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Arild Folkvord [a]

[a] Department of Fisheries and Marine Biology, University of Bergen, Bergen High-Technology Center, N-5020, Bergen, Norway

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PREY RECOGNITION IN STOMACHS OF CANNIBALISTIC JUVENILE COD (*GADUS MORHUA* L.)

ARILD FOLKVORD

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A series of experiments were undertaken to determine how long a cod (*Gadus morhua* L.) prey could be recognized in the stomach of a cannibalistic cod. Three-day old cod larvae were recognized 15–90 min whereas 6 cm cod could be confidently identified up to 8–9 hours after ingestion, based on external morphological features. The prey dissolved at different rates depending on subsequent feeding of the cannibalistic cod, with the digestion of cod larvae being more rapid when no additional food was offered. The rapid digestion of early cod larvae limit the feasibility of quantifying cannibalism from stomach contents of cod.

Arild Folkvord, Department of Fisheries and Marine Biology, University of Bergen, Bergen High-Technology Center, N-5020 Bergen, Norway.

INTRODUCTION

Predation is an important source of mortality in fishes (BAILEY & HOUDE 1989). This is particularly the case during the egg- and yolk sac stages where starvation is ruled out due to endogenous energy reserves in the yolk (HUNTER 1984). In contrast to a number of reports of piscivore predation on fish eggs, there are few reports of predation on early larval stages (SMITH & REAY 1991). A rapid digestion of early larvae as in the case of anchovy (*Engraulis mordax* GIRARD) and herring (*Clupea harengus* L.), may partly explain the relatively low incidences of larval fish found in fish stomachs (HUNTER & KIMBRELL 1980; CHRISTENSEN 1983).

This paper specifically deals with the feasibility of detecting and quantifying cannibalism among larval and juvenile cod (*Gadus morhua*) in juvenile rearing enclosures and in the field using a stomach analysis approach. The study was motivated by: a) the assumption that cannibalism is a main mortality factor in rearing enclosures, causing a rapid decline in numbers of the younger larval cod cohorts (ELLERTSEN & al. 1981; ØIESTAD & al. 1985); b) the observation that cannibalism is a common phenomenon during the early juvenile stage, under intensive rearing conditions (FOLKVORD 1991).

The digestion times of various sizes of larval and juvenile cod were determined experimentally in the laboratory. The results were used to calculate the number of stomachs required to account for observed mortality and potential cannibalism reported in the literature.

MATERIAL AND METHODS

All the prey and predators originated from a local broodstock at Austevoll Aquaculture Research Station, Norway. The juveniles used in the study (cod > 12 mm standard length), were reared in a nearby seawater enclosure (ØIESTAD & al. 1985), and were transported to the station before the experiments. Mean larval prey standard length (SL) were obtained from samples of the original population. All experiments were performed under ambient temperature conditions, ranging from 6 to 15° C. The large cod predators (> 6 cm) were fed dry feed whereas the smaller predators (≤ 6 cm) were fed live zooplankton up to the day of the experiment. The trials were conducted by adding one small cod together with a large potential cannibal into 2 l cylindrical tanks (larval prey) or 250 l cylindroconical tanks (juvenile prey). The cod were continuously monitored, and the time of ingestion in the respective tanks was noted. After a predetermined period the cannibals were removed from the tanks, and their gut contents analysed under a dissecting microscope. The experiments contained in total 98 trials of ingested cod (Table 1). In 52 cases the predators were fed live zooplankton (larval prey experiments) or dry feed (juvenile prey experiments) after ingestion of the single cod prey.

Morphological features were used to positively identify the cod prey in the gut, and the detail of stomach analysis was at a level applicable for a large sampling program. Remnants of skin with its typical pigmentation pattern, skull remains and fin structures were used as means of positive identification (identified cod). Pieces of vertebral columns and flesh were used to identify fish prey in the stomachs, but were not used in the classification of cannibalism. Otoliths of juvenile cod were not used in identification since indigestible solids will have more variable retention times in the gut, and may not be suitable for quantitative studies (SANTOS & JOBLING 1991a).

