



Cannibalism of Atlantic cod *Gadus morhua* larvae and juveniles on first-week larvae

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ABSTRACT: Cannibalism in Atlantic cod *Gadus morhua* is widespread under both field and culture conditions, but no studies have been conducted on the behavioural ontogeny of cannibalism in this species. We carried out an experiment to investigate the onset and ontogenetic changes in cannibalistic behaviour of Atlantic cod during early developmental stages. Cod larvae were separated into 4 size classes (6, 9, 12 and 15 mm) to monitor cannibalistic activity on first-week (~4 mm) conspecific larvae. Five cannibalistic behaviours (fixation, aggression, fin nipping, attacking and engulfing) were monitored when the predator was introduced to the observation chamber. Cannibalistic attacks initially appeared in 9 mm predators, although 6 mm larvae showed prey interest and engaged in fin nipping behaviour. The 9 and 12 mm larvae engaged in similar rates of cannibalistic activity, while 15 mm fish demonstrated a significant increase. These behavioural changes appear to coincide with the morphological and physiological changes associated with juvenile metamorphosis, namely fin ray, vertebrae and stomach development. More importantly, our observations indicate that cannibalism reduces survival of conspecifics at earlier developmental stages than indicated by diet analyses alone.

KEY WORDS: Conspecifics · Cannibalistic behaviour · Atlantic cod · Intra-cohort

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INTRODUCTION

Cannibalism is prevalent in most animal groups, including fishes, and is regarded as one of the most important events regulating population dynamics (Fox 1975). Cannibalism is a size-selective form of predation, and therefore has consequences on both the abundance and size structure of the entire population. Both inter-cohort (reported as a common occurrence) and intra-cohort cannibalism (less commonly reported) affect year class strength in various fish species (Smith & Reay 1991). While the predator to prey size ratio is likely the most important factor governing rates of cannibalism, other additional factors may also be important, such as food availability, fish density,

size variation, kinship and/or genetics (Smith & Reay 1991).

Atlantic cod *Gadus morhua* has been a commercially important fish species in the North Atlantic for centuries, in capture fisheries and more recently as an aquaculture species. Although most of the basic culture conditions are established, problems in certain areas still exist, including larval and juvenile mortalities due to cannibalism (Brown et al. 2003, Rosenlund & Halldórsson 2007). Cannibalism in Atlantic cod is a common occurrence in both wild fish stocks and in aquaculture, and the losses can be devastating under culture conditions if it is not managed properly (Folkvord 1991, Bogstad et al. 1994). Batch spawning over the course of 2 to 3 mo can lead to high within-year size

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variation, with first feeding larvae and early juveniles often co-occurring both spatially and temporally (Folkvord 1997). Due to this, cannibalism in Atlantic cod has received considerable attention in field and aquaculture studies and is assumed to significantly affect recruitment to the cod fishery as well as contribute to high economic losses in the cod aquaculture industry (Bogstad et al. 1994, Blom & Folkvord 1997). Surprisingly, no incidences of cannibalism have been reported in larval stages (Ellertsen et al. 1984, Perry & Neilson 1988). This may be because most cannibalism studies on cod have concentrated on the morphological constraints and causes of cannibalism (Folkvord 1991, Bogstad et al. 1994) and are largely based on stomach content analysis and mortality rates (Folkvord & Otterå 1993, Blom & Folkvord 1997). Furthermore, smaller conspecific prey tend to be digested faster and may not have been identified in stomach content analyses (Folkvord 1993).

To date, no studies have undertaken a behavioural approach to the phenomenon, thus leaving many of the underlying dynamics associated with cannibalistic activity in cod unknown. A better understanding of the underlying behavioural mechanism of cannibalism, along with existing information on morphological constraints, would be helpful in managing Atlantic cod both under field and culture conditions. The purpose of the present study was to directly observe cannibalistic behaviour of cod to: (1) determine the onset of predation on first-week cod larvae from conspecific fish and (2) understand how cannibalism and associated behaviours may change throughout development.

MATERIALS AND METHODS

Eggs of *Gadus morhua* were collected from a spontaneously spawning group of captive broodstock kept at the Ocean Sciences Center, Memorial University of Newfoundland, Canada. Larval cod acting as predators were reared from 2 egg batches separated by 14 d to ensure availability of 4 separate predator size classes; 6, 9, 12, and 15 mm. For the first-week post-hatch larvae, eggs were collected from the same group of broodstock when the older larvae were 5 wk post-hatch. Eggs were incubated in a flow through system using 250 l conical silos, with a water exchange rate of 5 l min⁻¹ at a temperature between 5 and 6°C. Aeration kept the eggs evenly distributed in the water column. Dead eggs were removed from the tank on a daily basis.

