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REVIEW PAPER

Biology and ecology of amphidromous Gobiidae of the Indo-Pacific and the Caribbean regions

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In the Indo-Pacific and the Caribbean regions, isolated rivers are host to amphidromous Gobiidae with a life cycle adapted to extreme climatic and hydrological seasonal variation. Although this is the most diverse family of freshwater fish, their biological cycle and the parameters and evolutionary processes that lead to such diversity are poorly understood. This paper reports on the current knowledge on reproduction (nidification, spawning, larval life and sexuality), recruitment into the rivers, upstream migration and distribution in the rivers. Management and restoration strategies to preserve amphidromous gobies, often endemic and bordering on extinction, require the development of research to have a better understanding of their life cycle. © 2003 The Fisheries Society of the British Isles

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INTRODUCTION

In the Indo-Pacific and the Caribbean regions, insular river systems are colonized by Gobiidae with a life cycle adapted to the conditions in these distinctive habitats which are young oligotrophic rivers and subject to extreme climatic and hydrological seasonal variation. These species spawn in fresh waters, the free embryos drift downstream to the sea where they undergo a planktonic phase before returning to the rivers to grow and reproduce (McDowall, 1997; Keith *et al.*, 2002*a*); hence they are termed amphidromous (McDowall, 1988, 1997). The practical details of their biological cycle and the parameters leading to such extreme evolution in amphidromous gobies are poorly known (McDowall, 1993), despite the fact that these gobies contribute most to the diversity of fish communities in the Indo-Pacific and the Caribbean insular systems and have the highest levels of endemism (Keith, 2002*a*; Keith *et al.*, 2002*a*; Lim *et al.*, 2002; Marquet *et al.*, 2003). For example, in the Marquesas Islands nine species of amphidromous gobies are endemic (64% of the freshwater fish species) (Keith *et al.*, 2002*a*). Amphidromous gobies belong mainly to the genus *Lentipes*, *Sicyopterus*, *Sicyopus*, *Stiphodon*, *Awaous*, *Stenogobius*, *Schismatogobius* and *Rhinogobius* for the Indo-Pacific area and *Sicydium* and *Awaous*

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for the Caribbean area. They comprise nearly 170 species (R. Froese & D. Pauly, 2003. FishBase electronic publication http://www.fishbase.org, Version 16, June 2003).

At certain times of the year, the biomass of larvae migrating upstream is so great that they contribute an important source of food for local human populations in certain island archipelagos (Manicop, 1953; Delacroix, 1987; Bell, 1999). Harvesting of this food resource, however, is highly unsustainable, on account of the complexity of the species' life cycle and the hydrological specificities of these islands. Hence there is an urgent need to address the biology and ecology of amphidromous Gobiidae, which is needed to form the basis of management and conservation policies.

REPRODUCTION

NIDIFICATION, SPAWNING AND LARVAL LIFE STAGES

Few studies have investigated the reproductive biology of freshwater Gobiidae, particularly in their natural habitat. Those species that have been studied live in various habitats, including middle reaches of rivers (Dotu & Mito, 1955; McDowall, 1965; Auty, 1978; Kim & Han, 1989; Daoulas *et al.*, 1993; Han *et al.*, 1998), streams with fast current (Delacroix, 1987; Fitzsimons *et al.*, 1993; Kinzie, 1993*a*; Ha & Kinzie, 1996; Takahashi *et al.*, 2001), lakes (Hidaka & Takahashi, 1987*a*, *b*; Ito & Yanagisawa, 2000), estuaries or lower reaches (Hirashima & Tachihara, 2000; Takahashi, 2000; Tamada, 2000).

Some amphidromous goby species are semelparous, others are annual spawners (Ego, 1956; Harrison *et al.*, 1991) while others spawn repeatedly (Torricelli *et al.*, 1985; Meadows & Meadows, 1988). Clutch size is known for only a few amphidromous species (Mizuno, 1960; Timbol *et al.*, 1980; McDowall, 1994), such as *Sicyopterus lagocephalus* (Pallas, 1770), on the island of Reunion, where the female fish produces 50 000–70 000 ova (Delacroix, 1987; Keith *et al.*, 1999), or (in Japan) *Sicyopterus japonicus* (Tanaka, 1909) which produces up to 225 000 ova (Dotu & Mito, 1955).

