Tadashi Kawai · Neil Cumberlidge
Editors

A Global Overview of the Conservation of Freshwater Decapod Crustaceans

Springer

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The white-clawed crayfish, *Austropotamobius pallipes* complex

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This book is dedicated to the late Professor Michael Türkay, who was a truly inspiring leader in the fields of crustacean biology and conservation

Foreword

More than 10 % of all described species on earth are concentrated in freshwater ecosystems. The fact that freshwaters are teeming with life but only occupy less than one per cent of the earth's surface makes these ecosystems the ultimate biodiversity hotspot. What's more, the beneficial services provided by freshwater ecosystems have been estimated to be worth more than $29 trillion US a year.

Despite the immense value of these ecosystems, we are losing them at a rapid pace, and it is estimated that more than 64 % of the world's wetlands on which freshwater species depend have been destroyed since 1900. Population monitoring of freshwater species dating back to 1976 indicates that the rate of species loss in freshwater ecosystems is double that seen in either terrestrial or marine ecosystems. The 2015 version of the IUCN Red List of Threatened Species confirms this trend is continuing in freshwaters, with an alarmingly high number of these species (one in three) assessed as threatened with extinction. The accelerating decline of freshwater species worldwide means that many will be lost forever before we have even had a chance to add them to the biodiversity literature.

Human actions are largely to blame for this catastrophic loss of natural capital. Pressures on freshwater resources everywhere are growing daily as the increasing world population adds to the demand for drinking water, improved sanitation, food, energy, and industrial products. However, questionable environmental accounting methods in use for development projects fail to factor in the benefits of the valuable ecosystem services provided by freshwater systems and often undercount the true costs of the detrimental impact of development. Too often the increasing exploitation of freshwaters for human use fails to recognise the needs of the species that live there, and equally does not recognise the valuable services that these species collectively provide to ensure the sustainable functioning of these ecosystems.

Freshwater decapod crustaceans are a key component of the biodiversity found in freshwater ecosystems around the world. As this volume clearly shows, these conspicuous and valuable macroinvertebrates are also falling victim to the ever-increasing threats to global biodiversity. Species extinction represents a tragic loss in itself, as well as being a tangible sign of the erosion of the natural resources upon which many people depend for their livelihood. The impact of this on human populations is felt through such things as a reduction in the number of species offered for direct consumption, or through a breakdown of ecosystem functions to the point where these wetlands fail to provide basic services (such as clean, abundant drinking water). In addition, research in Africa has demonstrated that healthy populations of freshwater crabs are critical for both nutrient recycling in freshwater ecosystems and for the continued survival of river otters and other predators of crustaceans.

Up-to-date information is a critical tool for addressing the urgent global challenge to conserve and sustainably manage the world's freshwater biodiversity. Knowledge of exactly where threatened species are located and the precise nature and origins of the threats that they face is invaluable for informing conservation actions aimed at avoiding or minimizing adverse impacts on freshwater biodiversity. Without current and comprehensive information, progress towards the conservation of our freshwater biodiversity is sure to continue to lag far behind that for other better known, and equally threatened, taxa.

This volume compiles for the first time the significant progress that has been made over the last 10 years to fill gaps in our knowledge of freshwater decapod crustacean conservation. It does this by providing specific examples of how this information can be applied in our efforts to conserve this important but rarely appreciated component of global biodiversity. I highly commend this volume and recognize the tremendous efforts of the many people who have worked tirelessly to make this information available in a single work. This book represents a truly valuable body of knowledge that is sure to make a significant contribution to help ensure the long-term future of freshwater decapod crustaceans around the world.

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Preface

Freshwater ecosystems worldwide, from high latitudes to the tropics, host highly diverse communities of aquatic invertebrates that are often dominated by large-bodied decapod crustaceans such as freshwater crabs, aeglids, crayfish, and shrimps. These conspicuous macroinvertebrates excite interest because of their large size, a characteristic that also makes them an attractive food source. As a consequence, the populations of these crustaceans are under increasingly heavy pressure. Moreover, the alteration of global ecosystems by humans has happened more in the past one hundred years than in any comparative period of time in history. Freshwater habitats, and the animals that depend on them, are now under imminent threat from a number of different sources, a fact that is reflected in the high rates of biodiversity loss in freshwater ecosystems in all parts of the world.

We became aware of the continuing demand for the latest information on the threats to freshwater ecosystems following the publication in 2014 of “Advances in Freshwater Decapod Systematics and Biology”, edited by Darren C.J. Yeo (National University of Singapore, Singapore), Sebastian Klaus (University of Heidelberg, Germany), and Neil Cumberlidge (Northern Michigan University, USA). This was the first multi-author English language book to be produced on the freshwater decapods, and it has become a much sought-after source of reference material for researchers, students, conservationists, citizen scientists, and regional managers. This realization is what motivated us to produce a book written by specialists in freshwater decapod conservation that highlights the scale of the problems facing all of us. We are especially aware of the importance of this message reaching the next generation of scientists and managers because they will be the ones facing the consequences of severe environmental disruption in their lifetimes.

Recent International Union for Conservation of Nature (IUCN) Red List assessments of the freshwater decapods from all parts of the world have revealed unexpectedly high numbers of species threatened with extinction and have specified the source of threats to each species. The majority of threatened species of decapods are restricted-range endemics living in habitats subjected to deforestation, alteration of drainage patterns, and pollution, and many species are over-harvested for human consumption. The stability of freshwater ecosystems is being seriously altered by the introduction of non-native species, urbanization, logging, and overexploitation of native species, and these negative impacts are increasing with globalization and human encroachment. In addition, the rate of global climate change in the coming century is projected to increase, and this will further impact all ecosystems more rapidly than any changes that have occurred in the last 10,000 years. It is clear that we are rapidly losing a good part of the biodiversity of the freshwater realm worldwide, and trends indicate that this situation is becoming increasingly serious. The locations of threatened species of decapods and the nature of their extinction threats are now better understood, and our global conservation efforts can now be focused on those species and habitats that are in most need.

Here, we review the current strategies aimed at monitoring and quantifying the decline of the world's threatened freshwater decapod species and highlight the efforts being taken to develop conservation measures to prevent further losses. Strategies for the sustainable management of inland aquatic resources depend heavily on baseline data on diversity, conservation status, and distribution patterns of the freshwater decapod faunas, all of which are now available on a global scale. The growing pressures on freshwater habitats and their species make it a priority to understand the effectiveness of current conservation strategies at the global and national levels in protecting freshwater systems and their inhabitants.

Future challenges include the increasing human population that is placing additional pressures on freshwater resources as demands for food, energy, transport, and water supply grow. In addition, there are significant emerging threats to freshwater ecosystems from future global climate change. However, the scale of the impact of these threats on freshwater ecosystems is still not well understood by the public, policymakers, and politicians, and there is a need to raise awareness of the urgent need for conservation action before it is too late. The limited resources available for conservation mean that we need to prioritize conservation interventions for those species that are on the edge of extinction based on their conservation status and the extinction threats that they face. Conservation action plans now need to be developed that are aimed at developing measures to prevent further losses, and these plans depend on cooperation between scientists, conservation managers, educators, funding agencies, and policymakers, as well as conservation agencies such as the IUCN.

Finally, the idea for the present volume arose at the 2013 summer meeting of The Crustacean Society in San Jose, Costa Rica, when we [Tadashi Kawai (TK) and Neil Cumberlidge (NC)] shared our common concerns for the urgent need to protect the hundreds of species of threatened decapod crustaceans that depend on freshwater habitats for their survival. As a result, we developed a proposal to Springer Publishers for a multi-authored invited volume that was based on two symposia on decapod conservation held at conferences in Germany and Japan. The first of these symposia was "Conservation and Biology of Freshwater Decapoda" held at the 2014 International Crustacean Congress 9 (ICC9) in Frankfurt, Germany, that included presentations by many of the authors who have contributed a chapter to this book. In addition, one of the editors (NC) was also an invited plenary speaker at ICC9 who presented a talk on “Developing Conservation Strategies for Threatened Freshwater Decapods Worldwide”. The second symposium was “Conservation of Freshwater Decapods” at the “International Association of Astacology (IAA) and Carcinological Society of Japan (CSJ) Joint international Conference on Crustacea, IAA 20” held later in 2014 in Sapporo, Japan. This conference was organized by TK and included presentations on decapod conservation by several authors of the present volume, and by NC, who gave a talk in the plenary session on “Freshwater Crabs and the Biodiversity Crisis: Meeting the Conservation Challenges”. These three meetings formed the core of the 15 chapters in the present volume that have been authored by 38 leading specialists from all parts of the world. In this way, we were able to obtain global coverage that provided us with global coverage of the latest information on the biology and conservation of freshwater decapods.

In organizing and editing this book, we have enjoyed the support and input from active specialists in decapod biology and conservation from around the world. We would especially like to acknowledge the following individuals and organizations for their help: Dr. Hanamura Yukio (Japan), Dr. Elena Tricarico (Italy), Ms. Heide Türkay (Germany), the International Association of Astacology, The Crustacean Society, The Carcinological Society of Japan, and Zarigani Kenkyukai (Japan). We are especially grateful for the capable support of Judith Terpos and Alexandrine Cheronet of Springer Publishers who have guided us expertly throughout all of the steps in this long and complex process.

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Contents

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Chapter 1
Global Diversity and Conservation of Freshwater Crabs (Crustacea: Decapoda: Brachyura)

Neil Cumberlidge

Abstract The global diversity of the almost 1400 species of primary brachyuran freshwater crabs that spend their entire lives in freshwater habitats is outlined, along with that of 220 species of secondary brachyuran freshwater crabs that spend part of their life in fresh water and part in salt water. Estimates of freshwater crab diversity based on the current rates of discovery and levels of exploration indicate that the field is still in a growth phase, and it is likely that there are a substantial number of undescribed taxa. The distribution pattern of the brachyuran freshwater crab families across zoogeographic regions is discussed, and the conservation status and current threats to the group are highlighted. It is likely that a greater proportion of the global fauna of freshwater crabs is actually threatened with extinction than is currently realized.

Keywords Primary and secondary freshwater crabs · Red List · Species estimates · Data deficiency

1.1 Introduction

The majority of crabs that live exclusively in freshwater habitats are brachyurans and these are referred to here as the primary freshwater crabs. These crabs comprise almost 1400 exclusively freshwater species assigned to five families: Pseudothelphusidae, Potamonautidae, Potamidae, Gecarcinucidae, and Trichodactylidae that are all in the Heterotremata (Ng et al. 2008; Cumberlidge et al. 2009; Cumberlidge 2014a; PKL Ng pers. com.). Primary freshwater crabs complete their life cycle independently of the marine environment, are never found in littoral saltwater habitats, and include species that are either semi-terrestrial or mostly terrestrial in habit. Four of the five primary freshwater families (Potamidae, Potamonautidae, Gecarcinucidae, and Pseudothelphusidae) share common ancestry,

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while the fifth family, the Trichodactylidae, is positioned on a separate part of the Brachyuran phylogenetic tree (Cumberlidge and Ng 2009; Tsang et al. 2014). There are another 220 species of brachyuran freshwater crabs worldwide (PKL Ng pers. com.) that belong to nine unrelated families (Tsang et al. 2014) whose members are mostly marine species: Sesarmidae, Varunidae, Gecarcinidae, Glyptograpsidae, and Dotillidae (Thoracotremata) and Hymenosomatidae, Chasmognathidae, Portunidae, and Xanthidae (Heterotremata) (Yeo et al. 2008; PKL Ng pers. com.). These paraphyletic families all include species that are found in fresh water, but all of these species also need to be in salt water at some point in their life (Yeo et al. 2008; PKL Ng pers. com.). Because of their euryhaline existence, these brachyurans are referred to here as secondary freshwater crabs. In South America there is a third group of exclusively (primary) freshwater crabs that are assigned to a single family (Aeglidae) in the decapod infraorder Anomura (that also includes hermit crabs). The aeglids are discussed in detail elsewhere in this volume (Chap. 2) and are distinguished here from other species that share the vernacular name ‘freshwater crabs’ by referring to them as anomuran primary freshwater crabs.

Although the brachyuran and anomuran primary freshwater crabs belong to widely separate evolutionary lineages of decapod crustaceans they nevertheless share similar adaptations for life in a freshwater habitat. For example, they all undergo direct development (with no larval stages) and they all produce large, yolky eggs that hatch directly into juvenile crabs. In contrast, the secondary freshwater brachyurans while fully adapted to freshwater/terrestrial living, do not show direct development [with a few exceptions (Ng and Tan 1995; Schubart and Koller 2005)]. The life cycle of these secondary freshwater animals is characterized by highly abbreviated development in which their eggs release larvae at an advanced stage that must pass through one or more stages before metamorphosing into hatchling crabs. This strategy of abbreviated development has evolved independently in each of the families with secondary freshwater species and these similarities are the result of evolutionary convergence.

1.1.1 Habitat

The primary brachyuran freshwater crabs occur in a wide variety of aquatic and terrestrial habitats around the world in the tropics and subtropics. These decapods are present in almost all freshwater bodies in the inland waters of the continents, from clear, fast-flowing montane streams to sluggish lowland rivers and streams, as well as peat and freshwater swamps, stagnant ponds and rice fields, tree holes, leaf axils, and underground caves (Cumberlidge et al. 2009). Most of the primary freshwater crabs do not survive for long in salt water, but there is evidence that species of potamids and gecarcinucids from Thailand are somewhat tolerant of saline conditions because they can survive immersion in salt water for up to three weeks in the laboratory (Esser and Cumberlidge 2011). Terrestrial freshwater crabs that live in tropical rain forests either move through forest floor litter or climb trees, and can live well away from permanent freshwater sources (Ng 1988; Cumberlidge 1991; Ng and Tay 2001; Bayliss 2002; Cumberlidge and Vannini 2004; Cumberlidge et al. 2005). These species do not require regular immersion in fresh water and can obtain water either from their food or from drinking dew or rainwater. Freshwater crabs are primarily nocturnal, and remain hidden during the day and come out at night to forage. These crabs are omnivorous scavengers that feed mainly on plant matter, but some species are opportunistic carnivores that feed either on live prey such as fish, molluscs, and prawns or on dead animals that they encounter (Ng 1988). Crabs also constitute an important food resource for many species of fishes, caymans, turtles, birds, and mammals in tropical freshwater ecosystems (Ng 1988; Magalhães 2003; Cumberlidge et al. 2009; Balian et al. 2010).

The distribution patterns of the secondary brachyuran freshwater crabs are mainly centred on the coastal/littoral regions of continents and islands, and are markedly different from those of the inland primary freshwater crabs that dominate the inland waters of the continents and are never found naturally in salt water of any kind (Esser and Cumberlidge 2011). Most species of secondary freshwater crabs do not wander very far inland, with a few exceptions (Schubart et al. 1998; Schubart and Koller 2005; Ng and Tay 1995). This littoral distribution pattern no doubt reflects their ties to saltwater and their need to spend part of their life cycle in freshwater and part of it in the sea.

1.2 Global Diversity

Although the primary freshwater crabs are one of the most species-rich groups within the Brachyura (Ng et al. 2008; Cumberlidge et al. 2009) these large and conspicuous tropical freshwater macro invertebrates were completely unknown until the late 18th century. Primary freshwater crabs were first discovered in 1783, and only six species (now in three different families) had been described by 1800 (Table 1.1). Even Linnaeus (1758) was unaware of the existence of these tropical and subtropical crustaceans. The very first freshwater crab species known to science was *Dilocarcinus septemdentatus* (Herbst 1783) (Trichodactylidae) from South America, followed two years later by *Potamon fluviatile* (Herbst 1785) (Potamidae) from southern Europe, and then by *Oziotelphusa senex* (Fabricius 1789) (Gecarcinucidae) from southern India. It took another 36 years for the first pseudothelphusid [*Guinotia dentata* (Latreille 1825)] to be discovered (in Trinidad), which was followed the next year by the discovery of the first potamonautid [*Potamonautes berardi* (Audouin 1826)] in Egypt. In terms of the modern understanding of the group, representatives of all five recognised families had been described between 1783 and 1826. After that no more primary freshwater crab families have been recognised [although at the high point 12 primary freshwater crab families had been proposed (Bott 1970; Cumberlidge et al. 1999)]. The rate of discovery of new species and genera of freshwater crabs increased slowly

Table 1.1 Number of described species and families of brachyuran primary freshwater crabs per century from 1783 to 2015

Year	Species	Family (families)
1783	1	1
1800	6	1
1900	167	1
2000	991	12
2015	1393	5

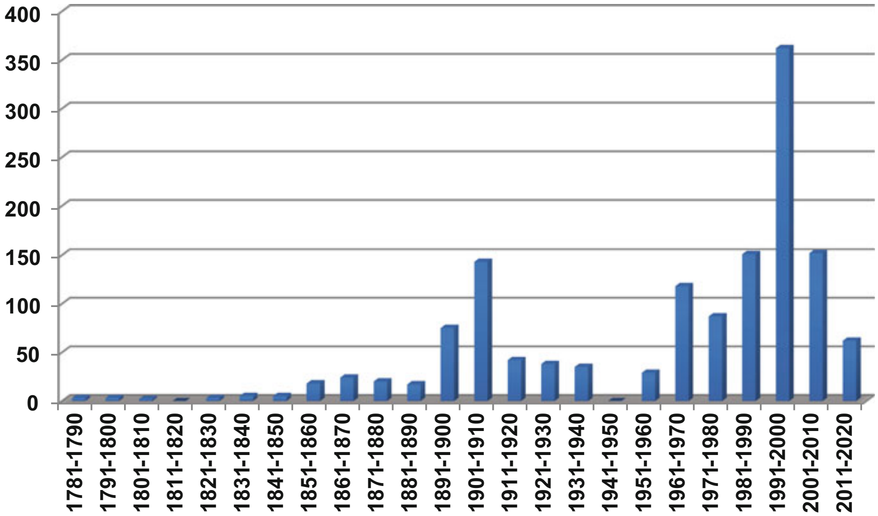

Fig. 1.1 Record of the number of species of freshwater crabs described per decade around the world from 1783 until the present day (*vertical axis*). All five families of primary brachyuran freshwater crabs are included. The *horizontal axis* shows time in ten-year blocks beginning with the discovery of the first species of freshwater crab in 1783

throughout the 19th century, reached a peak in the late 20th century, and continues to grow at a steady pace in the 21st century (Fig. 1.1; Table 1.2).

In 2009, there were 1280 known species of freshwater crabs, whereas in 2015 there are now 1394 species, and the consistently steady rate of species descriptions is showing no signs of slowing down (Fig. 1.1; Table 1.2). The five families of primary freshwater crabs have strikingly different numbers of species (Table 1.2). The breakdown of the described species by family in 2015 is as follows: Potamidae (548 species), Gecarcinucidae (361 species), Pseudothelphusidae (268 species), Potamonautidae (152 species), and Trichodactylidae (47 species) (Table 1.2). The rate of discovery of new species varies with the family under discussion. For example, while new species of Potamidae, Potamonautidae, Pseudothelphusidae, and Gecarcinucidae are still being discovered, no new species of Trichodactylidae have been described since 1996, despite active sampling in tropical South American

Table 1.2 Primary and secondary freshwater crab species discovery rates

Families of primary brachyuran freshwater crabs	Described species 2009	Described species 2015	# New species since 2009	Rate N. sp./ year	Estimated species (end 21st century); described + undescribed*
Potamonautidae	133	152	+19	3	152 + 255 = 407
Gecarcinucidae	344	372	+28	4.5	372 + 382 = 764
Potamidae	505	551	+46	8.0	551 + 680 = 1231
Pseudothelphusidae	251	271	+20	3	271 + 255 = 526
Trichodactylidae	48	48	0	0	48 + 0 = 48
Total primary FW crabs	1280	1394	+113	19	1394 + 1615 = 3009
Total secondary FW crabs	170	222	+52	9	737

*Assuming the current rate of species discovery continues for the next 85 years

lowlands including the Amazon basin (Table 1.2). This indicates that current numbers of species of trichodactylids may be close to the complete fauna for this family. Even so, it should be remembered that there are still large areas within the range of the Trichodactylidae that are as yet unexplored for freshwater crabs.

The number of undiscovered species of primary freshwater crabs is difficult to estimate accurately, but despite this, there have been attempts to estimate their true global diversity (Table 1.2). For example, Yeo and Ng (1999) used different methods to estimate the actual number of primary freshwater crabs globally. One approach was to extrapolate values from surveys of a well-sampled region and use this to estimate undescribed diversity in the unexplored freshwater crab habitats around the world. This involved calculating the number of species per unit area found in the intensively surveyed species-rich country of Thailand (1.8 species/km^2) and using this to estimate freshwater crab diversity based on estimates of the area of suitable freshwater crab habitat elsewhere. This gave an estimated global diversity of around 2155 species. However, the accuracy of this figure suffers from the fact that the actual species richness of primary freshwater crabs is not constant (Table 1.2) and varies a great deal across habitats in different parts of the world (Cumberlidge et al. 2009).

Another approach to estimate the number of undescribed species of primary freshwater crabs globally is to assume that the current rate of species discovery will continue for the rest of the 21st century. Cumulative data on the description of new species of primary freshwater crabs since their first discovery in 1783 up to the present time indicate that the boom in species discovery that began in the 1970s is still progressing strongly (about 15 species per year globally) (Table 1.2). This is a reasonable rate to use to estimate future additions for the rest of this century because the factors driving the current rate of species discovery are still adding to our knowledge of species richness, and are likely to continue to do so for many years to come, given the current encouraging levels of active taxonomic research in all

Table 1.3 Undiscovered biodiversity—vertebrates, invertebrates, and crustaceans

Group	Described species	Estimated species	% described
Vertebrates	62 k	80.5 k	81
Invertebrates	1.4 M	8–10 M	13–16
Crustaceans	47 k	150 k	~20

zoogeographical regions. The above factors include: (1) intensified biotic surveys targeted at the large areas of the tropics that are still poorly surveyed for freshwater crabs, (2) taxonomic revisions of described taxa including the resolution of synonymies and of the validity of subspecies, and (3) molecular studies aimed at discovering cryptic species using DNA sequences coupled with more refined taxonomic expertise (Cumberlidge and Daniels 2014). The latter approaches are likely to add to the species list even in the absence of new field collections.

A conservative worldwide estimate of the total number of species of primary freshwater crabs (those that are already discovered plus those not yet discovered) based on the assumption that the current rate of species description (about 19 new species a year globally) will continue throughout the 21st century (about 1614 more species) would give a total global fauna of more than 3000 species. This means that in 2015, with almost 1400 known species, we could be still only half way to our goal. Reality is probably somewhere in between the estimates obtained using the extrapolation method (2155 species) and those made using the species discovery rate method (3008 species). There could be between 755 and 1614 more species of primary freshwater crabs yet to be discovered.

When estimated numbers of undiscovered species of vertebrates (~80,500) are compared to the number of discovered species (~62,000) about 81 % are already known (Table 1.3). In contrast, estimated numbers of undiscovered species of invertebrates (~8,000,000) compared to the number of discovered species (~1,400,000) indicate that only about 17.5 % of this group are already known. When similar estimates are carried out for crustaceans as a whole (~150,000 undiscovered species; ~47,000 discovered species) then only about 31 % are already known. The present estimates that about 50 % of the primary freshwater crabs are still unknown indicates that although the above approaches bring us closer to our goals of understanding complete faunas, a more accurate system of estimating species numbers is clearly needed before the true diversity can be known.

1.3 Distribution and Zoogeography

The primary freshwater crabs have a circumtropical distribution and are today found in warm freshwater habitats in 122 countries in five zoogeographic regions (Neotropical, Afrotropical, Palaearctic, Oriental, and Australasian) (Cumberlidge et al. 2009). Interestingly, the present understanding of freshwater crab global distribution was established at the country level in the 19th century and no new countries that host these crustaceans have been added since then. These crabs are mainly found in the inland waters of the major continents and are notably absent from remote oceanic islands in the Pacific Ocean (such as the Galapagos, the Hawaiian Archipelago, the Society Islands), as well as from islands in the Atlantic and Indian Oceans. Primary freshwater crabs are also absent from cool freshwater habitats around the world in the Nearctic and from the cooler temperate zones of the Palaearctic, Neotropical, and Australasian regions (including New Zealand) (Yeo et al. 2008).

Globally, the primary freshwater crabs have two main centres of diversity: one centred in the Oriental region (923 species, 2 families, 66 % of the global fauna) and the other in the Neotropical region (319 species, 2 families, 23 % of the global fauna). In the Oriental region the countries with the highest species richness are China (243), Thailand (101), Malaysia (92), Indonesia (83), and India (90) (Cumberlidge et al. 2009; Cumberlidge et al. 2010). All of these Asian countries have representatives of the two most species-rich families—Potamidae and Gecarcinucidae. The species-rich countries in Indochina tend to have an even mix of species from both of these families (Yeo and Ng 2007). On the other hand, China's fauna is dominated by potamids and has only a few gecarcinucids (Cumberlidge et al. 2010), while India's fauna is dominated by gecarcinucids and has relatively few potamids (Cumberlidge et al. 2009).

In the Neotropical region the countries that have the highest species richness are Colombia (102), Mexico (67), Brazil (50), and Venezuela (44) (Cumberlidge et al. 2009, 2014). All of these countries have representatives of both Neotropical families—Pseudothelphusidae and Trichodactylidae. Mexico, Costa Rica, Colombia, and Venezuela have all been actively surveyed recently for freshwater crabs, and all have faunas dominated by pseudothelphusids especially in high-altitude habitats (the Cordilleras of the northern Andes, the Mexican Sierras, and the Guiana Massif). On the other hand, Brazil's freshwater crab fauna is dominated by trichodactylids that thrive in the vast lowland Amazon and Orinoco basins, and has fewer pseudothelphusids (perhaps because these crabs prefer highlands over lowland drainages). Although there has been active surveying for freshwater crabs in Brazil in recent years, this vast tropical area still has many under-sampled regions that have the potential for the discovery of many more new species. Similarly, the lower species numbers in Ecuador (26), Peru (22), Costa Rica (15), and Panama (15), and in most countries in Central America are almost certainly underestimates due to under-sampling (Cumberlidge et al. 2014; Magalhães et al. 2015).

The Afrotropical region is the most species-poor region in the world for primary freshwater crabs with only around 152 species in 2 families (11 % of the global fauna). There are two high diversity countries in this region one in Central Africa (Democratic Republic of Congo, 36) and one in East Africa (Tanzania, 25). However, with the possible exception of South Africa and Nigeria, most countries in this region are poorly surveyed (including the vast and largely unexplored Congo River basin), and the low numbers of species are almost certainly underestimates due to under-sampling. Increased recent surveying in a number of previously unexplored highland regions of southern Africa has produced several new species, and this approach promises to reveal a much greater diversity than is presently known (Daniels and Bayliss 2012; Phiri and Daniels 2013, 2014; Daniels et al. 2014; Cumberlidge 2014a).

1.3.1 Patterns of Species Richness and Endemism

The freshwater crab faunas within the different zoogeographical regions of the world typically include species that have one of two main distribution patterns: (1) widely distributed commonly encountered species with high population numbers, and (2) narrowly distributed rare species with a relatively restricted range and low population numbers. Widely distributed species include *Potamonautes niloticus* (Nile River drainage, East and North Africa) and *Sudanonautes africanus* (Lower Guinea forests, Congo river drainage, Central Africa) (Cumberlidge 1999, 2009). The wide distributional ranges of these species have been achieved as a result of the general lack of barriers to dispersal in the large river drainages and the long time periods available for species to spread out in these stable tropical ecosystems. These species have colonized vast areas of the tropics despite their relatively slow rate of dispersal (limited to adults) and their low fecundity (typical of reproduction by direct development). Abiotic barriers to their dispersal that restrict them to tropical warm water habitats include cool water temperatures (less than 0 °C, e.g., cold water rivers and high altitude mountain streams), a lack of year-round water (arid lands, deserts, extremely high mountain ranges), and prolonged contact with salt water (Esser and Cumberlidge 2011). Relatively restricted range species include *Potamonautes kundudo* (from a cave in Ethiopia, North Africa) and *Liberonautes nimba* (from high altitudes on Mount Nimba, West Africa) (Cumberlidge 1999, 2009; Cumberlidge and Clark 2012). Such species are found in just a few localized and isolating niches, despite the fact that they are living within a wider area of apparently favourable habitat. Over time the genetic isolation of populations of restricted-range freshwater crabs has resulted in the high levels of speciation and endemism that we observe today, especially in highland faunas (Cumberlidge 1999; Ng and Yeo 2007; Yeo et al. 2008; Cumberlidge et al. 2009).

Endemism in primary freshwater crabs is also evident at the family level. The Neotropical Pseudothelphusidae and Trichodactylidae and the Afrotropical Potamonautidae are strictly endemic to their zoogeographical regions. On the other hand the Potamidae is found in two regions: the southern Palaearctic region (North Africa, southern Europe, Middle East, Himalayas) and the Oriental region (southern China, Japan, and tropical Asia as far south as Wallace's line) (Cumberlidge et al. 2009; Cumberlidge et al. 2010). Similarly, the Gecarcinucidae is also found in the Oriental and Australasian regions (India, Sri Lanka, Indo-China, China, the Philippines, the Indonesian Archipelago, New Guinea, and northern Australia) (Cumberlidge et al. 2009). Endemism at the country level is high in primary freshwater crabs with 84 % of Palaearctic, Oriental, and Australasian species endemic to the country where they occur, as are 76 % of the Neotropical and 54 % of the Afrotropical species (Cumberlidge et al. 2009).

1.3.2 Islands

Significant numbers of species of primary freshwater crabs are found on large and small nearshore islands in the Neotropical, Afrotropical, Oriental, and Australasian regions. Because primary freshwater crabs are exclusively freshwater animals that have an aversion to salt water their presence on islands needs to be explained. One possibility is that crabs on islands close to continental landmasses were already in both places when past sea levels were lower than today, and became isolated when part of their range became an island as sea levels rose. However, this cannot explain the presence of primary freshwater crabs on remote oceanic islands (such as the Seychelles Archipelago and Madagascar that are fragments of the former Gondwanan landmass) because these ancient islands have been isolated for millions of years by deep seawater barriers (Cumberlidge 2008; Esser and Cumberlidge 2011). In these cases it is likely that the island freshwater crab faunas reached there by independent overseas rafting events millions of years ago, in a similar way to that proposed for saltwater-intolerant amphibians found on oceanic islands (Measey et al. 2007; Cumberlidge 2008; Daniels 2011; Cumberlidge and Daniels 2014).

1.3.3 Secondary Freshwater Crabs

Secondary freshwater crabs differ from primary freshwater crabs in that the former have the physiological ability to live both in saltwater and freshwater habitats for long periods of time, whereas primary freshwater crabs consistently avoid salt water. In addition, some species of secondary freshwater crab (e.g., *Varuna litterata*, Varunidae) have a widespread distributional range that not only includes tens of thousands of square kilometres of ocean, but also includes low salinity coastal waters and inland freshwaters. *Varuna litterata* is a common inhabitant of oceanic and freshwater habitats in the Indian Ocean (East Africa and Madagascar) and in the Pacific Ocean (Japan and Polynesia). Apart from phylogenetic separation at the family level (Tsang et al. 2014) differences between primary and secondary freshwater crabs relate to their life cycle strategies and their larval development. All brachyuran freshwater crabs are well adapted to life in freshwater, but primary freshwater crabs always reproduce by direct development, whereas most secondary freshwater crabs have abbreviated or reduced larval development with a few free-living larval stages and they complete their life cycle on land or in fresh water. Because these larval stages require saltwater for development the adult crabs need to return to the sea to breed. The retention of marine larval stages has the advantage of achieving a wide dispersal range in those species that produce planktonic larvae that are carried long distances by ocean currents before settling down on the benthos as young crabs (Vogt 2013). The only known exceptions to this strategy are species belonging to three genera of sesarmids: *Geosesarma notophorum* (a terrestrial freshwater crab from Sumatra, Indonesia), *Metopaulias* d*epressus* (a Jamaican terrestrial freshwater crab which lives in water pools in bromeliad leaves), and ten endemic species of *Sesarma* from Jamaica (Schubart and Koller 2005). These sesarmid freshwater species remain in fresh water for their entire life cycle and reproduce by direct development without producing any free-living larval stages (Ng and Tan 1995; Schubart and Koller 2005).

Five thoracotreme families (Varunidae, Sesarmidae, Gecarcinidae, Glyptograpsidae, and Dotillidae) include species that are found in freshwater habitats for either part or all of their life cycle. The Varunidae (7 genera, 55 species) are found in the coastal regions in the Palaearctic, Afrotropical, Oriental, Australasian and Pacific regions. A few species of varunids migrate long distances up rivers and spend most of their adult lives in fresh water (Schubart et al. 2002). The majority of varunids produce larvae that need to develop in sea water which means that the adults must either migrate from inland freshwaters to coastal waters, or release their larvae into rivers that carry them downstream to the sea (Anger 1995; Diesel et al. 2000). This family includes the euryhaline genera *Varuna* (2 species, including *V. litterata*) and *Eriochier* (4 species, including the Chinese mitten crab, *Eriochier sinensis*) that have wide distributional ranges and which live mostly in freshwater. The Varunidae also includes *Orcovita* (10 species) that are all karst and cave specialists, some of which live in freshwater habitats far inland and some of which have adapted to life in anchialine waters. The varunid genus *Ptychognathus* includes 25 species, most of which are estuarine, but some live in freshwater habitats and may venture several kilometres inland. Other varunid genera with species that are found in fresh water are *Utica* (7 species), *Pyxidognathus* (3 species), *Pseudograpsus* (2 species), and *Neoeriocheir* and *Platyeriocheir* (each with 1 species).

The Sesarmidae (8 genera, 95 species) is a large globally distributed family found in saltwater, brackish water, and freshwater habitats in the Palaearctic, Afrotropical, Neotropical, Oriental, Australasian, and Pacific regions. While the majority of species are found in soft-sediment coastal marshes and mangroves, some species live as adults in rivers (Diesel and Schuh 1998; Schubart et al. 2000), and others are found further inland and live exclusively in freshwater habitats. This family includes *Karstama* (15 species) that are all karst and cave specialists, some live inland in freshwater habitats, and some live near the coast in anchialine waters. The family also includes *Labuanium* (6 species) that are all tree climbers that live in phytotelm freshwater habitats and some species range several kilometres inland, often close to rivers. Another genus is *Pseudosesarma* (7 species) that are mostly found in mangrove forests, but some live in freshwater habitats. *Scandarma* (3 species) are tree climbers that live in freshwater pools in *Pandanus* palm leaves sometimes far inland. The Jamaican genus *Sesarma* (10 species) are primary freshwater specialists that live in mountain streams, bromeliad leaf axils, rock rubble, empty snail shells, and caves, and are all completely independent of salt water. Other sesarmid genera include *Geosesarma* (51 species, from Thailand, Taiwan, and Indonesia, that includes the exclusively freshwater species *G. notophorum*), *Sesarmops* (2 species, from phytotelm habitats in Madagascar), and *Metopaulius* (1 species, from a phytotelm habitat in Jamaica).

The Gecarcinidae (6 genera, 22 species) are the true land crabs that are found in coastal regions of the continents and islands throughout the tropics (in the Neotropical, Afrotropical, Oriental, Australasian, and Pacific regions), and includes some species that wander into freshwater habitats. This family comprises the genera *Johngarthia* (5 species), *Discoplax* (5 species), *Cardisoma* (4 species), *Gecarcinus* (3 species), *Epigrapsus* (3 species) and *Gecarcoidea* (2 species). The Glyptograpsidae (2 genera, 3 species) are found in the coastal regions in Central America and the east Atlantic. This family includes two genera *Glyptograpsus* (2 species) and *Platycheirograpsus* (1 species). *Glyptograpsus* spends its adult life in inland freshwater nhabitats (Schubart et al. 2002) but its adults must migrate downstream to release their larvae into the sea (Anger 1995; Diesel et al. 2000). Finally, the Dotillidae is a family of marine crabs with 59 species that includes two species of *Potamocypoda* from the coastal areas of the Australasian region that have adapted to a euryhaline life that includes both saltwater and freshwater habitats.

Four heterotreme families (Hymenosomatidae, Chasmocarcinidae, Portunidae, and Xanthidae) include species found in freshwater habitats for either part of, or all of, their life cycle. The Hymenosomatidae (9 genera, 26 species) are found in the coastal areas of the Neotropical, Afrotropical, Oriental, and Australasian regions. This family includes the genera *Amarinus* (11 species), *Neorhynchoplax* (4 species), and *Hymenosoma* (4 species) and most of these species are found in either estuarine or freshwater habitats. The Chasmocarcinidae (formerly Goneplacidae) (2 genera, 4 species) are from coastal areas in the Australasian Pacific regions and includes *Australocarcinus* (3 species) and *Trogloplax* (1 species). Finally the Portunidae and Xanthidae are two large marine crab families that include a few species that spend most of their lives in freshwaters. For example, *Scylla serrata* and *Callinectes sapidus* (Portunidae) and *Rhithropanopaeus harrisii* (Xanthidae) are common inhabitants of freshwaters but still need to migrate to the sea to breed.

1.4 Conservation Status

The International Union for Conservation of Nature (IUCN) Red List assessments of primary freshwater crabs by Cumberlidge et al. (2009) included the entire known fauna at that time (1280 species in 220 genera, 5 families) from 6 zoogeographic regions (Cumberlidge 2014b). Since that study was completed 114 more species of primary freshwater crabs have been described (Table 1.2) that are currently being assessed using IUCN Red List protocols, but are not yet part of the Red List. Therefore the conservation assessment data used here are based on the 1280 species that have already been assessed that are on the IUCN Red List site.

Although the study by Cumberlidge et al. (2009) included the entire global freshwater crab fauna, the extinction risk of 628 out of the 1280 species of freshwater crabs from all five families (almost 50 %) was not assessed due to a lack of relevant conservation information for them. The Red List protocols simply list such species as Data Deficient (DD) and exclude them from subsequent calculations of extinction threat. Cumberlidge et al. (2009) therefore based their assessments on the remaining 651 species in all five families, two-thirds of which (425 species) were not threatened (either LC or NT). However, high extinction threat levels were found for 209 assessed species: 32 critically endangered (CR), 52 endangered (EN), and 123 vulnerable (VU). Well over half (59 %) of these threatened species belong to just two families—Gecarcinucidae (Oriental and Australasian, 43 % of species Threatened) and Pseudothelphusidae (Neotropical, 34.2 % of species Threatened). The proportion of threatened African Potamonautidae (27.5 %) and Oriental Potamidae (26.5 %) is less than the global average (32.1 %), while only 10.3 % of the species of Neotropical Trichodactylidae appear to be at-risk (Cumberidge and Daniels 2007; Cumberlidge et al. 2009).

There are 43 countries (out of 122 with a freshwater crab fauna) that have a responsibility for the protection of at least one threatened species. So far, only one country (Singapore) has developed a conservation action plan aimed at protecting a freshwater crab: the critically endangered potamid, *Johora singaporensis* (Ng et al. 2015). This is the only threatened species of primary freshwater crab (out of 209) that is currently receiving any active conservation action (Ng et al. 2015). Elsewhere in Asia there are important concentrations of at-risk species (34.8 % of threatened species globally) in the highland forests of Sri Lanka and Taiwan, and in the rain forests of Indochina, Thailand, the Malay Peninsula, Borneo, and New Guinea. In the Neotropical region the highest numbers of threatened species are found in Colombia, Ecuador, Venezuela, Mexico, El Salvador, and Honduras. In the Caribbean, the entire freshwater crab fauna of the Dominican Republic and Haiti is threatened, but the faunas of these countries are species-poor (1-2 species). In the Afrotropical region the highest numbers of at-risk species are found in Liberia, Guinea, and Malawi, where there are alarmingly high proportions of threatened freshwater crabs (50–66.7 %).

The majority of threatened species of freshwater crabs are restricted-range (stenotopic) endemics whose habitat has been impacted by deforestation, alteration of drainage patterns, and pollution. Many of the threatened species of pseudothelphusids, potamonautids, potamids, and gecarcinucids are competent air-breathers that either live in burrows, or move between water and land in highlands, islands, caves, karsts, and phytotelms. These habitat specialists have small populations and restricted distributional ranges, and are especially susceptible to localized anthropogenic habitat disturbances (Collen et al. 2008, 2014).

The brachyuran secondary freshwater crabs have not yet been subjected to a global conservation assessment using the IUCN Red List protocols and so there is no information on the conservation status of any species in this important widespread group of freshwater decapods.

1.4.1 Data Deficiency

The primary freshwater crabs, like other invertebrate groups that have been studied at the global level (Richman et al. 2014; De Grave et al. 2014), include large numbers of DD species, which are species that lack data on population size and trends, distributional range, habitat quality, and threats (Cumberlidge et al. 2009). Many of these DD species (especially those collected before the 1950s) are not known beyond their original description, and their actual geographic range (other than type locality) is unclear due to inadequate on-the-ground knowledge. Once a species has been initially assessed as DD it is not included in any further analyses, because data necessary for the IUCN Red List assessment protocols are lacking.

High numbers of DD species are therefore a cause for concern because this designation may be masking the true number of threatened species, and could change IUCN Red List threat levels significantly when new field data enable their inclusion in future assessments. For example, the current estimates of threatened species of primary freshwater crabs (32 %) were made without the inclusion of 628 DD species (which represent almost 49 % of the global fauna) (Cumberlidge et al. 2009).

If improved future sampling targeted all DD species of freshwater crabs and provided sufficient new data to allow their assessment, then there would be two possible outcomes. If the result revealed that all DD species belonged to a threatened category (VU, EN, or CR), then the number of threatened species would increase dramatically (up from 32 to 66 %). On the other hand, if the result revealed that none of the DD species were threatened (all LC), then the number of threatened species would be halved (from 32 to 16 %). The wide difference in the results when these assumptions are applied undermines confidence in reported threat levels because a large proportion of the known global freshwater crab fauna has not been included. This is one reason that global Red List assessments are ideally carried out every 10 years, and why new field surveys that target threatened species should also include DD species.

The global study of the freshwater crabs identified 12 countries (Table 1.4) that have no DD species because the conservation status of their entire known freshwater crab faunas has been assessed. These countries can be used as models to estimate threat levels in countries that currently have a lot of DD species, and this can offer insights into the impacts that large numbers of DD species may have on the reported Red List threat levels. For example, Sri Lanka (50 species, 80 % threatened) is a comprehensively assessed country with an alarmingly high number of threatened species. On the other hand, Tanzania (25 species, 28 % threatened) is a comprehensively assessed country that has fewer than the average expected threatened species. When all 12 comprehensively assessed countries that lack DD species are considered together, the average percentage of threatened species amounts to 48 % of the fauna (range 100 to 8 %) in one of the three IUCN Red List threatened categories (Table 1.4). This average estimate is much higher than the current global estimate (32 % threatened, without DD species). In species-rich

Table 1.4 Extinction threat levels of primary freshwater crabs found in comprehensively assessed countries that have no data deficient (DD) species

Country	Total spp.	Thr. (%)	Endemic (%)	DD
Sri Lanka	50	80	98	0
Tanzania	25	28	16	0
South Africa	13	8	54	0
Turkey	9	11	22	0
Liberia	9	67	33	0
Australia	7	29	100	0
Honduras	6	33	17	0
Ghana	6	17	17	0
Malawi	4	50	50	0
Ethiopia	4	25	50	0
Singapore	4	75	75	0
Dominican Republic	2	100	100	0
Haiti	1	100	100	0
Totals	140	48	56	

China (8 % threatened) and in most of the African continent (21 % threatened), the high proportion of DD species means that the true number of threatened species is likely to be much greater than currently estimated (Cumberlidge et al. 2009; Cumberlidge 2011).

Multiple gaps in the exploration of freshwater crab faunas around the world make it likely that intensified surveying will not only add to the number of known species, it will also add to the number of threatened and DD species. The eventual inclusion in the Red List of little-known species currently treated as DD is likely to alter the current levels of biodiversity threat. Another factor that adds to the number of known species (and to the number of threatened species) is a lack of freshly caught samples because fresh tissues are required for the discovery of cryptic species using DNA sequence data. This is because the improved taxonomic clarity offered by molecular and morphological approaches allows detailed evaluations that can reveal cryptic species hidden within a morphologically similar widespread species. In these cases, the original range of a widespread species is fragmented when one or more cryptic species are identified within this range. The original species and cryptic species typically have restricted distributions, and some of these may prove to be concealed threatened taxa (Phiri and Daniels 2014; Cumberlidge and Daniels 2014). Taken together with the present high numbers of DD species, it seems highly likely that the true number of threatened freshwater crabs globally may be much higher than estimated.

Finally, highlighting DD species can serve as a focal point for further field studies aimed at filling gaps in our knowledge. With careful planning the implementation of conservation actions for threatened species could also have the added value of increasing our knowledge of DD species if they are found in the same area as the threatened species of interest.

1.4.2 Extinction

Some estimates place the current rate of species extinction as being at such high levels (i.e., eight species lost forever every day) that some authors have characterised modern times as the Earth's sixth major mass extinction episode (De Vos et al. 2015). Those authors estimated the current extinction rate to be approximately 100 extinctions per million species per year (1000 times higher than natural background rate), and predicted that future rates may be even worse (10,000 times higher than the natural background rate). The projections of those authors are based on estimates of about 8.7 million species found on the planet today (Mora et al. 2011), although only 1.9 million species have been formally described taxonomically.

Despite these high extinction rate estimates the IUCN Red List site actually lists only 901 species of animals or plants that are either extinct (EX) or extinct in the wild (EW) in recent times (Table 1.5). One reason for this relatively low number of extinctions is that in 2015 only 3.9 % of the 1.9 million described species have been assessed and are part of the Red List dataset (Stuart et al. 2010). Another reason is that before a species can be declared as extinct it is necessary to apply the IUCN Red List protocols that require exhaustive surveys examining the disappearance of a species suspected as being extinct (i.e., repeated investigations in the right habitats at the right time of year, and no sightings for over 60 years). At our present levels of knowledge no species of primary freshwater crabs are extinct (EX) or extinct in the wild (EW) using the IUCN Red List protocols. There are, however, 351 EX or EW species of vertebrates and 411 EX or EW species of invertebrates, including 12 extinct species of freshwater shrimps on the Red List. In the case of the primary freshwater crabs it is likely that some DD (and even CR) species may already be

Table 1.5 Number of species on the Red List that are extinct or extinct in the wild in 2015

Group	Total described species (k)	Species on Red List (% of total species known)	No. species RL EX/EW	% assessed species extinct
Invertebrates	1400	17,218 (1.2 %)	411	2.44
Vertebrates	62	39,223 (63 %)	354	0.93
Plants	300	19,738 (6.6 %)	136	1.40
Total: all organisms	1900	74,106 (3.9 %)	901	1.21

Invertebrates are the most poorly known group of organisms and most species have yet to be discovered (possibly because it is had to identify invertebrates without specialist knowledge). Invertebrates also have the smallest number of species represented on the IUCN Red List, but have the highest documented rate of extinction of any group studied extinct, but we cannot establish this as fact because we lack the necessary field data to make an evaluation. Freshwater crab habitats around the tropics are among the most severely disrupted ecosystems in the world. It is therefore likely that the current intense degradation of tropical freshwater ecosystems worldwide that are subjected to forest destruction, water diversion, and pollution (Stiassny 1999; Dudgeon et al. 2006) makes it likely that some freshwater species assessed as DD that have not been collected for many years since their original description may actually be extinct. The same lack of field data that warrants their status as DD may actually be masking their extirpation, but this information gap is preventing their formal assessment as extinct (Sodhi et al. 2004; Bahir et al. 2005; Ng and Yeo 2007). For example, the DD species *Louisea edeaensis* and *L. balssi* (Cameroon), *Afrithelphusa afzelii* (Guinea), *Thaipotamon siamense* (Thailand) and *Demanietta manii* (Thailand) may well already be extinct because there have been no records of them for over a century despite survey activities, or because their original habitats are now highly altered or located in densely populated urban areas (Ng and Naiyanetr 1993; Cumberlidge 1999; Sodhi et al. 2008).

1.5 Threats and Conservation Issues

The main threats to primary freshwater crabs include habitat destruction (accelerated by global climate change), alterations of river or stream flow patterns (from dams and other drainage diversions), and pollution (from mining, pesticides, and fertilizers) (Cumberlidge et al. 2009; Cumberlidge 2011). Other threats to these freshwater animals include displacement of native species by introduced species. For example, in Kenya, East Africa the introduction of the red swamp crayfish (or Louisiana red-claw crayfish) (*Procambarus clarkii*) into Lake Naivasha in 1970 impacted native populations of aquatic plants and freshwater crabs. Soon after the introduction of *P. clarkii* to the lake their populations rose to levels high enough to support a thriving commercial export fishery. However, the high densities of crayfish in the lake had a devastating impact on the aquatic vegetation due to overgrazing and there was a subsequent collapse of crayfish populations. The eventual recovery of the lake's aquatic plants allowed crayfish populations to expand and once again they overgrazed the lake's vegetation. The dominance of *P. clarkii* in Kenyan freshwater ecosystems and its cyclical effects on the lake's primary producers also caused population crashes of native freshwater crabs (*Potamonautes loveni*) (Gherardi et al. 2011). It may also have caused population crashes of the clawless otters that feed on these crabs (Ogada 2006). When freshwater crabs became scarce, the lake's otters switched from to eating crabs to eating crayfish, but the otters overall food supply was nevertheless reduced due to competition from numerous other predators attracted to feed on the abundant crayfish.

Other threats to freshwater crabs are over-harvesting for food and for the aquarium trade. Common species of freshwater crabs are harvested by human populations around the world, either for use as food or for the treatment of medical problems (such as stomach ailments and physical injuries). Locally abundant species of African freshwater crabs (e.g., *Potamonautes lirrangensis* in Lake Malawi and *Platythelphusa armata* in Lake Tanganyika) support small-scale fisheries. Even so, these species could still be vulnerable to population crashes. Species of brightly coloured primary and secondary Asian freshwater crabs are collected intensively for the aquarium trade and some of these restricted range habitat specialists may now be threatened with extinction (Cumberlidge et al. 2009).

Many widespread lowland species of freshwater crabs (e.g., *Parathelphusa maculata*) seem to be tolerant of change because these crabs continue to survive despite suffering severely altered lowland freshwater habitats as a result of land development, natural forest loss, and agriculture. On the other hand, many species of freshwater crabs are less tolerant of habitat alteration and are vulnerable to population crashes, and these species tend to be those that have a restricted distribution in highly threatened tropical freshwater habitats. For example, restricted range species such as the cave specialist *Cerberusa caeca*, and the cold mountain stream specialist *Johora grallator* are both vulnerable to, and have little tolerance of, habitat changes. Other restricted range species that inhabit inaccessible places (such as offshore islands, high mountains, caves, and karsts) with low human impact are less likely to be threatened. Studies of the conservation status of the freshwater crab faunas of Sri Lanka (Bahir et al. 2005), Malaysia (Ng and Yeo 2007), China (Cumberlidge et al. 2011a), Tanzania (Reed and Cumberlidge 2006), southern Africa (Cumberlidge and Daniels 2007), and the Neotropical region (Cumberlidge et al. 2014) have reached similar conclusions: it is the restricted range species living in disturbed habitats that are more likely to be threatened.

The conservation of freshwater crabs in general requires conservation actions tailored to bring about the long-term survival of a species threatened with extinction. Other approaches to species conservation focus more on habitat conservation. For example, there is a need for a network of carefully managed protected sites that are large enough to preserve natural forests in drainage basins that will maintain water quality in the rivers, streams, lakes, and wetlands where crabs live. This in turn would require the establishment of more nature reserves and national parks, and the development of integrated species conservation action plans for the world's increasing number of species of freshwater crabs that are threatened with extinction.

1.6 Conclusions

1. Primary and secondary freshwater crabs are abundant in tropical and subtropical freshwater habitats around the world in five zoogeographic regions (Neotropical, Afrotropical, Palearctic, Oriental, and Australasian). Primary freshwater crabs dominate the inland waters of continents and islands, while secondary freshwater crabs mostly occupy littoral freshwater and saltwater habitats, and many species migrate seasonally between the two.

2. Primary and secondary freshwater crabs are diverse and species rich (1394 and 223 species respectively in 2015) and they together constitute more than 20 % of all brachyurans The rate of new species discovery in four of the five families of primary freshwater crabs is high, and is likely to continue for the rest of the 21st century, given the vast areas on un-surveyed suitable habitats around the world, and the improving taxonomic precision. The species discovery rate in one family, the Trichodactylidae, has slowed in the past 20 years and this family may be close to being known comprehensively.
3. The extinction risk of 651 out of the 1280 species of freshwater crabs known in 2009 that were assessed using IUCN Red List protocols indicates that two-thirds (425) are not immediately threatened (either LC or NT); but that about one third (209) have a high extinction threat level: 32 critically endangered (CR), 52 endangered (EN), and 123 vulnerable (VU) species.
4. The main threats to primary freshwater crabs include habitat destruction (accelerated by global climate change), alterations of river or stream flow patterns (from dams and other drainage diversions), and pollution (from mining, pesticides, and fertilizers). Other threats to freshwater animals include displacement of native species by introduced species, and over-harvesting either for food or for the aquarium trade.
5. No species of primary freshwater crabs are known to be extinct (EX) or extinct in the wild (EW), but extinctions are difficult to confirm using IUCN Red List protocols. However, some 628 species of primary freshwater crabs (which represent almost 49 % of the global fauna) are designated as Data Deficient (DD). The large number of DD species of primary freshwater crabs is a cause for concern because their exclusion from conservation assessments due to a lack of relevant data may be masking the true number of threatened (and possibly extinct) species.
6. Some DD species may actually be extinct because there have been no records of them for over a century and their original habitats are now highly altered or located in densely populated urban areas. It is likely that a greater proportion of the global fauna of freshwater crabs is threatened with extinction than is currently realized.

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Chapter 2

A Remarkable Anomuran: The Taxon *Aegla* Leach, 1820. Taxonomic Remarks, Distribution, Biology, Diversity and Conservation

Sérgio Luiz de Siqueira Bueno, Roberto Munehisa Shimizu and Juliana Cristina Bertacini Moraes

Abstract The family Aeglidae comprises three genera, one extant (*Aegla*) and two extinct genera (*Protaegla* and *Haumuriaegla*), the latter two genera are known only from fossils from marine sediments (indicating a marine origin for the group). *Aegla* contains all extant species and constitutes a monophyletic group within the Anomura. All 78 species and subspecies described so far are entirely adapted to freshwater habitats and are endemic to temperate and subtropical regions of continental South America. While most species are found in epigean habitats, there are a few cave-dwelling species in southeastern Brazil. The reproductive period varies from 8 to 12 months (in species from colder higher latitudes), to 4–7 months (in species from lower latitudes where warm-rainy and cold-dry seasons alternate). The adult males of seasonally breeding species include two morphotypes, one non-reproductive and the other reproductive. Eggs are large and few in number, and post-embryonic development is epimorphic. Juveniles have limited dispersal capacity and recruits tend to remain with the parental population. *Aegla* is the most severely threatened group among South American freshwater decapods because of habitat degradation, high endemism, a restricted area of occupancy, and a severely fragmented spatial distribution with reproductively isolated subpopulations.

Keywords Aeglidae · Decapoda · Freshwater · Threatened species · Review

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2.1 Introduction

This chapter offers a multidisciplinary overview of the taxonomy, diversity, distribution, general biology, and conservation of a remarkable group of freshwater anomuran. The uniqueness of the genus *Aegla* Leach, 1820 was recognised well over 60 years ago when Schmitt (1942b) stated "There are no fresh-water Crustacea at all like *Aegla* anywhere else in the world." This contribution is timely because *Aegla* is probably the most severely threatened taxon of freshwater decapods in South America, with more than half (55.13 %) of the 78 known species and subspecies assessed as either Critically Endangered (15.38 %), Endangered (28.21 %), or Vulnerable (11.54 %).

2.1.1 Taxonomic Remarks

The family Aeglidae Dana, 1852 currently comprises three genera: *Haumuriaegla* Feldmann 1984; *Protaegla* Feldmann et al. 1998, and *Aegla*. The first two genera are monotypic and known only from fossil records (Fig. 2.1): *Protaegla miniscula* is found in Early Cretaceous marine deposits (about 110 million years old) in Mexico (Feldmann et al. 1998), and *Haumuriaegla glaessneri* is found in Late Cretaceous marine deposits (about 75 million years old) in New Zealand (Feldmann 1984). These fossil findings provide strong support for the marine origin of the family Aeglidae, possibly in the Indo-Pacific region (Feldmann 1986).

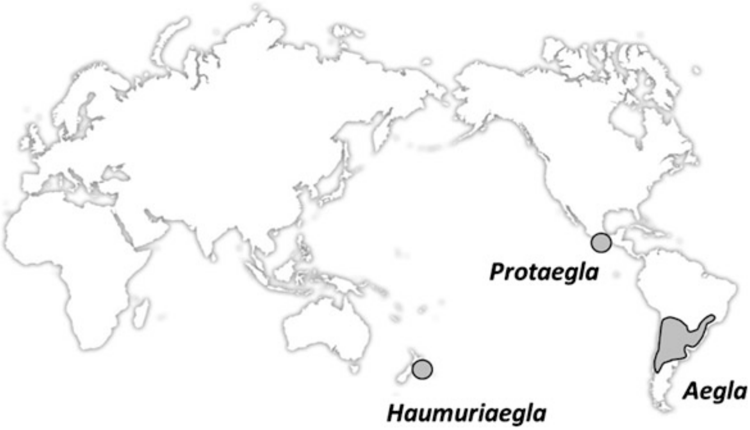


Fig. 2.1 World distribution of the family Aeglidae. World map represents today's configuration of the continents, and it is freely used here to show proximate locations of the marine fossil genera *Haumuriaegla* and *Protaegla* in the Indo-Pacific Region. All extant aeglids, genus *Aegla*, are endemic to temperate and subtropical regions of continental South America and are entirely adapted to freshwater habitats

The third genus, *Aegla*, contains all extant aeglid species. It is the only anomuran taxon entirely adapted to freshwater habitats and it is endemic to temperate and subtropical regions of continental South America (Schmitt 1942b; Bond-Buckup et al. 2008) (Fig. 2.1). With 78 described species and subspecies, these freshwater aeglids represent only 3 % of the extant anomuran assemblage of approximately 2500 species (sensu De Grave et al. 2009).

Until recently, the family Aeglidae was included in the superfamily Galatheoidea Samouelle, 1819, together with three other anomuran families: Chirostylidae Ortmann, 1892, Porcellanidae Haworth, 1825, and Galatheidae Samouelle, 1819 (Schmitt 1942b; Bowman and Abele 1982; Martin and Abele 1986; Martin and Davis 2001). This traditional view is based on morphological similarities such as the pyriform body shape, the dorso-ventral flattening of the cephalothorax and pleon, the presence of a well-developed rostrum, and the distinct dorsal cervical groove on the carapace; but none of these traits is exclusive to the aeglids, and many are also found in other anomurans (Martin and Abele 1988).

Recent investigations based on spermatozoal ultrastructure (Tudge and Scheltinga 2002), molecular data, and phylogenetic analyses (Martin and Abele 1988; Pérez-Losada et al. 2002a, c, 2004) have challenged the traditional view that the Aeglidae is part of the superfamily Galatheoidea. Furthermore, McLaughlin et al. (2007) proposed that the Aeglidae should be placed in the superfamily Aegloidea Dana, 1952.

The phylogenetic relationships of the Aegloidea with other anomuran taxa, however, still remains controversial and close phylogenetic affinities with the Paguroidea Latreille, 1802 and Hippoidea Latreille, 1825 have been suggested by several authors (Martin and Abele 1988; Pérez-Losada et al. 2002c; McLaughlin et al. 2007). Data from sperm morphology (Tudge and Scheltinga 2002) and phylogenetic analyses (Schnabel and Ahyong 2010; Tsang et al. 2011) strongly support close affinities between the Aegloidea and the Lomisoidea Bouvier, 1895, a monotypic taxon for *Lomis hirta* Lamarck, 1818 from the Australasian and Indo-Pacific regions.

Freshwater aeglids have unique traits that set them apart from other galatheoid families, such as *lineae* on the carapace, gill morphology, and postembryonic development.

1. *Lineae* on the carapace (Fig. 2.2a, b). Aeglids exhibit a unique pattern of sutures, or *lineae,* on the lateral and dorsal surfaces of the carapace. The dorsal sutures on the posterior half of the carapace demarcate well defined cardiac and branchial areas. The calcification along the *lineae* is weaker than the exoskeletal plates (Martin and Abele 1988) and the branchial plates can be easily broken along the *lineae* and gently removed creating an access window to the gill chamber that allows observation of the gills (Fig. 2.2c).
2. Gill morphology. *Aegla* has trichobranchiate gills and this separates them from the galatheoid families which have the phyllobranchiate gills seen in many marine anomurans (Martin and Abele 1986). Trichobranchiate gills are found in anomurans such as the blepharopodids (Hippoidea) (Boyko 2002).

