Fløde vigen rapportser., 1, 1984. ISSN 0333-2594
The Propagation of Cod *Gadus morhua* L.

GROWTH, MORTALITY AND FEEDING OF COD (*Gadus morhua* L.) LARVAE IN ENCLOSED WATER COLUMNS AND IN LABORATORY TANKS.

J.C. Gamble[1] and E.D. Houde[2]

1 Department of Agriculture and Fisheries for Scotland, Marine Laboratory, P.O. Box 101, Victoria Road, Aberdeen, Scotland
2 Center for Environmental and Estuarine Studies, Chesapeake Biological Laboratory, University of Maryland, P.O. Box 38 - Solomons, Maryland 20688, USA

ABSTRACT

Gamble, J.C. and Houde, E.D., 1984. Growth, mortality and feeding of cod (*Gadus morhua* L.) larvae in enclosed water columns and in laboratory tanks. In: E. Dahl, D.S. Danielssen, E. Moksness and P. Solemdal (Editors), The Propagation of Cod *Gadus morhua* L. Flødevigen rapportser., 1, 1984: 123-143.

In April 1982 cod larvae were reared in four 30 l laboratory tanks and in two 300,000 l columnar plastic enclosures for 3-4 weeks from hatching. North Sea oil "production water" was added to one of the enclosures immediately after introduction of the yolk sac larvae. Natural zooplankton at an initial copepod nauplii concentration of 5-7 l^{-1} provided the food source for enclosure larvae. Food in the tanks, mainly copepod nauplii and small copepodites, was maintained at about 300 items l^{-1}.

Post yolk sac specific growth rates of larvae in the enclosures were 10.0% and 10.4% d^{-1}. In the laboratory, cod larvae of Norwegian origin grew at 7.8% and 7.7% d^{-1}, while those of Clyde Sea origin grew at 1.7% and 6.0% d^{-1}. Natural daily mortality rates were 8.4% and 9.7% in the enclosures and 10.6%, 14.5%, 15.6% and 10.0% in the tanks. "Production water" had no detectable effect on the treated larvae.

Larvae in both systems started feeding at 4-5 days after hatching and feeding incidence was soon over 60%. The diet of enclosure larve consisted almost entirely of nauplii of the copepod *Pseudocalanus elongatus*. The relationship between numbers and sizes of food items relative to standard length and the relationship of maximum gut content weight to larval size were determined. Pump samples revealed that cod larvae in the enclosures preferred the top 7.5 m of the water column.

INTRODUCTION

Large enclosures have proved to be invaluable in the experimental study of aquatic pelagic ecosystems in general (Menzel and Steele, 1978; Gamble and Davies, 1982) and for pollution (Steele, 1979) and fish larvae (Øiestad, 1982) in particular. For several years replicated columnar enclosures have been deployed at a sheltered fjordic site, Loch Ewe, on the west coast of Scotland. The initial objective of these experiments was to test the effects of heavy metal pollutants on the enclosed pelagic system (Gamble et al., 1977; Davies and Gamble, 1979). More recently we reared larval herring successfully in the enclosures (Gamble et al., 1981).

Since there is considerable concern about possible deleterious effects of the oil drilling activity in the North Sea on the pelagic ecosystem, we have tested the effects of water soluble derivatives of oil production ("production water") on herring larvae and other pelagic components within the experimental enclosures (Davies et al., 1980; MacLachlan et al., 1981). However, herring spawn demersal eggs at specific sites distant from areas of oil production so we believed that it was desirable to test a pelagically developing fish species whose embryonic and larval stages might occur in such areas. We chose cod primarily because of the available information from experiments in the Flødevigen enclosures (e.g. Ellertsen et al., 1981a).

This paper does not focus on the effects of "production water", indeed the results indicated no discernable effects. We will compare the mortality, growth and feeding of cod larvae reared simultaneously in two very different systems; small laboratory tanks (tubs) and large in situ enclosures (bags). Larvae were reared in laboratory tanks as well as enclosures to check viability, to provide live larvae for ad hoc experiments and to compare larvae from two separate localities.

MATERIALS AND METHODS

Cod larvae in these experiments originated from parent fish from the Clyde Sea, Scotland (Ballantrae Bank) and from adults brought live to the fishmarket in Bergen, Norway. In both cases ripe gonads were removed from the fish and fertilization carried out in vitro. Norwegian eggs were fertilized on March 16 and Clyde eggs on March 22, 1982 but, due to different incubation temperatures, eggs from both localities hatched between 2-4 April. Eggs from four individuals, two from each locality, were used in both the bag and tub experiments, although in the bags most embryos (91%) were from the Norwegian material split 70:30 between the two females. The tub experiments compared larvae from Clyde and Norwegian localities.

Two 4.75 m diameter by 19.5 m deep, columnar, transparent PVC enclosures (Gamble et al., 1981) moored in a 30 m deep embayment of L. Ewe, L. Thuirnaig, were stocked with about 45,500 day-old cod larvae. The initial larval density was about 0.150 l^{-1} at an approximate bag volume of 300,000 l. In the tub experiments 200 newly hatched larvae were placed in static, black, plastic cylindrical tubs of 30 l capacity with a water depth of about 25 cm. Stocking density was 6.5 l^{-1}. Two tubs contained Clyde and two Norwegian larvae.

