

## Evolution of Diadromy in Fishes

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**Abstract.**—One of the major unresolved questions of diadromous fishes is how they evolved. In this paper, several issues in the evolution of diadromy are examined from the viewpoint of life history theory. The paper opens with a discussion of whether it is appropriate to use the term "strategy" in describing the biology of diadromous fishes since there is little evidence that diadromy arose through frequency-dependent intraspecific competition. Next, a comparison between diadromous and nondiadromous species reveals a similarity in their life history traits including egg size, fecundity, age at first maturity, and body size. Even comparisons between diadromous and nondiadromous populations within species reveals few life history differences. Thus, identification of fishes as "diadromous" is a subjective rather than an evolutionary classification. Third, one of the key questions for diadromy—when does natural selection favor habitat switching?—is addressed. The question is resolved through a life history model showing how natural selection operates on each component of a diadromous life cycle. To evolve, migration must maximize fitness or the lifetime product of reproductive success  $\times$  survivorship. Diadromy, therefore, occurs when the gain in fitness from using a second habitat minus the migration costs of moving between habitats exceeds the fitness from staying in only one habitat. The most important biological variable in explaining the presence and direction of diadromous migration is apparently the relative availability of food in sea and freshwater habitats. Since seas are often more productive than fresh waters in the temperate zone, while the reverse occurs in the tropics, both anadromy and catadromy can evolve. Finally, amphidromy is hypothesized to be an ancestral state in the evolution of anadromy and catadromy. Amphidromy will be evolutionarily stable, however, if there is insufficient advantage to completing adult development in a second habitat. This and future studies of life history evolution can provide much insight into the biology and effective management of diadromous fishes.

Although diadromous fishes have been the subject of numerous ecological (Foerster 1968; Leggett 1977; Northcote 1978; Peterman 1984), physiological (Hoar 1976; McKeown 1984), migrational (Groot et al. 1975; Quinn 1982; Hasler and Scholz 1983), systematic (Thomas et al. 1986; McDowall 1987, this volume), and distributional studies (Baker 1978; McDowall 1987), little attention has been directed towards understanding how diadromy evolved through natural selection. This paper aims to use life history theory to examine the evolution of diadromy in fishes. Its purpose is not to extensively review literature nor to examine a single topic in detail; rather, it attempts to clarify several key issues central to understanding how and why diadromy evolved.

The paper has three parts. The first focuses on clarifying the meaning of "strategies" and "tactics" as terminology for understanding the evolution of diadromous life histories. These terms

have been so often misapplied in the literature that their meaning now lacks substance (e.g., Kramer 1984). Since scientific progress and communication rely upon terminology (Ziman 1984; Cohen 1985), it is important to clarify the terms on which this symposium is based.

The second and major part of the paper addresses the evolution of diadromy by asking four questions. (1) What are diadromous fishes from a "life history" perspective rather than a "classification" perspective? (2) Why do fishes migrate? (3) What is the importance of sea and freshwater habitats in the evolution of diadromy? (4) What are the links between amphidromy, catadromy, and anadromy? A life history model is developed to help clarify how natural selection acts on the evolution of diadromy.

In the final part, some implications for the management of diadromous fishes arising from the study of their evolution are discussed.

### Strategies and Tactics

The term strategy is so widely used without definition that its meaning is often in doubt. From

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a life history perspective, strategy and tactic are defined as follows (Maynard Smith 1982; Gross 1984). A strategy is a genetically determined life history or behaviour program which has evolved because it maximizes fitness (lifetime reproductive success) under frequency-dependent intraspecific competition. Under intraspecific competition that is frequency-dependent, the fitness from a behaviour or life history depends upon the actions of others in the population. For example, if obtaining a territory were necessary for successful reproduction and depended upon body size, an individual's fitness at maturity would depend upon the size of other mature individuals in the population. In this case, size at maturity would evolve as a "strategy" because the optimal size for any individual would depend upon what size others in the population attained.

Strategies are composed of tactics: the ontogenetic stages of development or actions specifically used for achieving given life history or behaviour programs. Strategies therefore evolve through alterations in their tactics. For example, one tactic in a maturity strategy could involve an individual delaying maturity until it was larger in size than other members of the population. Should this tactic yield a higher fitness than other possible tactics, the maturity strategy which evolves in the population would include delaying maturity.

Not all genetic programs are strategic. Nonstrategic or "simple" life histories (Parker 1984) are those which evolve in the absence of frequency-dependent competition. For example, if fitness at maturity is not influenced by conspecific body size, then maturity will not be strategic; body size will evolve as a simple life history, independent of the size of conspecifics.<sup>2</sup>

Therefore, two very different kinds of life history evolution exist. On the one hand are strategic life histories which evolve to maximize fitness in response to competition among individuals sharing the same gene pool. On the other hand are simple life histories which evolve to maximize fitness in response to environmental conditions originating from outside the gene pool.