In the statistical analysis, time from ingestion was standardized to 10° C by using a Q_{10} of 2.8 (SANTOS & JOBLING 1991b). Prey recognition is affected mostly by surface digestion. A square root transformation of time

Table 1. Overview over experiments with corresponding predator and prey standard lengths, SL (± SD). Cannibals fed after ingestion of prey are indicated (n is number of trials in each experiment).

Experimental date	Pred SL (cm)	Prey SL (cm)	Pred/Prey SL ratio	Time from ingestion (hours)^n	Total n	Temp (°C)	Fed
4 May	2.3 ± 0.2	0.44 ± 0.11	5.2	$1/4^2$, $1/2^3$, 1^4, 2^4, 4^4	17	6.0	no
5 May	2.3 ± 0.2	1.01 ± 0.12	2.3	2^1, 4^4, 8^5	10	6.0	no
8 May	2.1 ± 0.3	0.43 ± 0.16	4.8	$1/2^3$, 1^3	6	6.0	yes
8 May	2.3 ± 0.2	0.94 ± 0.12	2.5	2^4, 4^4, 8^3, 11^4	15	6.0	yes
28 May	4.9 ± 0.4	1.6	3.0	2^2, 4^2, 8^2, 15^1	7	6.0	yes
30 May	16.3	3.9	4.2	6^1	1	6.0	yes
12 Aug	14.5 ± 0.6	5.7 ± 0.5	2.5	8^2, 16^4	6	8.5	no
13 Aug	14.6 ± 1.0	6.0	2.4	8^2, 20^4	6	8.5	yes
13 Aug	13.9 ± 1.1	6.0	2.3	22^7	7	8.5	no
14 Aug	14.1 ± 0.5	6.0	2.3	22^4	4	8.8	yes
14 Aug	15.0	6.0	2.5	6^1	1	9.9	no
14 Aug	15.1	6.0	2.1	6^1	1	15.1	no
15 Aug	14.1 ± 0.7	5.0	2.8	6^1, 8^4, 9^2, 10^1, 18^1, 20^1	10	10.2	yes
15 Aug	14.3 ± 0.9	5.0	2.9	16^1, 18^1, 19^1	3	15.1	yes
19 Sep	11.3 ± 1.5	3.5	3.2	6^2, 9^1, 10^1	4	10.0	no

from ingestion was therefore applied, since surface digestion is related to $W^{2/3}$ or L^2 of the prey (SANTOS & JOBLING 1991b). The functional relationship between prey size, time from ingestion and recognizability was modelled with NAG GLIM 3.77 (PAYNE 1987), by fitting a logistic regression model:

Eq. (1) $$\text{logit}(p_r) = \ln(p_r) - \ln(1-p_r) = \sqrt{t} + \text{fed} + \ln(SL) + \text{fed} \times \ln(SL)$$

where p_r is recognizability (binary response variable), t is the time from ingestion in hours (independent variable), ln(SL) is log prey standard length in cm (covariate), fed is subsequent feeding (categorical variable), and fed × ln(SL) is the interaction term representing different slopes of fed versus starved predators. The significance of each term in the full model was estimated by step-wise removal of the terms (DOBSON 1983). The digestion time was defined as the time when 50 % of the prey would be recognized, corresponding to $p_r = 0.5$ and $\text{logit}(p_r) = 0$. The equations for length dependent digestion times were then obtained by rearranging Eq. 1.

