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Chapter 18

Proximate and ultimate control of eel continental dispersal

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INTRODUCTION

Eels *Anguilla* spp. are fishes belonging to the elopomorph superorder, a group of phylogenetically ancient teleosts (Nelson 1994). Eels have ancestrally evolved a continental growth phase and thus migrate between marine breeding and continental feeding areas. In continental waters, eels colonize an extremely wide variety of salt (SW), brackish and freshwater (FW) habitats. Such a ubiquity is exceptional among teleost fishes. However, the mechanisms controlling eel continental dispersal, i.e., distribution in different growth habitats, remain largely unknown. Dispersal is here understood in ecological terms and thus refers to as movements leading to habitat colonization in general. Dispersal is a pivotal process for both species persistence and evolution, and involves a great diversity of ecological phenomena (Clobert et al. 2001). In the eel, dispersal in different habitats may influence survival, growth, sex differentiation, age and size at silvering [female size affects fecundity, egg-size and larval viability (Einum et al. 2004)], swimming ability during the spawning migration, and finally capacity to reproduce. In turn, decision-makings by individual dispersers for migration to, immigration in and emigration from different habitats depend on genetic, physiological, morphological and social attributes and are affected by a number of environmental parameters (Clobert et al. 2001).

In this chapter, we provide material to understand how (proximate control) and why (ultimate control) dispersal patterns by eels in continental habitats are what they are. In the first section, we describe the process of continental dispersal, focusing on the behavioural changes that occur during ontogeny. We emphasize the importance of considering separately migration, which is mainly an endogenously-controlled behaviour expressed by glass eels and elvers, from *ranging*, which is mainly an environmentally-controlled behaviour expressed by yellow eels. Based on this dichotomy, we review in the second and third sections the internal and external (environmental) drivers of movements. In the fourth section, we investigate the evolutionary forces acting on eel movements and we propose an evolutionarily stable strategy (ESS) model explaining how decision-making for movement by individual dispersers may be ultimately controlled. We further use this ESS model for qualitative predictions on the evolution of diadromy (i.e., colonisation of freshwater habitats) in response to anthropogenic changes in selective pressures. Finally, in the conclusion, we point out lack of knowledge and suggest future research directions.

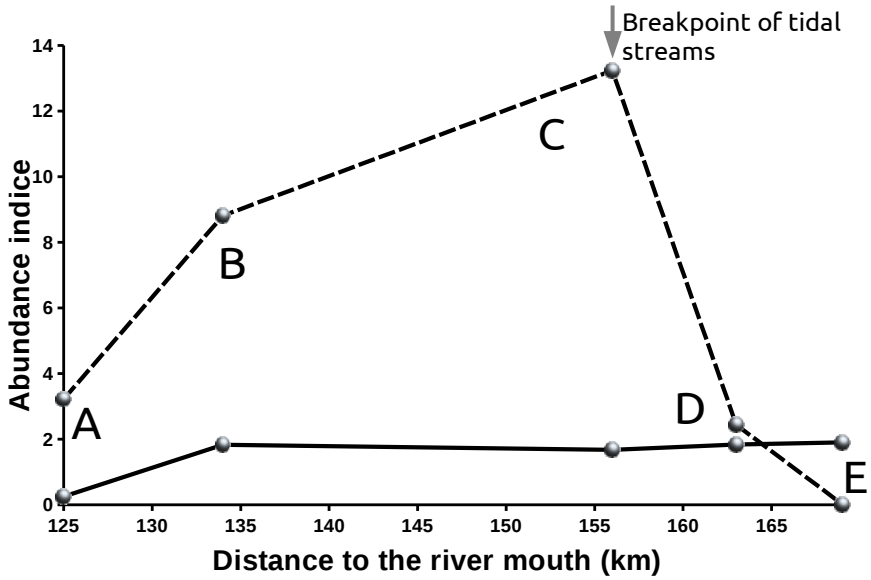
1. ONTOGENY OF EEL CONTINENTAL DISPERSAL

1. 1. Metamorphosis

Metamorphosis is a drastic developmental strategy consisting in a suite of morphological, physiological and behavioural adaptive changes. In the eel, metamorphosis of translucent leptocephalus larvae, drifting from the oceanic spawning grounds, into late-metamorphic, unpigmented glass eels occurs on the slope of the continental shelf (Schmidt 1909, Tesch 1977). This transformation is an adaptive shift from oceanic drift to river colonization, and marks the start of the continental dispersal phase. The larva's body changes from willow-leaf to eel-shape, undergoes a reduction in length and weight, and an 80 % drop in water content (Bertin 1951, Otake 2003). In addition, the brain structure is profoundly remodelled, with the external brain shape of the leptocephali gradually changing from laterally compressed to depressed elongated due to biased growth of the telencephalon and optic tectum (Tomoda and Uematsu 1996). Also, feeding activity stops due to the shedding of larval teeth and reorganization of the digestive system. Then, as shown in *A. anguilla* glass eels, the gut specializes for osmoregulation in FW,

independent of the environmental salinity (Ciccoti et al. 1993). This indicates that, although they keep the ability to live and grow in SW, eels are ontogenetically programmed for FW residency. Body pigmentation progressively develops throughout the glass eel phase over different pigment stages VA, VB, VIA_0, VIA_1, VIA_2, VIA_3, VIA_4 and VIB, as defined by Elie et al. (1982). In this chapter, we will not use the term "elver" but instead term "glass eel" all the development stages between the leptocephalus larvae and the newly transformed yellow eel (stage VII of Elie et al. 1982). Feeding resumption occurs around the pigment stage VIA_3 for most of individuals, after sufficient rearrangements of digestive organs and acquisition of a new set of teeth (Elie 1979). At feeding resumption, stomachs contain mainly a mixture of plant and algal detritus that may be assimilated by the developing gut (Bardonnet and Riera 2005). The true end of metamorphosis, marking the start of the juvenile growth phase (yellow phase), occurs at completion of body pigmentation (stage VII) and matches with the full development of gut and teeth (Vilter 1945, Elie 1979, Elie et al. 1982, Jegstrup and Rosenkilde 2003). At that stage, eels start feeding on macro-invertebrates and will progressively shift towards piscivory (Tesch 1977). The colonization of continental habitats is carried out by both the glass and yellow eels, but with quite different modalities.

1.2. Glass eel dispersal



1.3.

Fig. 1. Ontogeny of eel dispersal behaviour, adapted from Edeline et al. (2007). Distributions of glass eels (dotted line) and newly transformed yellow eels (solid line, body length < 15 cm, solid line) around the tidal limit of the Dordogne River (France, Site C). Eels were sampled at 5 sites (A, B, C, D and E) located at increasing distance from the river mouth. Site C was located at the breakpoint of tidal streams. Glass eels accumulated at site C, most likely due to the loss of tidal streams available for selective tidal stream transport (STST). In contrast, newly transformed yellow eels were homogeneously distributed around site C. This result is most parsimoniously interpreted as a behavioural shift from upstream migration to settlement and food search during the completion of larval metamorphosis (see Section 1.3). Abundance indices (y axis) were obtained by multiplying the estimated probability of presence of a fish at each sampling site, by the estimated abundance of fish when fish was present, taking into account the effects of several important environmental variables in generalized linear models (for further details, see Edeline et al. 2007).

