

For Phil
with best wishes,
Jenny

PREDATION ON FISH EGGS AND LARVAE BY PELAGIC CNIDARIANS AND CTENOPHORES

Jennifer E. Purcell

ABSTRACT

Predation is recognized as a major source of mortality in fish eggs and larvae. In this review, I consider pelagic cnidarians and ctenophores as an assemblage of predators that is distinct from other types of planktonic predators in that they do not actively attack prey organisms. Three basic approaches have been used to study their predation on larval fishes—laboratory observations, analysis of prey found in the gastric cavities of the predators, and modelling of predator-prey interactions. Laboratory experiments have identified many gelatinous zooplankters that can consume fish larvae. Fish larvae comprise 90–100% of the diets of cystonect siphonophores, but only small percentages of the natural diets of other gelatinous predators. High in situ predation rates have been found in the few studies, made in near-shore environments, that combined gut content analysis, digestion times, and abundances of larvae and their predators. I discuss the characteristics of pelagic cnidarians and ctenophores that make them of great potential importance as predators and food competitors of early stages of fish, and the characteristics of larval fishes that affect their vulnerability to these predators. The amount of predation is determined by the sizes and the spatial and temporal overlap of predator and fish larva populations. Future studies must quantify feeding rates on fish eggs and larvae over several consecutive years, and consider the combined effects of all potential predators.

Mortality in the egg and larval stages of marine fishes is extremely high, but the causes of mortality are not well documented. Starvation of the fish larvae and predation on them are suspected to be the two major causes of mortality (Hunter, 1981; 1984). Many laboratory and some field studies suggest that starvation is critically important; however, some recent field studies suggest that for some species it may not be the most important factor (Methot and Kramer, 1979; O'Connell, 1980; Ellersten et al., 1981). Also, starvation cannot account for mortality that occurs during the egg and yolk sac stages.

Studies of predation of larval fishes are few, probably because of the uncertainties of extrapolating laboratory results to field conditions, and because of the difficulties in collecting in situ data on predation. Recent interest in predation effects on larval fish populations has been stimulated in part because of the failures of starvation to account for the mortality observed. Hunter (1984) reviewed much of the literature on all predators of fish eggs and larvae. In the present review, I compile the scattered data on pelagic cnidarians and ctenophores as predators of fish eggs and larvae, and discuss the approaches to this research. These gelatinous zooplankters form an assemblage of predators that do not actively attack their prey, unlike the other predators of larval fishes—euphausiids (Theilacker and Lasker, 1974), hyperiid amphipods (Sheader and Evans, 1975; von Westernhagen and Rosenthal, 1976; von Westernhagen et al., 1979), copepods (Lillilund and Lasker, 1971; Bailey and Yen, 1983), chaetognaths (Kuhlmann, 1977), or fish predators (Daan, 1976; Hunter and Kimbrell, 1980). Recent research indicates that cnidarians and ctenophores are important predators on the early stages of fishes.

PREDATION ON FISH EGGS AND FISH LARVAE

Information on cnidarians and ctenophores as predators of fish eggs has accumulated incidentally from studies on their diets. In all but one case, fish eggs comprised a small portion of the prey consumed (Table 1). Only in the neustonic hydrozoan, *Velella lata*, did fish eggs constitute a large percentage of the prey. Huge numbers of *V. velella* are stranded along the western North American coast in the spring (Larson, 1980), and occur in abundance elsewhere. They could be important consumers of neustonic fish eggs.

A large number of pelagic cnidarians and some ctenophores have been reported to eat larval fishes (Table 2). I will discuss the basic approaches used in these studies below.

Laboratory Studies.—The most common approach in identifying predators of larval fishes has been to offer larvae to potential predators in laboratory containers. Some of these studies only state that predation occurred, and others give the numbers or proportions of the larvae that were consumed (Table 2). Almost invariably, when fish larvae were confined with medusae, the larvae were eaten. The only exceptions to this were the hydromedusae *Obelia* spp., *Proboscoidactyla flavicirrata* (Arai and Hay, 1982), and *Sarsia* sp., which killed but did not eat the larvae (Bailey and Yen, 1983), and the ctenophore *Pleurobrachia* sp. (Bailey and Yen, 1983). Other studies showed that species of *Sarsia* and *Pleurobrachia* did consume other species of larvae (Table 2); the results of Bailey and Yen (1983) are probably due to the small size of the predators used in the experiments (Bailey, pers. comm.).

