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

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RESUME.— *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.

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 very 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 Oceania (Pacific Oceanic Islands), Palearctic 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 undertaken by Quintero-Galvis & Castro (2013), using the genes COI and 16S rRNA. However, this 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).

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 Shigemiyama & 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* (*Hihīwai*) 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). *Hihīwai* 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 *hihīwai* 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 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 Kīnihapai 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 *hihiwai* to aggregate and form lines and mucus trails was observed. Several migrating *hihiwai* 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/m²). 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 (Burriss *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).

REFERENCES

- ALEXANDER, J.E. & COVICH, A.P. (1991).— Predation risk and avoidance behavior in two freshwater snails. *Biol. Bull.*, 180: 387-393.
- ALLIBONE, R.M. & WALLIS, G.P. (1993).— Genetic variation and diadromy in some native New Zealand galaxiids (Teleostei: Galaxiidae). *Biol. J. Linn. Soc.*, 50: 19-33.
- BAKER, H.B. (1923).— Notes on the radula of the Neritidae. *Proc. Acad. Nat. Sci. Philad.*, 75: 117-178.
- BANDEL, K. (2001).— The history of *Theodoxus* and *Neritina* connected with description and systematic evaluation of related Neritimorpha (Gastropoda). *Mitt. Geol.-Palaont. Inst. Univ. Hamburg*, 85: 65-104.
- BARBER, P.H., PALUMBI S.R., ERDMANN, M.V. & MOOSA, M.K. (2002).— Sharp genetic breaks among populations of *Haptosquilla pulchella* (Stomatopoda) indicate limits to larval transport: patterns, causes and consequences. *Mol. Ecol.*, 11: 659-674.
- BELL, K.N.I. (2009).— What comes down must go up: The migration cycle of Juvenile- Return anadromous taxa. *Am. Fish. Soc. Symp.*, 69: 321-341.
- BENSTEAD, J.P., MARCH, J.G. & PRINGLE, C.M. (2000).— Estuarine larval development and upstream post-larval migration of freshwater shrimps in two tropical rivers of Puerto Rico. *Biotropica*, 32: 545-548.
- BENSTEAD, J.P., MARCH, J.G., PRINGLE, C.M. & SCATENA, F.N. (1999).— Effects of low-head dam and water abstraction on migratory tropical stream biota. *Ecol. Appl.*, 9: 656-668.
- BIGGS, B.J.F. & SMITH, R.A. (2002).— Taxonomic richness of stream benthic algae: effects of flood disturbance and nutrients. *Limnol. Oceanogr.*, 47: 1175-1186.
- BISHOP, C.D., HUGGETT, M.J., HEYLAND, A., HODIN, J., BRANDHORST, B.P. (2006).— Interspecific variation in metamorphic competence in marine invertebrates: the significance for comparative investigations into the timing of metamorphosis. *Int. Comp. Biol.*, 46: 662-682.
- BLANCO, J.F. & SCATENA, F.N. (2005).— Floods, habitat hydraulics and upstream migration of *Neritina virginea* (Gastropoda: Neritidae) in Northeastern Puerto Rico. *Caribb. J. Sci.*, 41: 55-74.

- BLANCO, J.F. & SCATENA, F.N. (2006).— Hierarchical contribution of river-ocean connectivity, water chemistry, hydraulics, and substrate to the distribution of diadromous snails in Puerto Rico streams. *J. North. Am. Benthol. Soc.*, 25: 82-98.
- BLANCO, J.F. & SCATENA, F.N. (2007).— The spatial arrangement of *Neritina virginea* (Gastropoda: Neritidae) during upstream migration in a split-channel reach. *River Res. Appl.*, 23: 235-245.
- BLANCO-LIBREROS, J.F. & ARROYAVE-RINCÓ, A. (2009).— Daños por depredación y tamaño de concha del caracol diádromo *Neritina virginea* (Gastropoda: Neritidae) en el Río Mameyes, Puerto Rico. *Rev. Biol. Trop.*, 57: 1069-1080.
- BOWEN, B.W., BASS, A.L., ROCHA, L.A., GRANT, W.S. & ROBERTSON, D.R. (2001).— Phylogeography of the Trumpetfishes (*Aulostomus*): ring species complex on a global scale. *Evolution*, 55: 1029-1039.