Glass eels invade coastal and estuarine waters using selective tidal stream transport (STST), a saltatory transport mechanism with alternations of flow-carried swimming during flood tide and benthic sheltering behaviour during ebb tides *(Creutzberg 1958, McCleave and Kleckner 1982, Elie and Rochard 1994)*. STST allows important energy saving compared to constant counter-current swimming *(Weihs 1978)*. Glass eels orientate towards the river mouth and up-estuary

following decreasing salinity gradients *(Tosi et al. 1990)* and river water odours *(Creutzberg 1961)*. Thermal gradients could also play a role in glass eel orientation *(Tosi et al. 1990)*. As they reach the tidal limit (limit of flow reversals), migrating glass eels lose tidal advection for transport and have to switch from STST to constant counter-current swimming *(McCleave and Wippelhauser 1987)*. We have investigated glass eel migration at the obstacle-free tidal limit area of the Dordogne River (France) during a two-year field study *(Edeline et al. 2007)*. This tidal limit is located about 50 km upstream from the salinity front, and thus provides a rare opportunity to separate the effects of salinity and hydrodynamics on the migration process. We have monitored the distributions of glass eels (pigment stages VB to VIB) vs. newly transformed yellow eels (stage VII, body length < 15 cm) at 5 sites (coded A, B, C, D and E). Site C was located at the limit of flow reversals, i.e., at the point of the watershed where glass eels lose tidal advection for STST. The results indicate that glass eels arriving from the sea rapidly migrated up-estuary. Then, despite absence of any osmotic barrier, glass eels accumulated at the limit of flow reversals (site C, Fig.1). Upstream of this accumulation point, migration speed dropped and glass eels transformed into small yellow eels before reaching the non-tidal river area, where only small yellow eels and no glass eels were found (site E, Fig. 1). This finding is in accordance with other data indicating almost absence of glass eels among inland river colonizers *(Haro and Krueger 1988, Michaud et al. 1988, Naismith and Knights 1988, Dutil et al. 1989, McGovern and McCarthy 1992, White and Knights 1997b)*. Together, these results indicate that glass eels are strongly dependent on tidal streams for upstream movements and poorly adapted to colonization of non-tidal rivers. Therefore, the late-metamorphic glass eel should be considered as a transitory developmental stage between the oceanic larva and the continental juvenile, adapted to the colonization of tidal interface habitats by means of STST.

1.3. Yellow eel dispersal

The distribution pattern of small yellow eels in the tidal limit area of the Dordogne River was quite different from that of glass eels (Fig. 1), suggesting that completion of larval metamorphosis was related to a pronounced change in dispersal behaviour (Edeline et al. 2007). Upstream migratory movements by newly transformed yellow eels should have induced increased abundances upstream the site where they accumulated as glass eels (site C, Fig. 1). Instead, abundances remained almost constant between sites B and E, suggesting a loss of the upstream-oriented migratory behaviour at the onset of the growth phase. This result matches with experimental aquarium data indicating a shift from a pelagic towards a benthic behaviour during the transformation of glass eels into small yellow eels (Jegstrup and Rosenkilde 2003). Therefore, termination of metamorphosis and full development of feeding capacity seem to mark the end of the larval migratory period in the European eel, as commonly observed in benthic marine fishes (Moran 1994). Homogenous distribution of newly transformed small yellow eels after initial accumulation at the glass eel stage further suggests density-dependent dispersal (Edeline et al. 2007). This hypothesis is supported by recent studies suggesting that upriver movements by yellow eel are largely density-dependent (Smogor et al. 1995, Ibbotson et al. 2002, Feunteun et al. 2003, Briand et al. 2005a).

Based on the aforementioned results, we may propose a typical ontogenetic pattern for eel dispersal behaviour. According to Dingle (2006), during migration the individual is not distracted from movement by resource-based stimuli like food or living space. This definition clearly fits to glass eel movements because glass eels move upstream even if resources are more abundant in the estuary or on the coastline. In contrast, at the yellow stage, movements are driven by the search for food or other resources, and also aim at avoiding competitors and predators (see section 3.7). These movements are clearly not migratory because they cease when a resource is encountered (Dingle 2006). We here choose to refer to these non-migratory yellow eel movements as "ranging", because they occur at the home range scale – either within

or between home ranges [but see Dingle 2006 for further development]. Finally, we define settlement as the behavioural shift from migration to ranging.

1.4. Variability of the eel dispersal phenotype

We have now defined the typical ontogenetic pattern for European eel continental dispersal: eels migrate upstream at the glass eel stage, settle at the onset of the yellow stage and then shift to ranging behaviour. However, there is probably a large variability around this typical (or average) ontogenetic pattern. Indeed, settlement is a complex trait involving a number of morphological, physiological and behavioural changes, and complex traits generally show a large variability in populations. In accordance with the view that settlement timing is highly variable, otolith microchemistry shows that some eels never enter freshwater but settle at the glass eel stage at sea or in the estuary (Tsukamoto and Arai 2001, Daverat et al. 2006). Settlement may also occur after the onset of the yellow eel stage. Indeed, small yellow eels may show intense upriver migratory behaviour during spring "runs", and some larger ("pioneer") yellow eels may maintain density-independent, upstream migration (Feunteun et al. 2003).

After settlement, ranging may be aperiodic or instead occur on a periodic basis, and include movements within and between home ranges that may cross salinity boundaries. For instance, seasonal ranging movements by yellow eels may occur between the river and the estuary (Tesch 1977, Daverat et al. 2006). The combination of variability in settlement timing and ranging movements leads to a very large diversity of continental dispersal patterns – this diversity is stressed by otolith microchemistry studies. How the variability of pre- and post-settlement movements is controlled is discussed in the three following sections. The definition of migration given above – that a migrant is not responsive to resource-based stimuli – implies that migration is primarily driven endogenously. However, it should be kept in mind that environmental factors may still affect many internal drivers. Reciprocally, ranging behaviour is mainly controlled by the environment, but final decisions for moving or staying remain under endogenous control.

