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Interpopulation comparison of growth patterns of 14 fish species on Faroe Bank: are all fishes on the bank fast-growing?

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Individual growth and sexual maturity of 14 common fish species on Faroe Bank have been investigated and compared with published data from 36 geographical areas. To examine the importance of the Faroe Bank environment on fish growth, a discrimination between resident and migratory species was made. The present study shows that individuals of the resident species on Faroe Bank have higher growth performance and are, on average, 36% larger when they reach sexual maturity than individuals of the same age in other populations. For the migratory species, the difference is only 6%. Abundance of food and high temperatures are probably the main reasons for the high individual growth.

Key words: age at maturity; cross-system comparison; growth; growth-performance index; life-history traits; von Bertalanffy growth equation.

INTRODUCTION

Individual growth of fishes is one of the most important parameters in life-history theory (Stearns, 1997). Indeed, growth of living organisms is a very complex process. Besides its dependence on behaviour, fish growth depends on environmental factors (mainly food and temperature) and genetic properties. For coldwater fishes, Gjedrem (2000) found that 70–80% of the growth is determined by environmental factors, while the remaining part is ascribed to genetic properties. *In situ* it is difficult to separate these two factors. In laboratory experiments, however, environmental conditions can be held constant or controlled and the genetic influence on growth can be measured. Such experiments have been done by, for instance, Fjallstein & Magnussen (1996), who compared growth of Faroe Bank cod *Gadus morhua* L. and Faroe Plateau cod and by Purchase & Brown (2000, 2001), who compared different cod populations in the western part of the North Atlantic.

Unfortunately, laboratory growth experiments are often demanding with respect to time, equipment and manpower. Thus, satisfactory growth information,

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such as specific growth rates, food-conversion efficiencies, size effect and how temperature influences these parameters, are only available for some of the main fish species, *e.g.* cod (Jobling, 1988; Svåsand *et al.*, 1996; Bjørnsson *et al.*, 2001; Bjørnsson & Steinarsson, 2002) and whiting *Merlangius merlangus* (L.) (Andersen, 1998, 1999, 2001; Andersen & Riis-Vestergaard, 2003) and for fish species that are important in aquaculture, such as Atlantic salmon *Salmo salar* L. (Sveier *et al.*, 2000; Bendiksen *et al.*, 2002; Mente *et al.*, 2003; Lysfjord *et al.*, 2004) and rainbow trout *Oncorhynchus mykiss* (Walbaum) (Cowey, 1992; Murai, 1992; Sumpter, 1992; Nikki *et al.*, 2004).

The most common way to study environmental effects on fish growth in the field is by time-series analysis. In doing this, changes in growth are related to environmental variables, and thus the different environmental variables evaluated with respect to growth. Optimal environmental conditions for fishes are both species and size specific (Jobling, 1994; Bjørnsson *et al.*, 2001), which means that growth conditions in a certain ecosystem can be optimal for some species at a specific life stage, but not necessarily for other species or for the smaller and larger individuals.

As a general rule, it can be assumed that an abundant food supply, and usually also a high temperature, favour the growth rate. This implies that there may be great variation between areas. From other research, it is known that some areas (ecosystems) are more productive than others. Seamounts and banks are examples of such highly productive ecosystems (Boehlert & Genin, 1987; Comeau *et al.*, 1995; Genin, 2004). Characteristic of these ecosystems is an enhancement of demersal fishes and micronekton (Comeau *et al.*, 1995; Genin, 2004), and that the fishes living there often are fast-growing.

Faroe Bank is one such highly productive ecosystem (Gaard & Mortensen, 1993). The water on Faroe Bank is fairly isolated from the surrounding water masses (Hansen *et al.*, 1999), which makes the Faroe Bank its own ecosystem (Fig. 1). The position of the Faroe Bank as a separate ecosystem has resulted in specialization with respect to morphological, physiological and genetic properties for some of the fish species living there (Schmidt, 1930; Love *et al.*, 1974; Mattiangeli *et al.*, 2000, 2002). The best known of these is probably the extremely fast-growing Faroe Bank cod, which is considered to be one of the fastest growing cod in the world (Jones, 1966; Love *et al.*, 1974; Ursin, 1984). Examples of other fast-growing fish species on the Faroe Bank are poor cod *Trisopterus minutus* (L.) (Magnussen, 2004) and haddock *Melanogrammus aeglefinus* (L.) (Jones, 1962). These high growth rates may also occur in other fish species living on Faroe Bank. When comparing the size spectra of fish assemblages of Faroe Bank and the North Sea, Pope & Knights (1982) found the slope of the size spectra for the Faroe Bank to be lower than for the North Sea. Later work by Gislason & Rice (1998) demonstrates that higher individual growth rates reduce the slope of the size spectrum in fish assemblages. Higher growth rates of Faroe Bank fishes could therefore be one of the reasons for the difference in the size spectra between the North Sea and Faroe Bank ecosystems found by Pope & Knights (1982).

The potential of an ecosystem for growth can be tested by studying the individual growth of the fish species living in the ecosystem, and then comparing this with the growth for this species in other ecosystems. If a specific ecosystem

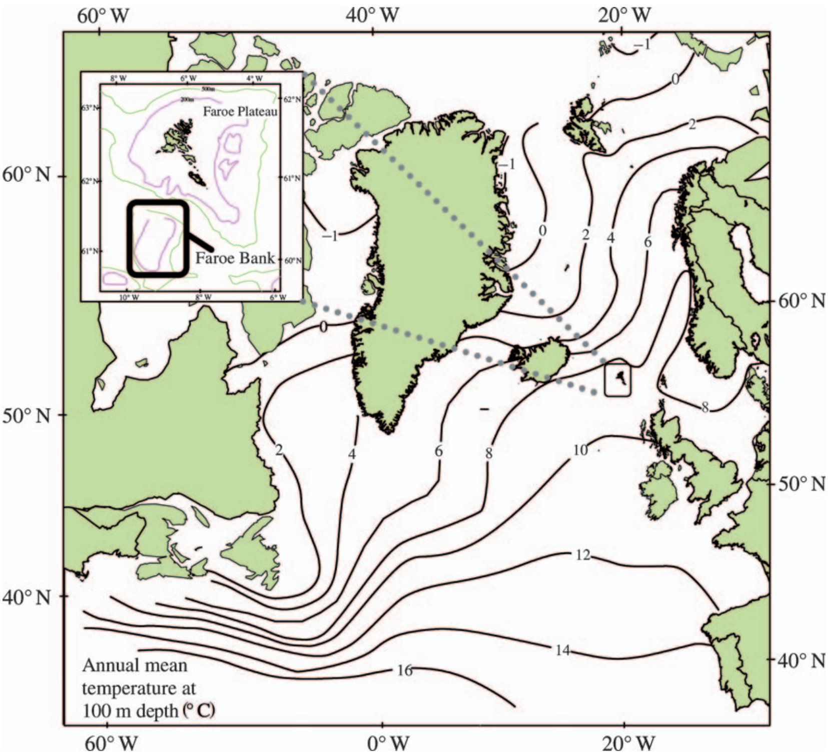

FIG. 1. Geographic location of Faroe Bank and annual mean temperature at 100 m depth in the North Atlantic. Temperatures are based on data from Antonov *et al.* (1998).

somehow is superior, it should be expected that the fishes living there will have higher individual growth rates than those found in other areas. Such evaluation of ecosystem quality is not common, and has probably not been performed before.