The number of predator stomachs required for identifying a single cod prey was estimated by the following procedure: the daily number of cod prey ingested per day, I (assuming all the mortality is cannibalism), is given by the equation:

Eq. (2) $$I = N_p \times M$$

where N_p is the cod prey abundance and M the daily mortality rate (per day). The number of cod prey in the cannibal stomachs during the feeding period, N_s (assuming constant ingestion rates during feeding period), is given by the equation:

Eq. (3) $$N_s = D \times I / F$$

where D is digestion time (in days) and F is the proportion of the day the fish are feeding. The proportion of the cannibal population with prey in the gut during the feeding period, p_c, is given by the equation:

Eq. (4) $$p_c = N_s / N_c$$

where N_c is cannibal abundance. The average number of stomachs required per positive identification, S, is thus (Eqs 2–4 combined):

Eq. (5) $$S = 1 / p_c = (N_c \times F) / (N_p \times D \times M)$$

The number of stomachs required to obtain at least one positive identification of cod in 95 % of the cases, n_d (n detection), can be regarded as a special binomial case, $b(r; n_d, p_c)$, where $P(R = 0) = 0.05$ (BHATTACHARYYA & JOHNSON 1977). Solving for n_d gives:

Eq. (6) $$n_d = \ln(0.05) / \ln(1-p_c)$$

The precision of calculated cannibalism rate depends on the precision of the estimated p_c. The number of stomachs required to meet any desired level of precision of p_c, n_q (n quantification), can be calculated as:

Eq. (7) $$n_q = (S - 1) / CV^2$$

where CV is the predetermined coefficient of variation of p_c.

RESULTS AND DISCUSSION

Digestion time increased with increasing prey size (χ^2 (chi square) = 18.5, df = 1, $p < 0.001$, Fig. 1). The digestion time of the largest prey (6 cm) was 8–9 hours.

The digestion pattern was also affected by subsequent feeding (slope, χ^2 (chi square) = 5.3, df = 1, $p < 0.03$). The cannibals fed after ingestion of the cod prey had a longer and more variable digestion time of early larvae than those subsequently starved. It has been shown for larger cod that the gastric half-life of herring meals increases with increasing meal size (SANTOS & JOBLING 1991b). The digestion times for starved individuals may represent minimum estimates because of minimal meal

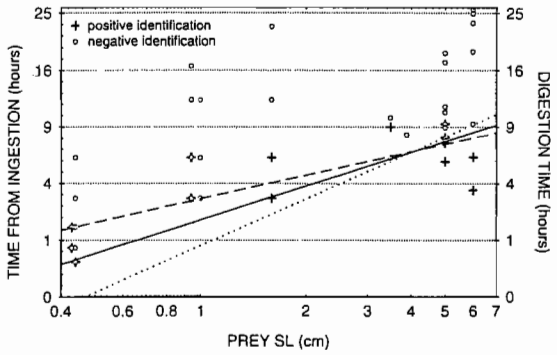

Fig. 1. Time from ingestion of cod larvae and juveniles (symbols). Lines and equations for average digestion time t (defined as the time when 50 % of the prey would be recognized) are presented: a) unfed (dotted line) $\sqrt{t}$ = 0.90 + 1.19 ln(SL), b) fed (broken line) $\sqrt{t}$ = 1.73 + 0.60 ln(SL), c) combined (solid line) $\sqrt{t}$ = 1.36 + 0.86 ln(SL). Values and equations are normalized to 10° C using a Q_{10} of 2.8.

size. On the other hand, the smallest predators fed copepods after ingestion of the cod prey, had filled their stomachs with other prey and had on average over 100 copepods in the stomach. Thus, the digestion of the larvae may have been delayed since excessive feeding will prolong digestion time (SANTOS & JOBLING 1991b). The digestion times under natural feeding conditions will therefore probably lie between the estimates obtained from the starved and fed predators. Although the predator size varied in the study, this effect will to some extent be counterbalanced by proportionate prey size (SANTOS & JOBLING 1991b).

The lack of both hard parts and multilayer integument in the larvae make them easily digestible. The model possibly underestimates the digestion time of cod prey of 1–3 cm. This may partly be due to a marked change in digestibility caused by initial ossification and integument formation around metamorphosis (PEDERSEN & FALK-PETERSEN 1992). The digestion times of early cod larvae of 15–90 min with starved and fed predators respectively, are of the same magnitude as observed for anchovy and herring larvae (HUNTER & KIMBRELL 1980; CHRISTENSEN 1983). In the following calculations, an estimated digestion time of 30 min from the combined groups is used, corresponding to larval size of 4.7 mm.

