Fol. 41 L

International Council for
the Exploration of the Sea

C.M.1983 (L:39)
Biological
Oceanography Committee
Ref.: Demersal Fish Committe

PREDATION ON FISH LARVAE AS A REGULATORY FORCE ILLUSTRATED IN ENCLOSURE EXPERIMENTS WITH LARGE GROUPS OF LARVAE

by

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ABSTRACT

In Norway enclosure experiments have been carried out every year since 1975 including a large number of commercial marine fish species (cod, herring, capelin and plaice) to study their populations dynamics in relation to food supply and predators.

The experiments have been carried out in enclosures with volumes of 2 500 m, 4 400 m and 60 000 m and with populations of fish larvae ranging from a few thousand to 1.2 million. Two main conclusions can be drawn for these experiments:

Presented at Fifth Annual Meeting, NAFO, Special session on Throphic relationships in marine species relevant to fisheries management in the Northwest Atlantic, 14-16 September, Leningrad, USSR.

(1): fish larvae have a very high survival potential to metamorphosis in systems without predators, as illustrated with herring (70%) and cod (50%). Even at marginal feeding conditions leading to reduced growth rates, high survival rates have been observed.

(2): fish larvae are very sensitive to predation and markedly reduced survival rates have been observed. This is illustrated with both evertebrates and fish larvae (in multi-species experiments) as predators including cannibalism.

These results have important implications for the understanding of populations dynamics for wild fish populations.

INTRODUCTION

Marine fish larvae have very high mortality rates, but the reasons for this mortality should be further investigated. Although number of hypotheses have been suggested, little evidence has been put forward for any of them. It has been almost dogma that starvation is the main reason, but few field studies seem to support this hypothesis, as starved larvae seldom have been identified from sea samples (Methot and Kramer 1979, O'Connel 1980). Given a daily mortality rate of 5-10%, a fairly large fraction of fish larvae should at any time be in some stage of starvation if this is a main cause of death.

Enclosure studies with fish larva populations, carried out for many years, have made it possible to look at trophic relationships related to the survival of fish larvae. The experiments have been reviewed by Øiestad (1982).

MATERIALS AND METHODS

Enclosure studies were carried out for six years at Flødevigen Biological Station (FBS) outside Arendal (1975-1980) and for four years at the Institute of Marine Research, Marine Aquaculture Station Austevoll (MASA), south of Bergen (1980-1983).

At FBS the experiments were mainly carried out in a land-sited basin with a volume of 4 400 m^3 and at MASA in a dammed pond with a volume of 60 000 m^3. For more detail, see Ellertsen et al. (1981), Øiestad et al. (1976) and Øiestad and Kvenseth (1981).

Basin experiments at FBS

In 1975 preliminary experiments were carried out with herring, cod, flounder and a flounder hybrid (Øiestad et al. 1976) . In 1976 and the following years, large populations of fish larvae at the end of the yolk sac stage (EYS) were transferred from the laboratory and released in the basin (Table 1). In all years more than one species was released in the basin in order to look at possible interactions between fish species. However, the main purpose was to study the effect of the ambient feeding regime on growth and survival of the released larva populations. As large populations were released in most cases, frequent sampling could be carried out, with net hauls giving information on growth and survival rates. Both hydrography and primary and secondary production were monitored weekly.

In 1976 and 1977 cod was the main species studied; other species were of secondary interest (Table 1). In 1978 and 1979, herring was the main species. In these two last years, the basin experiment was supplemented with plastic bag experiments to examine growth and survival at more marginal feeding conditions than those in the basin. In 1980, only experiments with turbot larvae were carried out.

Pond experiments at MASA

The larger volume of the MASA pond was compensated for by releasing larger populations of larvae (Table 2).

Some weeks before larval release, 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 in the pond to mid-June (about 3 months). The ecosystem in the pond was somewhat more diverse than that observed in the basin at FBS.

RESULTS

Basin experiments at FBS

Cod as main species

In 1976 three populations of fish larvae were released at about the same time: plaice, cod and the plaice-flounder hybrid. All populations had a rather high survival to metamorphosis (Table 1). The two flatfish species settled to the bottom at metamorphosis, but the cod fry were still pelagic, with a mean density of 5 fry/m^3. At about that time, yolk sac larvae of herring, plaice and the hybrid were released, and although the feeding conditions had improved (Table 1), they rapidly disappeared from the basin. A 24-hour sampling a fortnight after release, found them almost extinct. A parallel group of herring exposed to marginal feeding conditions had 50% survival to day 50 in a small basin (20 m^3).

