Adaptive phenotypic plasticity of eel diadromy

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ABSTRACT: Eels are marine teleosts that have ancestrally evolved a continental growth phase during which diadromy is facultative. This migratory plasticity reflects a fitness trade-off between search for the most productive habitats and competition avoidance favoring shift to less productive areas, while migration costs (increased mortality and reduced growth) hinder movements. To cope with these conflicting selective pressures acting in heterogeneous and unpredictable environments, eels have evolved a conditional evolutionarily stable strategy (ESS) with alternative tactics as a regulation mechanism for migratory plasticity. In this model, diadromy is considered as a threshold reaction norm to an individual's energetic status. In the population, this reaction norm evolves rapidly in response to changes in the cost/benefit fitness ratio of diadromy. This conditional ESS model may explain how the collapse of freshwater eel stocks results not only from decreased recruitment but also from an adaptive drop in the proportion of the diadromous phenotype in populations. Hence, I suggest that the decline in populations of eels has been less steep in salt than in freshwater habitats.

KEY WORDS: Anguilla spp. · Diadromy · Dispersal · Game theory · Migration · Phenotypic plasticity · Population decline · Rapid evolution

INTRODUCTION

Eels Anguilla spp. are semelparous marine fishes belonging to the elopomorph superorder, a group of phylogenetically ancient teleosts. Eels migrate between marine breeding and continental feeding areas where they grow for 3 to 20 yr (yellow stage) before beginning gonad maturation (silvering) and engaging in the spawning migration. Eels colonize an extremely wide variety of growth habitats including the littoral zone, estuaries, marshes (salt or fresh), rivers and lakes. Such ubiquity is almost unique among teleost fishes and results from an extreme migratory plasticity (Tsukamoto & Arai 2001, Daverat et al. 2006). However, the mechanisms controlling this plasticity remain largely unknown. Eel recruitment in freshwater habitats is crashing worldwide, raising well-founded concern about possible extinction of these legendary fishes (Dekker et al. 2003, Stone 2003). In this context, it is urgent to synthesize and improve knowledge for both ecological and conservation purposes. The aim of this essay is to provide an evolutionary mechanism for eel migratory plasticity. I apply the principles of game theory to analyze the alternative eel phenotypes in terms of cost and benefits to evolutionary fitness. For greater convenience, I will dichotomize these alternative migratory histories as diadromy, i.e. migration in freshwater (FW), vs. non-diadromy, i.e. settlement in saltwater (SW).

BENEFITS OF DIADROMY: HABITAT PRODUCTIVITY VS. COMPETITION AVOIDANCE

It is widely admitted that diadromy in fishes has evolved in response to gradients in food availability between marine and FW habitats. At low latitudes, the higher primary productivity of FW habitats may favor a
FW growth period by marine species; in contrast, at high latitudes, a marine growth phase may be advantageous for FW species (Gross et al. 1988). The genus *Anguilla* originates from tropical oceans where it probably developed diadromy (Tsukamoto et al. 2002), which may therefore be viewed as an ancestral trait. The shift of some *Anguilla* species to temperate latitudes promoted the evolution of a facultative diadromy (Tsukamoto & Arai 2001), likely because of the decreased relative productivity of rivers compared with the sea and estuaries. In Taiwan, where both tropical and temperate species co-occur (at the margins of both geographical ranges), the tropical *A. marmorata* inhabits the upper river reaches, while the temperate *A. japonica* mainly colonizes the estuary and the lower river reaches (Shiao et al. 2003). Indeed, *A. marmorata* elvers migrate up-river much more rapidly than temperate elvers (Robinet et al. 2003), consistent with the hypothesis that eels evolve a migratory behavior in response to the relative habitat productivity prevailing in their geographical range.

At first glance, colonization of FW habitats by temperate eels could be seen as a paradox: why maintain ancestral diadromy if productivity is higher in saline environments? In light of all evidence, diadromy allows reduction of both inter- and intra-specific competition, 2 pivotal components of migration and dispersal evolution (Cloître et al. 2001). Indeed, shift to FW probably allows temperate eels to avoid both strong marine predators, such as conger eels, and the high densities of conspecifics produced in brackish waters by intense primary productivity and limited habitat surface (Tesch 1977, Moriarty 2003). Therefore, evolution of eel migration may be driven by a trade-off between search for the most productive habitats and shift to less productive, lower density habitats. In *Anguilla anguilla*, the gut develops for osmoregulation in FW whatever the ambient salinity (Ciccoti et al. 1993), indicating ontogenetic programming for osmoregulation in FW. This suggests that diadromy remains the favored migratory tactic in *A. anguilla*, i.e. that competition avoidance is more prominent than relative habitat productivity in driving evolution of migration under temperate latitudes.

