflagellata; Diatomacea	Angel, 1970, 1972
Conchoecia spinirostris Claus 1874	Myctophid fish; Crustacea; Chaetognatha; Tintinnida; Radiolaria; Coccolithophorida; Foraminifera; Silicoflagelata; Diatomacea	Angel, 1970, 1972

TABLE V. Cont.

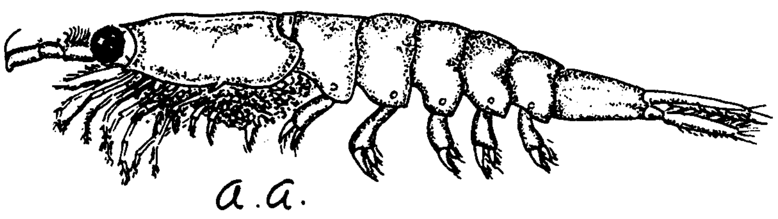
CLASS: ORDER Species	Food	Author
:AMPHIPODA		
Anomys sp.	Pteropoda; *P. pacifica* and other Amphipoda	Fukuchi, Yoshida, Hara, 1971
Calliopius sp.	*Clione limacina* (Pteropoda)	Fukuchi, Yoshida, Hara, 1971
Euthemismo sp.	Fish eggs; *Calanus*, *Temora* (Copepoda); Euphausiidae; Amphipoda; Decapod larvae	Bigelow, 1926
Euthemisto compressa = *Themisto gaudichaudi* Guérin-Méneville 1825	Copepoda; Euphausiidae	Conover, 1960
Hyperia galba (Montagu) 1813	Copepoda; Mollusca	Conover, 1960
Hyperoche medusarum (Krøyer) 1837	*Clupea pallasi* and flat fish larvae	Westernhagan and Rosenthal, 1976
Parathemisto gaudichaudi (Guerin) 1836	Copepoda; Euphausiidae; Diatomacea	Nemoto and Yoo, 1970
	Clupeidae, *Ammodytidae* fish larvae; *Acartia*, *Temora*, *Anomalocera*, *Calanus* (Copepoda); *Nyctiphanes cauchi*, *Thysanoessa inermis*, *T. raschii*, *Meganyctiphanes norvegica* (Euphausiidae); *Sagitta elegans* (Chaetognatha); Amphipoda; *Aequorea vitrina*, *A. aequorea* (Medusae) and larvae of other Invertebrates	Sheader and Evans, 1975
Parathemisto japonica Bovallius 1887= *Themisto japonica*	*Metridia* and other copepoda; Euphausiidae; Ostracoda; Medusae; Foraminifera; Radiolaria; Tintinnidae	Zhuravlev and Neyman, 1976
	Ammodytes personatus fish larvae	Yamashita and Joh (Communication)
Parathemisto libellula (Lichtenstein) 1822= *Themisto libellula*	Cod larvae	Lee, 1966
Parathemisto pacifica = *Themisto pacifica* (Stebbing) 1888	*Clione limacina* (Pteropoda); *P. pacifica* and other Amphipoda	Fukuchi, Yoshida, Hara, 1971
Pseudolibrotus sp.	Cod larvae	Lee, 1966
:DECAPODA		
Penaeus aztecus (Ives) 1891 *Penaeus brasiliensis* Latreille 1817 *Penaeus duorarum* Burkenroad 1939		

TABLE V. Cont.

