FRESHWATER NERITIDS (MOLLUSCA: GASTROPODA) OF TROPICAL ISLANDS: AMPHIDROMY AS A LIFE CYCLE, A REVIEW

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RÉSUMÉ.— *L'amphidromie en tant que cycle de vie des Néritidés (*Mollusca : Gastropoda*) des eaux douces dans les îles tropicales, une revue.*— Les eaux douces des îles tropicales abritent des mollusques de la famille des *Neritidae*, ayant un cycle de vie spécifique adapté à l'environnement insulaire. Les adultes se développent, se nourrissent et se reproduisent dans les rivières. Après l'éclosion, les larves dévalent vers la mer où elles passent un laps de temps variable selon les espèces. Ce cycle de vie est appelé amphidromie. Bien que cette famille soit la plus diversifiée des mollusques d'eau douce, le cycle biologique, les paramètres et les processus évolutifs qui conduisent à une telle diversité sont peu connus. Cet article fait le point sur l'état actuel des connaissances sur la reproduction, le recrutement, la migration vers l'amont et la dispersion. Les stratégies de gestion et de restauration pour la préservation des nérites amphidromes exigent de développer la recherche pour avoir une meilleure compréhension de leur cycle de vie.

SUMMARY.— Tropical island freshwaters are inhabited by Molluscs of the Neritidae family with a specific life cycle adapted to the insular environment. The adults grow, feed and reproduce in rivers. After hatching the larvae drift downstream towards the sea where they spend a variable amount of time. This life cycle is called amphidromous. Although this is the most diverse family of freshwater Molluscs, the biological cycle and the parameters and evolutionary processes that lead to such diversity are not well understood. This paper reports on the current knowledge on reproduction, recruitment, upstream migration and dispersal. Management and restoration strategies to preserve amphidromous Neritids require the development of research to get a better understanding of their life cycle.

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Within the open ocean, tropical insular freshwater environments usually represent highly isolated and fragmented habitats. The colonization of tropical insular rivers, subject to extreme climatic and hydrologic seasonal variations (McDowall, 2007; Crandall *et al*., 2010) requires specific adaptations of the life cycle of freshwater fauna occurring in these distinctive habitats. Diadromy is one of the evolutionary answers to the instability of freshwater habitats. Spending part of their life cycle at sea, diadromous species are indeed capable of escaping drought or cyclonic flood events while colonizing new environments via oceanic dispersal (McDowall, 2007; Crandall *et al*., 2010; Lord *et al*., 2012). This oceanic dispersal of freshwater organisms represents an essential element in the persistence and structuring of populations at both the local (stream, river, archipelago) and regional scales (Keith, 2003; McDowall, 2008; Lord *et al*., 2012)

Amphidromy is one of the modalities of diadromy. The adults grow, feed and reproduce in rivers. After hatching, larvae drift downstream towards the sea where marine salinities are necessary for larval development (Crandall, 1999; Crandall *et al*., 2010; Lord *et al*. 2010). After this marine larval stage, the post-larvae come back to rivers; they recruit in estuaries and from there colonize the adult freshwater habitat (Kano & Kase, 2003; Maeda *et al*., 2007; Iida *et al*., 2008; Gorbach *et al*., 2012). The practical details of the species biological cycle and the parameters leading to such evolution in amphidromous species are poorly known, but our knowledge increases each year.

Amphidromous species are known in many taxa throughout the Indo-Pacific area and the Caribbean insular systems, such as gastropods (Cook *et al*., 2009; Crandall *et al*., 2010), decapod crustaceans (Dennenmoser *et al*., 2010; Castelin *et al*., 2013) or fish mainly in the Eleotridae and Gobiidae families (Keith & Lord, 2011a, b). These species contribute most to the diversity of freshwater communities, and have the highest levels of endemism (Keith, 2003; McDowall, 2007; Keith & Lord, 2011a). At certain times of the year, the biomass of fish larvae migrating upstream is so great that they represent an important source of food for local human populations in certain archipelagos (*i.e.* the 'bichiques' (gobiids post-larvae) of La Réunion (Hoareau *et al*., 2007)). However, harvesting of this food resource is highly unsustainable, on account of the complexity of the species' life cycle (Lord *et al*., 2012; Castelin *et al*., 2013). As for adult neritids, some of them are used as food by coastal populations of oceanic islands in the West Pacific (Carpenter & Niem, 1998).