The present study intends to address the question: are all fishes living on the Faroe Bank fast-growing, or is the cod a special case? To do this, growth rates have been measured for 14 common fish species living on Faroe Bank. These growth rates are compared with growth data reported for other populations of these species elsewhere. To examine the importance of the Faroe Bank environment on fish growth, data have been collected for both resident and migratory species. If the Faroe Bank environment is somehow superior to most other habitats, it will be expected that the individual growth rates for the resident species on the Faroe Bank should be higher than those found in other populations. For the migratory species on the other hand, the growth curves are expected to be more blurred, because here the Faroe Bank environment only accounts for a narrow fraction of the individual growth.

Consumed energy in fishes is distributed partly to individual growth and partly to maturity development. In the context of energy budget, overall, 29% of consumed energy in fishes goes for growth (Brett & Groves, 1979). Before the maturity process is initiated, all this energy goes for somatic growth. After the fishes have become sexually mature, the main proportion of the available resources is channelled towards reproductive growth, and only 0–5% of the consumed energy goes for somatic growth (Jobling, 1994). Consequently, the individual growth of fishes slows down after they become mature. Because of this close link between somatic growth and maturity processes, the maturity age has also been included in the analysis.

MATERIALS AND METHODS

STUDY AREA

The Faroe Bank is located *c.* 70 km south-west of the Faroe Islands at 60°55′ N; 8°40′ W. (Fig. 1). It is separated from the Faroe Plateau by the narrow (20 km) and deep (850 m) Faroe Bank Channel, and thus resembles a seamount. Inside the 200 m depth contour, the Faroe Bank has an area of 45 × 95 km (3500 km^2). The shallowest part is *c.* 95 m deep. A general description of the Faroe Bank environment and its demersal fish assemblages is given by Magnussen (2002).

RESIDENCY STATUS

Six of the species investigated are characterized as resident stocks for the Faroe Bank (Table I), but assessments of residency status (*e.g.* tagging experiments, genetic analysis or morphometry) are available only for cod, poor cod and lemon sole *Microstomus kitt* (Walbaum).

Table I. Residency statement of the investigated species

Species		Resident population for Faroe Bank	Part of common population	References
Greater silver smelt	*Argentina silus* (Ascanius)		X	16
Cod	*Gadus morhua* L.	X		1–5
Saithe	*Pollachius virens* (L.)		X	10–12
Tusk	*Brosme brosme* (Ascanius)		X	14
Haddock	*Melanogrammus aeglefinus* (L.)	X		9
Poor cod	*Trisopterus minutes* (L.)	X		6, 7
Ling	*Molva molva* (L.)		X	15
Blue ling	*Molva dipterygia* (Pennant)		X	15
Silvery pout	*Gadiculus argenteus thori* Schmidt		X	9
Blue whiting	*Micromesistius poutassou* (Risso)		X	13
Grey gurnard	*Eutrigla gurnardus* (L.)	X		9
Witch	*Glyptocephalus cynoglossus* (L.)		X	9
Dab	*Limanda limanda* (L.)	X		9
Lemon sole	*Microstomus kitt* (Walbaum)	X		8

1, Joensen (1956); 2, Jones (1966); 3, Strubberg (1916); 4, Strubberg (1933); 5, Tåning (1940); 6, Mattiangeli *et al.* (2000); 7, Mattiangeli *et al.* (2002); 8, Tåning (1943); 9, Joensen & Tåning (1970); 10, Jakobsen & Olsen (1987); 11, Nicolajsen (1995); 12, Jones & Jónson (1971); 13, Bailey (1982); 14, Johansen & Nævdal (1995); 15, Magnússon *et al.* (1997); 16, Keysler (1968).

For the remaining three species [haddock, grey gurnard *Eutrigla gurnardus* (L.) and dab *Limanda limanda* (L.)], the residency statement is based on the following: that they spawn and mature on Faroe Bank, that the larvae grow up in the area and that fluctuations in these stocks are not synchronized with the corresponding stocks on the Faroe Plateau. Because of this, these species are also believed to be local stocks for the Faroe Bank. For the other eight species, such as saithe *Pollachius virens* (L.) and blue whiting *Micromesistius poutassou* (Risso), it is assumed that individuals on Faroe Bank are members of a wide-ranging stock, which includes Faroe Bank as a part of its range.

SAMPLING AND MEASUREMENTS

Fourteen fish species were selected for measuring growth and maturity variables on the Faroe Bank (Table II). Data were collected by the R/S Magnus Heinason on bottom surveys, during the years 1994 to 1999. The sampling protocol for these surveys is described by Magnussen (2002). Total length (L_T) and ungutted mass (M) of each fish was measured to the nearest mm and g respectively. Maturity stage was measured visually on a scale from 1 to 7, modified after FAO (1960), where stage 1 is immature and ≥ 2 are different stages for mature fishes. Ages of the fishes were determined from the otoliths.

GROWTH

Growth in L_T and M of the fish species are described as size at age (A), using the von Bertalanffy growth equations: $L_{T_{age}} = L_\infty(1 - e^{-K_{L_T}A})$ and $M_{age} = M_\infty(1 - e^{-K_M A})^3$, where L_∞ and M_∞ are the asymptotic L_T and M, respectively, and K_{L_T} and K_M are the rates of growth towards the asymptotic values. For some of the species, *e.g.* dab, the growth data were scarce, but these species were included only in the case of a high correlation. Otherwise, they were excluded. With respect to dab, there were only eight fish, but the data fitted the von Bertalanffy growth curve very well ($r^2 = 0{\cdot}9998$), giving a 95% CI on L_∞ of 43 $\pm$ 1 cm.