CLASS: ORDER Species	Food	Author
Penaeus kerathurus Forskal 1775	Fish larvae; Eupahusiidae; Amphipoda; other Crustacea; Polychaeta; Echinodermata	Burukovskyi and Froyerman, 1973
Sergestes similis Hansen 1903	Copepoda; Euphausiidae; Tintiniidae	Tchindonova, 1959; Renfro and Pearcy, 1966
Sergestes lucens Hansen 1903	Fish; *Calanus pacificus*, *Paracalanus parvus*, *Euchaeta marina*, *Candacia* sp, *Oncaea venusta*, *Clausocalanus arcuicornis*, *Mondilla typica*, *Pareuchaeta ruselli*, *Pleuromamma gracilis*, *Oithona plumifera*, *Gaetanus Euchirella* sp.(Copepoda); Chaetognatha; Mollusca; Diatomacea	Omori, 1969
Sergestes japonicus Bate 1881	Fish; Copepoda; Chaetognatha	Tchindonova, 1959
Decapod larvae	Young fish; small Crustacea	Steuer, 1910; Bigelow, 1926
Homarus americanus Milne-Edwards 1837 (larvae)	Other Crustacea	Weldon and Fowler, 1890
Homarus vulgaris Linnaeus 1758 (larvae)	Decapod larvae; Copepoda	Lebour, 1922
Palinurus vulgaris = *Palinurus elephas* Fabricius 1787	*Lophius piscatorius* larvae; Copepoda	Lebour, 1925
Squilla desmaresti= *Meiosquilla desmaresti* (Risso) 1816	*Temora longicornis* (Copepoda); Crustacea	Lebour, 1925
Phyllosoma of *Jasus lallandei*	Hydromedusae	Williamson (in Thomas, 1963)
Phyllosoma of *Scyllaridae*, *Scyllarus americanus* (S.I. Smith) 1869, *Scyllarus chacei* Holthuis 1960	*Liriope tetraphylla* (Medusae)	Shojima, 1963; Herrnkind et al 1976
Hymenodora frontalis Rathbum 1902	Fish larvae; Copepoda; Other Crustacea; Medusae; Chaetognatha; Tintinnidae	Tchindonova, 1959
Hymenodora glacialis S.I. Smith 1886	Copepoda; Amphipoda; Ostracoda; other Crustacea; Medusae; Polychaeta; Chaetognatha; Radiolaria	Tchindonova, 1959
Gennadas borealis Rathbum 1902	Copepoda; other Crustacea; Medusae; Chaetognatha;	

TABLE V. Cont.

CLASS: ORDER Species	Food	Author
	Radiolaria; Tintinnidae	Tchindonova, 1959
Physetocaris microphthalma	Copepoda; Ostracoda; Chaetognatha; Tintinnidae	Tchindonova, 1959
Acanthephyra sp.	Fish; other Crustacea	Tchindonova, 1959
Pasiphaea sp.	Fish; other Crustacea; Tintinnidae	Tchindonova, 1959



EUPHAUSIACEA: *Euphausia pacifica* **Hansen 1911**

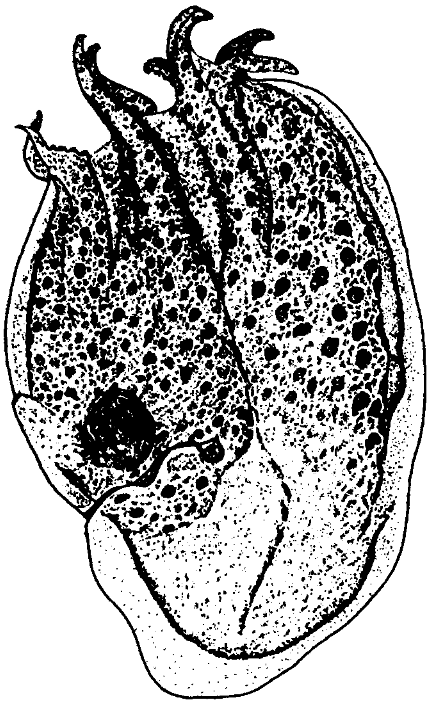
Information on the prey off of Pelagic mollusca appears compiled in Table VI.

CEPHALOPODS

Cephalopoda predation on young fish can have a drastic effect on some fisheries. Johnson (1942) described the behavior of *Paraoctopus apollyon* feeding on small fish and shrimps in Friday Harbor. The octopus obtained food by gliding forward with the tentacles extended in a canopy under which fish and shrimps are captured; contracting the tentacles, the catch is forced slowly into the mouth. The octopus repeated this process in a rapid succession, making 15 of these hauls in twenty minutes.