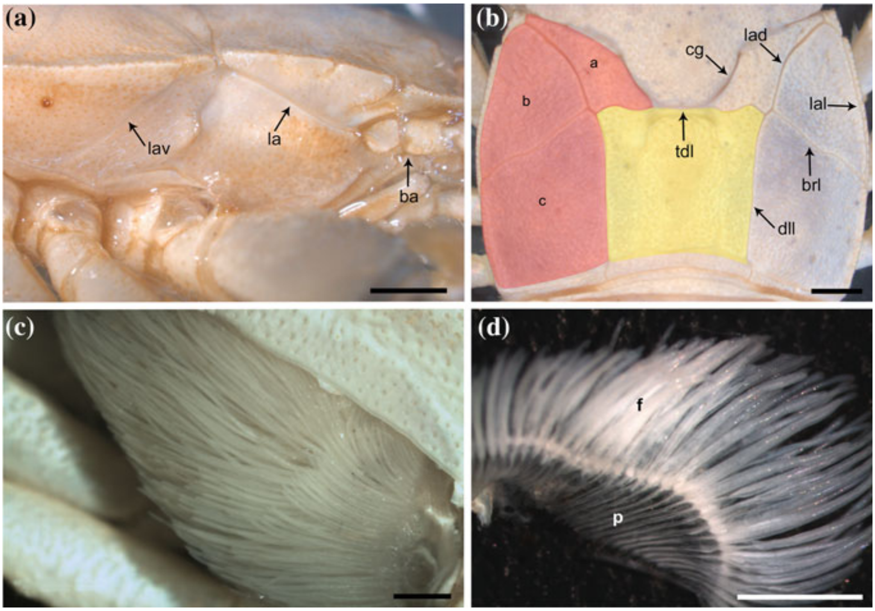


Fig. 2.2 Lineae and gill morphology. **a** *Aegla paulensis*: Lateral view of the carapace showing the *linea aeglica* (la) and the *linea aeglica ventralis* (lav); ba: base of the antenna. *Bar* 2 mm. **b** *Aegla strinatii*: Dorsal view of the posterior region of the carapace showing the cardiac area (*yellow*) and the three subdivisions of the branchial area (*red*): interior area (*a*), anterior area (*b*) and posterior area (*c*). Cervical groove (*cg*), *linea aeglica dorsalis* (lad), *linea aeglica lateralis* (lal), branchial linea (*brl*), transverse dorsal linea (*tdl*), and dorsal longitudinal linea (*dll*). *Bar* 2 mm. **c** *Aegla perobae*: General view of trichobranchiate gills in the branchial chamber as seen after the exoskeleton plates covering the anterior and posterior branchial areas have been removed. *Bar* 1 mm. **d** *Aegla perobae*: Trichobranchiate gill removed from the branchial chamber; arrangements of finger-like lamellae (*f*) on distal portion and of plate-like lamellae (*p*) on proximal portion. *Bar* 1 mm

The trichobranchiate gills in freshwater aeglids (Fig. 2.2d) have a unique structure, which was well described by Martin and Abele (1988, p. 23, 25) as follows: (The gills) “resemble trichobranchiate gills distally in that the gill filaments are long finger-like tubes; these extend forward from the base of the gill. The proximal portion of the gill resembles that of a brachyuran phyllobranch in having plate-like lamellae extending out over the branchial axis…” McLaughlin and de Saint Laurent (1998, p. 161) emphasized that “… It is not the shape of the gill elements, so much as their insertion on the rachis of the gill that determines gill type.” McLaughlin et al. (2007) described the gills of freshwater aeglids as having a quadriserial arrangement whereby the lamellar elements are not regularly inserted around the gill axis. Gills with quadriserial arrangements of lamellar elements have also been described in some paguroids (McLaughlin and de Saint Laurent 1998). It is clear that the gill morphology of freshwater aeglids needs further investigation.

3. Postembryonic development. The postembryonic development in marine anomurans is indirect, with eggs releasing zoeal larval stages. The zoeal stages are then followed by the megalopal stage that then moults into a juvenile "crab". Examples of this general pattern of development in marine anomurans are available in the literature for several families, such as Chirostylidae (Clark and Ng 2008; Fujita and Clark 2010), Galatheidae (Pike and Wear 1969; Fagetti and Campodonico 1971; Christiansen and Anger 1990; Fujita and Shokita 2005; Fujita 2010), Porcellanidae (Fujita et al. 2002; Fujita and Osawa 2005), Coenobitidae (Harvey 1992; Brodie and Harvey 2001), Hippidae (Knight 1967; Stuck and Truesdale 1986), Paguridae (McLaughlin et al. 1989, 1993; Gherardi and McLaughlin 1995; Barria et al. 2006), Lithodidae (Haynes 1982; Crain and McLaughlin 2000a, b; McLaughlin et al. 2003) and Lomisidae (Cormie 1993). The postembryonic development of marine fossil aeglids is not known, but it was most probably characterized by the presence of free-swimming larval form with a high capability for dispersal in ocean currents, similar to larval development observed in marine anomurans. Dispersal of ancient larval aeglids toward South America would have probably been favored by the counter-clockwise gyre of ocean circulation in the Pacific Ocean during the Oligocene Epoch (Feldmann 1986). In the freshwater aeglid genus *Aegla*, however, the postembryonic development is direct (=epimorphic), a life-history strategy that is a derived trait in this family. Aeglids hatch from eggs as benthic juveniles that resemble the adult form in general morphology (Mouchet 1932; Bahamonde and López 1961; Rodrigues and Hebling 1978; Bond-Buckup et al. 1996, 1999; Bueno and Bond-Buckup 1996; Francisco et al. 2007; Teodósio and Masunari 2007; Moraes and Bueno 2013, 2015).

2.1.2 *Origin and Biogeography*

The taxon *Aegla* probably originated in freshwater habitats in the Early Tertiary Period of the Cenozoic Era, about 60 mya (Pérez-Losada et al. 2004). While *Protaegla* and *Haumuriaegla* did not survive the great extinction of the Mesozoic/Cenozoic transition (Schweitzer and Feldmann 2005), the successful survivourship of *Aegla* during that geological period has been attributed to the occupation of buffered habitats less susceptible to the effects of the Cretaceous/Paleocene (K/P) transition (Schweitzer and Feldmann 2005). Factors that could have increased survivability of *Aegla* include inhabiting a refugium and eurytopy (Schweitzer and Feldmann 2005). The radiation and speciation of freshwater aeglids throughout the Cenozoic Era up to the present time corroborate the successful adaptation and colonization of freshwater habitats after the K/P event.

The point of origin of freshwater aeglids, whether from the Pacific side or from the Atlantic side of continental South America, was a matter of debate by past naturalists (Ortmann 1902; Schmitt 1942b; Ringuelet 1949; Morrone and Lopretto

1994). Over the past decades, however, the Pacific hypothesis has increasingly gained acceptance as data from different sources became available. This included evidence from fossil findings (Feldmann 1984; Feldmann et al. 1998), studies on the possible ancestral larval dispersal route of marine predecessor aeglids in the Indo-Pacific region (Feldmann 1986), and molecular phylogenetic analyses made in conjunction with data on the geological history and paleodrainage systems formations of continental South America (Pérez-Losada et al. 2004).

The dispersal of ancient marine aeglids on the western side of South America was favoured by marine transgressions during the early formation of the Andes Cordillera, in the Late Cretaceous-Early Tertiary Period, about 90–60 mya (Pérez-Losada et al. 2004). The evolutionary path of populations of land-locked marine aeglids would favour the acquisition of physiological adaptations and changes to life history strategies that helped them cope with increasing exposure to less saline waters. The successful adaptation to freshwater habitats marks the origin of the taxon *Aegla* and the beginning of its dispersal and speciation history throughout southern regions of South America from the Pacific to the Atlantic.

The uplifting of the Andes Cordillera represented an important physical barrier leading to the separation of *Aegla* populations on the western side of the Cordillera (mostly found in Chile today) from those on the eastern side. The uplifting of the Andes caused the drainage of many Pacific paleobasins to flow eastward toward the Atlantic side of South America (Potter 1997; Lundberg et al. 1998; Almeida et al. 2000). The west-to-east dispersal routes of *Aegla* through South American paleobasins were made possible by the eventual interconnection of continental western water masses with the paleobasins of Paraná and Uruguay rivers in the Late Eocene—Early Oligocene Epoch (43–30 mya) (Pérez-Losada et al. 2004). The east-northward dispersal route through the Paraná River paleobasin was one of the latest major events in the evolutionary radiation of the freshwater aeglids. Freshwater aeglids form a monophyletic assemblage with five recognized clades (sensu Pérez-Losada et al. 2004), and their current geographic distribution reflects the dispersal history of *Aegla* as described above.

2.1.3 Diversity, Distribution and Habitat

The present-day distributional range of freshwater aeglids includes six South American countries: Chile, Argentina, Bolivia, Paraguay, Uruguay, and Brazil (Bond-Buckup et al. 2008). The northernmost and the southernmost limits of the distributional range of *Aegla* are latitude 20 °S at Claraval, Brazil (*Aegla franca* Schmitt, 1942) and latitude 50 °S at Duque de York Island, Chile (*Aegla alacalufi* Jara and López 1981) (Bueno et al. 2007; Oyanedel et al. 2011). The highest known altitude (3613 m) is that for *Aegla septentrionalis* Bond-Buckup and Buckup 1994 from the Province of Jujuy, Argentina (Bond-Buckup et al. 2010a).

Based on a recent annotated checklist (McLaughlin et al. 2010), updated thereafter by descriptions of new species (Santos et al. 2012, 2013, 2014, 2015), the number of known species of freshwater aeglids is currently 78 (Table 2.2). More than half of these species (n = 47) are found in the south and southeastern regions of Brazil of which 89.4 % (n = 42) are endemic to Brazilian freshwaters (Fig. 2.3). Chile ranks second in number of species (21) and has the highest percentage of species that are country endemics (95.2 %, n = 20). There are currently 14 species reported for Argentina, with 7 (50 %) being endemic to that country. Uruguay follows next with 4 species, including *Aegla carinata* Bond-Buckup and Loureiro 2014 as the only endemic species (25 %) (Santos et al. 2014). Paraguay and Bolivia have one species each, *Aegla platensis* Schmitt 1942 and A. *septentrionalis* Bond-Buckup and Buckup 1994, respectively, neither of which is country endemic, because the distribution of these two species extends to other countries. Species richness increases from south to north in the distributional range of the genus, and this may be due to the latitudinal gradient effect (Morrone and Lopretto 1994).

Most species of *Aegla* inhabit lotic habitats, such as rivers and streams with fast moving and well oxygenated water flowing over bedrock strata (Fig. 2.4a). A few species inhabit lentic habitats such as lakes [e.g., *Aegla denticulata lacustris* Jara 1989 from Chile, and *Aegla prado* Schmitt, 1942 from Brazil and Uruguay (Jara 1989; Bond-Buckup et al. 2008)].

Most species of aeglids inhabit epigean habitats and show marked allopatric distributional patterns, and are usually restricted to one or more drainage systems belonging to a major hydrographic basin (Schmitt 1942b; Morrone 1996), although there are a few instances where two or more species with a sympatric distribution have been reported (Buckup and Rossi 1977; Castro-Souza and Bond-Buckup 2004; Santos et al. 2012). Several species of freshwater aeglids from epigean habitats are highly stenotopic and are restricted either to the type-locality or have a limited area of occupancy (Rodrigues and Hebling 1978; Bueno et al. 2007; Santos et al. 2010, 2012, 2013).

A few species (*Aegla microphthalma* Bond-Buckup and Buckup 1994, *A. cavernicola* Türkay 1972 and *A. leptochela* Bond-Buckup and Buckup 1994) are obligate cave dwellers or troglobites (Fig. 2.4b). Troglobitic species exhibit troglomorphic traits, such as depigmentation of the cuticle (Fig. 2.3i), shorter eyestalks, a reduced pigmented area of the cornea (Fig. 2.5), proportionately longer walking legs (Fig. 2.3d), and longer antennal flagella (Bond-Buckup and Buckup 1994; Moracchioli 1994; Alves 2007). Troglobitic species are highly endemic, with distributions restricted to the type-locality inside the cave (Türkay 1972; Trajano 1987; Bond-Buckup and Buckup 1994; Gnaspini and Trajano 1994; Moracchioli 1994, Maia et al. 2013; Fernandes et al. 2013).

Aegla strinatii Türkay 1972 (Fig. 2.3g) is an example of a facultative cave dwelling species, or troglophile, because it forms a self-sustaining, non-isolated reproductive population that moves about freely between both epigean and subterranean habitats (Türkay 1972; Rocha and Bueno 2004, 2011). Troglobitic and troglophilic species are found in the karst region of the Alto Ribeira in the State of São Paulo, southeastern Brazil.

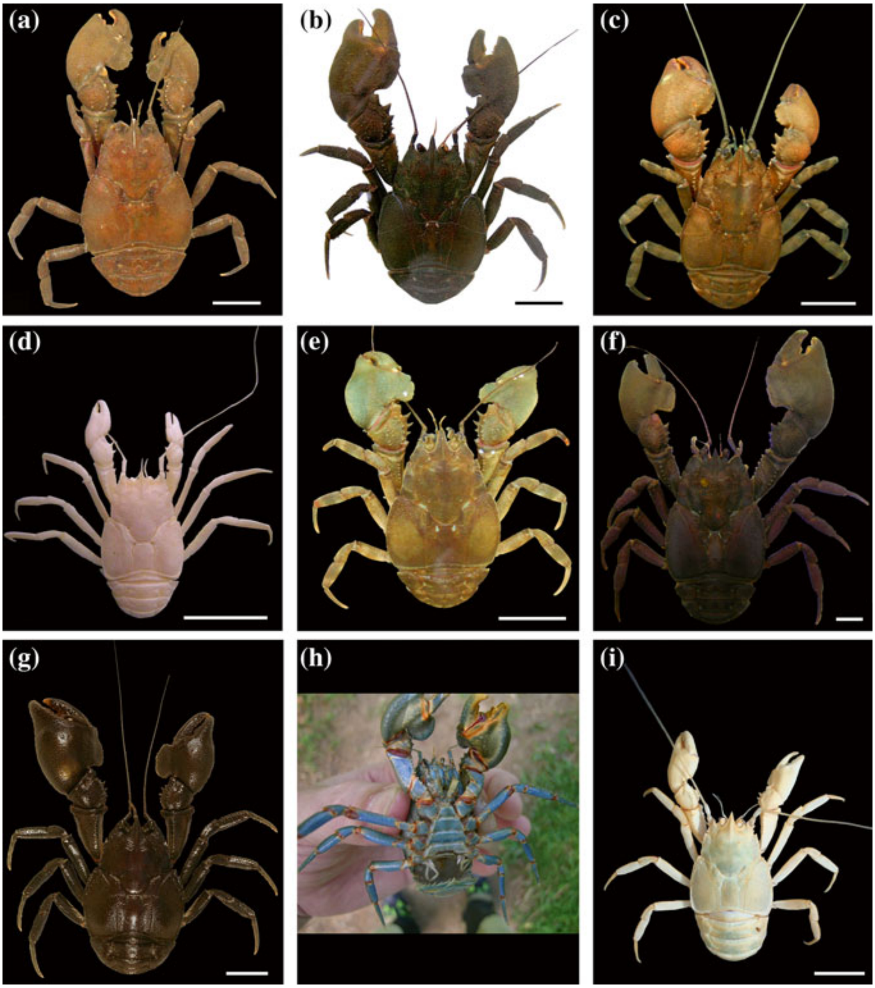


Fig. 2.3 A selection of *Aegla* species from Brazil. **a** *Aegla castro*, male, live specimen from Itatinga (SP), *Bar* 1 cm. **b** *Aegla franca*, male, live specimen from Claraval (MG), Bar. 1 cm. **c** *Aegla marginata*, male, live specimen from the type-locality, Morretes (PR), *Bar* 1 cm. **d** *Aegla microphthalma*, male, alcohol preserved specimen from the type-locality, Caverna Santana, Iporanga (SP), *Bar* 1 cm. **e** *Aegla paulensis*, male, live specimen from the type-locality, Paranapiacaba, Alto da Serra de Cubatão, (SP), *Bar* 1 cm. **f** *Aegla perobae*, male, live specimen from the type-locality, São Pedro (SP), *Bar* 5 mm. **g** *Aegla strinatii*, male, live specimen from the type-locality, das Ostras River/Gruta da Tapagem (also known as Caverna do Diabo), Jacupiranga (SP), *Bar* 1 cm, modified from original photo by Sérgio Schwarz da Rocha. **h** *Aegla schmitti*, male, live specimen from Iporanga (SP), note general body coloration on the ventral surface and leg joints; no bar included. **i** *Aegla cavernicola*, female, live specimen from the type-locality, Gruta das Areias, Iporanga (SP), *Bar* 1 cm; modified from original photo by Bruno Fernandes Takano. Key to Brazilian States: São Paulo (SP), Minas Gerais (MG), and Paraná (PR)

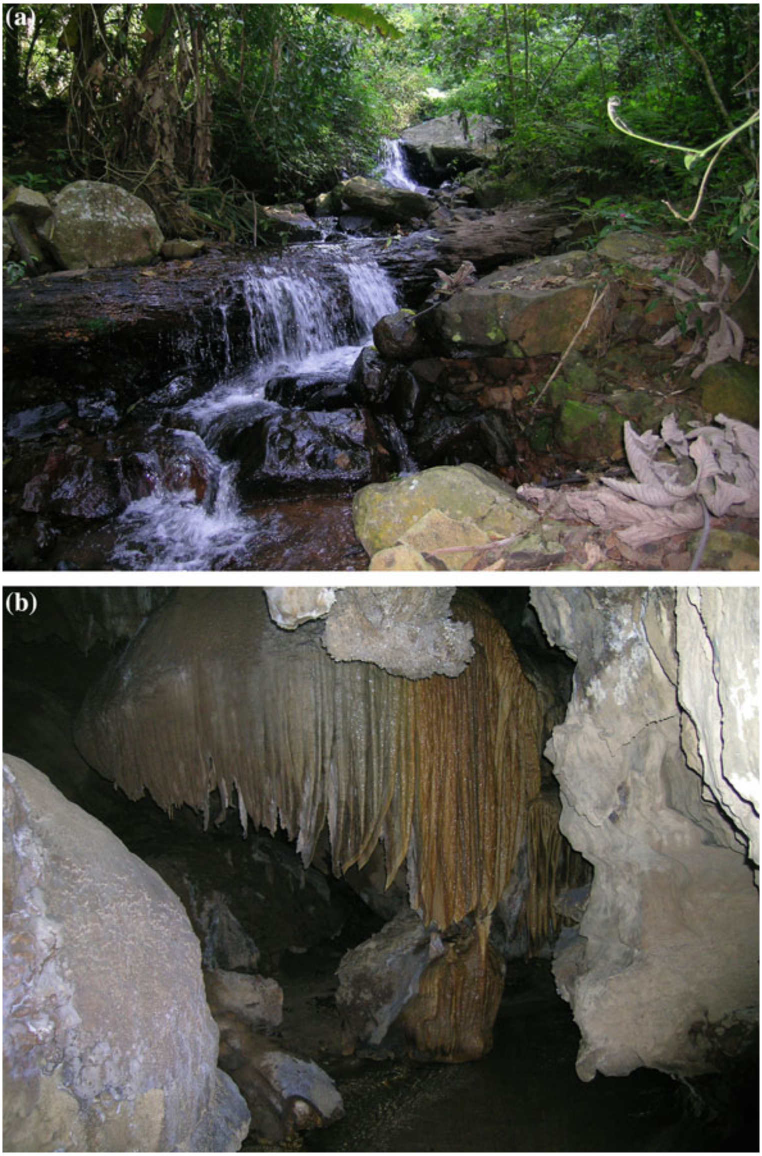


Fig. 2.4 Habitats. **a** Epigean habitat: type-locality of *Aegla perobae*, São Pedro, São Paulo state, Brazil. **b** Subterranean habitat: type-locality of an undescribed troglobite species from Gruta do Furo da Agulha, Alto Ribeira karst region, São Paulo state, Brazil

Freshwater aeglids are omnivorous, and feed on animal debris, algae, and the larvae of aquatic invertebrates (Bahamonde and López 1961; Rodrigues and Hebling 1978; Magni and Py-Daniel 1989; Castro-Souza and Bond-Buckup 2004; Bueno and Bond-Buckup 2004; Santos et al. 2008). During the day aeglids are

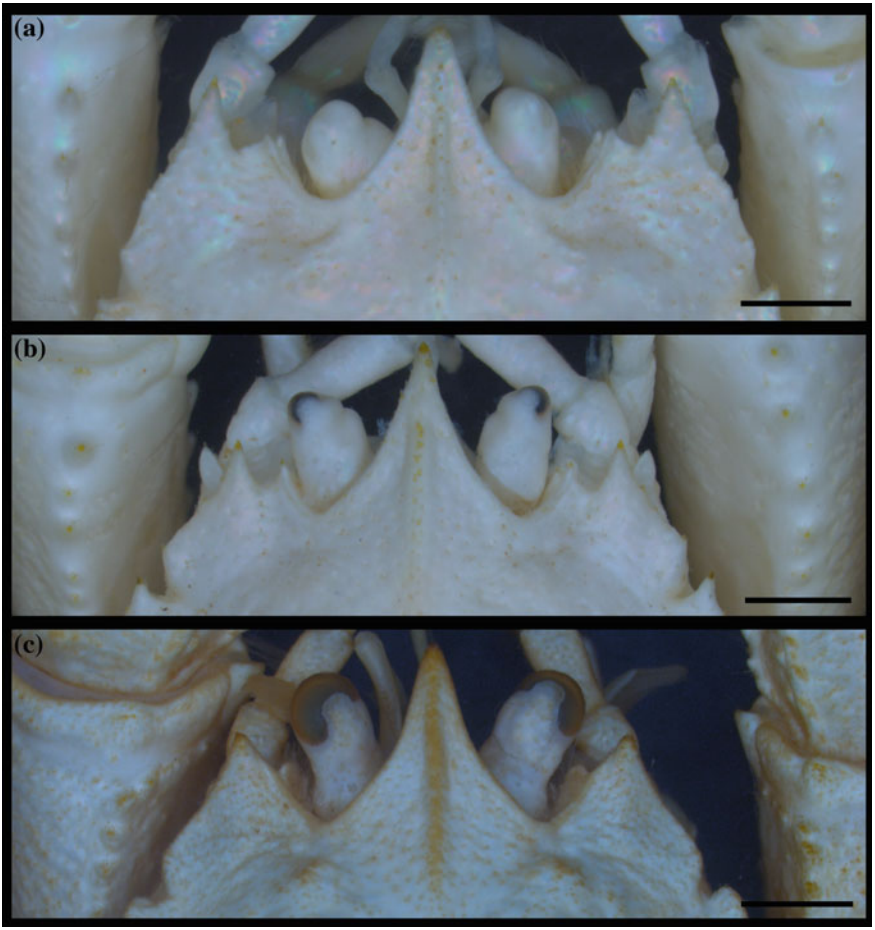


Fig. 2.5 Compound eyes. **a** Depigmentation of the cornea in the troglobitic species *Aegla microphthalma*. **b** Reduced pigmentation of the cornea in the troglobitic species *Aegla cavernicola*. **c** Pigmentation area of the cornea in *Aegla marginata* from epigean habitat. *Bar* 1 mm (**a**) and 2 mm (**b** and **c**)

usually inactive and seek protected spaces under rocks, pebbles, and leaf litter that accumulates on the riverbed (Noro and Buckup 2002; Gonçalves et al. 2006; Bueno et al. 2014). They are more active at night and move about in their quest for food and, when the time comes, for reproduction (Sokolowicz et al. 2007a; Bueno et al. 2007; Ayres-Peres et al. 2011b).

Population density estimates are available for a few species only. Density estimates for the troglobitic species, *Aegla microphthalma* and *A. leptochela*, are low, and less than one individual/m^2 (Moracchioli 1994; Maia et al. 2013). For species from epigean habitats, density estimates varied from as low as 2.8/m^2 for *Aegla* *franca* to as high as 9.05/m^2, 11.5 m^2 and 12/m^2 for *Aegla perobae, A. paulensis* and *A. platensis*, respectively (Bueno and Bond-Buckup 2000; Bueno et al. 2007, 2014b; Cohen et al. 2013).

2.2 Biology

2.2.1 *Population Size Structure and Sexual Dimorphism*

As a rule, male aeglids attain a larger body size than females (Swiech-Ayoub and Masunari 2001b; Noro and Buckup 2002; Fransozo et al. 2003; Boos et al. 2006; Viau et al. 2006; Bueno and Shimizu 2009; Teodósio and Masunari 2009; Cohen et al. 2011; Chiquetto-Machado et al. 2016). Body size dimorphism is a common feature in pleocyemate decapods, and has been generally interpreted to reflect different energy use by males and females (whereby females divert a significant amount of their energy toward reproduction, while males allocate most of their energy toward growth) (Hartnoll 1985). Other possible causes of body size dimorphism suggested for *Aegla* are differences in mortality rate, migration, responses to environmental conditions (Gonçalves et al. 2006), resource use (Silva-Gonçalves et al. 2009), and sexual selection (Cohen et al. 2011). Female aeglids tend to live longer than males (Silva-Castiglioni et al. 2006; Silva-Gonçalves et al. 2009; Cohen et al. 2011; Chiquetto-Machado et al. 2016), although the opposite (Trevisan and Santos 2011) as well as similar longevity in both sexes (Bahamonde and López 1961; Bueno and Bond-Buckup 2000; Swiech-Ayoub and Masunari 2001b; Boos et al. 2006) have also been reported.

Both adult male and female aeglids lack the first pair of abdominal pleopods. Female aeglids have well-developed uniramous two-segmented pairs of pleopods 2 through 5 (Fig. 2.6a), which they use for egg attachment and incubation. In males, pleopods 2 through 5 are either lacking altogether or are vestigial and resemble calcified knobs (Martin and Abele 1988) (Fig. 2.6b). This sexually dimorphic abdominal appendage trait can be used to determine the gender of freshwater aeglids. However, adult males with rudimentary pairs of pleopods 2–5 have been observed in two species: *Aegla perobae* Hebling and Rodrigues, 1977 (Moraes and Bueno 2015), and an undescribed troglobitic species (Bueno et al. 2014a) from Brazil (Fig. 2.6c). These rudimentary male pleopods are clearly shorter and less setose than the corresponding pairs of pleopods observed in adult females, but they are not vestigial, and, they are either one- or two-segmented.

Freshwater aeglids are heterochelous whereby the propodus and dactylus of the first pair of pereopods have a different size and shape to each other (Bueno and Shimizu 2009; Trevisan and Santos 2011) (Fig. 2.3), and there is only one reported exception (Noro and Buckup 2003). The heterochelous condition of the chelipeds is conspicuous in both sexes, and may even be noticeable in the late juveniles of some species (Bueno and Shimizu 2009). The chelipeds show a clear predominance for

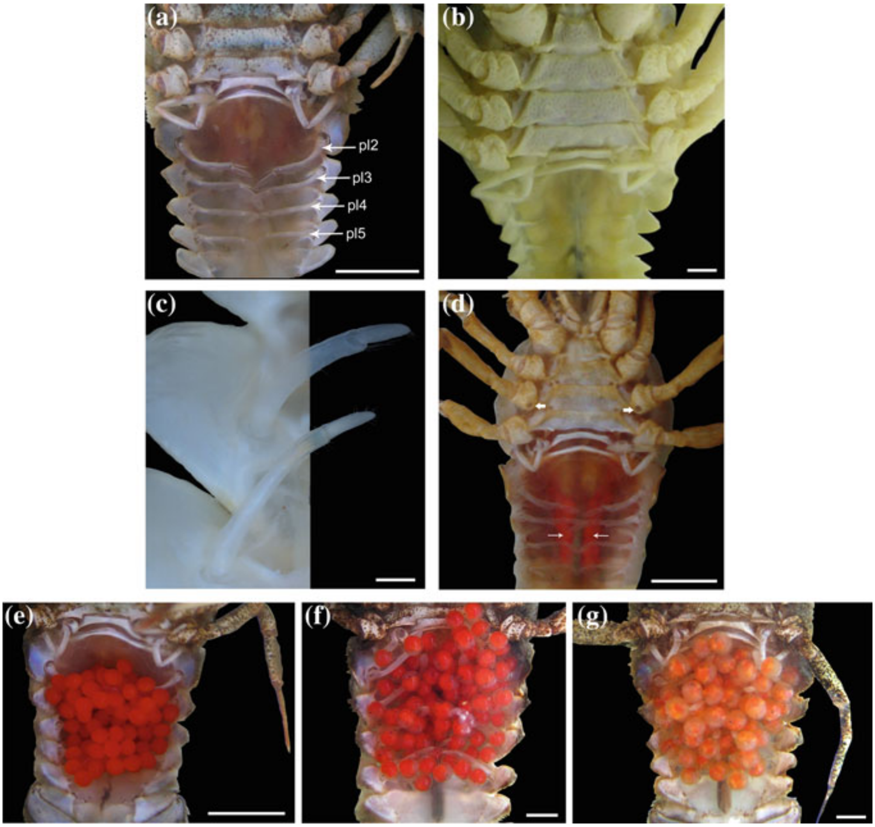


Fig. 2.6 Pleopods, late ovaries and eggs. **a** *Aegla franca*, adult female, live specimen from Claraval (MG); ventral view of pleon showing four pairs of well-developed uniramous and two-segmented pleopods 2 through 5; *Bar* 5 mm. **b** *Aegla paulensis*, adult male, alcohol preserved specimen from Jaraguá State Park, São Paulo (SP); ventral view of pleon. Note absence of pleopods 2 through 5; *Bar* 2 mm. Photo: Felipe P. A. Cohen. **c** Ventral view of pleon (one side only) of an undescribed troglobite, adult male, alcohol preserved specimen from Gruta do Lago Subterrâneo, Alto Ribeira karst region (SP), showing two (out of four) short two-segmented pleopods. *Black background* was positioned underneath distal portion of pleopods to provide contrast. *Bar* 0.5 mm. **d** *Aegla paulensis*, adult female, live specimen from Jaraguá State Park, São Paulo (SP). Ventral view of pleon showing the two posterior lobes of the ovaries at late maturation stage (*thin arrows*). Gonopore openings are also indicated (*bold arrows*) on the coxa of the third pair of pereopods. *Bar* 5 mm. **e**–**g** *Aegla franca*, ovigerous females, live specimens from Claraval (MG); **e** early eggs, *Bar* 5 mm; **f** intermediate eggs, *Bar* 2 mm; **g** late eggs, *Bar* 2 mm. Key to Brazilian States: São Paulo (SP) and Minas Gerais (MG)

left handedness, whereby the left is prevalently the most robust of the pair (Bahamonde and López 1961; López 1965; Rodrigues and Hebling 1978; Viau et al. 2006; Bueno and Shimizu 2009; Trevisan and Santos 2011). Adult males typically exhibit heavier and larger first chelipeds than adult females (Martin and Abele 1988) (Fig. 2.7a), and this sexually dimorphic trait has been well

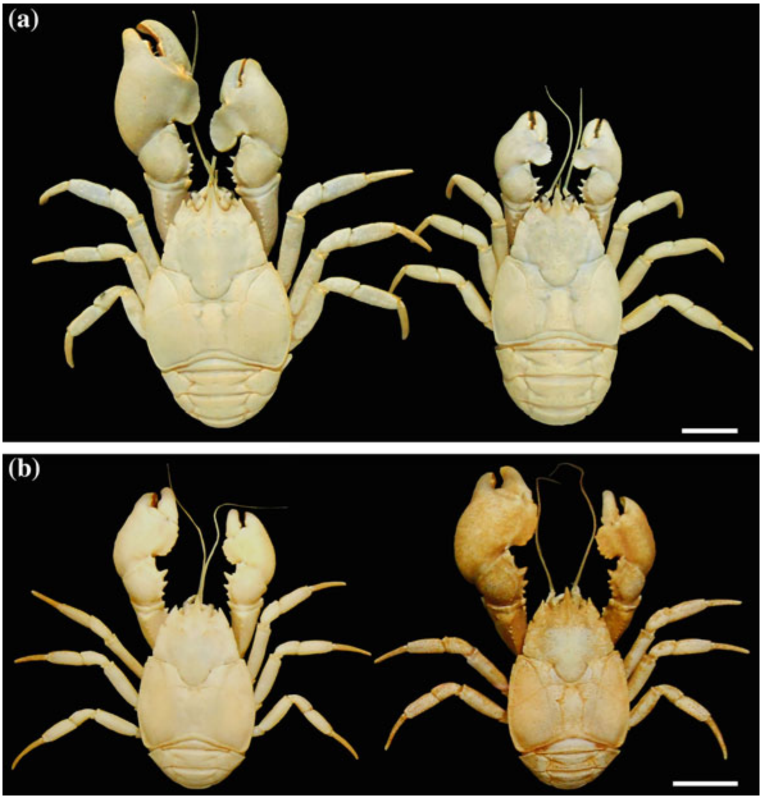


Fig. 2.7 Chelipeds: Sexual dimorphism and male morphotypes. **a** *Aegla schmitti*, sexual dimorphism of the pair of chelipeds between male (*left*) and female (*right*). Sexual dimorphism regarding the size of pleonal somites 2, 3 and 4 can also be noted. *Bar* 1 cm. **b** *Aegla franca*, morphotype I male (CL = 17.7 mm) and morphotype II male (CL = 18.7 mm) sampled in November 2005 and February 2006, respectively. CL: carapace length taken from right orbital sinus to posterior midpoint border of carapace. *Bar* 1 cm

documented in freshwater aeglids (Bahamonde and López 1961; López 1965; Colpo et al. 2005; Viau et al. 2006; Bueno and Shimizu 2009).

The increase in claw dimensions in adult male decapods is often associated with agonistic and/or reproductive behaviour (Mariappan et al. 2000). In most heterochelous decapod species reproductive activities are associated with the major chela, while non-sexual activities (such as food capturing and manipulation, and grooming) are usually associated with the minor claw (Mariappan et al. 2000). In *Aegla*, the major chela is often used in agonistic confrontations (Ayres-Peres et al. 2011a; Palaoro et al. 2014), and in *A. uruguayana* Schmitt, 1942, males use their major chela to defend females from other males (Viau et al. 2006).

The transition from juvenile to adult phase is referred to as morphometric maturity, and is usually marked by a pubertal molt to sexual maturity that has been achieved by allometric growth in some parts of the body in decapod crustaceans (e.g., chelipeds, abdomen, pleopods) (Hartnoll 1978). Dimensions of the chelae and the pleon are used to determine the average size at the onset of morphometric maturity in *Aegla* (Colpo et al. 2005; Viau et al. 2006; Bueno and Shimizu 2009). Females attain morphometric maturity at a smaller size than males (Swiech-Ayoub and Masunari 2001a; Colpo et al. 2005; Viau et al. 2006; Bueno and Shimizu 2009).

2.2.2 Reproduction

The development of gonads and the maturation of gametes probably start soon after the pubertal molt in both sexes. In females, the early development of the ovaries is initially confined to the cephalothoracic region (Viau et al. 2006; Sokolowicz et al. 2007b). Towards the end of the maturation phase the two posterior lobes of the ovaries gradually extend posteriorly into the pleon as two bright red colored strips, which can be easily observed through the thin and translucent cuticle covering the ventral surface of the pleon (Bueno and Shimizu 2008) (Fig. 2.6d). In the field, determination of the maximum extension of the posterior lobes of the ovaries along the pleon in relation to the pairs of pleopods is a helpful indicator of full ovarian maturation (gonadal or physiological maturity) and impending oviposition (Bueno and Shimizu 2008; Rocha et al. 2010). Functional maturity in female aeglids, therefore, coincides with full gonadal maturity.

Mating behavior has been described in detail in *Aegla platensis* by Almerão et al. (2010). Those authors report that males use their chelipeds to lift and rotate the body of the female during mating with fertilization probably occurring externally in the brood pouch. Fertilized eggs are held firmly attached to the pleopods. Eggs are large in size and few in number, usually in the lower hundreds [see Bueno and Shimizu (2008) for compilation on average egg size and number in some aeglid species]. There is a positive relationship between the number of eggs and the size of the female (Noro and Buckup 2002; Bueno and Shimizu 2008; Silva-Gonçalves et al. 2009). Three sequential stages of embryonic development are recognized according to the criteria established for *Aegla franca* by Bueno and Shimizu (2008): (1) early eggs, with an evenly distributed red yolk mass that occupies over 80 % of the egg volume, with no sign of developing compound eyes (Fig. 2.6e); (2) intermediate eggs, in which the yolk mass fills 50–80 % of the egg mass, with narrow dark pigmented area in each of the compound eyes (Fig. 2.6f); (3) late eggs, with the yolk mass reduced to less than 50 % of egg volume, with the embryo clearly discernible, and with large, round dark pigmented areas in the compound eyes (Fig. 2.6g).

The occurrence of ovigerous females in the population indicates the reproductive period in freshwater aeglids, and varies from markedly seasonal (4–7 months) to extended (8–12 months) (Table 2.1). In the southern hemisphere the seasonal reproductive period usually occurs between mid fall and late winter/early spring. Species with an extended reproductive pattern can be found in their reproductive phase for most of the year but they exhibit a conspicuous period of higher reproductive intensity that coincides with the same period of the year as the markedly seasonal pattern (López 1965; Bueno and Bond-Buckup 2000; Noro and Buckup 2002; Chiquetto-Machado et al. 2016), but *A. longirostri* Bond-Buckup and Buckup 1994 may be an exception to this (Colpo et al. 2005).

Aegla franca exhibits two adult male morphotypes (I and II), the latter (II) exhibiting larger and more robust first chelipeds than the former (I) (Fig. 2.7b). This difference is accomplished through changes in the allometry coefficient of claw dimensions (Bueno and Shimizu 2009). Adult male morphotypes have also been observed in *Aegla castro* (Takano et al. in press), *A. perobae*, *A. strinatii* and *A. paulensis* Schmitt, 1942 (Bueno, unpublished data), and all these species have a markedly seasonal reproductive period (Rodrigues and Hebling 1978; Rocha et al. 2010; Cohen et al. 2011; Bueno et al. 2014; (Takano et al. in press). It is not known whether adult male morphotypes also occur in aeglids that have an extended reproductive period.

Temporal variation in the proportion of coexisting morphotypes in the population of *Aegla franca* support the hypothesis that morphotype II adult males are the reproductive forms, because the proportion of morphotype II male in the population increases dramatically at the beginning of the mating season, coinciding with the period of late ovarian development of females (Fig. 2.8). Morphotype II male becomes numerically dominant by the time females are fully mature. Bueno and Shimizu (2009) suggested that morphotypes I and II represent a sequential shift from the non-reproductive to the reproductive phases respectively in the adult male population of *Aegla franca*. Functional maturity in adult males is therefore associated with the appearance of morphotype II, although mating will only take place when females are fully mature and ready to spawn. Larger and stronger chelae in adult males are advantageous in aggressive interactions between males during the mating period (Viau et al. 2006). In the case of *Aegla franca*, however, sexual selection would only involve adult male morphotype II individuals.

2.2.3 Postembryonic Development

The postembryonic development in *Aegla* is direct (see Sect. 2.1 this chapter), though morphological traits associated with zoeal and megalopal stages can still be recognized within the developing egg (Lizardo-Daudt and Bond-Buckup 2003) (Fig. 2.9a).

Morphological descriptions of newly-hatched juveniles are currently available for the following species from Brazil: *A. prado*, *A. violacea* Bond-Buckup and Buckup 1994, *A. platensis*, *A. ligulata* Bond-Buckup and Buckup 1994*, A. longirostri, A. franca*, *A. schmitti* Hobbs III, 1978, *A. paulensis* and *A. perobae*

Table 2.1 Reproductive period of freshwater aeglid species from different geographic localities

Aeglid species	Location (country)	Latitude (S)	Reproductive period (number of months)	References
Aegla franca (a)	Claraval (Brazil)	20°18′	May–August (4)	Bueno and Shimizu (2008)
Aegla parana (a)	União da Vitória (Brazil)	26°00′	April–July (4)	Grabowski et al. (2013)
Aegla castro (a)	Itatinga (Brazil) Ponta Grossa (Brazil)	23°09′ 25°05′	April–August (5) May–October (6)	Takano et al., (in press) Swiech-Ayoub and Masunari (2001b)
Aegla perobae (a)	São Pedro (Brazil)	22°31′ 22°33′	April–August (5) April–October (7)	Bueno et al. (2014) Rodrigues and Hebling (1978)
Aegla paulensis (a)	Paranapiacaba (Brazil) Jaraguá, (Brazil)	23°47′ 23°27′	May or June–October (5–6) March–July or August (5–6)	López (1965) Cohen et al. (2011)
Aegla strinatii (a)	Jacupiranga (Brazil)	24°38′	May–September (5)	Rocha et al. (2010)
Aegla franciscana (a)	São Francisco de Paula (Brazil)	29°26′	June–October (5)	Gonçalves et al. (2006)
Aegla leptodactyla (a)	São José dos Ausentes (Brazil)	28°38′	April–September (6)	Noro and Buckup (2002)
Aegla schmitti (b)	Alto Ribeira Touristic State Park (Brazil) Piraquara (Brazil)	24°31′ 25°29′	April–December (9) April–November (8)	Chiquetto-Machado et al. 2016 Teodósio and Masunari (2009)
Aegla laevis (b)	El Monte (Chile)	33°42′	March–October (8)	Bahamonde and López (1961)
Aegla longirostri (b)	Itaára (Brazil)	29°24′	July–March (9)	Colpo et al. (2005)
Aegla platensis (b)	Taquara (Brazil)	29°46′	January–December (12)	Bueno and Bond-Buckup (2000)
Aegla uruguayana (b)	San Antonio de Areco (Argentina)	34°14′	January–December (12)	Viau et al. (2006)

All species are from lotic environment

Reproductive period: (a) markedly seasonal, (b) extended. Modified and updated from Bueno and Shimizu (2008)

(Bond-Buckup et al. 1996; Bueno and Bond-Buckup 1996; Bond-Buckup et al. 1999; Francisco et al. 2007; Teodósio and Masunari 2007; Moraes and Bueno 2013, 2015). The resemblance between newly-hatched juvenile and adult forms in aeglids include general similarities in body shape, a complete set of body segments

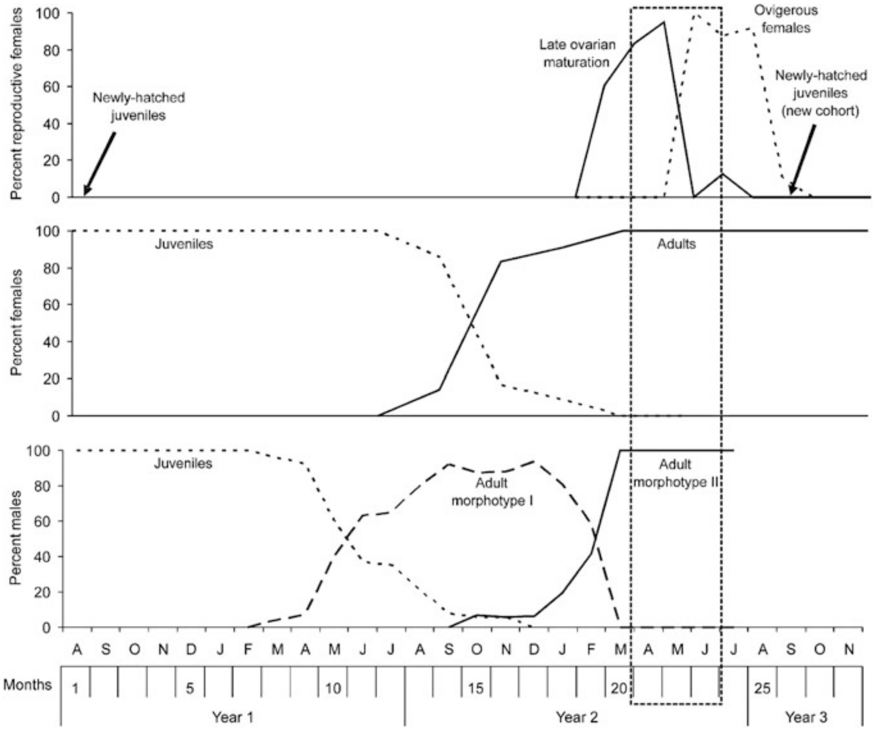


Fig. 2.8 Life cycle of *Aegla franca*. All representations refer to one single cohort. The following selected biological aspects are depicted: *Top section* the hatching moment of juveniles starting cohort, late ovarian development as seen through the thin cuticle of the pleon, followed by the markedly seasonal reproductive pattern (ovigerous females). *Middle* and *Bottom sections* Morphometric maturity for females (*middle*) and males (*bottom*) indicating the temporal transition from the juvenile to the adult phase. *Bottom section* includes temporal transition from morphotypes I and II in adult males. *Dashed line rectangle* indicates mating period (20–22 months after hatching of juveniles) when late maturation of the ovaries and the subsequent appearance of ovigerous females are highest, and when only the reproductive morphotype II males are present in the population

with corresponding functional pairs of appendages (except for pleopods), their general behavior, and benthic habits (Fig. 2.9b).

Though pleopods are reported to be absent in newly-hatched juveniles of *Aegla platensis*, *A. longirostri*, *A. ligulata*, *A. prado, A. violacea* and *A. schmitti* (Bond-Buckup et al. 1996, 1999; Bueno and Bond-Buckup 1996; Teodósio and Masunari 2007), four pairs of rudimentary pleopods have been observed in unsexed hatchlings of *Aegla franca* (Bueno unpublished data), *A. paulensis* and *A. perobae* (Moraes and Bueno 2013, 2015) (Fig. 2.9c). Moraes and Bueno (2013) speculated that those rudimentary pleopods might develop further in adult females, or might regress to calcified knobs in adult males [or develop further but still remain rudimentary as in males of *Aegla perobae* and males of an undescribed troglobitic species (Bueno et al. 2014a; Moraes and Bueno 2015)].

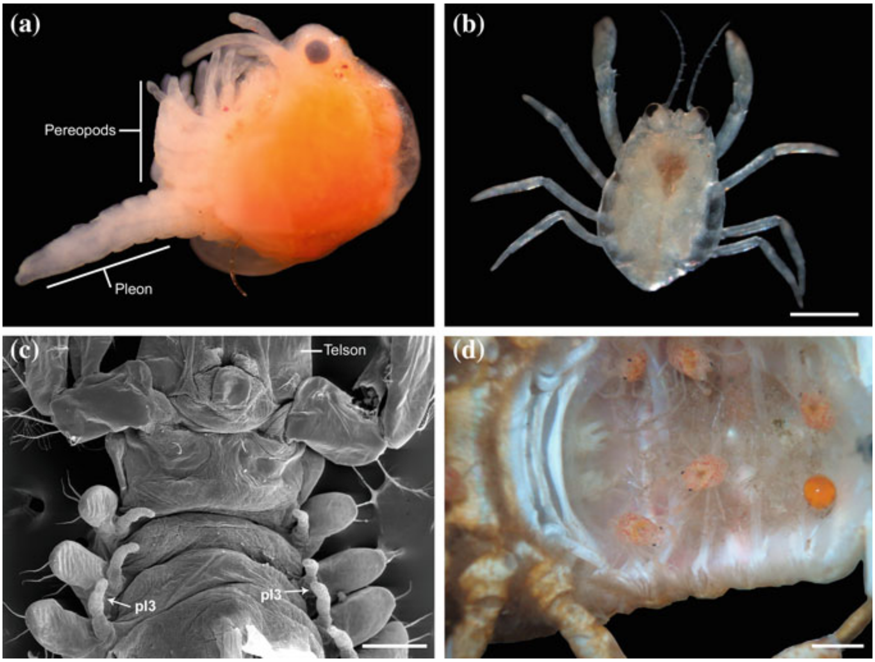


Fig. 2.9 Embryonic and post-embryonic development, and parental care. **a** Late embryo of *Aegla franca* removed from the egg shell. Note presence of larval traits such as non-functional pereopods, absence of uropods and slender pleon (as compared to the broader pleon in the newly-hatched juvenile); no bar included. **b** Newly-hatched juvenile of *Aegla perobae*. *Bar* 500 µm. **c** Newly-hatched juvenile of *Aegla paulensis*: Scanning Electron Microscopy (SEM) micrograph of the ventral surface of pleon showing pairs of rudimentary pleopods (third pair indicated). *Bar* 100 µm. From Moraes and Bueno (2013); Zootaxa 3635(5): 501–519. **d** *Aegla paulensis*: Live female still carrying one egg and few live newly-hatched juveniles in the brood chamber. *Bar* 2 mm

Newly-hatched juveniles remain in the abdominal brood chamber formed by the flexed female pleon where they are under maternal care for a few days (Bahamonde and López 1961; Rodrigues and Hebling 1978; Bueno and Bond-Buckup 1996; Bond-Buckup et al. 1999; López-Greco et al. 2004; Francisco et al. 2007; Moraes and Bueno 2013) (Fig. 2.9d). Later on, the epibenthic juveniles leave the brood chamber and move to areas of low water flow and seek protection under rocks, pebbles, and leaf and debris accumulated on the riverbed (López 1965). Aeglid juveniles tend to remain with the parental population and show limited dispersal capacity. Direct development, parental care, and limited juvenile dispersal are important life-history strategies observed in several true freshwater decapods, and these traits are related to the successful colonization of freshwater habitats (Vogt 2013; Chap. 6 in this book).

2.2.4 Latitudinal Gradient and Climate Effect

Extreme climatic conditions found within the distributional range of aeglids affects their distribution, development, and evolution (Schmitt 1942b). The latitudinal range of aeglid distribution (from 50 °S in Chile to 20 °S in Brazil) includes temperate and subtropical regions of Neotropical South America. The reproductive period in freshwater aeglids may also vary according to latitude and regional environmental differences in temperature and rainfall (Bueno and Shimizu 2008). Freshwater aeglids from colder temperate areas that live at high latitudes have an extended reproductive period (Bueno and Bond-Buckup 2000; Colpo et al. 2005; Viau et al. 2006), while those from streams at low latitudinal regions have a marked seasonal reproductive pattern (López 1965; Rodrigues and Hebling 1978; Bueno and Shimizu 2008; Rocha et al. 2010; Cohen et al. 2011; Grabowski et al. 2013; Bueno et al. 2014) (Fig. 2.10a). The effect of latitudinal gradient on the reproductive period of freshwater aeglids is the opposite of that observed in benthic marine decapods (where the reproductive period is extended in tropical species living at lower latitudes and seasonal in species from temperate regions at higher latitudes) (Bauer and Rivera Vega 1992; Bauer 1992; Castilho et al. 2007).

Contrasting regional climatic conditions of temperature and rainfall have a strong influence on the reproductive pattern in freshwater aeglids (Bueno and Shimizu 2008). The reproductive period is shorter in localities with a wide variation in rainfall (expressed as standard deviation >60 mm) than in sites with the opposite climate conditions (Bueno and Shimizu 2008; Fig. 2.10b). For example, the climate of Itaára, State of Rio Grande do Sul, southern Brazil (latitude 29 °S) is characterized by alternating warm and cool seasons and evenly distributed monthly rainfall that has only a minor effect on water flow velocity throughout the year (Fig. 2.11a). The reproductive period of *Aegla longirostri* extends for 9 months, from winter (July) to late summer (March), when species breed twice with two recruitment pulses per year (Colpo et al. 2005). Itaára has favorable conditions for the hatching and recruitment of juveniles for most of the year, which could explain the long reproductive and recruitment periods in the populations of species that live there.

In contrast, the climate in São Pedro, State of São Paulo, southeastern Brazil (latitude 22 °S) is characterized by the alternation of a hot rainy season with a cool dry season (Fig. 2.11b). *Aegla perobae* shows a marked seasonal reproductive period of 5 months (from April to August), with the production of a single egg mass, and a single recruitment pulse per year (Bueno et al. 2014). The reproductive period coincides with the cool dry season, whereby juveniles hatch between July and August when the rainfall and stream flow velocities are at their lowest. The timing of the hatching of juveniles to coincide with the times of the year with low rainfall is a key factor in the life cycle of that aeglid species because it benefits successful local recruitment and guarantees that juveniles will be large enough to withstand the stronger water currents associated with the peak of the following hot rainy season 6 months later. Similar relationships between a marked reproductive

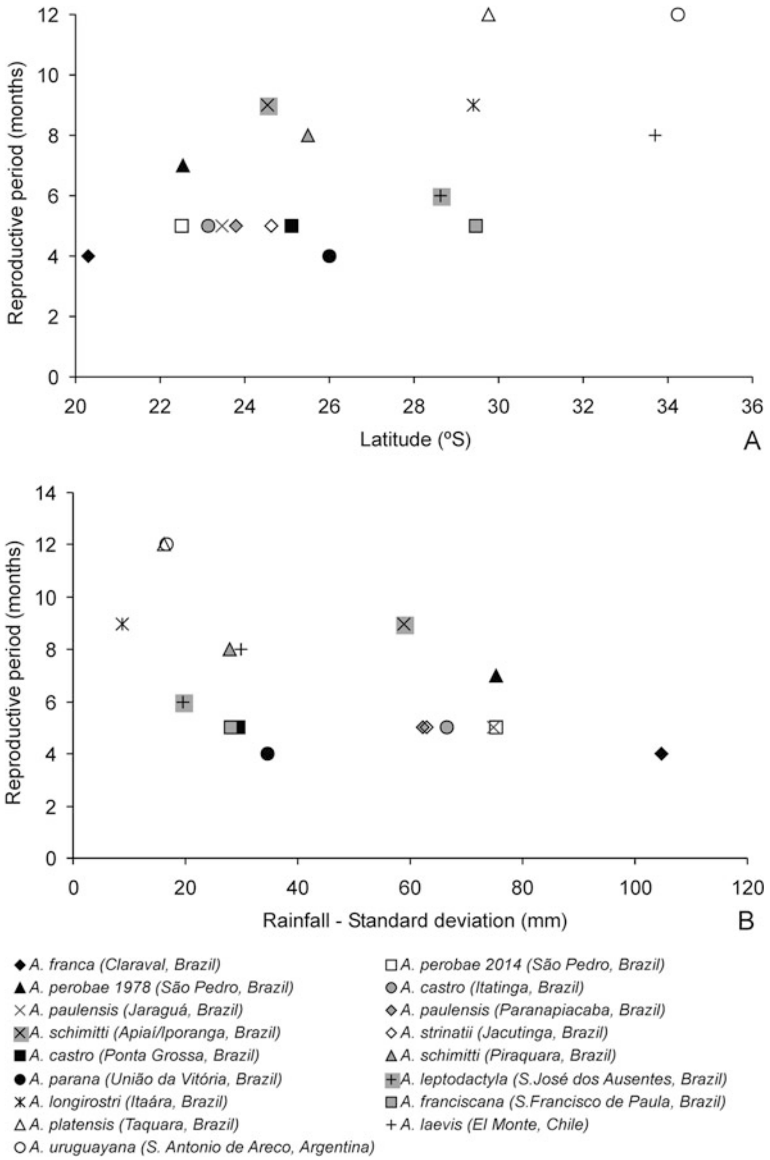
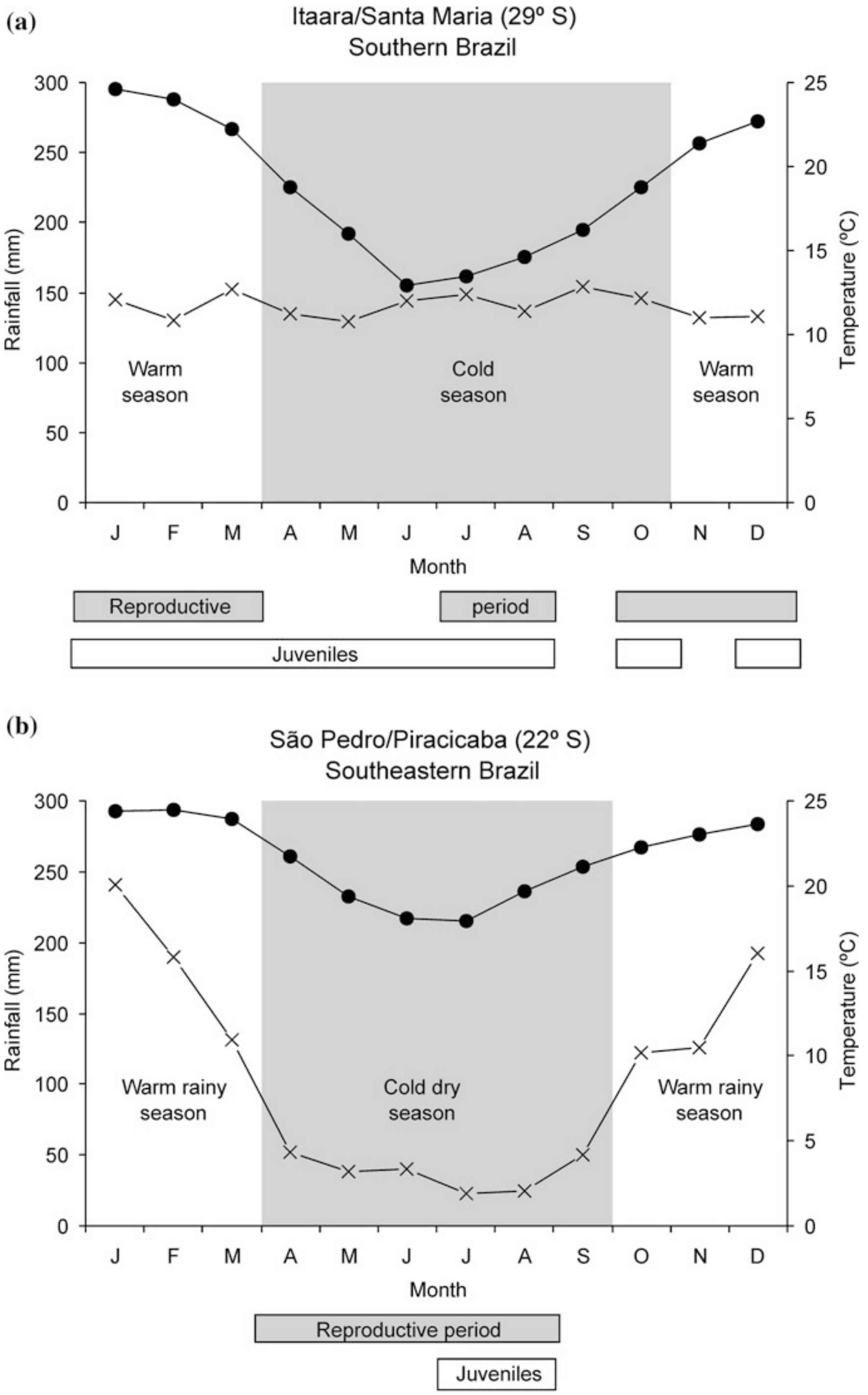


Fig. 2.10 Latitudinal gradient and rainfall effect on reproductive pattern. Variation in length of the reproductive period of aeglid species in relation to latitude (**a**), and rainfall variability (**b**). All species are from lotic habitats. References are the same as those indicated on Table 2.1

period and the regional climate characteristics have also been reported for other aeglid species from localities at low latitudes, such as *A. franca, A. strinatii* and *A. paulensis* (Bueno and Shimizu 2008; Rocha et al. 2010; Cohen et al. 2011).


(a)
Itaara/Santa Maria (29º S)
Southern Brazil
Rainfall (mm)
300
250
200
150
100
50
0
Temperature (ºC)
25
20
15
10
5
0
Warm season
Cold season
Warm season
J F M A M J J A S O N D
Month
Reproductive
period
Juveniles
(b)
São Pedro/Piracicaba (22º S)
Southeastern Brazil
Rainfall (mm)
300
250
200
150
100
50
0
Temperature (ºC)
25
20
15
10
5
0
Warm rainy season
Cold dry season
Warm rainy season
J F M A M J J A S O N D
Month
Reproductive period
Juveniles

◀ **Fig. 2.11** Contrasting climatic patterns, reproductive pattern and recruitment. Relationship between regional climatic pattern and reproductive pattern/timing of hatching of juveniles of *Aegla longirostri* from Itaára (**a**) and of *Aegla perobae* from São Pedro (**b**). Monthly means of rainfall and temperature from Itaára/Santa Maria and from São Pedro/Piracicaba were obtained from daily collection of weather data from each location, available at www.bdclima.cnpm.embrapa.br

These examples suggest the existence of environmental selective pressures at lower latitudes that favour a seasonal reproductive pattern. The increasingly harsh climatic conditions that are found at lower latitudes might have constrained the breeding period progressively as aeglids dispersed from high to low latitudes along the eastern side of South America in ancient times (Bueno and Shimizu 2008).

2.3 Conservation

Freshwater ecosystems are particularly vulnerable to human activities, so much so that they are currently suffering a more dramatic decline in biodiversity than terrestrial ecosystems (Abell 2002; Dudgeon et al. 2006). Freshwater decapods are important macroinvertebrates in benthic communities and their conservation status and global diversity have received a lot of recent attention (Bond-Buckup et al. 2008; Crandall and Buhay 2008; De Grave et al. 2008; Yeo et al. 2008; Cumberlidge et al. 2009; Pérez-Losada et al. 2009; Collen et al. 2014; De Grave et al. 2015).

Table 2.2 shows the conservation status of all 78 species of freshwater aeglids as of 2015. This data compilation is mostly based on the latest official lists from Brazil (Brazil—Ministério do Meio Ambiente 2014; ICMBio—Instituto Chico Mendes de Conservação da Biodiversidade 2014) and Chile (Chile—Ministerio del Medio Ambiente 2014a; Chile—Ministerio del Medio Ambiente 2014b). The conservation status of species not included on those official lists was based on information available in the scientific literature. All categories and criteria were assessed according to IUCN guidelines (IUCN 2013), and most species fall under criterion B, which uses data on geographic range [(extent of occurrence (EOO) and/or area of occupancy (AOO)], distribution patterns (high endemism and/or severe fragmentation in the distributional pattern of highly endemic species resulting in reproductively isolated subpopulations), and habitat quality (continued degradation of environmental conditions and habitat loss).

Aegla is probably the most severely threatened taxon of all decapod crustaceans found in South American freshwaters. More than half (43/78 species, 55.13 %) of freshwater aeglids belong to one of the three threatened categories in the following percentage (Fig. 2.12): Critically Endangered (CR) with twelve species (15.38 %), Endangered (EN) with 22 species (28.21 %), and Vulnerable (VU) with 9 species (11.54 %). The major threats impacting most of the threatened species of aeglids (CR, EN and VU) include the ongoing deterioration of habitat quality that fragments distributional ranges into small disjunct areas of occupancy.

