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SURVIVAL AND GROWTH OF TURBOT (*SCOPHTHALMUS MAXIMUS* L.) IN A LAND-SITUATED MESOCOSM

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ABSTRACT

Danielssen, D.S., Haugen, A.S. and Øiestad, V. 1990. Survival and growth of turbot (*Scophthalmus maximus* L.) in a land-situated mesocosm. Flødevigen rapportser. 2, 1990: 11-45.

A mesocosm study of turbot larvae was undertaken in a 2000 m^3 outdoor basin into which 15000 yolk sac larvae were released. Scarce food supply during first feeding gave high initial mortality and only 10% survived the first 10 days. The diet was dominated by nauplii through first feeding followed by a swift change to larger food items, mainly calanoid copepods. These were replaced from day 20 onwards by juvenile amphipods. The surviving turbot were distributed in the surface layer from day 15 until the onset of settlement on day 25. Standard length increased from 3 mm at release to 20 mm on day 30, and during the same period the dry weight increased from 0.030 mg to 32 mg. At termination on day 74, standard length was 38 mm and mean dry weight was 340 mg (wet weight being 1.9 g) with 600 juvenile turbot surviving to this stage (4%). All juveniles were normally pigmented and without any deformations.

INTRODUCTION

"What is left to be done in the culture of turbot?". The question has been echoing to us from the turn of the century, and it has taken almost 80 years to give a real answer. The question reflected the recent advances with turbot rearing at that time (Anthony 1910). The main achievements were:

- appropriate handling of the broodstock gave naturally fertilized eggs
- hatching was successful

- the first rearing experiment with larvae gave 90% survival through what was called a critical stage.

Anthony had reason to be optimistic and he saw the contours of a new industry and presented his vision at the Fourth International Fishery Congress in Washington in September 1908 (Anthony loc.cit.).

It is incredible that the next publication on the rearing of turbot (Jones 1972) appeared only after more than 60 years had elapsed. It represented the introduction to a new era for turbot culture. Within few years a number of European countries had their own turbot rearing programme.

Except for the cod larval release programme started in 1884, only minor Norwegian activity on rearing of marine fish species took place until a new fish larvae research programme was initiated in 1975. The research strategy in that programme deviated partly from the international approach in that large experimental ecosystems in out-door enclosures were applied to the study of the basic requirements for larval survival. As a spin-off from these studies, the research team postulated that these methods could be applied to the large-scale rearing of juveniles for aquaculture purposes (Øiestad et al. 1976).

The enclosure represents an ecosystem and as such contains the different trophic levels with their food web relations (Grice and Reeve 1982). The main strength of the method is that it represents a close-to-field situation, with an opportunity to sample on a true continuum population at all trophic levels. Application of mesocosms to the study of marine fish larvae has traditions in Norway (Rognerud 1887, Rollefsen 1946), and the method has gained a new momentum since transitional studies in early life history of fishes were recommended by an expert group in 1975 (Hunter 1976). While the CEPEX mesocosm programme active at that time mainly concentrated their attention on primary and secondary production (Reeve et al. 1982), a number of other studies have concentrated on fish larvae. Many of these have been reviewed by Lafontaine and Leggett (1987) and Øiestad (1990).

Most studies have been undertaken in water masses with a vertical axis, as in floating plastic bags, but as turbot larvae have a rather restricted vertical distribution, studies in systems with a horizontal axis seem more appropriate.

From 1975 to 1980, mesocosm studies in land-situated basins were carried out with a number of marine fish species at the Flødevigen Marine Research Station (Danielssen et al. 1981, Ellertsen et al. 1981, Moksness

1982, Øiestad 1983, Øiestad et al. 1976, Øiestad et al. 1978, Øiestad and Moksness 1981), but only one of these fish species was a premium aquaculture candidate, namely turbot. Preliminary plastic bag experiments with turbot larvae at the station in 1978 and 1979 had been fairly successful. As a consequence, basin studies were planned for 1980 at the station on larvae supplied from Scotland as no turbot broodstock was available in Norway.

MATERIALS AND METHODS

The study was carried out in a land-situated basin at Flødevigen Marine Research Station outside Arendal. The basin contained 2000 m^3 of sea water, had a surface area of 600 m^2 and a maximum depth of 5 m (Fig. 1). For a full description, see Moksness (1982).

The turbot larvae arrived on July 8 from the White Fish Authority (now the Sea Fish Industry Authority), Marine Farming Unit, Hunterston, Scotland. The eggs were fertilized on July 2 and hatched on July 7 (day 0). On day two, an estimated 15000 larvae, still with some yolk remaining, were released in the basin, while eight control groups each with 100 larvae were stocked in 5-l jars without food supply in the laboratory at the same temperature as at 1 m depth in the basin.

A monitoring programme was performed weekly (Table 1). This programme included measurements of temperature, salinity and oxygen content. Pump sampling for microzooplankton was carried out at two positions in the basin (stations A and B; Fig. 1). At station A, samples were taken at seven depths (0.0 m, 0.5, 1.0, 2.0, 3.0, 10 cm above bottom and at the bottom). At station B the 3.0 m sample was omitted. Sea water was filtered through 90 µm mesh size during 30 s pumping time (capacity 75 l/min). Net hauls were carried out daily for the first fortnight along one of two transects (Fig. 1), though occasionally net-hauls were taken along both. From day 2 to 5 a small net (350 µm, 0.1 m^2) and a large double-chambered net (500 µm, 0.5 m^2) were used. From day 6 only the larger net was used. The net hauls were normally taken at four depths (0.0, 1.0, 2.0 and 3.0 m depth) for sampling of fish larvae and macrozooplankton.

Net sampling continued every 3rd or 4th day from day 14 to day 28 when the fish disappeared from the samples. Subsequently, samples were taken only on days 37, 58 and 70 to sample macrozooplankton. Most of

Table 1

Sampling programme for hydrographic data and micro- and macro-zooplankton (net haul: number of net hauls indicated) relative to age of turbot larvae and number of turbot larvae caught with net type indicated (350µm and 500 µm).

Age in days	Hydrogr.	Zooplankton Pump	Zooplankton Net haul	Turbot larvae 350 µm	Turbot larvae 500µm
2	x	x	4	80	
3			15	382(24h)	
4			11	80	153
5			10	16	375
6			9		202
7	x	x	20		296 (24h)
8			10		261 (24h)
9			10		157
10			5		64
11			9		212
12			2		16
13			3		52
14			2		21
15	x	x			
17			10		60
21	x	x	11		22
24			2		11
28	x	x	3	10*	4
37	x	x		10*	
51	x	x			
58			4		
59	x	x			
70	x	x	4		

* On day 28 and 37 10 larvae were caught with dipnet

the samples were taken at 0900 h, 1500 h and 2100 h with two sets of around-the-clock sampling at 3 hour intervals (days 3 to 4 and 7 to 8).

The volume sampled was calculated as the product of haul distance (Fig. 1) and the area of the net opening. No allowance is made for the resistence of the net to less water filtered. The estimated concentations of zooplankton are therefore somewhat underestimated. Allocated volume to each depth range for standing stock calculations were:

Depth range (m):	0.0-0.5	0.5-1.5	1.5-2.5	2.5-3.5	3.5-4.5	4.5-5.0
Volume (m^3):	350	640	530	360	100	20

The bottom was partly gravel, sand and mud (Fig. 1) while the walls were made of concrete and rock. Water was exchanged at a rate of 2-3%

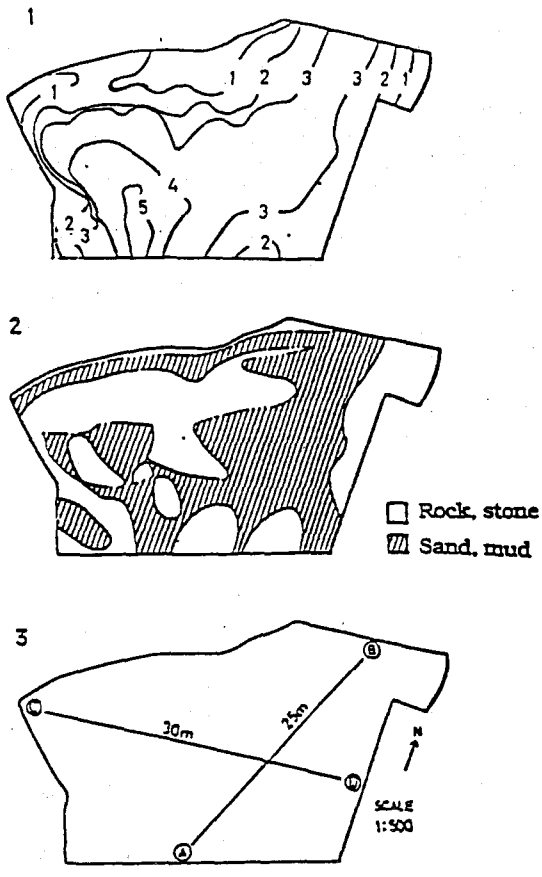

Fig. 1. Indication of bottom depth (1) and bottom types (2) in the basin. The positions of the pump sampling stations (A and B) and the net haul distances, A>B and C>D are also given (3); (modified from Moksness 1982).

per day with water from 75 m depth outside the station, having a temperature initially of 8°C increasing to 11.7°C and a salinity of about 34‰.

At the end of the study the basin was drained and on day 74 all surviving juveniles were collected from the bottom of the basin. No other fish species were observed in the basin.

