SEASONAL VARIATION IN PATTERNS OF COMPENSATORY GROWTH IN ATLANTIC SALMON

Neil B. Metcalfe
Fish Biology Group, Division of Environmental & Evolutionary Biology,
Graham Kerr Building, Glasgow University, Glasgow G12 8QQ, UK
Tel. +44 141 330 5968, Fax. +44 141 330 5971
e-mail n.metcalfe@bio.gla.ac.uk

Colin D. Bull
Conservation Department, John G. Shedd Aquarium,
1200 South Lake Shore Drive, Chicago, IL 60605, U.S.A.

Marc Mangel
Department of Environmental Studies and Institute of Marine Sciences,
University of California, Santa Cruz, CA 95064, U.S.A.

EXTENDED ABSTRACT ONLY – DO NOT CITE

This talk examines how evolution has shaped the interaction between animals and their food supply, so affecting their strategies of feeding, growth and resource allocation. In contrast to the resource allocation trade-off between reproductive and somatic tissues, that between growth and reserves has received little attention. In particular we address the problem faced by animals in a highly seasonal environment, where the food supply varies predictably over the course of the year as well as unpredictably from day to day. Here resources may have to be gathered at one time of year, to be used when conditions get more extreme. We consider how the allocation of those resources should vary both seasonally and when periods of reduced resource availability simultaneously cause depletion of reserves and a set-back in growth. The optimal strategy in this situation may be to exhibit seasonal variation in both the effort put into foraging (since intensive foraging in winter may be both risky and energetically expensive) and the relative allocation between reserve tissues and skeletal growth.

These principles are illustrated using juvenile Atlantic salmon *Salmo salar*, which have the added interest of having highly flexible feeding and growth patterns that are linked to alternative life history strategies (Metcalfe 1998). An experimental approach was adopted, in which the food supply to the fish was temporarily manipulated in both summer and winter, and their subsequent growth pattern recorded. Food deprivation experiments carried out in a single season have shown that juvenile salmon show a hyperphagic response such that they can at least partially compensate for a prior shortfall (Nicieza and Metcalfe 1997; Bull and Metcalfe 1997). However, in the present experiments the same nutritional deficit (as measured by the lipid content of the fish at the end of the food manipulation period) caused marked variation in response between seasons. In winter, fish primarily allocated new resources into restoring lost lipid reserves (so that skeletal growth was negligible), whereas in summer resources were divided between growth and lipid restoration. Moreover, this skeletal growth was faster than in control fish (i.e. a food shortage subsequently causes accelerated or compensatory growth in summer but not winter). Conventional growth or allocation models cannot explain this seasonal variation in response, since they would predict a single outcome for a given nutritional state and food supply.

We therefore developed a dynamic state variable model that takes account of the long-term fitness consequences of different acquisition and allocation strategies. Therefore it incorporates seasonal variation in expected food supply (so that prudent salmon ‘look ahead’ to anticipate periods of food shortage in the coming winter), and adjusts the risk of predation according to the intensity of feeding, since foraging exposes the animals to greater risk. It also balances the risk of predation against the risk of future starvation. This is an extension of a model that has previously been shown to be successful in predicting the pattern of overwinter fat regulation in juvenile salmon, where fish adjust their foraging to match long- rather than short-term energy requirements (Bull et al. 1996). The new model is parameterised for juvenile salmon, although it provides a more general framework for predicting allocation strategies for any growing organisms living in seasonal environments. The results reveal a close match between the experimental results and model predictions. This suggests that salmon are capable of altering their feeding and resource allocation rules in a manner that maximises their long-term (rather than immediate) survival: their appetite, time of day (or night) at which they feed, and relative allocation of resources to body reserves *versus* skeletal growth are all found to be flexible, and vary in an adaptive manner according to their current state, the time of year and the expected environmental conditions in the future.

Acknowledgements

This work was funded by a Natural Environment Research Council grant to NBM, a NERC PhD Studentship to CDB and a National Sea Grant College program grant to MM.

References

Bull, C.D. and N.B. Metcalfe. 1997. Regulation of hyperphagia in response to varying energy deficits in overwintering juvenile Atlantic salmon. J. Fish Biol. 50: 498-510.

Bull, C.D., N.B. Metcalfe and M. Mangel. 1996. Seasonal matching of foraging to anticipated energy requirements in anorexic juvenile salmon. Proc. R. Soc. Lond. B 263: 13-18.

Metcalfe, N.B. 1998. The interaction between behavior and physiology in determining life history patterns in Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sciences 55 (Suppl. 1): 93-103.

Nicieza, A.G. and N.B. Metcalfe. 1997. Growth compensation in juvenile Atlantic salmon: responses to depressed temperature and food availability. Ecology 78: 2385-2400.