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COMPARATIVE GROWTH AND SURVIVAL OF TWO GENETIC STRAINS OF ATLANTIC COD (*GADUS MORHUA* L.) REARED THROUGH THE EARLY LIFE STAGES IN A MARINE POND IN WESTERN NORWAY

by

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ABSTRACT

The investigation was carried out in a marine pond in western Norway during spring and summer 1990. Two genetic defined strains of Atlantic cod (*Gadus morhua* L.) were used as broodstocks. A total of 11.1 x 10^6 cod larvae and eggs were released in the pond from 16 to 22 March. Approximately 80 % of the specimens were homozygous for the rare 30-allele at the *PGI-1* locus (Strain-A), and the remaining were offspring from a farmed cod stock (Strain-B). Hydrographical parameters and feeding conditions of larval and juvenile cod were monitored. Gel electrophoresis of samples collected from the pond, revealed significant variation in the Strain-A/Strain-B frequencies with increasing age. The percentage of Strain-A dropped pronounced from the larval to the juvenile stage, and Strain-A had lower larval and juvenile growth rates than Strain-B, indicating size-dependent mortality during the pre-recruit period.

INTRODUCTION

Application of fish with genetic markers in stock enhancement and breeding programmes has been suggested by several workers (Moav *et al.*, 1976; Allendorf and Utter, 1979; Shaklee, 1983; Taggart and Ferguson, 1984), and genetic markers may be a useful way of controlling the effect of releases of reared fish (Nævdal and Jørstad, 1984).

Accurate estimates of growth and particularly survival of cohorts of fish larvae are difficult to obtain due to ageing and sampling problems (Houde, 1987), and use of genetically marked fish larvae in release experiments makes a unique opportunity to study early life dynamics and recruitment mechanisms of fishes (Svåsand *et al.*, in press). Important parameters as age and abundance of the released fish larvae are then known, and in 1988 a preliminary release experiment with genetically marked cod larvae was carried out in a small land-locked fjord in western Norway (Svåsand *et al.*, in press).

Modest changes in daily growth or mortality rates of fishes can cause major changes in recruitment levels, especially if they occur in the larval stage (Houde, 1987). Many of the factors critical to larval survival and growth (e.g. starvation and predation) are known to be size-dependent (Miller *et al.*, 1988). Size-dependent survival during pre-recruit stages may be a direct function of growth (Anderson, 1988). Even subtle differences in size between individuals may have profound effects on their fates (Miller *et al.*, 1988).

Recently, a genetically marked broodstock of Atlantic cod (*Gadus morhua*) was produced at the Institute of Marine Research (Jørstad *et al.*, 1987). These fish were homozygous for the rare 30-allele in the enzyme phosphoglucose isomerase (*PGI-1*) expressed in white muscle, and can be detected from the yolk-sac stage and onwards. The purpose of this study is to compare growth and survival of two genetic strains of Atlantic cod reared through the larval and early juvenile phase in a marine pond in western Norway, and subsequently use the reared juvenile cod in an enhancement programme.

MATERIALS AND METHODS

Production of egg and larvae

The egg and larval material originated from two different broodstocks of Atlantic cod kept at the Austevoll Aquaculture Station in western Norway. One of the broodstocks (A) was homozygous for the rare 30-allele at the *PGI-1* locus (Jørstad *et al.*, 1987). The other broodstock (B) was a farmed cod stock descendent from the artificially produced cod fry in 1983 and 1985 (Øiestad *et al.*, 1985). The A and B-broodstocks consisted of 203 (≈ 50/50 sex ratio) and 116 (58 ♀ and 58 ♂) mature cod, respectively. Mean length, weight, and Fulton's condition factor of cod in the broodstocks are given in Table 1. In early February 1990, the two broodstocks were transferred into separate spawning pens where they spawned naturally, and fertilized eggs were collected as described by Holm and Andersen (1989). Egg diameter (± 0.08 mm) of 40 eggs from each spawning pen were measured daily. In the following, progeny from the broodstocks A and B are termed Strain-A and Strain-B, respectively.

Table 1. Mean length, weight, and Fulton's condition factor [K = (weight/length^3)10^5] of mature Atlantic cod from two genetically different broodstocks. The cod were measured in the beginning of December 1989. Standard deviations and sample sizes are given in the parentheses.