MATURITY

Age at maturity (A_{50}) was derived from: $P_{age} = \pi[2(1 + e^{-m(A - A_{50})})]^{-1}$, as described by Chen & Paloheimo (1994), where P_{age} is the proportion of mature fishes at a particular age. There are two parameters in the model: A_{50} is the age where 50% of the population have reached maturity and the m-value represents the rate at which the population attains maturity. Parameterization is based on arcsine square-root transformation of proportion data. Given the maturity age, the corresponding L_T and M were estimated, using the von Bertalanffy growth equation with the respective parameters found for the species. For three of the species [poor cod, silvery pout *Gadiculus argenteus thori* Schmidt and witch *Glyptocephalus cynoglossus* (L.)] all the collected fish were mature. Because of this, it was not possible to estimate the A_{50} and m parameters for these species.

Calculations of all parameters were performed on a SYSTAT 8.0 PC-programme (SYSTAT, 1998), using a non-linear regression technique with least-squares estimates and the Gauss-Newton method.

INTRASPECIFIC COMPARISON

Growth parameters used for comparison have mainly been found in the scientific literature, either as explicitly published von Bertalanffy growth parameters, or calculated based on reported data. Means were calculated when sex-specific values were reported or multiple estimates were available.

TABLE II. Time schedule and number of fishes for which age, total length, mass and maturity were measured

	1994	1995	1996		1997		1998		1999	
Species	11–19 April	5–9 May	22–31 March	6–10 September	21–25 March	4–8 September	19–23 March	18–22 September	17–21 September	Total number
Greater silver smelt	19	18	78	25	20	19	20	—	—	209
Cod	—	—	—	—	304	—	—	—	—	304
Saithe	183	—	—	—	—	—	—	—	—	183
Tusk	4	5	4	1	5	—	—	—	—	19
Haddock	190	—	—	—	—	—	—	—	—	190
Poor cod	—	—	63	—	—	—	—	—	—	63
Ling	19	22	12	—	—	—	—	—	—	53
Blue ling	—	29	—	50	—	—	—	—	—	79
Silvery pout	—	—	29	—	—	—	—	—	—	29
Blue whiting	—	—	—	—	—	—	19	—	—	19
Grey gurnard	—	—	—	6	—	5	8	5	—	24
Witch	—	—	—	—	—	—	—	—	12	12
Dab	—	—	—	—	—	—	—	—	8	8
Lemon sole	—	—	—	—	—	—	—	—	22	22

Comparisons of growth among populations have been expressed using auximetric plots ($\log_{10}L_\infty$ *v.* $\log_{10}K_\infty$) and the growth performance index ($\Phi' = \log_{10}K + 2\log L_\infty$) as described in Froese & Pauly (2000). Additionally, comparison has been expressed using the term 'relative length' of the Faroe Bank fishes compared to the other populations. Based on the von Bertalanffy growth equation, L_T at a specific age was calculated for each population. 'Relative length' was then found as the size of the Faroe Bank fish divided by the median size of the fish in the other populations. Comparisons were performed at three age-stages: low, medium and high. As the low and high ages, the lowest and highest maturity ages found for the species in its geographical distributions area were chosen. Doing this, relative length of the fishes was obtained both before and also after they have become sexually mature. As medium age, maturity age of the Faroe Bank fishes was chosen, because it is between the two bounded ages.

BOTTOM TEMPERATURE

Bottom temperatures were measured by the R/S Magnus Heinason on eight trips to Faroe Bank from 1997 to 2000. There were four surveys in spring (19 March to 4 April) and four in autumn (4 to 22 September). A total of 203 trawl stations were sampled. The bottom temperature was recorded every minute with a calibrated data logger (MINILOG: resolution 0·2° C) connected to the trawl door. With tow duration of 1 h, the average temperature in each of the 29 statistical rectangles is based on 8 × 60 measurements.

RESULTS

In the spring, the bottom temperature on the Faroe Bank was more or less the same all over the bank, 7·6 to 8·1° C (Fig. 2). During the summer, water is heated and in autumn it reaches temperatures near 11° C on the shallowest part of the central bank. In depths down to *c.* 200 m, the temperature is of

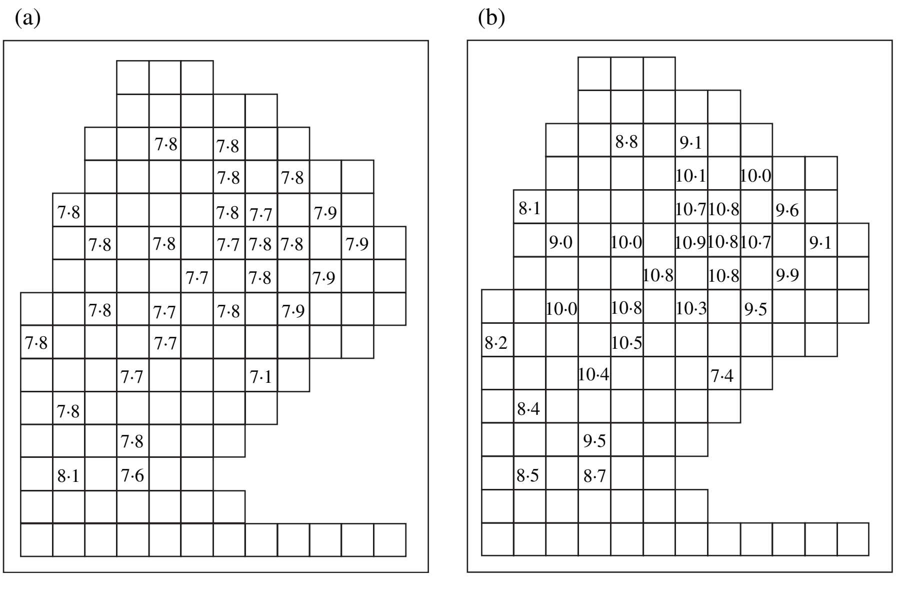

FIG. 2. Average bottom temperature on Faroe Bank in (a) spring (19 March to 4 April) and (b) autumn (4 to 22 September). Size of each statistical rectangle corresponds to 5 × 5 nautical miles.

the order of 10 to 11° C. In deeper water, it is in order of 8° C. The lowest temperature in both periods was found south-east of the Bank. The reason for this is the cold water of Arctic origin (<0° C) that flows north-west through the Faroe Bank Channel below 500 m depth. Interannual variations in bottom temperature on the Faroe Bank were small (range of averages for the whole Faroe Bank: spring: 7·7–8·0° C, autumn: 9·5–10·0° C).

The asymptotic length (L_∞) for the fish species on Faroe Bank varies from 16 to 160 cm [silvery pout and blue ling *Molva dipterygia* (Pennant) respectively] (Table III). These were also those species with the highest and lowest K values (0·847 and 0·110). The asymptotic mass goes from 182 g (poor cod) to 21 712 g (cod) and the K values related to mass from 0·085 [ling *Molva molva* (L.)] to 0·582 (grey gurnard).