Among Gastropods, most of the Neritidae species have been recognized as amphidromous (Myers *et al*., 2000; Kano & Kase, 2003; Blanco & Scatena, 2006) and they represent one of the commonest members of freshwater fauna on tropical islands. Amphidromy exists, however, in other gastropod families such as, for example, Neritiliidae and Thiaridae (Kano & Kase, 2003; Strong *et al*., 2008, 2011; Hidaka & Kano, 2014). Neritids seem to have their origin in the sea (Kano *et al*., 2011; Quintero-Galvis & Castro, 2013), comprise roughly 100 living species in a few marine genera (e.g. *Nerita*) and abundantly inhabit intertidal rocky shores. However, they are more diverse in freshwater and brackish-water environments in terms of the numbers of species and genera. There are some 200 limnic species worldwide in eight or more genera (Kano *et al*., 2011) and most of the freshwater lineages have retained a dispersive, planktotrophic marine larval stage.

The aim of this review is to give the main current knowledge in biology and ecology concerning amphidromous Neritidae, supplying the facts to be used in management and conservation policies.

TAXONOMY AND DISTRIBUTION

Neritidae is one of the most primitive families in the Gastropoda (Baker, 1923), belonging, with five other families (Hydrocenidae, Helicinidae, Neritiliidae, Phenacolepadidae and Neritopsidae) to the Neritimorpha superorder (Kano *et al*., 2002). Neritids have adapted to different environments in tropical and subtropical regions. They inhabit intertidal and supratidal rocks and mangroves, brackish-water and freshwater, on temperate to tropical coasts. The survival of this archaic family is probably dependent on its ability to live where few other forms compete with them (Baker, 1923). Most of the valid described species of freshwater neritids inhabit the main zoogeographical regions of Oceania (Pacific Oceanic Islands), Palaearctic and Australasian (Strong *et al*., 2008). The main genera of the family are distributed as follows. Marine genera (*Nerita*, *Smaragdia*, *Puperita*) are found mainly in tropical regions, particularly in the Indo-West Pacific and Caribbean; freshwater and estuarine genera (*Neritina, Clithon, Vittina, Neritodryas, Neripteron, Septaria*) occur in the Indo-Pacific; the freshwater genus *Theodoxus* is European, Central Asian, Middle Eastern and North African (Baker, 1923; Haynes, 2001; Bunje & Lindberg, 2007; Frey & Vermeij, 2008; Limpalaer, 2009; Frey, 2010; Quintero-Galvis & Castro, 2013).

There are few studies giving a classification of the Neritidae, such as that of Baker (1923), based on the radula, or the molecular phylogeny undertook by Quintero-Galvis & Castro (2013), using the genes COI and 16S rRNA. However, this last study remains in need of complementary analyses. Besides that, various genera are relatively well studied. This is the case, for example, of the genera *Theodoxus* (Bandel, 2001; Bunje & Lindberg, 2007), *Nerita* (Frey & Vermeij, 2008; Frey, 2010), and Neritina (Kano, 2009).

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REPRODUCTION

Female Neritids store sperm capsules (spermatophores) received from males for continuous spawning. Neritids lay flat, elliptical egg capsules on hard substrata including rocks and shells of other snails (Kano *et al.*, 2011). The capsules are 1-3 mm long depending on species and are covered with sand grains sorted from mother's faeces. Newly laid capsules are white and then become cream to brown in a few days. Each capsule contains up to 300 eggs that hatch several weeks after being laid (Kano *et al.*, 2011). Embryonic development was studied by Koike (1996), and growth rate by Shigemiya & Kato (2001). These last authors demonstrated that the number of growth lines was a good indicator of the age of a snail, and that the growth rate was higher and the life span was longer in females.

After hatching larvae are swept to the sea (Myers *et al.*, 2000). Similar to fish larvae (McRae, 2007), there appears to be a limited time window of opportunity for Neritids larvae to reach saltwater (Hau, 2007). Veligers held in fresh water died within six days (Ford, 1979).