Table 2.2 IUCN categories and criteria, and country of occurrence to all 78 known species and subspecies of *Aegla* as of 2015

IUCN categories and aeglid species	Countries	IUCN criteria	Remarks	References
Critically endangered (CR), EOO < 100 km^2*; AOO* < 10 km^2				
Aegla affinis Schmitt, 1942	AR CH	B1ab (iii) + 2ab (iii)	Previously suggested category: LC	3, 4, 5
Aegla brevipalma Bond-Buckup and Santos, 2012	BR	B2ab(iii)	Distribution restricted to one location	1, 2, 6
Aegla cavernicola Türkay, 1972	BR	B2ab(iii, v)	Troglobite; one location; Previously suggested category: VU	1, 2, 7, 8
Aegla denticulata lacustris Jara, 1989	CH	B1ab (iii) + 2ab (iii)	Previously suggested category: NT	3, 4, 5
Aegla franca Schmitt, 1942	BR	B2ab(iii)	No longer found in type-locality; fragmented distribution	1, 2, 9
Aegla lata Bond-Buckup and Buckup, 1994	BR	B1ab(i, iii, iv)	No longer found in type-locality; one location	1, 2, 10
Aegla leptochela Bond-Buckup and Buckup, 1994	BR	B2ab(iii, v)	Troglobite; one location; Previously suggested category: VU	1, 2, 8, 11
Aegla ludwigi Santos and Jara, 2013	BR	B1ab(iii)	Distribution restricted to one location	12
Aegla meloi Bond-Buckup and Santos, 2015	BR	B2ab(iii)	Distribution restricted to one location	27
Aegla microphthalma Bond-Buckup and Buckup, 1994	BR	B2ab(iii, v)	Troglobite; one location	1, 2, 11
Aegla perobae Hebling and Rodrigues, 1977	BR	B2ab(iii)c (iv)	Fragmented distribution; population size fluctuation observed and estimated	1, 2, 13
Aegla renana Bond-Buckup and Santos, 2010	BR	B2ab(iii)	Distribution restricted to one location	1, 2, 14
Endangered (EN) EOO < 5000 km^2*; AOO* < 500 km^2				
Aegla bahamondei Jara, 1982	CH	B1ab (iii) + 2ab (iii)	Previously suggested category: VU	3, 4, 5, 15
Aegla camargoi Buckup and Rossi, 1977	BR	B2ab(iii)	Previously suggested category: LC	1, 2, 16

(continued)

Table 2.2 (continued)

IUCN categories and aeglid species	Countries	IUCN criteria	Remarks	References
Aegla concepcionensis Schmitt, 1942	CH	B1ab (iii) + 2ab (iii)	Previously suggested category in 1998: VU (ref. 17); reported to be Extinct in the Wild (EX) in 2002 (ref. 5); suggested category in 2009: CR under A2ae + B1ab(I,iii,v) (ref. 16)	3, 4, 5, 15, 16, 17
Aegla expansa Jara, 1992	CH	B1ab (iii) + 2ab (iii)	Previously suggested category in 1998: Data deficient (DD) (ref. 17); reported to be Extinct in the Wild (EX) in 2002 (ref. 5)	3, 4, 5, 15, 17
Aegla georginae Santos and Jara, 2013	BR	B1ab(iii)	Number of locations < 5	12
Aegla inermis Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: VU	1, 2, 16
Aegla itacolomiensis Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: LC	1, 2, 16
Aegla laevis (Latreille, 1818)	CH	B1ab (iii) + 2ab (iii)	Previously suggested category: CR	3, 4, 5
Aegla lancinhas Bond-Buckup and Buckup, 2015	BR	B1B2ab (iii)	Number of locations = 5	27
Aegla leachi Bond-Buckup and Buckup, 2012	BR	B1ab (iii) + 2ab (iii)	Previously suggested category: VU	1, 2, 6
Aegla loyolai Bond-Buckup and Santos, 2015	BR	B1B2ab (iii)	Number of locations = 5	27
Aegla manuinflata Bond-Buckup and Santos, 2009	BR	B1ab (iii) + 2ab (iii)	Previously suggested category: VU; 3 locations	1, 2, 18
Aegla oblata Bond-Buckup and Santos, 2012	BR	B1ab(iii)	Previously suggested category: VU	1, 2, 6
Aegla obstipa Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: VU	1, 2, 16
Aegla occidentalis Jara et al., 2003	CH	B1ab (iii) + 2ab (iii)	Previously suggested category: LC	3, 4, 16
Aegla papudo Schmitt, 1942	CH	A2ce	Previously suggested category: CR	3, 4, 5

(continued)

Table 2.2 (continued)

IUCN categories and aeglid species	Countries	IUCN criteria	Remarks	References
Aegla plana Buckup and Rossi, 1977	BR	B1ab(iii)	Previously suggested category: LC	1, 2, 16
Aegla pomerana Bond-Buckup and Buckup, 2010	BR	B1ab(iii)	Distribution restricted to 2 locations	1, 2, 19
Aegla rossiana Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: LC	1, 2, 16
Aegla strinatii Türkay, 1972	BR	B2ab(iii)	Troglophile, two locations	1, 2, 20
Aegla talcahuano Schmitt, 1942	CH	B1ab (iii) + 2ab (iii)	Previously suggested category: VU	3, 4, 5, 15, 17
Aegla violacea Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: VU	1, 2, 16
Vulnerable (VU), EOO < 20,000 km^2*; AOO* < 2000 km^2				
Aegla cholchol Jara and Palacios, 1999	CH	B1ab (iii) + 2ab (iii)	Possible assemblage of cryptic species	3, 4, 21
Aegla grisella Bond-Buckup and Buckup, 1994	BR	B1ab(iii)		1, 2
Aegla inconspicua Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: LC	1, 2, 16
Aegla leptodactyla Buckup and Rossi, 1977	BR	B1ab(iii)	Previously suggested category: LC	1, 2, 16
Aegla ligulata Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: LC	1, 2, 16
Aegla manni Jara, 1980	CH	B1ab (iii) + 2ab (iii)	Previously suggested category: Data Deficient	3, 4, 17
Aegla spectabilis Jara, 1986	CH	B1ab (iii) + 2ab (iii)	Previously suggested category: CR under A2ae + B1ab(I,iii,v)	3, 4, 5
Aegla spinipalma Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: LC	1, 2, 16

(continued)

Table 2.2 (continued)

IUCN categories and aeglid species	Countries	IUCN criteria	Remarks	References
Aegla spinosa Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: LC	1, 2
Near threatened (NT)				
Aegla hueicollensis Jara and Palacios, 1999	CH		Previously suggested category: VU	3, 4, 5
Aegla muelleri Bond-Buckup and Buckup, 2010	BR		Category NT suggested by ICMBio/Ministério do Meio Ambiente (Brazil); publication due 2016	22
Aegla prado Schmitt, 1942	BR UR		Previously suggested category: LC; category NT suggested by ICMBio/Ministério do Meio Ambiente (Brazil); publication due 2016	16, 22
Aegla riolimayana Schmitt, 1942	AR CH			16
Least concern (LC)				
Aegla abtao Schmitt, 1942	CH			3, 4
Aegla alacalufi Jara and López, 1981	CH		Previously suggested category: VU	3, 4, 5
Aegla araucaniensis Jara, 1980	CH			3, 4
Aegla castro Schmitt, 1942	BR			16
Aegla denticulata denticulata Nicolet, 1849	CH			3, 4
Aegla franciscana Buckup and Rossi, 1977	BR		Possible assemblage of cryptic species	16, 21
Aegla humahuaca Schmitt, 1942	AR			16
Aegla intercalata Bond-Buckup and Buckup, 1994	AR			16
Aegla jarai Bond-Buckup and Buckup, 1994	BR		Possible assemblage of cryptic species	16, 21
Aegla jujuyana Schmitt, 1942	AR			16
Aegla longirostri Bond-Buckup and Buckup, 1994	BR		Possible assemblage of cryptic species	16, 23

(continued)

Table 2.2 (continued)

IUCN categories and aeglid species	Countries	IUCN criteria	Remarks	References
Aegla marginata Bond-Buckup and Buckup, 1994	BR		Possible assemblage of cryptic species	16, 21
Aegla neuquensis Schmitt, 1942	CH			3, 4
Aegla odebrechtii Müller, 1876	BR			16
Aegla parana Schmitt, 1942	BR AR		Possible assemblage of cryptic species	16, 21
Aegla parva Bond-Buckup and Buckup, 1994	BR			16
Aegla paulensis Schmitt, 1942	BR		Possible assemblage of cryptic species	16, 24
Aegla pewenchae Jara, 1994	CH			3, 4
Aegla platensis Schmitt, 1942	BR AR UR PA		Possible assemblage of cryptic species	16, 25
Aegla ringueleti Bond-Buckup and Buckup, 1994	AR			16
Aegla rostrata Jara, 1977	CH			3, 4
Aegla sanlorenzo Schmitt, 1942	AR			16
Aegla scamosa Ringuelet, 1948	AR			16
Aegla schmitti Hobbs III, 1978	BR			16
Aegla septentrionalis Bond-Buckup and Buckup, 1994	AR BO			16
Aegla serrana Buckup and Rossi, 1977	BR			16
Aegla singularis Ringuelet, 1948	BR AR			16
Aegla uruguayana Schmitt, 1942	BR AR UR		Possible assemblage of cryptic species	16, 26

(continued)

Table 2.2 (continued)

IUCN categories and aeglid species	Countries	IUCN criteria	Remarks	References
Not evaluated (NE)				
Aegla carinata Bond-Buckup and Loureiro, 2014	UR			
Aegla intermedia Girard, 1855	CH			
Aegla saltensis Bond-Buckup and Jara, 2010	AR			

Key to countries: *AR* Argentina; *BO* Bolivia; *BR* Brazil; *CH* Chile *PA* Paraguay; *UR* Uruguay

Key to Criteria (IUCN 2013)

A2: Population size reduction, observed, estimated, inferred, or suspected in the past where the causes of reduction may not have ceased OR may not be understood or may not be reversible, base on

(c): a decline in area of occupancy (AOO), extent of occurrence (EOO) and/or habitat quality, and

(e): effects of introduced taxa, hybridization, pathogens, pollutants, competitors or parasites

B1: Extent of occurrence (EOO); B2: Area of occupancy (AOO). Values of EOO and AOO to each threatened category (CR, EN or VU) indicated in the Table

(a) severely fragmented OR number of locations (CR = 1; EN $\leq$ 5; VU $\leq$ 10)

(b) continuing decline observed, estimated, inferred or projected in any of

(i) extent of occurrence

(iii) area, extent and/or quality of habitat

(iv) number of locations or subpopulations

(v) number of mature individuals

References: *1* Brazil–Ministério do Meio-Ambiente (2014); *2* ICMBio–Instituto Chico Mendes de Conservação da Biodiversidade (2014); *3* Chile–Ministerio del Medio Ambiente (2014a); *4* Chile–Ministerio del Medio Ambiente (2014b); *5* Pérez-Losada et al. (2002b); *6* Santos et al. (2012); *7* Türkay (1972); *8* Machado et al. (2008); *9* Bueno et al. (2007); *10* Galvês et al. (2007); *11* Bond-Buckup and Buckup (1994); *12* Santos et al. (2013); *13* Bueno et al. (2014); *14* Santos et al. (2010); *15* Jara et al. (2006); *16* Pérez-Losada et al. (2009); *17* Bahamonde et al. (1998); *18* Santos et al. (2009); *19* Bond-Buckup et al. (2010b); *20* Rocha and Bueno (2011); *21* Pérez-Losada et al. (2004); *22* Bueno SLS (personal communication); *23* Marchiori et al. (2014); *24* Moraes et al. (2014); *25* Marchiori et al. (2015); *26* Giri and Collins (2014); *27* Santos et al. (2015)

A few aeglid species were once considered extinct in the wild. The endemic Chilean species *A. concepcionensis* Schmitt, 1942 was initially assessed as vulnerable (VU) by Bahamonde et al. (1998), but a few years later this species, together with *A. expansa* Jara, 1992 from Chile, were both reported to be extinct in the wild (EX) (Pérez-Losada et al. 2002b). Later, in 2006, *A. concepcionensis* and *A. expansa* were rediscovered in a single hydrographic basin outside their previously known area of distribution (Jara et al. 2006; Pérez-Losada et al. 2009), and *A. concepcionensis* was assessed as CR under criteria A2ae + B1ab(i, iii, v) by Pérez-Losada et al. (2009). The most recent evaluation of the conservation status of these two species in 2014 indicates that both *A. concepcionensis* and *A. expansa* are now assessed as endangered (EN) (Chile—Ministerio del Medio Ambiente 2014a; Chile—Ministerio del Medio Ambiente 2014b).

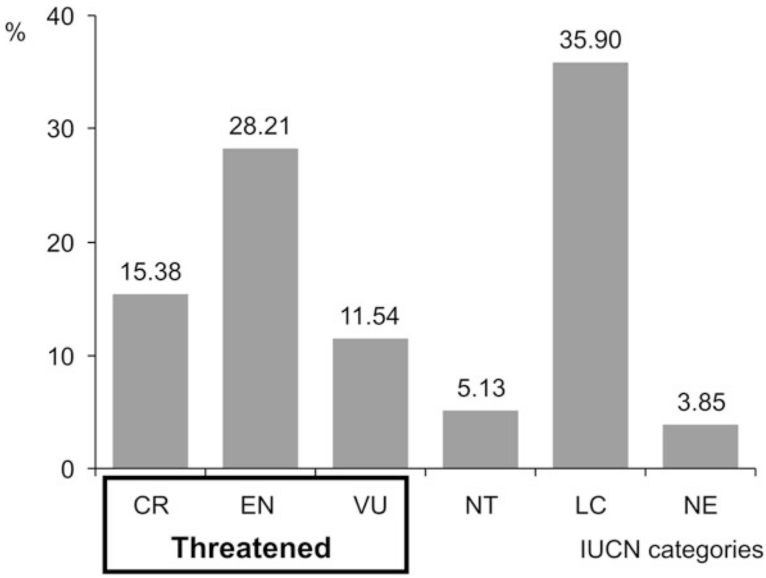


Fig. 2.12 Conservation status. Relative percentage of species and subspecies of *Aegla* (n = 78) according to the IUCN Red List Categories. *Cr* Critically Endangered; *EN* Endangered; *VU* Vulnerable; *NT* Near Threatened; *LC* Least Concern; *NE* Not Evaluated

Similarly, the endemic Brazilian species *A. lata* Bond-Buckup and Buckup 1994, was suspected of being extinct in the wild (EW) because this species was no longer found in the type-locality (then the only known location of the species) (Bond-Buckup and Buckup 1994). Recently, a population of *A. lata* was found in a single location far from its type-locality (Galvez et al. 2007). On the other hand, the Brazilian aeglid *A. brevipalma* Bond-Buckup and Santos 2012 was collected in 2000 from a single location (the type-locality), but has not been seen since then, despite attempts to collect more specimens from that location in 2010 (Santos et al. 2012).

Table 2.3 shows Brazil as the country where most of the 43 threatened species have been reported from (72.09 %, n = 31), followed by Chile (25.58 %, n = 11) and Argentina (2.33 %, n = 1). So far, there are no threatened species reported from Paraguay, Bolivia and Uruguay. In the latter country, however, the recently described *Aegla carinata* Bond-Buckup and Loureiro 2014 is known only from two locations in the northern region (Rivera Department) (Santos et al. 2014) but the conservation status of the species still requires proper evaluation. Of the twelve species which have been assessed or suggested as critically endangered, ten (83.33 %) are country endemics to Brazil (Table 2.3). Most species assessed as endangered (68.18 %) and vulnerable (66.67 %) are also endemic to that country.

All three formally described troglobitic species (*A. cavernicola*, *A. leptochela* and *A. microphthalma*) are included in the CR category. These subterranean freshwater aeglids are highly endemic, and the geographic distribution of each one

Table 2.3 Number and percentage of threatened aeglid species per country

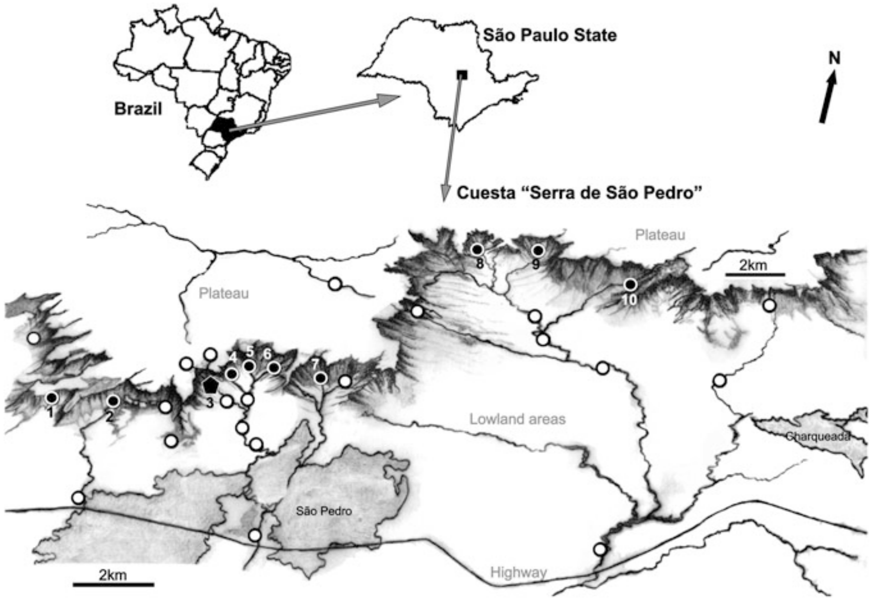
IUCN categories	BR + CH + AR	Brazil (BR)		Chile (CH)		Argentina (AR)	
	n	n	%	n	%	n	%
Critically endangered (CR)	12	10	83.33	1	8.33	1	8.33
Endangered (EN)	22	15	68.18	7	31.82	0	0
Vulnerable (VU)	9	6	66.67	3	33.33	0	0
Total	43	31		11		1	
% (CR + EN + VU)/country			72.09		25.58		2.33

Each number of species/country/IUCN category refers to country endemics, except the CR species *Aegla affinis* which occurs in both Argentina and Chile (see Table 2.2). That species is considered here exclusively as an Argentinean species because that is the country from where the species was originally described

is restricted to their respective type-localities. Troglobitic aeglids show allopatric distributions, whereby no two obligate cave-dwelling species are found inhabiting the same cave. Successful colonization of subterranean habitats occurred independently from different epigean ancestors (Fernandes et al. 2013). Although environmental conditions tend to be fairly stable in the subterranean world cave ecosystems are fragile and highly dependent on nutrients brought in from epigean habitats (Trajano 2000; Gibert and Deharveng 2002).

Other CR species are single locality endemics that live in epigean habitats (e.g., *A. renana* Bond-Buckup and Santos 2010, *A. lata, A. brevipalma* and *A. meloi* Bond-Buckup and Santos 2015 (Galvez et al. 2007; Santos et al. 2010, 2012, 2015). Other CR species are found in more than one location, but their distributional pattern is severely fragmented and the subpopulations are reproductively isolated from one another. For example, Fig. 2.13 shows all known sites of occurrence of *A. perobae* in São Pedro Cuesta, State of São Paulo, Brazil. The current distributional pattern of this species is highly fragmented (10 locations; combined area of occupancy of 0.02 km^2) due to severe and ongoing environmental degradation intrinsically associated with human occupation. In each of these locations a high-gradient stream runs through a steep valley with well-preserved forest cover on the cuesta wall. The plateau and the lowland are highly degraded areas used for cattle grazing and agricultural activities, and the streams in these areas are devoid of riparian vegetation. Both the plateau and lowland areas lack aeglids despite detailed surveys, so gene flow from encounters among individuals from these subpopulations in the lowlands where the streams merge are now unlikely.

Furthermore, due to the landscape characteristics of each location, all subpopulations of *A. perobae* are exposed to unpredictable disturbances on the slopes of the cuesta. Bueno et al. (2014) reported a sharp decrease in the population size of *A. perobae* from the type-locality, which was caused by unseasonal high-intensity flash floods in July 2007 during the dry and cool season that coincided with the period of intense hatching of juveniles (Fig. 2.11b). This adversely affected recruitment of the



1	Fazenda Campestre, Ribeirão do Meio	22°32'13.6"S; 47°53'41.3"W	MZUSP24575
2	Fazenda Santa Maria, Cachoeira do Bocainão	22°32'19.3"S; 47°57'52.5"W	MZUSP24574
3	Peroba stream, Fazenda Santa Rita (Type-locality)	22°31'26.6"S; 47°56'37.6"W	MZUSP24570
4	Cachoeiras da Furna III	22°30'56.1"S; 47°56'16.6"W	MZUSP24573
5	Cachoeiras da Furna II	22°30'33.1"S; 47°56'10.0"W	MZUSP24572
6	Cachoeiras da Furna I, Pousada Cachoeiras da Furna	22°30'42.5"S; 47°55'46.8"W	MZUSP24571
7	Fazenda Santo Antonio	22°31'03.7"S; 47°55'04.3"W	MZUSP24576
8	Fazenda São José, Serra Cruzeiro do Facão	22°26'14.9"S; 47°53'17.0"W	MZUSP24578
9	Fazenda São José, Cabeceira do Araquá	22°26'12.8"S; 47°51'49.8"W	MZUSP24579
10	Fazenda Cavalinho (Fazendão)	22°26'57.6"S; 47°50'05.9"W	MZUSP24577

Fig. 2.13 *Aegla perobae*: fragmented distribution. Bird's-eye perspective of São Pedro and Charqueada landscape, state of São Paulo (SP), Brazil, showing partial extension of the cuesta "Serra de São Pedro". Illustration redrawn from satellite view taken from Google Earth. Scales (2 km) vary with perspective. *Black pentagon* type-locality; *black filled circles* sites with positive sampling results; *white filled circles* sites with negative sampling results. See text for details. Names and geographic coordinates of all ten locations where sampling of *Aegla perobae* specimens were positive and their respective number of voucher material deposited in the Museu de Zoologia—University of São Paulo, Brazil (MZUSP) are also provided

cohort produced in that year, causing a severe impact on the size-class structure and on the reproductive output of the population in the years that followed.

Maintaining and encouraging the recovery of the riparian vegetation of the streams in the lowland area could help overcome reproductive isolation among populations of *A. perobae* and greatly diminish the adverse impact caused by unseasonal disturbances. Riparian canopy closure modifies heat and solar radiation received by streams (Gomi et al. 2002), prevents siltation (Magris et al. 2010), and contributes to establish and maintain favorable microhabitats for aeglids. Intact riparian vegetation along streams acts as an ecological corridor and could increase the area of occupancy of the species by providing viable dispersal routes between connecting sections of streams and thereby re-establishing gene flow among subpopulations.

The number of threatened species of aeglids is expected to increase dramatically in the near future, not only because there are several new and highly endemic species awaiting formal description, but also because species assessed as Least Concern (LC) may actually represent assemblages of cryptic species with limited ranges and small population sizes (Table 2.2). For example, *A. longirostri*, *A. platensis, A. marginata* Bond-Buckup and Buckup 1994, *A. franciscana* Buckup and Rossi, 1977*, A. parana* Schmitt, 1942, *A. jarai* Bond-Buckup and Buckup 1994, *A. uruguayana* and *A. paulensis* (Pérez-Losada et al. 2004; Moraes et al. 2014; Giri and Collins 2014; Marchiori et al. 2014, 2015) are all LC species with wide EOOs. Different interpretations of the taxonomic status of any of these species that lead to the recognition of several valid species where once there was one, would require a thorough revision of the conservation status of all taxa. One taxon assessed as LC may end up becoming several restricted range taxa each with the potential for being assessed as either belonging to one of the threatened categories, or to the Data Deficient category.

Aegla paulensis, for example, has a wide distribution over three hydrographic basins: Paraíba do Sul, Tietê, and Ribeira de Iguape (Fig. 2.14), with an extent of occurrence (EOO) of 30,000 km^2 (shaded area on the EOO map) (Schmitt 1942b;

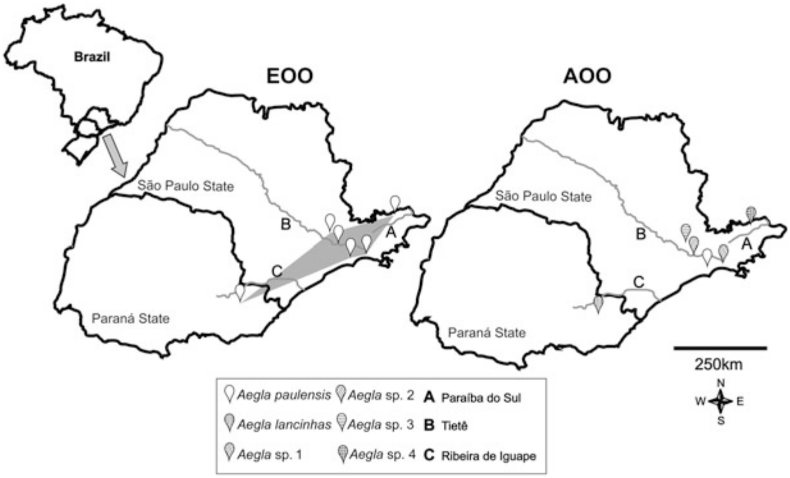


Fig. 2.14 *Aegla paulensis*: from Least Concern to threatened categories. The EOO (extent of occurrence) map shows some of the recorded sites of occurrence of *Aegla paulensis,* as one valid taxon, from three hydrographic basins (A, B and C), totaling an EOO of approximately to 30,000 km^2. The AOO (area of occupancy) map shows a different possible scenario of *Aegla paulensis* populations as a species complex assemblage, consisting of A. *paulensis* s. str., the recently described new species, A. *lancinhas*, plus several distinct taxonomic units showing distribution restricted to small AOO. See text for details

López 1965; Bond-Buckup and Buckup 1994, 2000; Cohen et al. 2011). However, the 6 locations indicated on the map represent populations that are geographically separated from one another, even those belonging to the same hydrographic basin (Tietê). Although the actual area of occupancy at each location may vary, all populations occupy a small area. Morphological comparisons indicate that the six populations of *A. paulensis* may not be monophyletic (Moraes et al. 2014), and quite recently the population from the Ribeira de Iguape was recognized as a new species, *Aegla lancinhas* Bond-Buckup and Buckup 2015 (Santos et al. 2015).

The continued degradation of freshwater environments has frequently led to habitat loss for aeglids and has contributed to the severely fragmented distribution patterns and the high rates of endemism observed. The discovery of new species, or range extensions of known species are most likely to be made in headwater areas or cryptic habitats. *Aegla* is a bioindicator species whose presence indicates a well-preserved freshwater habitat with clear, well-oxygenated freshwaters (Correa-Araneda et al. 2010). Freshwater aeglids are therefore a desirable target for conservation efforts using either a species-based or ecosystem-based approach.

The Aeglidae is a severely threatened family of South American freshwater decapods. However, aeglids are not charismatic as far as public awareness is concerned and would not make good candidates to raise government and public support for effective conservation actions. On the other hand, the recent IUCN Red List assessment of the extinction risk of aeglids is a solid step toward this goal. We recommend adopting an ecosystem-based conservation strategy with aeglids as flagships or umbrella species because they are a unique and irreplaceable component of the South American freshwater fauna. This is probably the best way to save this highly threatened endemic group of species from extinction.

Any conservation action plan would include an ecosystem-based approach aimed at habitat protection that conserves all native species in situ while maintaining functional ecosystem services (Mace et al. 2007). This approach is illustrated in Pérez-Losada et al. (2002b) for Chilean species of aeglids and in Pérez-Losada et al. (2009) for all species. In the latter work, a multidisciplinary approach based on genetic diversity, conservation status, species richness, distribution patterns, and phylogeny was used to prioritize conservation efforts according to ecoregions as defined by major hydrographic systems.

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Chapter 3
Global Diversity and Conservation of Freshwater Crayfish (Crustacea: Decapoda: Astacoidea)

Tadashi Kawai and Keith A. Crandall

Abstract The number of species in the three families of freshwater crayfish worldwide (Astacidae, Cambaridae, and Parastacidae) are updated by region. These are: Astacidae, western North America (5 species) and Europe (5 species), Cambaridae, eastern North America and Mexico (423 species) and Asia (6 species), and Parastacidae, Oceania (153 species), South America (12 species), and Madagascar (7 species). The conservation status of 611 species of crayfish worldwide is discussed, based on global assessments from the IUCN (International Union for Conservation of Nature) Red List protocols as well as regional assessments on governmental endangered species lists. The current threats to endangered species of crayfish include habitat destruction, water diversion, pollution, and threats from exotic species of crayfish (such as *Pacifastacus leniusculus*, *Procambarus clarkii* and *Cherax*) that have been introduced to other parts of the world where they are having an increasing impact. New threats posed by the parthenogenetic marbled crayfish *Procambarus fallax* f. *virginalis* to freshwater ecosystems in Europe and Madagascar are also discussed.

Keywords Alien crayfish · Conservation · Species diversity · IUCN Red List

3.1 Introduction

Freshwater crayfish (Astacoidea) globally comprise three families: the Astacidae and Cambaridae (Astacoidea) in the northern hemisphere, and the Parastacidae (Parastacoidea) in the southern hemisphere. Crayfish belong to the Decapoda, the largest crustacean taxon, and are conspicuous freshwater macroinvertebrates (Holdich 2002). Crayfish are easy to collect (Crandall 2016) and to raise in captivity

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and so over the years have become one of the best-studied crustacean taxa, serving as model organisms in zoology since Victorian times (Stebbing 1893; Huxley 1896). Freshwater crayfish have also long been exploited in inland aquaculture.

The International Association of Astacology founded in Hinterthal, Austria in 1972, has organized biannual international symposia and published the peer-reviewed journal "Freshwater Crayfish", from the 1970s to the 1990s. Significant recent multi-authored publications on crayfish include "Freshwater Crayfish: Biology, Management and Exploitation" (Holdich and Lowery 1988), and "Biology of Freshwater Crayfish" (Holdich 2002), and "Management of Freshwater Geodiversity, Crayfish as Bioindicators" (Reynolds and Souty-Grosset 2013) that all address the increasing need for the sustainable management of crayfish. Other major milestones include molecular studies on the phylogeny and global diversity of crayfish (Crandall and Buhay 2008), and the International Union for Conservation of Nature (IUCN) Red List conservation assessments of every known species of crayfish worldwide (Richman et al. 2015). Here we report on the extinction risks of all crayfish in the world by analyzing the patterns of population changes and threats as a guide for crayfish conservation (Richman et al. 2015). Equally important, we highlight the gaps in knowledge that still exist across all families of crayfish. In addition, the recent multi-authored volume "Freshwater Crayfish: Global Overview" (Kawai et al. 2015) focuses on the threats to all crayfish posed by the spread in several countries of the parthenogenetic marbled crayfish that arose in aquaria in Germany in the 1990s.

This chapter provides the latest information on crayfish biodiversity in every part of their range (eastern North America and Mexico, western North America, Central America, South America, Asia, Oceania, Madagascar, and Europe) as well as describing their conservation status and the major threats. Introduced species of crayfish can have a serious impact on native ecosystems which has been well documented for native European crayfish populations (Holdich 1999). A number of species of North American crayfishes have been introduced to other parts of the world and are spreading rapidly. The current global spread of alien species of crayfish in many parts of the world, and the threats posed by these exotic species, are summarized based on new data (Fig. 3.1).

3.2 Global Diversity

Freshwater crayfish (Astacidea) are distributed in the temperate parts of the northern and southern hemispheres. In North America the Cambaridae range from the eastern part of the continent as far south as Mexico, while the Astacidae (*Pacifastacus*) are found in the western part of the continent west of the Rocky Mountains. In Europe there are five species of astacids (in the genera *Astacus* and *Austropotamobius*), while in eastern Asia there are six species of cambarids (in the genus *Cambaroides*) (Fig. 3.1). The species richness of crayfish is significantly different among geographical regions with North American cambarids forming the

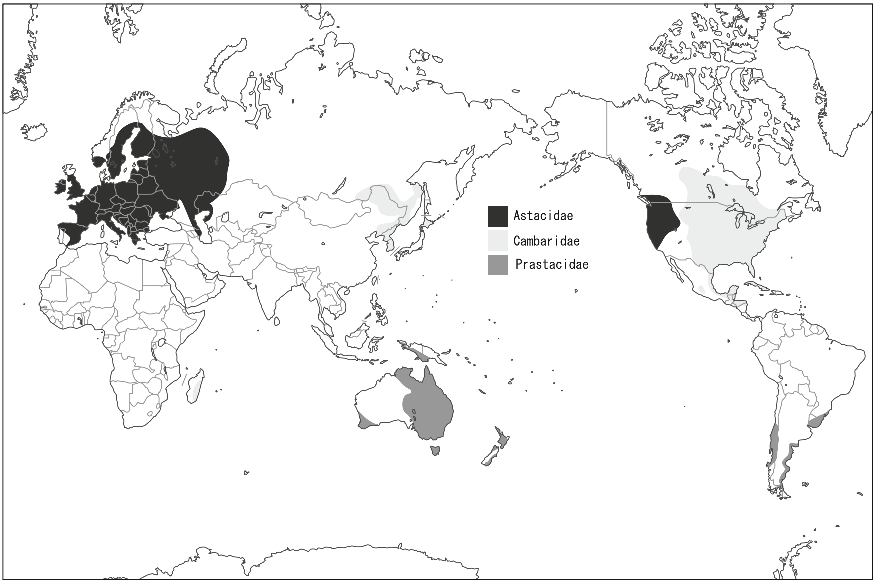

Fig. 3.1 Updated distribution of native species of freshwater Crayfish

most diverse group in the world. For example, North America has 423 species of Cambaridae and 5 species of Astacidae; Asia has 6 species of Cambaridae, Europe has 5 species of Astacidae, South America has 12 species of Parastacidae, Oceania has 153 species of Parastacidae, and Madagascar has 7 species of Parastacidae.

Scholtz (2002) and Vogt (2016, this book Chap. 6) suggest that direct development in freshwater decapods evolved as an adaptation to freshwater by their marine ancestors, and that extended maternal care has been responsible for the high rates of endemism and speciation. Freshwater crayfish have the most sophisticated paternal care between a mother and her offspring of all freshwater decapods. Although there are small differences in physiological and behavioral adaptations among the three families of crayfish from different parts of the world, molecular phylogenetic studies indicate that the group is monophyletic and that all crayfish share a common ancestor that invaded freshwaters only once. Two families of crayfish (Parastacidae and North American Cambaridae) produce an anal thread that connects recently hatched juveniles to the pleopods of the mother, and it is the third stage moult juveniles that become independent, whereas Asian Cambaridae and European Astacidae all lack an anal thread and it is the second stage moult juveniles that become independent. Scholtz and Kawai (2002) interpreted the regional differences in species richness shown by the three families of crayfish in terms of differences in the behavior and morphology of the juveniles. Those authors suggested that it was the more advanced maternal care of Parastacidae and North American Cambaridae that has contributed to their species richness, but they noted that there were two exceptions. For example, although the Madagascan Parastacidae (7 species) and the South American Parastacidae (13 species) have relatively advanced maternal care both groups have a low species richness.

3.3 Global Distribution and Zoogeography

All species of crayfish live their entire lives in freshwater and are unable to extend their distribution to other aquatic envoronments, but there are three notable exceptions to this: For example, *Astascus leptodactylus*, *Pacifastacus leniusculus*, and *Procambarus clarkii* can tolerate high salinities and occur naturally in brackish water estuaries and salt marshes (Kawai and Takahata 2010; Scholtz 2002). Hobbs (1988) explained the enigmatic distribution of these latter species as a reflection of significant variations in their external body shape, and suggested that some ancestors of crayfish had independently entered and colonized freshwater from marine habitats at different times, and that crayfish were therefore polyphyletic. On the other hand, the molecular phylogeny of the crayfish by Crandall et al. (2000a, b) supports the monophyly of the group. The oldest crayfish fossils date from the Triassic period which implies that this group originated on the single super continent of Pangea (Scholtz 2002; Bracken-Grissom et al. 2014). The supercontinent subsequently split up over time eventually forming the modern continents, with each continental piece carrying with it ancient crayfish populations that then diversified in isolation to produce the present global distribution patterns (Toon et al. 2010).

However, there are two enigmatic distributions that are difficult to explain. First, although the majority of the Cambaridae are found in eastern North America and Mexico, there is a small population in eastern Asia. Second, although the majority of the Astacidae are found in western North America (USA and Canada), there are some species of this family in western Europe (Fig. 3.1). Recent molecular analyses (Crandall et al. 2000a; Ahn et al. 2006; Braband et al. 2006; Owen et al. 2015) pointed out that the Asian Cambaridae and American Cambaridae may be polyphyletic and that the Asian cambarids (*Cambaroides*) may be a primitive stem group of all northern hemisphere crayfish.

3.4 Habitat

Freshwater crayfish live in streams, rivers, lakes, and marshes, and are completely dependent on permanent freshwater their whole lives. If the water levels of their habitat fall, or the stream bed dries up, then crayfish construct a verical burrow down to the water table so that their burrow has layer of water in the botton and humid air above it (Grow 1981). Fluctuations of water levels in freshwater habitats is commonplace and often seasonal, and construction of burrows is therefore a common adaptative behavior in crayfish (Kawai and Takahata 2010). The ability to dig a vertical burrow into muddy substrata is seen in the European Astacidae (Füreder 2015), North American Astacidae (Koese and Soes 2011), Madagascan Parastacidae (Jones et al. 2007), North American Cambaridae (Hobbs 1942), Asian Cambaridae (Kawai and Takahata 2010), Oceanaian Parastacidae (Riek 1969), and South American Parastacidae (Rudolph and Almerão 2015).

Constructing burrows is a trait that is also seen in marine lobsters (e.g., *Homarus americanus*) which are a sister group to the crayfish, as well as in the marine mantis shrimp *Oratosquilla oratoria* (Matsuura and Hamano 1984; Scholtz 2002). The oldest fossil burrows of crayfish are from freshwater depositis dating back to the Triassic or Jurassic (Hasiotis and Kirkland 1997; Hasiotis and Thomas 1997), which indicates that the ancestors of crayfish may well have constructed burrows (Kawai and Takahata 2010).

3.5 Regional Diversity, Distribution, and Conservation

3.5.1 Eastern North America and Mexico

3.5.1.1 Taxonomy and Population Levels

Eastern North America and Mexico has the most diverse crayfish fauna in the world and new species are still being described (Crandall and Buhay 2008) (Table 3.1). This region harbours 371 species in 11 genera and one family (Cambaridae), with three genera, *Cambarus*, *Orconectes*, and *Procambarus* that account for over 80 % of all camabarid species.

The IUCN Red List conservation status assessments identify species that are under the greatest risk of extinction, as well as providing critical information on each species including data on distribution and their ecology, population trends, and genetics (Rodrigues et al. 2006). The IUCN Red List uses detailed quantitative criteria to assign species to nine categories (Least Concern, Near Threatened, Vulnerable, Endangered, Critically Endangered, Extinct in the Wild, and Extinct, Data Deficient, and Not Evaluated) based on biological indicators of population levels such as rapid population declines, small population sizes, and the degree of threat. The Least Concern and Near Threatened categories indicate species that are presently doing well, while the threatened categories (VU, EN, CR) indicate that there is a significant risk of extinction (IUCN 2013). Species in Table 3.1 are marked by 2 “Endangered” which indicates that they have been petitioned for listing as endangered species based on regional criteria from governmental agencies such as the U.S. Fish and Wildlife Service (Thoma 2015). This list does not include

Table 3.1 Taxonomy and assessment information of Eastern North America and Mexico

Scientific name	IUCN Red List criteria	Regional criteria	English name
Barbicambarus cornutus (Faxon) 1884	Least concern		Bottlebrush Crayfish
Barbicambarus simmonsi Taylor and Schuster, 2010			
Bouchardina robisoni Hobbs, 1977	Data deficient		Bayou Bodcau Crayfish
Cambarellus blacki Hobbs, 1980	Data deficient		Cypress Crayfish
Cambarellus diminutus Hobbs, 1945	Data deficient		Least Crayfish
Cambarellus lesliei Fitzpatrick and Laning, 1976	Least concern		Angular Dwarf Crawfish
Cambarellus ninae Hobbs, 1950	Least concern		Aransas Dwarf Crawfish
Cambarellus puer Hobbs, 1945	Least concern		Swamp Dwarf Crayfish
Cambarellus schmitti Hobbs, 1942	Data deficient		Fontal Dwarf Crayfish
Cambarellus shufeldtii (Faxon, 1884)	Least concern		Cajun Dwarf Crayfish
Cambarellus texanus Albaugh and Black, 1973	Least concern		Brazos Dwarf Crayfish
Cambarus acanthura Hobbs, 1981			
Cambarus aculabrum Hobbs and Brown, 1987	Least concern	Endangered	
Cambarus acuminatus Faxon, 1884	Critically endangered		Benton County Cave Crayfish
Cambarus aldermanorum Cooper, 2010	Least concern		Acuminate Crayfish
Cambarus angularis Hobbs and Bouchard, 1994	Least concern		Angled Crayfish
Cambarus asperimanus Faxon, 1914	Least concern		Mitten Crayfish
Cambarus bartonii (Fabricius, 1798)	Least concern		Appalachian Brook Crayfish
Cambarus batchi Schuster, 1976	Least concern		Bluegrass Crayfish
Cambarus bouchardi Hobbs, 1970	Near threatened		Big South Fork Crayfish
Cambarus brachydactylus Hobbs, 1953	Data deficient		Shortfinger Crayfish
Cambarus brimleyorum Cooper, 2006	Data deficient		Valley River Crayfish
Cambarus buntingi Bouchard, 1973	Least concern		Longclaw Crayfish
Cambarus carinirostris Hay, 1914	Least concern		Rock Crayfish
Cambarus catagius Hobbs and Perkins, 1967	Data deficient		Greensboro Burrowing Crayfish
Cambarus causeyi Reimer, 1966	Least concern		Boston Mountains Crayfish
Cambarus chasmodactylus James, 1966	Least concern		New River Crayfish
Cambarus chaugaensis Prins and Hobbs, 1969	Least concern		Chauga River Crayfish
Cambarus clivosus Taylor, Soucek and Organ, 2006	Vulnerable		Short Mountain Crayfish

(continued)

Table 3.1 (continued)

Scientific name	IUCN Red List criteria	Regional criteria	English name
Cambarus conasaugaensis Hobbs and Hobbs, 1962	Data deficient		Mountain Crayfish
Cambarus coosae Hobbs, 1981	Least concern		Coosa Crayfish
Cambarus coosawattae Hobbs, 1981	Near threatened		Coosawattee Crayfish
Cambarus cracens Bouchard and Hobbs, 1976	Endangered		Slenderclaw Crayfish
Cambarus crinipes Bouchard, 1973	Least concern		Hairyfoot Crayfish
Cambarus cryptodytes Hobbs, 1941	Least concern		Dougherty Plain Cave Crayfish
Cambarus cumberlandensis Hobbs and Bouchard, 1973	Least concern		Cumberland Crayfish
Cambarus cymatilis Hobbs, 1970	Endangered		Conasauga Blue Burrower
Cambarus davidi Cooper, 2000	Least concern		Carolina Ladle Crayfish
Cambarus deweesae Bouchard and Etnier, 1979	Least concern		Valley Flame Crayfish
Cambarus diogenes Girard, 1852	Least concern		Devil Crawfish
Cambarus distans Rhoades, 1944	Least concern		Boxclaw Crayfish
Cambarus doughertyensis Cooper and Skelton, 2003	Data deficient		Dougherty Burrowing Crayfish
Cambarus dubius Faxon, 1884	Least concern		Upland Burrowing Crayfish
Cambarus eeseeohensis Thoma, 2005	Vulnerable		Grandfather Mountain Crayfish
Cambarus elkensis Jezerinac and Stocker, 1993	Vulnerable		Elk River Crayfish
Cambarus englishi Hobbs and Hall, 1972	Least concern		Tallapoosa Crayfish
Cambarus extraneus Hagen, 1870	Data deficient		Chickamauga Crayfish
Cambarus fasciatus Hobbs, 1981	Data deficient		Etowah Crayfish
Cambarus friaufi Hobbs, 1953	Least concern		
Cambarus gentryi Hobbs, 1970	Least concern		Linear Cobalt Crayfish
Cambarus georgiae Hobbs, 1981	Least concern		Little Tennessee River Crayfish
Cambarus girardianus Faxon, 1884	Least concern		Tanback Crayfish
Cambarus graysoni Faxon, 1914	Least concern		Twospot Crayfish
Cambarus halli Hobbs, 1968	Least concern		Slackwater Crayfish
Cambarus hamulatus (Cope, 1881)	Least CONCERN		Prickly Cave Crayfish
Cambarus harti Hobbs, 1981	Endangered		Piedmont Blue Burrower
Cambarus hatfieldi Loughman, 2013			
Cambarus hiwasseensis Hobbs, 1981	Least concern		Hiwassee Crayfish
Cambarus hobbsorum Cooper, 2001	Least concern		Rocky River Crayfish
Cambarus howardi Hobbs and Hall, 1969	Least concern		Chattahoochee Crayfish

(continued)

Table 3.1 (continued)

Scientific name	IUCN Red List criteria	Regional criteria	English name
Cambarus hubbsi Creaser, 1931	Least concern		
Cambarus hubrichti Hobbs, 1952	Data deficient		Salem Cave Crayfish
Cambarus hystricosus Cooper and Cooper, 2003	Least concern		Sandhills Spiny Crayfish
Cambarus jezerinaci Thoma, 2000	Data deficient		Spiny Scale Crayfish
Cambarus johni Cooper, 2006	Least concern		Carolina Foothills Crayfish
Cambarus jonesi Hobbs and Barr, 1960	Vulnerable		Alabama Cave Crayfish
Cambarus laconensis Buhay and Crandall, 2009	Critically endangered		Lacon Exit Cave Crayfish
Cambarus latimanus (LeConte, 1856)	Least concern		Variable Crayfish
Cambarus lenati Cooper, 2000	Near threatened		Broad River Stream Crayfish
Cambarus longirostris Faxon, 1885	Least concern		Longnose Crayfish
Cambarus longulus Girard, 1852	Least concern		Atlantic Slope Crayfish
Cambarus ludovicianus Faxon, 1884	Least concern		Painted Devil Crayfish
Cambarus maculatus Hobbs and Pflieger, 1988	Least concern		Freckled Crayfish
Cambarus manningi Hobbs, 1981	Least concern		Greensaddle Crayfish
Cambarus miltus Fitzpatrick, 1978	Least concern		Rusty Grave Digger
Cambarus monongalensis Ortmann, 1905	Least concern		Monongahela Crayfish
Cambarus nerterius Hobbs, 1964	Near threatened		Greenbrier Cave Crayfish
Cambarus nodosus Bouchard and Hobbs, 1976	Least concern		Knotty Burrowing Crayfish
Cambarus obeyensis Hobbs and Shoup, 1947	Critically endangered		Obey Crayfish
Cambarus obstipus Hall, 1959	Least concern		Sloped Crayfish
Cambarus ortmanni Williamson, 1907	Least concern		Ortmann's Mudbug
Cambarus parrishi Hobbs, 1981	Data deficient		Hiwassee Headwaters Crayfish
Cambarus parvoculus Hobbs and Shoup, 1947	Least concern		Mountain Midget Crayfish
Cambarus pecki Hobbs, 1967	Endangered		Phantom Cave Crayfish
Cambarus polychromatus Thoma Jezerinac and Simon, 2005	Least concern		Paintedhand Mudbug
Cambarus pristinus Hobbs, 1965	Data deficient		Pristine Crayfish
Cambarus pyronotus Bouchard, 1978	Data deficient		Red-black Crayfish
Cambarus reburrus Prins, 1968	Least concern		French Broad Crayfish
Cambarus reduncus Hobbs, 1956	Least concern		Sickle Crayfish
Cambarus reflexus Hobbs, 1981	Least concern		Pine Savannah Crayfish
Cambarus robustus Girard, 1852	Least concern		Big Water Crayfish

(continued)

Table 3.1 (continued)

Scientific name	IUCN Red List criteria	Regional criteria	English name
Cambarus rusticiformis Rhoades, 1944	Least concern		Depression Crayfish
Cambarus sciotensis Rhoades, 1944	Least concern		Teays River Crayfish
Cambarus scotti Hobbs, 1981	Least concern		Chattooga River Crayfish
Cambarus setosus Faxon, 1889	Near threatened		Bristly Cave Crayfish
Cambarus smilax Loughman Simon and Welsh, 2011			
Cambarus speciosus Hobbs, 1981	Near threatened		Beautiful Crayfish
Cambarus speleocoopi Buhay and Crandall, 2009	Endangered		Sweet Home Alabama Crayfish
Cambarus sphenoides Hobbs, 1968	Least concern		Triangleclaw Crayfish
Cambarus spicatus Hobbs, 1956	Data deficient		Broad River Spiny Crayfish
Cambarus stockeri Thoma, 2011			Ambiguous Crayfish
Cambarus striatus Hay, 1902	Least concern		Ambiguous Crayfish
Cambarus strigosus Hobbs, 1981	Data deficient		Lean Crayfish
Cambarus subterraneus Hobbs, 1993	Critically endangered		Delaware County Cave Crayfish
Cambarus tartarus Hobbs and Cooper, 1972	Critically endangered		Oklahoma Cave Crayfish
Cambarus tenebrosus Hay, 1902	Least concern		Cavespring Crayfish
Cambarus theepiensis Loughman, 2013			
Cambarus thomai Jezerinac, 1993	Least concern		Little Brown Mudbug
Cambarus truncatus Hobbs, 1981	Near threatened		Oconee Burrowing Crayfish
Cambarus tuckasegee Cooper and Schofield, 2002	Near threatened		Tuckasegee Stream Crayfish
Cambarus unestami Hobbs and Hall, 1969	Least concern		Blackbarred Crayfish
Cambarus veitchorum Cooper and Cooper, 1997	Critically endangered		White Spring Cave Crayfish
Cambarus veteranus Faxon, 1914	Data deficient		Big Sandy Crayfish
Cambarus williami Bouchard and Bouchard, 1995	Near threatened		Brawleys Fork Crayfish
Cambarus zophonastes Hobbs and Bedinger, 1964	Critically endangered	Endangered	Hell Creek Cave Crayfish
Distocambarus carlsoni Hobbs, 1983	Data deficient		Mimic Crayfish
Distocambarus crockeri Hobbs and Carlson, 1983	Data deficient		Piedmont Prairie Burrowing Crayfish
Distocambarus devexus (Hobbs, 1981)	Data deficient		Broad River Burrowing Crayfish
Distocambarus hunteri Fitzpatrick and Eversole, 1997	Vulnerable		Saluda Burrowing Crayfish
Distocambarus youngineri Hobbs and Carlson, 1985	Vulnerable		Newberry Burrowing Crayfish

(continued)

Table 3.1 (continued)

Scientific name	IUCN Red List criteria	Regional criteria	English name
Fallicambarus burrisi Fitzpatrick, 1987	Data deficient		Burrowing Bog Crayfish
Fallicambarus byersi (Hobbs, 1941)	Least concern		Lavender Burrowing Crayfish
Fallicambarus caesius Hobbs, 1975	Least concern		Timberlands Burrowing Crayfish
Fallicambarus danielae Hobbs, 1975	Near threatened		Speckled Burrowing Crayfish
Fallicambarus devastator Hobbs and Whiteman, 1987	Least concern		Texas Prairie Crayfish
Fallicambarus dissitus (Penn, 1955)	Data deficient		Pine Hills Digger
Fallicambarus fodiens (Cottle, 1863)	Least concern		Digger Crayfish
Fallicambarus gilpini Hobbs and Robinson, 1989	Near threatened		Jefferson County Crayfish
Fallicambarus gordoni Fitzpatrick, 1987	Near threatened		Camp Shelby Burrowing Crayfish
Fallicambarus harpi Hobbs and Robison, 1985	Near threatened		Ouachita Burrowing Crayfish
Fallicambarus hortoni Hobbs and Fitzpatrick, 1970	Critically endangered		Hatchie Burrowing Crayfish
Fallicambarus houstonensis Johnson, 2008	Least concern		Houston Burrowing Crayfish
Fallicambarus jeanae Hobbs, 1973	Vulnerable		Daisy Burrowing Crayfish
Fallicambarus kountzeae Johnson, 2008	Least concern		Big Thicket Burrowing Crayfish
Fallicambarus macneesei (Black, 1967)	Least concern		Old Prairie Digger
Fallicambarus oryktes (Penn and Marlow, 1959)	Near threatened		Flatwoods Digger
Fallicambarus petilicarpus Hobbs and Robison, 1989	Endangered		Slenderwrist Burrowing Crayfish
Fallicambarus strawni (Reimer, 1966)	Least concern		Saline Burrowing Crayfish
Fallicambarus wallsi Johnson, 2011			
Faxonella beyeri (Penn, 1950)	Least concern		Sabine Fencing Crayfish
Faxonella blairi Hayes and Reimer, 1977	Least concern		Blair's Fencing Crayfish
Faxonella clypeata (Hay, 1899)	Least concern		Ditch Fencing Crayfish
Faxonella creaseri Walls, 1968	Near threatened		Ouachita Fencing Crayfish
Hobbseus attenuatus Black, 1969	Data deficient		Pearl Riverlet Crayfish
Hobbseus cristatus (Hobbs, 1955)	Data deficient		Crested Riverlet Crayfish
Hobbseus orconectoides Fitzpatrick and Payne, 1968	Endangered		Oktibbeha Riverlet Crayfish
Hobbseus petilus Fitzpatrick, 1977	Data deficient		Tombigbee Riverlet Crayfish
Hobbseus prominens (Hobbs, 1966)	Least concern		Prominence Riverlet Crayfish

(continued)

Table 3.1 (continued)

Scientific name	IUCN Red List criteria	Regional criteria	English name
Hobbseus valleculus (Fitzpatrick, 1967)	Endangered		Choctaw Riverlet Crayfish
Hobbseus yalobushensis Fitzpatrick and Busack, 1989	Endangered		Yalobusha Riverlet Crayfish
Orconectes acares Fitzpatrick, 1965	Least concern		Redspotted Stream Crayfish
Orconectes alabamensis (Faxon, 1884)	Least concern		Alabama Crayfish
Orconectes australis (Rhoades, 1941)	Least concern		Southern Cave Crayfish
Orconectes barri Buhay and Crandall, 2008	Data deficient		Cumberland Plateau Cave Crayfish
Orconectes barrenensis Rhoades, 1944	Least concern		Barren River Crayfish
Orconectes bisectus Rhoades, 1944	Vulnerable		Crittenden Crayfish
Orconectes blacki Walls, 1972		Endangered	Calcasieu crayfish
Orconectes burri Taylor and Sabaj, 1998	Near threatened		Blood River Crayfish
Orconectes carolinensis Cooper and Cooper, 1995	Least concern		North Carolina Spiny Crayfish
Orconectes castaneus Johnson, 2010			
Orconectes causeyi Jester, 1967	Least concern		
Orconectes chickasawae Cooper and Hobbs, 1980	Least concern		Chickasaw Crayfish
Orconectes compressus (Faxon, 1884)	Least concern		Slender Crayfish
Orconectes cooperi Cooper and Hobbs, 1980	Least concern		Flint River Crayfish
Orconectes cristavarius Taylor, 2000	Least concern		Spiny Stream Crayfish
Orconectes cyanodigitus Johnson, 2010			
Orconectes deanae Reimer and Jester, 1975	Least concern		Conchas Crayfish
Orconectes difficilis (Faxon, 1898)	Least concern		Painted Crayfish
Orconectes durelli Bouchard and Bouchard, 1995	Least concern		Saddle Crayfish
Orconectes erichsonianus (Faxon, 1898)	Least concern		Reticulate Crayfish
Orconectes etnieri Bouchard and Bouchard, 1976	Least concern		Ets Crayfish
Orconectes eupunctus Williams, 1952	Vulnerable		Coldwater Crayfish
Orconectes forceps (Faxon, 1884)	Least concern		Surgeon Crayfish
Orconectes harrisonii (Faxon, 1884)	Least concern		Belted Crayfish
Orconectes hartfieldi Fitzpatrick and Suttkus, 1992	Vulnerable		Yazoo Crayfish
Orconectes hobbsi Penn, 1950	Data deficient		Pontchartrain Painted Crayfish
Orconectes holti Cooper and Hobbs, 1980	Data deficient		Bimaculate Crayfish
Orconectes hylas (Faxon, 1890)	Least concern		Woodland Crayfish
Orconectes illinoiensis Brown, 1956	Least concern		
Orconectes immunis (Hagen, 1870)	Least concern		Calico Crayfish

(continued)

Table 3.1 (continued)

Scientific name	IUCN Red List criteria	Regional criteria	English name
Orconectes incomptus Hobbs and Barr, 1972	Vulnerable		Tennessee Cave Crayfish
Orconectes indianensis (Hay, 1896)	Least concern		Indiana Crayfish
Orconectes inermis Cope, 1972	Least concern		Unarmed Crayfish
Orconectes jeffersoni Rhoades, 1944	Endangered		Louisville Crayfish
Orconectes jonesi Fitzpatrick, 1992	Data deficient		Sucarnoochee River Crayfish
Orconectes juvenilis (Hagen, 1870)	Least concern		Kentucky River Crayfish
Orconectes kentuckiensis Rhoades, 1944	Least concern		Kentucky Crayfish
Orconectes lancifer (Hagen, 1870)	Least concern		Shrimp Crayfish
Orconectes leptogonopodus Hobbs, 1948	Least concern		Little River Creek Crayfish
Orconectes limosus (Rafinesque, 1817)	Least concern		Spinycheek Crayfish
Orconectes longidigitus (Faxon, 1898)	Least concern		Longpincered Crayfish
Orconectes luteus (Creaser, 1933)	Least concern		Golden Crayfish
Orconectes macrus Williams, 1952	Least concern		Neosho Midget Crayfish
Orconectes maletae Walls, 1972	Data deficient		Kisatchie Painted Crayfish
Orconectes marchandi Hobbs, 1948	Near threatened		Mammoth Spring Crayfish
Orconectes margorectus Taylor, 2002	Near threatened		Livingston Crayfish
Orconectes medius (Faxon, 1884)	Least concern		Saddlebacked Crayfish
Orconectes meeki (Faxon, 1898)	Least concern		Meek's Short Pointed Crayfish
Orconectes menae (Creaser, 1933)	Least concern		Mena Crayfish
Orconectes mirus (Ortmann, 1931)	Least concern		Wonderful Crayfish
Orconectes mississippiensis (Faxon, 1884)	Data deficient		Mississippi Crayfish
Orconectes nais (Faxon, 1885)	Least concern		Water Nymph Crayfish
Orconectes nana Williams, 1952	Least concern		Midget Crayfish
Orconectes obscurus (Hagen, 1870)	Least concern		Allegheny Crayfish
Orconectes occidentalis Johnson, 2010			
Orconectes ozarkae, Williams, 1952	Least concern		Ozark Crayfish
Orconectes palmeri (Faxon, 1884)	Least concern		
Orconectes pardalotus Wetzel et al. 2005	Endangered		Leopard Crayfish
Orconectes pellucidus (Tellkampf, 1844)	Least concern		Mammoth Cave Crayfish
Orconectes perfectus Walls, 1972	Least concern		Complete Crayfish
Orconectes peruncus (Creaser, 1931)	Vulnerable		Big Creek Crayfish
Orconectes placidus (Hagen, 1870)	Least concern		Bigclaw Crayfish
Orconectes propinquus (Girard, 1852)	Least concern		Northern Clearwater Crayfish
Orconectes punctimanus (Creaser, 1933)	Least concern		Spothanded Crayfish
Orconectes putnami (Faxon, 1884)	Least concern		Phallic Crayfish
Orconectes quadruncus (Creaser, 1933)	Vulnerable		St. Francis River Crayfish

(continued)

Table 3.1 (continued)

Scientific name	IUCN Red List criteria	Regional criteria	English name
Orconectes quinebaugensis Mathews and Warren, 2008	Data deficient		
Orconectes rafinesquei Rhoades, 1944	Least concern		Rough River Crayfish
Orconectes raymondi Thoma and Stocker, 2009			
Orconectes rhoadesi, Hobbs, 1949	Least concern		Fishhook Crayfish
Orconectes ronaldi Taylor, 2000	Least concern		Mild River Crayfish
Orconectes rusticus (Girard, 1852)	Least concern		Rusty Crayfish
Orconectes sanbornii (Faxon, 1884)	Least concern		Sanborn's Crayfish
Orconectes saxatilis Bouchard and Bouchard, 1976	Vulnerable		Kiamichi Crayfish
Orconectes sheltae Cooper and Cooper, 1997	Critically endangered	Endangered	Shelta Cave Crayfish
Orconectes shoupi Hobbs, 1948	Endangered	Endangered	Nashville Crayfish
Orconectes sloanii (Bunday, 1876)	Least concern		Sloan's Crayfish
Orconectes spinosus (Bundy, 1877)	Least concern		Coosa River Spiny Crayfish
Orconectes stannardi Page, 1985	Least concern		Little Wabash Crayfish
Orconectes stygocaneyi Hobbs, 2001	Least concern		Caney Mountain Cave Crayfish
Orconectes taylori Schuster, 2008	Vulnerable		Crescent Crayfish
Orconectes texanus Johnson, 2010			
Orconectes theaphionensis Simon, Timm and Morris, 2005	Data deficient		Sinkhole Crayfish
Orconectes tricuspis Rhoades, 1944	Least concern		Western Highland Crayfish
Orconectes validus (Faxon, 1914)	Least concern		Powerful Crayfish
Orconectes virginiensis Hobbs, 1951	Data deficient		Chowanoke Crayfish
Orconectes virilis Hagen, 1870	Least concern		Virile Crayfish
Orconectes williamsi Fitzpatrick, 1996	Least concern		Williams Crayfish
Orconectes wrighti Hobbs, 1948	Vulnerable		Hardin Crayfish
Procambarus ablusus Penn, 1963	Least concern		Hatchie River Crayfish
Procambarus acherontis (Lonnberg, 1894)	Endangered		Orlando Cave Crayfish
Procambarus acutissimus (Girard, 1852)	Least concern		Sharpnose Crayfish
Procambarus acutus (Girard, 1852)	Least concern		White River Crayfish
Procambarus advena (LeConte, 1856)	Least concern		Vidalia Crayfish
Procambarus alleni (Faxon, 1884)	Least concern		Florida Crayfish
Procambarus ancylus Hobbs, 1972	Least concern		Coastal Plain Crayfish
Procambarus angustatus (LeConte, 1856)	Extinct	Endangered	Sandhills Crayfish
Procambarus apalachicolae Hobbs, 1942	Endangered	Endangered	Coastal Flatwoods Crayfish

(continued)

Table 3.1 (continued)

