RESEARCH NOTE

DRIFTWOOD AS A VECTOR FOR THE OCEANIC DISPERSAL OF ESTUARINE GASTROPODS (NERITIDAE) AND AN EVOLUTIONARY PATHWAY TO THE SUNKEN-WOOD COMMUNITY

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Although dispersal of marine benthos is typically accomplished by transport of planktonic larvae in ocean currents (e.g. Scheltema, 1986; Grantham, Eckert & Shanks, 2003), benthic invertebrate species with no pelagic stage sometimes have wide-ranging distributions across ocean basins (Johannesson, 1988; Gillespie *et al.*, 2012; Haydar, 2012; Winston, 2012). Explanations for such intriguing wide distributions include dispersal by rafting on floating objects or actively swimming animals (Thiel & Haye, 2006), flying on birds (Green & Figuerola, 2005), drifting as juveniles or small adults (Highsmith, 1985; Martel & Chia, 1991) and anthropogenic introduction (Miura *et al.*, 2006; McGlashan *et al.*, 2008). However, direct evidence of such dispersal has rarely been provided (e.g. Martel & Chia, 1991), except for the relatively common occurrence of sessile organisms on drifting logs and plastic and other debris (Barnes & Milner, 2005; Hoeksema, Roos & Cadée, 2012). Driftwood may even be an available vector for the dispersal of limnic and terrestrial animals that presumably have more difficulties in transoceanic dispersal (Trewick, 2000; Measey *et al.*, 2007) but, again, there are only few reports on actual observation of such phenomena (Censky, Hodge & Dudley, 1998; Green & Figuerola, 2005).

Here we report our direct observation in Papua New Guinea (PNG) of three estuarine species of neritid gastropods (Neritimorpha: Neritidae) that survived on driftwood in seawater for some extended period and were transported several kilometres to a fully marine shore. Furthermore, we found another species of typically estuarine Neritidae on sunken pieces of wood at depths of 105–135 m in Vanuatu, South Pacific. These supposedly non marine gastropods evidently have the potential to survive in fully marine conditions and to disperse as benthic adults and eggs. We suggest that driftwood from shallow-water environments, including estuaries, mangrove swamps and mudflats, might have an evolutionary significance for the establishment of the sunken-wood community and possibly other chemosynthetic faunas in the deep sea.

