Sub-populations of coastal cod with different behaviour and life-history strategies

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ABSTRACT: This study provides evidence of countergradient variations in life-history traits among coastal cod *Gadus morhua* off the Norwegian coast, suggesting the existence of sub-populations. One-yr-old wild-caught individuals from 70°N were smaller, grew slower, weighed less, and had a lower condition factor (CF) than southern cod from 60°N during the sampling period from June to February. In contrast, both a higher growth potential and an increase in CF were found in northern cod when offspring of northern and southern cod from the same area and of the same age as the wild cod were housed together in a 'common-garden' experiment. The rapid growth in northern cod was achieved by higher success in food competition when given a restricted amount of food. Active feeding behaviour and larger energy allocation to storage tissues, as suggested by the higher increase in condition, represents adaptations to the high-latitude environment for northern cod and countergradient variation. These differences suggest the existence of genetically distinct sub-populations along the Norwegian coast. Development of sub-populations that differ in behaviour and life-history strategies are discussed in relation to mechanisms for local retention of early life stages and local adaptation of older stages. Sub-populations with different life histories may respond differently to fisheries, and attention to this could be beneficial for improving fisheries management.

KEY WORDS: Coastal cod · Countergradient variation · Behaviour · Fisheries management · Local adaptation · Sub-populations

INTRODUCTION

Populations distributed over a wide range of environments may form distinct sub-populations that vary in life-history traits (Law 2000). The dynamics of sub-populations largely depend on growth and mortality rates, age and size at maturation and fecundity. These life-history traits all influence fitness and should therefore adapt to local selection regimes (Sutherland 1996, Carrol & Corneli 1999, Law 2000). Since individuals' size affects their survival, maturation and fecundity, maximising growth rate should be a major influence on life history (Arendt 1997).

However, evidence exists that most organisms are capable of growth rates far greater than what is found in nature (Calow 1982), suggesting trade-offs between growth and other life-history traits (Arendt 1997). For example, temperature is correlated with growth rate (Jobling 2002), and this may to varying degrees constrain the realised growth rate in different environments. Growth rates have also been found to a have a genetic component (e.g. Gjerde 1986, Elliott 1989, Law 2000), and should therefore respond to selection (e.g. Arendt 1997). Evolution of genetically differentiated sub-populations in species distributed over wide range of environments is therefore likely, as long as there are mechanisms ensuring local retention of early life stages (Asplin et al. 1999, Cowen et al. 2000).

Along a latitudinal gradient there will typically be changes in ambient temperature and seasonal variation in photoperiod, differences in encounter rates with prey, predators and competitors, and variations in the strength, temporal pattern and direction of ocean currents. In the Northern Hemisphere growth is generally

more constrained by a shorter growth season and lower temperature at higher latitudes. To counteract the negative effect of the environment on growth, high-latitude populations may evolve local adaptations to maximise growth, i.e. countergradient selection (Levins 1969, Hutchings & Morris 1985, Conover & Present 1990, Conover & Schultz 1995, Arendt 1997, Foster & Endler 1999, Jobling 2002). In species within which countergradient selection on growth occurs, high-latitude populations show higher growth potential than their southern conspecifics when their normal environmental stress is absent. This has been documented in plants, insects and poikoliterms (Partridge et al. 1994, Conover & Schultz 1995, Arendt 1997).

A likely hypothesis for countergradient selection in growth is that it occurs when limiting factors such as a short growth season exist (Arendt 1997). The length of the growth season depends on the integrated amount of daylight available for visual feeding during the entire growing season (Suthers & Sundby 1996), food availability and ambient temperature (Jobling 2002). The rates at which individuals grow also influence their survival probability. Winter mortality is greater in small fish because smaller energy reserves cause a higher risk of starvation during periods of food shortage. Small fish will also be at greater risk of being preyed upon by predators. Mortality is therefore assumed to be greater at higher latitudes (Conover & Present 1990), particularly if food competition is high. One way of surviving periods of food shortage is to allocate energy to reserves when food is plentiful. These reserves can then fuel metabolism in times of need. This strategy is affected by a trade-off between storage costs and needs (Bull et al. 1996). When encountering food, fish at high latitudes, which experience prolonged food shortage, should allocate more energy to storage tissues than fish less constrained by their environment (Bull et al. 1996).

The North Atlantic cod (*Gadus morhua* L.) consists of many populations and sub-populations with different life histories, which are distributed on the west and east coast of the North Atlantic (Mork et al. 1985, Brander 1994b, Bentzen et al. 1996, Svåsand et al. 1996, Fevolden & Pogson 1997, Ruzzante et al. 1998, Jonsdottir et al. 2002). Populations in warm water grow faster and mature earlier than those in colder water (Hutchings et al. 1993, Brander 1994b). Previous studies have reported photoperiod affecting growth in cod larvae, with those in northern latitudes having a longer time for visual feeding during summer (Suthers & Sundby 1996), and higher food-conversion efficiency in northern cod compared with southern cod off the coast of Canada (Purchase & Brown 2000). Some of the units are heavily overfished and have collapsed; they have shown slow recovery even under a complete fish-

ing moratoria (Hutchings 2000). Others are declining dramatically, including the coastal cod in Norwegian waters, which is distributed over a distance of more than 2000 km along the coast.

