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Effect of light intensity on the foraging and growth of Atlantic cod larvae: interpopulation difference?

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ABSTRACT: Studies have been conducted on the geographic variation of growth and survival among fish populations but little work has been done in this regard on the early larval stages of marine fish. We conducted experiments on larvae from 2 separate populations of Atlantic cod to determine their response to light. Preliminary experiments conducted in our laboratory suggested that the light intensity under which larvae were reared may affect the growth performance of Atlantic cod larvae from the Scotian Shelf (SS) and Northeast Grand Banks (NF) differently. We conducted experiments to test the hypothesis that light intensity differentially affects larvae from these 2 geographically distinct populations. Cod larvae from each population were reared under low (0.19 μE m^{-2} or 8.5 lx) and high (12.92 μE m^{-2} or 680 lx) light intensities. Results showed that NF larvae foraged, grew and survived better under high light than low light, while the SS larvae performed better under low light conditions. In nature, the population of SS cod we used spawn during late fall/early winter while NF cod spawn in spring/summer. Thus, SS larvae likely experience low winter light levels and NF larvae high summer light levels during first feeding. These results support our hypothesis and suggest that cod larvae from different latitudes are adapted to local environmental conditions.

KEY WORDS: Atlantic cod larvae · Population difference · Light intensity · Growth · Survival

INTRODUCTION

Geographic variation in growth and survival among populations of the same species has been well documented in reptiles (Ferguson & Talent 1993), fishes (Blaxter & Hempel 1963, Houde 1989, Fleming & Gross 1990, Castro & Cowen 1991, Present & Conover 1992, Mathias et al. 1993), and some invertebrates (Lonsdale & Levinton 1985). Although studies have examined geographic variation in growth and survival among fish populations, most of these have dealt with salmonids and adult fish (Fleming & Gross 1990, Present & Conover 1992, Mathias et al. 1993). In contrast, little work has been done on geographic variation in the early life history of fishes (Blaxter & Hempel 1963, Houde 1989, Castro & Cowen 1991). It has been hypothesized and demonstrated that animal populations which are geographically separated respond differently to particular environmental variables (Ferguson & Talent 1993). These differences could be interpreted as an evolutionary response or adaptation to the different levels of environmental constraints that each population experiences in nature (Ricker 1972). Although some of these differences appear to have a heritable (i.e. genetic) component, in many cases it has been difficult to establish how selective pressure has resulted in the suite of differences observed (Beacham et al. 1988).

Atlantic cod *Gadus morhua* is an ideal model for the study of geographic variation in the response to environmental characteristics. Its range extends from the arctic seas to temperate oceans and within each region there appears to be 1 or more separate stocks (Scott & Scott 1988). For example, Cross & Payne (1978), using electrophoric and immunochemical characteristics, suggested the existence of genetically discrete subpopulations of Atlantic cod within restricted geographic areas, off eastern North America. Despite its wide distribution, surprisingly little work has been done on the intra-population variation of Atlantic cod and nothing has been done to examine effects of geographic variation in the early life history of Atlantic cod.

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Light, in particular, plays an important role in the growth and survival of larval fish (Blaxter 1975, Batty 1987). Light can influence the behaviour of fish, through its variation in intensity, wavelength and polarization and diurnal and seasonal variation (Munz 1975, McFarland 1986). The availability of light during the early life stages of fishes also affects the normal development of the eye. Response of larval fish to a particular characteristic of light is species specific. In the cichlid *Haplochromis burtoni* (Zeutzius & Rahmann 1984) and rainbow trout *Salmo gairdneri* (Rahmann et al. 1979), light deprivation in the early larval stage affects the normal development of the eye and reduces visual acuity. In contrast, halibut *Hippoglossus hippoglossus* yolk-sac larvae develop abnormally in the presence of light (Bolla & Holmefjord 1988). Despite an impressive amount of research on the early life history of Atlantic cod larvae, no investigations have been done on the effects of light on growth and feeding.

Preliminary experiments on the foraging, growth and survival of cod larvae from the Scotian Shelf (SS; latitude 44° 30' N) and Northeast Grand Banks (NF; 47° 30' N) in our laboratory showed that performance between the 2 groups differed under different light intensity. We set up laboratory experiments to test the working hypothesis that light intensity differentially affects larvae from these 2 geographically separate cod populations.