Table 2 illustrates the effort required to detect predation on yolk sac cod larvae. The number of stomachs needed to confidently detect at least one incidence of cannibalism varies between 29 and 1700. Quantification of the cannibalism rate with a precision corresponding to a CV of p_c of 0.5, 0.31 or 0.1, would require on average 4, 10 and 100 positive identifications of cannibalism respectively (Eq. 7). It was therefore not feasible to estimate cannibalism among cod in the study by ØIESTAD & al. (1985) by stomach analysis (see Table 2).

The calculations in Table 2 rely on several assumptions; a) that unbiased sampling of the predator population is possible, b) that non-successful cannibalistic attacks do not cause added mortality as in other species (LOADMAN & al. 1986), c) all the observed mortality is directly due to cannibalism, d) a constant feeding level during the feeding period (EGGERS 1977), e) all cannibals have only one cod prey in the stomach. None of these assumptions are normally valid, but any violations of them would generally require even higher sampling effort to detect and correctly quantify cannibalism rates by stomach analysis. The digestion time used in the example were based on the combined experimental results, and using the digestion times from the separate equations of the fed and starved predators would imply using a third or twice the required sampling effort respectively.

Table 2. Number of stomachs required for detecting cannibalism on 3-day old cod larvae assuming cannibalism is responsible for all the mortality. (All population numbers in thousands).

Parameters		ØIESTAD & al. 1985			ELLERTSEN & al. 1981	FOSSUM 1988[a]
Cannibal population	N_c	750[b]	600[b]	475[b]	5	4×10^9
Prey population	N_p	250	150	80	100	20×10^9
Daily mortality rate	M (day^{-1})	0.19	0.5	1.0	0.18	0.12
Digestion time	D (day)	1/48	1/48	1/48	1/48	1/48
Part of day feeding	F	3/4	3/4	3/4	3/4	3/4
Results						
Average number of stomachs required to detect one incidence of cannibalism (Eq. 5)	S	568	288	380	10	60
Number of stomachs required to detect at least one incidence of cannibalism in 95 % of the cases (Eq. 6)	n_d	1700	862	1137	29	179

[a] assuming a 30-day age difference between predators and prey, and originally 10 times more abundant predator population.

[b] corresponding to the abundance of cohort 1 at the time of release of cohorts 3, 4 and 5 respectively.

The N_c/N_p ratio in Eq. 5 should be relatively low in order to successfully carry out a stomach analysis programme. As a consequence, abundant invertebrate predators are poor candidates for stomach analysis programmes to quantify predation on larvae. Recent radio immunoassay (RAI) techniques have enabled the detection anchovy yolk protein in krill stomachs up to 4 hours after ingestion (THEILACKER 1988), but the high ratio of predators to prey may still limit their application. The colour of the faeces can be used as a indicator of cannibalism in fish cultures. Sea bass (*Lates calcarifer* BLOCH) reared in the laboratory had orange coloured faeces when fed *Artemia*, while the cannibals had black gut contents and faeces (PARAZO & al. 1991). Although black gut contents were observed in this study, it is difficult to quantify cannibalism in the enclosures and in the field based on this criterium because other prey organisms, such as other larvae and decapods, also contain black pigments.

A hypothetical example in Table 2 based on field data from FOSSUM (1988), illustrates that on average 60 stomachs are required to detect cannibalism by cod juveniles originating from around peak spawning. However, to detect cannibalism by juveniles from the start of the spawning season will require substantially smaller sample sizes. Only 1 individual is needed if the N_c/N_p ratio at hatching is 1/500 instead of 1/5 as in the example in Table 2. Although higher sample sizes are required to obtain precise estimates of cannibalism rate, the few reports of larval intracohort cannibalism in the field may indicate that it is of minor importance compared to in experimental systems.

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