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NOTE

Predation on fish larvae by *Physalia physalis*, the Portuguese man of war*

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ABSTRACT: Larval fish comprised 70 to 90% of the prey types found in stomach contents of the neuston siphonophore *Physalia physalis* (Suborder Cystonectae). Specimens at one station were estimated to consume an average of 120 fish larvae daily, about 60 % of the larvae that were available at 0 to 5 m depth. Only soft-bodied prey were captured (fish and fish larvae, cephalopods, chaetognaths, leptocephalus larvae); this may be related to the structure of nematocysts found in cystonect siphonophores.

Predation has long been recognized as a potentially major cause of mortality in larval fish (e.g. Hunter, 1981), yet only a few studies have made quantitative estimates of predation *in situ* (Möller, 1980; Purcell, 1981a; Bailey and Yen, 1983). Analyses of gut contents have shown that fish larvae constitute only a small fraction of the diets of many soft-bodied zooplankters, including ctenophores (Fraser, 1970), chaetognaths (Pearre, 1976), scyphomedusae (Larson, 1978), siphonophores in the suborders Calycophorae and Physonectae (Purcell, 1981b), and hydromedusae (Purcell, unpubl.). In contrast, larval fish comprised 100 % of the natural diet the siphonophore *Rhizophysa eysenhardti* (suborder Cystonectae) (Purcell, 1981a). *Physalia physalis,* another cystonect siphonophore, is found world-wide at the surface in tropical and subtropical waters (Woodcock, 1956), and is a widely-recognized coelenterate due to its conspicuous blue float and its dangerous sting. On the US Gulf Coast, the public is warned of its presence at beaches daily in broadcasts of the National Weather Service at Corpus Christi, Texas. Observations of *P. physalis* eating fish 4 to 10 cm long, including herring, flying fish, and silversides, date back to 1864 (summarized in Wilson, 1947; additionally Lenhoff and Schneiderman, 1959; Mackie, 1960; Phillips et al., 1969), yet other reports state that the diet consists of small crustaceans (e.g. Lane, 1960). Here I show that fish larvae comprised 70 to 90 % of the prey found in specimens of *P. physalis.* Data indicate that cystonect siphonophores are the most specific invertebrate predators of fish larvae known.

In order to establish quantitatively the diet of *Physalia physalis,* specimens were collected using dip nets during December 4 to 11, 1981 (0900 to 1400 h) in the Gulf of Mexico off Pensacola, Florida at 29°30′ N, 85°06′–85°46′ W, and off Galveston, Texas at 29° N, 94° W–28° N, 93° W, and during February 19 to 24, 1982 (1000 to 1100 h), and May 23 to 24, 1982 (0000 to 0630 h) in the Sargasso Sea at approximately 30° N, 77°–78° W and 34° N, 73° W. The specimens, which had floats 1 to 20 cm in length with 10 to several hundred gastrozooids, were immediately preserved in 10 % formaldehyde solution, and examined for consumed prey. Any distended gastrozooids were dissected and examined for relatively undigested prey; then each siphonophore was homogenized for < 30 s at low speed of a Polytron (Brinkmann Instruments), and the tissue debris was searched for prey remains at 12 X magnification using a dissecting microscope.

Undigested prey remains included the spherical eye lenses of fish and fish larvae, the distinctive eye lenses, beaks, and pens of cephalopods, and the jaws of chaetognaths. The numbers of fish and cephalopod eye lenses were divided by 2 to give the numbers of prey consumed. A total of seven crustaceans were found in 4 (10 %) of the dissected *Physalia physalis,* but these were within the stomachs of the larger fish contained in the gastrozooids, and probably were food of the fish and not of the siphonophores. Fish and fish larvae clearly predominated in the diet of *P. physalis,* constituting 92.6 % of 662 prey items in 40 specimens

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Table 1. *Physalia physalis.* Prey removed from the gastrozooids; 32 specimens from Gulf of Mexico; 8 specimens from Sargasso Sea

Prey type	% of specimens containing prey type		% of total prey items		Length of prey (mm)	Prey per specimen (no.)
	Gulf	Sargasso	Gulf	Sargasso		
Fish and fish larvae	93.8	100.0	94.1	73.5	2–~40	1–120
Cephalopods	37.5	46.7	5.9	6.1	3.5–25 (pen)	1–13
Chaetognaths	0	62.5*	0	14.3	~35	1–2
Leptocephalus larvae	0	25.0*	0	6.1	~80	1

* Nighttime samples

examined (Table 1). The distribution of the diameters of lenses recovered from *P. physalis* gastrozooids, compared to the relations between lens diameter and standard length of intact fish larvae, shows that approximately 90 % of the captured fish were larvae between 2 and 20 mm in length (Fig. 1). Some fish beyond the larval stage also were captured.

The daily predation rate of *Physalia physalis* can be approximated from the equation

$$\text{Ingestion} = \text{P} \times \frac{24\ \text{h}}{\text{D}} \quad (1)$$

where P = average number of prey in each siphonophore; D = digestion time in hours. This calculation, which assumes no diurnal periodicity in feeding activity or prey availability, probably is overly simplified, but was used because adequate data on diurnal patterns were lacking. A total of 511 fish larvae were found in 15 *P. physalis* collected in daytime off Galveston, Texas. The time between ingestion and egestion of 15 mm fish larvae (Fam. Sciaenidae) averaged 7 h ± 2 (s. d.) for *P. physalis* at 21 °C in the laboratory (n = 35 measurements, J. E. Purcell, unpubl.). Thus an average of about 120 fish larvae were consumed daily by each *P. physalis*. The abundance of *P. physalis* averaged 1/200 m^{-2} at the sea surface (J. E. Purcell, unpubl.), and the abundance of fish larvae averaged 1/5 m^3 at 0 to 5 m depth (D. E. Hoss, pers. comm.). *P. physalis* tentacles may extend 10 m in length (Mackie, 1960), however the tentacles reach only shallow depths due to wind-induced motion (Woodcock, 1944). The above data indicate that about 60 % of the fish larvae at 0 to 5 m depth could have been consumed daily by *P. physalis* at this location. These data are of necessity very approximate, and are meant only to indicate that *P. physalis* could be a major cause of mortality in larval fishes.