In general, the eggs are laid on the substratum, often on the underside of various supporting structures such as stones, rocks and crevices, but sometimes also on, or among, the vegetation. In *Lentipes concolor* (Gill, 1860) found in Hawaii, nests are situated preferentially under a large rock, away from the main river channel, close to the banks where they are safe from the full strength of the river current. The eggs are found from October to June, with a peak occurrence in February. The number of eggs in the ovaries varies from 12 000 to 14 000 (Kinzie, 1993*a*). Following the courtship display, the male fish leads the female to the spawning site (Fitzsimons *et al.*, 1993; Way *et al.*, 1998). In *Awaous guamensis* (Valenciennes, 1837) from the Pacific area, the adult fish normally migrate downstream to the spawning grounds, which are situated in general in the first shallow rapids encountered upstream from the river mouth (Ego, 1956; Kido & Heacock, 1992). The females lay the eggs in the latter location, where they hatch within 24–70 h (Kido & Heacock, 1992; Lindstrom & Brown, 1994). The females lay a vast number (up to 700 000) of rather small eggs (*c.* 0·23 cm in diameter) between August and December (Ego, 1956; Ha & Kinzie, 1996). The

females usually leave the nest unattended, or are driven away by the male fish, immediately after releasing the eggs. The male fish care for and guard the eggs as in many other species of goby (Gibson, 1970; Cole, 1982; Thresher, 1984; Lindstrom & Brown, 1994).

In the rivers of Martinique (West Indies), Lim *et al.* (2002) showed that the female of *Sicydium punctatum* Perugia, 1896 produce 50 000–60 000 ova. The breeding season of *Sicydium plumieri* (Bloch, 1786) from Puerto Rico begins in early September and finishes in January with the end of the rainy season (Erdman, 1961; Lim *et al.*, 2002).

Species of the genus *Rhinogobius* live in the river courses of Japan, Taiwan and Korea, and exhibit paternal care over nests that are typically found on the underside of rocks on the river bottom (Takahashi, 2000; Sone *et al.*, 2001). The breeding season of the species *Rhinogobius* sp. DA (dark type) is from mid-April to early July and peaks in May. Half of the females spawn more than once in one breeding season and some guarding males receive eggs from several different females (Takahashi & Yanagisawa, 1999; Hirashima & Tachihara, 2000).

Tamada (2001) studied three species of the *Rhinogobius* complex in a Japanese stream and demonstrated that the distribution of their spawning grounds differed between species along the stream. The differences in spawning ground distribution and spawning season reduce interspecific competition for nest sites and enhance reproductive isolation. The difference in distribution of spawning grounds may be linked to other intraspecific differences in reproductive characteristics such as egg size. This is probably the result of a negative correlation between the survival of embryos during migration to the sea and the distance from the spawning ground to mouth of the river (Tamada, 2001). Hayashi (1972) noted for *Rhinogobius brunneus* (Temminck & Schlegel, 1845) that females were most abundant in the lower and middle reaches of streams while males were most abundant in the upper reaches of the stream.

Males of the stream goby *Rhinogobius* sp. DA (dark type) court females in deep pools in areas of streams with a fast current (Takahashi & Kohda, 2001) and care for their eggs under stones in shallow riffles. Although larger males won aggressive encounters with smaller male fish, large males did not monopolize courtship opportunities, and the frequency of successful courtships, after which males led the females to their nests, was not related to male body size (Takahashi *et al.*, 2001). Large males occupied larger nest stones, and the number of eggs received in the nest was correlated positively with nest size (area covered). Takahashi *et al.* (2001) suggested that male mating success of *Rhinogobius* sp. DA (dark type) is determined by male–male competition for large nests rather than competition for females. Takahashi & Kohda (2001) demonstrated that neither male body size nor the length of the dorsal fin (sexually dimorphic traits) was related to female selectivity. Females favoured males that courted at locations where the water current was relatively fast ($> 1\,\mathrm{l\,min^{-1}}$). Males in poor physical condition do not court in fast water currents. Hence this mate choice pattern enables females to mate with males with the highest fitness.

