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The Propagation of Cod *Gadus morhua* L.

INFERENCES REGARDING PREDATION ON THE EARLY LIFE STAGES OF COD
AND OTHER FISHES

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ABSTRACT

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Little information exists on the predation on the early life stages of marine fish in general and even less on cod. Thus the approach used in this review was to infer the predatory processes that may be significant in the early life history of cod using the general literature on the predators of marine fish eggs and larvae. The mortality of cod during the embryonic period is high indicating a high rate of predation and predation may continue to be the dominant source of mortality in later larval stages. The known predators of eggs and larvae are discussed as are intrinsic and extrinsic factors that affect vulnerability to predation. Recommendations are made for future research.

INTRODUCTION

The objective of this review was to characterize the process of predation on cod eggs and larvae in the sea. Little information exists on the predation on the early life stages of marine fish in general and even less on cod. Thus, the approach I have used in this review was to infer the predatory processes that may be significant in the early life history of cod using the general literature on the predators of marine fish eggs and larvae.

Predation, starvation, and certain abiotic effects (wave action, UV radiation, temperature and salinity changes) have been proposed as possible sources of the great mortality experienced by pelagic marine fish eggs and larvae in the sea. During the embryonic period (egg and yolk-sac stages) only abiotic effects and predation are sources of mortality because the embryo subsists on yolk. Abiotic effects occasionally may be important in the embryonic stages since these stages are the most susceptible to physical damage. Moribund eggs and larvae have been observed in plankton catches but these reports have been discounted in recent years and attributed to failure to wash plankton nets thoroughly between tows (May, 1974). Soleim's (1942) observation of a large number of dead or dying yolk-sac herring larvae, presumably killed by changes in temperature and salinity, appears to be an authentic case as the proper precautions were taken to avoid contamination from previous net hauls (Wiborg, 1976). Nevertheless, changes in temperature and salinity sufficient to kill large numbers of eggs or larvae in the open sea are probably rare, and experimental evidence indicates that other abiotic causes of mortality are unlikely. For example, pelagic eggs appear to be highly resistant to damage from wave action (Pommeranz, 1974) and significant damage from UV radiation seems to require sustained exposure for days in the upper 5 m of the water column, which seems unlikely in well mixed surface waters (Hunter et al., 1982). Thus the mortality during the

embryonic period is good evidence for the existence of predation as a cause of natural mortality.

The mortality rates of embryonic marine fishes are often very high indicating high rates of predation. Mortality rates (z) of cod eggs from the North Sea range from 0.03 to 0.41 over 11 years and averaged about 0.25, implying a loss rate of about 22% per day (Daan, 1979, 1981). Considering the long incubation period of cod eggs (15-18 days at 5-7°C) these rates seem surprisingly high, being comparable to those of temperate northern anchovy which has only a 3 day incubation period (Table 1). Thus in the North Sea typically 98% of the cod eggs are probably consumed by predators before they hatch.

TABLE 1

Mortality rates of pelagic eggs and larvae in percent per day.

Fish	Year(s)	Stage	Mean	Range	Reference
Cod	1968-1977	Egg	22	3-33	Daan, 1976
Plaice	1947-1977	Egg	7	2-13	Harding et al., 1978
Plaice	1947-1971	Yolk-sac larvae	10	3-22	Harding et al., 1978
Anchovy	1980-1983	Egg	21	13-36	Unpub. data SWFC ¹
Anchoveta	1981	Egg	-	67	Santander et al., 1983
Sole	1969-1970	Egg	-	42-65	Riley, 1974

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The range of mortality rates for cod eggs and for those of other species indicates that predation rates vary greatly from year to year, and such variation might account for the observed variations in recruitment, particularly if these predation rates persisted over subsequent life stages. Some evidence exists that the high predation rate encountered in the egg stage persists through the embryonic period, i.e., until the development of a functional eye and jaw and the onset of feeding. In plaice and northern anchovy the mortality rates of eggs do not differ much from that of yolk-sac larvae indicating no sharp transition in rates during the embryonic period (Harding et al., 1978; Hunter, 1982).

After the onset of feeding the argument for predation as the principle source of mortality is less compelling because starvation may also play an important role. All laboratory studies on pelagic fish larvae such as cod, herring, anchovy, and plaice (Hunter, 1981) indicate that they are highly vulnerable to starvation at the onset of feeding owing to their small size, short sighting distance for prey, slow cruising speeds during the search for food, low capture success, and high food density requirements. On the other hand, new studies in large semi-natural enclosures seem to indicate that predation is the major source of mortality in the sea. In such enclosures, 3-10% of cod larvae survived through metamorphosis at food densities equivalent to those encountered in the sea (Ellertsen et al., 1981). Since these survival rates are much greater than those of larvae in the sea, the absence of predators in the enclosure appears to be the reason for the remarkably high survival.

