Behavioural Ecology of Teleost Fishes

Edited by

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2 Fish migration: an evolutionary perspective

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2.1 Introduction

The study of fish migration has been dominated by the description of migratory trajectories and of the proximate control of orientation behaviour (e.g. Harden Jones 1968; McCleave *et al.* 1984; McKeown 1984; Smith 1985). Although fascinating in themselves, these themes are generally not concerned with the most central assumption of behavioural ecology, that individuals behave so as to maximise their reproductive success or, rather, their inclusive fitness (Krebs and Davies 1993). The purpose of this chapter is to relate migratory behaviour to reproductive success in fishes. The coverage of the subject is more selective than exhaustive. Although I focus principally (but not exclusively) on 'diadromous' migrations (between freshwater and marine habitats), I have not dealt with the ultimate causes of variability in the rates of homing to and straying from natal habitats. The reader is referred to Quinn (1985) and Kaitala (1990) for a treatment of the latter. The population genetic consequences of varying levels of gene flow among locally-adapted populations is beyond the scope of this chapter.

Migration means to move from one place to another. Landsborough Thompson (1942) classified three types of movement patterns: local and seasonal movements, dispersals, and true migrations. Harden Jones (1968) qualified local and seasonal movements as 'merely changes of ground at a particular time of the year' that may involve short or long distances. This category involves foraging behaviour, defined in the context of spatial displacement as 'reiterative locomotor activity that is readily interrupted by an encounter with a resource item of one particular kind' (Kennedy 1985). Such movements may occur at time periods ranging from seasonal to semi-diurnal and in both the horizontal and vertical planes. Dispersal involves wandering away from the breeding habitat over a wide area, but with the majority of individuals remaining near the breeding habitat. This is in contrast to a 'true' migration, which involves movement between widely-separated and well-defined areas, 'a shift in what may be called the centre of gravity of the population' (Landsborough Thompson 1942).

Given the great diversity of animal movements, attempts to place specific examples into discrete categories are inevitably unsatisfactory (McKeown 1984). I will not attempt such a categorisation here. Rather, I will limit my discussion of migration to the regular coming and going of fish on a seasonal basis that involves a shift in the distribution of all or part of a population between habitats (Harden Jones 1984). Such movements include a return to habitats previously occupied. From an evolutionary perspective, migration involves specialised behaviours that have arisen through natural selection (Dingle 1980). An appropriate starting point for behavioural ecology is to ask how migration influences the fitness of individuals that express such behaviour. Migration confers many advantages, including increased feeding, avoidance of adverse environmental conditions, and improved current reproductive success (Northcote 1978). Migration also has associated costs, including the actual energetic cost of displacement, risks of increased predation, the energetic and developmental costs of any special migratory adaptations, and potential reproductive costs due to decreased lifetime reproductive effort (Rankin and Burchsted 1992). Obviously, benefits must exceed costs on average for migratory behaviour to evolve. Fitness may be defined as the lifetime summation 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 (m_x). Therefore, a migratory life style will be favoured by natural selection if the contribution to $l_x m_x$ of each habitat occupied by a migrant, minus the cost of moving between habitats in terms of $l_x m_x$, exceeds the fitness of a non-migrant who completes the entire life cycle within one habitat (Gross 1987). This model, developed by Gross (1987) to explain the evolution of diadromous migrations, is based on the premise that a migratory strategy would be favoured by selection only if the adult feeding habitat provides a fitness benefit that exceeds the fitness advantage of staying in the juvenile rearing habitat. This assumes that the evolutionary origin of the migratory lifestyle is to be found in an advantage of leaving the habitat used for reproduction and early rearing.

The evolution of many migratory patterns may also be the result of reproductive adults placing their eggs in habitats in which the early survival and growth of their offspring are maximised. As density-dependent mortality occurs early in the life of fishes and declines with age (Cushing 1975), the greatest contributions to reproductive success in many migratory species may thus be achieved by maximising early survival. The location of spawning sites and the timing of reproduction in fishes is often population-specific and is thought to be linked, through natural selection, to ecological conditions (e.g. predation risk, habitat productivity) that favour early growth and survival (Leggett 1985, and references therein). Any evaluation of the evolution of migration should therefore begin with a consideration of the reproductive environment. This is not a new idea; Fulton (1889, cited in Sinclair 1988) originally proposed that offshore spawning areas were chosen as a function of the safety of floating eggs and larvae and their transport to places

suitable for the welfare of the juveniles. This point of view is most clearly illustrated by examples of reproductive habitats in which species could never have completed a non-migratory lifestyle. Capelin, *Mallotus villosus*, and grunions (e.g. *Leuresthes tenuis*) are marine fishes that spawn on beaches and their eggs develop in the gravel (Taylor 1990). Other high-intertidal spawners typically place eggs in protected sites near the high-tide line, including the mummichog, *Fundulus heteroclitus*, whose eggs develop in air (Taylor 1990). These species could not exist as non-migratory populations in such habitat. Ephemeral aquatic habitats such as flood plains and tide pools that are subject to periodic dessication, but used by many fishes as reproductive habitat, could never support non-migratory populations. Goulding (1980) identified 11 genera of large characins that descend nutrient-poor tributaries of the Rio Madera basin and spawn either adjacent to or in the nursery habitats of the expanded Rio Madera flood plain. On both Atlantic and Pacific coasts, sticklebacks (Family Gasterosteidae) spawn in tidal salt-marsh pools from which the young must migrate before the pools dry up or are choked by the growth of macroalgae (FitzGerald 1983). I am not implying that all reproductive and juvenile rearing habitats are unsuitable for adult fishes. Rather, the above examples serve to illustrate that the evolution of fish migration may best be understood by considering the fitness benefits that accrue to individuals who migrate to and exploit specific reproductive habitats, as well as the fitness benefits that accrue to fish following their emigration from the reproductive habitat.

2.2 Patterns of migration and the evolutionary significance of the reproductive habitat

Migration patterns have traditionally been described with reference to freshwater and marine habitats: oceanodromous migrations occurring entirely in the oceans, potamodromous migrations occurring entirely in fresh water, and diadromous migrations that involve crossing the saline–freshwater boundary (Harden Jones 1968). These simple categories hide a broad range of migration patterns and life-history adaptations and are not sufficient for an evolutionary consideration of migration. Since the salinity of aquatic habitats is only one of a large number of variables that may influence the reproductive fitness of fishes, the continued categorisation of migrations according to salinity serves no useful purpose beyond providing the most superficial of descriptive categories.

A large body of literature supports the contention that the associations of larvae and juveniles with specific environmental conditions are adaptations to increase fitness. Although such studies have mainly been the purview of population biologists, much of this work illustrates that spawning is coordinated in time and space with conditions that favour the survival of offspring during early life-history stages (see below). Stochastic fluctuations in these conditions may generate variations in reproductive success among individuals, as well as causing variations in population size. Migration of adults to particular spawning sites

and the subsequent passive or active migration of larvae to nursery sites may be considered adaptations to reduce the impact of environmental fluctuations on the survival of larvae and, consequently, on lifetime reproductive success (Leggett 1985).

