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

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1 **CHAPTER 11: New insights on biodiversity and conservation of amphidromous shrimps of**
2 **the Indo-Pacific islands (Decapoda: Atyidae: *Caridina*).**

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8

9 **Abstract**

10 Amphidromous shrimps of the genus *Caridina* (Crustacea: Decapoda: Atyidae) are essential
11 components of the tropical insular freshwater ecosystems. Due to an extremely confused taxonomy,
12 their biodiversity is poorly known, and their conservation status cannot be properly assessed.
13 However, thanks to recent advances of integrative taxonomy, the systematics of this genus
14 progressively becomes clearer, allowing us to draw conclusions about their biogeography and
15 conservation biology. In this chapter, we 1) review the current state of knowledge of amphidromous
16 *Caridina* diversity in the light of the latest results of integrative taxonomy on this model, 2) review
17 the threats faced by *Caridina* in Indo-Pacific Islands, and 3) discuss how integrative taxonomy
18 approaches can inform and support programs designed to limit the impacts of threatening processes
19 on the diversity of *Caridina*. Finally, we provide recommendations for the conservation of these
20 species and their habitats.

21

22 **11.1 Introduction**

23 Atyid shrimps (Crustacea: Decapoda) are essential components of tropical freshwater ecosystems,
24 playing a role of cleaner by shredding fallen leaves or filtering organic particular matter and being
25 preys to a number of organisms (Covich *et al.*, 1999 ; Crowl *et al.*, 2001). Among them, genus
26 *Caridina* H. Milne Edwards, 1837 is particularly diversified, comprising more than 300 described
27 species making it the most diversified of the infra-order Caridea (De Grave *et al.*, 2015). In Indo-
28 Pacific Islands, the majority of the species of *Caridina* have an original diadromous lifestyle, with a
29 planktonic marine larval phase and a benthic freshwater adult phase; amphidromy (McDowall, 2007
30 ; Bauer, 2013). This strategy allows the species to colonize isolated habitats, such as the rivers of
31 volcanic islands, and to survive to the instability of these environments (floods, droughts,
32 volcanism, etc.) by keeping a stock of larvae in the ocean, ready to recolonize depopulated rivers

33 (Keith *et al.*, 2010). Amphidromy, by isolating populations, has also contributed to establishing the
34 high diversity that exists among caridean shrimps. This diversity, however, is the source of an
35 extreme taxonomic confusion that impedes the monitoring of the species and the establishment of
36 appropriate conservation programs (Klotz & Rintelen, 2014). Recently, with the development of
37 new molecular biology techniques, integrative taxonomy is being increasingly used by
38 systematists attempting to achieve more precise species delineations by combining
39 morphological data with genetic, ecological and/or biogeographical information (Mazancourt *et al.*,
40 2017). In this chapter, we 1) review the current state of knowledge of amphidromous *Caridina*
41 diversity in the light of the latest results of integrative taxonomy on this model, 2) review the threats
42 faced by *Caridina* in Indo-Pacific Islands, and 3) discuss how integrative taxonomy approaches can
43 inform and support programs designed to limit the impacts of threatening processes on the diversity
44 of *Caridina*.

45

46 **11.2 Biodiversity**

47 *11.2.1 Taxonomy*

48 There is substantial confusion surrounding the taxonomy of many species of *Caridina* that has
49 resulted in the creation of several species complexes (N.B.: We consider a species complex a
50 monophyletic species group that share a common taxonomic history in having been synonymized at
51 one point, and/or that can be identified by morphological characters). In Indo-Pacific islands,
52 amphidromous shrimps have been grouped into seven main complexes, (1) *Caridina nilotica* (P.
53 Roux, 1833) complex (Johnson, 1963 ; Holthuis, 1978 ; Jalihal *et al.*, 1984 ; Choy, 1991 ; Richard
54 & Clark, 2005 ; Karge & Klotz, 2007), (2) *C. weberi* De Man, 1892 complex (Richard & Chandran,
55 1994 ; Cai & Shokita, 2006a), (3) *C. gracilirostris* De Man, 1892 complex (Cai & Ng, 2001,
56 2007), (4) *C. typus* H. Milne Edwards, 1837 complex (Karge & Klotz, 2007 ; Bernardes *et al.*,
57 2017), (5) *C. serratirostris* De Man, 1892 complex (Cai & Shokita, 2006b), (6) *C. brevicarpalis* De
58 Man, 1892 complex (Short, 2009) and (7) *C. propinqua* De Man, 1908 complex (WK,
59 unpublished). Little work has been done to differentiate among the species clustered within these
60 complexes, possibly due to the difficulty and costs associated with genetic analyses and the highly
61 similar morphology of shrimps from different populations.

