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Sexual and geographical variation in life history parameters of the shorthorn sculpin

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A total of 293 shorthorn sculpins *Myoxocephalus scorpius* from Tromsø, northern Norway, were sampled between November 1998 and April 1999 to determine sex, total length, age, growth, maturity and mortality. Females grew to larger sizes (L_∞=26·9 *v.* 18·5 cm), matured later (2 *v.* 1 year of age) at larger size (maturation length=16 *v.* 14 cm L_T), and had lower instantaneous mortality rates (0·93 *v.* 1·20 year^{-1}) than males. The life history parameters of shorthorn sculpins in northern Norway were more similar to the parameters of short-lived central European populations than to the parameters of the long-lived population of Newfoundland. This study confirms that northern Norwegian shorthorn sculpins exhibit sexual dimorphism as in other shorthorn sculpin populations. The relationships between growth pattern, age at maturity and mortality rates observed in the Tromsø population and in other shorthorn sculpin populations, correspond well with the predictions from a published life history model.

Key words: *Myoxocephalus scorpius*; population dynamics; life history; growth; mortality; geographic variation.

INTRODUCTION

The shorthorn sculpin *Myoxocephalus scorpius* (L.) is a widespread species that occurs on the coasts of eastern North America, Greenland, Iceland, the Baltic Sea, the Arctic Ocean, Svalbard and south to the north-west coast of France (Leim & Scott, 1966; Wheeler, 1969). Details on mortality and abundance of this species are scarce (Lamp, 1966; Ennis, 1970*a*, *b*; King *et al.*, 1983; Raciborski, 1984), and the population dynamics of the species at high latitudes have never been subjected to detailed investigation. Some intraspecific studies of life history parameters in other fish species have documented considerable variation between populations (Leggett & Carscadden, 1978; Beverton, 1992; Stearns, 1992; Goto, 1998). In shorthorn sculpins, there are notable differences between the population of Newfoundland (Ennis, 1970*a*, *b*), with slow growth and late age at maturation, and populations in central European waters (Lamp, 1966; King *et al.*, 1983; M. Fonds, A. Jaworski, A. Iedema & P. V. D. Puyl, pers. comm.), with relatively rapid growth and early age at maturation. Beverton (1992) pointed out that populations in the northerly and colder part of the species range

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were often more long-lived, matured at a larger size and reached a larger maximum size than in more southerly parts of the species range.

Correlation between growth patterns, age and size at maturity and the natural mortality rate may be caused by trade-offs between reproduction, growth and survival. With the onset of maturity, much of the energy will be directed towards gonad production and spawning activities (Pressley, 1981; Roff, 1984). This may result in a positive correlation between age and size at maturity and survival. Roff (1984) developed a model, which predicts age at maturity based on growth and mortality parameters. He also predicted the natural mortality rate based on estimates of age at maturity and growth pattern. Using another approach, Gunderson & Dygert (1988) found that the adult natural mortality rate increased linearly with increasing female reproductive effort (gonado-somatic index, I_G). Despite their success in explaining interspecies variability in life history parameters (Roff, 1984; Gunderson & Dygert, 1988), these models have not been widely employed to study intraspecific variation in life history parameters.

In shorthorn sculpins, there also seem to be sex-related differences in growth patterns, age and size at maturity and longevity (Lamp, 1966; Ennis, 1970*a*, *b*; King *et al.*, 1983; Raciborski, 1984). Published data on sexual differences in growth patterns and mortality rates are generally scarce in fishes (Gunderson & Dygert, 1988). This study investigated sexual dimorphism in life history characteristics of the shorthorn sculpin in northern Norway (70° N) and compared the findings with other published results. Based on sampling from one year, the following hypotheses were tested: (1) males and females have different life history parameters; (2) life history parameters in northern Norway are characterized by low mortality, slow growth and late age at maturity; (3) female mortality may be predicted from I_G (Gunderson & Dygert, 1988); (4) the relations between growth pattern, age at maturity and mortality can be predicted by the model of Roff (1984).