Males of another species of *Rhinogobius* sp. LD (large dark) selectively courted females of similar size prior to leading them to the nests; however, females preferentially followed courting males that had larger body size than the

female (Ito & Yanagisawa, 2000). Male–male competition for a female was relatively infrequent and the intensity was low. Developmental stages of eggs and egg numbers in one nest indicated that males receive 1–3 clutches during one breeding cycle. Males guarding multiple clutches frequently ate some of the eggs, but those guarding single clutches rarely consumed eggs. While in the nest, gravid females frequently cannibalized eggs laid by a previous female. This behaviour increases the area available for egg deposition and may reduce the competition for oxygen among eggs (Ito & Yanagisawa, 2000).

The spawning behaviour, development of eggs and larvae of the Korean freshwater goby, *R. brunneus* were studied by Han *et al.* (1998). The eggs were spawned as a monolayer, hanging from the underside of a small pebble and guarded by one male. The eggs were elliptic, *c.* 1·48 mm in length and 0·65 mm in breadth. Newly hatched larvae were 3·1–3·3 mm in total length, and their mouth and anus are not open at this point. When the yolk sac and oil globules were nearly absorbed, the mouth and anus were open, and they began to feed actively on rotifers.

Some experiments demonstrated that newly hatched larvae are better adapted physiologically to life in sea water, while prolonged exposure to fresh water retarded development and increased mortality markedly (Bell & Brown, 1994; Lindstrom & Brown, 1994; Lindstrom, 1999*a*; Keith, 2002*a*). Bell & Brown (1994) showed that there is an active salinity choice by the vesiculate larvae of *S. punctatum* in Dominica (West Indies).

Larvae of gobioids are known to drift to the sea (or lake for some *Rhinogobius* species) during the night (Dotu & Mito, 1955; Dotu, 1961; Iguchi & Mizuno, 1990, 1991; Moriyama *et al.*, 1998). Free embryos of *Sicyopterus stimpsoni* (Gill, 1860) from Hawaii and of *S. lagocephalus* from Reunion Island 'swim' repeatedly upwards until they contact the water surface, then for a while cease 'swimming' and sink and then move towards the surface again (Kinzie, 1993*a*; Keith *et al.*, 1999). This reaction facilitates their transport to the sea (Balon & Bruton, 1994).

The yolk was completely consumed in 3–7 days after hatching in *Rhinogobius* sp. (Hirashima & Tachihara, 2000). Moriyama *et al.* (1998) estimated that in normal or low river flow, embryos from the upstream reaches perish through starvation before they reach the sea. As a result, Iguchi & Mizuno (1999) suggested that early starvation of larvae limits reproductive success of fish located far from the sea which would have a strong selection for fish reproduction in certain regions of rivers within a given distance from the sea.

The free embryos are carried passively *via* river transport to the sea where they will lead a planktonic life for 90–169 days for the Hawaiian species (Radtke *et al.*, 1988; Radtke *et al.*, 1996) and for 30–163 days for Tawainese species (Shen *et al.*, 1998).

MATING SYSTEMS

To date, there are few studies of the mating systems in amphidromous gobies. In the non-Sicydiine goby species studied to date, polygamy appears to be the commonest pattern, with males guarding nests containing eggs laid by several different females (Hidaka & Takahashi, 1987*a*; Daoulas *et al.*, 1993; Takahashi

& Yanagisawa, 1999; Ito & Yanagisawa, 2000; Tamada, 2000). For gobies from the Sicydiines, aquarium-based studies indicate that they are not polygamous (Kinzie, 1993*b*).

Gobies from the Sicydiines show no hermaphroditism nor sex changes or other alternative sexual strategies, and this might also be the case for other freshwater gobioids. Watson (1991), however, reported two distinct phases in males of *Stenogobius caudimaculosus* Watson, 1991, from the Marquesas Islands. Though he added this was the only case of male dimorphism he had ever observed. These two distinct phases were not observed by Keith *et al.* (2002*a*) in the course of their studies on the Marquesas Islands.

