NAFO Sci. Coun. Studies, 8: 25-32

Predation on Fish Larvae as a Regulatory Force, Illustrated in Mesocosm Studies with Large Groups of Larvae*

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Abstract

Mesocosm studies were carried out during 1976-83 with a number of commercially important marine fishes (Atlantic cod, Atlantic herring, capelin, and European plaice) to examine their population dynamics in relation to food supply and to predators. The studies involved the release of populations of yolk-sac fish larvae in a 4,400 m^3 basin during 1976-79 and in a 60,000 m^3 pond during 1980-83. Larval populations ranged from 3,000 to 1.2 million. The main conclusions from these studies are that (a) fish larvae have a very high potential for survival to metamorphosis in systems without predators, as illustrated by survival rates of 70% and 50% for herring and cod respectively under good feeding conditions and survival rates of 10-20% for various species under marginal feeding conditions; and (b) fish larvae are very sensitive to predation and markedly reduced survival in the presence of predatory fish fry (including cannibalism) and certain invertebrates such as hydromedusae and jellyfish. These results have important implications to studies on the dynamics of natural fish populations.

Introduction

Mortality in marine fish larvae is very high but the reasons for this are not fully understood. Although several hypotheses have been suggested, little evidence has been presented for any of them. Most field and laboratory studies have been focused on food, feeding and starvation of larvae. Great emphasis has been put on the patchiness of food organisms for larval survival, and some laboratory studies of different fishes have indicated that the mean density of appropriate food organisms in the sea is not high enough to ensure growth and survival (Lasker, 1975; Laurence, 1974, 1977). It has been assumed that starvation is the main reason for the high mortality, but few studies support this hypothesis because starving larvae seldom have been observed in sea samples (Methot and Kramer, 1979; O'Connell, 1980). With a daily mortality rate of 5-10%, a fairly large proportion of the fish larvae at any time should be in some stage of starvation, if this is the main cause of death.

So far, little attention has been given to studies of predation, although this factor is considered to be a major cause of larval mortality, both alone and in conjunction with starvation (Cushing and Harris, 1973). Research in this field has been recommended by Hunter (1976) who indicated that, after the predators have been identified and their predatory potential evaluated, sea studies should be made to determine density and distribution of predators in relation to target prey species, and field models of predation should be developed.

Results from laboratory experiments have their limitations, and transitional studies have been proposed to link laboratory and field studies (Hunter, 1976). These transitional studies must be carried out in large water volumes, with groups of fish larvae exposed to conditions which can be manipulated and monitored. Different feeding regimes might be the variable in such experimental ecosystems whereby fish larvae serve as competitors and prey of specific organisms. In this way, direct and indirect effects of these factors on larval growth and survival can be quantified. Such transitional studies with populations of fish larvae were carried out in Norway during 1975-83, making it possible to examine trophic relationships with respect to the survival of fish larvae (Øiestad, 1982).

Materials and Methods

Mesocosm studies were carried out at the Fløddevigen Biological Station (FBS) near Arendal, Norway, during 1975-79 and at the Marine Aquaculture Station (MAS) in Austevoll, south of Bergen, during 1980-83. The studies were carried out at FBS in a land-sited basin with water volume of 4,400 m^3 and at MAS in a dammed pond with water volume of 60,000 m^3. Detailed descriptions of the systems have been reported by Øiestad *et al.* (1976), Ellertsen *et al.* (1981) and Kvenseth and Øiestad (1984).

Basin studies at FBS

In 1975, preliminary studies were carried out with Atlantic herring (*Clupea harengus*), Atlantic cod

* Based on a paper presented at the NAFO Special Session on "Trophic Relationships in Marine Species Relevant to Fisheries Management in the Northwest Atlantic", held at Leningrad, USSR, 14-16 September 1983.

(*Gadus morhua*), flounder (*Plathichthys flesus*) and European plaice (*Pleuronectes platessa*) (Øiestad *et al.*, 1976). In 1976 and subsequent years, populations of fish larvae (3,000 to 200,000) at the end of the yolk-sac stage were transferred from the laboratory and released in the basin. More than one species was released in each year in order to study possible inter-specific interactions. However, the main purpose was to study effects of the ambient feeding regime on growth and survival of the larval populations. The fish populations and zooplankton abundance were sampled frequently with plankton nets, and hydrographic conditions were monitored weekly.

