Effects of anthropogenic feeding on the growth rate, nutritional status and migratory behaviour of free-ranging cod in an Icelandic fjord

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The growth rate of wild, free-ranging cod increased substantially in a 17-month feeding experiment in Stödvarfjördur, a small Icelandic fjord. The feed, mainly capelin and herring, was dispensed in the fjord from a boat three times a week, 2–10 tonnes per month. During feeding an audio signal was transmitted and the response of the fish observed with an underwater video camera. Within a few weeks thousands of cod had been conditioned to feed. To study the growth rate and migratory behaviour, 2539 cod were tagged and released in Stödvarfjördur and three control areas. All the recaptured fish tagged in the control areas had liver indices less than 10% (unconditioned fish), whereas nearly half of the recaptured fish tagged in Stödvarfjördur had liver indices greater than 10% (conditioned fish); 95% of the conditioned cod were recaptured within 5 nmi from the feeding areas. The growth rate and liver index of cod tagged in Stödvarfjördur were significantly correlated. The mean growth rate was 8.3 and 15.4 cm·yr⁻¹ and 725 and 2254 g·yr⁻¹ for the unconditioned and conditioned cod, respectively.

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Introduction

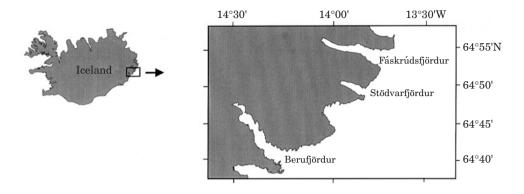
A 17-month fjord-ranching experiment was carried out in Stödvarfjördur, a small fjord in Iceland, to find out whether it might be technically possible and economically feasible to feed on a large scale wild, freeranging cod in an area closed to all commercial fishing (Björnsson, 1999a). The benefit of large-scale anthropogenic feeding of a predatory fish stock may be threefold. First, it may increase the growth rate and yield of a predatory fish stock. Second, it may reduce predation on valuable species. Third, it may lower the cost of fishing (Björnsson, 2001). The main purpose of the present paper is to estimate from tagging data the effects of feeding on the growth rate of cod in the Stödvarfjördur fjord-ranching experiment.

The growth rate of wild cod has been found to be food-limited in Icelandic waters (Björnsson, 1999b; Björnsson and Steinarsson, 2002). In a sea pen in Stödvarfjördur 40–50 cm captured cod (*Gadus morhua*

L.), receiving regular meals of pelagic fish, grew much faster (17 cm \cdot yr $^{-1}$) than wild cod in Icelandic waters (\sim 10 cm \cdot yr $^{-1}$) (Björnsson, 1999b). The liver index and the condition factor of the captive cod increased substantially.

There is an increasing interest in Norway, Iceland, Canada, and Scotland to grow cod commercially, either using captured wild cod or cod juveniles produced in hatcheries. However, feasibility studies have indicated that cod farming in sea pens using hatchery reared juveniles may not be profitable in Iceland (Björn Knútsson, University of Iceland, personal communication; Erlendur Steinar Fridriksson, University of Akureyri, personal communication).

In Japan, sound-conditioned hatchery reared red sea bream [Pagrus major (Temminck and Schlegel)] have been ranched on a commercial scale (Fujiya et al., 1980) and a three-month experiment in Norway showed that pond-reared juvenile cod could be conditioned by sound to return to the feeding site at specific times (Midling



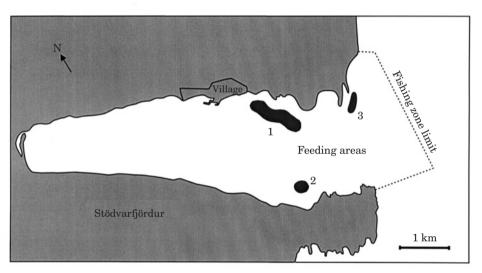


Figure 1. The experimental site, Stödvarfjördur, and the two control fjords. The three feeding areas (dark) and fishing zone limit are indicated.

et al., 1987). During the experiment some wild cod joined the school of conditioned cod.