Such studies are useful in identifying predators that are capable of consuming larval fishes, and those that are not. Laboratory observations are made under artificial conditions where both the predators and prey could be influenced by the effects of collection and laboratory conditions. Predators of larval fishes in laboratory experiments should not be assumed to be important in situ without supporting field data on the spatial and temporal overlap of predator and prey populations, their abundances, and the frequency of predation events. Laboratory data were confirmed by field observations of predation by Plotnikova (1961) and Sveshnikov (1963), and combined with field data on fish larva and predator abundances by Sveshnikov (1963) and Arai and Hay (1982).

In several laboratory studies of gelatinous zooplankters feeding on crustacean prey, predation rates measured at known prey concentrations have been combined with predator and prey abundances in situ to estimate the ecological impact of predation (Reeve, 1977 reviews this approach). This approach has not been used with gelatinous predators feeding on larval fishes because it would be particularly difficult to obtain meaningful feeding rates in the laboratory due to the large size and activity of the predators, the reactivity of fish larvae to their surroundings, and the low natural densities of most species.

The experimental approach used by Bailey (1984) and Bailey and Batty (1983; 1984) quantified behavioral parameters of the scyphomedusa *Aurelia aurita*, and its success at capturing several species of fish larvae at different sizes and densities. The mathematical model they proposed predicts predation rate based on capture success (related to medusa size, larval size and species) and encounter rate (related to prey density, medusa and larval sizes and swimming speeds). These are the only attempts to date to model jellyfish predation on larval fishes. Although this model was not designed for application to the field (Bailey, pers. comm.), similar models could be combined with field data on medusa and larval fish abundances

Table 1. Pelagic cnidarian and ctenophore predators of fish eggs

	Predator	Prey	Consumption	Methods	Location	Reference
Cnidaria						
Scyphozoa						
Rhizostomae	<i>Phyllorhiza punctata</i>	NI	incidental	dip, guts	Puerto Rico	Larson, 1978
	<i>Rhopilema verrilli</i>	NI	incidental	dip, guts	Delaware Bay, USA	Larson, 1978, pers. comm.
	<i>Stomalophus meleagris</i>	NI	NQ	dip, guts	North Carolina, USA	Larson, 1978, pers. comm.
Semaestomeae	<i>Aurelia aurita</i>	Sciaenidae	1.4%*	dip, guts	Gulf of Mexico	Purcell, 1983b
		NI	5-10%*	dip, guts	Puerto Rico	Larson, 1978
	<i>Chrysaora melanaster</i>	Sciaenidae	1%*	dip, guts	Gulf of Mexico	Purcell, 1983b
		NI	NQ	guts	Trivandrum, India	Nair, 1954
	<i>Cyanea lamarcki</i>	NI	NQ	lab	England	Delap, 1901
	<i>Pelagia noctiluca</i>	NI	av. 2.5 per medusa	dip, guts	Puerto Rico	Larson, 1978
Hydrozoa						
Chondrophora	<i>Porpita porpita</i>	NI	NQ	beachstranded, guts	Shirahama	Bieri, 1970
	<i>Velella lata</i>	jack mackerel	48%*	net and dipped, guts	California, USA	Bieri, 1961
Hydroida	<i>Aequorea victoria</i>	anchovy	3%*			
		Pleuronectidae	3%*	dip, guts	British Columbia, Canada	Purcell, 1984b
	<i>Eirene ceylonensis</i>	NI	NQ	guts	Trivandrum, India	Nair, 1954
	<i>Helgicirrha malayensis</i>	NI	NQ	guts	Trivandrum, India	Nair, 1954
	<i>Liriope tetraphylla</i>	NI	in 40% of medusae	net, guts	Belize	Larson, 1982
	<i>Phialidium hemisphaericum</i>	NI	NQ	guts	Trivandrum, India	Nair, 1954

Table 1. Continued

	Predator	Prey	Consumption	Methods	Location	Reference
	<i>Phialidium</i> sp.	hake	4 of 5 eggs consumed	lab	Washington, USA	Bailey and Yen, 1983
		sprat	1	net, guts	Plymouth, England	Lebour, 1923
	<i>Sarsia</i> sp.	hake	3 of 5 eggs consumed	lab	Washington, USA	Bailey and Yen, 1983
	<i>Steenstrupia rubra</i>	NI	1	net, guts	Plymouth, England	Lebour, 1923
Ctenophora						
Tentaculata						
Cydippida	<i>Pleurobrachia bachei</i>	NI	0.13%*	net, guts	California, USA	Hirota, 1974
	<i>P. pileus</i>	plaice	>6 in 33 specimens	net, guts	English Channel	Lebour, 1923
		NI	0-1.0%	net, guts	Scottish North Sea	Fraser, 1970
	<i>P. sp.</i>	hake	4 of 5 eggs consumed	lab	Washington, USA	Bailey and Yen, 1983
Lobata	<i>Mnemiopsis leidyi</i>	NI	1%*	net, guts	Chesapeake Bay, USA	Burrell and Engel, 1976
	<i>M. mccradyi</i>	Sciaenidae	0.2%*	dip, guts	Gulf of Mexico	Purcell, 1983b

Legend for Tables 1 and 2

NI = not identified;

NQ = not quantified;

* = % of number of prey in gastric cavities;

net = predators collected in a plankton net;

jar = predators collected individually in a jar by SCUBA divers;

dip = predators collected individually in surface waters;

lab = observations made in the laboratory;

guts = prey identified in gut contents of predators.