All larvae were preserved in 4% neutral formalin. Most of the 2 500 preserved larvae had their standard length measured and 700 had their dry weight determined (±1 µg) after being rinsed in distilled water and dried for 24 hours at 80°C. Altogether 700 larvae were gutted and all food items were identified and classified to species or groups. The length of a representative number of prey organisms were measured. The development stage of each larva was recorded in accordance with the following

scheme (modified from Ryland 1966):
1: yolk sac present or resorbed, no fin rays
2: fin rays present, but caudal of notochord unbent
3: caudal of notochord bent, no eye displacement, premetamorphosis
4: right eye in movement, but not in final position, metamorphosing
5: right eye in final position, postmetamorphosis

Transition to a stage was defined as the day when at least 50% of the larvae had reached that stage.

Standard length is given unless otherwise indicated. The mouth gape was measured as the distance between the upper jaw and the jaw hinge perpendicular to the body axis.

Examination for phytoplankton in the gut was carried out on 20 larvae on day 4 in addition to the ordinary gutting program. In addition, the otoliths of 10 larvae were examined on that day and following days until day 12. These results have been published separately by Rosenberg and Haugen (1982).

Zooplankton organisms in pump samples and net samples were also examined and classified to species or families and with intervals sub-samples were length-measured. Calanoid copepodites were not stage determined. Dry weight calculations from length measurements of prey organisms in the gut were carried out according to these equations:

$W = 4\ TL^{1.65}$

for nauplii of calanoid copepods (Laurence 1976, Miller et al. 1977) where TL is the total length;

$W = 10\ CL^{2.6}$

for juvenile and adult stages of calanoid copepods (Allen et al. 1977, Bogorov 1959), where CL is the length of cephalotorax;

$W = 5.76\ TL^{2.65}$

for all cladocera (Bottrell et al. 1976) and

$W = 3.8\ TL^{2.8}$

for amphipods (Øiestad 1983).

Dry weights were converted to calories assuming an equivalence of 1 g dry wt to 5000 cal (Laurence 1977). The instantaneous daily growth coefficient, G, was calculated from the equation (Ricker 1958):

$W_t = W_0\ e^{Gt}$

W_t = dry weight at day t

W_0 = dry weight at day 0

t = number of days between day t and day 0

Percent daily weight gains, SGR, were calculated as:

$100\ (e^{G}-1)$ (Houde and Schekter 1983).

Daily ration and ration as percent of body weight has been calculated from larval growth data applying a gross growth efficiency (K_1) of 40% (Houde and Schekter loc.cit.).

The survival curve was calculated by use of least square regression. Input data to the curve were the number transferred on day 2, the number alive at termination on day 74, and population estimates from net haul samples. The resulting function described a sigmoid function:

$$N_t = N_o \cdot e^{k_1 (1-e^{-k_2 \cdot t})}$$

N_t = number of larvae at day t

N_o = number of larvae at day 0

t = number of days between day t and day 0

and k_1 and k_2 are constants determined by the regression.

RESULTS

Hydrographic conditions

In the upper meter, the temperature was between 19 and 21°C until the turbot larvae metamorphosed. The thermocline was at a depth of 2-3 m (Fig. 2A). The temperature gradient between the surface and the bottom (5 m) was initially about 10°C, but had declined to 6°C when the turbot started settling on the bottom. The gradient was gradually reduced from day 40, and at termination on September 20 no gradient was observed.

The seawater was initially supersaturated with oxygen from 4 m to the surface, with a gradual reduction to day 40 (Fig. 2B). A supersaturation of 150% was observed at 1 m depth in early July. From day 50 the oxygen saturation in the deeper part of the basin was below 50%.

The salinity was between 33 and 34‰ throughout the study, except in the surface layer where it occasionally decreased to 27‰ after rainfall.

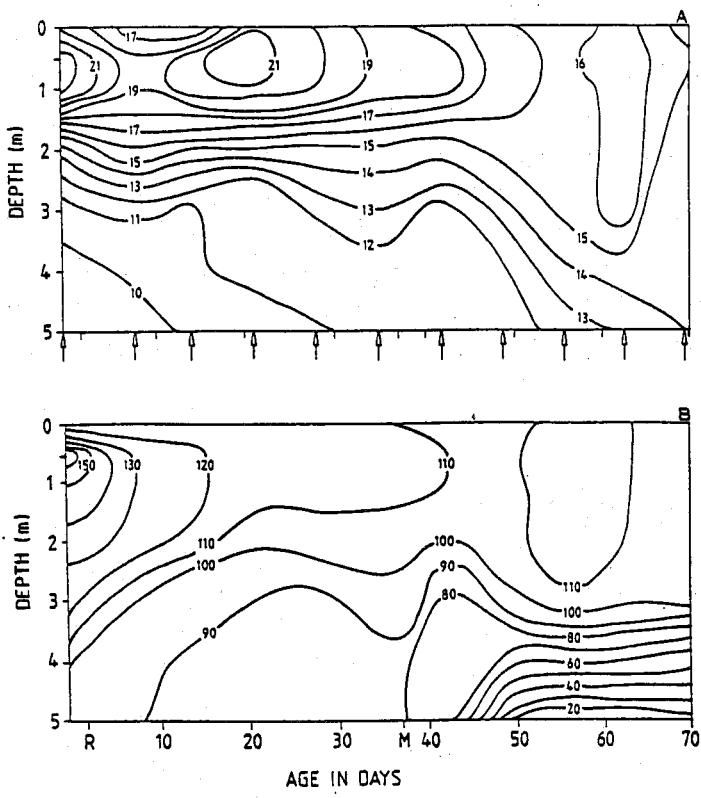

Fig. 2. Isoplet diagram from day 2 to 70 from the surface to 5 m depth of temperature (A) and oxygen saturation (B). R: day of release; M: mean day of metamorphosis. Arrows indicate days of sampling.

Zooplankton composition and densities

Ten different pelagic or semipelagic species dominated in the basin, but some of them, such as amphipods and *Sarsia tubulosa*, were at such a low density that they were only sampled representatively with net hauls. There could also be large differences in density between day and night samples among semipelagic organisms like amphipods and harpacticoid copepods.

S. tubulosa had a stable mean density of about $10/m^3$. During daytime they had a deeper distribution than during night time. The amphipod, *Gammarus* spp., occurred normally in low densities ($1\text{-}5/m^3$) during daytime, but at densities from $20\text{-}40/m^3$ around day 20. During night time in mid-July (on day 7) more than $400/m^3$ were observed in the surface whereas during the day there had been only $3/m^3$.

Podon spp. contributed during the first 30 days of the study with densities of 1-3/m^3, as determined by the net hauls. Then they disappeared from the basin.

The main calanoid copepods were *Centropages hamatus* and *Acartia* spp., while *Eurytemora* spp. contributed in low numbers. For the first two weeks, *C. hamatus* made up more than 60% of the standing stock while *Acartia* spp. had a similar strength from day 20 and onwards (Fig. 3). *Eurytemora* spp. contributed occasionally with more than 5%. As nauplii and copepodites were not allocated to species, the population dynamics of each species could not be described.

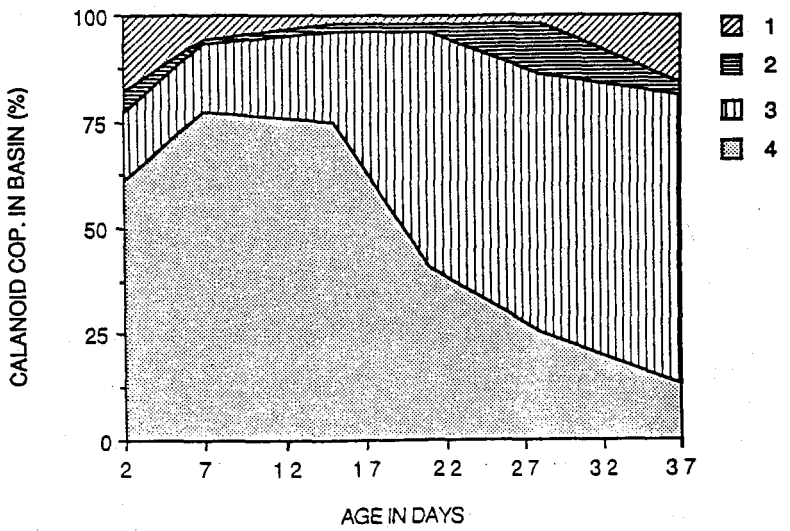

Fig. 3. Juvenile and adult calanoid copepods in the basin from day 2 to day 37. 1: Juveniles; 2: *Eurytemora* spp.; 3: *Acartia* spp.; 4: *Centropages hamatus*.

The mean nauplii density declined from 5/l during first feeding to a stable level of 2/l until day 28 followed by an increase to more than 10/l on day 60 (Fig. 4).

Calanoid copepods had a mean density of 7/l during first feeding declining to 4/l on day 21 followed by a further decline to almost zero on day 45, with a sudden and sharp increase during the next fortnight to more than 15/l.

Harpacticoid and cyclopoid copepods, as well as gastropod larvae, occurred at densities below 1/l during the whole period (Fig. 4).

The most numerous organism in the basin was spionid nectochaeta, a polychaete species, with mean densities fluctuating between 20 and 100/l during the first 50 days, followed by an abrupt decline to a level between 10 and 15/l. This organism had its main distribution close to the bottom below the thermocline with densities above the thermocline being between 0.3 and 3/l.

