132732

Journal of Fish Biology (2006) **68**, 1158–1176
doi:10.1111/j.1095-8649.2006.00990.x, available online at http://www.blackwell-synergy.com

Growth, maturity and fecundity of wolffish *Anarhichas lupus* L. in Icelandic waters

Á. GUNNARSSON*†‡, E. HJÖRLEIFSSON*, K. THÓRARINSSON§ AND G. MARTEINSDÓTTIR*†

**Marine Research Institute in Reykjavík, Skúlagata 4, P. O. Box 1390, 121 Reykjavík, Iceland, §The Federation of Icelandic Fishing Vessel Owners, Borgartúni 35, IS-105 Reykjavík, Iceland and ‡Biology, University of Iceland, suðurgata 7, 101 Reykjavík, Iceland*

(Received 2 February 2005, Accepted 8 October 2005)

Fecundity, maturity and the relationship between growth and maturity of common wolffish *Anarhichas lupus* were studied in Icelandic waters. A total of 788 female common wolffish were sampled in two areas: one in the relatively warm sea west of Iceland and the other in the colder sea east of Iceland. No difference was detected in fecundity of common wolffish between areas. The time from the onset of the cortical alveolus stage until spawning, was on average, 10 years in the east and 8 years in the west area. Common wolffish in the east area reached cortical alveolus stage, on average, at a greater age but similar size compared to common wolffish in the west area. Similarly, common wolffish started spawning, on average, at greater age and larger size in the east than in the west area. Common wolffish grew faster in the west than in the east area. Spawning common wolffish grew faster than common wolffish at the cortical alveolus stage in both areas. The relationship between growth and maturity for common wolffish in Icelandic waters appeared to be related to temperature, characterized by fast growth and early maturation in the west and slower growth and delayed maturation in the east.

Key words: age- and length-at-maturity; common wolffish; fecundity; growth.

INTRODUCTION

Genotype, mortality and growth rates are generally accepted as important factors affecting the onset of sexual maturity. Genotype determines the reaction norm to a particular environment and mortality acts as a selective force on delayed or early maturity *via* evolutionary effects of selection (Stearns, 1992; Law, 2000; Heino *et al.*, 2002). The relationship between growth and maturity is often characterized by either fast growth and early maturation or slow growth and delayed maturation (Lambert *et al.*, 2003).

Growth varies spatially and temporally, both between and within fish species (Pauly, 1980; Brander, 2000). As such, growth is influenced by abiotic factors as well as being dependent on genotype and biotic factors. Of the abiotic factors,

---

†Author to whom correspondence should be addressed. Tel.: +354-5752000; fax: +354-5752001; email: geiri@hafro.is

sea temperature appears to be the most important (Brett, 1979; Brander, 2000). For most fish species, maturation is usually associated with reduced growth, *i.e.* due to increased allocation of energy to gonads at the expense of investment in somatic growth (Love, 1970).

Studies have shown that length and age at maturity vary between populations within the same species (Lambert *et al.*, 2003). Life history models (Cole, 1954; Gadil & Bossert, 1970; Roff, 1984; Stearns & Crandall, 1984; Stearns & Koella, 1986) and energy allocation models (Choen, 1971; Kozlowski, 1992) generally assume that the faster the fishes grow, the younger they tend to mature. As such, an association between high growth rates and reduced age at maturation has been observed in cod *Gadus morhua* L. (Godø & Moksness, 1987; Marteinsdottir & Begg, 2002), salmonids (Alm, 1959), plaice *Pleuronectes platessa* L. (Rijnsdorp, 1993) and haddock *Melanogrammus aeglefinus* (L.) (Sonina, 1981).

In the common wolffish *Anarhichas lupus* L., growth has been studied in Iceland (Jónsson, 1982), the White Sea (Barsukov, 1959; Pavlov & Novikov, 1993), north Norway (Hansen, 1992), Skagerak (Gjøsæter *et al.*, 1990), the North Sea (Liao Lucas, 2000) and Canada (Nelson & Ross, 1992). These studies suggested that the growth rate of common wolffish increased with higher temperature.

Similarly, studies on maturity and fecundity in common wolffish have been conducted in Canada (Templeman, 1986), the White Sea (Maslow, 1944; Barsukov, 1959; Pavlov & Novikov, 1993), north Norway (Hansen, 1992) and Barents Sea, where only fecundity was studied (Gusev & Shevelev, 1997). These studies showed that fecundity was similar among areas, while maturity differed. As such, the data indicated that common wolffish matured at a greater size with increasing temperature, which is, however, opposite to what is generally observed among fish species.

Common wolffish spawn from late summer to early winter depending on the area. The spawning season is *c.* 2–3 months. Fertilization is internal and takes place 8–15 h before spawning (Kvalsund, 1990; Johannessen *et al.*, 1993; Pavlov & Moksness, 1994). Common wolffish is a determinate spawner and spawns all the eggs in single batch (Johannessen *et al.*, 1993). The eggs are demersal and 4–7 mm in diameter. After spawning the female fish coils around the eggs and creates an egg cluster that will later be guarded by the male (Barsukov, 1953; Keats *et al.*, 1985). The incubation period of the eggs is *c.* 800–1000 degree-days, depending on incubation temperature (Pavlov & Moksness, 1995).

Shortly before spawning, three generations of oocytes are present in the ovary of the common wolffish. Besides the eggs soon ready to be spawned, there are also oocytes at the cortical alveolus (CA) stage that will be spawned next year as well as primary oocytes that will be recruited to the CA stage next year. The generation time from oogonia to CA stage oocyte is therefore 2 years (Beese & Kändler, 1969). After the common wolffish has reached the CA stage, primary oocytes and oocytes at CA stages will always be present in the ovary. The CA stage belongs to a secondary growth of the oocyte and the protein synthesis is endogenous (Wallace & Selman, 1981; de Vlaming, 1983; Nagahama, 1983). Teleosts at the CA stage are generally deemed sexually mature. This has been shown for roughhead grenadier *Macrourus berglax* (Lacepède) (Murua & Motos, 2000), summer flounder *Paralichthys dentatus* (L.), (Merson *et al.*, 2000), Greenland halibut *Reinhardtius hippoglossoides* (Walbaum) (Fedorov, 1968), cod (Kjesbu & Kryvi, 1989) and peacock blenny *Blennius pavo* (Risso) (Patzner, 1983), which belongs to the same suborder as the common wolffish.

For stock assessment and fish management, it is important to know the reproduction mode of the fishes. Until now, no studies have been conducted to explore the relationships between growth and maturity in common wolffish. In Icelandic waters little information exists on growth of common wolffish, and no studies have been conducted to estimate fecundity or age and size at maturity. In this study samples of female common wolffish were collected from two areas west and east of Iceland to test the hypothesis that common wolffish from the warmer waters west of Iceland have a higher growth rate and mature at a younger age than common wolffish living in the colder waters east of the country.

MATERIAL AND METHODS

SAMPLING AREAS

Sampling areas were chosen so as to represent both the main distributional area of common wolffish (west of Iceland) as well as different temperature regimes. As such, the east area was on the average 2–3° C colder than the west area, according to pooled average sea-bottom temperature for the years 1936–1999 off Iceland (Fig. 1)