Temperatures in the bags matched that of the surrounding seawater and increased from 7°C to 9°C during the month-long experiment. Gross fluctuations in tub temperatures were avoided by immersion in a trough of flowing seawater pumped from L. Ewe. Temperature ranged from 5.5-11°C, averaging 8-10°C during the experiment. Lighting in the bags was natural but, due to the design of the bag system, was reduced to about 80% of ambient. Duration of surface light intensity above 0.1 lux in April at the latitude of L. Ewe (57° 49'N) was 16-18 h (Blaxter and Staines, 1971). Light in the tubs was enhanced by overhead fluorescent tubes set on a 14:10 h light: dark cycle.

No zooplankton was added to the bags after the stocking of the cod larvae although the originally enclosed zooplankton stocks were enhanced before larval addition with extra 68 µm

mesh netted zooplankton. In the tubs, net-caught zooplankton, filtered between 350 µm and 68 µm meshes was monitored, replenished when necessary and maintained near 300 l^{-1}. Aeration and circulation in the tubs was aided by a single airstone and 20-25% of the seawater was replaced on alternate days. There was no artificial circulation nor routine water exchange in the bags. Additions of "production water" from BP Forties Field in the North Sea were made to one bag (D) immediately after larval addition (age 1 day post-hatch) and on day 18 post-hatch. The concentration of the initial sample, 6 µm l^{-1} "oil-equivalents by fluorescence", was a 600-fold dilution of the "production water" and was aimed at simulating the conditions within 500-1000 m from a production platform. The second addition was 14 µg l^{-1}. The fluorescence method used to measure the concentration of hydrocarbons in "production water" (Davies et al., 1981) may seriously underestimate the concentration of total hydrocarbons since the major components are monoaromatic hydrocarbons, benzenes, xylenes etc. (J.M. Davies, DAFS, Aberdeen, personal communication, 1983). The second bag (C) containing cod larvae was an untreated control.

Larvae were collected at 4-day intervals in the bags at dusk using a 350 µm mesh metre plankton net hauled verically through 19 m up the centre of the bag on a counterweight system (Gamble et al., 1981). An in situ electric pump, capacity 170 $l.min^{-1}$, was also used on four dates to ascertain the depth distribution of the larvae. Plankton, including larvae, was collected in a 68 µm mesh sleeve fitted anterior to the pump. On 12 (9 day old larvae), 15 and 23 April, 2-min pump samples were taken at both the side and centre of Bag C at 1, 2.5, 7.5, 12.5 and 17.5 m depths on two occasions about 12 h apart. On 25-26 April water was pumped at the usual depths and at an additional depth, 15 m, at three times during a 24 h period, but with the pump being moved continuously across the bag at each depth. The pump was used regularly to assess zooplankton populations in both bags.

In the bags survival rates were determined from the metre net hauls while in the tubs they were estimated from the numbers of survivors at the end of the experiments. An exponential

decrease was assumed for the tub populations. In both cases adjustments were made for collection (i.e. fishing) mortality to permit estimation of expected survival rates (Ricker, 1975; Werner and Blaxter, 1980). A severe storm destroyed the bags on 3 May and all remaining larvae were lost.

Larvae collected by metre net from the bags were preserved immediately in 2% formalin:15 o/oo seawater solution (Blaxter, 1971). Larvae in a subsample of 20 randomly selected individuals, but including the largest and smallest from the haul, were measured and then freeze-dried prior to dry weight determination. A further sample of 20 individuals was taken for gut content analysis in which lengths of all food items were measured. Larvae in the tubs were sampled regularly for standard length measurement, feeding incidence and representative sizes were selected for subsequent dry weight determination. On one occasion 25 larvae at 7 days old were removed from both a Clyde and a Norwegian tub to estimate gut evacuation rate. Larvae from the pump samples in Bag C were counted only since too much damage was caused by the pump for detailed measurement or gut examination.

Material which settled into the bottom cone of the bag was pumped through a pipe to the surface. Collections of this settlement were made daily during the first two weeks of the experiment and then at two day intervals. Larval remains were removed and counted.

RESULTS

Mortality and Survival

Due to the premature storm destruction of the bags and consequent loss of surviving larvae, larval mortality rates were determined only from net sample data assuming an exponential decrease in population size. There was no significant difference ($P>>0.05$) between the two bag populations from the routine metre net hauls (Fig. 1a and Table 1), nor were there any obvious changes in mortality during the experiment. The similarity was confirmed independently by the nearly identical patterns of

fallout of dead larvae (Fig. 1b) which peaked 7 days after hatching. A secondary peak 20 days post hatch could represent fallout of larvae which failed to feed although it is later than the time of 14 days suggested by Tilseth and Strømme (1976) and by Ellertsen et al. (1980) for cod at 5°C.

Independent estimates of mortality were obtained from the pump samples (Table 1). These results confirmed the similarity between bag populations, but the slopes (mortality rates) of the zooplankton pump-sampled larvae and the metre net samples were significantly different ($p<0.01$). No significant difference was detected between the slopes of the Bag C metre net and the diurnal pump samples. The reason for the relatively high pump-sample estimates of mortality probably resulted in part from avoidance of the pump by growing larvae.