New tools now exist which can be used to determine if the apparent vulnerability to starvation inferred from laboratory work translates into a high rate of natural mortality. In fact, identification of starvation as a cause of mortality in the sea is now easier to assess

quantitatively than the effects of predation, because starving larvae can now be accurately identified using histological criteria (Theilacker, 1978; O'Connell, 1980), and slow growth of larvae can be detected using daily increments on larval otoliths (Methot and Kramer, 1979). Such measurements hold the key to determining the relative importance of starvation and predation (by the difference between starvation mortality and total mortality) during the post-embryonic phase of larval life. Sea studies using these new techniques are just beginning (no data exist on cod) but present evidence indicates predation plays the dominant role in larval mortality (O'Connell, 1980; Methot and Kramer 1979).

These lines of evidence seems to indicate that predation during the embryonic period is high and variable, and it probably remains the principle source of mortality throughout the rest of the early life history of cod. The latter conclusion is of course speculation, although the results of the enclosure studies seem quite convincing in this regard. Proof will await assessment of the rates of starvation in the sea.

KINDS OF PREDATORS

Crustacea and chaetognaths

Consumption of marine fish larvae by copepods, euphausiid shrimp, hyperiid amphipods and chaetognaths has been studied in small (0.2-3.5 litre) containers in the laboratory. For example, in the California Current region, 11 species of calanoid copepods, and euphausiid shrimp were capable of capturing or fatally injuring yolk-sac anchovy larvae (Lillelund and Lasker, 1971; Theilacker and Lasker, 1974), and to the north in Dabob Bay, Washington, the calanoid *Euchaeta elongata* and several species of crab larvae have

been identified as predators of yolk-sac hake larvae (Bailey and Yen, 1983). Additional species of calanoids observed preying on larvae are mentioned by Lebour (1925). Laboratory studies seem to show that small carnivorous arthropods (calanoid copepods, amphipods and euphausiids) can attack and kill significant numbers of marine yolk-sac fish larvae if the concentrations of larvae are suitably high (Table 2). Consumption of fish larvae by chaetognaths has been frequently inferred from examination of preserved specimens taken in plankton tows (Lebour 1922, 1923; Alvarino 1980). On the other hand, laboratory experiments on two species (*Sagitta elegans* and *S. setosa*) seem to indicate that they are not important predators. *Sagitta* required a 24h starvation period before consuming any larval fish, they strongly preferred copepods to larvae, and they ate only first feeding larvae, as younger larvae (yolk-sac) and older ones were not eaten (Kuhlmann, 1977). Clearly, more information is needed on larval predation by chaetognaths.

Few of the small invertebrate predators studied to date seem to be effective predators of pelagic fish eggs. Laboratory tests indicate that neither *Euphausia* (Lillelund and Lasker, 1971; Bailey and Yen, 1983), *Sagitta* (Kuhlmann, 1977) nor crab larvae (*Parathemisto* and others) and shrimp larvae, (Bailey and Yen, 1983) are significant predators of pelagic fish eggs. Presently, the only pelagic crustacean identified as a predator of pelagic eggs is the amphipod *Calliopius* (Bailey and Yen, 1983), but very few of the vast number of pelagic crustacea have been considered.

Only the yolk-sac stage of marine fish larvae appears to be vulnerable to these small carnivorous arthropods. These predators appear not to be able to consume significant numbers of pelagic eggs and the number of fish larvae attacked drops rapidly at the end of the yolk-sac period. For example, the number of yolk-sac anchovy larvae killed by *Labidocera* females declined from 16 newly hatched anchovy

Table 2. Results of various laboratory studies on the predators of marine fish larvae.

Predator species	Prey species	Relative life stage vulnerability ^a		Maximum prey attacked n/l per day	Minimum prey density and attack rate n/l per day	Natural incidences of predation on stomachs with prey	Projected effects	References
		egg	yolk-sac					
Copepods	anchovy	0	1	8.6	1.4	---	---	Lillelund & Lasker, 1971 Lillelund & Lasker, 1971 Bailey & Yen, 1963
		0	1	4.2	1.4	---	---	
		0	1	10-25	2.0	31-43	---	
Euphasiid shrimps	anchovy	1	0.2	11-14	5-6	---	---	Theilacker & Lasker, 1974
		"low"	1	10 ^c	6 ^c	---	---	
Amphipods	herring	---	X	100	10	24-58	---	Westernhagen & Rosenthal, 1976; Westernhagen, 1976
Chaetognaths	sprat, anchovy	0	0	N.E. ^e	7.5	---	---	Kuhlmann, 1977
		0	1.0 ^d	N.E. ^e	---	---	---	
Jellyfish	herring	---	X	9	0.5	9-40 ^g	Accounts for 4.4% of larvae per day	Müller, 1980 Bailey & Betty, 1983
		X	---	7/hour ^f	1/hour ^f	---	---	
Fish	anchovy	X	---	10	1	42	Accounts for 32% of the natural mortality of eggs	Hunter & Kimbrell, 1980b Hunter & Dorr, 1982
		---	X	---	---	---	---	
<i>Clupea harengus patuxi</i>	herring	---	X	---	---	---	---	Hourston et al., 1981
		---	X	14,000	2,000	---	---	

^a 1 = maximum vulnerability, other numerical values are relative to maximum; X = only the indicated life stage was examined.