Table 2. Pelagic cnidarian and ctenophore predators of fish larvae

	Predator	Prey	Consumption	Methods	Location	Reference
Cnidaria						
Cubozoa	<i>Carybdea marsupialis</i>	<i>Jenkinsia</i>	15%*	nightlight dip, guts	Puerto Rico	Larson, 1976; 1978
	<i>C. rastoni</i>	NI	NQ	dip, guts	Puerto Rico	Larson, 1976; 1978
	<i>Chiropsalmus quadrumanus</i>	small bumpers and harvestfish, larval sciaenids	in 10% of medusae	trawl, guts	Gulf of Mexico	Phillips and Burke, 1970 Phillips et al., 1969 Larson, 1976; 1978
	<i>Ch. quadrigatus</i> and <i>Chironex fleckeri</i>	NI	NQ	—	Australia	Barnes, 1966
Scyphozoa						
Rhizostomae	<i>Lorifera lorifera</i>	<i>Sillgo</i>	2 in single specimen	guts	Trivandrum, India	Nair, 1954
	<i>Rhopilema hispidum</i>	<i>Engraulis</i> sp.	NQ	guts	Trivandrum, India	Nair, 1954
Semaeostomeae	<i>Aurelia aurita</i>	various	NQ	lab	Plymouth, England	Lebour 1922; 1923
		various	NQ	lab	England	sum. in Gudger, 1934
		cod, flounder	115 in one month	lab	Newfoundland, Canada	Fraser, 1969
		NI	NQ	dip, guts	Puerto Rico	Larson, 1978
		herring	1.6–15.9/medusae/day	dip, guts	Kiel Bight, Germany	Moller, 1980; 1984
		herring	10 of 10 consumed	lab	British Columbia, Canada	Arai and Hay, 1982
		herring	6.64/hour maximum	lab, model	Oban, Scotland	Bailey and Batty, 1983
	<i>Chrysaora hysoscella</i>	NI	0.6%*	dip, guts	Gulf of Mexico	Purcell, 1983b
		various	NQ	lab	Plymouth, England	Lebour, 1922; 1923
	<i>Ch. melanster</i>	<i>Caranx kalla</i> , <i>Equula</i> sp.	many, 239 in one	guts	Trivandrum, India	Nair, 1954

Table 2. Continued

	Predator	Prey	Consumption	Methods	Location	Reference
	<i>Ch. quinquecirrha</i>	small harvest fish, bumpers, larval sciaenids	in 5% of medusae	dip, guts	Gulf of Mexico	Phillips et al., 1969
		blennies	a few	guts	Lafayette River, Va., USA	Larson, 1978 Feigenbaum and Kelly, 1984
	<i>Cyanea capillata</i>	NI	NQ	lab, guts	various	Gudger, 1934 Larson, 1978
		various	in 13% of medusae	lab	Murmansk, USSR	Plotnikova, 1961
		flatfish	6 in 17 days	lab	Newfoundland, Canada	Fraser, 1969
	<i>C. sp.</i>	hake	5 of 5 consumed	lab	Washington, USA	Bailey and Yen, 1983
	<i>Desmonema quadrichaudi</i>	epibenthic fish	incidental	dip, guts	Antarctica	White and Bone, 1972
	<i>Linuche unguiculata</i>	NI	NQ	field obs., lab	Haiti	in Gudger, 1934
	<i>Pelagia noctiluca</i>	NI	incidental	dip, guts	Puerto Rico	Larson, 1978
	<i>Phacellophora camtschatica</i>	NI	NQ	dip, guts	Oregon, USA	Larson, 1978, pers. comm.
		cod herring	1.2%* 28.9%*	dip, guts	British Colum- bia, Canada	Purcell, in prep.
Hydrozoa						
Chondrophora	<i>Porpita porpita</i>	NI	10%*	beach stranded, guts	Shirahama	Bieri, 1970
	<i>Velella lata</i>	one saury, NI	incidental	net and dipped, guts	California, USA	Bieri, 1961
Hydroida	<i>Aequorea victoria</i>	various	NQ	lab	Plymouth, Eng- land	Lebour, 1923
		herring	38 of 40 consumed	lab	British Colum- bia, Canada	Arai and Hay, 1982
		herring, flatfish, rockfish, scul- pins, cod, sti- chaeids	0-47%* depending on larval abundance	dip, guts	British Colum- bia, Canada	Purcell, 1984b, in prep.
	<i>Bougainvillia multitentaculata</i>	herring	20 of 20 consumed	lab	British Colum- bia, Canada	Arai and Hay, 1982
	<i>B. superciliaris</i>	sand eel	1	net, guts	Plymouth, Eng- land	Lebour, 1923

