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Editorial

Habitat as a Template for Life Histories of Fish

Bror Jonsson

Norwegian Institute for Nature Research, Sognsveien 68, 0855 Oslo, Norway; bror.jonsson@nina.no

Abstract

Life history traits are heritable and evolve through natural selection to maximize organisms' Darwinian fitness in their specific environments. The theory of life history evolution has developed during the last 100 years, and is rooted in the idea that these traits, to a certain extent, are heritable. Concurrently, ecologists have acquired evidence in support of the theory. Thus, a central focus of the present Special Issue is the adaptiveness of natural fish populations, and how environmental variables affect developmental processes within and across generations, which influence phenotypic developments. Habitat selection in stable and stochastic environments dampen abundance fluctuations and promotes phenotypically plastic life histories with morphs using different habitats. Reproduction is a major event in every life history, and the structure of mating systems depends on factors that allow males to obtain and monopolize mating resources. Habitat use and management, and the conservation of populations, are the other central themes of the volume. All habitats used by species require concern so that management actions do not impinge on their habitat selection. It is demonstrated how adult bull sharks use a seascape. For small demersal species, the structure and particle size in the bottom substratum is critical to secure feeding opportunities and shelter. Shelter is particularly important when invasive predators are introduced, and the native fauna meet a new threat against which they have no behavioral defense. Future research directions are discussed at the end of this introduction and in several of the separate papers.

Keywords: adaptive life history traits; conservation; habitat selection; niche; species management

1. Introduction

Life history is the science of how individuals in populations grow and survive where traits change in accordance with how the organisms allocate energy for growth, maintenance and reproduction. Life histories quantify how individual traits are expressed in response to how environmental variables change. The central theory is that traits, such as migration and dispersal, age at first maturity, length of life span, egg size and fecundity are heritable and evolve through natural selection to maximize organisms' Darwinian fitness in a specific environment [1,2].

Life history is a discipline in evolutionary ecology. The theory of life history has been developing with seminal papers such as Write [3], forming the concept of adaptive landscapes that map the relationship between life history traits and fitness. Peaks in the map represent optimal life history traits and valleys represent traits giving low survival. The evolution of a trait is a hill-climbing process. Then, Cole [4] observed that life history traits, such as age at first reproduction, fecundity and length of life span, are connected and evolve together to maximize an organism's reproductive fitness. Furthermore, Hamilton [5]

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developed a theory concerning aging, and Schaffer [6] demonstrated theoretically how environmental stability and demographic trade-offs dictate whether an organism evolves to breed once (semelparity) or multiple times (iteroparity), with contrasting effects of juvenile and adult mortality. In addition, there are several other highly influential theoretical papers such as [7,8], on how energy is allocated for survival versus reproduction, development and growth, and whether individuals should reproduce a few large or more but smaller offspring. Such trade-offs shape life histories of populations and species. It was realized that there are direct relationships between generation time, life history traits and the ability of populations to recover from disturbances, and that reaction norms of life history variables help us predict how individuals and their offspring react to future environmental impacts. The latter is a cornerstone of evolutionary ecology and conservation biology [9–11].

These early theoretical works inspired ecologists to seek empirical evidence for the fundamental relationships [12,13]. Fish ecologists realized the importance of studying the entire life cycle to understand life histories and modeled how to best manage harvested species [14,15]. It became important to include influences, such as temperature experienced by embryos and larvae, which affect later life history decisions such as metabolic rates [16–18], growth [16,19], migration [20] and reproductive effort [21,22]. Other variables affecting embryos and larvae, such as predator presence [23], chemical environment [24], salinity and oxygen content [25], have knock-on effects on later life history stages. Even environmental experiences perceived by parents can be transferred to offspring and affect life history variables across generations [26,27].

Movement ecology is an important part of life history studies with a recent shift from individual tagging studies to telemetry, biologging and global telemetry networks [28,29]. Fish move to find food, for predator avoidance and to find a safe place to reproduce [30,31]. Migration studies reveal how and when fish disperse and return [32,33], and how they navigate over long distances in the ocean [34,35]. By mapping their spatial dynamics, fisheries can accurately assess stock sizes, optimize the design of marine reserves, and regulate fishing pressure to prevent overexploitation [36]. Another important aspect is that migratory fish transport energy across ecosystems [37]. For example, fish that migrate from nutrient-rich seas into freshwater to spawn bring valuable marine nutrients into river systems, enriching the food web through excretions and carcass decomposition [38,39]. Human activities, such as dam building and alterations of waterways, disrupt migration routes. Selective overfishing is another widespread problem. Studying these paths allows scientists to evaluate where aquatic connectivity has been severed, design functional fishways and inform fishing regulators to protect fish during vulnerable stages such as under synchronized migration and spawning periods [40,41]. But still, these regulation issues are far from solved.