MATERIALS AND METHODS

SAMPLING

Shorthorn sculpins were sampled west of Grindø and at the north and south end of the island of Tromsø (69°40′ N, 18°50′ E). Fish were collected from November 1998 to March 1999 ($n=377$). Sampling was conducted with two to 12 fyke nets at depths of 0·5–11 m and at a distance of 1–30 m from the low tide mark. The fyke nets consisted of a central single leader arranged like a gillnet, but with two circular retainment sectors on each side (Nøstvik & Pedersen, 1999). The retainment sectors had three chambers with funnels in between. The fyke nets were emptied every 2 to 4 days, but occasionally a week or more passed before the nets could be emptied due to bad weather. On 18 January 1999 every other 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 as they were caught. During sampling, sea surface water temperature was measured at every sampling occasion and ranged from − 1·2 to 3·0° C, with mean temperatures from 2·1° C in January to 0·0° C in February to 1·05° C in March.

LABORATORY

A total of 293 fish (84 fish were used in a tag-recapture experiment) was available for laboratory analysis. Total length (L_T), total mass, gutted mass, sex and maturity stage were determined. Sagittal otoliths were dissected out and stored in 90% ethyl alcohol for subsequent examination. Maturity stage was determined by visual inspection according to the description provided by Ennis (1970*a*).

Otoliths were inspected with a binocular microscope (× 16) using reflected light. Age determination was based on assumed annuli according to Ennis (1970*a*). Winter rings appeared as dark and translucent and summer rings appeared as white and opaque (Bagenal, 1978). Age was determined as the number of summer rings minus one. Glycerol was added to enhance contrast between annuli. Some otoliths were too thick and had to be ground down with sandpaper (p400). To assess observer reliability, 50 otolith pairs (17·1% of 293) were taken at random and aged by a second person. Eight fish (16%) were determined differently, with five aged 1 year summer ring more and three aged 1 year summer ring less. It may be concluded that this age reading is sufficiently consistent for the purpose of this study. A birth date of 1 April was assumed (J. A. Luksenburg, T. Pedersen & I. B. Falk-Petersen, unpubl. data).

Growth

To test if frequency distributions of length and age of females and males were significantly different, the nonparametric Mann–Whitney *U*-test (Zar, 1984) was applied. A Von Bertalanffy growth equation (Von Bertalanffy, 1938), was fitted to the mean length-at-age data for females and males using nonlinear least square regression with error constant variance: $L_{\mathrm{Tt}}=L_{\infty}\ (1-\mathrm{e}^{-kt})$, where t is age in years, L_{Tt} is total length (cm) at age t, L_{∞} is maximum theoretical length and k is the rate at which maximum length is reached.

Initial attempts to fit the growth equation containing the t_0 parameter resulted in very strong parameter correlations (*c.* 0·95) between t_0 and k. Because strong parameter correlation may lead to unrealistic parameter estimates due to over-parametrization (Quinn & Deriso, 1999), the t_0 parameter was not used.

Maturity and length at age

A sigmoid maturity function (King, 1995) was fitted to the proportion of sexual mature female individuals as a function of either length (L_{T}) or age (t) using logistic regression: $P_{\mathrm{a}}=[1+\mathrm{e}^{-R(a-a50)}]^{-1}$ where P_{a} is the proportion of sexual mature females at length or age a, R is the slope, a is either length or age, and a_{50} is length or age when 50% are mature.

Since nearly all males became mature during their second year, and only two males were caught during their first year, no attempt was made to fit a sigmoid function to the male maturity data.

Mortality

Estimates of the annual natural mortality rate (M) for females and males were obtained using the catch curve equation (Quinn & Deriso, 1999): $\ln C_{\mathrm{t}}=a_1-Mt$, where C_{t} is numbers caught at age.

Since all by-catch should be landed under Norwegian law and mortality due to fishing appeared to be extremely uncommon it was assumed that the natural mortality rate was equal to the total mortality rate.

A linear regression was fitted to the data with $\ln(C_{\mathrm{t}})$ as the dependent variable, age (t) as the independent variable and a_1 as a constant. Age classes 1–5 and 2–6 years were used for mortality estimation of male and female fish respectively, since inspection of plots of $\ln C_{\mathrm{t}}$ against t revealed that these year classes appeared to be fully recruited by the fyke net fishery.