RECRUITMENT, DISTRIBUTION AND MICROHABITATS

RECRUITMENT INTO RIVERS

On some oceanic islands, thousands of miles away from any other freshwater habitat, amphidromy necessitates special migratory abilities in larvae and juveniles (McDowall, 1988). The post-hatch embryos appear in the marine environment when they have reached 1–4 mm in length (Han *et al.*, 1998; Keith *et al.*, 1999) where they spend only a few months before they must locate a source of fresh water when they have reached a length of 13–25 mm depending on the species and after their 'metamorphosis' into juveniles. In Reunion Island, larvae are sometimes caught with planktonic nets in the sea (Keith *et al.*, 1999). The various measurements of larvae made by Keith (2002*a*) in French Polynesia and New Caledonia indicate that larvae occur at sea with a length that ranges from 13 to 16 mm for *Lentipes*, *Stenogobius*, *Awaous* and *Eleotris* and 23–25 mm for *Sicyopterus*. These measurements are similar to those made in Hawaii (Tate *et al.*, 1992).

In Japan, Hayashi (1972) noted a larval length of 17 mm for *R. brunneus* and Yuma *et al.* (2000) recorded a larval length of 16–26 mm for *Rhinogobius* sp. (orange form). In the Caribbean, the larvae of *S. punctatum* reached 10–30 mm (Bell *et al.*, 1995; Lim *et al.*, 2002). Bell *et al.* (1995) showed that the age at recruitment could vary slightly (1·3–3·4 days) in the *Sicydium* species in Dominica (West Indies). In French Polynesia, the migration of postlarvae appears to be linked to body size (which is always approximately the same size for each species when they reach the estuary) (Keith, 2002*a*).

Recruitment of postlarvae at the river mouth is possible all year round, but occurs most markedly in the Spring in Hawaii (Tate, 1995; Nishimoto & Kuamo'o, 1997) and during July to September in Japan for *Rhinogobius* sp. (orange form) (Yuma *et al.*, 2000). Keith *et al.* (2002*a*) reported massive upstream movements of postlarvae of *S. lagocephalus* from December to February in Tahiti.

Soon after entering fresh waters, the juveniles undergo several changes in colour and fin shape (Manicop, 1953; Erdman, 1961, 1986; Tomihama, 1972; Lau, 1973; Keith *et al.*, 2002*a*). The body of these postlarvae is mostly translucent and light coloured when they enter the estuary, except for the eyes and internal organs. The tail is mainly forked but it gradually becomes truncated

and the body acquires pigments as it metamorphoses and changes from a larval planktonic life to an adult benthic life (Nishimoto & Kuamo'o, 1997). Pectoral and tail fins grow bigger, together with the pelvic disc needed for upstream movements. The mouth and the jaw structure are also modified, as well as the digestive system (Tomihama, 1972). The juveniles must switch from a planktonic feeding mode to a benthic feeding mode, when they 'graze' on the substratum. The rows of teeth will regularly be replaced so as to allow grazing such as in *S. japonicus* (Mochizuki & Fukui, 1983).

In *S. stimpsoni*, Schoenfuss *et al.* (1997) reported the observation of a kind of metamorphosis unique among Gobiidae. When the postlarvae of this species migrate from the ocean to rivers, they will remain in the estuary while undergoing a total restructuring of the cranium. Forty-eight hours after entering fresh waters, both the length of the snout and the height and width of the head increase considerably, whilst the total body length and the length of the head remain unchanged. The upper lip is enlarged and the mouth moves from a terminal to an almost ventral position. When the metamorphosis is complete, *S. stimpsoni* is able to negotiate waterfalls by using alternatively its pelvic suction cup and its lips, and these are also used to graze on the diatoms growing on rock surfaces. This metamorphosis is correlated with the changes in diet and spatial distribution between larvae and juveniles. All of these changes are closely related to a phase of rapid growth (Keith, 2002*a*).

Physical characteristics and morphotypes are sufficiently distinct to form the basis of larval identification keys used for amphidromous gobies (Tate *et al.*, 1992; Lindstrom, 1999*a*, *b*).

The recruitment of gobies is often associated with heavy rains (Delacroix, 1987; Delacroix & Champeau, 1992). The freshwater flow seems to trigger their migration inland. Even intermittent rivers that flow only after major storms attract postlarvae (Delacroix & Champeau, 1992). The movement of these young fish from the ocean to the rivers is the key link in completing their amphidromous cycle. The maintenance of this system is crucial to the long-term supply of resources in the fresh waters of insular systems (Keith, 2002*a*; Lim *et al.*, 2002).

