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Reproduction of the shorthorn sculpin *Myoxocephalus scorpius* in northern Norway

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Abstract

The reproduction and life history events of the shorthorn sculpin *Myoxocephalus scorpius* were studied in an unexploited high latitude population in Tromsø, northern Norway. Shorthorn sculpins were sampled from November 1998 to March 1999 to determine sex ratio, spawning period, oogenesis, fecundity, embryogenesis and hatching. Spawning occurred between January and March. The catches of males were maximal in January and February, while catches of predominantly immature females increased towards the end of the spawning period. This may be related to different migration patterns in males and females. It is possible that after spawning, females migrate to other areas, whereas males stay behind and guard the eggs. The spawned eggs were smaller than reported from other study areas. Larvae hatched after 7 weeks at an average egg incubation temperature of 3.3 °C. Fecundity in females ranged from 1200 to 29 000 eggs, with a length exponent of 3.0. The relatively large size (7.6–8.8 mm in length), advanced performance and developmental status at hatch of shorthorn sculpin larvae suggest that the reproductive strategy of the shorthorn sculpin is an intermediate between strategies that have many small larvae and those that have fewer, larger and more developed larvae.

Keywords: *Myoxocephalus scorpius*; Reproduction; Spawning seasons; Fecundity; Oogenesis; Embryonic development

1. Introduction

The shorthorn sculpin *Myoxocephalus scorpius* (Linnaeus, 1758) is a common and widespread species in the coastal areas of the northern Atlantic (Ennis, 1970a) and it is distributed from eastern North America to Greenland and Iceland to the Baltic Sea and south to north-western France (Wheeler, 1969; King et al., 1983; Raciborski, 1984). The reproductive biology of the shorthorn sculpin is poorly known, and in particular, with the exception of the study of Pavlov et al. (1992), little is known about the reproductive biology of the shorthorn sculpin in Norway and at high latitudes.

The oocytes of shorthorn sculpins increase in diameter during the months prior to spawning, as sea temperature decreases (Ennis, 1970b; King et al., 1983; James and Johnston, 1998). Shorthorn sculpin spawn eggs with diameters of about 2.4 mm from late November to early December to February in the Baltic Sea and Newfoundland (Ennis, 1970b; Lamp, 1966). In the White Sea they spawn eggs with

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diameter of 2.0–2.5 mm from November to January (Pavlov et al., 1992). The females deposit a clump of eggs between rocks or amongst seaweed (Wheeler, 1969). One male guards the eggs of one or more females but may also guard two egg masses from the same female (Ennis, 1970b). A concurrent study of the life-history of the shorthorn sculpin has shown that in northern Norway, males become sexually mature at the age of one year and that most females mature at the age of two (Luksenburg and Pedersen, 2002). Marked differences in growth and mortality patterns between males and females may be linked to the reproductive biology of the species (op. cit.).

This study aims to test whether reproductive output of the high latitude population in Tromsø is related to sex and fish size and whether the reproductive characteristics differ from shorthorn sculpin populations in other areas. We also compare the reproductive strategy of the shorthorn sculpin with other species.

2. Materials and methods

2.1. Sampling

Shorthorn sculpins were sampled at Grindøy, at the north end, and at the south end of the island of Tromsøy (N69°40′, E18°50′). Fish were collected from November 1998 to March 1999 (n = 377). Sampling was conducted with 2–12 fyke nets at a depth of 0.4 – 11 m at a distance of 0.5 – 30 m from the low tide mark. The fyke nets consisted of a central single leader arranged like a gill net, but with two circular retainment sectors on each side. The retainment sectors had three chambers with funnels in between (Nøstvik and Pedersen, 1999). The fyke nets were emptied every two to four days, but occasionally a week or more passed before the nets could be emptied due to bad weather. On 18 January 1999 every second chamber of the fyke nets was closed to prevent otters from being caught. Because there was no apparent difference in catch rate between closed and unclosed nets, all the second chambers of all fyke nets were closed from 22 January 1999. After capture, the shorthorn sculpins were killed by pithing and either immediately frozen at -20 °C or examined the same day.