We found, photographed and collected 23 neritid snails on a log drifting along a sand/rubble beach on Sek Island, Madang, PNG (Fig. 1A; 5°4′44″S, 145°48′53″E; Station number PM22 of PNG Expedition 2012–2013) during low tide at midnight on 15 November 2012. Sek is a barrier-reef island on the northeastern edge of the Madang Lagoon, which is the largest lagoon on the north coast of PNG, *c.* 17 km long and 1–4 km wide, with an approximate total area of 50 km^2 (Benet-Monico *et al.*, 2006). The narrow barrier reef has a steep slope dropping to the seabed at 400 m on its seaward side (Jebb & Lowry, 1995) and four passages that link the lagoon to the open sea, the northernmost of which is the Ottilien Passage (Fig. 1B). The inner coastline of the lagoon is greatly dissected, with shallow fringing reefs, mangroves and seagrass habitats. Inside the lagoon the bottom is even in depth at 30–40 m and there are numerous shallow patch reefs and coral-rubble islands that support rich fringing reefs (Stephenson & Williams, 1971). The northernmost area of the lagoon is called Sek Harbour and has a narrow westerly extension towards Bostrem Bay and a broad southerly extension towards Madang. There are three major inlets within the harbour: Biges and Sek (or Marrain) Rivers at the south and Maklay River at the north. These rivers carry silty water that traverses the harbour after heavy rains and generally leaves the lagoon rapidly without mixing appreciably (Jebb & Lowry, 1995). A few other minor creeks enter Bostrem Bay. River outlets and surrounding waters have highly variable but generally low salinity, while coastal sites consistently exhibit (nearly) full-strength seawater values; salinity levels of 1.7–33 and 33–35 psu, respectively, were recorded by Benet-Monico *et al.* (2006). Waves enter the harbour through the Ottilien Passage but subside within 1 km of entering the passage. The tidal exchange of surface water appears to affect only the outer half of the harbour; in the remainder, conditions are extremely sheltered (Stephenson & Williams, 1971). Temperatures of the water on the inner edge of the lagoon, at a depth of 4 m, vary from 27 to 29.5°C through the year (Jebb & Lowry, 1995). In Ottilien Passage, the bottom is of fine to coarse biogenic sand with coral debris, mollusc fragments and larger foraminiferal tests, and this extends southwards near the shore of Sek Island; it is muddier towards the west (Stephenson & Williams, 1971; Langer & Lipps, 2003).
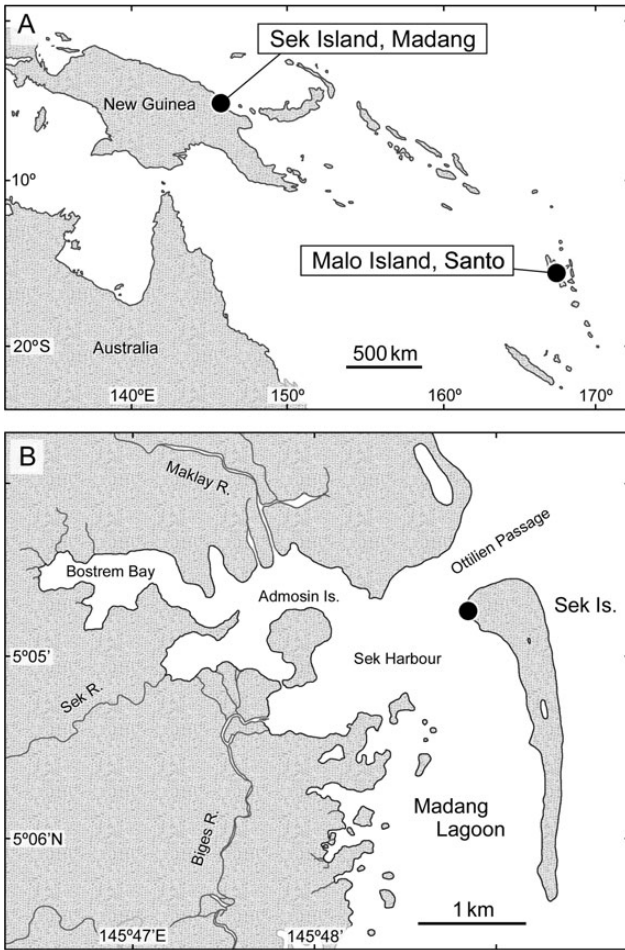
Figure 1. A. Map of Melanesia. Estuarine species of neritid gastropods were collected on a floating log at a sand/rubble beach on Sek Island, Madang, PNG, and in sunken pieces of wood at a depth range of 105–135 m, Station AT76, off Malo Island, Santo, Vanuatu. **B.** Map showing northern part of Madang Lagoon. Dot indicates sampling locality of neritids on the log. Their typical brackish habitats exist near the mouths of Maklay, Sek and Biges Rivers as well as in Bostrem Bay, all of which are more than 2 km away from the coast of Sek Island.

While Sek is the largest barrier island of the lagoon, with a length of 3.3 km from the northern to the southern tip and 150–750 m from east to west (Fig. 1B), it does not have any of typical habitats for the three neritid species, such as a river, an estuary or a mangrove swamp, along its coastline. The outer, eastern side of Sek Island has a rocky shore with crashing surf and the inner, western side facing Sek Harbour is a sand/rubble beach washed by calmer waves. There are a couple of small, land-locked ponds on the island, but it does not seem likely that these neritids would climb over the surrounding limestone covered with bush to reach the coast by crawling the distances of 100–200 m (Fig. 1B). The closest possible habitats of the three species are the estuaries of the Biges, Sek and Maklay Rivers and nearby mangrove swamps on the opposite side of Sek Harbour, all at distances more than 2 km from the beach where the driftwood log was found. The beach was located near the north-western corner of the island and characterized by seawater of normal salinity, sand in the upper intertidal zone and coral rubble in the lower intertidal zone. The associated gastropod fauna was typical for the coral-rubble shore of the Madang Lagoon, including large populations of Planaxidae, Muricidae, Conidae and other neogastropod families.