The distinction between simple and strategic life histories is an important one since simple life histories can be analyzed with optimization models (e.g., Alexander 1982; Jonsson et al. 1984),

while strategic life histories usually require more complex frequency-dependent or game theoretic models (e.g., Colman 1982; Gross and Charnov 1982; Maynard Smith 1982). Not only will the type of life history we expect to find influence our method of quantitative analysis, it will also affect our research hypothesis. As an example of why it is necessary to correctly distinguish between strategic and simple life history evolution, let us consider the case of precociously mature males in salmon populations. Precocious male salmon have long been viewed as a biological "mistake" because researchers were not aware of how precocity could evolve when all individuals were under the same environmental selection pressure. Recently, work analyzing precocity as a life history "strategy" (Gross 1984; 1985) has shown that precocious males can evolve as an alternative means for breeding. Through a combination of morphological and behavioural attributes, precocious males successfully circumvent the territorial defense of larger and older individuals.

At present, there is insufficient evidence to conclude whether diadromy has evolved as a simple or strategic life history in fishes. Some authors (e.g., Baker 1978; Northcote 1978; McDowall 1987) have summarized information which suggests that the migration of diadromous fishes may be a direct response to the environment (especially temperature, water level, or food availability). Others have suggested that migration behaviour may also be influenced by the actions of conspecific competitors (e.g., Gross 1985). Diadromy may, therefore, be a complex collection of life history traits, some of which are strategic and others simple in origin. Separating the relative contributions of competitive and environmental selection pressure should thus be an interesting direction for future studies of diadromy. Until the results of such studies are available, use of the term "strategy" to generally describe diadromous life histories is premature.

#### Evolution of Diadromous Habit

##### *What are Diadromous Fishes?*

The first question which should be addressed in a study of the evolution of diadromy is: What are diadromous fishes? In more detail: Are they different from other fishes? If so, in what way? Are diadromous fishes a real (biological) category, or an artificial category based on perceived needs to group and pigeonhole fishes?

<sup>2</sup>The term "simple" does not suggest triviality but designates that selection is from noncompetitive sources.

As defined by McDowall (1987), a diadromous fish is one which uses two habitats—specifically the sea and fresh water—during its life history. Use of these two habitats requires migration across a saline–freshwater boundary and thus the capability to osmoregulate in different salinities. While this provides a useful description of diadromous species, there are several problems with McDowall's definition.

First, multiple-habitat use, migration, and changes in osmoregulation are common to the biology of many fish species (Leggett 1977; Harden-Jones 1981; McKeown 1984). Desert pupfishes (*Cyprinodon* spp.), for example, cross salinity gradients in Arizona deserts that range from fresh water to several times the salinity of seawater (Hillyard 1981). Similarly, many fishes near inland saline lakes (e.g., the Great Salt Lake of Utah) regularly migrate between freshwater feeder streams and the lake's "estuaries" (Sigler and Miller 1963). Multiple habitat use and osmoregulatory changes during migration are, therefore, not unique biological features of diadromous fishes.

Second, crossing the sea–freshwater boundary is not an obligate but a facultative behaviour of many species labelled diadromous. For example, some populations of the brown trout *Salmo trutta* along the European coast migrate to the sea while others do not (Baker 1978). The same holds true for some Pacific salmon (*Oncorhynchus* spp.) in North America (e.g., kokanee *O. nerka*: Hanson and Smith 1967). An extreme form of facultative properties involves the coexistence within populations of both migratory and nonmigratory behaviour. In populations of Atlantic salmon *Salmo salar*, Arctic char *Salvelinus alpinus*, and brown trout, for example, some males and females may not take part in seaward migration at all (Jones 1959; Nordeng 1983; Jonsson 1985). Instead, they mature within fresh water. Since alternative migratory behaviours occur both among and within diadromous fish populations, crossing a sea–freshwater boundary is clearly not a biological requisite for being classified a diadromous species.

It is thus apparent that two of the three principal elements in McDowall's definition of diadromy—migration and the ensuing osmoregulatory changes—are not unique to diadromous fishes. Moreover, crossing the sea–freshwater boundary is only partially expressed in some species. While the key factor in defining diadromy may be crossing a geographical boundary, the biological importance of this remains open to question.

If diadromous fish species are a biological entity, uniquely different from other types of fishes, then a comparison of important life history traits such as egg size, fecundity, age at first maturity, and body size should reveal a significant general difference between diadromous and nondiadromous species. Past studies have shown that comparisons of such life history traits between evolutionary groupings invariably reveal differences (e.g., Stearns 1977). A comparison of representative diadromous and nondiadromous species from the same families reveals no generally significant differences (Table 1).<sup>3</sup> Diadromous species produce some of the smallest and largest egg sizes known, exhibit both early and late maturation, and are mature at both a small and large body size.

An even stronger test for differences in life history results from a comparison of diadromous and nondiadromous populations within species. The Salmoninae, a subfamily of the Salmonidae, has been selected for this analysis because a large, reliable data set is available. A comparison of eight life history traits between anadromous and nondiadromous populations of seven species reveals a significant difference in body size, with anadromous populations being larger for the same age at maturity (Table 2). As a consequence of this size difference, the anadromous form is more fecund (both in egg number and in ovary volume). However, this difference in growth rate is attributable to environmental differences (see below), and is not accompanied by changes in life history traits. Five of the eight traits examined, including age at maturity, maximum broods in lifetime, egg diameter, and hatching time, show no significant difference. Classifying fishes as diadromous or nondiadromous, therefore, provides little insight into their life history evolution. The answer to the question "Do diadromous fishes have unique life histories?" is no!