- BRASHER, A.M. (1997).— *Life history characteristics of the native Hawaiian Stream Snail Neritina granosa (hihiwai)*. Cooperative National Park Resources Studies Unit, University of Hawaii at Manoa, Hawaii. Technical Report 114.
- BRASHER, A.M. (2003).— Impacts of human disturbances on biotic communities in Hawaiian streams. *BioScience*, 53: 1052-1060.
- BRIGGS, J.C. (1974).— *Marine zoogeography*. McGraw Hill, New York.
- BROWN, W.M., GEORGE, M. JR. & WILSON, A.C. (1979).— Rapid evolution of animal mitochondrial DNA. *Proc. Natl. Acad. Sci. USA*, 76:1967-1971.
- BUNJE, P.M.E. & LINDBERG, D.R. (2007).— Lineage divergence of a freshwater snail clade associated with post-Tethys marine basin development. *Mol. Phyl. Evol.*, 42: 373-387.
- BURRIS, J.A., BAMFORD, M.S. & STEWART, A.J. (1990).— Behavioral responses of marked snails as indicators of water quality. *Environ. Toxicol. Chem.*, 9: 69-76.
- CARPENTER, K.E. & NIEM, V.H. (eds). (1998).— *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Volume 1. Seaweeds, corals, bivalves and gastropods*. Rome, FAO.
- CASTELIN, M., FEUTRY, P., HAUTECOEUR, M., MARQUET G., WOWOR, D., ZIMMERMANN, G. & KEITH, P. (2013).— New insight on the genetic connectivity of the widespread amphidromous prawn *Macrobrachium lar* (Fabricius, 1798) (Crustacea: Decapoda: Palaemonidae). *Mar. Biol.*, 160: 1395-1406.
- COOK, B.D., BERNAYS, S., PRINGLE, C.M. & HUGHES, J.M. (2009).— Marine dispersal determines the genetic population structure of migratory stream fauna of Puerto Rico: evidence from island-scale population recovery process. *J. North. Am. Benthol. Soc.*, 28: 709-718.
- COOK, B.D., PAGE, T.J. & HUGHES, J.M. (2012).— Phylogeography of related diadromous species in continental and island settings, and a comparison of their potential and realized dispersal patterns. *J. Biogeogr.*, 39: 421-430.
- COWEN, R.K., LWIZA, K.M.M., SPONAUGLE, S., PARIS, C.B. & OLSON, D.B. (2000).— Connectivity of marine populations: open or closed? *Science*, 287: 857-859.
- CRANDALL, E.D. (1999).— Early life history aspects of amphidromous neritid snails in Moorea, French Polynesia. *Berkeley Sci.*, 3: 98-103.
- CRANDALL, E.D., TAFFEL, J.R. & BARBER, P.H. (2010).— High gene flow due to pelagic larval dispersal among South Pacific archipelagos in two amphidromous gastropods. *Heredity*, 104: 563-572.
- CRANDALL, E.D., TREML, E.A. & BARBER, P.H. (2012).— Coalescent and biophysical models of stepping-stone gene flow in neritid snails. *Mol. Ecol.*, 21 (22): 5579-5598.
- CROWE, T. (1996).— Different effects of microhabitat fragmentation on patterns of dispersal of an intertidal gastropod in two habitats. *J. Exp. Mar. Biol. Ecol.*, 206: 83-107.
- DENNENMOSER, S., THIEL, M. & SCHUBART, C.D. (2010).— High genetic variability with no apparent geographic structuring in the mtDNA of the amphidromous river shrimp *Cryphiops caementarius* (Decapoda: Palaemonidae) in Northern-Central Chile. *J. Crustacean Biol.*, 30: 762-766.
- DOHERTY, P.J., PLANES, S. & MATHER, P. (1995).— Gene flow and larval duration in seven species of fish from the Great Barrier Reef. *Ecology*, 76: 2373-2391.
- DRINKWATER, K.F. & FRANK, K.T. (1994).— Effects of river regulation and diversion on marine fish and invertebrates. *Aquat. Conserv. Mar. Freshw. Ecosys.*, 4: 135-151.
- DUDGEON, D. (2003).— The contribution of scientific information to the conservation and management of freshwater biodiversity in tropical Asia. *Hydrobiologia*, 500: 295-314.