In the Stödvarfjördur experiment it was found that free-ranging cod could be conditioned to feed on whole capelin [Mallotus villosus (Müller)] and chopped herring (Clupea harengus L.) which were provided regularly (Björnsson, 1999a). By comparing successive samples of untagged cod it was clear that about half of the cod in Stödvarfjördur developed large livers and increased their growth rates substantially compared to the unconditioned fish. A tagging study can give a more accurate estimate of the growth enhancement. The aim of the study is to compare the growth rates, nutritional status and behaviour of the unconditioned and conditioned cod which were tagged in Stödvarfjördur and three nearby areas.

Materials and methods

The 17-month feeding trial was initiated in July 1995 in Stödvarfjördur, a small fjord on the east coast of Iceland (Figure 1). Two nearby fjords were selected as control fjords, Berufjördur and Fáskrúdsfjördur. Initially, fishing was prohibited inside the fjord from a line drawn between the two outermost points of the fjord. From 1 May 1996 to 30 April 1997 the closed area was enlarged somewhat (Figure 1).

The feeding was carried out three times a week, 0.5–3.5 t of whole capelin, chopped herring or herring offal per week (a total of 99 t in the project). Most of the feed was distributed in three distinct feeding areas (Figure 1). The feed was shovelled into a barrel attached to a flexible hose towed behind the boat (Figure 2).

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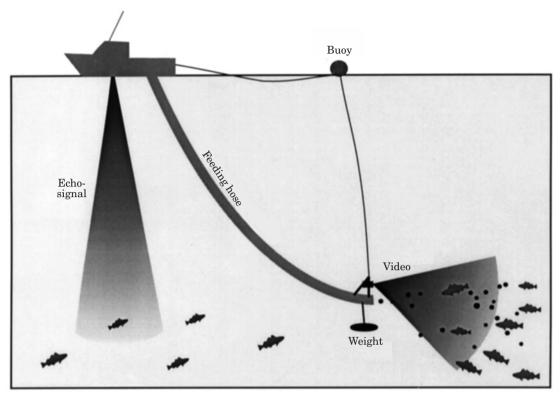


Figure 2. The feeding technique used. The feed was flushed down the feeding hose to a depth of 23 m. The fish were monitored with an underwater video camera and an echo-sounder on board the 5 t boat.

During feeding, an audio signal was emitted in short pulses with an underwater transmitter (Midling *et al.*, 1987). The feeding reaction of the fish was monitored by an underwater video camera (Figure 2). The amount of feed released was regulated in accordance with the number of fish seen on the screen and on the echosounder (Figure 2). It was estimated that within a few weeks thousands of cod had been conditioned to feed.

To study the growth rate and migratory behaviour, 2216 cod were tagged during the period 12 June to 13 July 1995. The fish were caught by handline with small hooks and tagged with T-bar anchor tags near the base of the anterior dorsal fin. The tagged fish, 96% of them 30-74 cm, were subsequently released at the site of capture, 522 in Berufjördur (mean length 52.7 cm), 550 in Fáskrúdsfjördur (mean length 50.5 cm), 651 in Stödvarfjördur (mean length 51.2 cm), and 493 off Stödvarfjördur in the area less than 3 nmi from the mouth of Stödvarfjördur (mean length 55.4 cm). Additionally, 323 cod were tagged and released in the feeding area in Stödvarfjördur on 12 July 1996 (mean length 56.2 cm). Local fishermen in the area from Berufjördur to Fáskrúdsfjördur were asked to freeze the tagged fish whole (ungutted) and were rewarded ~\$10 per tag + \sim \$2 per kg fish.