Maturity age for the fish species on the Faroe Bank goes from <2 years (poor cod and silvery pout) to 8·2 years [greater silver smelt *Argentina silus* (Ascanius)] (Table IV). The Faroe Bank fishes mature when they have reached an L_T between 49 and 88% of the L_∞ and an M between 9 and 80% of the M_∞ (Table IV).

The comparative life-history parameters for the resident and migratory species are given in Tables V and VI. In Figs 3 and 4, the fastest- and slowest-growing populations are plotted, together with the present results.

The growth of the Faroe Bank fishes seems to be high compared to their counterparts in other areas. The resident species for the Faroe Bank attain high values, both when plotting the L_∞ and K pairs (Fig. 5) and in the growth performance index (Φ') (Fig. 6). An exception to this is the lemon sole, which has a poor growth on the Faroe Bank compared to other areas. Excluding the

TABLE III. Parameter estimates for the von Bertalanffy growth equation for some common fish species living on the Faroe Bank. Total lengths (L_T) at various ages for the respective species are plotted in Figs 3 and 4

	Samples		Length		Mass	
Species	n	Age range (year)	L_∞ (cm)	K	M_∞ (g)	K
Greater silver smelt	199	4–20	44	0·234	802	0·183
Cod	304	2–16	122	0·304	21 712	0·314
Saithe	183	3–9	101	0·196	20 000	0·119
Tusk	19	8–17	69	0·188	4329	0·154
Haddock	190	2–10	63	0·452	2601	0·423
Poor cod	63	2–7	25	0·565	182	0·478
Ling	53	4–15	119	0·136	22 731	0·085
Blue ling	79	3–17	160	0·110	19 688	0·094
Silvery pout	29	2–4	16	0·847	NA	NA
Blue whiting	19	1–8	36	0·561	277	0·538
Grey gurnard	24	3–9	35	0·475	342	0·582
Witch	12	7–16	48	0·134	1058	0·102
Dab	8	2–7	43	0·390	1130	0·321
Lemon sole	23	7–24	50	0·154	2249	0·111

NA, data not available.

TABLE IV. Maturity parameters for some fish species on the Faroe Bank

Species	A_{50} (years)	m	L_{50} (cm)	M_{50} (g)	Ratio L_{50}:L_∞	Ratio M_{50}:M_∞
Greater silver smelt	8·2	0·23	38	376	0·85	0·47
Cod	3·0	17·14	73	4932	0·60	0·23
Sathe	5·8	1·45	69	2478	0·68	0·12
Tusk	7·9	15·26	53	1509	0·77	0·35
Haddock	2·8	1·14	46	870	0·72	0·33
Poor cod	<2	A.M	<17	—	—	—
Ling	7·2	0·58	74	2180	0·62	0·10
Blue ling	6·2	1·66	79	1696	0·49	0·09
Blue whiting	3·1	0·92	29	148	0·82	0·53
Silvery pout	<2	A.M	<12	—	—	—
Grey gurnard	4·5	12·00	31	273	0·88	0·80
Witch	<7	A.M	<29	—	—	—
Dab	3·5	37·00	32	347	0·74	0·31
Lemon sole	<8·2	25·00	36	480	—	0·21

A.M, all fish were mature: $P_{\text{age}} = \pi[2(1 + e^{-m(A - A_{50})})]^{-1}$, where A = age.

TABLE V. Comparative von Bertalanffy growth and maturity parameters for resident fish populations on Faroe Bank. The parentheses codes for the Newfoundland area refer to NAFO statistical area

Species	Ecosystem	von Bertalanffy growth parameters L_∞ (cm)	K (year^{-1})	t_0 (year)	Maturity parameters A_{50} (year)	L_{50} (cm)	References
Cod	Newfoundland area						
	(2H)	64	0·24	0·96	—	—	1
	(2J)	65	0·31	1·74	—	—	1
	(3K)	77	0·26	1·51	—	—	1
	(3L)	102	0·16	1·21	—	—	1
	(3M)	98	0·15	0·19	—	—	1
	(3NO)	130	0·12	1·03	—	—	1
	(3Ps)	101	0·17	1·48	6	—	1, 2
	(3Pn)	78	0·25	1·53	—	—	1
	Georges Bank (5Ze)	132	0·166	—	2·5	45·5	3, 4
	Gulf of Maine Bank (5Y)	167	0·118	—	3·2	43·2	3
	Iceland	149	0·121	—	—	—	7
	Faroe	—	—	—	2·7	—	8
	Faroe Plateau	115	0·19	−0·42	—	—	9
	Faroe Bank	110	0·40	0·73	—	—	9
	Irish Sea	99	0·39	—	2·5	60·9	10
	North Sea	126	0·217	—	3·8	70	11, 12, 6
	Southern Baltic	103	0·15	—	—	—	6
	N. Norway	154	0·069	—	—	—	7
	Barents Sea	134	0·109	—	8–10·5	—	7, 13

TABLE V. Continued

Species	Ecosystem	von Bertalanffy growth parameters			Maturity parameters		References
		L_∞ (cm)	K (year^{-1})	t_0 (year)	A_{50} (year)	L_{50} (cm)	
Poor cod	North Sea	20	0·51	—	2·0	15	11
	W. of Scotland	—	—	—	2	14·8	18
	English Channel	22	0·41	—	—	12	19
	Greece	30	0·213	−0·86	—	—	15
	Spain (Vinaroz & Colum. Isl.)	22	0·390	—	—	—	15
	Italy (Sicily Strait)	22	0·462	—	—	—	15
Lemon sole	Faroe Bank	52	0·080	—	2·9	—	27
	Faroe Plateau	48	0·189	—	2·9	—	27
	North Sea	40	0·315	—	4·0	27	11, 12
	W. of Scotland (North Rona)	28	0·193	—	—	—	28
	S. Norway (Karmøy)	36	0·254	—	—	—	21
Dab	N. Norway	41	0·302	—	—	—	21
	S. Norway (Karmøy)	36	0·325	—	—	—	21
	Faroe Plateau	36	0·367	—	—	—	22
	Iceland	35·0	0·269	—	3·5	17,5	23
	North Sea	29	0·208	−0·90	1·9	13	24, 25
	France (Brittany)	39	0·588	0·27	3	27	26
Grey gurnard	North Sea	46	0·16	—	3·0	23	11
	France (Douarnenez Bay)	36	0·815	—	—	—	20
	Greece (Pagasitikos Gulf)	26	0·22	—	—	—	20
Haddock	Georges Bank	73	0·33	—	2·1	35·0	3
	Gulf of Main	80	0·265	—	2·3	34·8	3
	Iceland	81	0·228	−0·25	—	—	14, 15
	Faroe	81	0·22	−0·24	2·9	—	16, 17, 8
	Rockall Island	44	0·269	−0·66	—	—	14, 15
	W. of Scotland	68	0·16	—	2·0	30·6	10
	North Sea	53	0·26	−0·76	2·5	34	16, 11
	Denmark, Skagerrak	115	0·084	−0·14	—	—	15
	Barents Sea	76	0·234	—	—	—	14, 15