^b Number attacked decreased when alternate prey present.

^c Number attacked unaffected by presence of alternate prey.

^d Larvae older than 4 days escaped.

^e Density had no effect (= N.E.) between 7.5 - 150 larvae/.

^f Hourly rates given because medusae began to satiate after ingesting 5-6 larvae.

^g 56-50 mm dia. Jellyfish.

larvae per day to about 7 per day for 168-h-old larvae.

The presence of an alternative prey (copepods) depresses the rate of larval predation in the carnivorous copepods (Lillelund and Lasker, 1971; Bailey and Yen, 1983) but apparently not in euphausiid shrimps. For example, at equal densities of *Pseudocalanus* and hake larvae the presence of *Pseudocalanus* depressed the predation rate of *Euchaeta* on hake larvae by 60% (Bailey and Yen, 1983). Since copepods, rather than larval fish dominate most plankton assemblages, this is an important effect. The predation rates observed in the laboratory probably are seldom realized in the sea because the larval fish densities are much lower in the sea and more numerous alternative prey exist for the predators. Yolk-sac herring are a possible exception as they appear to achieve remarkably high densities in the sea (20 larvae/litre at the surface; Westernhagen and Rosenthal, 1976).

Field evidence also indicates that, hyperiid amphipods and carnivorous calanoid copepods consume significant numbers of fish larvae although specific identification of remains of larvae in the stomachs is uncertain. Hyperiid amphipods co-occur with yolk-sac herring larvae for 40 days in Departure Bay, British Columbia, and remains of fish larvae are the most abundant item in their guts (Westernhagen and Rosenthal, 1976; Westernhagen, 1976). Fish larvae, especially herring and *Ammodytes*, make up 23% of the food of the hyperiid amphipod *Parathemisto gaudichaudi* during April and June in the North Sea (Sheader and Evans, 1975). Fish larvae (presumably yolk-sac stages of hake) occurred in 30 to 43% of the *Euchaeta* stomachs examined by Bailey and Yen (1983).

Field evidence from freshwater lakes indicates that marine cyclopoid copepods might be as important predators as the predacious calanoids. Adult female freshwater lake cyclopoid copepods (*Diacyclops thomasi* and *Acanthocyclops vernalis*) are reported to feed on alewife (*Alosa*

pseudoharengus) larvae; 1-4% of alewife larvae (typically 3-5 mm) taken in plankton tows had attached cyclopoid copepods; and all were taken at night, indicating that the larvae may be more vulnerable when less active (Hartig et al., 1982). Similarly, Brewer et al., (1983) found the cyclopoid copepod (*Corycaeus anglicus*) attached to 5% of white croaker larvae (*Genyonemus lineatus*) taken in net tows from nearshore waters of Southern California. Only small larvae were susceptible to capture as 93% of the larvae with attached copepods were less than 4 mm long. It is possible that the predation observed in these reports occurred in the plankton net. Nevertheless, it seems important to evaluate the predatory potential of marine cyclopoids because of their great abundance. For example, cyclopoid copepods constitute 20-30% of the total copepods occurring in Norwegian coastal plankton (Wiborg, 1954).

Predation by Jellyfish and Ctenophores

Laboratory and field observations over the years have identified at least 34 species of medusae and about 5 species of ctenophores as predators of the eggs and larvae of marine fishes. This probably represents a small fraction of potential predators given the hundreds of species and their carnivorous feeding habits. These records are based largely on casual observation in the laboratory or food habit studies of sea caught individuals where fish eggs and larvae are typically an incidental part of a zooplankton diet. Thus, it seems pointless to list all species and references here, but the majority are mentioned in various reviews or surveys (Lebour, 1922, 1923, 1925; Fraser, 1969; Bieri, 1961, 1970; Larson, 1976; Møller, 1980; Ari and Hay, 1982) and additional references are mentioned in the context of this review.

Consumption rates of fish larvae by large medusae and ctenophores at times can be very high. Fraser (1969), in

his review, speculates that a lifetime consumption of 50-250 larval fish by each hydromedusa, about 450-500 by each *Aurelia*, and about 15,000 by each *Cyanea* is probable. Stevenson (1962) commented that as many as 45% of the Pacific herring larvae taken in a sample had been or were being devoured by ctenophores (*Pleurobrachia* spp.) on one occasion in 1947, but he continues that predation by ctenophores is generally not a serious source of mortality; in almost 4,000 plankton samples containing larval Pacific herring, evidence of such a mortality occurred in fewer than 100 samples. In a shallow cove in the Gulf of California, the siphonophore *Rhizophysa eysenhardti* was estimated to consume about 8.8 fish larvae per siphonophore per day which may have represented about 26% of the various species of fish larvae present in the cove (Purcell, 1981). Major blooms of this species in the Gulf are probably sporadic, however.