Broodstock	Length (cm)	Weight (kg)	Fulton's K
A	63 (5.7; 203)	4.0 (1.1; 203)	1.54 (0.21; 203)
B	72 (12.0; 116)	5.6 (2.4; 116)	1.45 (0.21; 116)

The fertilized eggs were treated in a 1 % solution of Buffodine, and incubated in 180 l black, conical aerated tanks. Mean incubation temperature and salinity were 6.7 °C (range 5.7-8.6 °C) and 33.6 ppt (range 33.0 - 34.0 ppt), respectively.

Pond routines

The rearing pond, called Parisvatnet, is situated at 60°38'N 44°49E, 60 km northwest of Bergen, Norway. The pond has a maximum depth of 10 m, a surface area of 50 000 m^2, and a volume of 270 000 m^3. Further description of the pond is given by Blom *et al.* (in press).

The pond was treated with 200 l Gullviks rotenone (concentration ≈ 0.74 ppm) on 23 November 1989, to remove predatory fish prior to release of cod larvae. The pond was left stagnant from 16 March to 30 April 1990. From 30 April the tidal water was filtered through metal screens (1.5 mm screens from 30 April to 21 May; 2.0 mm screens from 21 May) to allow entry of zooplankton to the pond. Sea water (10 m^3 min^{-1}) from 30 m depth was pumped into the pond from 31 May. The pond was fertilized with inorganic fertilizer (chemical composition in percentages of weight for important elements: 21 % N; 3.5 % P; 10.5 % K; 0.5-1.0 % Si) on 10 March (200 kg) and on 2 April (100 kg).

Atlantic cod larvae (≤ 2 d post-hatching) and eggs close to hatching were released in the pond from 16 March to 22 March 1990, and the median date of release was 19 March (Day 0). A total of 11.1 x 10^6 cod larvae and eggs were released, and 80.1 % of the larvae and eggs were Strain-A (Table 2). Three samples (preserved in 4 % hexamine-buffered formalin) of cod larvae from the two genetic strains were taken, to estimate larval standard length and dry weight at release. Standard lengths were measured to the nearest 0.04 mm, and dried cod larvae (60 °C, 24 h) were weighed using an electrobalance weight (± 1 μg).

Table 2. Releases of Atlantic cod larvae and eggs in Parisvatnet in 1990.

Date	Strain-A		Strain-B	
	Larvae (x 10^3)	Eggs (x 10^3)	Larvae (x 10^3)	Eggs (x 10^3)
16 March	1 897	39	1 343	14
17 March	1 502	35	83	3
18 March	516	43	749	15
21 March	1 333	503		
22 March	1 302	1 693		
Total	**6 550**	**2 313**	**2 175**	**32**

Cod larvae preyed upon the natural zooplankton production in the pond during the larval period. In addition, larval and juvenile cod were offered zooplankton collected by a fine-meshed zooplankton trawl (opening area of 25 m^2) in the fjord areas within 20 km from the rearing pond between 25 April and 29 May, and dry feed from 25 April. Juvenile cod were also offered 40-60 kg frozen zooplankton (mainly *Calanus*) per day from 25 May to 7 June.

Sampling program

Temperature, salinity and oxygen saturation were measured weekly in the pond at depth intervals of 1 m from the surface to the bottom.

Microzooplankters (size range: 0.1-0.6 mm food items for larval cod) were sampled weekly by using an electrical pump of 72 l min^{-1} capacity, and filtered through a net of 30 μm mesh size. Samples were taken at depths of 1, 4, 5, 7 m and 10 cm above the bottom at one sampling site (8.5 m depth), and density estimates (organisms l^{-1}) of microzooplankton presented in this paper are means of the 5 samples. Macrozooplankters (size range: 0.6-4.0 mm food items for larval and juvenile cod) and cod larvae were sampled during night time (22.00 - 02.00 hours) once a week with a two-chamber 350 μm mesh, 0.1 m^2 mouth area net towed horizontally at a speed of 1 m s^{-1} at depth intervals of 1 m to a depth of 8 m. Density estimates (number m^{-3}) of macrozooplankton given are averages of 8 or 9

samples. Zooplankton and cod larvae were preserved in 70 % ethanol. Population estimates of juvenile cod (≥ Day 60) were carried out with a 200 kHz Furuno echo sounder during nighttime. Standing stocks of larval and juvenile cod were calculated by integrating density estimates (number m^{-3}) multiplied by water volume allocated to each depth stratum. A survival curve for the early life stages of cod was constructed from either pooled (2 subsequent samples) or single population estimates, and mean daily instantaneous mortality rates (z) during the intervals were calculated.