Many fish populations are divided in migratory and non-migratory (resident) individuals, a phenomenon called partial migration [42]. Partial migration is widespread among fish taxa, including anadromous, catadromous, potamodromous and oceanodromous fishes. It is also widely distributed across orders, with examples in many species from Salmonidae to Pleuronectidae [43]. However, in what way partial migration is genetically regulated is still open for discussion. Are migratory and resident phenotypes genetically distinct forms or are they polyphenic variants cued by environmental stimuli? Typically, in juveniles of Atlantic salmon, *Salmo salar* L. 1759, rapid growth increases the chance of early maturation and residency, instead of seaward migration and feeding in the ocean, suggesting that the forms are phenotypically plastic. In contrast, in whitebait *Galaxias brevipinnis* Günther, 1866, the migratory and resident phenotypes are genetically distinct. Iwikau et al. [44] found that migratory whitebait populations include jackpot individuals that carry allele sequences essential for residency. Because of these gene sequences, populations can exist

as a non-migratory form after land-locking. A similar mechanism may exist in brown trout, where residency is chiefly genetically determined [45], although in anadromous populations, the growth rate of juveniles may influence whether they will remain or migrate. Thus, there may be a continuum from phenotypical plasticity to genetically determined partially migratory populations, and the degree of heritability differs among conspecific populations.

Until recently, the genetics of life history traits was little investigated, but recent population genomics studies in Atlantic salmon have identified two unlinked genomic regions surrounding the genes *six6* in chromosome 9 and *vgll3* of chromosome 25, which are associated with life history traits of Atlantic salmon lineages [46,47]. Genes at the *six6* locus are associated with head morphology, which is crucial for their feeding strategy, and those at the *vgll3* locus are associated with swimming performance [48], aggressiveness, metabolic rate and aerobic scope [49,50]. Both loci influence age and size at first maturity and iteroparity, which are important for the fitness of the fish [47–50]. Thus, many life history traits in this species are strongly influenced by natural selection, and it may also be so for other fishes.

2. The Studies

The studies in the present Special Issue are grouped in one of two categories, (1) adaptive life histories and (2) habitat use, management and conservation.

2.1. Adaptive Life Histories

Fish populations are often polymorphic with different sized morphs. One morph is typically slow-growing and small-sized, attaining maturity at a young age, flaunting no or few secondary sexual characters in contrast to the other, faster-growing and larger-sized morph. In a literature review, Jonsson [51] summarizes how these morphs are adapted to different niches by living in different habitats and feeding on different food items. Environmental stimuli affect the diversification, but it is an open question to what extent genetic and epigenetic differences affect the morph divergence.

How environmental factors give cues leading to population diversification is central in Skúlason's [52] paper. How can environmental variables such as temperature, density, or predator presence affect developmental processes within and across generations that influence their phenotypic development? There seem to be inherited reaction norms related to specific signals that affect development. Such responses can even be transferred across generations.

Adaptive life histories through environmentally dependent effects are also a focus of Morris and Lundberg [53]. In a theoretical study, they simulated habitat selection in stable and stochastic environments. They demonstrated that ideal habitat selection dampen abundance fluctuations. Furthermore, habitat selection promotes phenotypically plastic life histories with morphs using different habitats as described above [51].

Reproduction is a major event in every life history, and Weir [54] reviewed how the structure of mating systems depends on factors that allow males to obtain and monopolize mating resources. Increases in temperature beyond optimal levels or decreases in oxygen availability may reduce the energy available for mating and for the defense of resources, and decrease variance in mating success. If individuals cannot monopolize resources, increases in density, extreme skews in sex ratios or the presence of alternative mating strategies within a sex can affect the nature of competition among individuals, with a change in mating system to an even or random distribution. Habitat alterations that result in increases in complexity because of vegetation or turbidity can affect the distribution of reproductive successes. While polygamy is typically considered the basal mating system of

fishes, deviations from this mating system can be related to habitat features that influence the fitness of the individuals.

2.2. Habitat Use, Management and Conservation of Populations

Several of the studies concern population preservation. Morris and Lundberg [53] maintain that all different habitats used by a species require concern, so that management actions do not impinge on their habitat selection. Thus, one needs to know all habitats and areas used by populations.

Venables et al. [55] used acoustic telemetry when studying how adult bull sharks *Carcharhinus leucas* (Valenciennes, 1839) used the Bazaruto Seascape, Mosambique. They showed that the important habitat for resident bull sharks extended beyond the protected seascape, and that migratory individuals from other parts of the coast visited the protected area. Thus, there is a need to look at the size of the protected area to protect the resident sharks, and develop a strategy for how one can protect individuals from other aggregations moving along the coast.

