A snapshot of cannibalism in 0-group Atlantic cod (Gadus morhua) in a marine pond

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Summary
Cannibalism in 0-group Atlantic cod (Gadus morhua) was investigated in a semi-natural marine pond using stomach content analysis. About 6000 individuals were eradicated by rotenone treatment of the pond in November 1991. Total lengths of cod ranged from 7.4-28.8 cm with a median of 14.4 cm. The proportion of cannibalistic cod in the population was estimated at 1.3%. Cannibalism accounted for a daily loss of 1.1% of the population. The frequency of cod with > 2 cod prey per stomach was higher in the population compared with a Poisson model. Predator-prey length ratios ranged between 1.6 and 3.2 when estimated from otolith-length relationships. Chesson's 1983 x-index indicated that cannibalistic cod had a positive selectivity for conspecifics < 9.0 cm in total length.

Introduction
Cannibalism may be an essential feature among teleosts as a regulating mechanism of population abundance, especially when food abundance is low (Polis 1981; Smith and Reay 1991). Also, the population size structure may be severely affected by cannibalism as it acts as a strongly size-selective mechanism (Patriquin 1967; Polis 1981; Folkvord and Otterå 1993). Cannibalism in Atlantic cod (Gadus morhua) has been reported to occur in most of the stocks in their natural habitats (Bogstad et al. 1994), acting mainly as intercohort cannibalism (i.e. between age groups) (Smith and Reay 1991). Intracohort cannibalism (i.e. within age groups) has also been documented for 0-group cod in Icelandic waters (Bogstad et al. 1994), but no quantitative studies have been performed. However, cannibalism has been a major obstacle in rearing of 0-group cod (Folkvord and Otterå 1993; Blom et al. 1994), and may occur from a size of 1.2 cm. Hecht and Pienaar (1993) regarded cannibalism as an alternative feeding strategy, most likely adopted by larvae and early juveniles which turn piscivorous when food resources become limiting.

In the field, the calculations of the magnitude of cannibalism are sensitive to biased estimates of stock biomass, stomach content data, and parameters in gastric evacuation models (Dwyer et al. 1987; Mehl 1989), or if sampling is not carried out at appropriate temporal and spatial scales (Bailey 1989; Bogstad et al. 1994). Reliable quantification of cannibalism in early life stages, in particular, is difficult due to the rapid digestion time of the small prey (Folkvord 1993). With rotenone sampling, reliable characterisations of prey availability and predator relationships can be derived, and, in addition, data on size and age structure of fish populations are effectively collected (Davies and Shelton 1983). Several marine ponds used for rearing of juvenile cod are treated with rotenone at the end of each production season, usually in October-November, to eradicate remaining fish (Blom et al. 1994). By rotenone treatment of a marine pond, the remaining cod population can be sampled almost simultaneously which should make an ideal basis for studying cannibalism among 0-group cod under semi-natural conditions. Marine ponds are considered as semi-natural systems since 0-group cod inhabiting the pools are offered an environment with naturally occurring prey species, natural hydrographic and light conditions and marine vegetation, but larger piscine predators are absent and migration out of the ponds by 0-group cod is prevented due to screens installed at the outlet of the ponds (Blom et al. 1991).

This investigation considers intracohort cannibalism in 0-group Atlantic cod under semi-natural conditions. Specifically, we examined (1) the prey size selectivity by cannibalistic individuals, and (2) cannibalism rate in connection with rotenone treatment of a marine pond in western Norway.

Materials and methods
Study area and collection of material
The investigation was conducted in 1991 in Parisvatnet, a marine pond in western Norway used for production of juvenile cod (Blom et al. 1991; Blom et al. 1994). The pond is situated 60 km northwest of Bergen, Norway, and has a maximum depth of 9 m, a surface area of 50 000 m², and a volume of 270 000 m³. A total of 7.1 × 10⁶ cod eggs and larvae were released in the pond from 23 to 25 March (Blom et al. 1994), and the pond was kept enclosed until 13 May. From 13 May, 2 mm metal screens were installed in the dam of the pond to allow entry of zooplankton to the pond via the tidal water. Full tidal cycle was allowed from early June, and metal screens with 4 mm × 20 mm mesh size were installed in the dam from late June. A total of 317000 juvenile cod were harvested from the pond between 4 June and 28 October. The cod population in the pond had been offered formulated feed daily from 10 May to 28 October. After that period supply of formulated feed was stopped and feeding of the remaining population was dependent on natural food organisms either occurring in the pond or advected into the pond via the tidal water.