62 To recognize amphidromous species, the egg size is often a good indicator. Small eggs indicate that
63 the species has an indirect development with several planktonic stages that are often marine.
64 Conversely, species with large eggs are most likely landlocked, with a direct development limiting

65 their dispersal abilities, meaning that they are often endemic. However, some species can have
66 small eggs and still be endemic. This can be due to particular conditions that limit the dispersal of
67 marine larvae. For example, oceanic currents or physical barriers (e.g. closed coral lagoons) may
68 prevent dispersal to nearby islands even if larvae are capable of surviving in oceanic conditions. It
69 is not unusual therefore for different types of larval development to occur within one species group.
70 Moreover, in some cases, like in *C. meridionalis* (see Mazancourt *et al.*, 2018) or *C. gracilipes*
71 (WK, unpublished), egg size varies within a single species, depending on the habitat, with generally
72 larger eggs found in upstream localities and smaller eggs near the estuary, suggesting the possibility
73 of facultative amphidromy.

74

75 *11.2.2 Phylogeny*

76 A recent work (Mazancourt *et al.*, 2019), object of a presentation at the 9th International Crustacean
77 Congress in Washington DC (May 2018), focused on producing a molecular phylogeny of two
78 species complexes from the Indo-Pacific islands, *C. nilotica* and *C. weberi* complexes. This work
79 demonstrated the importance of an integrative taxonomy approach in understanding the diversity of
80 *Caridina*. Non-integrated approaches are likely to underestimate the as the number of species for a
81 locality, with many cryptic/pseudocryptic species confused under a single name, or more rarely,
82 morphotypes of a single variable species described as separate species. As a result, geographical
83 ranges and ecological data concerning poorly delineated species are often misleading, which
84 impedes the establishment of programs that provide sufficient protection and management. The
85 work also found that habitat was often the most important factor leading to the separation of
86 complexes. Species belonging to different complexes live in different habitat types. Identification to
87 species level (or at least species complex level) and monitoring of *Caridina* diversity over time may
88 therefore provide an early warning system that provides information about changes in their
89 environment.

90

91 *11.2.3 Habitat*

92

93 (Figure 1 here)

94

95 Habitat is a critical factor influencing the distribution of *Caridina* species and it can often be used
96 as an identification tool to separate species (Mazancourt *et al.*, 2019). *Caridina* shrimps inhabit
97 different kinds of freshwater ecosystems, divided between lentic environments, such as lakes (n°7
98 in Fig. 1; Fig. 2L) or swamps (n°8 in Fig. 1; Fig. 2K), and lotic (river) environments for surface
99 waters, as well as for subterranean waters (n°9 in Fig. 1). Amphidromous shrimps, due to their
100 ability to migrate between freshwater and seawater are mainly found in rivers or lentic
101 environments connected to the sea.

102 On the tropical mountainous islands that are typical in the Indo-Pacific, rivers are subject to
103 important natural disturbances like droughts, floods, volcanic eruptions, or earthquakes. The flow of
104 rivers can therefore be subject to great temporal variations (strong during floods or zero for
105 temporary waterways) as well as spatial variations (depending on the slope, substrate type, or plant
106 cover). The morphology of rivers, for example, plays an important role in determining the
107 variability of environmental conditions that are often unique to the specific watershed that form
108 discontinuous units isolated from each other by the sea and geological formations, such as
109 ridgelines. The length of rivers depends on island morphology, ranging from short streams a few
110 metres in length to large rivers of several kilometres. Examples of the great diversity of river
111 lengths in the Indo-Pacific include the Diahot in New Caledonia and the Sigatoka in Fiji.