In the four tubs from 2 to 8 live larvae remained at 26-29 days after hatching (1-4%). However, because 48 to 77 of the original 200 larvae were sampled during the course of the experiment, expected survival rates were somewhat higher. Percentage daily mortality rates (M), derived from the instantaneous mortality coefficient (z), $M = 100\ (1-e^{-Z})$, together with

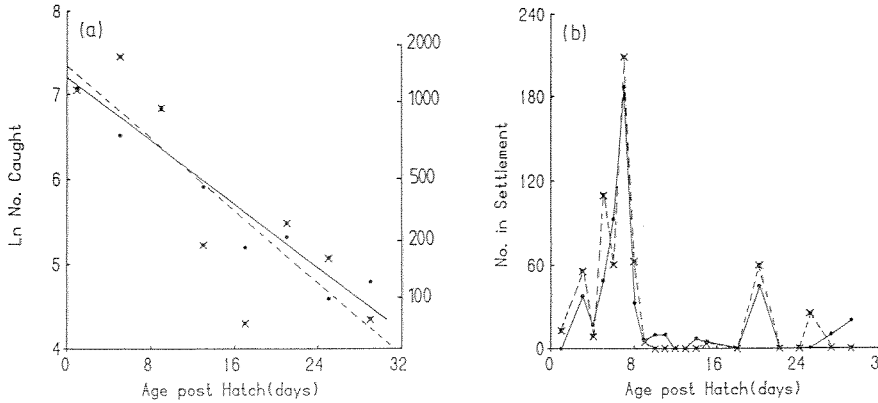

Fig. 1. Mortality of larvae in bag C (dots, continuous line) and in bag D (crosses, dashed line). (a) numbers caught in dusk metre net collections, (b) fallout of dead larvae into base of bags. Bag D was treated with oil well "production water".

TABLE 1

Bag cod larvae: regression parameters for equations relating exponential decrease in sample size with larval age (Ln Nt = LnNo - zt,t in days). S.E. - standard error.

Sampling Device	LnNo	S.E.	z	S.E.	r^2	n
Metre Net, Bag C	7.157	0.216	0.092	0.012	0.90	8
Metre Net, Bag D*	7.327	0.481	0.107	0.028	0.72	8
Pump, diurnal, Bag C	10.10	0.68	0.134	0.039	0.63	9
Pump, Zoopl. Bag C	5.15	0.39	0.184	0.020	0.83	18
Pump, Zoopl. Bag D*	5.81	0.41	0.212	0.021	0.86	18

* treated enclosure

TABLE 2

% daily mortality and % survival at 25 days post hatch in bag and tub cod larval populations.

	Bags		Tubs			
			Norway		Clyde	
	C	D*	1	2	3	4
Total Mortality	8.8	10.1	12.6	16.1	17.1	12.1
Natural Mortality	8.4	9.7	10.6	14.5	15.6	10.0
25 day Survival	10.9	7.9	6.1	2.0	1.4	7.2

* treated enclosure

the 25 day % survival, $S = 100e^{-zt}$, values are shown in Table 2; expected survival was calculated from natural mortality. There was greater mortality in the tubs than in the bags.

Growth

Growth in standard length, Fig. 2 and Table 3, was similar in bags and tubs except for tub "Clyde 3". Because the cod larvae did not grow for the first 4-6 days and were principally subsisting on yolk reserves, linear relationships adequately described the length increase of all populations from 5 day old onwards. Excluding "Clyde 3" the daily increases in standard length in the tubs were 0.080, 0.101 and 0.122 mm compared to 0.122 and 0.123 mm in the bags. Comparisons between the linear

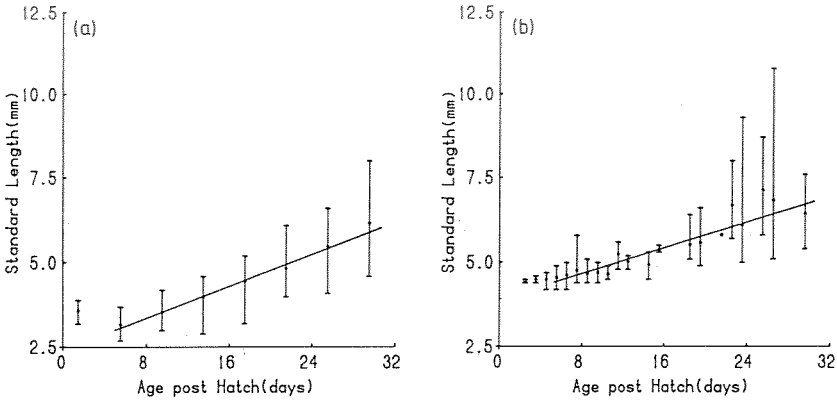

Fig. 2. Growth of cod larvae in (a) bags and (b) tubs. Combined data from each rearing system; means and absolute ranges indicated.