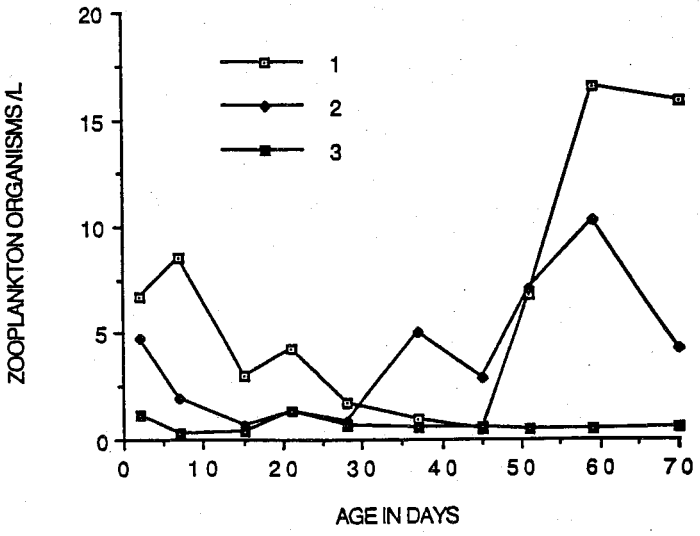

Fig. 4. Mean density per liter of zooplankton organisms in the basin from day 2 to 70. 1: nauplii of calanoid copepods; 2: juvenile and adult calanoids; 3: sum of harpacticoid and cyclopoid copepods and gastropod larvae.

Maximum densities of nauplii were observed in 2-3 m depth during first feeding and the following week with a maximum value of 15 nauplii/l. Mean densities in the upper 1 m were below 1/l in the same period (Fig. 5).

Larval distribution and behaviour

The turbot larvae had a shallow distribution from the very day of release with the majority in the depth range from 0-1 m (Table 2). From day 15 onwards larvae were observed close to the surface often with a rather patchy distribution. These aggregates moved slowly clockwise from the east side to the west side during the day. The larvae did not have a

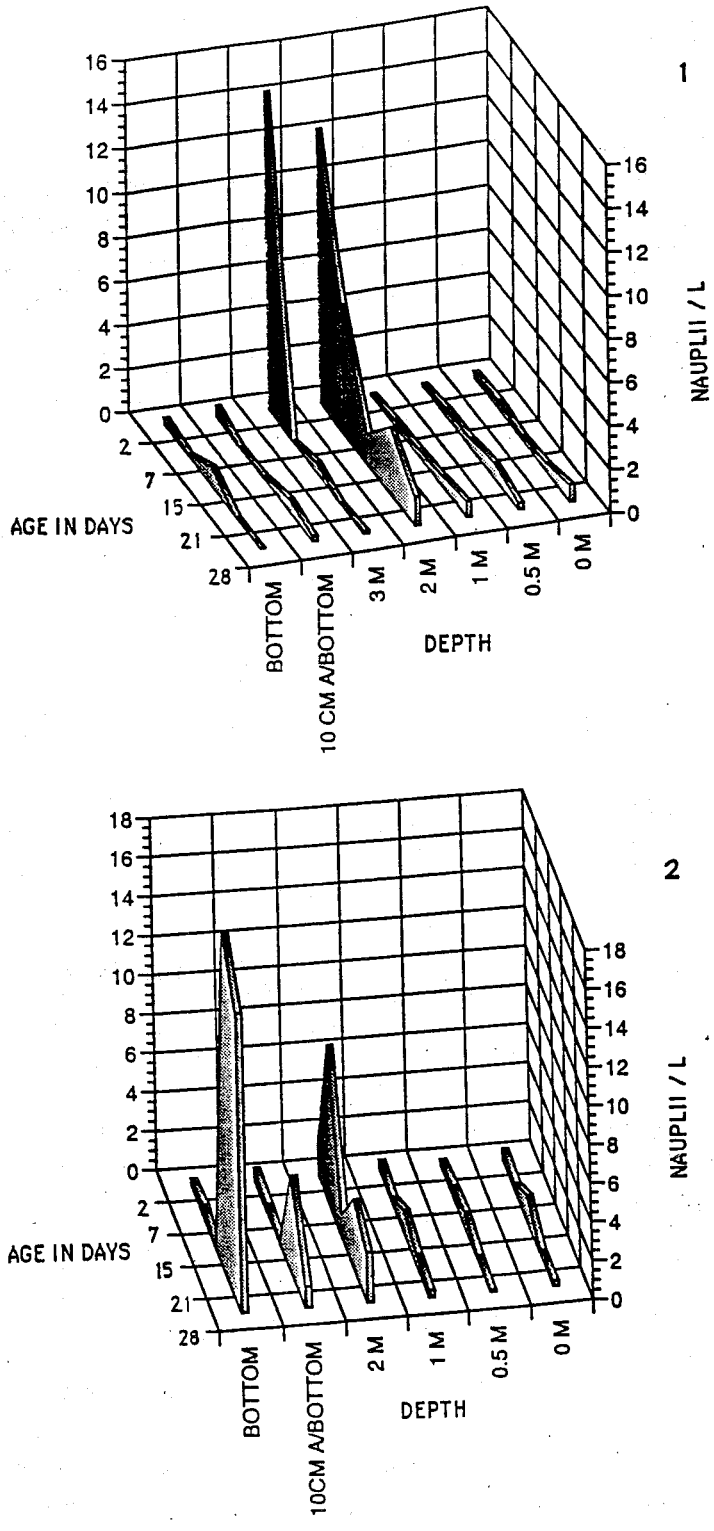

Fig. 5. Number of nauplii per litre in different depths from day 2 to day 28 at station A (1) and station B (2).

true schooling behaviour. They swam continuously and stopped from time to time for inspection of particles and made short bursts to attack food organisms. From day 30 they were more homogenously distributed in the surface layer, and during the next week the number declined sharply as they settled to the bottom.

Escape behaviour was very weak in the early stages and they could easily be netted from the surface, but as they approached metamorphosis, their ability to avoid capture improved radically.

Table 2

Vertical distribution of turbot larvae, percent of larvae with yolk sac and feeding incidence.

Age in days	Vertical distribution (%) 0 and 1 m	2 and 3 m	Yolk sac (%)	Feeding incidence (%)	Number examined
2	94	6	100	0	80
3	95	5	22	20	376
4	91	9	0	67	233
5	100	0	0	86	386
6	53	47	0	96	198
7	83	17	0	94	288
8	72	28	0	97	230
9	58	42	0	98	155
10	80	20	0	100	64

Standing stock estimates

Population estimates on day 3 and 4 were at the level of the initial population (Fig. 6). On day 8, while total mortality was observed in the control groups in the laboratory due to starvation, a population estimate from the basin indicated about 30% survival. Later estimates indicated a further decline giving a final survival on September 20 of 600 juvenile turbot (4%) without correction for the 2500 larvae sampled during the first 37 days.

The survival curve for the control groups in the laboratory is shown in Fig. 6. The calculated values of the standing stock of turbot larvae in the basin have been fitted to a survival curve (Fig. 6). The fitted curve to these points is described by the following equation which estimates the population for the whole experimental period:

$$N_t = 15000 - e^{9.57(1-e^{-0.438 \cdot t})}$$

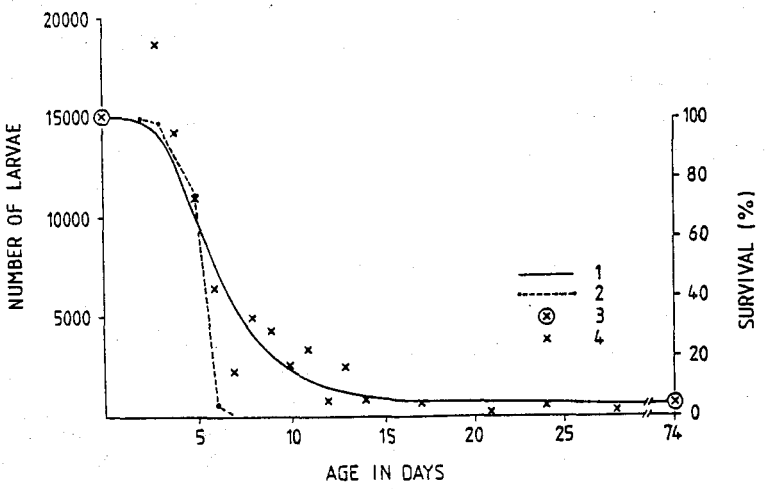

Fig. 6. Calculated survival curve for turbot larvae shown by solid line (1) while dashed line (2) indicates percentage survival of the starvation control groups in the laboratory. Number of released larvae on day 1 (15000), and surviving juveniles on day 74 (600) indicated by (3) and calculated standing stock from net hauls (4).

The instantaneous daily mortality rate, Z, has been calculated and was about 25% per day for almost a week, starting on day 5 (Fig. 7). The mortality rate after two weeks was negligible.

STAGES AND SWIMBLADDER DEVELOPMENT

Turbot larvae experience a spectacular transformation of their organs and body shape during the pelagic stage. The first major event is the formation of a swimbladder. It was not detected on day 4, but on day 5 it was observed among 74% of the turbot larvae (Fig. 8). On day 8 it was observed among 98% of examined larvae, and all the settled turbot had still swimbladder on day 74. The size of the swimbladder increased until day 37 (9.3 mm^3) and then declined. It had shrunk to 1.0 mm^3 by day 74 (Fig. 8).