A total of 4 samples of cod were collected from the pond to estimate the portion of genetically marked cod, and to compare length and weight distributions of individuals from each genetic strain. Sample no. 1 (216 larvae) and no. 2 (380 larvae) were collected with a two-chamber net at daytime on 19 April (Day 31) and 23 april (Day 35), respectively. Larvae from sample no. 2 were measured for standard length to the nearest 0.09 mm, and frozen at -70 °C within few hours after sampling. Sample no. 3 (384 juveniles) and no. 4 (287 juveniles) were collected with a dip net on 19 June (Day 92) and on 2 July (Day 105), respectively. The cod were measured for standard length to the nearest 0.1 mm and wet weight to the nearest 0.01 g. A small amount of white muscle was removed from each fish, and frozen at -70 °C within few hours after sampling. The frozen materials were later analysed by starch gel electrophoresis for identification of *PGI-1* genotypes (Jørstad *et al.*, 1987).

Estimation of growth

Growth rates of Strain-A and Strain-B were estimated as daily increase in average standard length between Day 0 and 35, and between Day 35 and 98.5 (averaging mean lengths in sample 3 and 4). Measured lengths at relase were corrected for shrinkage in formalin by assuming a preserved/fresh length ratio of 0.92 (Theilacker, 1980).

Mean daily instantaneous growth rates (g) of Strain-A and Strain-B were calculated as:

$$g = [(\ln WW_2 - \ln WW_1)/(t_2 - t_1)]100 \quad (1)$$

where WW_1 and WW_2 are mean wet weights at time t_1 and t_2, respectively. Mean g-values were estimated between Day 0 and 98.5 (averaging mean weights in sample 3 and 4). Dry weights at release were corrected for loss of weight due to fixation by assuming a preserved weight/fresh weight ratio of 0.79 (Hay, 1984), and a dry weight/wet weight ratio of 0.18 (Thorisson, 1989).

RESULTS

Size of eggs and yolk-sac larvae

Individuals in broodstock B were significantly longer ($P < 0.001$) and heavier ($P < 0.001$) than those in broodstock A, however, the mean condition factor of cod in broodstock A was significantly higher ($P < 0.001$) than that of cod in broodstock B. Generally, diameter of Strain-A eggs (1.34 mm) was significantly smaller (Table 3A; $P < 0.001$; *t*-test) than Strain-B eggs (1.38 mm). There was no significant difference in standard lengths of larval Strain-A and Strain-B at release; 4.21 and 4.25 mm, respectively (Table 3B; $P = 0.35$; *t*-test), however, mean larval dry weight of Strain-A (44.6 μg) at release was significantly lower ($P < 0.01$; *t*-test) than that of Strain-B (48.2 μg).

Hydrography

The mean temperature in the pond increased from 5.7 to 13.1 °C between Day 1 and 108 (20 March - 5 June) (Fig. 1A), and the average salinity ranged from 29.6 to 33.2 ppt between Day 1 and 87 (20 March - 14 June) (Fig. 1B). Salinity was lowest towards the end of the period when the rearing pond was stagnant. The average oxygen saturation levels in the pond were satisfactory during the study period with values varying from 83 to 115%.

Table 3. Comparisons (*t*-tests) of egg and larval sizes from to genetic strains of Atlantic cod. A. Egg diameter of fertilized eggs from the spawning pens on different dates. B. Standard length (SL), and dry weight (DW) of cod larvae at release (samples were taken from larval groups released from 16 to 18 March which originated from egg groups spawned between 28 February and 2 March). Standard deviations and sample sizes are given in parentheses. NS: not significant; ** $P < 0.01$; *** $P < 0.001$.

A.

Spawning date	Egg diameter (mm)		Probability
	Strain-A	Strain-B	
28 February	1.31 (0.06; 40)	1.37 (0.05; 40)	***
1 March	1.38 (0.05; 40)	1.38 (0.07; 40)	NS
2 March	1.34 (0.06; 40)	1.39 (0.05; 40)	***
7 March	1.34 (0.06; 40)	1.39 (0.05; 40)	***
8 March	1.37 (0.05; 40)	1.38 (0.07; 40)	NS
9 March	1.33 (0.07; 40)	1.38 (0.05; 40)	***
Pooled	1.34 (0.06; 240)	1.38 (0.06; 240)	***

B.