The temperature of the surface water was measured at every sampling and ranged from -1.2 °C to 3 °C, with mean temperatures from 2.1 °C in January to 0 °C in February and 1.05 °C in March.

2.2. Laboratory

A total of 293 fish (84 fish were used in a tag-recapture experiment) were available for laboratory analysis. Total length, total weight, gutted weight, gonad weight, sex and maturity were determined. Maturity stage was determined by visual inspection according to the criteria provided by Ennis (1970a).

Ovaries (n = 64) of mature females (fresh and frozen) were analysed for fecundity estimation. The paired ovaries were weighed to the nearest milligram. Three sub-samples of the anterior, middle, and posterior part of each ovary were dissected out, weighed and put in 9.1‰ NaCl to preserve the size of the eggs. For each sub-sample, the number of eggs and egg diameter was determined. The fecundity is defined as the number of mature eggs in the ovary before spawning (Raitt, 1968; Bagenal, 1978). Fecundity was determined by estimating the average number of mature eggs per gram and multiplying this by the total ovary weight. It was not possible to subtract the weight of the ovarian capsule (Lagler et al., 1977) after the number of eggs had been estimated, but a few known weights of ovarian capsules of ovulated females indicated that this weight was on average 2.36% of the total body weight, so it is assumed that inclusion of the ovarian capsule in the total ovary weight would not make a significant difference in fecundity estimates. The gonadosomatic index (GSI) was calculated as: GSI = 100(gonad weight/somatic body weight), where somatic weight is the weight of the body excluding the weight of the gonads.

To estimate the duration of embryogenesis and embryo development, nine egg masses were held in flow-through seawater incubators to allow hatching. The incubators were cylindrical with a diameter of 30 cm and water height of 20 cm. Eggs of six ovulated females were stripped and artificially dry fertilised with milt taken from dead, just caught males (dates of insemination: 27-1-99, 4-2-99, 5-2-99, 8-2-99, 11-2-99, 3-3-99). After careful mixing of the eggs and sperm, some water was added until the eggs were covered to a depth of 0.5 cm. The eggs were put in a cooler (4 °C) for two hours and then

Table 1
Summary of numbers of fish caught, sex ratio (number of females/males), and chi-square tests for equality in sex ratio of *Myoxocephalus scorpius* caught in the Tromsø area from November 1998 to March 1999

Month	Number of fish		Sex ratio	χ^2	Significance
	Females	Males			
November	29	11	2.64	8.1	S
December	26	16	1.63	2.38	NS
January	43	99	0.43	22.08	S
February	27	59	0.46	11.90	S
March	35	25	1.40	1.67	NS

S = significant, NS = not significant at the 5% level.

transferred to incubators. During sampling, three females which were close to spawning, and three mature males were put in three flow-through seawater tanks, making three pairs. The holding tanks were 104 x 104 cm with a water height of 20 cm. Two of these pairs spawned naturally (dates of fertilisation: 29-1-99, 21-2-99) and from one female the eggs were stripped and dry fertilised (date of insemination: 9-2-99). All three egg-masses were transferred to incubators. During February, the egg-masses were disinfected twice with 25% glutardialdehyde, initially with 150 ppm for 5 min, and subsequently with 150 ppm for 3 min. Temperature and egg development were determined regularly. Embryogenesis was studied by inspecting small samples taken from the egg masses through a binocular. Holt (1893) gives a precise description and realistic drawings of the embryogenesis and larva of the shorthorn sculpin.

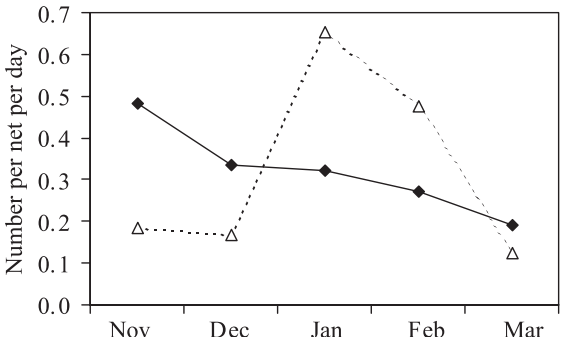

Fig. 1. Catch rates per net per day for male and female *Myoxocephalus scorpius* in the Tromsø area from November 1998 to March 1999; Δ males, ♦ females.