2. INTERNAL DRIVERS OF EEL CONTINENTAL DISPERSAL

2.1. Genetic factors

Despite its central importance for both ecological and conservation purposes, the genetic control of eel life history has been historically neglected. Indeed, many authors implicitly consider that phenotypic diversity results from a single genotype showing different norms of reaction in response to various environmental effects. However, assuming no genetic variation (i.e., one genotype) for migratory behaviour simply implies that migration cannot evolve, because evolution results from sorting of genotypes by selection (Futuyma 1998). Instead, in both vertebrates and invertebrates, migration is an heritable syndrome (i.e., a complex trait) that requires genetic programming for morphological, physiological and behavioural adaptations (Berthold 1991, Pulido et al. 1996, Futuyma 1998, Roff and Fairbairn 2001, Alerstam et al. 2003, Dingle 2006). Typically, these adaptations are controlled by many loci each with a small additive effect (polygenic model) together bearing considerable genetic variation (Berthold and Pulido 1994, Futuyma 1998, Roff and Fairbairn 2001). Accordingly, recent studies have shown significant genetic variation in *A. anguilla* (Daemen et al. 2001, Wirth and Bernatchez 2001, Maes and Volckaert 2002, Dannewitz et al. 2005), that may be correlated to fitness-related traits *(Pujolar et al. 2005)*. In the genus *Anguilla*, genetic diversity for migratory traits is necessary to explain evolution of diadromy from ancestral marine residency (Gross et al. 1988), as well as spatiotemporal shifts of migration loops (migration route and life cycle) that caused separation into subpopulations and speciation (Tsukamoto et al. 2002).

2.2. Body condition

Body condition, i.e., energetic status, is a parameter of major importance that influences dispersal in birds and mammals (Dufty and Belthoff 2001). In anadromous fishes, limitations in energy reserves constitute a major constraint for migration (Bernatchez and Dodson 1987, Jonsson et al. 1997, Forseth et al. 1999). Migrating glass eels, due to both their small size and non-trophic state, are likely prone to energetic constraints. Indeed, decreased body condition triggers a swap from FW- to SW-preference and a shift from migration to settlement in glass eels (Bardonnet et al. 2003, Edeline et al. 2004, Edeline et al. 2006). This energetically-controlled migratory plasticity likely reflects an adaptive threshold (see Section 4). Indeed, high body condition fishes will gain the highest fitness return by migrating to low-density river habitats (see Sections 3.7 and 4), while low body condition individuals increase their fitness by stopping migration-related energy expenditure and settling precociously in saline habitats. Glass eels are recruited into estuaries during migration peaks lasting for several months (Tesch 1977). The body condition of estuarine recruits decreases over this migration period in *A. anguilla* (Elie 1979, Charlon and Blanc 1982), *A. rostrata* (Jessop 1998), *A. japonica* (Kawakami et al. 1999), *A. reinhardtii*, *A. australis* (Sloane 1984) and *A. dieffenbachii* (Jellyman and Lambert 2003), possibly due to a decreased productivity of oceanic ecosystems during the larval migration period (Désaunay and Guerault 1997). Hence, the propensity to colonize river rather than marine and estuarine habitats is probably higher in early than in late recruits. Also, longer term oscillations in oceanic productivity (Désaunay and Guerault 1997) might plastically affect the proportion of diadromous individuals among recruits.

2.3. Endocrine factors

Because they integrate both the genetic and environmental influences and, in turn, regulate gene transcription, neuronal and metabolic activities, hormones are key behavioural mediators. Diadromous fish migrations are under endocrine control (Fontaine 1975). During salmonid smoltification, pre-adaptation to SW residency is controlled in synergy by growth hormone (GH) and cortisol (Boeuf 1993, McCormick 2001), while thyroid hormones (THs, thyroxine T_4 and triiodothyronine T_3) are involved in many adaptive processes including olfactory imprinting (Lema and Nevitt 2004), changes in muscle physiology (Katzman and Cech 2001), and rheotaxis (Specker et al. 2000). In the eel also, THs have a crucial role in controlling leptocephalus metamorphosis (Yamano et al. 1991, Ozaki et al. 2000), body pigmentation and gut transformations (Vilter 1946, Jegstrup and Rosenkilde 2003). In glass eels, THs further stimulate migratory behaviour (Edeline et al. 2004, Edeline et al. 2005b). Therefore, THs play a key role in the regulation of morphological, physiological and behavioural adaptations leading to the colonization of FW habitats by the eel. Thyroid gland activity decreases at the yellow stage (Callamand and Fontaine 1942), likely promoting the observed switch from migration to settlement during transformation of glass eels into small yellow eels (see Section 1.3). In yellow eels, individuals caught climbing water falls also have higher plasma T_4 levels and locomotor activity compared to sedentary individuals (Castonguay et al. 1990), suggesting that maintenance of a high thyroid gland activity at the yellow stage delays settlement.

It seems likely that cortisol and GH are also involved in the regulation of glass eel dispersal (fig. 2). Indeed, in both glass and yellow eels, cortisol promotes gill and intestine Na^+/K^+-ATPase activity, i.e., adaptation to SW residency, probably in synergy with GH (Epstein et al. 1971, Butler and Carmichael 1972, Wilson et al. 2004). In addition, cortisol injections decrease plasma THs levels (Redding et al. 1986), while THs exert a negative feedback on GH production by the pituitary, an eel-specific regulation (Rousseau et al. 2002). These crossed negative feedbacks between THs vs. cortisol-GH could mediate the swap of glass eels from FW-oriented migration to settlement induced by a lowered body condition (Fig. 2). Indeed, in teleosts, a lowered caloric status induces decreased thyroid gland activity (Eales 1988). In glass eels, a low body condition correlates to low thyroid gland activity (Edeline et al. 2004) and high GH levels (Lambert et al. 2003), while physiological stress and fasting in yellow eels stimulate GH and cortisol secretion through brain production of corticotropin-releasing hormone (Marchelidon et al. 1996, Rousseau et al. 1999, Dufour et al. 2001).

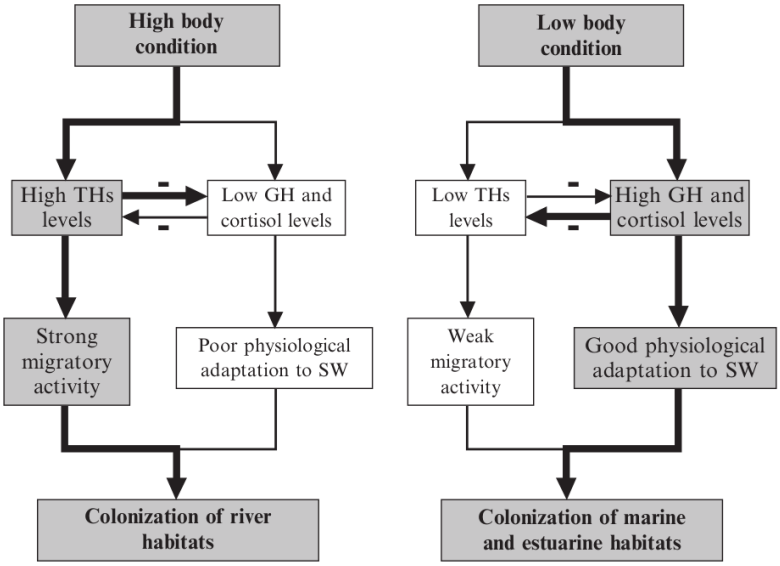


Fig. 2. Hypothetical endocrine mechanism for the control of glass eel migratory plasticity based on the results provided in Section 2.3. Bold arrows represent the dominant physiological pathway. Thyroid hormones (THs) induce a river-oriented migratory behaviour, but also exert a reciprocal negative feedback on cortisol and growth hormone (GH) production, which are both involved in saltwater (SW) acclimation. Left panel: individual's physiology is "THs-dominated". We suggest that a satisfying energetic status (high body condition, see Section 2.2) may stimulate thyroid gland activity. Then, high THs levels maintain low GH and cortisol levels and promote colonization of river habitats. Right panel: we depict a possible endocrine switch to a "GH-cortisol-dominated" physiology. Decreasing energetic status lowers THs production and increases GH and cortisol secretion, inducing low migratory activity and good hypoosmoregulatory ability. We suggest that shift from a "THs-dominated" to a "GH-cortisol-dominated" physiology occur when individual's energetic status reaches a switch point as described in Section 4 and Fig. 5.