In 1976 and 1977, cod was the main species studied, other fish being of secondary interest. In 1978 and 1979, capelin (*Mallotus villosus*) and herring were the main species studied. These basin experiments were supplemented in 1976 with a study of herring in a small 20 m^3 basin and in 1977-79 with plastic bag experiments (each bag containing 2 m^3 of seawater) to examine growth and survival of larvae under controlled feeding conditions (zooplankton injections) in the absence of predators. Larval density in the plastic bags (100-150/m^3) was much higher than in the basin experiments (1-45/m^3). Only the results from the plastic bag experiments with the highest food levels and with comparable duration to survival in the basin were included in this paper. A detailed account of the plastic bag method was given by Øiestad and Moksness (1981).

Pond studies at MAS

The pond studies during 1980-83 involved the release of large populations of fish larvae (up to 1.2 million) than were used in the basin experiments of 1976-79, and cod was the only fish species studied. Some weeks before the larvae were released, the pond was treated with rotenone to kill predatory fish. No other control of potential predators was carried out. In most years, the pond had an open connection to the sea, but this was closed from the day of larval release until mid-June (about 3 months).

The zooplankton community in the pond during 1980-83 was dominated by populations of hydromedusae and calanoid copepods, both of which varied greatly in abundance. The hydromedusa populations consisted of *Rathkea octopunctata*, *Sarsia tubulosa* and *Tiaropsis multicirrata*.

Results

Basin studies in 1976-79

In late March-early April 1976, three populations of fish larvae (plaice, cod and a plaice-flounder hybrid) were released in the basin, cod being the dominant group with a density of 45/m^3 (Table 1). Although feeding conditions were quite low, all three populations had about 10% survival to metamorphosis. The two flatfish species settled to the bottom at metamorphosis, but the cod fry were still pelagic with a mean density of 5/m^3. When the cod larvae were about to metamorphose in late April, yolk-sac larvae of herring, plaice and the hybrid flounder were released with densities less than 1/m^3. Although feeding conditions had improved considerably, these larvae disappeared by day 20 after their release. In fact, sampling at 3-hr intervals during a 24-hr period about 2 weeks after release indicated that they had become almost extinct. A parallel group of herring which had been exposed to marginal feeding conditions in a small 20 m^3 basin had 40% survival at day 54 (Table 2).

In late March 1977. a population of cod larvae was released in the basin with a density of 17/m^3 at extremely low feeding conditions, and only 0.5/m^3 (3%) survived to metamorphosis (Table 1). A week before metamorphosis of these larvae, relatively large groups of yolk-sac larvae of cod, capelin and herring were released under much improved feeding conditions. All three of these latter populations had high specific growth rates, and a 24-hr sampling exercise about 10-12 days after their release indicated that large proportions of the populations were still alive, although the numbers were declining. Night sampling a week later showed that all herring and capelin larvae had disappeared and cod larvae were present at low density, only 6% surviving to metamorphosis. In parallel plastic bag experiments with cod, capelin and herring (Table 2), survival was 26% for capelin and 20% for herring long after both species became extinct in the basin. For cod larvae, the 10% survival to metamorphosis in the 2 m^3 plastic bag was higher than in the basin (6%).

In April 1978, a rather small population of herring larvae (density 2.3/m^3) was released in the basin under moderate feeding conditions (Table 1). About 90% were still alive at metamorphosis, and 70% survived to termination of the experiment on day 135 after hatching. At the start of herring schooling in late May, a small population of capelin larvae was released in the basin. They became extinct within 2 weeks after release. A parallel group of capelin larvae in a plastic bag had 26% survival at the same age (Table 2), but the mean daily length increment (0.14 mm) was much lower than in the basin (0.35 mm). The main reason for the faster growth of larvae in the basin may have been the higher food density relative to larval density in contrast to the food supply in the densely-stocked plastic bag.

In May 1979, two populations of capelin larvae were released in the basin, which had been stocked with herring larvae in early April (Table 1). The first

TABLE 1. Transfer data, together with specific growth rates and survival to day 20 and to metamorphosis, for populations of fish larvae involved in the 1976-79 basin studies and in the 1980-83 pond studies. (Under specific growth rate, + indicates actual values not available.)