Passage time through the defined stages varied. Transition from stage 1 to stage 2 took place around day 8, while transition to stage 3 came four days later (Fig. 9). Stage 4 larvae appeared on day 17 and persisted for a

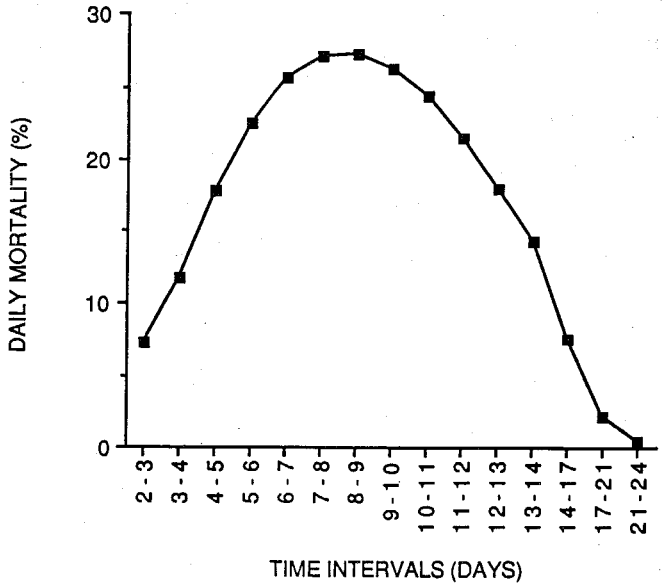

Fig. 7. Instantaneous daily mortality rate in percent from day 2 to day 21.

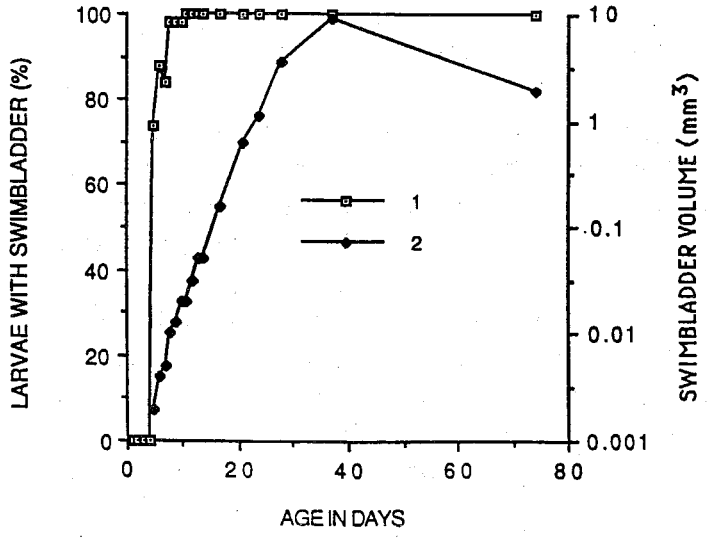

Fig. 8. Frequency of swimbladder (1) from day 1 to day 74 given in percentage (left abscissa) and volume (mm^3) of swimbladder (2) from day 5 to day 74 (log-scale; right abscissa).

longer time than other stages, lasting to day 33. The largest transformation took place during metamorphosis, a process started during stage 4 and being completed at stage 5 when the turbot settled to the bottom with a completely different body shape to that a few weeks earlier.

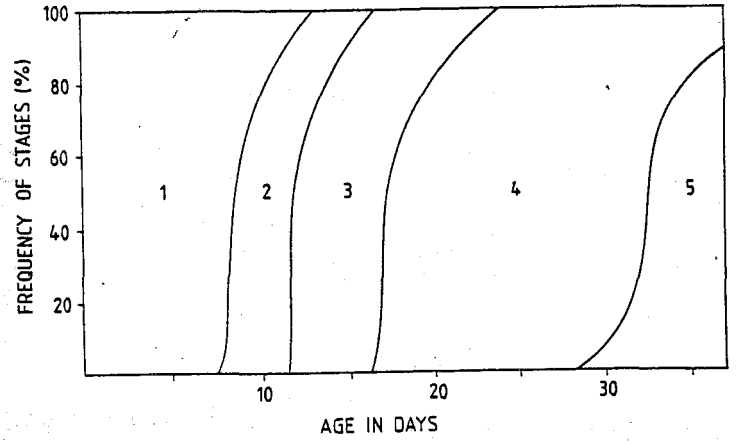

Fig. 9. Frequency of sampled turbot in the five different development stages from release to day 37.

GROWTH IN LENGTH AND DRY WEIGHT

During the first fortnight in the basin the larvae increased their mean standard length almost lineary from 3.0 mm to 6.6 mm, and then during the next fortnight to 20.1 mm (Fig. 10). At that time settling started and a decline in growth rate was observed after day 28. The final mean standard length was 38.4 mm on day 74 with a total length of 47.8 mm.

Dry weight increased during the first fortnight from 0.025 mg to 0.430 mg with a further sharp increase during the next fortnight to 32.4 mg (Fig. 11). At the end of the experiment it was 338.7 mg, with the largest examined juvenile being 910 mg, which is equivalent to a wet weight of almost 5 g. The mean live weight of 250 juveniles was 1.86 g on day 74.

Daily length increment (DLI) presented as a mean of three day values in Fig. 12, increased steadily from initial values between 0.3-0.4 mm to about 1.3 mm/day during metamorphosis. During the bottom stage it dropped back to the initial level.

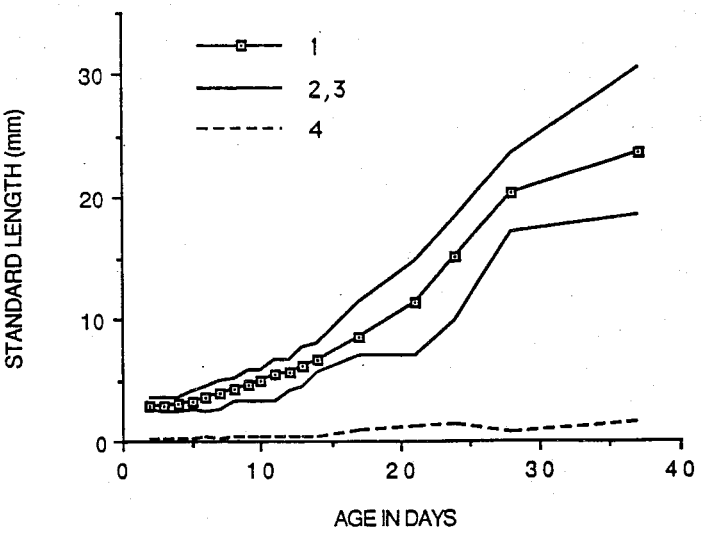

Fig. 10. Standard length of turbot larvae from day 2 to day 37 (1) with minimum (2) and maximum values (3) indicated. Standard deviation (4) is given separately for clarity.

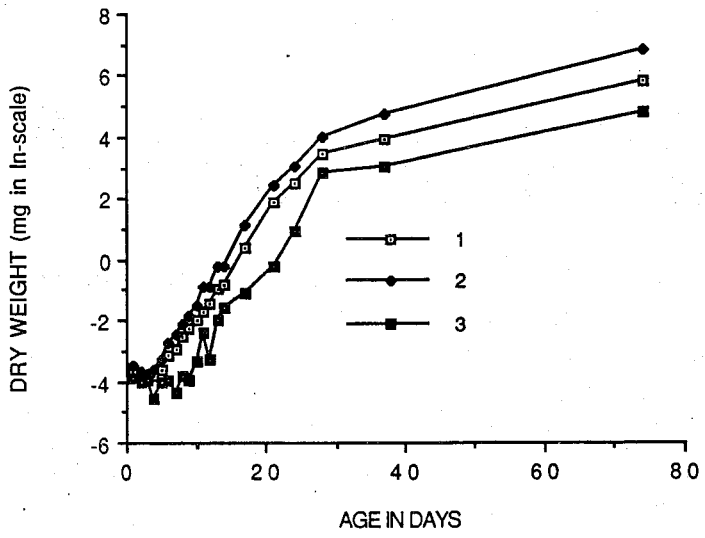

Fig. 11. Mean dry weight of turbot larvae in the basin from day 1 to day 74 (1) with the largest (2) and smallest (3) larvae on each day of sampling indicated (weight in ln-scale).

The daily weight gain in percent (SGR) calculated for time intervals similar to those for daily length increment gave initial values between 32-36% followed by a peak of 51%/day from day 14-17. The rest of the pelagic stage gave values between 27 and 38% while the bottom stage had values at about 5%/day (Fig. 12).

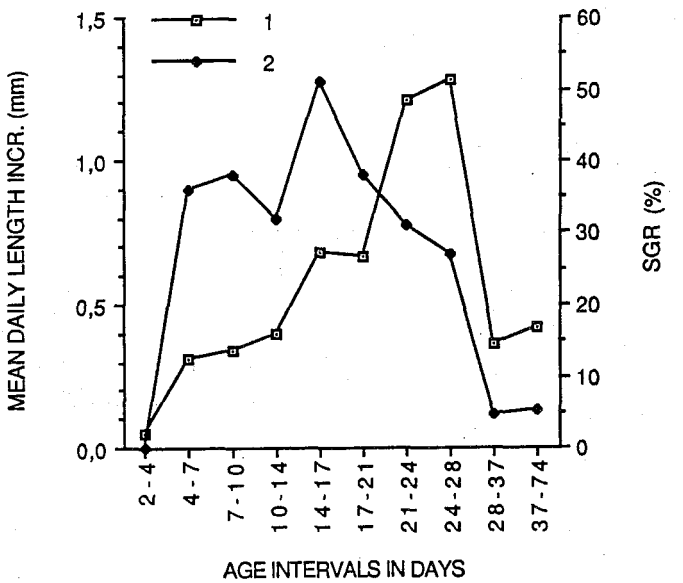

Fig. 12. Mean daily length increment (DLI) for three to five-day-intervals to day 28 and then for the time intervals from 28-37 and 37-74 (1). Mean specific growth rate in percentage (SGR; according to Houde and Schekter 1983) for the same time intervals (2: right abscissa).