What then are diadromous fishes? They are a group of species which have been artificially (versus biologically) classified based largely on their habit of migrating between the sea and fresh water. This geographical boundary is a conceptual (rather than biological) distinction since similar osmoregulatory boundaries are crossed by landlocked fishes (e.g., desert pupfish). The classifi-

<sup>3</sup>Comparing species within the same families largely controls for complications of phylogeny (Harvey and Mace 1982).

TABLE 1.—A comparison of life history traits of representative diadromous and nondiadromous species (as classified by McDowall 1987). The mean  $\pm$  1 SD is given for species within each family (midvalues were used for each species). The number of species examined is in parentheses. Data are from Breder and Rosen (1966), Hart (1973), Scott and Crossman (1973), and Hutchings and Morris (1985). Two-tailed *t*-tests (Sokal and Rohlf 1981) are used to compare diadromous against nondiadromous species. The only significant difference is in salmonid egg size ( $P < 0.05^*$ ).

Diadromy status	Egg diameter (mm)	Age at maturity (years)	Maximum body length (mm)	Fecundity (1,000s of eggs)
<b>Petromyzontidae (lampreys)</b>				
Diadromous	0.96 $\pm$ 0.27 (3)	8.0 $\pm$ 1.4 (2)	488 $\pm$ 265 (5)	30.1 $\pm$ 26.6 (5)
Nondiadromous	1.04 $\pm$ 0.05 (4)	6.4 $\pm$ 0.7 (5)	240 $\pm$ 107 (5)	4.1 $\pm$ 4.5 (4)
<i>t</i> <sub>df</sub>	<i>t</i> <sub>5</sub> =0.6	<i>t</i> <sub>5</sub> =2.2	<i>t</i> <sub>8</sub> =1.9	<i>t</i> <sub>7</sub> =1.9
<b>Salmonidae (salmons)</b>				
Diadromous	5.27 $\pm$ 0.96 (13)	4.6 $\pm$ 1.5 (13)	1,035 $\pm$ 241 (13)	4.2 $\pm$ 2.8 (13)
Nondiadromous	2.77 $\pm$ 1.05 (8)	5.8 $\pm$ 3.5 (8)	812 $\pm$ 465 (8)	52.0 $\pm$ 91.1 (8)
<i>t</i> <sub>df</sub>	<i>t</i> <sub>19</sub> =5.6*	<i>t</i> <sub>19</sub> =1.1	<i>t</i> <sub>19</sub> =1.5	<i>t</i> <sub>19</sub> =1.9
<b>Osmeridae (smelts)</b>				
Diadromous	0.95 $\pm$ 0.05 (3)	2.7 $\pm$ 0.6 (3)	185 $\pm$ 31 (3)	24.1 $\pm$ 5.7 (3)
Nondiadromous	1.00 $\pm$ 0.00 (2)	1.5 $\pm$ 0.7 (2)	203 $\pm$ 56 (10)	34.0 $\pm$ 21.7 (3)
<i>t</i> <sub>df</sub>	<i>t</i> <sub>3</sub> =1.3	<i>t</i> <sub>3</sub> =2.1	<i>t</i> <sub>11</sub> =0.5	<i>t</i> <sub>4</sub> =0.8
<b>Clupeidae (herrings)</b>				
Diadromous	0.95 $\pm$ 0.07 (2)	4.0 $\pm$ 1.4 (2)	296 $\pm$ 89 (3)	102.6 $\pm$ 31.9 (2)
Nondiadromous	1.31 $\pm$ 0.36 (8)	2.7 $\pm$ 0.8 (5)	230 $\pm$ 158 (4)	110.8 $\pm$ 153.5 (5)
<i>t</i> <sub>df</sub>	<i>t</i> <sub>8</sub> =1.4	<i>t</i> <sub>5</sub> =1.6	<i>t</i> <sub>5</sub> =0.6	<i>t</i> <sub>5</sub> =0.1

cation of fishes as being either diadromous or nondiadromous is thus based on convenience rather than biology.

While the habit of crossing a sea-freshwater boundary appears to have little effect on life history traits, this migratory behaviour may still provide the key to understanding the so-called diadromous fishes. Three major evolutionary questions concerning migration in diadromous fishes are: Why migrate? What is the selection importance of the sea and freshwater habitats for migration? What are the evolutionary links among amphidromy, anadromy and catadromy?

#### Why Migrate?

Migration behaviour is widespread among fishes (e.g., Leggett 1977; Northcote 1978). When viewed from an evolutionary perspective, the only significant difference between the migration of diadromous species and that of nondiadromous species is the osmoregulatory cost associated with crossing the sea-freshwater boundary (but note the "landlocked" exceptions above). Diadromous migration is therefore part of the larger question of why any fish should migrate.