Bottom particle size is important for demersal fishes, and habitat selection can differ with the size and sex of species. Yu et al. [56] showed how *Leptobotia elongata* (Bleeker, 1870) in the Yangtze River preferred coarse gravel and stones associated with habitat variability, good feeding opportunities and the formation of low-velocity refuges. Thus, restoring coarse substrate particles in the river will provide a good habitat for *Leptobotia elongata* and other species with similar habitat requirements.

Salmonidae include some of the world's most invasive species, such as rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792), which pose a threat to the southern smelt, dwarf galaxias *Galaxias divergens* Stockell, 1959 in New Zealand. Experimental research by Coughlan and Canning [57] demonstrated that dwarf galaxias do not change habitat in presence of this foreign intruder, making them vulnerable to predation. However, maintaining a coarse bottom substrate provides this galaxiid with shelter, and reducing fine substrate in rivers is a positive management action supporting dwarf galaxias in their home rivers.

Body sizes of similar-aged pairs of coho salmon *Oncorhynchus kisutch* (Walbaum, 1972) and cutthroat trout *Oncorhynchus clarkii* (Richardson, 1836) vary among stream and populations [58]. Important causes for size variations are the size of the catchment area, physical habitat structures such as substrate particle size, pools, boulders and dead wood, and salmonid density. Water temperature appears less important for growth variations in these fish. Management actions, such as improving the physical habitat by adding instream wood and creating pool areas, ensure a natural range of body sizes across watersheds, typical for healthy populations.

Body size influences activity levels of fish, and Dziubinska et al. [59] found that, in round goby *Neogobius melanostomus* (Pallas, 1814), large individuals shift habitats between day and night to a larger extent than smaller ones. Large individuals spend more time in vegetated areas during the day. At night, they showed a greater tendency to move to bare and rocky areas for feeding. Higher activity of larger individuals may be related to a reduced danger of mortality and a greater need for food. Thus, restoring benthic habitats provides good conditions for round goby.

Similarly, Chen et al. [60] showed habitat differences between small and larger gray snapper *Lutjanus griseus* (L., 1758). These are young and small fish, typically less than one year of age. Small juveniles were most often observed along the shore line and larger juveniles occurred more often on oyster reefs. Thus, habitat selection varies with size, as the niche requirements of small and large conspecifics are typically different, and often more so than those of competing species of similar-sized fish.

Thus, in a time with decreasing fish abundances, loss of habitat is a major threat, and habitat restoration is an urgently needed management action and a growing aspect of many life history studies of fish.

3. Future Research Directions

Anthropogenic-induced stress on aquatic habitats are stronger than ever before, and to better understand the meaning of these stresses for fishes, one needs to study the tolerance limits of the stressors by estimating reaction norms for life history traits in relation to the stressors, and to study the degree to which species perform adaptive developmental plasticity reactions [61,62]. Embryos and larvae are highly sensitive to the influences of environmental variables, such as temperature, oxygen concentration, salinity, water chemistry, turbidity and cues of predator presence, which may alter metabolic and developmental rates with a major effect on life history trajectories. Research into the breadth of reaction norms of traits to environmental stressors is in its infancy and needs to be conducted across conspecific populations.

The effects of the rapidly warming climate are presently of particular interest [63–65]. To what degree can species adapt genetically to a warmer habitat, and to what degree do they have short-term plastic life history responses developed in the past, which cause phenotypic changes making them more able to cope with the warming? Do they have adequate phenotypic mechanisms that dampen negative effects, and if so, how are these regulated by genetic and/or epigenetic mechanisms, and what are the limits of the adaptations? The limits may well vary among conspecific populations depending on their past history, but this has not yet been much studied.

Is there a relationship between developmental rate and the sensitivity to a warmer climate? Wang et al. [66] found by studying the literature that demersal and reef fish were more sensitive to a warmer climate than pelagic fish. They also found that slowly developing and long-lived fish were less sensitive to a warmer climate than faster developing, short-lived fish. To what degree are there general relationships between habitat use, life histories and the vulnerability to climate change? Are there universal laws that can be found?

Climate warming changes species ranges both horizontally and vertically towards colder water in search of a thermally optimal habitat [67]. However, feeding opportunities at higher latitudes or at greater depth may be poorer resulting in slower growth rate and smaller adult size, and may change age at maturity. Because of climate change, the strength and direction of ocean currents may be adjusted and nfluence the distribution of pelagic fish larvae, and if so, will the need for early feeding match with the opportunities to feed? This may affect local food webs. The match–mismatch hypothesis of larval presence relative to feeding opportunities is a prevailing theory for year-class variation in abundance of fish [68,69], and a mismatch is a likely outcome of climate warming.

Among anthropogenic stressors are size-selective fishing and the introduction of predatory fish variables that affect the life histories of fish [70]. With a growing human demand for fish protein, many populations are over-harvested and the life history effects of this can be strong [71], but more research is needed to see the full spectra of effects of these human actions.

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