CHAPTER 12

New Insights on Biodiversity and Conservation of Amphidromous Shrimps of the Indo-Pacific islands (Decapoda: Atyidae: *Caridina*)

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12.1 INTRODUCTION

Atyid shrimps (Crustacea: Decapoda) are essential components of tropical freshwater ecosystems, playing a role of cleaner by shredding fallen leaves or filtering organic particular matter and being preys to a number of organisms (Covich et al. 1999, Crowl et al. 2001). Among them, the genus *Caridina* H. Milne Edwards, 1837, is particularly diversified, comprising more than 300 described species, making it the most diversified of the infra-order Caridea (De Grave et al. 2015). In Indo-Pacific Islands, the majority of *Caridina* species have an original diadromous lifestyle, with a planktonic marine larval phase and a benthic freshwater adult phase (McDowall 2007, Bauer 2013). This strategy allows the species to colonize isolated habitats, such as the rivers of volcanic islands, and to survive the instability of these environments (floods, droughts, volcanism, etc.) by keeping a stock of larvae in the ocean, ready to recolonize depopulated rivers (Keith et al. 2010). Amphidromy, by isolating populations, has also contributed to establishing the high diversity that exists among caridean shrimps. This diversity, however, is the source of an extreme taxonomic confusion that impedes the monitoring of the species and the establishment of appropriate conservation programs (Klotz and Rintelen 2014). With the development of new molecular biology techniques, integrative taxonomy is increasingly used by systematists to achieve more precise species delineations by combining morphological data with genetic, ecological, and/or biogeographical information (Mazancourt et al. 2017).

12.2 BIODIVERSITY

12.2.1 Taxonomy

There is substantial confusion surrounding the taxonomy of many *Caridina* species resulting in the creation of several species complexes (we consider a species complex a monophyletic species group that share a common taxonomic history in having been synonymized at one point, and/or that can be identified by morphological characters). Indo-Pacific island amphidromous shrimps have been grouped into seven main complexes: (1) *Caridina nilotica* (P. Roux, 1833) complex (Johnson 1963, Holthuis 1978, Jalihal et al. 1984, Choy 1991, Richard and Clark 2005, Karge and Klotz 2007), (2) *C. weberi* De Man, 1892 complex (Richard and Chandran 1994, Cai and Shokita 2006a), (3) *C. gracilirostris* De Man, 1892 complex (Cai and Ng 2001, 2007), (4) *C. typus* H. Milne Edwards, 1837 complex (Karge and Klotz 2007, Bernardes et al. 2017), (5) *C. serratirostris* De Man, 1892 complex (Cai and Shokita 2006b), (6) *C. brevicarpalis* De Man, 1892 complex (Short 2009), and (7) *C. propinqua* De Man, 1908 complex (W. Klotz, unpublished). Little work has been done to differentiate among the species clustered within these complexes, possibly due to the difficulty and costs associated with genetic analyses and the highly similar morphology of shrimps from different populations.

Egg size is often a good indicator of amphidromous species. Small eggs indicate that the species has an indirect development with several planktonic stages that are often marine. Conversely, species with large eggs are most likely landlocked, with direct development limiting their dispersal abilities, meaning they are often endemic. However, some species can have small eggs and still be endemic – such as *C. longicarpus* and *C. meridionalis*, both endemic to New Caledonia (Marquet et al. 2003, Mazancourt et al. 2018) or *C. futunensis*, endemic to Futuna Island (Mazancourt et al. 2019a). This can be due to particular conditions that limit the dispersal of marine larvae. For example, oceanic currents or physical barriers (e.g., closed coral lagoons) may prevent dispersal to nearby islands even if larvae are capable of surviving in oceanic conditions. It is not unusual therefore for different types of larval development to occur within one species group. Moreover, in some cases, like in *C. meridionalis* (see Mazancourt et al. 2018) or *C. gracilipes* (W. Klotz, unpublished), egg size varies within a single species, depending on the habitat, with generally larger eggs found in upstream localities and smaller eggs near the estuary, suggesting the possibility of facultative amphidromy.

12.2.2 Phylogeny

Mazancourt et al. (2019b) produced a molecular phylogeny of two species complexes from the Indo-Pacific islands: the *C. nilotica* and *C. weberi* complexes. This demonstrated the importance of an integrative taxonomic approach in understanding *Caridina* diversity. Nonintegrated approaches are likely to underestimate the number of species for a given locality, with many cryptic/pseudocryptic species confused under a single name, or more rarely, morphotypes of a single variable species described as separate species. As a result, geographical ranges and ecological data concerning poorly delineated species are often misleading, impeding the establishment of programs that provide sufficient protection and management. Mazancourt et al. (2019b) also found that habitat was often the most important factor leading to the separation of complexes. Species belonging to different complexes live in different habitat types. Identification to species level (or at least species complex level) and monitoring of *Caridina* diversity over time may therefore provide an early warning system that provides information about changes in their environment.