TABLE 3

Growth of cod larvae: regression parameters relating linear increase in standard length (mm) on age post hatch (days). Minimum age of larvae is 5 days.

	a	S.E.	b	S.E.	r^2	n
Bag C	2.384	0.109	0.122	0.006	0.76	138
Bag D*	2.487	0.100	0.123	0.005	0.80	138
Tub, Norway 1	3.937	0.303	0.122	0.187	0.50	45
Tub, Norway 2	3.921	0.151	0.101	0.012	0.68	36
Tub, Clyde 3	4.775	0.151	0.029	0.008	0.28	38
Tub, Clyde 4	3.913	0.077	0.080	0.004	0.84	58

* treated enclosure

regression slopes for growth in length of the "Norway 1", "Norway 2" and "Clyde 4" larvae only showed a significant difference ($p<0.05$) between the two extremes, "Norway 1" and "Clyde 4" (Table 3). When these tub data were combined, the slope of the common regression differed significantly ($p<0.01$) from the combined slope for bags C and D although when "Clyde 4" was omitted from the tub data combination no difference was detectable. Both the bag-reared and tub-reared larvae developed distinct size hierarchies (Fig. 2). The tub populations were

more variable and erratic than the bag populations, possibly in part due to the small samples. The growth rates of the fastest and slowest growing larvae were 0.206 and 0.065 mm d^{-1} in the bags compared with 0.295 and 0.024 mm d^{-1} in the tubs.

Dry weight increases (Table 4) also were similar between the two bag populations despite the addition of "production water" to D. Exponential relationships were fitted to the data for larvae older than 5 days after hatching, since, prior to this period, some weight loss occurred. Because nc routine measurements of dry weight of tub larvae were made, weight increases were inferred from conversion of the standard length measurements to weights using a combined length:weight relationship (Table 5). Daily specific growth rates (SGR), calculated from instantaneous growth coefficients SGR = 100 (e^{g}-1), were 10.0% and 10.4% for bags C and D respectively, 7.8% and 7.7% for the Norwegian and 1.7% and 6.0% for the Clyde tubs.

The combined length:weight power relationship of the bag larvae differed significantly in slope ($p<0.001$) and intercept ($p<0.001$) from that of the tub larvae (Table 5). However, since the bag sample included a much larger proportion of larvae with yolk sacs, which initially lost weight without increasing in length, the power relationship did not describe the length: weight relationship for the smallest individuals. When a standard length of 3.5 mm was chosen as a minimum length, the

TABLE 4

Growth of cod larvae: regression parameters relating exponential increase in dry weight (mg) on age post hatch (days). Minimum age of larvae is 6 days. Relationship: LnWt = LnWo + gt.

	LnWo	S.E.	g	S.E.	r^2	n
Bag C	-4.047	0.102	0.095	0.005	0.75	120
Bag D*	-4.024	0.092	0.099	0.005	0.80	118
Tub, Norway 1	-3.006	0.199	0.075	0.116	0.52	40
Tub, Norway 2	-3.170	0.116	0.074	0.009	0.71	31
Tub, Clyde 3	-2.423	0.077	0.017	0.006	0.18	33
Tub, Clyde 4	-3.152	0.058	0.058	0.003	0.85	53

* treated enclosure

TABLE 5

Dry weight (mg) on standard length (mm) relationship of combined populations of bag and of tub cod larvae: log 10 transformation of power relationship. (S.L. - standard length).

	log a	S.E.	b	S.E.	r^2	n
Bags C + D, all data	-2.978	0.032	3.065	0.058	0.90	317
Bags C + D, >3.5 mm S.L.	-3.347	0.042	3.587	0.063	0.93	253
Tubs 1 + 2 + 4	-3.70	0.093	3.848	0.128	0.93	67

resultant relationship had an exponent closer to that of the tub larvae (Table 5). A notable difference was observed in standard length of the youngest larvae, about 3.5 mm in the bags compared to 4.5 mm in the tubs. The larvae collected by metre net in the bags were obviously shrunken despite rapid preservation. In contrast, tub larvae which had been sampled with a beaker and fixed by addition of formalin, apparently shrunk less than bag larvae.

Food and Feeding

First indications of exogenous feeding were noted 4 days post hatch in the tubs and 5 days in the bags (Fig. 3). In both rearing systems the incidence of feeding increased with larval age although the age-related increase in feeding incidence in the daytime collections of tub larvae was greater than in the dusk-caught bag larvae. The attempt to determine diurnal feeding periodicity from the in situ pump samples was not conclusive because of gut damage. Nevertheless, the lowest incidence noted was 8.3% at 0600 h in 12 day old larvae suggesting that little feeding had ocurred in the preceeding few hours.

Gut content analyses were done only on bag larvae. We found that during the experiment the diet consisted almost entirely of calanoid copepod nauplii of which *Pseudocalanus elongatus* formed 98% of the total. Food concentrations at the onset of first feeding, days 4-5 post hatching, were about 5 and 7 nauplii l^{-1} in the two bags. *P. elongatus* formed 80% of the bag copepod naupliar population at that time. Although no gut

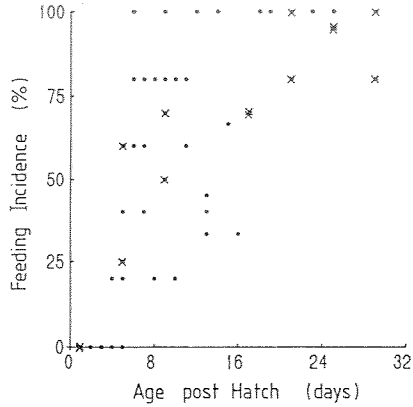

Fig. 3. Feeding incidence as determined by presence of mateial in guts of cod larvae from bags (crosses) and tubs (dots).