On 19 November, the pond was treated with 200 L (concentration: 0.74 ppm) of rotenone mixture (Gullvilt®), to eradicate the remaining cod and other small fish which had entered the pond through the metal screens during the production season. The rotenone treatment started at 0845 h and ended at 1215 h. About 4500 dead or dying cod were collected with landing nets in the surface layer from 0915 h to 1315 h. The collected fish were stored in a freezer at -21°C for further analyses. In addition, an estimated 1250 cod remnants were located at the bottom of the pond according to a diving inspection after the rotenone treatment, and subjectively about 250 cod were eaten by gulls during the rotenone treatment.

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Examination procedures

First, 520 individuals (hereafter called Group R) were first randomly chosen from a subsample of 3066 individuals. Second, 127 potential cannibals (hereafter called Group S) were selectively chosen from the remaining 2546 cod. The 647 individuals were measured for total length (TL) and wet weight (WW). Two weight measurements were excluded due to tissue loss of the fish. Measurements of one or both otolith (lagitta) lengths (OL) were done from 403 individuals (Group S + 276 smaller-than-average cod from Group R), and in 272 of these cod both left and right sagittae were identified and measured. Stomach contents of 257 individuals (Group S + 130 larger-than-average cod from Group R) were excised under a stereomicroscope at 6–25 × magnification, and fish prey were identified to species if possible and other prey were identified to higher taxonomic categories. Whole cod prey found in the stomach contents were measured for total length (TL) and wet weight (WW). Three weight measurements were excluded due to tissue loss of the fish. Measurements of one or both otolith (lagitta) lengths (OL) were done from 403 individuals (Group S + 276 smaller-than-average cod from Group R), and in 272 of these cod both left and right sagittae were identified and measured. Stomach contents of 257 individuals (Group S + 130 larger-than-average cod from Group R) were excised under a stereomicroscope at 6–25 × magnification, and fish prey were identified to species if possible and other prey were identified to higher taxonomic categories. Whole cod prey found in the stomach contents were measured for total length (TL) and wet weight (WW), and sagittae were dissected out from each individual. Fish remains which could not be identified to species by exterior characters, were, as far as possible, examined for sagittae. The appearance and shape of these otoliths in addition to loose otoliths found in the stomach contents, were used for positive recognition of engulfed cod (Härkönen 1986). Sagittae from 2 cod prey were broken, and thus were not length measured. TL and WW of juvenile cod were measured to the nearest 0.1 cm and 0.1 g, respectively. Sagittae were rinsed in 96% ethanol and measured for length to the nearest 0.1 mm.

Calculations and statistical analyses

Left and right sagitta of individuals in groups did not differ in length (Wilcoxon's signed-ranks test, P > 0.45, n = 272), and thus otolith lengths from each individual were averaged in further analyses when data on both otoliths were available. We examined the relationships between TL and WW of cod and matching otolith length from examined individuals by regression analyses. The regressions were used for estimating original TL and WW of engulfed cod based on their otolith lengths.

The proportion of provable cannibals (cod with whole conspecifics, remains or otoliths from conspecifics found in their stomach) as a function of predator size, was estimated by logistic regression using GLIM 3.77 (Dobson 1983). The occurrence of cod prey in the stomach was used as a binary response variable and the predator length as the explanatory variable. The extent of size-selective cannibalism was estimated in 1 cm size intervals by Chesson a-index given as:

$$x = \frac{(r_j/n_j)(\Sigma r_j/n_j)}{m} = \frac{(r_j/n_j)(\Sigma r_j/n_j)}{m}$$

(1)

where r, and n, are numbers of cod of size category i in the stomachs and in the population, respectively, and m is the number of size categories found in the stomachs. Total digestion time (DT, h) for each cod prey cod engulfed by cannibalistic cod was estimated according to Jones (1974) as:

$$DT = W_p^{0.54}(40 TL^{-1})^{1.4}/R$$

(2)

where Wp is the weight (g) of cod prey (40 TL−1)1.4 is a correction factor to allow for the length of the cannibalistic cod where TL is the total length (cm), and R is equivalent to the rate of elimination of 1 g food from the stomach of a fish with a TL of 40 cm. Jones (1978) used an R = 0.16 at 8°C for cod fed a combination of single meals and continuous feeding with saithe (Pollachius virens). We used this R-value but corrected it for temperature by using a Q10-value of 2.2 (Jones 1974). The average temperature in the pond was 6.2°C on 18 November.

To estimate the mortality rate due to cannibalism, the calculated DT was applied to indicate the probable ingestion time of individual cod prey. We assumed that the feeding period of cod lasted from 30 min before sunrise to 30 min after sunset, e.g. on 18 November from 0821 h to 1632 h. The daily mortality rate M(%) due to cannibalism on 18 November was calculated as:

$$M(\%) = 100\times N_p/(N_p + N_r)$$

(3)

where Np is the number of cod prey assumed to have been engulfed on 18 November, and Nr is the subsample of 3066 cod from 19 November.