12.2.3 Habitat

Habitat is a critical factor influencing *Caridina* distribution and it can often be used as a species identification tool (Mazancourt et al. 2019b). *Caridina* inhabit different types of freshwater ecosystems, divided between lentic environments, such as lakes (No. 7 in Figs. 12.1 and, 12.2L) or swamps (No. 8 in Figs. 12.1 and 12.2K), and lotic (flowing) environments in surface as well as subterranean waters (No. 9 in Fig. 12.1). Amphidromous shrimps are mainly found in rivers or lentic environments connected to the sea.

Tropical mountainous islands typical of the Indo-Pacific are subject to important natural disturbances like droughts, floods, volcanic eruptions, or earthquakes. River flow can therefore be subject to great temporal variations (strong during floods or zero flow in temporary waterways) as well as spatial variation (changes in slope, substrate, or plant cover). River morphology, for example, is important in determining environmental condition variability. This variability is often unique to a specific watershed, forming isolated, discontinuous units by the sea and geological formations, such as ridgelines. River length depends on island morphology, ranging from short streams a few meters in length to large rivers of several kilometers. Examples of the great river length diversity in the Indo-Pacific include the Diahot River in New Caledonia and the Sigatoka River in Fiji.

Keith et al. (2010) proposed an altitudinal zonation scheme for lotic habitats, divided into five zones with flexible boundaries, depending on the island studied to better characterize variable environmental conditions experienced by shrimp. The five zones are the spring zone (No. 1 in Figs. 12.1 and 12.2I), the higher course (No.

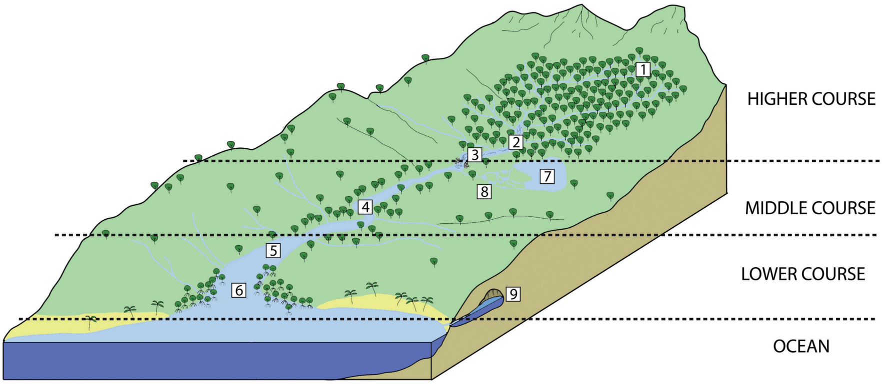


Figure 12.1 Schematic representation of different freshwater habitats. 1: spring zone; 2: higher course; 3: waterfall; 4: middle course; 5: lower course; 6: estuary; 7: lake; 8: swamp; 9: subterranean waters.

2 in Figs. 12.1 and 12.2A and B), the middle course (No. 4 in Fig. 12.1 and 12.2C and D), the low part of the stream (No. 5 in Figs. 12.1 and 12.2E and F), and the lower course (No. 6 in Figs. 12.1 and 12.2G and H). An additional sub-zonation exists, depending on current velocity, distinguishing calm zones (Figs. 12.2C and E), or pools (Fig. 12.2B) from riffles (Figs. 12.2A, D, and F). Usually the altitudinal zonation is further simplified into three functional levels (Fig. 12.1):

- The higher course, characterized by a steep slope (generally >10%), a fast current, and a boulder substrate.
- The middle course, characterized by an intermediate slope (<10%) and a substrate of pebbles and rocks or sand in slow flow areas. This level is typically separated from the higher course by a topographical feature, like a cascade (No. 3 in Figs. 12.1 and 12.2J).
- The lower course, characterized by a very low or zero slope, with a slow current and a pebble substrate with a progressive size decrease when approaching the estuary. The estuary is the lowest end of the river where environmental conditions are influenced by the tidal flux, as distinguished from the purely limnic area. This chemical boundary between seawater and freshwater is an essential habitat for some amphidromous species. The estuary size can vary, from very broad and long for large rivers (like the Jordan River in Santo, Vanuatu) to absent in some small streams flowing directly from the mountains to the sea.

Species living in rivers are subject to a range of biotic and abiotic conditions, depending on the river zone where they live. Differences in biotic and abiotic conditions often form gradients that apply over the entire length of rivers (Table 12.1):

- A current velocity gradient mainly linked to elevation. Water currents are typically fastest at high altitudes and slowest in the estuary, although local variations at a given altitude are also important, depending on the configuration of the river (calm zones vs. riffles).

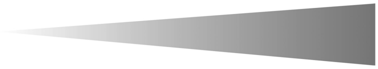
Figure 12.2 Examples of habitat types. (A) Higher course riffle, lotic mode (River Poitete, Kolombangara Island, Solomon Islands, credit PK). (B) Higher course pool, lentic mode (Ciu Waterfall, New Caledonia, credit VM). (C) Middle course, lentic mode (River Wénou, New Caledonia, credit VM). (D) Middle course riffle, lotic mode (River Nekouri, New Caledonia, credit VM). (E) Lower course, lentic mode (River Hienghène, New Caledonia, credit VM). (F) Lower course riffle, lotic mode (River Negropo, New Caledonia, credit VM). (G) Mangrove estuary (River Tanghène, New Caledonia, credit VM). (H) Estuary, low tide (Nera estuary, New Caledonia, credit VM). (I) Mountain stream (Unnamed tributary of the river Ciit, New Caledonia, credit VM). (J) Waterfall (Colnett waterfall, New Caledonia, credit VM). (K) Swamp (Plaine des Lacs, New Caledonia, credit VM). (L) Lake (Lac en Huit, New Caledonia, credit VM).