TABLE 6

Preference vectors, alpha (Chesson, 1978), calculated for grouped food items from guts of cod larvae from the bags. 20 larvae sampled in each bag on each occasion. Absence on any category in the guts is indicated by a dash.

Food Item	Bag	Preference Vectors at Age (days) 5	9	13	17	21	25	29
Copepod Eggs	C	0.29	0.01	0.20	-	-	-	-
	D	-	0.02	-	-	-	-	-
Copepod Nauplii	C	0.71	0.99	0.80	1.00	1.00	0.63	1.00
	D	0.52	0.53	0.15	0.86	0.93	0.90	1.00
Copepodites	C	-	-	-	-	-	-	-
	D	0.05	-	-	0.14	0.07	0.10	-
Cladocera	C	-	-	-	-	-	0.37	-
	D	-	-	-	-	-	-	-
Bivalve Veligers	C	-	-	-	-	-	-	-
	D	0.43	0.46	0.85	-	-	-	-

analyses were done on tub larvae, about 60% of the 300 food organisms l^{-1} were nauplii of *P. elongatus*.

The preference for copepod nauplii is further emphasized by the high values for Chesson's (1978) alpha listed in Table 6. Furthermore the vertical distribution patterns of cod larvae (Fig. 4) and of copepod nauplii (Fig. 5) obtained from pump sampling both endorsed the view that the larvae must have been selecting *P. elongatus* nauplii. While the cod larvae showed a distinct preference for the shallower regions of the water column, from the surface to 7.5 m depth, the nauplii were much more evenly distributed or concentrated below 12.5 m depth. There was also no detectable difference between the abundance of cod larvae at the side of the bag (44.7%) compared with the centre (55.3%).

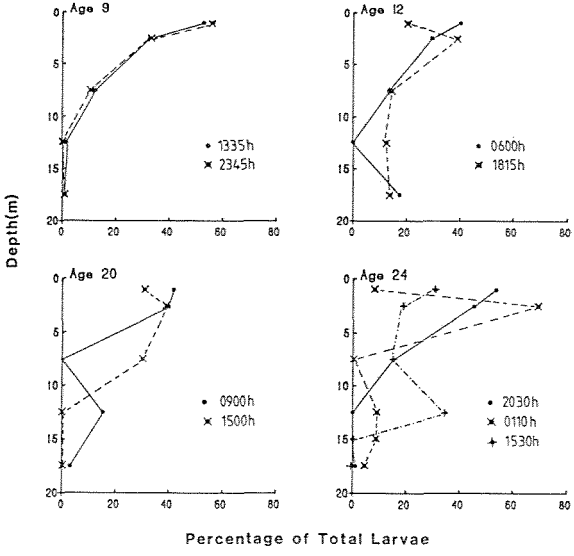

Fig. 4. Vertical distribution patterns of cod larvae on four different occasions (days post hatch) in bag C as determined by pump.

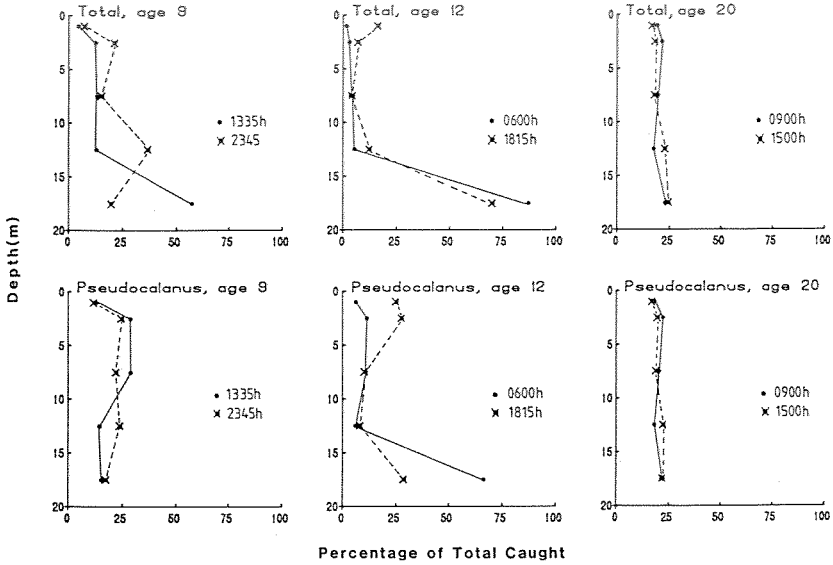

Fig. 5. Vertical distribution patterns of all copepod nauplii and of *P. elongatus* nauplii in Bag C on three separate occasions. Days and times of sampling refer to age of cod larvae specified in Fig. 4.

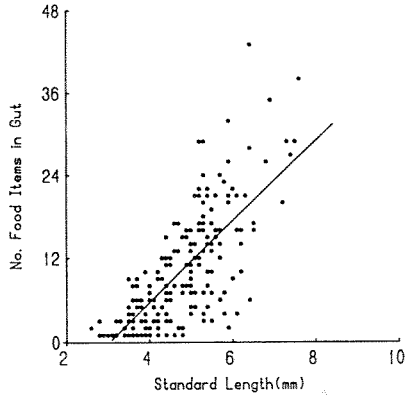

Fig. 6. Number of individual food items in guts of bag cod larvae collected at dusk.