Scientific name	IUCN Red List criteria	Regional criteria	English name
Procambarus attiguus Hobbs and Franz, 1992	Critically endangered	Endangered	Silver Glen Springs Cave Crayfish
Procambarus barbatus (Faxon, 1890)	Least concern		Wandering Crayfish
Procambarus barbiger Fitzpatrick, 1978	Data deficient		Jackson Prairie Crayfish
Procambarus bivittatus Hobbs, 1942	Least concern		Ribbon Crayfish
Procambarus blandingii (Harlan, 1830)	Least concern		Santee Crayfish
Procambarus braswelli Cooper, 1998	Data deficient		Waccamaw Crayfish
Procambarus brazoriensis Albaugh, 1975	Endangered		Brazoria Crayfish
Procambarus capillatus Hobbs, 1971	Data deficient		Capillaceous Crayfish
Procambarus caritus Hobbs, 1981	Least concern		Poor Crayfish
Procambarus ceruleus Fitzpatrick and Wicksten, 1998	Least concern		Blueclaw Chimney Crawfish
Procambarus chacei Hobbs, 1958	Least concern		Cedar Creek Crayfish
Procambarus clarkii (Girard, 1852)	Least concern		Red Swamp Crayfish
Procambarus clemmeri Hobbs, 1975	Least concern		Cockscomb Crayfish
Procambarus cometes Fitzpatrick, 1978	Endangered		Mississippi Flatwoods Crayfish
Procambarus connus Fitzpatrick,1978	Data deficient		Corrollton Crayfish
Procambarus curdi Reimer, 1975	Least concern		Red River Burrowing Crayfish
Procambarus delicatus Hobbs and Franz 1986	Critically endangered		Big-cheeked Cave Crayfish
Procambarus dupratzi Penn, 1953	Least concern		Southwestern Creek Crayfish
Procambarus echinatus Hobbs, 1956	Least concern		Edisto Crayfish
Procambarus econfinae Hobbs, 1942	Endangered		Panama City Crayfish
Procambarus elegans Hobbs, 1969	Data deficient		Elegant Creek Crayfish
Procambarus enoplosternum Hobbs, 1947	Least concern		Black Mottled Crayfish
Procambarus epicyrtus Hobbs, 1958	Least concern		Humpback Crayfish
Procambarus erythrops Relyea and Sutton, 1975	Endangered		Santa Fe Cave Crayfish
Procambarus escambiensis Hobbs, 1942	Endangered		Escambia Crayfish
Procambarus evermanni (Faxon, 1890)	Data deficient		Panhandle Crayfish
Procambarus fallax (Hagen, 1870)	Least concern		Deceitful Crayfish
Procambarus ferrugineus[a]	Least concern		Osage Burrowing Crayfish
Procambarus fitzpatricki Hobbs, 1972	Least concern		Spiny-tail Crayfish
Procambarus franzi Hobbs and Lee, 1976	Endangered		Orange Lake Cave Crayfish
Procambarus geminus Hobbs, 1975	Least concern		Twin Crawfish
Procambarus geodytes Hobbs, 1942	Data deficient		Muddiver Crayfish
Procambarus gibbus Hobbs, 1969	Data deficient		Muckalee Crayfish

(continued)

Table 3.1 (continued)

Scientific name	IUCN Red List criteria	Regional criteria	English name
Procambarus gracilis (Bundy, 1876)	Least concern		Prairie Crayfish
Procambarus hagenianus (Faxon, 1884)	Least concern		Southern Prairie Crayfish
Procambarus hayi (Faxon, 1884)	Least concern		Straightedge Crayfish
Procambarus hinei (Ortmann, 1905)	Least concern		Marsh Crayfish
Procambarus hirsutus Hobbs, 1958	Least concern		Shaggy Crayfish
Procambarus horsti Hobbs and Means, 1972	Endangered		Big Blue Spring Cave Crayfish
Procambarus howellae Hobbs, 1952	Least concern		Ornate Crayfish
Procambarus hubbelli (Hobbs, 1940)	Least concern		Jackknife Crayfish
Procambarus hybus Hobbs and Walton, 1957	Least concern		Smoothnose Crayfish
Procambarus incilis Penn, 1962	Least concern		Cut Crayfish
Procambarus jaculus Hobbs and Walton, 1957	Least concern		Javelin Crayfish
Procambarus kensleyi Hobbs, 1990	Least concern		Free State Chimney Crawfish
Procambarus kilbyi (Hobbs, 1940)	Least concern		Hatchet Crayfish
Procambarus lagniappe Black, 1968	Near threatened		Lagniappe Crayfish
Procambarus latipleurum Hobbs, 1942			
Procambarus lecontei (Hagen, 1870)	Least concern		Mobile Crayfish
Procambarus leitheuseri Franz and Hobbs, 1983	Endangered		Coastal Lowland Cave Crayfish
Procambarus leonensis Hobbs, 1942	Least concern		Blacknose Crayfish
Procambarus lepidodactylus Hobbs, 1947	Data deficient		Pee Dee Lotic Crayfish
Procambarus lewisi Hobbs and Walton, 1959	Data deficient		Spur Crayfish
Procambarus liberorum Fitzpatrick, 1978	Least concern		Osage Burrowing Crayfish
Procambarus litosternum Hobbs, 1947	Data deficient		Blackwater Crayfish
Procambarus lophotus Hobbs and Walton, 1960	Least concern		Mane Crayfish
Procambarus lucifugus (Hobbs, 1940)	Least concern		Vampire Crayfish
Procambarus lunzi (Hobbs, 1940)	Data deficient		Hummock Crayfish
Procambarus luxus Johnson, 2011			
Procambarus lylei Fitzpatrick and Hobbs, 1971	Endangered		Shutispear Crayfish
Procambarus machardyi Walls, 2006	Critically endangered		Caddo Chimney Crayfish
Procambarus mancus Hobbs and Walton, 1957	Least concern		Lame Crayfish
Procambarus marthae Hobbs, 1975	Data deficient		Crisscross Crayfish
Procambarus medialis Hobbs, 1975	Data Deficient		Pamlico Crayfish

(continued)

Table 3.1 (continued)

Scientific name	IUCN Red List criteria	Regional criteria	English name
Procambarus milleri Hobbs, 1971	Endangered		Miami Cave Crayfish
Procambarus morrisi Hobbs and Franz, 1991	Critically endangered		Putnam County Cave Crayfish
Procambarus natchitochae Penn, 1953	Least concern		Red River Crayfish
Procambarus nechesae Hobbs, 1990	Least concern		Neches Crayfish
Procambarus nigrocinctus Hobbs, 1990	Least concern		Blackbelted Crayfish
Procambarus nueces Hobbs and Hobbs, 1995	Least concern		Nueces Crayfish
Procambarus okaloosae Hobbs, 1942	Least concern		Okaloosa Crayfish
Procambarus orcinus Hobbs and Means, 1972	Endangered		Woodville Karst Cave Crayfish
Procambarus ouachitae Penn, 1954	Least concern		Ouachita River Crayfish
Procambarus paeninsulanus (Faxon, 1914)	Least concern		Peninsula Crayfish
Procambarus pallidus (Hobbs, 1940)	Near threatened		Pallid Cave Crayfish
Procambarus parasimulans Hobbs and Robison, 1986	Least concern		Bismark Burrowin Crayfish
Procambarus pearsei (Creaser, 1934)	Data deficient		Carolina Sandhills Crayfish
Procambarus penni Hobbs, 1951	Data deficient		Pearl Blackwater Crayfish
Procambarus pentastylus Walls and Black, 2008	Data deficient		
Procambarus petersi Hobbs, 1981	Data deficient		Ogeechee Crayfish
Procambarus pictus (Hobbs, 1940)	Near threatened		Spotted Royal Crayfish
Procambarus planirostris Penn, 1953	Least concern		Flatnose Crayfish
Procambarus plumimanus Hobbs and Walton, 1958	Least concern		Croatan Crayfish
Procambarus pogum Fitzpatrick, 1978	Data deficient		Bearded Red Crayfish
Procambarus primaevus (Packard, 1881)			Brushnose Crayfish
Procambarus pubescens (Faxon, 1884)	Data deficient		
Procambarus pubischelae Hobbs, 1942	Data deficient		Hookless Crayfish
Procambarus pycnogonopodus Hobbs, 1942	Data deficient		Stud Crayfish
Procambarus pygmaeus Hobbs, 1942	Least concern		Christmas Tree Crayfish
Procambarus raneyi Hobbs, 1953	Data deficient		Disjunct Crayfish
Procambarus rathbunae (Hobbs, 1940)	Data deficient		Combclaw Crayfish
Procambarus regalis Hobbs and Robison, 1988	Data deficient		Regal Burrowing Crayfish
Procambarus reimeri Hobbs, 1979	Data deficient		
Procambarus rogersi (Hobbs, 1938)	Data deficient		Field Crayfish
Procambarus seminolae Hobbs, 1942	Least concern		Seminole Crayfish
Procambarus shermani Hobbs, 1942	Least concern		Gulf Crayfish
Procambarus simulans (Faxon, 1884)	Least concern		Southern Plains Crayfish

(continued)

Table 3.1 (continued)

Scientific name	IUCN Red List criteria	Regional criteria	English name
Procambarus spiculifer (LeConte, 1856)	Least concern		White Tubercled Crayfish
Procambarus steigmani Hobbs, 1991	Data Deficient		Parkhill Prairie Crayfish
Procambarus suttkusi Hobbs, 1953	Least concern		Choctawhatchee Crayfish
Procambarus talpoides Hobbs, 1981	Least concern		Mole Crayfish
Procambarus tenuis Hobbs, 1950	Data deficient		Ouachita Mountain Crayfish
Procambarus texanus Hobbs, 1971	Data deficient		Bastrop Crayfish
Procambarus troglodytes (LeConte, 1856)	Least concern		Eastern Red Swamp Crayfish
Procambarus truculentus Hobbs, 1954	Least concern		
Procambarus tulanei Penn, 1953	Least concern		Giant Bearded Crayfish
Procambarus verrucosus Hobbs, 1952	Least concern		Grainy Crayfish
Procambarus versutus (Hagen, 1870)	Least concern		Sly Crayfish
Procambarus viaeviridis (Faxon, 1914)	Least concern		Vernal Crayfish
Procambarus vioscai Penn, 1946	Least concern		Percy's Creek Crayfish
Procambarus youngi Hobbs, 1942	Data deficient		Florida Longbeak Crayfish
Procambarus zonangulus Hobbs and Hobbs, 1990	Data deficient		Southern White River Crayfish
Troglocambarus maclanei Hobbs, 1942	Near threatened		Spider Cave Crayfish

[a] *Procambarus ferrugineus* is junior synonym of the species, *Procambarus liberorum*

subspecies and fossil species, and updated regional species lists based on the latest monographs of freshwater crayfish by regional taxonomic specialists (Thoma 2015).

3.6 Distribution

The river basins in the Atlantic drainage in the USA have more species than any other continent. The rich species diversity is particularly concentrated in the southeastern United States between the Ozark Mountains of Missouri and Arkansas, and new species are still being described. In the Appalachian Mountains species abundance is concentrated in the southern range in eastern Tennessee, northern Georgia, and western South Carolina and North Carolina (Thoma 2015).

3.7 Conservation

Crayfish conservation in the United States has risen in importance in recent years and several works have highlighted the numbers of rare and threatened species (Master 1990; Taylor et al. 2007). Some 371 species are known from the Atlantic drainages of Canada and the USA, of which 86 (23.2 %) are too poorly known to assess (Data Deficient). The IUCN Red List shows 53 (14.3 %) species of crayfish in Canada and USA to be threatened with extinction, while the U.S. Fish and Wildlife Service (USFWS) (Center for Biological Diversity 2010), additionally lists 8 species, total 61 species (total 16.4 % of the fauna) as endangered. It is likely that many of the newly described species of crayfish that have a small population and a restricted distribution are in a threatened category when their formal conservation assessments have been made.

Lodge et al. (2000) discussed the spread of crayfish species in North America and have evaluated the effects of non-native species on the indigenous fauna. Alien invasive species of crayfish impact both indigenous species of crayfish and fish, especially those species that rely on submerged aquatic vegetation (Lodge et al. 1998a, b). Despite this, some forty political units in Canada and the United States do not regulate the use of, or movement of, crayfish within their boundaries. Because of this it is likely that more non-native crayfish populations will become established in the U.S. and Canada and that this will increase the number of endangered species in these two countries (Thoma 2015).

3.7.1 North America, Pacific Drainages

Pacifastacus leniusculus has three subspecies (Miller 1960) but recent molecular analyses by Sonntag (2006), Larson et al. (2012), and Larson and Williams (2015) suggest that all three subspecies should properly be recognized as valid species (Table 3.2). About 40 % of North American species of crayfish living in the Pacific drainages are threatened with extinction and another 20 % are Data Deficient.

Table 3.2 Taxonomy and assessment information of Western North America, Pacific drainages

Scientific name	IUCN Red List criteria	English name
Pacifastacus connectence (Faxon, 1914)	Data deficient	Snake River Pilose Crayfish
Pacifastacus fortis (Faxon, 1914)	Critically endangered	Placid Crayfish or Shasta Crayfish
Pacifastacus gambelii (Girard, 1852)	Least concern	Pilose Crayfish
Pacifastacus leniusculus (Dana, 1852)	Least concern	Signal Crayfish
Pacifastacus nigrescens (Stimpson, 1857)	Extinct	Sooty Crayfish

3.8 Distribution

The native range of the genus *Pacifastacus* lies in the Columbia River system, but there is a lack of clarity of their exact historic distributions prior to widespread human-related introductions because it is known that *P. leniusculus* has been introduced into the U.S. states of California, Nevada, and Utah (Larson and Olden 2011, 2013; Martinez 2012),. This is proving to be a barrier to our understanding of the endemic range of these crayfish (Riegel 1959; Abrahamsson and Goldman 1970; Johnson 1986).

3.9 Conservation

The IUCN Red List for the North American Pacific drainages records one endangered species (*Pacifastacus fortis*), and another species (*P. nigrescens*) that is now extinct. The U.S. Endangered Species Act (http://explorer.natureserve.org/statusus.htm) (U.S. ESA) is the primary legislation that affords federal legal protection to threatened and endangered species in the United States, and is administered by the U.S. Fish and Wildlife Service (USFWS) (http://endangered.fws.gov/) and U.S. National Marine Fisheries Service (NMFS) (http://www.nmfs.noaa.gov/prot_res/overview/es.html). Recently, the U.S. Endangered Species Act recognised *P. fortis* as endangered, and *P. gambelii* and *P. connectens* as being of least concern. However, Bouchard (1977) assigned *P. fortis* as "Threatened" under the U.S. ESA, which was upgraded to "Endangered" in 1988 (Singleton 1987). Bouchard (1977) suggested that *P. nigrescens* was probably extinct owing to the effects of urbanization in the San Francisco area coupled with the impacts of the invasive crayfish *P. leniusculus*. *Pacifastacus fortis* appears highly impacted by range expansions of non-native species such as *P. leniusculus* and the cambarid *Orconectes virilis* (Eng and Daniels 1982; Light et al. 1995; Ellis 1999). Recent research has evaluated behavioral interactions between *P. fortis* and *P. leniusculus* (Pintor et al. 2008), and management actions have included the design and construction of impassable barriers to crayfish aimed at preventing the further spread of invasive species into critical habitats for *P. fortis* (Ellis 2005). The conservation status of the three nominal subspecies of *P. leniusculus* is as follows: *P. l. klamathensis* and *P. l. trowbridgii* are endangered, whereas *P. l. leniusculus* is not endangered.

3.10 Distribution

The crayfish of Mexico and Central America range from sea level wetlands and salt marshes to highland streams above 3000 m in parts of central Mexico (Table 3.3). Although the natural habitat of crayfish is generally limited to freshwater, species

Table 3.3 Taxonomy and assessment information of Mexico and Central America

Scientific name	IUCN Red List criteria
Cambarellus alvarezi Villalobos, 1952	Extinct
Cambarellus areolatus Faxon, 1885	Critically endangered
Cambarellus chapalanus Faxon, 1898	Near threatened
Cambarellus chihuahuae Hobbs, 1980	Extinct
Cambarellus lermensis Villalobos, 1943	Least concern
Cambarellus occidentalis Faxon, 1898	Least concern
Cambarellus patzcuarensis Villalobos, 1943	Endangered
Cambarellus prolixus Villalobos and Hobbs, 1981	Critically endangered
Cambarellus zempoalensis Villalobos, 1943	Least concern
Procambarus acanthophorus Villalobos, 1948	Least concern
Procambarus achilli López, Mejia and Alvarez, 2003	Least concern
Procambarus atkinsoni (Ortmann, 1913)	Data deficient
Procambarus bouvieri (Ortmann, 1909)	Endangered
Procambarus caballeroi Villalobos, 1944	Least concern
Procambarus catemacoensis Rojas, Alvarez and Villalobos, 2000	Critically endangered
Procambarus cavernicola Mejia-Ortiz, Hartnoll and Viccon-Pale, 2003	Vulnerable
Procambarus chacalli López-Mejia, Alvarez and Mejia-Ortiz, 2004	Data deficient
Procambarus citlaltepetl Rojas, Alvarez and Villalobos, 1999	Vulnerable
Procambarus clarkii (Girard, 1852)	Least concern
Procambarus contrerasi (Creaser, 1931)	Endangered
Procambarus cubensis (Erichson, 1846)	Data deficient
Procambarus cuetzalanae Hobbs, 1982	Near threatened
Procambarus cuevachicae (Hobbs, 1941)	Least concern
Procambarus digueti (Bouvier, 1897)	Endangered
Procambarus erichsoni Villalobos, 1950	Data deficient
Procambarus gonopodocristatus Villalobos, 1958	Least concern
Procambarus hidalgoensis López-Mejia, Alvarez and Mejia Ortis, 2005	Least concern
Procambarus hoffmanni (Villalobos, 1944)	Least concern
Procambarus hortonhobbsi Villalobos, 1950	Endangered
Procambarus llamasi Villalobos, 1954	Least concern
Procambarus maya Alvarez, López-Mejia and Villalobos, 2007	Data deficient
Procambarus mexicanus (Erichson, 1846)	Least concern
Procambarus mirandai Villalobos, 1954	Least concern
Procambarus niveus Hobbs and Villalobos, 1964	Data deficient
Procambarus oaxacae Hobbs, 1973	Least concern
Procambarus olmecorum Hobbs, 1987	Least concern
Procambarus ortmannii (Villalobos, 1949)	Critically endangered
Procambarus paradoxus (Ortmann, 1906)	Critically endangered
Procambarus pilosimanus (Ortmann, 1906)	Least concern

(continued)

Table 3.3 (continued)

Scientific name	IUCN Red List criteria
Procambarus regiomontanus (Villalobos, 1954)	Critically endangered
Procambarus riojai (Villalobos, 1944)	Least concern
Procambarus roberti Villalobos and Hobbs, 1974	Endangered
Procambarus rodriguezi Hobbs, 1943	Data deficient
Procambarus ruthveni (Pearse, 1911)	Vulnerable
Procambarus sbordonii Hobbs, 1977	Data deficient
Procambarus strenthi Hobbs, 1977	Data deficient
Procambarus teziutlanensis (Villalobos, 1947)	Data deficient
Procambarus tlapacoyanensis (Villalobos, 1947)	Data deficient
Procambarus toltecae Hobbs, 1943	Least concern
Procambarus williamsoni (Ortmann, 1905)	Data deficient
Procambarus vazquezae Villalobos, 1954	Near threatened
Procambarus veracruzanus Villalobos, 1954	Data deficient
Procambarus zapoapensis Villalobos, 1954	Data deficient
Procambarus villalobosi Hobbs, 1967	Data deficient
Procambarus xilitlae Hobbs and Grubbs, 1982	Data deficient
Procambarus xochitlanae Hobbs, 1975	Data deficient
Procambarus zapoapensis Villalobos, 1954	Near threatened
Procambarus zihuateutlensis Villalobos, 1950	Endangered

such as *P. clarkii* have been recorded from brackish water habitats (Huner and Barr 1991), and another species (*P. maya*) has been collected from a salt marsh with a salinity of 5.5 ppt in the Sian Ka’an Nature Reserve in Quintana Roo, Mexico about 1 km from the coast (Alvarez et al. 2011). Crayfish are not evenly distributed throughout Mexico and Central America. In Mexico, the majority of species are found along the Gulf of Mexico slope, while a less diverse group occurs along the Trans-Mexican Volcanic Belt, and a few species form a third disjunctive group distributed on the Pacific versant. Crayfish diversity reaches a high point along the Gulf of Mexico slope in a region where the States of Veracruz, Hidalgo, and Puebla come together (Armendáriz 2011).

3.11 Conservation

The IUCN published conservation assessments of all cambarid species of crayfish (IUCN 2013; Richman et al. 2015). In 2010 the Secretariat of Environment and Natural Resources (in Spanish: Secretaría del Medio Ambiente y Recursos Naturales, SEMARNAT) published the Mexican Red List of threatened species that is known as Nom-059-Semarnat-2010 (SEMARNAT 2010), which is an updated version of the IUCN Red List. These two reports included the same number of species with 30.5 % of the Mexican and Central American species endangered and another 28.8 % Data Deficient.

In Mexico and Central America only a few species of crayfish have been used for aquaculture. The U.S. red swamp crayfish *Procambarus clarkii* has been introduced into a number of lakes and ponds in northern Mexico and has since spread to the states of Tamaulipas, Nuevo Leon, Coahuila, Durango, Chihuahua, Sonora, Baja California, and Chiapas (Campos and Rodríguez-Almaraz 1992; Hernández et al. 2008). Torres and Álvarez (2012) found that one non-native population of *P. clarkii* was genetically more similar to each other than to other introduced populations *of P. clarkii* found elsewhere in Mexico and Costa Rica, although overall genetic variation within this species was low. In addition, populations of *Orconectes virilis* (which is native to the northeastern parts of North America) have now become established in Mexico (Campos and Contreras 1985). And the Australian redclaw crayfish, *Cherax quadricarinatus,* was brought into Mexico in 1995 to start experimental cultures but some have escaped and established wild populations. Mendoza-Alfaro et al. (2011) reviewed the status of *C. quadricarinatus* in Mexico, but there have been no studies that have focused on the impact of this alien species on the native fauna, especially in nearby Tamaulipas and San Luis Potosi, where there is an important hotspot of native crayfish species diversity.

3.12 South America

The genus *Parastacus* includes taxonomically problematic species such as *P. saffordi, P. pilimanus,* and *P. varicosus* whose external morphological characters closely resemble each other (Table 3.4). Unfortunately, the type series of *P. saffordi* and *P. varicosus* comprise only a few specimens and the type specimens of *P. pilimanus* have been lost. This remains a difficult problem because no additional specimens of these three species have been collected since their original descriptions (Buckup and Rossi 1980; Rudolph and Almerão 2015).

3.13 Distribution

Thirteen species of crayfishes are native to South America and are distributed in southern Brazil, Uruguay, northeast and southern Argentina, and central-southern Chile (Crandall et al. 2000a, b; Buckup 2003; Rudolph 2013), with Chile (six species) hosts the greatest diversity (Rudolph 2010).

Table 3.4 Taxonomy and assessment information of South America

Scientific name	IUCN Red List criteria	Regional criteria
Parastacus brasiliensis (von Martens, 1869)	Near threatened	
Parastacus defossus Faxon, 1898	Data deficient	Near threatened
Parastacus laevigatus Buckup and Rossi, 1980	Data deficient	
Parastacus nicoleti (Philippi, 1882)	Data deficient	Near threatened or vulnerable
Parastacus pilimanus (von Martens, 1869)	Least concern	
Parastacus pugnax (Poeppig, 1835)	Data deficient	Least concern or vulnerable
Parastacus saffordi Faxon, 1898	Data deficient	
Parastacus varicosus Faxon, 1898	Data deficient	
Samastacus spinifrons (Philippi, 1882)	Data deficient	Least concern or vulnerable
Virilastacus araucanius (Faxon, 1914)	Data deficient	Vulnerable
Virilastacus jarai Rudolph and Crandall, 2012		Critically endangered
Virilastacus retamali Rudolph and Crandall, 2007	Data deficient	Endangered
Virilastacus rucapihuelensis Rudolph and Crandall, 2005	Data deficient	Endangered or critically

Regional criteria based on Almerão et al. (2014) and Rudolph and Almerão (2015)

3.14 Conservation

The differences between the conservation status of the South American species of crayfish reported by the IUCN Red List and that reported by the Regional Evaluation agencies are mainly due to differences in the protocols used (Almerão et al. 2014; Buckup 2010; Rudolph and Crandall 2007, 2012; Marques et al. 2002; MMA 2013a, b). For example, the IUCN Red List shows 7.7 % of South American parastacids as threatened with extinction (and 10 species (76.9 %) as Data Deficient), while the Regional Criteria considers 6 species (46.2 %) to be endangered. Threats to the South American parastacid species are mostly from the negative impacts of human activities. In Uruguay and Brazil stream channel diversion and water pollution have affected natural crayfish habitat, while in Chile deforestation for agriculture is the main threat (Rudolph and Almerão 2015). Introduced alien crayfish such as *Procambarus clarkii* (Girard 1852) are also posing new threats to the freshwater ecosystems of South America, because this U.S. species has been recorded to occur in Ecuador and Brazil (Magalhães et al. 2005; Silva and Bueno 2005; Torres and Álvarez 2012). Species Distribution Models (SDMs) have demonstrated that *P. clarkii* represents a potentially serious threat to large areas of southern South America (Paraguay, Chile, Argentina, Uruguay and Brazil) (Palaoro et al. 2013). Several other non-native species of crayfish have also been introduced into South America from Australia: *Cherax quadricarinatus* (von

Martens 1868), *C. tenuimanus* Smith 1912, and *C. cainii* (Austin and Bunn 2010) (Lawrence and Jones 2002; Mendoza-Alfaro et al. (2011)). These Australian species have been cultivated in commercial farms in Ecuador, Paraguay, Colombia, Peru, Uruguay, Argentina, and Chile, and it is likely that these alien species will become a greater threat to South American Parastacidae in the future.

3.15 Oceania (Australia, New Guinea, New Zealand)

The freshwater crayfish of Oceania all belong to the Parastacidae (Holdich 2002). Eleven out of the 15 genera of the Parastacidae are found in Oceania, with 9 genera endemic to Australia (*Astacopsis*, *Engaeus*, *Engaewa*, *Euastacus*, *Geocharax*, *Gramastacus*, *Ombrastacoides*, *Spinastacoides*, and *Tenuibranchiurus* (cf., Riek 1969, 1972; Hobbs 1988; Hansen and Richardson 2006)), one genus (*Cherax*) that is found in Australia, New Guinea, and nearby islands (Clark 1936; Holthuis 1986), and one genus (*Paranephrops*) that lives in New Zealand (Archey 1915; Hopkins 1970) (Table 3.5).

3.16 Distribution

The eleven parastacid genera found in Oceania: *Astacopsis* (Tasmania), *Cherax* (Australia and some offshore islands and New Guinea), *Engaeus* (Victoria and Tasmania), *Engaewa* (western Australia), *Euastacus* (eastern and southeastern Australia), *Geocharax* (Victoria and Tasmania), *Gramastacus* (southeastern Australia), *Ombrastacoides* (Tasmania), *Paranephrops* (New Zealand), *Spinastacoides* (Tasmania), and *Tenuibranchiurus* (central and eastern Australia) (Furse 2014; Lukhaup and Herbert 2008).

3.17 Conservation

The crayfish fauna of Oceania has a significantly high species diversity with 153 species in 11 genera. The threat levels and conservation status of each genus can be summarized as follows: *Astacopsis* spp. are threatened by habitat loss and degradation due to land clearance or by catchment disturbance for agriculture, forestry, or mining. The largest species, *A. gouldi*, is still threatened by illegal fishing (Threatened Species Sect. 2006) and is listed as Vulnerable under Tasmanian and Commonwealth of Australia legislation.

The common threats to *Cherax* have been identified by Wells et al. (1983) as habitat destruction, pollution, human exploitation, and the introduction of exotic species. The 2010 IUCN Red List assessed 17 species (50 %) in the genus *Cherax*

Table 3.5 Taxonomy and assessment information of Oceania (Australia, New Guinea, New Zealand)

Scientific name	IUCN Red List criteria	English name
Astacopsis franklinii (Grey, 1945)	Least concern	
Astacopsis gouldi Clark, 1936	Endangered	Tasmanian Giant freshwater Lobster
Astacopsis tricornis Clark, 1936	Least concern	
Cherax austini Coughran and Hobson, 2012		
Cherax barretti Clark, 1941		
Cherax boschmai Holthuis, 1949		
Cherax buitendijkae Holthuis, 1949		
Cherax cainii Austin and Ryan, 2002	Least concern	Smooth Marron
Cherax cairnsensis, Riek, 1969		
Cherax cartacoolah Short, 1993		
Cherax cid Furse and Dawkins, 2012		
Cherax communis Holthuis, 1949		
Cherax crassimanus Riek, 1967		
Cherax cuspidatus Riek, 1969	Least concern	
Cherax depressus Riek, 1951		Orange-fingered Crayfish
Cherax destructor Clark, 1936	Vulnerable	Yabby
Cherax dispar Riek, 1951	Least concern	
Cherax glaber Riek, 1967		
Cherax holthuisi Lukhaup and Pekny, 2006	Data deficient	
Cherax leckii Coughran, 2005	Critically endangered	
Cherax longipes Holthuis, 1949		
Cherax murido Holthuis, 1949		
Cherax nucifraga Short, 1991	Data deficient	
Cherax pallidus Holthuis, 1949	Endangered	
Cherax panaicus Holthuis, 1949		
Cherax papuanus Holthuis, 1949	Vulnerable	
Cherax parvus Short and Davie, 1991	Data deficient	
Cherax peknyi Lukhaup and Herbert, 2008	Data deficient	
Cherax preissi (Erichson, 1846)	Least concern	
Cherax punctatus Clark, 1936		
Cherax quadricarinatus (von Martens, 1868)	Least concern	Red-claw, Tropical Blue Crayfish
Cherax quinquecarinatus (Gray, 1845)	Least concern	
Cherax rhynchotus Riek, 1951	Least concern	
Cherax robustus Riek, 1951		
Cherax rotunadus Clark, 1941		

(continued)

Table 3.5 (continued)

Scientific name	IUCN Red List criteria	English name
Cherax setosus (Riek, 1951)		Setose Yabby
Cherax solus, Holthuis, 1949		
Cherax tenuimanus (Smith, 1912)	Critically endangered	Marron
Cherax urospinosus Riek, 1969	Data deficient	
Cherax wasselli Riek, 1969		
Engaeus affinis Smith and Schuster, 1913	Data deficient	
Engaeus australis Riek, 1969	Near threatened	Lilly Pilly Burrowing Crayfish
Engaeus cisternarius Suter, 1977	Least concern	
Engaeus cunicularius (Erichson, 1846)	Least concern	
Engaeus curvisuturus Horwitz, 1990	Data deficient	
Engaeus cymus (Clark, 1936)	Least concern	
Engaeus disjuncticus Horwitz, 1990	Endangered	
Engaeus fossor (Erichson, 1846)	Least concern	
Engaeus fultoni Smith and Schuster, 1913		
Engaeus granulatus Horwitz, 1990	Critically endangered	
Engaeus hemicirratulus Smith and Schuster, 1913	Least concern	
Engaeus karnanga Horwitz, 1990	Data deficient	
Engaeus laevis (Clark, 1941)	Data deficient	
Engaeus lengana Horwitz, 1990	Least concern	
Engaeus leptorhynchus Clark, 1936	Least concern	
Engaeus lyelli (Clark, 1936)	Least concern	
Engaeus mairener Horwitz, 1990	Least concern	
Engaeus mallacoota Horwitz, 1990	Critically endangered	Malacoota Burrowing Crayfish
Engaeus martigener Horwitz, 1990	Endangered	Furneax Burrowing Crayfish
Engaeus merosetosus Horwitz, 1990	Least concern	
Engaeus nulloporius Horwitz, 1990	Data deficient	
Engaeus rientalis Clark, 1941		
Engaeus orramakunna Horwitz, 1990	Near threatened	Mount Arthur Burrowning Crayfish
Engaeus phyllocercus Smith and Schuster, 1913	Endangered	Narracan Burrowing Crayfish
Engaeus quadrimanus Clark, 1936	Least concern	
Engaeus rostrogaleatus Horwitz, 1990	Vulnerable	Strzelecki Burrowing Crayfish
Engaeus sericatus Clark, 1936	Least concern	
Engaeus spinicaudatus Horwitz, 1990	Critically endangered	Scottsdale Burrowning Crayfish

(continued)

Table 3.5 (continued)

Scientific name	IUCN Red List criteria	English name
Engaeus sternalis (Clark, 1936)	Critically endangered	Warracul Burrowing Crayfish
Engaeus strictifrons (Clark, 1936)	Least concern	
Engaeus tayatea Horwitz, 1990	Least concern	
Engaeus tuberculatus Clark, 1936	Least concern	
Engaeus urostrictus Riek, 1969	Vulnerable	
Engaeus victoriensis Smith and Schuster, 1913	Near threatened	
Engaeus yabbimunna, Horwitz, 1994	Vulnerable	Burnie Burrowing Crayfish
Engaewa pseudoreducta Horwitz and Adams, 2000	Critically endangered	
Engaewa reducta Riek, 1967	Endangered	Dunsborough Burrowing Crayfish
Engaewa similis Riek, 1967	Least concern	
Engaewa subcoerulea Riek, 1967	Least concern	
Engaewa walpolea Horwitz and Adams, 2000	Endangered	Walpole Burrowing Crayfish
Euastacus angustus Coughran and Dawkins, 2013		
Euastacus armatus (von Martens, 1866)	Data deficient	Murray River Crayfish, Murray Spiny Crayfish
Euastacus australasiensis (H. Milne Edwards, 1837)	Least concern	
Euastacus balanesis Morgan, 1988	Endangered	
Euastacus bidawalus Morgan, 1986	Endangered	
Euastacus bindal Morgan, 1989	Critically endangered	
Euastacus binzayedi Coughran and Furse, 2013		
Euastacus bispinosus Clark, 1936	Vulnerable	Glenelg River Crayfish, Prickley-backs
Euastacus brachythorax Riek, 1969	Endangered	
Euastacus clarkae Morgan, 1997	Critically endangered	
Euastacus claytoni Riek, 1969	Endangered	
Euastacus crassus Riek, 1969	Endangered	Alpine Spiny Crayfish
Euastacus dalagarbe Coughran, 2005	Critically endangered	
Euastacus dangadi Morgan, 1997	Least concern	
Euastacus dharawalus Morgan, 1997	Critically endangered	Fitzroy Falls Crayfish
Euastacus diversus Riek, 1969	Endangered	Orbost Spiny Crayfish
Euastacus eungella Morgan, 1988	Critically endangered	

(continued)

Table 3.5 (continued)

Scientific name	IUCN Red List criteria	English name
Euastacus fleckeri (Watson, 1953)	Endangered	
Euastacus gamilaroi Morgan, 1997	Critically endangered	
Euastacus girurmulayn Coughran, 2005	Critically endangered	
Euastacus gumar Morgan, 1997	Endangered	
Euastacus guruhgi Coughran, 2005	Critically endangered	
Euastacus guwinus Morgan, 1997	Critically endangered	
Euastacus hirsutus (McCulloch, 1917)	Endangered	
Euastacus hystricosus Riek, 1951	Endangered	
Euastacus jagabar Coughran, 2005	Critically Endangered	
Euastacus jagara Morgan, 1988	Critically endangered	
Euastacus kershawi Smith, 1912	Least concern	Spinybacks, Gippsland Spiny Crayfish
Euastacus maccai McCormack and Coughran, 2008	Endangered	
Euastacus maidae (Riek, 1956)	Critically endangered	
Euastacus mirangudjin Coughran, 2002	Critically endangered	Ochre-bellied Crayfish
Euastacus monteithorum Morgan, 1989	Critically endangered	
Euastacus morgani Coughran and McCormack, 2011		
Euastacus neodiversus Riek, 1969	Endangered	
Euastacus neohirsutus Riek, 1956	Least concern	
Euastacus pilosus Coughran and Leckie, 2007	Endangered	
Euastacus polysetosus Riek, 1951	Endangered	
Euastacus reductus Riek, 1969	Least concern	
Euastacus rieki Morgan, 1997	Endangered	
Euastacus robertsi Monroe, 1977	Critically endangered	
Euastacus setosus (Riek, 1956)	Critically endangered	
Euastacus simplex Riek, 1956	Vulnerable	
Euastacus spinichelatus Morgan, 1997	Endangered	
Euastacus spinifer (Heller, 1865)	Least concern	

(continued)

Table 3.5 (continued)

Scientific name	IUCN Red List criteria	English name
Euastacus sulcatus Riek, 1951	Vulnerable	
Euastacus suttoni Clark, 1941	Vulnerable	New England Crayfish
Euastacus urospinosus (Riek, 1956)	Endangered	
Euastacus valentulus Riek, 1951	Least concern	
Euastacus woiwuru Morgan, 1986	Near threatened	
Euastacus yanga Morgan, 1997	Least concern	
Euastacus yarraensis (McCoy, 1888)	Vulnerable	Yarra Spiny Crayfish
Euastacus yigara Short and Davie (1993)	Critically endangered	
Geocharax falcata Clark, 1936	Vulnerable	
Geocharax gracilis Clark, 1936	Least concern	
Gramastacus insolitus Riek, 1972	Near threatened	Western Swamp Crayfish
Gramastacus lacus McCormack, 2014		
Ombrastacoides asperrimanus Hansen and Richardson, 2006	Near threatened	
Ombrastacoides brevirostris Hansen and Richardson, 2006	Least concern	
Ombrastacoides decemdentatus Hansen and Richardson, 2006	Least concern	
Ombrastacoides denisoni Hansen and Richardson, 2006	Critically endangered	
Ombrastacoides dissitus Hansen and Richardson, 2006	Near threatened	
Ombrastacoides huonensis Hansen and Richardson, 2006	Least concern	
Ombrastacoides ingressus Hansen and Richardson, 2006	Data deficient	
Ombrastacoides leptomerus (Riek, 1951)	Least concern	
Ombrastacoides parvicaudatus Hansen and Richardson, 2006	Critically endangered	
Ombrastacoides professorum Hansen and Richardson, 2006	Data deficient	
Ombrastacoides pulcher (Riek, 1967)	Vulnerable	
Paranephrops planifrons White, 1842	Least concern	
Paranephrops zealandicus (White, 1847)	Least concern	
Spinastacoides catinipalmus Hansen and Richardson, 2006	Least concern	
Spinastacoides inermis (Clark, 1939)	Least concern	
Spinastacoides insignis (Clark, 1939)	Least concern	
Tenuibranchiurus glypticus Riek, 1951	Endangered	Swamp Crayfish

(three Australian and two New Guinean species) to be threatened with extinction, with another 5 species considered to be Data Deficient.

A number of species of *Engaeus* are restricted-range endemics (Horwitz 1990; Harvey 2002) whose habitat is threatened by agricultural activities (including ploughing), dam construction, and clearance of riparian vegetation (Richardson and Doran 2008). Approximately 60 % of the species of *Engaeus* are listed as VU or EN by the IUCN Red List, or as endangered by State legislation (the Commonwealth Environment Protection and Biodiversity Conservation Act), while four species of *Engaeus* (*E. granulatus, E. spinicaudatus, E. sternalis*, and *E. urostrictus*) are considered to be Critically Endangered by both the IUCN Red List and the State legislation.

Species of burrowing crayfish in the genus *Engaewa* require moist habitats, and arid conditions render them vulnerable to extinction (Wardell-Johnson and Horwitz 1996). Identified threats to *Engaewa* include the drainage of swamps for agriculture, and dam construction (Horwitz 1995; Horwitz and Adams 2000). About 40 % of species of *Engaewa* are assessed by the IUCN Red List as Least Concern.

The extensive distribution of *Euastacus* exposes many of the species in this genus to a broad array of threats including habitat destruction, pollution and reduced water quality, the introduction of exotic species, and illegal collection by humans (Furse and Coughran 2011). The 2010 IUCN Red List assessment listed 82 % of the species of *Euastacus* as threatened, 16 % as Least Concern, and 2 % as Data Deficient. The emerging threats to *Euastacus* are discussed in Furse (2014), including the effects of global climate change which especially threaten cool adapted organisms such as the members of this genus (Horwitz 1990).

Threats to species of *Geocharax* include habitat alteration, trampling by cattle, and phosphate run-off in agricultural areas (March and Robson 2006). Although *G. gracilis* is assessed as Least Concern by the 2010 IUCN Red List, the conservation status of this species was recently upgraded to Endangered under state legislation in Victoria.

Ombrastacoides denisoni is listed as Critically Endangered by the IUCN Red List and as a Priority Species by the Tasmanian Forest Practices Authority, and is currently listed as threatened under Tasmanian or Commonwealth legislation.

The 2010 conservation assessment of *Paranephrops* in the IUCN Red List is Least Concern, but populations of two species (*P. planifrons* and *P. zealandicus*) are now declining due to the combined effects of habitat reduction through the draining of wetlands, collection for human consumption, and predation by exotic species (Whitmore et al. 2000).

The distribution of all species of *Spinastacoides* extends throughout western Tasmania and each species in this genus has an extensive range (Hansen and Richardson 2006), but climate change is a potential threat (but none of these species are currently threatened).

Tenuibranchiurus is a monotypic genus that is endemic to the central and eastern coastal regions of Australia. One species (*T. glypticus*) is assessed by the IUCN Red List as Endangered, but it is not listed as threatened by any of the Australian conservation protocols. The main threats to species of *Tenuibranchiurus* are habitat destruction, pollution, and salt water intrusion (Furse et al. 2015).

In summary, 40.5 % of Oceanian parastacid species are listed as threatened with extinction and 7.8 % of species are Data Deficient.

3.18 Madagascar

Seven species of parastacid crayfish in the genus *Astacoides* Guérin, 1839 are endemic to Madagascar (Boyko 2015; Boyko et al. 2005) (Table 3.6).

3.19 Distribution

Crayfishes in the genus *Astacoides* are unevenly distributed in Madagascar. All of them are restricted to an inland area of about 60,000 km^2 in the southeast highlands between 18° and 25°S and 46° and 48°E, from the Hauts Plateau near Anjozorobe in Analamanga Region, 90 km north-east of Antananarivo, to the Isaka Valley int eh Anosy Region some 700 km to the south (Hobbs 1987; Rabeharisoa 1996). Reports suggesting a broader range (Dixon 1992) including the Masoala peninsula (approximately 17°S, 50°E) and the mountains of Andapa (approximately 14°S, 49° E) are uncorroborated and not supported by specimens (Crandall 2003).

Table 3.6 Taxonomy and assessment information of Madagascar

Scientific name	IUCN Red List criteria	Malagasy name
Astacoides betsileoensis Petit, 1923	Endangered	Orana mena or Oramaintso or Orana Satria or Anjatsy or Pepeo or Orambanonga or Orambato
Astacoides caldwelli Bate, 1865	Endangered	Orana Mena
Astacoides crosnieri Hobbs, 1987	Data deficient	Orampotoka or Orambory or Oramalemy
Astacoides granulimanus Monod and Petit, 1929	Least concern	Orandambo
Astacoides hobbsi Boyko, 2005	Data deficient	Orapotsy
Astacoides madagascariensis H. Milane Edward and Audouin, 1839	Data deficient	Orambato or Orana Maintso or Orana Mainty or Orana Satria or Oramaintso
Astacoides petiti Monod and Petit, 1929	Data deficient	Orambato

3.20 Conservation

Threats to *Astacoides* in Madagascar include overharvesting, habitat loss, and competition with introduced species. Crayfish harvesting is common throughout the range of *Astacoides* (Jones et al. 2005, 2006, 2007), and a recent study in and around Ranomafana National Park (Jones et al. 2005) suggested that the harvest of *A. granulimanus* is potentially sustainable under the current conditions. However, the effect of harvesting on other species such as *A. betsileoensis* that have a lower fecundity is a cause for concern. Differences in reproductive strategy influence a species' vulnerability to harvesting (Milner-Gulland and Lhagvasuren 1998; Kokko et al. 2001), but aquaculture is not a viable solution, given the slow growth rates of *Astacoides* (Jones et al. 2007). Crandall (2003) suggested that the recent destruction of most of the lowland forests of Madagascar has had little impact on crayfish populations in the highlands (between 800 and 2000 m above sea level, asl) because slash-and-burn activities in Madagascar tend to be below 900 m asl. However, habitat loss at low altitudes could become a very serious threat to Madagascar's crayfish because habitat destruction is taking place throughout that island and could spread to higher altitudes (Hawkins and Horning 2001). Other threats to Madagascar's crayfish come from the introduction of non-native crayfishes and from the predatory Asian snake-head fish, *Channa maculata* (whose local name: is fibata) (Raberisoa et al. 1996). These threats suggest that the IUCN Red List assssments that list 28.6 % of Malagasy crayfish as endangered may prove to be an underestimate, especially because the vast majority of the species (57.1 %) are too poorly known to assess (Data Deficient).

There are no species of crayfish found naturally anywhere on continental Africa, but five species of crayfish have been introduced there, from North America (*Procambarus clarkii,* and *P. fallax*), Australia (*Cherax destructor, C. quadricarinatus, C. tenuimanus*), and Europe (the marbled crayfish). There are notable populations of alien crayfish established in South Africa (Holdich 1999), Sudan, Kenya, Uganda, Zambia, and Zimbabwe. *Procambarus clarkii* has spread rapidly from the intial release points of introduction in Kenya (Hobbs et al. 1989; Howard and Matindi 2003; Foster and Harper 2007).

In 2005 biologists at the University of Antananarivo in Madagascar noticed that an unusual non-native decapod (the marbled crayfish or Marmorkrebs) was being sold at markets close to the capital by fishermen who had collected them locally. To date, the marbled crayfish has been found only in the vicinity of Ambohimangakely (Antananarivo), most commonly in rice fields (Jones et al. 2007). Marbled crayfish are likely to compete with native *Astacoides* species, and have the potential to transmit the crayfish plague, *Aphanomyces astaci* that is lethal to crayfish (Jones et al. 2006; Kawai et al. 2013; Feria and Faulkes 2011). Marbled crayfish grow rapidly, much faster than species of *Astacoides* (that are among the slowest growing of all crayfish) (Jones et al. 2007). Marbled crayfish also are six times more fecund than species of *Astacoides* and marbled crayfish can breed more than once per year, compared to *Astacoides* that breeds once a year (Jones et al. 2005). Because of

Table 3.7 Taxonomy and assessment information of Europe

Scientific name	IUCN Red List criteria	English name
Astacus astacus (Linnaeus, 1758)	Vulnerable	Noble Crayfish
Astacus leptodactylus Eschscholtz, 1823	Least concern	Narrow-clawed crayfish or Slender-clawed Crayfish
Astacus pachypus Rathke, 1837	Data deficient	Thick-clawed Crayfish
Austropotamobius torrentium (Schrank, 1803)	Data deficient	Stone Crayfish
Austropotamobius pallipes (Lereboullet, 1858)	Endangered	White-clawed Crayfish

these attributes, marbled crayfish have an immense potential to outcompete native crayfish and may even be able to outcompete Madagascar's endemic freshwater crabs (Cumberlidge et al. 2004). To date, marbled crayfish have not been found in the high altitude forested areas where *Astacoides* lives (Jones et al. 2007), but their present wild range overlaps with the distribution of several species of freshwater crabs.

3.21 Europe

3.21.1 Taxonomy and Conservation

Five indigenous species of astacid crayfish occur in European freshwaters (Table 3.7).

3.22 Distribution

Four European species, *Astacus astacus, A. leptodactylus*, *Austropotamobius pallipes*, and *A. torrentium* are heavily consumed for food and have long been translocated between Euopean countries and islands (Füreder et al. 2009). The range of *A. astacus* extends from Russia and Ukraine in the east, to Finland, Sweden, and Norway in the north, to Greece in the south, and the United Kingdom and France in the west. The occurrence of this species within Andorra, Cyprus, UK, Liechtenstein, Luxembourg, Morocco and possibly Montenegro and Italy, is probably the result of introductions from neighbouring countries (Kouba et al. 2014). *Astacus leptodactylus* is presently found in 32 countries (Holdich et al. 2009), including extensive areas in Russia and Ukraine (Kouba et al. 2014), and in southeast Europe including Bulgaria (Stoynov et al. 2013; Trichkova et al. 2013), Romania (Györe et al. 2013), Serbia (Simić et al. 2008), and Croatia (Maguire 2009; Maguire and Gottstein-Matočec 2004; Maguire et al. 2011). *Astacus pachypus* is reported to occur in Azerbaijan, Kazakhstan, European Russia, and Ukraine (Holdich et al. 2009). *Austropotamobius pallipes* has a wide distribution throughout Europe (Holdich et al. 2009), with its western limits in Portugal (but it is now thought to be extinct there), its eastern limits in Montenegro, its southern limits in Spain, and its northern limits in Scotland. *Austropotamobius torrentium* is found in at least 20 countries in central and southeastern Europe (Holdich et al. 2009; Kouba et al. 2014) including Bosnia and Herzegovina (Trožić-Borovac 2011), Serbia, Montenegro (Simić et al. 2008), and Germany (Groß et al. 2008; Martin et al. 2008). It is likely that the populations of this species in England may have originally been introduced there from France (Kouba et al. 2014; Grandjean et al. 1997; Diéguez-Uribeondo et al. 2008), and that populations in Sardinia may also be the result of past introductions (Bertocchi et al. 2010).

3.23 Conservation

The IUCN Red List assesses 40 % of astacids as endangered with another 40 % being too poorly known to assess (Data Deficient). EU countries have a regional list of criteria for the designation of endangered species (the EU Habitat Directive) that has 6 criteria or levels (http://lhnet.org/eu-habitat-directive/). The EU Habitat Directive protocols assess 60 % of European astacid species as endangered species. *Austropotamobius torrentium* is Data Deficient according to the IUCN Red List, but it is an endangered species according to the EU Habitat Directive regional criteria Appendix V (animal and plant species of community interest whose capture in the wild and exploitation may be subject to management measures). This situation is complicated by the fact that *A. pallipes* may be a species complex formed by two distinct species, *A. pallipes* and *A. italicus* (Fratini et al. 2005) according to molecular analyses by Santucci et al. (1997), Grandjean et al. (2002), and Pedraza-Lara et al. (2010). Reports of the recent population and distribution trends of *Astacus pachypus* are considered here to be speculative (Kouba et al. 2014).

A number of European species of indigenous crayfish are in decline and there are growing concerns that unless there is concerted action to conserve them they will be progressively replaced by invasive non-indigenous crayfish species in most or all of their range (Peay and Füreder 2011; Tricarico et al. 2010; Weinländer and Füreder 2009). North American and Australian crayfish species have been introduced into European freshwaters since the end of the 19th century. For example, U.S. crayfish such as the spiny-cheek crayfish, *Orconectes limosus*, the signal crayfish, *Pacifastacus leniusculus*, and the red swamp crayfish, *Procambarus clarkii*, have all been introduced into European waters between 1890 and the mid-1970s. Similarly, Australian crayfish such as *Cherax destructor* and *C. quadricarinatus,* and North American crayfish such as *Orconectes immunis, O. limosus, O. juvenilis, O.* cf. *virilis, Procambarus* cf. *acutus,* have all been recorded from European freshwaters (Füreder 2015). The Marmorkrebs or marbled crayfish (Scholtz et al. 2003) appears to be a hybrid that originated in captivity in aquaria in Germany and reproduces by parthenogenesis (virgin females produce fertile eggs without needing to mate with a male) which is the first time that this strategy has been reported for any decapod crustacean. The marbled crayfish was formally named as *Procambarus fallax* form *virginalis* (Martin et al. 2010). Rumors of the existence of the marbled crayfish first surfaced in online discussions by amateur aquarium enthusiasts, who were aware of an enigmatic crayfish species of unclear origin. Marbled crayfish were first sold by an aquarium shop in Germany in the mid-1990s (Vogt et al. 2004). Since then, reports of wild populations of marbled crayfish living in European freshwaters include Germany (Martin et al. 2010; Chucholl and Pfeiffer 2010; Chucholl et al. 2012), the Netherlands (Holdich and Pöckl 2007), Italy (Marzano et al. 2009), Sweden (Bohman et al. 2013), and Slovakia (Stloukal 2009).

3.24 Asia

3.24.1 Taxonomy and Conservation

3.25 Distribution

Large areas of Asia lack crayfish but there is a single genus *Cambaroides* that is native to the eastern corner of the continent in far-eastern Russia (ranging from the northern part of Sakhalin Island, the Amur River and the Ussuri River basin), the Korean Peninsula, northern China, Mongolia, and Hokkaido and northern Honshu in Japan (Kawai 2012; Kawai and Arai 2000; Kawai et al. 2015) (Table 3.8).

3.26 Conservation

The IUCN Red List shows that four species (*Cambaroides dauricus, C. japonicus*, *C. schrenckii, C. similis)* are too poorly known to assess (Data Deficient), and that two species (*C. wladiwostokensis* and *C. koshewnikowi*) have not been assessed (NA). However, the Government of Mongolia protects *C. dauricus* as an endangered species (Ministry for Nature and the Environment at Mongolia 1997), and The Environmental Agency and other official organizations of Japan have designed *C. japonicus* as an endangered species (Kawai and Fitzpatrick 2004). In Russia, *C. schrenckii* was listed as threatened in the Red Data book of the Sakhalin region in the Russian Federation (as *Cambaroides sachalinensis* Birstein and Vinogradow 1934, a junior synonym of *C. schrenckii*) (Kawai et al. 2013; Labay 2000). Populations of *Cambaroides wladivostokiensis* in Russia have been declining

Table 3.8 Taxonomy and assessment information of Asia

Scientific name	IUCN Red List criteria	Regional criteria	Russian name	Chinese name	Mongolian name	Japanese name	Korean name
Cambaroides dauricus (Pallas, 1773)	Data deficient		Daursky Rechnoy Rak	东北黑螯虾 Dōngběi hēi áo xiā or Rako (Changu-F and Chun-Lin 1959; Hart 1994) or dong bei la gu	Hafuchi (Ministry for Nature and the Environment at Mongolia 1997; Kawai and Arai 2000)		
Cambaroides japonicus (De Haan, 1841)	Data deficient			日本黑螯虾 Rìběn hēi áo xiā		Zarigani or Nihon-Zarigani (Kawai and Fitzpatrick 2004)	
Cambaroides similis (Koelbel, 1892)	Data deficient			朝鲜黑螯虾 Cháoxiăn hēi áo xiā			Kajae (Kawai and Min 2005)
Cambaroides schrenckii (Kessler, 1874)	Data deficient			南京黑螯虾 Nánjīng hēi áo xiā			
Cambaroides wladiwostokensis Birstein and Winogradow, 1934		Endangered Species		海参崴黑螯虾 Hăishēnwăi hēi áo xiā			
Cambaroides koshewnikowi Birstein and Winogradow, 1934		Extinct					

Regional criteria based on Kawai et al (2015) sharply over the past several decades due to habitat loss, particularly along the rivers flowing into the Peter the Great Bay which is where their main distribution lies (Barabanshchikov 2003; Marin 2013). *Cambaroides koshewnikowi* (Starobogatov 1995) is found in the Amur River delta, the Nikolaevsk-na-Amure estuary, and in the Tatar Strait where it lives in both fresh water and brackish water. However, there have been no records of *C. koshewnikowi* for the last 30 years and it may even be extinct (Kawai et al. 2015). In Korea, *C. similis* is ranked as a "monitored species", which means that this crayfish is a candidate for recognition as an endangered species (Kored 2015). The criteria used in the Korean red list protocols are evaluated and updated every 5 years based on monitoring. The most recent evaluation recognises *C. similis* as an endangered species (G. S. Min, personal communication). The IUCN Red List records all species of *Cambaroides* as Data Deficient (Richman et al. 2015), but recent research (Kawai and Takahata 2010; Labay 2000; present chapter) suggests that all species of *Cambaroides* might be threatened with extinction in their native ranges, and that one species may already be extinct. Clearly, conservation actions are urgently needed.

Interestingly, *C. schrenckii* has been illegally introduced by anglers into Russian freshwaters beyond its natural range since the 1970s, and has also been legally live-stocked in rivers and water reservoirs in and near Vladivostok (Barabanshchikov 2003; Kawai and Min 2005). Subsequently, the range of this species has expanded on its own following flooding and now includes rivers and reservoirs in the Bay of Peter the Great and in the eastern part of Primorye region as well as basins of the Ussuri River and Khanka Lake (Barabanshchikov 2003). In those areas where *C. schrenckii* is an alien species it has had a negative impact on native crayfishes such as *C. dauricus* and *C. wladivostokiensis* that are now endangered because their populations have drastically declined or have become locally extinct following contact with *C. schrenckii* (Barabanshchikov 2003).

Astacus leptodactylus Eschscholtz, 1823 is a large-sized species that is endemic to Europe and which impacts the European river ecosystems wherever it is found (Füreder 2015). In August 2012, this western European crayfish was reported from Siberia in far-eastern Russia (Kawai et al. 2015) which will probably become a new threat to the native ecosystems in Asia.

In 1997 KBS, a broadcasting company in South Korea, announced that the red swamp crayfish, *Procambarus clarkii* had been found for the first time in a lake in Yongsan Park, Seoul City. This crayfish population has now become well established in water bodies around Seoul and its distributional range is slowly increasing. Live individuals of *P. clarkii* are imported into Korea from other Asian countries and sold at pet shops in markets in major cities such as Seoul, and it is highly probable that some of these individuals have been released in the rivers around Seoul City (HS Ko, personal communication).

Two exotic species of crayfish, *P. clarkii* and *Pacifastacus leniusculus*, have been introduced into Japan. *Procambarus clarkii* was introduced into Kamakura City, Honshu on 12th May, 1927 by a private company (Kawai and Kobayashi 2006), and has since spread across the Japanese Archipelago. *Procambarus leniusculus* was released into Hokkaido Prefecture on 28th July, 1930, and was subsequently released in Shiga Prefecture, on 4th November, 1927, by the Japanese Government (Kawai et al. 2003). Current localities of *P. leniusculus* are Hokkaido, Fukushima, Nagano, Chiba, Fukui, Shiga, where they are having a negative impact on native Japanese ecosystems (Nakata and Goshima 2003, 2006). In 2007, several individuals of the parthenogenetic marbled crayfish *Procambarus fallax* f. *virginalis* (Scholtz et al. 2003) were collected from Sapporo City, Hokkaido, Japan (Kawai and Takahata 2010). This is of concern because this parthenogenetic highly fecund macroinvertebrate has the portential to constitute a serious threat to freshwater systems in Japan, especially if it gains access to rice fields (Faulkes et al. 2012). So far, there have been no further records of the marbled crayfish in Japan.

It is likely that *P. clarkii* has not invaded the Primorye Territory in far-eastern Russia near to the border with China but this crayfish is intensively cultured by China in large ponds (Kawai et al. 2015).

3.27 Threats and Conservation Issues

Recent molecular studies have shown that several widespread species of crayfish (such as *Cambaroides japonicus* (Koizumi et al. 2012) and *Pacifastacus leniusculus* (Larson and Williams 2015) may be species complexes that include one or more cryptic species (Füreder 2015). The presence of possible cryptic new species is of concern to crayfish taxonomists and conservation specialists because the number of endangered species is likely to increase if some of the existing species prove to include cryptic new species with a small population and a narrow distribution.

The IUCN Red List is the most reliable source when seeking the conservation status of a species, but it needs to updated regularly every time new data on a species population levels, distributional ranges, or threats are collected. Richman et al. (2015) summarizes the results of a global conservation assessment of every species of crayfish known, and draws on the expertise of 23 crayfish specialists from a number of countries. The IUCN Red List includes data on the major global threats to species-rich geographical regions such as climate-change, logging, invasive species, disease, urban development, agriculture, dam management, harvesting, pollution, and human disturbance (Richman et al. 2015). However, the IUCN Red List contains many Data Deficient species that are often assessed as endangered when regional conservation protocols are applied. For example, all Asian cambaroid crayfishes are assessed as Data Deficient by the IUCN Red List, but all of them are assessed as endangered species (and one of these, *Cambaroides koshewnikowi*, may even be extinct).

Freshwater crayfish distribution globally is mostly in the temperate regions of the world (Fig. 3.1) where urbanization and agricultural exploitation are intense. Crayfish are aquatic animals that depend on permanent water sources and they reproduce by direct development rather than producing planktonic larval stages, and this adaptation alone contributes to their isolation, high speciation rate, and endemism. Gelder and Williams (2015) point out that crayfish have numerous kinds of

Fig. 3.2 Current distribution of the signal crayfish, *Pacifastacus leniusculus*

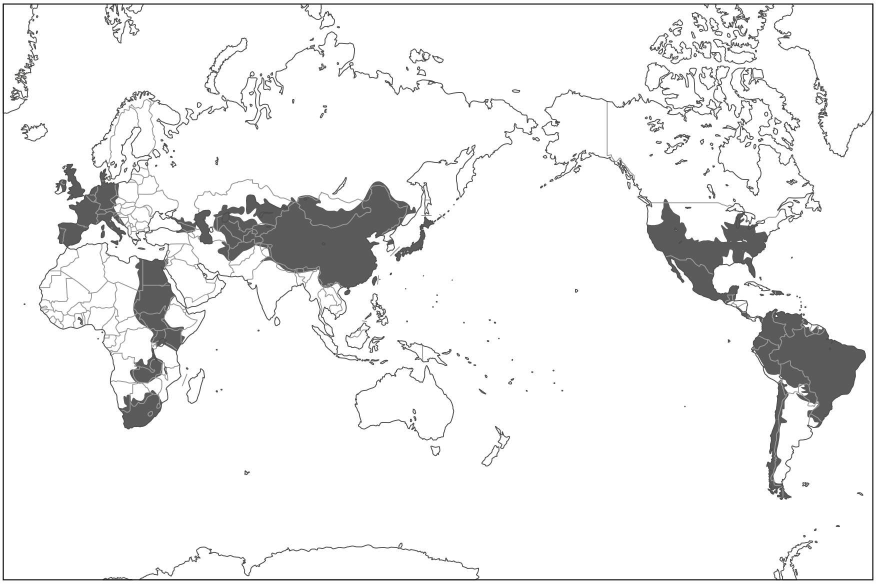

Fig. 3.3 Current distribution of the red swamp crayfish *Procambarus clarkii*

symbiontic organisms on their bodies that would also become extinct should crayfish species disappear. The introduction of alien crayfish species is prohibited in Oceania because non-native crayfish species particularly impact restricted-range endemic endangered species. Figures 3.2 and 3.3 show the native distributions of freshwater crayfish in Africa, Asia, Europe, and North, Central, and South America, as well as the expanding ranges of alien species such as *Procambarus clarkii* and *P. leniusculus* in Europe, Japan, Africa, and South America.