Figure 12.2 Continued.

- A temperature and oxygen gradient, with cool and oxygen-rich waters typical of the higher course and warm and low-oxygen waters typical of the lower course.
- A width and depth gradient, from small rivulets in the spring zone to large rivers near the mouth.
- A salinity gradient that is typically limited to the lower course. Salinity tends to decline rapidly outside of the areas influenced by tidal flux.
- A sediment-size gradient, from bedrock in the spring zone to boulders and rocks in the higher course, pebbles in the middle course, and sand and silt in the lower course.
- A particulate organic matter gradient, with clear, oligotrophic waters in the spring area to turbid, eutrophic waters in the estuary.
- A riparian vegetation gradient, with riverbanks consisting of naked rocks in the higher course switching to dense riparian vegetation in the lower course.
- A predation gradient, with the greatest density and diversity of predatory species (birds, fish) present in the lower course. Predators of shrimps in the higher course are mostly limited to eels (*Anguilla* spp.) or insects (dragonfly larvae, etc.).

Gradients in abiotic and biotic factors overlap in many combinations to create a considerable variety of microhabitats (Gehrke et al. 2011) to which *Caridina* species have adapted. We can observe a species vertical zonation, depending on the variation of these factors linked to elevation, as well as horizontal variables linked to the river configuration, according to lotic or lentic facies in the area or microhabitats (sunken

Table 12.1 **Variation of Environmental Gradients (Abiotic and Biotic) along the River Course**

Variable	Low altitude	High altitude
Current		
Temperature		
Oxygen		
Width and depth		
Salinity		
Sediment size		
Organic matter		
Vegetation		
Predation		

wood, roots, aquatic macrophytes, rocks, etc.). Indeed, different species assemblages are observed at different levels of the rivers and in different flowing facies. The lower course supports species of the *C. nilotica* species complex (Mazancourt et al. 2018), the *C. gracilirostris* species complex, or species allied to *C. serratirostris* and *C. brevicarpalis*. Higher in the river, two species groups are found: *C. weberi* complex in lotic areas and *C. nilotica* complex in lentic areas. Species of the *C. typus* group seem to have a broader range of habitats, present virtually the entire river length (de Mazancourt pers. obs.).

As observed for fish in tropical rivers by Pouilly et al. (2006) and Lorion et al. (2011) in continental systems and by Keith et al. (2015) in insular systems, *Caridina* demonstrates an altitudinal diversity gradient with maximum diversity in the lower course, decreasing with elevation. This diversity gradient is explained by the greater concentration of organic particulate matter in the lower reaches, allowing establishment of higher biomass (Angermeier and Karr 1983). Alternatively, diversification may be promoted by higher habitat heterogeneity (Gorman and Karr 1978) and stronger predator pressure in the lower course (Deacon et al. 2018). The lower course proximity to the ocean also presents the advantage of reducing the distance that dispersing larvae and returning juveniles have to travel. In contrast, resources are more limited but predator pressure is weaker at higher altitudes, which often leads to low biodiversity but high abundance (Leberer and Nelson 2001). Some species living in these environments have adopted a life cycle completed entirely in freshwater, with reduced larval stages or even direct development, avoiding migration hazards (Hancock 1998).

It is important to note that diversity patterns across zones can sometimes be more nuanced than the zonation framework may suggest. Diversity patterns can be dominated by a single parameter, such as the nature of the substrate. In New Caledonia, ultramafic rocks of the south of the island leach high concentrations of metals (nickel, chromium, cobalt) into the water of the rivers. These metals are toxic for most species, but some species have evolved to tolerate these high levels of dissolved metals (Marquet et al. 2003). These rivers thus exhibit a different fauna than rivers on sedimentary substrate, with different altitudinal zonations.

12.2.4 Biogeography

Caridina can be found in virtually all tropical Indo-Pacific and African rivers, ranging from West Africa (Richard and Clark 2009), Egypt (Hussein and Obuid-Allah 1990, Richard and Clark 2005, Mazancourt et al. 2018), and South Africa (Mirimin et al. 2015) to mainland Japan (Saito et al. 2012), Polynesia (Keith et al. 2013), and South Australia (Davie 2002), extending to the Middle East (Christodoulou et al. 2016) (Fig. 12.3).