In 1977 a population of cod larvae were released at extremely poor feeding conditions. Only 3% or 0.5/m^3, survived to metamorphosis. A week before metamorphosis, three populations of yolk sac larvae were released: cod, herring and capelin (Table 1). The feeding conditions had improved and all three populations had a high specific growth rate (Table 1). During a 24-hour sampling 10-14 days after release, large populations of the released larvae were still alive although the number was declining. Night sampling a week later showed that all larvae had disappeared or occured at very low density (cod 2).

Herring as main species

In 1978 a rather small population of herring larvae was released (Table 1) giving an initial density of 2.3/m^3. At metamorphosis about 90% were still alive, and 70% survived to final termination (day 135 post-hatching).

At start of schooling, a small population of capelin larvae was released. Within a fortnight they were brought to extinction.

Parallel groups of capelin larvae in plastic bags had high survival rates to the same age.

In 1979 two populations of capelin larvae were released in the basin stocked with herring larvae. The first group, released when the herring were 30 days old, had a very high survival rate to a size of 17 mm (about 100%). At that time the herring started schooling, and within a week the capelin disappeared (Fig. 1). The second population was released during the initiation of herring schooling. This population also declined immediately and very rapidly, although its specific growth rate was high (16%) and its first-feeding conditions were unusually good (Fig. 1 and Table 2). In parallel plastic bag experiments, the survival rate was far higher at lower specific growth rates.

Pond experiments at MASA

Most years the zooplankton community was dominated by populations of hydromedusae although they changed in density from year to year (Fig. 2), with 1981 outstanding. By number, *Rathkea octopunctata* dominated in all years. *Sarsia* sp. and *Tiaropsis* sp. also were rather numerous in all years.

The other main component of zooplankton was different species of calanoid copepods (Fig. 3a). Among first feeding organisms for cod larvae, rotifers were of great importance (Fig. 3b).

In all years the feeding conditions during first feeding were sufficient to give a rather high specific growth rate for the first two weeks after release, i.e. beyond point of no return and point of mass mortality in the laboratory (between day 16-20).

In 1980 and 1981 cod larvae mortality was high (Figs. 4a and b), although starving larvae were not observed or were observed in small numbers (Fig. 5).

In 1982 a more thorough rotenone treatment eradicated a large population of eels and nearly all types of zooplankton. The resulting bad water quality due to decomposing fish and zooplankton biomass gave a high immediate mortality of cod larvae. The population of hydromedusae did not reach the high level of the preceeding year (Fig. 2), and the cod larvae surviving the first week in the pond had a 15% survival to metamorphosis in this year (Fig. 4).

In 1983 a new strategy was tried: repeated release of cod larvae before the onset of hydromedusa reproduction, and in larger numbers than before. Altogether, 2 million cod larvae were released in the last part of March (Table 2). In April about half a million cod larvae were released (Table 2).

R.octopunctata had a rather slow increase to a moderate high density (Fig. 2), and the two other common species maintained nearly constant populations. The improved feeding conditions due to little competition from hydromedusae resulted in high specific growth rates of the two first-released cod population to metamorphosis (Fig. 3a and Table 2). Of more importance, survival rates to metamorphosis were very high (50% and 30%) compared with 1980 and 1981 (2%) (Fig. 4).

The third population (released 9 April) had a low survival rate to day 20 (4%), and the fourth and fifth populations of cod (20 and 29 April) were brought to extinction within a few days although feeding conditions were rather good (Table 2).

DISCUSSION

The enclosure experiments demonstrate that marine fish larvae potentially have very high survival rates beyond metamorphosis. This should clearly indicate that the high mortality rates observed in the sea must 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 in the 1975 basin experiment was unsuccessful (Øiestad et al. 1976).