3. EXTERNAL DRIVERS OF EEL DISPERSAL

3.1. Tidal streams: the importance of STST

As indicated by their behavioural adaptation to tidal streams (the STST), glass eels are strongly constrained in their movements by the water current, that may either represents a transport vector or a migration barrier depending on its direction. At the tidal limit, migrating glass eels accumulate because tidal advection is no longer available to support upstream movements (see Section 1.2). In estuaries, glass eels may be found swimming in the water column during ebb-

tide, while the use of STST for migration implies sheltering close to the bottom during ebb-tide. These ebb-tide glass eels present signs of physiological stress, similar to settling glass eels that remain on the bottom of the estuary during flood tide (Edeline et al. 2004). These results suggest that an inefficient use of tidal streams (by ebb-tide glass eels) is one of the mechanisms that could lead precocious settlement in saline habitats at the glass eel stage through a sequence presented in Fig. 3.

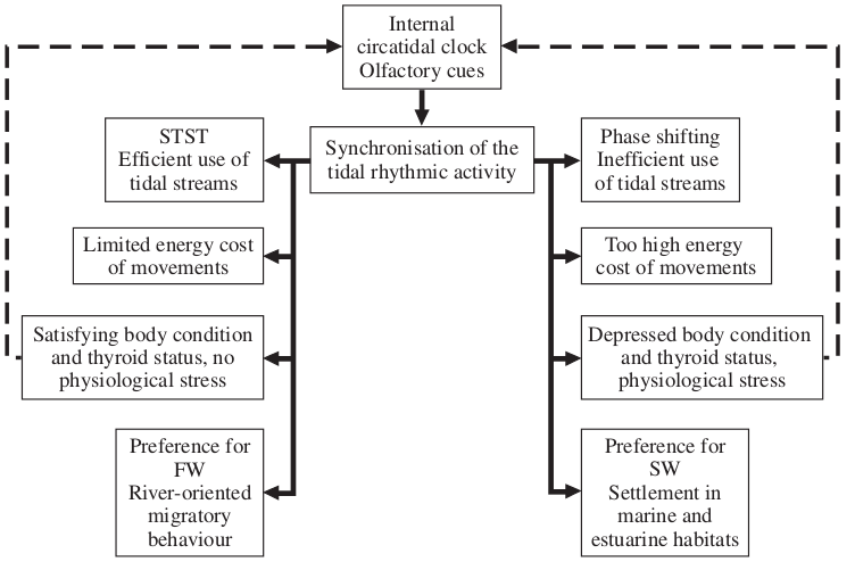


Fig. 3. Proximate mechanism for the control of glass eel dispersal by tidal streams based on the results provided in Section 3.1. The rhythmic activity during selective tidal stream transport (STST) is triggered by both endogenous (internal clock) and exogenous (olfactory) cues. A rhythmic swimming activity in phase with flood tides allows energy saving and maintenance of satisfying energetic status and high thyroid gland activity, which promote preference for freshwater (FW) and a river-oriented migratory behaviour. In contrast, a phase shifting in activity rhythm, preventing glass eels from efficient use of tidal streams as transport means, leads to physiological stress through the resultant high energy cost of movements. This decreases thyroid gland activity and promotes preference for saltwater (SW), loss of migratory behaviour and finally settlement. We suggest that the physiological condition could possibly exert a feedback on the synchronization of rhythmic activity (dotted arrows) because THs may be involved in olfactory sensitivity (see Section 2.3).

The rhythmic activity during STST is triggered by both exogenous olfactory cues (Creutzberg 1959, Barbin et al. 1998) and endogenous cues produced by an internal circatidal clock, which rhythm is synchronized by flow reversals (Wippelhauser and McCleave 1988). Disruption of these phasing mechanisms could hinder effective utilization of tidal streams (Fig. 3). For instance, pollutants could affect fine sensory processing of water currents and odours necessary for synchronization of the internal clock. Indeed, pollutants may damage olfactory neurons (Halpern 1982) and may also affect a variety of behaviours through the upsetting of sensory, hormonal, neurological, and metabolic systems (Scott and Sloman 2004). Also, in poikilotherms, temperature is a very strong synchronizer of internal oscillators. Slight temperature changes may induce phase shifting of endogenous rhythms through alterations of the clock molecular machinery (Rensing and Ruoff 2002). Accordingly, in *A. japonica* glass eels kept under free-running conditions, a slight temperature change may shift the rhythm of the internal circatidal clock (Kim et al. 2002). Such temperature-mediated phase shifting in the internal tidal clock may be one of the processes leading to an inefficient use of tidal streams by glass eels (see Fig. 3).

3.2. Salinity

Salinity is a major environmental factor that affects fish distribution *(Jung and Houde 2003)* and growth (Boeuf and Payan 2001). In the eel, salinity tolerance varies during development. Both glass eels and silver eels show an extraordinary capacity to cope with abrupt salinity transfers (Fontaine and Raffy 1932, Wilson et al. 2004), but osmotic tolerance decreases in small yellow eels (Boucher-Firly 1935), which may suffer high mortalities during acute transfer from FW (0 ppm) to SW (35 ppm) (E. Edeline, unpubl. data: 100% mortality among 197 newly transformed small yellow eels previously held and fed in FW for 2 months). Salinity is likely to influence eel movements during both migration and ranging. Indeed, despite exceptional osmotic tolerance, glass eels arriving from the sea need a delay period before voluntary entry into FW (Petit and Vilter 1944, Deelder 1958), indicating that salinity preference may reflect subtle processes that are not revealed by osmoregulation studies. Salinity preference tests show that, at arrival from the sea, the proportion of FW-seeking glass eels varies between 50 and 70 % (Tosi et al. 1988, Tosi et al. 1989, Tosi et al. 1990), suggesting inter-individual variation in salinity preference that could possibly influence migration and/or habitat selection.

