

Limitations of Early Seaward Migration Success in Amphidromous Fishes

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Abstract

Amphidromous fishes are abundant in insular streams and rivers which have a comparatively short length, whereas they are less common in continental rivers which are relatively larger in scale. This presents a challenging question about the adaptive role of amphidromy to freshwater habitats. This study overviews amphidromy, with a focus on the early survival of amphidromous fishes. Similarity in diel periodicities during downstream and vertical migrations of larval gobies suggests that, in running waters, seaward migration starts automatically as a result of phototaxis inherited from marine ancestors. Goby larvae feed on plankton, and during the downstream migration, loss of larvae from starvation prior to reaching the comparatively plankton rich brackish and marine zone can be regarded as a function of the distance they must be carried by water currents or the time spent without food. Smaller eggs may have an adaptive significance with respect to larvae reaching the sea more quickly, but such an evolutionary “countermeasure” is limited by the higher vulnerability of smaller embryos. Topographical features such as long, slow-flowing lower courses make typical continental rivers unsuitable as a habitat for amphidromous fish due to the high costs of dispersal. Disruptive selection, which is expected to favor both large- and small-sized eggs, may allow an evolutionary breakthrough by the abandonment of a migratory life cycle. In fact, some fishes which originated from amphidromous species have established effective landlocked populations within longer rivers. These fluvial species generally spawn large eggs, from which well-developed larvae emerge that are able to support themselves in running water.

Introduction

Fishes that inhabit freshwaters are conventionally classified according to their capacity to tolerate different salinities, and this can be useful in understanding their ecological and evolutionary status in local aquatic communities. Myers (1949) analyzed the categories of freshwater fishes and listed some definitions. Many fishes that are strictly confined to low salinity are defined as primary freshwater fish. Those that are strictly confined to freshwater, but are relatively salt tolerant, at least for a short period, are defined as secondary freshwater fish. However, some species are more adaptable and tolerant of a wide range of salinities. Those that regularly migrate between freshwater and seawater at a definite stage of their life cycle are defined as diadromous fishes. Marine species which move freely into freshwater are defined as peripheral fish. The dynamics of immigration and local extinctions are important factors in the ecology and evolution of species and populations dwelling on islands (MacArthur, 1972; Otto & Endler, 1989; Futuyma, 1998). Compared with freshwater fish faunas in mainland areas, those on islands can be characterized by a low occurrence of genuine primary and secondary freshwater species. Instead, euryhaline species fill this vacant niche in insular fish communities, especially in the middle and upper courses of rivers and streams where species of diadromous fishes are often dominant (Hayashi *et al.*, 1992; Shinomiya & Ike, 1992). Because suitable habitats on islands have less of an opportunity to be invaded by genuine freshwater fishes from mainland streams and rivers, insular freshwater fish faunas more plausibly depend upon euryhaline migratory fishes.

Diadromy, a term used to describe migrations of fishes between freshwater and the sea, includes three sub-categories: anadromy, catadromy, and amphidromy (Myers, 1949). Their definitions are as follows: anadromous fishes spend most of their lives in the sea and migrate to freshwater to breed,

catadromous fishes spend most of their lives in freshwater and migrate to the sea to breed, and amphidromous fishes that are spawned in freshwater, migrate downstream to the sea and then go upstream at a juvenile stage for further growth and reproduction (McDowall, 1992, 1997a). Salmon and eels, representative of anadromous and catadromous fishes, respectively, can inhabit continental areas as well as insular areas, showing their ability to reproduce in large rivers. In contrast, habitats of amphidromous species are limited largely to islands with small streams such as those known from Japan, Hawai'i, Australia, and New Zealand (McDowall, 1997b). Amphidromy has developed among a wide variety of taxa involving several families such as Osmeridae, Galaxiidae, Aplocheilichthyidae, Prototroctidae, Cottidae, and Gobiidae (McDowall, 1988). Like anadromous and catadromous fishes, amphidromous fishes have a potential to disperse through the ocean to some extent during their marine stages. However, establishment of populations of amphidromous fishes in large rivers running through continents is a rare occurrence. Such an asymmetry in the distribution of amphidromous fishes, biased toward insular habitats, is a challenging question requiring assessment.