The squid *Ommatostrephes todaratus* was observed by Hjory and Dahl (1900) as reported in Murray and Hjort (1912), pursuing the herring in Norwegian waters. Those authors explained that these squids "generallly appear in enormous shoals coming from the open ocean in pursuit of the herring shoals on which they gorge themselves greedly". The coincidence of great quantities of *Ommatostrephes* sp. together with several hydromedusae (Lucas and Henderson 1936) coincided with the breakdown of the Shetland herring fishery during 1931.

Octopus vulgaris, *Loligo vulgaris* and *Sepia officinalis hierredda* appeared in great abundance (Cort and Pérez-Gândaras 1973) in the Sahara Bank during 1966-1967 in a region about 50m deep, off the Spanish Sahara. The Sparids *Dentex dentex*, *D. canariensis*, *Pagrus pagrus* and other fish used to be extremely abundant in that region, but this abundance has decreased drastically since 1960 due to overfishing. Coincident with this condition, the population of cephalopods in the region has increased due to lack of natural predators. Thus the abundant cephalopod population will be preying on the young and larvae of Sparidae, preventing these populations from regaining strength. Examination of stomach contents of cephalopods in this area indicated that they feed on young Pleuronectidae, Sparidae, Mollusca, and Crustacea. However, in the far offshore adjacent region off Spanish Sahara, large Sparidae, *Trachurus trachurus*, and *Scomber scombrus* were abundant and preyed on Cephalopoda larvae. In this manner, the cephalopod populations are controlled by the predatory activity of Sparidae and other fish populations. In the Sahara Bank region the depleted Sparidae populations do not harm the Cephalopoda larvae, and so the great number of squids and Octopoda devour the young and larval fish occurring in the region. It appears that the fish population can only be limited by scarcity of food and by the fishery. A cephalopod fishery has started to develop in the Sahara region, and it is expected that it will help to restore the predatory/prey equilibrium. Similarly, absence or scarcity of *Panulirus regius* (spiny lobster) off Sahara (Maigret 1976) coincided with abundance of *Octopus vulgaris* and *Sepia officinalis*.



a.a.

CEPHALOPODA, OCTOPODA: *Alloposus mollis* **Verrill 1880**

TABLE VI. OBSERVATIONS ON THE FOOD OF PELAGIC MOLLUSCA

CLASS: ORDER Species	Food	Author
GASTROPODA: HETEROPODA		
Heteropod spp.	Fish larvae; Ctenophora; *Phronima* sp. (Hyperiidae); Salps (Tunicata)	Tesch, 1949
Cardiapoda placenta (Lesson) 1830	Fish larvae; *Phyllirhoe atlanticum* (Nudibranchia) *Firoloida desmaresti* (Heteropoda); *Salpa cylindrica* (Tunicata)	Hamner et al, 1975
Pterotrachea coronata Forskal 1775	Physonectae bracts (Siphonophorae)	Hamner et al, 1975
Carinaria cristata f. japonica Spoel 1972	*Myctophidae* fish larvae; *Nematoscelis difficilis*, *Euphausia recurva* (Euphausiidae); *Hyperia* sp., *Phronima Sedentaria* (Amphipoda); *Conchoecia spinosa* (Ostracoda); *Muggiaea atlantica*, *Stephanomia bijuga*, *Nectodroma* sp., and other Siphonophorae; *Tomopteris elegans* (Polychaeta); Chaetognatha; *Limacina*, *Carinaria japonica* (Pteropoda); *Atlanta gaudichaudi* (Heteropoda); *Thalia democratica*, *Doliolum denticulum* Thaliacea); *Oikopleura* sp. (Appendicularia)	Seapy, 1980
Carinaria sp.	*Sardina ocellata* fish eggs and other fish larvae; Crustacea; Scyphozoa Medusae	Graham, 1955
Carinaria japonica Okutani 1955	*Paracalanus parvus*, *Calanus* sp., *Oithona plumifera* (Copepoda); Euphausiid larvae; juvenile Amphipoda; *Evadne* sp. (Cladocera); *Sagitta nagae* (as *S. bedoti*) (Chaetognatha); *Thalassiotrix longisima* (Diatomacea)	Okutani, 1961
: GYMNOSOMATA		
Clione limacina (Phipps) 1774	*Limacina* (*Spiratella*) *helicina*, *Spiratella retroversa* (Pteropoda)	Conover and Lalli, 1974
CEPHALOPODA: OCTOPODA		
Octopus vulgaris Cuvier 1797	Fish larvae; Euphausiidae; other Crustacea; Cephalopoda	Burukovskyi and Froyerman, 1973; Cort and Pérez-Gándaras, 1973
Paraoctopus apolyon = *Octopus apollyon* (Berry) 1912	Fish larvae; Decapod Crustacea	Johnson, 1942
: DECAPODA		
Illex coindeti (Verany) 1837		