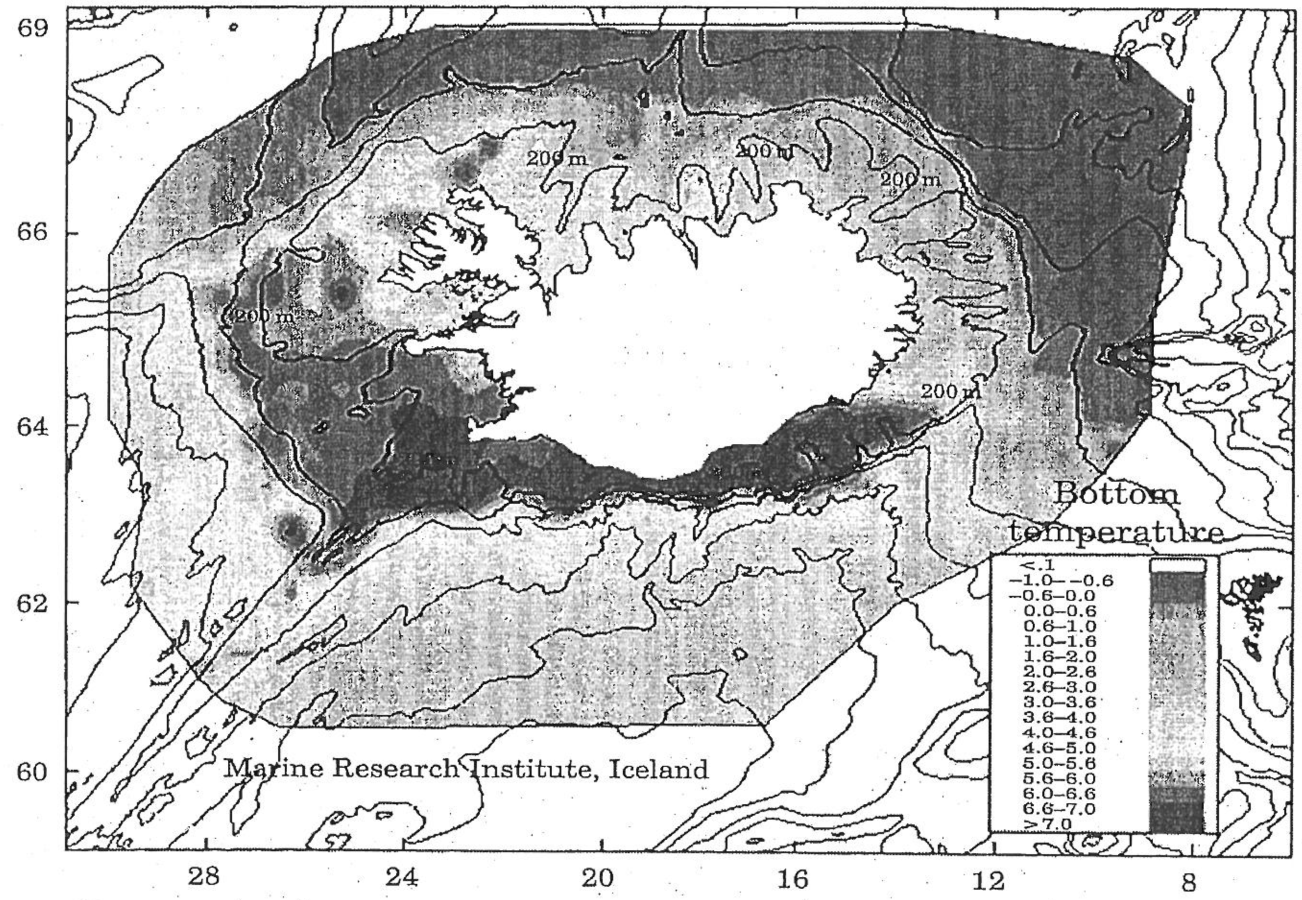

FIG. 1. Polled average sea-bottom temperature for the years 1936–1999 off Iceland.

Further measurements of sea-bottom temperature off Iceland show that in 2002, the year of this study, the mean bottom temperature was similar to the long-term average (Guðmundsson *et al.*, 2003).

SAMPLING

The sampling was done in July-December, east and west of Iceland in 2001 (for fecundity only) and 2002 (Fig. 2). This particular period was chosen in an attempt to cover the whole spawning season. Three different sampling methods were used to obtain the data for this study. First, random sampling was preformed in the annual ground fish survey (AGFS) conducted by the Marine Research Institute, in October 2002. All females $\geq$15 cm in total length (L_T) were sampled. Second, stratified samples were collected from commercial landings, to secure enough data for each length group. A total of 15 females were sampled in each 5 cm L_T interval, ranging from 30 to 85 cm. Third, random samples were obtained from commercial landings, sampled by researchers at the Marine Research Institute for common wolffish stock assessment purposes (Table I and Fig. 3). During the random sampling from landed catch, only samples from the west area were obtained, *i.e.* as commercial landings of common wolffish from the east area are generally rare in early winter.

During the AGFS sampling and the stratified sampling, maturity stages were determined both visually in the laboratory and from histological samples. During the random sampling from commercial landings, maturity stages were only determined visually in the field.

The L_T (cm), whole body mass (M, g) and gutted mass (M_S, g) were measured for each fish. Sagittal otoliths were extracted from all individuals for ageing. Gonads were

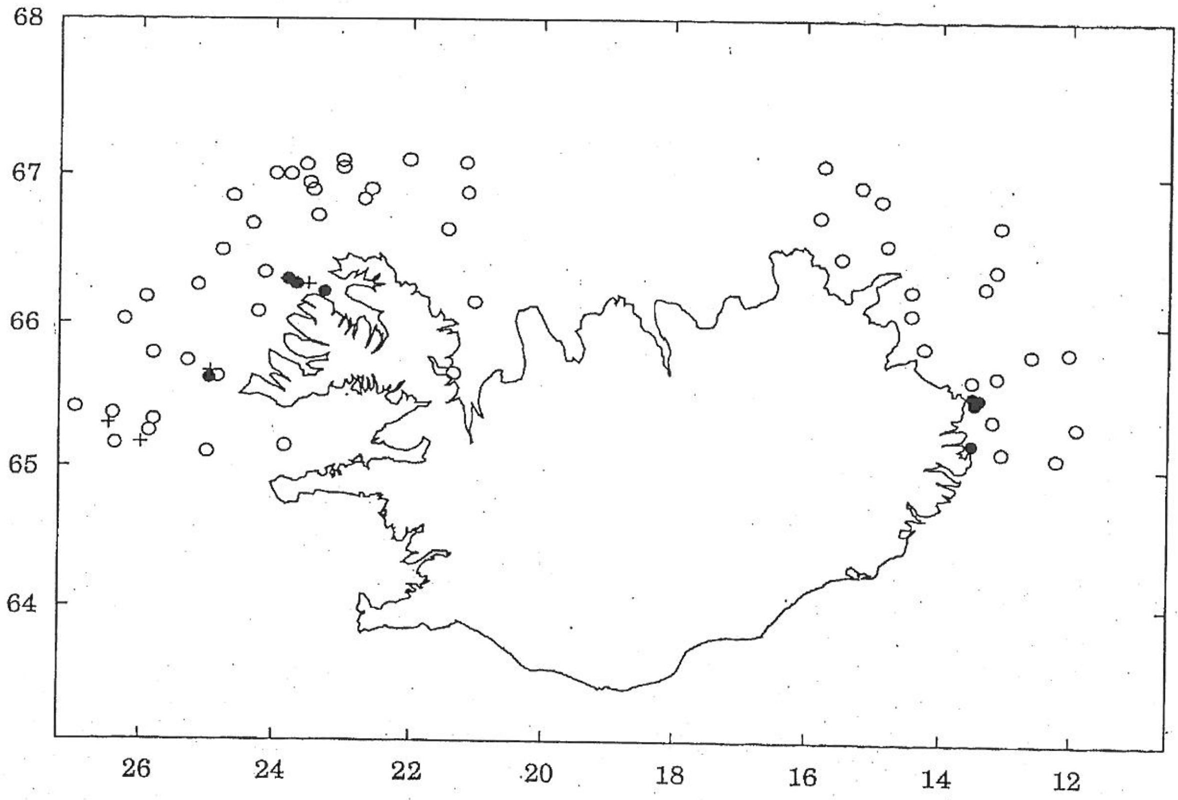

FIG. 2. Sampling areas and locations of samples in 2002. Samples were from the research survey (o), and from landed catches [stratified (•) and random (+) samples].

TABLE I. Number of female common wolffish collected by sampling method, area and months in 2002

Sampling gear	Sampling method	Months	West (*n*)	East (*n*)
Groundfish survey	Random	October	260	90
Commercial catch	Stratified	August to September	102	139
Commercial catch	Random	July to December	197	0

removed and weighed (M_G, g), gonads for laboratory examination were placed in permutable plastic bags and saturated in 10% formalin.

MATURITY STAGES

Maturity stages were determined according to the maturity scale of Barsukov (1959) and revised by Mazhirina (1988). The revised scale of Mazhirina (1988) included seven maturity stages. For simplification, however, only four maturity stages were used in this study (Table II). According to Barsukov (1959), in female common wolffish the cortical alveolus (CA) stage can last for several years. Therefore it was decided to use two criteria for sexual maturity in this study (Table II). The first is the CA stage (MC1), which refers to fish that has reached CA stage but has however not spawned before. This is represented as stage 2 in both scales in Table II. The second is the spawning stage (MC2), the same as stages 3 and 4 in this study. Stage 3 in this study refers to fish that intend to spawn during the present year, and stage 4 refers to fish that have recently completed spawning or is recovering after spawning (Fig. 4 and Table II).