Once in the river, the juveniles then migrate upstream, towards the adult habitat. The timing and direction mechanisms required for the success of this migration remain mostly unknown. Three studies, however, have been undertaken on how gobies orientate over short distances. *Coryphopterus nicholsi* (Bean, 1882), from the Pacific Ocean, is able to memorize the location of a refuge after a brief reconnaissance and is thus able to retreat to safety if a predator is detected (Markel, 1994). It takes only one high tide for the Caribbean goby, *Bathygobius soporator* (Valenciennes, 1837), to memorize the spatial location of neighbouring water pools and, at low tide, it can jump from one to the next when chased by a predator (Aronson, 1971). Finally, under experimental conditions, *A. guamensis*, *S. stimpsoni* and *L. concolor* locate quickly (in under 10 min) the freshwater current ($1\,l\,min^{-1}$ into the test pool) that will allow them to swim upstream, even if the flow is interrupted (Smith & Smith, 1998). The rapid acquisition of such directional preferences for upstream migration is crucial to these juveniles if they are to clear obstacles in intermittent flows.

Rheotaxis might not be the only phenomenon involved. Studying directional mechanisms is important if one is to understand the phenomena. The existence of a solar or a magnetic compass may also be uncovered for the marine phases of migration. Leis *et al.* (1996) demonstrated that, in coral reefs, fish larvae could maintain their direction beyond the reefs. Kobayashi (1989) reports visual orientation in *Psilogobius* larvae towards the reef. These studies suggest that visual (non-rheotaxic) parameters can also be used during the oceanic larval phases (Smith & Smith, 1998).

To access the rivers, the larvae most often choose to swim close to the shoreline, where the current is less strong and can even be reversed (*i.e.* a counter-current) with the tide or the swell (Tate, 1997). Some larvae travel with their spindle-shaped body facing the current and climb from one rock to the next using their pelvic suction cups. Others can reach fresh waters following passages through cracks in the rocks, thus avoiding turbulence (Tate, 1997). Postlarvae first congregate near the shore. They will begin migrating into the estuary at first light and at various moments during the day, depending on the species (Miller, 1984; Fièvet, 1999; Lim *et al.*, 2002).

In *L. concolor*, the postlarvae enter rivers mainly during the daylight hours, with the waves of the incoming tide (Nishimoto & Kuamo'o, 1997). Migration peaks in the hours following sunrise, when they are bourne on the rising tide thereby reducing their energy expenditure. The same phenomenon has been reported for *Lentipes kaaea* Watson, Keith & Marquet, 2002, from New Caledonia (Watson *et al.*, 2002). When they enter fresh waters, *Lentipes* postlarvae swim immediately upstream. No amphidromous goby species (whether adults or young) appears to develop strict nocturnal activities; thus a morning-initiated migration enables larvae to reach higher up into the river system.

In *S. lagocephalus* the postlarvae are strong swimmers. Their well-developed fins and strongly effective pelvic suction cup allow them to access rapidly the upper reaches of the catchment area (Keith *et al.*, 1999; Keith *et al.*, 2002*a*; Marquet *et al.*, 2003), which is also the case for the *Sicydium* species of the Caribbean (Fièvet & Le-Guennec, 1998; Lim *et al.*, 2002).

Tate (1997) and Nishimoto & Kuamo'o (1997) reported that in *A. guamensis*, the postlarvae were transported to the river mouth by waves and that they entered fresh waters either by day or by night, with a peak occurring early in the night. *Awaous guamensis* is a slower climber and it depends on tidal inundation to move upstream (Keith *et al.*, 2000). In *Stenogobius hawaiiensis* Watson (1991), the postlarvae appear to move with the incoming tide during the day (Tate, 1997), or, at night, using cracks in the rocks. In comparison, in *Eleotris fusca* (Forster, 1801) (Eleotridae), the postlarvae have difficulties manoeuvring and swimming in turbulent waters, and this determines recruitment periods. They are transported mainly at night by the waves of the incoming tide. In the absence of a pelvic suction cup, this species move upstream by attaching itself to the substratum (Keith, 2002*a*).