MATERIALS AND METHODS

Collection of eggs. Naturally spawned fertilized eggs were collected from Scotian Shelf (SS) broodstock maintained at Dalhousie University, Halifax, Nova Scotia, and from the Northeast Grand Banks (NF) broodstock maintained at the Ocean Sciences Centre (OSC), Memorial University of Newfoundland. The SS broodstock spawn naturally from November through January (Brander & Hurley 1992) while the NF broodstock spawn from April through July (Fahay 1983). Thus, experiments were conducted at different times of the year, but the experimental protocols were identical. SS eggs were collected in early December 1993, while NF eggs were collected in late May 1993. At the time of egg collection temperature in the brood stock tanks was between 4 and 6°C for the NF broodstock and 5 and 7°C for the SS broodstock. Similar temperatures were reported in the field during late fall for the SS (Smith 1989) and summer for NF (Myers et al. 1993). SS eggs were transported to OSC and incubated under the same condition as NF eggs. Light intensity in the incubation room was 300 to 400 lx. We will provide light intensities in both lx and μE m^{-2}. Eggs were incubated at 6 ± 1°C in 250 l circular tanks with water flow and aeration. Dead eggs were siphoned out daily and antibiotic solution [mixture of tetracyclene (100 mg l^{-1}) and penicillin (60 mg l^{-1})] was sprayed on the eggs to control any bacterial and fungal infections. Incubation time for both NF eggs (13 d) and SS eggs (14 d) was similar. When 50% of the eggs had hatched, larvae were transferred to experimental tanks and this was taken as Day 0 of the experiment.

Preliminary experiments. Prior to the main experiment a series of preliminary experiments were carried out to develop protocols for the rearing of cod larvae through metamorphosis. In one experiment, we duplicated the conditions used by Norwegian scientists (Ellertsen et al. 1980, Solberg & Tilseth 1987) including low light intensities (<100 lx). In these experiments we used a light intensity of ~10 lx and a 16 h light:8 h dark photoperiod and temperature was maintained at 8 ± 1°C. Laboratory reared rotifers (*Brachionus plicatilis*) and/or *Artemia* sp. were used at prey concentrations, ranging from 500 to 4000 prey l^{-1}. The results showed that SS larvae grew and survived better than NF larvae. Both the populations did better in 4000 prey l^{-1}.

In a second preliminary experiment, we used a 24 h light (of appropriate intensity) photoperiod for both NF and SS cod larvae and prey levels of 4000 prey l^{-1}. For both populations, survival was higher under the continuous light regime than under 16 h light:8 h dark. Previous studies have indicated that other fish species achieve a better growth and/or survival using a 24 h photoperiod (Kiyono & Hirano 1981, Duray & Kohno 1988).

Experimental setup. All experiments were carried out at the OSC in a temperature controlled cold room maintained at 8°C. Water temperature in the experimental tanks was measured daily in the morning. The room was subdivided into 2 chambers by an opaque black plastic curtain. One chamber was assigned as a high light (HL) intensity treatment (12.92 μE m^{-2}/680 lx) and the other a low light (LL) intensity (0.19 μE m^{-2}/ 8.5 lx) treatment. These light intensities were chosen based on the results from our preliminary experiments. The experimental tanks were 30 l rectangular glass aquaria (38 cm in depth) with 2 tanks per treatment. Three sides of each aquarium were covered with opaque black plastic. The front was not covered to facilitate the behavioural observations. Two 90 W incandescent bulbs, one above each of the HL tanks, and two 7.5 watt incandescent bulbs, one above each of the LL tanks, were used. Both type of bulbs produce a smooth continuous spectra ranging from 400 to 700 nm [GE electronic company, 4400 Cox Road, PO Box 4410, Glen Allen, VA 23058-4410, USA). All tanks were covered by a sheet of blue-green plastic to ensure an even distribution of light into the tanks. LL tanks were covered with 2 blue green plastic sheets to achieve

8.5 lx. Light intensity inside the tanks was measured using a light meter (SPER Scientific light meter 840006 for measurements in lux and Li-Cor Quantum photometer model L1-189 for measurements in $\mu E\ m^{-2}$), held just above the water surface. All measurements were taken when the covers were on. A 24 h photoperiod was used.