2.2.1 Survival of the early life-history stages

The major determinants of survival during early life-history stages are considered to be starvation and predation (Wooster and Bailey 1989). Cushing's (1975) match–mismatch hypothesis emphasises the importance of starvation, and states that larval mortality is determined by the availability of food when fish larvae switch to exogenous feeding after yolk-sac absorption. Yolk-sac absorption should therefore coincide with the abundance peak of their food resources. Since planktonic crustaceans (mainly copepods) are the most important single source of food for most fish larvae (Bone and Marshall 1982), the magnitude of primary production and the fraction of it consumed by copepods may well determine survival during early life-history stages. Ephemeral and localised mixing events in the water column allow rapid bursts in production of large phytoplanktonic cells, which may account for most production that is grazed by copepods (Legendre and Le Fèvre 1989). Such events, including the pycnocline on the vertical axis, eddies, fronts and upwelling areas on the horizontal axis, and temporal transitions in vertical stability with periodicities ranging from annual to tidal along the time axis, may be tracked by the reproductive cycles and migratory patterns of fishes if their occurrence is predictable in both time and space.

A number of field studies have demonstrated that the spawning of marine fish is linked to tidal and coastal shelf fronts, and the accumulation of larval fish in these areas has been interpreted as a process likely to enhance survival (reviewed by Heath 1992). The relationship between fish spawning patterns and the timing of annual plankton production cycles is not clearly established and remains controversial. For example, peak spawning for several important marine species in continental shelf waters of northeastern United States is synchronised temporally with increasing abundance levels of their copepod prey, whereas other species continuously produce larvae over more prolonged periods, possibly allowing these populations to respond rapidly to favourable conditions (Sherman *et al.* 1984). The timing of cod, *Gadus morhua*, spawning is coupled to the timing of plankton production in the Northwest Atlantic ocean, but only a general correspondence between larval fish production and planktonic production exists rather than a precise one as required by the original match/mismatch hypothesis (Myers *et al.* 1993).

In temperate coastal areas, patterns of migration and spawning may be adaptive responses to historical patterns of predation (Frank and Leggett 1985). The inverse correlations observed between the abundance of macroinvertebrate predators and ichthyoplankton in coastal Newfoundland (Canada) result from their occupation

of discrete water masses, whose presence in the coastal area oscillates temporally in response to changes in wind direction. Frank and Leggett suggested that such adaptations involve active behavioural responses of fish to reliable physical and/or biological signals indicative of the existence of ecological 'safe sites'. For example, capelin spawn on gravel beaches at the head of bays along the eastern coast of Newfoundland, where their eggs and young are exposed to different types of coastal water masses. Prevailing westerly winds cause warmer water to be blown seaward and to be replaced by cold, subthermocline waters that upwell along the coast. Easterly winds re-establish the warmer coastal water masses, but are infrequent, unpredictable and of short duration. The biomass of the principal food of larval capelin is 2–3 times greater in the warm surface water mass, whereas the densities of their major predators are 3–20 times lower. Upon hatching, capelin larvae accumulate in the top 20 cm of the beach gravel and then emerge synchronously during onshore, wind-induced coastal water-mass exchanges. As a result, larvae are associated with water masses that are rich in food and poor in predators; these conditions should enhance larval survivorship (reviewed by Leggett 1985).

Refuge from predation may also influence patterns of migration and spawning in tropical waters. In the coastal tropics, many marine species move offshore to spawn in deep waters and larvae are subsequently transported onshore by prevailing currents (Johannes 1978). Whereas offshore tropical surface waters are relatively plankton-poor and provide less food for pelagic larvae, the threat of predation there is greatly reduced because these waters contain fewer planktonic and pelagic predators than inshore waters and are devoid of demersal and benthic predators. Johannes (1978) thus views offshore spawning as an adaptation to remove offspring from the intense predation pressure occurring in nearshore regions.

The transport of eggs and larvae away from favourable nursery areas may result in increased predation or starvation and has been demonstrated to reduce survival (Wooster and Bailey 1989). Parrish *et al.* (1981) hypothesised that spawning by fishes in the upwelling zone of the California current is adapted to counteract the adverse effects of offshore transport of eggs and larvae. They provided examples of species that spawn at particular times and places to minimise offshore transport. In contrast, Sinclair (1988) proposed that starvation and predation (identified as food chain processes) are not the principal determinants of spawning strategies, presenting examples of populations whose spawning times were not related to the annual production cycle. Sinclair (1988) viewed the aggregation and retention of planktonic larvae within specific areas as principally an adaptation to insure population persistence. Individuals that are 'lost' (vagrancy) from their population at any point in the life cycle and do not find a mate that is a member of the same population do not contribute to population persistence. Loss of individuals from the rearing area may thus influence individual fitness in two ways: mortality due to unfavourable conditions, and the possibility that lost individuals are unable to

reproduce with members of their own population. Implicit in the latter proposal is that individuals who spawn with members of other populations suffer a reduction in fitness. However, if vagrants successfully reproduce in new areas, great selective value may accrue to such individuals if their offspring are associated with areas that are favourable for survival. It seems evident that vagrancy (*sensu* Sinclair 1988), or straying, is necessary to avoid extinction. As climatic fluctuations alter the availability of suitable habitat, straying promotes the colonisation of new habitats (Northcote 1978; Bowen *et al.* 1992).

2.2.2 The evolution of diadromy

Few topics in fish migration have generated more debate than the evolutionary origins of diadromy. Anadromous fish reproduce in fresh water and migrate to sea where they grow to maturity, whereas catadromous fish reproduce at sea and grow to maturity in fresh water. Amphidromous fish migrate between the sea and fresh water, but not for the purpose of breeding. The migrations occur regularly at some other stage of the life cycle. Two forms of amphidromy have been recognised: marine amphidromy, in which spawning is marine and the larvae or juveniles reside temporarily in fresh water before returning to sea to grow to maturity, and freshwater amphidromy, in which spawning is in fresh water and the larvae or juveniles are temporarily marine before returning to fresh water to grow to maturity (see McDowall (1988) for definitions and a review of diadromy). Baker (1978) noted a latitudinal trend in the occurrence of diadromy, with anadromy occurring more frequently at higher latitudes and catadromy being more frequent in the tropics. Northcote (1978) proposed that this trend may be a result of oceanic waters usually being less productive in the tropics than in temperate or polar areas. Expanding on this hypothesis, Gross (1987) and Gross *et al.* (1988) postulated that diadromy evolved as a response to the productivities of the marine and freshwater environments. Assuming that access to food resources for the growth of adults is the most important fitness benefit accrued from diadromous migrations, these authors demonstrated that oceans are more productive than fresh waters in temperate latitudes where anadromous species predominate. In contrast, catadromous species generally occur in tropical latitudes where freshwater productivity exceeds that of the ocean.