Rhinogobius sp. (orange form) from Japan migrates between a lake and its tributaries (this is a landlocked form) (Kawanabe & Mizuno, 1989; Yuma *et al.*, 1998). The species spawns in rivers and from where the larvae drift down into the lake (Hidaka & Takahashi, 1987*b*). They live in the lake for 1 or 2 months,

whereupon the juveniles ascend the river en masse during July to September. The upstream migration begins after 0900 hours, was most active from 1400 to 1800 hours and ceased around 1800 hours just before sunset (Yuma *et al.*, 2000).

SCHOOLING

Schooling has an antipredator and foraging function (Pitcher & Parrish, 1993). As a result of the journey undertaken by the postlarvae from the sea to the river, with inevitable encounters with predators, some amphidromous goby species have developed a strategy of migrating in schools. Major predators would include open water predators such as *Kuhlia* sp. and ambush predators such as *Eleotris* sp. (Kinzie, 1992; Kido, 1996*a*; Keith *et al.*, 2002*a*). Schooling behaviour is present only in postlarvae and never occurs in either juveniles or adults. In *L. concolor*, the postlarvae do not swim in schools, while in *A. guamensis* they swim in pairs, in single species schools or in mixed species schools of 30–100 individuals (Tate, 1997).

In the Indo-Pacific region, *S. lagocephalus* postlarvae travel alone or in small single or mixed schools of some 30–100 individuals, depending on the islands concerned: mass movements of 'bichique' (a local name for the postlarvae) schools in Reunion Island (Delacroix, 1987; Keith *et al.*, 1999), smaller schools in Tahiti (Keith *et al.*, 2002*a*) and even smaller ones in New Caledonia (Keith, 2002*a*; Marquet *et al.*, 2003).

In Indonesia, large aggregations of *Stiphodon semoni* Weber, 1895, were observed undertaking a migration upstream from the estuary (Martin, 1999). In the Caribbean, the *Sicydium* species in the streams of Guadeloupe (West Indies) (Gillet, 1983; Hostache, 1992; Fièvet & Le-Guennec, 1998; Fièvet, 1999), Martinique (Lim *et al.*, 2002), Puerto Rico (Nieves, 1999), Costa Rica (Bussing, 1996), Dominica (Watson, 2000) are known to undertake mass migrations.

UPSTREAM MIGRATION

The juveniles must migrate from the lower reaches of river habitats to the habitats they will occupy as adults. Out of the three genera living highest up river systems (*Lentipes*, *Sicyopterus* and *Sicyopus*), *Lentipes* is the only one to swim directly towards the upper reaches, while the other two take more time to complete their migration (Keith, 2002*a*). In *L. concolor*, for example, postlarvae remain in the estuary no longer than 1 day and they migrate directly upstream at a speed of $90\,\mathrm{m\,h^{-1}}$, until they reach the first physical obstacle to migration upstream (usually a waterfall). When this obstacle is cleared they gain refuge where predators are less numerous (Tate, 1997). Yuma *et al.* (2000) noted for *Rhinogobius* sp. an upstream migration speed of $4{\cdot}2$–$8{\cdot}9\,\mathrm{m\,min^{-1}}$ depending on current velocities. Beyond the first major waterfall which acts as barrier against predators, schooling and escape behaviours are replaced by agonistic interactions between juveniles competing for space and food.

On the Opunohu River, in Moorea (French Polynesia), Keith (2002*a*) showed that in *S. lagocephalus* the numbers of adults increased while the numbers of juveniles decreased with distance from the river mouth. Yuma *et al.* (2000) showed that the number of upstream-migrating juveniles of *Rhinogobius* sp. decreased progressively from the river mouth. They supposed that riffles in

the mid- and upper reaches, having few slow current areas, probably presented barriers to upstream migration of the juvenile gobies, although both adults and subadults of the species are found in upper reaches beyond these obstacles. Balon & Bruton (1994) showed that the distribution of *S. lagocephalus* in Comoros Islands separated the smallest juveniles in the estuary and largest adults on the volcanic slopes.