	Strain-A	Strain-B	Probability
SL (mm)	4.21 (0.22; 100)	4.25 (0.25; 50)	NS
DW (μg)	44.64 (6.64; 92)	48.21 (7.80; 47)	**

Zooplankton

Average density of microzooplankton in the pond increased from 11 organisms l^{-1} on Day 4 (23 March) to 210 organisms l^{-1} on Day 22 (10 April), and then decreased to 4 organisms l^{-1} on Day 44 (2 May) (Fig. 2A). Larvae of the common mussel (*Mytilus edulis*) were dominating in numbers among microzooplankters during the larval stage of cod. Copepod nauplii occurred in mean abundances between 2.7 to 29 l^{-1} from Day 4 to 44. Mean density of macrozooplankton increased from 177 m^{-3} on Day 3 (22 March) to a maximum of 1 490 m^{-3} on Day 22 (10 April), and then decreased rapidly to < 100 m^{-3} on Day 38 (26 April) (Fig. 2B). Macrozooplankton abundances were very low after Day 38 with numbers < 130 organisms m^{-3}. Copepodites of the calanoid copepods *Temora longicornis* and *Centropages hamatus* were the most abundant macrozooplankters in the pond. The collection of zooplankton by the trawl carried out from late April to late May, resulted in daily catches of zooplankton < 2 kg dry weight. *Calanus finmarchicus* was almost absent in samples taken from the trawled zooplankton.

Growth and survival of cod

The total cod population (Strain-A & B) decreased from 11.1 x 10^6 individuals (including eggs) at release to 2.1 x 10^6 individuals at metamorphosis (≈ Day 40, 28 April), giving an estimate of 19 % survival to metamorphosis (Fig. 3). On Day 92 (18 June) the number of juvenile cod was estimated to 161 000, giving an estimated survival of 7.7 % from Day 40 to 92. The abundance of juvenile cod on Day 105 (2 July) was estimated to 116 000 individuals which corresponds to a total survival of 1 % from release. Estimated instantaneous mortality rates (z) employed in the survival curve were 0.08 d^{-1} between Day 0 and 20, 0.005 d^{-1} between Day 20 and 45, 0.11 d^{-1} between Day 45 and 63, and 0.02 d^{-1} between Day 63 and 105.

During the larval phase, the percentage of Strain-A seemed to be fairly constant (Fig. 4), however, from the larval to the juvenile stage the portion of genetically marked cod dropped pronounced with values decreasing from 79.6 % on Day 31 to 37.8 % on Day 92. The frequencies of Strain-A and Strain-B varied significantly (*G*-test; G = 159.7; df = 3;

$P < 0.001$) between the samples. The average size (length and weight) of Strain-A were significantly smaller than that of Strain-B in all samples (Table 4). Daily increases in length of Strain-A and Strain-B between Day 0 and 35 were 0.15 and 0.16 mm, respectively. From Day 38 to 98.5, the average increase in length was 0.66 mm d^{-1} in Strain-A and 0.70 mm d^{-1} in Strain-B. The mean growth rate (g) of Strain-A was slightly lower than that of Strain-B during the study period; 8.6 % and 8.7 % d^{-1}, respectively.

Table 4. Comparisons (*t*-tests) of mean standard lengths (SL), and wet weights (WW) of Atlantic cod from two genetic strains related to days after release (DAR) in the pond. Standard deviations and sample sizes are given in parentheses. * $P < 0.05$; ** $P < 0.01$: *** $P < 0.001$.

DAR	SL (mm)			WW (g)		
	Strain-A	Strain-B	Probability	Strain-A	Strain-B	Probability
35	9.98 (0.88; 280)	10.30 (0.89; 100)	**			
92	51.28 (7.85; 145)	54.42 (9.01; 239)	***	1.49 (0.72; 144)	1.86 (1.05; 239)	***
105	52.96 (4.73; 139)	54.52 (4.99; 148)	**	1.61 (0.52; 138)	1.75 (0.60; 148)	*

DISCUSSION

Within a larval fish population, growth rates are determined by abiotic factors such as temperature, and biotic factors such as feeding conditions (Anderson, 1988). The agents of mortality in early stages of fish are thought to be predation, starvation, and abiotic factors such as anomalous oceanographic conditions (Houde, 1987). However, survival of early life stages tends to be a direct function of growth (Anderson, 1988), and seems to be positively related to body size at hatching (Rosenberg and Haugen, 1982; Miller *et al.*, 1988). Growth and survival in young fish are affected by density-dependent mechanisms such as competition and cannibalism (Ware, 1975; Smith, 1985). However, density-

dependent responses might first become important in the stages following the larval stage (Anderson, 1988; Blom *et al.*, in press).