In Norwegian waters the sub-population concept has largely been ignored in fisheries management (Anon 2003). Some evidence of differentiation along the Norwegian coast has been found, however. Variation in noncoding DNA shows a north–south gradient in the frequency distribution of neutral isozymes among coastal cod (Mork & Giaever 1999). There has, however, been no study on the geographic structure of genes influencing fitness and the possibility of countergradient variation and sub-populations for Norwegian coastal cod. The extent of local adaptation and the existence of sub-populations is likely to be underestimated by selectively neutral molecular genetic traits (Conover 2000), and 'common-garden' experiments examining traits related to fitness, such as growth, are needed to address this issue (e.g. Conover & Schultz 1995, Foster & Endler 1999).

Higher growth potential could be achieved by higher food consumption through a more active feeding behaviour and higher competitive ability. Higher food-conversion efficiency, or a combination of both effects, would also result in a higher growth potential in northern forms. This study is the first to employ 'common-garden' rearing, using cod reared from eggs from 'northern' (70° N) and 'southern' (60° N) Norway to test whether they differ in (1) feeding behaviour, growth and food-conversion efficiency and (2) energy allocation between skeletal growth and storage tissues. Consistent differences imply adaptation to different environments and hence sub-populations. Field data derived from Svåsand et al. (2000), from the area of origin of the parental fish, are included for comparison of growth between northern and southern coastal cod in the field.

MATERIALS AND METHODS

Study species. Cod develop through pelagic egg and larval stages with vertical distributions in the intermediate dynamic water masses (0 to 50 m depth), potentially causing a wide dispersal of early life stages by non-local, wind-driven transport, which allows advection between fjords and coastal areas (Asplin et al. 1999). For cod in Norwegian waters the classic view is that there are only 2 major populations: the Northeast Arctic and the coastal cod populations, which differ in growth performance (Svåsand et al. 1996). The Northeast Arctic population has its nursery area in the Barents Sea and undertakes yearly spawning migrations from the Barents Sea to the north Norwegian coast from 7 to 8 yr of age (Bergstad et al. 1987, Nordeide & Pettersen 1998). Coastal cod have a less migratory life

style, remaining more or less in the same area from settlement at 4 to 5 mo of age and onwards; they will also reproduce locally in fjords and coastal areas from an age of 3 to 5 yr (Jakobsen 1987, Salvanes & Ulltang 1992, Nordeide & Pettersen 1998).

Environmental gradients. Water temperature decreases as one moves in a northerly direction along the Norwegian coast. The major current is the Norwegian coastal current, which flows northwards with a speed between 30 and 50 cm s^{-1} down to 500 m depth (Blindheim 2004). The fjords of southern Norway have relatively high temperatures (12 to 16°C) during summer and autumn, but substantially lower temperatures during winter and spring (Svåsand et al. 2000). The fjords and coastal areas of northern Norway have a sub-arctic climate, with a temperature of 5 to 7°C all year round (Svåsand et al. 2000). Summer day length increases and winter day length decreases with latitude, causing latitudinal differences in opportunities for visual feeding (Suthers & Sundby 1996) and seasonal differences in prey-encounter rates. The average cod biomass in northern fjords (3.5 t km^{-2}) is about 4 times that of southern fjords (0.8 t km^{-2}), due to higher recruitment and density of juveniles, the presence of few competing species and relatively low fishing mortality (Svåsand et al. 2000). This implies different selection regimes between high and low latitudes.

Fish. The northern brood stock consisted of wild-caught individuals from 70° N kept in an environmental regime characteristic of northern cod during maturation and spawning (natural photoperiod, 3.5 to 4.5°C). The southern brood stock were comprised of first-generation cod from 60° N reared in hatcheries. These fish were kept in an environmental regime typical of southwestern Norway during maturation and spawning (natural photoperiod, 6 to 7°C). The brood stocks spawned voluntarily in large tanks. The southern group consisted of 15 females and 10 males, and the northern group of 45 individuals with approximately 50% females. Eggs were collected over a 24 h period. Female cod release batches approximately every other day, implying that approximately 7 to 8 and 12 to 13 females mothered larvae for the southern and northern fish, respectively. For the southern population this is likely a minimum number, since eggs were collected on days with a particularly high egg density. Fertilized eggs from the southern strain were spawned at Austevoll Aquaculture Station (near Bergen), but hatched in egg incubators at the University of Bergen (UoB) in April 2000, whereas fertilized eggs from the northern strain were spawned at Troms Marin Yngel (near Tromsø) before being transported to UoB and gradually acclimated to 5 to 6°C. The eggs from both strains were then housed at a temperature of 5 to 6°C until 2 d before hatching; the temperature was then gradually increased to 10°C, which was

reached 2 d after hatching. The day for 50% hatching was identical for the 2 groups.