In *S. stimpsoni*, two forms access the rivers (Nishimoto & Fitzsimons, 1986). The first form develops coloured body markings used in signalling to defend a feeding territory; the second form does not develop such markings and individuals migrate further upstream when they are disturbed by the more colourful and aggressive form. The species' distribution along the river is determined by the aggression by coloured postlarvae and subsequent migration upstream of the least coloured individuals. When the least coloured postlarvae reach a site with a lower density of competitors, they stop migrating and develop coloured signals. At this time aggression becomes important in the distribution of the species, when adults and coloured juveniles displace non-coloured young (Nishimoto & Fitzsimons, 1986). Males of adjacent territories show no, or little, aggressive behaviour among themselves because the boundaries are exactly defined; however, they will chase males passing through their territory (Nishimoto & Fitzsimons, 1986; Osugi *et al.*, 1998).

In the genus *Lentipes*, the adults are territorial (especially the males) (Fitzsimons & Nishimoto, 1990; Watson *et al.*, 2002). In *L. concolor*, males establish a territory between sea level and 1000 m. These territories are always situated in areas that experience strong currents and good water clarity and vary in size from 0·1 to 4 m^2 (Fitzsimons & Nishimoto, 1990) and are larger in still waters (pools) and smaller in riffles. The size of this territory does not appear to be affected by the density of *Lentipes*, including the number of available females and the number of competing males or the size of the males (Fitzsimons & Nishimoto, 1990).

Outside the mating season, the male attaches itself to one or more observation posts close to the centre of its territory to detect the presence of other males or drifting food. This contrasts sharply with observations made in coral reefs where the butterfly fish uses predetermined routes to move from one site to another within a territory (Reese, 1988). The same male may use the same territory for up to four and a half years (Fitzsimons & Nishimoto, 1990). The females move between the territories of different males and are courted when gravid. A number of females, however, have been reported on the same territory for 32 months (Fitzsimons & Nishimoto, 1990).

In *A. guamensis*, many individuals spend over 4 weeks in the estuary. This was revealed due to a study on helminth parasites. Indeed, *Camallanus cottii*, an estuarine parasitic nematode, has been found in the stomach of the postlarvae of this species, and it takes 4 weeks for this parasite to become adult (Font & Tate, 1994). Beyond the 'barrier' of the first waterfalls, most juveniles will develop dark colours and defend a temporary feeding and resting territory, forcing others of the same species to migrate upstream. In some species, the adult population is redistributed when adults swim downstream for reproduction, which creates space upstream for the juveniles (Ego, 1956).

PREFERENTIAL HABITATS AND ZONATION

As a rule, whatever the island studied, the first major waterfall is a crucial factor in species distribution along a river. This zonation has been described for the Arakitoach River in Palau (Fehlmann, 1960), the Asmafines River in Guam (Parham, 1995), the Pohnpei rivers (Maciolek & Ford, 1987), the rivers of Martinique Island (Lim *et al.*, 2002) and in Puerto Rican streams (Holmquist *et al.*, 1998).

Keith *et al.* (2002*a*) and Fossati *et al.* (2002) showed a specific longitudinal distribution in adult amphidromous gobies and decapod crustaceans inhabiting Polynesian rivers. *Lentipes* are often the species present at the highest altitudes: in Hawaii, *L. concolor* is found at an altitude of up to 1000 m high, beyond a 130 m waterfall and multiple other falls adding up to 600 m of obstacles (Fitzsimons & Nishimoto, 1990; Nishimoto & Kuamo'o, 1991), while in the Marquesas Islands, *Lentipes rubrofasciatus* Maugé, Marquet & Laboute, 1992, is found at an altitude of up to 500 m (Keith *et al.*, 2002*a*). In French Polynesia, *Eleotris*, *Awaous* and *Stenogobius* are not normally found below the lower reaches and the first waterfall (Keith *et al.*, 2002*b*); *Stiphodon* do not reach beyond the major falls (5–10 m) (Keith *et al.*, 2002*c*), while *Sicyopus* swim a little further up; *Sicyopterus* clear major falls and may swim up to the upper reaches where they mix with *Lentipes* (Keith *et al.*, 2002*a*). In the Caribbean, *Sicydium plumeri* (Bloch, 1786) may swim up to the upper reaches and can climb major waterfalls (Nieves, 1999; Lim *et al.*, 2002) and *Sicydium adelum* Bussing (1996) is found between 10 and 800 m elevation in the streams of Costa Rica (Bussing, 1996).