The length frequency distribution, during the first feeding period, from day 5 to day 10, had a narrow range, and the mean point of the distribution moved gradually, day by day, from between 3-4 mm on day 5 to beyond 5 mm on day 10, with a small fraction of the larvae still being less than 4 mm (Fig. 13). Three days later, on day 13, all larvae were longer than 5 mm, with a range from 5.3 mm to 7.7 mm, while on day 17, the range had increased to between 5.6 mm and 11.9 mm. A further increase in the range took place in the proximate week.

The dry weight frequency distribution from day 5 to 10, indicated formation of a double-peak distribution on day 7 with remnants of slow-growing larvae kept alive beyond day 10 (Fig. 14). The smallest larva observed on day 10 was 0.038 mg or about the same as at first feeding. On

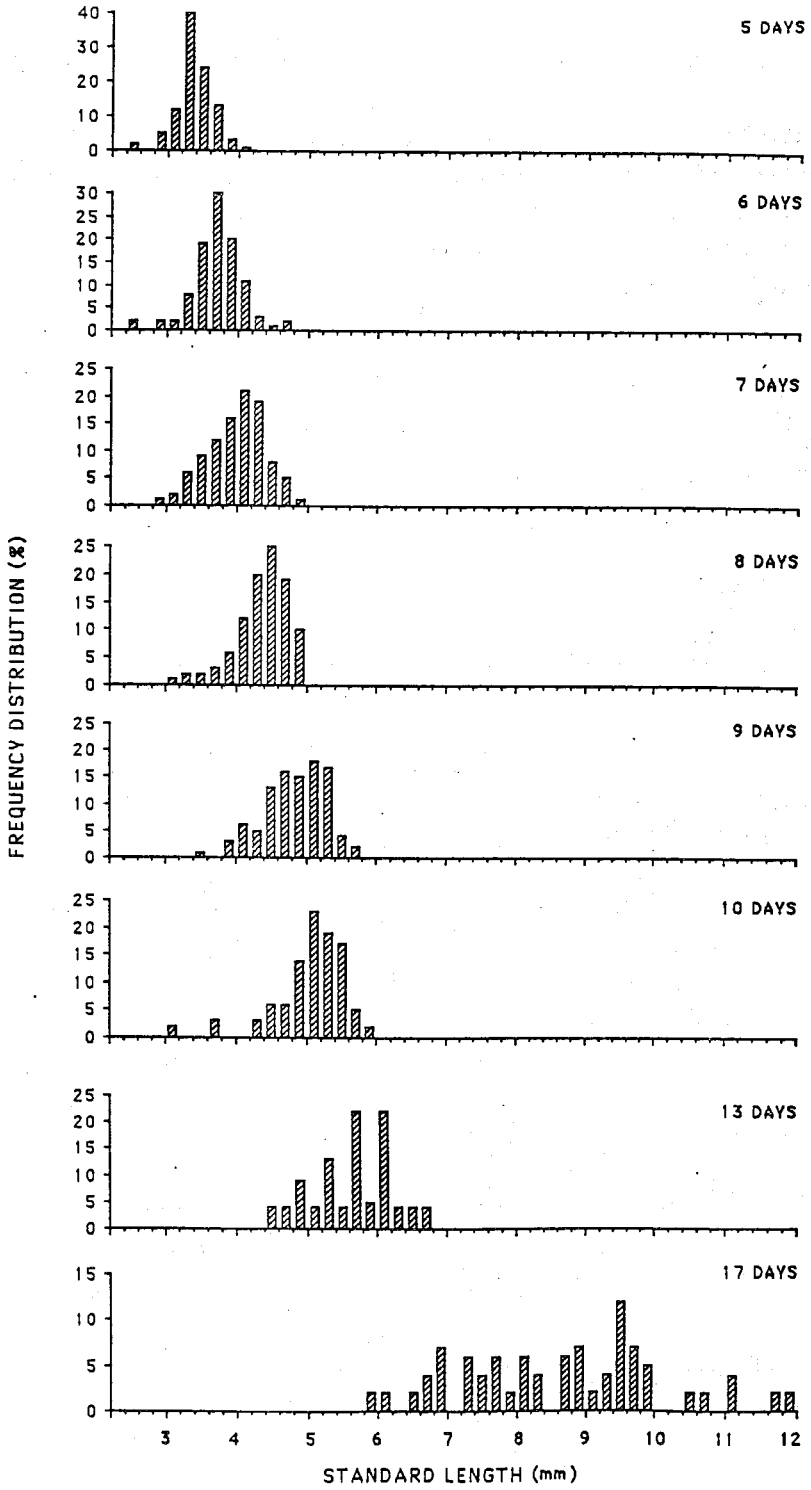

Fig. 13. Frequency distribution of standard length of turbot larvae sampled in the basin from day 5 to 17.

day 12, larvae with a dry weight below 0.1 mg were observed for the last time.

The ratio between the largest and smallest larvae increased from a minimum value of 1.2 on day 3 to a maximum value of 14.7 on day 21 with high values on a number of days from day 9 (8.5) to day 24 (8.0) (Fig. 15). Metamorphosed turbot had a ratio increasing from a low level before settling of 3-6 to 7.2 on day 74.

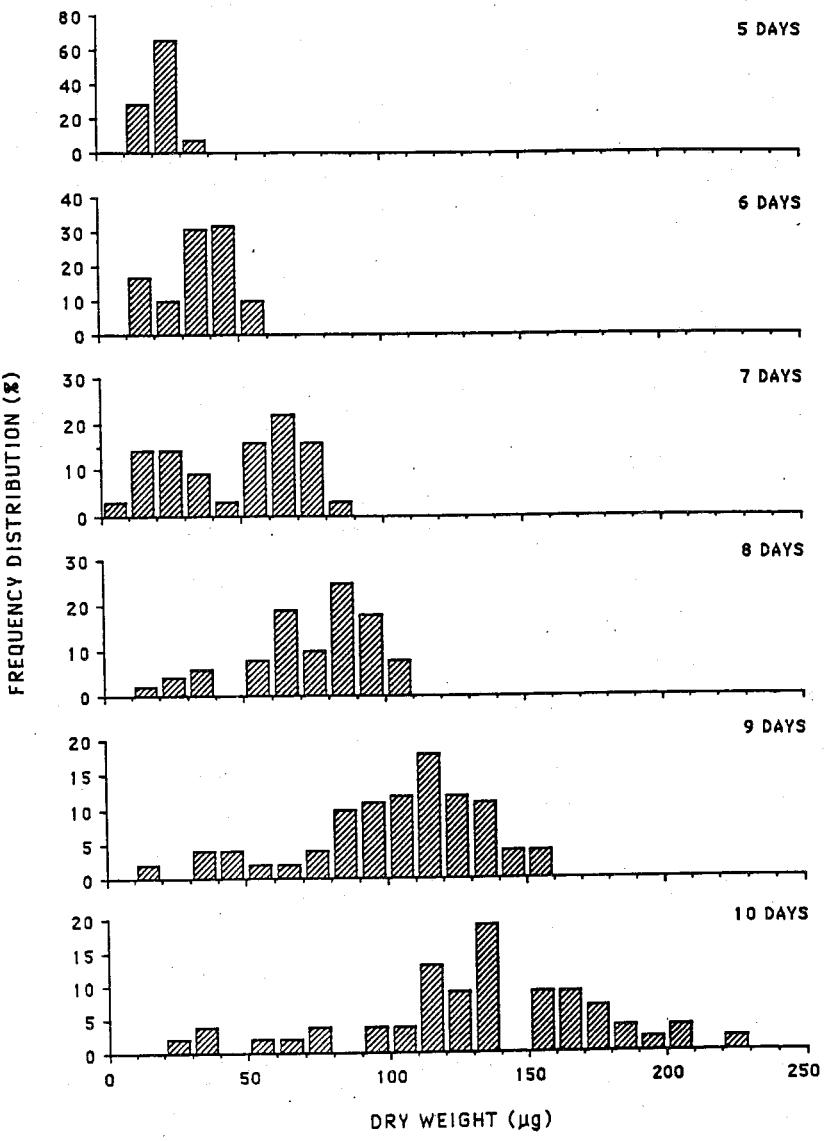

Fig. 14. Frequency distribution of dry weight of turbot larvae sampled daily in the basin from day 5 to 10.

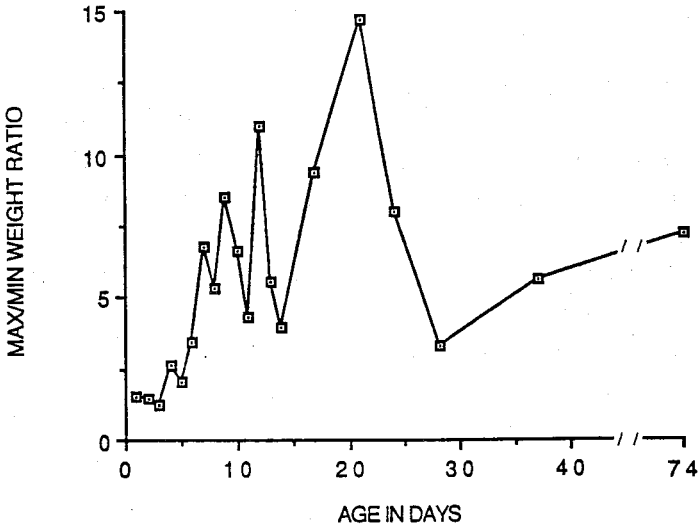

Fig. 15. The ratio between the highest and lowest dry weight of larvae within single days from day 1 to day 74.