Larvae were fed natural zooplankton until late June, and thereafter commercial fish feed (Supra Marine; Felleskjøpet, Norway). The cod were housed under typical natural light and temperature conditions representative of Bergen (60° N), and from June onwards they were provided with a water renewal rate of 5 l h^{-1}. Northern and southern cod were housed in separate aquaria prior to the experiments. Both groups of fish were treated identically prior to the experiments. The larvae were not sorted into size groups. A few cannibals were removed from both the northern and southern fish, but only over a 1 wk period approximately 10 wk after hatching to avoid further cannibalism. The temperature varied seasonally between 8 and 10°C. In May 2001, samples of 30 individuals were selected at random from each population and transferred to 2 separate 7000 l aquaria. At this time the diet was changed to natural cod food: herring (*Clupea harengus*) pieces, which were provided in small amounts during a 3 wk acclimation period and from late May given as 2 larger meals per week for 6 wk. During this period, 2 individuals from the southern population escaped from the aquaria, and another individual was removed from the experiment.

The experiment. From the start of and throughout the experiment, northern and southern cod shared two 7000 l aquaria (i.e. 'common-garden' rearing), in which there was a continuous water renewal rate of 2000 l h^{-1} in each, and a natural light cycle for Bergen.

The experiment started on 11 July. After anaesthetisation (Metakain), every individual was measured (total length, cm), weighed (total weight, g) and individually tagged. Feeding trials were conducted twice a week. The experimental groups were given similar-sized pieces of herring (4.4 g; SE = 0.16). Food items were provided sequentially in order to allow competition for each piece. Feeding terminated when food equivalent to 5% of the total biomass in each aquarium had been eaten or 4 items of food in a row had been rejected. Which individual took which food item was recorded.

Every other month the cod were anaesthetised, weighed and measured. After each measurement the food ration per aquarium was adjusted to 5% of the current biomass. The experiment was terminated on January 24. Four measurements were taken for individual fish (measuring dates were 11 July, 11 September, 13 November and 24 January). Hereafter, Period 1 refers to July–September, Period 2 to September–November, and Period 3 to November–January.

Field data. Data for wild cod of the same age (Svåsand et al. 2000) from the same areas as the origin of the brood stock were used to compare weight, length and condition factor for northern and southern coastal cod in their natural habitats.

Data analysis. *Wild cod:* Foulton's condition factor, CF = $(W/L^3) \times 100$, was calculated from weight (W) and length (L). CF was calculated to serve as an index of energy allocation. Growth in length, weight and CF were modelled by linear regression comparing population differences in slope and intercept. The equation used was

$$y_{il} = \mu_0 + \beta_{0l} + (\mu_1 + \beta_{1l})t_{il} + e_{il} \qquad (1)$$

where y_{il} denotes the measurement of the ith fish from the lth population. Subscript 1 refers to a slope and 0 to a constant (i.e. intercept), μ_0 and μ_1 are the overall intercept and slope values, while β_{0l} and β_{1l} are the population specific effects and e_{il} is the unexplained error. The dates were coded as $t = 0$ for 1 July, $t = 4.5$ for 15 November and $t = 7$ for 1 February. The NLME library of the Splus software was used in this and the following tests (Pinoheiro & Bates 2000). A contrast treatment using the northern population as the reference value was used for all tests. β_{02} (SN-diff) and β_{12} (time:SN-diff) thus show the differences between the southern and northern population at the start of the experimental period (intercept, β_{02}) and differences in growth rate during the experimental period (slope, β_{12}) for all tests (see Tables 1–3). A positive value implies larger values for the southern population.

Reared cod: CF was calculated for each individual measurement. Growth curves were modelled for individual fish for W, L and CF. This was done by regressing the quantity in question using time and some of the other explanatory quantities, with an individual slope for each fish varying randomly around a mean slope. The model that fit the data best was

$$Y_{ijkl} = \mu_0 + \alpha_{0k} + \beta_{0l} + b_{0i} + (\mu_1 + \alpha_{1k} + \beta_{1l} + b_{1i})t_j + e_{ijkl} \qquad (2)$$

The subscripts k and i denote aquaria and fish, respectively. The time t_j was coded as 0, 1, 2, 3. A Greek letter denotes a fixed effect and a Latin letter denotes a random effect. Other variables are identical to those in Eq. (1).