In most cases specific growth rates to metamorphosis were fairly high indicating good feeding conditions in the enclosures (Tables 1 and 2). It should be noted that feeding conditions were comparable to those on spawning grounds all over the world (Arthur 1977) and consequently far lower than those used in laboratory experiments with the same species (Laurence 1978, Werner and Blaxter 1980). Furthermore, larval densities in the enclosure experiments were comparable to those observed in the sea during first feeding (Dragesund 1970), and far below those used in laboratory experiments (Laurence 1978, Werner and Blaxter 1980). The grazing pressure from the fish larvae should initially have been about the same as in the sea, but in later stages it was higher, and about metamorphosis far higher due to the high survival rates in enclosures compared with the sea. Nevertheless, the natural production of food organisms in enclosures was sufficient to bring the larval populations through metamorphosis even at fry densities of $15/m^3$ (1983). Against this background it seems obvious that larval grazing in the open sea should seldom be the main reason for a decline in zooplankton, as the production rate in coastal waters should be comparable to that in enclosures. Consequently, other organism groups competing with fish larvae would be more likely to exhaust the food supply. Potential competitors would be jellyfish, older schooling young fish and eupheusiids.

Another aspect is the rather high survival at marginal feeding conditions in the 1976 and 1977 (first group of cod) basin experiments. Obviously, marine fish larvae are opportunistic and are able to some extent to favour survival over growth in contrast to that suggested by Jones (1973). This ability is 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, fish larvae themselves seem to be predators when they reach a certain size. Metamorphosing cod (12 mm) are cannibalistic and maintain this behaviour for the rest of their lives, as demonstrated in 1977 and 1983 (pond experiment) (Table 3). In addition they prey on other fish larvae. Even when they cannot ingest the prey organisms because they are too large, they attack and mortally wound fish larvae. This behaviour has been observed in our laboratory experiments.

The effect of cod fry density is obvious when the 1976 and 1977 basin experiments are compared as in 1976 first-feeding larvae were rapidly eradicated while at the low predator density in 1977, they survived for weeks (Table 3). In areas with metamorphosed cod fry, one would expect these fry to prey on other fish larvae with similar distributions.

Herring larvae seemingly do not prey on other fish larvae until they start schooling (25 mm; Table 3). Then they seem to change their behaviour towards other fish species; even rather large and healthy capelin larvae (17 mm) were eradicated within a week (Fig. 1). Probably the herring did not ingest the capelin, but wounded them badly by attacking them.

The repeated extinction of capelin yolk-sac larvae exposed to schooling herring (1978 and 1979) supports this view. A possible predator - prey relationship between herring and capelin in the Barents Sea has been suggested by Hamre (1977) to explain the dramatic increase in the stock of capelin after the decline of Norwegian spring-spawning herring. Similarly, the outburst of cod in the North Sea has been linked with the decline in autumn-spawning herring in that area (Cushing 1980). Altogether, marine fish larvae seem very sensitive to predation. Facing a fish predator, even fast-growing fish larvae have little chance to escape and survive. Vertical or horizontal segregation of different species and stages of the same species may have been favoured (Courtois _et al_. 1982) because they reduce the effect of this phenomenon in nature.

In the pond experiments, predation from hydromedusae is the most likely explanation for the rapid reduction of cod larvae for the first 20 days after release in 1980 and 1981 (Table 3). This reduction was closely correlated with the density of medusae; in 1983, with low medusae density, survival was high (Fig. 6). All hydromedusae species present are known to be predators on fish larvae. As with fish predators, the large mortality might have been due to damage caused by encountering the medusae. This phenomenon has been observed in numerous laboratory experiments with the species discussed here (Bailey and Bates 1983).

Besides being predators, the hydromedusae are important competitors. In the 1980 and 1981 pond experiments their grazing was far more important than that of the cod larvae. In April 1983, without this grazing pressure, the populations of calanoid copepods was larger than preceeding years (Fig. 3a). The delayed and reduced hydromedusae reproduction in 1983 might be explained by heavy grazing on microzooplankton by the cod larvae that were released every 10 days beginning 20 March. This never permitted the less competetive hydromedusae recruits to have a realy proper first-feeding food supply (Fig. 3b).