Although appealing in its apparent explanatory power, the simplicity of this food-availability hypothesis hides the complexity of the diadromous life style and the possibility that diadromy may have evolved for different reasons. An important problem concerns the classification of fishes as anadromous or catadromous, a categorisation that is overly simplistic and at times misleading. The hypothesis was based on the global geographic distribution of diadromous species as classified by McDowall (1988). A reading of the detailed analyses of anadromous and catadromous species presented by McDowall (1988) reveals that only 34% of anadromous and 34% of catadromous species actually match the generally accepted definitions of the two groups (Fig. 2.1). The classification of 24 and 42% of

Anadromous fishes (n=110)
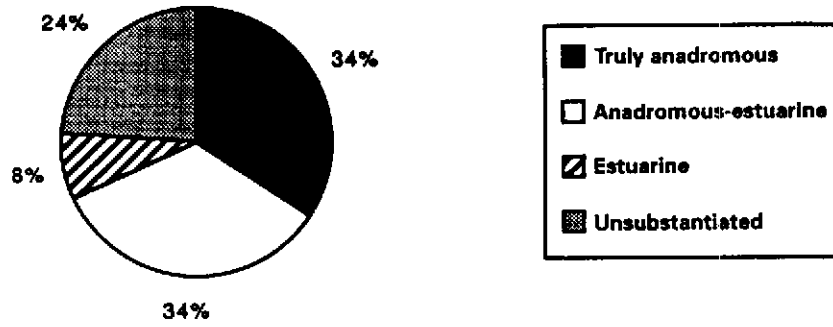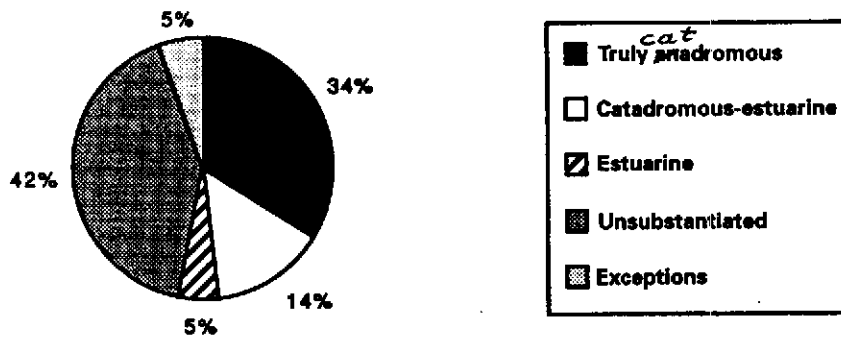

Catadromous fishes (n=56)

Fig. 2.1   The reclassification of 110 anadromous species and 56 catadromous species classified by McDowall (1988). See text for definition of categories.

species as anadromous and catadromous, respectively, was not substantiated in the detailed analyses presented by McDowall (1988). The life histories of these latter species are so poorly documented that insufficient knowledge precludes any reliable classification beyond euryhaline or 'marginally' diadromous. More detailed information on the life cycle of these species and the habitats that they exploit are needed to improve our understanding of diadromy.

A significant proportion of fishes classified as anadromous or catadromous exhibit life cycles that occur largely in estuaries or coastal areas influenced by freshwater outflow. The life history descriptions of 8 and 5% of species classified as anadromous and catadromous, respectively, suggest that these fishes

were estuarine residents, spawning and growing to maturity in estuaries. Another 34% of species classified as anadromous spawn in fresh water but grow to maturity largely in estuaries (anadromous–estuarine, Fig. 2.1). Similarly, 14% of species classified as catadromous spawn at sea, but grow to maturity in estuaries (catadromous–estuarine, Fig. 2.1). Finally, 5% of species classified as catadromous exhibit life histories that are so exceptional that they do not fit any of the above categories. *Galaxias maculatus* experiences half its growth in fresh water and half at sea. *Lates calcarifer*, the barramundi, grows to maturity in fresh water, but post-spawners never return to fresh water. They continue to feed and spawn in tidal waters, where some males change to females following the first spawning. *Rhombosolea retiaria* grows to maturity in fresh water, spawns at sea and stays there to complete its life cycle (McDowall 1988).

A second potential shortcoming of the food-availability hypothesis is that primary productivity data used to quantify the productivity of 'freshwater' and 'ocean' waters may not reflect the production actually exported to higher trophic levels or represent the habitat actually occupied by many diadromous species. In open oceanic waters, two production systems exist within the euphotic system (Goldman 1988). The first (microbial food loop) consists of tiny phytoplankton cells (< 5 μm, ultraplankton), heterotrophic bacteria and protozoa. The primary production of this system is the one measured by standard incubations at sea. An unknown proportion of this production is exported, but much of the energy stored by the ultraplankton is dissipated within the loop (recycled production). The second system is based on larger cells (i.e. diatoms) growing in response to ephemeral and localised mixing events. These events allow rapid bursts in production that remain mostly undetected by bottle incubations. These large cells may account for most production that is exported from the euphotic zone by sedimentation or grazed by copepods (Legendre and Le Fèvre 1989). In fresh water, the young of many anadromous salmonids exploit a rich insect fauna that is largely independent of primary aquatic productivity (Groot and Margolis 1991). For example, over 50% of the energy obtained by young coho salmon, *Oncorhynchus kisutch*, in wooded streams in Oregon (USA) was estimated to be derived from primary production that did not occur in the water (Chapman 1965, cited in Hynes 1970). Because the production calculations used to support the food-availability hypothesis were based on published annual primary productivity estimates of freshwater and ocean habitats at different latitudes (Gross *et al.* 1988), they may not be accurate estimates of production that is available to higher trophic levels. Furthermore, the predominance of estuarine habitat occupied by many diadromous fishes (Fig. 2.1) is not reflected in the calculations of production. Estuaries are among the most productive systems in the world (Lalli and Parsons 1993). Since estuaries and coastal areas account for 10% of the world's oceans, latitude-averaged annual estimates of primary productivity greatly underestimate the importance of these areas to diadromous species.

Diadromy may have evolved to improve fitness, relative to a non-migratory

strategy, by improving the survival of the early life-history stages rather than by improving the growth of older fish. Greater adult body size may be an important determinant of reproductive success in species that compete strongly for mates (Andersson 1994; see also Berglund, Chapter 9 and Dugatkin and FitzGerald, Chapter 10). These species are generally characterised by conspicuous secondary sex traits and sexual dimorphism. Among diadromous fishes, the seven species of Pacific salmon are all sexually dimorphic. Males are territorial and aggressive towards other males on the spawning grounds, with larger males gaining access to females (Groot and Margolis 1991). However, the reproductive success of individuals of species that do not build nests and compete over mates, but rather broadcast their gametes, may be far less influenced by sexual selection. In these species, improving the survival of the vulnerable egg and larval stages may represent a significant contribution to lifetime reproductive success. For example, anadromous American shad, *Alosa sapidissima,* and and alewife, *A. pseudoharengus,* release and scatter eggs in open waters (Balon 1975). Although sperm competition may be important, differences in reproductive success due to competition over mates may be far less important than differences in reproductive success due to variations in the mortality of the larvae. As the Clupeidae are primarily a marine group (Nelson 1994), anadromy in shad, alewife and other anadromous clupeids may be considered a derived evolutionary state to exploit fresh waters for reproduction. Similarly, anadromy among species belonging to predominantly marine families such as the Gadidae, Percichthydae and Gasterosteidae (McDowall 1993) may be considered a derived evolutionary state to exploit fresh waters for reproduction. This is in contrast to the salmonines, in which freshwater residency is the ancestral state (Stearley 1992) and migration to sea may be considered a derived state to exploit marine feeding grounds (Gross 1987).