1, May *et al.* (1965); 2, Chen & Mello (1999); 3, Begg *et al.* (1999); 4, Hunt (1996); 5, Penttila & Gifford (1976); 6, Pauly (1980); 7, Taylor (1958); 8, Kristiansen (1992); 9, Jones (1966); 10, Jennings *et al.* (1998); 11, Jennings *et al.* (1999); 12, Gislason & Rice (1998); 13, Jørgensen (1990); 14, Blacker (1971); 15, Froese & Pauly (2000); 16, Jones (1962); 17, Parrish & Jones (1952); 18, Cooper (1983); 19, Beverton & Holt (1959); 20, Booth (1997); 21, based on data from Albert *et al.* (1998), 22, based on data from M. Dam (unpubl. data); 23, based on data from Jónson (1966); 24, Lozan (1989); 25, Rijnsdorp *et al.* (1992); 26, Daniel (1990); 27, based on data from Rae (1939); 28, based on data from Rae (1965).

TABLE VI. Comparative von Bertalanffy growth and maturity parameters for migratory fish species on Faroe Bank

		von Bertalanffy growth parameters			Maturity parameters		
Species	Ecosystem	L_∞ (cm)	K (year^{-1})	t_0 (years)	A_{50} (years)	L_{50} (cm)	References
Saithe	Nova Scotia	111	0·100	—	3·6	45·7	8, 7
	Iceland	118	0·170	—	—	—	9
	Faroe	113	0·178	—	5·0	—	9, 10
	North Sea	106	0·16	—	—	—	11
	N. North Sea	119	0·146	—	—	—	9
	N. Norway	112	0·164	—	—	—	9
Blue whiting	Iceland	45	0·14	−2·95	—	—	16
	Faroe	33	0·23	−2·94	—	—	16
	W. Scotland	36	0·28	−2·48	—	23·3	16
	N. North Sea	35	0·24	−1·58	—	—	16
	Mediterranean	28	0·54	−1·26	—	—	16
Tusk	Nova Scotia (4X)	—	—	—	5·6	47·1	12
	Faroe Plateau	78	0·106	—	—	—	14
	N. North Sea	83	0·105	—	—	—	14
	North Sea	89	0·08	—	7·0	50	13
	Norwegian Sea	79	0·099	—	—	—	14
	W. of Scotland	73	0·152	—	—	—	14
	Rockall	75	0·130	—	—	—	14
Ling	Faroe	124	0·163	—	—	—	14
	N. North Sea	189	0·080	—	—	—	14
	W. of Scotland	166	0·103	—	—	—	14
	Rockall	158	0·087	—	—	—	14
	Norwegian Sea	141	0·143	—	—	—	14
Blue ling	Faroe	110	0·184	0·57	7·3	—	15
	W. of Shetland	123	0·158	0·52	7	—	15
Greater silver smelt	Nova Scotia Banks	40	0·137	−0·75	—	—	1
	Newfoundland	45	0·197	—	—	—	2
	Greenland	56	0·151	—	—	—	2
	Iceland	54	0·091	−4·37	8·5	37	3
	Faroe	46	0·185	−0·17	4	30·3	4
	N.W. of Scotland	38	0·567	—	4·0	—	5
	Rockall Bank	42	0·300	—	3·9	—	5
	S.W. Ireland, Porcupine Bank	37	0·435	—	4·0	—	5
	S. Ireland, Coral Bank	34	0·622	—	3·4	—	5
	N.E. North Sea	41	0·200	−1·95	—	—	6
	Norway	45	0·244	—	—	—	2
	N. Norway	46	0·185	—	6·7	—	5
Silvery pout	France (Bay of Biscay)	16	0·693	−0·37	—	—	8

TABLE VI. Continued

Species	Ecosystem	von Bertalanffy growth parameters L_∞ (cm)	K (year^{-1})	t_0 (years)	Maturity parameters A_{50} (years)	L_{50} (cm)	References
Witch	Iceland	47	0·221	—	—	—	17
	N. Norwegian Sea	31	0·229	—	—	—	17
	S. Norwegian Sea	40	0·208	—	—	—	17
	S. Norway (Karmøy)	41	0·215	—	—	—	18
	Irish Sea	38	0·291	—	—	—	17
	North Sea	42	0·238	—	4·5	29	13, 17
	Denmark (Kattegat)	47	0·259	—	—	—	17

1, Zukowski (1972); 2, based on data from Keysler (1968); 3, Magnússon (1996); 4, Westhaus (1982); 5, based on data from Wood & Raitt (1968); 6, Bergstad (1993); 7, Trippel *et al.* (1997); 8, Froese & Pauly (2000); 9, Based on data from Schmidt (1959); 10, Kristiansen (1992); 11, Gislason & Rice (1998); 12, Oldham (1972); 13, Jennings *et al.*(1999); 14, based on data from Bergstad & Hareide (1996); 15, Thomas (1987); 16, Bailey (1982); 17, based on data from Bowers (1960); 18, based on data from Albert *et al.* (1998).