Gobies comprise one of the largest families of marine fishes, have diverse life histories (Nelson, 1984), and often become predominant members of the freshwater fish faunas on oceanic islands in the tropics and subtropics [e.g. the Hawaiian Chain; Nishimoto & Kuamo'o (1991)]. It is readily comprehensible that amphidromous species are derived from marine ancestors. In fact, some amphidromous gobies known from the Japan Archipelago have coastal relatives neighboring with them near the stream mouth (Mukai, 2001; Senou *et al.*, 2004). Early migration of amphidromous gobies begins with passive drift (i.e. movement due to currents) just after hatching. The frequency of drifting larvae changes hourly within a day, and different species exhibit similar periodicities (Iguchi & Mizuno, 1990). Such diel drift patterns are principally explicable by larval phototaxis (Iguchi & Mizuno, 1991). Rather than being particular to amphidromous fishes, larval phototaxis is also prevalent among marine fishes and governs their diel vertical migrations (Woodhead & Woodhead, 1955). This leads to the idea that the mechanism which triggers downstream movement in amphidromous fishes did not evolve after invasion of freshwater habitats but is a pre-adaptive behavioral characteristic inherent in their marine ancestors. Drift and vertical migrations in larval fishes, therefore, are hypothesized to be homologous behaviors that evolved in different conditions, running water and lentic water. The aim of this study is to examine this hypothesis through the comparison of diel phenomena shown within a single species that inhabits both lotic and lentic habitats. Then, evolution and limitations of amphidromy are discussed on the basis of the life histories of gobies.

Materials and Methods

Study fish

Rhinogobius sp. CB, Shima-yoshinobori in Japanese, is a member of the *Rhinogobius* species complex formerly called *R. brunneus* Cross Band type (Kawanabe & Mizuno, 1989; Shimizu *et al.*, 1993; Aonuma *et al.*, 1998). This goby is common throughout Japan, inhabiting steep and moderately sloped reaches with stony riverbeds (Mizuno, 1960a). In marked contrast to continental rivers, watercourses on the Japan Archipelago are short in length but high in average water velocity, owing to the insular topography characterized by small coastal plains and mountains close to the coast. To evaluate watercourse landscapes in Japan, a reach type classification defined by the combination of the arrangement of rapids and pools (A or B) with the mode of flow from rapids to pools (a, b or c) is often adopted for convenience (Kani, 1944; Mizuno & Kawanabe, 1981). Aa-type reaches have two or more sets of a rapids and a pool in a single reach separated by clear falls, and usually occurs along steep courses in mountains. Bb-type reaches have a couple of turbulent rapids and pools in a single reach with no waterfall separating them, and usually appears along gentle courses in plains. Along the gentlest and lowest courses, Bc-type reaches which lack the distinguishable boundary of rapid and pool can be found. This reach type is rare in Japan, but constitutes the main part of continental rivers. Reach types, therefore, determine the capacity of watercourses to function as conveyors of larvae. Amphidromous gobies usually use Bb and Aa-type reaches as habitats for growth and breeding. However, landlocking of amphidromous fishes in lakes, reservoirs or ponds results in the establishment of new populations without the seaward migration (Mizuno, 1960a).

Rhinogobius species complex spawns on the undersurfaces of stones, and males, as in many other gobiid species, are the sole providers of parental care, maintaining nests and taking care of eggs until hatching (Breder & Rosen, 1966; Ito & Yanagisawa, 2003). Newly hatched larvae of *Rhinogobius* sp. CB are characterized by their pigmentation pattern, a yolk with oil globules somewhat larger than the eye in diameter and membranous fins without rays (Sakai & Yasuda, 1978). They are approximately 4 mm long in notochord length and have a specific gravity more than one (i.e. negatively buoyant in freshwater). They show a positive phototaxis to 500 lux ambient light but a negative response to light more than 5000 lux, even though their swimming ability is negligible (1.5 cm/sec maximum in still water) (Iguchi & Mizuno, 1991). Their diel drift pattern is variable along river courses, and corresponds to the environmental conditions present in the reach they occur in. In the case of the Mina River, which is typical of short rivers in Japan at just 12 km in length, downstream migration occurs throughout the day in upper courses with Aa-type reaches, whereas drifting larvae becomes nocturnal with a peak in number soon after sunset in the lower courses with Bb-type reaches (Iguchi & Mizuno, 1990). As is commonly the case in streams and rivers in Japan, the diel drift pattern of larval gobies corresponds to the reach type. Diel periodicity in larval drift is not specific to gobies but is known from other amphidromous fishes including ayu *Plecoglossus altivelis* (Tago, 1999).