To study the condition and growth of the recaptured cod, each fish was measured as follows: total length, total (ungutted) weight, gutted weight, weight of liver, sex, sexual maturity (four stages), weight of gonads, and weight of the stomach contents. The following indices of nutritional status and growth rate were used: stomach fullness index [100 weight of stomach contents \cdot (gutted weight)⁻¹], liver index [100 \cdot weight of liver · (gutted weight) - 1], condition factor (100 · gutted weight · length - 3), and yearly growth rate in length $[(L_2 - L_1) \cdot t^{-1}]$ and weight $[(W_2 - W_1) \cdot t^{-1}]$, where L_1 and W₁ are the length and total weight at tagging and L₂ and W2 the length and total weight at recapture and t the length of the period from tagging until recapture in years. Fish recaptured less than 3 and more than 22 months from the time of tagging were omitted in the data analysis. In the fish samples from the feeding area, a clear distinction could be made between fed (conditioned) and unfed (unconditioned) cod, based on relative liver size. The applied definition of a conditioned cod was one with a liver index $\geq 10\%$.

To minimize the effects of short term compensatory growth response on the estimate of yearly growth rate, a regression was found between growth in length $(L_2 - L_1)$ and time from tagging to recapture (t) for wild and conditioned fish. The slope of the linear regression

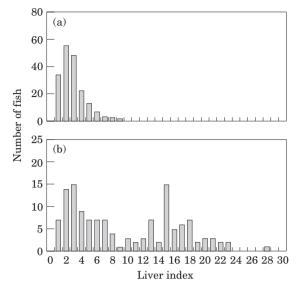


Figure 3. Liver index (% of gutted weight) of cod tagged (a) outside Stödvarfjördur (off Stödvarfjördur, Fáskrúdsfjördur and Berufjördur) and (b) in Stödvarfjördur.

through the origin, gave the best estimate of the mean yearly growth rate. The 95% confidence limits of the slope was calculated according to the method described by Rawlings (1988). A chi-square test was used to determine differences in recapture ratios. For further details of the methodology see Björnsson (1999a).

Results

All the recaptured fish tagged outside Stödvarfjördur had small livers (liver index <10% of gutted weight) (Figure 3a) whereas about half (63/134) of the recaptured fish tagged in Stödvarfjördur had large livers (liver index $\ge 10\%$ of gutted weight) (Figure 3b). The time of

tagging in Stödvarfjördur had a marked effect on the percentage of fish recaptured with large livers. It was 33% (27/82) for the cod tagged in July 1995, 6–12 days before the feeding started and 69% (36/52) for the cod tagged one year later in Stödvarfjördur (χ^2 =16.84, p<0.001).

For all the recaptured cod there was a positive correlation between growth rate (cm·yr⁻¹) vs. liver index, growth rate vs. condition factor and condition factor vs. liver index but no correlation between growth rate vs. stomach fullness index (Table 1). The best correlation was between growth rate vs. liver index, 47% of the variation being explained. Therefore this relationship was also considered for fish according to their tagging location. The correlation was positive and highly significant for the fish tagged in Stödvarfjördur 1995 and in Stödvarfjördur 1996, but not significant in the area off Stödvarfjördur and barely significant in the two control fjords, negatively correlated in Fáskrúdsfjördur and positively correlated in Berufjördur (Table 1).

There was a highly significant correlation (r^2 =0.48) between the growth rate and liver index of all the fish tagged in Stödvarfjördur but not significant for all the fish tagged outside Stödvarfjördur (Table 1, Figure 4). All the fish tagged outside Stödvarfjördur had growth rates $\leq 17 \text{ cm} \cdot \text{yr}^{-1}$ whereas in Stödvarfjördur almost one third of the fish (43/137) had growth rates $\geq 17 \text{ cm} \cdot \text{yr}^{-1}$ (Figure 4). The mean liver index $\pm 95\%$ confidence limits was 3.6 ± 0.2 and $16.6 \pm 0.9\%$, the mean condition factor 0.816 ± 0.007 and 0.918 ± 0.018 , and the mean growth rate $9.1 \pm 0.4 \text{ cm} \cdot \text{yr}^{-1}$ and $19.8 \pm 1.6 \text{ cm} \cdot \text{yr}^{-1}$ for all the unconditioned and conditioned fish, respectively (Table 2).