After 100% hatch, larvae were transferred to 250 l conical silos at a larval density of 50 larvae l⁻¹. All larval batches used for predators and prey in the experiment were reared under similar conditions. Larval

rearing temperature was maintained between 8 and 12°C throughout the experimental period. Water exchange was initially 1 l min⁻¹ and gradually increased to 5 l min⁻¹ towards the end of the rearing period. Larvae were fed enriched rotifers (Super Selco, INVE Aquaculture) from 2 to 40 d post-hatch (dph) and enriched *Artemia* from 35 to 55 dph. Larvae were reared under continuous light (24 h) at a light intensity of 2000 lux (see Brown et al. 2003).

Predators were removed from their rearing tanks, measured to the nearest 0.25 mm on a delineated petri dish, and withheld from food for 24 h prior to observation trials. Then, 3 predators of the same size class along with 60 first-week cod larvae (prey) were placed into 2 l glass bowls submersed in a water bath maintained at rearing temperature. Behavioural observations of predator and prey were taken for a 15 min period. Behavioural observations on 9 replicates of 4 predator size classes were conducted over a period of 6 d for a total of 36 trials.

Prey sizes averaged (\pm SD) 4.3 \pm 0.3 mm (1 to 6 dph) during the 6 d period of observations, as measured by a sub-sample of 20 larvae on Days 1, 3 and 5 of the observation trials. To account for prey growth over the course of the experiment and to reduce the bias, 6 and 12 mm predators were observed on Days 1, 3 and 5, while 9 and 15 mm predators were observed on Days 2, 4 and 6. None of the predators or prey was used again during the experiment.

Observations were made by 1 observer sitting behind a curtain to reduce disturbances by any movements of the observer. The observer sat 50 cm away to permit a full-field view of the tank and larvae. Overall, 5 types of behaviour were observed in each 15 min trial period (Table 1), and the frequency of each behaviour was recorded using an event counter. Attack likelihood and prey capture ability were calculated as:

$$\text{Attack likelihood} = \text{attacking} / \text{fixation}$$

$$\text{Capture success} = \text{engulfing} / \text{attacking}$$

Table 1. *Gadus morhua*. Definitions of the 5 observed cannibalistic behaviour types of larval and pre-juvenile Atlantic cod

Behaviour	Description
Fixation	Interest shown by the predator on a prey item, often characterized by a 'C' posture
Aggression	Short chase of the prey item after fixation, which may or may not result in fin nipping
Fin nipping	Non-fatal bite on a fish prey, which may or may not proceed to an attack
Attacking	Attempt to strike and engulf a prey item which could result in a miss or engulfing
Engulfing	Successful cannibalistic attack in which the prey is consumed

Changes in behaviour with predator size were analysed using ANOVA. Subsequent comparisons between size classes were conducted using Scheffé post hoc tests. If the assumptions of normality could not be met, data were randomized following procedures outlined by Manly (1991) and Adams & Anthony (1996). Significance was set at 0.05.

RESULTS

Size of Atlantic cod *Gadus morhua* had a significant effect on cannibalistic behaviour (Table 2). All predator sizes performed fixation, aggression and fin nipping behaviour, but the frequencies increased with predator size (Fig. 1). The 6 mm predator showed an interest (fixation) in first-week larvae and performed occasional fin nipping, but did not attack and engulf any larvae during the course of the experiment. The 9 mm predators were able to attack and consume first-week larvae, but were also observed fin nipping larvae they did not consume. The 15 mm predators did not show much interest in fin nipping, and instead showed

Table 2. ANOVA results for effect of size on cannibalistic behaviour

Behavior	$F_{3,35}$	p
Fixation	53.57	<0.001
Aggression	30.74	<0.001
Fin nipping	5.71	<0.003
Attacking	45.49	<0.001
Engulfing	52.84	<0.001

