Individual variation in competitive performance of juvenile cod and its consequences for growth

Paul J.B. Hart* and Anne Gro V. Salvanes

Department of Fisheries and Marine Biology, University of Bergen, High Technology Centre, N–5020 Bergen, Norway.
*Present address: Department of Biology, University of Leicester, Leicester, LEl 7RH. E-mail: pbh@leicester.ac.uk

This communication reports on experiments, which studied the variation in competitive performance of juvenile cod (*Gadus morhua* L.) and their growth rates. The fish were held in groups of five in either summer or winter conditions and tested for their individual response to prey offered sequentially. There was marked individual variability. Fish that took the highest share of prey tended also to be those that took prey earlier than others. In winter conditions these fish were the largest, but in summer conditions size had no effect. There was a positive influence of the indices of competitive performance on individual growth rate but the relationship was not significant.

Since Darwin (1859), competition has been considered a driving force in evolution, although its effects have often been hard to detect (see Strong et al., 1984; Grant, 1986; Schluter, 1994). Given that growth is an important proxy for fitness in fish (Schluter, 1994) it is possible that it is positively correlated with competitive ability which is likely to vary from individual to individual. An animal competing against conspecifics for limited resources has to ensure it receives a sustaining share as food is required for positive growth. Competitors either have to have superior physical attributes, or they must evolve strategies for overcoming their physical shortcomings. Such strategies are living in stable groups and cooperating, living in kin groups, holding resource rich territories or developing dominance. If competition is a scramble then who is successful at obtaining food will be determined by phenotypic properties such as who swims faster, reacts first to an encountered prey or has a bigger gape than others (Parker, 1982; Milinski & Parker, 199l; Gill & Hart, 1996). In this study we subjected groups of juvenile cod to scramble competition for sequentially delivered prey. Our purpose was to determine the degree of individual variability in competitive performance and its possible influence on growth.

The cod used in the experiment were hatchery reared and originated from the western Norway coastal cod populations. Thirty fish were taken from stock at random and placed in six groups of five fish which were held separately in 500-l tanks of seawater in two separate rooms, each containing three tanks. These had a water inlet in one corner and an outlet in the centre of the tank bottom. The rate of water renewal was approximately $5\,\mathrm{l\,min}^{-1}$ and the water was circulated through the tank.

At the start of the experiment the fish had a mean weight of 210.0 ± 49.2 g (N=30). In each group, four fish were marked with either a red, blue, yellow or white spaghetti tag inserted into the muscle below the dorsal fin. This allowed identification of the fish taking each prey, an event recorded onto a Dictaphone. Data later showed that the unmarked fish did not behave differently to the others in the group.

We simulated midsummer (temperature, $15.5 \pm 0.3\,°C$; photoperiod, 22:2 h light:dark (L:D) regime) and midwinter (temperature, $5.9 \pm 0.1\,°C$; photoperiod, 8.5:15.5 h L:D) both matching conditions in Bergen which is at $60°25'N\;05°20'E$. Fish were adapted to the conditions for 25 d before the experiment started.

Individual dead gobies (*Gobiusculus flavescens*) were given sequentially at the start of the day. New prey was only delivered when the previous one had been taken and swallowed or had sunk to the bottom and been ignored. More prey were offered either 3, 7 or 24 h after the first feed, each interval being termed a treatment. The trial was stopped when three prey in a row had been rejected. To reduce the carry-over effects between tanks, the order in which each tank was treated each day was varied. A new treatment was started every other day and three repeated observations per group of fish per treatment were completed.

The acclimatization period allowed the cod to feed in the same way so that they could get to know the protocol and each other. Each individual in a group had the same opportunity of taking every prey item introduced into the tank. There were no observed aggressive interactions or signs of territorial defence during the experiments.

Individuals that were the first to feed and ate most of their prey early in the trial were defined as having the highest competitive performance. To quantify this, prey offered were numbered 1 to n as they were thrown into the tank, n being the total number of gobies taken by all the fish. For each cod, the mean rank of prey taken from the sequence of n offered during a trial was used as one index of competitive performance. We used the frequency with which a fish had rank one (the highest competitive performance) over all trials in all further analysis and label the variable as 'earliest feeder' in all subsequent discussion. The best competitor had the smallest value of this index, meaning that it most often took prey at the start of the trial. A second index was the average proportion of prey taken by an individual over the trials, labelled in further discussion as 'prey share'.

Analysis of variance (ANOVA) was used to test four relationships; the effect of initial size on earliest feeder using two size categories (<200 g or $\geqslant 200$ g), the effect of the earliest feeder, using two categories (<0.3 and $\geqslant 0.3$) on the prey share taken per trial for each individual, the effect of the prey share taken per trial using two categories (<0.25 and $\geqslant 0.25$) on the specific growth rate and the effect of earliest feeder on the growth rate. For each relationship we also tested for the effects of temperature.