A regression between growth in length vs. time from tagging to recapture (Figure 5) indicated that the mean growth rate $\pm 95\%$ confidence interval was 8.3 ± 0.09 ($r^2=0.581$, n=256) and 15.4 ± 0.79 cm \cdot yr $^{-1}$ ($r^2=0.742$, n=63) for the unconditioned and conditioned fish,

Table 1. Regression analysis of tagged cod recaptured 3–22 months from the time of tagging. The fish were tagged in Stödvarfjördur 1995 (St.95), off Stödvarfjördur 1995 (Off.St.95), Fáskrúdsfjördur 1995 (Fá.95), Berufjördur 1996 (Be.95) and Stödvarfjördur 1996 (St.96). Cod tagged in Stödvarfjördur (St.95 and St.96) and outside Stödvarfjördur (Off.St.95, Fá.95 and Be.95).

Group	Regression	n	a	b	r^2	Sign.
All fish	Growth rate (cm · yr - 1) vs. liver index	319	6.75	0.721	0.471	***
All fish	Growth rate $(\text{cm} \cdot \text{yr}^{-1})$ vs. condition factor	335	-23.12	41.019	0.269	***
All fish	Growth rate $(cm \cdot yr^{-1})$ vs. stomach fullness	321	11.03	0.057	0.002	n.s.
All fish	Condition factor vs. liver index	319	0.79	0.0075	0.319	***
St.95	Growth rate (cm · yr - 1) vs. liver index	82	6.84	0.541	0.402	***
Off.St.95	Growth rate $(\text{cm} \cdot \text{yr}^{-1})$ vs. liver index	54	9.85	-0.390	0.037	n.s.
Fá.95	Growth rate $(cm \cdot vr^{-1})$ vs. liver index	84	9.44	-0.364	0.062	*
Be.95	Growth rate $(\text{cm} \cdot \text{yr}^{-1})$ vs. liver index	47	8.60	0.794	0.111	*
St.96	Growth rate $(cm \cdot vr^{-1})$ vs. liver index	52	7.24	0.893	0.474	***
In Stödvarfjördur	Growth rate $(\text{cm} \cdot \text{yr}^{-1})$ vs. liver index	134	6.48	0.765	0.477	***
Outside Stödvarfjördur	Growth rate (cm · yr - 1) vs. liver index	185	9.85	-0.250	0.017	n.s.

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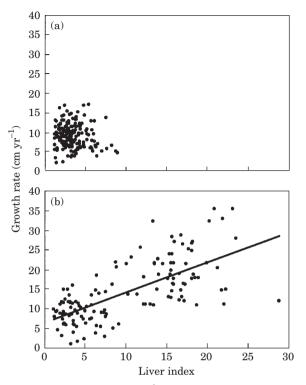


Figure 4. Growth rate (cm · yr ⁻¹) from tagging to recapture vs. liver index (% of gutted weight) for cod tagged (a) outside Stödvarfjördur (off Stödvarfjördur, Fáskrúdsfjördur and Berufjördur) and (b) in Stödvarfjördur.

respectively. A corresponding analysis for the weight gain, $W_2 - W_1$ (g), indicated that the mean growth rate was 725 ± 35 ($r^2 = 0.451$, n = 256) and 2254 ± 204 g·yr⁻¹ ($r^2 = 0.589$, n = 63) for the unconditioned and conditioned fish, respectively.