- FORD, J.I. (1979).— *Biology of a Hawaiian fluvial gastropod Neritina granosa Sowerby (Prosobranchia: Neritidae)*. MSc thesis, University of Hawaii, Honolulu, Hawaii.
- FORD, J.I. & KINZIE III, R.A. (1982).— Life crawls upstream. *Natur. Hist.*, 91: 60-67.
- FREY, M. (2010).— A revised classification of the gastropod genus *Nerita*. *The Veliger*, 51: 1-7.
- FREY, M. & VERMEIJ, G.J. (2008).— Molecular phylogenies and historical biogeography of a circumtropical group of gastropods (Genus: *Nerita*): implications for regional diversity patterns in the marine tropics. *Mol. Phyl. Evol.*, 48: 1067-1086.

- GAITHER, M.R., BOWEN, B.W., BORDENAVE, T.R., ROCHA, L.A., NEWMAN, S.J., GOMEZ, J.A., VAN HERWERDEN, L. & CRAIG, M.T. (2011).— Phylogeography of the reef fish *Cephalopholis argus* (Epinephelidae) indicates Pleistocene isolation across the Indo-Pacific barrier with contemporary overlap in the coral triangle. *BMC Evol. Biol.*, 11: 189.
- GAITHER, M.R., TOONEN, R.J., ROBERTSON, D.R., PLANES, S. & BOWEN, B.W. (2010).— Genetic evaluation of marine biogeographical barriers: perspectives from two widespread Indo-Pacific snappers (*Lutjanus kashmira* and *Lutjanus fluvius*). *J. Biogeogr.*, 37: 133-147.
- GORBACH, K.R., BENBOW, M.E., MCINTOSH, M.D. & BURKY, A.J. (2012).— Dispersal and upstream migration of an amphidromous neritid snail: implications for restoring migratory pathways in tropical streams. *Freshw. Biol.*, 57: 1643-1657.
- HAU, S. (2007).— *Hihiiwai* (*Neritina granosa* Sowerby) recruitment in Iao and Honomanu streams on the island of Maui, Hawaii. In: N.L. Evenhuis & J.M. Fitzsimons (eds), *Biology of Hawaiian Streams and Estuaries*. Bishop Mus. Bull. Cult. Environ. Stu., 3, 171-181.
- HAU, S., WAY, C.M. & BURKY, A.J. (1992).— *Life cycle of the endemic limpet Neritina granosa* (Sowerby), in Palauhulu Stream, Maui. 43rd Annual Meeting of American Institute of Biological Sciences. Ecological Society of America, 9-13 August, Honolulu, Hawaii (abstract).
- HAYNES, A. (2000).— The distribution of freshwater gastropods on four Vanuatu islands: Espiritu Santo, Pentecost, Efate and Tanne (South Pacific). *Ann. Linnol.*, 36: 101-111.
- HAYNES, A. (2001).— A revision of the genus *Septaria* Férussac, 1803 (Gastropoda : Neritimorpha). *Ann. Naturhit. Mus. Wien*, 103 B: 177-229.
- HAYNES, A., TAYLOR, B.J.R. & VARLEY, M.E. (1985).— The influence of the mobility of *Potamopyrgus jenkinsi* (Smith, A.E.) (Prosobranchia: Hydrobiidae) on its spread. *Arch. Hydrobiol.*, 103: 497-508.
- HIDAKA, H. & KANO, Y. (2014).— Morphological and genetic variation between the Japanese populations of the amphidromous snail *Stenomelania crenulata* (Cerithioidea: Thiariidae). *Zool. Sci.*, 31: 593-602.
- HIRATA, T., NISHIWAKI, S., UEDA, H., TSUCHIYA, Y. & SATO, T. (1992).— Seasonal changes in moving activity of *Clithon retropictus* (Prosobranchia: Neritidae). *Venus*, 51: 57-66.
- HOAREAU, T.B., LECOMTE-FINGER, R., GRONDIN, H.P., CONAND, C. & BERREBI, P. (2007).— Oceanic larval life of La Réunion 'bichiques', amphidromous gobiid post-larvae. *Mar. Ecol. Prog. Ser.*, 333: 303-308.
- HODGES, M.H. & ALLENDORF, F.W. (1998).— Population genetics and pattern of larval dispersal of the endemic Hawaiian freshwater amphidromous gastropod *Neritina granosa* (Prosobranchia: Neritidae). *Pacific Sci.*, 52: 237-249.