To answer this question, we need to consider how migration increases the evolutionary fitness of individuals that migrate relative to those that do

not. Fitness ( $W$ ) can be quantified by the lifetime summation ( $\Sigma x$ ) of an individual's probability of surviving to reproduce at any age  $x$  ( $l_x$ ) multiplied by its fecundity (or male fertility) and breeding success at that age ( $b_x$ ):

$$W = \Sigma l_x b_x.$$

Because migration involves switching habitats, we need to understand the contribution of each habitat to  $l_x$  and  $b_x$  as well as the costs of moving between these habitats (also in terms of  $l_x$  and  $b_x$ ). Migration costs include the energy and physiological mechanisms for osmoregulation, energetic demands of swimming, and exposure to predators or disease. Since the main characteristic of diadromy is alternation between habitats, a single migration model can be developed to explain the evolution of all three diadromous forms: amphidromy, anadromy, and catadromy (Figure 1).

The conditions for the evolution of diadromy in a nondiadromous population can be modeled as follows. In a nondiadromous population, individuals complete their entire life cycle in one habitat ( $H_1$ ). By contrast, a diadromous life history includes the use of one habitat ( $H_1$ ) for reproduction and early rearing, a juvenile removal migration ( $M_1$ ) which involves crossing the sea-freshwater

TABLE 2.—A comparison of eight life history traits of anadromous (A) and nondiadromous (ND) forms of seven species of *Salmo* and *Salvelinus*. Data are from Hutchings and Morris (1985). Two-tailed sign tests (Siegel 1956) are used to test for significant differences between A and ND means ( $P < 0.05^*$ ).

Species or statistic	Age at maturity (years)		Maximum broods in lifetime		Egg diameter (mm)		Hatching time (d)	
	A	ND	A	ND	A	ND	A	ND
<i>Salmo clarki</i>	4.0	3.5	6.0	7.0	4.70	4.70	45.5	45.5
<i>S. gairdneri</i>	4.0	4.0	5.0	5.0	4.00	4.00	47.5	47.5
<i>S. salar</i>	5.0	5.0	11.0	10.0	6.00	5.25	175.0	175.0
<i>S. trutta</i>	4.0	3.5	10.0	11.0	4.50	4.25	89.5	115.0
<i>Salvelinus alpinus</i>	7.0	8.0	18.0	12.0	4.35	4.30	180.0	72.0
<i>S. fontinalis</i>	4.5	2.5	5.0	8.0	4.25	3.85	125.0	125.0
<i>S. malma</i>	8.0	5.5	11.0	12.0	4.50	3.55	225.0	225.0
Mean	5.2	4.6	9.4	9.3	4.61	4.27	126.8	115.0
SD	1.6	1.8	4.6	2.7	0.65	0.56	69.6	67.1
Sign test	$P=0.376$		$P=0.688$		$P=0.062$		a	

<sup>a</sup> Excessive ties; data not significantly different.

boundary,<sup>4</sup> a second habitat for adult rearing ( $H_2$ ), and an adult return migration ( $M_2$ ) to  $H_1$  for reproduction. Thus the cost of the total migration  $M_T$  equals those of  $M_1$  and  $M_2$ . For simplicity, the analysis will be restricted to females and will assume that  $b_x$  is linearly related to growth, that growth rate is independent of size but dependent upon habitat, and that the species is semelparous (breeds once and dies). Under such conditions, the diadromous life cycle (D) may evolve in a nondiadromous population (ND) if:

$$W(D) > W(ND) \quad (1)$$

or

$$W(H_1 + H_2 + M_T)_D > W(H_1)_{ND}; \quad (2)$$

$$W(H_1)_{ND} = 1;$$

$g$  = growth rate of D relative to ND (D/ND);

$s$  = survivorship rate of D relative to ND;

$t$  = proportion of D spent in each life zone (i.e., for zones  $H_1 + H_2 + M_T$ ,  $t_1 + t_2 + t_m = 1$ ).

For a diadromous individual,

$$W(H_1) = t_1 W(H_1)_{ND} = t_1;$$

$$W(H_2) = t_2(g_2 \cdot s_2);$$

<sup>4</sup>Initial removal migration may be of eggs (rare), newly hatched larvae (common), or well-grown individuals (very common) (McDowall 1987). For simplicity, I consider the removal migration of well-grown individuals.

$$W(M_T) = t_m(g_m \cdot s_m).^5$$

It follows from expression (2) that

$$t_2(g_2 \cdot s_2) + t_m(g_m \cdot s_m) > 1 - t_1, \quad (3)$$

or

$$[t_2(g_2 \cdot s_2) + t_m(g_m \cdot s_m)]/[t_2 + t_m] > 1. \quad (4)$$

Diadromous migration will therefore evolve in a nondiadromous population (if there are appropriate mutations) when expression (4) is satisfied.

I now digress and explain why growth ( $g_x$ ) was substituted for the  $b_x$  benefit of migration. The answer is that fecundity in many species (Bagenal 1967), including diadromous fishes (Table 2), increases with body size and hence growth. Moreover, body size can also contribute to success during breeding since intrasexual fighting determines access to territories and mates in many species (Schroder 1982; Sargent et al. 1986; van den Berghe and Gross 1986). Finally, as will be shown later in this paper, growth is a key variable in diadromous migration.

