

Estuarine dependency and life history evolution in temperate sea basses

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SUMMARY: The Asian temperate sea bass, *Lateolabrax japonicus* has strong taxonomic affinities with the North American *Morone saxatilis* and European *Morone labrax*, despite wide geographic separation. *L. japonicus* and *M. labrax* populations exhibit varying levels of estuarine dependency (facultative amphidromy), while *M. saxatilis* shows varying levels of coastal dependency (facultative anadromy). Based upon phylogenetic evidence, it is hypothesized that anadromy in *M. saxatilis* evolved from a marine-spawning ancestor, contrary to the prevailing view for salmonids: that anadromy evolved from freshwater ancestors. Higher stability of east coast North American estuaries in comparison to European and Asian estuaries may explain the unique pattern of anadromy and freshwater radiation in North American temperate basses.

KEY WORDS: anadromy, contingents, life history strategy, migration, temperate sea bass

INTRODUCTION

Two commercially important temperate sea basses, the striped bass *Morone saxatilis* (Moronidae) and the Japanese sea bass *Lateolabrax japonicus* (Percichthyidae; common name “suzuki”) are respectively found along the East Coast of North America and the marginal seas of Japan, Korea, and China. To the casual observer they are remarkably similar in appearance and taste. Indeed, this has led Japanese-Americans to often call the striped bass - *Amerikano suzuki*. With the inclusion of European temperate sea bass, *Morone labrax* (a.k.a. *Dicentrarchus labrax*), the temperate sea bass group shows circumglobal distribution. Members of this group show strong taxonomic affinities, nearshore coastal distributions, and support important fisheries. The apparent similarity in morphology is more than superficial and ichthyologists have long debated the interrelationship of these species within the lower Perciformes. Ongoing biochemical studies may ultimately provide more definitive evolutionary relationships. Important taxonomic affinities among temperate sea basses and the similarity of marine habitats that they occupy has stimulated interest in their comparative physiology and ecology.

In this paper, I provide a brief description of the phylogeny, distribution, life history, and ecology for the three temperate sea basses *L. japonicus*, *M. labrax*, and *M. saxatilis*. A major underlying theme in the life history of the temperate sea basses is estuarine dependency, which varies in pattern and degree among and within temperate sea basses. From perspectives of divergent life cycles among the three temperate sea basses, I propose that anadromy in *M. saxatilis*, and freshwater dependency in other North American *Morone* is derived from facultative amphidromy, now manifested in the life cycles of *L. japonicus* and *M.*

labrax.

ZOOGEOGRAPHY AND PHYLOGENY

Based upon adult characters and early life history attributes, Johnson¹⁾ placed *Morone*, *Dicentrarchus*, *Lateolabrax* and *Sinoperca* into the single family Moronidae. Prior to this revision, Gosline²⁾ had placed these genera into the polyphyletic Percichthyidae. Waldman³⁾ provided a more comprehensive morphometric analysis of *Morone* sp. and concluded that Moronidae should not include *Lateolabrax* and *Sinoperca*, but that *Morone*, *Lateolabrax* and *Perca* (Percidae) showed very strong taxonomic affinities despite disparate family membership. These included the presence of extended epioccipital processes, and common features of the preopercle and scales. An early phylogeny⁴⁾ had proposed that genera of Moronidae, Percidae, and Lateolabracidae (*Lateolabrax*) all formed a monophyletic group. While genetic affinity among these taxa has not been reported, strong taxonomic affinities suggest a common phylogeny among temperate sea basses.

That the three temperate sea basses are separated by the Atlantic and Pacific ocean basins is an apparent conundrum. The phylogeny of freshwater eels (Anguillidae) presents the same issue - what historical pattern of lineage and dispersal led to the current pan-global distribution of species? Based upon molecular analysis that date back to the late Cretaceous, Tsukamoto and Aoyama⁵⁾ proposed that the Tethys Sea (which closed c. 30 Ma) served as a corridor for *Anguilla* spp. linking the present Pacific, Indian, and Atlantic Oceans. A similar explanation could be proposed for past dispersal and speciation within Moronidae. Nolf and Stringer⁶⁾ describe Moronidae otolith fossils from North America in late Cretaceous sandstone deposits. Thus, if the three sea basses are

monophyletic, then their lineage has been sufficiently long to account for dispersal through the shallow Tethys Sea and their current pan-hemispheric distribution.

LIFE HISTORY AND ECOLOGY

The three temperate sea basses are large top predators in estuarine and coastal ecosystems. Populations of each species occur over a wide latitudinal range and contribute to important fisheries. *L. japonicus* and *M. labrax* spawn in inshore marine habitats and larvae are transported into embayments and estuarine nursery habitats⁷. As advanced-stage juveniles and adults, the two species exhibit seasonal migrations between estuarine and deeper coastal waters. Both species occasionally use freshwater tidal habitats as juveniles and adults. Due to the variable nature of estuarine and freshwater habitat use, these species should be considered facultatively amphidromous. In contrast to the marine spawning sea basses, *M. saxatilis* is anadromous, spawning in freshwater tidal reaches of major estuaries along the broad coastal plane of eastern North America. Converse to the other sea basses, *M. saxatilis* is facultatively anadromous, where sub-adults and adults show varying degrees of marine habitat use⁸.