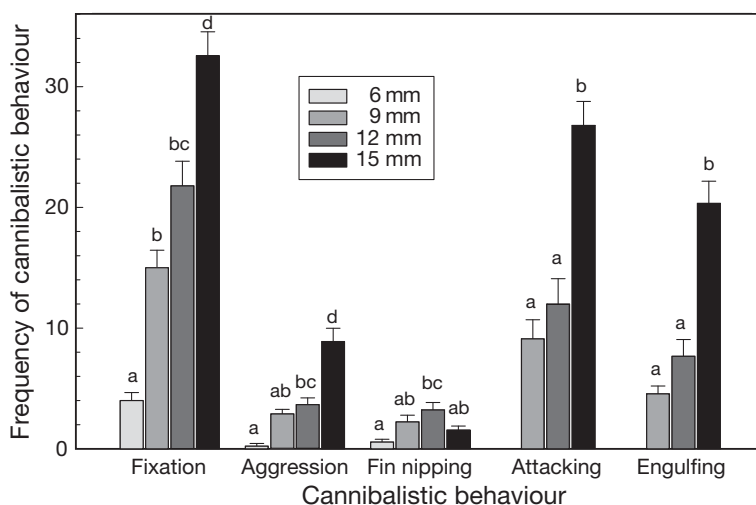


Fig. 1. *Gadus morhua*. Frequency of cannibalistic behaviour (mean \pm SD) of 6 to 15 mm Atlantic cod on the first-week conspecific larvae during a 15 min observation period. Different letters within a behavioural response indicate significant difference ($\alpha = 0.05$)

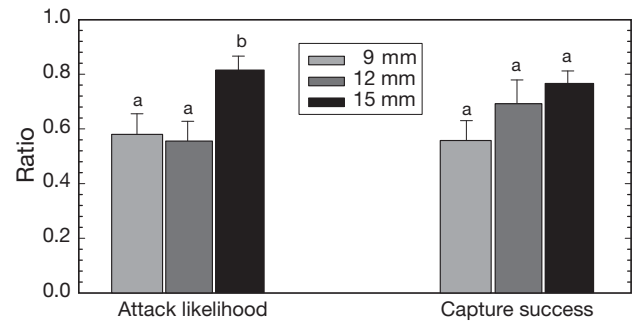


Fig. 2. *Gadus morhua*. Mean attack likelihood and capture success (\pm SD) of 9 to 15 mm Atlantic cod on the first-week conspecific larvae. Different letters within a behavioural response indicate significant difference ($\alpha = 0.05$)

higher rates of attacking and engulfing than the smaller predator size classes. Among the 3 larger predators, the number of incidents of attacking and engulfing increased with increasing size (Fig. 1). While no significant differences were found in any of the observed behaviours between 9 and 12 mm predators, 15 mm predators showed higher frequencies of fixation, aggression, attacking and engulfing (Fig. 1).

Fixation did not always end in an attack, nor did an attack always lead to the consumption of prey (Fig. 1). Attack likelihood was similar between 9 and 12 mm predators ($p = 0.064$), but 15 mm predators had higher attack likelihood ($p = 0.033$) (Fig. 2). Capture success consistently increased with increasing predator body size. The 15 mm predator represented the greatest threat in terms of absolute number of attacks and engulfments to 1 wk old cod larvae; however, 9 and 12 mm predators also demonstrated similar threats when considering the capture success (Fig. 2).

DISCUSSION

To date, studies on cannibalism in Atlantic cod have been restricted to larger-sized individuals than those examined in our study (Folkvord 1993, Folkvord & Otterå 1993, Blom & Folkvord 1997, Uzars & Plikshs 2000). While most field studies on cannibalism have analysed the gut contents of cod >350 mm (Uzars & Plikshs 2000), the smallest cod studied were about 21 mm in a laboratory study (Folkvord 1993) and about 130 mm in a semi-intensive system (Blom & Folkvord 1997) (Fig. 3).

Few studies have so far investigated the ontogeny of cannibalistic behaviour in fishes (Loadman et al. 1986, Sakakura & Tsuka-