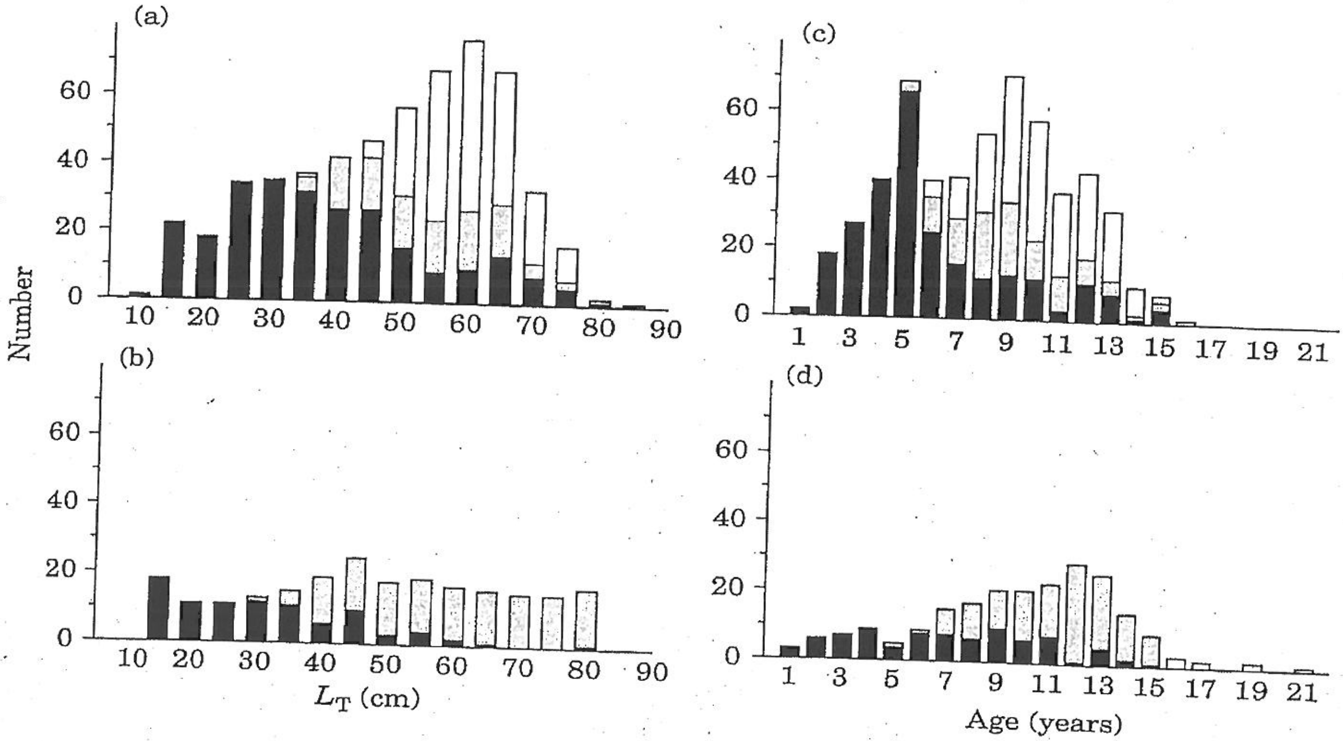

FIG. 3. (a), (b) total length and (c), (d) age frequency distributions of female common wolffish from the areas (a), (c) west and (b), (d), east of Iceland, collected in the autumn ground fish survey (■) and from landed catches, which were collected using both stratified (▨) and random (□) methods.

TABLE II. Female common wolffish maturity stages of Barsukov (1959), revised by Mazhirina (1988), and maturity stages used in this study. On both scales, stage 1 represents immature fish, other stages represent mature fish

Barsukov (1959), revised by Mazhirina (1988)		This study	
Stages	Description	Stages	Description
I	Oocytes half-clear and grey-white. Size <0·5 mm	1	Immature. Only primary oocytes in the ovary
II	White eggs. Size 0·5–1·8 mm Vacuolization phase	2 (MCI)	Cortical alveolus stage. Primary and cortical alveolus oocytes in the ovary
III	Yellowish-orange eggs. Size 2·5–4·8 mm Yolk phase	3 (MC2)	Vitellogenesis. Primary, cortical alveolus and vitellogenic oocytes in the ovary
IV	Red-orange eggs at the size 5–7 mm Yolk phase	3 (MC2)	Vitellogenesis. Primary, cortical alveolus and vitellogenic oocytes in the ovary
V	Spawning	3 (MC2)	Spawning
VI	Some clear residual eggs and few white eggs at the size 0·5–2·2 mm	4 (MC2)	Spent. Primary, cortical alveolus and residual oocytes in the ovary
VII	Few white eggs. Size 0·5–3·2 mm	4 (MC2)	Recovering. Primary, cortical alveolus and residual oocytes in the ovary

To confirm visual evaluation of maturity stages 1–4 in this study, 20 histological samples were taken from all stages including additional sampling if the visual evaluation was doubtful, which was mainly between stages 1 and 2 or immature and CA stages. In an attempt to recognize the differences between these two stages, 20 additional histological samples were taken, 10 samples from gonads with no visible eggs and 10 samples from gonads with few eggs, vaguely visibly to the naked eye. The result showed that gonads with visible eggs, belonged to fish at a CA stage and gonads with no visible eggs belonged to fish containing only primary oocytes in the ovary, except one fish that was in a CA stage. As a result, 10 additional histological samples were taken from gonads with no visible eggs. All of these samples contained only primary oocytes. As a result, all gonads containing no visible eggs were classified as immature (stage 1, only primary oocytes present in the ovary), while gonads with visible eggs were classified as being at a CA stage.

Generally the CA stage begins with the appearance of so called yolk vesicles that are believed to be the precursor of the cortical alveolus (de Vlaming, 1983; Selman *et al.*, 1988; Wallace & Selman, 1990), therefore fish can be classified to a CA-stage before cortical alveolus have been constructed. Whether the fish classified to a CA-stage had only yolk vesicles or both cortical alveolus and its precursor in its oocytes is beyond the scope of this study. In both cases it was conventional to classify the fish to a CA stage.

To determined if the CA stage in this study was identical to stage II in the maturity scale by Barsukov (1959) revised by Mazhirina (1988), described as visible egg through the egg membrane at the size 0·5–1·8 mm at vacuolization stage, a total of 100 oocytes were measured from 10 common wolffish at a CA stage or 10 oocytes from each fish, using Leica image Q500 MC and Sigmascan. The diameter of these oocytes ranged from 0·725–1·110 (mean ± s.d. = 0·916 ± 0·077 mm). This indicated that the CA stage in this study was identical to stage II in the maturity scale by Barsukov (1959), revised by Mazhirina (1988). Further histological samples from fish visually classified to a CA stage, in this study, showed that the most advanced oocytes were at vacuolization stage or CA stage [Fig. 4(e)].

For histological preparation, the ovary samples were dehydrated in ethanol, embedded in historesin, sectioned (3 μm) and stained with toluidine blue (Óskarsson *et al.*, 2002). The slides were examined under a microscope, Olympus Bx50 connected to a Leica image analyser Q500 MC.

AGE DETERMINATION

For ageing, otoliths were washed in water and embedded in 50% glycerine with thymol and kept in this solution for 1 or 2 months, to increase the contrast between the winter and

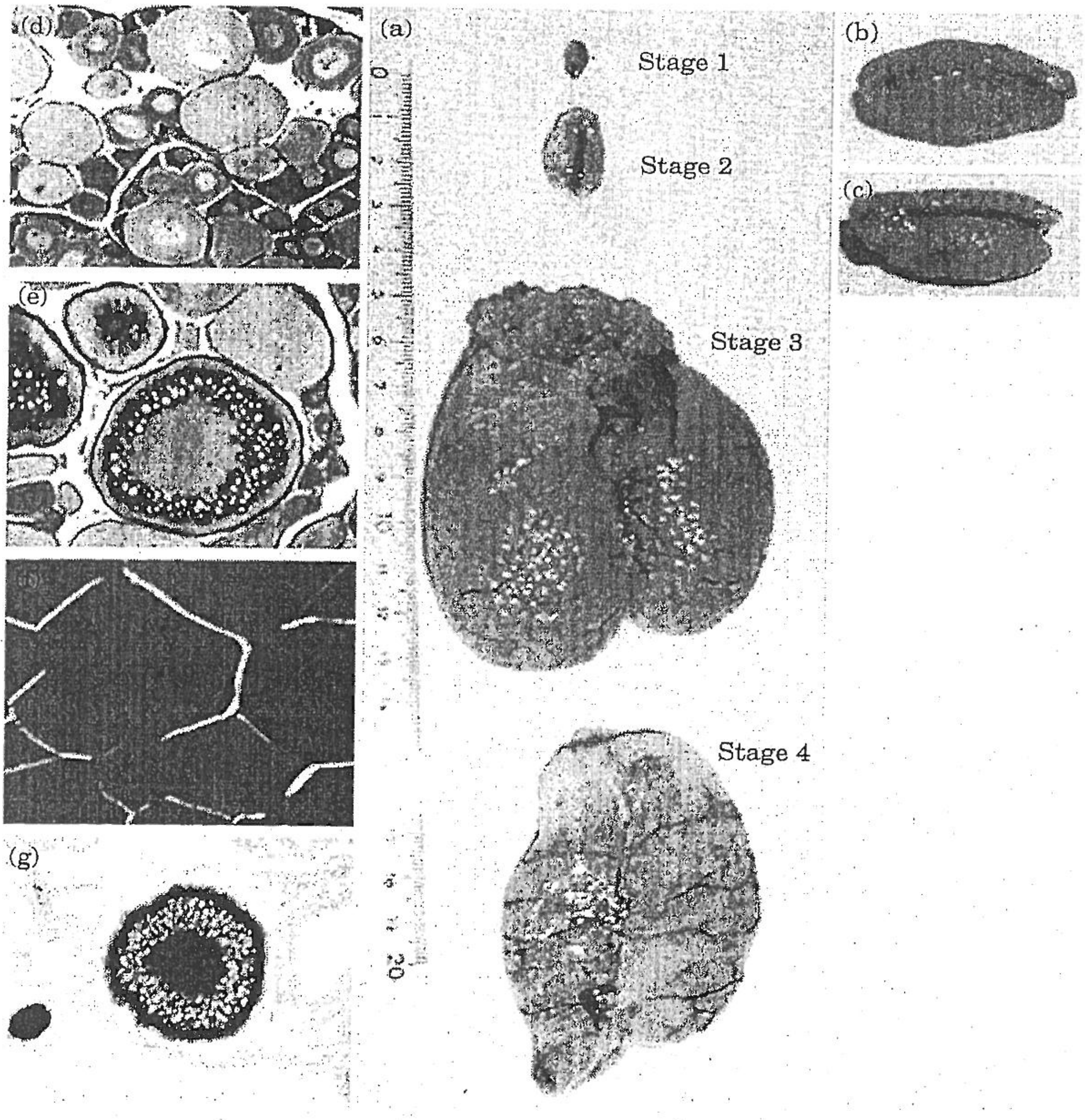

Fig. 4. Staging of gonads as used in this study: (a) stages 1–4, (b) stage 1, ×10, (c) stage 2, ×2 and (d)–(g) histological samples from stages 1–4 respectively, ×40.

summer zones. To determine the boundary of the first winter zone, pairs of sagittal otoliths from five individuals as well as a single sagittal otoliths from two individuals were extracted from juvenile common wolffish collected during the annual 0 year group survey in August.