The driftwood log was 4.5 m long with diameters of 10 cm and 25 cm at the distal and proximal ends, respectively (Fig. 2A). It was floating close to the shore at a depth of *c*. 0.5 m at the low-tide level, while the thinner end and branches were found partly stuck in the rubble. The attached neritids include 13 specimens of *Neripteron auriculata* (Lamarck, 1816), nine *Septaria tessellata* (Lamarck, 1816) and one *S. clypeolum* (Récluz, 1842). The first species is a relatively flat snail with a large aperture and fine spiral threads on the whorls (Fig. 2C), sometimes reported under other names (e.g. Lozouet & Plaziat, 2008: pl. 13, figs 4, 5). The latter two species of the patelliform genus *Septaria* are morphologically similar and their taxonomy has been subject to confusion in most previous literature. The shape of the deck or septum and position of the apex are good discriminating shell characters (see Haynes, 2001: figs 18, 19 for *S. tessellata* and fig. 17 for *S. clypeolum*; Lozouet & Plaziat, 2008: pl. 13, figs 1–3 for the former and figs 7–9 for the latter). Nucleotide sequence comparison of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene using our data library verified the morphological species identification of the present specimens (Y. Kano & H. Fukumori, unpubl.). The mean maximum shell lengths were 11.8 ± 2.8 mm (range: 6.0–13.5 mm) for *N. auriculata*, 18.6 ± 7.8 mm (13.1–30.4 mm) for *S. tessellata* and 21.0 mm for *S. clypeolum*. These sizes suggest that these are sub-adult to fully grown adult individuals (see Lozouet & Plaziat, 2008; Kano *et al.*, 2011).

Many of the snails and limpets were attached to the lateral sides of the log, which were covered with green macro- and microalgae. The upper surface of the log was exposed to the air above the water level and lacked neritids and algal growth (Fig. 2A). All species of *Neripteron* and *Septaria* are grazers and usually feed on microalgae, including diatoms, in their typical habitats (Kano & Fukumori, 2010; Kano *et al.*, 2011). The present neritids evidently fed on the microalgae; zigzag traces of radular rasping were clearly etched on the surface of the log. This may explain their apparently good, not starved, condition with ordinary size of soft parts and active movement of the head-foot. Both macro- and microalgae seemed to be fully marine species but not of an estuarine origin, as the nearby rubble and other driftwood were covered with algae of the same appearance. Some of the shells were also covered with the same algae (Fig. 2B). More than a thousand egg capsules of *N. auriculata* and *S. tessellata* were scattered on the surface of the log around the adult individuals of each species (Fig. 2B, C). Some of the capsules were white and thus newly deposited, probably less than a few days old (see Kano & Fukumori, 2010; Fukumori, Chee & Kano, 2013), suggesting that oviposition might have occurred during the drift, after leaving the original, brackish-water habitat of the snails.