Initially, tanks were filled with filtered, UV treated sea water. Larval stocking density was 40 larvae l^{-1}. For the first week, there was no exchange of water. After 1 wk a flow of 100 to 200 ml min^{-1} was started, which was gradually increased to 700 to 800 ml min^{-1} during the fourth week (Howell 1984). Green algae (*Isochrysis* sp.) was added to the tanks daily from Day 1 to the end of the experiment. Cultured, enriched rotifers and/or *Artemia* sp. were used as prey. From Day 3 to Day 10 post-hatch rotifers were used as prey. As the larvae grew a mixture of rotifers and *Artemia* sp. (1:1) were used. Prey concentration was maintained at 4000 prey l^{-1} (Laurence 1978, Gotceitas et al. 1996). To maintain this prey level, a 10 ml water aliquot was sampled daily from each tank at different depths (just below surface, mid water column, and just above bottom). The number of prey was counted and prey levels were adjusted to 4000 prey l^{-1}, if necessary. The blue-green covers and presence of an air bubble and an air lift helped to reduce the patchiness of the prey (Ellertsen et al. 1980, Gulbrandsen 1991).

Data collection. Ten larvae were sampled on Day 0 and thereafter 5 larvae from each tank (10 per treatment) were arbitrarily chosen for morphometric measurements and dry weights at 5 d intervals over the duration of the experiment (43 d). Using a dissecting microscope, the following were recorded: standard length (mm), head depth (measured posterior to the eye), eye diameter and myotome height (measured at anus). The presence or absence of food in the gut, in proportion to gut volume, was also recorded. After measurements, each larva was rinsed in fresh water and placed on a pre-weighed piece of aluminium foil and dried in an oven for 24 to 48 h at 65°C. To calculate the larval dry weight, larvae and foils were weighed to nearest 0.0001 mg using a electro microbalance.

Behavioural observations were recorded from Day 1 to Day 31 post-hatch for NF stock, and from Day 1 to Day 43 post-hatch for SS stock using a Tandy 102 event recorder. We could not collect behavioural data for NF cod larvae beyond Day 31 due to technical problems. Observations were conducted twice a week and all the observations were made by an observer seated in front of each tank between 10:00 and 12:00 h. During each observation period, a larva was observed for 1 min. The occurrence (beginning and end of the event) of any of 5 foraging Modal Action Patterns or 2 activities (swim or motionless) (MAPs; Barlow 1977; Table 1) performed by the larva was recorded. In total, 5 larvae were observed in each tank (10 per treatment). In this paper, we combined the frequencies (MAPs min^{-1}) of orient, success, miss, and pass into a category termed foraging.

Table 1 Operational definitions of feeding Modal Action Patterns (MAPs) for larval cod

MAP	Definition
Swim	Forward movement of larva through water column accomplished by caudal fin action
Motionless	Larva is not swimming
Orient	Larva stationary and fixates on a prey item
Bite	Larva attempts to capture prey
Success	Prey is captured
Miss	Prey is not captured
Pass	Larva orients on a prey item but does not bite; larva then swims in another direction

Foraging = Orient + Success + Miss + Pass

The experiment was carried out for 43 d and terminated when the majority of the larvae were past metamorphosis. Metamorphosis was determined externally by the disappearance of the continuous fin fold and subsequent formation of discrete fins. At the end of the experiment, the number of surviving larvae were recorded.

Data analysis. All data were tested for normality (SAS Institute 1988). The foraging frequency and gut content index data were not normal, and a non-parametric 1-way analysis of variance (ANOVA) (Wilcoxon's rank sum test) was used to determine the effect of light level ($p \leq 0.05$).

The effect of light level and age on standard length and swimming of cod larvae were analysed by 2-way ANOVA ($p \leq 0.05$). Tukey's test was used for a multiple comparison among different light treatments and locations (SS/NF) for each week.

RESULTS

By the end of the second week, there was a significant difference in growth (ANOVA; $F = 29.3$; $p < 0.0001$) among NF cod larvae raised under HL and LL intensity conditions. NF larvae reared under HL grew better from Week 3 until the end of the experiment (Fig. 1a, Table 2). In contrast, SS cod larvae grew significantly better under LL. In fact, SS larvae reared under HL did not survive beyond the fourth week (Fig. 1b). Analysis of the data for the first 4 wk showed that the standard length of the SS larvae reared under LL was significantly higher ($F = 5.99$; $p < 0.00163$) than that of SS larvae reared under HL.