Mating and spawning seems to occur year round (Hau, 2007; Kano *et al.*, 2011). In Hawaii, larvae of *Neritina granosa* (*Hïhïwai*) were effectively found all year round in drift collections in Palauhulu Stream in Ke'anae with a major period from June to August (Hau *et al.*, 1992; Hau, 2007). *Hïhïwai* larvae were present three to five months prior to juvenile recruitment upstream (Hau, 2007). They are often found in pool and run areas during low flow conditions, and the first major freshet after that period often causes a sudden decrease in water temperature and an increase in dissolved oxygen. This scouring flow provides optimum conditions for *hïhïwai* egg cases to be laid on hard substrate and the transport of hatched larvae to the ocean as quickly as possible (Hau, 2007). Records of gastropod density and egg laying in French Polynesia (Resh *et al.*, 1990, 1992) and Japan (Nishiwaki *et al.*, 1991b; Hirata *et al.*, 1992) suggest a seasonal occurrence of downstream migrations, but the controlling factors remain unknown.

LARVAL DISPERSAL

Given the high levels of larval mortality and the effects of diffusion (Cowen *et al.*, 2000), it seems unlikely that significant numbers of larvae that drifted away from their natal archipelago would be able to find suitable freshwater habitat for settlement (Crandall *et al.*, 2012). Therefore, local selection for traits that favour self-recruitment could be particularly strong for amphidromous species as shown for fishes (Sponaugle *et al.*, 2002; Strathmann *et al.*, 2002). Similar homing behaviours have been suggested for the larvae of amphidromous shrimps and snails (Benstead *et al.*, 2000; Haynes, 2000; Crandall *et al.*, 2012). Such larval retention could result in limited realized dispersal and pronounced genetic structure among archipelagos. However, weakly swimming veliger larvae of amphidromous lineages have a Pelagic Larval Duration (PLD) that is estimated to be from a few weeks to a few months, by size-frequency distributions analysis and by growth lines counting (Scheltema, 1971; Underwood, 1975; Kano, 2006; Crandall *et al.*, 2010). Freshwater species with an amphidromous life cycle and marine species with a pelagic larval stage exhibit higher dispersal abilities and potentially a lower degree of population structure than strictly freshwater species or marine species of low vagility (Allibone & Wallis, 1993; Doherty *et al.*, 1995; Cook *et al.*, 2009; Crandall *et al.*, 2010). Genetic studies confirm that larvae from amphidromous lineages are capable of pelagic dispersal across broad expanses of open ocean (Hodges & Allendorf, 1998; Myers *et al.*, 2000; Crandall *et al.*, 2010). In the South Pacific, neritid larvae are much more likely to encounter a reef or atoll than a high island with freshwater streams, and as such there are more stepping-stones to facilitate dispersal in marine species than amphidromous species (Crandall *et al.*, 2012). Consistent with this high dispersal potential, genetic structure within high-island archipelagos is low or non-existent in amphidromous Neritid and Neritiliid snails (Hodges & Allendorf, 1998; Myers *et al.*, 2000; Kano & Kase, 2004), suggesting

that populations of amphidromous species are genetically structured at scales similar to fully marine species. Species persistence in these island freshwater systems (*i.e.* amphidromous gastropods, fishes and crustaceans) partially depends on colonisation or recolonisation events. This is influenced by the proximity of environments, species dispersal capacities, island biogeography, and the presence of favourable oceanic currents (Murphy & Cowan, 2007; McDowall, 2007; Crandall *et al.* 2010; White *et al.*, 2010; Lord *et al.*, 2012; Castelin *et al.*, 2013). An important finding of these last population genetic studies has been the identification of a certain degree of spatial genetic structuring among biogeographic provinces, reflecting the effectiveness of biogeographical barriers for limiting larval dispersal.

As the planktotrophic larvae of amphidromous species must settle in a rare, unstable habitat, they could be selected for the ability to delay metamorphosis and extend their planktonic life indefinitely ('death before dishonor' hypothesis, Bishop *et al.*, 2006), (Crandall *et al.*, 2012).