Comparison with other studies

To compare the results with previous investigations, an attempt was made to estimate M, k and L_{∞} from published data containing age-distributions, and length at age. Data with obvious large variable year-class strengths were not used for the estimation of natural mortality rates, since large year-class variability may bias the estimation of mortality rates (Quinn & Deriso, 1999). For the Newfoundland population, the data set contained pooled age distributions for both sexes, but since the ages of the oldest males and females were similar, 14 and 15 years respectively (Ennis, 1970*a*), the same M values calculated from the pooled distribution were allocated to both sexes. In some of the published data, the additional term age at zero length (t_0) was originally included in the Von Bertalanffy function. The Von Bertalanffy function without t_0 was refitted to obtain values of mean L_T at age so that they would be comparable to estimates of L_∞ and k in the present study (Table I).

Application of life history models

The model of Roff (1984) is based on a relation for how reproductive output ($l_t m_t$) changes during lifetime as a function of mortality (M) and the Von Bertalanffy growth parameters.

The age at maturity T was found when the derivative ($\partial l_t m_t / \partial_t$) was set equal to zero and solved for t to find the maximum of the $l_t m_t$ function:

$$T_m = \{\ln[(3k + M)M^{-1}]\}k^{-1} \tag{1}$$

where T_m is the predicted age at maturity.

When equation 1 was solved for M (Roff, 1984), and given estimates of T and k, M was estimated from:

$$M_m = (3k\mathrm{e}^{-kT})(1 - \mathrm{e}^{-kT})^{-1} \tag{2}$$

and compared with catch curve estimates of M.

Another estimate of the adult natural mortality of female fish was calculated using the linear regression equation given by Gunderson & Dygert (1988):

$$M_g = 0{\cdot}03 + 1{\cdot}68 I_G \tag{3}$$

where I_G is the gonado-somatic index [(gonad mass)(somatic body mass)$^{-1}$] of fish with fully developed gonads. In Tromsø fish with fully developed gonads were sampled from January to March (J. A. Luksenburg, T. Pedersen & I. B. Falk-Petersen, unpubl. data).

RESULTS

AGE AND GROWTH

Total length varied from 7·8 to 30·1 cm for females and from 11·1 to 21·2 cm for males [Fig. 1(a)]. Males had lower median length (14 cm) and age (1·9 years) than females (16·3 cm, 2·9 years). The length- and age-frequency distributions differed significantly (length; $U = 5018$, d.f. $= 1$, $P < 0{\cdot}001$, age; $U = 6339$, d.f. $= 1$, $P < 0{\cdot}001$). The most abundant age class was age 2 years (31·2%) for the females and age 1 year (59%) for males [Fig. 1(b)]). Maximum age was 6 years for females and 5 years for males. The smallest fish were four fishes of age 0 years (3·2%) with L_T ranging from 7·1–9·0 cm that were caught after 26 January (Fig. 1).

The growth of both sexes was relatively rapid during the first 1·8 years of life, but the growth subsequently decreased, particularly in males (Fig. 2). After *c.* 2 years, females continued to grow fast while the growth of males was reduced. Females had a significantly higher L_∞ (26·9, s.e. $= 1{\cdot}65$ cm) and lower k (0·37, s.e. $= 0{\cdot}05$ year^{-1}) than males (18·5, s.e. $= 0{\cdot}52$ cm and 0·67, s.e. $= 0{\cdot}05$ year^{-1}) (Table I).

TABLE I. Overview of estimates from published data on L_∞, k, M, age (T) and size (L_{50}) at maturation, maximum age and length observed for shorthorn sculpin. f, Females; m, males; b, pooled data of both sexes. All lengths are given as total length. The age-classes used in estimating M is given. —, S.E. could not be calculated