The exploitation of estuaries as nursery areas by a large number of diadromous fishes (Fig. 2.1) may best be understood as adaptations to increase survival of the vulnerable larval stages. Estuaries have long been recognised as important nursery areas, providing high concentrations of food and possible refuge from predators because of their greater turbidity (Miller *et al.* 1985). Estuarine nursery areas are exploited by species spawning in rivers flowing into estuaries, offshore marine spawners and estuarine resident species (Miller *et al.* 1985). Two different larval migratory patterns have been observed: (1) larvae of freshwater or brackish spawners drifting downstream, and (2) larvae of some marine spawners 'drifting' inshore. For example, over 85% of the annual commercial catch of fish off North Carolina (USA) is composed of five species that spawn offshore in the winter. Larvae migrate about 100 km to inlets in the barrier islands and another 100 km to estuarine nursery areas, a migration that may be largely achieved by drifting passively in warm onshore currents at intermediate depths. These currents arise to compensate for offshore surface currents associated with prevailing offshore winter winds (Miller *et al.* 1984; Govoni and Pietrafesa 1994).

The exploitation of the estuary of the St. Lawrence River (Canada) by four migratory fish species illustrates the variety of migratory patterns that may evolve in relation to estuarine frontal zones. The salinity front formed by the upstream limit of salt-water intrusion in this river represents an important early-summer nursery area for larvae and juveniles of rainbow smelt, *Osmerus mordax*, and Atlantic tomcod, *Microgadus tomcod*, (Laprise and Dodson 1989, and references therein). Smelt spawn in the main river and tributaries adjacent to the estuary in the spring, and are concentrated at the frontal zone by a combination of residual circulation and active vertical migration. Tomcod spawn 150 km upstream in winter and, following spring hatching, larvae drift passively to the frontal zone where they occupy deep waters and are retained by residual circulation. Larvae and juveniles of both species feed on mesozooplankton that occur at peak abundances in the frontal zone as temperatures increase in early summer. Moving 150 km downstream from the salinity front, a tidally-induced stratification front associated with an abrupt change in bottom topography separates shallow, well-mixed inshore waters from deep, stratified offshore waters. This area is the spawning site of Atlantic herring, *Clupea harengus*, that migrate upstream from the Gulf of St. Lawrence in the spring and fall. The stratification front appears to limit the seaward drift of yolk-sac larvae, and the subsequent colonisation of inshore mixed waters located upstream of the stratification front is largely due to upstream residual circulation. Suitable prey for first-feeding larvae is initially produced uniquely at the front and is subsequently transported upstream toward shallower areas of the estuary in concert with the upstream movement of postlarvae (Fortier and Gagné 1990, and references therein). Located even further downstream along the Gaspé peninsula is a quasi-permanent 150 km-long estuarine front. In the spring, capelin migrate upstream from the Gulf of St. Lawrence and spawn on beaches of the estuary located between the upstream limit of salt-water intrusion in the river and the tidally-induced stratification front where herring spawn. Upon hatching, larvae occupy surface waters and are rapidly transported downstream where, as first-feeding larvae, they encounter high concentrations of copepod eggs and nauplii on which they feed. The high concentration of copepods is triggered by the production and accumulation of large diatoms related to freshwater runoff and mixing along the Gaspé frontal zone (Fortier *et al.* 1992, and references therein). In all of these cases, the spawning season and the migratory trajectories of adults and larvae in the St. Lawrence Estuary appear to have evolved to exploit estuarine frontal systems that offer predictable and dense mesozooplankton food resources favourable for larval survival.

In conclusion, fitness may be improved by migrating to habitats that provide food resources for greater growth and survival, or that provide better protection from unfavourable conditions for offspring. For pelagic or demersal spawners that broadcast gametes, differences in reproductive success among individuals may be caused mainly by early life-history mortality. Thus, the greatest contribution to reproductive success may be achieved by improving survival during the vulnerable

egg and larval stages. In species that protect their young by building nests and/or by providing parental care, differences in reproductive success may be caused mainly by competition over mates. In such cases, a significant contribution to fitness may be achieved by improving growth during the adult stages. In the seasonally fluctuating environments of temperate and polar regions, variation in adult and juvenile mortalities due to periodic unsuitable conditions in the feeding habitat may be sufficient to favour the evolution of migration (Northcote 1978). The formulation of general evolutionary models of migration patterns must take into account the relative contributions to individual fitness of all habitats occupied during the migratory cycles of the species under study. Knowledge of the phylogenetic relationships between the species under study provides insights about their ancestral habitats and the part of the migratory cycle that may best be defined as the derived state.

2.3 Migration and life-history evolution

The evolution of migratory behaviour cannot be understood without considering the evolution of life history. Migratory behaviour and other life-history traits should coevolve to form adaptive strategies that convey selective advantage in specific environmental settings (Hutchings and Morris 1985). The complexity of the interaction between migration and other life-history traits is well illustrated by the American eel, *Anguilla rostrata*. Juvenile American eel (elvers), upon metamorphosis at sea, enter freshwater systems from latitudes 9°N to 60°N, with body size and the proportion of females increasing to the north (Helfman *et al.* 1987). These authors suggest that males and females have evolved different life histories, and hence different migratory strategies, in response to different selection pressures. Male eels mature rapidly at small sizes and are most common in estuaries of southeastern United States that are relatively close to their spawning grounds in the Sargasso Sea. In contrast, females maximise fecundity through increased size and are generally found further upstream in rivers and farther north than males within the species' range (Helfman *et al.* 1987). Females grow to maturity in fresh water further upstream and/or at higher latitudes (with greatest sizes being attained farthest to the north), where estimates of freshwater production are below that of temperate marine waters and tropical freshwaters (Gross *et al.* 1988). Greater size is associated with longer periods of residence in fresh water and late maturity (Helfman *et al.* 1987). In contrast, males occupy highly productive estuaries close to their oceanic spawning grounds, grow rapidly and mature at small sizes. Thus, for males, highly productive waters are occupied to grow rapidly and mature early, not to attain larger body sizes (Helfman *et al.* 1987). This time-constrained strategy contrasts with that of females, which increase their fecundity through increased body size and thus are selected to reproduce at the largest size possible. Large body size has little relative effect on male fitness, assuming that size-related social interactions do not affect spawning (Helfman *et al.* 1987).

The evolution of migratory and other associated life-history strategies may depend on (1) the energetic cost of migration, (2) the relationship between fecundity and body size, and (3) environmental uncertainty. These factors are addressed below.

2.3.1 The energetic cost of migration

The energetic cost of returning to spawning grounds can be great enough to reduce the somatic reserves of reproductive adults and contribute significantly to the cost of reproduction. Current reproduction may reduce lifetime reproductive success because of its adverse effect on future adult survival and breeding success (Rankin and Burchsted 1992). In the case of anadromous migrations, energy expenditures can be high and contribute significantly to the cost of reproduction. During the freshwater migration of iteroparous anadromous coregonines of James Bay (Canada), the energetic cost of migration was 1.6 times higher than the total energy invested in gonads by female cisco, *Coregonus artedii*, and equal to the total energy invested in gonads by female lake whitefish, *C. clupeaformis* (Lambert and Dodson 1990a, b). This cost of migration represented 20 to 29% of the somatic energy content of reproductive fish of both species. Iteroparous York River (USA) shad expended about 30% and iteroparous Connecticut River shad 40–60% of their energy reserves to migrate, spawn and return to sea (Glebe and Leggett 1981a, b). Evidence from several anadromous species show that expenditures in excess of approximately 70% of stored energy reserves results in complete spawning mortality (Glebe and Leggett 1981a, b).