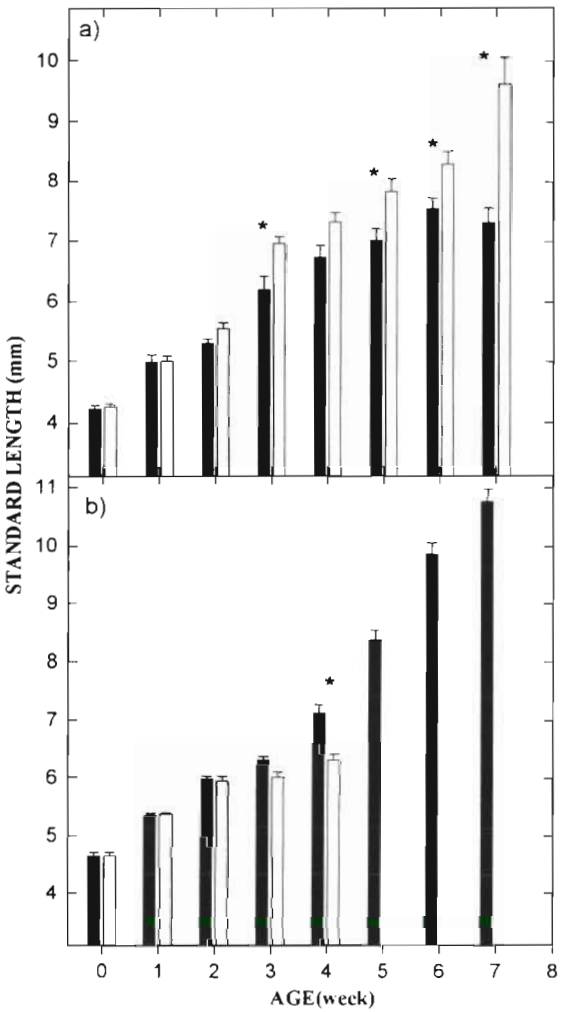

Fig. 1 *Gadus morhua*. Standard length of (a) Northeast Grand Banks and (b) Scotian Shelf cod larvae reared under low (8.5 lx or 0.19 µE m^{-2}; ■) and high (680 lx or 12.92 µE m^{-2}; □) light conditions over age. Values are mean +SE. *Significant difference. n = 10 to 20 larvae wk^{-1}

Overall, there was no significant difference between the growth of SS larvae reared under LL and NF larvae reared under HL (F = 1.27; p < 0.2622). However, at hatching the SS larvae were larger than the NF larvae but NF larvae reared under HL exceeded the size of SS larvae by the end of Week 2. There was no significant difference between the growth of NF larvae under HL and SS larvae under LL at Weeks 3 and 4, but NF larvae reared under HL were significantly larger than SS larvae reared under HL at Weeks 3 and 4 (Table 2). SS larvae reared under LL were significantly larger than NF larvae reared under same condition (F = 87.09; p < 0.0001), but there was no significant difference at Weeks 3 and 4. After 4 wk, SS larvae were significantly larger than the NF cod larvae (Table 2).

The duration of swimming of NF larvae was significantly higher (F = 25.28; p < 0.0001) under HL than LL (Fig 2a, Table 3). This higher swimming activity probably resulted in a higher encounter rate with the prey which resulted in an increased foraging frequency under the HL condition. The mean foraging frequency of NF larvae was significantly higher under HL (Wilcoxon's rank sum test; Z = −4.27284, df = 1; p = 0.0001) than for larvae under LL (Fig. 2b). The gut fullness analysis also confirmed higher rate of successful prey encounter of NF larvae under HL than under LL. The index of gut fullness of NF cod larvae was significantly higher (Z = 4.46398, df = 1; p = 0.0001) under HL than LL conditions (Fig. 2c).

There was no significant difference in swimming duration (F = 0.86; p = 0.356) between SS larvae reared under LL and HL (Fig. 3a, Table 3). However, the foraging frequency of larvae under LL conditions was significantly higher than that under HL conditions (Z = −7.02919, df = 1; p = 0.0001) (Fig. 3b). This was reflected in gut fullness index (Fig. 3c), which was significantly higher under LL (Z = −2.91237, df = 1; p = 0.0036) than HL conditions. At the end of the experiment the survival of NF cod larvae was higher in HL compared to LL. SS larvae did not survive in HL, but in LL survival of SS larvae was much higher than NF larvae (Fig. 4).