- HORNE, J.B., VAN HERWERDEN, L., CHOAT, H.J. & ROBERTSON, D.R. (2008).— High population connectivity across the Indo-Pacific: congruent lack of phylogeographic structure in three reef fish congeners. *Mol. Phyl. Evol.*, 49: 629-638.
- HURYAN, A.D., & DENNY, M.W. (1997).— A biomechanical hypothesis explaining upstream movements by the freshwater snail *Elimia*. *Funct. Ecol.*, 11: 472-483.
- IIDA, M., WATANABE, S., SHINODA, A. & TSUKAMOTO, K. (2008).— Recruitment of the amphidromous goby *Sicyopterus japonicus* to the estuary of the Ota River, Wakayama, Japan. *Environ. Biol. Fishes*, 83: 331-341.
- JOHNSON, P.D., & BROWN, K.M. (1997).— The role of current and light in explaining the habitat distribution of the lotic snail *Elimia semicarinata* (Say). *J. North Amer. Benthol. Soc.*, 16: 545-561.
- KANO, Y. (2006).— Usefulness of the opercular nucleus for inferring early development in neritimorph gastropods. *J. Morphol.*, 267: 1120-1136. (doi:10.1002/jmor.10458).
- KANO, Y. (2009).— Hitchhiking behaviour in the obligatory upstream migration of amphidromous snails. *Biol. Lett.*, 5: 465-468.
- KANO, Y., CHIBA, S. & KASE, T. (2002).— Major adaptive radiation in neritopsine gastropods estimated from 28S rRNA sequences and fossil records. *Proc. R. Soc. Lond. B*, 269: 2457-2465. (doi:10.1098/rspb.2002.2178).
- KANO, Y. & KASE, T. (2003).— Systematics of the *Neritilia rubida* complex (Gastropoda: Neritiliidae): three amphidromous species with overlapping distributions in the Indo-Pacific. *J. Mollusc. Stud.*, 69: 273-284.
- KANO, Y. & KASE, T. (2004).— Genetic exchange between anchialine cave populations by means of larval dispersal: the case of a new gastropod species *Neritilia cavernicola*. *Zool. Scr.*, 33: 423-437.
- KANO, Y., STRONG, E.E., FONTAINE, B., GARGOMINY, O., GLAUBRECHT, M. & BOUCHET, P. (2011).— Focus on freshwater snails. Pp 257-264. in: P. Bouchet, H. Le Guyader & O. Pascal (eds) *The Natural History of Santo*. Patrimoines Naturels. vol. 70. Muséum National d'Histoire Naturelle, Paris.
- KEITH, P. (2003).— Biology and ecology of amphidromous Gobiidae in the Indo-Pacific and the Caribbean regions. *J. Fish. Biol.*, 63: 831-847.
- KEITH, P. & LORD, C. (2011a).— Systematics of Sicydiinae. Pp 243-277. in: R.A. Patzner, J.L. Van Tassell, M. Kovacic & B.G. Kapoor (eds). *The biology of gobies*. Science Publishers Inc.
- KEITH, P. & LORD, C. (2011b).— Tropical freshwater gobies: Amphidromy as a life cycle. Pp 119-128. in: R.A. Patzner, J.L. Van Tassell, M. Kovacic & B.G. Kapoor (ed.). *The Biology of Gobies*. Science Publishers Inc.

- KOBAYASHI, S. & IWASAKI, K. (2002).— Distribution and spatiotemporal variation in the population structure of the fluvial neritid gastropod *Clithon retropictus*. *Benthos Res.*, 57: 91-101.
- KOIKE, K. (1996).— Embryonic development and larval dispersal in the Neritidae (Gastropoda: Prosobranchia). *Galaxea*, 13: 129-130.
- LAVERY, S., MORITZ, C. & FIEDLER, D.R. (1995).— Changing patterns of population structure and gene flow at different spatial scales in *Birgus latro* (the coconut crab). *Heredity*, 74: 531-541.
- LAVERY, S., MORITZ, C. & FIEDLER, D.R. (1996).— Indo-pacific population structure and the evolutionary history of the coconut crab *Birgus latro*. *Mol. Ecol.*, 5: 557-570.
- LESSIOS, H.A., KANE, J. & ROBERTSON, D.R. (2003).— Phylogeography of the pantropical sea urchin *Tripneustes*: contrasting patterns of population structure between oceans. *Evolution*, 57: 2026-2036.