Field survey

Larvae of *Rhinogobius* sp. CB were collected from the Shimanto River, Mina River and Yoshifuji Pond in 1984. Sampling sites established in each location were different in topographical features. The Shimanto River is 190 km in length (the largest river on Shikoku Island, Japan) and has adult gobies distributed as far as 100 km upstream of the river mouth. The sampling site in the Shimanto River was located just upstream of the salt wedge, 9.1 km from the river mouth (32°59'N, 132°56'E). In the Mina River, which is 12 km in length, adult gobies occur as far as 5 km upstream of the river mouth; a sampling site was located in a tidal zone estuary in the river mouth (33°2'N, 133°3'E). The Yoshifuji Pond (33°50'N, 132°47'E) is a small reservoir (325,000 m³ volume) constructed in 1957 for agricultural use in which gobies have been landlocked.

Fish collection was conducted two or three times at each locality from June to August corresponding to the breeding season of *Rhinogobius* sp. CB. In each sampling trial, netting was repeated at hourly intervals over a 24-hour period beginning at noon. Drifting larvae in the Shimanto River were captured using a drift net with a 30 x 30 cm mouth anchored for 10 min. Larvae in the surface layers of both the mouth of the Mina River and the Yoshifuji Pond were captured using a plankton net with a mouth of 25 cm in diameter by making ten 10m-castings in succession from the shore. Goby samples were fixed in 10% formalin immediately after being caught for later sorting and counting in the laboratory. Samples that contained a mix of the four sympatric *Rhinogobius* species were tentatively divided into two size classes; larvae that were approximately 4 mm notochord length were assorted into *Rhinogobius* sp. CB or DA, and those that were approximately 3 mm notochord length were assorted into *Rhinogobius* sp. CO or LD. Further identification of larvae relied on the pattern of pigmentation on the dorsal surface (M. Miwa & N. Mizuno, 1978, unpubl. data). Detection of their external characteristics required the aid of a microscope.

Results

At the lower course of the Shimanto River, the number of drifting larvae increased rapidly after sunset, peaked between 1900 and 2300 hours and then decreased, while few larvae also drifted during the daytime (Fig. 1A). Small numbers of larvae were observed to have already exhausted their yolk. Surface-netting in the tidal area of the Mina River revealed diel changes in the density of larval gobies with lower amount of remaining yolks. Larvae in the river mouth were nocturnal, appearing in the surface layer soon after sunset with a peak between 1900 and 2300 hours (Fig. 1B). In the Yoshifuji Pond, larval numbers in the surface layer increased immediately after sunset, peaking between 1800 and 2200 hours and then quickly decreasing, while small numbers also emerged in the daytime (Fig. 1C). Every sampling trial confirmed that diel periodicity was consistent across localities.