The observed effects could be unduly influenced by small sample sizes so that some effects might be statistically insignificant as a result of this. To check this possibility we calculated the power of the *F*-test for the ANOVA (Zar, 1984).

There was a pronounced variability in the frequency with which individual fish took prey first (earliest feeder) for both winter and summer conditions. The frequency was positively related to initial weight for fish at $6\,°C$ (Figure 1A; $F=4.91$,
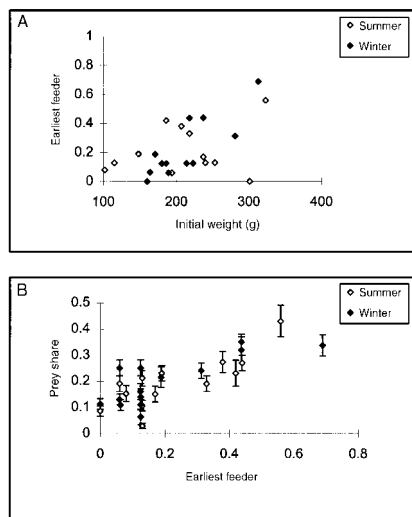
Figure 1. (A) Earliest feeder plotted against the initial weight of the fish for summer and winter conditions; (B) prey share plotted against earliest feeder. Data are separate for summer and winter conditions. The bars represent ±SE.

Figure 2. (A) The specific growth rate for individual fish plotted against prey share for summer and winter; (B) the specific growth rate for individual fish plotted against earliest feeder. Data are divided into winter and summer records. The bars represent ±SE.

$P=0.045$), but not at 15 °C ($F=0.85$, $P=0.378$). Earliest feeder had a positive effect on prey share (Figure 1B; $F=28.13$; $P<0.001$), but there was no significant effect of temperature ($F=0.57$, $P=0.45$). The power of the overall ANOVA F-test was high with $\beta=0.88$ and $r^2_{adj}=0.48$.

Average daily growth rate of individual fish showed considerable variability at both temperatures and Figure 2A,B suggests a positive correlation with both the intake of prey and competitive performance. Temperature had a significant effect ($F=5.93$, $P=0.026$) on the relationship between the prey share and growth but the relationship between prey share and growth was marginally non-significant ($F=3.76$; $P=0.069$; $0.3<\beta<0.65$, $r^2_{adj}=0.33$). In contrast the effect of earliest feeder was clearly not significant ($F=1.16$; $p=0.296$; $\beta \approx 0.41$ $r^2_{adj}=0.24$). Since the power (β) and unexplained variance were low these results could be due to low sample sizes and other unspecified effects.

Our study has demonstrated considerable variability in competitive performance (Figure 1A,B) and suggests that the individuals that take the highest share of a meal also tend to take prey earlier in a trial. Under winter conditions fish that were initially large tended to have a competitive performance that was higher than those that were small.

The competitive status of the fish has an effect on the amount of food that an individual takes (Figure 1B), a relationship unaffected by temperature. If competitive excellence is so important in determining how much food an individual cod takes it is also likely that it will affect growth rate. Many studies have shown that in fish, growth rate is strongly linked to food intake (e.g. Jobling, 1994; Elliott, 1994). There was a positive trend between the specific growth rate of the cod in our experiment and prey intake and competitive performance (Figure 2A,B). Individual variation was pronounced suggesting that many other factors play a part. We have shown in a separate paper (Salvanes & Hart, 2000) that one contributing factor is haemoglobin genotype which seems to be linked to the fish's metabolic rate with fish that have a higher rate feeding more vigorously.

The pronounced heterogeneity in competitive performance can be discussed in the broader context of processes regulating cod population dynamics. If a cohort of fish consists of individuals with varying competitive abilities then competition between them 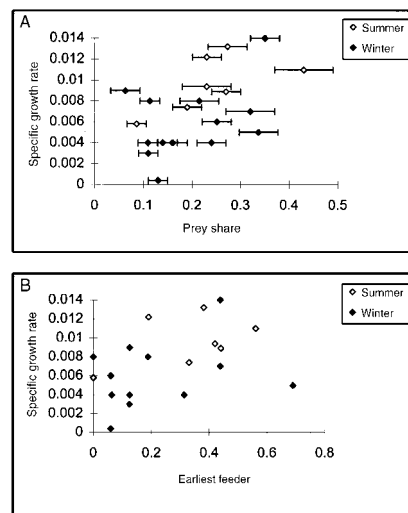for food can be expected to lead to increased size variation in the cohort. As a consequence, the advantage of being the best competitor and feeder is expected to amplify the heterogeneity and increase the size range of the cohort. The largest competitor may even be cannibalistic towards the smallest individuals as demonstrated by, for example, Folkvård et al. (1994). As a result, limited resources may amplify heterogeneity in competitive performance which could have a profound influence on the density-dependent regulation of a cod population.

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