Images of the otoliths were compared to images of sagittal otoliths from adult common wolffish, using Leica image Q500 MC and Sigmascan. The diameter (mean = 0·67 mm, range = 0·62–0·80 mm) of the sagittal otoliths of the 0 year group common wolffish was compared with the core in sagittal otoliths from adult common wolffish (Fig. 5).

For further comparison, diameters of the core of 14 pairs of sagittal otoliths from adult common wolffish sampled in the spring survey in March, were measured. The mean diameter of the otoliths was 0·78 mm, ranging from 0·68–0·96 mm. The difference between the mean diameters of the sagittal otoliths of 0 year group common wolffish and the core of an adult was 0·11 mm. It was assumed that this difference could not account for a first winter zone, in addition to the first summer zone. The 0 year group common wolffish was sampled in mid August or when the growth phase of its first summer zone, *i.e.* the core, was not completed. For adult common wolffish this growth phase was probably 1–2 months longer than for the 0 year group common wolffish that was sampled in this study. This may explain the difference in the diameter of otoliths of the 0 year group common wolffish and the core of the otoliths of the adult common wolffish.

ESTIMATION OF FECUNDITY

Potential fecundity (F_P) was estimated gravimetrically (Bagenal & Braum, 1978). A total of 72 prespawning females were included in the analysis. Of these, 36 were

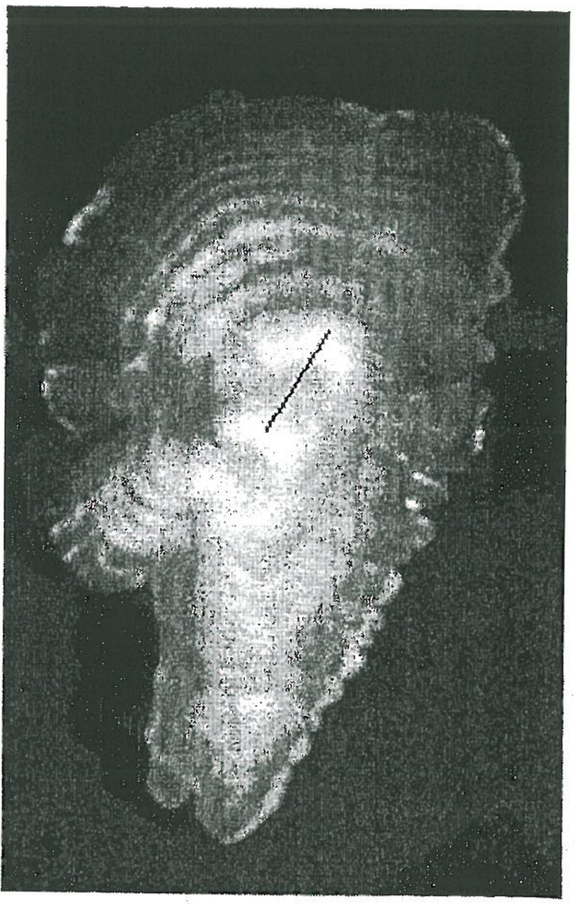

FIG. 5. Sagittal otolith from an adult common wolffish. —, the mean diameter of 12 sagittal otoliths from seven 0 year group common wolffish collected in August 2000.

from the west area and 23 from the east area. Also included were 13 females from the AGFS conducted in October 2001 (11 from the west and two from the east). To estimate F_P, all the eggs were removed from the fixed ovary, blended together and washed with water. After most of the water had drained, the sample (M_E, cg) was weighed. A total of three subsamples (M_{SE}, cg) were collected from each ovary. All eggs >2 mm were counted in each subsample (n). The F_P was calculated for each fish from: $F_P = M_E M_{SE}^{-1}$ n. A coefficient of variation (CV) multiplied with a correction factor (V) was used to compare the total number of eggs, based on two of the subsamples. $CV = (100\ \text{s.d.} \cdot \bar{x}^{-1}) \cdot V$, and due to a low number of subsamples (Sokal & Rohlf, 1981) V was calculated from: $V = 1 + 4n^{-1}$, where n is the number of subsamples. If the difference (CV) was >5%, eggs of a third subsample were also counted. In only four cases out of 72 was it necessary to include a third sample.

STATISTICAL ANALYSIS

Statistical analysis was performed using Splus 6·1. Logistic regression analysis (Crawley, 2002) was used to estimate maturity ogives, which were used to determine total length (L_{T50}) and age (A_{50}) at 50% maturity. χ^2 tests were used to compare maturity ogives between areas (Crawley, 2002). Measure of model fit was based on a pseudo-coefficient of determination [$r^2 = 1 -$ (residual deviance null deviance $^{-1}$)], which was the fraction of the total variation explained by the model. Residual deviance is analogous to residual sums of squares and null deviance to total sums of squares (Swartzman *et al.*, 1995).

The F_P and L_T relationship was described with a power function using $\log_{10}$-transformed data, and compared between areas with analysis of covariance (ANCOVA).

The analyses of growth of female common wolffish was based on length at age data. The following growth models were tested: logistic (Fresco, 1973), Gompertz (Winsor, 1932) and von Bertalanffy (von Bertalanffy, 1938). The logistic model gave the lowest residual sum of squares and was therefore used in the present analyses. The estimation of the coefficients L_∞, K and t_0 was done by employing non-linear optimization (Gauss-Newton method) (Bates & Chambers, 1992). To assess the difference in parameters between the two locations t-tests was used (Zar, 1999). Two-way ANOVA was used to compare the growth of common wolffish at CA (MC1) and spawning (MC2) stages within an area. Dunnett multiple comparison tests with 95% CI (Crawley, 2002) were used to compare size in same age class between common wolffish on CA and spawning stages. To compare mean age and mean L_T between areas a t-test was used.

RESULTS

LENGTH AND AGE

Female common wolffish ranged from 1–16 years in the west, with a mean age of 8 years, and 1–21 years in the east, with a mean age of 10 years. These differences were significant (t-test, $n = 782$, $P < 0.001$). The L_T of female common wolffish in the west ranged from 14–86 cm, with a mean size of 51 cm, and 15–83 cm in the east, with a mean size of 50 cm (Fig. 3). These differences were not significant between areas (t-test, $n = 381$, $P > 0.05$).

SPAWNING TIME

Main spawning of common wolffish in the west area appeared to start in the beginning of October. In this area all spawning fish were at stage 3 from late July to October. In the beginning of October 70% had spawned ($n = 46$) and in late

November all MC2 (spawning) fish had spawned ($n = 44$). In the east area it was impossible to estimate the time of spawning time, because of insufficient distribution of data over the spawning season.

MATURITY

In the east area, female common wolffish reached the CA or MC1 stages at a greater age, but at a similar size, compared to fish in the west area. As such, in the east area L_{T50} and A_{50} were 21·5 cm and 3·8 years, while in the west area they were 19·7 cm and 2·7 years (Table III). For females at stage MC1, maturity ogives were significantly different between areas with respect to age (χ^2, d.f. $= 1$, $P < 0{\cdot}001$), but not L_T (χ^2, d.f. $= 1$, $P > 0{\cdot}05$; Fig. 6).

Similarly for stage MC2, spawning females were both longer and older in the east, than in the west area (Fig. 6). As such, in the east area L_{T50} and A_{50} were 72·6 cm and 13·8 years, while in the west area L_{T50} and A_{50} were 63·6 cm and 10·6 years (Table III). For females at stage MC2, maturity ogives were significantly different between areas with respect to both age (χ^2, d.f. $= 1$, $P < 0{\cdot}001$) and L_T (χ^2, d.f. $= 1$, $P < 0{\cdot}001$; Fig. 6).

FECUNDITY

Neither the slopes nor the intercepts of the F_P and L_T relationship were different between areas (ANCOVA, $n = 72$, $P > 0{\cdot}05$; Fig. 7). Therefore, fecundity data from both areas were pooled.

The F_P ranged from 400–16000 eggs, for 25 and 83 cm L_T common wolffish, respectively. The relationship between F_P and L_T was best described with a power function ($F_p = 0.0437 \times L_T^{2.8633}$; $r^2 = 0{\cdot}96$, $n = 72$; Fig. 7).