In order to investigate the role of glass eel salinity preference in the control of eel migration, Edeline et al. (2005a) sorted groups of *A. anguilla* glass eels (hereafter termed "contingents") over 2 consecutive salinity preference tests. This allowed us to study the link between salinity preference and locomotor activity (i.e., positive rheotaxis), and to separate contingents of glass eels that were either plastic or fixed in their preference for FW or SW. During the first trial series, 3,193 glass eels were tested for salinity preference 1, 2 and 3 days after capture; 864 were active (i.e., actively swam towards either a FW or a SW flow). All the active glass eels, as well as a batch (n = 543) of inactive fishes, were kept to perform the second behavioural test. The other fishes (the rest of the inactive glass eels) were released. During the second trial series, we tested these 2 batches (543 inactive and 864 active glass eels) for their salinity preference, 9 and 10 d after capture. After the second trial, the 543 glass eels that had been inactive during the first trial were released. Among the 864 glass eels that had been active during the first trial series, 526 were again active during the second trial series. These 526 fishes were used to carry out a growth experiment (see below), while the others were released. We classified the 526 glass eels that were active during the 2 trials into contingents according to their salinity preference: FWC (n = 240) for FW contingent (double preference for FW), SWC (n = 47) for SW contingent (double preference for SW), and PCC (n = 239) for plastic contingent (shift in salinity preference over the acclimatization period: from SW to FW, or from FW to SW). Somatic growth of these 3 contingents was then monitored during 2 months under excess feeding in controlled FW and SW conditions (Edeline et al. 2005a).

During the 2 behavioural tests, locomotor activity and salinity preference were significantly linked. Indeed, the glass eels that were active during the first trial (preferring either FW or SW) showed a high locomotor activity during the second trial but also a sharp preference for FW, even if SW had been preferred first. This result indicated that a high locomotor activity was associated with FW preference in glass eels, a behavioural syndrome likely promoting migration to the river (Edeline et al. 2005a). In contrast, inactivity during the first trial was associated with a low locomotor activity during the second trial, but also to a preference for SW if the fish were active. This result indicated that low locomotor activity was associated with SW preference in glass eels, a behavioural syndrome probably promoting an early settlement in marine and estuarine habitats (Edeline et al. 2005a).

Additionally, the behavioural syndromes observed during the behavioural tests were associated with growth patterns that fitted with the observed growth patterns of yellow eels in the wild. Indeed, the FWC (i.e. glass eels that preferred FW twice) had the lowest growth rates in both FW and SW rearing conditions. In contrast, the SWC (i.e. glass eels that preferred SW twice)

had the highest growth rates in SW rearing conditions. These results suggest a trade-off (negative correlation) between migration and growth, in accordance with data from the wild showing that freshwater eels grow more slowly than estuarine eels (Tzeng et al. 2003, Jessop et al. 2004, Daverat and Tomás 2006). Additionally, growth was higher in SW than in FW in all contingents, indicating that, in addition to the migration/growth trade-off, habitat salinity may directly affect growth (Edeline et al. 2005a). The PCC (i.e. glass eels that swapped their salinity preference) had an intermediary growth status that could be related to the nomad life style of eels migrating between different habitat types during their life (Feunteun et al. 2003, Daverat and Tomás 2006). The results from this behavioural-growth experiment provide a comprehensive ecological mechanism for the control of habitat distribution and growth patterns in glass and yellow eels, as presented in Fig. 4.

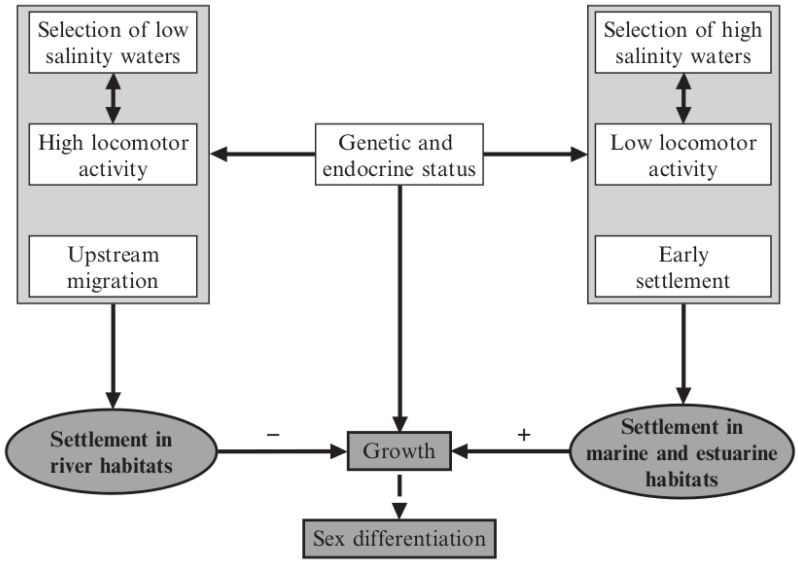


Fig. 4. A simple mechanism for the proximate control of eel life history in continental habitats based on the results provided in Section 3.2. Non-filled boxes refer to processes occurring in glass eels and elvers (hereafter simply termed glass eels), while grey boxes refer to processes occurring in yellow eels. In glass eels, locomotor activity and salinity preference are correlated (double arrows) and participate in driving upstream migratory behaviour. High locomotor activity and preference for FW lead to upstream migration and diadromy, while a low locomotor activity and preference for SW favour an early settlement and non-diadromy. At the yellow stage, habitat salinity and primary productivity directly influence somatic growth (+ and -). We further suggest occurrence of a trade-off between migration and somatic growth, presumably through endocrine and genetic pathways (Edeline et al. 2005a): high migratory propensity at the glass eel stage seems to be correlated with low juvenile growth rates, while a low migratory propensity by glass eels seems to be related to high juvenile growth rates. Following other authors (for review see Davey and Jellyman 2005), it is suggested that growth rate during the first year of continental life could affect sex differentiation (dotted line).

Trade-offs between migration and other fitness-related traits are frequent because migration incurs heavy fitness costs (Roff and Fairbairn 2001). This trade-off may involve various ecological, physiological, and genetic pathways (Zera and Harshman 2001). In juvenile eels, the links between locomotor activity, salinity preference and growth probably involve complex interactions of several mediators, including metabolic hormones and genes (Fig. 4). The speculations presented in Fig. 4 are based on the fact that (1) THs promote locomotor activity in glass eels (Edeline et al. 2005b) and have also been shown to affect salinity preference (Baggerman 1960, 1962, Iwata 1995) and growth (Higgs et al. 1982) in other teleosts, (2) GH affects growth, acclimation to SW (see Section 2.3) and locomotor activity in salmonids (Øverli et al. 2002, Johansson et al. 2004), (3) genes (allozyme heterozygosity) affects both salinity tolerance in teleosts (Shikano et al. 2000) and growth performance in *A. anguilla* (Pujolar et al.

2005). Finally, migratory behaviour could also be correlated to sex differentiation through growth (Fig. 4). Indeed, recent data suggest that slow growth rates during the first year of continental life may favour female sex differentiation (Holmgren and Mosegaard 1996, Holmgren et al. 1997, Davey and Jellyman 2005).