The best documented example of predation by jellyfish on fish larvae is for the scyphomedusa *Aurelia aurita* which appears to be an important predator of yolk-sac herring larvae. In Kiel Fjord (western Baltic) consumption rates of *Aurelia* averaged about four larvae per medusa per day during May, indicating that at least 2-5% of the total stock of yolk-sac herring larvae are eaten per day (Möller, 1980). No correlation existed between the size of the medusa and the percentage of medusae containing larvae but the number of larvae per medusa increased with increasing medusa diameter from up to 10 larvae in 12 mm medusae to 68 larvae in 42 mm medusae. Laboratory work indicates that *Aurelia* (12-14 mm) have the capacity to kill herring larvae at rates up to 7/h with satiation occurring after consumption of 5-6 larvae (Bailey and Batty, 1983). These authors also point out that both efficiency of capture and encounter rates increase greatly with medusa size, corroborating Möller's field observations. The evidence for this species and perhaps other large jellyfish being a major predator of cod

larvae is not strong. *Aurelia*, and other large jellyfish are most abundant during the summer, whereas peak months of spawning of cod are February and March (at least in the Baltic; Möller, 1979). On the other hand, the ephyrae stage might be important because they become abundant in March (Möller 1979) and ephyrae of *Aurelia* only a few days old will eat larval fishes (Lebour, 1922).

The size-specific vulnerability of cod and other fish larvae to jellyfish is essential for estimating overall impact on the population and interpreting mortality rates, yet little data exist other than for the yolk-sac stages. The vulnerability of cod must decline greatly over the larval stages since late larval and pelagic juvenile cod are known to accompany and seek shelter beneath large jellyfish (*Cyanea capillata*, *Aurelia aurita*, *Rhizostoma pulmo*) as do many other gadoid fishes (Ward, 1912; Mansueti, 1963). Young whiting, *Gadus merlangus*, which show the same behaviour appear to have developed a certain degree of immunity from the discharge of nematocysts of *Cyanea* and presumably cod are similarly immune (Dahl, 1961). Thus these large jellyfish seem unlikely predators of older cod larvae and juveniles.

Consumption of pelagic fish eggs by jellyfish and ctenophores seems to be mentioned much less frequently in the literature than predation on larvae. About five species of medusae (Lebour, 1922, 1923; Phillips et al., 1969; Bailey and Yen, 1983), two chondrophora (Bieri, 1961, 1970), and two ctenophores, *Pleurobrachia* (Lebour, 1922, 1923; Bailey and Yen, 1983) and *Mnemyopsis leidyi* (Burrell and Engel, 1976), have been reported to consume pelagic fish eggs as well as larvae. *Pleurobrachia* might be a significant predator of cod eggs and early larvae as it reaches peak abundance in January-February in the Baltic, which corresponds to peak production of cod larvae (Möller, 1979). At filtering rates that range from 5 ml/day for animals less than 0.8 mm to 1,150 ml/day for 7.2-8.3 mm

animals (Reeve and Walter, 1976), dense swarms of *Pleurobrachia* certainly would have the capacity for removing significant quantities of eggs and yolk-sac larvae. Eggs and larvae that concentrate at the sea surface are probably highly vulnerable to the neustonic jellyfish *Vevellella* and *Porpita* (Chondrophorae) (Bieri, 1961, 1970). Off the coast of California in May, fish eggs (*Trachurus symmetricus*) were the most important and common food item (48% of prey) of *Vevellella* (Bieri, 1961).

The occurrence of swarms of ctenophores or jellyfish appears to be very episodic. Ctenophore populations, for example, appear to be capable of very rapid growth resulting in the sudden appearance of dense swarms. Reeve and Walter (1976) conclude from studies of growth of *Pleurobrachia* in large bags (68 m³) that populations are capable of increasing by more than 50% per day. Although patches or swarms of ctenophores and jellyfish are known to occur in the open sea, the most frequent reports are from inshore and often partially enclosed areas such as bays, fjords and estuaries. Burrell and Engel (1976) mention that concentrations of ctenophores seem to be short lived in neritic or oceanic water but they may persist for months in confined areas such as estuaries. Thus, significant predation by jellyfish and ctenophores may only occur on the occasions when spawning and outbursts of jellyfish occur together; the probability of such events seems to be greater in partially enclosed areas than in the open sea. An inverse relationship between *Aurelia* and larval herring abundances in Kiel Fjord clearly illustrates this point, as the highest larval abundances occurred in years in which significant numbers of herring had hatched before the annual outburst of *Aurelia* (Möller, 1982). These inverse correlations between jellyfish or ctenophore abundance and larval abundance are relatively common (Alvariño, 1980), but only in herring is it good evidence for consumption by the medusae, since herring have geographically fixed spawning

grounds and the parents can not move elsewhere to avoid concentrations of medusae. On the other hand, low abundance of eggs and larvae of pelagic spawners could also be attributed to avoidance of such regions by the parents. This seems likely for planktivorous fishes since the zooplankton foods of these fishes are consumed by medusae and ctenophores, and spawning schools may not remain long in areas where forage is low.