At hatching, several individuals were fixed in 2.5% glutardialdehyde and 2.5% paraformaldehyde in 0.02 N cacodylate buffer (modified Karnovsky fixation medium), some of which were embedded in paraplast and Epon epoxy medium and sectioned to study the histomorphological organ differentiation of the shorthorn sculpin larvae.

2.3. Relation between fecundity and body size

The relationships between fecundity and size took the form: $F = a_1 L^{b1}$ and $F = a_2 W^{b2}$, and $W = a_3 L^{b3}$, with F = fecundity, L = length in cm and W = somatic weight in gram. F, L and W were transformed taking the natural logarithms, and the coefficients *a* and *b* estimated by linear regression. Calculations were performed with SYSTAT (Wilkinson, 1992). A t-test was

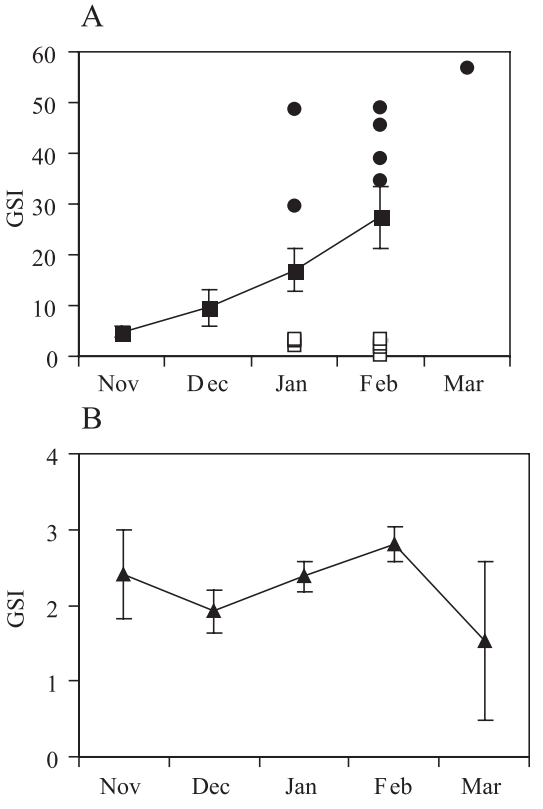

Fig. 2. Changes with time in gonadosomatic index (GSI) for (A) females and (B) males; ■ maturing females, ● ovulated females, □ spent females, Δ mature males; bars indicate 95% confidence intervals.

used to check whether the slopes (b1, b2, b3) in the regressions differed from published values (Zar, 1984).

3. Results

3.1. Sex ratio and catch rate

Of the 377 fish caught, 160 were female, 210 were male and 7 fish could not be sexed, giving a female: male sex ratio of 0.76:1. This is significantly different from the 1:1 sex ratio ($\chi^2 = 6.76$. d.f. = 1, $P < 0.05$). During November significantly more females than males were caught (72.5%) (Table 1). In December, the percentage of females dropped to 61.9. In January and February the situation reversed with more than twice as many males caught (69.7% and 68.6%, respectively). In March, the difference between females and males became less pronounced (58.3% and 41.7%), and was not significantly different from the 1:1 sex ratio. There was a steady decrease in the catch per unit effort (cpue) for females from November (c. 0.50) to March (c. 0.20). In contrast, the cpue for males peaked in January and February (Fig. 1).

3.2. Allocation of resources to gonads

Of the 293 fish, 54 were immature and 70 were mature females. Of the males, two were immature, 149 were mature and 11 were undetermined. Seven fish could not be sexed.

Immature females and males had an average GSI of 0.5 and 0.2, respectively. The average GSI for maturing females increased from 4.8 in November to 27.4 in February (Fig. 2A). Ovulated females were caught from January to March and had an average GSI of 41.4 (c.i.: 33, 50) with a range from 27.6 to 56.7. Spent females were caught in January and February with an average GSI of 2.5 (c.i.: 1.7, 3.5). The average GSI of mature males was much lower than for females and did not increase much from November to March (Fig. 2B).