3.3. Water temperature

Water temperature profoundly affects the whole metabolic machinery and is thus a crucial driver for eel dispersal plasticity. In glass eels, both the estuarine migration and river recruitment are conditioned by temperature thresholds (Vøllestad and Jonsson 1988, McGovern and McCarthy 1992, Elie and Rochard 1994, Jessop 2003). Accordingly, under experimental conditions, a temperature increase from 10 to 18°C enhances both locomotor activity (i.e. positive rheotaxis) and FW-preference (Edeline et al. 2006). Runs of small yellow eels in rivers are also triggered by a rise in water temperature; the temperature-dependency of movements decreases with increasing body size (Moriarty 1986, Naismith and Knights 1988, White and Knights 1997b). There are several physiological mechanisms by which temperature may affect locomotion. Decreased environmental temperatures primarily act in reducing enzymatic activities and fluidity of both membranes and internal liquids, causing a drop in the power output from muscles (Johnston and Temple 2002). Water temperature also affects endocrine secretions. In *A. anguilla* yellow eels, thyroid gland activity decreases with water temperature (Leloup 1958, Leloup and De Luze 1985) and, in glass eels, a fall in water temperature slows down the process of metamorphosis (Briand et al. 2005b). Finally, habitat selection at the patch scale may be affected by water temperature (Chen and Chen 1991, Richardson et al. 1994). Thermal preferences match with optimal temperatures for growth (Elie and Daguzan 1976), suggesting that preference is related to optimal functioning of the enzymatic machinery relative to both high and low temperature limits.

3.4. Water odour, migration and habitat selection

Odours are widely known to guide salmon to their native stream during spawning migration (Døving and Stabell 2002). According to the definition of Harden-Jones (1984), migratory fishes may use water odour as a "cue" triggering movements (i.e., shift from inactivity to activity) above sensitivity thresholds, and/or as a "clue" orienting movements through odorous gradients once the fish is in motion (i.e., after the cue triggered onset of movement). In glass eels, the smell of inland waters is thought to provide a cue triggering the onset of swimming during STST (see Section 3.1), but also clues orienting movements towards rivers (Creutzberg 1961). Attraction is due to several earthy compounds (Sorensen 1986, Tosi and Sola 1993, Sola 1995), that may either attract or repel glass eels depending on environmental salinity (Sola and Tongiorgi 1996). It has been hypothesized that orientation towards earthy odorants during migration evolved because these compounds are indicative of habitat primary productivity (Sorensen 1986). Odours also transmit social information. Both glass eels (Briand et al. 2002) and yellow eels (Saglio 1982) are attracted by the odour of conspecifics, possibly through epidermal mucous compounds (Saglio 1982), bile salts (Sola and Tosi 1993) and amino acids (Sola et al. 1993, Sola and Tongiorgi 1998). Chemoattraction could promote glass eel's grouping behaviour during migration, and mediate conspecific recognition and allow food location during ranging (Sola and Tongiorgi 1998). Therefore, odorous signals may be seen as mediators of optimal foraging and optimal habitat selection by dispersers during ranging.

3.5. Light and photoperiod

In both plants and animals, light is one of the most important synchronizers of internal rhythms (Hastings et al. 1991). Photoperiodic (seasonal) information is transformed into a melatonin

secretory rhythm that, through hypothalamic stimulation, regulates many biological functions such as growth and reproduction (Bolliet et al. 1996, Boeuf and Le Bail 1999, Falcon et al. 2003). In teleosts, photoperiod affects circulating levels of numerous hormones, including GH (Björnsson et al. 1994), THs (Leiner and McKenzie 2001) and reproductive hormones (Blázquez et al. 1998). In salmonids, the spring increase in day length is one of the factors triggering smoltification (Hoar 1988). In the eel, the effects of photoperiod variations on physiology and behaviour remain unexplored, but it is well known that light inhibits eel movements. Glass eels are strongly photonegative (Bardonnet et al. 2003, Dou and Tsukamoto 2003), and light avoidance increases with body pigmentation (Bardonnet et al. 2005). In estuaries, glass eels avoid both the daylight and moonlight by remaining on the bottom or swimming deeper in the water column (Creutzberg 1961, Elie and Rochard 1994, De Casamajor et al. 2000). Yellow eels also present a nocturnal foraging activity (Bertin 1951, Tesch 1977, Baisez 2001), reduced during full moon periods (Adam and Elie 1994). This light inhibition of eel movements is mediated by increased secretion of brain catecholamines (Le Bras 1978, 1984). Finally, both glass eels (Wippelhauser and McCleave 1988) and silver eels (Edel 1976) have circadian activity rhythms in free-running conditions, suggesting occurrence of an internal circadian clock.

3.6. Anthropogenic pressures

Anthropogenic pressures on aquatic environments may be considered critical to eel continental dispersal (Feunteun 2002). First, global warming affects oceanic gyres, reduces nutrient availability and slows down oceanic migration, and could thus increase larval mortality through enhanced starvation and predation (Knights 2003). On the other hand, continental influences should not be neglected. Overharvesting, habitat fragmentation and loss, and introduction of exotic species are strong agents of selection and may drive species to extinction (Stockwell et al. 2003). For instance, estuarine fisheries may deplete a large proportion of the migrating glass eels. In the Vilaine River, where a dam blocks upstream movement, the fishery removes up to 99% of the glass eel stock (Briand et al. 2003). In barrier-free estuaries, exploitation rates are probably sharply reduced but glass eel fisheries, by selectively targeting migrants using STST, could possibly favour evolution towards reduced migratory behaviour in the population on a decadal time scale (see Section 4). Indeed, fisheries may induce rapid life history evolution in fish populations (Law 2000). Furthermore, dams dramatically decrease habitat accessibility (White and Knights 1997a, Lafaille et al. 2005), and could possibly increase mortality in migrants that accumulate below the obstacle. Introduction of strong FW predators such as *Silurus glanis* could also seriously impair the benefits from colonizing river habitats. Finally, pollution impacts fitness through decreased individual condition and genetic erosion (Maes et al. 2005), and probably also disrupts complex behaviours through various endocrine and metabolic pathways (Robinet and Feunteun 2002, Scott and Sloman 2004).

3.7. Social interactions

Social interactions are critical to animal dispersal (Clobert et al. 2001). In the eel, social entrainment to migration (i.e., positive density-dependent migration) is likely to occur through schooling behaviour (Tesch 1977). However, it is probably during ranging that social interactions play their major role in driving eel continental dispersal patterns. Indeed, yellow eels are strongly antagonistic and confrontations may induce severe injuries or even death of the defeated individual (Bertin 1951, Tesch 1977, Peters et al. 1980). This antagonistic behaviour is coupled to cannibalism (Degani and Levanon 1983, Knights 1987) and results in negative density-dependent survival (Vøllestad and Jonsson 1988, Briand et al. 2005a) and growth (Degani et al. 1988, Beentjes and Jellyman 2003). In mammals, competition for food and space and antagonistic interactions are known to induce positive density-dependent dispersal (Sutherland et al. 2002). The same is likely to be true for the eel. In other words, how far yellow eels

disperse from the habitat where they settled (the tidal limit area for many individuals) should be positively related to the density of dominant eels present in this habitat. Indeed, several recent studies indicate that river colonization by yellow eels is positively density-dependent, i.e., is a process equivalent to random diffusion of particles driven by density at the point source (Smogor et al. 1995, Ibbotson et al. 2002, Feunteun et al. 2003, Briand et al. 2005a).