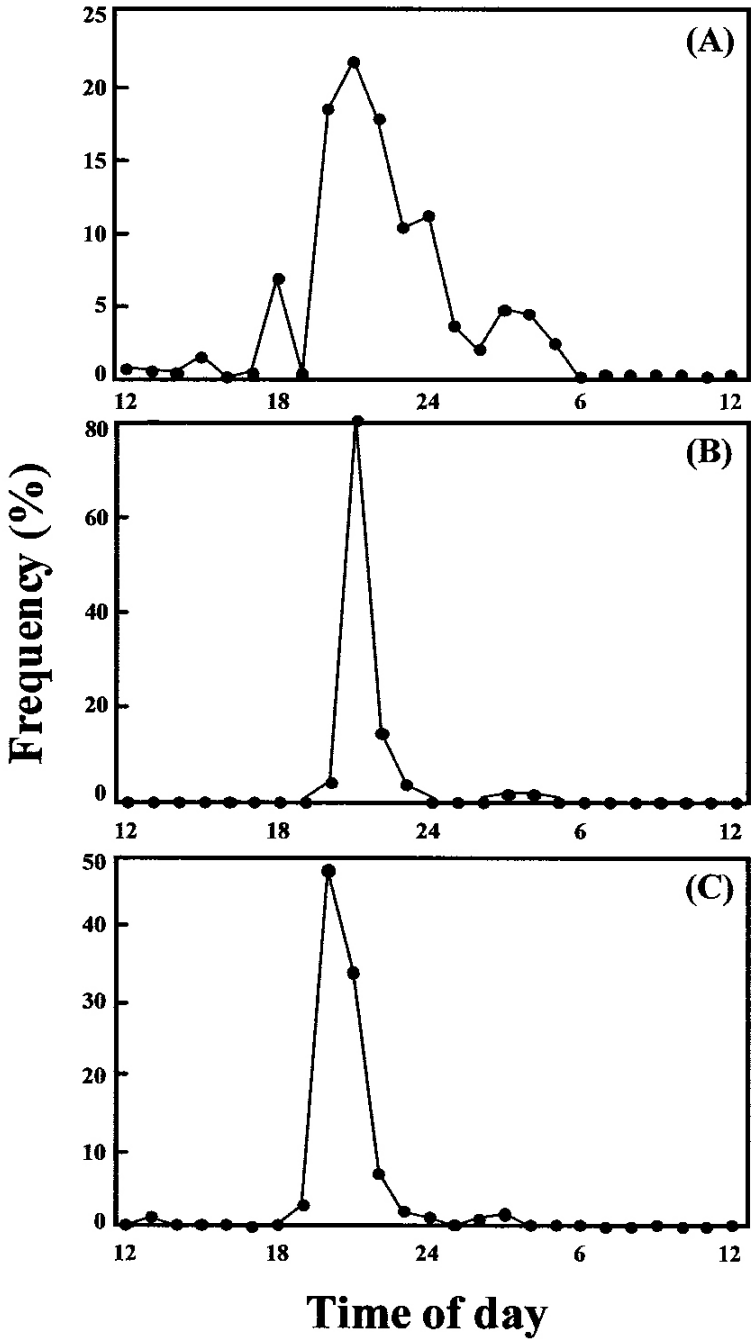


Figure 1. Diel changes in the frequency of larvae captured from (A) the Shimanto River on 11–12 July 1983 (N = 862), (B) the Mina River on 23–24 July 1983 (N = 200), and (C) the Yoshifuji Pond on 14–15 June 1983 (N = 652).

Discussion

Origin of drift migration

It is difficult for the appearance of larvae in the surface layer of water to be explained by horizontal movements from elsewhere because of the fact that larval *Rhinogobius* sp. CB have such poor swimming ability. Changes in the surface density of larvae in the river mouth of the Mina River as well as in the Yoshifuji Pond are therefore attributable to the vertical movement of larvae. Vertical migration is a widespread phenomenon among zooplankton including pelagic larvae of fishes (Motoda, 1972; Seliverstov, 1973; Takahashi, 1981; Fortier & Legget, 1983). In Lake Biwa, the largest lake in Japan, larvae of *Rhinogobius* sp. nocturnally ascend during their vertical migration (Nagoshi, 1982). Their lacustrine life has been estimated to have evolved during the diluvial epoch, 100,000 years ago (Takaya, 1963). On the other hand, for the population in the Yoshifuji Pond, it has only been, at most, 26 years since the transition from an amphidromous life to a landlocked life. Larvae in the mouth of the Mina River are still actively migrating to the sea. Thus, early vertical migration seems to be an instinctive action of goby free embryos regardless of what type of habitat they occur in. Similar to the larvae in the Shimanto River, those in the river mouth of the Mina River and in the Yoshifuji Pond share a pattern of diel periodicity, which indicates a common mechanism.

Diel drift patterns of larval gobies in comparatively small rivers are variable along courses, as was observed in the Mina River (Iguchi & Mizuno, 1991), and can be attributed to larval reactions to ambient light together with their vertical mobility in running water (Iguchi & Mizuno, 1991). Once leaving the nest, daytime larvae in upper courses can do nothing but be carried away by water currents, no matter how they may prefer to avoid strong illumination. The poor swimming ability of larvae is responsible for their all-day drifting through Aa-type reaches. Sizable pools formed in the lower courses of rivers allow larvae their directional movement, and negative phototaxis lets them halt drifting until twilight induces them to rise from the dark adjacent to the bottom. Phototaxis explains the marked increase in the number of drifting larvae in the Bb-type reaches that exist in relatively large rivers in Japan such as the Shimanto River. Likewise, the vertical position of larvae in lentic water changes in a similar pattern. Close to evening, positive phototaxis to weak illumination stimulates larvae to swim upward in the water column, and at dusk a high density of them occur in the surface layer. At night, larvae that stop moving sink due to their negative buoyancy and disappear from the surface layer. Periodical appearance of larvae at the surface layer observed at the river mouth of the Mina River and in the Yoshifuji Pond is, thus, explained chiefly by phototaxis. It can be concluded, then, that for amphidromous gobies, seaward drift migration and vertical migration can be considered homologous phenomena expressed under different conditions, running water and lentic water. A key factor in this homology is phototaxis, suggesting that early seaward migration in amphidromous gobies is driven by instinctive behaviors inherited from marine ancestors.