Table 2. Continued

Predator	Prey	Consumption	Methods	Location	Reference
<i>Cosmetira pilosella</i>	wrasse, cottids	NQ	lab	—	Gudger, 1934
<i>Eirene ceylonensis</i>	NI	NQ	guts	Trivandrum, India	Nair, 1954
<i>Eutima</i> (= <i>Saphenia</i>) <i>gracilis</i>	various	NQ	lab	Plymouth, England	Lebour, 1923
<i>Eutonina indicans</i>	herring	20 of 20 consumed	lab	British Columbia, Canada	Arai and Hay, 1982
<i>Gonionemus murbachii</i>	<i>Fundulus</i>	NQ	lab	Woods Hole, Massachusetts	Gudger, 1934
<i>Helgicirrha malayensis</i>	NI	NQ	guts	Trivandrum, India	Nair, 1954
<i>Laodicea undulata</i>	blennies	several	lab	Plymouth, England	Lebour, 1923
		5 in 6 days	lab	Newfoundland, Canada	Fraser, 1969
<i>Leuckartiara nobilis</i>	NI	22 in 26 days	lab	Newfoundland, Canada	Fraser, 1969
<i>Liriope tetraphylla</i>	NI	NQ	guts	Trivandrum, India	Nair, 1954
<i>Melicertum octostatum</i>	NI	35 in 4 days	lab	Newfoundland, Canada	Fraser, 1969
<i>Mitrocomella polydiademata</i>	herring	incidental	net, guts	British Columbia, Canada	Purcell, in prep.
<i>Obelia</i> sp.	whiting, clupeoid	occasional	net, guts	Plymouth, England	Lebour, 1923
<i>Obelia</i> spp.	herring	0 of 10 consumed	lab	British Columbia, Canada	Arai and Hay, 1982
<i>Phialidium hemisphericum</i>	various, clupeoids, cottids	15 of over 70 prey	lab, net and guts	Plymouth, England	Lebour, 1922; 1923
	NI	NQ	guts	Trivandrum, India	Nair, 1954
<i>P. gregarium</i>	herring	12 of 12 consumed	lab	British Columbia, Canada	Arai and Hay, 1982
<i>P. sp.</i>	hake	5 of 5 consumed	lab	Washington, USA	Bailey and Yen, 1983
<i>Proboscoidactyla flavicirrata</i>	herring	0 of 20 consumed	lab	British Columbia, Canada	Arai and Hay, 1982

Table 2. Continued

	Predator	Prey	Consumption	Methods	Location	Reference
Siphonophora Calycophorae	<i>Rathkea octopunctata</i>	herring, sprat, sardine	10 of 38 prey	net, guts	Plymouth, England	Lebour, 1922; 1923
	<i>R. punctata</i>	3 spp. flatfish, capelin	NQ	lab	Murmansk, USSR	Plotnikova, 1961
	<i>Sarsia princeps</i>	NI	19 by 2 specimens	lab	Newfoundland, Canada	Fraser, 1969
	<i>S. tubulosa</i>	capelin, flatfish	NQ	guts and lab	Murmansk, USSR	Plotnikova, 1961
		herring	20 of 20 consumed	lab, field obs.	British Columbia, Canada	Arai and Hay, 1982
	<i>S. (=Coryne) tubulosa</i>	herring	est. 10% larvae eaten/day	lab	White Sea	Sveshnikov, 1963
	<i>S. sp.</i>	hake	1 of 5 consumed, 4 killed	lab	Washington, USA	Bailey and Yen, 1983
	<i>Staurophora mertensi</i>	NI	8 in a few hours	lab	Newfoundland, Canada	Fraser, 1969
	<i>Steenstrupia rubra</i>	<i>Ammodytes</i> , clupeoid	incidental	net, guts	Plymouth, England	Lebour, 1923
	<i>Stomotoca atra</i>	herring	2 of 2 consumed	lab	British Columbia, Canada	Arai and Hay, 1982
	<i>Tiaropsis multicirrata</i>	capelin, flatfish	NQ	lab	Murmansk, USSR	Plotnikova, 1961
	<i>Tima formosa</i>	sand eels	2-3 per medusa	net, guts	Massachusetts Bay	in Gudger, 1934
	<i>Turris pileata</i>	whiting, cottid	incidental	net, guts	England	Lebour, 1923
	<i>Rosaca cymbiformis</i>	NI	present, 0-2.4%*	jar, guts	Sargasso Sea, Gulf Stream, California, USA	Purcell, 1981b
	<i>Sulculeolaria quadrivalvis</i>	NI	0-1.6%*	jar, guts	Sargasso Sea, Gulf Stream, California, USA	Purcell, 1981b
	<i>Bathypphysa sibogae</i>	NI	only prey seen	jar, guts	Sargasso Sea	Purcell, 1981b
	<i>Physalia physalis</i>	NI	93%*	dip, guts	Northern Gulf of Mexico, USA Gulf Stream, Sargasso Sea	Purcell, 1984c