112 To better characterize the variable environmental conditions experienced by shrimp in different
113 rivers, Keith *et al.*, (2010) proposed an altitudinal zonation divided into five zones with flexible
114 boundaries depending on the island studied. The five zones are the spring zone (n°1 in Fig. 1; Fig.
115 2I), the higher course (n°2 in Fig. 1; Fig. 2A and B), the middle course (n° 4 in Fig. 1; Fig. 2C and
116 D), the low part of the stream (n°5 in Fig. 1; Fig. 2E and F), and the lower course (n°6 in Fig. 1;
117 Fig. 2G and H). An additional sub-zonation exists depending on the current velocity, distinguishing
118 calm zones (Fig. 2C and E) or pools (Fig. 2B) from riffles (Fig. 2A, D and F). Usually, the
119 altitudinal zonation is further simplified into three functional levels (Fig. 1):

120 - The higher course, characterized by a steep slope (generally >10%), a fast current and a boulder
121 substrate.

122 - The middle course, characterized by an intermediate slope (<10%) and a substrate of pebbles and
123 rocks or sand in calm areas. This level is typically separated from the higher course by a
124 topographical feature, like a cascade (n°3 in Fig. 1; Fig. 2J).

125 - The lower course, characterized by a very low or zero slope, with a slow current and a substrate of
126 pebbles whose size decreases when approaching the estuary. The estuary is the lowest end of the

127 river where environmental conditions are influenced by the tidal flux of seawater, as distinguished
128 from the purely limnic area. This chemical boundary, between seawater and freshwater, is essential
129 in terms of habitat, for some amphidromous species. The size of the estuary can vary, from very
130 broad and long for large rivers (like the Jordan in Santo, Vanuatu) to absent in some small streams
131 flowing directly from the mountains to the sea.

132 Species living in rivers are subject to a range of biotic and abiotic conditions depending on the zone
133 of the river where they live. Differences in biotic and abiotic conditions often form gradients that
134 apply over the entire length of rivers (Tab. 1):

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

138 - A temperature and oxygen gradient, with cool and oxygen-rich waters typical of the higher course
139 and warm and low-oxygen waters typical of the lower course.

140 - A width and depth gradient, from small rivulets in the spring zone to large rivers near the mouth.

141 - A salinity gradient that is typically limited to the lower course. Salinity tends to decline rapidly
142 outside of the areas influenced by tidal flux.

143 - A sediment size gradient, from bedrock in the spring zone, to boulders and rocks in the higher
144 course, pebbles in the middle course, and sand and silt in the lower course.

145 - A particulate organic matter gradient, with clear, oligotrophic waters in the spring area to turbid,
146 eutrophic waters in the estuary.

147 - A riparian vegetation gradient, with riverbanks consisting of naked rock in the higher course
148 switching to dense riparian vegetation in the lower course.

149 - A predation gradient, with the greatest density and diversity of predatory species (birds, fish)
150 present in the lower course. Predators of shrimp in the higher course are mostly limited to eels
151 (*Anguilla spp.*) or insects (dragonfly larvae, etc.)

152

153 (Table 1 here)

154

155 Gradients in abiotic and biotic factors along rivers overlap in many combinations to create a
156 considerable variety of micro-habitats (Gehrke *et al.*, 2011) to which species of *Caridina* have
157 adapted. We can observe a vertical zonation of species depending on the variation of these factors
158 linked to the elevation, as well as horizontal variables linked to the river configuration, according to
159 the lotic or lentic facies in the area, or micro-habitats (sunken wood, roots, aquatic macrophytes,
160 rocks, etc.). Indeed, different species assemblages are observed at the different levels of the rivers
161 and in the different flowing facies. In the lower course will be encountered species of the *C. nilotica*
162 species complex (Mazancourt *et al.*, 2018), the *C. gracilirostris* species complex or species allied to
163 *C. serratirostris* and *C. brevicarpalis*. Higher in the river, two species groups are found, *C. weberi*
164 complex in lotic areas and *C. nilotica* complex in lentic areas. Species of the *C. typus* group seem to
165 have a broader range of habitats, present virtually in the whole length of the rivers (pers. obs.).