Early survival in rivers

Adhesive eggs, which need a hard substrate to attach to, are common among marine and freshwater gobies and are also known from many amphidromous fishes other than gobies [e.g., sculpins (genus *Cottus*), Goto (1990); ayu, Ishida & Ohoshima (1959)]. Such a phylogenetic constraint in spawning mode, which requires appropriate substrata on which to attach eggs, results in amphidromous fishes moving upstream until encountering reaches with stony riverbeds suitable for spawning grounds (Tamada, 2000). Herbivores found among amphidromous fishes include specified grazers such as the monk goby *Sicyopterus japonicus* and ayu (Fukui, 1979; Iguchi & Hino, 1996). Attached algae needs stony substrata on which to grow and moderate flow velocities to maintain their growth (Tanimizu *et al.*, 1981). These types of spawning and grazing habitats are less abundant in the lowest part of typical rivers in Japan because of the combination of muddy riverbeds and low flow velocities. Many species of amphidromous gobies have evolved pelvic fins fused to form a sucking disk that is helpful to climb up the steep waterfalls that frequently interrupt insular streams and rivers (Nishijima & Shikatani, 1994).

Low availability of food due to the lack of zooplankton in running water practically prohibits seaward drifting larvae from foraging even after the absorption of their yolk (Tsukamoto, 1991). The degree of starvation is, therefore, correlated with the distance from the hatching site to the sea or the

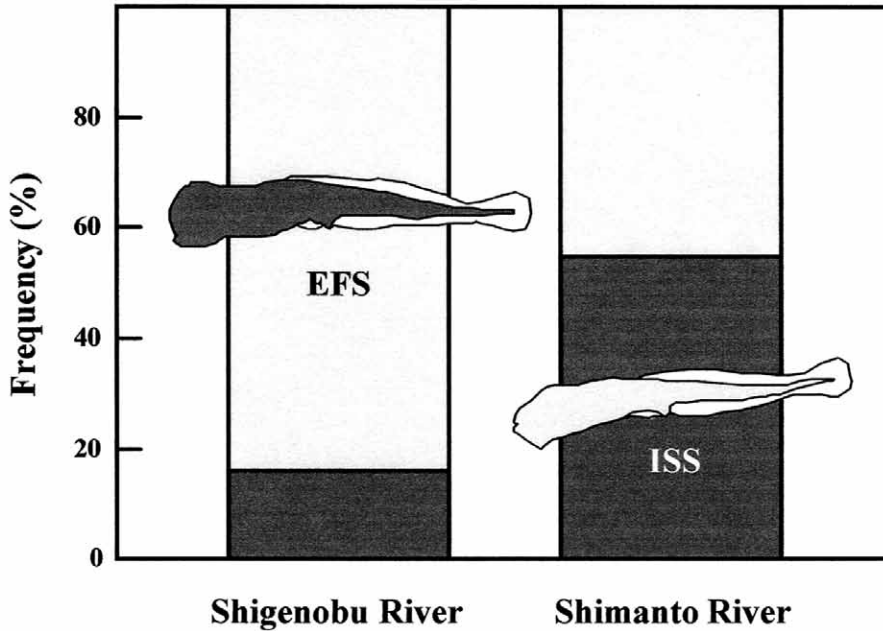


Figure 2. Frequency of larvae in endogenous feeding state (EFS) and irrecoverable starvation state (ISS) compared between samples (each N-100) from the headwater area in the Shigenobu River (33°46'N, 133°48'E) and from the beginning of the salt wedge of the Shimanto River (32°59'N, 132°56'E). Reanalysis was based data given in Iguchi & Mizuno (1999).