Most of the conclusions that can be drawn from these experiments have already been suggested:

- Marine fish larvae have a very high potential survival rate, even at marginal feeding conditions;

- Even fast-growing and healthy larvae are very sensitive to predation;

- Some species of marine fish larvae are voracious predators against other fish larvae from metamorphosis onward;

- Predation does not mean that the predators are ingesting the prey; in many and perhaps most cases the prey is only injured.

The relevance of these results to field studies is obvious. Primarily: less attention should be paid to feeding conditions <u>per se</u> and far more to predation and competition. Very seldom have starving larvae been caught in sea samples, although if starvation explained a 5-10% daily mortality rate, 30-50% of fish larvae should be in a state of starvation. A selective predation, i.e. predators searching for starving larvae, is less likely, as that implies the presence of a predator surveying the whole water volume daily. It is more likely that predators are not looking for weak larvae, as most of the predators are either fast-swimming (fish fry and eupheusiids) or encounter fish larvae accidentally (most medusae).

The main attempt in a new strategy should be to study processes, i.e. to carry out enclosure studies in the open sea (Hunter 1976). Relevant equipment and hypotheses should enable researchers to determine why a potential 50-90% survival to metamorphosis, as demonstrated for cod and herring, can become an actual rate far below 1°/oo in the open sea.

AKNOWLEDGEMENTS

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

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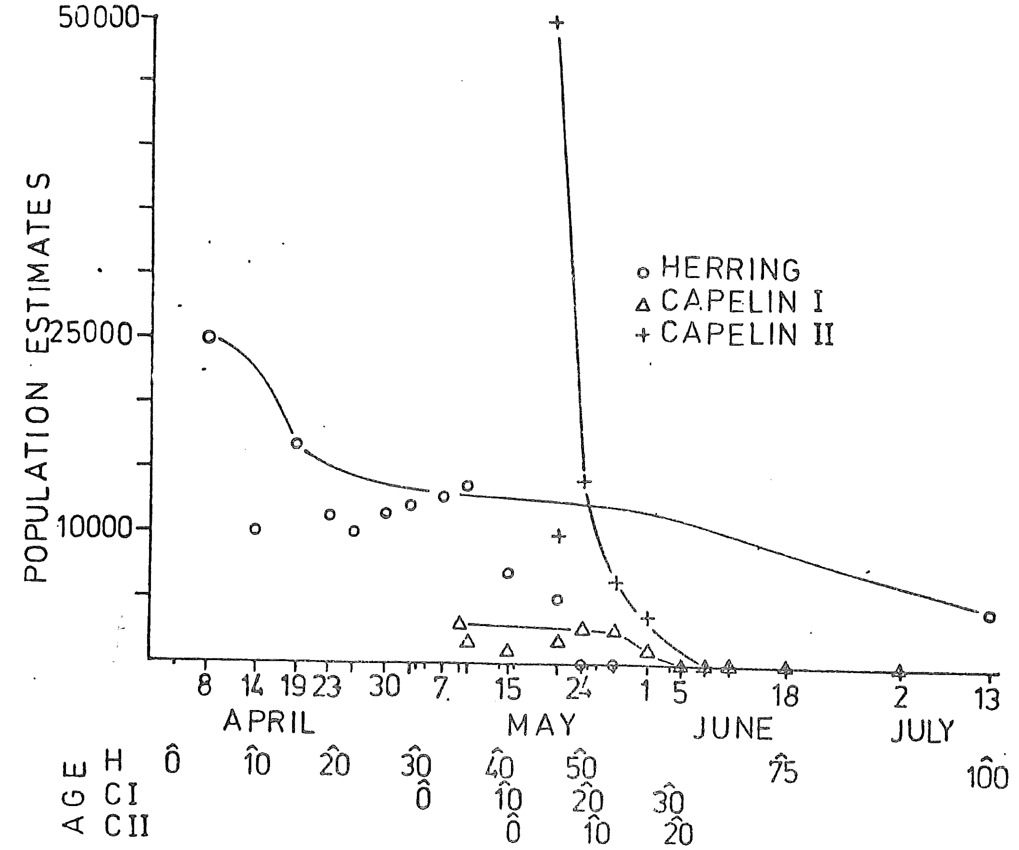


Fig. 1. Estimates of the herring population (circle) from release to termination on day 100; of the capelin population released in early May (CI, triangle) and of the capelin population released in late May (CII, cross). All estimates are based on night haul samples in the basin in 1979 with two-chambered nets.