The differing life cycles between amphidromous and anadromous temperate sea basses may be associated with early life history attributes and reproductive schedules. *L. japonicus* and *M. labrax* show similar spawning habitat and behaviors, egg size, spawning temperatures, larval nursery habitats and larval growth rates (Table 1). Females of the two species mature at similar ages, and exhibit similar fecundity, longevity and maximum size. Mean generation times range between 3 and 5 years. *M. saxatilis*, in contrast spawns 5-fold larger eggs at substantially higher temperatures in much more restricted freshwater habitats. Larval growth rates are higher due to higher temperatures, but so too are mortality rates, which are tightly linked to volatile spring weather conditions⁹. As a possible consequence of highly variable recruitment, striped bass have a long reproductive life span accomplished through relatively late maturation, high fecundity, and high longevity and maximum size¹⁰. The mean generation for this species is 10 years. Landings data suggest that *M. saxatilis* may be a less productive species than amphidromous temperate sea basses, which corresponds to the higher generation time (10 years).

ESTUARINE DEPENDENCY

A common theme in the life history of temperate sea basses is the use of estuaries as nursery habitat. Catch

Table 1. Life history attributes of temperate sea basses.

Attribute	<i>L. japonicus</i>	<i>M. labrax</i>	<i>M. saxatilis</i>
Reproductive Ecology	Gonochoristic Multi-batch spawner, 2-3 month spawn season	Gonochoristic Multi-batch spawner, 2-3 month spawn season	Gonochoristic, Single batch spawner 1-2 month spawn season
Spawning habitat	Sea margin	Sea margin	Freshwater tidal estuary
Egg size	200 µg (pelagic)	200 µg (pelagic)	1000 µg (pelagic)
Larval habitat	Sea margin, estuary	Sea margin, estuary	Estuary
Larval stage temp.	16 C	16.5 C	18 C
Larval growth rate	0.10 mm d ⁻¹	0.13 mm d ⁻¹	0.20 mm d ⁻¹
♀ age at maturation	3-6 years	2-3 years	5-8 years
♀ longevity	20 years	15 years	31 years
♀ maximum fecundity	2.2 10 ⁶	2.5 10 ⁶	8.0 10 ⁶
♀ generation time (T _g)	5 years	3 years	10 years
♀ maximum size	15 kg	12 kg	57 kg

data and mark-recapture studies indicate that juvenile and sub-adult *M. labrax* reside in estuaries for varying lengths of time, and may occasionally invade freshwater¹¹. Young-of-the-year (YOY) juveniles may concentrate in regions adjacent and down-estuary to the saltfront, but also occur in shallow waters of coastal embayments, and near shore habitats. Juveniles and sub-adults may reside up to four years in estuarine habitats; adults more typically occur in coastal habitats over hard bottom and reefs. Much the same ontogenetic pattern of habitat use occurs for *L. japonicus*. Eggs and larvae occur in marine habitats and YOY tend to occur in shallow coastal or estuarine regions. Sub-adults and adults are known to occur in estuaries, but estuaries are not thought to be primary habitats for these stages.

Recently, otolith microchemistry has been employed to investigate estuarine dependency. In the Chikugo Estuary (Ariake Sea), Ohta¹² observed that a substantial fraction of newly transformed juveniles invaded freshwater and occurred above the saltfront. The other fraction of juveniles remained in coastal or polyhaline estuarine habitats - a clear demonstration of facultative amphidromy.

For striped bass, estuarine dependency during the larval and juvenile stage is obligate. However, during sub-adult and adult stages, there are variable patterns of estuarine and coastal habitat use. Based upon otolith microchemistry of Hudson River striped bass, Secor⁸ suggested that groups of fish - "contingents" - could be classified based upon their life-time occurrence in estuarine or coastal habitats. Further, otolith elemental fingerprints were distinct for individuals that spent the majority of their sub-adult and adult life in freshwater, estuarine, or marine habitats¹³. This contingent phenomenon indicates that facultative behaviors of amphidromy or anadromy may have common causes (genetics, environment) within populations^{8,12}.