Given the consequences of migration for current and future reproductive success, selection should favour the evolution of behavioural traits that minimise energetic expenditures (assuming that such traits are 'simple' life-history traits which evolve to maximise reproductive success in response to environmental conditions (*sensu* Gross 1987)). Because any reduction in current energy expenditure will permit an accumulation of stored energy that may enhance future reproductive success, selection may be expected to favour traits that minimise energetic cost per unit distance travelled.

2.3.2 The energetic efficiency of migration

To empirically test the hypothesis that fish migrants minimise energetic cost per unit distance travelled, Bernatchez and Dodson (1987) documented the migration energetics of 15 anadromous fish populations involving nine species. Anadromous fishes do not generally feed in fresh water, but derive energy required for migration from somatic reserves stored in muscles and viscera while at sea. Thus, studies of the energetic cost of anadromous migrations, based on observations of lipid and protein metabolism during the freshwater phase of the migration in combination with observations of migration length and duration, provide reliable estimates of energy cost per unit distance for a variety of species and hydrological conditions.

Table 2.1 Characteristics of the freshwater reproductive migrations of 15 anadromous fish populations. Populations are presented in ascending order of body weight. Adapted from Bernatchez and Dodson (1987).

| Species	(No.) Population-river	Mean weight (g)	Mean length (cm)	Migration distance (km)	Migration distance (Body lengths)	Vertical gradient (m km^{-1})	Total migration cost (kJ kg^{-1})	Cost per unit distance (kJ kg^{-1} km^{-1})	Mean swimming speed (bl s^{-1})	Mean displacement rate (km d^{-1})
River lamprey (*Lampetra fluviatilis*)	(1) Severn	55	30	100	3.30x10^5	0.10	5109	51.09	0.33	0.6
Cisco (*Coregonus artedii*)	(2) Eastmain	310	29	33	1.10x10^5	0.45	2114	64.06	0.86	0.6
Alewife (*Alosa pseudoharengus*)	(3) La Have	327	32	32	1.00x10^5	-	884	27.62	-	5.4
Sea lamprey (*Petromyzon marinus*)	(4) St. John (N.B.)	896	77	140	1.80x10^5	0.02	2280	16.29	0.13	1.8
American shad (*A. sapidissima*)	(5) St Johns (Florida)	1000	40	370	5.90x10^5	0.00	6463	17.47	1.50	8.8
American shad	(6) York	1300	45	80	1.86x10^5	.	1520	19.00	1.00	4.6
American shad	(7) Connecticut	1800	55	137	2.49x105	0.22	2863	20.89	1.09	6.0
Sockeye salmon (*Oncorhynchus nerka*)	(8) Skeena	2200	57	380	6.30x10^5	1.84	3778	9.94	2.77	18.0
Sockeye salmon	(9) Fraser (Stuart Lake run)	2545	58	1152	1.74x10^6	0.66	4555	3.95	2.71	42.6
Sockeye salmon	(10) Fraser (Chilko Lake run)	2545	58	596	1.00x10^6	1.75	5070	8.51	2.25	33.0
Atlantic salmon (*Salmo salar*)	(11) Northwest Miramichi	2900	74	113	1.50x10^5	1.77	2032	17.98	0.10	0.9
Chum salmon (*O. keta*)	(12) Amur	3900	64	1193	1.86x10^6	0.25	6140	5.15	2.43	45.0
Atlantic salmon	(13) Spey	4100	77	105	1.40x10^3	.	1262	12.02	-	-
Chinook salmon (*O. tshawytscha*)	(14) Sacramento (Mc Cloud R.)	10000	86	1000	1.15x10^6	1.00	3856	3.86	0.67	7.1
Chinook salmon	(15) Columbia (Snake R.)	15000	104	1134	1.10x10^6	0.53	2852	2.52	1.40	26.0
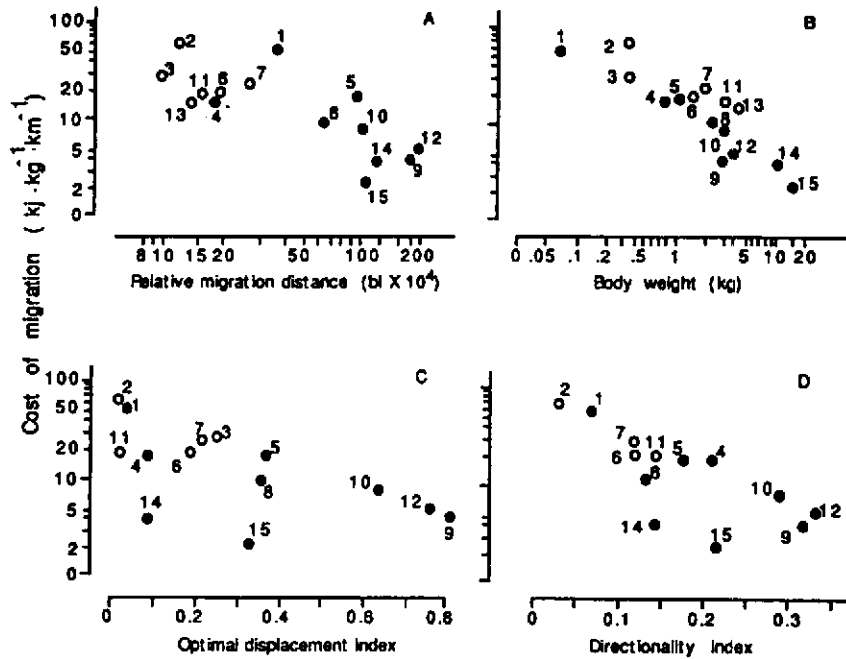
Fig. 2.2 Relationship between the energetic cost of migration (logarithmic scale) and (A) relative migration distance (log scale), (B) body weight (log scale), (C) optimal displacement index (arithmetic scale), and (D) directionality index[1] (arithmetic scale). Numbers refer to anadromous populations identified in Table 2.1. Open circles identify iteroparous species and closed circles, semelparous ones. Adapted from Bernatchez and Dodson (1987).

The anadromous freshwater migrations summarised in Table 2.1 are very different in terms of the body size of migrating fish, type of river, distance travelled and cost of migration. To compare the energetic efficiency of observed displacement rates (km per day), an index of optimal displacement was calculated for each population. The index was calculated by dividing observed displacement rate by a calculated optimal displacement rate, the empirically-determined ground speed at which energy cost per per unit distance is minimised (see Bernatchez and Dodson 1987 for calculations). An optimal displacement index of 1 corresponds to the

[1]An index of directionality was calculated by dividing the mean rate of displacement (km per day) by the mean swimming speed relaive to the water (calculated from regressions relating energy expenditure per unit time with swimming speed that are empirically determined using respirometry techniques). The maximum value of the index is 1 and corresponds to the ideal situation where all swimming activity is translated into upstream displacement. Values less than 1 imply meandering (low degree of upstream orientation) or holding station. Although water currents affect the swimming activity of fish, current speed was not correlated with the directionality index and we proposed that the index represents a comparative estimate of the directionality and persistence of upstream movement (Bernatchez and Dodson 1987).

situation where observed mean displacement rate minimises energy cost per unit distance. Index values less than 1 indicate ground speeds below optimal.