Year	Type of larvae	Date	Transfer data: No. of larvae	Transfer data: Larvae (N/m³)	Transfer data: Food[a] (N/l)	Specific growth rate (%): Day 20[b]	Specific growth rate (%): Met.	Survival (%): Day 20	Survival (%): Met.
			Basin studies at FBS (volume 4,400 m³)						
1976	Plaice (1)	18 Mar	3,000	0.7	1	+	+	>9	9
	Cod	25 Mar	200,000	45.0	2	5.0	6.0	50	12
	Hybrid (1)	04 Apr	5,400	1.2	4	+	+	>10	10
	Plaice (2)	27 Apr	3,500	0.8	6	—	—	0	0
	Hybrid (2)	27 Apr	3,000	0.7	6	—	—	0	0
	Herring	29 Apr	3,000	0.7	6	—	—	0	0
1977	Cod (1)	25 Mar	75,000	17.0	1	4.2	8.2	10	3
	Cod (2)	22 Apr	100,000	23.0	8	12.5[c]	10.8	10	6
	Capelin	24 Apr	40,000	9.1	8	15.0[d]	—	0	0
	Herring	28 Apr	51,000	12.0	8	7.0[c]	—	0	0
1978	Herring	18 Apr	10,000	2.3	18	9.5	13.6	96	88
	Capelin	22 May	3,000	0.7	100	— (0.35)[d]	—	0	0
1979	Herring	08 Apr	25,000	5.7	12	7.5	11.8	88	56
	Capelin (1)	08 May	3,000	0.7	140	13.9(0.44)	—	100	0
	Capelin (2)	20 May	50,000	11.0	100	16.0(0.28)[c]	—	0	0
			Pond studies at MAS (volume 60,000 m³)						
1980	Cod	12 Apr	500,000	8.3	110	11.0	13.4	7	2
1981	Cod	29 Mar	610,000	10.0	10	8.1	12.3	9	3
1982	Cod	06 Apr	60,000[e]	1.0	1	11.3	11.8	50	15
1983	Cod (1)	20 Mar	1,200,000	20.0	6	10.4	12.0	75	50
	Cod (2)	30 Mar	700,000	12.0	10	13.2	10.8	65	30
	Cod (3)	09 Apr	250,000	4.2	8	11.1	—	4	0
	Cod (4)	20 Apr	150,000	2.5	4	—	—	0	0
	Cod (5)	29 Apr	80,000	1.3	3	—	—	0	0

[a] Mean density of food organisms (mainly copepod nauplii and rotifers) in the layer of maximum concentration near the bottom.
[b] Values in parentheses are daily length increments (mm/day).
[c] To day 13 posthatching.
[d] To day 10 posthatching.
[e] Corrected for immediate mortality, as initial number released was 2 million larvae.

TABLE 2. Small mesocosm experiments with groups of fish larvae in a small basin and in plastic bags in parallel with the larger basin experiments listed in Table 1, indicating specific growth rate (SGR), daily length increment (DLI) and percent survival to termination of the studies.

Year	Type of larvae	Date	Mesocosm (volume)	No. of larvae	Density (N/m³)	SGR (%)	DLI (mm/day)	Survival: Days	Survival: %
1976	Herring	29 Apr	Basin (20 m³)	400	20	4.4	0.17	54	40
1977	Cod (2)	22 Apr	P. bag (2 m³)	200	100	12.5	0.22	35	10
	Capelin	24 Apr	P. bag (2 m³)	200	100	—	0.24	36	26
	Herring	28 Apr	P. bag (2 m³)	300	150	5.1	0.18	42	20
1978	Capelin	22 May	P. bag (2 m³)	300	150	—	0.14	18	23
1979	Capelin (1)	08 May	P. bag (2 m³)	200	100	—	0.46	29	3[a]
	Capelin (2)	20 May	P. bag (2 m³)	200	100	—	0.15	21	40

[a] Survival was 12% on day 20.

group, released when the herring were 30 days old, had a very high survival rate (almost 100%) and a high specific growth rate (14%) to day 20 (28 May). The herring had already begun schooling in late May, and the capelin larvae disappeared within a week although food was plentiful (Table 1, Fig. 1). The second group of capelin larvae was released on 20 May when the herring had just begun to school. This population declined immediately and rapidly, although its specific growth rate was high (16%) and feeding conditions were unusually good. In the parallel plastic bag experiments (Table 2), survival of the first group of capelin was only 12% on day 20 compared with almost 100% in the basin, due possibly to improper inoculation at the