DISCUSSION

Overall, our results showed a significant difference in the swimming, foraging, growth and survival of Atlantic cod larvae from 2 populations in relation to light intensity. For example, NF cod larvae foraged more, grew faster and had higher survival under high light intensity, while SS cod larvae performed better under low light conditions. Even though eggs/larvae were col-

Table 2. Results of the Tukey analysis comparing the standard length (mm) of cod larvae from the Scotian Shelf (SS) and Northeast Grand Banks (NF) under low light (LL) and high light (HL) levels from Week 1 to Week 7 post-hatch. *Significant difference between the treatments (p < 0.05)

Treatment	Weeks post-hatch						
	1	2	3	4	5	6	7
NFHL and SSLL	−0.388*	−0.430*	0.268	0.194	−0.536	−0.728*	−1.141
NFHL and NFLL	0.006	0.241	0.421*	0.582	0.823*	1.443*	2.318*
NFHL and SSHL	−0.397*	−0.400*	0.574*	1.024*	–	–	–
NFLL and SSLL	−0.394*	−0.671*	−0.153	−0.388	−1.359*	−1.493*	−3.459*
NFLL and SSHL	−0.403*	−0.641*	0.153	0.441	–	–	–
SSLL and SSHL	−0.007	0.030	0.306	0.829*	–	–	–

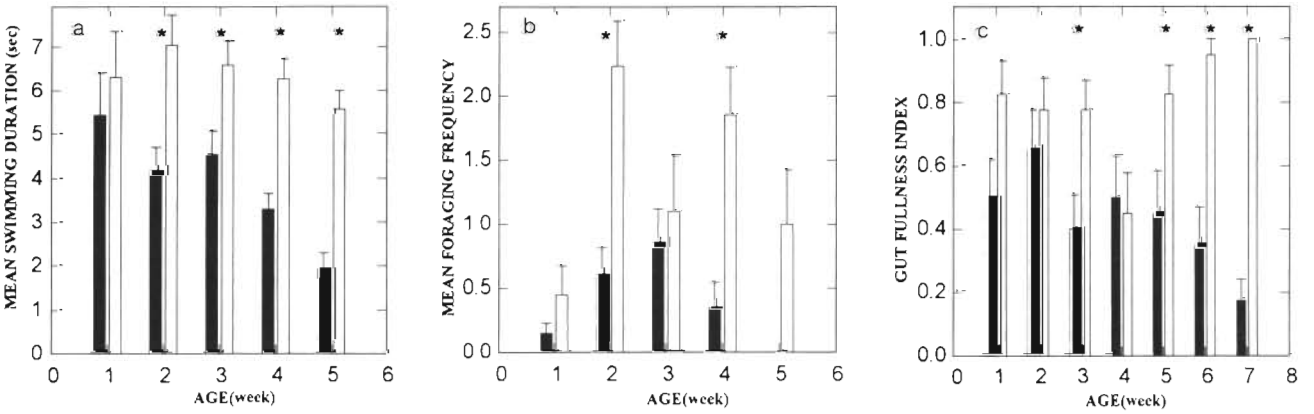

Fig. 2. *Gadus morhua*. (a) Mean swimming duration, (b) mean foraging frequency, and (c) mean gut fullness index of Northeast Grand Banks cod larvae reared under low (■) and high (□) light conditions. Values are mean + SE. *Significant difference. n = 20 larvae wk^{-1}

Table 3. Results of the Tukey analysis comparing the mean swimming duration(s) of cod larvae from the Scotian Shelf (SS) and Northeast Grand Banks (NF) under low light (LL) and high light (HL) levels from Week 1 to Week 5 post-hatch. *Significant difference between the treatments ($p < 0.05$)

Treatment	Weeks post-hatch				
	1	2	3	4	5
NFHL and SSLL	1.515	1.153	0.550	1.025	1.510*
NFHL and NFLL	0.875	2.873*	2.055*	2.965*	3.650*
NFHL and SSHL	2.940*	1.288	1.565	1.515	–
NFLL and SSLL	0.640	−1.720	−1.505	−1.940*	−2.140*
NFLL and SSHL	2.065	−1.585	−0.490	−1.450	–
SSLL and SSHL	1.425	0.135	1.015	0.490	–

lected at different times of the year from naturally spawning broodstock, the experimental conditions (temperature, light intensity, photoperiod, prey type/density) were identical for both populations. It is apparent that light intensity affected the foraging ability of larvae differentially. The ecological reason for this result may be traced to the different spawning seasons of each population. The population of cod we studied from the SS typically spawn over the period of November to January (Brander & Hurley 1992), while cod on NF typically spawn from April to July (Fahay 1983). Winter sea surface light levels at the latitude of the SS range from 3180 to 1360 lx from November to January respectively, while the spring/summer sea surface light levels at the latitude of NF range from 13 000 to 20 000 lx from April to July (Nielsen 1974, Blaxter & Batty 1990). Thus, larvae on NF might be expected to experience 10-fold higher light levels compared to cod larvae on the SS from the fall/winter spawning. As such, the differences between larvae from these 2 populations noted in our study may reflect an adaptation of these larvae to local conditions.