166 As observed for fish in tropical rivers by Pouilly *et al.* (2006) and Lorion *et al.* (2011) in continental
167 systems and by Keith *et al.* (2015) in insular systems, there seems to be an altitudinal diversity
168 gradient in *Caridina*, with a maximum diversity in the lower course, decreasing with elevation. This
169 diversity gradient may be explained by the greater concentration of organic particulate matter in the
170 lower reaches, allowing the establishment of a higher biomass (Angermeier & Karr, 1983).

171 Alternatively, diversification may be promoted by higher heterogeneity in habitats (Gorman &
172 Karr, 1978) and stronger predator pressure in the lower course (Deacon *et al.*, 2018). The proximity
173 to the ocean of the lower course also presents the advantage of reducing the distance that larvae of
174 amphidromous species have to travel to the sea as larvae and to the upper course as juveniles. In
175 higher altitudes, in contrast, resources are more limited but predator pressure is weaker, which often
176 leads to low biodiversity but high abundance (Leberer & Nelson, 2001). Some species living in
177 these environments have adopted a life cycle completed entirely in freshwater, with reduced larval
178 stages or even direct development, avoiding the hazards of migration (Hancock, 1998).

179 It is important to note patterns in diversity across zones can sometimes be more nuanced than the
180 zonation framework proposed by Keith *et al.* (2010) may suggest. In some cases, patterns in
181 diversity can be dominated by a single parameter, such as the nature of the bedrock. In New
182 Caledonia, ultramafic rocks of the South of the island leach high concentrations of metals (nickel,
183 chromium, cobalt) into the water of the rivers. These metals are toxic for most species, but some
184 species that have evolved to tolerate high levels of dissolved metals live there (Marquet *et al.*,
185 2003). These rivers flowing over ultramafic substrate thus exhibit a different fauna than rivers on
186 sedimentary substrate, with different altitudinal zonations.

187

188 (Figure 2 here)

189

190 *11.2.4 Biogeography*

191 The genus *Caridina* can be found in virtually all the rivers of the tropical Indo-Pacific and Africa,
192 ranging from West Africa (Richard & Clark, 2009), Egypt (Hussein & Obuid-Allah, 1990; Richard
193 & Clark, 2005; Mazancourt *et al.*, in press) and South Africa (Mirimin *et al.*, 2015) to mainland
194 Japan (Saito *et al.*, 2012), Polynesia (Keith *et al.*, 2013) and South Australia (Davie, 2002),
195 stretching to Middle East localities (Christodoulou *et al.*, 2016) (Fig. 3).

196

197 (Figure 3 here)

198

199 As expected for such a wide-ranging genus, regional differences in diversity of *Caridina* exist in the
200 Indo-Pacific. When focusing on endemic species of *Caridina* (Fig. 4A), the maximum diversity
201 occurs around the Coral Triangle (Veron *et al.*, 2009), between the Philippines, Indonesia, and
202 Papua-New Guinea. The number of endemic species tends to be substantially lower in rivers further
203 away from this area, although large continental islands such as Madagascar or Sri Lanka, and
204 archipelagos such as the Solomon Islands, constitute local hotspots of endemism. Some of these
205 hotspots have been exposed by previous studies on freshwater shrimps, including Madagascar (De
206 Grave *et al.*, 2008; De Grave *et al.*, 2015; Cumberlidge *et al.*, 2017) and Sulawesi (De Grave *et al.*,
207 2008; Klotz & Rintelen, 2013; De Grave *et al.*, 2015). Islands of relatively old geological origin
208 like New Caledonia, Fiji, or Mauritius also appear to harbor a high diversity of endemic species. In
209 contrast, younger and often isolated islands like those of Polynesia or Micronesia harbor fewer
210 endemic species. Localities at the northern and southern limits of the distribution area (Japan and
211 South Australia for example) show low endemism.

212

213 (Figure 4 here)

214

215 It appears regional patterns in the diversity in *Caridina* of the Indo-Pacific are explained by the age,
216 size, and latitude of islands. Diversity will likely be high in a large continental island close to the

217 equator and low in a small young volcanic island or in an area away from the equator (Paulay, 1994
218 ; Willig *et al.*, 2003). Geologically old islands have had more opportunity to be colonized by
219 shrimps, and had time for colonizers to adapt and specialize to the different habitats and form new
220 species. Chen & He (2009) showed that the number of speciations in islands, and thus their
221 biodiversity, increases with time, whereas the number of colonizations decreases. According to the
222 same study, the number of endemic species correlates to the size of the island, due to the greater
223 diversity of habitats (geological or climatic differences, for example), which agrees with our
224 observations for large islands such as Madagascar, Sri Lanka, or New Caledonia.