Table 2. Continued

Predator		Prey	Consumption	Methods	Location	Reference
Physonectae		anchovies	> 100 in 1 specimen	dip, guts	Gulf of Mexico	Phillips et al., 1969
		various	NQ	dip, guts	Plymouth, England	sum. in Wilson, 1947
	<i>Rhizophysa eysenhardti</i>	various reef and midwater	100%*	jar, guts	Gulf of California, Mexico	Purcell, 1981a; 1981b
	<i>R. filiformis</i>	NI	only prey seen	jar, guts	Sargasso Sea	Purcell, 1981b
	<i>Agalma elegans</i>	NI	0-18%*	jar, guts	Sargasso Sea, Gulf Stream	Purcell, 1981b
	<i>A. okeni</i>	NI	present	jar, guts	Sargasso Sea	Purcell, 1981b
	<i>Apolemia uvaria</i>	NI	0-1%*	jar, guts	California, USA	Purcell, 1981b
	<i>Athorybia rosacea</i>	NI	0-56%*	jar, guts	Sargasso Sea	Purcell, 1981b
Ctenophora Tentaculata Cydippida	<i>Forskalia</i> sp.	NI	present	jar, guts	Sargasso Sea	Biggs, 1977
	<i>Pleurobrachia bachei</i>	herring	31%*	net, guts	British Columbia, Canada	Purcell, in prep.
	<i>P. pileus</i>	NI	<0.1%	net, guts	Scottish North Sea	Fraser, 1970
		flounder	incidental	net, guts	Wadden Sea, Netherlands	van der Veer and Zijlstra, 1982
	<i>P. sp.</i>	plaice, herring hake	> 33 in 43 specimens 0 of 5 consumed	net, guts lab	English Channel Washington, USA	Lebour, 1923 Bailey and Yen, 1983
	<i>P. spp.</i>	herring	up to 45% of herring in tow	net, guts	British Columbia, Canada	Stevenson, 1962
	<i>Bolinopsis (=Bolina) infundibulum</i>	angler fish	NQ	lab	Plymouth, England	Lebour, 1925
	<i>B. infundibulum</i>	herring	NQ	dip, guts	British Columbia, Canada	Purcell, in prep.
	<i>Mnemiopsis mccradyi</i>	red drum (sciaenid)	0.4%*	dip, guts	Gulf of Mexico	Purcell, 1983b
	<i>M. leidyi</i>	NI	0.4%*	net, guts	Chesapeake Bay, USA	Burrell and Engel, 1976
Lobata	<i>Ocyropsis</i> spp.	NI	NQ	lab	Sargasso Sea	Harbison et al., 1978
		NI	incidental	jar, guts	Sargasso Sea	Purcell, pers. obs.

Legend as in Table 1.

and size distributions to predict the predation impact of the medusae. Any such model must be used with caution due to possible laboratory effects on behavior.

Field Studies.—Fish larvae comprise a small portion of the prey found in the gastric cavities of numerous pelagic cnidarians and some ctenophores from field collections (Table 2). Fish larvae are eaten by most, if not all, cubomedusae, and sennaeostome scyphomedusae. Little published information exists on the diets of hydromedusae; fish larvae may be consumed incidentally (Table 2), but other zooplankters predominate in the diets (McCormick, 1969; Zelickman et al., 1969; Larson, in prep.; Purcell, in prep.). Fish larvae were found only occasionally in calyophoran siphonophores (2 of 14 species examined), and more frequently in physonecks (5 of 7 species examined) (Purcell, 1981a); however, larval fish comprised 90–100% of the diets of cystonect siphonophores (4 of 5 recognized species were examined). The diets of lobate and tentaculate ctenophores generally contained only a small proportion of larval fish. In many reports on predator gut contents, there is no information on predator, fish larva, or zooplankton abundance. Therefore selection by the predator cannot be determined, nor can the magnitude of the predation be estimated.