This simple life history model specifies the growth and survivorship contribution of each habitat and can account for the migration costs between them. Substitution of appropriate values into expression (4) should allow us to calculate the fitness advantage of diadromy. Unfortunately, data appropriate for the model are not presently available because research on diadromous fishes

<sup>5</sup>Write  $t_{m,1}(g_{m,1} \cdot s_{m,1}) + t_{m,2}(g_{m,2} \cdot s_{m,2})$  to consider removal (1) and return (2) migration separately.

TABLE 2.—Extended.

Species or statistic	Maximum length (cm)		Length at maturity (cm)		Fecundity (number of eggs)		Egg production (egg size × number)	
	A	ND	A	ND	A	ND	A	ND
<i>Salmo clarki</i>	99.0	99.1	39.3	20.0	2,323	1255	10,918	5,899
<i>S. gairdneri</i>	122.0	91.5	50.0	42.0	4,483	1500	17,932	6,000
<i>S. salar</i>	140.0	99.0	67.0	21.5	11,196	2384	67,176	12,516
<i>S. trutta</i>	102.0	82.6	51.5	29.0	1,510	738 <sup>b</sup>	6,399	1,390
<i>Salvelinus alpinus</i>	96.0	55.0	63.0	27.7	4,582	1576	19,932	6,777
<i>S. fontinalis</i>	80.0	86.0	27.0	20.0	2,550	2550	10,838	9,818
<i>S. malma</i>	127.0	75.0	37.5	15.1	4,250	1412	19,125	5,013
Mean	109.4	84.0	47.9	25.0	4,413	1631	21,760	6,773
SD	20.9	15.5	14.3	8.9	3,223	635	20,657	3,552
Sign test	P=0.454		P=0.016*		P=0.016*		P=0.016*	

<sup>b</sup> Calculated from the original reference (Lee 1971) to replace the value in Hutchings and Morris (1985), which is incorrect.

has proceeded without the theoretical and evolutionary direction necessary to understand why diadromy exists.

Some insight into the costs and benefits of diadromy from existing data may be provided by a comparison of diadromous and nondiadromous forms within species (Table 2). Egg production by anadromous forms is, on average, threefold greater than that of their nondiadromous conspecifics. Therefore, the fitness advantage of anadromy may be threefold through the enhancement

of  $b_x$ .<sup>6</sup> These data do not, however, indicate the  $l_x$  cost in obtaining the threefold  $b_x$  advantage. In our model, egg production must be devalued by the survivorship costs incurred as a consequence of migration. Moreover, mortality during maturation in the sea could exceed potential adult mortality in fresh water. Perhaps the only reasonable conclusion from these data is that diadromous fishes may have as much as a threefold higher mortality than nondiadromous fishes and still be favored in evolution.

Thus, one important use of the life history model is that it allows us to quantify the relationship between growth and mortality in the evolution of diadromy. The model also clarifies how growth and mortality may interact. The variables  $g$ ,  $s$ , and  $t$  each have three or more values—one for each habitat and one for the costs of migration.<sup>7</sup> The combination of these independent variables can result in some surprising conclusions about fitness.

The effect of combining the variables is illustrated in the following example. Figure 2 has four time periods: (1) while fish are in the early rearing habitat ( $H_1$ ); (2) during juvenile migration ( $M_1$ ); (3) while adults are in the rearing habitat ( $H_2$ ); and (4)

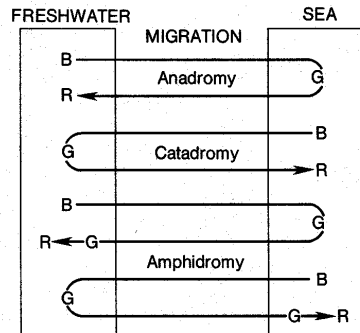


FIGURE 1.—The three life histories of diadromous fishes (McDowall 1987). Each life history includes occupation of freshwater and sea habitats and migration between them. Anadromous, catadromous, and amphidromous life histories are defined by the habitat in which birth (B), growth (G), and reproduction (R) take place. Some growth may occur in the habitat of birth.

<sup>6</sup>Threefold is probably a minimum estimate since the larger size of diadromous individuals will further increase  $b_x$  through increased success in breeding competition.

<sup>7</sup>The variables contribute independently in our model. "Dynamic optimization," however, would allow for interaction among the variables (see Mangel and Clark 1986).