Area investigated	Sex	L_∞ (cm)	S.E. (cm)	k (year^{-1})	S.E. (year^{-1})	M (year^{-1})	S.E. (year^{-1})	Age-class used	T (year)	L_{50} (cm)	Max. age (year)	Max. L_T (cm)
Tromsø, northern Norway[1]	f	26·9	1·65	0·37	0·05	0·94	0·12	2–6	2	16·0	6	30·1
	m	18·5	0·52	0·67	0·05	1·20	0·09	1–5	1	13·6	5	21·2
Newfoundland[2]	f[12]	57·1	0·14	0·17	0·01	0·33	0·06	5–15	6	35·0	15	50·6
	m[12]	42·5	1·19	0·19	0·01	0·33			5	30·0	14	42·2
Kiel Fjord[3]	f	24·7	1·67	0·57	0·09	1·35	0·26	2–4	1[11]	15	6	26·8
	m	19·4	0·23	0·77	0·03	1·47	0·30	1–4	1	15	6	22·7
Gdansk Bay[4]	f	33·5	—	0·48	—				2			34·5[9]
	m[12]	24·0	0·57	0·85	0·07				2			34·5
Wadden Sea[5]	f	25·5	0·61	0·65	0·05							
	m	19·4	0·29	0·98	0·07							
Galway Bay, Ireland[6]	f[12]	27·0	0·83	0·54	0·03	1·16	—	2–3	2	11·9[10]	3	26·5
	m[12]	18·4	0·09	0·76	0·01	2·37	—	2–3	1	7·5[10]	3	19·4
Büsum[7]	f	23·1	1·52	0·75	0·15							22·0
Helgoland[7]	f	26·4	0·68	0·57	0·04							25·0
Den Helder[7]	f	22·8	1·22	0·76	0·12							21·0
Fiskebäckil[7]	f	24·4	1·61	0·63	0·12							26·0
Limfjord[7]	f	31·1	1·91	0·34	0·04	1·59	0·11	3–5				29·0
Kieler Bucht[7]	f	25·5	0·84	0·56	0·05							27·0
	m	21·4	0·24	0·66	0·02							
Pommerse Bucht[7]	f	30·1	2·93	0·41	0·07							25·0
Samlandsküste[7]	f	30·4	2·23	0·57	0·12	1·87	0·12	3–5				35·0
Vega, Norway[8]	b										11	30·0
Torbjørnsskjær, Norway[8]	b										10	42·0

[1] This study; [2] Ennis, 1970*a*; [3] Lamp, 1966; [4] Raciborski, 1984; [5] M. Fonds, A. Jaworski, A. Iedema & P. V. D. Puyl, pers. comm.; [6] King *et al*., 1983; [7] Hass, 1936; [8] Jensen *et al*., 1994; [9] largest length in samples of both sexes; [10] minimum size; [11] some females became mature at age 2 years; [12] Von Bertalanffy growth function without the t_0 term refitted to data.

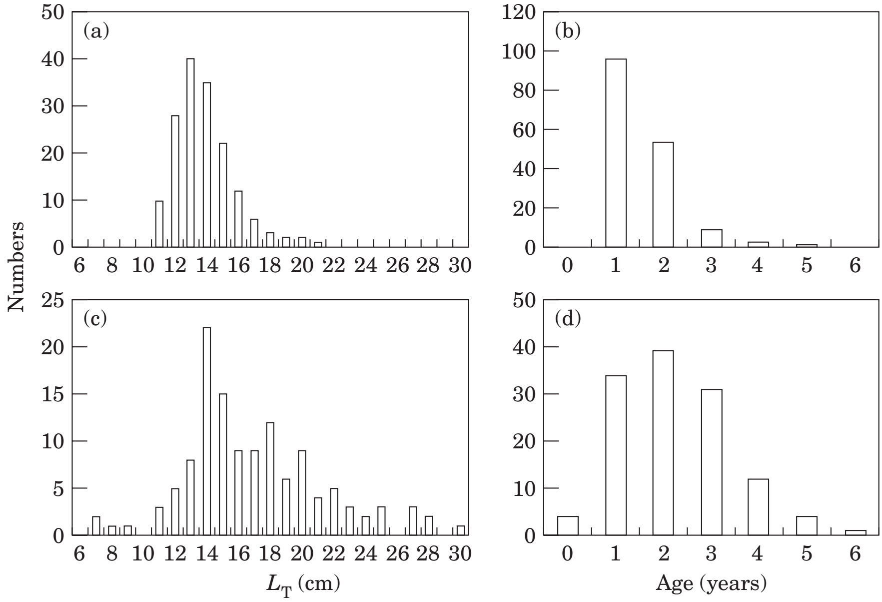

FIG. 1. Male (a) length and (b) age and female (c) length and (d) age of *M. scorpius* sampled in the Tromsø area