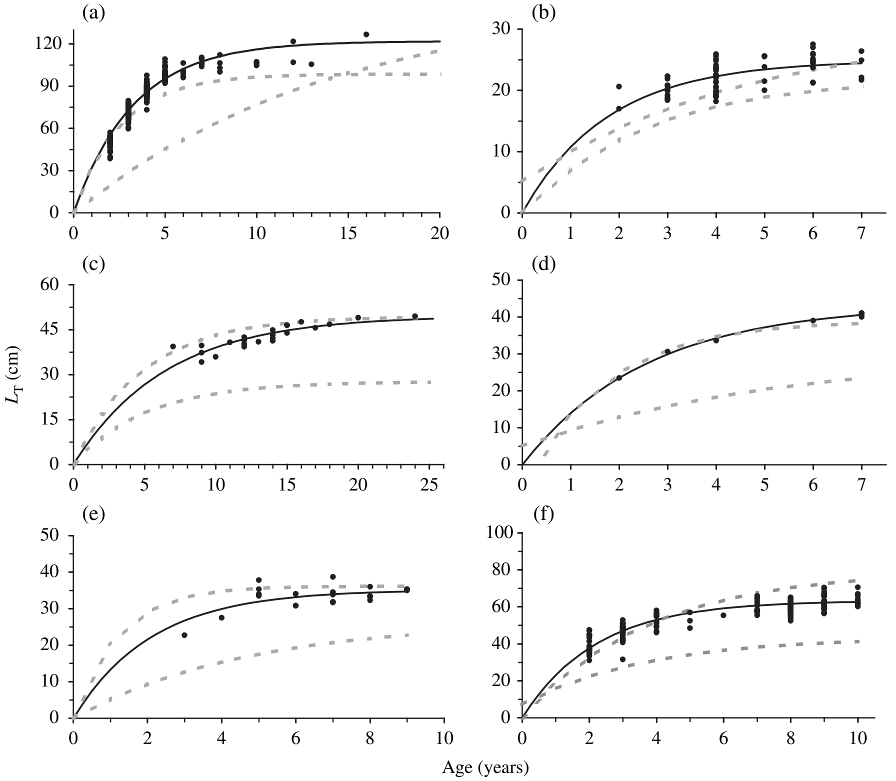

FIG. 3. von Bertalanffy growth curves fitted to observed total length (L_T) observations for resident species (a) cod, (b) poor cod, (c) lemon sole, (d) dab, (e) grey gurnard and (f) haddock on the Faroe Bank (——). For comparison of growth strength, the fastest and slowest growing populations described in Table V are also plotted (- - -).

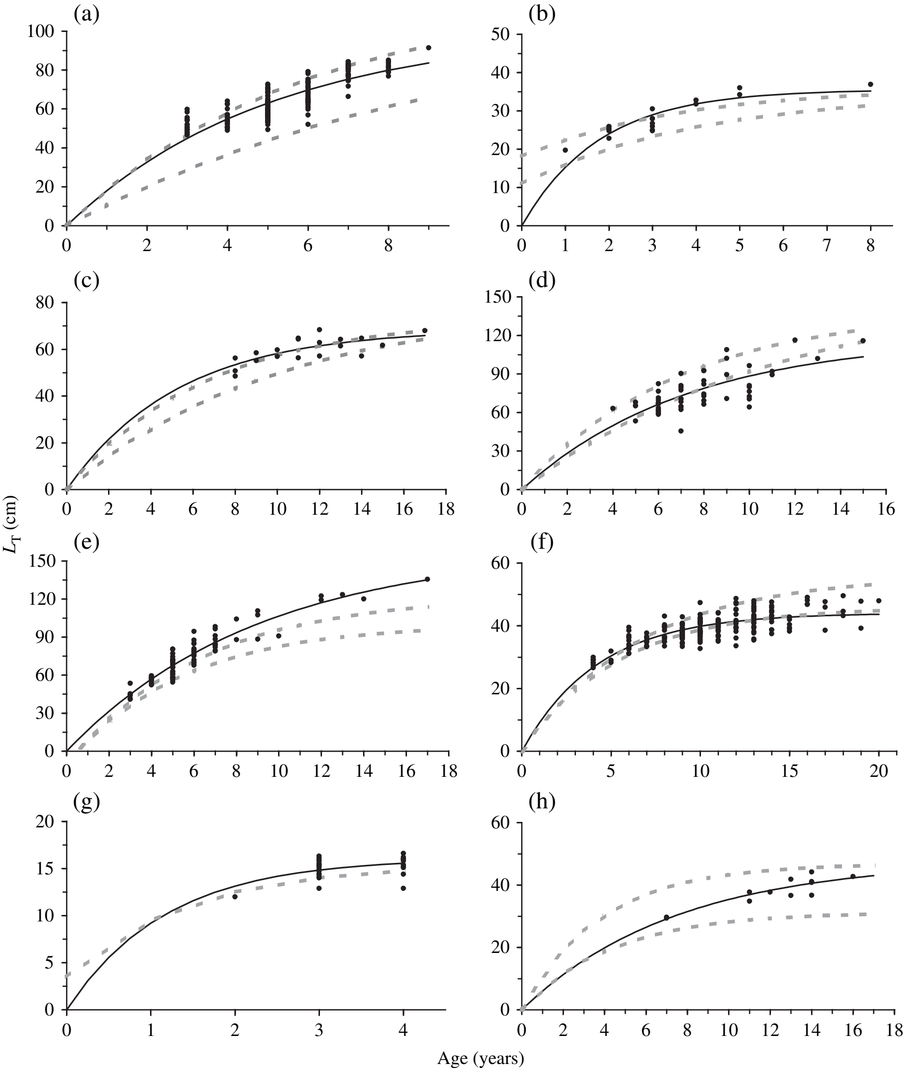

FIG. 4. von Bertalanffy growth curves fitted to observed total length (L_T) observations for Faroe Bank migratory species (a) saithe, (b) blue whiting, (c) tusk, (d) ling, (e) blue ling, (f) greater silver-smelt, (g) silvery pout and (h) witch (——). For comparison of growth strength, the fastest and slowest growing populations described in Table VI are also plotted (- - -).

lemon sole, the Faroe Bank fishes had significant higher values than fishes from other areas, both in the $\log_{10}L_\infty$ and $\log_{10}K$ relationship (ANCOVA; d.f. 1, 47; $P < 0{\cdot}001$) and in the in the L_∞ and Φ' plot (ANCOVA; d.f. 1, 47; $P < 0{\cdot}01$). For the migratory species on the other hand, the results were less clear and no differences were detected between the slopes representing the fishes caught on the Faroe Bank and those caught in other areas, either for the L_∞ and K pairs (ANCOVA; d.f. 1, 49, $P > 0{\cdot}05$) or for the growth performance index (Φ') (ANCOVA; d.f. 1, 49, $P > 0{\cdot}05$).

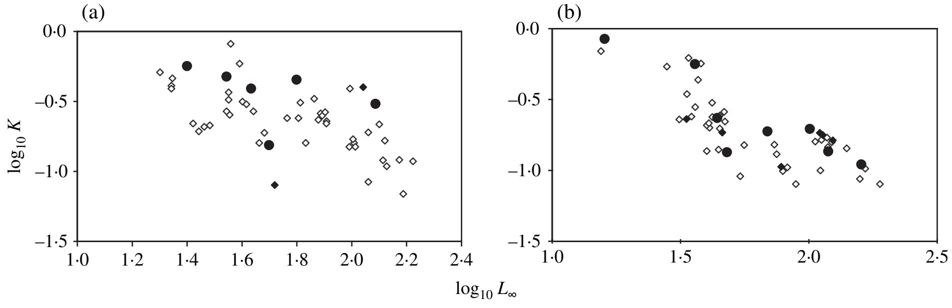

FIG. 5. Relationship between the von Bertalanffy growth parameters L_∞ and K for a variety of (a) resident and (b) migratory fish populations: ● and ◆, Faroe Bank populations; ●, results from the present study; ◆ and ◇, reported data.