For most populations, cost per unit distance is not minimised and observed displacement rates are less than 40% of optimal displacement rates (Fig. 2.2c). The optimum situation was approached only in the case of Stuart Lake sockeye salmon and by Amur River chum salmon. Increasing energy efficiency of migration is associated with distance travelled, as shown by the strong negative relationship between the cost of migration per unit distance travelled and migration distance (Fig. 2.2a). This analysis suggests that migration distance may lead to improved migratory efficiency by selecting for larger body size (Fig. 2.2b), more accurate upstream migration (Fig. 2.2d) and travel speeds that optimise energy efficiency (Fig. 2.2c).

Water currents represent an obvious transport system which marine fishes may exploit for both directional information and energy savings, and which provide another means of examining behavioural adaptations for the efficient use of energy during migration. Weihs (1978) demonstrated mathematically that, in areas where tidal currents are directional, fish may achieve considerable energy savings by swimming in midwater at a constant speed relative to the bottom when the tide flows in the direction of migration and by holding station on the sea floor when the tide flows in other directions. Such behaviour, known as selective tidal stream transport, has been demonstrated in plaice, *Pleuronectes platessa*, and several other marine species (reviewed by Arnold and Cook 1984), and can save up to 40% in energy cost compared with the alternative strategy of swimming continuously in the direction of overall movement. Metcalfe *et al.* (1990) attempted to identify whether plaice use selective tidal stream transport in an energetically effective way by calculating the metabolic cost of transport for individuals tracked at sea. The metabolic cost of transport was 20% less than the cost of continuous swimming at the optimal swimming speed. When in midwater, most fish swam at speeds less than 50% of the optimal speed and headed downtide, but this orientation was not precise. It was, however, sufficient to achieve 88% of the maximum energy saving that could have been made with precise downtide orientation.

These examples demonstrate that the migratory lifestyle is associated with the evolution of a number of behavioural traits improving migratory performance and energetic efficiency. However, it is evident that not all migrants behave to maximise energetic efficiency. Pacific salmon are semelparous and, despite their outstanding energetic efficiency, many populations (but not necessarily all) exhaust their 'fuel' reserves to complete spawning (Groot and Margolis 1991). In such cases, fuel economy is essential for successful reproduction. Iteroparous species could also benefit from minimising costs to improve the probability of survival and/or increased fecundity. However, this does not appear to be a strong selective factor. Overall energy storage may be more important than the energetic efficiency of locomotion; hence the importance of large body size to store sufficient energy reserves for the spawning migration. Only when sufficient energy reserves cannot

be stored to successfully migrate and spawn does energetic efficiency approach theoretically optimal levels (Bernatchez and Dodson 1987).

2.3.3 Migration, body size and fecundity

Large body size provides benefits to migrants other than the opportunity to accumulate greater energy stores. Larger body size increases metabolic efficiency, in terms of energy expended per unit body weight, and swimming capacity (Beamish 1978). As the distance moved for one tail beat is the same fraction of a fish's body length, regardless of its size, big fish can migrate farther than small fish and exploit a far greater area during their life cycle (Schmidt-Nielsen 1984). Since fecundity generally increases with body size in fishes (Bagenal 1978), larger size will also contribute to increasing female breeding success through an increase in the number of eggs produced. In addition, larger size will contribute to the fitness of territorial species through success in breeding competition (e.g. van den Berghe and Gross 1989; see also Berglund, Chapter 9 and Dugatkin and FitzGerald, Chapter 10). Larger size at maturity may be achieved by growing faster or staying longer on feeding grounds. Thus, we may predict that the body size of migratory species and populations should be greater than those of non-migratory ones (Roff 1988). In addition, fecundity should also be greater among migratory species because of their larger body size. However, the suggestion has been made that populations allocating a greater proportion of their energy reserves to migration accomplish this by reducing the energy allocated to gonads, thereby reducing relative fecundity (Leggett and Carscadden 1978). Thus, these two hypotheses predict different trends in fecundity with migration distance.

In support of the hypothesised positive relationship between body size, fecundity and migratory life style, a comparison of anadromous and non-anadromous populations of seven salmonid species (*Salmo* and *Salvelinus* spp.) revealed that anadromous fish were significantly bigger and more fecund (number of eggs and total biomass of eggs produced) than non-anadromous ones (Gross 1987). Similarly, migratory marine teleosts are generally bigger than non-migratory species (Roff 1988). The bioenergetic analysis of Bernatchez and Dodson (1987) summarised above revealed that the average adult body size for 15 anadromous populations was positively correlated with migration distance. Positive associations between body size and migration distance and spawning site altitude, with greater growth at sea associated with delayed reproduction, have been observed among Atlantic salmon, *Salmo salar*, (Schaffer and Elson 1975) and anadromous brown trout, *Salmo trutta*, populations (L'Abée-Lund 1991). In a study of Atlantic salmon in Norwegian waters, water discharge was more important than river length in influencing body size (Jonsson *et al.* 1991). A comparison of anadromous and freshwater brook charr, *Salvelinus fontinalis*, inhabiting the same river system revealed that anadromous forms exhibited greater longevity, greater maximal length and a greater age and length at maturity than freshwater forms (Castonguay *et al.*

1982). Female chinook salmon originating in the upper Columbia River (USA) were both larger and more fecund than those sampled in the lower river (Beacham and Murray 1993). Genetically-based variation in growth rate and body size among populations of sticklebacks, *Gasterosteus aculeatus*, that exhibit different migratory strategies is also consistent with the positive body-size/migration-distance relationship (Snyder 1991).

There are, however, intraspecific comparisons that do not support the hypothesised positive relationship between body size, fecundity and migration length. St. John's River (USA) shad suffer complete post-spawning mortality. Despite being the smallest of the Atlantic coast shad studied by Glebe and Leggett (1981b), they displayed the longest and most costly migrations and allocated 1.3 and 3.3 times the absolute energy allocated to migration by Connecticut River and York River shad, respectively (Table 2.1). The St. John's fish also had the greatest fecundity, allocating 1.4 and 1.8 times the absolute energy allocated to the gonad by Connecticut River and York River shad (Leggett and Carscadden 1978). Among Pacific salmon, female chum salmon, *Oncorhynchus keta*, in the long-migrating Yukon River (Canada) populations were smaller and less fecund than those in more coastal populations. In the odd-year broodline of pink salmon, *O. gorbuscha*, upper-Fraser River populations had lower fecundities and were smaller than populations spawning in the lower river. Female sockeye salmon, *O. nerka*, in upper river populations in both the Skeena and Fraser Rivers were less fecund than lower-river populations, but there was no consistent size differential. Upper Fraser River chinook salmon, *O. tshawytscha*, were smaller than those in lower-river populations, but not necessarily less fecund. Female coho salmon in long-distance migrating, upper-river populations were smaller and less fecund than those in more coastal populations (Beacham and Murray 1993). Similarly, Fleming and Gross (1989) reported a negative relationship between female body length and migration distance in coho salmon. Egg production in coho salmon (total biomass of eggs produced) also showed a tendency to decrease with elevation of spawning grounds and migration distance, but the trends were not statistically significant. The majority of these data support the alternative hypothesis mentioned above, namely that fecundity is reduced to pay the costs of longer migrations (Leggett and Carscadden 1978). However, the smaller average body sizes of fish migrating longer distances is not consistent with the positive body-size/migration-distance relationship. Differences in the contribution of body size to breeding success among populations of territorial salmonids may be partially responsible for these trends, although other phenomena may be involved (see Section 2.3.5).