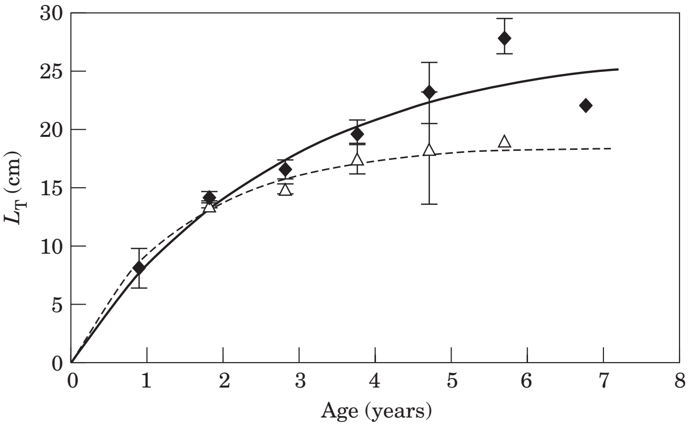

FIG. 2. Mean ± 95% CI length at age of female (◆) and male (△) *M. scorpius* sampled in the Tromsø area. Lines indicate the von Bertalanffy's growth equation fitted for males (---) and females (—).

MATURITY

The mean length at 50% sexual maturity for females was 16·0 cm [Fig. 3(a)], and the mean length for males at age 1 was 13·6 cm. Males matured at a smaller size and at a younger age than females. The age at 50% sexual maturity for females was close to 2 years [Fig. 3(b)]. The majority of the females were sexually mature by the end of their third year. In contrast, almost all males (98·9%) were mature at the end of their second year (age class 1), and all were immature at age 0 years (age class 0).

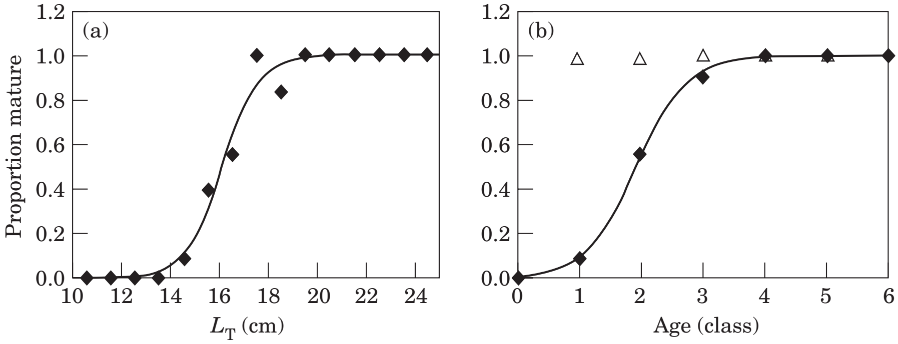

FIG. 3. Length (a) and age (b) at maturity for female (◆) and male (△) *M. scorpius* sampled during 1998–99 in the Tromsø area. The line indicates a sigmoid maturity function fitted to the female maturity data.

FIG. 4. Annual instantaneous mortality rates (*M*) of male and female *M. scorpius* estimated from the linear regressions of ln(numbers caught) of each age group and age. Females (——, ◆), males (- - -, △).

MORTALITY

The catch curve method resulted in mortality rate (*M*) estimates of 0·94 (S.E.=0·12) year^{-1} for females and 1·20 (S.E.=0·09) year^{-1} for males (Fig. 4). Analysis of covariance indicated a significant higher mortality rate for males than for females ($F_{1,7}$=21·2, P=0·002). The annual natural mortality rates (*M*) at the study site were relatively high compared to the mortality rates of other populations of shorthorn sculpin: 2·37 for males and 1·16 for females in Galway Bay (King *et al.*, 1983), 1·35 for females and 1·47 for males in Kiel Fjord (Lamp, 1966) and 0·33 for combined sexes in Newfoundland (Ennis, 1970*a*) (Table I).

COMPARISON OF LIFE HISTORY PARAMETERS

In the Tromsø population and other populations, for which published data were available, males had a lower L_∞, higher *k* and higher *M* than females (Table I). All the life history parameters L_∞, *k*, *M* and age at maturity (*T*) were significantly correlated when data from the Tromsø population and published data were considered together. L_∞ was negatively correlated to *k* ($r=-0·84$,