Results

TL of Group R ranged from 7.4 to 28.8 cm with a median TL of 10.4 cm, and WW ranged from 2 to 295 g with a median WW of 8.7 g. TL and WW of Group S ranged from 11.2 to 28.3 cm and 12 to 289 g, respectively, and the fish were among the 35% largest in the population. Juveniles had allometric growth as shown by the exponent of 3.42 (statistically different from 3, t-test, P < 0.001) in the length-weight relationship (Table 1). Body sizes of individuals used for stomach content analyses ranged from 11.0 to 28.8 cm and 10.3 to 295.4 g, all larger than the median size in the population. We found log-linear relationships between TL, WW and mean OL, and >96% of the total variation was explained by the regressions (Table 1). We found a total of 40 provable cannibals (individuals with whole or parts of conspecifics in their stomachs) among 3066 cod. This figure corresponds to a binomial proportion (+95% C.I.) of cannibals in the population of 1.3 ± 0.4%.

Crustacea was the most frequent taxon (44%) in the stomach contents of juvenile cod (Table 2), and Mysidae, Gammaridea, Craugus sp.

Table 1

<table>
<thead>
<tr>
<th>Linear regressions</th>
<th>R²</th>
<th>P</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length-weight relationship</td>
<td>0.991</td>
<td>&lt;0.0001</td>
<td>645</td>
</tr>
<tr>
<td>Otolith-size relationships</td>
<td>0.966</td>
<td>&lt;0.0001</td>
<td>403</td>
</tr>
</tbody>
</table>
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Table 2

<table>
<thead>
<tr>
<th>Prey taxa</th>
<th>Frequency of occurrence (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Empty</td>
<td>12.8</td>
</tr>
<tr>
<td>Undetermined</td>
<td>17.9</td>
</tr>
<tr>
<td>Algae</td>
<td>20.6</td>
</tr>
<tr>
<td>Mytilus edulis</td>
<td>1.9</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>1.2</td>
</tr>
<tr>
<td>Polychaeta</td>
<td>6.6</td>
</tr>
<tr>
<td>Crustacea</td>
<td>44.0</td>
</tr>
<tr>
<td>Insecta</td>
<td>0.4</td>
</tr>
<tr>
<td>Undetermined Pisces</td>
<td>6.2</td>
</tr>
<tr>
<td>Sprattus sprattus</td>
<td>1.2</td>
</tr>
<tr>
<td>Gadus morhua</td>
<td>15.6</td>
</tr>
<tr>
<td>Gobidae</td>
<td>4.3</td>
</tr>
</tbody>
</table>
and *Carcinus maenas* dominated among crustaceans. Atypical prey including macroalgae, blue mussels and insects were also found. The stomach contents of cannibalistic cod contained a total of 60 cod prey of which 9 were newly ingested, 35 were partly digested, and 16 were identified from finds of loose otoliths. The occurrence of cod with 2 cod prey per stomach was overrepresented in the population relatively to a Poisson model ($\chi^2 = 6.46$, d.f. = 1, $P = 0.011$; Fig. 1).

Cannibalistic cod ranged from 16.7 to 28.3 cm and 49 to 289 g in TL and WW (Table 3), respectively, and they were among the 10% largest fish in the population. The proportion of provable cannibals exceeded 50% for individuals >24 cm (Fig. 2), and decreased to 0 for individuals <16 cm. The mean size of cod prey estimated from findings of loose otoliths was significantly lower than that of cod prey estimated from otoliths in remnants, possibly due to partial digestion of the loose otoliths, and thus we decided to exclude estimated sizes from the former prey group in subsequent analyses. Lengths and weights of directly measured cod prey were slightly lower than that of corresponding estimated ones from otolith-size regressions (Wilcoxon's signed-ranks tests, $P < 0.026$, n = 8). Predator-prey length ratios estimated from otoliths and from whole prey ranged from 1.6 to 3.2 and 2.1 to 3.3 (Fig. 3), respectively. Estimated and observed predator-prey length ratios did not differ statistically (Mann-Whitney U-test, $P > 0.16$). We found no apparent relationship between TL of cod prey and cannibals (Table 1).

Chesson's (1983) $\alpha$-index indicated that cannibalistic cod had

### Table 3

Total lengths and wet weights of cannibalistic 0-group Atlantic cod and cod prey estimated from lengths of sagittal otoliths. Mean lengths and weights of cod prey groups having different letters (Mann-Whitney U-tests) are significantly different at $P < 0.05$.