2.3.4 Life-history evolution and reproductive uncertainty

Various authors examining the relationship between reproductive success and the frequency of reproduction have concluded that when reproductive success is unpredictable and the variance of juvenile survival exceeds that of adults, iteroparity

significantly increases population stability, lowers the probability of extinction and will thus be selected for (Leggett and Carscadden 1978, and references therein). Such a strategy is generally associated with delayed reproduction, greater size and age at first maturity, lower fecundity and a greater number of lifetime reproductive events. The proximate influence of the energetic requirements of migration on life-history traits cannot be considered independently of the ultimate influence of reproductive uncertainty in the spawning and early rearing habitats. Iteroparity and exhausting migrations are incompatible. The reduction in longevity and lifetime reproductive events associated with increased post-spawning mortality is limited by the probability of extinction associated with high variance in the survival of early life-history stages. Iteroparous populations must maintain a certain level of post-spawning survival by limiting somatic depletion during reproduction. This may be achieved by accumulating sufficient somatic reserves prior to migration and subsequently expending a smaller proportion of these reserves. For example, post-spawning survival in the iteroparous Connecticut River shad population appears to be assured by greater somatic reserves afforded by larger body size and reduction in energy invested in gonads and migration, due to a shorter migration, relative to the semelparous Florida population (Leggett and Carscadden 1978; Table 2.1).

Bell (1980) provided evidence for a negative correlation between migration distance (degree of anadromy) and adult survivorship. Anadromous species that make extensive ocean migrations are semelparous, whereas those exhibiting short oceanic migrations confined to coastal and estuarine waters are all iteroparous. However, semelparity may be selected only if mean juvenile survival is higher, or if its variance is lower, relative to adult survivorship (Bell 1980), regardless of the difficulty of the spawning migration. In fact, complete post-spawning mortality may have little to do with the energetic requirements of migration. Because complete spawning mortality occurs in certain populations of sockeye salmon, pink salmon and American shad that exhibit relatively short freshwater migrations at apparently minimal energetic costs, Glebe and Leggett (1981b) concluded that semelparity was not simply a result of somatic exhaustion due to long migrations. However, the actual energetic cost of these short, semelparous migrations has not been documented. I can think of no reason why such fish would accumulate energy reserves beyond those needed to migrate and spawn, unless the nutrient enrichment of juvenile rearing habitats caused by the death and decomposition of post-spawning adults results in improved juvenile survival (Northcote 1978, and references therein). Intraspecific bioenergetic studies of semelparous populations migrating different distances are required to establish the relationship between body size and energy stores, and the costs of migration and spawning. Considering the potential importance of body size to breeding success in territorial salmonids (van den Berghe and Gross 1989; see also Dugatkin and FitzGerald, Chapter 10), the proportion of energy stores available to compete for mates (and thus the intensity of intrasexual selection) may be far less in salmon populations migrating long

distances than in those migrating short distances. For example, the deeper body profile of male sockeye salmon spawning on beaches relative to river spawners within the Kvichak River system of Alaska may be related to differences in the difficulty of their respective migrations (Blair *et al.* 1993). These authors proposed that the relatively short migration distance and the little energy needed to hold position in the lake permit these fish to invest more energy in secondary sexual characteristics (such as body depth) relative to river spawners who must expend more energy to hold position in the river and, in some cases, invest energy in more demanding upstream migrations. In addition, natural selection against deep-bodied forms may be less intense in beach-spawning populations as the lake's depth affords protection from predatory bears and permits the deepest bodied fish access to all spawning areas (Blair *et al.* 1993).

An example of how migration interacts with other life-history traits in iteroparous populations is provided by a comparative study of sympatric populations of anadromous cisco and lake whitefish of James Bay (Canada). Lambert and Dodson (1990a, b) demonstrated that the smaller size and earlier age at first maturity of cisco was associated with higher growth rates and greater adult mortality rates relative to lake whitefish. For the same freshwater migration distance, cisco allocated twice as much energy to migration than lake whitefish did. The resultant higher post-spawning mortality rates in cisco were associated with a less iteroparous lifestyle than that of whitefish, with the expected lifetime fecundity of cisco being achieved in about half the number of spawnings than that of lake whitefish. Thus, for cisco, greater somatic depletion during migration and spawning appears to be associated with smaller size at maturity, greater fecundity and fewer lifetime spawning events. Furthermore, the persistence of anadromous cisco in the geologically younger rivers of Hudson Bay (Canada) is related to migration distances to reach spawning grounds that are much shorter than those in more southern rivers in James Bay. In spite of decreases in pre-migratory energy accumulation in the north of their range due to shorter growing seasons, cisco maintain a similar somatic cost of reproduction without reducing fecundity, which has resulted in similar life-history patterns among populations over a large latitudinal gradient (Kemp *et al.* 1992). Because more difficult migrations in the north of their range would result in greater post-spawning mortality and an almost semelparous lifestyle, the probability of population extinction would be high due to reproductive uncertainty. Anadromous cisco may have succeeded in extending their range to the northernmost rivers because freshwater spawning habitats are closer to marine feeding habitats than in the southern part of their range.

The relative energetic inefficiency of the few iteroparous anadromous migrations studied to date (Table 2.1) may be the result of a strategy to store sufficient energy reserves to insure a level of post-spawning survival appropriate for the uncertainty of the reproductive environment. I speculate that sufficiently high levels of energy accumulated prior to migration may accommodate a wide variety of migration patterns and mechanisms of displacement, with little selective pressure

on the evolution of specialised migratory behaviour, physiology or morphology. Sufficient directional bias may be provided by the 'reactive' responses of fish to external stimuli that may simply depend on ortho- and klinokineses (reviewed by Dodson 1988). The observed circuitous routes of many migratory fishes (Leggett 1984, and references therein), with some populations spending from weeks to months residing on spawning grounds prior to spawning (Bernatchez and Dodson 1987), is consistent with this view. This view also implies that adaptations for fuel economy among iteroparous populations are positively correlated with migration distances, and that there exist maximum migration distances beyond which the sedentary lifestyle is favoured or population extinction occurs. The data base presently available to test these predictions is inadequate. Intraspecific comparisons of iteroparous populations that migrate different distances are required to establish how body size and energy stores are related to the difficulty of migration and how the demands of post-spawning survival limit the extent of migration.