EVOLUTION OF ANADROMY

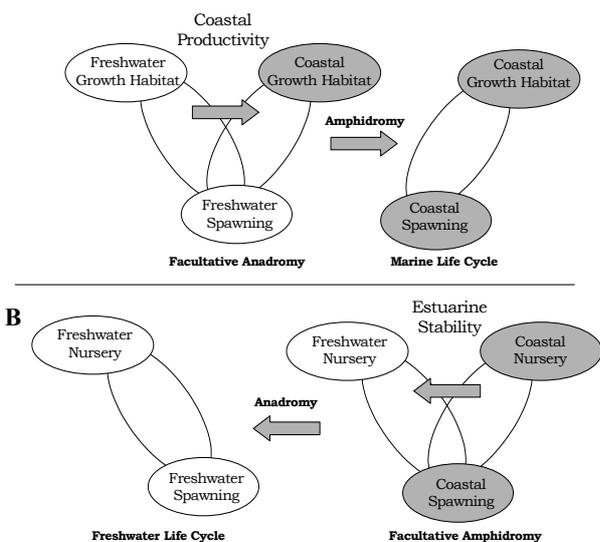
The plausibility of a common phylogeny for amphidromous and anadromous sea basses raises the question, is amphidromy or anadromy the ancestral state? One could speculate that hypertrophy and more specialized migration and reproductive behaviors in *M. saxatilis* represent a derived condition. Evidence from renal histology (simplified nephrons, lacking distal tubules) supports marine ancestry of striped bass¹⁴. Assuming that marine spawning is ancestral in temperate sea basses, corollary questions are, 1. how did freshwater spawning evolve? and 2. why does

anadromy only occur along the east coast of North America?

As late stage larvae and YOY juveniles, all three temperate sea basses are known to utilize up-estuary regions. A growing body of literature supports the view that regions adjacent to the salt front (and associated

A

Figure 1. Concept of anadromy as proposed by (A) Gross¹⁸ and in this paper (B). See text for details.



turbidity maxima) are essential nursery habitats¹⁶. Such regions often afford higher levels of zooplankton forage and refuge from predators. Larvae and juveniles of many important coastal spawning fish disperse into estuarine environments utilizing such mechanisms as selective tidal stream transport or oriented swimming. Still, mechanisms of dispersal into estuaries¹⁶ are imperfect. In contrast to coastal spawning, an anadromous life cycle would guarantee arrival of young to estuaries. Why then are not all

temperate sea basses anadromous?

Temperate estuaries are characterized as highly variable ecosystems, due to the combined influences of adjacent marine and continental watershed hydrology, hydrography, biota, and anthropogenic effects (e.g. eutrophication, invasive species). Over geological time, estuaries are influenced by climate change, sea level rise, glaciation, erosion, and orogeny. Thus, it might be expected that nearshore coastal habitats are more stable (albeit, perhaps less productive) over millennia than are estuaries. Facultative amphidromy would serve as a strategy to hedge bets across predictable less productive coastal habitats versus unstable productive estuarine habitats.

Temperate estuaries of Europe and Japan are considerably smaller than those in North America. In Europe and Japan, the largest estuaries are the Gironde (Bay of Biscay) and the Chikugo (Ariake Sea), respectively, and both of which serve as important nursery habitat for temperate sea basses. The Gironde estuary (635 km²) is closely framed by the Cévennes and Pyrenees mountain chains, and the slightly smaller Chikugo estuary is closely bordered by several active volcanos. Thus, over geological time, these estuaries represent unstable productive habitats. The Eastern continental divide of North America is characterized by an ancient and highly eroded mountain chain and a broad coastal plane. This erosional landscape has favored the formation of the world's largest temperate estuaries. The largest of these, the Chesapeake Bay (11,000 km²) supports an abundant stock of striped bass.

If eastern North American estuaries are unique in their size and stability, this might have led to the evolution of freshwater spawning by a progenitor of *M. saxatilis*. For salmoniform and other teleosts, anadromy is thought to have evolved from the exploration of marine environments by juveniles or adults of freshwater spawned fish¹⁷. If marine temperate environments are more productive, then the costs of migration and increased predation may be balanced by increased growth rate. Further, Gross¹⁸ suggested that marine spawning could ultimately evolve from freshwater spawning based upon differences in production between freshwater and marine habitats (Fig. 1). In contrast, I propose that for temperate sea basses, the relative stability of North American estuaries permitted initial exploration of freshwater tidal regions as spawning habitat. This led to adoption of an anadromous life cycle (Fig. 1). Given the inherent instability of estuaries, large or small, evolution of anadromy may have entailed changes in life history traits such as increased reproductive lifespan, higher fecundity, and increased egg size (Table 1). It is also conceivable that anadromy led to freshwater life cycles as evidenced by the radiation of the other three North American Moronidae: one of which completes its life cycle in estuaries (*M. americana*) and two of which are exclusively freshwater (*M. chrysops*, *M. mississippiensis*). Congeneric species of *L. japonicus* and *M. labrax* are

marine fishes.

Circumstantial evidence for the evolution of anadromy from marine spawning comes from the work of M. Tanaka, his students, and colleagues on Chikugo estuary *L. japonicus*¹⁹⁻²³. Larvae of this population are uniquely adapted in their dispersal behavior and physiology to utilize freshwater tidal estuaries as late stage larvae and juveniles. Conceivably, if the system were to remain stable over geological time, a "mutant" spawning behavior that increased the probability of larvae occurring in freshwater tidal habitats (i.e. anadromy) would be favored. Further investigation of the larval ecology of *L. japonicus* and *M. labrax* particularly in large estuarine systems could provide additional support for the hypothesis that evolution of anadromy in temperate sea basses was due to the comparative habitat values of marine and estuarine nurseries.

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