Regional differences in *Caridina* diversity exist in the Indo-Pacific as expected for such a wide-ranging genus. Focusing on endemic *Caridina* species (Fig. 12.4A), the maximum diversity occurs around the Coral Triangle (Veron et al. 2009), between the Philippines, Indonesia, and Papua-New Guinea. The endemic species number tends to be substantially lower in rivers further away from this area, although large continental islands such as Madagascar or Sri Lanka, and archipelagos such as the Solomon Islands and Sulawesi, constitute local endemism hotspots (De Grave et al. 2008, 2015, Klotz and Rintelen 2013, Cumberlidge et al. 2017). Islands of relatively old geological origin like New Caledonia, Fiji, or Mauritius also appear to harbor a high diversity of endemic species. In contrast, younger and often isolated islands like those of Polynesia or Micronesia harbor fewer endemic species. Localities at the northern and southern limits of the distribution area (Japan and South Australia, for example) show low endemism.

Regional patterns in Indo-Pacific *Caridina* diversity are explained by island age, size, and latitude. Diversity tends to be high on large continental islands close to the equator and low on small young volcanic islands as well as in areas away from the equator (Paulay 1994, Willig et al. 2003). Geologically old islands have had more opportunity to be colonized and had time for colonizers to adapt and specialize. Chen and He (2009) showed that the number of island speciations, and thus their biodiversity, increases with time, whereas the colonization rate decreases. According

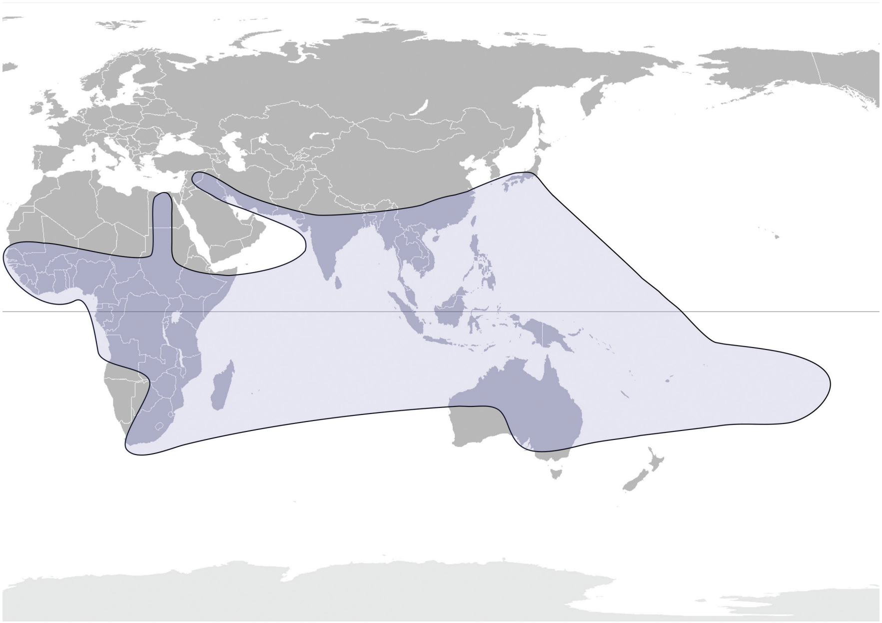


Figure 12.3 Distribution area of *Caridina*.

to the same study, the number of endemic species correlates to the size of the island, due to greater habitat diversity (geological or climatic differences, for example), which agrees with our observations for large islands such as Madagascar, Sri Lanka, and New Caledonia.

Patterns in endemic diversity (Fig. 12.4C) vary considerably from the patterns in amphidromous species diversity (Fig. 12.4A). The greatest amphidromous species diversity is in the Solomon Islands and Vanuatu. This may also include the Coral Triangle, as *Caridina* diversity from the area is poorly known. The high *Caridina* diversity in this region is explained by the complex geological history of the area, which lies at the convergence of three tectonic plates. The region contains islands of continental and volcanic origin, as well as historical connections to Papua in the north.

The lowest amphidromous species diversity is found in Polynesia and at the borders of the *Caridina* distribution area in general (Fig. 12.4C). Important areas of endemism, such as Madagascar, are not diversity hotspots for amphidromous species. Localities with low endemism, like the Polynesian or Micronesian islands, often have a higher proportion of amphidromous species.

Amphidromous species diversity patterns may be explained by the recent colonization of the islands by taxa with great dispersal abilities, allowing them to colonize without becoming reproductively isolated. Small islands often exhibit unstable conditions in which endemic landlocked populations could not maintain themselves. In contrast, amphidromous species can repopulate islands following disturbance as