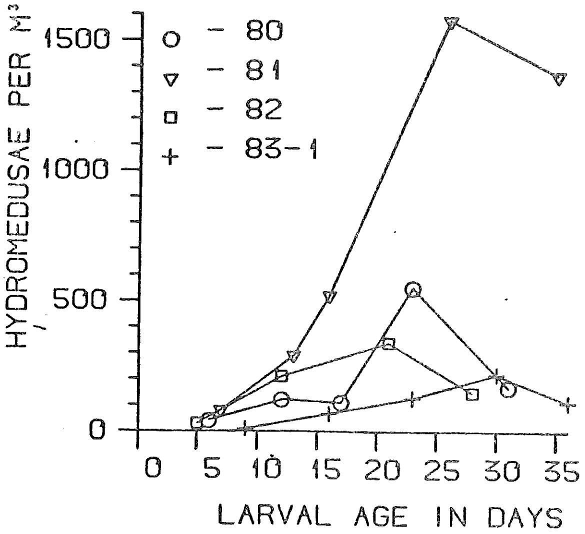


Fig. 2. Mean densities of hydromedusae in the 1980-1983 pond experiments from larval release to metamorphosis (about day 35).

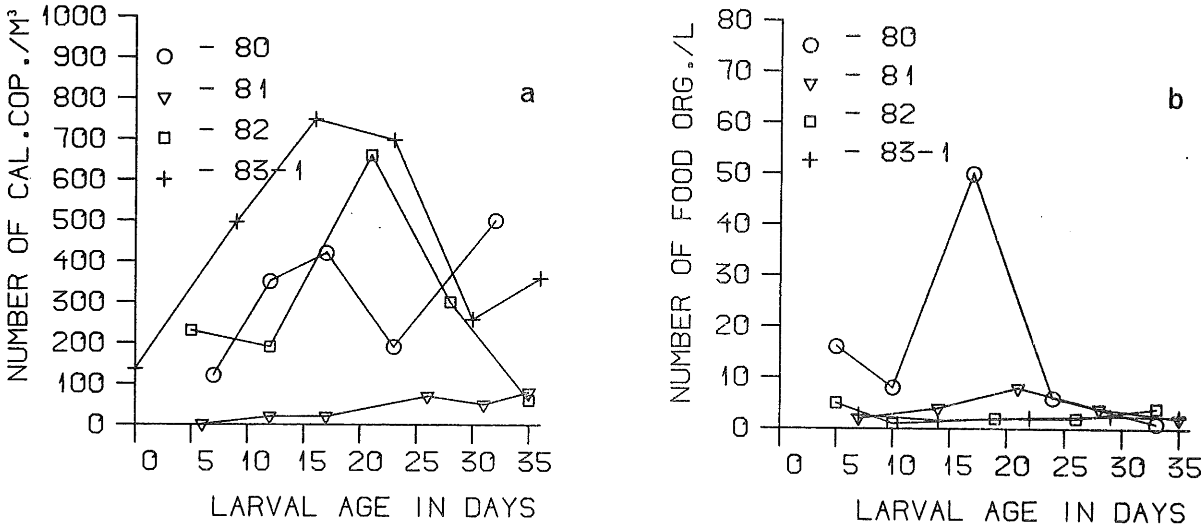


Fig. 3. Mean densities of calanoid copepods (a) and nauplii and rotifers (b) in the 1980-1983 pond experiments from larval release to metamorphosis (day 35).