Of the 63 conditioned cod tagged in Stödvarfjördur, 46 (73%) were recaptured in Stödvarfjördur, 14 (22%) off Stödvarfjördur (≤ 5 nmi), 2 in Fáskrúdsfjördur (≤ 8 nmi) and 1 off Berufjördur (13 nmi from the feeding area). Of the 71 unconditioned cod tagged in Stödvarfjördur, 47 (66%) were recaptured in Stödvarfjördur, 21 (30%) off Stödvarfjördur (≤ 5 nmi), 1 cod in Fáskrúdsfjördur and 2 cod > 5 nmi off the coast. It is not possible to conclude that more unconditioned than conditioned cod left the feeding area, as similar proportions of unconditioned 34% (24/71) and conditioned cod 27% (17/63) were recaptured outside Stödvarfjördur (χ^2 =0.73, p=0.39).

Discussion

In the study area, cod with large livers were so uncommon in the wild population (Björnsson, 1999a; Björnsson, 1999b) that liver index could be used as a marker of fish conditioned to anthropogenic

Table 2. Cod recaptures. Comparison of unconditioned (liver index <10%, n=256) and conditioned (liver index $\ge10\%$, n=63) fish with respect to length at tagging, length at recapture, liver index, condition factor and growth rate (s.d. is standard deviation).

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Variable	Unconditioned fish	Conditioned fish				
Length at tagging (cm)						
Mean	51.0	52.7				
s.d.	9.7	8.7				
Min	30	36				
Max	78	75				
Length at recapture (cm)						
Mean	58.7	64.3				
s.d.	9.5	9.4				
Min	38	48				
Max	85	87				
Liver index (%)						
Mean	3.63	16.64				
s.d.	1.80	3.54				
Min	1.16	10.02				
Max	9.11	28.74				
Condition factor						
Mean	0.816	0.918				
s.d.	0.061	0.072				
Min	0.654	0.746				
Max	0.979	1.072				
Growth rate $(cm \cdot yr^{-1})$						
Mean	9.10	19.80				
s.d.	3.32	6.50				
Min	1.12	10.80				
Max	21.84	35.44				
Growth rate $(g \cdot yr^{-1})$						
Mean	752.9	2691.6				
s.d.	451.0	1569.8				
Min	-1214.7	-682.2				
Max	2600.1	8327.7				

feeding. Nearly half of the recaptured fish tagged in Stödvarfjördur had liver indices $\geq 10\%$ whereas all the fish tagged outside Stödvarfjördur had liver indices <10%. The conditioned fish had a much higher condition factor and growth rate than the wild (unconditioned) fish.

Why were half of the recaptured cod tagged in Stödvarfjördur not affected by feeding? It is possible that some of the fish tagged in July 1995 may have left the fjord before a feeding routine with a large number of fish had been established. The results show that relatively fewer fish tagged in Stödvarfjördur in July 1995 were conditioned to anthropogenic feeding than the fish tagged in Stödvarfjördur in July 1996 when feeding had been carried out for almost 12 months. Furthermore, the limited amount of feed released in the experiment may not have been sufficient for all the cod in Stödvarfjördur, the most dominant individuals in the feeding areas may have taken it all. Therefore, it is likely that many of

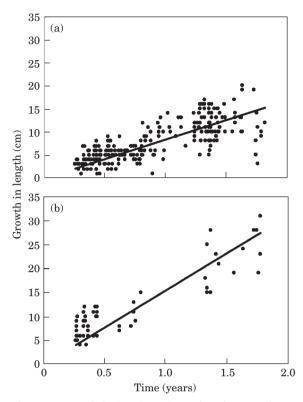


Figure 5. Growth in length (cm) vs. time from tagging to recapture for (a) unconditioned cod (liver index <10% of gutted weight) and (b) conditioned cod (liver index $\ge 10\%$ of gutted weight).

the subordinate fish had to make do with the less energy rich invertebrate prey available in Stödvarfjördur (Björnsson, 1999b).