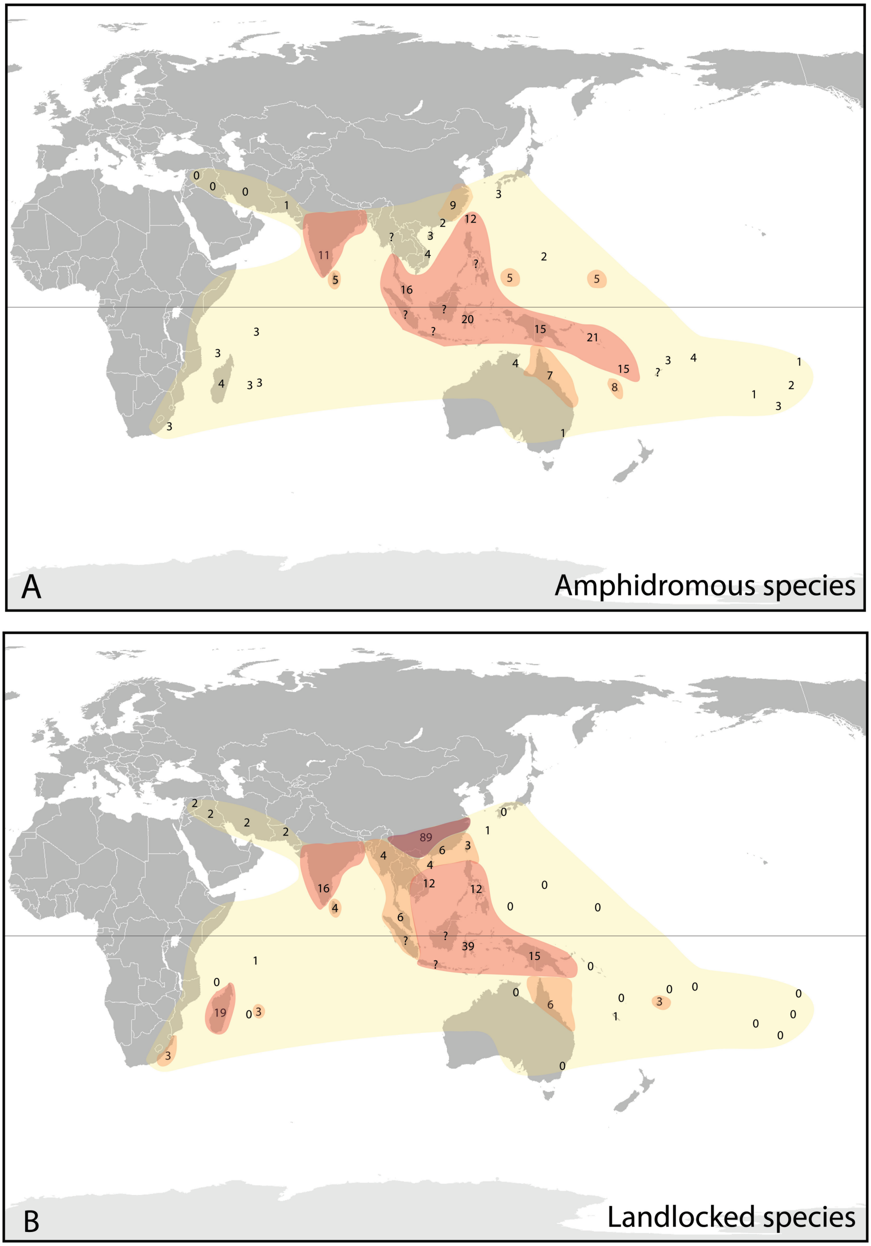


Figure 12.4 Heat maps representing the species richness by locality. (A) Numbers of amphidromous species (eggs < 0.8 mm). (B) Numbers of landlocked species (eggs > 0.8 mm).

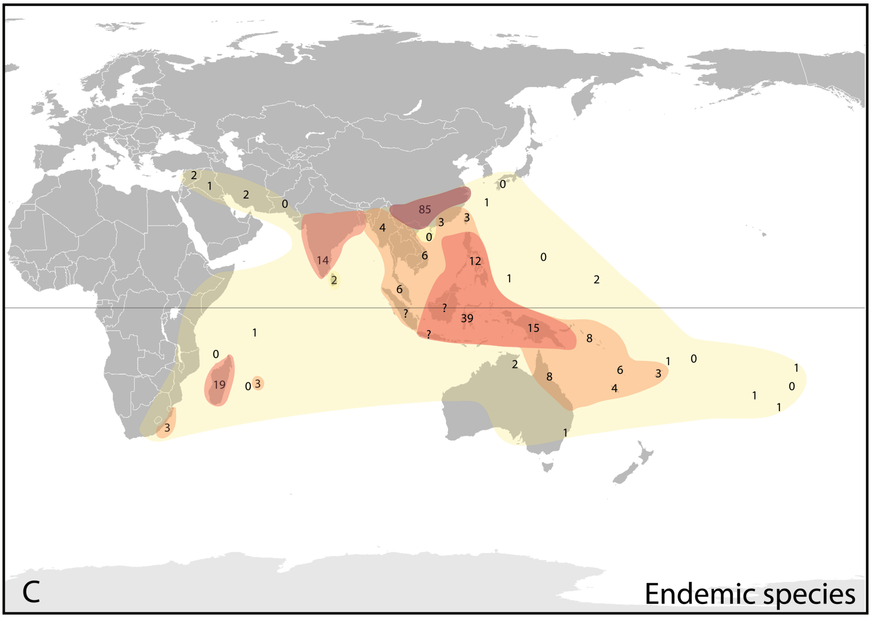


Figure 12.4 (C) Numbers of endemic species (known from a single locality/area).

they maintain a stock of larvae in the ocean, ready to recolonize depopulated habitats (McDowall 2007).