During the last period some of the fish did not compete for food, possible indicating maturation (Fordham & Trippel 1999), and there was food left in the aquaria after the feeding trials. All data were therefore analyzed both including and excluding the last measurement.

Differences in the total food intake of the 2 populations for the periods between each of the measurement points were tested using a mixed-effect model with population-specific components in the intercept and slope. The population component in the slope was not significantly different from zero including $(p = 0.18)$ or excluding the last period $(p = 0.12)$. The population-

Table 1. *Gadus morhua*. Results of growth in length, weight and condition factor (CF) using linear regression model on field data of coastal cod from northern and southern Norway

	Value	SE	df	t	p
Length					
Intercept, μ_0	17.51	1.43	304	12.1	<0.0001
Time, β_1	0.92	0.27	304	3.37	<0.001
SN-diff, β_{02}	9.40	1.70	304	5.55	<0.0001
Time:SN-diff, β_{12}	0.306	0.316	304	0.97	0.33
Weight					
Intercept, μ_0	43.82	50.07	304	0.87	0.58
Time, β_1	9.02	9.47	304	0.95	0.34
SN-diff, β_{02}	9.40	58.9	304	2.88	<0.01
Time:SN-diff, β_{12}	24.13	10.98	304	2.20	<0.05
Condition factor					
Intercept, μ_0	0.78	0.078	304	10.12	<0.0001
Time, β_1	0.0005	0.015	304	0.003	0.997
SN-diff, β_{02}	0.36	0.09	304	3.98	<0.0001
Time:SN-diff, β_{12}	−0.038	0.017	304	−2.26	<0.05

specific term in the slope could therefore be omitted and the equation becomes

$$y_{ijkl} = \mu_0 + \alpha_{0k} + \beta_{0l} + b_i + \mu_1 t_j + e_{ij.} \qquad (3)$$

The symbols have the same meaning as above. The same model was used on the data after food intake had been standardized to weight at the start of each time period in order to correct for size. Again, the population component in slope was not significant (including last period, $p = 0.19$; excluding last period, $p = 0.60$).

Differences in gross food conversion efficiency (GFCE) were tested by a separate analysis of co-variance (ANCOVA) test for each time period. The test was done on the relationship between food eaten relative to initial size versus weight gain relative to initial size using populations and aquaria as fixed effects. Homogeneity of slopes was tested for all measurement dates for both aquaria and populations.

$$y_{ikl} = \mu_0 + \alpha_{0k} + \beta_{0l} + \mu_1 x_{ikl} \qquad (4)$$

where x is food eaten relative to initial weight.

RESULTS

Wild cod

Southern cod were heavier, longer and had a higher CF when they were the same age as experimental reared cod at the start of Period 1 (Fig. 1, Table 1: β_{02}). The southern cod had higher weight increase, but significantly lower increase in CF than northern cod (Fig. 1, Table 1: β_{12}). There was no difference in length increase (Fig. 1, Table 1: β_{12}).
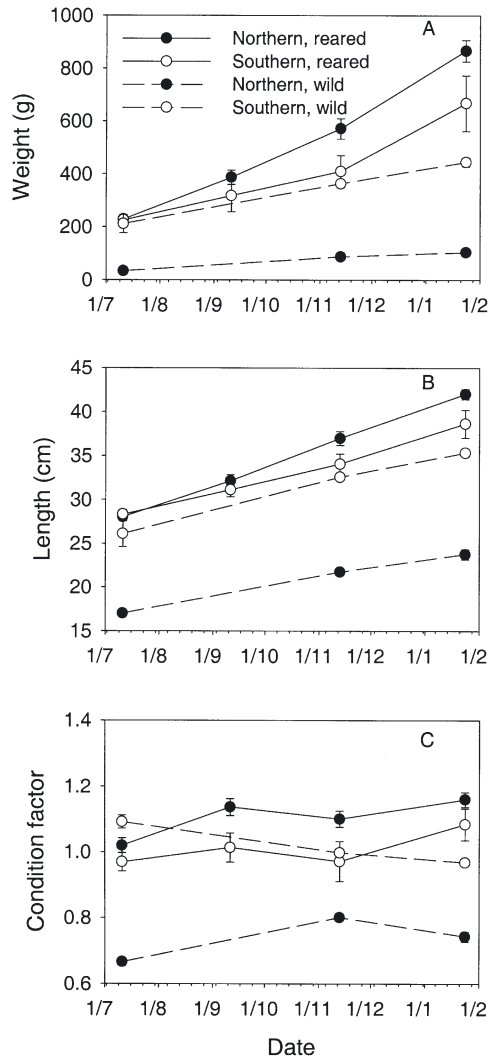
Fig. 1. *Gadus morhua.* Growth in (A) mean weight, (B) length and (C) condition factor (CF) in reared and wild cod. Date: date of measurement for the reared fish. Measurements for the wild cod are taken from the same month using fish of the same age (field data from Svåsand et al. 2000). Mean values of each measurement for the reared cod include all individuals alive at that point in time. Error bars: standard error

Reared cod

Contrasting results were obtained for reared cod from the 'common-garden' rearing experiment. There were no differences between aquaria in any of the variables measured (Fig. 1, Table 2). The interaction of aquaria:SN-diff was never significant (p > 0.5), and it was therefore excluded from the model.