Other invertebrates

Marine polychaetes and squid undoubtedly consume marine fish larvae but little is known regarding their importance in larval mortality. Lebour (1923) mentions that the polychaete *Tomopteris helgolandica* consumes herring, and other fish larvae and squid are known piscivores. Owing to their size, agility, and piscivorous habits, they are capable of feeding on many life stages of fishes, not just the youngest larval stages, as is the case for most invertebrate predators. Newly hatched squid (*Loligo opalescens*) prefer fish larvae to brine shrimp adults, and the daily ration of a newly hatched individual is equivalent to 14 yolk-sac anchovy per day, and at 8 mm their daily ration is 135 anchovy larvae (Hurley, 1976).

Fishes

Ample evidence exists that pelagic planktivorous fishes consume pelagic eggs and larvae. In the southern North Sea cod eggs are consumed by herring, sprat, and stickleback. The highest mean rates were 5-6 cod eggs per sprat or herring with the eggs of plaice and other species being consumed in considerable quantities as well (Daan, 1976). Cod eggs were more abundant in the plankton than plaice but herring and sprat seemed to consume more plaice eggs. This might be related to the fact that plaice have larger eggs or

possibly that the eggs of plaice were more concentrated than those of cod. Daan's study also identified herring as a major consumer of fish larvae, as herring larvae comprised 10-60% of the weight of the stomach contents of herring in some of the collections.

That herring and other planktivorous fishes are major consumers of fish eggs and larvae is also indicated by a number of other studies. For example, 54% of the stomach contents of herring and 45% of sprat were composed of fish eggs and larvae in the southern North Sea (Pommeranz, 1981), and in southern New England waters and Georges Bank, eggs and larvae of fishes represented 4.5% of the Atlantic mackerel diet by weight and 0.4% of that of herring (Maurer, 1976). Similarly, 83% of the prey consumed by Atlantic mackerel larvae (13-19 mm) were other mackerel larvae. Cannibalism probably occurred at night during an upward migration of the larger larvae as they passed through layers where smaller individuals were abundant (Grave, 1981). Pacific mackerel larvae, *Scomber japonicus*, are also larval fish predators (Hunter and Kimbrell, 1980a). Along the Peruvian coast, fish larvae and appendicularians were the principal foods of Pacific mackerel larvae, with sardine and Pacific mackerel larvae occurring in larval mackerel stomachs; larvae as small as 3.7 mm were piscivorous (Lipskaya, 1982). Young pelagic stages of cod co-occur with Atlantic mackerel in the North Sea (Jones, 1983); consequently nearly all life stages of mackerel can be considered as potential predators of cod larvae. Harding et al. (1978) examined the stomach contents of fish predators taken in egg patches in the southern North Sea. Sixty-two percent of the prey items in the stomachs of herring, and 96% of those in the stomachs of anchovy (*Engraulis encrasicolus*) were fish eggs or larvae, whereas other potential predators, *Merlangius merlangus*, *Melanogrammus aeglefinus*, *Limanda limanda*, *Eutrigla gurnardus*, and *Sprattus sprattus* contained only a few fish eggs or larvae.

Capelin are also indicated as possible consumers of cod eggs and larvae since cod eggs, as well as other fish eggs and larvae have been identified in their stomachs (Pozdnyakov, 1961).

Cod larvae and pelagic juveniles are likely predators of larval cod. Laurence et al. (1981) inferred that cannibalism occurred in cod rearing tanks because variability in length declined and survival decreased in groups of cod larvae maintained at low food densities. Variability in length increased until an age of one month after which it decreased in direct proportion to the density of prey in the container, indicating the existence of cannibalism. Ellertsen et al. (1981) also suggests that cannibalism occurred in their enclosure study because the survival of a group of cod larvae reared with older, near metamorphic individuals, was much lower than expected.

This discussion indicates that planktivorous fishes such as herring, sprat, pilchard, mackerel and others consume eggs and larvae of cod and other marine fishes. This could be expected since pelagic fish eggs and larvae differ little in size and avoidance capabilities from the typical foods consumed by such fishes, and if encountered they would be consumed along with their typical foods (copepods and euphausiids).