These and earlier data (Purcell, 1981a, b) indicate that all of the 4 species examined out of 5 recognized cystonect species (Totton, 1965) consume primarily fish larvae, and only soft-bodied prey. This implies selectivity by the siphonophores, because data from plank-

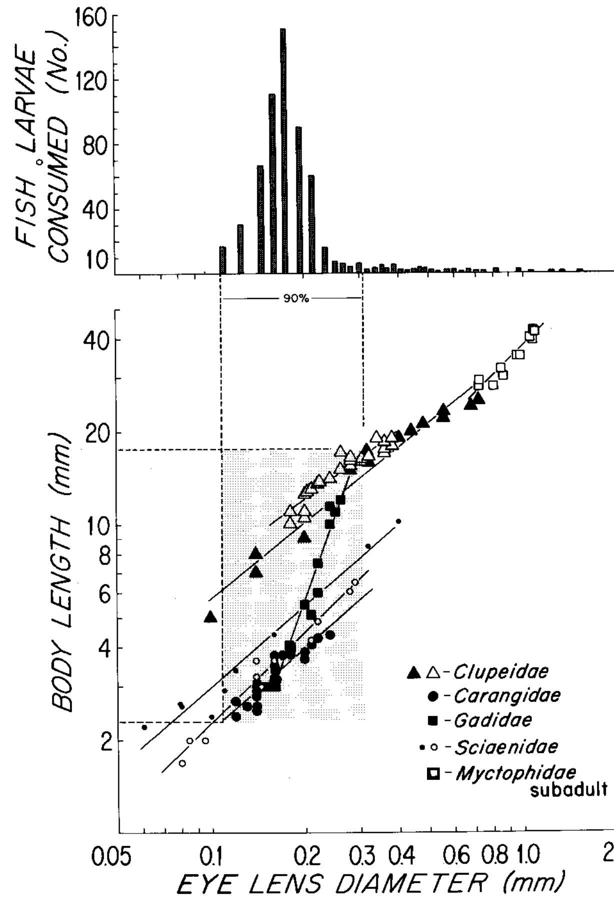

Fig. 1. *Physalia physalis.* Distribution of eye lens diameters of fish larvae found in gastrozooids (top), compared with lens diameter to body length relations of intact fish larvae and subadults (bottom). Regressions of isolated lens diameter against standard length (measured from intact fish collected from surface waters of the Gulf of Mexico and preserved in 5 % formaldehyde) are as follows: Fam. Clupeidae, *Brevoortia* spp. (menhaden): ▲, log y = 0.75 log x + log 39.73, r = 0.98; △, log y = 0.82 log x + log 37.37, r = 0.94 (larvae collected at 2 different locations and years); Fam. Carangidae: log y = 0.97 log x + log 21.07, r = 0.99; Fam. Sciaenidae, *Leiostomus xanthurus* (spot) ●: log y = 0.88 log x + log 16.49, r = 0.93; *Sciaenops ocellata* (red drum) ○: log y = 0.86 log x + log 21.42, r = 0.98; Fam. Gadidae: ■ log y = 2.79 log x + log 501.7, r = 0.97; Fam. Myctophidae, *Gonicthyes cocco* subadults: □ log y = 0.99 log x + log 37.55, r = 0.96

ton net tows clearly show that crustaceans of comparable size and activity were more abundant than fish larvae in the environments sampled (Purcell, 1981a, b; D. E. Hoss, P. B. Ortner, and J. C. Stepien, pers. comm.), and the larval fish diets of cystonects contrast markedly with the primarily crustacean diets of other siphonophores collected concurrently (Purcell, 1981b).

The process of prey selection by cystonect siphonophores could be attributed to 3 characteristics of the nematocysts, the structures responsible for prey capture in these non-visual predators: (1) Nematocyst discharge is thought to require a combination of chemical and mechanical stimuli (Mariscal, 1974). No experiments have tested the sensitivities of cystonect nematocysts; the possibility that crustaceans do not present the stimuli necessary for discharge cannot be judged based on present evidence. (2) The toxins of cystonect nematocysts may not be effective to crustaceans; however, toxin extracted from *Physalia physalis* killed crabs and fish when injected (Lane and Dodge, 1958). (3) The structure of nematocyst threads may not permit cystonects to capture hard-bodied prey. The tentacles of siphonophores of the suborders Calycophorae and Physonectae have 4 to 5 kinds of nematocysts, most of which adhere to and entangle crustacean prey; in contrast, cystonect siphonophores have 1 kind of nematocyst, which penetrates soft-bodied prey, but appears not to entangle or pentrate crustaceans (Purcell, 1984). Thus, differences in prey capture among siphonophores appear to be related to the structure of the nematocyst threads.

Cystonect siphonophores are the most selective invertebrate predators of larval fish known. *Physalia physalis* was shown to consume large numbers of fish larvae daily. The importance of *P. physalis* as a cause of mortality in larval fish probably depends on yearly and seasonal variations in abundance and distribution of both predator and prey (Purcell, unpubl. results). *P. physalis* and other cystonects could potentially influence the size of harvestable fish stockes in areas supporting major commercial fisheries, such as the Gulf of Mexico.

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