225 The patterns in the diversity of endemic species (Fig. 4C) vary considerably from the patterns in the
226 diversity of amphidromous species (Fig. 4A). The greatest diversity of amphidromous species is
227 found in the Solomon Islands and Vanuatu. This may also include the Coral Triangle, as the
228 diversity of *Caridina* from the area remains poorly known. The high diversity of *Caridina* in this
229 region may be explained by the complex geological history of the area, which lies at the
230 convergence of three tectonic plates. The region contains islands of both continental and volcanic
231 origin, as well as historical connections to Papua in the North.

232 The lowest diversity of amphidromous species is found in Polynesia and at the borders of the
233 distribution area in general (Fig. 4C). Important areas of endemism, such as Madagascar, are not
234 hotspots of diversity for amphidromous species. Localities with low endemism, like the Polynesian
235 or Micronesian islands, often have a higher proportion of amphidromous species.

236 Patterns in the diversity of amphidromous species may be explained by the recent colonization of
237 the islands by amphidromous shrimps with great dispersal abilities, allowing them to colonize these
238 isolated habitats without becoming reproductively isolated. Small islands often exhibit unstable
239 conditions in which endemic landlocked populations could not maintain themselves. In contrast,
240 amphidromous species can repopulate islands following disturbance as they maintain a stock of
241 larvae in the ocean, ready to recolonize depopulated habitats (McDowall, 2007).

242 The landlocked or amphidromous lifestyle of a species is not always linked to it being endemic or
243 widespread, with examples of amphidromous species that are known from a single island for
244 instance. The patterns of diversity of landlocked species are shown in Fig. 4B. Globally, the highest
245 diversity of landlocked species is found in the Coral Triangle with a diminution when one moves
246 away from it, until they completely disappear at the borders of the distribution area of the genus.
247 However, the differences between landlocked and endemic or amphidromous species is that
248 landlocked species are mainly absent from volcanic islands such as Polynesia, Micronesia, Solomon

249 Islands, or Vanuatu, where the majority of species are amphidromous. In contrast landlocked
250 species often constitute the majority of the species in continents (India, China, Australia, South
251 Africa) or large continental islands (Madagascar). This supposes that habitats for landlocked species
252 need to have been available for sufficient time for new species to evolve a landlocked lifestyle from
253 amphidromous ancestors, or for species to diverge from landlocked ancestors that were already
254 present.

255

256 **11.3 Conservation**

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

266

267 *11.3.1 Threats to amphidromous Caridina*

268 The main threats faced by *Caridina* almost always originate from anthropization of their
269 environment.

270 *Habitat degradation.* Many anthropic activities induce habitat degradation. The direct impacts of
271 habitat degradation occur through impact through pollution of the rivers by pesticides (Kumar *et al.*,
272 2010a ; Kumar *et al.*, 2010b), industrial accidents (Dominique, 2014), illegal poisoning (Greathouse
273 *et al.*, 2005), use of the rivers as dumps (Keith *et al.*, 2006), eutrophication by fertilizers, poisoning
274 and causing the proliferation of algae clogging the rivers, or increased sedimentation from mining,
275 gravel extraction, or constructions (dams, roads, etc.) smothering the stream bed, and increasing
276 water turbidity (Boseto *et al.*, 2007; Keith *et al.*, 2013). Habitat destruction also occurs through the
277 removal of water from river systems for agriculture, industry or tourism, causing physical changes
278 (e.g. lower flow rates) and the disappearance of lotic zones (Keith *et al.*, 2013) that are the
279 exclusive habitat of some species (e.g. *Caridina weberi* species complex). The cause and effects of