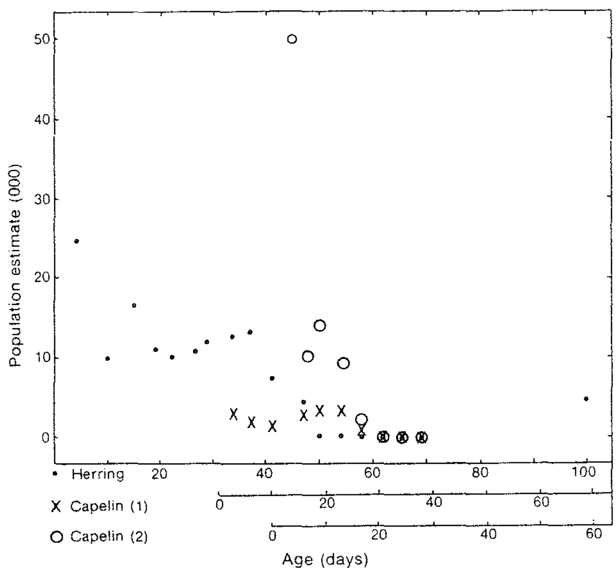

Fig. 1. Estimates of the herring population from release on 8 April 1979 to termination on day 100, and of the capelin populations released on 8 May and 20 May, based on sampling in the basin at night with two-chambered nets.

initiation of the plastic bag experiment. However, survival of the second group of capelin larvae was 40% to day 21 when the basin population had already become extinct, but the growth rate was lower (0.15 mm/day) than that for the basin experiment (0.28 mm/day), due possibly to more intense competition for food in the densely-stocked plastic bag. Even on day 35, survival was 30% in the plastic bag.

Pond studies in 1980-83

The pond studies involved the release of generally much larger populations of larvae than in the basin experiments of 1976-79 (Table 1), and cod was the only fish species studied. The zooplankton community of the pond in these years was dominated by populations of hydromedusae and calanoid copepods, both of which varied greatly in abundance from year to year (Fig. 2). Hydromedusae dominated in 1981 when copepod abundance was very low, and copepods dominated in 1983 when hydromedusae abundance was quite low. The hydromedusae population was composed of three species (*R. octopunctata*, *S. tubulosa* and *T. multicirrata*), the first being the dominant one in all years. In most years, their total density increased rapidly from less than 50/m³ in March to 200-500/m³ in April (Fig. 2A). Copepods were also abundant during the same period (Fig. 2B). Among the food organisms utilized during the first feeding of cod larvae, rotifers were important (Fig. 2C). In all years, feeding conditions at the time when the larvae began to eat were sufficient to give rather high specific growth rates (8-13%) up to day 20 (Table 1).

In 1980 and 1981, mortality of cod larvae was quite high (Table 1, Fig. 3) and only 2-3% of the initial popu-