Pelagic planktivorous fishes can be abundant in cod spawning habitats and therefore could be responsible for a significant proportion of the mortality of cod eggs and larvae as well as that of other species. For example, Edwards and Bowman (1979) list 16 important species of pelagic planktivorous fishes from a cod habitat in the western Atlantic (continental shelf off New Jersey and Nova Scotia) without even considering the pelagic planktivorous life stages of the demersal fishes in that area. They estimated the zooplankton consumed by the two most abundant planktivorous species (Atlantic herring and Atlantic mackerel) varied from $2 \cdot 10^6$ to $26 \cdot 10^6$ tons annually for

herring and from $4 \cdot 10^6$ to $28 \cdot 10^6$ tons for mackerel depending on their population sizes. Clearly, fluctuations in the size of these two major planktivorous fish stocks might induce major variation in the mortality of cod eggs and larvae even if cod early life stages were an incidental part of their diet. This suggests that a direct causal relationship might be responsible for the observed antagonistic behaviour of pelagic stocks (herring and sprat) and demersal stocks (cod and plaice) in the North Sea (Daan, 1976).

The proportion of egg and larval mortality that can be attributed to predation by planktivorous fishes has rarely been determined for any species. Daan (MS presented at the ICES council meeting in 1983) estimates that at least 1% of the eggs produced by cod and at least 7% of those produced by plaice are consumed by herring. This may be an underestimate because he assumed the digestion time for an egg was one day and because the herring stock in the North Sea is still at a rather low level. The only published study where cannibalism or predation has been related to natural mortality is that of Hunter and Kimbrell (1980b). They estimated that northern anchovy stomachs contained a mean of 5.1 anchovy eggs/stomach and using an instantaneous coefficient of gastric evacuation of 0.71/h they estimated the daily consumption of eggs to be 85.8 eggs/fish or about 17% of the daily egg production. MacCall (1980), using a new estimate of natural mortality of eggs ($Z = 0.39$) and a few other modifications, estimated from their data that cannibalism on eggs could account for 28% of total egg mortality.

Hunter and Kimbrell (1980b) noted that the eggs were eaten by filtering, but this process appears to be non-random, since consumption of eggs in the sea increased as the 1.6 power of egg abundance although the form of the relationship is unclear. At times anchovy schools probably aggregate on patches of eggs rather than taking them

incidentally when feeding on other zooplankton, because egg densities in the sea are at times high enough to stimulate selective filtration (Hunter and Dorr, 1982).

VARIATION IN VULNERABILITY

The vulnerability of a larva to its predators is controlled by the intrinsic characteristics of size and maturational state, and by various extrinsic variables including larval forage, temperature, alternative prey for the predator, and visibility.

Intrinsic factors

The most important factor affecting vulnerability of larvae to predation is without a doubt the maturational state. The least mature stages (egg and yolk-sac) are also the most defenceless, suffer the highest losses, and are vulnerable to the greatest variety of predators ranging from small invertebrates to fishes. I know of only two studies in which the decline in vulnerability to predation with larval maturation has been directly studied, although the marked decline in the capture success of plankton nets with larval size is an important source of indirect evidence (Smith and Richardson, 1977; Hunter, 1981). In her thesis work, L. Dowd (University of Miami, personal communication, 1983) finds that the consumption rates of juvenile bay anchovy (*Anchoa mitchilli*) decline exponentially from about 80 sea bream larvae per hour (*Archosargus rhomboidalis*) for 2.5 mm larvae to about 10/h for 4.5 mm larvae. She found that the yolk-sac stages and eggs were less vulnerable than 2.5 mm larvae because lower activity levels made the yolk-sac larvae less visible. Webb (1981) provided a study on changes in vulnerability of northern anchovy to capture by the aquarium fish *Amphiprion percula*. The success of anchovy in avoiding capture increased linearly with size,

with the percentage of larvae that responded to attack increasing from 9% in yolk-sac larva to 85% in 12 mm larvae.

The improvement in the avoidance of predators with maturation may be due to decreases in the latency of the escape response, increases in the speed and stamina of avoidance movements or some combination of these factors. Webb (1981) found that the critical element in the enhanced ability of longer larvae to escape the predator was the latency of the startle response, as only larvae that responded too late or not at all were caught. Thus the maturation of sensory systems seems to be more important than an increase in burst speed for this particular predator.

The mode of attack of a predator determines which factors are of greatest importance in avoiding capture. For example, the striking behaviour of fishes range over a continuum from sustained pursuit to sudden lunges (Webb and Skadsen, 1980). Lungers usually start an attack with the body position in an "S" shape, strike at the prey at high speed from short range and seldom pursue the prey if the attack fails, whereas pursuers start with the body positioned in a "C" shape, strike at slower speed from greater distances, and persistently chase the prey if the first attempt fails (Webb and Skadsen, 1980; Webb, 1983; Webb, Univ. of Mich., personal communication, 1983). Clearly maturation of sensory systems will be of utmost importance in avoiding the attack of lunging predators, whereas both locomotor and sensory systems are important in avoiding pursuing predators.