Gut fullness, defined as numbers of items per gut increased with larval size (fig. 6). A linear regression was fitted to the highly variable data:
no. food items = -18.5 + 6.02 x standard length (mm), r^2 = 0.53. Gut contents increased by 6 items, on average, per mm increase in length. The preference for *P. elongatus* nauplii facilitated estimation of weight of gut contents using the naupliar length:dry weight relationship of Klein-Breteler et al. (1982):
$\log_{10}$ naupliar dry weight (µg) = -5.57 + 2.27 x $\log_{10}$ carapace length (µm).
The calculated relationship between weight of gut contents and cod larval dry weight was:
dry weight gut contents (µg) = -1.19 + 62.83 x dry weight larva (mg), r^2 = 0.64. Thus on average about 6% of the total dry weight of a cod larva at that time of day would be gut contents.

The dry weight relationship also incorporated increase in size of maximum food item with increasing size of larva (Fig. 7). While there was an obvious positive relationship for the smaller larvae, the food item size range was limited by the maximum size of the *P. elongatus* nauplii. The few items longer than 0.40 mm were copepod stages. The relationship between dry weight of gut contents and larval age (Fig. 8) also was variable; the data appear to mirror the progressive hierarchical structure of the enclosed populations. A good relationship between maximum gut content weight and larval age was observed in Fig. 8. The power function describing it was:
Max. weight of gut content (µg) = 0.057 x larval age(d)$^{1.89}$, r^2 = 0.9.

Zooplankton

The most abundant organisms were copepod nauplii whose numbers in both enclosures generally increased throughout the experiment from 6-40 individuals l^{-1}. However, for a very short period, about 4 days in each enclosure, very large

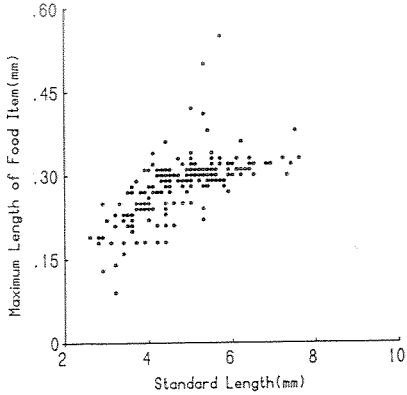

Fig. 7. Size of largest food item in the guts of individual cod larvae.

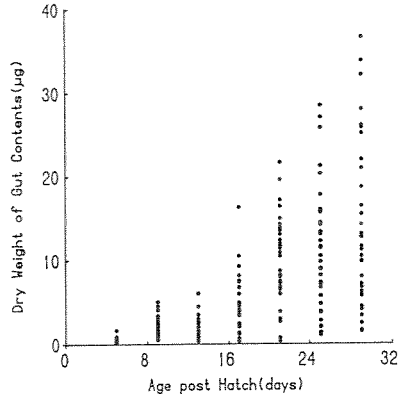

Fig. 8. Dry weight of gut contents in relation to age of cod larvae.

samples (up to 200 l^{-1}) of stage 1 (N1) nauplii of *Temora longicornis* were collected from the base of the bags. It was suspected that these were from a synchronous hatch of eggs but the nauplii neither appeared to survive nor were they identified in the gut contents of the cod larvae. Other mesozooplanktonic organisms; mostly copepodites, cirripede nauplii and cyprids, cladocera and bivalve veligers, were at least an order of magnitude less abundant than the copepod nauplii and their population levels in both bags tended to decline throughout the experiment. The bag zooplankton populations were very similar throughout despite the addition of "production water".

Copepod nauplii comprised about 60%, by number, of the zooplankton population in the tubs. Although the population was maintained at a nominal 300 individuals l^{-1}, as sampled, ranged between 150 and 450 l^{-1}.

Some potential invertebrate predators of cod larvae were present in the bags. Commonest were *Pleurobrachia pileus*, *sarsia tubulosa* and *Lizzia blondina*. The largest were *Pleurobrachia* which ranged in size from 3-12 mm in polar length and which maintained their numbers in both bags at 1-2 m^{-3}. Of the two hydromedusae, *Sarsia* was much larger, up to 15 mm bell height, but was less abundant averaging 0.3 m^{-3} in both enclosures. The much smaller *Lizzia*, with a maximum bell height of 2 mm, increased from 1 m^{-3} to 7 m^{-3} and 17 m^{-3} in bags C and D respectively during the experiment.

DISCUSSION

The cod larvae in the bag, as previously observed with herring (MacLachlan et al., 1981) were not discernably affected by exposure to oil well "production water". Such results suggest that "production water" at realistic dilution levels might not be a critical factor affecting the recruitment of cod in the sea.

Survival of cod larvae was better in the bags than in the tubs, especially the Norwegian larvae. This was despite the

presence in the bags of the *Pleurobrachia pileus*, the *Lizzia blondina* and other planktonic predators of fish larvae (Lebour, 1923; Fraser, 1969). In recent large impoundment experiments Øiestad and Kvenseth (1981) noted that larval cod mortality levels could be related to the abundance of gelatinous predators.