Anderson & de Young (1995) reported that cod larvae in the offshore and inshore areas of NF occupy the top 40 m (5 to 35 m) of the water column during summer months. Field data from Conception Bay in NF showed that light intensity during the month of July, at 40 m

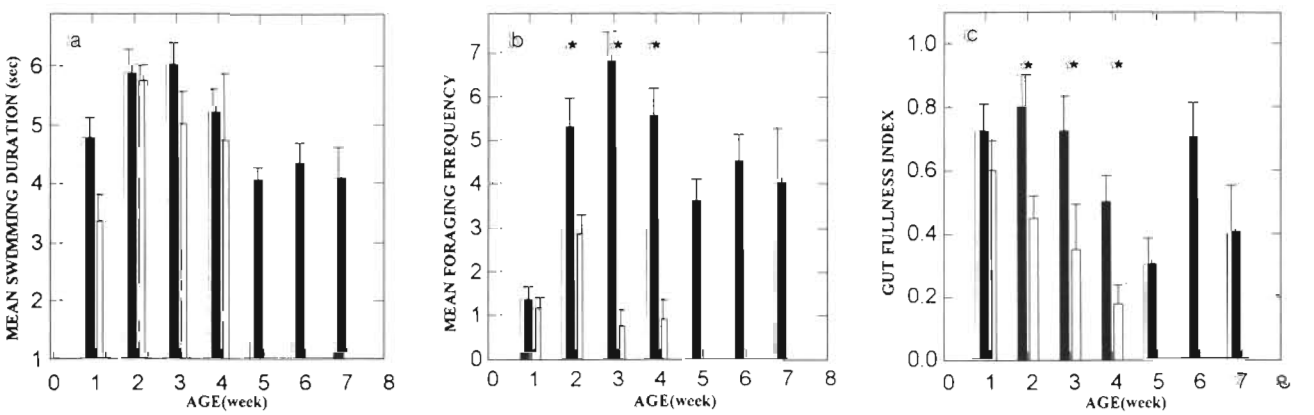

Fig. 3. *Gadus morhua*. (a) Mean swimming duration, (b) mean foraging frequency, (c) mean gut fullness index of Scotian Shelf cod larvae reared under low (■) and high (□) light conditions. Values are mean + SE. *Significant difference. n = 20 larvae wk^{-1}

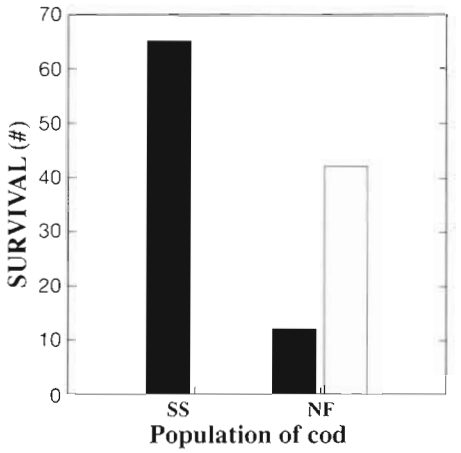

Fig. 4. *Gadus morhua*. Total number of Scotian Shelf (SS) and Northeast Grand Banks (NF) cod larvae surviving at the end of the each experiment in relation to the light levels (■: low light; □: high light) at which they were reared

depth, ranges between 10 and 30 μE m^{-2} (R. Rivkin unpubl. data). Thus, in nature, cod larvae from NF experience similar light intensities to those of our high light treatment. On the other hand, cod larvae from SS occur at a depth of 20 to 30 m in late fall (McKenzie 1940). O'Reilly et al. (1987) reported that the surface sun light over the SS diminishes to 1% between 20 and 45 m. The larvae from SS therefore would likely experience a light intensity of 13 to 31 lx in late fall, which is comparable to the low light intensity (8.5 lx) used in our experiment.