PHYLOGEOGRAPHY AND BARRIERS TO DISPERSAL

Oceans are partitioned into biogeographical provinces, which are recognized by habitat discontinuities (Briggs, 1974; Gaither *et al.*, 2010; Lord *et al.*, 2012). Physical entities separate these biogeographical provinces, and these barriers have been intermittently shaping species distribution and intraspecific population structure over time. These barriers mainly act on species displaying dispersal potential through the marine environment as larvae, juveniles or adults (Gaither *et al.*, 2010, 2011). This is, for example, the case for many fishes (Gaither *et al.*, 2010; 2011; Winters *et al.*, 2010; Lord *et al.*, 2012) and invertebrates (Lavery *et al.*, 1995, 1996; Barber *et al.*, 2002; Lessios *et al.*, 2001, 2003) across the Indo-Malay archipelago, widely recognized as the Indo-Pacific Barrier (IPB; an intermittent barrier of throughflow current and chain of islands, depending on sea level fluctuations over geological time scale) that separates the Indian and the Pacific Oceans. Some marine organisms however lack any structure across the IPB (Bowen *et al.*, 2001; Lessios & Robertson, 2006; Horne *et al.* 2008) suggesting different evolutionary histories and dispersal capabilities between organisms.

Crandall *et al.* (2010) undertook a large-scale population genetic study on two species of amphidromous gastropods (*Neritina canalis* and *Neripteron dilatatus*) distributed from the Philippines to Eastern Pacific locations. Sampling localities for this study are islands in the West Pacific archipelagos of Vanuatu, Fiji and Samoa, and the Society and Marquesan archipelagos in the Central Pacific. A 658-bp region of mitochondrial cytochrome oxidase I (COI) was amplified. Both species show no evidence of genetic structure within Vanuatu, Samoa and Fiji archipelagos, which promotes long-distance dispersal abilities. But, while *N. dilatatus* showed no evidence of regional structure between western Pacific locations and Polynesia, authors found a strong genetic structure in the amphidromous gastropod *N. canalis*. Similar results on other amphidromous species suggest that unstable freshwater habitats promote long-distance dispersal capabilities. Hodges & Allendorf (1988) studying the population genetics of the endemic Hawaiian freshwater amphidromous gastropod *Neritina granosa*, showed that gene flow was substantial and was generally sufficient to maintain similar allele frequencies among stream populations. However, significant heterogeneity among populations was observed and was due primarily to three geographically disparate streams.

RECRUITMENT AND UPSTREAM MIGRATION

After a few weeks spent at sea metamorphosed juveniles recruit at river mouths and then migrate (often over 10 km) upstream where they spend the rest of their life (see Kano *et al.*, 2011, fig. 307). Massive upstream snail migration has been hypothesized to be density and body size

dependent and juvenile forms have been observed to move together in long lines and ∕ or dense aggregations (Schneider & Frost, 1986; Schneider & Lyons, 1993; Brasher, 1997; Kobayashi & Iwasaki, 2002; Pyron & Covich, 2003; Blanco & Scatena, 2005; Hau, 2007; Kano, 2009; Gorbach *et al.*, 2012). Such migrations of freshwater neritids were reported for example in Hawaii (Ford, 1979; Ford & Kinzie, 1982 ;Hau, 2007), Costa Rica (Schneider & Frost, 1986; Schneider & Lyons, 1993), Japan (Nishiwaki *et al.*, 1991a; Hirata *et al.*, 1992 ; Kano, 2009), French Polynesia (Resh *et al.*, 1990, 1992; Liu & Resh, 1997), and Puerto Rico (Pyron & Covich, 2003; Gorbach *et al.*, 2012).