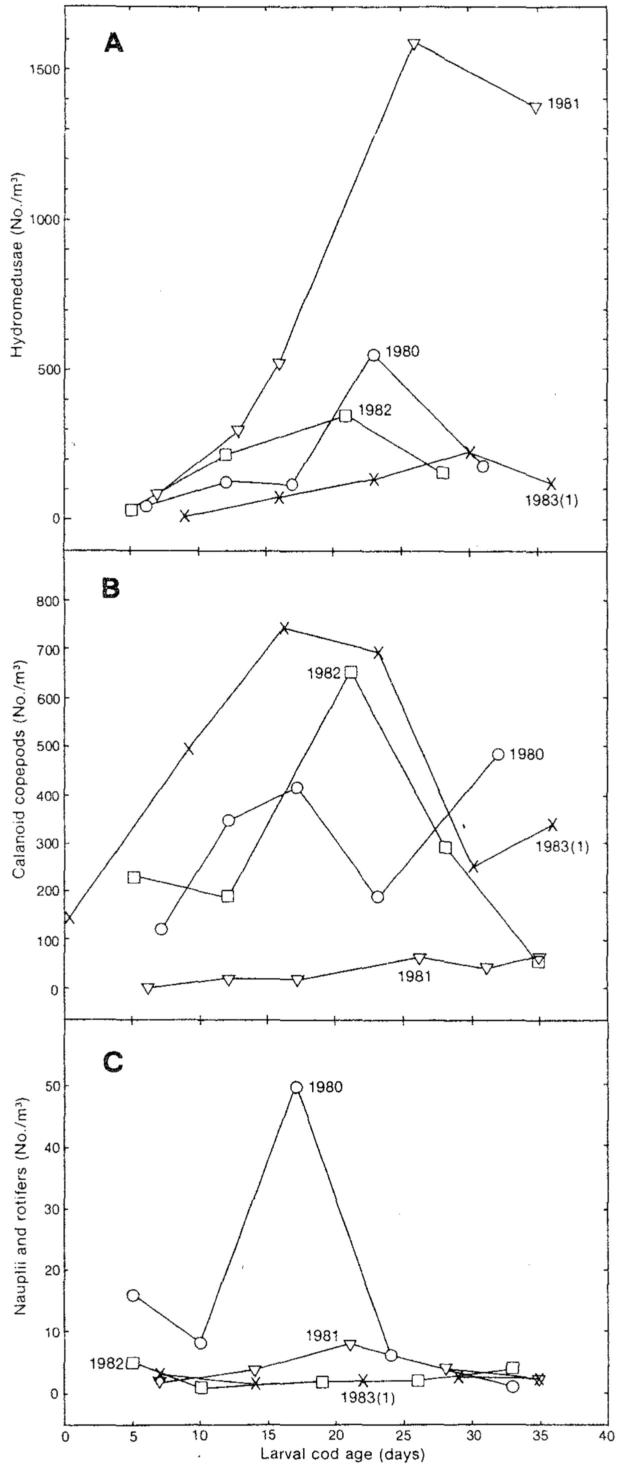

Fig. 2. Estimates of the density of (**A**) hydromedusae, (**B**) calanoid copepods, and (**C**) nauplii and rotifers, in the 1980-83 pond experiments from release of cod larvae to metamorphosis (about day 35 posthatching).

lations survived to metamorphosis (about 35 days after release). Starving larvae either were not observed or were found in very small numbers during periodic sampling. For example, the size distributions of larvae about day 15 in 1981 was similar to those in 1980 and

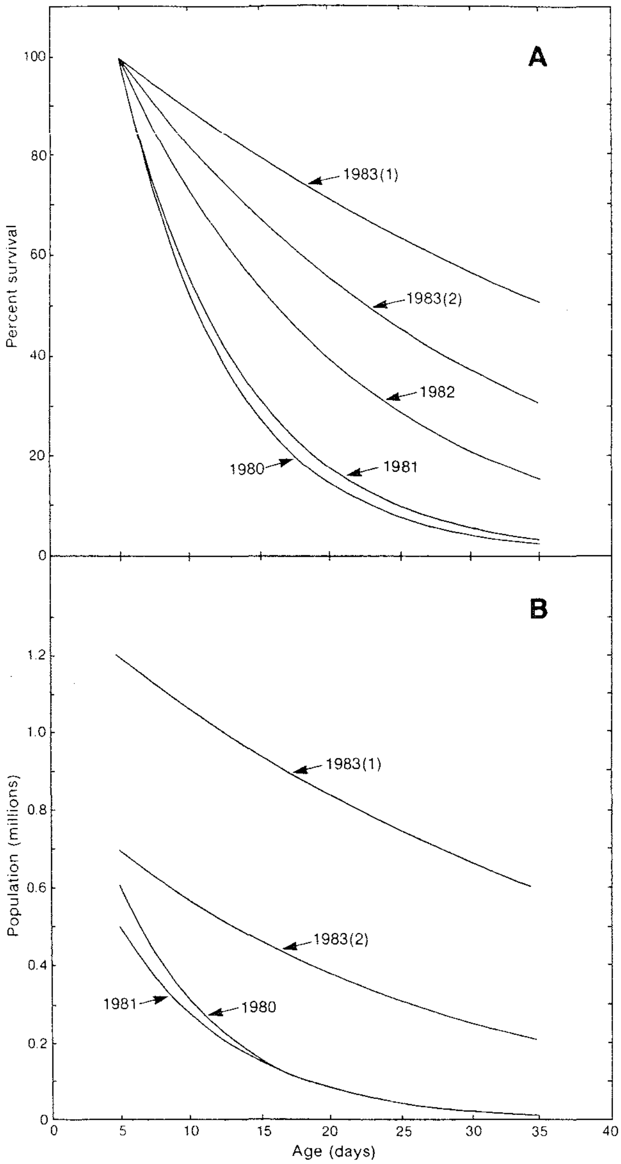

Fig. 3. Decline in population numbers (**A**) and percentage survival (**B**) of cod larvae in the 1980-83 pond experiments from release to metamorphosis (about day 35).

