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and fall. Little growth was observed during the winter, probably because of low water temperature (1-3°C). Growth resumed in the late winter and spring coincident with the parr-to-smolt transformation. Migrating smolts were larger than the resident parr and transitional fish. Condition factor was high in the summer, declined during winter, and then increased sharply in the spring. Smolt migrants had reduced condition factor as is characteristic of smolts. Liver glycogen declined during the winter and then increased markedly in the spring in resident fish. Liver glycogen was depleted in smolt migrants. Body lipid levels were highest in the summer, declined in the winter, and then became elevated again in the spring in resident fish. Body lipid levels of migrant smolts were low (1-3%), among the lowest that we have seen in salmonids. Stomach fullness was correlated with growth and energy storage; it was high in the summer, low in the winter, and then increased sharply in the spring.

The pattern of change in body weight, stomach fullness, and body energy storage of resident fish is dynamic during the year. The high anabolic state in the summer contrasts with the low levels of energy in the winter. In the late winter and spring parr begin feeding and resume growth, coincident with body lipid and liver glycogen stores becoming replenished. Both live glycogen and body lipid are depleted in the smolt migrants, which were captured after only one-third of the seaward migration had been completed. This suggests that additional energy to support migration must come from food captured during migration or from stored protein. We speculate that large body size and growth during the parr-smolt transformation are important in building up stored energy as protein to be used to support smolt migration.

V. EVOLUTION OF LIFE HISTORY AND MIGRATION IN FISH

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Abstract

This paper reviews my hypothesis for the evolution of diadromous migration in fish (Gross, 1987; Gross *et al.*, 1988), and suggests additional hypotheses for amphidromy and intraspecific variation in migration.

Introduction

Movement from one location to another is common in fish. A different location may have fewer costs, such as less predation, competition or disease. Or it may provide higher

benefits, such as more food or mates. Switching locations to obtain greater net benefits (benefits minus costs) and thus maximize fitness (lifetime reproductive output) is a behavior that is often favored by natural selection.

In biology, the study of costs and benefits to behavior is known as behavioral ecology (Gross and Maekawa, 1989; Krebs and Davies, 1991; Gross, 1994), a field that has greatly increased our understanding of animal behavior. Here I take a behavioral ecology approach to understanding the evolution of diadromous fishes. First I note that diadromous species are not biologically unique, although they have unique migratory pathways. Next I review my hypothesis for the evolution of anadromous and catadromous migration (Gross, 1987; Gross *et al.*, 1988). I then suggest that amphidromous migration may be understood through differential costs, and end with a cost/benefit model to explain intraspecific variation in migration.

1. Definitions

Migration usually refers to a specific movement between habitats, typically involving departure and return within the lifetime of an individual. Fish which migrate between freshwater and ocean habitats are called diadromous, a terminology discussed in detail by McDowall (1987, 1988, 1992). The three major life histories of diadromous fishes are shown in Figure 6. Anadromy, catadromy and amphidromy are useful terms for

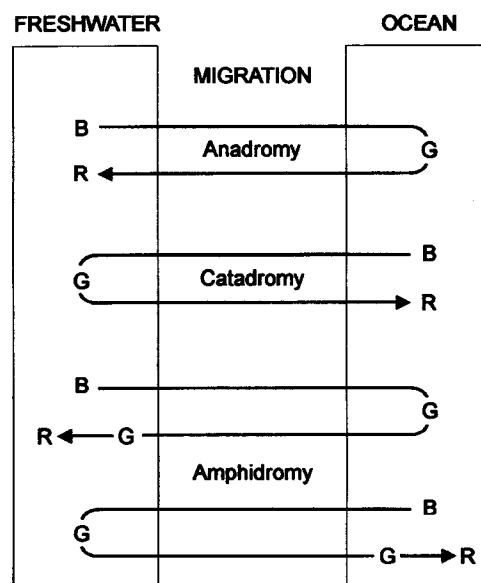


Fig. 6. The three life histories of diadromous fishes include occupation of freshwater and ocean habitats and migration between them. Anadromy (>87 species), catadromy (>41) and amphidromy (>60) are defined by the habitat in which birth (B), growth (G) and reproduction (R) take place. Modified from Gross (1987).

classifying migratory pathways; however, it is worth noting that diadromous species are not uniquely different from other fish species: (1) changes in osmoregulation similar to that between freshwater and ocean are found in many nondiadromous species; (2) diadromous species may be facultative with some populations or individuals not migrating across the freshwater/ocean boundary; and (3) diadromous species are generally similar in their life history traits such as egg size, age at maturity, body size or fecundity to nondiadromous species in the same taxonomic family (Gross, 1987). Therefore, diadromous fishes are not biologically unique and their migratory pathways can be understood evolutionarily from a consideration of costs and benefits as in any other fish species.

2. A hypothesis and test

The existence of contrasting pathways of migration such as anadromy and catadromy has long been perplexing. I hypothesized that anadromy has evolved when food resources in the ocean exceed those in fresh water while catadromy has evolved when freshwater food resources exceed those in the ocean (Gross, 1987). This hypothesis focuses on food and growth as being the primary selective agent favoring migratory behaviour. I tested this hypothesis in the following way. With my graduate student Ronald Coleman, I gathered together all known information on freshwater and ocean productivity along all latitudes in the Northern and Southern hemispheres. Next, with Robert McDowall, I reanalyzed data (McDowall, 1987) on the latitudinal ranges of all known anadromous ($N = 87$) and catadromous ($N = 41$) species. Both the productivity and species data were