The presence of rare alleles in a population may be attributed to some kind of disadvantage under natural conditions. For that reason, Allendorf and Utter (1979) proposed that fitness of individuals possessing a genetic marker should be evaluated under controlled conditions. They also recommended that alleles occurring at frequencies < 0.01 should be avoided in experiments with genetically marked fish. The genetic marker *PGI-1(30)* used in our experiment, is present at a frequency between 0.02 and 0.05 in wild cod populations in Norwegian seawaters. Jørstad *et al.* (1987) found no difference in growth of larvae and juveniles homozygous for the genotype *PGI-1(30)* compared to individuals having other *PGI-1* genotypes. The frequency of genetically marked individuals in the reared population was constant from the yolk-sac stage to mature fish 3 - 4 years of age (Jørstad *et al.*, in press). This suggests equivalent fitness among *PGI-1* genotypes, at least under farm conditions.

In our study, the percentage of genetically marked cod (Strain-A) in the pond decreased significantly with age, and in general, growth rate of Strain-A was lower than that of cod with other genotypes (Strain-B). During the larval stage (< Day 40), including the critical first feeding, the frequency of Strain A was approximately constant. In spite of a total larval mortality of 81 % during the larval phase apparently no changes in the frequency of genetically marked cod were noticed, and these observations are in agreement with the studies of Jørstad *et al.* (1987).

Strain-A had significantly smaller egg diameter than Strain-B, and hatched at a smaller size. This size disparity remained throughout the study, demonstrating a persistent size hierarchy. Knutsen and Tilseth (1985) showed that large eggs from the same spawning stock produced significantly larger larvae with respect to dry weight and standard length than small eggs. The egg size seems to be controlled by the diet, condition factor, and size of mature females, spawning group and time of spawning (Blaxter, 1988; Kjesbu, 1988). The

mean size of cod in broodstock A (genetically marked) was considerably smaller than that of cod in broodstock B, however, cod in broodstock A had a significantly higher average condition factor than cod in broodstock B.

The sharp reduction of Strain-A coincided with the increased mortality rate of the cod population after metamorphosis (Figs. 3 and 4). Food availability declined rapidly during the late larval stage (30 - 40 days after release) and remained low during the early juvenile stage, suggesting that competition for food and subsequent cannibalism were initiated (Blom *et al.*, in press). These density-dependent mechanisms are likely to be responsible for the increased post-metamorphosis mortality. The effect of selection for size should be most noticeable when mortality is highest (Rosenberg and Haugen, 1982). Strain-A had significant smaller body length than Strain-B towards the end of the larval stage (Day 35), indicating that size-selective mortality might be a reasonable explanation of the decrease in the portion of Strain-A in the population beyond metamorphosis. Predation, included cannibalism, may be the main process through which size-selection operates (Shepherd and Cushing, 1980; Smith, 1985). A larger part of the genetically marked larvae (55 %) were released on 21 and 22 March, while the first larval groups were released on 16 March. Thus, parts of Strain-A started exogenous feeding several days later than the initial larval groups which probably resulted in delayed growth, and hence reduced survival capability of Strain-A.

In spite of improvement in otolith analyses (Campana and Neilson, 1985), reliable estimates of larval abundances at different ages are difficult to obtain (Houde, 1987), and thus analysis of mortality rates are obscured. As shown by Svåsand *et al.* (in press), releases of genetically marked fish larvae in the sea offer the possibility of direct age and abundance measurments of field-collected larvae, and hence estimates of growth and mortality. In the pond experiment, we compared growth and survival of two genetic strains of Atlantic cod during the larval and juvenile stage. Growth was somewhat lower in the strain with a genetic marker, and the increased post-metamorphosis mortality of genetically marked individuals probably was the result of size-selective mortality. As observed, size-selective

mortality did not seem to prevail until a density-dependent response occurred due to insufficient food supply. Our findings support the view of Miller *et al.* (1988) and Anderson (1988) that small differences in size and growth between individuals may directly influence their survivorship.