The ratio between total length and standard length was at about 1.05 to a larval size of 7 mm standard length. After a transition period from 7 to 12 mm (from day 15 to 22), the ratio stabilized at a level of 1.20-1.25 reflecting the change in tail shape and bending of the notochord (Fig. 16).

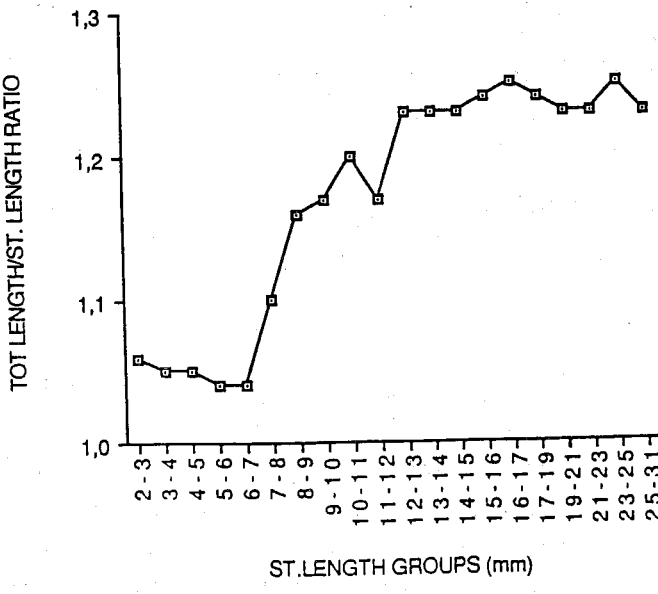

Fig. 16. The ratio between total length and standard length of preserved turbot larvae from the basin within the size range from 2 to 31 mm standard length.

FEEDING ASPECTS

Feeding incidence and number ingested

The feeding incidence was close to 100% from day 6 onwards. Only 20% had gut contents on day 3 when 22% of the larvae still had some yolk sac left (Table 2).

Gut examinations every day from day 2 to 14 at 0900 h indicated a steady increase in mean number ingested from 1.2 on day 3 to 8.6 on day 14 (Fig. 17). The increase continued and reached a maximum on day 28 with 118 organisms/gut.

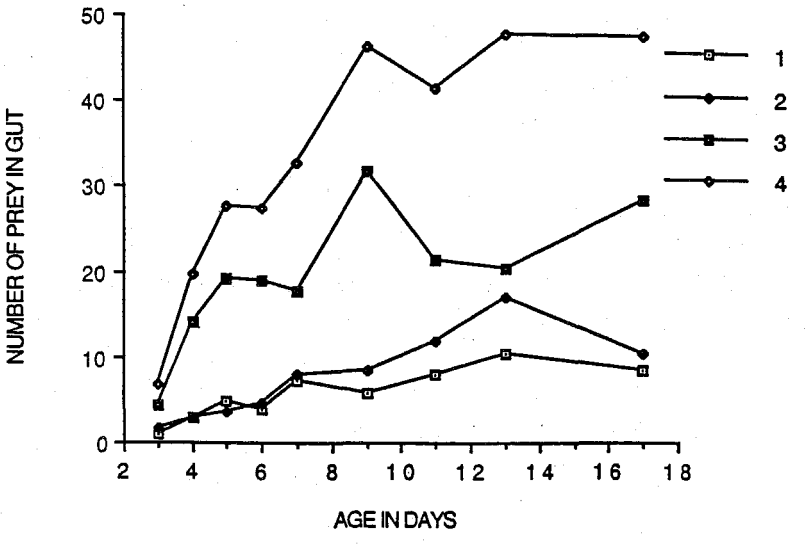

Fig. 17. Number of prey organisms in the gut of turbot larvae at nine different age groups from day 3 to day 17 at 0900 h (1), 1500 h (2) and 2100 h (3) indicated together with the total number of food organisms in the three samples (4).

A 24 hour sampling period carried out on days 7 to 8 (July 15-16) revealed that the main feeding took place from 1800 h to midnight, while minimum gut content was observed at 0600 (Fig. 18). Observed values were low and almost equal at 0900. on both days. This situation with far higher numbers of food organisms in the gut in the evening, was observed repeatedly from day 3 to day 17 with 9 series of observations (Fig. 17).

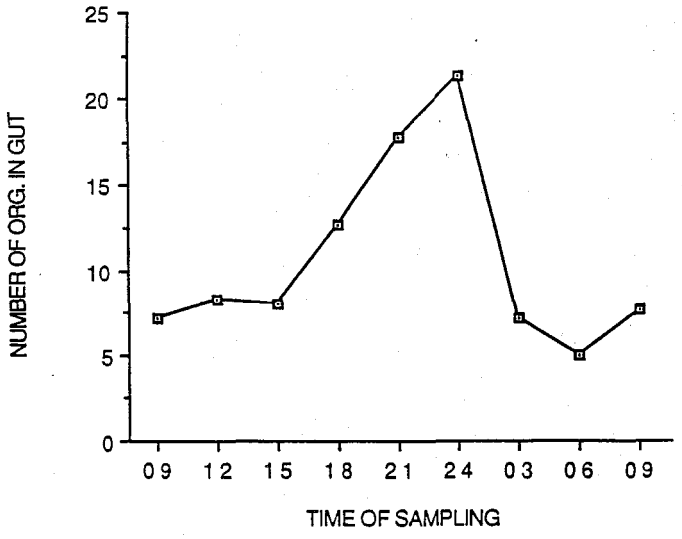

Fig. 18. Number of food organisms in the larval gut throughout a 24 hour sampling period from day 7 to 8.

Diet; composition and calorific contribution

Nauplii dominated by number to day 10 when calanoid copepods replaced them after a gradual increase starting on day 4 (Fig. 19). No phytoplankton was observed in larval guts examined on day 4. From day 10 to day 20 almost all the pelagic organism groups were represented in the diet, including *Podon* spp., cyclopoid and harpacticoid copepods and gastropod larvae. The three last organism groups, pooled as miscellaneous in Fig. 19, represented more than 40% of the ingested food organisms on day 13 to 17. Calanoid copepods continued to increase their importance making up 90% of the ingested food items on day 21. On the same day, the first amphipod occurred in the diet and gradually they replaced the calanoids and made up 75% of the organisms in the gut on day 37. Their importance continued after settling as they made up 80% of the identified organisms in guts examined on day 74.

The picture is somewhat different with respect to the relative importance of different groups when calorific contribution is considered (Fig. 20). The dominance of calanoids during the first three weeks increased at the expense of nauplii and specially of the miscellaneous items from day 10 to 20. This effect was reversed during the second part

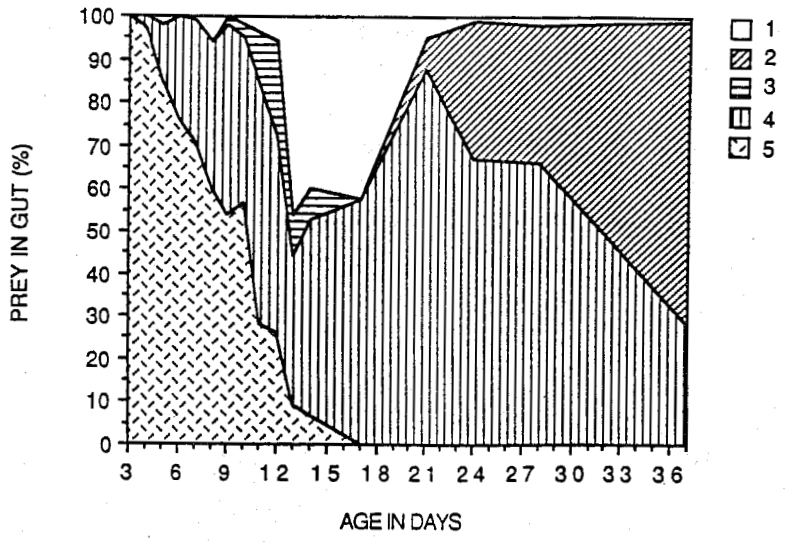

Fig. 19. The frequency in percent of different types of organisms in examined guts from the time period day 3 to day 37. 1: Miscellaneous; 2: amphipods; 3: *Podon* spp.; 4: calanoid copepods; 5: nauplii of calanoid copepods.

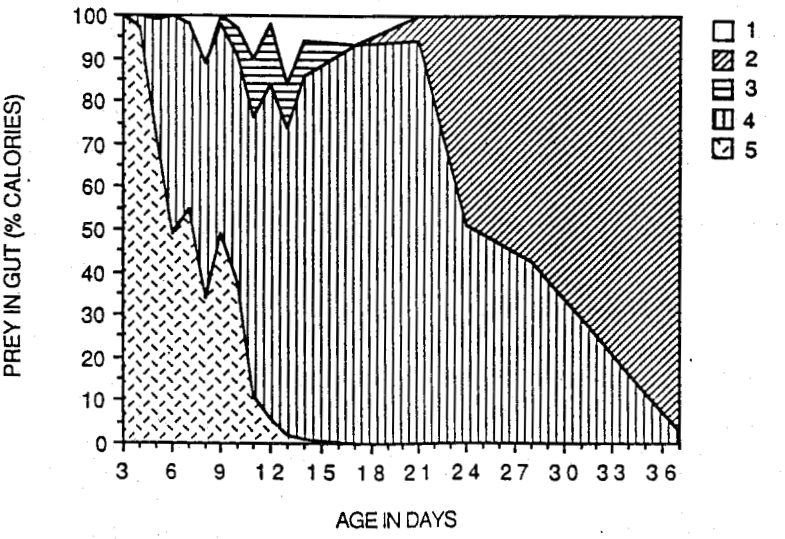

Fig. 20. The calorific contribution in the diet of turbot larvae of each organism group from day 3 to day 37. 1: Miscellaneous; 2: amphipods; 3: *Podon* spp.; 4: calanoid copepods; 5: nauplii of calanoid copepods.

of the pelagic stage as amphipods contributed 50% of the calorific value on day 24 increasing to 95% on day 37 at the expence of calanoids.