The native range of *P. clarkii* spans from northern Mexico to a number of states in the USA including Florida, Illinois, New Mexico, Oklahoma, Tennessee, and Texas. *Procambarus clarkii* has been widely introduced across the globe in the past 20 years not only to other states in the USA (Alabama, Arizona, Arkansas, California, Georgia, Hawaii, Idaho, Indiana, Maryland, North Carolina, Nevada, Ohio, Oregon, South Carolina, Utah, and Virginia, West Virginia), but also to Europe (Belgium, Cyprus, France, Germany, Italy, Majorca, The Netherlands, Portugal, Spain, Switzerland, United Kingdom), Central and South America (Belize, Chile, Colombia, Costa Rica, Dominican Republic, Ecuador, Venezuela), Africa (Egypt, Kenya, South Africa, South Sudan, Sudan, Uganda, Zambia, Zimbabwe), and Asia (China, Japan, Philippines, Taiwan) (Hobbs et al. 1989; Holdich 1999; Howard and Matindi. 2003; Foster and Harper 2007) (http://maps.iucnredlist.org/map.html?id=153877). Furthermore, recent studies have reported the presence of *P. clarkii* in Austria (Füreder 2015), Brazil (Amazon, Paraguay/Lower Parana River Basin, San Paolo) (Magalhães et al. 2005; Silva and Bueno 2005; Torres and Álvarez 2012), Mexico (Chiapas Region, Alvarez and Villalobos 2015), and South Korea (near Seoul City, Kawai pers. obs.).

Although the native range of *P. leniusculus* is well known in the western colder regions of North America, it is still not sufficiently understood in detail (Larson and Olden 2011, 2013; Martinez 2012). Given this provisio, *P. leniusculus* has been introduced into many countries well beyond its native range over the last century including Austria, Belgium, Czech Republic, Croatia, Cyprus, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Italy, Latvia, Lithuania, Luxembourg, Netherlands, Norway, Poland, Portugal, Russian Federation (Europe), Slovenia, Slovakia, Spain, Sweden, Switzerland, and the United Kingdom (Füreder 2015; Hefti and Stucki 2006), as well as in Japan (Kawai and Takahata 2010), and some of the U.S. western states including California, Nevada, and Utah. The areas where the distributions of alien crayfishes overlap and co-exist are noticeably expanding.

Other North American cambarid species (*Orconectes immunis, O. juvenilis, O. limosus, O.* cf. *virilis, Procambarus* cf. *acutus, P. fallax* f. *virginalis*), and Australian parastacid species (*Cherax destructor,* and *C. quadricarinatus*) have been introduced into Europe and *Orconectes virilis* and *Cherax quadricarinatus* have been introduced into Central America. Populations of Australian parastacids *Cherax destructor, C. quadricarinatus, C. tenuimanus,* and the North American cambarid *P. clarkii* are have become established in many parts of continental Africa, and the parthenogenetic marbled crayfish *P. fallax* f. *virginalis* is established and is spreading in Madagascar. The parthenogenetic marbled crayfish represents a new threat for global crayfish conservation because this alien species outcompetes native crayfish and has the potential to transmit crayfish plague (Jimenez and Faulkes 2010; Jones et al. 2007; Kawai and Takahata 2010; Feria and Faulkes 2011).

3.28 Conclusion

1. Freshwater crayfish are mainly distributed in the temperate parts of the southern and northern hemispheres, although there is a significant difference in the species richness among geographical regions. The most species rich area is found in the USA and Mexico, east of the Rocky Mountains, with 432 species represented by 11 genera one family (Cambaridae) while the most species-poor region is far-east Asia with only 6 species in a single genus, *Cambaroides*.
2. All members of Astacoidea can construct burrows, which is probably an apomorphic adaptation for life in freshwater.
3. The conservation status of all crayfish species worldwide has been assessed using the IUCN Red List protocols as well as by regional governmental red data lists. It is clear that there are a significant number of species that are threatened with extinction: 22.1 % of Cambaridae in Canada and the USA, 40 % of American Astacidae, 29.3 % of American Cambaridae (in Mexico and Central America), 69.2 % of South American Parastacidae, 34 % of Oceanian Parastacidae, 28.6 % of Madagascan Parastacidae, 40 % of European Astacidae, and 100 % of Asian Cambaridae (Table 3.9).
4. The present range of two alien crayfishes, *Pacifastacus leniusculus* and *Procambarus clarkii,* has been updated here. The distributional ranges of these two species are spreading in Asia, Africa, South America, and Europe and their impact on the native ecosystems and native species of crayfishes is becoming of increasing global concern. The new threat presented by the exotic

Table 3.9 Summary of the 2010 IUCN Red List and regional red list of freshwater crayfish (data: Kawai et al. 2015)

	Total of species number	Data deficient	IUCN endanger species[a]	Update based on local red list
Atlantic side of North America	371	86	53	55
Pacific side of North America	4	1	1	
Middle America	59	17	18	18
South America	13	10	1	6
Oceania	153	12	62	
Africa	7	4	2	
Europe	5	2	2	3
Asia	6	4	0	6

[a] Endangered species according to the following categories; "Vulnerable, Endangered, Critically Endangered, Extinct in the wild, and Extinct" and not endangered species "Least Concern, and Near Threatened". "Not Evaluated and Data Deficient"

parthenogenetic marbled crayfish, *Procambarus fallax* f. *virginalis* which was first found in European aquaria, has now been reported living in wild populations in Europe, Madagascar, and Asia (only one record).

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Chapter 4
A Brief History of Freshwater Crab Research

Michael Türkay, Tadashi Kawai, Moritz Sonnewald and Neil Cumberlidge

Abstract The history of the study of the biology of freshwater crabs is described from the first records in ancient Greece up to the present day. Today, hundreds of scientists from all parts of the world are engaged in the study of all aspects of freshwater crab biology from field studies of their ecology to molecular studies of their systematics and genetics. The first mention of the occurrence of freshwater crabs is by the Roman author Claudius Aelianus, then Aristoteles, Belon, Linne, A. Milne-Edwards, James wood-Mason, Mary Jane Rathbun, Major Alfred Alcock, Stanley Kemp, Jean Roux, Heinrich Balss, and Richard Bott in Europe developed the study.

Keywords Biology · Freshwater crab · Natural history · Scientific name · Taxonomy

4.1 Introduction

Our knowledge of freshwater crab biology is very old and dates back to Ancient Greece. Freshwater crabs were used as food and were of cultural significance in ancient Mesopotamia and there are detailed observations of their biology available

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(Brandis and Schuster 1999). For example, about 2000 years BC, Dumuzi, the God of Fecundity of Animals and Crops wrote about a dream that he had in which the river crabs were asked to weep for him because he was dying (etcsl.orinst.ox.ac.uk/section1/tr143.htm). This was taking place in July when the river crabs produce their eggs and leave the rivers in search of food on land. The ancient observation that freshwater crabs leave the rivers at the same time each year is the earliest record on the biology of any members of this group. This freshwater crab exodus still takes place each July, and was the original inspiration for the name of the month of July —Tammuz—in the old Babylonian calendar, that was adopted (as Temmuz) by the Hebrew, Arabic and Turkish calendars. There are other ancient links between crabs and astrology, because the sun rises in the zodiac sign of Cancer from mid-June to mid-July, and might be the reason for naming this zodiac sign the crab (Cancer), a usage that dates back to the old classical Sumerian texts (Brandis and Schuster 1999).

Freshwater crabs were well known to scholars in ancient Greece and the Roman Empire. For example, freshwater crabs are featured on a number of Greek coins such as the one from Acragas [=Agrigento] in Sicily that dates back to the 4thC BC. The Greek scholar Aristoteles writing in 350 BC mentions freshwater crabs in Historia Animalium (‘περί Ζώων Ιστορίαί’, book IV, part 2) as a “distinct variety” of crabs under the name “ποτάμιοι” but did not supply any more details. However, this does at least indicate that freshwater crabs were known at that time, but it is not possible to assign Aristoteles’ freshwater crab to a species recognized today from Greece (although all of the species from that country belong to the genus *Potamon*).

The first mention of freshwater crabs occurring outside of Europe is by the Roman author Claudius Aelianus (175–235 AD), who refers to the occurrence of freshwater crabs in the Nile in book 5 of his handwritings “De Nature Animalium”. Two comprehensive works—Belon (1553) and Rondelet (1555)—in the pre-Linnean European literature include freshwater crabs. The figure published by Belon (1553) does not represent a European freshwater crab (as stated in the caption) and therefore his account must be regarded as either inaccurate or as a reference to the next species “Cancer marinus” treated on the same page. In contrast, the figure published by Rondelet (1555) clearly shows *Potamon fluviatilis* from Italy, a country where he stayed during his 1549 voyages and where he made the illustration. Rondelet (1555) also provided a short description of that species and wrote that freshwater crabs also occur in Greece, Crete, Sicily, Italy, Etruria, and the Nile. Gesner (1558, 1563) included these early contributions on freshwater crabs in his multi-volume series “Historiae Animalium”. Freshwater crabs were also included in the book “Historia Animalium” by Aldrovandi (1606) although the figure of a crab in that work is not a freshwater crab (but might represent *Carcinus aestuarii* a portunid crab that is found brackish water in the Mediterranean region).

In Mexico and Central America freshwater crabs (probably pseudothelphusids) have been depicted in sculptures and other artifacts from Guatemala and El Salvador as early as the late classic Cotzumalhuapan culture (around 800 AD) (Moreira unpublished). In South America, indigenous populations (such as the Yanomami of northern Brazil) have long recognized different species of freshwater crabs and they have a good knowledge of their biology and occurrence, and use them for food and cultural rituals (Magalhães et al. 2006). For example, the pseudothelphusid *Kingsleya hewashimi* Magalhães and Türkay (2008), is used by the Yanomami of the Orinoco in a ritual that marks the transition of young girls to womanhood (Herzog-Schröder 2003). The recognition of different species of freshwater crabs by indigenous people in South America (Magalhães et al. 2006) must have been the same in many local inland tribes from the beginning of their existence (da Silva et al. 2014).

Although this information on freshwater crabs was available it is surprising that Linnaeus did not include these decapods in his "Systema Naturae" (Linnaeus 1758). The first freshwater crab to be formally described was *Dilocarcinus septemdentatus* Herbst, 1793 [original spelling: *Cancer septemdentatus*]. After that almost 70 species from different continents were described up to 1869, mostly as single species. In 1853 H. Milne Edwards published an account of the Ocypodoids s. l. of the Paris Museum collection that included 66 species of Thelphusinae that he described as the "Première tribu satellite des Gécarcinacés". In 1869 A-Milne-Edwards published a summary of all known species of freshwater crabs that included only 36 species because some of the earlier described taxa were not considered to be valid and were listed in synonymy (Milne-Edwards 1869).

Milne-Edward's (1869) revision prompted a new wave of species descriptions of freshwater crabs from many parts of the world. This included 63 new species descriptions between 1870 and 1892, including the important monograph by Wood-Mason (1871) on the Indian and southwest Asian freshwater crabs that added 19 new species.

Mary Jane Rathbun (1860–1943) published a series of revisionary works on crabs including monographs on the trichodactylids (1893), the pseudothelphusids (1898), and a monographic trilogy on the freshwater crabs of the world (Rathbun 1904, 1905, 1906). Her contributions influenced research on the freshwater crabs for the first half of the 20th century, and were the main source of information on their taxonomy and distribution well up until the 1950s. In her works Rathbun established a series of important morphological taxonomic characters of the carapace and mouthparts that were widely used for the identification of freshwater crabs from anywhere in the world.

The comprehensive keys and detailed figures in Rathbun's works allowed a great deal of further progress on freshwater crab biogeography and systematics. For example, Major Alcock (1909, 1910) published important taxonomic contributions on the Indian freshwater crabs that included 51 new species, while Kemp (1913, 1923) described 18 more new species of freshwater crabs from Southeast Asian, and Jean Roux published a series of works between 1904 and 1936 on the Southeast Asian and Indo-Malayan freshwater crabs.

The massive growth in species descriptions in the 20th century brought with it problems of accommodating these new species using the classification systems established by Rathbun (1904, 1905, 1906). Grouping species together based on Rathbun's carapace and mouthparts characters resulted in biogeographically improbable taxonomic groups whereby families and subfamilies were spread across different continents and geographical regions. It became clear that Rathbun's taxonomic characters were subject to a great deal of ontogenetic and geographical variability, and that in some cases characters were convergent and did not reflect common ancestry.

This realization prompted a search for more reliable morphological taxonomic characters to use for higher classifications as well as for species identification. Heinrich Balss (1886–1957) was the first person to realize that the pleopods of adult male freshwater crabs (gonopods 1 and 2) could be used as conservative morphological characters for species identification and for grouping specimens into higher taxonomic groups. Although the gonopods of freshwater crabs were described by Rathbun (1904) and by Colosi (1920), these characters were not at that time considered to be especially important for classification and systematics. Balss (1937) did published on the importance of using the gonopods in freshwater crab taxonomy but then left his position as chief conservator at the *Zoologische Staatssammlung* (Bavarian State Zoology Collection) at the University of Munich in 1937 and did not resume his work on decapod taxonomy again. When he returned to work in 1946 he spent his time compiling a major series of works on decapods and stomatopods in Heinrich Georg Bronn's *Klassen und Ordnungen des Tierreichs* (Classes and Orders of the Animal Kingdom) (Balss 1957; Tiefenbacher 1989).

However, in the early 1950s Balss enthusiastically expressed his ideas on the taxonomic importance of the gonopods of freshwater crabs to Richard Bott during a visit by Bott to the museum in Munich. This inspired Bott who was also considering the importance of the gonopods while working on the first monograph of the African freshwater crabs (Bott 1955).

Richard Bott was appointed as the curator of the Crustacea Section of the Senckenberg-Museum in Frankfurt, Germany in 1948. Between 1940 and 1944 Bott worked at the German School in Istanbul, Turkey where he became fascinated with the biology of the local species of freshwater crabs (*Potamon*), especially their copulatory activities. It was there that he became convinced that differences in gonopod morphology could help to distinguish between species of freshwater crabs, because the gonopods were protected under the male abdomen, whereas carapace characters were subject to variations prompted by changing environmental influences. Bott was able to study only one species in Turkey and his comparative studies had to wait until 1948 when he had access to collections of a larger group of species in the Senckenberg Museum in Frankfurt. However, the collection of freshwater crabs in Frankfurt at that time was relatively small, and his first large revisionary work in which he could test his concepts depended on his examining a more comprehensive selection of specimens held in other museums. Such a collection became available to Bott in the early 1950s when Edmond Dartevelle of the Belgian Congo Museum in Tervuren, Belgium sent a large series of specimens of African freshwater crabs to Bott in Frankfurt. These specimens, together with material from other sources, formed the basis of Bott's first monographic work (Bott 1955) that dealt with the freshwater crabs of Africa. Bott (1955, 1959, 1960, 1965) developed his ideas of using the gonopods to distinguish between species and to construct a new classification system for the freshwater crabs found on that continent. These landmark publications in freshwater crab systematics established identification systems and classifications that used the gonopods as primary characters. The works on African freshwater crabs were followed by major monographs on the American freshwater crabs (Bott 1969a, b, c), and the Asian and European freshwater crabs (Bott 1970a, b). The American monograph (Bott 1969a, b, c) was based mainly on material collected by Harald Sioli (Schaller 2004) and Ernst Joseph Fittkau (Hausmann et al. 2012) in the Brazilian Amazon.

Acknowledgments Sadly, the author of this chapter, Professor Michael Türkay, passed away just before completing the manuscript. The editors have taken the liberty of putting the finishing touches to this work, which is the final manuscript in the long and productive academic career of this great scientist, whose numerous contributions to crustacean biology have helped to lay the foundations of our present understanding of the field.

Appendix

In remembrance of Professor Michael Türkay (1948–2015).

Professor Michael Türkay passed away suddenly on 9th September 2015 in Frankfurt am Main, Germany, immediately before submitting the manuscript of his chapter on the history of freshwater decapods (Sect. 4.1, this volume). The second author (MS) was a colleague of MTs at the Senckenberg Research Institute in Frankfurt and completed the unfinished manuscript along with one of the editors (NC). The following is an account of MTs contributions and leadership in the field of freshwater decapod biology.

In August 2014 the first author (TK), visited Professor Michael Türkay (MT) the Curator of the Crustacean Section at the Senckenberg Research Institute and Natural History Museum in Germany (hereafter Senckenberg Museum) who was hosting the 8th International Crustacean Congress (ICC-8). TK and MT discussed the history of freshwater decapod systematics and the natural history of freshwater crayfish, and the importance of the museum's collection of crayfish. This meeting is summarized here to make it available to other scientists interested in the biology of freshwater decapods, and to serve as an illustration of Michael Türkay's vast knowledge of crustacean biology.

Michael Türkay succeeded Dr. Richard Bott as the Curator of the Crustacean Section of the Senkenberg Research Institute (Türkay 1974a, b, 1975). At that time Dr. Bott was one of the most accomplished freshwater crab taxonomists and had also published the first comprehensive revisionary work on Europe's freshwater crayfish (Decapoda: Astacidae) (Bott 1950). Freshwater crayfish (Astacidae, Cambaridae, and Parastacide) are a monophyletic group (Scholtz 1995) of exclusively freshwater decapods that are never found in marine environments (Crandall et al. 2000; Scholtz 2002). The distribution of crayfish worldwide is disjunctive: for example, astacid species are found only in northwestern North America and in western Europe but this family is absent from the rest of the USA. Bott tried to answer this enigmatic distribution of astacid crayfish but found it difficult to collect samples in Europe immediately after the end of World War II. But despite this, he collected samples of *Pacifastacus leniusculus* from the Pacific northwest of the USA with the help of the French Army, and these specimens are still in the Crustacean collection of the Senckenberg Research Institute (Fig. 4.1). While collecting in the USA Dr. Bott hid his collecting equipment (including a microscope) under a large winter overcoat, and managed to publish detailed taxonomic revisions of astacid crayfish. Dr. Bott established the American astacid genus *Pacifastacus* based on his specimens from North America that contributed to his systematic studies of the European astacid species of *Astacus* and *Austropotamobius*. This taxonomic work is still one of the best taxonomic contributions of its time that was produced at a time when relations between Germany and other European countries and the U.S.A. were still delicate immediately following the end of World War II.

The efforts of Dr. Bott to establish international partnerships that contribute to the understanding of crustacean systematics and morphology were continued by his successor, MT, who was already known for his friendship with Japan. MT visited Japan in 1979 to meet the past president of the Carcinological Society of Japan, Dr. Tune Sakai, and they subsequently established a productive scientific partnership, including the gift of a large number of specimens of crustaceans collected by Dr. Sakai that are now in the Senckenberg Museum as the "Tune Sakai Collection". Dr. Sakai also gave MT his Japanese name "美蛙鶴飼" (meaning keeper of beautiful frogs and cranes (birds)) (Türkay 1981, 1987).

Fig. 4.1 Specimens of *Pacifastacus leniusculus* from Portland, Jonson Creek, Oregon, U.S.A. (lot number SMF 1438, in Senckenberg Research Institute and Natural History Museum)

MT spent a great deal of time promoting developments in crustacean research including hosting large international conferences such as the 21st International Senckenberg-Conference on the Biology of Freshwater Decapods (2010), and the ICC-8 world congress (2014) that were of immense value to the entire international scientific community. It was during the world crustacean congress (ICC-8) on the 3rd day of the conference that MT became ill. Despite this setback he was eager to return, telling his wife Heide: "I must get better and go back to the conference". The sharing of knowledge throughout the international crustacean community was a great passion in his life. After the conference MT gave the first author souvenir gifts from the ICC-8 that bore his signature, and indicated that these could be sold at a charity auction to raise support for research on crustacean biology. There is no doubt that Michael Türkay's contributions to crustacean science deserve to be recognized by carcinologists worldwide.

Contributions by Michael Türkay to Freshwater Decapod Biology

Besides organizing the ICC world congress in 2014, Michael Türkay also organized the 21st International Senckenberg-Conference in 2010 on the Biology of Freshwater Decapods in Frankfurt am Main from December 8–10. There were 45 full participants from 10 countries and five continents at the conference who presented 27 papers and/or 12 posters on recent taxonomy, phylogenetics, biogeography, life history, and conservation of freshwater crabs, anomurans, prawns, and crayfish. The proceedings of the conference were published in a book entitled: "Advances in Freshwater Decapod Systematics and Biology" that was edited by Darren Yeo, Neil Cumberlidge, and Sebastian Klaus, and published by Crustaceana Monographs 19, Brill, 296 pp.

Michael Türkay authored over 300 publications, The following is a list of publications by MT that focus on freshwater decapods.

1. Magalhães C and M Türkay (1986). Brasiliothelphusa, a new Brazilian freshwater-crab genus (Crustacea: Decapoda: Pseudothelphusidae). Senckenbergiana biologica 66: 371–376, Abb.1-2; Frankfurt a. M.
2. Türkay M and P Naiyanetr (1987). The identity of Potamon rangoonense Rathbun 1904 and Thelphusa larnaudii A. Milne-Edwards 1869, with introduction of Neolarnaudia botti n.g. n.sp. (Crustacea: Decapoda: Potamidae). Senckenbergiana biologica 67: 389–396, Abb.1–6; Frankfurt a. M.
3. Türkay M (1987). Freshwater crab records of the Northern Sporades (Crustacea: De-capoda: Potamidae). Biologia Gallo-Hellenica 13: 47–50; Athen.
4. Türkay M and P Naiyanetr (1989). Ranguna Bott, 1966 and Larnaudia Bott, 1966 (Crustacea, Decapoda): proposed fixation of Thelphusa longipes A.Milne-Ed-wards, 1869 and Thelphusa larnaudii A.Milne-Edwards, 1869 as the respective type species. The Bulletin of zoological nomenclature 46: 101–103, London.

5. Türkay M and R Diesel (1994). Description of a new species of Sesarma from Jamaica with notes on its occurrence and biology. Senckenbergiana biologica 74): 157–161; 1–5.
6. Magalhães C and M Türkay (1996). Taxonomy of the neotropical freshwater crab family Trichodactylidae. I. The generic system with description of some new genera (Crustacea: Decapoda: Brachyura). Senckenbergiana biologica 75: 63–95, Figs. 1-50, Tables 1-2.
7. Magalhães C and M Türkay (1996). Taxonomy of the neotropical freshwater crab family Trichodactylidae. II. The genera Forsteria, Melocarcinus, Sylviocarcinus, and Zilchiopsis (Crustacea: Decapoda: Brachyura). Senckenbergiana biologica 75: 97–130, Figs. 1-57; Frankfurt a. M.
8. Magalhães C and M Türkay (1996). Taxonomy of the neotropical freshwater crab family Trichodactylidae. III. The genera Fredilocarcinus and Goyazana (Crustacea: Decapoda: Brachyura). Senckenbergiana biologica 75: 131–142, Figs. 1-11; Frankfurt a. M.
9. Schubart CD, J. Reimer, R Diesel, M Türkay (1997). Taxonomy and ecology of two endemic freshwater crabs from western Jamaica with the description of a new Sesarma species. Journal of Natural History 31: 303–419, Figs. 1-7.
10. Türkay M and AY Dai (1997). Review of Chinese freshwater crabs previously placed in the genus Malayapotamon Bott, 1968 (Crustacea: Decapoda: Brachyura: Potamidae). Raffles Bulletin of Zoology 45: 189–207, Text-Figs. 1-7, pl.1; Singapore.
11. Dai AY and M Türkay (1997). Revision of the Chinese freshwater crabs previously placed in the genus Isolapotamon Bott, 1968 (Crustacea: Decapoda: Brachyura: Potamidae). Raffles Bulletin of Zoology 45: 237–264, Text-Figs. 1-11, plates 1-2; Singapore.
12. Brandis D, Storch V and M. Türkay (1998). The status of the freshwater crab populations of the Khabur River (Syria). Journal of Natural History 32: 1439–1445, Abb. 1-3.
13. Türkay M (1998). Notes on the Mediterranean nematocarcinid shrimps (Crustacea: Decapoda: Caridea). Journal of Natural History 32: 1787–1794, Table 1, Abb. 1-4.
14. Brandis D, Storch V and M Türkay (1999). Morphology and function of the copulatory system in freshwater crabs of the genus Potamon. Journal of Morphology 239: 157–166, Text-Figs. 1-4.
15. Brandis D, Storch V and M Türkay (2000). Taxonomy and zoogeography of the freshwater crabs of Europe, North Africa, and the Middle east (Crustacea, Decapoda, Potamidae). Senckenbergiana biologica 80: 5–56, Table 1, Text-Figs. 1-18.
16. Magalhães C and M Türkay (2008). Taxonomy of the Neotropical freshwater crab family Trichodactylidae, IV. The genera Dilocarcinus and Poppiana (Crustacea, Decapoda, Trichodactylidae). Senckenbergiana biologica 88: 185–215, Text-Figs. 1-25.
17. Magalhães C and M. Türkay (2008). Taxonomy of the Neotropical freshwater crab family Trichodactylidae, V. The genera Bottiella and Rotundovaldivia

(Crustacea, Decapoda, Trichodactylidae). Senckenbergiana biologica 88: 217–230, Text-Figs. 1-18.

18. Magalhães C and M. Türkay (2008). A new species of Kingsleya from the Yanomami Indians areain the upper Rio Orinoco, Venezuela (Crustacea, Decapoda, Brachyura, Pseudothelphusidae). Senckenbergiana Biology 88: 231–237, Text-Figs. 1-4.
19. Magalhães C, Türkay M and DB Means (2009). The status of *Kunziana* Pretzmann, 1971 (Crustacea: Decapoda: Pseudothelphusidae), with a redescription of the holotype of *K. irengis* Pretzmann, 1971. Zootaxa 2276: 40–48, Text-Figs. 1-4.
20. Magalhães C and M Türkay (2010). A new freshwater crab of the genus *Brasiliothelphusa* Magalhães and Türkay, 1986 from Rio Aripuanã, southern Amazon Region, Brazil (Decapoda: Pseudothelphusidae). Nauplius 18: 103–108, Text-Figs. 1-7.
21. Magalhães C and M. Türkay (2012). Taxonomy of the Neotropical freshwater crab family Trichodactylidae. VI. The genera Avotrichodactylus and Rodriguezia (Decapoda: Brachyura: Trichodactylidae). Nauplius 20: 27–40, Text-Figs. 1-20.
22. Magalhães C, Campos MR and M Türkay (2013). Freshwater crabs from eastern Panamá: a new species of *Potamocarcinus* H. Milne Edwards, 1853, and new records of two little-known species (Crustacea: Decapoda: Pseudothelphusidae, Trichodactylidae). Zootaxa 3702: 348–356, Text-Figs. 1-3.
23. Klaus S and Türkay M (2014). Freshwater crab systematics and biogeography: The legacy of Richard Bott (*1902–†1974). In: Yeo D, N Cumberlidge, S Klaus (eds.), Advanced Freshwater Decapod Systematics and Biology. Crustaceana Monographs 19: 7–16, Figs. 1-3.

The following is a collection of biographies of carcinologists who have contributed to the present-day knowledge of freshwater crab systematics.

African Freshwater Crab Carcinologists

Heinrich Balss
Keppel Harcourt Barnard
Richard Bott
Louis-Eugene Bouvier
William Thomas Calman
Fenner Albert Chace
Colosi
Neil Cumberlidge
Savel Daniels
Isabella Gordon
Franz Hilgendorf
Johannes Govertus de Man
Alphonse Milne-Edwards
Henri Milne-Edwards
Theodore Monod

Nobili
Mary Rathbun

Europe and Asian Freshwater Crabs

Alfred William Alcock
Heinrich Balss
Richard Bott
Louis-Eugene Bouvier
Colosi
Ai Yun Dai
Johannes Govertus de Man
Stanley Wells Kemp
Franz Hilgendorf
Lipke Bijdeley Holthuis
Alphonse Milne-Edwards
Henri Milne-Edwards
Phaibul Naiyanetr
Peter K. L. Ng
Nobili
Mary Jane Rathbun
Hsi-Te Shih
Darren Yeo

New World

Fernando Alvarez
Jose-Luis Villalobos
Richard Bott
Fenner Albert Chace
Célio Magalahães
Alphonse Milne-Edwards
Henri Milne-Edwards
Gerhard Pretzmann
Gilberto Rodriguez
Alfred Smalley
Ingo Whertmann
Mary Jane Rathbun

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Chapter 5
Adaptation to Life in Fresh Water by Decapod Crustaceans: Evolutionary Challenges in the Early Life-History Stages

Klaus Anger

Abstract The Decapoda evolved in the Palaeozoic as a marine group and have since then shown limited radiation in limnic and terrestrial environments. About 80 % of the extant decapod species still live in the sea. The colonization of non-marine environments required physiological adaptations such as hyper-osmoregulate (for fresh water) and hypo-osmoregulate (for terrestrial and hypersaline habitats). Osmoregulatory abilities are strong in juvenile and adult freshwater decapods, but are typically absent in larval stages. Diadromous breeding migrations to estuaries or the sea are part of an adaptive strategy that allows adult life in non-marine habitats in combination with a conservation of the ancestral life-history pattern (extended planktonic larval development in salt water). Phylogenetically old groups of hololimnetic decapods (crayfish, aeglids, primary freshwater crabs) have completely eliminated the larval phase, showing direct development and brood care. Recent colonisers generally show intermediate patterns with an abbreviated and partially or fully lecithotrophic larval phase. Macroevolutionary patterns support possible colonization routes from the sea to fresh water and land. It is suggested that ecologically transitional habitats such as brackish mangrove swamps, salt marshes, seasonally inundated wetlands, and anchialine caves have been the principal entrance portals, rather than direct invasion through estuaries and rivers.

Keywords Diadromy · Abbreviated development · Larval ecology · osmoregulate · Brood care

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5.1 Introduction

The Decapoda represent the largest order of crustaceans, comprising almost 15,000 known extant species plus about 3000 fossil species (de Grave et al. 2009; Martin et al. 2009). According to the fossil record, decapods originated in the oceans in the Late Devonian about 360 mya, which was followed by a rapid radiation during the Mesozoic (Schram et al. 1978; Schram 2009). Model-based analyses of phylogenetic divergence times suggest that decapods made an even earlier appearance in the Silurian (>437 mya) (Porter et al. 2005; Bracken et al. 2009). Today almost 80 % of all extant decapod species are still living in their ancestral environment, the oceans, while less than 20 % have successfully conquered brackish and freshwater environments, and less than 2 % are terrestrial (de Grave et al. 2009; Vogt 2013). The relatively small percentage of non-marine decapod species indicates that the transition from marine to a limnic or terrestrial life style presents serious challenges.

The most dramatic change in environmental conditions in fresh water is that the concentrations of inorganic ions are greatly reduced compared to sea water. Dilute freshwater habitats not only limit the availability of essential minerals, they also challenge freshwater animals with an enormous reduction of osmotic pressure. Decapods living in fresh water face both osmotic gradients that cause water to flow into the body, and diffusion gradients that cause ions to leave the body; decapods living on land face dehydration of their body tissues and a physiologically dangerous increase in the concentration of their internal ions. The conquest of non-marine environments by ancestral marine decapods therefore required major adaptations in morphological and physiological traits that are necessary for osmotic and ionic protection. However, phylogenetic constraints mean that these evolutionary adaptations to life in a dilute medium have only evolved in a few decapod lineages (McNamara and Faria 2012; McNamara et al. 2015). The first part of this chapter discusses the principal mechanisms, structures, and functions of osmoregulate in freshwater decapods. Moreover, the transition from a marine to a limnic or terrestrial life style is accompanied by significant changes in nutritional conditions and in biotic factors such as competition and predation. This has required major adaptive changes in their reproductive, behavioural and developmental patterns, which will be treated later in this chapter.

The early developmental stages of decapods are structurally more delicate and physiologically more vulnerable than adults, so it is essential to consider the ontogeny of biological key variables such as feeding and osmoregulate (Strathmann 1993; Charmantier 1998; Charmantier and Charmantier-Daures 2001; Susanto and Charmantier 2001; Padilla and Miner 2006). Developmental changes are closely related to changing needs of the different life-history stages, which often live in different ecological conditions. Evolutionary transitions from the sea to fresh water and land can therefore only be understood if adaptive traits are considered in the context of life-history patterns. Particular attention is given here to changes in morphology, growth, locomotion, osmoregulate and feeding of the early ontogenetic stages. Macroevolutionary trends in adult life styles are discussed, as well as possible routes of colonization of non-marine environments by marine ancestors.

5.2 Physiological Adaptation to Non-marine Conditions: Osmoregulate

In aquatic crustaceans, variations in salinity can cause physiologically dangerous changes in the ionic concentration of extracellular body fluids (the haemolymph), cytosol osmolality, and cell volume. Freshwater decapods face the dilution of their body fluids from the gain of water by osmosis and from the loss of ions by diffusion. Selectively advantageous evolutionary adaptations include passive osmotic protection from a thick cuticle with reduced permeability to ions and water, highly specialised cell and tissue structures, and active metabolic pumps that move ions into the body and bring about osmoregulate (Rabalais and Cameron 1985a; Susanto and Charmantier 2000; Charmantier et al. 2009; Henry et al. 2012; McNamara and Faria 2012). These adaptations enable decapods living in brackish and fresh water to oppose the dilution of their body fluids from the gain of water and the loss of ions. These same adaptations protect decapods living on land against water loss and critically enhanced ion concentrations due to evaporation. This section summarises the basic physiological principles of osmoregulate in decapods including a brief account of the key molecules, cells, tissues, and organs involved.

Most groups of marine decapods are osmoconformers, regulating their blood concentration within a narrow range around the concentration of seawater ($\sim$1000 mOsm/kg). When faced with a low salinity environment, they suffer a hazardous dilution of their body fluids (Charmantier et al. 2009; Henry et al. 2012; McNamara and Faria 2012). Marine decapods are therefore stenohaline, tolerating only small fluctuations in environmental salinity.

Stenohaline marine decapods rely on intracellular isosmotic regulation that is based on changes in the concentrations of osmotically active free amino acids. Low salinities cause free amino acids in cells to decrease as they are released from the cytosol into the haemolymph, where they are catabolised and excreted as ammonia. High salinities cause free amino acids in cells to increase as they are obtained from food or from the breakdown of cellular proteins. These processes of intracellular osmoregulate cause significant metabolic losses of organic matter and energy and can only compensate for quite small fluctuations in habitat salinity.

Extracellular ionic regulation is an energetically more efficient mechanism which consists of a complex set of active (energy-consuming) processes that bring about ion transport through cell membranes in highly specialised epidermal cells called ionocytes. Extracellular ionic regulation is typically found in freshwater, estuarine, and terrestrial habitats. When decapods live in dilute media (brackish or freshwater), they hyper-osmoregulate whereby ion concentrations in the extracellular haemolymph space are up-regulated to compensate for passive osmotic ion losses and water ingress. In hypersaline or terrestrial habitats, they hypo-osmoregulate whereby ion concentrations in the extracellular haemolymph space are down-regulated to compensate for a passive increase in osmotic pressure due to water loss. The main emphasis here is on hyper-osmoregulate in freshwater decapods.

Ionocytes show characteristic ultrastructural features that allow them to be electron-microscopically identified and localized (Fig. 5.1). Their apical and basal cell poles face the external medium and the extracellular lacunar haemolymph space, respectively. The cell membrane shows deep basal infoldings that increase the surface area, closely associated with dense mitochondria populations that provide energy for the active transport of ions against their concentration gradients. Large-size apical microvilli, rough endoplasmic reticulum, Golgi bodies, and microtubules are also characteristic of ionocytes.

The principal processes of extracellular hyper-osmoregulate are illustrated in Fig. 5.2. A recent hypothetical model (Charmantier et al. 2009; McNamara and Faria 2012) can be summarised as follows. At the apical pole of the ionocyte, V-type (vacuolar) H^+-ATPase pumps protons (H^+) into the subcuticular space, hyperpolarizing the cell membrane. As the apical cytosol becomes electronegative, Na^+ ions move from the external medium through Na^+ channels into the cytosol in exchange for intracellular HCO_3^- and H^+ ions provided by carbonic anhydrase. In addition, extracellular Cl^- is absorbed through an apical Cl^-–HCO_3^- antiporter. At the basal cell pole, Na^+–K^+-ATPase drives the transport of Na^+, K^+ and Cl^- ions out of the cytosol and into the extracellular haemolymph space, and recycles K^+ back into the cytosol via K^+ channels. The enzymes V-H^+-ATPase and Na^+–K^+-ATPase produce chemical energy through dephosphorylation of ATP and generate an electrochemical potential that energises ion transport through the cell membrane and the overlying cuticle in the apical region (not shown in Fig. 5.2). As a result

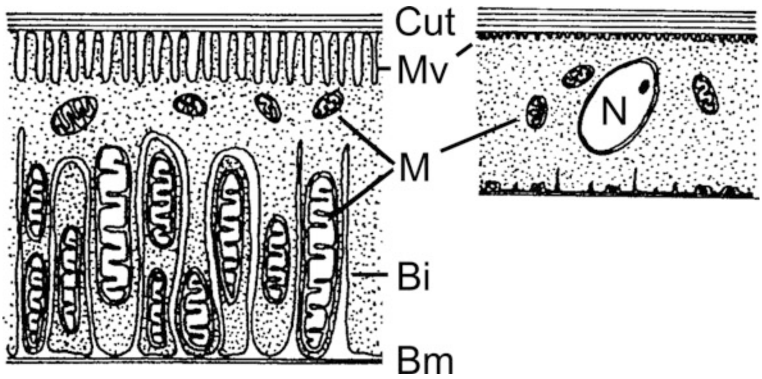

Fig. 5.1 Ultrastructure of a ionocyte (*left*) compared to a regular epidermal cell (*right*). *Cut* cuticle; *Mv* Microvilli; *M* mitrochondria; *Bi* basal infoldings; *Bm* basal membrane; *N* nucleus (schematic drawings, after Cieluch 2004 with permission of the author)

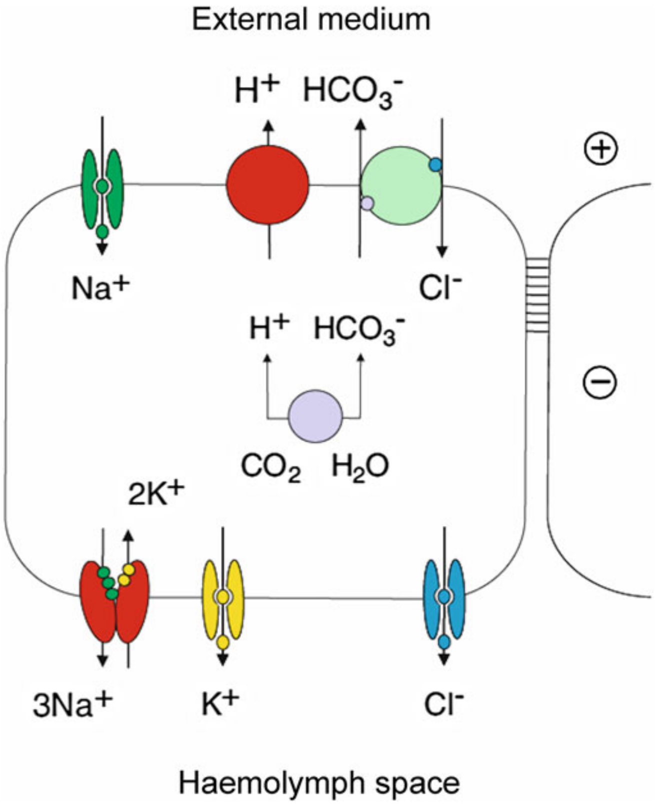

Fig. 5.2 Schematic illustration of the principal processes of extracellular hyper-osmoregulate (from McNamara and Faria 2012 with permission of Springer Science + Business Media). As a net result, Na^+ and Cl^- ions are taken up from the diluted external medium and transported against strong osmotic gradients, passing through the cuticle (not shown) and the apical membrane into the cytosol, eventually into the haemolymph; for further explanations, see text

there is a net uptake of Na^+ and Cl^- ions from the diluted external medium that are actively transported against strong diffusion gradients into the haemolymph, thereby compensating for the passive loss of ions.

Ion-transporting cells and tissues are found in various organ systems including the integument, the digestive tract, the excretory organs (especially the antennal gland), and the gills and surrounding branchial chambers (Freire et al. 2008; Charmantier et al. 2009; Boudour-Boucheker et al. 2013). The precise localization of ionocytes is possible using transmission electron microscopy which reveals their characteristic ultrastructural features (Fig. 5.1). The key enzymes involved in ion transportation are detected by immunohistochemistry (Khodabandeh et al. 2006; Cieluch et al. 2004; Fig. 5.3). Besides these qualitative methods for the localization of osmoregulating cells, tissues and organs, there are also quantitative cryoscopical

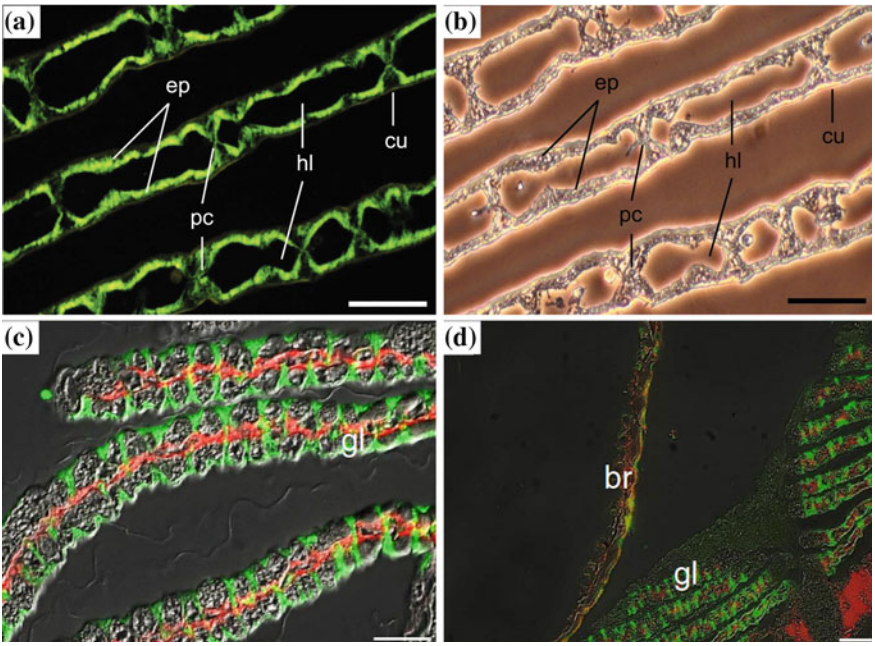

Fig. 5.3 Immunohistochemical localization of two key enzymes involved in osmoregulate; *upper pictures* posterior gills of a juvenile euryhaline crab, *Carcinus maenas* (from Cieluch et al. 2004); **a** fluorescent micrograph, showing Na^+–K^+-ATPase; **b** corresponding phase-contrast micrograph; *cu* cuticle; *ep* epithelium; *hl* hemolymph lacuna; *pc* pillar cells; *bars* 50 mm. *Lower pictures* transverse sections of gill lamellae (*gl*. **c**, **d**) and branchiostegites (*br*, **d**) of early juvenile diadromous shrimp, *Macrobrachium amazonicum* (from Boudour-Boucheker et al. 2014); micrographs taken with differential interference contrast, showing V-H^+-ATPase (*green*) and Na^+–K^+-ATPase (*red*); *scale bars* 20 µm

techniques that measure osmolality in haemolymph samples with respect to those in the external medium. These data can be graphically displayed showing variation in haemolymph osmolality plotted against the osmolality of the external medium and in relation to the isosmotic line (internal = external osmolality). Figure 5.4 shows these patterns in two strongly hyper-hypo-osmoregulating species, the semiterrestrial sesarmid crabs *Armases ricordi* (H. Milne Edwards) and *A. miersii* (Rathbun).

The difference between the internal and external osmolalities at a given salinity is called the osmoregulatory capacity, OC (Fig. 5.5). The OC is used to quantitatively compare osmoregulate between different species, developmental stages, or environmental conditions (salinities, temperatures, nutritional levels, exposure to toxic pollutants, etc.) (Lignot et al. 2000; Silvestre et al. 2005).

Most comparative studies of osmoregulate have exclusively focussed on the adult phase. However, it is obviously necessary to compare the physiological traits of all life-history stages, because developmental changes in these traits may reflect changing needs in different stages that do live in different ecological conditions

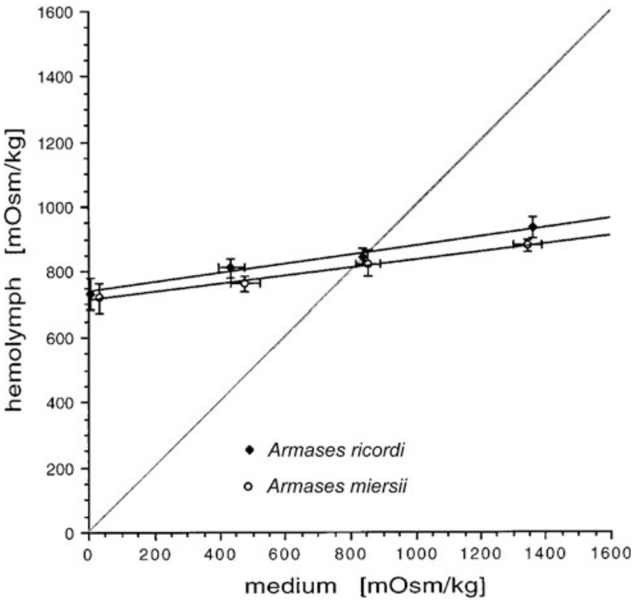

Fig. 5.4 Haemolhymph osmolality plotted against the osmolality in the external medium in two strong hyper-hypo-osmoregulators, the semiterrestrial sesarmid crabs *Armases ricordi* and *A. miersii* (from Schubart and Diesel 1998, with permission of Bulletin of Marine Science; slightly modified); *straight line* isosmotic line (internal = external osmolality)

(Charmantier 1998; Anger 2003). The ontogeny of osmoregulatory functions will be treated in Sect. 5.4.

5.3 Principal Life-History Patterns in Decapod Crustaceans

5.3.1 Extended Larval Development

Most marine decapods pass through a biphasic or "complex" life cycle (Wilbur 1980) which includes a benthic phase from juvenile to adult, and a planktonic larval phase (Anger 2001). As an exception, dendrobranchiate shrimps (superfamilies Penaeoidea and Sergestoidea; de Grave et al. 2009) pass through a holopelagic life cycle with planktonic embryos and larvae, including a naupliar phase (Martin et al. 2014a, b). The Dendrobranchiata are considered as the most plesiomorphic clade among the extant Decapoda (Bowman and Abele 1982; Scholtz and Richter 1995; Scholtz et al. 2009), and their life-history is presumed to represent the ancestral pattern of reproduction and development (Anger 2001). The Dendrobranchiata are

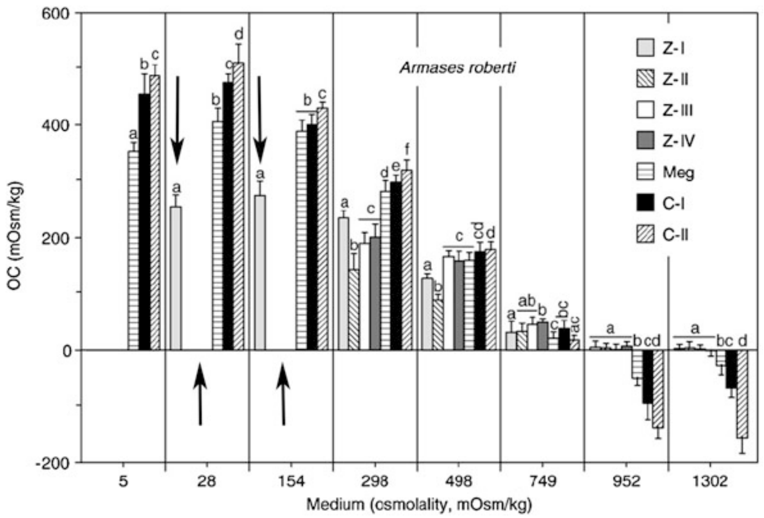

Fig. 5.5 *Armases roberti*. Variations of osmoregulatory capacity (*OC*) in different ontogenetic stages (zoeal stages I–IV; megalopa; crab stages I and II) in relation to the osmolality of the external medium; note that the megalopa is a strong hyper-osmoregulator in fresh water (5 m Osm/kg), showing also incipient hypo-regulation in sea water and at hypersaline conditions; *arrows* hyper-osmoregulate at oligohaline conditions (28–154 m Osm/kg or 1–5 PSU) is present in the zoea I, but absent in the zoeal stages II–IV; from Anger et al. (2008; modified; with permission of Elsevier BV)

exclusively marine and will therefore not be further considered here. Hence, “Decapoda” will from here on refer to Pleocyemata.

Compared to the Dendrobranchiata, the Pleocyemata have an abbreviated larval phase whereby the entire naupliar phase is not free-living but develops inside the egg case (Jirikowski et al. 2013; Martin et al. 2014b). Juvenile and adult Pleocyemata are mostly benthic and live in aquatic environments, or on land. Their females carry internally fertilised eggs and developing embryos under their pleon. This means that all Pleocyemata show some degree of brood care which is absent in most Dendrobranchiata. After hatching from the egg case, zoea larvae leave their mothers’ abdominal brood chamber, enter the water column, and become free-living members of the planktonic community.

Most marine decapods have an extended larval development through at least four zoeal stages and one or more decapodid stages (see e.g. *Galathea intermedia* Lilljeborg in Fig. 5.6). Brachyura and Anomura have a single decapodid stage that is called megalopa or glaucothoe (Anger 2001). Although larval decapods drift in water currents, their swimming behaviour contributes significantly to both their vertical and horizontal distribution (Queiroga and Blanton 2004; Anger et al. 2015). The larvae are planktotrophic, that is they feed on other plankton (Boidron-Métairon 1995; Fileman et al. 2014). In species with an extended larval phase, planktonic development takes several weeks or months, or may take up to

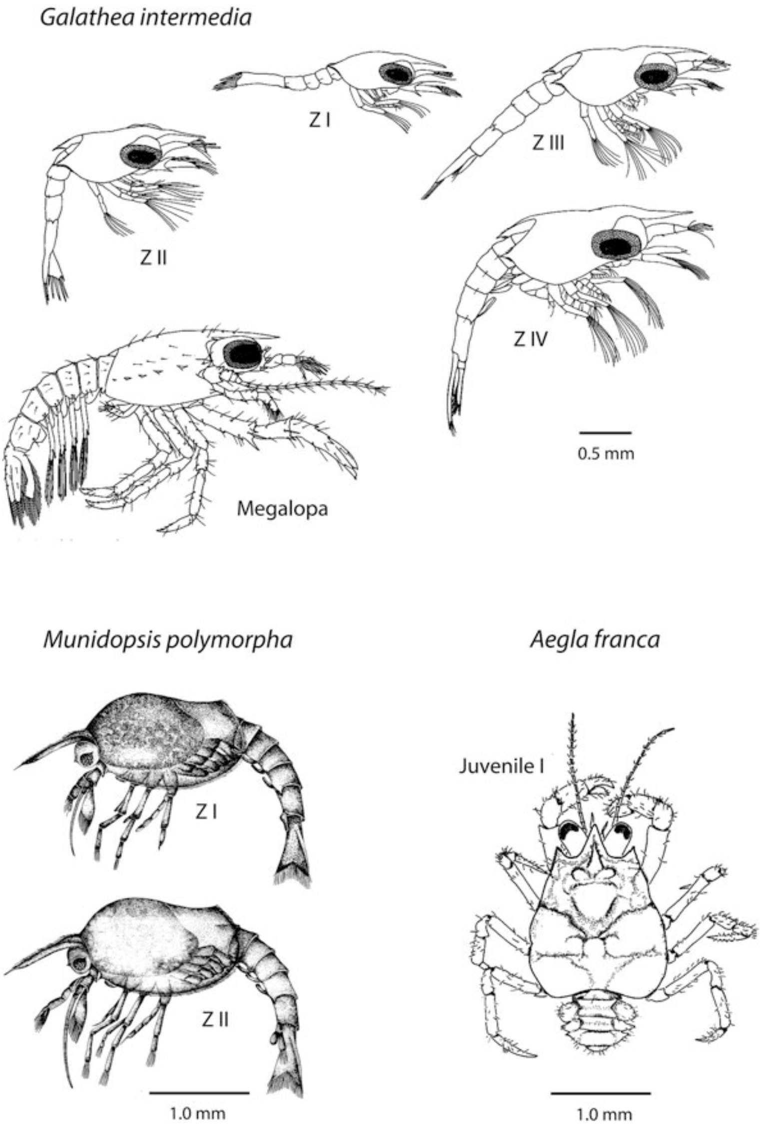

Fig. 5.6 Developmental patterns in Galatheoidea (Decapoda, Anomura): extended larval development in the marine species *Galathea intermedia* (Galatheidae) (from Christiansen and Anger 1990); abbreviated larval development in *Munidopsis polymorpha* (Galatheidae) from anchialine caves (from Wilkens et al. 1990); direct development to a first-stage juvenile in the inland freshwater crab *Aegla franca* (Aeglidae) (from Francisco et al. 2007 with permission of Magnolia Press). Z I–Z IV: zoeal stages I–IV

two years in the case of some spiny lobsters (Achelata) that can have more than 30 morphologically distinct stages (Lipcius and Eggleston 2000; Säwström et al. 2014). Extensive dispersal via ocean currents facilitates a wide geographical distribution and enhances the genetic exchange between separate populations (Macpherson and Raventos 2006).

5.3.2 Abbreviated Larval Development

Many decapods show an abbreviated larval development, which is characterised by "*shorter duration than that normally seen in the majority of related species in a taxon, and which results in fewer morphologically discrete instars and/or reduced ontogenetic duration*" (Rabalais and Gore 1985). Figure 5.6 shows as an example the larvae of a cave-dwelling anomuran crab, *Munidopsis polymorpha* Koelbel.

In addition to having a shorter development, the larvae shift from planktonic to benthic behaviour, and from planktotrophy to deposit-feeding or lecithotrophy (non-feeding development). In some species only the initial larval stages are independent of external food sources. Lecithotrophy of decapod larvae is based on enhanced maternal energy stores, mainly triacylglycerides, that are deposited in the egg yolk and remain available after larval hatching (Kattner et al. 2003; Anger et al. 2007). Compared to species with an extended planktonic phase, the larvae show thus a reduced dependence on planktonic food sources and an increasing importance of benthic food items such as sedimented detrital matter. Hence, abbreviated development not only shortens the time of larval exposure to physical stress and predation pressure in the pelagic zone, it also reduces the "nutritional vulnerability" (Sulkin 1978) during the larval phase.

5.3.3 Direct Development

Many Decapoda including some higher taxa (e.g. superfamilies Astacoidea and Parastacoidea) show direct development without any free-living larval phases. In these groups the embryos utilise egg yolk as their exclusive metabolic energy source and as the raw material for organogenesis, after which they emerge from the egg case as adult-like juveniles (Fig. 5.6, *Aegla franca* Schmitt). Morphologically distinct larval stages can still be identified microscopically in the embryos which are encapsulated inside the egg membrane (Xue et al. 2010; Jirikowski et al. 2013; Martin et al. 2014b). This supports the view of a secondary reduction of an originally free-living larval phase in the Decapoda.

After hatching the juveniles stay close to their mothers, from which they receive brood care (reviewed in detail in Chap. 6 of this volume). This life-history pattern is most frequently observed in fresh water, but occurs also in brackish and marine environments. In contrast to biphasic life cycles, the earliest postembryonic stages remain completely protected from the physical or nutritional stresses in the pelagic environment, as maternal brood care extends into the benthic juvenile phase.

5.4 Relationships Between Adult Life Style, Life-History Patterns, and Osmoregulate

5.4.1 *The "Freshwaterization" Paradigm*

Comparisons of the life-history patterns of decapods in terrestrial, marine, brackish or limnic environments reveal conspicuous macroevolutionary trends: (1) most marine and terrestrial species pass through a complex life cycle with an extended planktonic larval phase in the sea; (2) many decapods living in limnic or brackish habitats, in physically and nutritionally harsh polar and deep-sea environments, or in anchialine caves with no primary production, have an abbreviated larval phase; (3) most species that spend their entire life cycle in fresh water show direct development, i.e. a monophasic life history without a larval phase.

The sea is the ancestral environment of the Decapoda, and the conquest of brackish and limnic habitats was a later adaptation (Schram 2009). Hence, the tendency towards a reduction or even a complete elimination of the larval phase reflects a life-history adaptation associated with the evolutionary transition from a marine to a limnic life style. Jalihal et al. (1993) observed this trend in the caridean shrimp genus *Macrobrachium* which typically lives in freshwater and brackish habitats, and termed it "freshwaterization". Various reviews of abbreviated and direct development in decapods showed that the same trend occurs also in other lineages (Rabalais and Gore 1985; Anger 2001; Vogt 2013).

5.4.2 *The "Part-Time" Freshwater Species: Diadromous Life Histories*

Numerous decapods live as juveniles and/or adults in terrestrial, freshwater, or brackish habitats, but have an extended larval development in the sea ("export" strategies, Sandifer 1975). This ecological split of the life cycle is necessary in species whose larval stages (in contrast to their juveniles and adults) are not physiologically adapted to osmotic stress conditions (Charmantier 1998; Charmantier et al. 2009; McNamara et al. 2015). Export strategies require that the larvae are transported out of the limnic or oligohaline parental habitat towards the ocean, or at least from fresh water to adjacent estuarine or coastal waters. The late larval or early postlarval stages make their own way back upstream in rivers or other freshwater systems where they mature into juveniles and adults (Fig. 5.7). Decapods whose adults live in fresh waters and whose larvae develop in salt water are thus dependent on the sea to complete their life cycle, and so are considered to be secondary ("part-time") rather than primary ("full time") freshwater species.

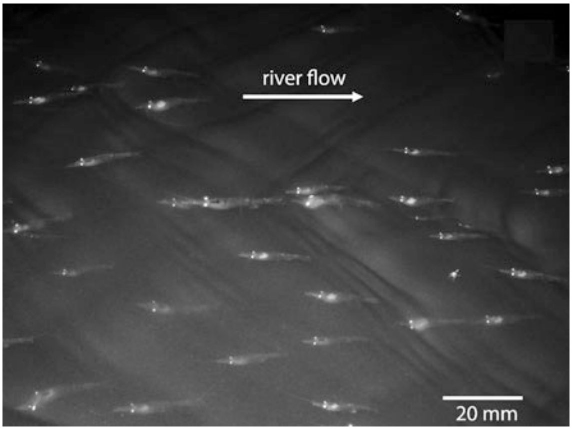

Fig. 5.7 Diadromous upstream migration of juvenile palaemonid shrimps, *Macrobrachium ohione*; *scale bar* 20 mm (from Bauer and Delahoussaye 2008)

5.4.2.1 Terminology: "Diadromous" Versus "Amphidromous"

Species with a larval export strategy are commonly referred to as either diadromous or amphidromous (Sandifer 1975; Bauer 2004, 2013). *Diadromy* (from Greek, meaning "running through") is the general term used to describe migrations between fresh water and the sea. According to Myers (1949), McDowall (2007), there are three diadromous strategies: *catadromy* (living as adults in fresh water, migrating downstream to breed in the sea; best known example: anguillid fishes); *anadromy* (living as adults in the sea, migrating upstream to breed in fresh water; typical example: salmonid fishes); *amphidromy* (migrating both upstream and downstream, with an adult return migration to feeding grounds). The first two terms denote migrations with a reproductive background. Amphidromy, by contrast, occurs in species (mostly fishes) that "*do not undertake a return migration to the biome in which they hatched in relation to spawning—their return migration is 'trophic' rather than 'gametic'*" (McDowall 2007). Since the migratory strategies of decapods show primarily a reproductive background, I use here the general term "diadromous" (or in cases where it clearly applies, the more specific "catadromous"), rather than "amphidromous". Catadromous life histories have been documented in numerous decapods (see below), whereas anadromy is unknown in this group.

Larval export strategies of non-marine decapods whose larval stages develop in brackish or coastal marine environments require either active adult breeding migrations followed by larval release in salt water, larval hatching in fresh water followed by their passive downstream transport by river currents, or a combination thereof. Recruitment to the adult population depends in all cases on active upstream migrations of freshwater-tolerant late larval or early juvenile stages, or a colonization of land by desiccation-resistant stages in terrestrial species, respectively.

5.4.2.2 Breeding Migrations in Terrestrial Decapoda

Adult land crabs possess (1) a structurally enhanced cuticle that protects them against water loss and a subsequent accumulation of metabolic waste products, (2) gills and adjacent organs modified for respiration in air, and (3) a digestive system that can utilise terrestrial food sources (Burggren and McMahon 1988; Burggren 1992; Greenaway 1999; Adamczewska and Morris 2000; Morris 2002; Linton and Greenaway 2007). The larvae of these land crabs, by contrast, have a thin and permeable cuticle (no effective protection against rapid dehydration in air), respiratory organs that depend on the diffusive uptake of dissolved oxygen from water, and a digestive system that can only process planktonic food. These larval traits mean that water is essential for their survival. Hence, they cannot develop in the same terrestrial habitats used by adults and juveniles, so that export strategies are necessary.

As land crab larvae generally require salts to survive and develop, terrestrial decapods cannot simply release their larvae into nearby rivers, lakes, or other freshwater habitats, because (unlike conspecific juveniles and adults) their zoeal stages are incapable of hyper-osmoregulate (Little 1990; McNamara and Faria 2012). It should be noted, however, that the larvae of a small number of species of terrestrial decapods do develop entirely in fresh water, but their larval phases are abbreviated and at least partially lecithotrophic. These exceptions may be explained with different evolutionary routes of colonization (see Sects. 5.4.3.1 and 5.5).

The inability of the larvae of nearly all terrestrial decapods (e.g. crabs in the brachyuran families Gecarcinidae and Ocypodidae and the anomuran family Coenobitidae) to survive in fresh water means that the adults must perform active breeding migrations to the sea. Most of these species live within 10 km of salt water (Nieves-Rivera and Williams 2003; Hartnoll et al. 2007). The Christmas Island Red Crab, *Gecarcoidea natalis* Pocock lives up to 5 km inland. During the breeding season it retreats to its burrow where it copulates and incubates its eggs. When these are ready to hatch, armies of adult crabs migrate overland to the coast where females immerse themselves in seawater and release their larvae into the ocean (Hicks 1985; Adamczewska and Morris 2001). After an extended development of about four weeks in the marine plankton (according to characteristics of the family Gecarcinidae probably passing through five or more zoeal stages, Cuesta et al. 2007), the megalopae return to land and metamorphose in the moist fringes of beaches or tide pools. Later juvenile stages migrate inland, eventually recruiting into the adult population (Hicks 1985). Similar migrations have been reported in other Gecarcinidae species including the congener *G. lalandii* Milne Edwards in Southeast Asia (Liu and Jeng 2007), *Discoplax celeste* Ng and Davie on Christmas Island (Turner et al. 2013), and *Gecarcinus ruricola* Linnaeus in the Caribbean region (Hartnoll and Clark 2006).