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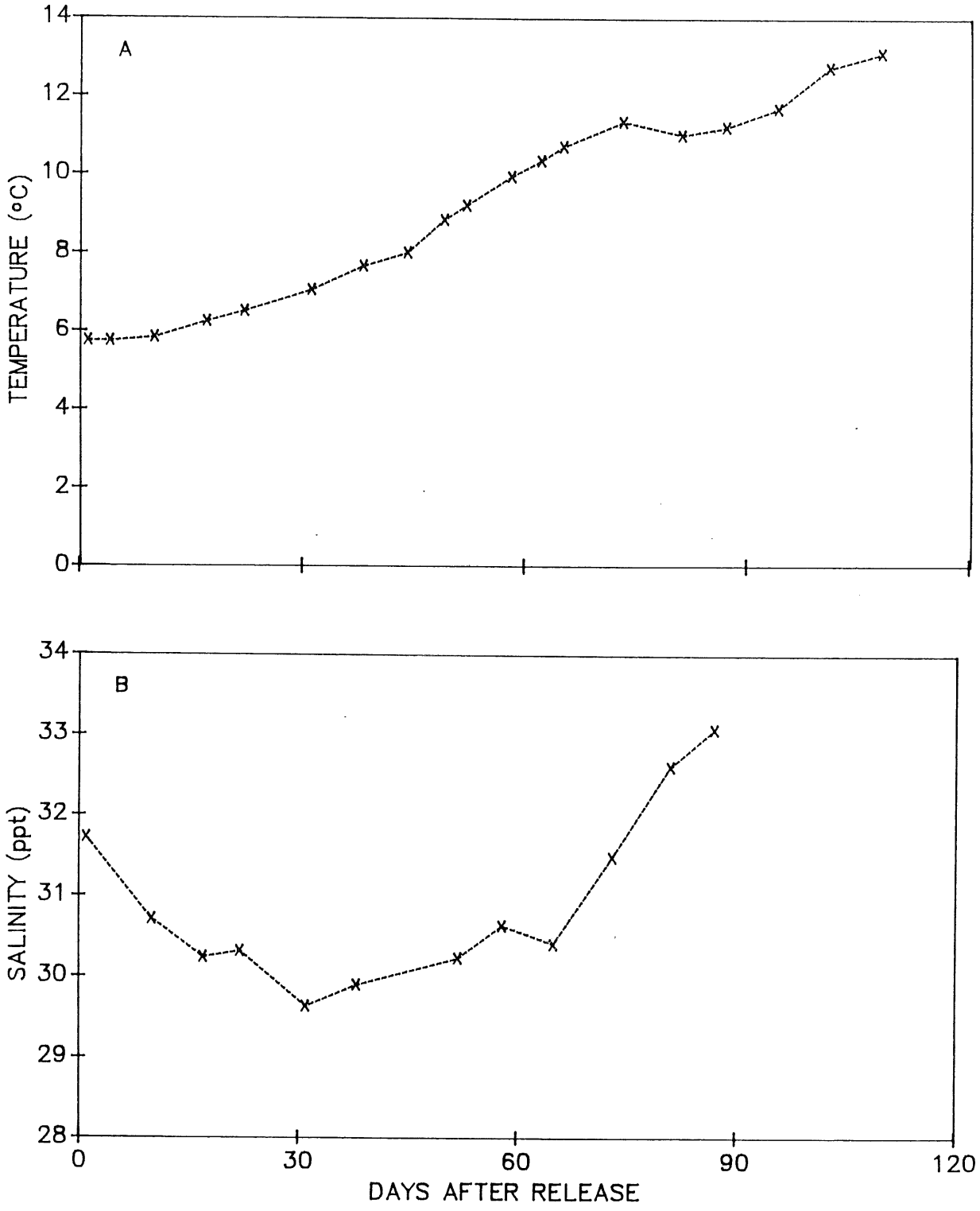

Fig. 1. Mean temperature (A) and salinity (B) in the pond. Measurements from 2 m depth to the bottom (1 m depth interval) are averaged. Day 0 corresponds to 19 March.