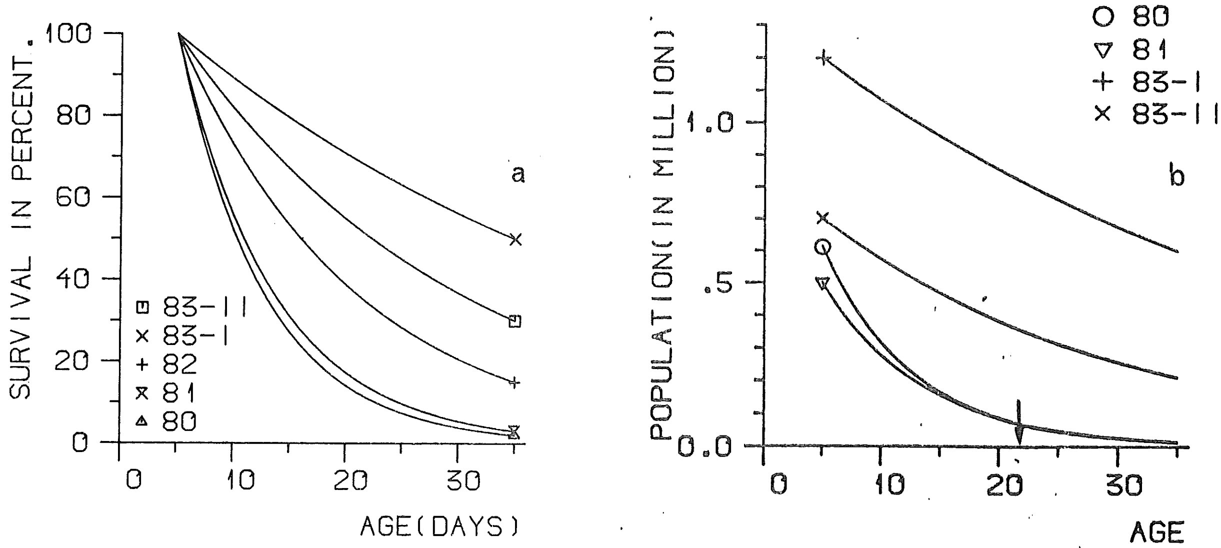
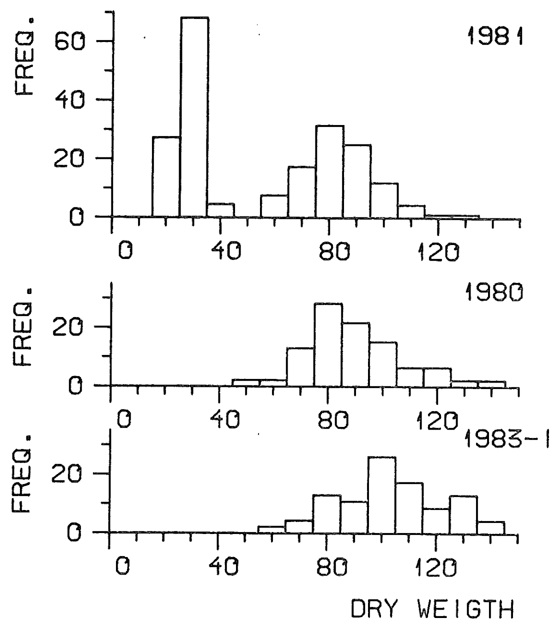


Fig. 4. Cod population survival in percentage (a) and in number (b) from release to metamorphosis in the 1980-1983 pond experiments.



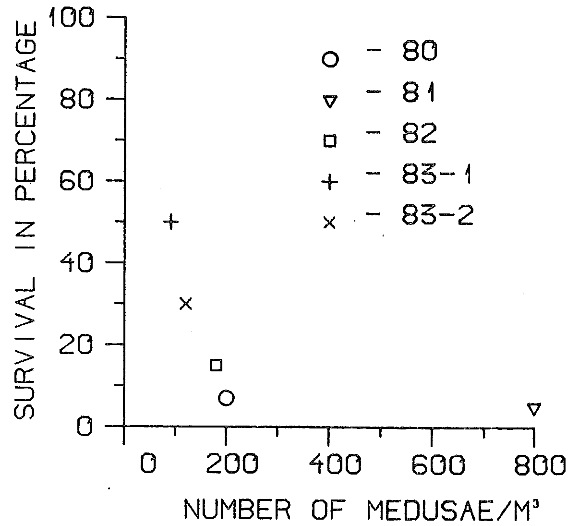


Fig. 5. Dry weight-frequency distribution of cod larvae about day 15 in the 1980-1983 pond experiments. This period coincided with mass mortality in the laboratory of starving larvae (mean dry weight 20-30 ug, left histogram 1981).

Fig. 6. The relation between mean densities of hydromedusae in the premetamorphose period of cod larva survival to beyond metamorphosis (Survival figures are based on population estimates after release in the pond).