The return migration inland by the megalopal stage of land crabs implies that this larval stage has at least modest osmoregulatory abilities. This has indeed been shown in a semiterrestrial sesarmid crab, *Armases ricordi*, that undergoes breeding migrations to the coast where its larvae have an extended development in the sea. The zoeal stages in the plankton are osmoconformers, but the megalopa that presumably settles in moist terrestrial beach habitats shows incipient hyper-hypo-regulatory abilities as found in juvenile and adult *A. ricordi* (Anger et al. 2008).

5.4.2.3 Diadromous Migrations in Freshwater-Inhabiting Decapoda

Estuarine and freshwater-inhabiting decapods (mainly varunid, grapsid and portunid brachyuran crabs; palaemonid and atyid shrimps) make long-distance breeding migrations to the sea. Some species of *Callinectes* swimming crabs (Portunidae), for instance, live in brackish habitats with very low salinities and are occasionally also found in fresh water (Almeida et al. 2008). Ovigerous females migrate up to more than 100 km from their oligohaline or limnic habitats to release their larvae in coastal marine waters. These migrations are supported by an ebb-tide horizontal transport mechanism based on vertical swimming behaviour, with an ascend in the water column during ebb tides and a descend during flood tides, so that the females use outflowing tidal currents near the surface and avoid inflowing bottom currents (Carr et al. 2005). The zoeae complete their development in marine continental shelf waters, after which the megalopae move inshore, using tidal and wind-driven onshore currents. Metamorphosis occurs in nursery areas in brackish coastal inlets and lagoons with freshwater inflow (Etherington and Eggleston 2003).

Another iconic example for catadromous migrations in Decapoda is the mitten crab *Paraeriocheir sinensis* (Milne Edwards) (Varunidae; formerly *Eriocheir sinensis*; for recent changes in taxonomy, see Sakai 2013). It is native to southern China and has become an extremely successful invasive species in temperate regions of the northern hemisphere (Dittel and Epifanio 2009). Juvenile and adult *P. sinensis* spend their whole lives exclusively in freshwater habitats, having a life span ranging from one year in subtropical regions in China (Jin et al. 2002) to about four years in cold-temperate waters of central and northern Europe (Panning 1938). Adult mitten crabs make catadromous downstream migrations over vast distances of up to 1500 km to the sea to breed (Panning 1938; Ojaveer et al. 2007). Tagging experiments revealed downstream migration speeds of up to 12 km/day, so that coastal areas are reached within a few months (Panning 1938). Mating takes place in the lower reaches of rivers (still in fresh water), while hatching occurs in estuarine or coastal marine waters, where the spent adults die.

This species has an extended larval development including five (occasionally six) zoeal stages and a megalopa (Montú et al. 1996). The zoeal stages require salinities of ≥ 15 PSU and temperatures >10 °C for survival and development (Anger 1991; Montú et al. 1996; Cieluch et al. 2007; Blumenshine et al. 2012). The circulation patterns of the coastal waters limit zoeal dispersal and advection, so that metamorphosis into the megalopa stage occurs in near-shore regions (Tilburg et al. 2011). As mitten crab megalopae are extremely euryhaline, they can swim upstream into estuaries and rivers and metamorphose into juvenile crabs in oligohaline or freshwater habitats (Panning 1938). Juvenile mitten crabs migrate further upstream, wandering up to about 1.5 km/day until they reach sexual maturity (Panning 1938).

The Mississippi shrimp, *Macrobrachium ohione* Smith (Palaemonidae), also can live up to 1500 km inland; it migrates long distances downstream to estuarine or coastal waters because its larvae require salt water for their development (Olivier et al. 2012; Bauer 2013). This species shows similar migratory patterns as mitten crabs but, in contrast to *P. sinensis*, it can release its larvae in fresh water already before the migrating females reach brackish or marine waters (Bauer and Delahoussaye 2008; Rome et al. 2009). The first-stage zoea larvae can survive for several days in river water until they are transported downstream to oligohaline estuarine waters (Bauer and Delahoussaye 2008; Rome et al. 2009). This indicates that hyper-osmoregulatory capabilities must already be expressed at hatching. Moreover, the zoea-I stage does not feed, which makes it independent of a supply of estuarine or marine plankton. The zoea II, by contrast, requires planktonic food and salt water at salinities of about 6–15 PSU to moult to the next stage. Hatching can therefore take place in the lower reaches of rivers that are not far from the sea, where further transport to estuarine waters only takes a few days. After an extended larval phase through at least 10 morphologically distinct stages (Conner and Bauer, unpublished data), juvenile *M. ohione* return to rivers and migrate upstream where they recruit into the limnic inland populations (Fig. 5.7). Similar ontogenetic patterns of larval feeding, salinity tolerance and osmoregulate have been observed also in the South American congener *M. amazonicum* (Heller) (Anger and Hayd 2009; Charmantier and Anger 2011).

Some species of freshwater decapods do not migrate downstream but release their larvae in the limnic adult habitat (March et al. 1998). In such species, larval needs for salts and planktonic food require rapid transport times to reach estuarine or coastal waters. Hence, the adult habitat must be located in fast-flowing rivers rather than in stagnant inland waters, and the distance between the adult habitat and the sea must be much shorter than in species with adult migrations. The semiterrestrial crab *Armases roberti* (Sesarmidae) from the Caribbean provides an example for diadromous strategies without adult migrations. This species lives on the banks of rivers and streams up to about 10 km inland (Chace and Hobbs 1969; Abele 1992), and releases its larvae directly into fresh water (Anger et al. 2006; Guerao et al. 2007). Physiological studies revealed that zoeal-I larvae can hyper-osmoregulate in oligohaline water at 1–5 PSU, whereas later zoeal stages cannot (Fig. 5.5). The megalopa, by contrast, can hyper-hypo-osmoregulate which enables it to return from the sea into rivers. After metamorphosis in the adult habitat, the early juveniles can leave the water and begin a semiterrestrial and limnic life.

Experimental observations on larval salinity tolerance suggest that similar ontogenetic migrations and changes in osmoregulate occur in the semiterrestrial and freshwater-tolerant crab *Armases angustipes* (Dana) from the Atlantic coast of South America (Anger et al. 1990). Diadromous strategies with hatching in the adult habitat, but without adult downstream migrations, have been observed also in the varunid crabs *Cyrtograpsus angulatus* Dana, *C. altimanus* Rathbun, and *Neohelice granulata* (Dana) from the same region. These species are found in oligohaline habitats (*C. angulatus* also in fresh water) with hydrological connections to the ocean. Their larval export to marine waters is based on the coordination of hatching rhythms and larval migrations with regularly occurring variations in physical factors (Bas et al. 2009). Field observations showed that maximum hatching intensity occurs at night (when predation by visually oriented planktivorous fish is low) and at ebb tides (when the outflowing currents ensure rapid seaward transport). An extended planktonic development through 4–5 zoeal stages takes place in coastal marine waters, from where the megalopae return to their settlement sites (Luppi et al. 2002). In all these species, the first larval stage must tolerate very low salinities, suggesting that osmoregulatory functions appear already at hatching.

In diadromous decapods, in general, larval transport toward the sea depends mainly on complex interactions between larval behaviour and physical factors such as riverine, tidal and coastal currents, vertical salinity stratifications, and cues from gravity, light cycles, and sound from coastal wave action (Sandifer 1975; Christy and Stancyk 1982; Strathmann 1982; Epifanio 1988; Garrison and Morgan 1999; Bilton et al. 2002; Queiroga and Blanton 2004; Anger et al. 2015). The larval responses to physical and chemical cues from the environment change substantially after the planktonic zoeal development (Queiroga et al. 2006; Tilburg et al. 2008). This results in onshore-directed return migrations of the final semibenthic decapodid (megalopa) stage which shows morphological, physiological, and behavioural traits resembling those of early juveniles (Anger 2001).

Settlement in or near to benthic locations inhabited by adult crabs is stimulated by specific chemical and physical properties of the habitat such as polychaete reefs that allow newly settled megalopae and early juveniles to hide from cannibalism and other predation (Luppi et al. 2002). Chemical cues released by adults may stimulate recruitment by signaling that a location is suitable for later survival and growth (Forward et al. 2001; Gebauer et al. 2004; Krimsky and Epifanio 2008; Anderson and Epifanio 2010; Simith et al. 2013).

5.4.2.4 Diadromous Life Histories: Conclusions, Evolutionary Considerations, and Implications for Conservation

Diadromous strategies comprise a combination of far-reaching morphological and physiological adaptations in juveniles and adults (but not in larvae), as well as highly complex ontogenetic migrations in various life-history stages. Similar migratory patterns have independently evolved in many different decapod clades as well as in other invertebrates and fish. These strategies allow a successful (though incomplete) evolutionary conquest of fresh water and/or land.

Diadromous decapods with adult long-distance migrations to salt water (e.g. mitten crab) can live for extended periods of time (up to several years) in fresh water far from the sea (up to 1500 km). Some of those species (e.g. Mississippi shrimp) release their offspring in fresh water just before the maternal downstream migration has reached brackish or marine waters. In these cases, the first-stage larvae show an early (transitory) expression of osmoregulatory capabilities, so that they can tolerate the initial exposure to fresh water. This allows them sufficient time to reach the salt water that the subsequent larval stages need for survival and development to metamorphosis. An initial larval freshwater tolerance occurs also in some riverine species that do not show adult migrations but depend exclusively on passive larval downstream transport to salt water; as their early larvae tolerate fresh water only for a limited time (up to a few days), the adult habitats must be located near estuarine or coastal marine waters. The habitat distance from salt waters is strongly restricted also in terrestrial species, in this case due to dehydration stress that the adults and egg masses may suffer during breeding migrations.

The life-history patterns of diadromous decapods, especially their breeding migrations and extended planktonic larval development, have conservation implications. Extended planktonic larval development facilitates wide dispersal and a wide geographic distribution. The larvae of intertidal crabs (for instance *Cyrtograpsus* spp.) may be transported more than 100 km, and this brings about gene flow between populations living in different estuaries (Dellatorre et al. 2013). Swimming crabs such as *Callinectes* spp. provide further examples for connectivity between different estuarine populations through larval exchange (Epifanio 1995). Genetic data indicate that there is also large-scale connectivity among populations of widely distributed diadromous freshwater shrimp that live on remote islands in the Caribbean (Cook et al. 2012; Page et al. 2013). All these observations indicate that species with extended larval development in the marine plankton are less prone to extinction by human activities or catastrophic natural events than species with abbreviated or direct development. Extended larval development serves as a buffer against large-scale extinction, because local populations that are extirpated are likely to be replaced by allochthonous larvae.

While extended patterns of larval dispersal in the sea are advantageous for the conservation of diadromous species, their obligatory adult downstream as well as juvenile upstream migrations are threatened by anthropogenic barriers such as dams, reservoirs, and other river control structures (Concepcion and Nelson 1999; Olivier et al. 2013; Richardson et al. 2004; Rodríguez-Uribe et al. 2014). The conservation of such species thus requires cautious planning of river regulation projects including the construction of artificial passage facilities (Fièvet 2000).

5.4.3 The "Newcomers" in Non-marine Environments: Transitional Life Histories

Many limnic and some terrestrial species of decapods have retained larval stages that can survive and develop in fresh water and do not have to be exported to salt-water environments. This requires adaptations, in particular osmoregulatory capabilities, that allow for survival and development in fresh water throughout the life cycle. The great majority of these decapods have an abbreviated larval phase, which is intermediate between a biphasic life cycle with an extended planktotrophic development and a monophasic cycle without larvae (direct development). Such clades show a tendency towards lecithotrophy, where partial or full independence from food is based on the availability of enhanced lipid stores remaining from egg yolk, especially triacylglycerides (Kattner et al. 2003; Anger et al. 2007). This nutritional strategy is intermediate between planktotrophy and direct development within the egg membrane. Additionally, maternal brood care has in many cases been observed, which is a typical trait of freshwater-breeding decapods with direct development (cf. Chap. 6).

5.4.3.1 Abbreviated Development in Terrestrial and Limnic Decapoda

Due to phylogenetic constraints, only few decapod lineages have evolved larval adaptations to non-marine conditions that make breeding migrations unnecessary. Abbreviated development in terrestrial and limnic decapods occurs most frequently in sesarmid and ocypodid crabs (Brachyura), coenobitid and diogenid hermit crabs (Anomura), and in palaemonid and atyid shrimps (Caridea) (Rabalais and Gore 1985; Anger 2001; Vogt 2013; Chaps. 6 and 7 of this volume).

The endemic Jamaican crab *Metopaulias depressus* Rathbun (Sesarmidae) lives in mountain forests in the interior of the island (Hartnoll 1964; cf. Chap. 6, Fig. 6.4 b). This terrestrial species does not perform diadromous breeding migrations to the sea but releases its larvae into rainwater-filled leaf axils of large bromeliad plants. The larvae develop through two non-feeding zoeal stages directly to a fully benthic stage with reduced, non-functional pleopods, i.e. morphological traits of an early juvenile rather than a megalopa (González-Gordillo et al. 2010). Juvenile and adult bromeliad crabs live on land but their larvae develop in fresh water, making the reproductive patterns in *M. depressus* an unusual version of an export strategy.

The complete independence of *M. depressus* from salt water indicates that all its life-history stages have evolved physiological adaptations to the physical and nutritional stresses in its unusual breeding habitat. It is likely, therefore, that not only the juvenile and adult crabs (Schubart and Diesel 1999), but also the embryonic and larval stages must have strong hyper-osmoregulate abilities that allow for their survival and development in fresh water. Moreover, this species exhibits full zoeal lecithotrophy as an adaptation to the lack of planktonic food sources in the small quantity of rainwater collected in bromeliad leaf axils. Early juvenile bromeliad crabs, in contrast to the zoeal stages, show benthic crawling behaviour, and their maxillipeds change from swimming to feeding appendages (González-Gordillo et al. 2010). These behavioural and morphological traits allow after metamorphosis the consumption of benthic food sources such as detritus, dead insects, and other sedimented organic matter.

Besides a strongly abbreviated larval development and adaptations to physical and nutritional stress, *M. depressus* also shows maternal brood care behaviour (Diesel 1989; cf. Chap. 6 of this volume). Brood care for early juveniles is common among decapods that breed in fresh water, but in *M. depressus* it is provided also to the larvae. Maternal care for the earliest life-history stages has, together with larval osmoregulate, enhanced lipid reserves, and an abbreviation of the time of larval exposure to physical and nutritional stresses, contributed to the success of this species as a colonizer of an unusual and demanding non-marine environment. The life-history strategy of *M. depressus* is considered to be an intermediate step in the evolutionary conquest of non-marine environments.

Other endemic Jamaican species of freshwater-breeding sesarmid crabs (*Sesarma fossarum* Schubart, Reimer, Diesel and Türkay; *S. dolphinum* Reimer, Schubart and Diesel; *S. bidentatum* Benedict) have reproductive traits that are similar to those observed in *M. depressus*. Their larval development probably takes place in burrows dug into river banks, passing also through two non-feeding zoeal stages and a juvenile-like megalopa (Anger 2005; Anger and Schubart 2005). Some non-burrowing species (*S. meridies* Schubart and Koller; *S. windsor* Türkay and Diesel; *S. ayatum* Schubart, Reimer and Diesel) have larvae that probably develop in shallow puddles on densely vegetated shady river banks (Anger et al. 2007). These breeding microhabitats are protected from aquatic predation, strong river currents, and solar radiation. A fully terrestrial species, *S. jarvisi* Rathbun, breeds inside empty snail shells where juveniles live in small quantities of rainwater introduced by the females (Diesel and Horst 1995). In this case, the larval phase may have been completely eliminated, reaching a direct mode of development. More detailed life-history studies are necessary to reveal the precise course of the early development in endemic Jamaican sesarmid crabs such as the terrestrial *S. cookei* Hartnoll, where nothing is known about reproduction and development. In all these species, maternal brood care seems to play an important role as an adaptive trait.

Similar patterns of development have been observed in the semiterrestrial sesarmid *Geosesarma perracae* (Nobili) from Southeast Asia, which releases its larvae into rainwater-filled burrows dug by the adults (Soh 1969). Their development is also abbreviated, comprising two short zoeal stages and a megalopa. Direct development inside the egg membrane is seen in *G. notophorum* Ng and Tan, *G. krathing* Ng and Naiyanetr, and *G. dennerle* Ng, Schubart and Lukhaup (Ng et al. 2015; cf. Chap. 6 of this volume, Figs. 6.3 and 6.4a). This suggests that the genus *Geosesarma* may represent another model for evolutionary transitions towards a hololimnetic life style, associated with a trend towards the elimination of the planktonic larval phase (“freshwaterization” sensu Jalihal et al. 1993). Direct development has been observed also in the limnic hymenosomatid crabs *Amarinus lacustris* Chilton from Australia and *A. angelicus* Holthuis from Papua New Guinea (Lucas 1980).

Abbreviated development in combination with physiological adaptations to extreme physical and nutritional conditions have been described also for the terrestrial fiddler crab *Uca subcylindica* Stimpson that lives in semi-arid inland environments up to 35 km from marine or estuarine waters in southern Texas. This species has a short breeding season in ephemeral rainwater puddles where the salinity varies between freshwater and hypersaline conditions (Rabalais and Cameron 1983). Its larvae have strong osmoregulatory capabilities that enable them to survive in salinities ranging from 0.08 to 50 PSU (Rabalais and Cameron 1985a, b). Larval development in these food-limited ephemeral pools is fueled by lecithotrophy, and the larval phase comprises only two non-feeding zoeal stages (compared to five planktotrophic stages in marine and estuarine congeners) and a megalopa. Maternal brood care, however, has not been observed in *U. subcylindica*.

Caridean shrimps provide numerous further examples of limnic decapods with a biphasic life cycle (cf. Chap. 7 of this volume), especially the speciose palaemonid genus *Macrobrachium* (>240 species) which is widely distributed in freshwater and brackish habitats in tropical and subtropical regions (Bauer 2004). Besides species with diadromous life histories and an extended mode of larval development in salt water, there are also many hololimnetic congeners with an abbreviated and lecithotrophic larval phase (Murphy and Austin 2005; Mejía-Ortíz and López-Mejía 2011; Anger 2013; Vogt 2013). Most of these hololimnetic species have a restricted distribution, being endemic to a particular river system or even a single subterranean cave (Mejía-Ortíz and López-Mejía 2011; Botello and Alvarez 2013). Some inland species such as *Macrobrachium potiuna* (Müller), however, have a wide geographic distribution, which raises the possibility of genetic divergence and an occurrence of cryptic species (Carvalho et al. 2013).

The limnic atyid shrimps *Dugastella valentina* Ferrer Galdiano from southern Spain and *D. marocana* Bouvier from North Africa have abbreviated larval development with only two non-feeding zoeal stages and a decapodid, and both species show extensive brood care which continues throughout the zoeal phase (Huguet et al. 2011; Rodríguez and Cuesta 2011; cf. Chap. 7 of this volume, Fig. 7.1b). The larvae remain after hatching in the maternal brood pouch, where they moult to a second zoeal stage and later to a juvenile-like benthic decapodid. The decapodid is the first feeding stage, and is the stage that leaves the brood pouch. This combination of a strongly abbreviated larval phase and maternal brood care may not only shield the larvae from nutritional stress but also protect them from irreversible advection in the fast-flowing streams where these shrimp species typically live.

5.4.3.2 Transitional Life Histories: Conclusions, Evolutionary Considerations, and Implications for Conservation

The life cycles of marine and diadromous decapods with extended development include planktonic larvae that bring about wide dispersal and the colonization of new habitats. Allochthonous larvae aid in the long-term stability of populations and communities because they can recolonise habitats that have previously been lost due to local or regional extinction. The planktivorous larval stages are planktonic suspension feeders and exploit food resources that are not available to conspecific adults (typically benthic predators or deposit feeders), so that competition between different life-history stages is reduced. Furthermore, self-reliant larval nutrition allows for low maternal energy investment per offspring and, in consequence, high fecundity. This trait buffers against generally high larval mortality in the plankton (Morgan 1995; Kerr et al. 2014; Yannicelli and Castro 2013; Anger et al. 2015).

In freshwater habitats, by contrast to the oceans, physical and nutritional stress (critically low osmotic pressure, poor or unreliable food production) appear to select against an extended planktonic larval phase, causing the "freshwaterization" trend towards an abbreviation or elimination of the larval phase. The benefits of extended larval development, however, are concomitantly reduced or completely lost when the planktonic phase is shortened or eliminated. Partial or full lecithotrophy is based on enhanced maternal energy investment per offspring and thus implies reduced or lacking exploitation of planktonic food sources. The larvae hatch with large body size and high fat content, and they show typically little if any swimming activity, remaining hyperbenthic rather than planktonic. All this makes the larvae attractive to predators and reduces their potential for dispersal, the colonisation of new habitats, or the replacement of previously extinct populations. These larval traits, together with low fecundity, make species with abbreviated and lecithotrophic development prone to pelagic predation and other environmental stress (Rasmuson et al. 2014; Wasserman et al. 2014; Hansen and Beauchamp 2015).

While species with transitional life histories have lost the advantages of the plesiomorphic pattern with high fecundity and an extended planktonic phase, they have not evolved to the evolutionary end point, where they could profit from the benefits of direct development in the benthos. Non-diadromous limnic species with a biphasic life cycle are thus not perfectly adapted to their habitats and may be evolutionarily transitory or unstable, persisting for some time but then tending to disappear. Losses of previously advantageous reproductive and developmental traits are probably offset by evolutionary gains of other traits that are adaptive in non-marine environments. This includes the early development of osmoregulatory organs, the partial or complete independence of larvae from planktonic food sources, and maternal brood care that reduces larval mortality. Intermediate life-history patterns may illustrate transitional stages that should have occurred during the course of evolution of terrestrial and limnic species from their marine ancestors. However, evolutionary explanations of life-history patterns or developmental traits based on presumptions of adaptive advantages or disadvantages in relation to selective forces are often speculative and need further scrutiny through both field and laboratory studies. This would enhance our understanding of evolutionary transitions and help to reconstruct invasion routes towards limnic and terrestrial life styles in decapods.

Transitional life-history patterns have conservation implications. Populations of marine and diadromous species threatened with local or regional extinction by natural or man-made catastrophic events have a good chance of rapid recovery through recolonization by allochthonous larvae. By contrast, species with abbreviated or direct development with a limited potential for dispersal and (re)-colonization are prone to long-lasting or even permanent population losses. Such species also have a restricted geographic distribution and need to be protected in the specific habitats where all of their life-history stages live closely together. Threats to these species may mean the loss of the regional population or even the entire species (Schubart et al. 2010; Schubart and Santl 2014; Mejía-Ortíz and López-Mejía 2011).

5.4.4 The "Natives": Monophasic Life Histories in Hololimnetic Species

The endpoint of life-history modifications that follow the "freshwaterization" trend is the complete elimination of the larval phase, i.e. a monophasic life cycle. Crayfish (Astacida) represent the oldest and best known monophyletic decapod clade that exclusively inhabits fresh water and shows direct development and brood care (Holdich 2001). The origin of crayfish dates back at least to the Late Jurassic—Early Triassic (185–225 mya), i.e. before the breakup of Pangea (Rode and Babcock 2003; Crandall and Buhay 2008; Breinholt et al. 2009). Earlier fossil records from the Permian (265 mya) seem to indicate an even older age for this group (Hasiotis and Mitchell 1993). Phylogenetic antiquity explains the complete adaptation of crayfish to freshwater habitats, and continental drift explains their almost world-wide distribution. The lack of a planktonic larval phase and reduced dispersal abilities favour allopatric speciation, which explains their great diversity (>640 species in two superfamilies, Astacoidea and Parastacoidea de Grave et al. 2009; cf. Chap. 3 of this volume).

Although the great majority of crayfish live exclusively in aquatic habitats, some species such as the burrowing parastacid *Engaeus* show distinct terrestrial tendencies (Hobbs 1988). The ability of semiterrestrial species of crayfish such as the cambarid *Orconectes limosus* Rafinesque to disperse between different river systems is one means of range expansion in these decapods (Puky 2014).

The more than 1300 species of primary freshwater brachyuran crabs are assigned to five families. Their phylogeny, biogeography, ecology, and life histories are discussed by Ng et al. (2008), Yeo et al. (2008), Cumberlidge and Ng (2009), Vogt (2013), Yeo et al. (2014) (cf. other chapters of this volume). None of these families has marine members, and all species show direct development and maternal brood care. In contrast to crayfish, these families are probably polyphyletic (four of them form a monophyletic group that excludes the fifth family), and there have been at least two independent evolutionary colonization events since the Late Cretaceous.

The anomuran family Aeglidae, which has no marine members, represents another monophyletic clade that has successfully colonised freshwater environments (Bond-Buckup et al. 2008; McLaughlin et al. 2010; cf. Chap. 2 of this volume). The marine ancestors of this endemic South American group came from the eastern South Pacific Ocean and invaded continental waters probably in the Late Cretaceous (ca. 75 mya). Its radiation occurred over shorter time and in a more limited geographic area than in crayfish and freshwater crabs, which may explain its low diversity (about 85 extant species). All Aeglidae show direct development, hatching as adult-like juveniles (Fig. 5.6).

Direct development in all crayfish, primary freshwater crabs and aeglids has conservation implications. As their embryonic stages depend entirely on maternal energy investments in yolk production, only a small number of large, energy-rich eggs are produced. The low number of offspring combined with their limited dispersal capacities reduces their ability to compensate for population losses following natural or man-made local or regional extinction threats.

5.4.5 Exceptions from the "Freshwaterization" Rule

5.4.5.1 Abbreviated and Direct Development in the Sea

The "freshwaterization" rule (Jalihal et al. 1993) suggests that a reduction in the number of larval stages in combination with lecithotrophy and maternal brood-care are essential adaptations for the successful conquest of freshwater environments (cf. Chap. 6 of this volume). Interestingly, however, these same evolutionary modifications are also found in the oceans. Most marine decapods from polar regions (e.g. Makarov 1968; Thatje et al. 2005a; Stevens 2014) and the deep sea including scattered hydrothermal vent communities (Saito and Konishi 1999; Thatje et al. 2005b; Goy 2010; Thatje and Mestre 2010) have abbreviated, lecithotrophic, or even direct developments. In such extreme environments with unpredictable or highly seasonal plankton production, food limitation selects against extended planktotrophic larval development (Rogers et al. 2012). In the boreal-arctic shrimp *Sclerocrangon boreas* (Phipps), for instance, the larvae remain in the brood pouch and pass through two brooded, lecithotrophic stages followed by a free-living benthic juvenile (Guay et al. 2011). The fact that all these species are marine and not limnic means that such unusual life history patterns have evolved independently (convergently) in different groups and in different environments. Reproductive traits that are otherwise associated with "freshwaterization" may have evolved here as adaptations to planktonic food limitation and/or may protect the larvae from benthic predation or advection by bottom currents.

Abbreviated and direct developments have exceptionally also been observed in decapods living in shallow coastal waters with sufficient planktonic food production. In some cases, commensal, parasitic, or otherwise highly specialised habitat demands may have selected against an extended larval development that incurs a high risk of larval advection away from specific hosts or other habitats with limited availability (Thiel 2000; Bolaños et al. 2005). This may explain the life history of the sponge-dwelling alpheid shrimp *Synalpheus regalis* Duffy, which has evolved direct development and far-reaching brood-care behaviour resembling eusociality in insects (Duffy 1996; Duffy and Macdonald 2010).

In other marine species with abbreviated or direct development, predation pressure has been suggested to be the principal selection factor. An undescribed diogenid hermit crab species belonging to the genus *Calcinus*, for example, hatches its eggs inside a host snail shell where its abbreviated, non-feeding larval stages develop into juveniles, well protected from predators (Calado et al. 2006). Similarly, the coastal axiid *Callichirus kraussi* Stebbing from South Africa produces two lecithotrophic larval stages that develop inside the burrows of the adults into a feeding juvenile (Forbes 1973). This reproductive pattern is remarkably similar to that of the terrestrial brachyuran crab *Geosesarma perracae* and may be another example of the convergent evolution of brood care.

There are various cases where no particular selection factors for the evolution of abbreviated or direct development in the sea could be suggested (Rabalais and Gore 1985; Clark 2005; Vogt 2013). Interestingly but for unknown reasons, such exceptions have most frequently been observed in the southern hemisphere. In the xanthid crab *Heterozius rotundifrons* Milne-Edwards from New Zealand, for instance, there are only two zoeal stages, whereas most other Xanthidae have four (Wear 1968). In the same geographic region, two reef-inhabiting pilumnid crab species, *Pilumnus lumpinus* Bennet and *P. novaezealandiae* Filhol, have no zoeal stages at all, hatching as megalopae (Wear 1967). In the former species, these late larvae are free-living, hiding in crevices of corals or stones, while those of *P. novaezealandiae* and probably *P. vestitus* Haswell remain clinging under the female pleon and receive maternal brood care. These megalopae can undertake exploratory swimming excursions, but return thereafter to the protecting brood chamber beneath the maternal pleon. The coenobitid hermit crab *Coenobita variabilis* McCulloch from coastal mangrove swamps in Australia has two lecithotrophic zoeal stages and a feeding megalopa whereas most other members of this family pass through five planktivorous zoeal stages and a megalopa (Harvey 1992). Another coastal marine hermit crab from Australia, the diogenid species *Paguristes frontalis* Milne Edwards, lacks the zoeal phase and hatches as a megalopa (Morgan 1987a). The spider crab *Paranaxia serpulifera* Guérin from Australia and the hymenosomatid crab *Neorhynchoplax bovis* Barnard from South Africa and Mozambique (Barnard 1950) show direct development and brood care for the early juveniles that stay beneath the female's abdomen, similar to primary freshwater crabs (Morgan 1987b).

In all these cases, no extant habitat conditions are known that may have selected against an extended larval development in the plankton. Abbreviated or direct developments might have evolved during a past geologic period when these reproductive traits were advantageous, and then persisted in some clades. More field and laboratory studies of ecological and life-history traits, in combination with data from the fossil record and molecular genetics, are necessary to better understand the occurrence of these unusual reproductive patterns in marine decapods.

5.4.5.2 Extended Larval Development in Fresh Water

Extended planktotrophic larval development in freshwater Decapoda has only been documented for a few species of palaemonid and atyid shrimps from tropical and warm-temperate zones. One example is the recently described hololimnetic species *Macrobrachium pantanalense* dos Santos, Hayd and Anger (previously considered as an inland population of the closely related congener *M. amazonicum* (Heller)). This palaemonid shrimp is found in the inundation zones and densely vegetated river banks in the Pantanal region, southwestern Brazil, and its adjacent lowlands in Paraguay and Argentina (dos Santos et al. 2013; Weiss et al. 2015). Reproductive females of this species prefer shallow, stagnant and productive freshwater lagoons with temporal connections to nearby rivers (Hayd and Anger 2013). The number of larval molts is highly variable, ranging from nine to as many as 30, even among sibling larvae from the same brood when reared under identical conditions in the laboratory. This extended development in fresh water is possible because the larvae of this species all have strong hyper-osmoregulatory capabilities (Charmantier and Anger 2011). Moreover, shallow lentic breeding habitats produce sufficient planktonic prey and provide places for hiding from predatory fish, especially between the roots of floating aquatic plants such as water hyacinth, *Eichhornia crassipes* (Mart.). The first larval stage, is fully lecithotrophic, and also the zoeal II can still develop to the next stage in complete absence of food (facultative lecithotrophy; Anger and Hayd 2010). This suggests that limited availability of food with suitable size has selected against planktotrophy in the earliest post-hatching stages.

In spite of their osmoregulatory capabilities, the larvae of this species develop in laboratory experiments better at 1–5 PSU than in pure fresh water (Anger and Hayd 2010). An explanation for their successful development in limnic inland waters might be found in trace metals that originate from Late Tertiary marine transgressions (Hoorn et al. 2010) and may be released from seasonally flooded soils. In some areas of the Pantanal there are even salt lakes, indicating the presence of mineral deposits (Almeida et al. 2011). Future studies of the hydrological and biogeochemical conditions in the Pantanal region are necessary to explain the persistance of an extended larval development in limnic inland habitats. The apparently incomplete adaptation in larval physiology as well as molecular genetic data (Weiss et al. 2015), support in this species a recent invasion.

Other hololimnetic shrimps with extended larval development include *Macrobrachium lanceifrons* (Dana) from the Philippines (Rasalan et al. 1969), *M. niloticum* (P. Roux) from Lake Chad, Africa (Williamson 1972), *M. walvanense* Almelkar, Jalihal and Sankolli from northwestern India (Almelkar et al. 2000), *M. lanchesteri* de Man from Singapore (Chong and Khoo 1988), *Palaemonetes argentinus* Nobili from Argentina and Uruguay (Menú-Marque 1973), *Atyaephyra desmaresti* Millet from the Mediterranean region (Anastasiadou et al. 2011; cf. Chap. 7 of this volume), and *A. mesopotamica* Al-Adhub from Iraq (Salman 1987). The world-wide occurrence of hololimnetic decapod species that have conserved the ancestral extended mode of larval development indicates independent lines of evolution in recent invaders of fresh water (Anger 2013). All these species must have evolved an early expression of osmoregulatory functions, and their early larvae may be non-feeding or facultatively lecithotrophic, which reduces their dependence on small-sized plankton immediately after hatching. Such life history patterns have very little been studied, and it remains unknown why these have evolved only in few exceptional cases.

5.5 Possible Colonization Routes to Non-marine Environments

5.5.1 Basic Considerations and Currently Proposed Routes

The phylogenetically and geographically widespread occurrence of non-marine life styles in different lineages of Decapoda indicate the repeated and independent colonization of fresh water and land. These transitions in life style are based on the convergent evolution of various key adaptations (diadromous migrations, osmoregulate, abbreviation or elimination of the larval phase, decreasing larval dependence on planktonic food, brood care) in response to repeatedly occurring selection pressures in limnic and terrestrial habitats. The current view of possible evolutionary invasion routes into non-marine environments is as follows (Little 1990; Schubart and Diesel 1999; Diesel et al. 2000; Freire et al. 2003; Vogt 2013):

- Plesiomorphic decapods live in physically stable marine environments and are osmoconformers. They typically show extended planktonic larval development, high fecundity, and an absence of brood care beyond the embryonic phase.
- Hololimnetic decapods invaded fresh water directly via estuaries (Route #1).
- Terrestrial decapods colonised land either
  - directly via the sea shore (Route #2a), or
  - indirectly in two steps, first from the sea to fresh water (= Route #1), then from fresh water to land (Route #2b).

Route #1: The ancestors of freshwater decapods invaded limnic habitats through riverine upstream migrations; adaptions to life in fresh water including the function of hyper-osmoregulate in all life-history stages, abbreviation or elimination of the larval phase, lecithotrophy and extended brood care, evolved gradually.

Route #2a: The direct transition from the sea to land selects in juvenile and adult decapods for the evolution of hypo-osmoregulate and other physiological and structural adaptations to terrestrial life; no such adaptations have evolved in the larval stages. The conservation of plesiomorphic reproductive traits (extended larval development, lack of brood care) requires adult breeding migrations to the sea. Typical examples are species of Gecarcinidae and Ocypodidae (Brachyura) and Coenobitidae (Anomura) (Vogt 2013).

Route #2b: An indirect transition from the sea to land via fresh water requires as a first step the same life-history modifications as Route #1. In a second step, hololimnetic species evolve juvenile and adult adaptations that provide protection against dehydration in terrestrial habitats (enhanced thickness and reduced permeability of the cuticle, respiration in air). Hololimnetic ancestry is reflected by an absence of hypo-osmoregulate (Schubart and Diesel 1999) and reproduction in fresh water. This rare invasion route has been suggested for *Metopaulias depressus* and the terrestrial endemic Jamaican species of *Sesarma*. However, conflicting interpretations of the same data, even within the same working group (cf. Schubart and Diesel 1999; Diesel et al. 2000), show that terrestrial colonizations are not yet fully understood and require further experimental and field studies.

5.5.2 Alternative Hypotheses for Limnic Invasions

5.5.2.1 Is There "Direct" Colonization of Fresh Water via Estuaries and Rivers?

Routes #1 and #2b involve the direct route for the colonization of the upstream reaches of rivers, streams, and inland lakes via estuaries and rivers. Transitional habitat types such as the upper reaches of estuaries and the lower reaches of rivers would then be expected to have a high incidence of transitional life-history patterns such as moderately expressed capabilities of hyper-osmoregulate in all larval stages, abbreviated and partially lecithotrophic larval development, and incipient brood care. However, most estuarine and riverine decapods have extended planktotrophic larval development, no brood care, and their larvae lack the ability to osmoregulate. This lack of intermediate patterns makes it unlikely that hololimnetic clades evolved from marine ancestors that invaded fresh water directly via estuaries and rivers, and this excludes Route #1 and parts of Route #2b.

It is suggested here that evolutionary upstream migrations into estuaries and rivers lead exclusively to diadromous strategies associated with a conservation of the ancestral pattern of extended and planktotrophic larval development, absence of brood care, and osmoconforming larvae. Diadromous species show adaptive physiological, morphological and behavioural modifications only in the freshwater-inhabiting juveniles and adults, but not in the larvae (except for transitionally expressed hyper-osmoregulate in the first stage of some species that release their larvae in fresh water, close to estuaries, e.g. *Macrobrachium ohione, M. amazonicum, Armases roberti*; see above, Fig. 5.5).

The evolutionary invasions of upper estuaries and rivers (Route #1) and the direct colonization of land (Route #2a), i.e. the evoloution of diadromous life histories, may have been driven by selection pressures on juvenile and adult decapods either searching for new food sources in non-marine habitats or evading predators in estuarine and coastal marine ecosystems. Increases in the distance of adult habitats from the sea may then have selected for adaptive traits in juvenile and adult life-history stages. The evolution of larval adaptations to non-marine environments seems to be strongly limited by phylogenetic constraints, so that more extended invasions of fresh water and land became possible only through the evolution of large adult breeding migrations towards coastal marine waters such as those seen in *Paraeriocheir sinensis* and *Macrobrachium ohione*.

In diadromous species, an extended larval development in salt water allows for a production of smaller but many more eggs (higher fecundity) compared to abbreviated and direct modes (see Rabalais and Gore 1985; Anger 1995; Vogt 2013). This compensates for high larval mortality from starvation in food-limited rivers, or from strong pelagic predation pressure in estuarine environments (Morgan 1995). Hence, riverine and estuarine conditions select against, and not for, the production of a low number of large non-feeding larval stages. It is high fecundity and extended larval development that produces late larval or early juvenile recruits capable of successful dispersal and the recolonization of estuaries and rivers. Hence, diadromous life-history patterns appear to be evolutionary old and ecologically stable rather than a transitional step in the conquest of fresh water and land by ancestrally marine decapods. This makes it unlikely that rivers and estuaries have ever been direct colonization routes in the evolution of hololimnetic decapods such as crayfish, aeglids, and primary freshwater crabs.

Likewise, there is no evidence that terrestrial decapods are derived from diadromous ancestors. The need for larval feeding and development in an aquatic environment, coupled with a lack of larval osmoregulate, requires adult terrestrial breeding migrations to the sea. This limits the distribution of terrestrial species with extended larval development (e.g. *Gecarcinus*, *Ocypode*, *Coenobita*) to a narrow fringe of no more than about 10 km away from the sea shore or an estuary. Terrestrial life further inland (e.g., *Uca subcylindrica*, *Metopaulias depressus*) requires adaptations of the larval stages to the conditions found in land-locked breeding habitats and an abbreviation of the larval phase. Also in these cases, it is suggested that the colonization of terrestrial habitats did not occur through ancestral upstream migrations via estuaries and rivers, nor through a diadromous strategy as an intermediate step. An alternative hypothesis is discussed in the following section.

5.5.2.2 Land-Locked Transitional Environments as Putative Entrance Portals

The end products of evolutionary transitions from marine to freshwater habitats (e.g., crayfish, aeglids, and primary freshwater crabs) are all phylogenetically old and occupy a variety of limnic habitats; all these groups are exclusively freshwater and all lack extant marine or brackish water species. Transitional steps in the adaptation to non-marine habitats may be illustrated looking at the ecological, physiological and life-history traits of more recently evolved and less completely adapted clades of freshwater decapods ("*newcomers*") that have extant marine relatives. Also, it should be useful to consider exceptions from the "freshwaterization" rule.

Macrobrachium pantanalense from the seasonally inundated Pantanal lowlands is one of those exceptions because it shows extended planktonic and planktotrophic larval development in spite of living in land-locked, fully limnic habitats. Anger (2013) proposed that ancestral *Macrobrachium* from the Caribbean coast invaded South American inland waters during the Miocene when continental flooding created a huge brackish wetland system named Lake Pebas (Hoorn et al. 2010). Later in the Miocene the uplifting of the northern Andes isolated Lake Pebas from the Caribbean Sea, and the system became land-locked, increasingly limnic, and ecologically similar to the modern Pantanal wetlands. The large-scale environmental changes from estuarine to freshwater habitats have gradually selected for evolutionary adaptations in physiological and life-history traits in the ancestral *Macrobrachium*, in particular for increasing hyper-osmoregulatory capabilities. During the late Miocene and Pliocene, an uplifting watershed separated the Paraguay River basin (including the Pantanal) from the Amazon basin and drove allopatric speciation within the former Pebas system populations. The permanent colonization of fresh water occurred here as a consequence of large-scale geological processes that lead to genetic isolation of populations in land-locked habitats rather than through the direct invasion of fresh water via estuaries and rivers. Remarkably, the life-history pattern of *M. pantanalense* indicates that the physical and nutritional conditions of the Pantanal region have not selected against an extended planktonic larval phase. While an evolution of larval osmoregulate was indispensable (Charmantier and Anger 2011), it must have been high plankton productivity that allowed for the persistance of larval planktotrophy (Anger and Hayd 2010). The occurrence of ancestral marine reproductive and developmental traits in fresh water is an interesting subject for further research.

Transitional patterns in physiological and developmental characteristics are not found in estuaries with widely open connections to the sea, but in inland-locked environments that are transitional between the sea and fresh water, for instance in mangroves and salt marshes which connect marine, brackish, freshwater, and terrestrial habitats. Mangroves are the largest, most productive, and most diverse coastal ecosystems in tropical and subtropical regions world-wide with a complex habitat structure and a high species diversity of fish and invertebrates including Decapoda (Wilson 1989; Echeverría-Sáenz et al. 2003). Mangrove swamps and salt marshes are characterised by great temporal and local variability in salinity (due to extreme seasonal and short-term fluctuations caused by variations in rainfall and seawater intrusions), plankton productivity (varying with hydrological connections to the sea), and vegetation structure (affecting species composition and diversity) (Sheaves 2005; Cannicci et al. 2008; Lee 2008). Mangroves and salt marshes receive fresh water from inflowing streams and rivers creating brackish and limnic habitats for colonization by hyper-osmoregulating coastal species. Hypersaline conditions occur in shallow water bodies in the upper supralitoral zones where evaporation exceeds precipitation; adult decapods that live here must be able to hypo-osmoregulate (Anger et al. 2008).

In the Amazon delta, it has been observed that ocypodid crab species that live in mangrove habitats with strong freshwater inflow and high connectivity to the sea typically have larval export strategies and an extended planktonic phase (Diele and Simith 2006; Simith et al. 2014). In more stagnant, shallow and highly productive zones, by contrast, atyid, palaemonid, hippolytid, and other shrimp lineages use mangrove habitats as nursery grounds where all life-history stages are living together, showing strong hyper-osmoregulatory capabilities and a tendency to invade oligohaline and freshwater environments (Bauer 2004; Crona and Ronnback 2005). It is quite possible that such transitional habitats may have served as a starting point in the evolution of hololimnetic life histories.

The semiterrestrial mangrove-inhabiting crabs *Sesarma curacaoense* Rathbun and *Armases miersii* from the Caribbean have abbreviated and partially lecithotrophic larval phases and an early development of hyper-hypo-osmoregulatory capacities (Anger and Charmantier 2000; Anger et al. 2008). *S. curacaoense* is closely related to the ancestors of the endemic Jamaican lineage of hololimnetic and terrestrial crabs (Schubart et al. 1998), which suggests that breeding in shallow, partially land-locked coastal mangrove habitats may have been the starting point of that freshwater invasion and adaptive radiation. Likewise, the colonization of inland habitats by the ancestor of the terrestrial fiddler crab *Uca subcylindrica* may have begun in nearby coastal mangroves and salt marshes. This species shows strong hyper-hypo-osmoregulatory capabilities in all life-history stages and an abbreviated, non-feeding larval development in land-locked rainfall puddles with highly variable salinities ranging from freshwater to hypersaline (Rabalais and Cameron 1985a, b).

On Jamaica and other tropical islands and coasts, limestone caves may have served as stepping stones for freshwater invasions. They were initially connected to the sea and became later land-locked and filled with fresh water following geological uplifting (Brinkmann and Reeder 1994). This may explain why subterranean caves in mountain regions in the interior of Jamaica are inhabited by specialised endemic crabs such as *Sesarma verleyi* Rathbun, *S. windsor*, and some morphologically distinct populations or subspecies of *S. fossarum* (Schubart et al. 1998; Stemmer and Schubart 2013, 2015). Other endemic Jamaican crabs (*S. dolphinum*, *S. meridies*) have colonised the upper reaches of inland rivers possibly via caves and mountain streams, while the terrestrial species *Metopaulias depressus*, *S. jarvisi* and *S. cookei* probably evolved later from hololimnetic ancestors (Schubart and Diesel 1999).

Anchialine pools and caves of karst or volcanic origin are land-locked habitats with subterranean connections to the ocean. They are filled with marine or brackish water and may also have been starting points for limnic and terrestrial invasions. These habitats experience tidal fluctuations, strong salinity stratifications, and low oxygen concentrations. These conditions select for physiological adaptations including osmoregulate and anaerobic metabolism (Havird et al. 2014a, b, 2015). Adult decapods living in anchialine caves are protected from predation, while they can feed on benthic food sources such as chemoautotroph bacteria, soil from nearby forests, and freshwater algae from connected open pools (Pohlmann et al. 1997). Primary production is either weak or non-existent, and planktonic food is therefore limited. Decapods that have been reported to occur in anchialine caves include brachyuran crabs (Davie and Ng 2012), caridean shrimps (Anker 2008), and anomurans (Wilkens et al. 1990). Although the larval development of most of these species is unknown, it would be expected that they do not have an extended planktotrophic larval phase. Rather, it is abbreviated and lecithotrophic, as is the case for the atyid shrimp *Halocaridina rubra* Holthuis from Hawaii (Couret and Wong 1978) and the anomuran crab *Munidopsis polymorpha* from Lanzarote in the Canary Islands (Fig. 5.6). Due to tectonic uplift, anchialine cave systems may gradually be isolated from the sea and filled with fresh water (Brinkmann and Reeder 1994), so that they become living places for hololimnetic decapods.

Numerous species of freshwater-inhabiting shrimps live in caves (Hobbs et al. 1977; Anker 2008; Wowor et al. 2009; Baldari et al. 2010). In Mexico and Belize, for example, there are stygobitic species of *Macrobrachium* with strongly abbreviated and lecithotrophic modes of larval development (Hobbs and Hobbs 1995; Mejía-Ortíz and López-Mejía 2011). Diadromous congeners living in the same region in large rivers show no tendencies towards "freshwaterization", i.e. no intermediate life-histories (Anger 2013). This suggests that hololimnetic *Macrobrachium* with abbreviated and non-feeding larval developments colonised their habitats independently via land-locked aquatic habitats, while diadromous species reached freshwater habitats by direct invasions via estuaries and rivers (Route #1).

In conclusion, transitional biota between the sea, fresh water and land, especially mangrove swamps, salt marshes, seasonally inundated wetlands, and anchialine caves were the most likely entrance portals for the colonization of non-marine habitats by physiologically robust coastal marine Decapoda. Land-locked aquatic microhabitats including supratidal pools, caves, and wetlands may have served as stepping stones on the way from the sea towards life in fresh water and on land. All these transitional habitats are characterised by highly variable physical and biotic conditions which select for direct development, extended maternal brood care, and physiological adaptations such as osmoregulate, rather than an extended planktotrophic larval phase.

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Chapter 6
Direct Development and Posthatching Brood Care as Key Features of the Evolution of Freshwater Decapoda and Challenges for Conservation

Günter Vogt

Abstract Direct development and posthatching brood care are among the key evolutionary adaptations of decapod crustaceans to life in fresh water. Direct development is obligatory in aeglid anomurans, primary freshwater crabs, and freshwater crayfish. It also occurs in some species of secondary freshwater crabs and freshwater shrimps. Posthatching brood care is the rule in aeglids, primary freshwater crabs, and crayfish, infrequent in secondary freshwater crabs, and rare in freshwater shrimps. Extended brood care is most intense in crayfish where it includes the attachment of hatchlings by a safety line, and specific behaviours of the mother and her offspring. Direct development and posthatching brood care are associated with reduced dispersal and reduced gene flow among populations, which may explain the high degree of endemism and speciation in freshwater decapods. Due to the reduced dispersal and recolonization abilities aeglids, primary freshwater crabs, and crayfish that live in stressed freshwater habitats may face a higher threat of extinction than do species of amphidromous shrimps and crabs that can undergo long-distance migrations.

Keywords Freshwater Decapoda · Direct development · Posthatching brood care · Evolutionary adaptation · Speciation · Endemism · Conservation

6.1 Introduction

The abbreviation or complete suppression of larval development and the extension of brood care after hatching are among the key adaptations of decapod crustaceans to life in fresh water. These characteristics are also seen in other taxa found in fresh waters including the species-rich gastropods and fishes (Gross and Sargent 1985;

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Anger 1995; Strong et al. 2008; Vogt 2013). Freshwater decapods show the entire range of developmental strategies from extended larval cycles to direct development, but the latter is by far the most common (Anger 1995, 2001, 2013; Schubart et al. 2000; Bauer 2013; Vogt 2013). Direct development is the complete abolishment of planktonic larvae and the release of benthic juveniles or juvenile-like decapodids from the mother (Rabalais and Gore 1985; Anger 2001). This is achieved either by carrying the embryos on the maternal pleopods until they hatch as juveniles, or by the brooding of earlier hatched zoeal stages either on the maternal pleopods, or in freshwater nursery pools or burrows until the juvenile stage has been reached.

This chapter starts with a detailed account of direct development and posthatching brood care in freshwater shrimps, aeglid anomurans, primary and secondary freshwater crabs, and freshwater crayfish. Thereafter, the evolutionary origin of direct development and posthatching brood care in freshwater decapods is described and the relevance of these adaptations for the conquest of freshwater environments is discussed. The chapter ends with reflections on the impact of direct development on the biogeography and conservation of freshwater decapods.

6.2 Direct Development and Posthatching Brood Care in Freshwater Shrimps

Freshwater shrimps have either an amphidromous life history characterized by extended planktonic development in salt or brackish water, or they have a freshwater life cycle characterized by abbreviation of their larval development (Chap. 5 of this book; Jalihal et al. 1993; Bauer 2011, 2013; Anger 2013). In amphidromous species, egg numbers per clutch are often in the tens of thousands, whereas in species with highly abbreviated development the number of eggs is reduced to less than one hundred (Cavalli et al. 2001; Rodríguez and Cuesta 2011).

In the Atyidae, the largest freshwater shrimp family, complete suppression of all larval development has evolved in a number of landlocked species of the genus *Caridina* and in all 30 species and subspecies of the genus *Neocaridina* (Karge and Klotz 2008; De Grave and Fransen 2011). For example, the 21 species of *Caridina* from ancient lakes of Sulawesi produce less than 50 eggs that hatch into either an advanced decapodid or a juvenile stage (Karge and Klotz 2008; Von Rintelen and Cai 2009; Von Rintelen et al. 2012b). A good example of direct development in the genus *Neocaridina* is *N. ishigakiensis* (Fujino and Shokita) from the Ryukyu Islands in Japan which produces eggs that hatch as decapodids with well developed appendages, eyes, and sensory setae on the antennae (Shokita 1976).

In the Palaemonidae, the second largest freshwater shrimp family, direct development has evolved in two genera, *Macrobrachium* and *Palaemonetes*. Shokita et al. (1991) listed 13 species of *Macrobrachium* that have highly abbreviated development, 10 of which produce only benthic larvae, e.g., the Indian hill stream species *M. dayanum* (Henderson) (Jalihal et al. 1993; Karge and Klotz 2008). The reduction of larval development to a single benthic stage is also found in *Palaemonetes mercedae* Pereira from blackwater forest creeks in the Amazon basin in South America whose hatchling stage closely resembles adults except that their uropods are not yet free (Magalhães and Walker 1988).

The members of the species-poor freshwater shrimp families Desmocarididae, Typhlocarididae, and Euryrhynchidae have small numbers of large eggs (Fig. 6.1a) and their larval development is either reduced to a single stage or completely suppressed (Bauer 2004). For instance, in *Desmocaris trispinosa* (Aurivillius), a species endemic to west and central African forests, the hatchling has a juvenile-like appearance except that the uropods are not yet free (Powell 1979). In the blind *Typhlocaris galilea* Calman, which is endemic to a warm sulphur spring in Israel, the hatchling is a decapodid that moults after a short period into a juvenile with similar morphology and behaviour as the adults (Tsurnamal 1978). The three *Euryrhynchus* species from the Amazon basin produce a benthic larval stage that walks slowly on the river bed and resembles adults except the larval stage lacks free uropods (Magalhães and Walker 1988).

Posthatching brood care is rare in freshwater shrimps. In the Atyidae it is only known for *Dugastella valentina* (Ferrer Galdiano) from Spain (Table 6.1) and *D. marocana* Bouvier from Morocco (Cuesta et al. 2006; Huguet et al. 2011; Rodríguez and Cuesta 2011). These species retain their larval stages (two zoeal stages and one decapodid) for 5–9 days in a brood chamber formed by the L-shaped arrangement of pleopods 1–4 and the laterally expanded pleonal tergites (Fig. 6.1b). The larvae and the first two to three juvenile stages have sufficient yolk reserves to ensure nutritional independence. Stage-2 zoeae and decapodids have well-developed chelae and can grip the setae of the maternal pleopods, but stage-1 zoeae lack chelae and are held within the brood chamber solely by the maternal structures (Rodríguez and Cuesta 2011). When the zoeal stages are transferred to culture vessels they remain inactive. The decapodids can walk but are usually inactive as well (Rodríguez and Cuesta 2011).

In the Palaemonidae, brooding of posthatching stages on the mother's body has never been observed, but there is a kind of brood protection in species of the *Macrobrachium hendersoni*-group from hill streams of northern India and Myanmar that have a single benthic larval stage. In the aquarium, females of *M. hendersoni* (De Man), *M. a. assamense* (Tiwari), and *M. dayanum* hide with their hatchlings for days and do not feed (Karge and Klotz 2008), which is typical of mothers caring for their young (Thiel 2007).

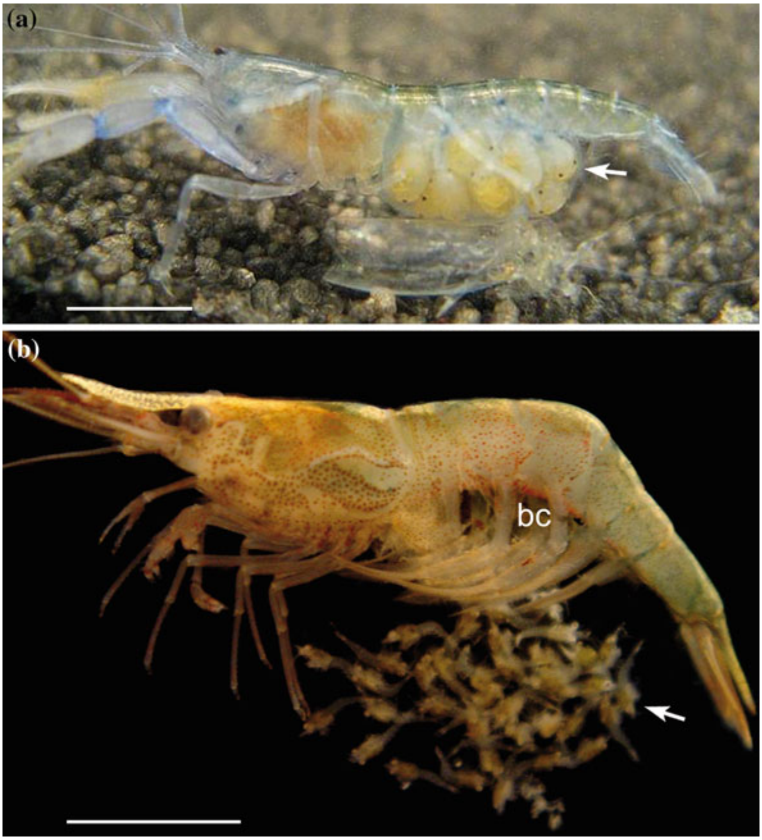


Fig. 6.1 Direct development and brooding of posthatching stages in freshwater shrimps. **a** *Euryrhynchus wrzesniowskii* Miers with a few advanced embryos (*arrow*) on the pleopods. Scale = 5 mm (*Photo* Murathan Kilic). **b** Brooding female of *Dugastella valentina* with zoea-2 larvae (*arrow*) removed from the brooding chamber (*bc*). Scale = 5 mm (from Cuesta et al. 2006)

6.3 Direct Development and Posthatching Brood Care in Aeglid Anomurans

All Aeglidae exhibit direct development and posthatching brood care (Bond-Buckup et al. 1999; Lizardo-Daudt and Bond-Buckup 2003; Francisco et al. 2007; Teodósio and Masunari 2007; Moraes and Bueno 2013, 2015). The number of eggs per clutch is in the upper tens to the lower hundreds, depending on species and size of female (Tudge 2003; Bond-Buckup et al. 2008). The eggs are carried on the four pairs of female pleopods (Fig. 6.2a), are incubated for about 4–8 months (Bond-Buckup et al. 2008), and are regularly aerated and groomed to avoid fouling.

The hatchlings remain for some days attached to the pleopods (Fig. 6.2b) in the maternal brood chamber formed by the flexed pleon. The hatchlings have an

Table 6.1 Posthatching brood care and brood protection in freshwater Decapoda

Species	Duration	References
Freshwater shrimps		
Dugastella valentina	5–9 days	Cuesta et al. (2006)
Aeglid anomurans		
Aegla uruguayana	3–4 days	López Greco et al. (2004)
Aegla platensis	5 days	López Greco et al. (2004)
Aegla perobae	8–12 days	Rodrigues and Hebling (1978)
Aegla castro	15 days	Swiech-Ayoub and Masunari (2001)
Freshwater crabs		
Geosesarma notophorum	4 days	Rademacher and Mengedoht (2011)
Austrothelphusa transversa	Some days	Powers and Bliss (1983)
Geosesarma bicolor	Some days	Rademacher and Mengedoht (2011)
Geosesarma peraccae	8–9 days	Lam (1969)
Candidiopotamon rathbunae	9–16 days	Liu and Li (2000)
Sylviocarcinus pictus	>17 days	Sant'Anna et al. (2013)
Potamonautes lirrangensis	Some weeks	Rademacher and Mengedoht (2011)
Sesarma jarvisi	2–3 months[a]	Diesel and Horst (1995)
Spiralothelphusa hydrodroma	38–100 days[b]	Pillai and Subramoniam (1984)
Metopaulias depressus	3 months[a], >1 year[c]	Diesel and Schubart (2007)
Freshwater crayfish		
Astacus astacus	6–17 days[d]	Bieber (1940)
Pacifastacus leniusculus leniusculus	20 days	Andrews (1907)
Orconectes neglectus chaenodactylus	20 days	Price and Payne (1984)
Virilastacus araucanius	20 days	Rudolph and Rojas (2003)
Cherax destructor	22 days[d]	Sandeman and Sandeman (1991)
Orconectes limosus	16–24 days	Mathews (2011)
Astacus leptodactylus	20–25 days	Köksal (1988)
Austropotamobius pallipes	25 days	Gherardi (2002)
Cherax quadricarinatus	18–29 days	Levi et al. (1999)
Procambarus fallax f. virginalis	14–38 days	Vogt (2008)
Cherax cainii	28–38 days	Burton et al. (2007)
Orconectes pellucidus	27–40 days	Bechler (1981)
Paranephrops planifrons	40–50 days[d]	Hopkins (1967)
Astacopsis gouldi	44–58 days	Hamr (1992)
Cambaroides similis	6 weeks[d]	Ko and Kawai (2001)

(continued)

Table 6.1 (continued)

Species	Duration	References
Procambarus clarkii	3 weeks, 3 months[b]	Huner (1988), Gherardi (2002)
Engaeus cisternarius	73–95 days	Suter (1977)
Paranephrops zealandicus	4–5 months	Whitmore and Huryn (1999)
Ombrastacoides pulcher	>14 months[b]	Hamr and Richardson (1994)
Engaeus orramakunna	>1 year[b]	Duffy (2010)

Data give carriage on maternal pleopods if not otherwise indicated
[a] Brooding of free larval and juvenile stages in water-filled nursery
[b] Carriage of young on pleopods plus subsequent protection of free juveniles in burrow
[c] Prolonged protection of juveniles in family group
[d] Firmly attached stages only

adult-like morphology (Fig. 6.2c) but lack pleopods, except for *Aegla paulensis* Schmitt, which has rudimentary pleopods (Moraes and Bueno 2013). Juvenile aeglids have no special structures for attachment. They remain in the female brood chamber by gripping pleopodal structures of the mother with the robust chelae of their first pereopods (López Greco et al. 2004; Francisco et al. 2007; Moraes and Bueno 2013, 2015).

Hatchlings of aeglids (stage 1 juveniles) have well-developed locomotory appendages and sense organs and can walk. They explore their environment, and show escape reactions by flapping their pleon (Moraes and Bueno 2013). Examples of well-developed sense organs are the olfactory aesthetascs on the antennules (Fig. 6.2d) and the gustatory setae on the pereopods (Fig. 6.2f). The mouthparts are also equipped with numerous sensory setae and the mandibles have well-developed sclerotized teeth (Fig. 6.2e) which suggests that stage-1 juveniles are able to feed. However, according to Lizardo-Daudt and Bond-Buckup (2003), juveniles of *A. platensis* Schmitt do not feed during the first few days of life subsisting on the yolk reserves in their cephalothorax. They only search for food after this endogenous resource has been exhausted.