- LESSIOS, H.A., KESSING, B.D. & PEARSE, J.S. (2001).— Population structure and speciation in tropical seas: global phylogeography of the sea urchin *Diadema*. *Evolution*, 55: 955-975.
- LESSIOS, H.A. & ROBERTSON, D.R. (2006).— Crossing the impassable: genetic connections in 20 reef fishes across the eastern Pacific Barrier. *Proc. R. Soc. Lond. B. Biol.*, 273: 2201-2208.
- LIMPALAER, L. (2009).— Coup de projecteur sur les *Neritidae*. Introduction : situation chez les gastropodes, histoire, autres familles. Caractères morphologiques, taxonomie. *Xenophora*, 128: 29-33.
- LIU, H.T.T. & RESH, V.H. (1997).— Abundance and microdistribution of freshwater gastropods in three streams of Moorea, French Polynesia. *Ann. Limnol.*, 33: 235-244.
- LORD, C., BRUN, C., HAUTECEUR, M. & KEITH, P. (2010).— Insights on endemism: comparison of the duration of the marine larval phase estimated by otolith microstructural analysis of three amphidromous *Sicyopterus* species (Gobiidae: Sicydiinae) from Vanuatu and New Caledonia. *Ecol. Freshw. Fish.*, 19: 26-38.
- LORD, C., LORION, J., DETTAI, A., WATANABE, S., TSUKAMOTO, K., CRUAUD, C. & KEITH, P. (2012).— From endemism to widespread distribution: phylogeography of three amphidromous *Sicyopterus* species (Teleostei: Gobiidae: Sicydiinae). *Mar. Ecol. Prog. Ser.*, 455: 269-285.
- MAEDA, K., YAMASAKI, N. & TACHIYAMA, K. (2007).— Size and age at recruitment and spawning season of sleeper, genus *Eleotris* (Teleostei: Eleotridae) on Okinawa Island, southern Japan. *Raff. Bull. Zool. Suppl.*, 14: 199-207.
- MCDOWALL, R.M. (2007).— On amphidromy, a distinct form of diadromy in aquatic organisms. *Fish Fish.*, 8: 1-13.
- MCDOWALL, R.M. (2008).— Diadromy, history and ecology: a question of scale. *Hydrobiologia*, 602: 5-14.
- MCRAE, M.G. (2007).— The potential for source-sink population dynamics in Hawaii's amphidromous fishes. In: N.L. Evenhuis & J.M. Fitzsimons (eds), *Biology of Hawaiian Streams and Estuaries*. *Bishop Mus. Bull. Cult. Environ. Stud.*, 3: 87-98.
- MURPHY, C.A. & COWAN, J.H. (2007).— Production, marine larval retention or dispersal, and recruitment of amphidromous Hawaiian Gobioids: Issues and implications. *Bishop Mus. Bull. Cult. Environ. Stud.*, 3: 63-74.
- MYERS, M.J., MEYER, C.P. & RESH, V.H. (2000).— Neritid and thiarid gastropods from French Polynesian streams: how reproduction (sexual, parthenogenetic) and dispersal (active/passive) affect population structure. *Freshw. Biol.*, 44: 535-545.
- NISHIWAKI, S., HIRATA, T., UEDA, H., TSUCHIYA, Y. & SATO, T. (1991a).— Studies on the migratory direction of *Clithon retropictus* (Prosobranchia: Neritidae) by marking-and-recapture method. *Venus*, 50: 202-210.
- NISHIWAKI, S., HIRATA, T., UEDA, H., TSUCHIYA, Y. & SATO, T. (1991b).— Egg-laying season and monthly change in egg capsule production in the Naka River of Izu Peninsula. *Venus*, 50: 197-201.
- PAULINI, E. (1963).— Field observations on the upstream migration of *Australorbis glabratus*. *Bull. W.H.O.*, 29: 838-841.
- PRINGLE, C.M., FREEMAN, M.C. & FREEMAN, B.J. (2000).— Regional effects of hydrologic alterations on riverine macrobiota in the New World: tropical-temperate comparisons. *BioScience*, 50: 807-823.
- PYRON, M., & COVICH, A.P. (2003).— Migration patterns, densities and growth of *Neritina punctulata* snails in Río Espíritu Santo and Río Mameyes, Northeastern Puerto Rico. *Carib. J. Sci.*, 39: 338-347.