The landlocked or amphidromous lifestyle of a species is not always linked to it being endemic or widespread; amphidromous species are known from a single island. The diversity patterns of landlocked species are shown in Fig. 12.4B. The highest diversity of landlocked species globally is found in the Coral Triangle with a diminution by distance, until they disappear at the distribution area borders. However, the difference between landlocked and endemic or amphidromous species is that landlocked species are largely absent from volcanic islands such as Polynesia, Micronesia, Solomon Islands, or Vanuatu, where the majority of species are amphidromous. In contrast, landlocked species are often the majority of species in continents (India, China, Australia, South Africa) or large continental islands (Madagascar). This suggests that habitats of landlocked species have been available for sufficient time for new species to evolve a landlocked lifestyle from amphidromous ancestors, or for species to diverge from landlocked ancestors that were already present.

12.3 CONSERVATION

Taxonomic confusion has been a substantial obstacle for the establishment of programs aimed at *Caridina* conservation. Some ill-delineated species like *C. longirostris* or *C. weberi* were thought to be widespread. However, studies using an integrative taxonomic approach (Mazancourt et al. 2018) showed that these "species" are actually comprised of several species with restricted distributions (some being endemic). Furthermore, a better knowledge of systematics allows greater understanding of these species habitat and ecology, since each species is adapted to a different environment. These new data will impact the way in which the conservation status of these species will be assessed. Species with small distributions and specific habitat needs are more vulnerable to extinction than widespread and tolerant species (Purvis et al. 2000).

12.3.1 Threats to Amphidromous *Caridina*

The main threats faced by *Caridina* almost always originate from anthropogenic factors (Table 12.2).

Habitat degradation. Many anthropic activities induce habitat degradation. The direct impacts of habitat degradation occur through pollution of the rivers by pesticides (Kumar et al. 2010a,b), industrial accidents (Dominique 2014), illegal poisoning (Greathouse et al. 2005), use of the rivers as dumps (Keith et al. 2006), eutrophication by fertilizers, poisoning and causing the proliferation of algae clogging rivers, or increased sedimentation from mining or construction (dams, roads, etc.), and increasing water turbidity (Boseto et al. 2007, Keith et al. 2013). Habitat destruction also occurs through the water extraction for agriculture, industry, or tourism, causing physical changes (e.g., lower flow rates) and the disappearance of lotic zones (Keith et al. 2013) that are the exclusive habitat of some species (e.g., *Caridina weberi* species complex). The cause and effects of habitat destruction can also be associated with human activities that do not impact rivers directly but have flow effects that impact shrimp habitats and threaten the viability of populations (i.e., indirect effects). For example, the disappearance of perennial rivers and associated loss of habitat for shrimp due to deforestation in Rodrigues Island (Keith et al. 2006) in Madagascar for rosewood, in Anjouan (Mirhani et al. 2014) for firewood, and Ylang-ylang plantations in the Marquesas islands and Rapa for goats and livestock, or in New Caledonia due to bushfires. As some species of amphidromous shrimps live in mangroves (like those of the *C. gracilirostris* complex), they are threatened during both their larval and adult stages by the degradation of their habitat by aquaculture. Together, the impacts of aquatic and terrestrial habitat destruction affect the physiology, reproduction, and migration of caridean shrimps and remain one of the most important threats for carideans and other freshwater species (De Grave et al. 2015).

Reduced connectivity. The construction of instream barriers suppresses habitat connectivity (Dudgeon 2000, March et al. 2003). The construction of dams, such as the Yaté hydroelectric plant in New Caledonia, are instream barriers that result in the rapid disappearance of amphidromous species across the upstream watershed. Indeed, shrimps need to be able to migrate along the river course, depending on water level in order to not get trapped during the dry season. For amphidromous species, it is critical to have a continuum between the adult habitat and the sea in order to maintain populations.

Introduced species. The introduction of exotic species can lead to local extinctions of indigenous species due to predation, competition, habitat alteration, or

Table 12.2 **Potential Direct and Indirect Effects of Climate Change on Amphidromous and Endemic (Freshwater) Caridean Shrimp in the Indo-Pacific**

	Amphidromous species	Endemic species (limited to freshwater)	Status of knowledge	References
Direct effects				
Reduction in pH of water due to increased CO_2 dissolution from atmosphere (ocean acidification)	• Unknown	• Unknown (likely species-specific)	Crustaceans appear to be highly robust to increased CO_2 levels and/or decreased pH	Wittmann and Portner (2013)Kroeker et al. (2013)
Increased mean water temperature	• Effects likely to be species-specific • Small changes are likely to increase growth rates, reduce time to reproductive maturity, and decrease overall size • Large changes may exceed thermal tolerances, with consequences for the maintenance of populations • Changes in species distributions as species move to new habitat • Changes in phenology (timing of natural events, such as reproduction, migration, etc.)	• Effects likely to be species specific • Small changes are likely to increase growth rates, reduce time to reproductive maturity, and decrease overall size • Large changes are likely to exceed thermal tolerances, with the potential to reduce population size due to limited options for migration to new habitat • Changes in phenology (timing of natural events, such as reproduction, migration, etc.)	Little research on effects for estuarine or freshwater crustaceans. Effects on marine crustaceans are well studied	Kroeker et al. (2013)
Lower dissolved oxygen levels due to increased temperatures	• Unlikely to be important given strong turbulence promoting dissolution of oxygen in upper catchment, except following weather events that cause high levels of organic matter to be deposited in waterways.	• Unlikely to be important given strong turbulence promoting dissolution of oxygen in upper catchment, except following weather events that cause high levels of organic matter to be deposited in waterways.	Little research on effects for estuarine or freshwater crustaceans.	Ficke et al. (2007)