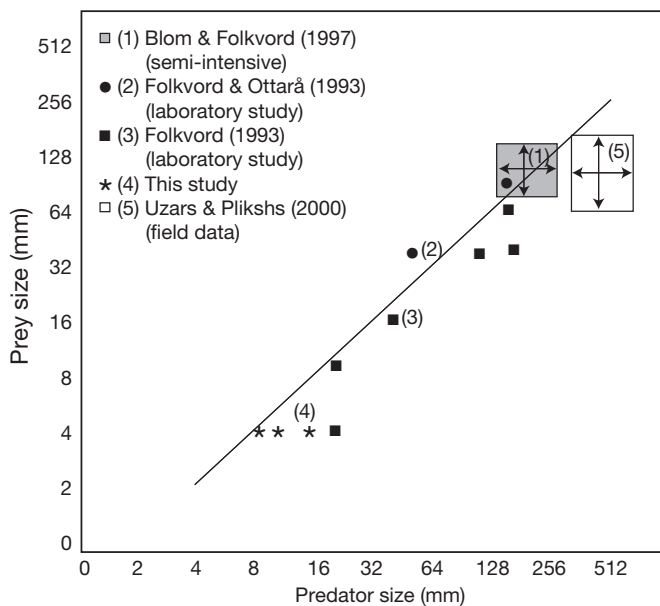


Fig. 3. *Gadus morhua*. Prey–predator length relationships in present and previous cod cannibalism studies. The line represents the 1:2 ratio of prey and predator size

moto 1996, Baras 1999, Baras & Jobling 2002). Of the studies that have incorporated behavioural observations, most were designed to characterize the mechanics of cannibalism (e.g. attack orientation) rather than its onset (Loadman et al. 1986, Baras 1999, Baras & Jobling 2002) and examined larger juveniles than reported in our study (e.g. Baras 1999). Cannibalism studies on larval and early juveniles of cod received less attention, likely because the available field information rules out intra-cohort cannibalism (Ellertsen et al. 1984, Perry & Neilson 1988). However, studies of semi-intensive systems, such as large marine ponds, suggest intra-cohort cannibalism in cod (Folkvord et al. 1994, Blom & Folkvord 1997). Sakakura & Tsukamoto (1996) showed that young yellowtail *Seriola quinqueradiata* exhibit strong cannibalistic behaviour at 23 dph (10 mm total length), and they attributed this elevated aggression to greater size variation within the cohorts. In the present study, the frequencies of aggressive and cannibalistic behaviours increased as the size differences between prey and predator increased. The age difference between prey and both the larger and smaller predators in our study was 48 and 34 d, respectively, and Folkvord et al. (1994) showed that cannibalism could be a major cause of mortality when the age difference among cohorts is >10 to 20 d and the food supply is limited.

Cannibalistic behaviour of larger conspecifics on first-week cod larvae appears to develop sometime between 6 and 9 mm. Although 6 mm larvae showed some interest (fixating) on smaller first-week larvae,

they did not fully attack (but did nip the fins) the larvae despite being starved 24 h prior to the onset of the experiment. This fin nipping aggressive behaviour has been seen as the precursor of cannibalism in other fish species, as could also be the case for cod (Sakakura & Tsukamoto 1996). Cod larvae are gape-limited predators; thus, the relationship between prey body depth and predator mouth gape is a limiting factor (Otterå & Folkvord 1993, Puvanendran et al. 2004). Using an empirical model, Otterå & Folkvord (1993) suggested that a 6 mm larva has the ability to cannibalize a 4.5 mm larva, as the body depth of the prey and mouth gape of the predator would be similar. But they have acknowledged that it is unlikely that cod, as a gape-limited predator, would consume a prey of similar body height to its own mouth gape and suggested that larger conspecifics would comfortably cannibalize a prey having 75% of the body depth of its mouth gape. Thus, failure to attack the 4.3 mm prey by the 6 mm predator in our experiment could be due to the morphological constraint of having a smaller mouth gape (0.69 mm) compared to the body depth (0.72 mm with yolk sac) of the 4.3 mm cod larvae (Folkvord 1997, Puvanendran et al. 2004, V. Puvanendran unpubl. data). Studies on the relationship between prey body depth to predator mouth gape ratios and cannibalism or piscivory are limited, compared to body-length relationships. However, few studies show a tight correlation between prey body depth to predator mouth gape ratios or prey length to predator length ratios (Nilsson & Brönmark 1999, Juanes 2003). The fixation period may be part of the decision making process in which the predator determines whether it can successfully ingest its prey. Other behavioural studies involving Atlantic cod larvae reported 'passes' (Puvanendran et al. 2002) or 'aborted attacks' (Hunt von Herbing & Gallagher 2000) in which the larvae terminate pursuit of a prey item, possibly because another suitable prey item enters the field-of-view and/or the prey item is determined to be too large to handle.

Fin nipping is an aggressive behaviour that could have some competitive importance, yet the significance of this behaviour is not clear, as it varies depending on the species. In salmonids, fin nipping has been interpreted as social behaviour in escalated conflicts, with the severity of fin damage sustained by different individuals possibly reflecting their position in a social hierarchy (Abbott & Dill 1985, Moutou et al. 1998). Although fin nipping in our study increased in predators from 6 to 12 mm, it appears that fin nipping is not an important cannibalistic behaviour of larval and juvenile cod of any of the sizes tested. Moreover, fin nipping frequency was reduced in 15 mm predators to the level found in 6 mm predators, possibly reflecting the improved predatory skills of larger predators.