Gonad weight and body size of non-ovulated mature females had the following relations: Gonad

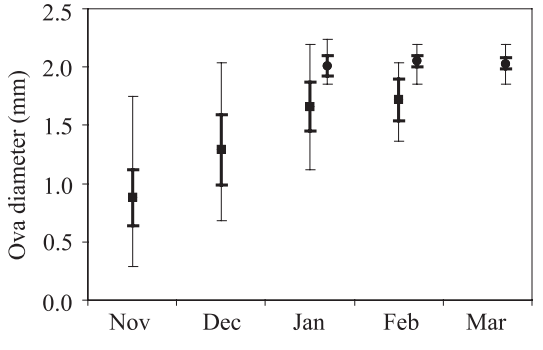

Fig. 3. Average diameter of maturing (■) and ovulated (●) oocytes from November 1988 to March 1999. Thin bars show range and thick bar shows average ± 1*SD.

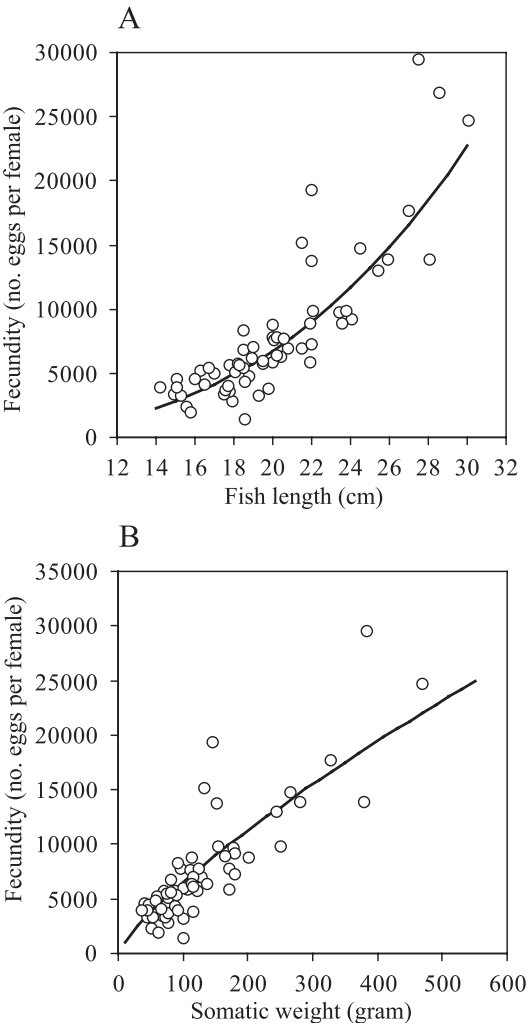

Fig. 4. Relation between (A) fecundity and length, and (B) between fecundity and somatic weight. Lines indicate re-transformed regression lines.

Table 2
Duration of embryonic development of two egg masses

Egg mass No.	1		2	
	days	T	days	T
Blastulation	3	1.8	6	3.7
Gastrulation	7	2.0		
Embryo visible on yolk sack	13	2.0	12	3.3
Embryo 1/2 around yolk sack	20	2.0	16	3.8
Embryo 3/4 around yolk sack			21	3.8
Embryo 3/4 around yolk sack, slight pigmentation of eyes	28	3.7	22	4.0
Embryo completely around yolk sack, eyes pigmented			26	4.0
Body pigments appearing along sides above the stomach	34	3.5	30	3.7
Body pigments very large, heart beating			34	4.2
Vitelline vein visible	43	3.8	37	4.2
Tail pigmented	44	9.1		
Start of hatching	44		42	4.7
50% hatching	50	4.2	47	4.4

Days since insemination and water temperature (T) in °C in the incubators are given.

weight = $1.2*10^{-2}$*Length$^{2.09}$ ($r^2 = 0.13$) and Gonad weight = 0.32*Somatic weight$^{0.65}$ ($r^2 = 0.14$). The exponent in the gonad weight – length relation was not significantly different from 3.0 (t = 1.21, d.f. = 52, $P>0.10$), nor was the exponent of the gonad weight – somatic weight relation significantly different from 1.0 (t = 1.52, d.f. = 51, $P>0.10$). Males had the following relations: Gonad weight = $2.9*10^{-4}$*Length$^{2.98}$ ($r^2 = 0.48$) and Gonad weight = 0.033*Somatic weight$^{0.89}$ ($r^2 = 0.49$). The exponent in the gonad weight – length relation was not significantly different from 3.0 (t = 0.08, d.f. = 143, $P>0.10$), nor was the exponent of the gonad weight – somatic weight relation significantly different from 1.0 (t = 1.25, d.f. = 135, $P>0.10$).