Calanoid copepods in the diet were dominated by the juvenile stages during the first week. Thereafter, *C. hamatus* contributed to 80-90% of the diet, but their numbers declined sharply from day 27 to day 37 when *Acartia* spp. and *Eurytemora* spp. and also juvenile calanoids increased in importance with numerical representation in the diet of about 35%, 25% and 30% respectively on day 37 (Fig. 21).

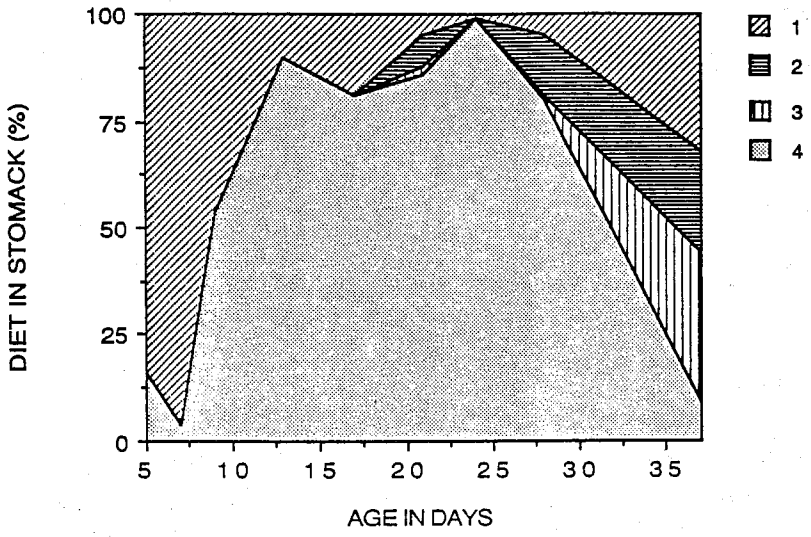

Fig. 21. The composition of calanoid copepods in the diet of turbot larvae from day 5 to day 37. 1: copepodites (not allocated to species); 2: *Eurytemora* spp.; 3: *Acartia* spp.; 4: *Centropages hamatus*.

Mouth size and size of food organisms

The mouth size increased almost lineary from 0.2 mm on day 3 to 1.4 mm on day 21 with a further increase to 3.3 mm on day 37 (Fig. 22), together with an increase in size of the food organisms in the gut in the same period. Nauplii, so important in the diet for the first 10 days, were in the length range from 0.13 to 0.20 mm while amphipods increased their mean length from 1.1 mm on day 20 to 2.1 mm on day 37. Calanoids also increased their mean size from 0.3 mm during the first days of feeding to 0.8 mm two weeks later when this group dominated in the diet (Fig. 22).

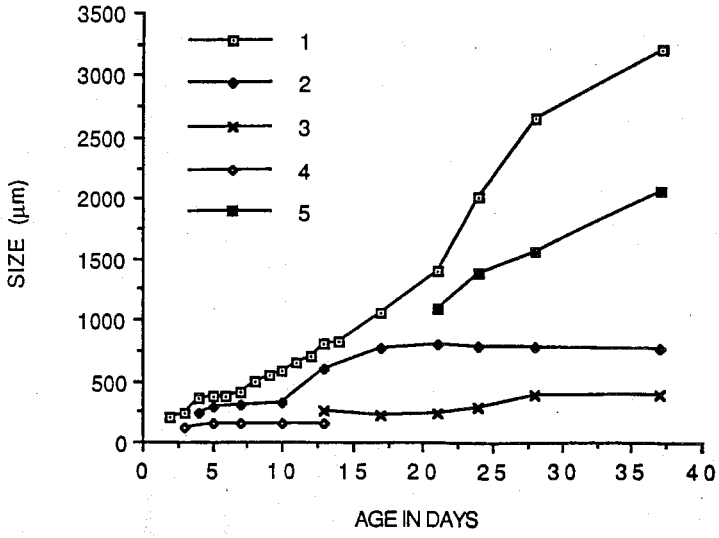

Fig. 22. Increase in mouth size from first feeding to day 37 and the length in µm of important food organisms observed in the gut on different days. 1: mouth size; 2: calanoid copepods; 3: harpacticoid and cyclopoid copepods; 4: nauplii of calanoid copepods; 5: amphipods.

Instantaneous and calculated ration

Calculation of the theoretical daily ration needed to obtain the observed growth rates, gave initial values of 15 µg on day 5 and 110 µg on day 11 with a further increase to 1230 µg dry weight on day 17 (Fig. 23). With an 18 hour feeding period, ingestion should be 0.8 µg/h on day 5. This should be equivalent to an ingestion of 2 nauplii/h. The ingestion increased to 6 µg/h on day 11 or about 3 calanoids/h and with a further increase to about 15 calanoids/h on day 17. On that day a mean of 9 food organisms were observed in gutted larvae in the morning and 28 organisms in the evening (Fig.17).

As a percent of larval size, the ration was 56% on day 5 increasing to a fluctuating level between 50-90% beyond day 20 followed by a decrease to 53% on day 28 (Fig. 23). During the bottom stage it was 13%.

The summation of gut content at 0900 h, 1500 h and 2100 h increased from 7 µg on day 5 to 163 µg on day 17 (Fig. 24). The relation between mean observed ration in the gut and the theoretical ration per hour with a 18 h feeding period declined from 2.8 on day 5 to 0.8 on day 17. This indicates that the larvae initially had a low digestion rate as they

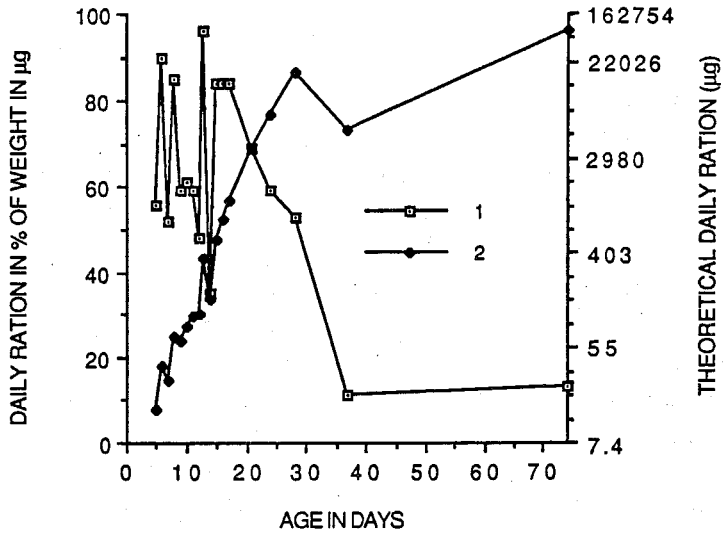

Fig. 23. Theoretical daily ration as percentage of larval body weight (1) from day 5 to 74 and theoretical daily ration in µg from the same period (2) in ln-scale.

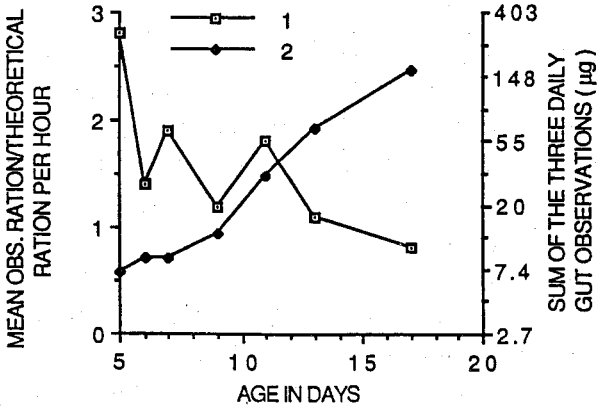

Fig. 24. Mean observed ration based on the sum of the gut content at 0900 h, 1500 h and 2100 h divided by the theoretical ration per hour (assuming K_1= 40% and 18 hour feeding period) from day 5 to 17 (1), and the sum of the gut content (µg) of the three daily observations from the same period (2). Observed ration is given in ln-scale.

had almost three hours ration in the gut at one time. On day 17 the turn over rate was below 1 hour.

Weight relation of prey/predator

The first day of feeding the weight ratio between a prey and a predator was 1 to 70 while on day 10 a diet of nauplii would give a ratio of 1 to 400. The change to copepodites gave on that day a ratio of 1 to 140 which did not change much during the next week as the increase in larval weight was paralleled by an increase in the size of calanoids ingested as on day 17 the ratio was 1 to 250. Further increases in larval weight could not be matched by the calanoids present in the basin. On day 21 the ratio had changes to 1 to 1000. The ratio 1 to 1000 also hold true for amphipods ingested on day 21. However, further growth in larval size was now paralleled by an increase in the size of amphipods ingested, so that on day 28 the relation was still 1 to 1000. On the same day the ratio for calanoids ingested had deteriorated to 1 to 10000.