The coefficient β_{02} (SN-diff intercept) was not significant for weight, length or CF (Table 2). Hence, the 2 populations were equal at the start of the experiment. The coefficients α_{02} (aquaria intercept) and α_{12} (slope

of aquaria) were never significant (Table 2), i.e. the start and changes in the measured variables did not differ between aquaria. No aquarium effects were therefore detected in the study.

The most interesting coefficient, β_{12} (time:SN-diff), which measures differences in increase in weight, length and CF for the southern population relative to the northern population, was highly significant for all variables including and excluding the last measurement (Fig. 1, Table 2). The negative value implies a smaller increase in southern fish (Table 2).

Food intake

Total food intake did not differ between aquaria (Table 3). As expected, the lower growth rate of southern cod was caused by significantly lower food intake due to lower success in feeding competition (consistent when including and excluding the last measurement; Fig. 2, Table 3). Normalised food intake gave the same results (Table 3).

Gross food conversion efficiency

We found no difference in GFCE between populations or aquaria (Fig. 2). The p-values for population comparisons were p > 0.53, p > 0.24 and p > 0.29 for Periods 1, 2 and 3, respectively. For aquaria they were p > 0.80, p > 0.81 and p > 0.12, respectively, for Periods 1, 2 and 3.

DISCUSSION

The common-garden study presented here provides evidence of countergradient variations in life-history traits and suggests the existence of sub-populations of coastal cod in Norwegian waters. Wild individuals from 70° N were shorter, weighed less and had a lower CF at 1 yr of age than southern cod caught at 60° N off western Norway (Fig. 1, and see Svåsand et al. 2000). From June to February the increase in weight of northern cod was also significantly lower, but they had a larger increase in CF than southern cod (Fig. 1). The latter implies a relatively higher allocation of energy to storage tissues (Fig. 1). In contrast, similar-age offspring of northern cod had a higher growth rate in length, weight and CF than southern cod when housed in a common-garden environment typical of the southern cod. No difference was found in GFCE (Fig. 2).

Two potential causes of bias concerning the parental fish need consideration: the number of generations in captivity, and the number of fish siring offspring for the reared southern and northern cod. The northern,

Table 2. *Gadus morhua.* Effects on weight, length, and condition factor (CF) of population, aquaria and time for experimental coastal cod, estimated from random-effects modelling

	Including last measurement					Last measurement removed				
	Value	SE	df	t	p	Value	SE	df	t	p
Weight										
Intercept, μ_0	144.2	63.3	139	2.28	<0.05	198.7	54.7	96	3.63	<0.001
Aquaria, α_{02}	18.2	17.8	51	1.02	0.31	8.0	15.4	51	0.52	0.604
SN-diff, β_{02}	10.4	18.0	51	0.58	0.56	0.3	15.5	51	0.02	0.98
Time, μ_1	235.9	67.3	139	3.51	<0.001	157.4	55.6	96	2.83	<0.01
Time:Aquaria, α_{12}	−11.8	19.0	139	−0.63	0.54	2.14	15.7	96	0.14	0.89
Time:SN-diff, β_{12}	−71.3	19.3	139	−3.69	<0.001	−57.7	15.8	96	−3.65	<0.001
Random effects	SE	Corr				SE	Corr			
Intercept, b_{0i}	32.77					51.6				
Time, b_{1i}	59.12	0.805				53.8	0.644			
Residual, e_{ijkl}	66.0					24.0				
Length										
Intercept, μ_0	25.9	1.8	139	14.3	<0.001	26.7	1.72	96	15.5	<0.001
Aquaria, α_{02}	0.62	0.51	51	1.21	0.23	0.38	0.49	51	0.78	0.44
SN-diff, β_{02}	0.26	0.51	51	0.50	0.62	0.26	0.49	51	0.54	0.59
Time, μ_1	5.39	0.97	139	5.56	<0.001	4.25	1.17	96	3.64	<0.001
Time:Aquaria, α_{12}	−0.32	0.27	139	−1.16	0.25	0.020	0.33	96	0.06	0.95
Time:SN-diff, β_{12}	−0.93	0.28	139	−3.33	<0.01	−0.94	0.33	96	−2.83	<0.01
Random effects	SE	Corr				SE	Corr			
Intercept, b_{0i}	1.68					1.66				
Time, b_{1i}	0.85	0.349				1.084	0.326			
Residual, e_{ijkl}	0.93					0.65				
Condition factor										
Intercept, μ_0	1.03	0.11	139	9.34	<0.001	1.04	0.108	96	9.6	<0.001
Aquaria, α_{02}	<0.01	0.03	51	0.085	0.93	0.001	0.030	51	0.025	0.98
SN-diff, β_{02}	−0.05	0.03	51	−1.65	0.10	−0.05	0.031	51	−1.52	0.13
Time, μ_1	0.034	0.041	139	0.825	0.41	0.025	0.050	96	0.49	0.62
Time:Aquaria, α_{12}	<0.01	0.012	139	0.127	0.90	0.004	0.014	96	0.31	0.76
Time:SN-diff, β_{12}	−0.026	0.012	139	−2.18	<0.05	−0.04	0.014	96	−2.39	<0.05
Random effects	SE	Corr				SE	Corr			
Intercept, b_{0i}	0.094					0.091				
Time, b_{1i}	0.022	−0.15				0.008	0.86			
Residual, e_{ijkl}	0.074					0.069				