In the Flødevigen enclosures Ellertsen et al. (1981a), observed low larval cod mortality over the 130-180 day long experiments, but they noted a much higher initial rate, about 10% daily, during the first 15 days after hatching. When calculated over a 25 day period, survival of three separate groups was approximately 8%, 13.5% and 22% which, on average, was better than we observed in the L. Ewe bags. The higher mortality rate in the tubs is more difficult to explain; there appeared to be more deaths initially and towards the end of the experiment larger larvae seemed to be "stalking" the smaller ones, but no acts of cannibalism were observed.

Larvae from the Norwegian cod eggs grew better than those from Clyde cod eggs in the tub experiments. Because only two females were tested from each source it is premature to conclude that Norwegian larvae have a better potential for growth, but the preliminary result encourages further experiments to determine whether there might be differences in viability or growth potential of larvae between cod stocks. The enclosures had been stocked mostly with Norwegian larvae from the same females used in the tub experiments. Thus, survival and growth comparisons between the systems are most appropriate considering only the Norwegian larvae from the tub experiments. Growth of Norwegian tub larvae was approximately equal to that of bag larvae while Clyde tub larvae grew at slower rates.

We were surprised that the growth rates in the tubs and bags were similar (Table 3) despite the differences in food concentration of one or two orders of magnitude (bags increasing from 6 to 40 individuals l^{-1} during the experiment, tubs averaging 300 individuals l^{-1}). Our tub larvae grew well, giving a daily SGR of 6-8% at 5.5-11.0°C and nominal food concentration of 0.3 plankton ml^{-1} compared to daily SGR of 8.8% at 10°C at 2-3 plankton ml^{-1} (Laurence, 1978) and 2.8%, 4.7%

and 7.8% daily SGR values measured by Laurence et al. (1981) for cod larvae at 7°C and food levels of 0.5, 1.0 and 3.0 items ml^{-1} respectively. Our better growth rates at the low food concentration could have been due in part to a longer light period, about 14 h, compared to 12 h in Laurence's experiments.

The most striking feature of the cod larval growth in the enclosures was the similarity between the systems. The growth rates obtained in our bags, 10.0% and 10.4% daily SGR, were higher over a 28 day period than the daily rates measured in the Fløde vigen enclosure experiments in 1976, SGR 6.2%, and in 1977 (no. 1), SGR 6.0% (Ellertsen et al., 1981a). In the L. Ewe bags more food was available since the zooplankton levels in Fløde vigen remained below 4 l^{-1}.

It is evident from Houde's (1978) results and others that improved techniques and husbandry can reduce the supposed critical food levels to less than the nominal 1.0 ml^{-1} believed necessary to ensure larval survival in laboratory studies (Hunter, 1981). We reared cod larvae in 30 l tubs at 0.3 food items ml^{-1}, which Laurence et al. (1981) found marginal for survival. The high survival in the bags, and in other large scale experiments (Øiestad, 1982), is evidence that fish larvae can survive and grow well at average natural food concentrations. We searched for patchy distribution patterns of preferred food items with the pump sampler but only detected localised populations of N1 nauplii, especially *Temora longicornis*, hatching from eggs sedimented on the bottom of the bags (Fig. 4). Such small nauplii, however, were not noted in the gut contents. Hence we conclude along with Ellertsen et al. (1981a) that the feeding performance of cod larvae in large systems, like that of herring (Gamble et al., 1981), is better than that predicted from laboratory observations and we infer that chance encounters with favourable patches of food may not be essential to ensure larval survival.

The preference of the cod larvae in the bags for the upper part of the water column parallels field observations made, for example, by Ellertsen et al. (1981b) in which most first-feed-

ing cod larvae were in the top 20 m. The dominant food items in the guts of bag cod larvae, *Pseudocalanus elongatus* nauplii, were not similarly distributed (Fig. 4). These relative distribution patterns together with the consistent high preference vectors for copepod nauplii (Table 6) suggest selective predation by the cod larvae. Copepod nauplii are the predominant food of young cod larvae in the sea (e.g. Wiborg, 1948; Marak, 1960; Sherman et al., 1981) although, in many cases, the nauplii of *Calanus finmarchicus* were most common (Ellertsen et al., 1981b). Comparison with gut contents of herring larvae reared previously in bags (Gamble et al., 1981; MacLachlan et al., 1981) demonstrated the dietary specificity of cod larvae. Herring invariably commenced feeding on copepod nauplii but rapidly graduated to larger and more varied food items.

ACKNOWLEDGEMENTS

We would like to thank Snorre Tilseth of the Institute of Marine Research, Bergen for his generosity in providing us with fertilized cod eggs. We are also indepted to the members of the Plankton Section, Marine Laboratory, Aberdeen who contributed to these experiments. Norman Nicoll identified the cod larval gut contents while Audrey Smith was responsible for the zooplankton analysis. Duncan Seaton and Tony Hawkins critically commented on the manuscript.

REFERENCES

Blaxter, J.H.S., 1971. Feeding and condition of Clyde herring larvae. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 160: 128-136.

Blaxter, J.H.S. and Staines, M.E., 1971. Food searching potential in marine fish larvae. In: D.J. Crisp (Editor), Fourth European Marine Biology Symposium, Cambridge University Press, Cambridge, pp. 467-485.

Chesson, J., 1978. Measuring preference in selective predation. Ecology, 59: 211-215.

Davies, J.M. and Gamble, J.C., 1979. Experiments with large enclosed ecosystems. Phil. Trans. R. Soc. Lond. B, 286: 523-544.