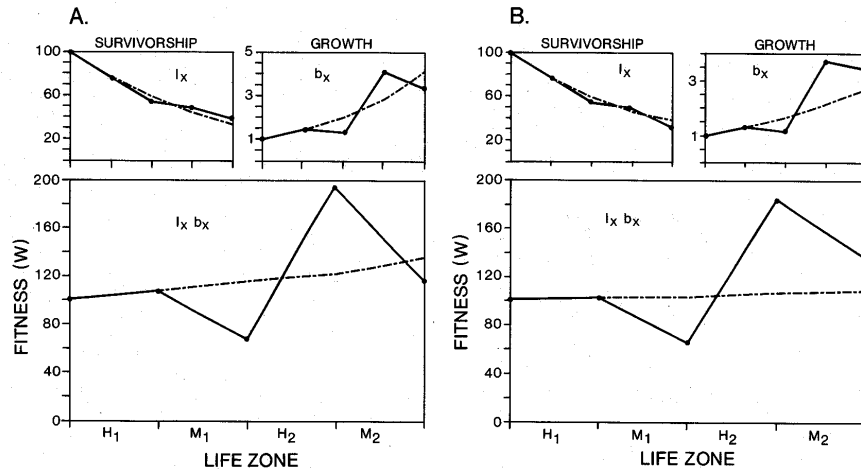


FIGURE 2.—Responses (A, B) of the fitness of diadromous fishes to growth and survivorship in the habitat for early rearing ( $H_1$ ), during juvenile migration ( $M_1$ ), in the habitat for adult rearing ( $H_2$ ), and during adult migration ( $M_2$ ). The solid line indicates the diadromous life history, the broken line the nondiadromous life history. In case B,  $H_1$  survivorship has been increased 2.6% and growth rate decreased 7.0% from those of case A.

during adult return migration ( $M_2$ ). For simplicity, the amount of time spent in each period is assumed equal ( $t_1 = t_2 = t_m$ ), and the following values are held constant:  $g_2 = 3.2$ ;  $s_2 = 0.9$ ;  $g_m = 0.9$ ;  $s_m = 0.7$ . These values mean that in  $H_2$ , a fish's growth is more than tripled and 90% of individuals survive. However, migration decreases body size by 10%, and survivorship during migration is only 70% (assumed the same for both juvenile and adult migration).

In Figure 2A,  $H_1$  provides 76% survivorship ( $s_1 = 0.76$ ) and 40% increase in body size ( $g_1 = 1.4$ ). From survivorship considerations alone, a diadromous life history is favored because the enhanced survivorship in  $H_2$  relative to that in  $H_1$  is greater than the mortality costs of migration between the habitats. However, growth favors the nondiadromous life history even though the growth in  $H_2$  exceeds that of  $H_1$ . The difference is simply not enough to allow for the costs of migration. Thus, while a survivorship advantage favors diadromy, growth does not. Which life history will evolve can be determined through a fitness calculation ( $\sum l_x b_x$ ) and, in this case, a nondiadromous life history is favored (Figure 2A). Thus, even when the potential fitness gains in  $H_2$  exceed those in  $H_1$ , migration will not be favored because of the costs in moving between these habitats.

Now imagine that a change in  $H_1$  increases survivorship by 2.6% ( $s_1$  now equals 0.78 rather than 0.76) and decreases growth by 7.0% ( $g_1 = 1.3$  rather than 1.4) (Figure 2B). When survivorship alone is considered, a nondiadromous habit is favored. By contrast, the growth advantage realized in  $H_2$  will favor a diadromous habit even when the migration costs are included. Here, the calculation of fitness shows that the growth advantage outweighs the survivorship costs and that a diadromous life history will evolve.

This example shows how even minor changes in  $g$  and  $s$  will have a major impact on the evolution of diadromous fishes. The sensitivity of the model's results may also explain why closely related species, and even populations within a species, have evolved different life histories.

In summary, our model shows that differences in growth rate alone or mortality alone between habitats will not predict migration behaviour. Furthermore, the difference in habitat quality,  $W(H_2) - W(H_1)$  where  $W(H_1) = 1$  by definition, must be positive for migration to evolve. That is,  $H_2$  must give a greater growth rate  $\times$  survival advantage if natural selection is to favor a migratory strategy. Finally, the costs of migration,  $t_m(g_m \cdot s_m)$ , including, the physiological costs of changing osmoregulation, increased predation, and the energetics of

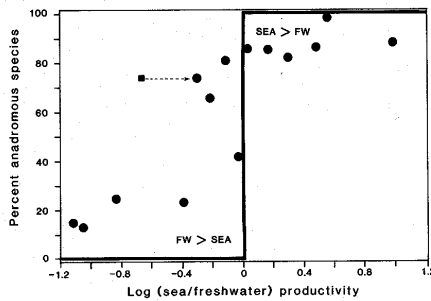


FIGURE 3.—The relationship between percent anadromous species,  $100(\text{anadromous species})/(\text{anadromous} + \text{catadromous species})$ , and the relative productivity of neighbouring seas and fresh waters (FW). Productivity is grams carbon fixed per square meter per year (from Gross et al., unpublished). The point marked by the square would be further to the right, as indicated by the arrow, were it not for a single anomalous value for freshwater productivity.

moving between habitats, must be considered. Even if  $W(H_2) - W(H_1) > 1$ , fish will be favored to remain in  $H_1$  when this difference is less than  $t_m(g_m \cdot s_m)$ .

#### What is the Importance of Sea and Freshwater Habitats?

The use of both sea and freshwater habitats is by definition the single pattern characteristic of diadromous species. Can the relative effects of these two habitats on  $b_x$  and  $l_x$  explain why diadromy evolves?

Baker (1978) and Northcote (1978) suggested several biological reasons why  $b_x$  and  $l_x$  could be enhanced by movement between sea and freshwater habitats. For example,  $b_x$  could be affected by differences in food resources or temperature conditions between the seas and fresh waters. Decreased predation, less disease, or favorable abiotic conditions could increase  $l_x$ . These authors could not determine, however, which of these selective factors was most critical to the evolution of diadromy.