Table 3. *Gadus morhua.* Results of linear mixed-effect model on total food intake and food intake normalised to weight at the start of each period for experimental coastal cod

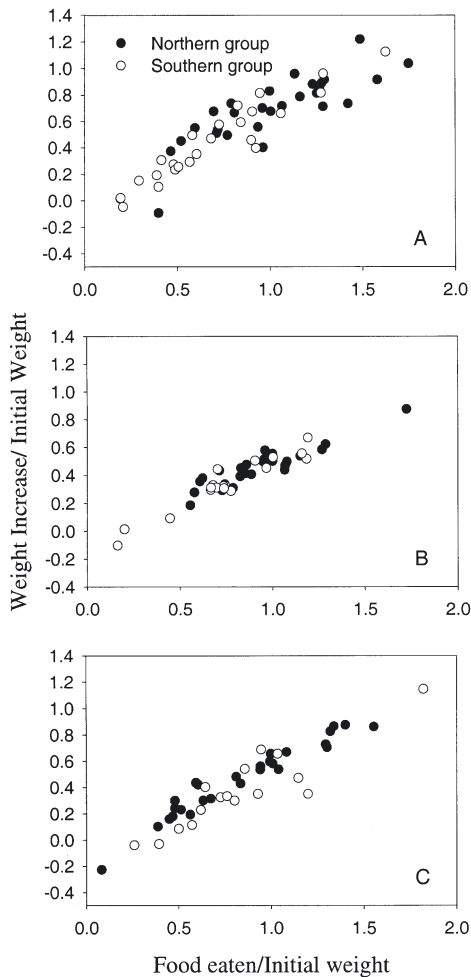|	Including last period					Last period removed				
	Value	SE	df	t	p	Value	SE	df	t	p
Total intake										
Intercept, μ_0	311.7	58.9	87	5.29	<0.001	254.2	49.1	44	5.18	<0.001
Aquaria, α_{02}	5.61	27.3	44	0.2	0.84	26.6	23.1	44	1.15	0.26
SN-diff, β_{02}	−81.2	27.7	87	−2.93	<0.01	−57.6	22.6	44	−2.55	<0.05
Time, β_1	110.8	12.8	87	8.63	<0.001	93.4	13.2	44	7.1	<0.001
Random effects	SE					SE				
Intercept, b_{0i}	59.1					63.0				
Residual, e_{ijkl}	118.9					61.6				
Normalised intake										
Intercept, μ_0	1.11	0.13	87	8.76	<0.001	1.11	0.15	44	7.65	<0.001
Aquaria, α_{02}	−0.013	0.06	44	−0.22	0.82	0.048	0.07	44	0.73	0.47
SN-diff, β_{02}	−0.124	0.06	87	−2.08	<0.05	−0.18	0.07	44	−2.60	<0.05
Time, β_1	110.8	12.8	87	8.63	<0.001	93.4	13.2	44	7.1	<0.001
Random effects	SE					SE				
Intercept, b_{0i}	59.1					63.0				
Residual, e_{ijkl}	118.9					61.6				

Fig. 2. *Gadus morhua.* Food conversion efficiency: relationship between food eaten/initial weight and growth/initial weight in northern and southern cod during Periods 1–3: (A) Period 1, (B) Period 2 and (C) Period 3

distance dispersal of early stages via coastal currents. This is based on the assumption that egg and larval stages are transported passively by advective forces that allow extensive mixing. How can genetic isolation be maintained between northern and southern cod? Selection of spawning grounds in relation to stratified water masses, the following distribution of early life stages and adult migration strategies may explain this.