Among them, Schneider & Frost (1986) reported the first gregarious upstream migrations of freshwater snails *Neritina latissima*, in the Rio Claro, a small coastal river in Corcovado National Park, Costa Rica. Snails migrated in narrow lines up to 32 meters long, containing thousands of snails. The migration covered over 1 km of the stream. In Hawaii, after the pelagic larval stage, *Neritina granosa* recruits at a stream mouth and begins an upstream migration until finding adult habitat (Ford, 1979; Way *et al.*, 1993; Hau, 2007 ; Gorbach *et al*, 2012). During the upstream migration, juveniles (6 mm) of *Neritina granosa* grow to about 9 mm over several months; growth then continues at a rate of 1-3 mm year^{-1}, slowing until they reach a mean maximum adult length of 29 mm (Brasher, 1997). Ford (1979) suggested a 10-year lifespan, while studies undertaken by Brasher (1997) implied a 6- to 10-year lifespan, and Gorbach *et al*. (2012) confirm a potential lifespan > 10 years, after they recovered tagged snails in Kinihapai Stream, Maui, in 2009 that were released in 1994. The upstream movement of this species has been reported by Hau (2007). It appears to be influenced by several factors. In general, there is limited upstream movement in diverted streams because of intermittent stream flows. Migration lines appear to be an efficient way to move *en masse* during times of increasing stream flow. The tendency of *hїhїwai* to aggregate and form lines and mucus trails was observed. Several migrating *hїhїwai* were found carrying smaller ones. This "hitch-hiking" behaviour was also reported for *Cochliopina tryoniana* migrating with *Neritina latissima* in the Rio Claro in Costa Rica (Schneider & Lyons, 1993). Kano (2009) reported another example of 'hitch-hiking' behaviour in the Neritid snail *Neritina asperulata* which appears to travel several kilometres as minute juveniles by firmly attaching to the shells of congeneric, subadult snails in streams of Melanesian Islands, presumably to increase the success rate of migration.

Published studies of Neritids species migrating *en masse* or in long lines under natural situations suggested that *Neritina granosa* could migrate above stream diversions within 72 days-2.5 years (when in an aggregation) and 29 days-1.1 years (when following in long lines of individuals) (Gorbach *et al.*, 2012). Mean upstream migration rate of *N. granosa* in Hawaii was 0.25, 0.66 and 1.16 m day^{-1} under reduced flow, natural flow and natural flow with increased snail density, respectively (Gorbach *et al.*, 2012).

Mark-and-recapture studies in northeastern Puerto Rico suggested that neritid gastropods are more active and travel longer distances during given periods of the year and that upstream migration may be seasonal (Pyron & Covich, 2003). However, other one-year mark-and-recapture study on a Neritid Gastropod in southern Japan showed no seasonal occurrence of upstream migrations, nor seasonal changes in mean distance movement (Nishiwaki *et al.*, 1991a) ; the movement distance of *Clithon* seems longer in spring to summer (June to September). Another study in the same area showed that maximum travel distance varies over the year, being greater during the period of high water temperature between April and August (Hirata *et al*. 1992; Blanco & Scatena, 2005). Blanco & Scatena (2006, 2007) concluded that younger snails prefer fast, turbulent and erosive habitats and that densities were greater in deep habitats with heterogeneous substrata, thus indicating that migration might ultimately be influenced by stream discharge and channel hydraulics.

Blanco & Scatena (2005) observed in Puerto Rico massive upstream migrations of *N. virginea* (500-3000 ind/m^2). While aggregations occurred at random time intervals, they were

clumped during rainy periods. Migratory aggregations consisted mostly of small individuals (5-7 mm). *N. virginea* density and size dynamics differed between reaches as a function of habitat hydraulics. While juveniles used the stable riffle as a permanent habitat and preferred passageway, they also used an adjacent, unstable reach after storm events. Upstream migrations are relatively frequent (once every 15 days), promoted by floods, and are strongly influenced by reach-level habitat stability (Blanco & Scatena, 2005).

Gorbach *et al*. (2012) suggested that upstream migration of Neritids relates to the search for food and space (Paulini, 1963), predator avoidance (Schneider & Lyons, 1993; Blanco-Libreros & Arroyave-Rincon, 2009), a response to accidental downstream drift (Schneider & Frost, 1986), constraints imposed by body architecture and hydrodynamics (Haynes *et al*., 1985; Way *et al*., 1993; Huryn & Denny, 1997), the availability of breeding sites (Soderstrom, 1987) and variation among adults and juveniles in tolerance of physical factors such as salinity and temperature (Pyron & Covich, 2003). For some authors, the energy cost of migration is compensated by lower predation pressure in the upper reaches of streams and by the increased upstream availability of food for these animals, all of which graze on microalgae (Schneider & Lyons, 1993; McDowall, 2007). Schneider and Lyons (1993) proposed that upstream migrations of Neritids in a Costa Rican stream were related with increased fish predation in the estuary. Small-sized individuals were more abundant within migratory groups, and they were also more responsive to the presence of predators, as similarly observed in other freshwater Gastropods (Alexander & Covich, 1991). The distribution of predatory fish, and the quantity and quality of periphytonic food (Johnson & Brown, 1997; Biggs & Smith, 2002) can also be correlated with the spatio-temporal variations in discharge and water velocity (Blanco & Scatena, 2005).