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Table 12.2 (Continued) **Potential Direct and Indirect Effects of Climate Change on Amphidromous and Endemic (Freshwater) Caridean Shrimp in the Indo-Pacific**

	Amphidromous species	Endemic species (limited to freshwater)	Status of knowledge	References
Hypoxic zones	• May be encountered in estuaries or in oceans during the larval stage • Adults and juveniles only likely to encounter hypoxic zones following weather events that cause high levels of organic matter to be deposited in waterways	• Unlikely to be encountered except following weather events that cause high levels of organic matter to be deposited in waterways	Research on the effects for crustaceans focused in marine systems	Vaquer-Sunyer and Duarte (2008)Breitburg et al. (2018)
Stronger rainfall events, increased likelihood of stronger and more frequent storms and cyclones	• Induce modifications in habitats (e.g., more depth, more flow) • Exacerbate existing problems (e.g., land clearing, turbidity) • Increased likelihood of pollution events (e.g., sewage overflow) • Changes in phenology (timing of natural events, such as reproduction, migration, etc.)	• Induce modifications in habitats (e.g., more depth, more flow) • Exacerbate existing problems (e.g., land clearing, turbidity) • Increased likelihood of pollution events (e.g., sewage overflow) • Changes in phenology (timing of natural events, such as reproduction, migration, etc.)	Substantial number of studies modeling changes in the probability of adverse weather events	Gehrke et al. (2011)Lough et al. (2011)
Changes in ocean currents	• Changes in dispersal of larvae • Interruptions to population connectivity • Potential to isolate populations	• No direct effect	Substantial number of studies on modeling changes in larval dispersal for marine invertebrates, no studies for *Caridina*	Keith et al. (2015)

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Table 12.2 (Continued) **Potential Direct and Indirect Effects of Climate Change on Amphidromous and Endemic (Freshwater) Caridean Shrimp in the Indo-Pacific**

	Amphidromous species	Endemic species (limited to freshwater)	Status of knowledge	References
Changes in multi-year weather patterns (e.g., El Niño)	• Likely to exacerbate the effects of adverse weather events (see above) • Limited rainfall causing reduction in available habitat	• Likely to exacerbate effects of adverse weather events (see above) • Limited rainfall causing reduction in available habitat	Climate change is closely linked with changes in multi-year weather patterns	Cai et al. (2018)
Rising sea levels	• Likely to increase the amount of estuarine habitat available • Influx of seawater into freshwater systems, reducing available habitat. Most severe for small islands • Increased barriers to migration due to engineered structures designed to prevent storm surges and combat sea level rise	• Reduction in potential habitat due to influx of seawater into freshwater habitat • Potential disappearance of freshwater habitat on islands inundated by sea level rise	Many studies modeling projected seawater inundation, but it is not clear the extent to which this will reduce the availability of freshwater habitats and/or increase the availability of estuarine habitats	Mcleod et al. (2010)
Effects of climate and nonclimate stressors combined	• Additive, synergistic, and antagonistic effects possible, dependent on the stressors combined	• Additive, synergistic, and antagonistic effects possible, dependent on the stressors combined	The effects of combined stressors in freshwater and estuarine systems remain understudied	Staudt et al. (2013)Jackson et al. (2016)
Indirect effects of climate change				
Movement of species	• New ecological interactions • Exposure to new pathogens and parasites	• New ecological interactions • Exposure to new pathogens and parasites	Movement of species into naive freshwater habitats has been documented. Little known about the ecological effects	Comte and Grenouillet (2013)Pecl et al. (2017)Mos et al. (2017)

(*Continued*)

Table 12.2 (Continued) **Potential Direct and Indirect Effects of Climate Change on Amphidromous and Endemic (Freshwater) Caridean Shrimp in the Indo-Pacific**

	Amphidromous species	Endemic species (limited to freshwater)	Status of knowledge	References
Changes in the abundance of ocean plankton (linked to changes in ocean currents and stronger rainfalls)	• Changes in food availability for larvae • Potential for changes in the timing of reproduction to match phytoplankton production • Changes in the success of larval migration to freshwater habitat due to reduced larval energy reserves • Potential for the larval stage to be a bottleneck, limiting recruitment to some populations	• No direct effects	No studies available for amphidromous species. Limited research for marine larvae	Hays et al. (2005)Beaugrand and Kirby (2018)
Changes in the diversity of ocean plankton (linked to changes in ocean currents and stronger rainfalls)	• Changes in the quality of food for larvae • Changes in the success of larval migration to freshwater habitat due to reduced larval energy reserves • Potential for the larval stage to be a bottleneck, limiting recruitment to some populations	• No direct effects	No studies available	Rosenblatt and Schmitz (2016)
Changes in carbon (C) uptake by algae and plants	• Alter C to N ratios in food • Potential changes in diet to seek out N-rich foods	• Alter C to N ratios in food • Potential changes in diet to seek out N-rich foods	The importance of C to N ratios is well documented across a variety of taxa	Rastetter et al. (1992)Sterner and Elser (2002)

disease transmission (Keith 2002a, b, De Grave et al. 2015). Another important but little studied threat associated with introduced species is the potential for hybridization with nonnative caridean species. The ease with which caridean shrimp hybridize is well noted in the hobby aquarium literature. There have been no reports of hybridization of introduced and native carideans in the wild, but the extinction of local populations due to hybridization following translocation within a catchment has occurred in other atyid genera (Hughes et al. 2003, Fawcett et al. 2010).