The high growth of the resident populations is especially clear for the Faroe Bank cod, of which the growth performance index was 13% higher than the median (3·24) for the 17 other cod populations. On average, 3 year-old cod from Faroe Bank, has a L_T of 73 cm (Fig. 3) compared to only 21 cm for the slow-growing cod in the 2J-area in Newfoundland. For the 17 cod populations in the North Atlantic (the Faroe Bank cod not included), the median of a 3 year-old fish is 35·5 cm.

Together, the resident fishes on Faroe Bank are on average 36% (median 32%) larger at the age of sexual maturity compared with fishes at the same age in other areas included in the present investigation (Fig. 7). For the migratory species, the corresponding size is only 6% (median 4%). Also, when the comparisons are based on the low and high ages, the results are positive for the resident species, which on average are 42 and 25% larger on Faroe Bank than in other areas (the medians are 32 and 28%, respectively). For the migratory species, the corresponding numbers are 6 and 9% (median 4 and 9%) (Fig. 7). On average, the level of the growth performance index (Φ') was 5% higher for resident species on the Faroe Bank than for the migratory species. Comparing growth metrics, a high correlation was found between Φ' and the 'relative length' at all three age levels compared, both for the resident

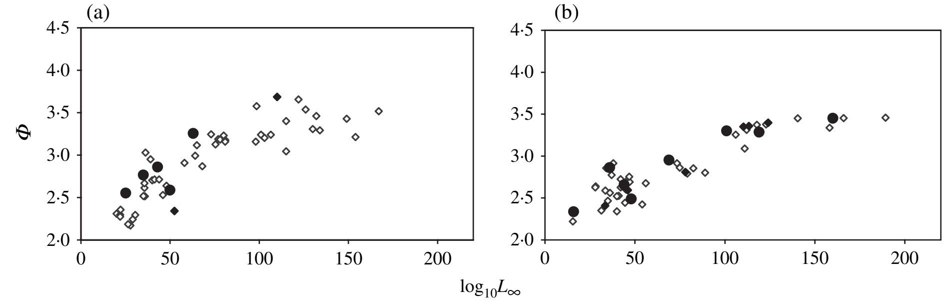

FIG. 6. Relationship between the von Bertalanffy growth parameter L_∞ and the growth performance index ($\Phi' = \log_{10}K + 2\log_{10}L_\infty$) for a variety of (a) resident and (b) migratory fish populations: ● and ◆, Faroese populations; ●, results from the present study; ◆ and ◇, reported data.

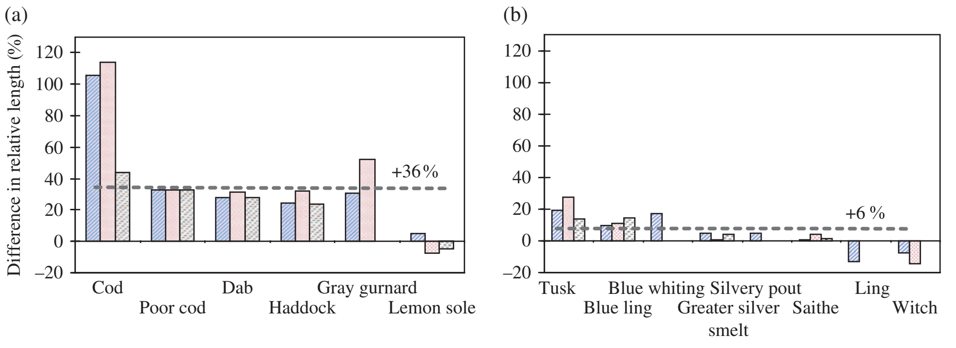

FIG. 7. Difference in relative total length of (a) resident and (b) migratory fish species on Faroe Bank compared to other populations. For each species, sizes are compared at three ages: when the fish reach sexual maturity on Faroe Bank (▨) and for the lowest (▨) and highest (▨) maturity ages found for the species in its geographic distribution range. - - -, Average level for all species.

species on the Faroe Bank(r = 0·79, 0·99 and 0·86) and for the migratory (r = 0·63, 0·97 and 0·67).

The Faroe Bank fishes have an intermediate L_∞. The L_∞ are between 83 (haddock) and 132% (lemon sole) compared to average of the L_∞ for the other populations (Tables V and VI). In general, the relative L_∞ are of the same order of magnitude for the resident and migratory species.

On average, the relative maturity age of cod on the Faroe Bank is 6% below the median for other cod populations, which varies from 2·5 years on Georges Bank to up to 10·5 years in the Barents Sea. For haddock and greater silver smelt, relative maturity ages are 22 and 105% above the medians for the other populations.

DISCUSSION

The present investigation provides evidence that the individual growth of most demersal fish species is high on Faroe Bank compared with most other areas. Additionally, it is shown that individual growth of the resident species is significantly greater than the growth of the migratory species. Most of the high growth observed can probably be explained by environmental factors, which include an abundant food supply and high temperatures, but genetic makeup must also be important.

With average water temperature around 8° C in spring and near 11° C in the autumn, the water temperature on Faroe Bank is relatively high (Figs 1 and 2). Also the food supply seems to be good on the Bank but, unfortunately, satisfactory information on food and feeding conditions confirming this hypothesis are scarce for most of the species on the Faroe Bank. Present knowledge, however, on the growth of the Faroe Bank cod and its condition in general, support a high food supply. High growth rate, low water content in the cod flesh and high liver glycogen (Love *et al.*, 1974) all indicate good food conditions and large amounts of stored energy. The importance of food is furthermore confirmed by studies comparing cod stomach-content data from Faroe Bank with that of other areas (Ursin, 1984; Ursin *et al.*, 1985; Magnussen, 1994). These show that stomach content of the Faroe Bank cod was much higher than in the other populations compared.

The present study tested whether Faroe Bank appears as an ecosystem with exceptionally fast-growth fishes compared to other ecosystems. In doing this, a difference between resident and migratory species was found. Gjedrem (2000) has shown that 70–80% of the growth for coldwater fishes is determined by environmental factors. It was therefore expected that, if Faroe Bank somehow is superior to most other ecosystems, individuals of species that are resident on the Faroe Bank should enjoy an advantage in terms of growth rate, compared with individuals that spend only part of their lives or part of the year on the Faroe Bank. This hypothesis is supported by the present investigation: species that are resident on the Faroe Bank have a higher growth performance and are on average 36% larger at the age of sexual maturity compared with fish at the same age in other populations (Figs 5–7). For the migratory species, on the other hand, there is only a slight difference in growth patterns between fishes caught on the Faroe Bank and in other areas. This obvious difference in the individual growth between the resident and migratory species clearly indicates that the environment on the Faroe Bank must somehow be superior to that of other areas.