2.3.5 Intraspecific migration phenotypes

The greatest opportunity for insight into the evolution of migratory patterns and their relationship with life-history evolution lies in the study of intraspecific migration phenotypes. An evaluation of lifetime fitness ($\Sigma l_x m_x$) among different phenotypes would be an excellent test of the validity of evolutionary models in explaining variations in migratory pattern and life-history traits. When life-history trait optima differ among environments that are inhabited at random within and among generations, selection acts on a trait's norm of reaction (the alteration of a life-history trait in response to environmental change) (Hutchings and Myers 1994, and references therein). Potentially the most important reaction norm with respect to the evolution of migration is a negative correlation between age at maturity and growth rate (Hutchings and Myers 1994). Such adaptive phenotypic plasticity may be responsible for the phenomenon of precocious male maturity among young Atlantic salmon that do not migrate to sea prior to reproduction, but mature in fresh water at a much smaller size (Hutchings and Myers 1994). These authors proposed a simple model incorporating polygenic thresholds of age at maturity (largely environmentally controlled) as a mechanism by which an evolutionary stable continuum of phenotypes could be maintained within a population. Many other examples of alternative migratory and reproductive strategies related to differences in growth rate exist, and these could also be analysed in the same way. Populations of Atlantic salmon may include several migratory phenotypes: the entire life cycle may either occur in fresh water, involve different combinations of freshwater, estuarine and sea residency, or resemble more closely the typical anadromous lifestyle (Power *et al.* 1987). These authors proposed that conditions for growth in the estuary vary from year to year and may determine the proportions of the various migration phenotypes in a population. Smolts may terminate their seaward migration in the estuary when growth exceeds a threshold value at

which the reproductive success of non-migrants is equivalent to that of migrants. Equivalent reproductive success may be caused by a greater degree of iteroparity and higher relative fecundity among estuarine salmon relative to anadromous forms. These propositions may be tested using a variety of species exhibiting plasticity of life history and migratory patterns, a situation that appears common among salmonids (Northcote 1978).

The anadromous (sockeye salmon) and non-anadromous (kokanee) forms of *O. nerka* may spawn sympatrically but are genetically distinct in several rivers of British Columbia, Canada (Wood and Foote 1990, and references therein). Kokanee mature at smaller sizes and often at younger ages than sockeye. Genetic differentiation among sockeye and kokanee populations in British Colombia led these authors to suggest that the two forms have diverged in sympatry on numerous, independent occasions. Genetic differentiation is promoted by assortative mating by size and by selection against hybrid progeny (reviewed by Wood and Foote 1990). A possible key to understanding the initial divergence of the two forms may be found in understanding the development of 'residual' sockeye, which do not migrate to sea and are, in part, the progeny of anadromous parents (Burgner 1991). These forms are characterised by faster growth rates among certain age groups (Burgner 1991), suggesting that a negative association between growth rate and age at maturity may be the basis for the evolutionary origin of the non-anadromous form. The relative production rates of anadromous and residual progeny from the spawning of residuals and the genetic component of the phenomenon are unknown. Given that anadromy is considered to be, in phylogenetic terms, a derived character state among salmonines (Stearley 1992), the evolutionary reversal to freshwater residence (the ancestral state) demonstrated by kokanee provides an opportunity to search for the selective factors that have taken precedence over those selecting for anadromy (McLennan 1994).

The different body-size/fecundity relations relative to migration distance among semelparous Pacific salmon species and populations documented by Beacham and Murray (1993) (see above) may be related to different migration phenotypes exhibiting different mortality and fecundity schedules. Among chinook salmon, two such phenotypes exist (Healey 1991). The 'stream-type' phenotype stays longer in fresh water as juveniles, migrates further at sea, matures later and is more fecund, whereas the 'ocean-type' phenotype migrates to sea soon after hatching, remains largely in coastal waters while at sea, matures earlier and is less fecund. Males and females of both phenotypes exhibit a range of ages at first maturity that may span three years. Since the stream-type is distributed further to the north than the ocean-type, it is possible that the two phenotypes evolved as different races in different glacial refugia (Gharret *et al*. 1987) such that differences in life-history traits may be the result of selection in different environments rather than alternative reproductive strategies evolved in a common environment. In the case of coho salmon, two phenotypes are also distinguished on the basis of their marine migrations (Sandercock 1991): an 'ocean' or 'coastal' form that occupies outer

coastal or offshore waters, and an 'inshore' or 'interior' form that remains inshore during the marine phase of the life cycle and migrates further upstream during the freshwater phase. If these phenotypes represent evolutionary stable strategies, then their respective lifetime reproductive success ($\Sigma l_x m_x$) should be the same in sympatry, a prediction that requires building life tables for each phenotype to test. Thus, for these semelparous species, smaller body size and/or lower fecundity should be associated with higher pre-spawning survival rates. It is important to note, however, that in cases where the fitness benefits of an increase in fecundity is equalled by its cost in terms of lowered survival, any change in survival or fecundity is selectively neutral (Bell 1980). In such cases, age at maturity may be highly variable within a population.

2.4 Conclusions

If the cost of migration was insignificant, relatively minor benefits to survivorship or breeding success afforded by habitat switching would favour the evolution of migration. As many aquatic organisms drift with oceanic and tidal currents to achieve long-range directed movements, long-distance migration may entail minor costs. In both spring and autumn spawning Atlantic herring of western Newfoundland, reduction in somatic condition due to spawning and overwintering did not attain critically low levels that would reduce survival probability, indicating no survival cost due to reproduction based only on somatic depletion (Y. Lambert, personal communication). It is possible that while somatic costs due to migration and reproduction may be relatively minor, costs due to predation on adults may be major determinants of post-spawning survival. Studies exploring the fitness consequences of the predation-risk component of migrations are needed.

Passive transport is particularly important when considering the displacements of early life-history stages. Given the limited storage capacity and vagility of larvae and the high larval growth requirement associated with survival and reproductive success, most migrations of larvae must be assisted by currents (Miller *et al*. 1985). In the case of immature spot, *Leiostomus xanthurus*, and croaker, *Micropogonias undulatus*, on the east coast of the United States, their 100 km migrations from winter spawning areas near the Gulf Stream to the inlets of Pamlico Sound takes 50 days, during which they grow from 2 to 15 mm (Miller *et al*. 1985). Assuming a net benefit of migration, largely related to the growth of larvae, the migratory lifestyle would have evolved even if there were no additional benefits from switching habitats. Therefore, the evaluation of costs or benefits associated with each leg of a migration becomes important to interpret predicted relationships among life-history traits. As an example, Gross (1987) calculated that egg production by diadromous forms is, on average, three fold greater than that of non-diadromous conspecifics. Therefore, the fitness advantage of migration may be three fold through the enhancement of age-specific fecundity (m_x). Devaluating m_x by the survivorship costs incurred as a consequence of migration, migrants may

have as much as a three-fold higher mortality than non-migrants and still be favoured by natural selection. However, recruitment in some pelagic marine fishes can vary by as much as five fold, indicating that placing early life-history stages in favourable habitat through migration may provide at least a five-fold increase in fitness relative to a non-migratory strategy. Thus, adult migrants may have as much as a five-fold higher mortality than non-migrants and still the migratory strategy could be favoured by natural selection. For species whose reproductive success depends largely on the survival of the vulnerable early life-history stages, the passive displacement of larvae and juveniles to favourable rearing habitats hypothetically may provide sufficient benefits in terms of growth and survival to favour the evolution of a migration strategy in the absence of any apparent benefits to switching adult habitats. Variations in the survival of eggs and larvae in the early-rearing habitat may, in many cases, be the most critical variable to consider in the evolution of large-scale migration.

Acknowledgements

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