Compensatory growth in young juvenile Atlantic cod

Maja Walter(1), Edward A. Trippel (2), Myron A. Peck (1)
(1) Institute of Hydrobiology and Fisheries Science, University of Hamburg; Hamburg Germany; (2) Fisheries and Oceans Canada, St. Andrews Biological Station, St. Andrews, NB, Canada. Presenter contact details: myron.peck@uni-hamburg.de, Phone +49 494 94 9000

Summary
Atlantic cod (*Gadus morhua*) juveniles may experience sub-optimal foraging as they transition from the pelagic to demersal habitat due to competitive interactions but maintaining high growth rates may be important to increasing the chances for survival. A 9-wk laboratory experiment tested whether juveniles exhibited compensatory growth in response to different types of food deprivation. Group swimming and feeding activity as well as individual growth responses were monitored. Juveniles were either (1) fed to satiation (control), or experienced (2) a 3-wk food deprivation and 6-wk re-feeding period (3WD), or (3) 1-wk cycles of feeding and food deprivation (DFDF). During the re-feeding period, juveniles in the 3WD group had higher weight-specific growth rate (SGR) and gross growth efficiency (GGE) than control fish. Marked inter-individual variability in SGR was observed in all groups, suggesting inherent differences in growth capacity. Swimming activity significantly decreased during food deprivation of 3WD fish but was unchanged in fish receiving weekly cycles of food availability. Partial growth compensation was possible in young, demersal juveniles experiencing food shortage but the magnitude of behavioral modification and growth response depended upon both the severity of prey deprivation and intrinsic differences among individuals in their growth physiology.

Introduction
A wide range of terrestrial and marine animals exhibit compensatory growth (CG), a period of accelerated growth displayed by well-fed organisms that previously experienced a phase of partial or total prey deprivation (Metcalf and Monaghan 2001). The ability of young marine fish to exploit CG may help individuals cope with fluctuations in prey availability and grow rapidly through the developmental period when mortality rates are high. For example, when pelagic juvenile Atlantic cod (*Gadus morhua*) descend to benthic habitats they may experience altered food types and sizes and may experience food shortage, particularly during winter months. Maintaining a high growth rate is important for settled juveniles since smaller fish face a greater risk of mortality from predators (including cannibalism from larger consepecifics) and suffer more competitive exclusion from shelters and prey resources. We examined whether young juvenile cod deprived of food for different periods of time could exhibit compensatory growth and the potential, underlying mechanisms.

Materials and Methods
Juveniles were produced by broodstock maintained at the St. Andrews Biological Station, New Brunswick, Canada. Fish were maintained using standard methods (5°C, large flow-through tanks, filtered Bay of Fundy seawater, 8L:16D light regime, fed a formulated dry pellet diet once a day). For the experiment, 240 juveniles (mean 45.4 g wet weight) were randomly distributed among eight flow-through tanks and fish were acclimated to 12L:12D and 10.0°C. Tanks were randomly assigned to one of three treatments: Control, 2 tanks fed ad libitum twice a day for 9 wks; '3WD', 3 tanks unfed the first 3 weeks and re fed *ad libitum* for 6 weeks, "DFDF", 3 tanks, fish experienced 1-wk cycles of feeding and food deprivation. Tanks were checked daily for mortalities and any dead fish were removed (5% mortality occurred). At 9:00 and 13:30 each day, fish were given an ad libitum ration of a dry pellet diet. All tanks (including tanks that did not receive food) were siphoned to remove uneaten pellets and fecal waste. The weight of food consumed was calculated. Fish were anaesthetized and PIT tagged at week 0, and total length and wet body weight were measured every three weeks (week 0, 3,

6, 9). During weeks 2, 5, 8, and 9, the swimming activity of fish in all tanks was estimated three times every day; twice in daylight (before and between feedings) and once in darkness (at night).

Results and Discussion

Specific growth rate of fish differed among the treatment groups (Figure 1A) and a key finding was that growth efficiency was higher in 3WD juveniles compared to those in controls and DFDF (cycles of feeding) (Figure 1B). Juveniles exhibited diel rhythms in activity (lower activity during darkness) in all treatments and, when food deprived (week 1 to 3), the mean activity of 3WD fish was lower than that of fish in the other treatments (Figure 1C).