The high individual growth found for the fishes on the Faroe Bank can probably be explained by a high primary production in the area (Gaard & Mortensen, 1993). Generally, bank and seamount ecosystems are characterized by high biological productivity, which causes an enhancement of demersal fishes and micronekton (Boehlert & Genin, 1987; Rogers, 1994; Comeau *et al.*, 1995; Genin, 2004). The enhanced production on the Bank and seamounts can in most cases be explained by different physical mechanisms, *e.g.* upwelling, physical aggregation mechanisms (anticyclonic circulation and topographic blockage) and an extended retention time of the water masses (Boehlert & Genin, 1987; Genin, 2004). It is difficult to assess precisely which of the mechanisms mentioned above are responsible for the higher biological productivity and high individual growth of the fish species on the Faroe Bank; however, it has been demonstrated that there is an anticyclonic circulation on the Faroe Bank (Hansen *et al.*, 1999). It is also known that both the phyto- and zooplankton compositions on the Faroe Bank differ, and that the biomass and production are higher on Faroe Bank than in the surrounding waters (Gaard & Mortensen, 1993).

It is well known that ecosystems with a high primary productivity also provide high biomasses of fish stocks (Iverson, 1990; Mann & Lazier, 1996; Moloney *et al.*, 2005; Ware & Thomson, 2005). In the same way, it should also be expected that the individual growth of fishes in these energy-rich ecosystems should be high. It has not been possible, however, to find intersystem references confirming this hypothesis, *i.e.* that a high primary production also provides high individual growth. Even so, some studies have given indications of such a relationship. On a more local scale, Basilone *et al.* (2004) found a high correlation between chlorophyll *a* concentrations and individual growth of the European anchovy *Engraulis encrasicolus* (L.) in 14 different regions in the Mediterranean Sea, and in time-series analysis of the Faroe Plateau, a high correlation was found between primary production and individual growth of cod and haddock (Gaard *et al.*, 2002; Steingrund & Gaard, 2005).

Genetic adaptation to local conditions plays a role in development of life-history characteristics. Indeed, isolated populations often have developed specific genetic properties that optimize them to live in a certain ecosystem. This kind of evolution has often caused the local organisms to be more competitive in order to live in their ecosystem, compared with other such organisms. This is probably also the case for the growth characteristics of the Faroe Bank fishes, of which the resident species must be expected to be optimized to the environmental conditions on the bank.

Although superior growth quality on the gene level has not yet been found for the Faroe Bank fishes, the Faroe Bank fishes have in many ways been found to differ genetically from fishes in other areas. During the last decade, applications of DNA-analyses have generated many new insights in the population structure of marine fishes. Of the commercially important marine fishes, most attention has been focussed on cod (Jonsdottir *et al.*, 1999, 2003; Nielsen *et al.*, 2005; Sarvas & Fevolden, 2005) and the results have revealed genetic differentiation among cod populations in the North Atlantic.

Applications of DNA techniques have also been performed on Faroese fishes. Dahle (1995) showed substantial genetic differentiation between the Faroe Bank cod and three cod populations in northern Norway. Based on microsatellite markers, Faroe populations are significantly different from surrounding populations in the eastern part of the North Atlantic. Further, small albeit significant genetic differentiation can be found between populations at the Faroe Plateau and the Faroe Bank (E. E. Nielsen, pers. comm.). Using single locus minisatellites and allozymes, Mattiangeli *et al.* (2000, 2002) found a distinct poor cod population on the Faroe Bank and by microsatellites and mitochondrial DNA, Hoarau *et al.* (2004) found a significant differentiation between the continental shelf populations of plaice *Pleuronectes platessa* L. and those from Iceland and the Faroe Plateau.

Although, growth of fishes depends mainly on environmental factors (mainly food and temperature), genetic properties are also important. For coldwater fishes, the heritability on growth rate (proportion of genetic to phenotypic variation) ranges from 0·2 to 0·3 (Gjedrem, 2000). For cod, it has been found to be 0·29 (Gjerde *et al.*, 2004). *In situ* it is difficult to separate the genetic and environmental factors. In laboratory experiments, environmental conditions can be held constant or controlled and the genetic influence on growth thus can be measured. This has been done for Faroe Bank and Faroe Plateau cod by Fjallstein & Magnussen (1996), whose experiment shows that Faroe Bank cod have good growth characteristics. They changed from being significantly smaller at the beginning to being significantly larger at the end of the experiment (Fjallstein & Magnussen, 1996). The Fulton condition factor was also found to be higher for the Faroe Bank cod, both at the start and at the end of the experiments.

The uniform growth pattern found for each of the migratory species in the present study is probably caused by high migration between areas. For fishes in general, life-history parameters are often geographically correlated. This implies that there may be great variation in the life-history parameters between areas. The high variations found in the growth pattern of cod (Brander, 1995) and in the spawning characteristics of long rough dab *Hippoglossoides platessoides* (Fabricius) in the North Atlantic Ocean (Walsh, 1994) are examples of such high variations. For the migratory species included in the present investigation, there are large environmental differences from south to north in the distribution area for many of the species. Migration between areas will thus diminish differences that naturally would arise if the populations were resident. For some of these species, the migrations patterns are well known, whereas for others they are less clear. For saithe, for example, there is high migration among geographic areas (Jones & Jónson, 1971; Jakobsen & Olsen, 1987; Nicolajsen, 1995). In British tagging experiments of saithe on the Faroe Bank, 66% were recaptured outside the Faroe Bank. Of these, 21% were caught in Iceland (Jones & Jónson, 1971). Blue whiting, on the other hand, pass the Faroes when they migrate between the spawning area west of the British Isles and the feeding area in the Norwegian Sea (Bailey, 1982).

For the 14 fish species on the Faroe Bank included in the present study, the relative maturity length was between 0·49 (blue ling) and 0·88 (grey gurnard) (Table IV) which is of the same order of magnitude as found by Beverton & Holt (1959). On average, the L_{50}:L_{∞} ratio was 0·70, which is close to the theoretical value (0·66) that optimizes the trade-off between survival and fecundity (Jensen, 1996).

In conclusion, the present study shows that individual growth of the resident species for the Faroe Bank is significantly greater than the growth of most of the migratory species. Species belonging to the resident populations on the Faroe Bank have higher growth performance and are, on average, 36% greater when they reach sexual maturity compared to fishes at the same age in other populations, whereas the corresponding size of the migratory species is only 6% larger. An abundant food supply and high temperatures are probably the main reasons for the high individual growth found for the Faroe Bank fishes.

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