Extrinsic factors

Two of the most important extrinsic factors that affect vulnerability to predation are temperature and the abundance of larval forage. Low temperature or lack of food slows growth and thereby increases the duration that larvae remain

in the smaller and most vulnerable life stages. Poor year-classes of Pacific sardine were associated with cold water temperatures and high food abundance, and it may have been the prolongation of the larval phase by low temperature resulting in higher predation that led to weak year-classes (Murphy, 1961). In support of this argument Murphy calculated that a 3° decline in water temperature (17-14° C) could decrease by 10 fold the number of sardine larvae that attain 21 mm. Prolongation of the early life stages of cod by low temperature might also increase mortality rates as a 3° decline in temperature (10-7° C) increases the time from fertilization to metamorphosis by about 20% (Laurence and Roger, 1976; Laurence, 1978).

An increase in vulnerability to predators as a result of slow growth can be caused by low food abundance as well as by temperature. Dowd (University of Miami, personal communication, 1983) found that sea bream larvae reared on low food rations were much more vulnerable to predation by juvenile bay anchovy than were those reared on a higher ration. She demonstrates that the increase in vulnerability can be explained entirely by the smaller size of larvae fed the lower ration. Lack of food may also increase vulnerability because of a deterioration of escape response of starved larvae. Twice as many hake larvae were attacked by the carnivorous copepod *Euchaeta* when they were starved for 3-4 days than when not starved (Bailey and Yen, 1983). As the larvae differed little in size the increased vulnerability may be attributed to a degenerated escape response.

Other extrinsic factors such as presence of alternative prey, abundance of predators, and patchiness of eggs and larvae were mentioned previously. I will not dwell on these factors here other than to point out that the presence of alternative prey consistently reduces predation rates in most laboratory studies to date. Other factors which have yet to be studied in larval fishes are the effect of the

onset of schooling, shelter-seeking beneath jellyfish, effects of vertical movements or currents which may concentrate eggs or larvae, visibility of predators and prey at different times of day and in different water types, and temperature-specific activity levels of larvae, any of which may alter the attractiveness of larvae for certain predators.

DISCUSSION

All the well documented accounts for consumption of eggs and larvae by invertebrate predators and most of those for fish, are for species other than cod; the clupeoids, anchovies and herring comprise the majority of such records. Owing to the similarity in size of pelagic eggs and larvae, it seems likely that cod larvae at the same life stage would be vulnerable to the predators discussed in the previous sections if cod larvae co-occurred with them. Two undocumented accounts seem to support this view; Lee (1966) mentions that the amphipods *Parathemisto libellula* and *Pseudolibrotus* sp. consume cod larvae, and it is noted in Fraser (1962) that *Pleurobrachia* also feed on cod larvae.

The well documented high mortality of cod eggs is certainly the best evidence for a high rate of predation during cod early life history, yet, the identity of the predators primarily responsible for these losses still remains in doubt. The planktivorous fishes, sprat, herring and others consume cod eggs but on the basis of present evidence it seems unlikely that they can account for all the losses. Certainly, medusae and ctenophores (particularly *Pleurobrachia*) may consume significant quantities of cod eggs. The identification of the major predators of cod eggs is not a trivial question since cod exist as eggs for about 20% of the period between fertilization and metamorphosis. In addition, consumers of eggs (the planktivorous fishes and

ctenophores) are also likely to be important consumers of yolk-sac stages as well, but yolk-sac stages are less commonly detected because of fast digestion rates (see next section). In fact, mortality rates of anchovy (Hunter, 1982) and plaice (Harding et al., 1978) often do not differ much between egg and yolk-sac stages, indicating that eggs and yolk-sac stages may be vulnerable to the same predators.

The taxa of predators that may be the most important in the early life history of cod at any life stage are unknown. The literature I have discussed for other species of fishes indicates that the small crustaceans (copepods, euphausiids and amphipods) are important consumers of only the yolk-sac stages, whereas planktivorous fishes consume eggs, yolk-sac stage and older larvae as well. The larger invertebrates (ctenophores, squid, and some of the medusae) are also certainly able to consume larger larvae as well. The consumption rates of fishes increase much more with an increase in egg or larval density than do consumption rates of the smaller invertebrates. Herring or sprat would be capable of consuming thousands of cod eggs or yolk-sac larvae per day if the density were sufficiently high, whereas the smaller invertebrates satiate rapidly and maximum attack rates are only 2-6 larvae per day. This is an important distinction because it indicates that predation by fishes is more likely to have a stronger dependence on prey density than predation by small invertebrates. It seems appropriate, owing to the lack of information on predation and the inherent difficulty of such studies, to conclude this review with a discussion of the problems inherent in investigations of the predators of marine fish eggs and larvae.

Problems in estimating effects of predators

Accurate estimation of the effect of pelagic predators on the success of year-classes of fishes is perhaps the most

difficult of all research on recruitment processes. Some of the major difficulties in a quantitative assessment of predation on eggs and larvae are: the incidental nature of eggs and larvae in the diets of their predators, which requires an assessment of the role of alternative prey; the patchiness of the youngest stages (egg and yolk-sac stages) and the rarity of the older stages in the plankton; the rapid digestion of early eggs and early larvae in the stomach of predators; biases resulting from predators feeding within net catches, and from undersampling large jellyfish and ctenophores; and, of course, the great diversity of potential predators. I discuss some of these issues below and suggest some approaches.