3.3. Oogenesis

Three size classes of oocytes were found in a ripe ovary. The smallest oocytes had diameters from 0.05 to 0.2 mm and were completely transparent. The medium-sized oocytes had diameters from 0.24 to 0.49 mm and were opaque in the centre with a transparent ring. The largest and most yolk-filled oocytes had diameters above 0.54 mm.

In November, a wide range of oocyte diameters of the largest group were found between and within the ovaries. In December and January, the average diameter of the oocytes increased (Fig. 3). During this period the diameters of the oocytes within each ovary

Fig. 5. Newly hatched shorthorn sculpin larva (live specimen).

became more uniform. Eggs from ovulated females did not differ more than 0.27 mm in one ovary. The coloration of the mature eggs varied from pale orange to dark red.

Ovulated egg diameters ranged from 1.85 to 2.24 mm, and the average egg diameter was 2.04 mm. The ova diameter averages of ten fish with spawned or ovulated ova ranged from 1.95 to 2.11 mm. Thus,

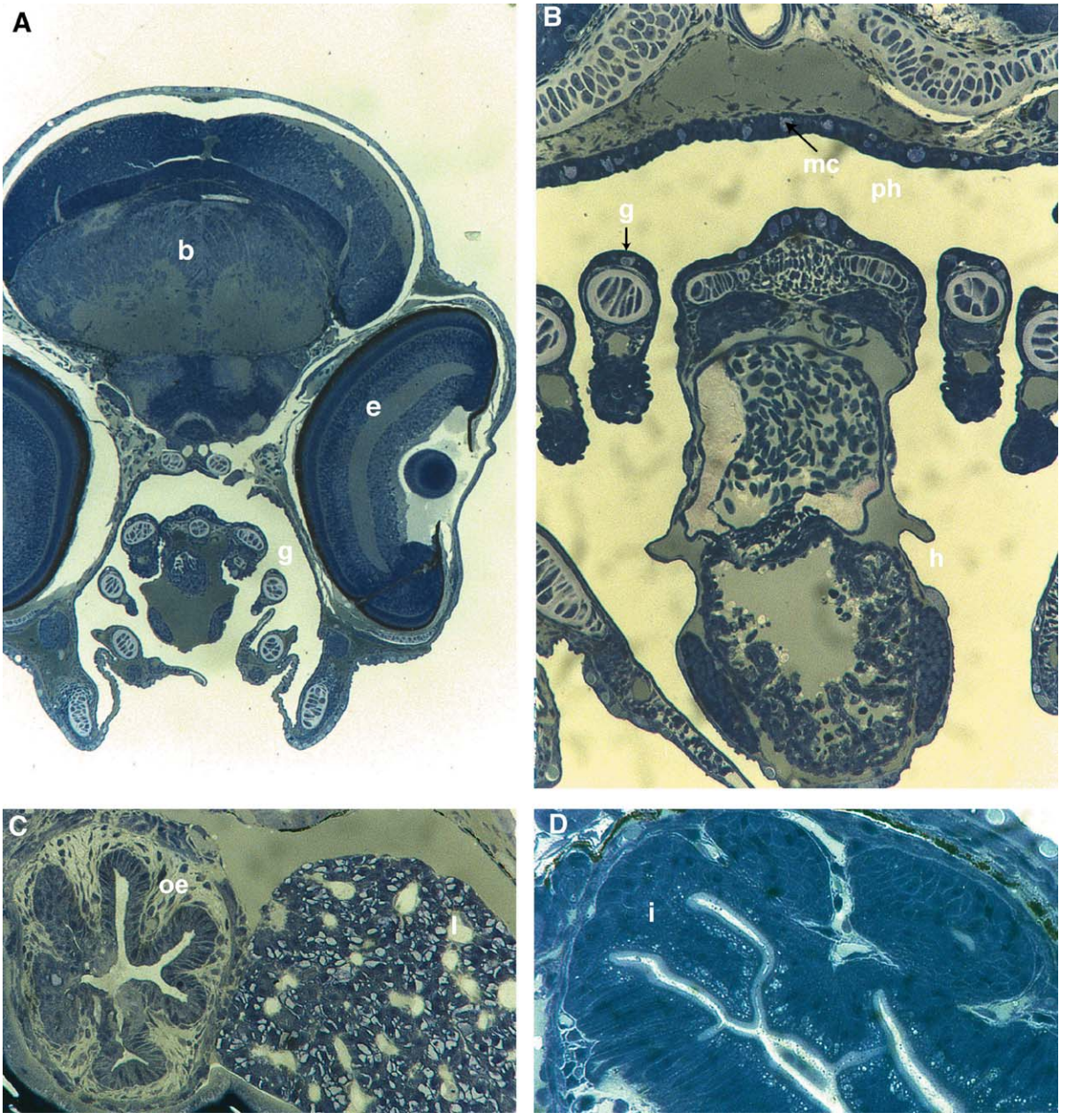

Fig. 6. (A) Transverse section through brain (b), eye (e) and gill region (g) of a newly hatched larva. (B) Transverse section of pharynx (ph)/gill (g)/heart-region (h). Note mucous epithelial cells (mc) lining the pharynx lumen. (C) Transverse section of liver (l) and hind part of oesophagus (oe). Note vacuolisation of hepatocytes. (D) Oblique section of the intestine (i). Note pinocytotic or absorptive vesicles in epithelial cells.

eggs were spawned when they reached a diameter of about 2.0 mm. In spent ovaries, only the smallest and medium-sized oocytes (0.05–0.49 mm) were abundant, but some residual ova were left.

3.4. Fecundity