Survival of NF cod larvae at the end of the experiment was higher under high light than low light. In contrast, SS larvae survived only under low light. The reason SS larvae did not forage or survive beyond 4 wk in high light intensity is difficult to explain. Swimming of SS larvae was not significantly different between high and low light intensity, but the foraging activity and the gut fullness of larvae were lower in high light. The latter result suggests that at high light intensity, SS larvae did not forage as efficiently as they did at low light intensity. The reason SS cod larvae foraged poorly under high light is not obvious. In nature, larvae can vertically migrate, so that, if unfavourable conditions occur, they can migrate to more favourable depths in the water column (Lough & Potter 1993).

As in most marine larval fishes, cod larvae have a poorly developed visual system at hatching. The eyes of most fish larvae become more pigmented during first feeding (Blaxter 1986). Most pelagic larvae investigated so far have a pure cone retina at first feeding (Blaxter & Staines 1970). During metamorphosis, this pure cone retina becomes a duplex retina and the juveniles move down into the water column (Shand 1994). The changes in the visual system could be associated with changes in both habitat and feeding behaviour In contrast, some deep-sea larvae (e.g. an anguillid and a macrourid larva) have a pure rod retina at hatching (Munz 1958). It would appear that the variation and change in eye pigments and structure pigments can be related to the diversity of the environments larvae encounter and reflect the different visual tasks the animals have to face. Regardless, all these observations imply that the presence of rods in the retina help the larval fish to cope with a darker environment. If this is the case, then fish larvae which experience low light levels may have a higher concentration of rods in their retina to facilitate searching for prey. Based on our results, SS larvae might be expected to develop a greater concentration of rods in their retina early in the first feeding stage compared to NF larvae, which begin foraging in a high light environment.

Sizes of marine fish larvae are influenced by egg size, which in turn is influenced by female condition (Chambers & Waiwood 1996) and the environmental conditions experienced during the embryonic stage (Miller et al. 1993). In our study, incubation conditions were similar for eggs from both NF and SS populations. Thus, the size difference at hatching between the larvae from 2 populations may be due to the differences in egg size. Unfortunately, we could not verify this as the egg sizes were not measured. Further, egg size varies substantially over years within the same populations (McKenzie 1940, Miller et al. 1993). Thus, even though our results were consistent with our hypothesis, precautions should be taken when comparing with other studies.

Lagomarsino & Conover (1993) reported variation in the environmental sex determination (ESD) process in Atlantic silverside from different latitudes. In their studies, larvae from higher latitudes, experiencing low temperatures, produced a higher percentage of females, while fish from lower latitudes, experiencing higher temperatures, produced mainly males. This incongruity was mainly attributed to differences in temperature experienced during the spawning season and suggested that sex determination in silverside is controlled by an interaction among genetic factors, phylogenic factor and temperature. A similar scenario may apply in the case of the SS and NF cod populations. A portion of cod in the SS spawn during winter, larvae experience low light levels, and, based on our results, display better growth and survival at low light conditions. In contrast, NF cod spawn during summer (high light), and larvae performed better under high light conditions. What the underlying mechanisms for the difference are remain to be determined.

The other attribute of light which has been shown to have an effect on aquatic organisms is the spectral

quality (Munz & McFarland 1973, Hobson et al. 1981, Levine & McNichol 1982). The studies reporting these effects have been field studies dealing with adult populations, and to the best of our knowledge no study has experimentally determined how spectral quality might influence the performance of larval fish. Shand (1993) reported that the abrupt change in the spectral sensitivity of the goatfish eye coincided with metamorphosis and the benthic mode of life. Juvenile pollack *Pollachius pollachius* also showed a progressive change in spectral absorbency during their late pelagic stage (Shand et al. 1988). In both cases, changes in the spectral sensitivity correspond to changes in life style, i.e. from pelagic to benthic life. Since we investigated only the pelagic stage up to late larvae of Atlantic cod, spectral quality may not affect feeding behaviour. Shand et al. (1988) also showed that the change in spectral sensitivity in pollack is correlated more with age/size than to season. Thus, the early life-stage larval cod that we investigated may not go through the developmental changes of the eye related to spectral sensitivity until later in larval life.

In summary, our results demonstrate that different light intensities had a influence on activity, foraging, growth and survival of 2 populations of Atlantic cod larvae. This result also suggests that, for the successful rearing of fish larvae, we have to understand the roles various environmental factors play in influencing larval growth and survival.

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