Although hatchlings appear to be ready to live independently they nevertheless remain under maternal protection for some days. Posthatching brood care has been documented in detail for *A. uruguayana* Schmitt, *A. platensis*, *A. perobae* Hebling and Rodrigues and *A. castro* Schmitt, which brood their young for 3–4, 5, 8–12 and 15 days, respectively (Table 6.1). The juveniles of laboratory-reared *A. uruguayana* are attached to the maternal pleopods for only the first day after hatching after which they explore their surroundings but return to their mother and rest on the pleopods for two further days. On the fourth day they leave their mother's protection and live independently (López Greco et al. 2004).

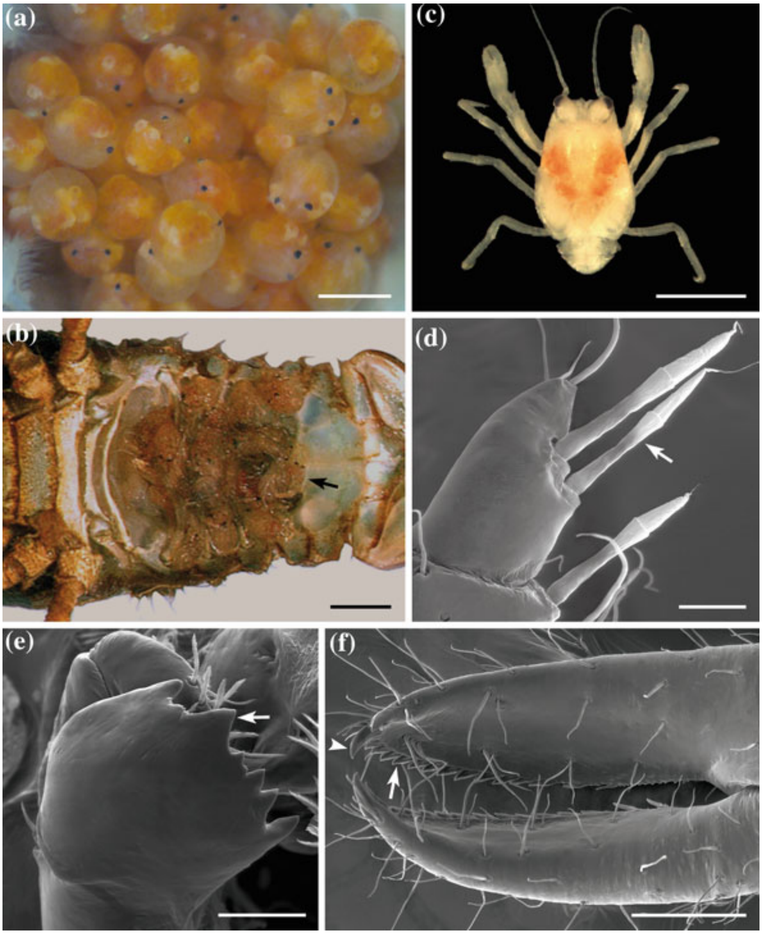


Fig. 6.2 Direct development and brooding of posthatching stages in aeglid anomurans. **a** Late stage embryos on the maternal pleopods of *Aegla paulensis*. Scale = 1 mm (*Photo* Sérgio L.S. Bueno). **b** Ventral aspect of adult female of *Aegla platensis,* with juveniles (*arrow*) on the pleopods. Scale = 2 mm (*Photo* Ludwig Buckup). **c** Freshly hatched juvenile of *A. paulensis*. Scale = 1 mm (*Photo* Juliana C.B. Moraes). **d** Tip of antennule of hatchling of *A. paulensis* showing well-developed olfactory aesthetascs (*arrow*). Scale = 20 µm (from Moraes and Bueno 2013). **e** Mandible of hatchling of *A. paulensis* with prominent teeth (*arrow*). Scale = 50 µm (from Moraes and Bueno 2013). **f** Cheliped of hatchling of *A. paulensis* showing relatively small terminal spines (*arrowhead*) and well-developed gustatory setae (*arrow*). Scale = 100 µm (from Moraes and Bueno 2013)

In most of the aeglids investigated, brood care is confined to the first juvenile stage. An exception is *A. franca* Schmitt, in which brood care is extended to stage-2 juveniles. Interestingly, in this species the mandibles become well developed only after stage-1 juveniles moult (Moraes and Bueno 2013).

6.4 Direct Development and Posthatching Brood Care in Freshwater Crabs

Freshwater crabs can be subdivided into primary freshwater crabs consisting of exclusively freshwater families and secondary freshwater crabs that belong to primarily marine brachyuran families (Yeo et al. 2008; De Grave et al. 2009; Klaus et al. 2011). In both groups there are fully aquatic species, semi-terrestrial species that divide their time between water and land, and terrestrial species that live most of their time out of water (Cumberlidge and Ng 2009). Egg numbers are in the tens to the lower thousands in primary freshwater crabs and in secondary freshwater crabs with direct development, but large specimens of amphidromous secondary freshwater crabs can produce up to one million eggs (Veilleux and de Lafontaine 2007; Wehrtmann et al. 2010).

6.4.1 Primary Freshwater Crabs

The members of the primary freshwater crab families Gecarcinucidae, Potamidae, Potamonautidae, Pseudothelphusidae, and Trichodactylidae all exhibit direct development, hatching as fully developed juveniles (Pace et al. 1976; Yeo et al. 2008; Cumberlidge and Ng 2009; Wu et al. 2010). Posthatching brood care is apparently the rule although detailed studies are scarce (Wu et al. 2010). Reports of posthatching brood care are available for representatives of all five primary freshwater crab families: the potamonautid *Liberonautes latidactylus* (De Man), the potamid *Candidiopotamon rathbunae* (De Man), the pseudothelphusid *Kingsleya ytupora* Magalhaes, the gecarcinucid *Parathelphusa maculata* De Man, and the trichodactylid *Sylviocarcinus pictus* (Milne Edwards) (Cumberlidge 1999; Liu and Li 2000; Wehrtmann et al. 2010; Rademacher and Mengedoht 2011; Sant'Anna et al. 2013).

The juveniles are carried in the abdominal brood pouch (Fig. 6.3a) which is formed by the concave sternum, the pleon folded under the cephalothorax, and the broad blade-like parts of the pleopods that enclose the lateral spaces between the sternum and the pleon. Carriage of the juveniles in the abdominal brood pouch lasts between ten days and a few weeks (Table 6.1). Hatchling crabs of *Liberonautes latidactylus*, *Potamonautes lirrangensis* (Rathbun), and *Kingsleya ytupora* moult while still living in the maternal brood chamber (Cumberlidge 1999; Wehrtmann et al. 2010; Rademacher and Mengedoht 2011). They cling to the pleopods and other maternal structures with their well-developed chelae (Pace et al. 1976). The visual, olfactory and tactile sense organs of the hatchlings are all well developed, allowing the young crabs to make regular excursions in the environment close to their mother and to find their way back to the maternal brood pouch for shelter (Pace et al. 1976; Liu and Li 2000).

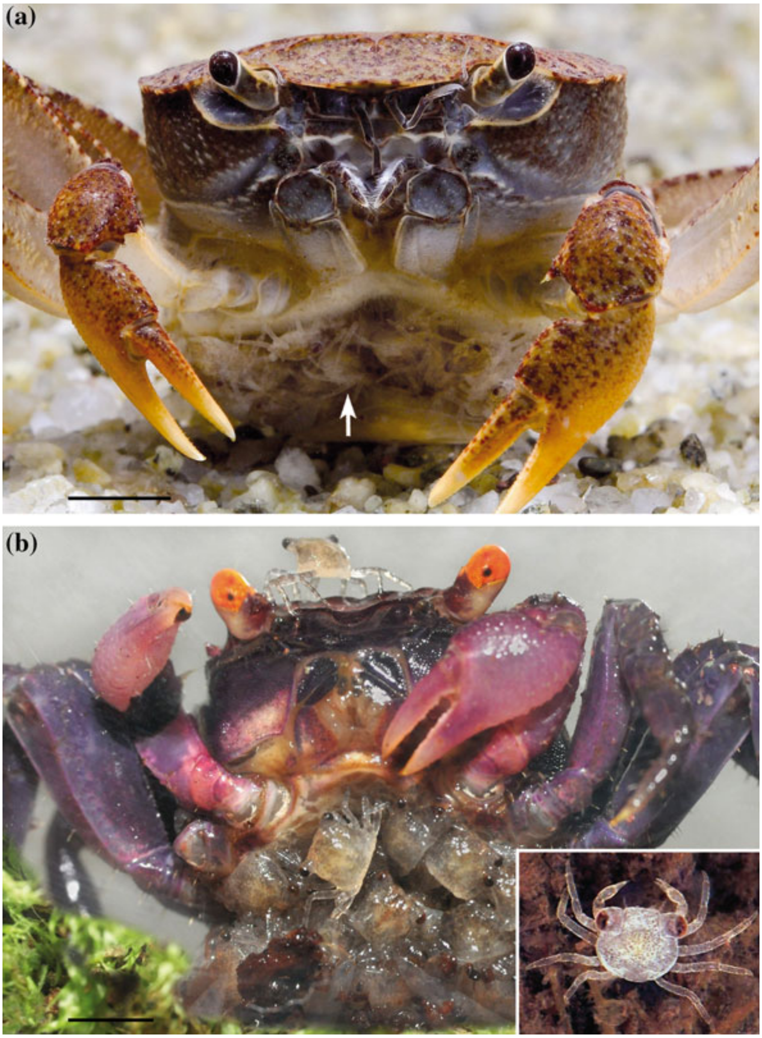


Fig. 6.3 Typical mode of posthatching brood care in freshwater crabs. **a** Primary freshwater crab *Irmengardia johnsoni* Ng and Yang with juveniles in brood pouch (*arrow*). Scale = 5 mm (*Photo* Choy Heng Wah). **b** Secondary freshwater crab *Geosesarma dennerle* with juveniles in brood pouch and on other body parts. Scale = 5 mm (from Rademacher and Mengedoht 2011). *Inset* Hatchling of *Geosesarma krathing* Ng and Naiyanetr showing well-developed eyes and chelipeds (*Photo* Oliver Mengedoht)

The burrowing field crab *Spiralothelphusa hydrodroma* (Herbst) from Madras, India exhibits an unusual type of brooding behaviour. Embryogenesis and hatching take place when temperatures are high and their habitat is at its driest. These conditions are unfavourable for the release of juveniles. Therefore, the offspring are brooded in the maternal burrow until the onset of monsoon rains which bring cooler temperatures and fill up the wetlands. The duration of posthatching brood care in *S. hydrodroma* is adapted to these conditions and varies considerably, e.g. between 38 and 100 days over a three-year observation period (Pillai and Subramoniam 1984).

Prolonged brood protection has also been observed in the arboreal crab *Potamonautes raybouldi* Cumberlidge and Vannini from closed canopy forests in the Usambara Mountains in Tanzania and the Shimba Hills in Kenya (Bayliss 2002, 2011; Cumberlidge and Vannini 2004). This species raises its young in water-filled natural tree holes that form at the base of branches. The mother crab cleans these brooding pools and manipulates the pH and calcium concentration of the pool water by adding empty snail shells. On one occasion, two different juvenile broods with mean carapace widths of 9.47 and 18.97 mm were found in the same tree hole together with a larger female, implying an advanced social system (Bayliss 2002).

6.4.2 Secondary Freshwater Crabs

Direct development and posthatching brood care are not the rule in secondary freshwater crabs because the larvae of most of these species must develop in saltwater and pass through the same series of larval stages as their family members that are fully marine (Anger 1995). A few species of secondary freshwater crabs have abbreviated limnic larval cycles, and only a small number of species develop without any larval stages at all (Chap. 5 of this book; Anger 1995; Ng and Tan 1995; Schubart et al. 2000; Vogt 2013). For example, the hymenosomatids *Amarinus lacustris* (Chilton) from Australia and *A. angelicus* (Holthuis) from Papua New Guinea lack larval stages (Lucas 1980), as does the sesarmid genus *Geosesarma*, whose eggs hatch as fully developed juveniles (Fig. 6.3b) (Ng and Tan 1995; Rademacher and Mengedoht 2011).

Posthatching brood care is only known for some Sesarmidae (Table 6.1). As an example, the semi-terrestrial vampire crab *Geosesarma dennerle* Ng, Schubart and Lukhaup carries its juveniles until all of the eggs in the clutch have hatched, which may take several days (Fig. 6.2b) (Rademacher and Mengedoht 2011). Mothers of the blue vampire crab, a colour variant of *G. dennerle* (Ng et al. 2015) allow their juveniles to return under the pleon for two weeks after hatching (Rademacher and Mengedoht 2011). The more terrestrial crab *Geosesarma notophorum* Ng and Tan carries the juveniles for approximately four days on the dorsal surface of the maternal carapace covered by a film of water (Fig. 6.4a) before releasing them onto the moist substratum (Ng and Tan 1995; Rademacher and Mengedoht 2011).

Another special mode of brood protection in secondary freshwater crabs is shown by the Jamaican bromeliad crab *Metopaulias depressus* Rathbun, which broods its larvae and juveniles in the water-filled leaf axils of bromeliads (Fig. 6.4b). Clutches of between 20 and 100 eggs per female are carried under the pleon for about 10–12 weeks. The hatching stage is an advanced zoeal larva that is released into the nursery pool where it develops for 13 days passing through two lecithotrophic zoeal stages into a facultative lecithotrophic juvenile

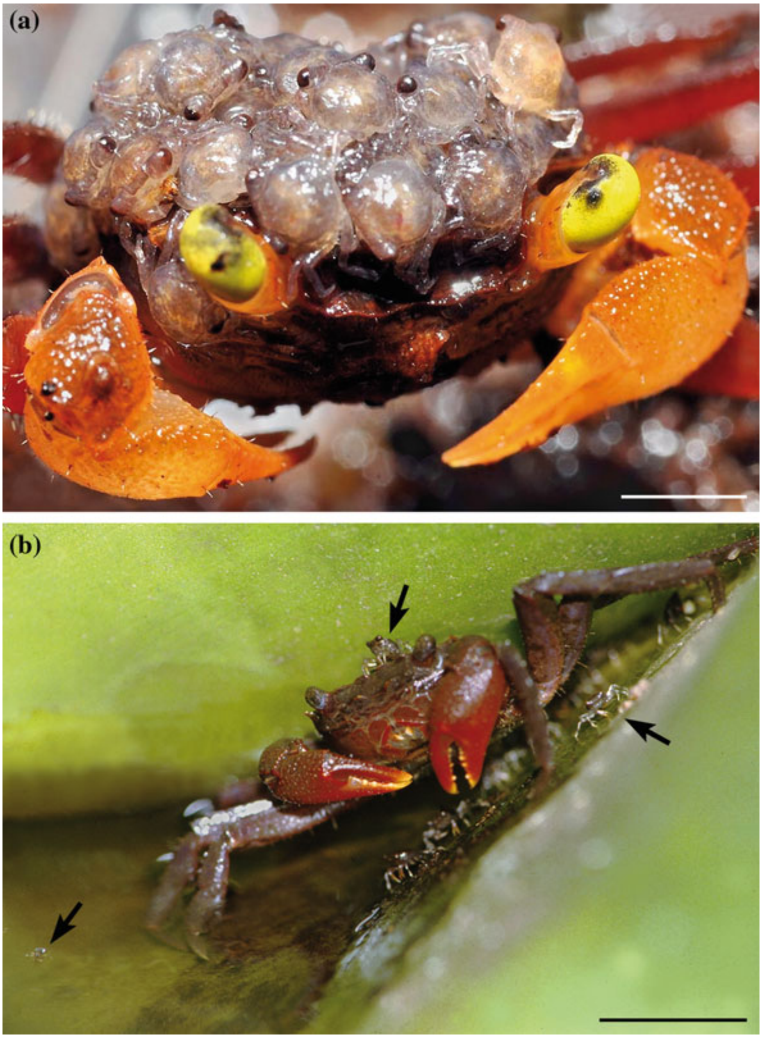


Fig. 6.4 Atypical mode of posthatching brood care in secondary freshwater crabs. **a** Terrestrial *Geosesarma notophorum* carrying juveniles on top of carapace. Scale = 3 mm (*Photo* Oliver Mengedoht). **b** Mother and young (*arrows*) of Jamaican bromeliad crab *Metopaulias depressus* in water-filled leaf axil of bromeliad. Scale = 2 cm (from Diesel and Schubart 2000)

(González-Gordillo et al. 2010). The mother crab supplies her offspring with food and optimizes the water quality in the brooding pool by oxygenation, removal of detritus, and the addition of snail shells. The latter measure buffers the pH of the water and increases its calcium content (Diesel 1992; Diesel and Schuh 1993; Diesel and Schubart 2007).

After about three months juveniles of the bromeliad crab leave their nursery pools in search of their own leaf axil pool, but if suitable habitat is not available they remain in the maternal pool as part of a family colony. The majority of bromeliad crab colonies investigated (80 %) consisted of at least two annual broods. The largest colony included one large female, 12 juveniles from an older brood, and 71 recent juveniles (Diesel and Schubart 2007). Mother crabs can distinguish between colony members and unfamiliar crabs, and defend their brooding pools vigorously. Such maternal care has been shown to reduce predator-related mortality of the offspring by 60 % (Diesel 1992). Moreover, the presence of older siblings in the maternal pool enhanced survivorship and growth of the younger siblings, indicating an advanced social system (Diesel and Schubart 2007).

6.5 Direct Development and Posthatching Brood Care in Freshwater Crayfish

Freshwater crayfish have egg numbers per clutch in the tens and hundreds and less frequently in the lower thousands (Reynolds 2002; Lukhaup and Pekny 2008). All freshwater crayfish investigated exhibit direct development and posthatching brood care, with both eggs and juveniles carried on the maternal pleopods (Fig. 6.5a–c). Embryonic development until the eggs hatch can be as short as 2–3 weeks as observed in *Procambarus clarkii* (Girard) or as long as one year as observed in *Paranephrops zealandicus* (White) (Whitmore and Huryn 1999; Reynolds 2002). Transport of the posthatching stages on the mother's pleopods can last from 1–2 weeks as reported for *Astacus astacus* (Linnaeus) to up to five months as reported for *Paranephrops zealandicus* (Table 6.1) (Andrews 1907; Whitmore and Huryn 1999). Brood protection in the maternal burrow may even exceed one year (Richardson 2007; Duffy 2010).

6.5.1 *Differences in Brood Care Between Families*

The hatchlings (stage-1 juveniles) of freshwater crayfish are unusual within the Decapoda because they are neither larvae characterized by specific larval characters nor completely developed juveniles (Fig. 6.6a) (Andrews 1907; Scholtz 2002; Vogt and Tolley 2004). The morphology of the hatchlings is rather uniform in the three crayfish families Astacidae, Cambaridae, and Parastacidae, because they all lack external sense organs such as the olfactory aesthetascs on the antennules, hydrodynamic and tactile setae on the antennules and antennae, and gustatory corrugated setae on the chelae of the pereopods (Fig. 6.6b). Moreover, crayfish hatchlings have incompletely developed eyes (Figs. 6.6b), statocysts, mouthparts, and gastric mill

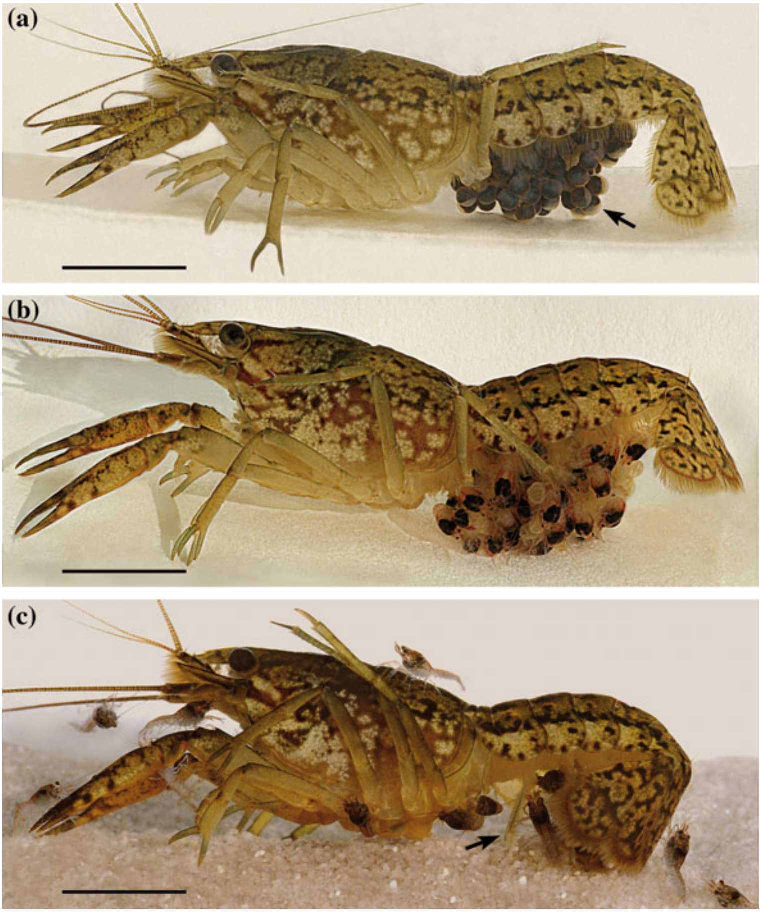
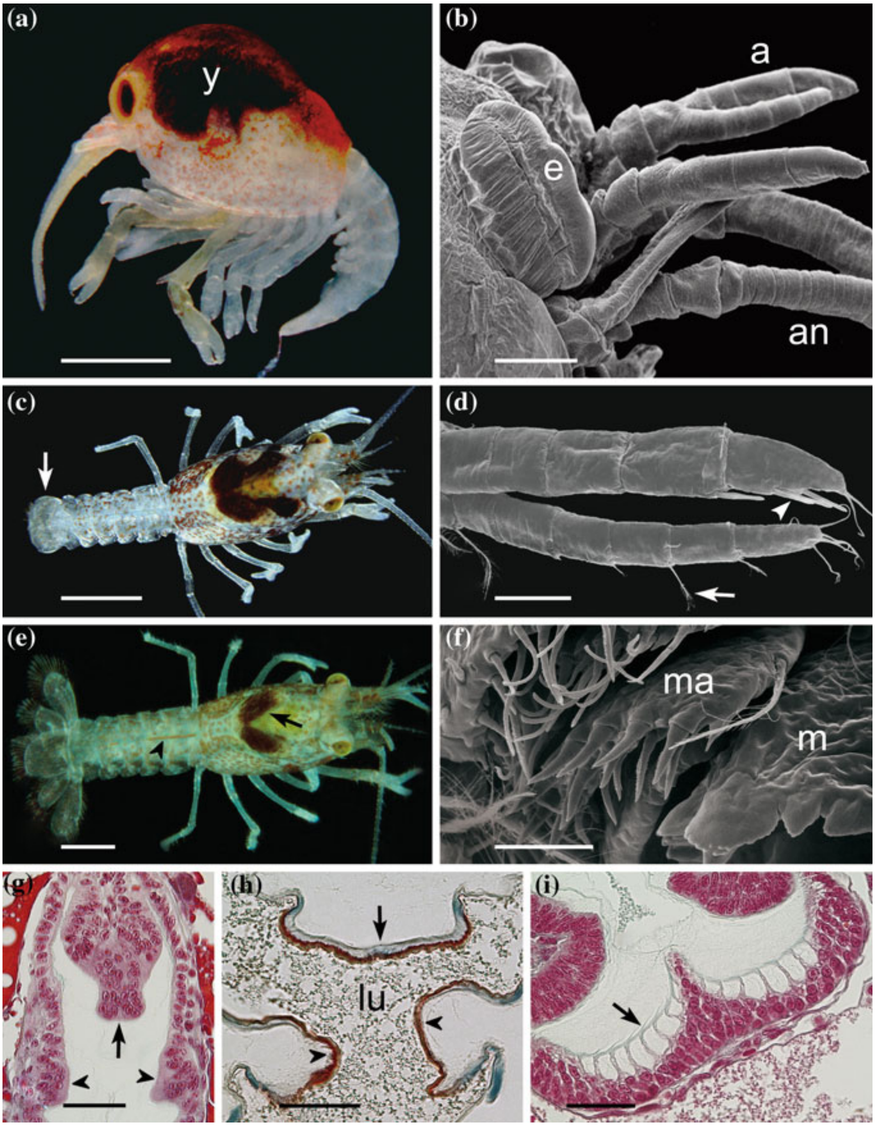


Fig. 6.5 Posthatching brood care in freshwater crayfish. **a** Female of marbled crayfish *Procambarus fallax f. virginalis* carrying embryonized eggs (*arrow*) on the pleopods. Scale = 1 cm (from Vogt et al. 2004). **b** Same specimen with stage-2 juveniles on the pleopods. Scale = 1 cm (from Vogt and Tolley 2004). **c** Same specimen collecting her foraging stage-3 juveniles with the pleopods levered to the ground (*arrow*), tolerating juveniles on all parts of her body. Scale = 1 cm (from Vogt and Tolley 2004)

(Fig. 6.6g) (Thomas 1973; Scholtz 1995; Vogt 2008), while the pyloric filters of the stomach are structurally complete (Fig. 6.6i) but not yet functional (Vogt 2008).

Stage-2 juveniles (Fig. 6.6c) differ among families with respect to maturity and activity. In the Astacidae, stage-2 juveniles possess fully-developed sense organs and mouthparts and leave the mother periodically (Andrews 1907), whereas stage-2 juveniles in the Cambaridae and Parastacidae still have developmental deficiencies and remain permanently attached to the maternal pleopods (Scholtz and Kawai 2002; Vogt et al. 2004; Noro et al. 2005). For example, in the cambarid marbled crayfish



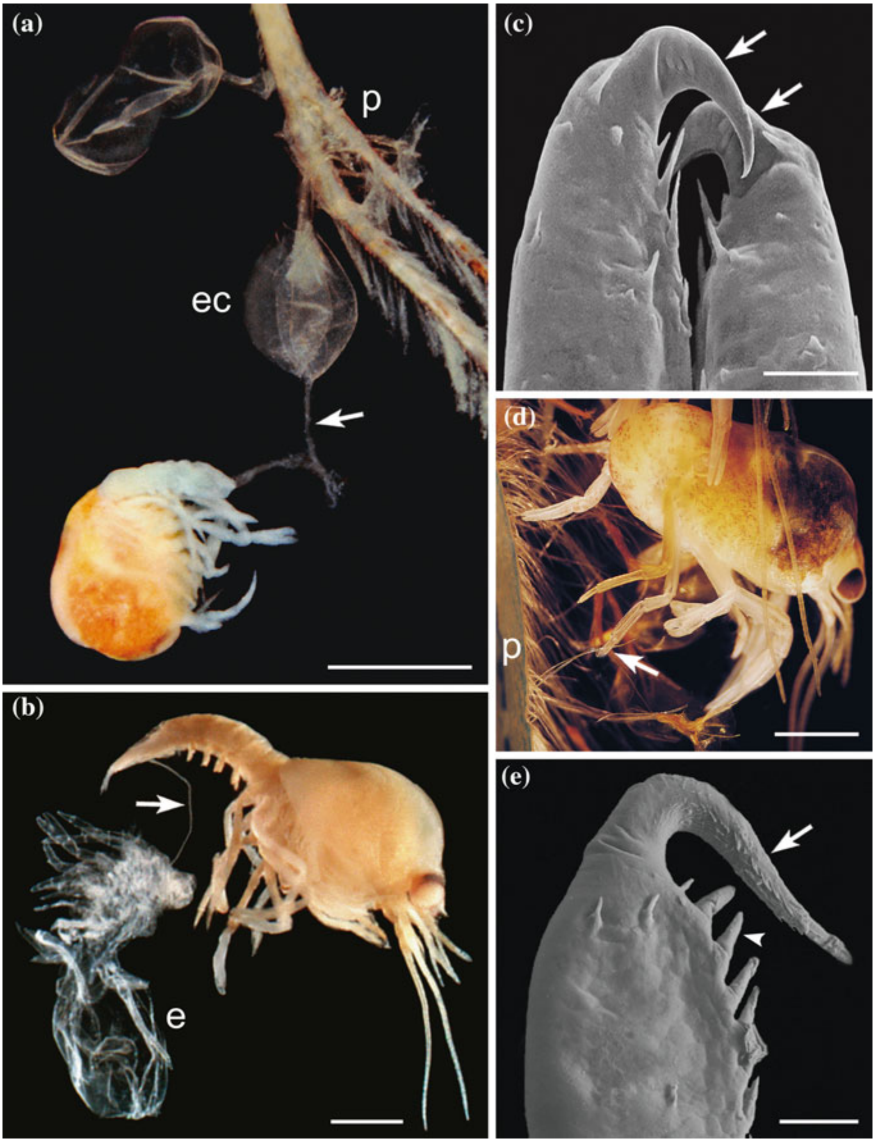
Procambarus fallax (Hagen) *f. virginalis* the stage-2 juveniles have well developed eyes (Fig. 6.6c), aesthetascs (Fig. 6.6d), tactile setae and corrugated setae, whereas their statocysts, mouthparts and gastric mill (Fig. 6.6h) are underdeveloped so stage-2 juveniles remain attached to the maternal pleopods. Stage-2 juveniles taken from the maternal pleopods can walk, but only unsteadily due their incompletely developed statocysts, and when offered food they examine it but do not feed.

◀ **Fig. 6.6** Developmental deficiencies in brooded juveniles of marbled crayfish. **a** Helpless hatchling with large yolk sac (*y*) in cephalothorax. Scale = 1 mm (from Vogt et al. 2004). **b** Head of hatchling showing incompletely developed eyes (*e*) and seta-free antennules (*a*) and antennae (*an*). Scale = 200 µm (from Vogt and Tolley 2004). **c** Stage-2 juvenile, the first stage with external sense organs. *Arrow* denotes incompletely developed tail fan. Scale = 1 mm (from Vogt et al. 2004). **d** Antennule of stage-2 juvenile studded with some olfactory aesthetascs (*arrowhead*) and feathered setae (*arrow*). Scale = 100 µm (from Vogt 2008). **e** Stage-3 juvenile, the first feeding stage. The tail fan is now complete. The specimen has already fed on external food as indicated by the gut content (*arrowhead*), but still has some yolk reserves (*arrow*). Scale = 1 mm (from Vogt et al. 2004). **f** Cutting edges of mouthparts of a stage-3 juvenile showing well-developed masticatory and sensory structures. *m* mandible; *ma* 1st maxilla. Scale = 50 µm (from Vogt 2008). **g** Gastric mill of hatchling showing primordia of median tooth (*arrow*), and lateral teeth (*arrowheads*). Scale = 40 µm (from Vogt 2008). **h** Gastric mill of stage-2 juvenile. The medial tooth (*arrow*) and the lateral teeth (*arrowheads*) are moderately developed and are beginning to be sclerotized (*brown layer*). The empty spaces underneath the teeth are fixation artefacts. *lu* lumen of stomach. Scale = 40 µm (from Vogt 2008). **i** Pyloric filters in a hatchling, showing well developed filter tubes covered by filter setae (*arrow*). Scale = 30 µm (from Vogt 2008)

The period of attachment of the hatchling crayfish to the maternal pleopods lasts between one and three weeks, depending on family and species. The release of the hatchlings is followed by a sheltering period, in which the juveniles leave the mother temporarily to feed but remain on the pleopods for the rest of the day (Vogt and Tolley 2004). This sheltering period is typical for stage-2 juveniles in the Astacidae, and for stage-3 juveniles in the Cambaridae and Parastacidae. The sheltering period may be expanded when conditions are unfavourable. For example, in laboratory-reared marbled crayfish the normal 10 day sheltering period was extended to 27 days and to stage-4 and stage-5 juveniles when the dens were removed from the culture vessel (Vogt 2008). The first feeding stages of all three crayfish families still have some yolk reserves (Fig. 6.6e) that fuel metabolism for a few days, and allow juveniles to slowly adapt to an independent life. In these first feeding stages the sense organs and the masticatory structures of the mouthparts (Fig. 6.6f) and the gastric mill are now fully developed.

6.5.2 Attachment of Crayfish Juveniles to the Maternal Pleopods

There are three different structures in freshwater crayfish that accomplish attachment of the early juveniles to their mother: (1) the telson thread, (2) the anal thread, and (3) recurved hooks on the pereopods. These structures are not permanent and only appear during the attachment phase. The telson thread occurs in all three crayfish families (Andrews 1907; Scholtz 1995; Vogt and Tolley 2004) and emerges during hatching. This thread is composed of a secretion and the detaching inner layer of the egg case (Vogt 2008) and extends from the posterior end of the telson of the hatchling to its egg case (Fig. 6.7a). During eclosion the telson thread acts as a safety line, keeping the helpless hatchling passively secured to the mother



and preventing it from being dislodged by the water currents. Thereafter, the telson thread secures the hatchling during its attempts to actively attach to the pleopods with its pereopodal hooks.

In the Cambaridae and Parastacidae, moulting of the hatchling is secured by an additional safety line, the anal thread (Fig. 6.7b). This structure is composed of the cuticle of the hindgut and originates from delayed moulting of the hindgut (Scholtz 1995; Rudolph and Rojas 2003; Vogt 2008). The anal thread links the emerging

◀ **Fig. 6.7** Attachment structures of the brooded stages in crayfish. **a** Safeguarding of hatching in marbled crayfish. The hatchling is passively linked to the maternal pleopod (*p*) via a telson thread (*arrow*) and the egg case (*ec*). Scale = 2 mm (from Vogt and Tolley 2004). **b** Safeguarding of first moulting in marbled crayfish. The freshly emerged stage-2 juvenile is passively linked to its exuvia (*e*) via the anal thread (*arrow*). In vivo the exuvia remains hooked to the mother's pleopodal structures. Scale = 1 mm (from Vogt 2008). **c** Strongly recurved terminal hooks (*arrows*) on the cheliped of a marbled crayfish hatchling used for active attachment to the maternal pleopods. Scale = 40 µm (from Vogt 2008). **d** Attachment of the hatchling of *Cherax cainii* Austin and Ryan to the oosetae of the maternal pleopod (*p*) by the 4th pereopod (*arrow*). Scale = 1 mm (from Burton et al. 2007). **e** Recurved terminal hook (*arrow*) and opposing spines (*arrowhead*) on the 5th pereopod of a hatchling of *C. cainii* used for attachment. Scale = 40 µm (from Burton et al. 2007)

stage-2 juvenile to its exuvia which remains hooked into the pleopodal structures of the mother during moulting. In vitro tests have revealed that the anal thread is firm enough to secure the emerging stage-2 juveniles and to prevent them from being washed away (Vogt 2008). Once the juveniles have attached to the female's pleopods with their peropodal hooks the anal thread is disconnected by flapping movements of the juveniles. There is no anal thread in the Astacidae (Andrews 1907).

The stage-1 juveniles of the Astacidae and stage-1 and stage-2 juveniles of the Cambaridae are equipped with recurved terminal hooks on the chelae of the first pereopods (Fig. 6.7c) (Andrews 1907; Scholtz and Kawai 2002; Vogt 2008). These hooks either pierce into remnants of the egg attachment system or hook onto the oosetae (Vogt and Tolley 2004). In contrast, the stage-1 and stage-2 juveniles of the Parastacidae hold on with specialized terminal hooks on the 4th and 5th pereopods (Fig. 6.7d, e) (Scholtz 1995; Burton et al. 2007). Later brooded juvenile stages lack terminal hooks and grip onto maternal structures with the well-developed chelae of pereopods 1–3 (Noro et al. 2005; Vogt 2008).

6.5.3 Special Behaviours of Brooding Mother Crayfish and Their Offspring

Behaviour related to brood care has been well investigated in freshwater crayfish, whereas little is known in most other freshwater decapods. Brood care behaviour includes defence of the offspring, ventilation and cleaning of eggs and juveniles, active attachment of hatchlings to the maternal pleopods, and maintenance of mother-juvenile associations during sheltering.

Berried females remain in their shelters, drastically reduce their movements, cease feeding, and become more aggressive against approaching conspecifics

(Mason 1970; Levi et al. 1999; Gherardi 2002; Reynolds 2002; Thiel 2007). Laboratory experiments with *Procambarus clarkii* revealed that females carrying eggs or juveniles won a significantly higher proportion of their agonistic encounters than non-maternal crayfish (Figler et al. 2001). The decreased locomotor activity of the females minimizes the risk of egg loss and their increased aggressiveness successfully repels cannibalistic conspecifics.

During the brooding period, the eggs and juveniles are fanned regularly by shaking movements of the female's pleopods. The frequency of ventilation is increased under conditions of low oxygen (Hazlett 1983), and in extreme cases, the mother leaves the water to ventilate the brood in the air. The eggs and juveniles are also regularly groomed by the female with her pereopods, and decaying eggs and dead juveniles are removed and eaten (Thiel 2007; Aquiloni and Gherardi 2008).

The freshly hatched hatchlings try to attach reflexively to the maternal pleopods using their pereopodal hooks, an action that has been observed in marbled crayfish juveniles raised under natural conditions and in vitro (Vogt 2008). These reflexes include stereotyped upward movements when dangling on the telson thread, rotating searching movements of the pereopods, and snapping of the chelae.

When juvenile crayfish start to make feeding excursions in the surroundings of their mother they are attracted back to their mother by a pheromone as shown by two-choice maze experiments with *Orconectes sanbornii* (Faxon), *O. virilis* (Hagen) and *Procambarus clarkii* (Little 1975; Ameyaw-Akumfi 1976; Aquiloni and Gherardi 2008), However, such a pheromone has never been isolated and biochemically characterized. There is also clear evidence of optical maternal signals directing the returning juveniles onto the pleopods. In red swamp crayfish and marbled crayfish the juveniles are lured to the maternal pleopods by walking slowly with the pleon stretched horizontally and the pleopods levered to the ground (Fig. 6.5c) (Gherardi 2002; Vogt and Tolley 2004; Aquiloni and Gherardi 2008). Figler et al. (1997), Aquiloni and Gherardi (2008) concluded from laboratory experiments with *P. clarkii* that brooding mothers not only accept their own offspring but also accept the offspring of other females, and aggressiveness against juveniles is generally inhibited (Fig. 6.5c). The juveniles of *P. clarkii* attach to the pleopods of both biological and foster mothers but move away from non-brooding adults, which are usually cannibalistic (Gherardi 2002).

Perpetuation of mother-juvenile bonds is governed by two factors, the number of returning juveniles, and the tolerance of the mother. The mother terminates brood care if the number of returning juveniles falls below a certain threshold, probably sensed as changes in the weight load on the pleopods (Thiel 2007; Aquiloni and Gherardi 2008). The mother then ceases the behaviours that lure returning juveniles to the pleopods, and instead repulses approaching juveniles with an intense shaking of her body which I have observed in the marbled crayfish.

Usually, crayfish mothers become cannibalistic against their offspring after dissolution of the mother-juvenile bond. For example, in *P. clarkii*, mothers begin to attack and cannibalize their offspring when the number of juveniles on the pleopods drops below ten (Little 1976). However, mothers of the South American burrowing crayfish *Parastacus pilimanus* (Von Martens) were not observed to be aggressive against their free offspring during a period of more than six months, which may be a consequence of burrow-living in this species (Dalosto et al. 2012).

The first feeding stages of crayfish eat food particles that escape from their mother's mouthparts (Gherardi et al. 2010). Moreover, laboratory experiments with marbled crayfish revealed that the first feeding stage prefers maternal faeces to other food (Vogt 2008). Sharing of food by the mother and her offspring and coprophagy is not uncommon in crustaceans (Thiel 2007). Such feeding preferences of juveniles may simply be due to the availability of food particles from the mother of an optimal size and consistency, but may also reflect an innate behaviour to obtain reliable information on suitable and safe food sources. Coprophagy could additionally help with the acquisition of beneficial symbiotic bacteria.

6.5.4 Brood Protection in Burrowing Crayfish

Brood protection beyond carriage of the first juvenile stages has evolved in species of burrowing semi-terrestrial and terrestrial crayfish. Semi-terrestrial crayfish are active on land but have their burrows close to open waters, while terrestrial species spend almost their entire lives underground in burrows without connection to open bodies of water (Gherardi et al. 2010). Burrows may run horizontally for several meters and descend more than 4 m into the soil, and may be found many kilometres away from open water. Such burrows contain water in the bottom either because they extend down to the water table, or because they trap surface drainage water (Gherardi 2002; Richardson 2007).

Species of semi-terrestrial and terrestrial crayfish are common among the Parastacidae and the Cambaridae (Richardson 2007; Duffy 2010). These crayfish usually have egg numbers in the lower tens, which is less than that of open-water species (Richardson 2007; Lukhaup and Pekny 2008). An example of a burrowing crayfish with prolonged brood protection is *Engaeus leptorhynchus* Clark that lives in burrows that do not connect with other burrows. This species was found living in family groups: one of them consisted of three adults (a male, an egg-carrying female, and a non-reproducing female), plus 52 juveniles in two age classes (Horwitz et al. 1985). Another example is the biennially breeding Tasmanian *Ombrastacoides pulcher*, whose juveniles remain in the maternal burrow for at least 14 months. The eggs hatch in austral spring, the young are on the maternal pleopods until mid-summer, and the free juveniles remain in the maternal burrow for the following 12 months (Richardson 2007).

6.6 Direct Development and Posthatching Brood Care as Key Features of the Evolution of Freshwater Decapoda

Comparisons of the reproductive strategies of decapods from marine, freshwater, and terrestrial environments suggest that direct development and posthatching brood care are typical adaptations to fresh water. These life history strategies are rare in marine species and are confined to a few species living in harsh environments (Anger 2001; Vogt 2013). However, an important precondition for the evolution of direct development evolved in marine decapods, namely the ability to attach the eggs to the female pleopodal oosetae by means of a firm but elastic egg stalk (Cheung 1966; Talbot 1991; Saigusa et al. 2002; Vogt and Tolley 2004). Egg attachment is an autapomorphy of the Pleocyemata (Burkenroad 1963) and probably arose about 430 million years ago (Porter et al. 2005). The efficiency of the egg attachment system in decapods is best demonstrated by wild American lobsters which lose only 15–36 % of their attached eggs during the ~9 month incubation period from mechanical and non-mechanical causes (Factor 1995).

There are striking differences in the number of eggs produced between marine, freshwater, and terrestrial decapods (Vogt 2013). Most marine species of decapods produce egg numbers per clutch in the thousands to the hundreds of thousands, and even in the millions in some large species. Amphidromous freshwater decapods and terrestrial species that have invaded land via the sea shore produce eggs in the tens of thousands as do their marine relatives. By contrast, in the primary freshwater decapod species egg numbers are usually in the tens to the hundreds and sometimes in the lower thousands. Terrestrial species of decapods that invaded land via fresh water also produce small numbers of large eggs (Rabalais and Gore 1985; Corey and Reid 1991; Hines 1991; Anger 1995, 2001).

Direct development occurs in 70–75 % of freshwater decapods with a further 15–20 % showing abbreviated larval development (Vogt 2013). This is in sharp contrast to the marine decapods, in which direct development has been reported in only 20–30 species (Anger 2001; Vogt 2013). Direct development is the rule in aeglids and the species-rich freshwater crayfish and primary freshwater crabs. It is unknown in land crab families such as the Gecarcinidae, Ocypodidae, and Coenobitidae that have invaded terrestrial habitats via the sea shore. These crabs show no significant abbreviation of larval development. In contrast, non-planktonic larval development with brood care are common reproductive strategies in semi-terrestrial and terrestrial species of sesarmid secondary freshwater crabs that have a long evolutionary history of living in freshwater environments (Anger 1995; Schubart et al. 2000; Vogt 2013).

Posthatching brood care occurs in an estimated 70 % of freshwater Decapoda. In freshwater shrimps it has been reported for only two species, both in the same genus. In aeglids, freshwater crayfish, and primary freshwater crabs, brood care is the rule and the brooded stages are generally carried under the female's pleon. In aeglids and primary freshwater crabs the hatchling stages are fully developed juvenile crabs. Crayfish, in contrast, produce helpless hatchlings lacking external sense organs and functional chewing structures and so brood care lasts longer in crayfish than in aeglids and primary freshwater crabs. In secondary freshwater crabs brood care is rare and variable, and includes carrying offspring either on the pleopods or on top of the carapace. In a few species free-living larvae and juveniles are brooded in nest-like brooding pools.

Decapods have invaded freshwater multiple times beginning in the Triassic and continuing up to the Holocene. Freshwater crayfish originated from lobster-like marine ancestors about 240 million years ago (Toon et al. 2010), and most authors favour the hypothesis of a single invasion of freshwater before the break-up of Pangaea (Scholtz 2002; Rode and Babcock 2003). Direct development and extended brood care in crayfish may have evolved soon after this invasion event because there is no other mode of development in this taxon. The closest marine relatives of freshwater crayfish, the clawed lobsters (Nephropidae), develop indirectly through three zoeal stages and one decapodid (Anger 2001). The close spatial proximity of parents and offspring in the directly-developing crayfish stem population may have promoted their colonization of freshwater habitats. A detailed account of the evolution of direct development and brood care in freshwater crayfish and of the origination of differences among families is found in Scholtz (2002), Scholtz and Kawai (2002).

The evolutionary history of the two lineages of primary freshwater crabs, the Potamoidea and Trichodactylidae, is still a matter of debate (Tsang et al. 2014). Recent articles favour divergence of the Potamoidea from unknown marine crab ancestors in the early Cretaceous some 125 million years ago. The extant families and superfamilies probably arose during the late Cretaceous to early Tertiary (Klaus et al. 2011; Tsang et al. 2014). The origin of the Trichodactylidae is estimated to about 80–90 million years ago (Tsang et al. 2014). Paraphyly within the primary freshwater crabs suggests that direct development and posthatching brood care must have evolved at least twice in this group.

The Aeglidae are thought to have colonized fresh water approximately 75 million years ago from the Pacific side of South America (Pérez-Losada et al. 2004), and evolved direct development and posthatching brood care soon afterward. Their closet living marine relatives, the Lomisidae and Chirostyloidea (Schnabel et al. 2011) show extended development through four to five zoeal stages and one decapodid (Anger 2001; Guerao et al. 2006).

The caridean shrimps invaded freshwater several different times: in the Jurassic, early Cretaceous, and the Holocene. The first shrimps to colonize fresh water were the Atyidae, which had settled in freshwater habitats by the Mesozoic. Freshwater life cycles independent of sea water developed separately in several major lineages of the Atyidae (Karge and Klotz 2008; De Grave and Fransen 2011). The same holds for the Palaemonidae which invaded fresh water habitats during the Eocene about 50 million years ago (Feldmann et al. 1981; Bauer 2004; Anger 2013).

The multiple origins of direct development and extended brood care in freshwater decapods at different geological times, their scarcity in marine decapods and their absence in terrestrial decapods that have invaded land via the sea shore suggest that these reproductive strategies originated in fresh water and were strongly favoured by natural selection. There is no evidence for an early origin of direct development and brood care in the marine ancestors of the groups that colonized freshwater habitats and a possible pre-adaptive role of these reproductive traits for the conquest of fresh water.

6.7 Direct Development as a Booster of Endemism and Speciation

The evolutionary shift from extended larval development to direct development should have had considerable consequences for the biogeography of the taxa concerned because direct developers have reduced dispersal abilities compared to planktonic developers. Most species of aeglids, freshwater crayfish, primary freshwater crabs, and directly developing freshwater shrimps have a narrow geographical range, indeed, whereas this is not the case in amphidromous shrimps and crabs (Bond-Buckup et al. 2008; Crandall and Buhay 2008; De Grave et al. 2008; Cumberlidge et al. 2011; Von Rintelen et al. 2012a).

Low dispersal plays a significant role in the evolution of endemism, and therefore, endemic species are common among directly developing freshwater decapods. For example, the primary freshwater crabs of China comprise 243 species in 37 genera, 96 % of which are country endemics at the species level and 78 % are endemic at the genus level (Cumberlidge et al. 2011). Endemism is also apparent in the freshwater crayfish found in the Central Highlands region of the United States, which harbours 49 endemic species of *Orconectes* and 34 endemic species of *Cambarus* (Crandall and Templeton 1999). Data on endemism in aeglids are provided by Pérez-Losada et al. (2009) and data on endemism in shrimps with suppressed larval stages are provided by Karge and Klotz (2008) and von Rintelen (2011).

Hansen (1983) predicted that direct developers will speciate more rapidly than species with planktonic larvae due to restricted geographical distributions leading to reproductive isolation and decreased gene flow. The directly developing freshwater crayfish, primary freshwater crabs, and aeglids seem to support Hansen's (1983) concept. The freshwater crayfish contain 634 species whereas their indirectly developing marine sister group, the geographically widespread Nephropidae, contains only 53 species (Scholtz 2002; De Grave et al. 2009). The aeglids (69 species) are also relatively species-rich considering their relatively small geographical range in the southern part of South America. The closest marine sister group, the Lomisidae contains only one species (De Grave et al. 2009; Schnabel et al. 2011). The Trichodactylidae from Central and South America, which represent a separate lineage of primary freshwater crabs, includes about 50 species, whereas their closest marine relatives of the family Orithyiidae has only one species (De Grave et al. 2009; Tsang et al. 2014). The closest marine relatives of the four families of primary freshwater crabs in the Potamoidea are unknown (Tsang et al. 2014), but the latter superfamily is species-rich with more than 1300 species (about one fifth of the Brachyura) (Ng et al. 2008; Cumberlidge and Ng 2009) suggesting a particularly high degree of speciation in this taxon.

6.8 Conservation Challenges Resulting from Direct Development

The reduced gene flow and diminished dispersal ability in direct developers not only boosts endemism and speciation, it also boosts genetic diversity among populations of the same species. Conservation programmes therefore need to be aimed at primary freshwater decapods and also need to include a consideration of protecting valuable gene pools aside of protecting threatened species as a whole. This approach is not usually necessary in species of amphidromous shrimps and crabs that have a high gene flow (Dennenmoser et al. 2010).

A second conservation issue related to direct development concerns present-day environmental challenges like habitat destruction, pollution and global warming. These challenges threaten directly developing aeglids, crayfish, and primary freshwater crabs more than indirect developers living in the same habitat because, as a result of low dispersal, the three directly developing groups may not always be able to recolonize lost habitats. For example, if an endemic crayfish population is eradicated in a particular river by a short-term wave of toxins, then it may be lost forever even if the water quality was soon restored. Planktonic dispersers could repopulate such a lost habitat rather rapidly from neighbouring rivers via estuary hopping.

Global analyses and model projections have shown that the threat of extinction is indeed higher for restricted range species of crayfish, aeglids, and primary freshwater crabs (Ricciardi and Rasmussen 1999; Thiel 2003; Cumberlidge 2011; Cumberlidge et al. 2011; Richman et al. 2015). In freshwater shrimps, which contain only a small percentage of directly developing species, the situation is less alarming and almost all threatened species of freshwater shrimps are narrow-range endemics that have suppressed larval development (De Grave et al. 2008).

6.9 Conclusions

1. Direct development has evolved in an estimated 70–75 % of the freshwater Decapoda, including all aeglid anomurans, all freshwater crayfish, and all primary freshwater crabs, some secondary freshwater crabs, and some landlocked shrimps. Brood care beyond the hatching stage is typical of the aeglids, primary freshwater crabs, and crayfish, and occurs in some secondary freshwater crabs, but has only been documented for two species of freshwater shrimps.
2. The duration and intensity of posthatching broad care varies considerably among higher taxa and species. Special attachment structures that provide firm adherence of the young to the maternal pleopods have only evolved in crayfish, along with sophisticated behaviours of mother and progeny that maintain mother-offspring associations. Prolonged brood protection beyond carrying the young on the maternal pleopods has evolved in primary and secondary freshwater crabs living in phytotelmata, and in crayfish that live in burrows.
3. Direct development and posthatching brood care have evolved several times independently in the freshwater Decapoda and are therefore interpreted as

specific adaptations to the harsh conditions of the freshwater environment. These life history adaptations increase the fitness of the early life stages by making them independent from fluctuating food sources and by protecting them from predation. There is no evidence for the early evolution of direct development in the marine ancestors of freshwater decapods.

4. The abolishment of planktonic larval stages in direct developers is associated with a marked reduction in dispersal and gene flow, and has favoured endemism and speciation in the aeglids, primary freshwater crabs, crayfish, and landlocked shrimps. Since direct development also boosts genetic diversity among populations of the same species conservation measures for direct developers should not only protect species, they should also preserve valuable gene pools.
5. Freshwater decapods with direct development have a reduced ability to recolonize lost habitats and to replace lost populations when compared to indirect developers. Therefore, under conditions of rapid habitat destruction, environmental pollution, and global warming these constraints put the direct developers more at risk of extinction than the amphidromous taxa.

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Chapter 7
Freshwater Shrimps (Atyidae, Palaemonidae, Typhlocarididae) in the Broader Mediterranean Region: Distribution, Life Strategies, Threats, Conservation Challenges and Taxonomic Issues

Magdalini Christodoulou, Chryssa Anastasiadou, Jure Jugovic and Theodoros Tzomos

Abstract The turbulent and intricate geology of the Mediterranean region has been responsible for connections, redirections, and interruptions of freshwater systems that have been instrumental in the speciation and distribution of many organisms, including freshwater shrimps. There are 50 species and subspecies currently reported from the freshwater systems of the broader Mediterranean region that belong to 11 genera and three families. Three of these are exotic species that have been introduced to the region's ecosystems from elsewhere. The majority of species of Mediterranean freshwater shrimps belong to the Atyidae, followed by the Palaemonidae, and the Typhlocarididae, and most species have a very restricted distributional range. Among the three Mediterranean Peninsulas, the Balkan Peninsula fosters the highest biodiversity and is the species hotspot within the region. Subterranean (hypogean) and surface (epigean) habitats of the broader

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Mediterranean region are equally dwelled by shrimps. Currently 14 native species of freshwater shrimps are assessed by the IUCN Red List as threatened with extinction from increased freshwater ecosystem degradation which underlines the urgent need for conservation action.

Keywords Biodiversity · Epigean shrimps · Europe · Middle East · North Africa · Subterranean shrimps · Troglobite

7.1 Introduction

The location of the Mediterranean basin at the intersection between Europe, Asia, and Africa, the topographical diversity of the surrounding land, and the varied climate have all contributed to the development of a highly diverse mosaic of inland water habitats that today harbour a rich and highly endemic fauna (Tockner et al. 2009; Blondel et al. 2010; Tierno de Figueroa et al. 2013). Moreover, the Mediterranean region's history of turbulent geology has been responsible for connections, redirections, and interruptions of its freshwater ecosystems over the years which has been instrumental in the speciation and distribution of many of its freshwater organisms including the shrimps (Zakšek et al. 2007; Perea et al. 2010; Jesse et al. 2011; Jugovic et al. 2012; Christodoulou et al. 2012; García Muñoz et al. 2014; Tzomos and Koukouras 2015).

Despite the Mediterranean region being one of the most well known and most intensely studied parts of the world our knowledge of its inland water organisms is still incomplete and unevenly divided between groups (fish are better studied than shrimps) and between regions (the north is better known than the south). The continued description of new species within well-known groups is a strong indication that there is a great deal of undiscovered diversity across the full taxonomic spectrum (Tierno de Figueroa et al. 2013).

The freshwater habitats of the Mediterranean region host a rich shrimp fauna belonging to three (Atyidae, Palaemonidae, Typhlocarididae) out of the seven freshwater shrimp families. Of these, the Atyidae and Palaemonidae, with 43 and 14 freshwater genera (anchialine species included) respectively are the most speciose freshwater shrimp families (De Grave et al. 2008; De Grave and Fransen 2011). Atyid shrimps are characterized by chelipeds (claw-bearing pereiopods) tipped with setal brushes that are used for filtering suspended matter or sweeping up microbial films (Bauer 2004; De Grave et al. 2008). Palaemonid shrimps are characterised by the size of their second chelipeds that range from a little larger than the first cheliped to several times larger in some species (Bauer 2004; De Grave et al. 2008). Representatives of the Atyidae and Palaemonidae are found in epigean and hypogean habitats in tropical and temperate regions around the world, including the Mediterranean region (De Grave et al. 2008; von Rintelen et al. 2012). Typhlocaridid shrimps are found only in the Mediterranean region and all species are troglobitic, characterised by the absence of eyes and body pigmentation and the presence of a longitudinal post-antennal suture on the lateral surfaces of their carapace (Bauer 2004; De Grave et al. 2008; De Grave and Fransen 2011).

7.2 The Freshwater Systems of the Broader Mediterranean

Strictly speaking, the freshwater systems of the Mediterranean region include all the drainage systems flowing into the Mediterranean Sea, except the upstream portions of the Nile and Rhone Rivers that originate outside this biogeographical region (Blondel et al. 2010). The present work includes freshwater shrimps from epigean and hypogean lentic and lotic systems of the circum-Mediterranean countries as well as of their adjacent countries, comprising thus a large part of Europe, the Middle East, and North Africa. This broader Mediterranean region, as defined herein, includes three biodiversity hotspots (the Mediterranean Basin, the Irano-Anatolian region, and the Caucasus Mountains) that each have an exceptionally high number of endemic species. Of concern is that these three biodiversity hotspots have all lost at least 70 % of their natural habitats (Mittermeier et al. 2011). Nevertheless, a patchwork of different epigean and hypogean habitats dwelled by endemic species of freshwater shrimps can be found today in the broader Mediterranean region.

The Danube River (2862 km) is the longest river in the broader Mediterranean region (and 29th in the world), and drains an area of 80,093 km^2, passing through 10 countries (Tockner et al. 2009), while the Ombla River (0.30 km) in south-eastern Croatia is one of the shortest rivers in the region and drains an area of between 600 and 1000 km^2 (Roje-Bonnaci and Bonnaci 2013). Other freshwater habitats in the Mediterrenan region of special interest include ancient lakes (Lakes Ohrid, Prespa and Pamvotis) that existed long before the last glacial period (Wagner and Wilke 2011). The rivers existing today and their associated lakes appeared in the Middle Miocene, emerging first as coastal rivers from the surrounding mainland and as streams on the Paratethys islands. Since then, there have been only local exchanges between neighbouring basins (Tockner et al. 2009).

An important geological feature of the region that has a strong biogeographic influence is the karstic subterranean rivers systems found in the Balkans but also in other parts of the broader Mediterranean region such as the Caucasus, France, Spain, Italy, and Israel (Klimchouk 2004; Garay 2005; Jaume and Bréhier 2005; Sket 2012). In the Balkan Peninsula the Dinaric Karst stretches across six countries from northeast Italy to southern Slovenia, Croatia, Bosnia and Herzegovina to Montenegro and northwestern Albania, and to south and western Serbia (Sket 2012). The Balkan Karst region is part of the Adriatic microplate that rose above the sea level 30 million years ago as an island surrounded by the Paratethys Sea and a narrow strip of the Tethys Ocean.

Finally, a special type of cave systems, dwelled by shrimps, is the anchialine caves. These caves are found within few kilometres inland from the Mediterranean coast and typically posses a highly stratified water column, with surface freshwater or brackish water layers, separated by a thermo-chemocline from underlying marine waters low in dissolved oxygen (Sket 1996).