The three species have been recorded from the lower reaches of rivers and streams as well as in creeks, ponds and mangrove swamps in Pacific islands (e.g. Tina Liu & Resh, 1997; Lozouet & Plaziat, 2008; Kano *et al.*, 2011), while rarely from freshwater reaches with no tidal influence and never from a fully marine habitat with no limnic influence. However, the markedly eury-haline nature of some neritids, particularly several species of *Neripteron* and *Septaria*, has been observed in laboratory experiments. Specimens of *N. auriculata* collected from a lower river reach all survived in full seawater during a 1-week experiment (Tina Liu & Resh, 1997). The usual absence of the three species in the fully marine environment may therefore not be due to physiological constraints. Rather, other physical and biological factors including substrate types, water velocity, food availability, competition and predation may play more important roles. The time the driftwood log spent in full seawater cannot be estimated accurately, but the distance from suitable brackish habitats in combination with a preceding period of calm weather and smooth water without appreciable turbulence, as well as the
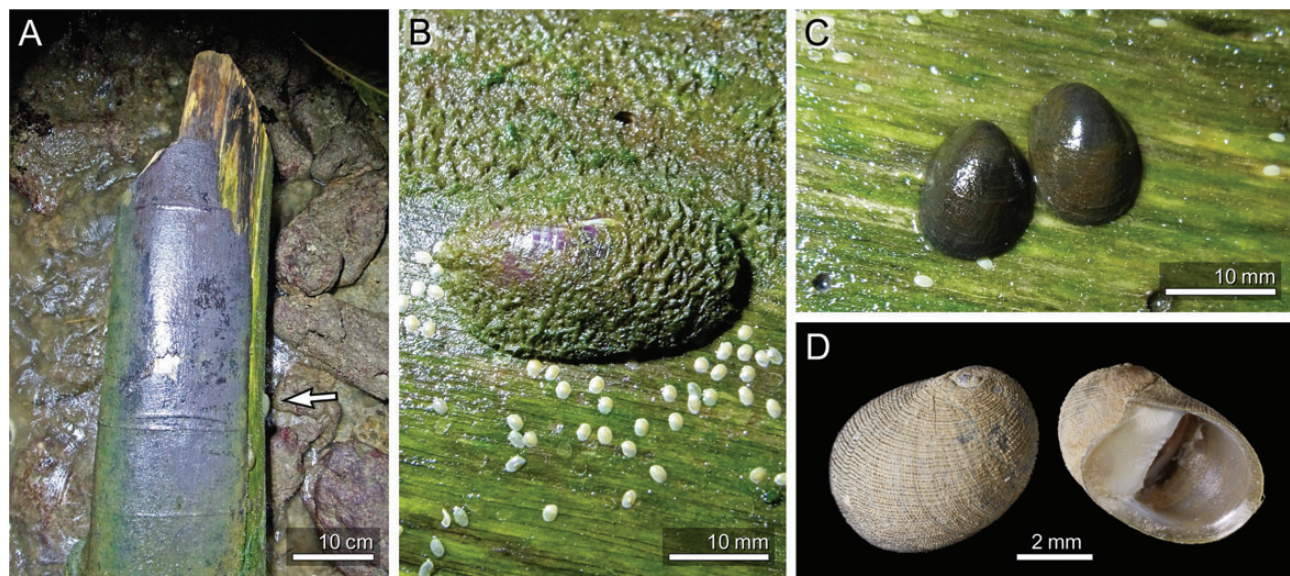
Figure 2. A. Proximal end of driftwood log (*c.* 4.5 m long) with estuarine neritids at a shore on Sek Island, Madang, PNG. Arrow points to *Septaria tessellata* shown in **B**. Note that the log was floating near the beach line and pulled up on the coral-rubble shore for observation and photo-documentation. **B.** Adult female of *S. tessellata* with numerous egg capsules laid on the surface of the log. Some of capsules seemed to have been deposited recently, possibly after the log was washed from a brackish environment. **C.** Adult specimens and egg capsules of *Neripteron auriculata* on the driftwood log. **D.** Single subadult specimen of *Neripteron spiralis* found in a piece of sunken wood from 105 to 135 m deep, Santo, Vanuatu, together with typical sunken-wood fauna. This is another species of Neritidae previously known only from estuarine and other brackish habitats.

thick layer of marine algae, may allow us to assume a minimum of several days.

We believe that the log was suspended in brackish water with enough buoyancy and remained stationary for a sufficiently long time for the snails to colonize the log before it floated down the estuary to the lagoon and then drifted to the shore of Sek Island. *Neripteron auriculata* and *S. tessellata* are known to prefer attaching to wood, *Nipa* palm leaves and other plant material, rather than to rocks and stones in their typical habitats, whereas *S. clypeolum* is found equally on both types of substrate (e.g. Haynes, 2001; Lozouet & Plaziat, 2008). Such a preference obviously increases the probability of being transported on driftwood. The flat shape of *N. auriculata* and even the limpet form of the *Septaria* species also increase that probability, because their low profile makes them less susceptible to dislodgement from hydraulic forces and because the larger aperture and consequently larger foot provide higher traction and better clinging ability (Vermeij, 1993). Other common neritid taxa on wood in the estuarine habitats of the Melanesian region, including a few species of *Clithon* and *Vittina* (Lozouet & Plaziat, 2008; Kano *et al.*, 2011), were absent on the log, probably because they fell off due to wave action acting on their more rounded shell shapes, and because of their smaller foot and consequently weaker adhesion strength.