Oocytes with a diameter larger than 0.5 mm were assumed to be maturing and were counted in fecundity estimates. The 64 mature females caught from November to March ranged in length from 14.2 to 30.1 cm, and the number of eggs per female ranged from 1200 to 29 000 (Fig. 4A). The relations between fecundity and body size were: $F = 0.87L^{2.99}$ ($R^2 = 0.69$), $F = 174W^{0.79}$ ($R^2 = 0.62$). Thus fecundity increased isometrically with fish length ($b2 = 2.99$), but fecundity was not proportional to weight (Fig. 4B), because the exponent (0.79) was significantly different from 1.0 ($t = 2.68$, d.f. = 60, $P = 0.009$). The relation between somatic weight and length was: $W = 4*10^{-3}L^{3.39}$ ($R^2 = 0.91$), with the exponent (3.39) significantly greater than 3.0 ($t = 2.72$, d.f. = 60, $P = 0.008$).

3.5. Spawning period

Ovulated females were caught from 20 January to 3 March and spent females were caught from 22 January to 19 February, indicating that the spawning started in late January and lasted until the beginning of March. After 5 March only immature females were caught.

3.6. Embryogenesis and hatching

Embryogenesis of the shorthorn sculpin took about 7 weeks at an average water temperature of 3.3 °C (Table 2). The length of the larva was 7.6 – 8.8 mm at hatching. A small yolk sac, with a colourless oil globule in the anterior part and a large, vitelline blood vessel, is left at hatching (Fig. 5) (see also Holt, 1893). The overall morphology and anatomy of the larvae are relatively advanced. The eyes are intensely pigmented and pronounced black melanophores are present on the top of the head, in the pectoral girdle area and on the peritoneum of the dorsal abdomen. Yellow pigment is also present in the same areas. A thin band of smaller black melanophores is also visible ventrally in the postanal region. Mouth and jaw apparatus are well developed, the intestine convoluted and liver, gall bladder and urinary bladder present. The blood is reddish. The pectoral fins are well developed, while no differentiation of the larval finfold has occurred.