Predatory species of the genus *Kuhlia* (Kuhliidae) abound in the lower reaches, below the first waterfall, but are absent beyond it; this is the case for *Kuhlia malo* (Val. *in* Cuvier et Valenciennes, 1831) in Polynesia (Keith *et al.*, 2002*a*) as well as for *K. marginata* (Cuvier, 1829) and *Kuhlia rupestris* (Lacepède, 1802) in New Caledonia (Keith, 2002*a*; Marquet *et al.*, 2003). This limitation in the movements of predators of the genus *Kuhlia* affects the distribution of other organisms. Gobies, Palaemonid crustaceans of the genus *Macrobrachium* or Atyids are often more abundant in the areas situated above the cascades where predators are less numerous (Fossati *et al.*, 2002).

In Guam, Parham (1995) showed that the type of habitat (riffle, pool, *etc.*) and the type of substratum determine species distribution and abundance. This is also the case in Pohnpei and Palau (Nelson *et al.*, 1997). The positive correlation between gobies' density and the proportion of hard substratum is the result of the diet of these herbivorous species. These gobies feed by scraping diatoms or algae from hard surfaces in the river. Many of these species have teeth adapted for scraping (Kido, 1996*a*, *b*). Although the site with the highest density of gobies is the site with the highest proportion of hard substratum, the wide differences reported even for areas with large amounts of hard substratum show that other factors are to be taken into consideration (Nelson *et al.*, 1997).

The amount of plant cover on the banks of the river is another important factor where gobies' habitat is concerned. Fish density is highest where plant cover is poorest. This is probably because primary productivity on rocks is higher in sunny locations, which provides more algae for the gobies to feed on. This might, however, not be the only reason: it is possible that light plays a part

in propagating the iridescent colours of displaying males (Keith, 2002*a*). Whatever the cause, vegetation cover on river banks is a contributing factor in the distribution of gobies within streams.

Understanding the role of these two factors (density/plant cover and density/hard substratum) is the first step towards ascertaining the main habitat factors that are important for amphidromous gobies and towards predicting the ecological impact of any environmental disturbance or modification of the habitat. Working on fish populations in Sri Lanka, Moyle & Senanayake (1984) determined an 'ecological key' for the species, based on current speed, substratum, depth and diet. Detailed ecological data on amphidromous gobies are required if one is to build and refine such 'ecological keys' and use them with enough precision in management and conservation programmes.

CONCLUSIONS

The current state of knowledge on amphidromous gobies' life cycle (biology and ecology), the length of the larval phase and the part it plays in the dispersal of larvae is of direct relevance for management and conservation. The management and the conservation of amphidromous species must take into account both the dependency of adult populations on the larval pool for replacement and the contribution of each reproductive population to the larval pool. The length of the marine phase might increase the probability of finding a river for colonization as will the strength and the direction of marine currents (Radtke *et al.*, 2001; Keith, 2002*a*). The survival of the species depends also on the ability of existing populations to provide enough larvae to maintain appropriate numbers of adults.

Seasonal variables (*e.g.* rainfall, drought, floods and typhoons) have a major impact on the survival of populations: biological events such as reproduction, spawning and the dispersal of larvae, are dependant on these events and are synchronized with them (Keith, 2002*a*). On the islands, the impact of humans on aquatic habitats is highly significant, particularly on estuarine habitats which are crucial to amphidromous species. These have to undertake two migrations between fresh waters and the sea. The success of such a life cycle, *i.e.* production of larvae and restocking rivers, depends on maintaining the mountain ocean corridor open to allow movements between both habitats (Fitzsimons *et al.*, 1997; McDowall, 1997; Radtke *et al.*, 2001; Keith *et al.*, 2002*a*). As a result of industrialization and the development of tourism, the island rivers have been channelled, reconfigured and degraded. Habitats were reduced and species were at extreme risk of extinction (Maciolek, 1979). It is therefore necessary to understand their biology to the best of our ability and to develop management and restoration strategies in order to preserve stocks for the future (Keith, 2002*b*; Keith & Marion, 2002).

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