Rafting on floating vegetation may be an important mechanism for the transoceanic dispersal, gene flow and geographic range expansion of benthic brackish animals, as suggested for the mangrove species of the littorinid snail genus *Littoraria* (see Reid, 1986: 66). Limnic species that lack a free-living larval stage and reproduce by direct development depend more on such supposedly rare stochastic events. Freshwater crabs with physiological tolerance to an extended period of immersion in full seawater represent such an example (Esser & Cumberlidge, 2011). However, most species of limnic nerites in the Indo-West Pacific region, including the three species found on the driftwood log, have an amphidromous life cycle with their planktotrophic larvae migrating to the sea (Kano, 2006; Kano *et al.*, 2011). The duration of the marine larval phase may exceed a few months (see Kano, 2006; Lesoway & Page, 2008), which more plausibly explains the widespread geographic distribution and genetic homogeneity of many of freshwater and estuarine species in the family (Kano, 2009; Crandall, Taffel & Barber, 2010). The three species on the driftwood indeed have very wide distributions: *N. auriculata* from Mauritius to French Polynesia, *S. tessellata* from Natal, South Africa to Vanuatu, and *S. clypeolum* from Okinawa, Japan to PNG (Y. Kano & H. Fukumori, unpubl.). Thus driftwood dispersal may have only limited significance for these species, although adult snails in a cluster, with suitable substrate for egg laying, could possibly be more efficient colonizers of new habitats than a small number of larvae (see Highsmith, 1985; Thiel & Haye, 2006). Even a single female neritid may keep laying fertilized eggs with sperm from previous matings, which are retained for a long time in the spermatophore sac and/or seminal receptacle (Andrews, 1937; Shigemiya & Kato, 2001). Each egg capsule of *Neripteron* and *Septaria* species contains several dozen eggs (e.g. Tan & Lee, 2009). The more than a thousand capsules found on the log may therefore have yielded tens of thousands of larvae, and the snails may have kept laying their egg capsules. Although it is not known if the larvae of amphidromous neritids tolerate full seawater conditions from the time of hatching, the fluctuating salinity typical of estuarine environments may well favour euryhaline tolerance, not only in adults, but also in the hatchlings of the present species.

A similar but even more intriguing finding was the occurrence of another estuarine species of *Neripteron* from sunken wood at shelf depth. One of us (A.W.) found two specimens of *N. spiralis* (Reeve, 1855) in separate sunken pieces of wood, both collected by a trawl haul from a depth range of 105–135 m, *c.* 3 km northwest of Malo Island, Santo, Vanuatu (Fig. 1A; 15°38′42″S, 167°03′36″E; Station number AT76 of Santo 2006 Expedition) on 10 October 2006. Both wood pieces were well eaten by teredinid or pholadid bivalves, and the surface and inside were dominated by a variety of typical sunken-wood animal species. The gastropod fauna included *Dillwynella* sp. (Trochoidea: Skeneidae), *Notocrater* 2 spp. (Lepetelloidea: Pseudococculinidae)

and another unidentified lepetelloid species (Warén, 2011: figs 498E, 499C, 500A). *Dillwynella* and *Notocrater*, at least, are confined to sunken wood and other plant remains (Marshall, 1986, 1988; Warén, 2011). Their presence in significant numbers suggests that the two wood pieces had been on the seabed for an extended period, probably months, during which the estuarine neritids survived at the shelf depth. One of the two individuals of *N. spiralis* was discarded when the first piece of wood was examined at the field-based laboratory, due to suspected contamination from intertidal material. However, the second specimen (Fig. 2D) was found well within an empty shipworm burrow and then preserved in ethanol for morphological and genetic examination.