DISCUSSION

Behaviour and distribution

The patchy distribution of the turbot observed visually on day 15 seemed to be influenced by the position of the sun during the day. As this behaviour was most pronounced in sunny weather it might be the effect of light-shadow that triggered it. A similar behaviour has been observed repeatedly among advanced cod larvae in enclosure experiments (Rognerud 1887, Øiestad, pers. comm.).

In addition it might be that zooplankton is triggered by the same light effect and that their aggregation might be the ecological explanation for this otherwise irrational behaviour in a food-deprivated system. Regrettably no specific zooplankton sampling was undertaken with respect to this question.

Food and feeding aspects

The preferred first food for turbot is considered to be nauplii (Quantz et al. 1980, Quantz 1985). The low densities at which they occurred in

the basin, represented a challenge for the turbot larvae and was compensated for by a swift change to larger and somewhat more numerous calanoid copepods (Fig. 4).

The maximum observed nauplii density during first feeding (15/l; Fig. 5) and the mean value of 5 nauplii/l, were both far below the value considered to be required for larval survival and growth. In a laboratory study, Quantz (1985) had total mortality of turbot larvae offered 500 nauplii/l and with reduced growth rate at 1000 nauplii/l compared with 2000/l, all at 21°C. Howell (1979) and Olesen and Minck (1983) maintained a level of 3-5000 rotifers/l to obtain high survival and growth rate of turbot larvae. The fairly high survival in the basin raises the question as to why such significant differences in performance can be observed between two rearing systems. Obviously the ability of each single larva should need to be fully exploited in the basin and, as observed, only a minor fraction of the larvae were able to get the ration needed for growth and survival. In a number of other mesocosm studies, food densities from 1-5 food organisms/l has been sufficient to give fairly high survival rates for such species as cod, herring and capelin (Ellertsen et al. 1981, Moksness 1982, Øiestad and Moksness 1981). The swimming pattern of turbot combined with their high activity rate (Huse and Skiftesvik 1985) should favour high feeding success on organisms encountered. For those larvae surviving the pelagic stage, a very high daily weight gain has been observed (Fig. 12), indicating that this type of performance existed. Rashevsky (1959) postulated that at marginal feeding conditions every food particle perceived would be inspected and ingested if suited to the fish in question. This strategy named "capture-frequency maximizing" (Vinyard 1980) might be adopted whenever the situation is so critical that the fish larvae can afford neither "optimal foraging" nor "prey-size maximizing".

Patchiness of food organisms has been set forward as an explanation for survival of fish larvae at generally low food densities. Patchiness was observed in the basin (Fig. 5), but even the highest density was far from what has been considered needed for growth and survival. More extensive studies have been undertaken to evaluate the importance of patchiness in other mesocosms. The conclusion drawn from these has been that sampling programmes of the type described, give a reliable picture of the density situation for zooplankton (Blom 1987, Øiestad 1983). Furthermore, similar growth results have been obtained in low food density studies on turbot by Paulsen and Andersen (1989) in

mesocosms, even in those tanks where artificial turbulence prevented patchiness.

According to Rothschild and Osborn (1988) and Sundby and Fossum (1990), microturbulence might partly explain why fish larvae can survive at food densities that give no survival in the laboratory. They report that with a windspeed of 6 m/s the encounter rate between food organisms and fish larvae will triple due to microturbulence. Nevertheless, still densitiy values 100 times higher than those observed seem to be needed to experience similar survival and growth rates in laboratory tanks (Quantz 1985).

The sharp increase of food items in the gut in the evening with a maximum at midnight (Fig. 18) might indicate scarcity of food organisms available during daytime in the surface layer where most fish larvae occurred (Table 2). The high gut filling in the evening might be due to prey behaviour, such as vertical movement to the surface layer during hours of twilight. Another possibility is light contrast phenomena making zooplankton more visible and therefore more vulnerable to predation at dusk and dawn. A similar gut filling increase at that time of the day has been observed in another mesocosm study with a more affluent food supply (Meeren 1991) and from the field (Last 1979), while under artificial conditions in the laboratory, Nellen et al. (1981) did not observe a feeding rhythm. Increased food intake at dusk and dawn has been observed among cod and herring larvae in mesocosm studies (Ellertsen et al. 1976, Gamble et al. 1981).

An almost 24 h food intake might indicate a strong feeding drive even at marginal light conditions, and the almost empty guts observed by Last (loc.cit.) at night time, was not observed in this study (Fig. 18). The proximity to mid-summer of the present study might be a contributing explanation for a continuous feeding through 24 hours (Blaxter 1966).

From day 10 onwards those larvae present that survived to the end of the study shifted their main diet from nauplii to calanoids (Fig. 19). During the following period of ten days a variety of food items were ingested, some being of the size of nauplii, others of the size of calanoids. From an energetic point of view the chosen strategy should be sound: without any information on what should be their main future food item, they ingested all those encountered. At the end of this period of opportunism, they selected the energetically more favorable amphipod (Fig. 20). This event might have been enforced by a coincidental decline in calanoid density (Fig. 4).

Obviously the calanoids on day 20 started to represent a small food item with a prey:predator weight ratio of 1:1000, although the relation was the same for amphipods on that day. The ratio maintained that level to day 37 for amphipods to turbot, while it was 1:10000 on day 37 for calanoids to turbot.

The small prey size made frequent food intake necessary. The ideal prey:predator ratio of 1:100 set forward by Ursin (1977) could not be realized during the pelagic stage, but might have been closer to its realization during the bottom stage with access to the bottom fauna including all stages of amphipods and sedentary polychaetes of settled spionids. In the study by Paulsen and Andersen (1989), the only food supply during the pelagic stage was calanoids, but still a high SGR was observed indicating that the prey size is of lesser importance than an affluent food supply.

Survival and growth

The sharp decline in the population of turbot levelled out a fortnight after hatching with only 6% of the population still alive. Almost 35% of the population had a mortality pattern equal to that observed from the starvation groups in the laboratory while about 60% had a somewhat delayed mortality as a result of food intake, though at a suboptimal rate (Fig. 6 and 7).

Identification of a starving subpopulation in this basin study was possible from day 6 onwards as many larvae still had the same dry weight as at first feeding. This subpopulation was distinctly segregated on day 7 by their dry weight frequency distribution making up almost 50% of the total population on that day (Fig. 14). The slow growing fraction was eroding day by day with only remnants left on day 10. Starvation as an explanation for the mortality is in accordance with minor further mortality in the population as only 15% of those alive on day 14, died later on. Similar observations have been made by Meeren (1991) in his mesocosm study on turbot in a plastic bag. He also detected suboptimal feeding conditions and a slow-growing subpopulation. Rosenberg and Haugen (1982) have examined otoliths from turbot larvae in the present basin study and back calculated individual growth trajectories. They verified that each single larva maintained its position relative to each other in accordance with their specific growth rate. This gives as a result an almost permanent ranking relative to other larvae in the same group.

They could also detect a size-selective mortality being particularly intense around day 7, and they also concluded that the smallest larvae in the population at any time was exposed to a far higher mortality rate than the larger ones. Their observation gives strong support to the assumption that the decline in the population was due to mortality among larvae in the slow-growing subpopulation and further, that starvation was the main reason for the mortality. It supports also an assumption that there exists a large variation in larval ability to hunt successfully, and that this might be the reason for the wide range in observed growth rates among a cohort of larvae. This variability in performance would be crucial at marginal feeding conditions and makes it possible for a few larvae to grow beyond 200 µg by day 10 while others still would be below 50 µg. There is no evidence to suggest that any one of these two categories of larvae have had better feeding conditions in such a shifting system as a mesocosm. Nevertheless, observed differences in the range from 15 nauplii/l to less than 1 nauplius/l should give room for behavioral adapations as suggested theoretically by Vlymen (1977). The anchovy larvae where able to detect concentrations of food organisms and maintain their position in the patch by frequent turns.

The minimum weight observed on day 14 was 204 µg which gives a specific growth rate of 23% (Fig. 11). Similar minimum SGR values were observed on day 17 and 21 indicating that a barrier SGR for survival beyond the stage of mass mortality was about 20-25% at the prevailing temperature (20°C). Meeren (1991) rearing the larvae at a far lower temperature of 12°C, observed a minimum SGR of 13% to a similar size. Specific growth rates observed in Danish mesocosms have been about 20% with high final densities of larvae (40-60 /m^3) and from 29-34% with low final larval densities (3-17 /m^3), all at similar temperatures to that of the present study.

Minimum larval growth rate barriers have been postulated for a number of temperate water marine fish species, all in the range 3-10% (Beyer and Laurence 1980, Jones 1973, Øiestad 1985, Øiestad et al. 1985).

Quality aspects with the juveniles

All the juveniles collected from the basin on day 74 had a normal pigmentation and no deformities while among flatfish of most species reared in indoor tanks, a variable proportion of the juveniles are mal-

pigmented; deformities have also frequently been observed although seldom reported. Flatfish species reared on a natural diet in out-door rearing systems, always have normal pigmentation (Øiestad et al. 1978, Øiestad et al. 1976, Øiestad and Berg 1989). The explanation should be sought in the quality of the diet. The fatty acid composition has been considered as a trigger for pigmentation (Scott and Middelton 1979). The composition will be influenced by the larval diet, particularly with respect to polyunsaturated fatty acids as illustrated by Witt et al. (1984) as 22:6 (n-3) almost disappeared in turbot larvae fed nauplii of *Artemia salina*.

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