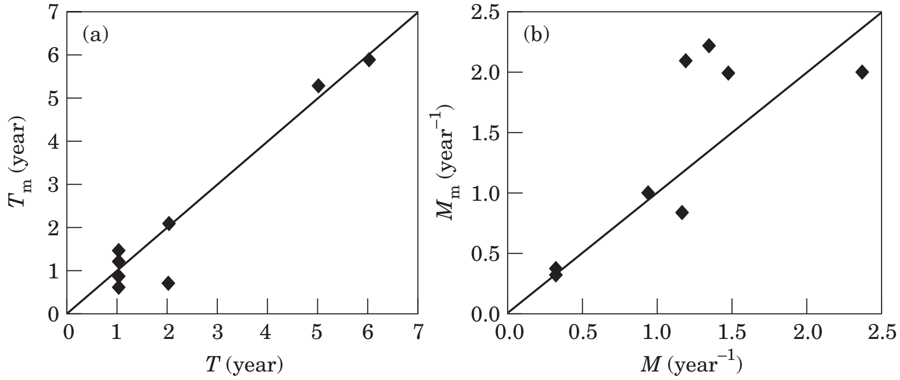

FIG. 5. Comparison of observed (T) and modelled (T_m) age at maturity using the equation from Roff (1984) (a), and mortality rates estimated by the catch curve method (M) and modelled for different populations of *M. scorpius* from the equation given by Roff (1984) (b). Straight line indicates equality.

d.f.=19, $P<0{\cdot}001$) and to M ($r=-0{\cdot}72$, d.f.=8, $P=0{\cdot}018$), and M and k were positively correlated ($r=0{\cdot}78$, d.f.=8, $P=0{\cdot}008$). T was negatively correlated to k ($r=-0{\cdot}84$, d.f.=6, $P=0{\cdot}002$) and to M ($r=-0{\cdot}82$, d.f.=5, $P=0{\cdot}024$), and positively to L_∞ ($r=0{\cdot}96$, d.f.=8, $P=0{\cdot}001$). Except for the correlation between k and L_∞, the correlations were not significant when the data on the population from Newfoundland were excluded.

The modelled age at maturity (T_m), using Roff's (1984) equation (1), gave values that correlated well with observed age at maturity (T) ($r=0{\cdot}96$, d.f.=6, $P<0{\cdot}001$) [Fig. 5(a)]. Estimates of mortality rate using Roff's equation (2) also gave values that were significantly correlated to the catch curve estimates ($r=0{\cdot}79$, d.f.=6, $P=0{\cdot}02$) [Fig. 5(b)]. These correlations were not significant when the Newfoundland data were excluded. For the Tromsø population the model from Roff (1984) (equation 2) predicted M_m to be 1·01 for females and 2·11 year^{-1} for males.

The Gunderson & Dygert (1988) equation (3) gave an estimate of $M_g=0{\cdot}72$ year^{-1} for females, using the average I_G value of 0·41 for ovulated females (J. A. Luksenburg, T. Pedersen & I. B. Falk-Petersen, unpubl. data), and M_g values of 0·58 and 0·87 year^{-1} corresponding to the low (0·33) and high (0·50) 95% CI of the average I_G.

DISCUSSION

Since fishes have to swim in order to be caught in fyke nets, a possible fish size dependent movement rate may bias the age-distributions and hence the mortality rates. Since most of the shorthorn sculpins used for mortality rate estimates were sexually mature and had a narrow length range (13–22 cm L_T, Fig. 1), it is unlikely that mortality rates would be biased much.

At the study site, maximum longevity was estimated to be 6 years for females and 5 years for males, which is similar to the data reported by Lamp (1966) for Kiel Fjord, Germany (6 years for females; 5–6 years for males), but higher than the maximum age recorded in Galway Bay, Ireland (3 years for both sexes) (King *et al.*, 1983). The present results are similar to the earlier findings by Hass (1936) that, in Europe, shorthorn sculpins do not exceed the age of 6 years. Larger and older shorthorn sculpins, however, have been recorded at localities with similar temperatures further south in Norway (Torbjørnsskjær, Table I) and at West-Greenland (Hovgaard, 1996). This indicates that some variation in longevity exists at similar latitude and temperature regimes in Europe. In Newfoundland, longevity is 15 years for females and 14 years for males (Ennis, 1970*a*). The present data thus suggest the existence of differences in longevity between Newfoundland and European populations. More data from north-west Atlantic populations, however, are needed to indicate whether this reflects a general difference across the Atlantic.