Histomorphological studies of tissues and organs confirm the impression of an advanced developmental status at hatch (Fig. 6A-D). The retina of the eyes (Fig. 6A) and the olfactory organs are well differentiated. The skin is supplied with numerous mucous cells and similar cell types are also present in the bucco-pharyngeal region and in the peripheral epithelial mucosa cells of the oesophagus (Fig. 6B). The mucosa of the digestive channel is highly differentiated. Numerous pinocytotic or absorptive vesicles are noted in the posterior intestine (Fig. 6D). The hepatocytes of the liver are vacuolised (Fig. 6C) and zymogen granules are present in the pancreatic tissue.

4. Discussion

The spawning period at our study sites commences in the second half of January, reaches its peak in early February, and continues into early March. In northern Norway, the spawning period is later than that observed in Kiel Fjord, where the onset of the spawning period is in late November/December, and where spawning continues until February (Lamp, 1966), and in Newfoundland and the White Sea, where the spawning period commences in late November/December and lasts until January (Ennis, 1970b; Pavlov et al., 1992). In our study, the embryogenesis lasted for about seven weeks at 3 °C, but under natural conditions the embryogenesis may last longer because of lower ambient temperatures and the larvae probably hatch in April.

The occurrence of first-feeding larvae appears to match the increase in copepod nauplii and copepodites in April and May in the coastal waters in northern Norway (Pedersen et al., 1989; Tande, 1991). Ennis (1970b) and Wheeler (1969) noted that smaller planktonic organisms become particularly abundant just before the eggs hatch.

The average egg diameter of ovulated females in the Tromsø area (2.0 mm) was smaller than in Newfoundland (2.4 mm) (Ennis, 1970b) and Kiel Fjord (2.4 mm) (Lamp, 1966). Detailed descriptions

of the measurements used by Ennis (1970b) and Lamp (1966) are not given for these areas. Marshall (1953) argued that variation in egg size is modulated by behavioural and ecological factors (e.g. feeding conditions). Wootton (1990) suggested that large eggs (with greater yolk content) are likely to have an adaptive advantage if food supply for the larvae is sparse or variable or if the period spent in the egg stage is long or relatively unpredictable.

The newly hatched larvae in our study (7.6–8.8 mm) are similar in length to those measured in the North Sea (7.4–8.6 mm) and the White Sea (6.6–8.6 mm) (Ehrenbaum, 1904; Pavlov et al., 1992), but are longer than the average length of 6 mm recorded in Kiel Fjord (Lamp, 1966). Thus, in Kiel Fjord larger eggs apparently result in smaller larvae than in northern Norway, but it is unclear whether this reflects biological variation or different measurement methods. Incubation temperature also influences larval size at hatch. Low temperatures increase incubation time but result in larger larvae (Blaxter, 1992; Pryor and Brown, 1998; Hansen and Falk-Petersen, 2001).

Our histological data on newly hatched shorthorn sculpin larvae confirm the impression of the establishment of apparently functional tissues and organs at this stage. The larvae of the shorthorn sculpin are ready to feed immediately after hatch. The larvae are probably distributed in relatively shallow water masses and spend several weeks in a pelagic environment before becoming benthic at c. 22 mm length (Andryashev, 1964; Pavlov et al., 1992). Their relatively large size, advanced performance and developmental status at hatch in addition to the timing of hatching may be a competitive advantage for the species. Cod, other gadoid and flatfish larvae predominate later in the season (Falk-Petersen, 1982), and are much smaller and less developed at hatch (Ellertsen et al., 1980). Larvae of herring (*Clupea harengus*) and capelin (*Mallotus villosus*) hatching from demersal eggs of similar size as the shorthorn sculpin also appear later in the season, and so do those of the lumpfish (*Cyclopterus lumpus*). Wolffishes (*Anarhichas* sp.), which spawn during autumn, hatch well-developed large larvae (22-24 mm in length) in March and April (Falk-Petersen et al., 1990; Falk-Petersen and Hansen, 2001).

Body musculature and fin fold are more developed in wolffishes than in sculpins, and so is the digestive channel which includes a stomach long before hatching. The shorthorn sculpin develops a stomach not long after hatching (Holt, 1893). The shorthorn sculpin larvae are more transparent at hatch than wolffish larvae, a phenomenon which may represent an advantage in the shallow pelagic environment.