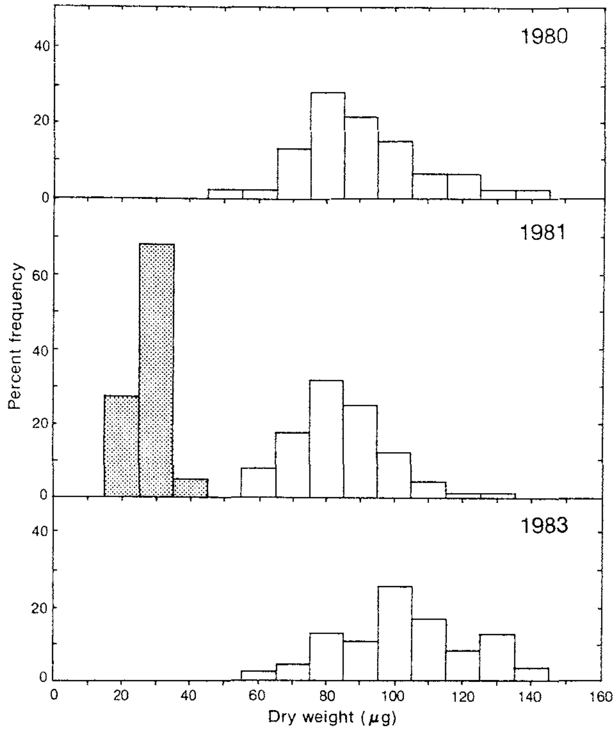

Fig. 4. Size distributions (based on dry weight measurements) of cod larvae about day 15 posthatching in the 1980-83 pond experiments (unshaded) compared with that of starving larvae of the same age in a 1981 laboratory experiment (shaded).

1983, indicating rapid growth of most of the larvae in the pond experiments of these years, in contrast to the slow growth of starving larvae of the same age in a 1981 laboratory experiment (Fig. 4). During the period of high larval mortality about 5-25 days after release in 1980 and 1981, the average density of hydromedusae was high, being 200 and 800/m^3 respectively (Table 3).

In 1982, a thorough rotenone treatment of the pond eradicated a large population of eels and nearly all types of zooplankton. When the group of cod larvae was released on 6 April (Table 1), the bad quality of the water due to decomposing fish and zooplankton resulted in high immediate mortality of the larvae. The population of hydromedusae did not reach the high level of the preceding year (Fig. 2A), and the cod larvae which survived the first week in the pond had 15% survival at metamorphosis (Table 1, Fig. 3).

In 1983, new strategy involved the successive release of cod larvae before the onset of hydromedusae reproduction. About 1.9 million larvae were released in late March and 480,000 were released in three groups at approximately 10-day intervals in April (Table 1). The hydromedusae population increased rather slowly in 1983 and remained at a much lower level than in the preceding years (Fig. 2). At the same time, copepods were very abundant. The improved feeding conditions and low competition by hydromedusae resulted in high specific growth to metamorphosis for the first two cod populations (Table 1). Of greater importance was the high survival of both populations to metamorphosis (50% and 30%) in contrast to the very low survival rates (2-3%) in 1980 and 1981 (Table 1, Fig. 3). Despite the favorable feeding conditions, the third population of cod larvae (released on 9 April) had very low survival (4%) to day 20, and the fourth and fifth groups (released on 20 and 29 April) became extinct within a few days (Table 1).

Laboratory observations on predation

A study on predation potential of various organisms was carried out in the laboratory, involving cod

TABLE 3. Summary of predator and prey characteristics from basin and pond experiments in 1976-83. (See Table 1 for other details.)

	Predator				Prey					
Year	Population	Density (N/m³)	Size (mm)	Age (days)	Population	Density (N/m³)	Period[a] (days)	Size (mm SL)	Survival (days)	%
1976	Cod	5.4	>12	>50	Herring	0.7	5–8	10	5	0.0
					Plaice (2)	0.8	5–8	6	10	0.0
					Hybrid (2)	0.7	5–8	6	10	0.0
1977	Cod (1)	0.5	>12	>50	Cod (2)	~4	5–15	5–7	>35	6.0[b]
					Herring	11.6	5–15	9–14	20	0.0
					Capelin	9.1	5–15	6–12	20	0.0
1978	Herring	2.0	>25	>40	Capelin	0.7	5–10	6	14	0.0
1979	Herring	3.2	>25	>40	Capelin (1)	0.7	25–30	6–17	25	0.0
					Capelin (2)	11.4	5–10	6–10	10	0.0
1980	Hydromedusae	~200	2–15	—	Cod	10.0	5–25	5–7	>35	2.0[b]
1981	Hydromedusae	~800	2–15	—	Cod	12.2	5–25	5–7	>35	3.0[b]
1982	Hydromedusae	~180	2–15	—	Cod	1.2	5–25	5–7	>35	15.0[b]
1983	Hydromedusae	~10	2–15	—	Cod (2)	~5	25–50	8–20	>35	30.0[b]
	Cod (1)	~10	>10	>35	Cod (3–5)	~2–4	5–30	5–10	<30	0.0