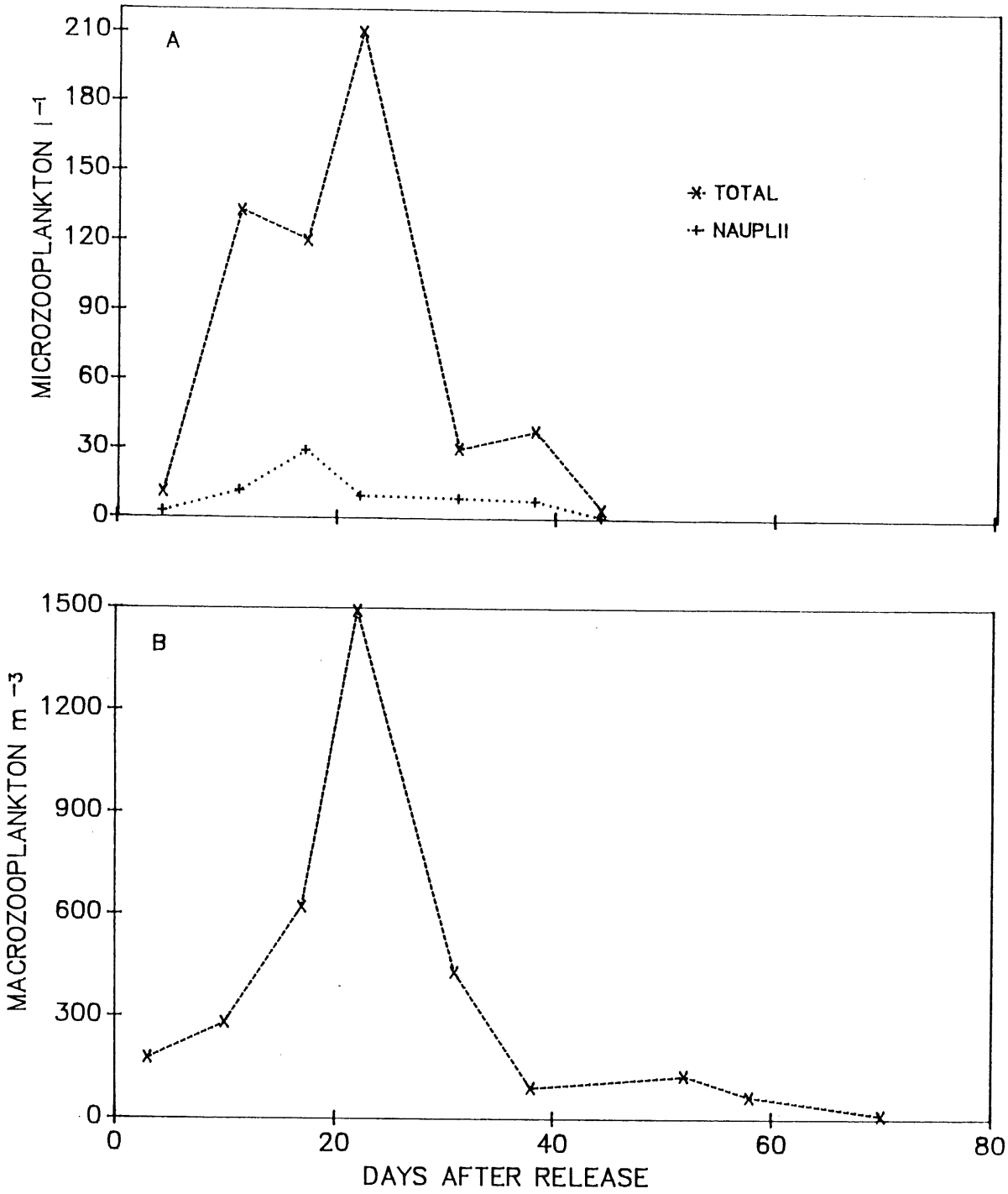

Fig. 2. Mean densities of microzooplankton (A) and macrozooplankton (B). Day 0 corresponds to 19 March.