Under density-dependent ranging, the many environmental (seasonal or not) variations that may alter the social structure of local populations will promote a reorganization of distributions, following a model of a patchy "fluid mosaic" (Feunteun et al. 2003). Depending on availability of habitat resources (space, water temperature, food availability, dissolved oxygen…) and/or demographic parameters (density, proportion of dominant eels…), subordinate eels shift towards habitats where survival and growth conditions are better (see also Section 4.2). This density-dependent ranging period is by far the longest of the continental phase, giving opportunity for generation of a very large variety of dispersal patterns. How often an individual will cross salinity boundaries during this period may partly depend on its osmotic capacities (see Section 3.2). In conclusion, social interactions combined with habitat variations represent major cues inducing plastic dispersal responses through ranging movements. However, we suggest that social interactions further represent a major selective force for the evolution of migration and timing of settlement because they induce habitat-specific survival and growth. This point is developed in the following section.

4. ULTIMATE CONTROL OF EEL DISPERSAL

Game theory and associated concepts such as the Evolutionarily Stable Strategy (ESS) provide a framework for studying eel alternative phenotypes in terms of their costs and benefits to evolutionary fitness. We have analysed eel continental dispersal in the context of evolutionary stable strategies, considering movement as a threshold trait with two alternative values: moving or staying. For the sake of clarity we have equated moving with diadromy (i.e. colonization of FW habitats) and staying with non-diadromy (i.e. colonization of SW habitats), but we suggest that the approach is valid for any type of movement.

4.1. The cost/benefits fitness ratio of diadromy

Evolution of diadromy should be seen as driven by a ratio between its costs and benefits in terms of fitness (Gross et al. 1988, Edeline 2007). Diadromy provides evolutionary benefits because it may give access to increased food resources (Gross et al. 1988). In eels, diadromy may be considered as an ancestral trait. Indeed, eels appeared in tropical oceans where they probably evolved diadromy from a marine ancestor because primary productivity is higher in FW than in SW under low latitudes (Aoyama et al. 2001, Tsukamoto et al. 2002). Colonization of temperate oceans by several eel species has promoted evolution of a facultative diadromy (i.e., a fraction of the population never enter FW), presumably because relative productivity of rivers decreases compared to the sea, estuaries or deltas (Tsukamoto and Arai 2001). However, diadromy remains the predominant migratory tactic in temperate eels, as suggested by the ontogenetic programming of *A. anguilla* for osmoregulation in FW (Ciccoti et al. 1993). Most likely, maintenance of diadromy by temperate eels is selected for because it allows reduction of both inter- and intraspecific competition, two pivotal components of dispersal evolution (Clobert et al. 2001). Indeed, shift to FW permits temperate eels to escape both strong marine predators (Jonsson and Jonsson 1993), such as conger eels (Moriarty 2003), and high conspecific densities (Tesch 1977). In that sense, social interactions may be considered as major drivers for the evolution of migration in the eel.

However, migration and diadromy incur a strong energetic cost (Roff 1991), that results in increased mortality. Indeed, depletion of energy stores by migration induces exhaustion that

could lead to death, either directly or through reduced competitive ability and increased sensitivity to predation and infections (Bernatchez and Dodson 1987, Gandon and Michalakis 2001). In addition, migration probably incurs growth costs as already discussed in Section 3.2. Indeed, in the eel, energy requirements of digestion and locomotor activity are conflicting (Owen 2001), and glass eel's migratory propensity is negatively correlated to their juvenile growth performance (Edeline et al. 2005a). Therefore, evolution of eel diadromy may be driven by a trade-off between search for the most productive habitats and competition avoidance favouring shift to less productive areas, while costs of dispersal hinder movements. We now provide an ESS model that may explain how eels cope with these conflicting selective pressures.

4.2. Evolutionarily stable strategy model

Conditional strategies are ESSs that are commonly invoked to explain occurrence of alternative phenotypes (i.e., threshold traits) among populations because they allow individuals to cope with physiological- and environment-dependent fitness trade-offs (Hazel et al. 1990, Gross 1996, Roff 1996, Hazel et al. 2004). Conditional strategies depict a special case of phenotypic plasticity in which the reaction norm is not continuous but instead takes a number of discrete values – most often 2 values – constituting the threshold trait under scrutiny (Schlichting and Pigliucci 1995). Classical examples of conditional strategies include predator-induced protected morphs, trophic polymorphisms or male alternative reproductive behaviours (but see Roff 1996 for review). The alternative phenotypes may be cued by internal (physiological) cues, and/or by external (environmental) cues if that they are reliable indicators of environment quality (Hazel et al. 2004). Following Gross (1996), we hereafter term "tactic" the value taken by the phenotype (or decision taken by the individual), and "status" the value of the internal cue triggering the tactic ("status" is not convenient for environmental cues). Tactics change at the status at which fitness benefits switch from favouring one tactic to favouring the alternative: the ESS switch point (Gross 1996).

Edeline (2005) and Edeline (2007) suggested that glass eel diadromy is a conditional strategy cued by individual energetic status, based on the observation that shift from migration to settlement by glass eels as their body condition decreases has an adaptive significance (Edeline et al. 2006) (see also Section 2.2). Edeline (2007) considered as parsimonious to consider a model in which both the switch point and the status (energy stores) of the conditional strategy as polygenic traits influenced by environmental factors. Hence, in an individual, both traits (the switch point and the status) are genetically fixed but they vary with environmental conditions. For instance, energy stores may possibly be influenced by the amount of food encountered during the larval stage (Désaunay and Guerault 1997). Also, the switch point may change with temperature, as indicated by the fact that low water temperature increases preference for SW in *A. anguilla* glass eels (Edeline et al. 2006). At the population level however, variations for the cue and the switch point result from both genetic and environmental variations, resulting in normal distributions for both traits (Hazel et al. 1990, Roff 1996, Hazel et al. 2004) (Fig. 5).