GROWTH

Common wolffish in the east area grew slower and had greater maximum size than common wolffish in the west area, according to the logistic growth model. (Fig. 8 and Table IV). The parameter K was larger for common wolffish in the west area than in the east area (t-test, $n = 768$, $P < 0{\cdot}001$) and the parameter L_∞

TABLE III. Estimates ± S.E. of total length and age at 50% maturity, for MC1 and MC2 stages, in the west and east areas. A pseudo-r^2 value is also given

Area	Criteria	L_{T50}	r^2	n	A_{50}	r^2	n
West	MC1	19·73 ± 0·53	0·84	260	2·71 ± 1·11	0·90	256
East	MC1	21·45 ± 0·50	0·72	90	3·83 ± 0·52	0·73	85
Total	MC1	20·44 ± 0·34	0·78	350	2·79 ± 0·29	0·67	346
West	MC2	63·56 ± 0·12	0·29	559	10·61 ± 0·13	0·31	551
East	MC2	72·58 ± 0·23	0·38	229	13·84 ± 0·25	0·35	223
Total	MC2	66·09 ± 0·11	0·29	788	11·98 ± 0·11	0·25	763

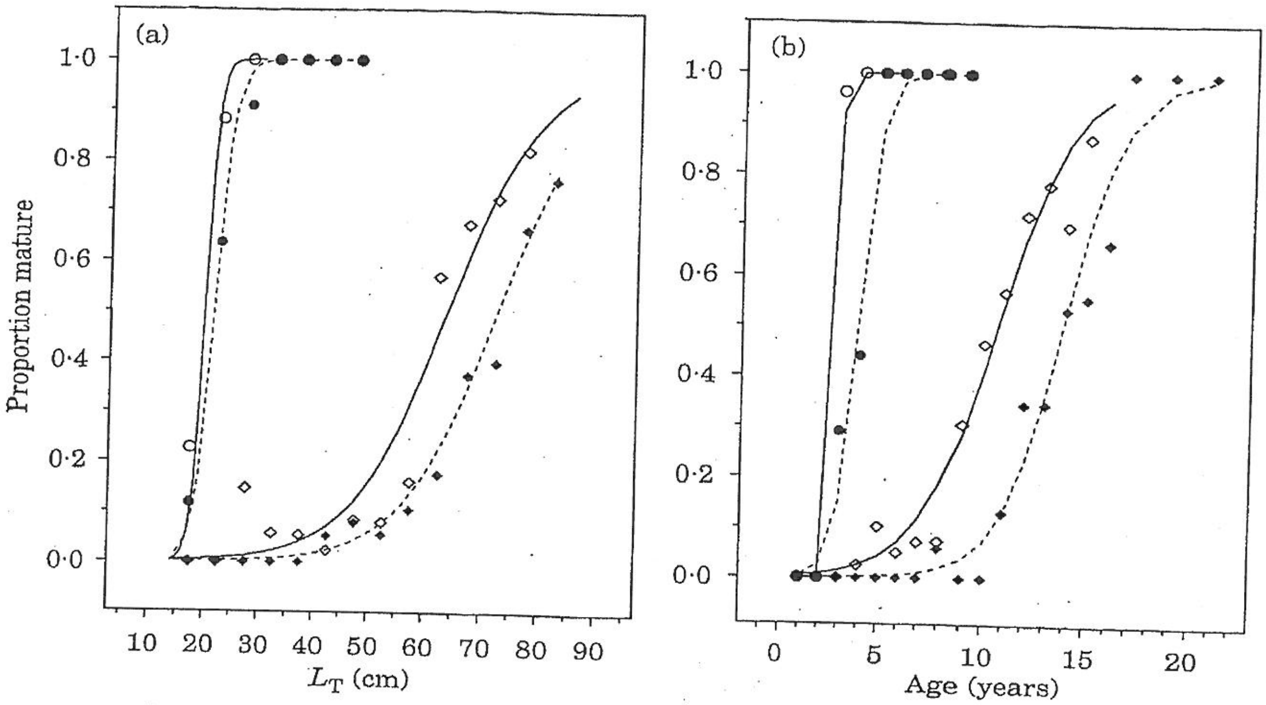

FIG. 6. Observed proportion of mature female common wolffish in each (a) total length and (b) age class for east MC2 (◆), west MC2 (◇), east MC1 (●), and west MC1 (○). Maturity ogives (lines) are based on logistic regressions.

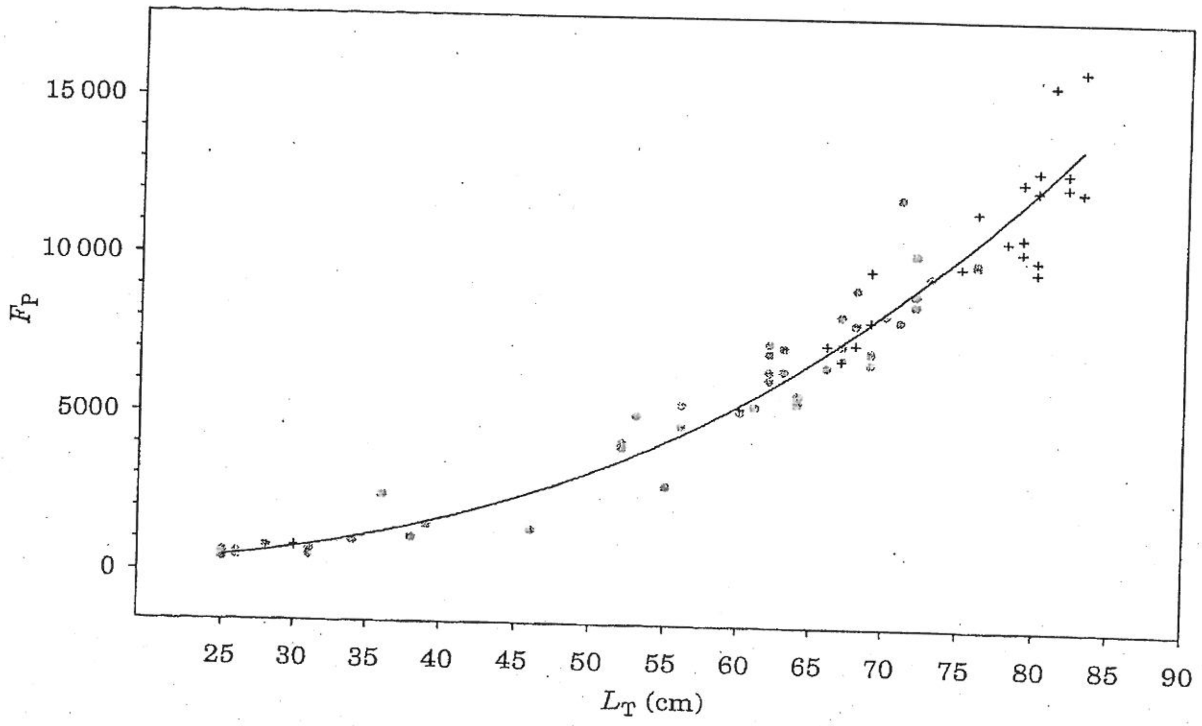

FIG. 7. Relationship between potential fecundity and total length for common wolffish. Values are from combined samples from the west (●) and the east (+) areas. The curve is a power function derived from these observations and was fitted by: $y = 0{\cdot}0437x^{2{\cdot}8633}$ ($r^2 = 0{\cdot}96$, $n = 72$, $P < 0{\cdot}001$).

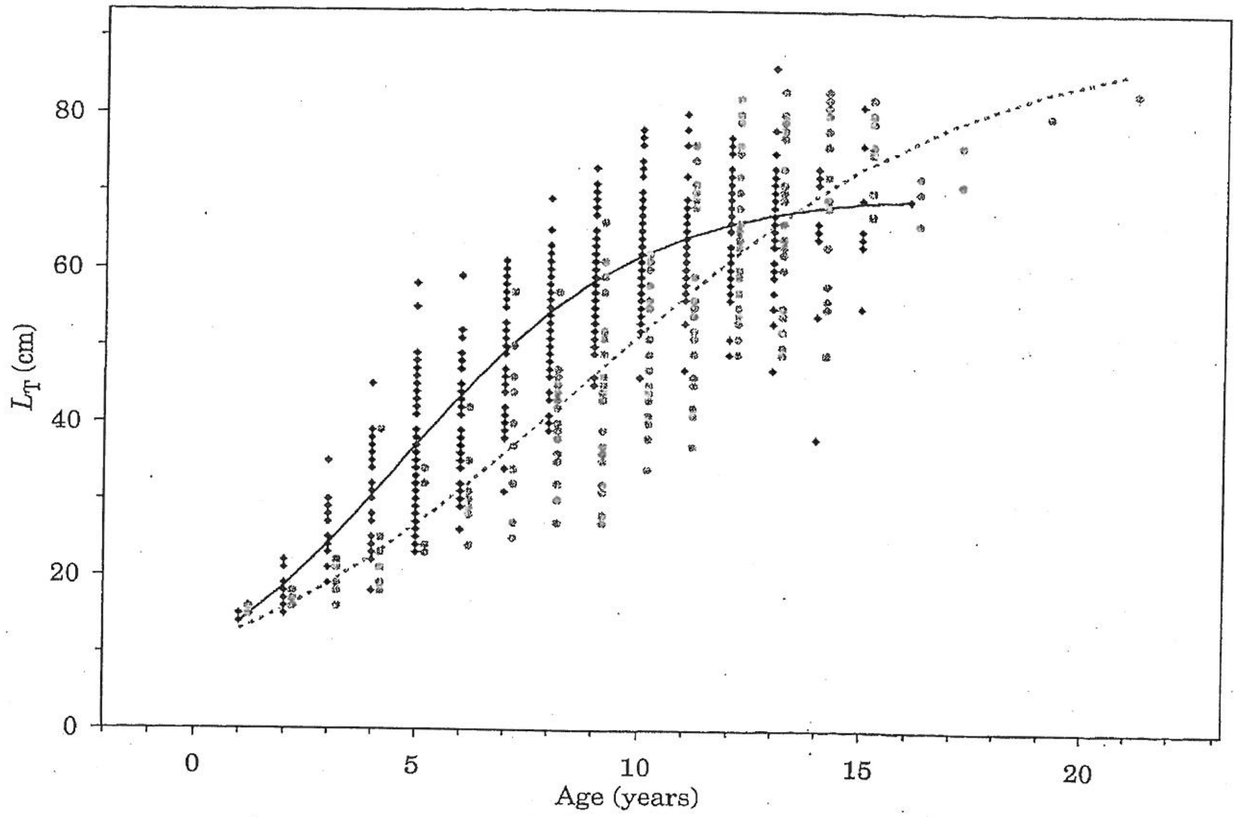

FIG. 8. Length-at-age of female common wolffish in the west (◆,—) and east (●, ---) areas. The logistic growth curves have been fitted (see Table IV).

was larger for common wolffish in the east than in the west area (*t*-test, $n = 768$, $P < 0{\cdot}001$; Fig. 8 and Table IV).