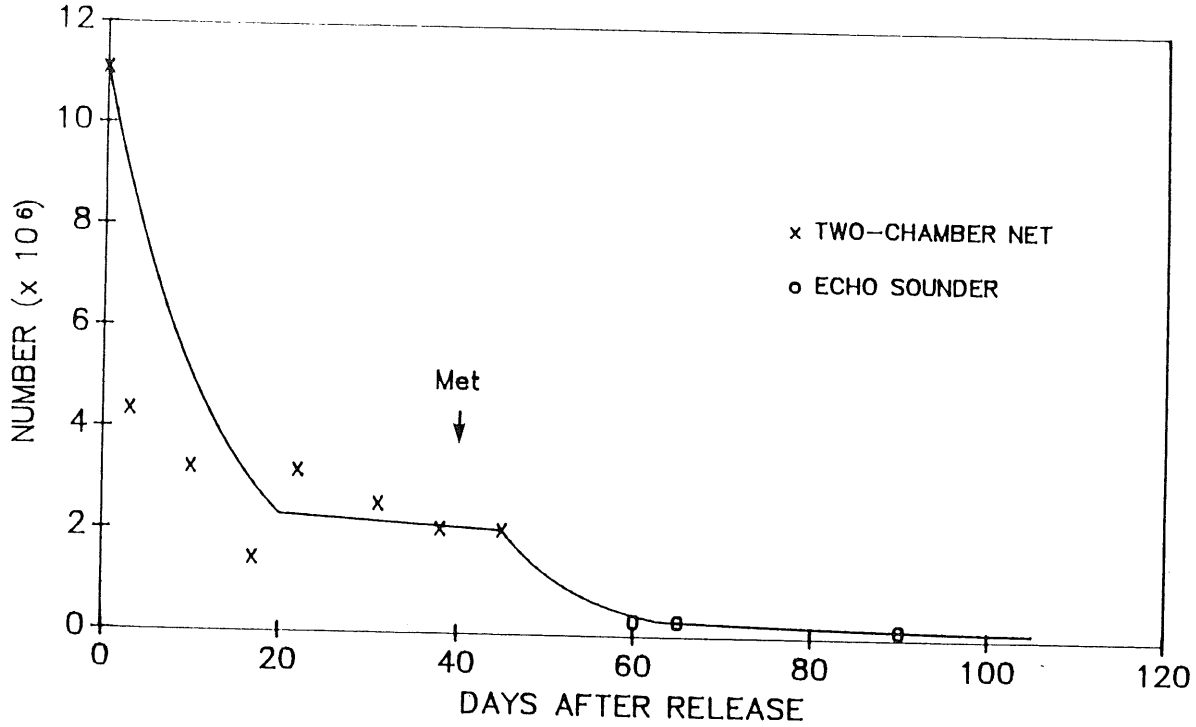

Fig. 3. Estimated survival curve for Atlantic cod fitted to the observed data (crosses and open circles). The arrow indicates metamorphosis.

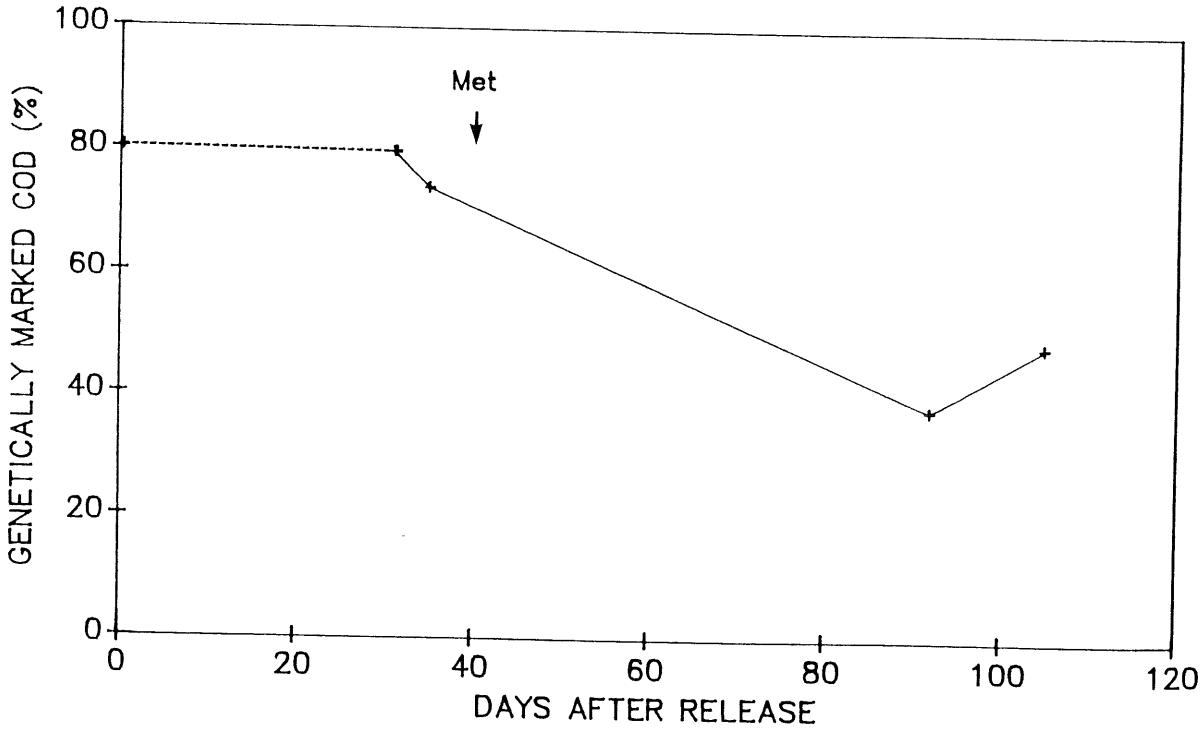

Fig. 4. Percentage of genetically marked cod (Strain-A) related to days after release. Observations on the solid line were included in the *G*-test. The arrow indicates metamorphosis.