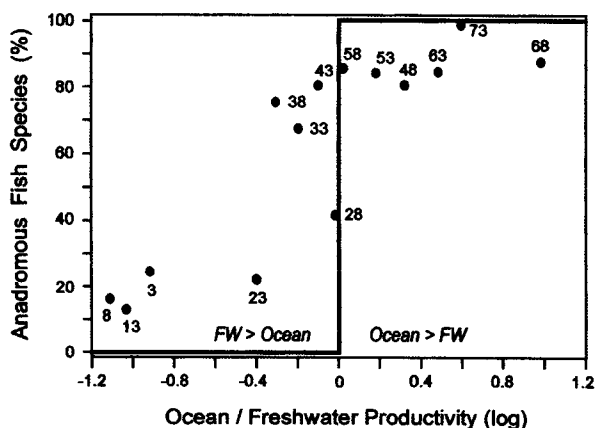


Fig. 7. The relation between relative productivity of the world's oceans and freshwaters and the proportion of diadromous fishes that are anadromous or catadromous. Ocean productivity is divided by freshwater productivity and both are measured as grams of carbon per meter per year. These calculations were made for each 5° latitude and thus approximate neighbouring oceans and freshwaters. Log productivity is zero when the productivity of neighbouring oceans and freshwaters is equivalent. The heavy bar is the theoretically predicted frequency of anadromy. The latitude for each point is shown. Modified from

analyzed for each 5Åinterval. The results, summarized in Figure 7, show that the occurrence of anadromy and catadromy follows the prediction: where the productivity of the ocean exceeds that of neighboring freshwaters, as many as 100% of diadromous fishes are anadromous. Conversely, where freshwater productivity exceeds that of neighbouring oceans, catadromy is the dominant form of diadromy. Where neighbouring oceans and freshwaters are similar in productivity, a threshold exists in the relative frequency of anadromy and catadromy. Thus, the differential productivity of aquatic habitats seemingly explains the contrasting directions of diadromous migration in fishes. Additional details of this analysis are provided in Gross *et al.* (1988). It will certainly be true that costs of migration and other possible benefits will help explain variation in the data, but the food availability hypothesis is surprisingly useful in explaining where diadromous fishes occur in the world, why they migrate across the freshwater-ocean boundary, and their direction of movement.

3. Why be amphidromous?

At present we do not have a particularly useful hypothesis for explaining the evolution of amphidromy. Although I suggested that amphidromy may have evolved from the habit of euryhaline wanderer (Gross, 1987), at the time I thought that amphidromy had most of its growth in the habitat to which the fish first migrated, and only some of its growth in the habitat to which it returned and was born. To my understanding now, however, most of the growth in amphidromy occurs after returning back to the habitat of birth (suggested by R. McDowall). In such case, amphidromy would seem to function more as escaping from the habitat of birth until being large enough to be able to profit from the resources there. I would suggest that for an explanation of amphidromy we look in the future at differential costs of occupying the habitat of birth compared to the alternative habitat, while small in size. Perhaps there tends to be higher predation rates on small individuals in the habitat of birth, for example. If so, it will make an interesting contrast that differential costs are the primary selective agent in the evolution of amphidromy, while differential benefits are the primary selective agent in the evolution of anadromy and catadromy.

4. Intraspecific variation

It is well established that not all members of a species or population are equally migratory. There is often a size-related pattern, as in salmonids where larger individuals are more likely to migrate anadromously (e.g., Kaeriyama, 1996). Gross (1987) gives a detailed life history model to show how even slight differences in costs and benefits of migration can affect whether diadromy occurs. This concept is visualized in Figure 8 for different body sizes within a population. Imagine that the benefit B for migrating, which is the difference in benefit gained in habitat 2 minus habitat 1 such as in growth, is relatively constant with juvenile body size, but that as in many fishes, the costs of migration C such as in mortality

decrease with body size perhaps because of greater swimming ability or energy storage. In such case, only certain individuals in the population, those individuals with a size above the threshold of $C = B$, are favored to migrate. Changes to C , such as the difficulty of migration due to water levels, or in B , such as in population size and thus competition for food resources in habitat 1, will alter the optimal size of migrating juveniles due to individual choice. It may also cause some populations not to migrate at all, if $C > B$ for all individuals. Thus, diadromous migration and its variability among species, populations and individuals can be understood through the study of costs and benefits, and fitness consequences from the movement between habitats.

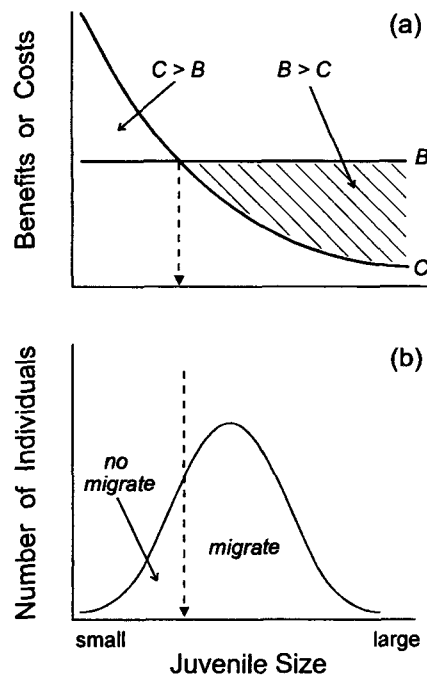


Fig. 8. Model for intraspecific variation in migration. (a) The benefit B is calculated from the difference in benefit in the birth habitat 1 and the alternative habitat 2, as for example the additional growth that can be obtained in habitat 2 above that in habitat 1. The cost C is due to migrating between habitats, as for example reduced survivorship or growth relative to staying in habitat 1. Although B is modeled as independent of body size, C decreases with increasing body size perhaps because larger individuals are better at migrating. (b) Only juveniles larger in body size than the intersection $B = C$ are favoured by natural selection to migrate. Smaller individuals should stay, or migrate later when they are larger.

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