TABLE VI. Cont.

CLASS: ORDER Species	Food	Author
Todarotes sagittatus (Lamarck) 1979 *Loligo pealei* Lesueur 1821	Larvae and juvenile fish; Euphausiidae; crabs and other Crustacea; Cephalopoda	Burukovskýi and Froyerman, 1973
Loligo opalescens Berry 1911	*Scomber japonicus* larvae; adult *Artemia* (Crustacea)	Hurley, 1976
	Fish; Copepoda; Euphausiidae; Amphipoda; Cumacea; Mysidacea; Ostracoda; other Crustacea; Gastropoda; Polychaeta; Cepahlopoda; Radiolaria	Karpov, 1979
Loligo vulgaris Lamarck 1822 *Sepia officinalis hierredda* Rang 1837	Fish larvae; Crustacea; Mollusca	Cort and Pérez-Gándaras, 1973
Symplectoteuthis (*Stenoteuthis*) *oualaniensis* (Lesson) 1830	Young fish; Crustacea; Cephalopoda	Filipova, 1974
	Myctophidae fish, flying fish and other fish; Crustacea; Squids	Neis, 1977
Symplectoteuthis luminosa Sasaki 1915 *Ommastrephes bartrami* (Lesueur) 1821 *Ommastrephes pteropus* (Steenstrup) 1885 *Todarotes angolensis* Adam 1962	Young fish; Crustacea; Cephalopoda	Filipova, 1974

OTHER PREDATORY ZOOPLANKTERS

Predation by fish is not considered in this work. Other predatory planktonic organisms are the pelagic worms. Little is known on the feeding characteristics of these animals, and the few observations on the food of pelagic Polychaeta appear compiled in Table VII.

TABLE VII. FOOD OF PELAGIC WORMS

CLASS: ORDER Species	Food	Author
ANNELIDA: POLYCHAETA		
Tomopteris sp.	Young herring; *Agalma elegans* (Siphonophorae)	Akesson, 1962
	Chaetognatha	Uschkov, 1972
Tomopteris helgolandica Greeff 1879	*Clupea harengus* and other fish larvae; Chaetognatha; Unicellular organisms	Lebour, 1923
Typhloscolex mulleri Bush 1851	Chaetognatha	Fernández Alamo (personal communication)

SUMMARY

The data gathered on the food of carnivorous zooplankters, together with observations on the failure of year-class of fish coincident with great abundance of predatory planktonic organisms, indicate that it is paramount for fisheries research to systematically analyze plankton, as food as well as plankton predators. Studies should be increased on the feeding of various fish larvae and carnivorous zooplankters, together with determinations on the voracious capacity of each of the plankton predator species related to the fish larvae. Larval fish and their basic food are greatly utilized by the planktonic carnivores, a factor which contributes to the source of mortality directly by predation, and indirectly by competition for food when the predators consume food of larvae available in the ocean. Continuous monitoring by oceanic surveys on the spawning region of fish and other invertebrates of commercial interest should be accomplished together with the qualitative and quantitative distribution of food and predatory zooplankters.

The study of long and short-term fluctuations in the abundance and distribution of zooplankters (Glover et al 1961) appears to hold a considerable promise to detect and analyze physico-chemical-biological changes in the environment, and consequently in the commercial fish stocks, as well as the effect of predation on the abundance of recruits to integrate the fish stocks. Once this multiple facies of research is properly achieved (Hardy 1956) "can we safely think of trying to predict the effect of such changes in the fishery".

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