time spent in migration toward the sea. Based on the morphological transition of larvae from endogenous feeding state to irrecoverable starvation state, Iguchi & Mizuno (1999) hypothesized that early survival of amphidromous fishes varies according to the length of river. A test using *Rhinogobius* sp. CB individuals from different populations strongly supported the hypothesis that the longer the distance of migration without food, the higher the mortality rate for larvae (Fig. 2). Total survival of larvae tends to be overestimated, because dead individuals sink to the bottom before passing by a sampling site (see Moriyama *et al.*, 1998). Starved larvae are too weak to feed even if food ultimately becomes available (Blaxter & Ehrlich, 1974) and are vulnerable to potential predators that forage selectively on an easy catch (Paradis *et al.*, 1996). A convincing argument can be made, then, that rivers with long, slow-flowing lower courses are unsuitable habitats for amphidromous gobies. Even though adults are successful in spawning in upper courses, their larvae must travel a long way to the sea to the detriment of early survival. This may be a critical reason why amphidromous fishes are abundant in insular streams and rivers but hardly maintain populations in large continental rivers. Generally, insular streams and rivers are comparatively short with short, slow-flowing courses, which enables larvae to finish their travel to the sea quickly.

Pathway to another life

It is a natural assumption that young amphidromous gobies entering the mouth of a freshwater habitat would keep on going upstream until encountering a vacant niche for growth and reproduction. From an evolutionary standpoint, amphidromy will be favored, when invading individuals are able to enhance their fitness while balancing this with the costs of migration (Gross, 1987). Reproductive success associated with the early survival of larvae varies among parental individuals with the dis-