**ENERGETIC COSTS OF DIADROMY: INCREASED MORTALITY, REDUCED GROWTH**

Bioenergetics strongly constrain the evolution of migration (Bernatchez & Dodson 1987). Indeed, migration-induced exhaustion may lead to death, either directly or through reduced competitive ability and increased sensitivity to predation and infection (Cloître et al. 2001). Therefore, energetic limitations represent an immediate constraint for migrants, especially when they are non-feeding and have limited swimming capacities, as do glass eels. Accordingly, recent data from both the laboratory and field indicate that the energetic status controls migratory behavior in glass eels. First, sedentary individuals in an experimental flume are shorter than swimmers (Bardonnet et al. 2003). Second, under constant experimental conditions, glass eels switch from FW- to SW-preference as their body condition decreases (Edeline et al. 2006). Third, glass eels that precociously settle in the estuary are lighter than river colonizers (Edeline et al. 2004). These data strongly support the view that glass eels migration is conditional on the fact that individuals have sufficient energy stores with which to migrate, as also observed in juvenile salmonids (Forseth et al. 1999, Thériault & Dodson 2003).

In addition to an immediate survival problem, the energetic cost of migration may have consequences on the longer term because migratory and foraging behaviors are in direct opposition in eels. Indeed, digestion and locomotion compete for energy and oxygen allocation, indicating that a feeding individual cannot migrate and vice versa (Owen 2001). Also, benthic foraging behavior by yellow eels requires territoriality (Bertin 1951), and a migratory individual cannot defend a territory. Therefore, a dual physiological and behavioral conflict between migration and foraging induces reduced or arrested growth during migration periods. This conflict was confirmed under experimentally controlled conditions where the glass eel migratory propensity was negatively correlated with juvenile growth performance over a period of 2 mo (Edeline et al. 2005). Hence, diadromy in the eel may be seen as a risky investment tactic: migrants lose immediate fitness through reduced growth but invest in future fitness gain through competition avoidance.

**CONDITIONAL EVOLUTIONARILY STABLE STRATEGY (ESS) MODEL**

The term ‘conditional strategy’ is used in evolutionary game theory to define a type of phenotypic plasticity in which a single individual can express different phenotypes (the tactics of the conditional strategy) depending on its environmental, social and physiological status (cueing trait). Based on the above cost and benefits analysis, I suggest that eel diadromy is a conditional strategy cued by individual energetic status, i.e. individual eels choose the migratory tactic (diadromy vs. non-diadromy) that maximizes fitness depending on the level of their energy stores (Edeline 2005) (Fig. 1). Indeed, diadromy is the most beneficial tactic for individuals with high energetic status be-
cause it allows competition avoidance. However, as energetic status decreases, costs of diadromy increase and eventually outweigh its benefits. Tactics change at that point where fitness benefits switch from favoring one tactic to favoring the alternative: the ESS switch point. The strategic model of Gross (1996) is particularly illustrative. I have here combined this model with the quantitative genetic model developed by Hazel et al. (2004), which allows inheritance of both the cueing trait and switch point, and coexistence of both conditional and unconditional individuals in the population (Fig. 1). The switch point and the cueing trait are allowed to vary both within and among individuals. At the individual level, the switch point and the cueing trait are genetically fixed and vary only in response to environmental effects (temperature, trophic and demographic parameters etc.). However, at the population level, variations in the switch point and the cueing trait result from both additive genetic and non-genetic sources (Hazel et al. 1990, 2004, Roff 1996, Garant et al. 2003), giving rise to normal distributions for both traits (grey curves in Fig. 1). The proportion of each alternative phenotype in the population (D vs. ND in Fig. 1) is controlled by the distribution of switch points relative to the distribution of the cueing trait.

In Fig. 1, I illustrate how Anguilla anguilla glass eels maximize their fitness by either migrating to FW habitats or settling in SW habitats, depending on their energetic status. The conditional ESS model presented here may be extended to other behaviors and developmental stages. For instance, in non-migratory yellow eels, individual status also depends on body size, which conditions the hierarchy in agonistic interactions. Residency is favored in (large) dominant eels, while (small) subordinate eels derive higher fitness from dispersal towards habitats where competition is less strong. The model may also be used to qualitatively predict evolution of diadromy under changing selective pressures. For instance, lowered population densities in SW habitats owing to population decline will increase fitness return from the non-diadromy tactic, and result in a shift to the right and increased variance in the distribution of switch points (as illustrated in Fig. 1). Hence, I suggest that decreased recruitment over the last 2 decades has not only decreased the number of migrants, but also their proportion in the population. Another prediction from the model is that river colonizers should now have higher energetic status than before population collapse.

Now, consider anthropogenic changes that act selectively on FW habitats, e.g. dam construction, wetland drainage, fishing and pollution. These artificial selective pressures will increase selection against migrants, lower the D fitness function and thus further push the
distribution of switch points to the right, i.e. further reduce the proportion of migrants in the population. Note that if you also consider selection on the cueing trait (against high energetic status), the decrease in the proportion of migrants will be even stronger. In conclusion, diadromy in eels may be viewed as a threshold reaction norm to a high energetic status, favored by selection when the cost/benefit fitness ratio of diadromy is low. Increase in this ratio during the last few decades induced a rapid evolutionary shift in the reaction norm and consequently reduced the proportion of diadromous phenotypes in populations. Long-term time series of marine eel abundances would allow the hypothesis that population decline has been less steep in SW than in FW to be tested.

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