Davies, J.M., Baird, I.E., Massie. L.C., Hay, S.J. and Ward, A.P., 1980. Some effects of oil-derived hydrocarbons on a pelagic food web from observations in an enclosed ecosystem and a consideration of their implication for monitoring. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 179: 201-211.

Davies, J.M., Hardy, R. and McIntyre, A.D., 1981. Environmental effects of North Sea oil operations. Mar. Poll. Bull., 12: 412-416.

Ellertsen, B., Moksness, E., Solemdal, P., Strømme, T., Tilseth, S., Westgård, T. and Øiestad, V., 1980. Some biological aspects of cod larvae (*Gadus morhua* L.). FiskDir. Skr. Ser. HavUnders., 17: 29-47.

Ellertsen, B., Moksness, E., Solemdal, P., Tilseth, S., Westgård, T. and Øiestad, V., 1981a. Growth and survival of cod larvae in an enclosure. Experiments and a mathematical model. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 178: 45-57.

Ellertsen, B., Solemdal, P., Sundby, S., Tileth, S., Westgård, T. and Øiestad, V., 1981b. Feeding and vertical distribution of cod larvae in relation to availability of prey organisms. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 178: 317-320.

Fraser, J.H., 1969. Experimental feeding of some medusae and chaetognatha. J. Fish. Res. Board Can., 26: 1743-1762.

Gamble, J.C. and Davies, J.M., 1982. Application of enclosures to the study of marine pelagic systems. In: G.D. Grice and M.R. Reeve (Editors), Marine Mesocosms. Biological and chemical research in experimental systems. Springer-Verlag, New York, pp. 25-48.

Gamble, J.C., Davies, J.M. and Steele, J.H., 1977. Loch Ewe bag experiment, 1974. Bull. Mar. Sci., 27: 146-175.

Gamble, J.C., MacLachlan, P., Nicoll, N.T. and Baxter, I.G., 1981. Growth and feeding in Atlantic herring larvae reared in large plastic enclosures. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 178: 121-134.

Houde, E.D., 1978. Critical food concentrations for larvae of three species of subtropical marine fishes. Bull. Mar. Sci., 28: 395-411.

Hunter, J.R., 1981. Feeding ecology and predation of marine fish larvae. In: R. Lasker (Editor), Marine fish larvae. Morphology, ecology and relation to fisheries. Washington Sea Grant Program. University of Washington Press, Seattle, pp. 33-77.

Klein-Breteler, W.C.M., Fransz, H.G. and Gonzalez, S.R., 1982. Growth and development of four calanoid copepod species under experimental and natural conditions. Neth. J. Sea Res., 16: 195-207.

Laurence, G.C., 1978. Comparative growth, respiration and delayed feeding abilities of larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as influenced by temperature during laboratory studies. Mar. Biol., 50: 1-8.

Laurence, G.C., Smigielski, A.S., Halavik, T.A. and Burns, B.R., 1981. Implications of direct competition between larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in laboratory growth and survival studies at different food densities. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 178: 304-311.

Lebour, M.V., 1923. The food of plankton organisms. II. J. mar. biol. Ass. U.K., 13: 70-92.

MacLachlan, P., Seaton, D.D. and Gamble, J.C., 1981. Developmental patterns of experimentally enclosed populations of autums and spring spawned Atlantic herring larvae. Coun. Meet. int. Coun. Explor. Sea, 1981 (L:21): 1-7 (Mimeo.)

Marak, R.R., 1960. Food habits of larval cod, haddock and coalfish in the Gulf of Maine and Georges Bank area. J. Cons. perm. int. Explor. Mer, 25: 147-157.

Menzel, D.W. and Steele, J.H., 1978. The application of plastic enclosures to the study of pelagic marine biota. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 173: 7-12.

Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can., 191: 1-382.

Sherman, K., Maurer, R., Byron, R. and Green, J., 1981. Relationship between larval fish communities and zooplankton prey species in an offshore spawning ground. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 178: 289-294.

Steele, J.H., 1979. The uses of experimental ecosystems. Phil. Trans. R. Soc. Lond. B, 286: 583-595.

Tilseth, S. and Strømme, T., 1976. Changes in buoyancy and activity during starvation of cod larvae (*Gadus morhua* L.) Coun. Meet. int. Coun. Explor. Sea, 1976 (F:33): 1-12 (Mimeo.)

Wiborg, K.F., 1948. Investigations on cod larvae in coastal waters of Northern Norway. Occurrence of cod larvae and occurrence of food organisms in the stomach contents and in the sea. FiskDir. Skr. Ser. HavUnders., 9: 1-26.

Werner, R.G. and Blaxter, J.H.S., 1980. Growth and survival of larval herring (*Clupea harengus*) in relation to prey density. Can. J. Fish. Aquat. Sci., 37: 1063-1069.

Øiestad, V., 1982. Application of enclosures to studies on the early life history of fishes. In: G.D. Grice and M.R. Reeve (Editors), Marine Mesocosms. Biological and chemical research in experimental systems. Springer-Verlag, New York, pp. 49-62.

Øiestad, V. and Kvenseth, P.G., 1981. Large-scale rearing of cod fry (*Gadus morhua*) in an inlet. Coun. Meet. int. Coun. Explor. Sea, 1981 (F:1): 1-6 (Mimeo.)