The results indicate a compensatory growth (Pedersen and Jobling, 1989) of the conditioned cod as a response to sudden improvements in the availability of energy rich diet. The mean growth rate was 9 and 20 cm · yr ⁻¹ for the wild and conditioned fish, respectively, calculated without considering the length of time from tagging to recapture. This may overestimate the yearly growth rate since many of the fish were recaptured between three and four months from tagging and these fast initial compensatory growth rates can not be maintained for the whole year (Björnsson, 1999b; Björnsson and Steinarsson, 2002). Therefore, it was found more appropriate to estimate the mean yearly growth rate as a regression of growth in length vs. time from tagging to recapture.

The results show clearly that there was a large improvement in the nutritional condition and growth rate of approximately half of the cod tagged in the feeding area but no change in the three control areas. The average yearly growth rate of the unconditioned cod was only $8.3 \, \mathrm{cm} \cdot \mathrm{yr}^{-1}$ and $725 \, \mathrm{g} \cdot \mathrm{yr}^{-1}$ compared to

 $15.4 \,\mathrm{cm} \cdot \mathrm{yr}^{-1}$ and $2254 \,\mathrm{g} \cdot \mathrm{yr}^{-1}$ for the conditioned cod. In the Icelandic groundfish surveys 1989–97 the mean yearly growth rate from age 3 to 5 was $10.2 \,\mathrm{cm} \cdot \mathrm{yr}^{-1}$ north of Iceland and $10.4 \,\mathrm{cm} \cdot \mathrm{yr}^{-1}$ south of Iceland (Björnsson, 1999b).

The growth rate estimate for the conditioned cod is similar to an earlier estimate of 15.8 cm \cdot yr $^{-1}$, based on periodic sampling of untagged cod in the feeding area (Biörnsson, 1999a). The growth rate estimate of wild tagged cod reared in a sea pen in Stödvarfjördur was slightly higher, 17.1 cm · yr⁻¹ (Björnsson, 1999b). In the sea pen all the fish received regular meals of herring and capelin all year round. In the fjord-ranching experiment there was no way of knowing how many months the recaptured cod had made use of the anthropogenic feeding. Some of the fish tagged in July 1995 may not have discovered or learned to accept the additional food resource until in the summer of 1996. A few months feeding on capelin is sufficient to enlarge the liver and qualify the cod as conditioned fish but not sufficient to maximize the mean yearly growth rate.

There was no apparent difference in the environmental conditions between Stödvarfjördur and the two control fjords. Continuous temperature records were almost identical in the three fjords with a mean yearly temperature of 3.7°C at a depth of 5 and 30 m (Björnsson, 1999b). Prior to the feeding study indicators of nutritional status of cod were similar in all three fjords (Björnsson, 1999a). A stomach content analysis of cod in five fjords, including Stödvarfjördur, Fáskrúdsfjördur and Berufjördur, two years prior to the feeding experiment, showed that the diet of cod in all five fjords consisted almost entirely of invertebrates (82–93%), mostly euphausids, crabs, bivalves and polychaetes (Björnsson, 1999b), with much lower caloric content than the feed used in the feeding experiment (Brawn et al., 1968). The release of energy rich feed in Stödvarfjördur seems to be the only plausible explanation for the growth enhancement of the cod. In fact, almost all the conditioned cod sampled had nothing in their stomachs but the feed given (Björnsson, 1999a).

The strong response to anthropogenic feeding indicates that the growth rate of wild cod may generally be food-limited as suggested earlier (Braaten, 1984; Björnsson, 1999b). In nature there is usually not a surplus supply of easily available and nutritious prey for wild cod to attain their full growth potential as found in laboratory experiments where sumptuous meals are provided all year round (Björnsson *et al.*, 2001; Björnsson and Steinarsson, 2002). The most important nursery areas for juvenile cod in Iceland are thought to be in the fjords and shallow waters north and east of Iceland (Pálsson, 1980) where cod is the dominant demersal fish species. Thus, there may be a strong intraspecific competition for the available food. In nature cod may have to use much energy to search for, pursue and catch wild

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prey, especially when preying on fish (Björnsson, 1993). Even unlimited consumption of some invertebrate prey species of poor nutritional quality may not result in maximum growth rate.