Overharvesting. Shrimps are harvested for human consumption. In the Philippines, Madagascar, Indonesia, India, and China, caridean shrimp are caught in large quantities using nets to be eaten fresh, dried, or salted, and to feed animals or used as fertilizer (Holthuis 1980), or in Reunion Island where they are called "chevaquines" (GM, pers. comm.). Another threat for *Caridina* spp. is their harvest for the aquarium trade, particularly for the colorful species living in Sulawesi (De Grave et al. 2015) or "Bee shrimps" from mainland China, some species being known only from a single stream of about 150 m in length (WK pers. comm.). While most species impacted are lacustrine landlocked, in the future growing global demand could see the expansion of the collection of amphidromous species. Currently, only a few amphidromous species appear in the trade, but whether these are collected legally, poached, or bred in captivity is difficult to determine due to long and complex supply chains. It is unclear how many shrimps are traded globally, but there is substantial anecdotal evidence suggesting local populations experience severe declines due to overcollection, particularly where a local color or pattern variant becomes highly sought-after in the trade. For example, Klotz and Lukhaup (2014) reported the disappearance of *Caridina trifascata* Yan and Cai, 2003, from locales near Zuhai, China, over a period of less than 12 months, likely associated with overharvesting for the aquarium trade.

Climate change. Climate change is likely already impacting and will continue to impact caridean shrimp through a variety of direct and indirect mechanisms (Table 12.1). Unfortunately, while crustaceans generally appear to be robust to some changes in their environment associated with climate change (e.g., ocean acidification), little research has been done to address the gaps in our knowledge about indirect effects of climate stressors, and the effects of interactions of climate stressors (e.g., temperature) with nonclimate stressors (e.g., pesticide pollution). This is concerning given studies that have examined the indirect and interactive effects of climate stressors on marine taxa have highlighted how these effects may be more important than the direct effects of climate stressors (e.g., Kroeker et al. 2012, Boyd and Brown 2015, Rosenblatt and Schmitz 2016, Kamya et al. 2017).

12.3.2 Conclusions and Recommendations

Integrative study of *Caridina* led to the discovery of unsuspected diversity in Indo-Pacific Islands, with recognized species complexes that present differences in habitat use. Therefore, when making river freshwater fauna inventories, if it is not possible to identify specimens to species level, the species complex can be sufficient to provide useful data. Keys and diagnoses of the different species complexes are detailed in another publication (Mazancourt *et al.* 2020). Now that species are better delineated through integrative taxonomy, their distribution (including micro- and macrohabitats) can be more informative and their specific conservation status (threats, IUCN status, etc.) needs to be reassessed.

Our recommendations to protect these amphidromous *Caridina* species revolve around three main points:

1. Taking Biological and Ecological Specificities into Consideration

Arguably, the best way to enable conservation is by changing people's mindset directly through education and example. Managing caridean species requires resource managers to have a minimum knowledge of their biology (i.e., amphidromous life cycle) and to take these specificities into consideration when making decisions. Understanding amphidromous species life cycles highlights the importance of maintaining the natural flow of waterways. Maintaining population connectivity through natural water flows supports a range of life stages. This limits local or regional extinction potential as breeding populations depend on the larval pool for recruitment (and conversely, the larval pool depends on the breeding populations). Successful implementation of conservation measures designed to maintain and enhance natural water flows may be best achieved through the inclusion of all project stakeholders (e.g., farmers, fishers, water management authorities, local government, community conservation groups, international conservation organizations, etc.).

2. Limiting Anthropic Impacts on Amphidromous Species

The most efficient way to protect amphidromous species is to limit anthropic impacts. This requires an integrated management approach, which accounts for both terrestrial and aquatic impacts. For example, water catchments should always have a minimum flow in line with their natural seasonal variations to support the upstream juvenile migration, which is often triggered by greater freshwater pulses to the sea during floods. Therefore, management decisions effects, such as not altering water flow, designing roads and dams that maintain connectivity between sea and mountains, maintaining healthy riparian corridors, and preserving estuaries need to be considered in an integrated manner.

3. Establishing priorities for species conservation

The priority must be to protect *Caridina* habitats, as conservation status is not known for many species. Identification of those habitats most in need of special protection, with management and implementation of the recommendations from the previous points would be the best starting point. Caridean shrimps seem to be good indicators of water and habitat quality. They may be a very useful tool for resource managers as indicators of impacts in tropical aquatic systems. Preventing exotic species introductions is another important recommendation. Finally, supporting research on the biology and ecology of these species would help to improve our knowledge and assess the threats they face.

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