Consumption of larval fish often is presented as a percentage of total number of prey items in the gastric contents (Table 2). Gut content data must be combined with digestion times of fish larvae and other prey to determine the proportion of fish larvae in the diets, and the number consumed per unit time per predator. Times required for digestion of fish larvae are available for the hydromedusae *Rathkea octopunctata*, *Sarsia tubulosa*, and *Tiaropsis multicirrata* [14–19.5 h, 3–3.5 h, and 18 h, respectively (Plotnikova, 1961)], and *Aequorea victoria* [2–4 h (Purcell, in prep.)], for the siphonophores *Rhizophysa eysenhardti* [3–7 h (Purcell, 1981b)], *Physalia physalis* [av. 7 h (Purcell, 1984c)], and *Forskalia* spp. [4–7 h (Purcell, 1983a)], and for the scyphomedusa *Aurelia aurita* [2 h (Fraser, 1969); 3.5–9.5 h (Möller, 1980)]. Fish larvae are large relative to most other zooplankton, and may represent a greater contribution to the diet than suggested by the percentage of prey items.

Measures of predator abundance are essential for estimating the impact of predators on larval fish populations. Surprisingly few studies give quantitative data on cnidarian or ctenophore abundances, and only a few of those have a connection with ichthyoplankton research: Sveshnikov (1963), Fraser (1970), Hay and Adams (1975), Alvarino (1977; 1980), Arai and Hay (1982), Arai and Mason (1982), Frank and Leggett (1982), Möller (1979; 1980; 1984), Purcell (1981b; 1984c; in prep.), and van der Veer and Zijlstra (1982).

To estimate the extent of predation on larval fish populations in nature, the mean number of larvae in the gastric cavities of each predator species, the time required for digestion at in situ temperatures, and the abundances of predators and prey must be determined. In studies where these criteria have been met, substantial predator impacts on fish larva populations were found: Möller (1980) calculated that *Aurelia aurita* consumed 2–5% of the yolksac herring per day; Purcell (1981b) calculated that *Rhizophysa eysenhardti* consumed 28% of the fish larvae available each day; and Purcell (1984c) estimated that 60% of the fish larvae could have been consumed by *Physalia physalis* in one location. Work in progress assesses the impact of a variety of gelatinous predators on larvae at herring spawning grounds in British Columbia (Purcell, 1984b; in prep.).

In in situ studies, the predators' gut contents must not be contaminated by net feeding, and predator and prey abundances must be determined accurately. Diel activity and distribution patterns also must be considered. Purcell (1981b; 1984b) found diel differences in predation to be important, however Möller (1980) found

no diel differences in predation. Gelatinous predators and fish larvae occurred in very high numbers in nearshore environments where studies have demonstrated substantial predation in situ on fish larva populations (Möller, 1980; 1984; Purcell, 1981b; 1984c; in prep.). Low rates of predation probably occur at typical larval fish densities of 1–100/100 m³, and would be difficult to demonstrate using microscopic gut analysis methods. However, the application of immunological techniques (Boreham and Ohiagu, 1978; Feller, 1982) to identify fish larvae in predators' guts would facilitate such work because many more specimens could be processed, highly-digested prey identified, and additionally, predators that masticate their prey and species living at depth could be studied.

Some studies have revealed an inverse relationship between the abundances of potential predators and fish eggs or larvae (Hattori, 1962; Alvarino, 1980; Möller, 1979; 1980; 1984; Frank and Leggett, 1982). Without concomitant information on predation, such as supplied by Möller (1980; 1984), the inverse relationship cannot be assumed to result from predation. The alternative explanations are numerous, for example, occurrence in different water masses (Frank and Leggett, 1982), different depth distributions, or different behavioral patterns of the predators and prey.

PELAGIC CNIDARIANS AND CTENOPHORES AS PREDATORS

Pelagic cnidarians and ctenophores are distinguished from nearly all other predators of fish larvae and eggs [except *Noctiluca*, Hattori (1962)], because they do not actively attack their prey. They are nonvisual predators that also do not detect the prey items by their movements as do chaetognaths (Kuhlmann, 1977) and copepods (Bailey and Yen, 1983), or by other sensory modes [the ctenophore *Beroë* (Class Nuda) chemically locates its ctenophore prey (Swanberg, 1974)]. Most feed with tentacles, which in the cnidarians contain toxic penetrating and entangling nematocysts, and in the cydippid ctenophores contain adhesive colloblasts. The effectiveness of the various predators in feeding upon larval fish is related to the different characteristics of these microscopic structures; siphonophores primarily entangle hard-bodied (crustacean) prey and penetrate soft-bodied prey (including fish larvae) (Purcell, 1984a); ctenophores, which cannot penetrate prey, consume mostly crustaceans (Fraser, 1970; Hirota, 1974). The most effective predators of larval fishes may be those that can penetrate soft-bodied prey; the mucus surface on larvae may protect them from adhesive tentacles. Conversely, the chorions of fish eggs may better protect them from penetration than from adhesion.