The k values, obtained with the Von Bertalanffy growth equation, in this study are lower (0·37 for females, 0·67 for males) than those found in Gdansk Bay, Poland (0·48 for females, 0·85 for males) (Raciborski, 1984) (Table I). In contrast, k values obtained in the Newfoundland population (0·17 for females, 0·19 for males) (Ennis, 1970*a*) are much lower. It appears that European shorthorn sculpins reach L_∞ much faster than the Newfoundland population.

The present results indicate that, at the study site in northern Norway, females become mature after 2 years and at a mean length of 16·0 cm and that males reach maturity after 1 year at a mean length of 13·6 cm. Alm (1959) suggested that maximum size attained and longevity are associated with size and age at maturity. Similar results have been obtained at Kiel Fjord, where both females and males mature at the end of their second year, at an average length of 15 cm (Lamp, 1966), and at Galway Bay, where females mature in their third year at minimum length of 11·9 cm and males become mature in their second year at minimum length of 7·5 cm (King *et al.*, 1983). In contrast, in Newfoundland maturity is reached at 5–7 years of age, at an average length 34–35 cm for females and 30 cm for males (Ennis, 1970*a*). Therefore, the most profound differences in the age and length at which shorthorn sculpins reach maturity are those between European and Newfoundland populations.

The difference in growth patterns between females and males is evident in both the data from Tromsø and the other locations. The pattern of sexual dimorphism in life history charateristics appears to be consistent across populations (Table I). This indicates the existence of different energy allocation patterns in the two sexes. The fact that large differences in growth patterns between males and females were found at locations with no sex-difference in age at maturity (Gdansk Bay and Kiel Fjord, Table I), also indicates that males either allocate more of their gained energy towards reproductive activites than females or that they have lower food intake rates than females or both.

The fact that high mortality corresponds with a high k value, low L_∞, and early maturation suggest that these life history parameters are linked in shorthorn sculpin. The high mortality rates of males compared to those of females (Table I and Fig. 4) could be due to higher exposure to predation during the period that males guard the eggs, as has been observed in three-spined sticklebacks *Gasterosteus aculeatus* L. (Pressley, 1981). In support of this, shorthorn sculpins and egg masses have been observed in cod *Gadus morhua* L. stomachs during the egg guarding period (T. Pedersen, unpubl. data), which may last for *c.* 7 weeks in the Tromsø area (J. A. Luksenburg, T. Pedersen &

I. B. Falk-Petersen, unpubl. data). During the egg guarding period the males do not avoid other animals but try to attack them regardless of their size (Ennis, 1970*b*).

Life history theory predicts that adult mortality is positively correlated with reproductive effort (Gunderson, 1997). The model for estimation of mortality based on the gonado-somatic index produced a female mortality estimate (M_g=0·72 year^{-1}) not very different from that estimated by the catch-curve method (M=0·94 year^{-1}). Thus the I_G may be a proper measure for reproductive effort in shorthorn sculpin females and be used to estimate mortality rates. This approach could not be applied to mature males, however, which have a very low I_G ($\leq$0·028) (J. A. Luksenburg, T. Pedersen & I. B. Falk-Petersen, unpubl. data), but apparently have a high reproductive effort and relatively high mortality rate estimated by the catch curve method (M=1·20 year^{-1}).

Intraspecific variation in life history parameters has been related to variation in environmental factors such as fish density (Goto, 1998; Kristoffersen & Salvanes, 1998), temperature (Sandstrøm *et al.*, 1995) and predation pressure (Reznick, 1996). These factors may in turn be related to juvenile and adult mortality rate, growth patterns and recruitment variability that ultimately determine life history parameters (Pauly, 1980; Roff, 1992; Stearns, 1992). Despite the fact that the northern Norwegian shorthorn sculpins live at high latitude (70° N), they do not have the expected slow growth and late maturity. The life-history parameters of shorthorn sculpin in Tromsø are much more similar to those of populations in central Europe than to those of the Newfoundland population. The data of both sexes within locations and within sexes between locations (Table I) support the predicted association between high adult mortality and low age at maturity (Roff, 1984). In particular the Newfoundland population, living in a cold environment, had a low mortality rate (M=0·33 year^{-1}) and a high age at maturity (5–6 years) for both sexes, compared to the European populations (Table I). Furthermore, the correspondence between measured and modelled age at maturity using the equation from Roff (1984) [Table I and Fig. 5(a)] indicates that intraspecific variation in shorthorn sculpin is similar to the general interspecific patterns in teleosts.

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