The tag returns do not indicate significant migration of cod from the control fjords to the feeding area. Not a single recaptured cod of the 185 tagged outside Stödvarfjördur showed evidence of enriched feeding. The minimum distances from the tagging areas in Berufjördur, Fáskrúdsfjördur and off Stödvarfjördur to the feeding areas were 16, 6 and 3 nmi, respectively. Assuming that the mean swimming speed was 0.5 body lengths \cdot s⁻¹ (Björnsson, 1993) and the mean length of the tagged cod was 56 cm it would have taken the cod only 29.4, 11.0 and 5.5 h, respectively, to swim the required distances. In an enhancement study in western Norway more than 96% of the cod were recaptured in shallow nearshore waters less than 10 km from the release site (Svåsand and Kristiansen, 1990). The daily home ranges measured with ultrasonic tracking near the Scottish coast were less than 200 m for immature cod (Hawkins et al., 1980). Limited home ranges of immature cod may explain why none of the 54 cod tagged off Stödvarfjördur did locate and make use of the feed released only 3 nmi away.

In the development of large-scale feeding of cod (Björnsson, 2001) the non-migratory behaviour of inshore cod must be taken into account. The present results indicate that it may be necessary to distribute the feed rather precisely according to the distribution of inshore cod. If the amount of feed is adjusted carefully to the amount of fish, the feed will be taken and the nutritional status and the growth rate of the fish will increase. However, the migratory activity of cod increases with age and size (Svåsand and Kristiansen, 1990; Jónsson, 1996) and can vary between stocks, the Arcto-Norwegian cod for example is more migratory than the Norwegian coastal cod (Godø, 1984, 1995).

Some of the cod tagged in Stödvarfjördur migrated out of the fjord in autumn. There was not a significantly higher percentage of the unconditioned than conditioned cod emigrating out of Stödvarfjördur. Thus, it is clear that regular feeding does not prevent the conditioned cod from leaving the feeding area. No conditioned cod was captured outside Stödvarfjördur from May to September whereas 17% of the unconditioned cod were recaptured outside Stödvarfjördur in the same period. This indicates that the conditioned cod do not leave the feeding areas during the main feeding season which is in agreement with the observations by Björnsson (1999a) who found that after the spawning season, in spring, the cod in Stödvarfjördur were hungry and easy to condition. Cod fed on maximum rations at constant temperatures in laboratory experiments (Björnsson and Steinarsson, 2002) showed reduced appetite in autumn. Apparently, the motivation of the conditioned cod to feed decreased in autumn when they had built up their energy reserves for the next spawning season.

The emigration of conditioned cod from the feeding areas in autumn may pose a problem to a party licensed to ranch and harvest cod. Therefore the area of exclusive fishing rights must be large enough to contain most of the conditioned fish throughout the entire feeding period. In the Stödvarfjördur experiment 95% of the conditioned cod were recaptured within 5 nmi from the feeding areas. Also it may be advisable to start harvesting the largest fish with size-selective gear, such as gillnets, before the fish leave the feeding areas in autumn, without harming the smaller fish. It is likely that a high percentage of the preconditioned fish will return to their previous feeding areas in spring.

The experimental feeding in Stödvarfjördur shows that it is possible to condition wild cod to feed on regular meals and it may have large effects on their yearly growth rates. Although, the results show that it is technically possible to condition wild cod to feed on capelin and chopped herring, it is clear that feeding of wild cod must be carried out on a much larger scale than was done in the Stödvarfjördur experiment to make it economically feasible (Björn Knútsson, University of Iceland, personal communication). Whether anthropogenic feeding of the Icelandic cod stock can be implemented on a large enough scale to increase the economic yield from the fishery substantially remains yet to be seen (Björnsson, 2001). It is hoped that this study may be of some help in the search for ways to enhance the sustainable yield from the ocean.

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