The lobate ctenophores, unlike the preceding tentaculate predators, move mouth first through the water, and prey are drawn by a ciliary current into the inner surface of their lobes, where they are captured either in mucus or by muscular action of the lobes (Harbison et al., 1978). This mode of feeding probably is most effective on eggs and early larvae that could not escape from the feeding current.

The gelatinous predators form two groups that differ in how they encounter prey. Lobate ctenophores, cubomedusae, most scyphomedusae, and many hydromedusae swim and the water currents generated by their motion bring prey into the tentacles for capture (Larson, 1978; Mills, 1981). The siphonophore *Physalia physalis*, the Portuguese man of war, is moved passively through the water by wind (Woodcock, 1944). Thus, one group of predators consists of species that move through the water while encountering prey. In contrast, cydippid ctenophores and all siphonophores other than *Physalia* feed while drifting with the water with their tentacles spread, and do not feed during the brief bouts of swim-

ming which spread the tentacles. These predators rely on the prey to swim into contact with their tentacles. Prey encounter is different for these two predator groups, and this could affect the types of prey captured. Gerritsen and Strickler (1977) proposed a mathematical model based on optimal encounter probabilities that predicted that "cruising" (moving) predators should eat slow moving prey and "ambush" (stationary) predators should eat rapidly swimming prey. It is not known how the various swimming patterns affect capture of larval fishes by these diverse planktonic predators.

Many pelagic cnidarians, especially the Scyphozoans, are much larger than fish larvae. Each predator potentially is able to eat a large number of larvae daily, unlike other planktonic predators that are similar in size to fish larvae and only can consume relatively few daily [amphipods, copepods, or chaetognaths, von Westernhagen and Rosenthal (1976); Bailey and Yen (1983); and Kuhlmann (1977), respectively]. Siphonophores and chondrophores have numerous "stomachs," each of which can contain more than one larva (Purcell, 1981b). Most of the hydromedusae are very small with small gastric cavities (*Aequorea victoria* is one exception), and probably could consume only a few larvae daily (Fraser, 1969, Table 2). Ctenophores, especially cydippids like *Pleurobrachia*, have small gastric cavities that probably can contain only a few larvae simultaneously. Many of these predators have rapid digestion rates and gut contents could be exchanged quickly.

Gelatinous zooplankters, in general, have low percentage composition of organic matter, which can lead to rapid growth, maturation, and population increases under favorable conditions (Kremer, 1976; Reeve et al., 1978; Purcell, 1981b; 1982). In scyphomedusans and many hydromedusans, population size depends on the budding rate of medusae from the benthic stages, and may be related to food levels. Growth of the medusae can be very rapid [hydromedusae—Rees (1975); Arai (1980); Purcell (unpubl.), and scyphomedusae—Hamner and Jenssen (1974); Hernroth and Grondahl (1983)], and also may be related to food levels. Many pelagic cnidarians and ctenophores occur in epidemic numbers, usually seasonally and in nearshore environments—ctenophores (Kremer and Nixon, 1976; Reeve et al., 1978; Reeve, 1980), scyphomedusae (Hedgpeth, 1954; Russell, 1970; Yasuda, 1970; Möller, 1979; 1980; 1984; Hamner and Hauri, 1981; Vucetic, 1982; Purcell, 1983b; Feigenbaum and Kelly, 1984), chondrophorans (Larson, 1980), hydromedusae (Zelickman, 1969; Zelickman et al., 1969; Purcell, in prep.), and siphonophores (Rogers et al., 1978; Purcell, 1981b).

The gelatinous zooplankters ingest their prey whole, making prey identification easier than for crustaceans, which masticate the prey. This advantage is offset by difficulties in collecting these predators and working with them in the laboratory. Standard plankton nets often destroy the specimens, and the abundances, or even presence, of fragile ctenophores cannot be determined (Harbison et al., 1978; Stretch, 1982). Special collecting techniques such as those described by Hamner (1975) and Reeve (1977) are recommended. The large size, active swimming, and tentacular feeding of many of the gelatinous predators make them especially difficult to study under typical laboratory conditions. Large containers in the laboratory or enclosures in situ may provide adequate experimental environments (Reeve, 1977).