Jobling et al. (1994) reported CG in larger cod which agrees with our findings for smaller, settlement-stage juveniles. Our age-0 juveniles appear to also possess potentially adaptive flexibility in their growth physiology to changes in food availability but poorly fed fish did not "catch-up" to fish continually well fed. The 6-week re-feeding period may not have been long enough to see the full CG response of previously unfed individuals.

Swimming activity is tightly coupled to feeding level in juvenile cod (Björnsson 1993) and rapid increases in activity upon re-feeding are often observed. Excess feeding (hyperphagia), often the principal mechanism involved in CG (Jobling et al. 1994; Metcalfe and Monaghan 2001), was not observed. In our study, reduced activity when deprived of food, and increased growth efficiency when re- fed appeared to be the most important mechanisms.

Finally, the reasons for the large differences in growth responses among individuals (data not shown) are unknown. Tupper and Boutilier (1995) observed social hierarchy in newly settled cod, with the largest fish having the fastest growth rates and controlling the largest territories. In conditions of habitat limitation, strong social interactions may be more important than food availability and the ability to perform CG in setting the potential of juvenile cod to grow well after settlement and to survive their first winter period.

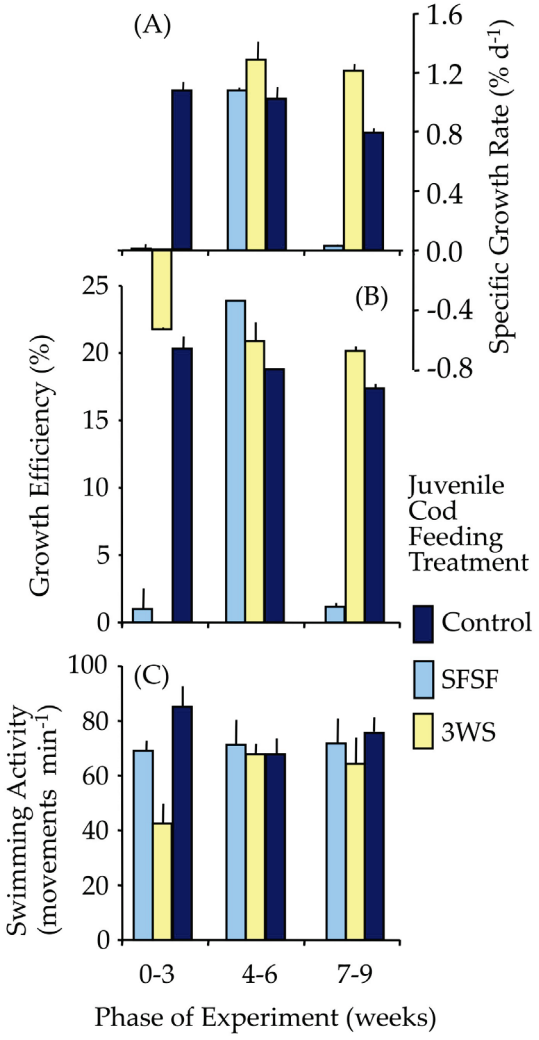

Figure. 1 Juvenile cod mean (+SE) growth rate (A), growth efficiency (B) and swimming activity (C) for fish in each of three feeding treatments (see text) over the course of a 9-week experiment.

References

Björnsson, B. 1993. Swimming speed and swimming metabolism of Atlantic cod (*Gadus morhua*) in relation to available food: a laboratory study. Canadian Journal of Fisheries and Aquatic Science, 50: 2542-2551.

Jobling, M., Meloy, O.H., dos Santos, J., Christiansen, B. 1994. The compensatory growth response of the Atlantic cod: effects of nutritional history. Aquaculture International, 2: 75-90.

Metcalfe, N.B., Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? Trends in Ecology and Evolution, 16: 254-260.

Tupper, M., Boutilier, R.G. 1995. Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. Marine Ecology Progress Series, 118: 295-300.