Similar fin nipping incidences were reported in winter flounder and Atlantic cod juveniles (55 to 450 g), whereby smaller juveniles were subjected to more fin nipping compared to larger juveniles, but no direct mortalities were related to this behaviour (Fairchild & Howell 2001, Hatlen et al. 2006). Fin nipping may not be beneficial for the predator in terms of energy gains, but it could have serious negative impacts on the prey, as the damaged fin may impair their swimming, foraging and predator escape capabilities. These weakened and stressed individuals may eventually benefit the predator, because they may become easier to catch and consume (Sogard & Olla 1994). Studies on walleye *Stizostedion vitreum* (Loadman et al. 1986) and wall-eye pollock *Theragra chalcogramma* (Sogard & Olla 1994) showed that 19 and 36% of the fish that were attacked died within 24 h, respectively. In our study, the fish were not observed beyond the observation period; thus, the fate of these fin-nipped fish is unknown.

Our results showed that the cannibalistic acts of attacking and engulfing 4.3 mm first-week larvae first developed in 9 mm predators. Folkvord et al. (1994) reported that in situations where cohorts of Atlantic cod larvae separated by 20 d in age were reared together, mortality rates in the younger cohort were higher when copepod densities were low. At that time, the cohorts had standard lengths of 9 to 15 mm (older) and 5 to 7 mm (younger). They suggested that the early juveniles from older cohorts had the ability (having the length ratio of 1.3:1 to 3:1) and motivation (low copepod density) to cannibalize the younger cohort. Folkvord et al. (1994) therefore concluded that cannibalism was the most probable explanation for the high rates of mortality, rather than food availability or other unexplained environmental factors. Our results support their prediction, which showed that the attack frequencies increased significantly as the predator size increased from 12 to 15 mm. As the larvae grew, the fixation period was more frequently followed by an attack on a prey item, but such attacks commonly missed the prey. The failure to capture prey could be a result of the enhanced escape behaviour of the prey. Similar observations of limited success are reported in other behavioural investigations involving marine finfish foraging on zooplankton (Hunt von Herbing & Gallagher 2000, Puvanendran et al. 2002). However, absolute number of attacks and engulfments increased with increasing predator size, a result which agrees with observations from other studies based on morphometrics that cannibalistic mortality increases as size variation increases in the cohort (Folkvord 1997).

Not surprisingly, 15 mm fish represented the greatest cannibalistic threat to first-week larvae in terms of incidents of attacking and engulfing. There appears to

be a significant ontogenetic shift in behaviour between 12 and 15 mm, which would correspond with the morphological and physiological changes associated with juvenile metamorphosis (Pedersen & Falk-Petersen 1992). Between 11 and 15 mm cod larvae develop vertebrae and fin rays that contribute to increased predatory skills through higher sustained and burst swimming speeds and improved manoeuvring (Pedersen & Falk-Petersen 1992). Pedersen & Falk-Petersen (1992) found that the stomach and the pyloric caeca of Atlantic cod start to develop at 15 mm and that the capacity of the stomach to hold more food begins to increase significantly at 20 mm. This could have enabled the 15 mm cod to consume significantly more prey than the smaller predators used in our study.

Our study was conducted in a small container, and the contact rate could have been higher than in natural environments; thus, comparison of the results from our study with *in situ* conditions should be done cautiously. With the difficulties involved in the simulation natural environments of fish larvae in mind, results from these studies nonetheless provide greater depth to our understanding of larval behaviour (Munk 1995, Laurel et al. 2001, Puvanendran et al. 2002, 2004).

In conclusion, our study demonstrated that aggressive behaviour develops as early as in 6 mm Atlantic cod larvae and that it increases as relative predator to prey size increases. The cannibalistic acts of attack and capture start as early as in 9 mm larvae. Previous cannibalistic studies based on gut contents and mortality data have not indicated that cannibalistic behaviour and acts begin this early in larval cod, despite providing insight into the morphological constraints of cannibalism. Although, our study demonstrated possible intra-cohort cannibalism in Atlantic cod using behavioural observation alone, further studies of cannibalism between different size classes in combination with behavioural observations, gut content and mortality data are warranted to enhance our knowledge of ontogeny of cannibalism in Atlantic cod.

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