Coastal cod select spawning sites commonly situated in fjord backwaters and areas with a water residence time higher than that on the shelf banks (Hutchings et al. 1993, Brander 1994a, S. Sundby pers. comm.). The dynamics of the stratified water masses in coastal and fjord areas (Asplin et al. 1999), and the evolved buoyancy of both eggs and larvae allowing early life stages to ascend at a vertical speed (1 mm s^{-1}) that much exceeds the typical speed of downwelling water (0.1 mm s^{-1}; Sundby 1983, 1991), may prevent egg stages from being transported away from the spawning site (Asplin et al. 1999). There is, however, a potential for downstream transport of early life stages to higher latitudes by the strong northward current, unless larvae counteract this through vertical migration (Asplin et al. 1999, Sponaugle et al. 2002). Switching between stratified water masses of inflowing and outflowing currents by active swimming is known for decapod crustaceans and fish larvae in coastal areas, and this strongly influences local retention and self-recruitment in sub-populations (Sponaugle et al. 2002).

In addition to local retention of eggs and larvae, homing to the same spawning ground augments differentiation into sub-populations (Cowen et al. 2000). Mature Northeast Arctic cod have returned to the same spawning area since the ninth century (Brander 1994a). This phenomenon has also been reported recently for cod in Canadian waters (Robichaud & Rose 2001). Genetically distinct sub-populations in bays, inlets and fjords have been identified in Canada (Ruzzante et al. 1996a, 1997, 2000) and Iceland (Jonsdottir et al. 2002), and among local spawning populations in the North Sea (Hutchinson et al. 2001). Tag–release–recapture experiments have shown that the juvenile and adult coastal cod in Norwegian waters tend to remain in their local areas (Salvanes & Ulltang 1992, Jakobsen 1987, Nordeide & Pettersen 1998, Svåsand et al. 2000). The different coastal and fjord sub-populations therefore have the potential to evolve life-history strategies adapted to local environmental conditions.

reared cod had wild-caught parents, while the southern fish were offspring of first-generation reared cod, which could be a potential source of bias if growth is under strong selection. However, it is not likely that selection for growth in the hatcheries could be strong enough to explain the results (see Law 2000). The observed differences are neither likely to be due to individual family effects, since a likely minimum of 7 to 8 and 12 to 13 females mothered the southern and northern offspring, respectively. Parental stocks adapted to different environments, and hence the existence of sub-populations is therefore likely to cause the results.

Local retention of early life stages

Marine species without parental care of offspring are generally thought to be well connected via long-

Countergradient variation and life-history strategies

Our study suggests that feeding strategies are likely to be associated with differences in growth potential between northern and southern coastal cod. No differ-

ence in growth was found during the pre-experimental period, when northern and southern cod were housed for 450 d in identical environments in separate aquaria and fed until satiation. Northern and southern cod were therefore of equal size at the start of the experiment. During the common-garden experimental period fish competed for limited amounts of food. Due to their higher feeding success, northern cod achieved higher growth rates than southern cod.

Size and time constraints may select for active feeding

Environmental stress differs between high and low latitudes. Rapid growth is selected for when there are time constraints on reaching a minimum size. An example is size-dependent winter mortality in juvenile fish. Due to a shorter growth season at high latitudes, selection for rapid growth is strong to counteract the negative effect of the environment (Conover & Present 1990, Conover 1992). Despite environmental stress at high latitudes, the potential growth rate evolves to a level beyond what local stress conditions dictate (Arendt 1997). This was found in the present study, in that reared northern cod (Fig. 1) had higher growth rate than southern cod when sharing aquaria under temperature conditions typical for the southern population.

A shorter growth season requires a more active strategy when prey is encountered, because it will be of great importance to catch every prey item, since the time frame for searching for and feeding on prey is limited. A more active feeding strategy is likely to explain the higher growth rate found in reared northern cod. Similarly, differences in food consumption between high- and low-latitude populations of Atlantic silverside (*Menida menida*) was explained by adaptation of high-latitude populations to a shorter growth season than southern populations (Present & Conover 1992). Another abiotic environmental factor that constraints growth is low ambient temperature (Jobling 2002) due to temperature influences on enzymatic processes such as digestion (Knutsen & Salvanes 1999), and thus assimilation and growth. Selection for individuals capable of fast growth under low temperature or other environmentally limiting circumstances might therefore also be favoured at high latitudes.

Density-dependent food competition may select for active feeding

An additional explanation for the development of higher intrinsic growth in northern cod is density-dependent food competition. Variation in prey type and density, as well as density of competitors and predators are all factors likely to influence feeding strategies in different environments (Reznick 1993). Northern fjords have a higher density of juvenile fish ($3.5 \; t \; km^{-2}$) than southern fjords ($0.8 \; t \; km^{-2}$), but there are fewer competing species in northern fjords and coastal areas (Svasånd et al. 2000). The lower CF in wild northern cod, which reflects an individual's recent feeding history and physiological allocation of resources (Jobling 2002), suggests food limitations in the north and indicates that the lower growth rate of northern cod is not solely due to delayed growth in response to the stress of low temperature. Food shortage caused by high intra-specific competition will result in lower net energy return per individual throughout the growth season and also a low CF in the wild. The higher intra-specific competition in the north thus selects for an active feeding strategy in juvenile cod to obtain prey whenever they are available.