The microdistribution and abundance of freshwater gastropods were studied by Liu and Resh (1997) in lower reaches of three streams on Moorea, French Polynesia. Seven species were examined; five species are in the Neritidae, the latter two in the Thiaridae. Most Gastropod species had higher densities during Austral Fall with higher densities being found in riffle than in pool habitats. No relationship between substrate type and either species presence-abundance or shell size was observed. Their study indicated that velocity, depth, and substrate roughness were determinants of gastropod abundance for some species within these streams.

Finally, habitat partitioning sustains dozens of species in a single river system. Distance from the river mouth, water velocity, salinity and riverbed condition are the primary factors that determine species composition at a certain area of rivers and streams. At a smaller scale, a different set of species occupies a different type of microhabitats (e.g. stream mouth, estuary, cascades, rapids) in a short stretch of rivers (Kano *et al*., 2011).

CONSERVATION

Freshwater Neritids in tropical islands have developed a specific life cycle. This group of Gastropod is highly diverse, mainly in the Indo-Pacific area. The mechanisms explaining the distribution of amphidromous species (e.g., neritids, fishes) and including larval production, retention, dispersal, and recruitment to freshwater are governed by both biological and physiological processes (Murphy & Cowan, 2007; Crandall *et al*., 2010). Seasonal variables (e.g. rainfall, drought, floods, typhoons), channel substratum, distance from the ocean, flow hydraulics and water depth may affect migration at different spatial scales (Way *et al*., 1993; Pyron & Covich, 2003; Blanco & Scatena, 2005) and have a major impact on the survival of populations: biological events such as reproduction, spawning, and the dispersal of larvae, are dependent on these events and are synchronized with them (Keith, 2003; Lord *et al*., 2012). On the islands, the impact of humans on aquatic habitats is highly significant, particularly on estuarine habitats which are crucial to amphidromous species. Thus Bell (2009) and Cook *et al*. (2012) have shown that lower reaches of rivers may be more important areas than upper reaches of rivers for conservation

of amphidromous species. These have to undertake two migrations between freshwaters and the sea. The success of such a life cycle – i.e. on the one hand for larvae's downstream migration after hatching, and on the other hand for the post-larval and juvenile upstream colonization after recruitment in freshwaters – depends on maintaining the mountain-ocean corridor open to allow movements between both habitats (Radtke *et al.*, 2001; Keith, 2003). The current state of knowledge on amphidromous Neritids' life cycle (biology, ecology), the length of the larval phase and the part it plays in the dispersal of larvae, will directly apply in matters of management and conservation. Anthropogenic alterations of the environment such as water withdrawals, channel modifications, deforestation and sewage inputs may have an impact on the performance of species, on their ability to find adequate food and to colonize the streams in altitude (Gorbach *et al.*, 2012). Nerites require hard substrata for their grazing and they cannot be found on mud bottom in estuaries. Man-made developments on these streams can alter larval dispersion and therefore the recruitment success (Brasher, 2003). Indeed, diversions and dams are responsible for modified flow regimes, fragmented populations, obstructed breeding migrations and the loss of navigational cues (Drinkwater & Frank, 1994; Crowe, 1996; Benstead *et al.*, 1999; Pringle *et al.*, 2000; Dudgeon, 2003).

In other words, the lack or a reduced number of new recruits of amphidromous Neritids might serve as an indicator of long-term health of estuaries (Burris *et al.*, 1990). With their large biomass, elimination of the Neritids may result in food-web alternation in a river system (Kano *et al.*, 2011).

The current state of knowledge on tropical freshwater Neritids' life cycle is of direct relevance for management and conservation (Radtke *et al.*, 2001; Keith, 2003). But, in addition to the scarcity of knowledge on their life history traits, species taxonomy has not been adequately resolved and boundaries between intra- and interspecific variation should be clarified for many taxa (Hidaka & Kano, 2014).

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