<table>
<thead>
<tr>
<th>Total length (cm)</th>
<th>Wet weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
</tr>
<tr>
<td>Cannibals</td>
<td>40</td>
</tr>
<tr>
<td>Cod prey</td>
<td></td>
</tr>
<tr>
<td>Estimated from loose otoliths</td>
<td>15*</td>
</tr>
<tr>
<td>Estimated from otoliths in remnants</td>
<td>45*</td>
</tr>
</tbody>
</table>

* one fish omitted due to loss of otoliths
a relatively high selectivity for conspecifics <9.0 cm in TL (Fig. 4), and juveniles ranging from 7.7 to 10.0 cm accounted for 76.7% of the cannibalised cod. Juveniles > 14 cm did not appear to be cannibalised.

We estimated an average digestion time of cod prey of 45.7 h (SD = 13.2). Three marked digestion stages of cod prey were registered in this study; newly eaten, partly digested, or completely digested (except for loose otoliths). Hence, the different digestion stages should correspond to cod ingested on the day of rotenone treatment, the day before, and 2 days before the treatment. The difference in digestion stage between cod prey is the basis to assume the number of cod prey (Np) equal to 35 on 18 November. By using this figure, we estimated a daily mortality rate M(%) due to cannibalism of 1.1% on 18 November applying eqn 3.

Discussion

Our work is the first quantitative study of cannibalism among 0-group cod in a semi-natural or natural environment. In rearing experiments, cannibalism has been suggested to be the main mortality factor in cod after metamorphosis (i.e., lengths > 1.2 cm) (Folkvord and Otterå 1993; Blom et al. 1994). Specifically, Folkvord (1991) reported higher cannibalism rates among 0.2 g cod juveniles than among 8 g juveniles, and he suggested that the higher growth rates of the former group could partly explain the differences in cannibalism rates. In this study, the proportion of cannibalistic individuals in the population was estimated at 1.3%, and we estimated a daily mortality rate due to cannibalism of 1.1%. Applying this mortality rate and given a remaining population of 6000 0-group cod on 19 November, around 1700 individuals or 22% of the population were cannibalised in the pond between 28 October and 19 November.

The extent of intracohort cannibalism tends to be density-dependent among fishes under semi-natural and natural conditions (DeAngelis et al. 1979; Densen 1985; Bry et al. 1992). The mean density of 0-group cod in the pond was estimated at 0.12 cod m⁻², and this density is not unnaturally high compared to those reported from some field studies. A stock found in the field cod stock of the landlocked Ogac Lake in Baffin Island, lack of alternate prey of suitable size made cannibalism a vital source of energy. Thus, in the field cod seem to be opportunistic cannibalistic. With respect to 0-group cod, we have demonstrated in this study that intracohort cannibalism is a mortality agent among 0-group cod under semi-natural conditions.

We observed a higher number of 0-group cod with two or more cod prey per stomach than expected from a Poisson model, indicating that some individuals had a predilection for cannibalism. Amundsen et al. (1995) reported that cannibalism in Arctic char (Salvelinus alpinus) appeared to involve a strong individual food specialisation. When groups of large char were given the opportunity to feed on juveniles 1 day every 2 weeks, the same individuals were cannibalistic throughout the sampling period. In this study, cannibalistic 0-group cod had a positive selectivity for the smallest conspecifics in the population; similar results were reported by Folkvord and Otterå (1993) in 0-group cod under intensive culture conditions. Amundsen et al. (1995) found that cannibalistic Arctic char selected the small conspecifics in laboratory experiments, and suggested that the exclusion of the largest prey from the diet was not due to a physical gape limitation but rather related to a steep increase in pursuit or handling time with increasing prey size. Cannibalistic juvenile sea bass (Lateolabrax calcarifer) exhibited prey preference, and the largest prey were maximally 61–67% of their total lengths (Parazo et al. 1991). In our study, the average size of cod prey was estimated at 42.1% (range: 30.5–61.3%) of the cannibal's length.

Cannibalism is well known as a generalist and an opportunistic carnivore, feeding on several types of prey when these are available (Mehl 1989). Predation on conspecifics is generally a minor source of food for cod, except for the largest individuals (Bogstad et al. 1994). Patriziin (1976), however, reported that the cod stock of the landlocked Ogac Lake in Baffin Island, lack of alternate prey of suitable size made cannibalism a vital source of energy. Thus, in the field cod seem to be opportunistic cannibalistic. With respect to 0-group cod, we have demonstrated in this study that intracohort cannibalism is a mortality agent among 0-group cod under semi-natural conditions.

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References


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