Feeding from the pelagic food web select for active feeding

The diet in the different areas could also influence feeding behaviour. Cod in fjords of northern Norway feed mainly off the pelagic food web (shrimp, krill, herring, capelin) (Klemetsen 1982, dos Santos & Falk-Petersen 1989, Kanapathippilai et al. 1994). This implies that the nearly non-migrating northern coastal cod depend on high lipid prey migrating between fjords and the outer coast (Falk-Petersen 1981, Lawson et al. 1998) and on organisms drifting in advective water masses. In southern fjords cod rely more on prey associated with the bottom layers, the proportion of benthic prey consumed increasing with distance from the coast (Table 5 in Salvanes et al. 1995). Pelagic feeding implies high prey abundance at times, but also greater uncertainty regarding food availability (Salvanes et al. 1995, Marshall et al. 1999). In contrast, feeding on less-abundant local benthic prey allows for a lower but constant food supply for non-migratory southern coastal cod (Salvanes et al. 1995). To successfully catch prey from the pelagic food web, northern cod may therefore have evolved a more active feeding behaviour than southern cod.

Time constraints on feeding favours storage

Throughout the experiment, differences in the energy-allocation patterns of the 2 populations were observed (CF; Fig. 1, Tables 1 & 2). The northern group had higher growth in CF both in the wild and in the

'common-garden' experiment, implying a relatively larger allocation to storage tissues. As has been shown for salmon (Bull et al. 1996), this indicates that the prolonged period of food shortage in the north selects for higher and earlier energy allocation to storage. The lower absolute CF (Fig. 1, Table 1) among the northern cod is likely due to low individual energy intake caused by the environmental constraints, since the relative changes in CF was higher in the northern population. Thus, relatively more of the energy was allocated to storage tissues also in the wild, consistent with our hypothesis and with what Bull et al. (1996) found for salmon.

Gross food conversion efficiency

We did not find any differences in GFCE between northern and southern cod. Although the existence of differences in GFCE is somewhat debated, since it does not come with any apparent costs (e.g. Conover & Schultz 1995), it has been reported for several species including turbot (*Scophthalmus maximus*; Imsland et al. 2001) and cod from separate populations on the coast of Canada (Purchase & Brown 2000). In the study of Purchase & Brown (2000), strains were kept in separate tanks and fed to satiation, thus reducing the need for competition. In the present study the focus was on behavioural adaptations of the strains. Prey were therefore offered sequentially to target competition. Individuals of northern cod were rewarded by higher success in food consumption apparently caused by higher activity. Higher activity would, however, be linked with elevated energy expenditure that potentially could mask the effect of a higher GFCE. Further studies are therefore required to test for differences in GFCE among coastal cod sub-populations.

Costs of high growth rate

Energy and nutrients are budgeted among numerous of functions in an organism. Given a limited amount of resources, an increase in allocation for one function will decrease allocation for another. The functions may be categorized to growth including storage, development, maintenance, repair, defence, reproduction and movement (modified from Arendt 1997). Rapid growth in Atlantic salmon (*Salmo salar*) was correlated to a poor immune system (Saunders et al. 1992), and in Atlantic tomcod (*Microgadus tomcod*) increased liver damage was found after detoxification. Active feeding occurs at the expense of vigilance for predators (e.g. Lima 1998, Houston & McNamara 1999, Skalski & Gilliam 2002), since less time is spent to evaluate predation risk. Such costs could have counteracted the evolution of a higher intrinsic growth rate in the southern population.

Conclusions

Fisheries represent additional 'human predation', potentially influencing the selection of life-history traits (e.g. Law 2000, Conover & Munch 2002). Populations allowed to recover from over-fishing will therefore experience altered selection pressure. Sub-populations having different life histories may respond differently to both fisheries and altered selection pressures. Even though one cannot draw conclusions on how the observed behavioural differences found in this experiment will affect vulnerability to fishing, such behavioural traits could be important. This study has shown that there may be localised, behaviourally different populations of cod along the Norwegian coast. Frank & Brickman (2000) suggested that the slow recovery of exploited species such as the Atlantic cod could be because behavioural differences between sub-populations are associated with differences in vulnerability to fisheries, and that this is masked and not accounted for when data are aggregated for fisheries-management purposes. Future studies may therefore show that differences such as those found in this study also need to be considered for improving fisheries management.

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