Baker and Northcote also noted a latitudinal trend in the incidence of anadromy and catadromy. Conclusive evidence that anadromy is more frequent in cold temperate latitudes while catadromy is relatively more common in the tropics has been provided by McDowall (1987). In terms of life history theory (see also Baker 1978), the selection gradient for northern fishes must

therefore be positive in the sea direction while that for tropical fishes is in the freshwater direction.

Following Northcote (1978), Gross, R. M. McDowall, and R. C. Coleman (unpublished) assimilated existing data on primary productivity in freshwater and sea habitats to test the importance of food production in the evolution of diadromy. They found that in northern latitudes sea productivity exceeded that of fresh water, while in tropical latitudes freshwater productivity exceeded that of the sea. Moreover, the incidence of diadromy increased with the relative differences in freshwater and sea productivity. Finally, when relative productivity is plotted in relation to the frequency of anadromous and catadromous fishes, it becomes clear that differential productivity and thus growth resources are a key factor in the evolution of anadromy and catadromy (Figure 3). In short, diadromous migrations have evolved to track aquatic productivity.

Experimental evidence also supports this conclusion. Norwegian populations of Arctic char have both resident and anadromous individuals that belong to the same gene pool—that is, a single individual may become either anadromous or resident. Nordeng (1983) experimentally produced crosses between resident and anadromous individuals and reared the progeny under three feeding regimes: low, moderate and high. He found that increasing the amount of food significantly increased the proportion of resident individuals in his crosses at the expense of anadromous fish. The fish were thus able to facultatively adjust to the increased productivity of their freshwater habitat and respond by not migrating. In terms of our model, expression (4) was no longer satisfied, at least for some individuals, when Nordeng increased  $g_1$  relative to  $g_2$ .

In summary, while survivorship considerations are important for understanding diadromy, the relative productivity or growth advantage of sea and freshwater habitats appears to be key to its evolution. The productivity differential can probably explain why fish migrate across the sea-freshwater boundary, predict their direction of movement, and account for where in the world diadromous species occur.

#### Amphidromy, Anadromy, and Catadromy

Considerable insight may be obtained into the phylogeny of amphidromous, anadromous, and catadromous fishes by analyzing their relationships in light of the above results. For example,



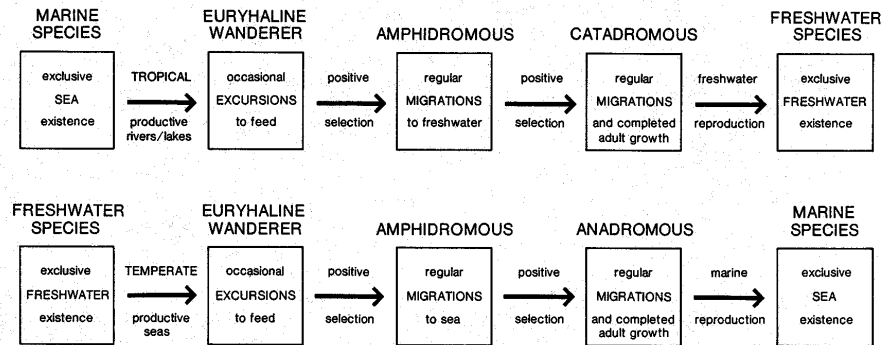


FIGURE 4.—Overview of the evolution of diadromy in fishes.

tropical marine fishes will be more likely to cross into fresh water as facultative wanderers than temperate marine fishes, because freshwater productivity often exceeds that of marine waters in the tropics. This would suggest that amphidromous fishes in the tropics are of marine origin. Moreover, continued residual selection after amphidromy, favoring adult specialization in the tropical freshwater habitat, will give rise to the evolution of catadromy (Figure 4). By contrast, freshwater fishes are more likely to cross into the sea as facultative wanderers in cold temperate and subpolar regions. Selection will first favor the evolution of an amphidromous habit. Continued selection will eventually give rise to an anadromous life history. Temperate amphidromous fishes may thus be of freshwater origin (Figure 4). Finally, selection may favor including the reproductive phase within the habitat of adult growth because this removes the costs of migration. Therefore, some marine fish species in temperate latitudes are probably of freshwater origin, while some freshwater species in tropical latitudes may be of marine origin (Figure 4).

Several lines of evidence support the above evolutionary hypothesis. First, several taxonomic groupings of fishes are known to include both marine and freshwater species (Nelson 1984). Second, the freshwater fauna of New Zealand, Australia, and the Hawaiian Islands is suspected to be of marine origin (McDowall 1978; Merrick and Schmida 1984). Third, some populations of pink salmon *Oncorhynchus gorbuscha* spawn in saline estuaries and spend the rest of their lives in the high seas (Morrow 1980), a behaviour suggesting that the pink salmon, classified as a diadro-

mous freshwater species (McDowall 1987), could be evolving towards exclusive use of marine habitats.

#### Management Implications

Several implications for the management of diadromous fishes emerge from this study of their evolution.