- QUINTERO-GALVIS, J. & CASTRO, L.R. (2013).— Molecular phylogeny of the Neritidae (Gastropoda: Neritimorpha) based on the mitochondrial genes cytochrome oxidase I (COI) and 16S rRNA. *Acta Biol. Colomb.*, 18: 307-318.
- RADTKE, R.L., KINZIE, R.A. III & SHAFER, D.J. (2001).— Temporal and spatial variation in length and size at settlement of the Hawaiian amphidromous goby *Lentipes concolor*. *J. Fish. Biol.*, 59: 928-938.
- RESH, V.H., BARNES, J.R., BENIS-STEGER, B. & CRAIG, D.A. (1992).— Life-history features of some invertebrates in a French Polynesian stream. *Stud. Neotrop. Fauna Environ.*, 27: 145-153.
- RESH, V.H., BARNES, J.R. & CRAIG, D.A. (1990).— Distribution and ecology of benthic invertebrates in the Opunohu river catchment, Moorea, French Polynesia. *Ann. Limnol.*, 26: 195-214.
- SCHELTEMA, R.S. (1971).— Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biol. Bull.*, 140: 284-322.
- SCHNEIDER, D.W. & FROST, T.M. (1986).— Massive upstream migrations by a tropical freshwater neritid snail. *Hydrobiologia*, 137: 153-157.

- SCHNEIDER, D.W. & LYONS, J. (1993).— Dynamics of upstream migration in two species of tropical freshwater snails. *J. N. Am. Benthol. Soc.*, 12: 3-16.
- SCHNEIDER, D.W. & FROST, T.M. (1986).— Massive upstream migrations by a tropical freshwater neritid snail. *Hydrobiologia*, 137: 153-157.
- SODERSTROM, O. (1987).— Upstream movements of invertebrates in running waters – a review. *Arch. Hydrobiol.*, 111: 197-208.
- SPONAUGLE, S., COWEN, R.K., SHANKS, A., MORGAN, S.G., LEIS, J.M., PINEDA, J.S. *ET AL.* (2002).— Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. *Bull. Mar. Sci.*, 70: 341-375.
- STRATHMANN, R., HUGHES, T.R., KURIS, A.M., LINDEMAN, K.C., MORGAN, S.G., PANDOLFI, J.M. *ET AL.* (2002).— Evolution of local recruitment and its consequences for marine populations. *Bull. Mar. Sci.*, 70: 377–396.
- STRONG, E., FONTAINE, B., GARGOMINY, O., GLAUBRECHT, M. & BOUCHET, P. (2011).— Thiaridae and other freshwater snails. Pp 260-264. *in*: P. Bouchet, H. Le Guyader & O. Pascal (eds) *The Natural History of Santo*. Patrimoines Naturels. Vol. 70.
- STRONG, E., GARGOMINY, O., PONDER, W. & BOUCHET, P. (2008).— Global diversity of gastropods (Gastropoda; Mollusca) in freshwater. *Hydrobiologia*, 595: 149-166.
- UNDERWOOD, A.J. (1975).— Comparative studies on the biology of *Nerita atramentosa* Reeve, *Bembicium nanum* (Lamarck) and *Cellana tramoserica* (Sowerby) (Gastropods: Prosobranchia) in S.E. Australia. *J. Exp. Mar. Biol. Ecol.*, 18: 153-172.
- WAY, C.M., BURKY, A.J. & LEE, M.T. (1993).— The relationship between shell morphology and microhabitat flow in the endemic Hawaiian stream limpet (Hihiwai), *Neritina granosa* (Prosobranchia: Neritidae). *Pac. Sci.*, 47: 263-275.
- WHITE, C., SELKOE, K.A., WATSON, J., SIEGEL, D.A., ZACHERL, D.C. & TOONEN R.J. (2010).— Ocean currents help explain population genetic structure. *Proc. R. Soc. B.*, 277: 1685-1694.
- WINTERS, K.L., VAN HERWERDEN, L., CHOAT, H.J. & ROBERTSON, D.R. (2010).— Phylogeography of the Indo-Pacific parrotfish *Scarus psittacus*: isolation generates distinctive peripheral populations in two oceans. *Mar. Biol.*, 157:1679-1691.