It has long been recognized that abnormal feeding may occur among raptorial copepods, amphipods, and chaetonaths in the crowded conditions of plankton samples. Many of the food habit studies may yield unnaturally high predation rates on larvae because chance encounters are greatly increased. Records of feeding on larvae by chaetonaths might fall in this category because laboratory work does not seem to identify them as important larval predators (Kuhlmann, 1977). Insertion of dyed larvae within the net prior to a tow might be a method of correcting for this possible bias as this technique has been successfully used in stomach analyses of trawl caught fishes (Lancraft and Robinson, 1979; Robinson and Bailey, 1982).

The rapid digestion of yolk-sac larvae by jellyfish and fishes, and their total destruction by crustacean predators greatly reduces the chance of detection of predation. Within 5 hours, yolk-sac herring larvae are digested beyond recognition by *Aurelia* at 10-12°C (Möller, 1980), and digestion of the smaller yolk-sac larvae of pelagic spawners proceeds much more rapidly. Larvae of American flounder and *Gadus saida* are totally digested except the eyes in 1.5 hours in *Aurelia* stomachs and take only 2 hours to disappear completely (Fraser, 1969). Similarly, the yolk-sac to first

feeding stages of northern anchovy are digested beyond recognition in the stomachs of adult anchovy in 0.5 hours at 16°C (Hunter and Kimbrell, 1980b). Eggs in anchovy stomachs disappear at a rate of about 50%/h; eggs are detectable somewhat longer than yolk-sac anchovy larvae, presumably because the chorion is more resistant to digestion than is the larva. The rapid digestion of eggs and early larvae has two important implications. Low average numbers in the stomachs of predators may indicate a much greater impact than anticipated because the daily ration increases markedly when adjusted by a rapid gastric evacuation rate (Hunter and Kimbrell, 1980b). Secondly, net tows or trawls should be of short duration since typical duration of trawl hauls may exceed the duration of detectability of yolk-sac stages. To my knowledge no one has examined the change in the rate of digestion of larvae in predator stomachs as a function of larval size, although it is clear that older larvae may remain in the stomach for much longer periods than yolk-sac stages. Ironically, the most abundant stages which have the highest probability of occurring in predator stomachs, disappear from those stomachs at the highest rate, whereas larger larvae which are presumably more resistant to digestion may be so rare that quantitative assessment through stomach examination may be impractical.

The maceration of larvae when ingested by crustacea make specific identification of larvae and estimates of consumption rates difficult. There is some reason for optimism, however, since crustacean predators seem to have low daily consumption rates, and immunological techniques which give only incidence might be useful for assessment of consumption in crustacean predators. These techniques have been used to trace food webs (Boreham and Ohlagu, 1978; Feller, 1982). Laboratory studies are required to check for cross reactions and to determine the duration that larvae can be detected in predator stomachs using immunological techniques.

Accurate estimates of the impact of predators also require that the consumption by predators be measured at the height of the spawning season, and since consumption by predators may increase non-linearly with the abundance of eggs and larvae, measurements of both consumption rates and larval abundance must be done at the same place and time. Eggs and early larvae are sufficiently concentrated at times for predators to feed selectively rather than consuming them incidentally with other foods. This seems to be the case for schools of anchovy feeding on their own eggs (Hunter and Kimbrell, 1980a) and may be important for the planktivorous predators of cod as well, but such effects can only be detected by simultaneous plankton and predator catches.

The great variety of potential predators of cod eggs and larvae makes it impractical to study systematically every one. Thus the most reasonable approach is to select several that seem to be the most influential. Such predators must have a high population biomass, a high population consumption rate, and a preference for the size or taxon in question, but still be able to maintain a high abundance on alternative prey and have recruitment that is relatively independent of the prey organism abundance (Rothschild and Rooth, 1982). The planktivorous fishes (herring and sprat) and some of the invertebrates may fit this role for cod eggs and larvae.

The predation problem seems so complex that it may take a long time before mortality rates of cod can be partitioned among the different groups of predators or predator-feeding models tested against accurate field estimates of consumption. Thus, as a first step, it may be preferable to assess the incidence of starvation in the sea, and thereby determine by difference the proportion of total mortality caused by predation. Accurate field work can be done now on starvation using histological criteria and growth increments on otoliths, whereas field work on predation has many more uncertainties. In addition, various laboratory studies on

predation seem very important to do, including the size-specific avoidance ability of all life stages from egg through metamorphosis using lunging, pursuing, and filter feeding predators; digestion rates of larvae in predator stomachs as a function of larval size; calibration of immunological techniques for detection of predation; and experiments on predation rates in large semi-natural enclosures.

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