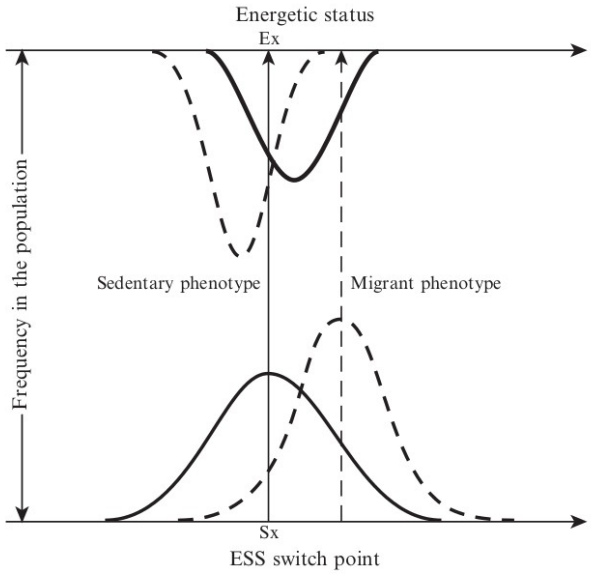


Fig. 5. Ultimate control of eel migratory behaviour. Conditional evolutionarily stable strategy (ESS) with alternative migratory tactics after Edeline (2007) and adapted from the quantitative genetic model of Hazel et al. (1990, 2004). In this model, both traits (switch point and cue) are plastic traits, i. e., polygenic traits influenced by environmental variation. The distributions of switch points and cues are therefore normal in the population. Consider first the solid curves and arrow. The distribution of the ESS switch points in the population (lower axis) is scaled with exposure to the cueing trait (energetic status, upper axis). An individual x (mean individual with regards to the switch points) will be sedentary if its energetic status Ex is lower than its switch point Sx, and migrant if its energetic status is higher than Sx. The proportion of migrants in the population therefore depends on the distribution of the switch points relative to the distribution of energetic status. For distributions corresponding to solid curves, the majority of the population presents a migratory phenotype (the mean energetic status is higher than the mean switch point). This situation may correspond to the historical state of Atlantic eel populations when recruitment in freshwater was abundant. Note that variation for the switch point is larger than variation for the energetic status, leading to the existence of unconditional migrants and unconditional sedentary individuals in the population (Hazel et al. 2004). Now, consider the effects of increased selection against migrants due to anthropogenic pressure on FW habitats (see Section 3.6). Individuals with a low switch point and/or a high energetic status are counter-selected, resulting in shifted distributions to a new equilibrium (dashed curves). This displacement of the curves induces a drop in the proportion of migrants in the population (dashed arrow). Such evolutionary shift could explain the collapse of eel recruitment into FW during the last decades (Edeline 2005, 2007). We suggest that increased selection against migrants strengthens stabilizing selection and thus results in reduced variance in distributions. Note that because the surface below a curve is held constant, reduced variance induces increased peak.

In Fig. 5, we depict this conditional strategy model in glass eels. Individual glass eels switch from migration to settlement if their energetic status decreases below their switch point. The proportion of migrants in the population is thus determined by the distribution of switch points relative to the distribution of energetic status (Fig. 5). In this model THs vs. GH and cortisol are presumably the proximate mediators of the alternative tactics, as described in Section 2.3. This conditional ESS model, initially designed for glass eel migration, may be adapted to ranging behaviour by yellow eels provided that the cue (internal or environmental) is a reliable proxy for fitness gain from dispersal decisions. For instance, individual body size relative to that of the opponent (hierarchical status) is probably a reliable cue for risk of injury during antagonistic interactions. Hence, the relationship between fitness of the alternative dispersal phenotypes and status in yellow eels will be the opposite of that found in glass eels: residency will be favoured in (large, high status) dominant eels, while (small, low status) subordinate eels will derive higher fitness from dispersal to lower density habitats (Edeline 2007). In that case, variation in the switch point for fighting or avoiding confrontation is related

to individual "personality" [aggressiveness or boldness for instance (Stamps 2007)]. In other words, not all subordinate eels of the same size will skip confrontation with a given larger opponent. The view that relative body size is a reliable cue for post-settlement dispersal decisions is supported by data showing that the intensity of movements by yellow eels is inversely proportional to their size (Feunteun et al. 2003).

Ecological events may change selective pressures acting on migrants and sedentary individuals and thus generate equilibrium displacements in the distributions of both switch points and status. For instance, in Fig. 5, we have depicted the effects of an anthropogenic increase in selection against migrants (see Section 3.6). Enhanced mortality, acting selectively on migrants (individuals with a low switch point and/or a high body condition), pushes distributions away from each other and then dramatically reduces the proportion of migrants in the population. Concurrently, global population collapse will decrease densities in SW habitats and thus favour non-migrant individuals (individuals with a high switch point and/or a low body condition), further contributing to separate the two distributions. As underlined in Section 3.6, such evolutionary shifts may be rapid. Hence, we suggest that the collapse of FW eel stocks monitored during the last decades (Dekker et al. 2003, Stone 2003) may have anthropogenic sources. This collapse would not only results from decreased recruitment, but also from a decrease in the proportion of diadromous individuals in the population (Edeline 2007).

CONCLUSION AND SUGGESTED FUTURE RESEARCH DIRECTIONS

Eel dispersal in different growth habitats impacts survival, growth, sex differentiation, age and size at silvering and finally capacity to reproduce. Therefore, understanding the mechanisms controlling continental dispersal is crucial to eel biology and conservation. Glass eels and elvers present a marked upstream migratory behaviour. Completion of metamorphosis into a yellow eel (onset of the growth phase) triggers settlement and shift to ranging behaviour characterised by search for resources and density-dependent dispersal. However, the timing of settlement is variable and some individuals settle precociously at the glass eel or elver stages, or continue exhibiting density-independent, upstream migration at the yellow stage. These alternative migratory patterns are underlaid by genetic variation that allows migration evolution. Migratory behaviour is strongly constrained by bioenergetics and is also influenced by salinity, currents, temperature and odours through different mechanisms. Thyroid hormones integrate both genetic and environmental effects, and are pivotal in mediating the alternative migratory patterns. Post-settlement, movements mainly result from competition for habitat patches, which generates a large variety of dispersal patterns due to aperiodic or seasonal variations in resource availability and demography. Ultimately, eel migratory plasticity reflects a fitness trade-off between search for the most productive habitats and competition avoidance favouring shift to less productive areas, while migration costs (increased mortality and reduced growth) hinder movements. To cope with these conflicting selection pressures acting in heterogeneous and unpredictable environments, eels have evolved a conditional strategy in which the alternative migratory tactics (e.g. diadromy vs. non-diadromy) are cued by the level of energy stores. We provide a conditional evolutionarily stable strategy model that explains how the crash of river recruitment during the last decades may reflect an adaptive drop in the proportion of migrants in response to anthropogenic change in selective pressures.

There still remain many gaps in our knowledge, as shown by the many speculative or purely theoretical parts of this review. Future works should aim at investigating the genetic basis of the alternative migratory tactics, such as for instance correlations between migratory behaviour and fitness-related genetic markers. More generally, mapping correlations among

fitness-related traits could greatly help in dissecting both the proximate and ultimate constraints shaping the eel life history. At the endocrine level, the roles of THs, GH and cortisol in regulating the morphological, physiological and behavioural processes governing dispersal should be explored more deeply. Also, the mechanisms controlling the glass eel rhythmic activity during STST are poorly understood, but additional studies could bring fascinating insights about the fine tuning of glass eels coastal and estuarine movements. At the environmental level, our understanding of the social control of dispersal remains limited, and the importance of olfaction in conspecific interactions could be underestimated. Finally, a better evaluation of the anthropogenic impacts on eel life history is critical for better management of the endangered eel populations.

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