Spawning common wolffish (MC2) in the west and east areas grew faster than common wolffish at CA stage (MC1). As such, the mean L_T of spawning common wolffish in west area was greater than the mean L_T of common wolffish at the CA stage within age groups 5–14 years (two-way ANOVA, $F_{1,435}$, $P < 0{\cdot}001$; Fig. 9). In the west area there was an interaction in mean L_T between

TABLE IV. Parameters of the logistic growth model for female common wolffish from the east and the west areas

		L_∞	K	t_0
West	Values	70·046	0·378	4·691
	S.E.	1·104	0·020	0·114
	t (548)	63·458	19·292	41·312
	P	$P < 0{\cdot}001$	$P < 0{\cdot}001$	$P < 0{\cdot}001$
East	Values	90·919	0·230	8·837
	S.E.	5·937	0·023	0·654
	t (220)	15·315	10·161	13·506
	P	$P < 0{\cdot}001$	$P < 0{\cdot}001$	$P < 0{\cdot}001$

common wolffish at spawning and CA stages ($F_{1,435}$, $P < 0{\cdot}05$), and the difference in L_T within same age groups between common wolffish at spawning and CA stages was only significant for age group 9 years (Bonferroni *t*-test, $P < 0{\cdot}01$). Similar, the mean L_T of spawning common wolffish in the east area was greater than the mean L_T of common wolffish at CA stage within age groups 11–15 years (two-way ANOVA, $F_{1,92}$, $P < 0{\cdot}001$; Fig. 9). Difference in L_T within same age groups between common wolffish at spawning and CA stages in the east area, was only significant for age group 12 years (Bonferroni *t*-test, $P < 0{\cdot}05$).

DISCUSSION

This study demonstrates that significant difference exist in several reproductive traits among common wolffish from two areas west and east of Iceland. It also shows that compared to other species the duration of the CA stage in common wolffish is relatively long, and may extend over several years. Oocytes at the CA stage are therefore ready years before the spawning takes place. For most teleost, oocytes at such an advanced stage are not present in the ovary until just before spawning. Such an extended duration of the CA stage is unknown for other species of teleosts in the North Atlantic, except wolffishes (Barsukov, 1959), and perhaps Greenland halibut *Reinhardtius hippoglossoides* (Walbaum) (Rideout *et al.*, 1999).

Based on the difference in A_{50} between MC1 and MC2, the duration from onset of the CA stage to maturation (MC2) is 8 years in the west area and 10

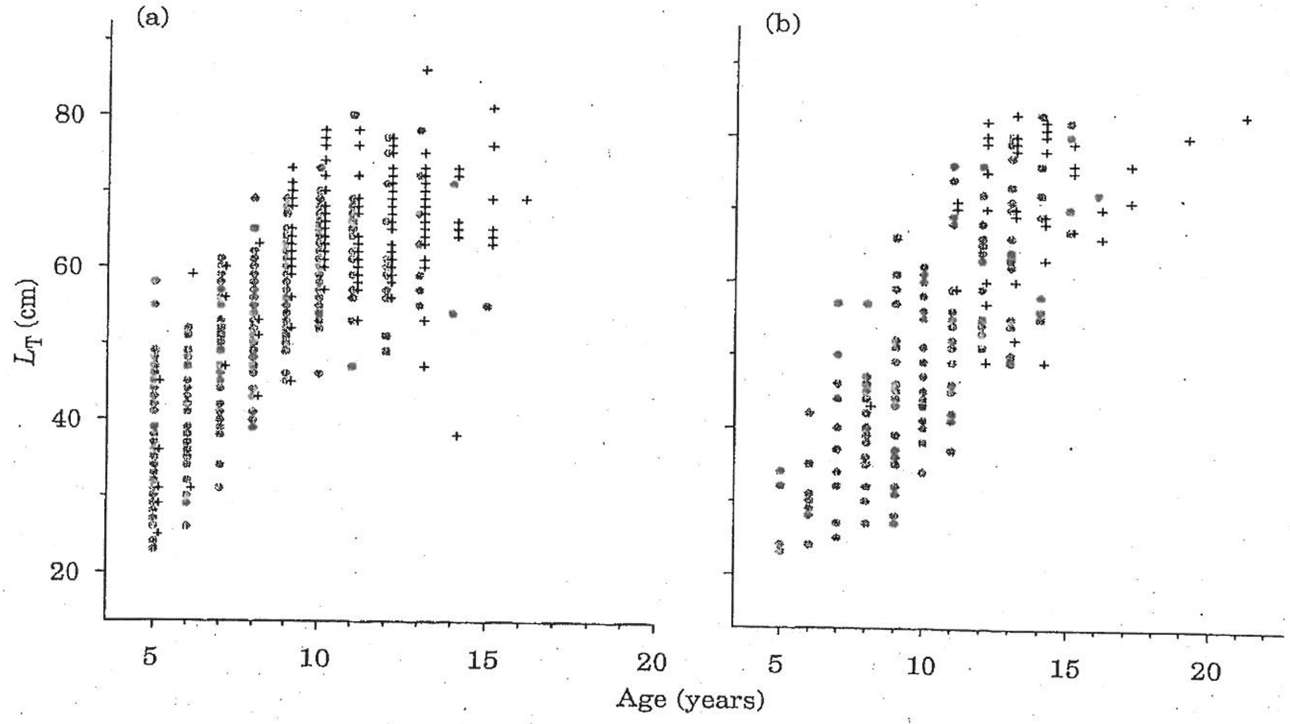

FIG. 9. Length-at-age from the (a) west and (b) east areas, among female common wolffish at spawning (+) and CA (●) stages.

years in the east area (Table III). For common wolffish in the White Sea, the duration from the onset of the CA stage to first spawning was 2–6 years (Barsukov, 1959), which is considerably less time than for common wolffish off Iceland.

The smallest common wolffish at a CA stage in this study were 19 cm in both areas. In the Barents Sea the smallest common wolffish found at the CA stage was 15 cm at Lofoten Island, 22 cm near Medvezhii Island and 24 cm in the southern part of the Barents Sea (Barsukov, 1959). This could indicate that common wolffish off Iceland and in the area between Lofoten Island and Medvezhii Island in the Barents Sea reach the CA stage at a similar size, or at *c.* 20 cm. In this study the youngest common wolffish that reached the CA stage were 3 years old (total of 25 from the west area and two from the east area). This is in accordance with the findings of Dzerzhinskiy & Pavlov (1992), *i.e.* that common wolffish in the White Sea must be at least 3 years old in order to attain the CA stage. The oldest immature (stage 1) common wolffish in this study were 4 years (total of five fish, all from the east area). This is in accordance with the findings of Barsukov (1959) for common wolffish in the White Sea, where the oldest immature common wolffish were also 4 years old. This means that common wolffish off Iceland and in the White Sea reach the CA stage at 3–4 years.

In this study, spawning common wolffish (MC2) attained maturity at a larger size and greater age in the cold sea in the east area than in the warm sea in the west area. The L_{T50} and A_{50} for the common wolffish in the east area are the highest values documented for common wolffish hitherto (72·6 cm and 13·8 years). In the west area these values were 63·6 cm and 10·6 years. This contradicts the results indicated by other studies, *i.e.* that common wolffish mature at a larger size when residing in relative warmer areas (Hansen, 1992; Pavlov & Novikov, 1993; Templeman, 1986). For spawning common wolffish in the west area, L_{T50} is similar to the L_{T50} that Templeman (1986) obtained for common wolffish in the intermediate and the warm sea off Newfoundland, which were 61 and 68 cm respectively. No other estimates of L_{T50} or A_{50} for common wolffish from other areas are available. Therefore direct comparison are difficult. As such, it seems that common wolffish mature at a larger size and greater age in Iceland than common wolffish in the White Sea and off north Norway. Pavlov & Novikov (1993) claimed that common wolffish in the White Sea matured (MC2) at 35 cm at 5–7 years of age. Hansen (1992) claimed that most common wolffish off north Norway were mature (MC2) when they had reached 40 cm and age 5–6 years.

The present study shows that common wolffish in the west area grew faster than common wolffish in the east area. These results are in accordance with other studies, suggesting that the growth rate of common wolffish increases with increasing temperature. Spawning common wolffish (MC2) grew faster than common wolffish at a CA stage (MC1) in both west and east areas. A similar relationship between growth and maturity, is frequently detected among other fish species (Lambert *et al.*, 2003).

Life expectancy has been hypothesized to decrease with higher growth rate (Beverton & Holt, 1959). Accordingly common wolffish in the east area should live longer than common wolffish in the west area. This is possibly true for the common wolffish in Iceland as the oldest common wolffish in the east area was

21 years old but in the west area only 16 years old (Fig. 3). This does probably explain also why common wolffish in the east area has greater average L_T at age infinitum (L_∞) in the logistic growth model than common wolffish in the west area.