Table 1. A review of larval fish populations transferred to the basin from 1976 - 1979: their density, feeding condition, spesific growth rate and survival. (f = female, m = male, + = actual value not monitored).

Year and species	Transfer data				SGR (%)		Survival (%)	
	Date	Number	Density m^3	Food density /litre	day 20	metam.	day 20	metam.
1976								
plaice-1	18.3	3000	0.7	1	+	+	+	9
cod	25.3	200000	45	2	5.0	6	50	12
plaice (f)x flounder (m)-1	4.4	5400	1.2	4	+	+	+	10
plaice-2	27.4	3500	0.8	6	-	-	0	-
plaice (f)x flounder (m)-2	27.4	3000	0.7	6	-	-	0	-
herring	29.4	3000	0.7	6	-	-	0	-
1977								
cod-1	25.3	75000	17	1	4.2	8.2	10	3
cod-2	22.4	100000	23	8	12.5^{x}	10.8	10	6
capelin	24.4	40000	9.1	8	15.0^{+}	-	0	-
herring	28.4	51000	12	8	7.0^{x}	-	0	-
1978								
herring	18.4	10000	2.3	18	9.5	13.6	96	88
capelin	22.5	3000	0.7	100	-	-	0	-
1979								
herring	8.4	25000	5.7	12	7.5	11.8	88	56
capelin-1	8.5	3000	0.7	140	13.9	-	100	0
capelin-2	20.5	50000	11	100	16.0^{x}	-	0	-

+: to day 10 posthatching; x: to day 13 posthatching

Table 2. A review of cod populations transferred to the pond from 1980 - 1983: their density, feeding condition during first feeding, specific growth rate and survival.

Year	Transfer data				SGR (%)		Survival (%)	
	Date	Number	Density /m^3	Food org. /litre	Day 20	Metam.	Day 20	Metam.
1980	12.4	500000	10	110	11.0	13.4	7	2
1981	29.3	610000	12	10	8.1	12.3	9	3
1982	6.4	60000	1.2	1	11.3	11.8	50	15
1983								
Cod-1	20.3	1200000	24	6	10.4	12.0	75	50
Cod-2	30.3	700000	14	10	13.2	10.8	65	30
Cod-3	9.4	250000	5	8	11.1	-	4	0
Cod-4	20.4	150000	3	4	-	-	0	-
Cod-5	29.4	80000	1.6	3	-	-	0	-

Table 3. Biological characteristics of predator and prey organisms

Year	Species	Predator SL mm	Predator Dry weight µg	Predator Age§	Predator Density /m³	Prey SL mm	Prey Dry weight µg	Prey Pred. period	Prey Density /m³	Detectable (days); survival (%)
1976	Cod	>12	>1000	>50	5					
	Herring					10	100	5-8	1	5 days; 0.1
	Plaice-2					6	60	5-8	1	10 days; 0
	Hybrid-2					6	60	5-8	1	10 days; 0
1977	Cod-1	>12	>1000	>50	0.5					
	Cod-2					5-7	50-250	5-15	4	>35 days; 15 (metam.)
	Herring					9-14	90-300	5-15	12	20 days; 0
	Capelin					6-12	60-200	5-15	9	20 days; 0
1978	Herring	>25	>10000	>40	2.0					
	Capelin					6	60	5-10	1	14 days; 0
1979	Herring	>25	>10000	>40	3.0					
	Capelin-1					6-17	60-800	25-30	1	25 days; 0
	Capelin-2					6-10	60-150	5-10	12	10 days; 0
1980	Hydromedusae	2-15	15-300	-	200					
	Cod					5-7	50-300	5-25	10	>35 days; 2 (metam.)
1981	Hydromedusae	2-15	15-300	-	800					
	Cod					5-7	50-300	5-25	9	>35 days; 3 (metam.)
1982	Hydromedusae	2-15	15-300	-	180					
	Cod					5-7	50-300	5-25	1	>35 days; 15 (metam.)
1983	Hydromedusae	2-15	15-300	-	10					
	Cod-1	>10	>1000	>35	14					
	Cod-2					8-20	500-10000	25-50	5	>35 days; 30 (metam.)
	Cod-3/4/5					5-10	50-800	5-30	2-4	30/5/1; 0/0/0

§ Period with main predation