In fish, there is a potential trade-off between producing many small or fewer but larger offspring. A comparison of the fecundity of shorthorn sculpins from Tromsø, Kiel Fjord and Newfoundland (Fig. 7) indicates that fish of the same length from Kiel Fjord had a slightly higher fecundity than fish from Tromsø, but a much higher fecundity than fish from Newfoundland. Thus a 25 cm long fish would have a fecundity of 14 000 in Kiel Bay, 13 100 in Tromsø, and 9500 in Newfoundland. The total average egg volume spawned by a 25 cm fish is similar in Newfoundland and Tromsø (44 and 51 cm^3) but much higher in Kiel Fjord (76 cm^3). Thus, it appears that the sculpins from Newfoundland invest energy in producing relatively fewer but larger offspring (eggs) than in Tromsø. The value of the weight exponent in the fecundity-body weight relation (0.79) indicates that the fish produce fewer eggs per unit somatic body weight as body weight increases. However, the fecundity estimates increase isometrically with length be-

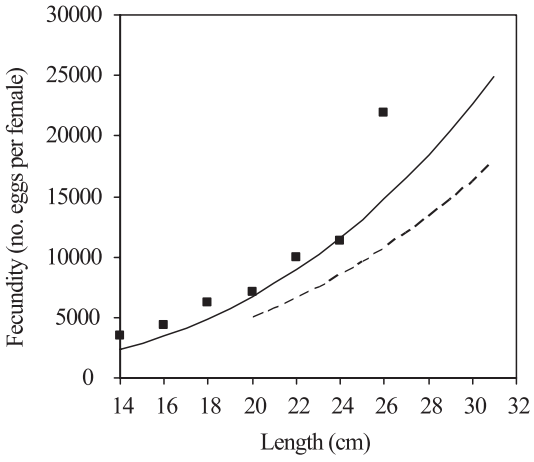

Fig. 7. Relation between fecundity and fish length for female shorthorn sculpin at Tromsø (—), compared to populations studied by Lamp (1966) in the Bay of Kiel (■) and by Ennis (1970a) in Newfoundland (- - - -). The data from Kiel are shown as average fecundity for two cm length intervals.

cause the exponent in the length – body weight relation was greater than 3.0. None of the fecundity studies of shorthorn sculpin have data from more than one season, and although there is usually a good correlation between fecundity and length, fecundity at a given size can vary from year to year (Bagenal, 1978). It would be necessary to sample through several years to investigate effects of environmental factors on fecundity.

The lower growth rates and higher mortality rates of males compared to females (Luksenburg and Pedersen, 2002) suggest that the reproductive effort and reproductive related mortality may be larger in males than in females. However, the effort is less directed towards production of gametes in males than in females, since mature males had a much lower gonadosomatic index than females (c. 2 in males versus c. 40 in females).

The significant difference in sex-ratio, with more males in the catches during the spawning period, is similar to observations from Kiel Fjord, Germany (Lamp, 1966), Gdansk Bay, Poland (Raciborski, 1984), and Galway Bay, Ireland (King et al., 1983). A likely explanation is that during the spawning period male shorthorn sculpins in search of unmated females are more mobile, and more easily caught, than females. Females appear to have lower swimming velocity when they are mature because of their increased girth and starvation (James and Johnston, 1998). During March, the males probably take care of the eggs during the guarding period and are less mobile and more difficult to catch by fyke nets. At the same time, females are more actively feeding and hence more easily caught (Raciborski, 1984). This interpretation is consistent with the observation that as the spawning period approached, the females had no food in their stomachs, whereas after spawning their stomachs were full (pers. obs.).

The predominance of immature females in the catches at our study site in late February and March may be due to movement into deeper waters of adult females after spawning (cf Ennis, 1970b), while immature females remain. In contrast to our data, Ennis (1970b) did not find a reduction in the portion of male shorthorn sculpins but instead found relatively more males during the guarding period. A possible explanation is that in Ennis' study divers were used to search for fish and therefore the proportion of males and females did not depend on the movement of the fish.

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