VULNERABILITY OF FISH EGGS AND LARVAE

Spawning and hatching must occur when annual planktonic predator populations are abundant if their predation is to be important. Many temperate fish

species spawn in late winter or early spring, which is before most predators become abundant. However, the relative timing of spawning and plankton abundances can vary annually and result in the eggs and larvae encountering different assemblages and sizes of predator populations, which can drastically affect the intensity of predation (Möller, 1984; Purcell, in prep.). Very few data document the yearly variation in zooplankton, fish larva, and predator populations.

Some fish species having pelagic eggs or larvae spawn in large groups, which may present planktonic predators with a superabundance of food. Larval densities of capelin and Pacific herring, which have intertidal demersal eggs, can be 100–1,000/m³ for a short time after hatching (Frank and Leggett, 1982; Purcell, in prep.). Many types of gelatinous predators can consume numerous prey if available, and only reach satiation at extremely high prey densities (Reeve et al., 1978; Frank and Leggett, 1982; Bailey and Batty, 1983; Purcell, in prep.). Some fish species spawn nocturnally, presumably reducing visual predation on the eggs. This would not reduce feeding by nonvisual gelatinous predators, most of which are active day and night.

The duration of the egg and larval stages determines how long they are vulnerable to the various planktonic predators. Herring have attached eggs, and are planktonic only as larvae. Egg stages last from less than 24 h in some warm-water fish to more than 2 weeks in cold-water species. The lengths of the larval stages vary similarly with climate. Large egg size, potentially an effective deterrent to small planktonic predators, would not inhibit predation by most gelatinous zooplankters.

The size and activity of the larvae at hatching may determine their vulnerability to planktonic predators. Large larvae, herring for example, may be immune to the smaller predators. Swimming abilities and associated escape responses develop quickly in fish larvae; evidence from field and experimental work suggests that the yolk sac and early post-yolk sac larvae are most vulnerable to medusae (Möller, 1980; 1984; Bailey, 1984; Bailey and Batty, 1983; 1984; Bailey and Yen, 1983; Purcell et al., submitted¹). Different species of larvae have different vulnerabilities to predators, related to larval length and escape speed (Bailey, 1984; Bailey and Batty, 1984).

Ample evidence suggests that the diets of larval fishes (Wailles, 1936; Cohen and Lough, 1983; Govoni et al., 1983) and the diets of gelatinous predators (Fraser, 1970; Burrell and Van Engel, 1976; Purcell, 1981a; 1982; 1983b; 1984b) contain many of the same prey items. Possible competition between jellyfish and larval fishes for food has been suggested many times (Plotnikova, 1961; Sveshnikov, 1963; Fraser, 1970; Burrell and Van Engel, 1976; Möller, 1979; 1980; Purcell, 1983b). In order for jellyfish to affect fish larvae through competition, jellyfish and fish larvae must consume the same zooplankton prey, and jellyfish must limit zooplankton stocks to levels detrimental to feeding by larval fishes. The reduced food levels could cause starvation of the larvae, reduce growth rates and increase the period that the larvae are vulnerable to predators, or weaken the larvae and decrease their abilities to avoid or escape predators. Some experimental evidence indicates that unfed larvae are more vulnerable to predation (Bailey and Yen, 1983; Bailey, 1984; Bailey and Batty, 1983; 1984; Purcell et al., submitted¹).

¹ Purcell, J. E., T. D. Siferd and J. B. Marliave. Vulnerability of larval herring (*Clupea harengus pallasii*) to capture by the jellyfish *Aequorea victoria*. Mar. Biol. submitted.

CONCLUSIONS

Fish eggs and larvae are incidental prey in the diets of most pelagic cnidarians and ctenophores. These predators can occur in epidemic numbers, and each can consume numerous prey daily. Their potential importance as predators on early stages of fish, and as competitors for food, is great. The relative importance of starvation and predation as causes of mortality in larval fishes cannot be determined by studying starvation or predation independently, because the effects of food limitation contribute to larval vulnerability to predation. In order to determine the extent of predation, it is critical to quantify feeding rates on fish eggs and larvae. In situ gut content analysis, in combination with digestion rates and data on predator and prey populations is the most direct method. Laboratory techniques also may be useful if combined with field data. To date, single predator species have been studied, however the combined effects of all potential predators in an area is important to total mortality. Yearly variation in predation may be substantial, and is related to variations in the sizes and temporal and spatial overlap of predator and larval fish populations. The impact of predation on larvae on their subsequent adult population size has not been examined. Large annual differences in mortality due to predation reasonably could be expected to correlate with differences in year-class strength.

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DATE ACCEPTED: April 18, 1985.

ADDRESS: College of Oceanography, Oregon State University, Corvallis, Oregon 97331.