The growth rate of common wolffish in the west area was similar to the growth rate reported from north Norway (Hansen, 1992). The growth rate of common wolffish in the east area was slightly less than in the White Sea (Pavlov & Novikov, 1993). Despite this similarity in growth rates, there seems to be a large difference in L_T and age at maturity among common wolffish from these areas, which indicates that other factors (*e.g.* biotic, abiotic, mortality and genotype) are also important in shaping the growth maturity reaction norm. One of the most important factors that affect growth and maturation is food availability (Brett, 1979). Kristinsson (1997) examined stomach and gut content of common wolffish around Iceland. His results showed that composition and the magnitude of food consumed by common wolffish was similar in the eastern and western waters off Iceland, thus indicating that food availability was similar in both areas. Spatial variation in growth and maturity may also result from different fishing mortality. Preliminary analysis of data from autumn and spring ground fish surveys conducted in 2000–2004 indicated that exploitation rate was indeed greater in the west area than the east area. If this exploitation rate is representative of a long-term pattern, such difference may account for some of the difference in maturity between the areas, *via* evolutionary effects of selection (Law, 2000).

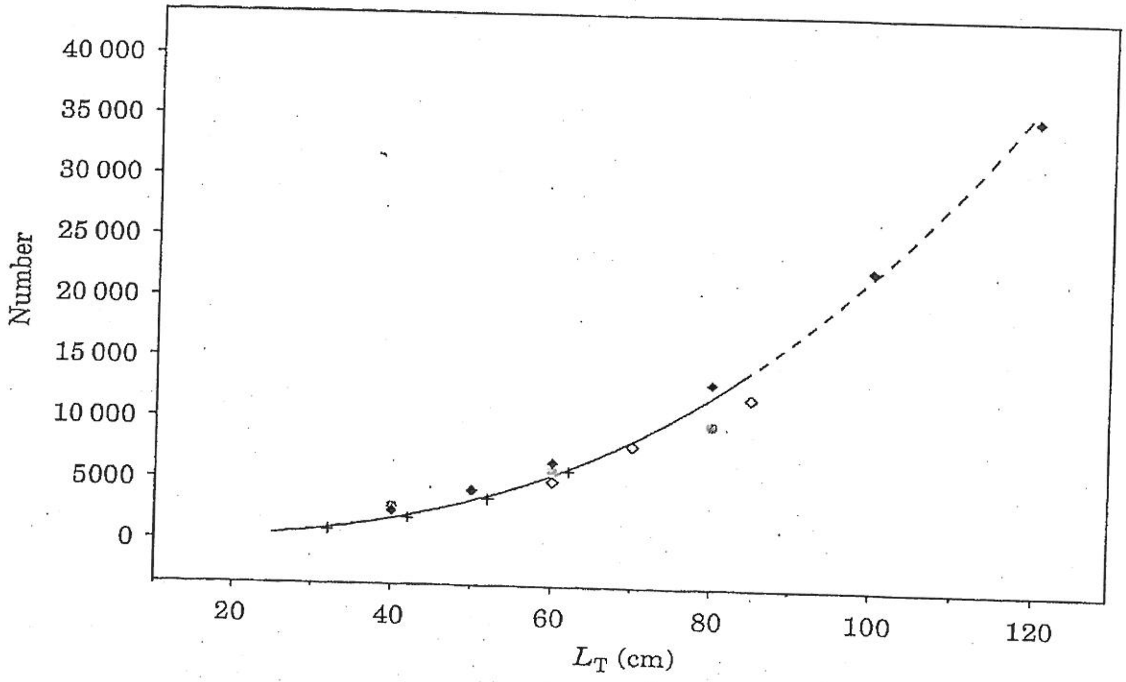

FIG. 10. Relationship between potential fecundity and total length of common wolffish from Newfoundland (◆), White Sea (+), Barents Sea to West Greenland (○) and north Norway (◇). The curve is a power function derived from observed values of potential fecundity from combined samples from the west and the east areas (this study; see Fig. 7). ---, beyond observed values in this study.

The findings showed no difference in potential fecundity and total length relationships between areas. This seems to be in accordance with other studies on F_P and L_T relationships for common wolffish, *e.g.* from White Sea (Barsukov, 1953), north Norway (Hansen, 1992), Barents Sea to West Greenland (Beese & Kändler, 1969) and Newfoundland (Templeman, 1986) (Fig. 10). From these areas, the F_P and L_T relationship of common wolffish was similar, despite a great difference in sea temperature. This suggests that the F_P of common wolffish in general is highly dependent on L_T, as is commonly observed among other fish species (Bagenal, 1978; Wootton, 1979).

Common wolffish reached the CA stage at the age of 3–4 years old and *c.* 20 cm, or relatively early considering that most of them would not spawn until 8–10 years later. A small portion of the fish, however seemed to spawn in the following year, *e.g.* 1 year after reaching the CA stage. In this study the smallest spawning common wolffish were 25 cm L_T (total of three fish, all from the west area) and the youngest were two 4 year old fish (26 and 28 cm, both from the west area). The smallest spawning common wolffish in the study by Jónsson (1982) was 25 cm and 7 years old.

Comparing age of common wolffish at the L_T range 25–29 cm from the west area, at MC2 (spawning; $n = 6$) and CA stage ($n = 29$) with a *t*-test, showed that MC2 fish were significantly older than fish at the CA stage ($P < 0{\cdot}05$), despite smaller average L_T (but greater age), which was 25·8 cm (4·8 years) for spawning fish and 27·3 cm (3·9 years) for fish at the CA stage. This may indicate that maturation of the small common wolffish (MC2; 25–29 cm) was related to slow growth. Small common wolffish are probably vulnerable prey. For example, common wolffish are known to be captured by cod and as large 55 cm individuals have been observed in cod stomachs (Marine Institute Reykjavík, unpubl. data). According to life history models (Stearns, 1992), increased juvenile mortality leads to earlier maturation. Therefore, it is possible that some of the slow growing common wolffish in the west area attained maturity as early as possible, *i.e.* as they were at a greater risk due to predation than the faster growing common wolffish. On the contrary, the faster growing common wolffish tended to mature at a much larger size, *c.* 60 cm, or at a size when they were likely to suffer from less predation.

The Marine Research Institute, Reykjavík, supported this project. We thank D. Teague, K. Gunnarsson, F. Á. Sigurðardóttir and G. Jónsson for comments on the manuscript. Also, S. Guðmundsdóttir, H. Karlsson, A. Þorsteinsson, B. Bárðarson and H. Pétursson for their assistance during sampling. We thank K. Harðardóttir for her help with histological samples and S. Steingrímsson for providing Fig. 1.

References

Alm, G. (1959). Connection between maturity and age in fishes. *Report of the Institute of Freshwater Research Drottningholm* **40**, 5–145.

Bagenal, T. B. (1978). Aspects of fish fecundity. In *Ecology of Freshwater Fish Production* (Gerking, S. D., ed.), pp. 75–101. Oxford: Blackwell Scientific Publication.

Bagenal, T. B. & Braum, E. (1978). Eggs and early life history. In *Methods for Assessment of Fish Production in Fresh Waters* (Bagenal, T. B., ed.), pp. 165–201. Oxford: Blackwell Science Publications.

Barsukov, V. V. (1953). On the biology of reproduction of the White Sea wolffish (*Anarhichas lupus* L.). *Zoologicheskii Zhurnal* **32,** 1211–1216.

Barsukov, V. V. (1959). *Wolffish family (Anarhichadidae).* New Delhi: Indian National Documentation (translated by Smithsonian).

Bates, D. M. & Chambers, J. M. (1992). Nonlinear models. In *Statistical models in S* (Chambers, J. M. & Hasties, T. J., eds), pp. 421–454. Pacific Grove, CA: Wadsworth & Brooks.

Beese, G. & Kändler, R. (1969). Beitrage zur Biologie der drei nordatlantischen Katfischarten *Anarhichas lupus* L., *A. minor* Olafsen und *A. denticulatus* Krøyer. *Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung* **20,** 21–59.

von Bertalanffy, L. (1938). A quantitative theory of organic growth. *Human Biology* **10,** 181–213.

Beverton, R. & Holt, S. (1959). A review of the lifespan and mortality rates of fish in nature in relation to growth and other physical characteristics. *Ciba Foundation Symposium* **5,** 142–180.

Brander, K. (2000). Effects of environmental variability on growth and recruitment in cod (*Gadus morhua*) using a comparative approach. *Oceanologica Acta* **23,** 485–496.

Brett, R. J. (1979). Environmental factors and growth. In *Fish Physiology*, Vol. **VIII** (Hoar, W. S., Randall, D. J. & Brett, J. R., eds), pp. 599–675. New York: Academic Press.

Choen, D. (1971). Maximizing final yield when growth is limited by time or limiting resources. *Journal of Theoretical Biology* **33,** 299–307.

Cole, L. (1954). The population consequences of life history phenomena. *Quarterly Review of Biology* **29,** 103–137.

Crawley, M. J. (2002). *Statistical Computing: An Introduction to Data Analysis using S-Plus.* Chichester: John Wiley & Sons Ltd.

de Vlaming, V. L. (1983). Oocyte development patterns and hormonal involvements among teleost. In *Control Processes in Fish Physiology* (Rankin, J. C., Pitcher, T. J. & Duggan, R. T., eds), pp. 176–199. London: Croom Helm.

Dzerzhinskiy, K. F. & Pavlov, D. A. (1992). Gametogenesis in the white sea wolffish, *Anarhichas lupus marisalbi. Journal of Ichthyology* **32,** 87–99.