This specimen from the shelf-depth sunken wood perfectly agrees in shell morphology with the conspecific snails from driftwood in estuaries and mangrove swamps in Santo and other western Pacific islands. Genetic data also justified the conspecific treatment. Sequence comparison of the COI gene revealed less than 1% genetic distances between the sunken wood specimen and four individuals of *N. spiralis* from brackish waters in various western Pacific islands, while the distances were greater among the latter four (Y. Kano & H. Fukumori, unpubl.). *Neripteron spiralis* is similar to the phylogenetically close *N. auriculata* mentioned above, in sharing a brown shell with fine spiral threads on the whorls, although the aperture is more narrowly constricted with a thickened rim inside, and the spire is taller and protruding in the former species (Kano *et al.*, 2011: figs 305H, I). The maximum shell length of 5.9 mm and a rather sharp margin of the outer lip of the shell aperture (Fig. 2D) suggest subadult status of the present specimen, presumably less than one year old. *Neripteron spiralis* shares wood-associated brackish habitats with *N. auriculata* and has not been found previously in fully marine conditions with no limnic influence (see above), but it probably also shares a markedly euryhaline nature. This is another species of the Neritidae with an amphidromous life cycle, a long planktotrophic larval period and a wide-ranging geographic distribution (Kano, 2006). No observation was made on the possible diet or the presence or absence of egg capsules in the sunken pieces of wood. However, it is certainly possible that *Neripteron* species on the sunken and drifted pieces of wood in shelf and estuarine waters graze on bacterial mats along with microalgae, considering the wide variety of food items identified in previous studies for limnic and marine neritids (see Kano & Fukumori, 2010).

Driftwood eventually becomes washed up on a shore or sinks to the seabed as it loses buoyancy, but the wood-associated faunas in the intertidal mangrove swamps and the deep sea have been considered quite different from each other (e.g. Lorion *et al.*, 2010: 77). However, sunken wood in shallow-water environments harbours rich prokaryotic and protozoan faunas that form sulphide-oxidizing symbioses, as is the case in bathyal and abyssal waters (Laurent *et al.*, 2009; see also Palacios *et al.*, 2009). An evolutionary link between the shallow sea and deep-sea hydrothermal vents and seeps via 'wooden steps' has been proposed by Distel *et al.* (2000) for bathymodioline mussels that associate with sunken wood and other chemosynthetic habitats in the deep sea, such as vents and seeps. This evolutionary transition from a shallow-sea ancestor to vent and seep descendants with intermediate species associated with organic falls has been verified by rigorous phylogenetic reconstructions for the Mytilidae (including Bathymodiolinae), but not in other groups (e.g. Lorion *et al.*, 2010; Bienhold *et al.*, 2013). However, such phylogenetic studies have concentrated on the relationships among deep-sea species themselves, and the direct ancestor of the sunken-wood taxa has not been identified among the shallow-water fauna. In this regard, the present specimen of *N. spiralis* may possibly represent a unique example of an ongoing invasion of the deep-sea chemosynthetic environments by a shallow-water animal species.

Evolutionary transitions from wood associated with estuarine and mangrove waters to wood in the deep-sea environments do exist in the Phenacolepadidae, the sister family of Neritidae (Kano, Chiba & Kase, 2002). Several species of the type genus *Phenacolepas* live exclusively on the underside of deeply buried driftwood in mud sediment, while some others are found in large numbers in the burrows of shipworms in sunken wood from shelf and bathyal waters in PNG and Vanuatu (Kano & Haga, 2011; Warén, 2011). Interestingly, one of the species is abundant in both shallow and deep waters, with no genetic difference between specimens from the two environments, although their shell shapes differ greatly from each other, reflecting the different substrates upon which they grow (Y. Kano & A. Warén, unpubl.). Our ongoing phylogenetic analysis of phenacolepadids, including species from both estuarine and offshore wood, as well as rocky shores, hydrothermal vents and seeps, should shed new light on the evolutionary origins of the deep-sea chemosynthetic fauna.

While the availability of anthropogenic flotsam has increased, the abundance of driftwood has decreased in the global marine environment (Thiel & Haye, 2006). This most probably has affected the frequency of rafting opportunities for wood dwellers and also the sustenance of the wood-fall community in the deep sea. New Guinea and Santo along with other Melanesian islands with high mountains are particularly rich in drifting and sunken pieces of wood, thanks to the presence of dense native forest and the near-absence of dams and other artificial constructs that hinder the downstream passage of floodwaters and plant material (Pailleret *et al.*, 2007; Warén, 2011; Pante *et al.*, 2012; see also Thiel & Haye, 2006). The observation of these presumably rare phenomena—of driftwood transportation and the possible evolutionary transition in progress from the estuarine to seabed habitats—may have been possible due only to an abundant supply of wood from these islands into the sea.

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