[a] Posthatching period of main predation.
[b] Survival to metamorphosis.

fry (20 mm), hydromedusae (*R. octopunctata*, *S. tubulosa*, *T. multicirrata*), juvenile jellyfish (*Aurelia aurita*, *Cyanea* sp.) and comb jellies (*Bolinopsis* sp.). A starved cod fry was observed to ingest up to 20 yolk-sac larvae of herring and/or capelin within 1 hr. Larger larvae up to about the same size as the predatory cod fry were attacked and an attempt made to ingest them, often without success. In any case, the attacks were generally fatal for the larvae. Fish larvae were attacked upon contact with all five species of cnidarians (hydromedusae and jellyfish), but only *Bolinopsis* sp. was observed to make directed movements toward the larvae. The hydromedusae were observed to ingest several larvae (5–10), but *R. octopunctata* more often killed than ingested larvae.

Discussion

These mesocosm studies have demonstrated that, in the absence of predation, marine fish larvae potentially have very high survival rates beyond metamorphosis (Table 1). Thus, the high mortality rates that are generally observed in the sea are likely to be due mainly to external factors such as lack of food and predation. Abiotic factors should have little direct effect on larval survival, although hatching of pelagic eggs within the basin in 1975 was unsuccessful (Øiestad *et al.*, 1976).

In most cases, specific growth rates to metamorphosis were quite high, indicating good feeding conditions in the mesocosms (Table 1). The feeding conditions were at least comparable to those on spawning grounds in boreal waters of the oceans (Arthur, 1977) and much lower than those generally used in laboratory experiments with the same species (Laurence, 1978; Werner and Blaxter, 1980). Furthermore, larval densities in the mesocosm studies were comparable to those observed in the sea during first feeding (Dragesund, 1970) and much lower than those used in the laboratory experiments of Laurence (1978) and Werner and Blaxter (1980). The grazing pressure from the fish larvae initially should have been about the same as in the sea, but it increased as the larvae developed and was much higher at metamorphosis due to the high survival rates in the mesocosms compared with those in the sea. Nevertheless, the natural production of food organisms in the mesocosm studies was sufficient to bring the larval populations through metamorphosis even at larval densities of 24/m³ initially and 16/m³ on day 20, as indicated by the 1983 pond experiment (Table 1). Against this background, it seems obvious that larval grazing in the open sea should seldom be the main reason for the decline in zooplankton, because the production rate in coastal waters should be comparable to that in the mesocosms. Consequently, other organisms which compete with fish larvae would more likely be responsible for depleting the food supply. Potential competitors are jellyfish, euphausiids and schooling juvenile fishes.

An interesting aspect of the mesocosm studies is the rather high survival of cod larvae at marginal feeding conditions in 1976 and 1977 when food density was about 1/l (Table 1). Obviously, marine fish larvae are opportunistic and are able to some extent to favor survival over growth, in contrast to the suggestion of Jones (1973). This ability was even more pronounced in herring, as shown in a plastic bag experiment (Øiestad and Moksness, 1981).

So far, systems without predators and competitors have been considered. However, the fish larvae themselves become predators of other larvae when they reach a certain size. Metamorphosing cod (12 mm) are cannibalistic and maintain this behavior, as demonstrated in the 1977 and 1983 studies (Table 1). In addition, they prey on other fish larvae. Even when they cannot ingest their prey because of size, they attack and mortally wound the larvae, as was observed in the laboratory experiments with starved cod fry.

The effect of predator density on first-feeding larvae is evident in the 1976 and 1977 experiments (Table 1). The comparatively large population of young cod remaining from the group released in late March 1976 rapidly eradicated the three groups of fish larvae released in late April, whereas the much smaller population of young cod remaining from the group released in late March 1977 has a lesser effect on the three groups of fish larvae released in late April, especially on the second group of cod although the capelin and herring larvae had essentially disappeared by day 20. Thus, when metamorphosed cod fry are abundant in an area, they would be expected to prey on smaller larvae of other fishes prevalent in the area.