Fedorov, K. E. (1968). Ovogenez i polovoi tsikl chernogo paltusa. [Oogenesis and the sexual cycle of the Greenland halibut.] *Trudy PINRO* **23,** 425–450. (*Canadian Fisheries and Aquatic Sciences Translation* **4558,** 1979).

Fresco, L. (1973). Model for plant-growth-estimation of parameters of logistic function. *Acta Botanica Neerlandica* **5,** 486–489.

Gadil, M. & Bossert, W. (1970). Life history consequences of natural selection. *American Naturalist* **104,** 1–24.

Gjøsæter, J., Lønnhaug, H. & Moksness, E. (1990). Vekst av steinbit i Skagerrak. *Norsk Fiskeoppdrett* **15**(10A), 16–17.

Godø, O. R. & Moksness, E. (1987). Growth and maturation of Norwegian coastal cod and northeast arctic cod under different conditions. *Fisheries Research* **5,** 235–242.

Guðmundsson, K., Gíslason, A., Ólafsdóttir, S., Sveinbjörnsson, S. & Valdimarsson, H. (2003). Environmental conditions and plankton communities. *Marine Research Institute (Reykjavík), Report* **96,** 9–16.

Gusev, E. V. & Shevelev, M. S. (1997). New data on the individual fecundity of the wolffishes of the genus Anarhichas in the Barents Sea. *Journal of Ichthyology* **37,** 381–388.

Hansen, T. K. (1992). Reproduksjonsbiologiske undersøkelser av gråsteinbit *Anarhichas lupus* (L.) i nordnorske farvann. Candidata scientiarum thesis, University of Tromsø, Norway.

Heino, M., Dieckmann, U. & Godø, O. R. (2002). Estimating reaction norms for age and size at maturation with reconstructed immature size distribution: a new technique illustrated by application to Northeast Arctic cod. *ICES Journal of Marine Science* **59,** 562–575.

Johannessen, T., Gjøsæter, J. & Moksness, E. (1993). Reproduction, spawning behaviour and captive breeding of the common wolffish *Anarhichas lupus* L. *Aquaculture* **115,** 41–51.

Jónsson, G. (1982). Contribution to the biology of catfish (*Anarhichas lupus*) at Iceland. *Rit Fiskideildar* **4,** 3–26.

Keats, D. W., South, G. R. & Steele, D. H. (1985). Reproduction and egg guarding by Atlantic wolffish (*Anarhichas lupus*: Anarhichidae) and ocean pout (*Marcozoarces americanus*: Zoarcidae) in Newfoundland waters. *Canadian Journal of Zoology* **63,** 2565–2568.

Kjesbu, O. S. & Kryvi, H. (1989). Oogenesis in cod, *Gadus morhua* L., studied by light and electron microscopy. *Journal of Fish Biology* **34,** 735–746.

Kozlowski, J. (1992). Optimal allocation of resources to growth and reproduction: implication for age and size at maturity. *Trends in Ecology and Evolution* **7,** 15–19.

Kristinsson, K. (1997). Fœòa steinbits (*Anarhichas lupus*) og hlýra (*A. minor*) viŏ Ísland. [Food of common wolffish (Anarhichas lupus) and spotted wolffish (*A. minor*) in lcelandic waters]. *Marine Research Institute (Reykjavik) Report* **57,** 79–88 (in Icelandic).

Kvalsund, R. S. (1990). Reproduction in wolffish. *Norsk Fiskeoppdrett (Norway)* **15**(10A), 4–5.

Lambert, Y., Yaragina, N. A., Kraus, G., Marteinsdottir, G. & Wright, P. (2003). Using environmental and biological indices as proxies for egg and larval production of marine fishes. *Journal of Northwest Atlantic Fishery Science* **33,** 115–159.

Law, R. (2000). Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science* **57,** 659–668.

Liao, Y.-Y. & Lucas, M. C. (2000). Growth, diet and metabolism of common wolf-fish in the North Sea, a fast-growing population. *Journal of Fish Biology* **56,** 810–825. doi:10.1006/jfbi.1999.1202

Love, M. R. (1970). *Chemical Biology of Fishes*. London: Academic Press.

Marteinsdottir, G. & Begg, G. (2002). Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series* **235,** 235–256.

Maslow, N. A. (1944). The bottom food-fishes of the Barents Sea. *Trudy PINRO, Murmansk* **8,** 3–186.

Mazhirina, G. P. (1988). Sex cycle of the Barents Sea catfishes. In *The Biology of the Fish in the Seas of the European North* (Glukhov, A. A., ed.), pp. 151–162. Murmansk: PINRO.

Merson, R. R., Casey, C. S., Martinez, C., Soffientino, B., Chandlee, M. & Specker, J. L. (2000). Oocyte development in summer flounder: seasonal changes and steroid correlates. *Journal of Fish Biology* **57,** 182–196. doi:10.1006/jfbi.2000.1300

Murua, H. & Motos, L. (2000). Reproductive biology of roughhead grenadier (*Macrourus berglax* Lacepède, 1801) (Pisces, Macrouridae), in Northwest Atlantic waters. *Sarsia* **85,** 393–402.

Nagahama, Y. (1983). The functional morphology of teleost gonads. In *Fish Physiology*, Vol. **IX** (Hoar, W. S., Randall, D. J. & Donaldson, E. M., eds), pp. 223–264. New York: Academic Press.

Nelson, G. A. & Ross, M. R. (1992). Distribution, growth and food habits of the Atlantic wolffish (*Anarhichas lupus*) from the Gulf of Maine-Georges Bank Region. *Journal of Northwest Atlantic Fishery Science* **13,** 53–61.

Óskarsson, G., Kjesbu, O. S. & Slotte, A. (2002). Predictions of realised fecundity and spawning time in Norwegian spring-spawning herring (*Clupea harengus*). *Journal of Sea Research* **48,** 59–79.

Patzner, R. A. (1983). The reproduction of Blennius pavo (Teleostei, Blenniidae). I. Ovarial cycle, environmental factors and feeding. *Helgoländer Meeresunters* **36,** 105–114.

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour L'Exploration de la Mer* **39,** 175–192.

Pavlov, D. A. & Moksness, E. (1994). Production and quality of eggs obtained from wolffish (*Anarhichas lupus* L.) reared in captivity. *Aquaculture* **122,** 295–312.

Pavlov, D. A. & Moksness, E. (1995). Development of wolffish eggs at different temperature regimes. *Aquaculture International* **3,** 315–335.

Pavlov, D. A. & Novikov, G. G. (1993). Life history and peculiarites of common wolffish (*Anarhichas lupus*) in the White Sea. *ICES Journal of Marine Science* **50,** 271–277.

Rideout, R. M., Maddock, D. M. & Burton, M. P. M. (1999). Oogenesis and the spawning pattern in Greenland halibut from the North-west Atlantic. *Journal of Fish Biology* **54,** 196–207. doi: 10.1006/jfbi.1998.0859

Rijnsdorp, A. D. (1993). Relationship between juvenile growth and the onset of sexual maturity of female North Sea plaice (*Pleuronectes platessa*). *Canadian Journal of Fisheries and Aquatic Sciences* **50,** 1617–1631.

Roff, D. A. (1984). The evolution of life history parameters in teleosts. *Canadian Journal of Fisheries and Aquatic Sciences* **41,** 989–1000.

Selman, K., Wallace, R. A. & Barr, V. (1988). Oogenesis in *Fundulus heteroclitus*. V. The relationship of yolk vesicles and cortical alveoli. *The Journal of Experimental Zoology* **246,** 42–56

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*. New York: W. H. Freeman and Company.

Sonina, M. A. (1981). Growth rate and sexual maturation of the haddock *Melanogrammus aeglefinus*. *Journal of Ichthyology* **21,** 85–97.

Stearns, S. C. (1992). *The Evolution of Life Histories*. New York: Oxford University Press.

Stearns, S. C. & Crandall, R. E. (1984). Plasticity for age and size at sexual maturity: A life-history adaptation to unavoidable stress. In *Fish Reproduction: Strategies and Tactics* (Potts, G. W. & Wootton, R. J., eds), pp. 13–33. London: Academic Press.

Stearns, S. C. & Koella, J. C. (1986). The evolution of phenotypic plasticity in life-history traits: Predictions of reaction norms for age and size at maturity. *Evolution* **40,** 893–913.

Swartzman, G., Silverman, E. & Williamson, N. (1995). Relating trends in walleye pollock (*Theragra Chalcogramma*) abundance in the Bering Sea to environmental factors. *Canadian Journal of Fisheries and Aquatic Sciences* **52,** 369–380.

Templeman, W. (1986). Some biological aspects of Atlantic wolffish (*Anarhichas lupus*) in northwest Atlantic. *Journal of Northwest Atlantic Fishery Science* **7,** 57–65.

Wallace, R. A. & Selman, K. (1981). Cellular and dynamic aspects of oocyte growth in teleosts. *American Zoologist* **21,** 325–343.

Wallace, R. A. & Selman, K. (1990). Ultrastructural aspects of oogenesis and oocyte growth in fish and amphibians. *Journal of Electron Microscopy Technique* **16,** 175–201.

Winsor, C. (1932). The Gompertz curve as a growth curve. *Proceedings of the National Academy of Sciences of the United States of America* **18,** 1–8.

Wootton, R. J. (1979). Energy costs of egg production and environmental determinants of fecundity in teleost fishes. *Symposia of the Zoological Society of London* **44,** 133–159.

Zar, J. H. (1999). *Biostatistical Analysis*. New Jersey: Prentice-Hall Inc.