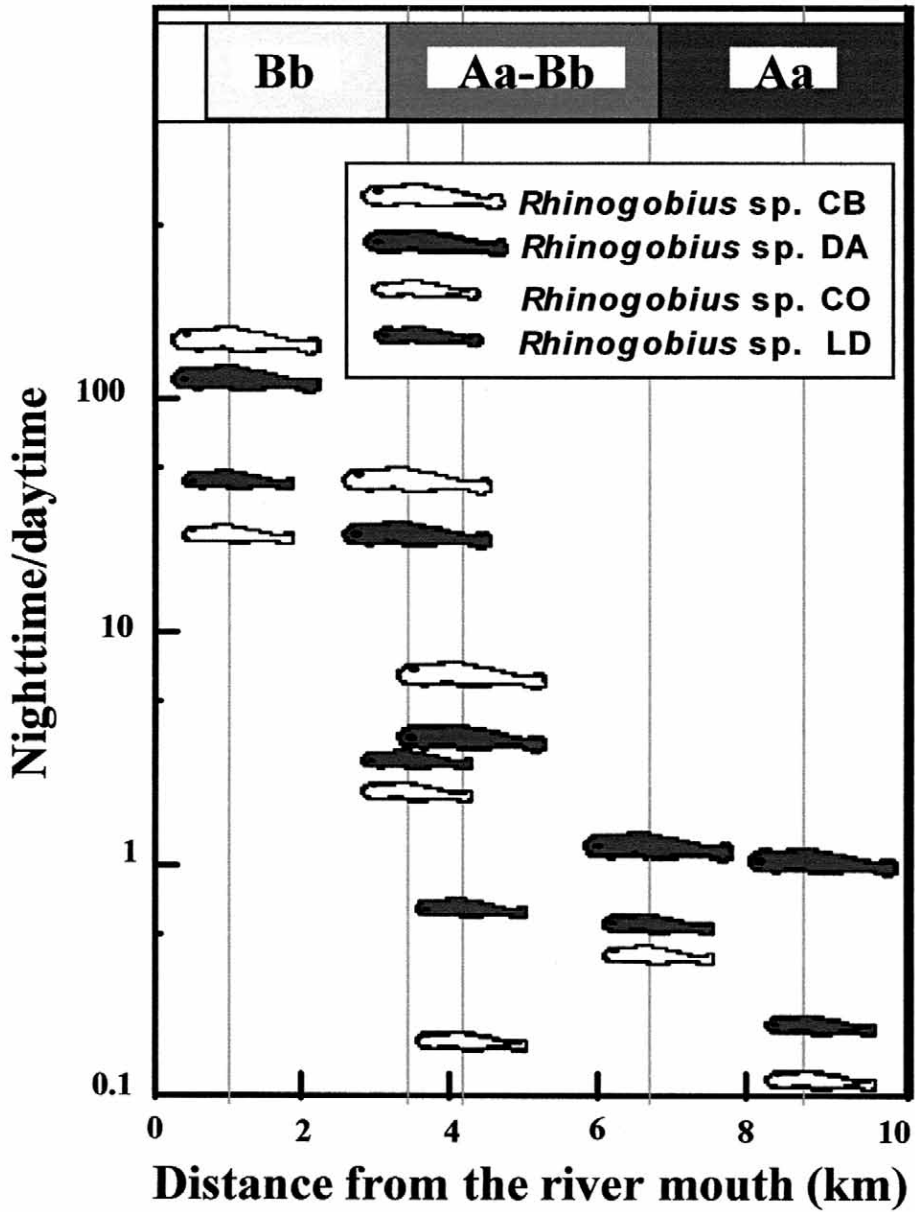


Figure 3. Night/day ratios of drifting larvae based on hourly collections along the the Mina River courses from June to July 1983. *Rhinogobius* sp. CB and DA are 4 mm in notochord length, while CO and LD are 3 mm. Natural photoperiod (L:D) was approximately 14:10. Upper horizontal bars indicate reach types. Reanalysis was conducted based on Iguchi (1985).

tance their offspring are required to drift. By replacing distance with time spent in-transit, it can be predicted that accelerated seaward migration will reduce early mortality from starvation. In one view, nocturnal activity of larvae wastes daytime hours available for further downstream movement. Meanwhile, daytime drift occurs inevitably according to the body size of larvae, a characteristic that primarily regulates swimming ability (Tsukamoto *et al.*, 1975). Downstream movement of smaller larvae during the daytime, even though involuntary, must shorten the total time spent migrating to sea. Some *Rhinogobius* species sympatric within a river have different egg sizes that correspond to differences in their distributional ranges, and species with small eggs prefer habitats in upper tributaries (Mizuno *et al.*, 1979; Tamada 2000). Egg size has an influence on the occurrence of daytime drift (Iguchi, 1985); larvae from small eggs gain more distance during the day than those from large eggs, although overall trends become nocturnal as they move downstream (Fig. 3). Egg size within a species is variable between populations from different rivers, suggestively involved in the distributional difference in spawning site (Tamada, 2005). Having smaller eggs that hatch into smaller larvae which are more likely to drift during the day results in higher dispersal efficiency and appears to be advantageous to populations living in the upper courses of streams and rivers.

The intraspecific variation in egg size indicates that larval body size can be an adaptive trait selected for in the process of invading. The trade-off between size and number of eggs leads to an increase in fecundity with decreasing egg size (Smith & Fretwell, 1974), which may be beneficial to some extent. However, the advantage of small eggs would attain a plateau rapidly because of the minimum size to exist. Monk gobies, famous for being the smallest larvae among vertebrates, often ascend to the headwaters of insular streams and rivers. It is, nevertheless, rare that populations that inhabit the upper courses of continental rivers are able to successfully reproduce (Dôtu & Mito, 1955). A complete turnabout in adaptive strategy, required to provide countermeasures against early mortality, is essential for populations of amphidromous fishes to successfully expand their distributions into habitats in longer rivers. This evolutionary turnabout is the abandonment of amphidromy. In terms of egg size evolution, sympatric speciation is subject to disruptive selection rather than directional selection (Kishi, 1978). It is estimated that large eggs from which larvae hatch at a well-developed stage and that are able to support themselves in running water allows for the evolution of a non-migratory freshwater life. Actually, fluvial species that have larger eggs than their amphidromous congeneric relatives have been identified from gobies; *Rhinogobius flumineus* (Mizuno, 1960b), *Rhinogobius* sp. BB, and *Rhinogobius* sp. YB (Hirashima & Tachihara, 2000), as well as from sculpins; *Cottus nozawae*, and *Cottus pollux* large-egg type (Goto, 1990; Goto & Andoh, 1990). In conclusion, the shift from an amphidromous to a fluvial life is highly likely to allow fish with large eggs to establish populations in longer rivers running through continents (e.g. *Rhinogobius* species from the mid Mekong River, Chen *et al.*, 1999).

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