Herring larvae seemingly do not prey on other fish larvae until they start schooling at about 25 mm SL and change their behavior toward attaching other larvae (Table 3). Rather large and healthy capelin larvae (up to 17 mm SL) were eradicated within a few days after predation began. The herring larvae probably did not ingest the capelin larvae but severely wounded them. The repeated exposure of yolk-sac capelin larvae to schooling herring fry in 1978 and 1979 (Table 3) supports this view. The extinction of capelin larvae took place during periods when food density was high and the capelin larvae had a high growth rate, with competition from herring seemingly being of minor importance. The second capelin population in 1979 was also exposed to hydromedusae (up to 300/m^3), and, although capelin larvae were not found in their guts, they may have caused many of the casualities. However, the schooling herring fry, with their far superior searching capacity, seems to be a more likely explanation for the rapid decline (Fig. 1).

A possible predator-prey relationship between herring and capelin in the Barents Sea has been suggested by Hamre (MS 1977) to explain the rapid increase in the stock of capelin after the decline of the Norwegian spring-spawning herring stock. Similarly, the outburst of cod in the North Sea has been linked to the decline of the autumn-spawning herring stock in that area (Cushing, 1980). Developing fish larvae are evidently very susceptible to predation. In the presence of predators, even fast-growing larvae have little chance to escape and survive. Vertical or horizontal segregation of different species and different stages of the same species may be favored (Courtois *et al.*, 1982), because such behaviour reduces the effects of predation in nature.

In the pond studies, predation by hydromedusae was the most likely cause of the rapid reduction of cod larvae during 20 days after release in 1980 and 1981 (Table 3), the reduction being closely correlated with the density of hydromedusae, whereas survival was high in 1983 when the density of hydromedusae was low. All hydromedusae species in the pond are known to be predators of fish larvae (Fraser, 1969; Møller, MS 1980; Arai and Hay, 1982). However, part of the mortality may have been due to damage from encountering the hydromedusae. This phenomenon was noted in our laboratory experiments and has been observed in numerous experiments by others (e.g. Bailey and Batty, 1983).

Besides being predators, hydromedusae may be important as competitors. Their grazing was particularly significant in the 1981 pond studies when their density exceeded 1,500/m^3 (Fig. 2A) in contrast to a density of 0.2/m^3 for cod larvae at metamorphosis (Table 1). The unusually low density of calanoid copepods in that year (Fig. 2B) was probably due to high grazing pressure by hydromedusae. The highest density of copepods was observed in 1983 when the density of hydromedusae was lowest. The low level of hydromedusae reproduction in 1983 may have been the result of heavy grazing on microzooplankton by cod larvae which were released at 10-day intervals from 20 March to 29 April. This prevented the less competitive hydromedusae recruits from an adequate food supply during their first feeding.

The conclusions that can be drawn from the basin and pond experiments in 1976–83 may be summarized as follows: (a) marine fish larvae have a very high potential survival rate, even at marginal feeding conditions; (b) fast-growing and healthy larvae may be very susceptible to predation; (c) from metamorphosis onward, larvae of some fish species are voracious predators of other fish larvae; and (d) predation involves not only the prey that are ingested but also those that succumb to injuries inflicted by predators.

The relevance of these results to field studies is obvious. Less attention should be devoted to feeding conditions and more should be given to studies of predation and competition. In nature, if starvation accounted for a daily mortality rate of 5–10%, about 30–50% of the fish larvae should be in a state of starvation, but very seldom have starving larvae been found in sea samples. Selective predation (i.e. predators searching for starving larvae) is not very likely, because this implies that the water column is surveyed daily by predators looking for weak larvae. Most of the predators either are fast-swimming (fish fry and euphausiids) or encounter fish larvae accidently by co-occurrence (hydromedusae).

Future research should emphasize *in situ* studies in the open sea (Hunter, 1976). Relevant equipment and hypotheses should enable researchers to determine why a potential 50–90% survival of fish larvae to metamorphosis, as demonstrated for cod and herring in this paper, becomes much less than 1% in the open sea.

Acknowledgements

The experiments at Flødevigen Biological Station were carried out in cooperation with Erlend Moksness and those at the Marine Aquaculture Station were assisted by Per Gunnar Kvenseth. The experiments at both stations were to a large extent funded by the Norwegian Council of Fishery Research.

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