280 habitat destruction can also be associated with human activities that do not impact rivers directly
281 but have flow-on effects that impact shrimp habitats and threaten the viability of populations (i.e.
282 indirect effects). For example, the disappearance of perennial rivers and associated loss of habitat
283 for shrimp due to deforestation, like in Rodrigues Island (Keith *et al.*, 2006), in Madagascar for
284 rosewood, in Anjouan (Mirhani *et al.*, 2014) for firewood and Ylang-ylang plantations, in the
285 Marquesas islands and Rapa for goats and livestock, or in New Caledonia due to bushfires. As some
286 species of amphidromous shrimps live in mangroves (like those of the *C. gracilirostris* complex),
287 they are threatened during both their larval and adult stages by the degradation of their habitat by
288 aquaculture activities. Together, the impacts of aquatic and terrestrial habitat destruction are well
289 documented to affect the physiology, reproduction and migration of caridean shrimp and remain
290 one of the most important threatening processes for carideans and other freshwater species (De
291 Grave *et al.* 2015).

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

299 *Introduced species.* The introduction of exotic species can lead to local extinctions of indigenous
300 species due to predation, competition, habitat alteration, or disease transmission (Keith, 2002a,
301 2002b; De Grave *et al.*, 2015). For caridean shrimp, another important but little studied threat
302 associated with introduced species, is the potential for hybridization with non-native caridean
303 species. The ease with which caridean shrimp hybridize is well noted in the aquarium literature.
304 There have been no reports of hybridization of introduced and native carideans in the wild, but the
305 extinction of local populations due to hybridization following a translocation within a catchment
306 has already occurred in other genera within the family Atyidae (Hughes *et al.*, 2003; Fawcett *et al.*,
307 2010).

308 *Overharvesting.* Shrimps are harvested for human consumption. In the Philippines, Madagascar,
309 Indonesia, India, and China, caridean shrimp are caught using nets in large quantities to be eaten
310 fresh, dried, or salted, and to feed animals or used as fertilizer (Holthuis, 1980), or in Reunion
311 Island where they are called “chevaquines” (GM, pers. comm.). A unique threat for *Caridina* spp. is
312 the capture of individuals for the aquarium trade, particularly for the colorful species living in

313 Sulawesi (De Grave *et al.*, 2015) or “Bee shrimps” from mainland China, some species being
314 known only from a single stream of about 150m in length (WK pers. comm.). While most of the
315 species impacted are lacustrine landlocked, in the future growing global demand could see the
316 expansion of the collection of amphidromous species. Currently, only a few amphidromous species
317 appear in the trade, but whether these are collected legally, poached, or bred in captivity is difficult
318 to determine due to long and complex supply chains. It is unclear how many shrimp are traded
319 globally, but there is substantial anecdotal evidence suggesting local populations experience severe
320 declines due over-collection, particularly where a local colour or pattern variant becomes highly
321 sort after in the trade. For example, Klotz & Lukhaup (2014) reported the disappearance of
322 *Caridina trifascata* from locales near Zuhai, China over a period of less than 12 months, likely
323 associated with over-harvesting for the aquarium trade.

324 *Climate change.* Climate change is likely already impacting and will continue to impact caridean
325 shrimp through a variety of direct and indirect mechanisms (Table 1). Unfortunately, whilst
326 crustaceans generally appear to be robust to some changes in their environment associated with
327 climate change (e.g. ocean acidification), little research has been done to address the gaps in our
328 knowledge about indirect effects of climate stressors, and the effects of interactions of climate
329 stressors (e.g. temperature) with non-climate stressors (e.g. pesticide pollution). This is concerning
330 given studies that have examined the indirect and interactive effects of climate stressors on marine
331 taxa have highlighted how these effects may be more important than the direct effects of climate
332 stressors (e.g. Kanya *et al.*, 2017; Rosenblatt & Schmitz, 2016; Kroeker *et al.*, 2012; Boyd &
333 Brown, 2015).

334

335 (Table 2 here)

336

337 *11.3.2 Conclusions and recommendations*

338 The integrative study of *Caridina* led to the discovery of unsuspected diversity in Indo-Pacific
339 Islands, with species complexes that are now recognized and present differences in habitat.
340 Therefore, when making inventories of the freshwater fauna of rivers, if it is not possible to identify
341 specimens to species level, the species complex can be sufficient to provide interesting data. Keys
342 and diagnoses of the different species complexes will be presented in an upcoming study
343 (Mazancourt *et al.* submitted). Now that species are better delineated thanks to integrative

344 taxonomy, their distribution (including micro and macro-habitats) can be more informative and
345 their specific conservation status (threats, IUCN status, etc.) needs to be re-assessed.