(1) The life history model presented here and the experimental work of Nordeng (1983) demonstrate that growth perturbations can have profound and possibly deleterious effects on diadromous fish management. A case in point is the recent practice by North American hatcheries of releasing smolts of Pacific salmon (*Oncorhynchus* spp.) at a larger than natural size to increase survivorship. This practice resulted in a significant increase in precocious maturity among males (Bilton et al. 1982) and, as a consequence, a decrease in total fish biomass—an outcome contrary to management objectives.

We should thus expect any alteration in natural habitats which affects food resources to perturb the selective pressures for migration. The increasing eutrophication of freshwater habitats, for example, will likely result in some fresh populations no longer migrating to the sea. Continued "fertilization" of freshwater lakes to enhance the growth rate of juvenile sockeye salmon *Oncorhynchus nerka* (Hyatt and Stockner 1985) could well select for nonanadromous populations of this species. Without consideration of the life history consequences of migration, such management of diadromous fishes is an unscientific exercise.

(2) The increased growth, fecundity, and thus

biomass characteristic of diadromous species may suggest that they have robust life cycles. However, such logic is not sound from the perspective of life history theory. Consider, for instance, that evolutionarily "robust" species are often low in abundance (e.g., top-level predators), and that many species which were once abundant have been driven close to extinction by a slight alteration to their environment (Soule and Wilcox 1980). The absence of a relationship between abundance and robustness results because no species gets "ahead" in evolution—each evolutionary progression forward is eventually matched by a balanced cost (red queen hypothesis: Van Valen 1973).

Furthermore, because diadromous fishes do not have strikingly different life histories from nondiadromous fishes, it is unlikely that the stability of their recruitment process will differ. Therefore, no theoretical justification exists for proposing different stabilities of anadromous and marine stocks simply based on freshwater-sea migration behaviour.

(3) Because diadromous fishes depend upon the integrity of multiple habitats, their life histories may be more "fragile" than those of nonmigratory species. Imagine a 0.5 probability of habitat degradation by humans. If the degradation of habitats is an independent event, and the time spent by fishes in each habitat is equal, then the probability that two habitats remain suitable is  $0.5 \times 0.5 = 0.25$ . However, since destruction of any one habitat may prevent successful reproduction and survival of a diadromous fish, we must calculate the probability that either one or the other is degraded. This probability is 0.75 or  $1 - (0.5 \times 0.5)$ . Thus, a fish using only one habitat has a 25% better chance of survival than one using two habitats.

Why then do fish species become dependent upon multiple habitats when this decreases their long-term probability of survivorship? The answer is that neither "foresight" nor "group selection" (where population rather than individual traits are favored: Williams 1966) is molding life history evolution in most fishes. What may be maladaptive in the long term is a natural consequence of fitness advantages at some point in an evolutionary history.

#### Conclusions

Whether or not diadromous life cycles have evolved as "strategies" remains open for question. Research directed at determining the relative

contribution of conspecific "conflict" and environmental "opportunity" in the natural selection of diadromy may resolve this issue.

Diadromous species do not have life history traits which are uniquely different from nondiadromous species. A classification system which groups fishes as being either diadromous or nondiadromous is a subjective one, based on crossing a geographical boundary (sea-fresh water). It is not a biological or evolutionary one, based on life history theory.

The key to the evolution of diadromy lies in understanding natural selection for habitat switching. Switching habitats may impact on two important life history parameters: reproductive success ( $b_x$ ) and survivorship ( $l_x$ ). Since selection for diadromy will occur only if  $\Sigma l_x b_x$  is maximized, increasing either reproductive success alone or survivorship may not favor diadromy. The migration model formulated here suggests that the necessary conditions for diadromy to evolve are:

$$[t_2(g_2s_2) + t_m(g_m s_m)] / (t_2 + t_m) > 1,$$

where  $g$  and  $s$  are the measurements of  $b_x$  and  $l_x$  in alternative habitats, and  $t$  is the proportion of time spent in each part of the life cycle. Therefore the growth and survivorship advantages of utilizing a second habitat, plus the costs of moving between habitats, must exceed the advantages of staying in only one habitat ( $=1$ ) for the same period of time. Even slight variations in these three variables may greatly influence natural selection for the evolution of diadromy. This model could be successfully used to direct future research into the biology of diadromous fishes.

The relative availability of food in sea and freshwater habitats appears to be the key factor driving the evolution of diadromy. Anadromy has evolved when food resources in the sea exceed those in fresh water while catadromy has evolved when freshwater food resources exceed those in the sea.

Selection for diadromy has probably been responsible for the colonization of tropical fresh waters by certain marine fishes. It may also have contributed to the marine fauna of temperate latitudes. Species of Pacific salmon (*Oncorhynchus* spp.) are an interesting example of the possible divergence of a freshwater genus into primarily marine, anadromous, and freshwater species (pink, coho, and "residual" sockeye salmon, respectively). Studies in fish phylogeny will gain considerable insight from a consideration of the evolution of diadromy.

The life histories of diadromous fishes are sensitive to changes in growth rate. Therefore, any management programs which impact on growth rate (e.g., hatcheries and lake fertilization) will perturb the behaviour of diadromous fishes. Examples include the overproduction of precociously mature males in salmon as a consequence of hatchery practices and the possible unintentional production, through lake fertilization, of freshwater populations from species which are presently anadromous.

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