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

348 1) Taking biological and ecological specificities into consideration

349 Arguably the best way to enable conservation is by changing the mind-set of people directly
350 implicated through education and example. For example, managing caridean species requires
351 managers to have a minimum knowledge of their biology (i.e. amphidromous lifecycle) and to
352 take their specificities into consideration when making decisions. Understanding of the
353 lifecycles of amphidromous species highlights the importance of maintaining the natural flow of
354 water ways in a good state. Maintaining population connectivity through natural water flows
355 allows populations to be comprised of a range of life stages. This limits the potential for local or
356 regional extinctions as breeding populations depend on the pool of larvae to replace them (and
357 conversely, the pool of larvae depends on the breeding populations). Successful implementation
358 of conservation measures designed to maintain and enhance natural water flows may be best
359 achieved through the inclusion of a range of stakeholders in projects (e.g. farmers, fishers, water
360 management authorities, local government, community conservation groups, international
361 conservation organisations, etc.).

362

363 2) Limiting anthropic impacts on amphidromous species

364 The most efficient way to protect amphidromous species is to protect their environment by
365 limiting anthropic impacts. This requires an integrated management approach that takes into
366 account the role of both terrestrial and aquatic impacts. For example, water catchments should
367 always have a minimum flow in line with their natural seasonal variations, considering the
368 upstream migration of the juveniles is often triggered by greater freshwater arrival in the sea
369 during floods. Therefore the effects of a variety of management decisions, such as avoiding
370 man-made structures altering water flow, design of roads and dams that maintain the
371 connectivity from the sea to the mountains, maintaining riparian vegetation in a good state, and
372 preserving estuarine habitats, need to be considered in an integrated manner.

373

374 2) Establishing priorities for species conservation

375 As conservation status is not known for many species, the priority is to protect their habitats. It
376 would thus be useful to identify those habitats that need special protection and make sure to
377 apply to them the recommendations of the previous point. Caridean shrimps seem to be good
378 indicators of water and habitat quality. They could thus be a very useful tool for managers as
379 indicators of anthropic effects and the impact of climate change in tropical rivers. As exotic
380 species are often harmful to native fauna, preventing their introduction would be an important
381 recommendation to preserve freshwater shrimps. Finally, supporting research on the biology
382 and ecology of these species would help to improve our knowledge and assess the threats they
383 face.

384

385

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630 **Figures captions:**

631 **Figure 1.** Schematic representation of the different freshwater habitats. 1: Spring zone; 2: Higher
632 course; 3: Waterfall; 4: Middle course; 5: Lower course; 6: Estuary; 7: Lake; 8: Swamp; 9:
633 Subterranean waters.

634 **Figure 2.** Examples of habitats types. A: Higher course riffle, lotic mode (River Poitete,
635 Kolombangara Island, Solomon Islands, credit PK); B: Higher course pool, lentic mode (Ciu
636 waterfall, New Caledonia, credit VM); C: Middle course, lentic mode (River Wénou, New
637 Caledonia, credit VM); D: Middle course riffle, lotic mode (River Nekouri, New Caledonia, credit

638 VM); E: Lower course, lentic mode (River Hienghène, New Caledonia, credit VM); F: Lower
639 course riffle, lotic mode (River Negropo, New Caledonia, credit VM); G: Mangrove estuary (River
640 Tanghène, New Caledonia, credit VM); H: Estuary, low tide (Nera estuary, New Caledonia, credit
641 VM); I: Mountain stream (Unnamed tributary of the river Ciit, New Caledonia, credit VM); J:
642 Waterfall (Colnett waterfall, New Caledonia, credit VM); K: Swamp (Plaine des Lacs, New
643 Caledonia, credit VM); L: Lake (Lac en Huit, New Caledonia, credit VM).

644 **Figure 3.** Distribution area of *Caridina*.

645 **Figure 4.** Heat maps representing the species richness by locality. A: numbers of amphidromous
646 species (eggs < 0.8mm); B: numbers of landlocked species (eggs > 0.8mm); C: numbers of endemic
647 species (known from a single locality/area).