7.2.1 Overview of the Freshwater Shrimps of the Broader Mediterranean

The freshwater shrimp fauna of the broader Mediterranean region is highly endemic at both the genus and species levels and has a completely endemic family, the Typhlocarididae (Tsurnamal 2008; Sket and Zakšek 2009; Christodoulou et al. 2012; Jugovic et al. 2012; Tzomos and Koukouras 2015). The taxonomic diversity of this region comprises three families (Atyidae, Palaemonidae, Typhlocarididae), with 11 genera and 50 species and subspecies (Table 7.1). The largest of these is

Table 7.1 List of freshwater shrimp species and subspecies with remarks on general distribution, habitat and IUCN status

A/A	Species/subspecies	Native distribution	Habitat	IUCN status
	Atyidae			
1.	*Atyaephyra acheronensis* Christodoulou et al.	Balkans (Slovenia, Croatia, Albania (?), Greece)	E	LC
2.	*Atyaephyra desmarestii* Millet	Europe (native: Spain, Portugal, France, Italy; non-native: Belgium, The Netherlands, Germany, Czech Republic, Poland, Switzerland, Austria), NW Africa (Morocco, Algeria, Tunisia)	E	LC
3.	*Atyaephyra orientalis* Bouvier	Middle East (Turkey, Syria, Israel, Jordan, Iran, Iraq)	E	LC
4.	*Atyaephyra stankoi* Karaman	FYROM, Greece	E	LC
5.	*Atyaephyra strymonensis* Christodoulou et al.	E Greece (Strymonas and Nestos Rivers)	E	VU
6.	*Atyaephyra thyamisensis* Christodoulou et al.	W Greece (including Corfu and Lefkada Islands)	E	LC
7.	*Atyaephyra tuerkayi* Christodoulou et al.	Syria (Nahr Al-Kabir River)	E	DD
8.	*Caridina babaulti basrensis* Al-Adhub and Hamzah	Iraq, Iran	E	LC
9.	*Caridina fossarum* Heller	Iran	E	LC
10.	*Dugastella marocana* Bouvier	Morocco	E	EN

(continued)

Table 7.1 (continued)

A/A	Species/subspecies	Native distribution	Habitat	IUCN status
11.	*Dugastella valentina* Ferrer Galdiano	Spain	E	NT
12.	*Gallocaris inermis* (Fage)	S France (Gard and Hérault departments)	S	NT
13.	*Neocaridina davidi* (Bouvier)[b]	China	E	–
14.	*Puteonator iraqiensis* Gurney	Iraq (Samawa)	S	–
15.	*Typhlatya miravetensis* Sanz and Platvoet	Spain (Ullal de la Rambla de Miravet cave)	S	VU
16.	*Typhlatya arfeae* Jaume and Bréhier	France (Grotte des Fées de Leucate cave and spring Font Estramar)	S (A)	–
17.	*Troglocaris* (*Troglocaridella*) *hercegovinensis* (Babić)	SE merodinaric (Bosnia and Hercegovina, Montenegro, Croatia (?))	S	NT
18.	*Troglocaris* (*Troglocaris*) *anophthalmus anophthalmus* (Kollar)	SE Slovenia (NW Dolenjska, Suha Krajina)	S	NT
19.	*Troglocaris* (*Troglocaris*) *anophthalmus intermedia* Babić	NW Croatia (around Ogulin)	S	NT
20.	*Troglocaris* (*Troglocaris*) *anophthalmus legovici* Jugovic et al.	Croatia (Istria)	S	NT
21.	*Troglocaris* (*Troglocaris*) *anophthalmus ocellata* Jugovic et al.	SE Slovenia and NW Croatia	S	NT
22.	*Troglocaris* (*Troglocaris*) *anophthalmus periadriatica* Jugovic et al.	Croatia (including Adriatic islands: Brač, Ugljan), Bosnia and Hercegovina	S	NT
23.	*Troglocaris* (*Troglocaris*) *anophthalmus sontica* Jugovic et al. 2012	Slovenia, NE Italy (Friuli-Venezia, Giulia)	S	NT
24.	*Troglocaris* (*Troglocaris*) *planinensis* Birštein	NW merodinaric (Italy, Slovenia, Croatia)	S	NT
25.	*Troglocaris* (*Troglocaris*) *bosnica* Sket and Zakšek	NW Bosnia and Hercegovina (isolated karst in Bosanska Krajina)	S	VU
26.	*Troglocaris* (*Spelaeocaris*) *prasence* Sket and Zakšek	SE merodinaric (Bosnia and Hercegovina, Montenegro)	S	VU
27.	*Troglocaris* (*Spelaeocaris*) *pretneri* (Matjašič)	SE merodinaric [Bosnia and Hercegovina, Croatia (?)]	S	NT
28.	*Troglocaris* (*Spelaeocaris*) *neglecta* Sket and Zakšek	S Croatia (Dalmatia)	S	VU

(continued)

Table 7.1 (continued)

A/A	Species/subspecies	Native distribution	Habitat	IUCN status
29.	*Troglocaris* (*Spelaeocaris*) *kapelana* Sket and Zakšek	Croatia (Kapela Mountains)	S	VU
30.	*Troglocaris* (*Spelaeocaris*) sp. (cf. Sket and Zakšek)[a]	NW Bosnia and Hercegovina (isolated karst in Bosanska Krajina)	S	VU
31.	*Troglocaris* (*Xiphocaridinella*) *ablaskiri* Birštein	Caucasus (NW Georgia, Abkhaziya, Atap)	S	DD
32.	*Troglocaris* (*Xiphocaridinella*) *fagei* Birštein	Caucasus (NW Georgia, Abkhaziya, Psyrzthka)	S	DD
33.	*Troglocaris* (*Xiphocaridinella*) *jusbaschjani* Birštein	Caucasus (Russia, Sochi, Mazesta)	S	DD
34.	*Troglocaris* (*Xiphocaridinella*) *kutaissiana* (Sadowsky)	Caucasus, (West Georgia, Abkhaziya, Kutais)	S	DD
35.	*Troglocaris* (*Xiphocaridinella*) *osterloffi* Juzbašjan	Caucasus (NW Georgia, Abkhaziya, Suchumi Zebelda)	S	DD
	Palaemonidae			
36.	*Macrobrachium dayanum* (Henderson)[b]	India, Nepal	E	LC
37.	*Macrobrachium nipponense* (De Haan)[b]	China, Japan, Korea, Vietnam, Myanmar, Taiwan	E	LC
38.	*Palaemon antennarius* H. Milne Edwards	Italy (including Sicily and Sardinia), Balkan Peninsula (Slovenia, Croatia, Albania, Greece)	E	LC
39.	*Palaemon colossus* Tzomos and Koukouras	Greece (Rhodes Island, Epta Piges), Turkey (Antalya)	E	–
40.	*Palaemon mesogenitor* (Sollaud)	Algeria, Tunisia	E	DD
41.	*Palaemon mesopotamicus* (Pesta)	Syria, Turkey	E	CR
42.	*Palaemon migratorius* (Heller)	Egypt	E	–
43.	*Palaemon minos* Tzomos and Koukouras	Greece (Crete, Kourna Lake)	E	–
44.	*Palaemon turcorum* (Holthuis)	Turkey (Sakarya river)	E	DD
45.	*Palaemon varians* Leach (in Leach)	Europe (Norway, Sweden, Denmark, Germany, Ireland, UK, the Netherlands, Belgium France, Portugal, Spain), NW Africa (Morocco, Algeria, Tunisia)	E	–

(continued)

Table 7.1 (continued)

A/A	Species/subspecies	Native distribution	Habitat	IUCN status
46.	*Palaemon zariquieyi* (Sollaud)	Spain (Valencia)	E	–
	Typhlocarididae			
47.	*Typhlocaris ayyaloni* Tsurnamal	Israel (Ayyalon Cave)	S (A)	EN
48.	*Typhlocaris galilea* Calman	Israel (Ein-Nur octagonal pool)	H	EN
49.	*Typhlocaris lethaea* Parisi	Libya	H	DD
50.	*Typhlocaris salentina* Caroli	Italy	H	VU

DD Data deficient; *LC* Least concern; *NT* Near threatened; *VU* Vulnerable; *EN* Endangered; *CR* Critical endangered; *E* Epigean waters; *S* Subterranean; *A* Anchialine. Holodinaric, whole Dinaric Karst. SE merodinaric, and NW merodinaric, two vicarious centres (SE and NW) within the Dinaric Karst (Sket 1994). ? Genetic evidence missing

[a] Close relative to *T. (S.) kapelana* (a female from Suvaja pećina in Bosanska Krajina, NW Bosnia and Herzegovina; Sket and Zakšek 2009)

[b] Exotic species

the Atyidae (8 genera, 35 species and subspecies) with representatives in epigean and subterranean systems throughout the broader Mediterranean region (Table 7.1). The next largest family is the epigean Palaemonidae (2 genera, 11 species), followed by the strictly subterranean Typhlocarididae (1 genus, 4 species) (Gurney 1987; Gorgin 1996; Tsurnamal 2008; Sket and Zakšek 2009; Huguet et al. 2011; Jugovic et al. 2012; Christodoulou et al. 2012; Christodoulou 2014; García Muñoz et al. 2014; Tzomos 2014; Tzomos and Koukouras 2015).

The most speciose area within the broader Mediterranean region is the Balkan Peninsula with at least 16 species that belong to three different genera (Sket and Zakšek 2009; Christodoulou et al. 2012; Jugovic et al. 2012; Tzomos and Koukouras 2015; Table 7.1). The next most species rich area is the Middle East (5 genera, 10 species), followed by North Africa (4 genera, 6 species), the Iberian Peninsula (4 genera, 5 species), and the Caucasus (1 genus, 5 species) (Table 7.1).

There are 43 atyid genera worldwide, comprising 492 species and subspecies distributed in all of the world's biogeographic regions except Antarctica (De Grave and Fransen 2011; Richard et al. 2012; Castelin et al. 2013; De Grave and Page 2014). The Indo-Malayan region is the most species rich province (13 genera, 257 species) harbouring five times more atyid species than the Palaearctic region (9 genera, 43 species), of which nine genera and 34 species (excluding the exotic species), are found in the broader Mediterranean region (De Grave et al. 2008; Sket and Zakšek 2009; Christodoulou et al. 2012; Jugovic et al. 2012). The genera

Atyaephyra de Brito Capello, *Caridina* H. Milne Edwards, and *Dugastella* Bouvier are epigean, while *Gallocaris* Sket and Zakšek, *Puteonator* Gurney, *Typhlatya* Creaser, and *Troglocaris* Dormitzer are found only in hypogean waters (von Rintelen et al. 2012). The Palaearctic region harbours the highest stygobitic species diversity within the family Atyidae (23 species and subspecies), which is found exclusively in the areas immediately surrounding the Mediterranean Sea (De Grave et al. 2008; Sket and Zakšek 2009).

The first epigean species that was described in the broader Mediterranean region was *Atyaephyra desmarestii* Millet (Rafinesque 1814), which for many years was thought to be a monotypic genus (Anastasiadou et al. 2004). Since then the number of species of *Atyaephyra* has risen to at least seven (García Muñoz et al. 2009, 2014; Christodoulou et al. 2012; Christodoulou 2014). Other epigean species found in the region are two species of *Dugastella,* two species of *Caridina*, and the non-native species *Neocaridina davidi* (Bouvier) (Gorgin 1996; Huguet et al. 2011; Klotz et al. 2013).

The diverse subterranean shrimp fauna of the Mediterranean region is the result of karstification starting at the end of Pliocene that created hydrographic changes and numerous cave systems that splintered the distributional range of many taxa (Sket 2012). Over time, populations that evolved in isolated habitats such as the Dinaric Karst of the western Balkans produced a number of highly endemic hypogean species with narrow distributions (Trontelj et al. 2009; Zakšek et al. 2009). Despite its relatively small area the Dinaric Karst region has a remarkable subterranean diversity: ~900 troglobitic species (obligate terrestrial or aquatic cave dwelling), 330 of which are stygobitic (strictly subterranean aquatic dwelling). The Planina-Postojna cave system in southern Slovenia harbours the world's highest diversity of cave biota with 99 obligate cave dwelling species (Culver and Sket 2000; Sket 2012).

The first subterranean shrimp species known from the Mediterranean region was *Troglocaris anophthalmus* (Kollar), from a karst cave (Kompoljska jama) in southern Slovenia (Holthuis 1956). Since then eight more hypogean species of *Troglocaris* from the Dinaric karst in the western Balkans have been described, while the discovery of *Troglocaris kutaissiana* (Sadovskij) signalled the existence of cave shrimp species in the Caucasus (Sket and Zakšek 2009; Marin and Sokolova 2014). Later discoveries include four more subterranean species assigned to three genera, *Typhlatya* (2 species), *Puteonator* (1 species) and *Gallocaris* (1 species) (Gurney 1987; Sanz and Platvoet 1995; Jaume and Bréhier 2005; Sket and Zakšek 2009).

The majority of palaemonid species live in marine and brackish waters, in contrast to the Atyidae, an almost exclusively freshwater family (De Grave et al. 2008). Nevertheless, species of freshwater palaemonids are found worldwide in five major biogeographic regions (but are absent from Antarctica). The highest generic and species diversity of palaemonids is found in the Neotropical region (8 genera, 89 species) and in the Indo-Malayan region (6 genera, 157 species), while the Palaearctic region has only 2 genera and 14 species (De Grave et al. 2008; Tzomos and Koukouras 2015). The genus *Palaemon* comprises 87 species worldwide (De Grave and Ashelby 2013; Carvalho et al. 2014; Tzomos and Koukouras 2015), nine of which are found in surface water systems of the broader Mediterranean region (Tzomos and Koukouras 2015). Finally, two non-native *Macrobrachium* species have recently been added to the fauna of the region (Table 7.1).

Freshwater shrimps of the family Typhlocarididae are restricted to the Mediterranean part of the Palaearctic region and comprise a single genus, *Typhlocaris* Calman, with four species that are all stygobionts (Tsurnamal 2008; Table 7.1).

7.3 Distribution

The distributional ranges of the epigean and subterranean shrimps of the broader Mediterranean region (Figs. 7.1, 7.2, 7.3, 7.4 and 7.5, Table 7.1) are based on literature sources (Tsurnamal 2008; Sket and Zakšek 2009; Jugovic et al. 2012; Christodoulou et al. 2012; Christodoulou 2014; Tzomos 2014; Tzomos and Koukouras 2015; and other references herein) and on unpublished information.

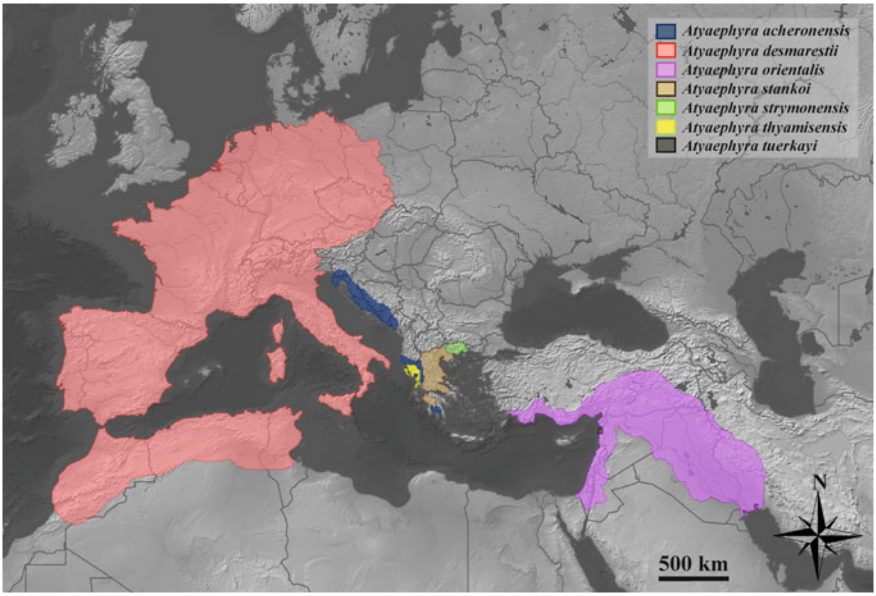

Fig. 7.1 Geographic distribution of epigean species of *Atyaephyra* (Atyidae)

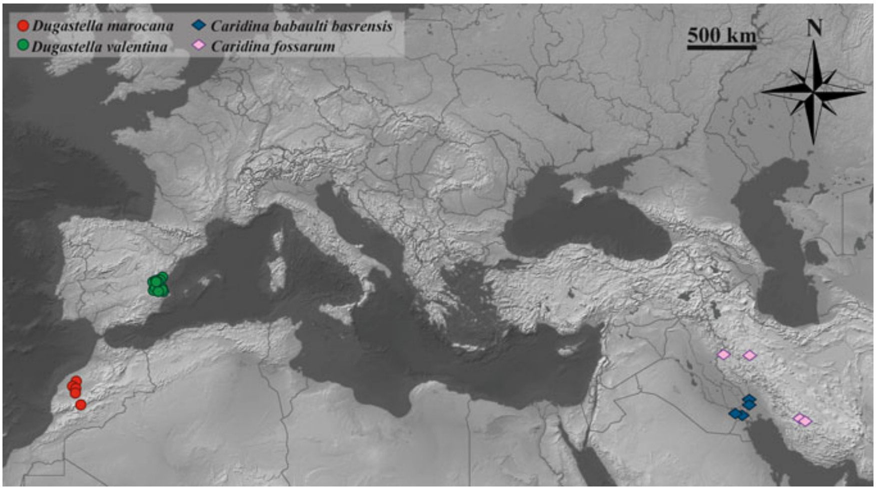

Fig. 7.2 Geographic distribution of epigean species of *Caridina* and *Dugastella* (Atyidae) in the broader Mediterranean region

7.3.1 Native Shrimp Species

The genus *Atyaephyra* is a widespread taxon whose range spans the Middle East, North Africa and a large part of Europe including some of the Mediterranean islands (Christodoulou et al. 2012; Christodoulou 2014; Fig. 7.1). *Atyaephyra desmarestii* is primarily a Mediterranean species that has a native distribution in southern Europe including the Atlantic drainages (Christodoulou et al. 2012; Christodoulou 2014; Fig. 7.1, Table 7.1). Its presence in northern Europe, until the Oder River in Poland (Grabowski et al. 2005) and central Europe until the Danube River in Austria (Moog et al. 1999), is most probably due to past anthropogenic transfers. The opening of the canals connecting the major rivers of Europe that began in the 17th century and resulted to the today's dense shipping channel network seems to be a possible pathway for the northerly dispersal of *A. desmarestii*. Today the channel network extends throughout Europe and joins the southern seas (Azov, Black and Mediterranean Seas), the northern European seas (Baltic and White Seas) and the Atlantic Ocean (Galil et al. 2007; Panov et al. 2009). It is likely that *A. desmarestii* spread from France to north and central Europe through this network (Christodoulou et al. 2012; Christodoulou 2014). Four out of the seven species of *Atyaephyra* (*A. acheronensis* Christodoulou et al., *A. thyamisensis* Christodoulou et al., *A. stankoi* Karaman, and *A. strymonensis* Christodoulou et al.) are found in the Balkan Peninsula (Fig. 7.1, Table 7.1). Two of these (*A. thyamisensis* and *A. strymonensis*) are endemic to Greece, the third (*A. stankoi*) is found in Greece as well as in the adjacent Former Yugoslav Republic of Macedonia, and *A. acheronensis* is distributed throughout the Balkan region (Christodoulou et al. 2012; Christodoulou 2014; Fig. 7.1, Table 7.1). *Atyaephyra acheronensis* and *A.*

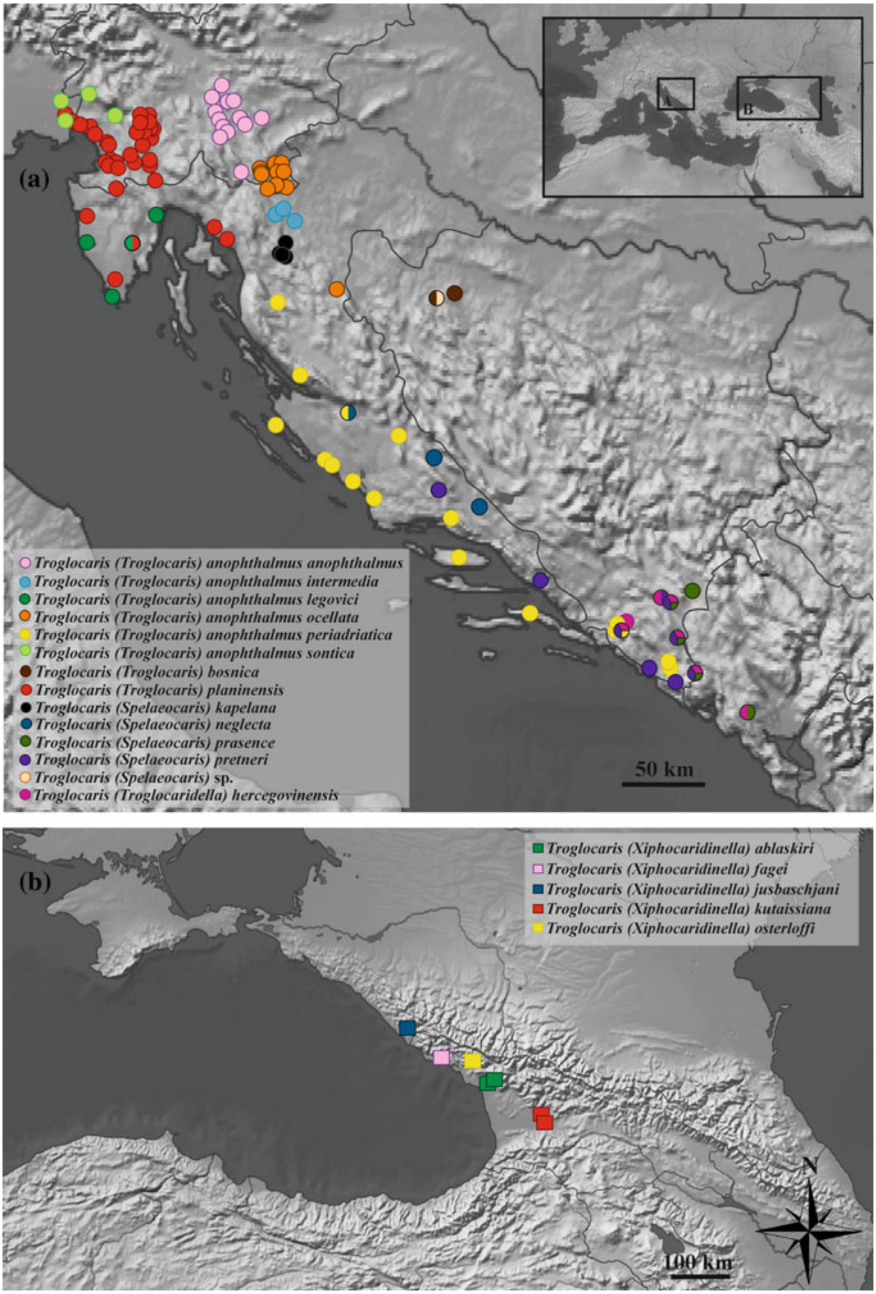

Fig. 7.3 Geographic distribution of subterranean species of *Troglocaris* (Atyidae) in **a**, the Balkan Peninsula (Dinaric Karst), and **b**, the Caucasus

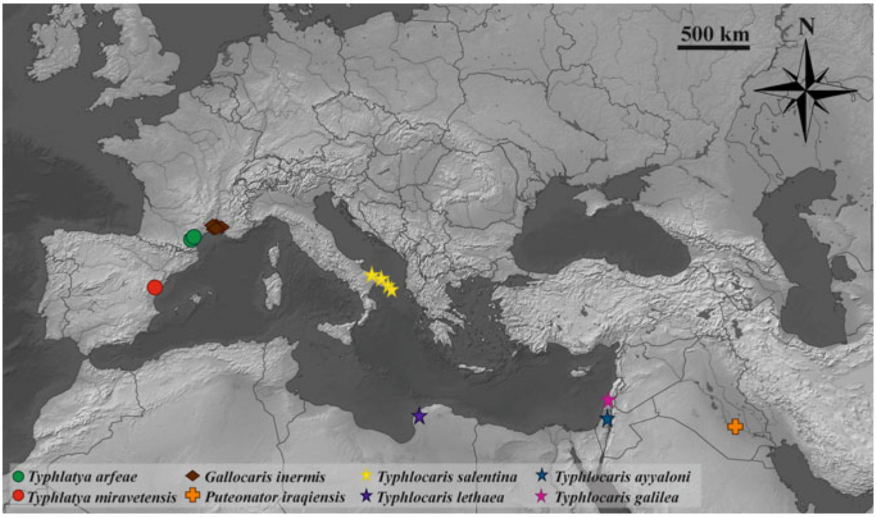

Fig. 7.4 Geographic distribution of subterranean species of the genera *Gallocaris*, *Puteonator*, *Typhlatya* (Atyidae) and *Typhlocaris* (Typhlocarididae) in the broader Mediterranean region

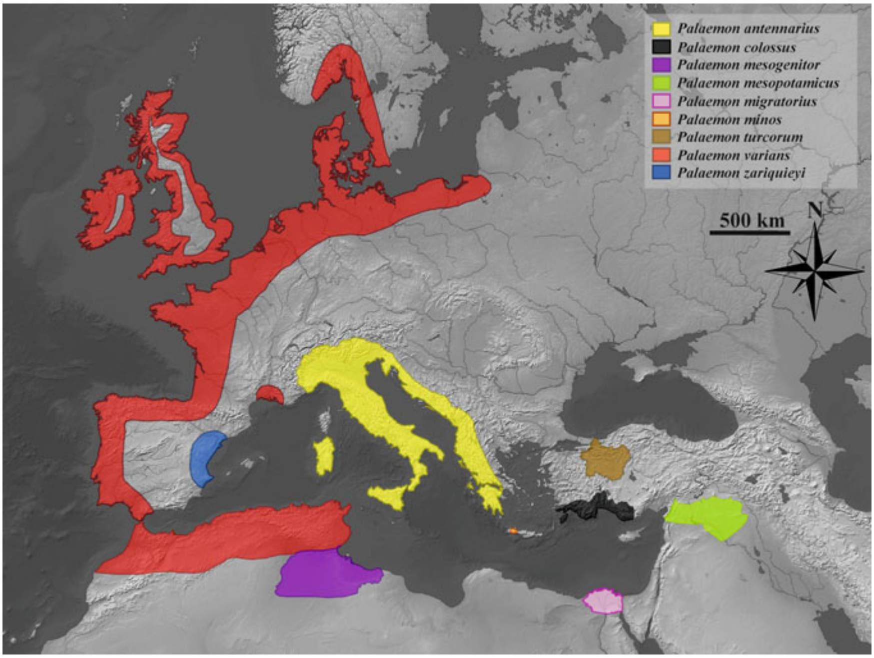

Fig. 7.5 Geographic distribution of epigean species of the genus *Palaemon* (Palaemonidae) in the broader Mediterranean region

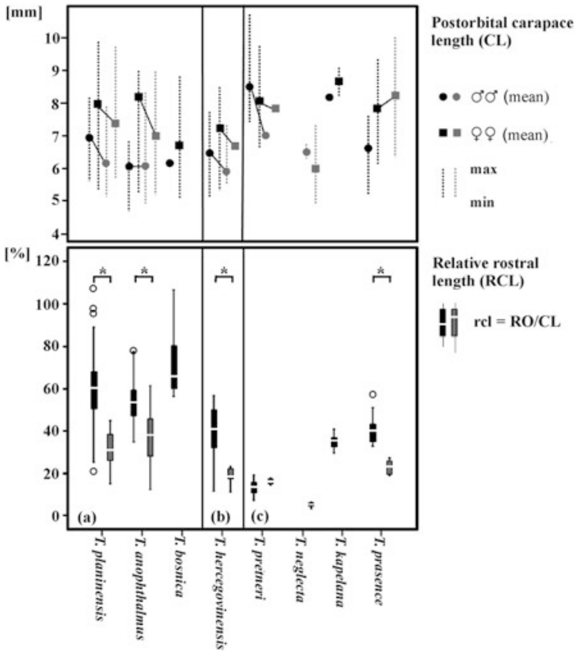

Fig. 7.6 Variation in A, the relative postorbital carapace length (*CL*), and B, the relative rostral length (*rcl*) in three Dinaric subgenera of cave shrimp: **a** *Troglocaris* (*Troglocaris*), **b** *Troglocaris* (*Troglocaridella)*, and **c** *Troglocaris* (*Spelaeocaris*) in relation to the presence of the predatory amphibian *Proteus anguinus*. All specimens were adult males except for *T. bosnica,* which was a juvenile. *Black Proteus* present; *grey Proteus* absent. Statistically significant differences in the relative rostral length at $p < 0.001$ (T-test) are denoted with an *asterisk*

thyamisensis co-occur at the mouths of the Louros and Thyamis Rivers in western Greece, but only *A. thyamisensis* is found further inland (Christodoulou et al. 2012; Christodoulou 2014). The syntopic occurrence of these shrimp species at river mouths may be the result of the accidental transport of *A. acheronensis* together with glass eels (*Anguilla anguilla* (Linnaeus) from the nearby Acherontas River by local fishermen for restocking purposes (Economidis et al. 2000; Anastasiadou, unpublished data). In Sardinia, the introduction of shrimps (*Palaemon antennarius* H. Milne Edwards) was probably a by-product of fish restocking efforts and aquaculture projects (Froglia 2006). However the natural coexistence in syntopy of *A. acheronensis* and *A. thyamisensis* cannot be ruled out. *Atyaephyra acheronensis* (as *A. desmarestii*, see García Muñoz et al. 2014) has also been found near the mouth of the Acheloos River that lies within the distributional range of *A. stankoi*, and this may be the result of either natural sympatry or translocation.

Two allopatric species, *A. orientalis* Bouvier and *A. tuerkayi* Christodoulou et al., are found in the Middle East (Fig. 7.1, Table 7.1) but the apparent absence of shrimp in the biggest part of Turkey as well as in the northeast Greece (Evros River) where there is an abundance of suitable shrimp habitats (perennial lotic and lentic systems) may be an artifact of undersampling (Bouvier 1913; Holthuis 1961; Kinzelbach and Koster 1985; Al-Adhub 1987; Gorgin 1996; Christodoulou et al. 2012; Christodoulou 2014; Özcan et al. 2013; García Muñoz et al. 2014; Fig. 7.1).

Two species of *Caridina* (the most speciose atyid genus with 302 species worldwide) are found in the eastern Mediterranean Basin (Fig. 7.2, Table 7.1). These species are *C. babaulti basrensis* Al-Adhub and Hamzah from Iraq and Iran and *C. fossarum* Heller from hypogean and epigean habitats in Iran (Al-Adhub and Hamzah 1987; Gorgin 1996; Zare et al. 2011). *Caridina babaulti basrensis* occurs in sympatry with *A. orientalis* (Gorgin 1996), while a third species (*C. syriaca*) from Syria is treated as a junior synonym of *C. fossarum* (De Grave and Fransen 2011).

The epigean genus *Dugastella* is found in the western Mediterranean (Fig. 7.2, Table 7.1). The kangaroo shrimp, *D. valentina* Ferrer Galdiano is restricted to the area around the gulf of Valencia (Spain) where it inhabits springs, canals, lowland rivers, estuaries, and freshwater lagoons, while *D. marocanna* Bouvier occurs in rivers in Morocco (Sanz and Gónez 1984; Huguet et al. 2011). Both species are found in sympatry with *A. desmarestii*, and *D. valentina* is found together also with the palaemonid species *Palaemon zariquieyi* (Sollaud) (Sanz and Gónez 1984; Huguet et al. 2011).

The majority of the atyid subterranean taxa are distributed in the Dinaric Karst in the Balkan Peninsula (Fig. 7.3a), while some are found in karst systems in the Caucasus, France, and Spain (Sket and Zakšek 2009; Marin and Sokolova 2014; Figs. 7.3b and 7.4). The distribution of these subterranean shrimps corresponds to mid-latitude regions where the highest diversity of terrestrial cave dwelling animals occur (Culver et al. 2006). The genus *Troglocaris* has four subgenera three of which, *T.* (*Troglocaris*), *T.* (*Spelaeocaris*), and *T.* (*Troglocaridella*), inhabit underground streams and rivers in caves in the Dinaric karst region mainly along the Adriatic coast but also further inland (Sket and Zakšek 2009; Moritsch et al. 2014; Fig. 7.3a, Table 7.1). The fourth subgenus, *T.* (*Xiphocaridinella*), is found in karst habitats in the Caucasus (Georgia and Sochi, Russia) and comprises five species (Marin and Sokolova 2014; Fig. 7.3b, Table 7.1). Nine species of *Troglocaris* (one species has been separated into 6 subspecies) occur in caves between Italy and Montenegro and most have an allopatric distribution, while a few are found in sympatry. Two up to three taxa can be found dwelling the same cave (e.g., Vjetrenica cave in southeast Bosnia and Herzegovina, with the majority of co-occurring species to belong to different subgenera; Fig. 8.3a, Tables 7.1 and 7.2).

The genus *Typhlatya* contains at least 17 species and exhibits a broad but disjunct transoceanic distribution throughout the tropical and temperate latitudes (Botello et al. 2012). Only two species of *Typhlatya* occur in the Mediterranean region (Fig. 7.4, Table 7.1). Most species of *Typhlatya* inhabit anchialine caves, but *T. miravetensis* Sanz and Platvoet is restricted to a freshwater cave system and two wells in eastern Spain (Botello et al. 2012). The second Mediterranean species of this genus, *T. arfeae* Jaume and Bréhier, is found in an anchialine cave and in a well in southwest France (Jaume and Bréhier 2005). The monotypic cave dwelling

Table 7.2 Differentiation of pleopods I–II and pereiopods (III–V) in adult males of atyid shrimp from the broader Mediterranean region [based on Sket and Zakšek (2009)]

Taxon	Shape of pleopods		Pereiopods
	I	II	
Atyaephyra	9-shaped	AM narrow and cylindrical, with long or medium spiniform setae, AM longer than AI	III–IV (slightly)
Caridina	0-shaped 9-shaped	AM narrow and cylindrical, with long spiniform setae, AM longer than AI	III–IV (slightly)
Dugastella	9-shaped		–
**Gallocaris inermis*	9-shaped	AM narrow and cylindrical, with long spiniform setae, AM shorter than AI	undiffer
**Puteonator iraqiensis*	9-shaped	AM narrow and cylindrical, with long spiniform setae, AM shorter than AI	III–IV (strongly)
**Troglocaris* (*Troglocaris*)	0-shaped	AM flattened, shield-like, with short spiniform setae, AM longer than AI	III–IV (strongly)
**Troglocaris* (*Spelaeocaris*)	9-shaped	AM narrow and cylindrical, with short spiniform setae, AM longer than AI	
**T. kapelana*			
**T. prasence*			
**T. pretneri*			III–V (strongly)
**T. neglecta*			
**Troglocaris* (*Troglocaridella*)			
**Troglocaris* (*Xiphocaridinella*)			
**Typhlatya*	9-shaped	AM vestigial, shorter than AI	undiffer

AM Appendix Masculina; *AI* Appendix Interna
*Hypogean taxa

genus *Gallocaris* is known only from five caves in a karst region of southern France (Sket and Zakšek 2009; Fig. 7.4, Table 7.1). Finally, *Puteonator iraqiensis* Gurney is only known from the type locality in the Samawa region of Iraq in an anchialine well at a depth of 160 m (Gurney 1987; Fig. 7.4, Table 7.1).

The genus *Palaemon* has a worldwide distribution (De Grave and Ashelby 2013) and nine species are known from the fresh and brackish waters within the area covered here (De Grave and Ashelby 2013; Tzomos and Koukouras 2015; Fig. 8.5, Table 8.1). The ditch shrimp *P. varians* Leach is the most widespread palaemonid species and is found in brackish and freshwater systems throughout most of the region (Gelin and Souty-Grosset 2006; Tzomos and Koukouras 2015; Fig. 8.5, Table 8.1). The species *P. zariquieyi* is endemic to Spain in fresh and brackish waters around Valencia (Zariquiey Alvarez 1968). In North Africa, *P. mesogenitor* (Sollaud) is found in Tunisia and Algeria (Azzouna 1994), while *P. migratorius* (Heller) occurs in Egypt, however the exact type locality and distribution of the species are unknown (Tzomos and Koukouras 2015). Greece hosts three species of

Palaemon (*P. antennarius*, *P. colossus* Tzomos and Koukouras, *P. minos* Tzomos and Koukouras), one of which (*P. minos*) is endemic to just a lake (Lake Kourna) in Crete (Tzomos and Koukouras 2015; Fig. 8.5, Table 8.1). In the Middle East, three species of *Palaemon* are found in Syria and Turkey: *P. colossus*, *P. mesopotamicus* Pesta and *P. turcorum* Holthuis (Pesta 1913; Özcan et al. 2013; Holthuis 1961; Tzomos and Koukouras, 2015). *Palaemon* and *Atyaephyra* co-occur, especially close to river mouths (Anastasiadou 2002). The following species groupings are found in sympatry: (1) *A. desmarestii* and *P. varians*; (2) *A. thyamisensis*, *A. acheronensis*, and *A. stankoi* with *P. antennarius*; and (3) *A. orientalis* and *P. mesopotamicus* (Holthuis 1961; Anastasiadou 2002; Bataller and Porras 2007; Özcan et al. 2013).

The family Typhlocarididae includes four stygobiotic species endemic to the broader Mediterranean region (Froglia and Ungaro 2001; Tsurnamal 2008; Fig. 8.4, Table 8.1). In Israel, there are two species of *Typhlocaris*: *T. galilea* Calman from a single chamber of a Roman cistern (the Ein-Nur octagonal pool), which collects water from surrounding springs on the shores of Lake Kinneret, near Tabgha (Calman 1909; Tsurnamal 1978), and *T. ayyaloni* Tsurnamal from Ayyalon karst cave near Ramla (Tsurnamal 2008). In Libya, *T. lethaea* Parisi is also known only from a cave near Bengazi (Parisi 1921), while in Italy *T. salentina* Caroli is found only in three caves (Zinzulusa, Grotte di Diavoli, L' Abyssi) in the Salento karst system, and in three wells near Brindisi and Bari (Froglia and Ungaro 2001).

7.3.2 Non-native Shrimp Species

The atyid shrimp *A. desmarestii* is native to southern Europe and North Africa (Mediterranean origin) but has actively spread throughout central and northern Europe using the canal network (western corridor) that connect the European river basins (Van der Velde et al. 2000; Galil et al. 2007). Numerous old navigable canals in France, Belgium, the Netherlands and Luxemburg, nowadays of little commercial importance, connect major river basins and may have served as early dispersal routes for species from the Mediterranean such as *A. desmarestii* (Galil et al. 2007). Additionally, *A. desmarestii* is a relatively eurythermal and euryhaline species, able to cover long distances, showing great versatility and ability to colonize new habitats (van den Brink and Van der Velde 1986; Fidalgo and Gerhardt 2003). Nevertheless, the population densities do not reach sizes that could affect native species and thus so far, *A. desmarestii* impact on the native fauna is considered neutral (van den Brink and Van der Velde 1986; Wittenberg 2005; Gollasch and Nehring 2006; Straka and Špaček 2009).

In Germany, two exotic species of Asian atyid freshwater shrimps, *Neocaridina davidi* (Bouvier) and *Macrobrachium dayanum* (Henderson), have been reported from two localities (Gillbach stream and the Erft River, a tributary of the Rhine River). Both of these water bodies suffer from warm water thermal pollution from mining operations and power plants that may have allowed these two non-native warm water species to become established after release by aquarium hobbyists (Klotz et al. 2013). *Neocaridina davidi* is a popular aquarium species that is native to China and can tolerate cool water temperatures (Englund and Cai 1999; Liang 2004; Klotz et al. 2013), while *M. dayanum* is native to India, Nepal, and Myanmar (Jayachandran 2001; Cai and Ng 2002) and requires subtropical water temperatures throughout the year (Klotz et al. 2013). Hence the dispersal of *N. davidi* to cooler parts of the Rhine basin is possible but in contrary for *M. dayanum* is unlikely.

Macrobrachium nipponense is a commercially important palaemonid species both for fishing and aquaculture (New 2005) and is native to China, Japan, Korea, Vietnam, Myanmar, and Taiwan (De Grave and Ghane 2006). The growing use of *M. nipponense* in aquaculture (New 2005) has resulted in its introduction to Iran and Iraq either from aquaculture escapes or unintentional transfers (De Grave and Ghane 2006; Salman et al. 2006). *Macrobrachium nipponense* is a competent coloniser of new areas because it is tolerant to changes in salinity and temperature and because its egg size and larval characters show significant intra-population and inter-individual variation that aid in adaptation to new conditions (Mashiko and Numachi 2000; Alekhnovich and Kulesh 2001; Salman et al. 2006).

7.4 Life Cycles and Adaptations

The life history strategy of a species describes the anatomical, physiological, and behavioral adaptations that control investment in reproduction and self-maintenance in response to environmental conditions. The Mediterranean epigean and subterranean shrimps have developed a large diversity of life history strategies despite their similarities in morphology, diet, and habitat utilization (Sket and Zakšek 2009; Christodoulou et al. 2012). For example, larval development ranges from the production of high numbers of small eggs with several different planktonic larval stages (extended development), to direct development where no free-swimming larvae exist and hatching from the egg results in an adult-like benthic juvenile stage (Hayashi and Hamano 1984; Anger 2001).

7.4.1 Life in the Light

All members of the genus *Atyaephyra* are phytophylous and prefer sheltered, well-oxygenated waters with soft substrata and submerged plants (e.g., *Mentha aquatica* L., *Ranunculus trichophyllus* Chaix, *Persicaria amphibia* (L.) Delarbre), or stands of emergent macrophytes (e.g., *Cyperus papyrus* L., *Phragmites australis* (Cav.) Steud, *Typha angustifolia* L.) (Gottstein Matočec and Kerovec 2002; Fidalgo and Gerhardt 2003; Anastasiadou et al. 2014; Christodoulou 2014). Similarly, species of *Caridina* are common in lentic vegetated habitats with dense reed beds where abundant food is available and the shelter helps them to avoid predators (Al-Adhub and Hamzah 1987; Zare et al. 2011).

The life history strategies of most shrimps inhabiting lotic and lentic surface waters of the region are poorly known, and only a few have been studied in detail. The majority of atyid species has either many larval stages (extended development) or a few larval stages (abbreviated development), while a few species lack all larval stages (direct development) (Hayashi and Hamano 1984; Rodríguez and Cuesta 2011). The Atyidae can be divided into three groups based on life history strategy and habitat requirements: (1) those with a small number of large eggs and either abbreviated larval development or direct development, that are found mainly in the headwaters of rivers; (2) those with an intermediate number of medium-sized eggs and abbreviated larval development that are found in a wide range of freshwater habitats; and (3) those with a large number of small eggs and extended larval development, often requiring saltwater, that are found in lowland freshwater habitats (Hayashi and Hamano 1984; Hancock et al. 1998; Anger 2001; Page and Hughes 2007).

The species of epigean atyid shrimps found in the broader Mediterranean region exhibit either abbreviated or extended larval development. *Atyaephyra desmarestii*, *A. thyamisensis*, *A. orientalis* have extended development with six zoeal stages and one decapodid stage that takes between 22 and 75 days to develop from newly hatched larval stage to the juvenile stage depending on species (Gauthier 1924; Salman 1987a; Anastasiadou et al. 2011). The first three zoeal stages do not feed and break down their internal reserves for nutrition (lecithotrophic), while the fourth larval stage feeds on plankton (planktotrophic) (Anastasiadou et al. 2011). The eastern species *A. orientalis* completes its larval development faster than the two western species (*A. desmarestii* and *A. thyamisensis*), which may reflect the adaptation of *A. orientalis* to differences in regional temperatures (Gauthier 1924; Salman 1987a; Anastasiadou et al. 2011). The larval development of *C. babaulti basrensis* has five zoeal stages and a decapodid that lasts between 15 and 19 days and its development is more abbreviated in comparison to *Atyaphyra* species (although its development is still considered to be extended), while the atyid *Dugastella* has abbreviated development (Salman 1987b; Rodríguez and Cuesta 2011; Huguet et al. 2011). The kangaroo shrimp, *D. valentina*, has just two zoeal stages and a decapodid stage, all of which are lecithotrophic (Rodríguez and Cuesta 2011). Both species of *Dugastella* exhibit, a unique for atyids, extended parental care where females carry their offsprings in their brood chamber long after the larvae have hatched (Rodríguez and Cuesta 2011; Huguet et al. 2011).

Egg size is an important life-history trait that is linked to the duration of embryonic and larval development, the number and type of larval stages, and to juvenile size (Anger et al. 2002). Egg size is highly heritable within atyids and is a key taxonomic character for species identification, whereas egg number may be more environmentally dependent and more variable (Hancock et al. 1998). In the Middle East species of *A. orientalis* carry a small number (32–158) of larger eggs compared to other species in this genus (*A. desmarestii*, with 133–848 small eggs) (Bouvier 1913; Christodoulou 2014), while species of *Caridina* and *Dugastella* carry small numbers of large eggs, 3–75 and 16–42 respectively (Zare et al. 2011; Rodríguez and Cuesta 2011; Huguet et al. 2011).

The sex ratio in *Atyaephyra* tends towards more females than males in the population (Anastasiadou and Leonardos 2008). The reproductive period lasts from six to nine months, from February to late October, although ovigerous individuals can be found throughout the year (Gottstein Matočec and Kerovec 2002; Dhaouadi-Hassen and Boumaïza 2009; Anastasiadou et al. 2014). Reproduction in *Atyaephyra* is seasonal, but reproductive periods vary according to region (Dhaouadi-Hassen and Boumaïza 2009). Similarly, the sex ratio of *Caridina* tends towards more females than males in the population and the reproductive period of *C. fossarum* lasts for five months and is more abbreviated in comparison with other representatives of this family (Zare et al. 2011).

The three types of larval development are also seen in the Palaemonidae (Sollaud 1923; Guerao 1993). Many freshwater species of *Palaemon* have abbreviated larval development with a reduced number of larval stages (Anger 2001). *Palaemon zariquieyi* has three zoeal stages and its decapodid stage takes between 6.6 and 8.5 days to reach the juvenile stage (Guerao 1993). *Palaemon antennarius* has abbreviated development with three lecithotrophic zoeal stages and two planctotrophic decapodids and takes between 11 and 13 days to reach the juvenile stage (Falciai and Palmerini 2001). *Palaemon mesopotamicus* and *P. mesogenitor* also have abbreviated larval development (Sollaud 1919), while *P. varians* has a more extended development with five zoeal stages (Fincham 1979). The abbreviated larval development in some freshwater species makes it less likely that their poorly-swimming benthic larvae will be carried away to unfavorable habitats or be exposed to predators (Froglia 1978).

The sex ratio in species of *Palaemon* tends towards more females than males in the population (Sanz Brau 1986; Gottstein Matočec et al. 2006; Anastasiadou et al. 2009), although male biased populations have been reported (Gelin and Souty-Grosset 2006). Generally, female palaemonids produce small numbers of large eggs and have a reproductive period from April to October (Gelin and Souty-Grosset 2006; Gottstein Matočec et al. 2006), although ovigerous females of *P. zariquieyi* are found throughout the year (Sanz Brau 1986). The reproductive period of the lake-living populations of the species *P. antennarius* starts 2 months earlier than in the river-living populations of the same species due to the faster rise of water temperatures in the lakes the spring, and the slower fall in water temperatures in the autumn (Gottstein Matočec et al. 2006; Anastasiadou et al. 2014).

Although information exists on only a limited number of epigean Mediterranean species it is likely that most of them have a life span of one year although some individuals survive for a second winter (Sanz Brau 1986; Gottstein Matočec et al. 2006; Dhaouadi-Hassen and Boumaïza 2009). *Palaemon varians* has been reported to have a life span between 1 and 2 years (Gelin and Souty-Grosset 2006).

7.4.2 Life in the Dark

Shrimps of the genus *Troglocaris* inhabit different hypogean habitats including sinking rivers and cave streams (but not pools of percolated water), and one species from the Caucasus (*T. jusbashjani*) inhabits hydrogen sulphide baths (Marin and Sokolova 2014). Some species of troglobitic shrimps aggregate in groups in the calmer parts of underground streams and rivers (Marin and Sokolova 2014; Jugovic et al. 2015). *Gallocaris inermis* lives in sinking rivers and pools that remain after periodic floods (Fage 1937). Subterranean shrimps feed by sweeping up small clay particles with the tufts on their chelae and passing them to their mouthparts. Most probably they digest bacteria, protozoans, other small biota and organic detritus from clay particles that can be observed when their digestive tract is full (Leitheuser and Holsinger 1984; Hobbs 1998). Marin and Sokolova (2014) suggested that *T. jusbaschjani* also feed on sulphide bacteria that grow on their appendages. *Typhlocaris* feeds by probing the substrate with its maxillipeds and first pereiopods and passing organisms or organic debris to their mouth with their first pereiopods (Tsurnamal 1978).

Obligate cave dwelling animals typically adapt to life in permanently dark subterranean habitats with scarce organic resources with a reduction or loss of their eyes and body pigments, and by modifications of their feeding strategies. Troglobitic species typically have well-developed extraoptical sensory organs and they are sciaphilic and higrophilic, while their energy demands are low. Changes in morphology typical of cave dwelling taxa (troglomorphies) are challenging to explain, and the adaptative nature of special features that are common to all cave dwelling animals is still an ongoing debate (Culver and Pipan 2010). The most obvious changes are elongation of appendages (e.g., antennae, pereiopods) and the development of additional extraoptical sensory organs that aid orientation and more effective movements in the dark (Sket 1985). The extracellular lipid reserves (oleospheres) in the hepatopancreas of cave shrimps enable them to withstand up to two years of starvation (compared to the surface-living *A. desmarestii* that can only last for four weeks without feeding) (Vogt and Štrus 1999; Jugovic et al. 2015). For example, cave peracarids such as *Niphargus rheorhodanensis* Schellenberg, *N. virei* (Chevreux) and *Stenasellus virei* Dollfus all have pigment loss, elongated limbs, well-developed extraoptical sensory organs, altered lipids, and low metabolic demands in comparison to the epigean species *Gammarus fossarum* Koch and *Asellus aquaticus* (Linnaeus) (Hervant et al. 1998).

Only some aspects of the life history of species of *Troglocaris* shrimps have been studied, and there is an almost total absence of information on the other atyid subterranean genera. Matjašič (1958) studied the abbreviated larval development of *Troglocaris* (only five stages). The first three larval stages do not feed at all (Juberthie-Jupeau 1972), fourth stage larvae feed on clay, while the vitellum disappears and until the end of the next stage the digestive tract differentiates. Females of species of *Troglocaris* produce a small number of relatively large eggs, such as *T. anophthalmus sontica* from northwestern Dinarides that produces only 10 eggs, while *T. planinensis* produces between 20 and 45 eggs (Juberthie-Jupeau 1974; Jugovic et al. 2015).

The sex ratio of cave dwelling species of *Troglocaris* tends towards more females than males (Jugovic et al. 2010a, 2015). The darkness of cave habitats results in a significant regression of reproductive patterns in troglobionts, but despite this egg production in *T. planinensis* seems to exhibit temporal reproductive patterns that reach a maximum in the autumn months (Juberthie-Jupeau 1974, 1975; Langecker 2000; Jugovic et al. 2015). Not much is known about the biology of the cave-living shrimps *Troglocaris* (*Xiphocaridinella*) from subterranean habitats in the Caucasus.

Regarding the life strategies of Typhlocarididae very limited information has been given (Tsurnamal 1978). *Typhlocaris galilea* (Typhlocarididae) lives beyond four years and reproduces annually. Females of *T. galilea* carry a small number of large eggs (35–42) and its juveniles hatch directly into the decapodid (post larval) stage, while the zoeal stages are lacking (Tsurnamal 1978).

7.5 Threats

Threats to freshwater habitats in the broader Mediterranean region generally, and to freshwater shrimps in particular are mostly anthropogenic in origin, including climate change (Dudgeon et al. 2006; Strayer and Dudgeon 2010; De Grave et al. 2015; Fig. 7.7). Demographic and demotechnic increase result in human activities such as intense agricultural inputs and practices, increased human settlements, increased industrial production, and widespread pollution that have changed land use and impacted landscapes and surface water bodies. The overexploitation of freshwater fishes and crustaceans is associated with sharp population declines or even extinctions. Moreover irrigation, nutrient and toxic pollution have contributed to habitat and species loss. Dam construction is one of the worst anthropogenic effects on freshwater bodies, because dams insert barriers that fragment habitats and this impacts migratory species (Blondel et al. 2010; Roje-Bonnaci and Bonnaci 2013). Habitat fragmentation via dams and human terracing construction in rivers' basins could be a severe threat for larvae and juveniles' up- and down-stream colonisations of amphidromous freshwater shrimps (whose larvae must develop in salt water) that perform long distance migrations (Bauer 2011). In the broader Mediterranean freshwater shrimps' movements along the river's length, in search of more suitable habitats or food could be likewise inhibited by the presence of dams (Anastasiadou 2010).

Climate change is also a major threat to freshwater biodiversity (Dudgeon et al. 2006; Strayer and Dudgeon 2010). Small increases in the mean surface temperature of the planet have already resulted in glacier melting and changes in precipitation patterns. This has affected freshwater bodies and their faunas by causing changes in water flow, water quantity, and water levels. Alterations to the flow in freshwater ecosystems have strong impacts on habitat loss, aquatic vegetation, substratum

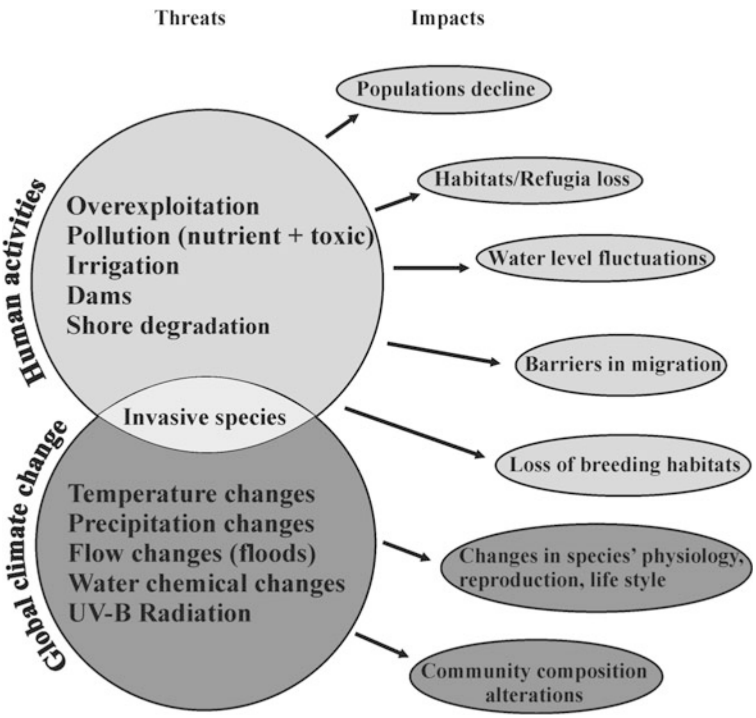

Fig. 7.7 Threats from increased human activities including global climate change on freshwater ecosystems and the observed or predicted impact on freshwater shrimps

conditions, and water chemistry, all of which affect the physiology, reproductive strategies, and life cycles of freshwater organisms (Brönmark and Hansson 1998). For example, species of *Palaemon* living near submerged aquatic vegetation and are sensitive to pH fluctuations migrate to deeper waters to feed when the pH of the water near the surface changes (Dalla Via 1986; Anastasiadou et al. 2014).

Serious threats to freshwater shrimp include highly adaptable and quickly dispersing invasive species that out-compete native species. Invasive non-native species disperse into new habitats either because of climate change or human activities (Fig. 7.7), and alter the structure of the habitat, compete for food resources, or predate the native fauna. The red swamp crayfish, *Procambarus clarkii* Girard, is native to the USA and is an alien species in European freshwaters including caves in Portugal and Italy (Mazza et al. 2014). Throughout its range, *P. clarkii* out-competes native species of crayfish (Gherardi 2006), native species of stygobitic shrimp (*T. salentina*) (Mazza et al. 2014) and threatens native species of subterranean asellid isopods and amphipods (Mazza et al. 2014). Besides non-native crayfish, invasive species of fish such as *Gambusia holbrooki* Girard found in the same habitats as native freshwater shrimps *A. thyamisensis* and *P. antennarius* competes with the shrimps for food and refuges (Gkenas et al. 2012).

In Germany the introduction of *M. dayanum* has had only a local impact because this species requires warm water to complete its life cycle. On the other hand, the introduction of the Asian shrimp species *N. davidi* might lead to a successful invasion into cool European waters since it can tolerate low water temperatures (Klotz et al. 2013). However, there is no evidence that either of these exotic species are having a negative impact on the native fauna in Germany, but in other parts of the world *N. davidi* out-competes native species for food and space, and it may be a carrier of non-native symbiotic organisms (Englund and Cai 1999; Niwa and Ohtaka 2006). Finally, in Iran the robust non-native palaemonid shrimp *M. nipponense* co-occurs with the native atyids *C. fossarum*, *C. babaulti basrensis*, and *A. orientalis* which could lead to the replacement of the native species as reported from other regions (Chong et al. 1987). It should be noted that although some species (e.g., *M. dayanum*) seem to have no impact on the native Mediterranean fauna their presence nevertheless alters the diversity, and may have long-term consequences that take years to become apparent (Wittenberg 2005; Gollasch and Nehring 2006; Klotz et al. 2013).

7.6 Value and Conservation Challenges of Freshwater Habitats

Freshwater ecosystems comprise only 0.01 % of the water on the planet and occupy only 0.8 % of the Earth's surface, yet they support an extraordinarily high proportion (about 10 %) of the world's total biodiversity (Dudgeon et al. 2006; Strayer and Dudgeon 2010). In addition, freshwater ecosystems are intensively used for human activities and play a vital role in the lives of many people, providing water for drinking and irrigation, food, recreation, and employment. Human activities have altered the composition of biological communities in a negative way through habitat loss, pollution, and species invasions all of which are associated with an increasing rate of species extinctions (Revenga and Mock 2000). Although a few freshwater species have a large geographic range, the insular nature of freshwater habitats has led to the evolution of many species with a narrow distribution, often only a single location, which is especially apparent in the troglobitic taxa (Trontelj et al. 2009). The high habitat fragmentation of freshwater ecosystems and the high endemism of freshwater organisms makes them very sensitive to human impacts whereby habitat isolation and limited dispersal increase the risk of species extinction.

Freshwater ecosystems face increasing degradation and this poses serious threats to ecosystem functions and to native species (Brooks et al. 2002). These impacts have caused severe declines in the range and abundance of many freshwater species. As a result, freshwater animals are among the most threatened groups worldwide and are more threatened than their marine or terrestrial counterparts (Strayer and Dudgeon 2010).

Natant freshwater decapods such as atyid shrimps contribute significantly to the ecological integrity of ecosystems through their high feeding plasticity and their role in plant litter breakdown. Atyid shrimps using the tufts on their first two pereiopods to sweep up detritus can recycle fine organic matter from muddy substrata and move it up the trophic pyramid (Fidalgo and Gerhardt 2003). Palaemonid shrimps also recycle organic matter either by means of their chelae or by scavenging dead vegetation and animal pellets. Apart from their ecological role, freshwater shrimps are used as a food source in many areas through fishing and have been proposed as alternative food to fish aquaculture (Anastasiadou 2002; Fidalgo and Gerhardt 2003).

Current river basin conservation efforts are focused either on specific species or on areas with a high biodiversity, while the ecosystem complexity and dynamism is ignored. However, techniques common in terrestrial systems do not work in freshwater ecosystems because the latter are subject to more frequent and dramatic disturbances (Moss 2000). This means that the conservation and management of river ecosystems should focus on the aquatic system as a whole rather than being limited to a specific protected area. The Water Framework Directive 2000/60/EC, (WFD) of the European Water Policy emphasized the value of developing water strategies that contribute to sustainable management. Analytical frameworks for determining pressures and impacts on freshwater ecosystems include “driving forces” (causes), “pressures” (e.g., pollutants), “states” (physical, chemical, biological), and “impacts” on ecosystem structure and function, that eventually lead to “responses” (policy).

The conservation and management of freshwater ecosystems is directly related to sustainable social, economic, and environmental practices (Moss 2000; Kallioras et al. 2006). Lakes and river basins are biodiversity hotspots that harbour a wide variety of species of conservation interest for which a number of protected areas have been established (Drakou et al. 2008). Lakes and rivers also support a wide array of socio-economic activities such as fisheries, recreation, agricultural water supply, water for hydropower, and water for drinking. Studies on water quality and ecological profiles are not readily converted into easily accessible management tools (Tockner et al. 2009; Chatzinikolaou et al. 2010). Thus a key challenge is to set up management plans based on a framework philosophy that includes the identification of pressures within the catchment, the establishment of a monitoring plan within each lake or river basin district, and the reorganization of the administrative system for freshwater ecosystem management.

The freshwater shrimp fauna of the broader Mediterranean region has been assessed using the IUCN Red List and includes nine data deficient species (DD), eight least concern species (LC), 11 near threatened species (NT), eight vulnerable species (VU), three endangered species (EN), and one critically endangered species (CR) (Table 7.1). The IUCN threatened status (VU, EN, CR) is a significant indication that conservation actions are needed to protect 12 species of Mediterranean shrimps from extinction. However, at present, there is no actual conservation action plans for the Mediterranean shrimps besides a preliminary effort for the cave-living species *T. anophtahlmus sontica* (CR) from Vipavska jama in southeast Slovenia (Jugovic et al. 2015).

7.7 Taxonomic Issues

The taxonomy of freshwater shrimps has been somewhat neglected in the past and is only now becoming more stable, as collections are able to include more remote locations. Morphological identification of atyid species is complicated by high intra- and interspecific variability and by sexual dimorphism (Sket and Zakšek 2009; Jugovic et al. 2010a). Primary and secondary sexual characters in the Atyidae are taxonomically important and are useful to estimate the age of animals but these characters are not well developed in young animals (Sket and Zakšek 2009; Jugovic et al. 2010a; Christodoulou et al. 2012; Table 8.2). Moreover, reliable identification requires the examination of adult males because secondary sexual characters of females that would be useful in taxonomy have not been observed so far (Jugovic et al. 2010a).

The current increased interest in the Mediterranean epigean and hypogean atyids is based on more comprehensive sampling, molecular studies, and a posteriori examination of morphological characters and has resulted in a generally improved taxonomy (Sket 1999a, b; Zakšek et al. 2007; Christodoulou et al. 2012; Christodoulou 2014; García Muñoz et al. 2014). Over the past two decades the number of epigean species of freshwater shrimps in the Mediterranean has increased from 5 to 11, although controversies still remain about the precise number of species (e.g., *Atyaephyra* spp.), while is possible that new species await discovery (Christodoulou et al. 2012; García Muñoz et al. 2014). Likewise the number of troglobitic species has increased from 6 to 16, and there are more species still awaiting description (Sket and Zakšek 2009). Molecular analysis not only enables better taxonomic resolution it also provides insights into the relationships of morphologically similar troglobitic species living in disjunct areas where the convergent evolution of troglobitic characters has given rise to a number of taxonomic problems (Sket 1999a; Zakšek et al. 2007; Trontelj et al. 2009). Despite the increased interest on the Mediterranean epigean and hypogean atyids and the new methods applied the taxonomy of these shrimps still remains unsettled.

7.7.1 The Troglocaris-Proteus Paradigm

A characteristic example of repeatedly erroneous use for taxonomic purposes which proved to be very variable due to the predatory pressure is the rostral length and dentition in *Troglocaris*. The amphibian *Proteus anguinus* Laurenti is a predator of *Troglocaris* shrimps in the Dinaric cave systems in Croatia. It was recently shown that where *Proteus* exerts a predation pressure the selection for individuals with a long rostrum lined by numerous teeth takes part. In contrast, *Troglocaris* populations without such predation pressure are characterized by a shorter rostrum armed with only a few teeth (Jugovic et al. 2010b). Although the rule applies mainly to the subgenus *Troglocaris*, variations in rostral length in some species within the subgenera, *Spelaeocaris* and *Troglocaridella* in relation to the presence of *Proteus* were also observed (Jugovic et al. 2010b). After being assumed that *Proteus* is present also in some caves where the species *T. (T.) hercegovinensis* and *T. (S.) prasence* are found, the same pattern in rostral length and dentition became clear (Jugovic, unpublished data; Fig. 7.6) for them too. Furthermore, two species of cave shrimps from central Dinarides (*T. (S.) kapelana*) and from Bosanska Krajina (*T.* (*S.*) sp.) that are both exposed to predation pressure from *Proteus* have relatively long rostra (Jugovic et al. 2010b, Fig. 8.6). On the other hand, shrimps from Russia and Georgia (*T. Xiphocaridinella*) and shrimp from karst areas outside the Dinarides that live in caves where *Proteus* is absent all have a short rostrum with few teeth (Marin and Sokolova 2014).

7.7.2 *Cryptic Species*

The application of molecular analysis and PC-supported multivariate statistical analysis are indispensible for the identification of cryptic diversity where populations appear morphologically identical but prove to be phylogenetically distinct (Bickford et al. 2007; Jugovic et al. 2012). Cryptic species are hard to recognize morphologically due to a high level of similarity between some characters coupled with high intraspecies variation.

7.7.2.1 *Atyaephyra*

Currently seven species are being recognized within the genus *Atyaephyra* although some controversy exist on which these species are (Christodoulou et al. 2012; García Muñoz et al. 2014). *Atyaephyra acheronensis* is a cryptic species proposed by Christodoulou et al. (2012), which was later questioned by García Muñoz et al. (2014) and was considered as a synonym of *A. desmarestii*. García Muñoz et al. (2014) did not consider the COI divergence rates found between *A. desmarestii* and *A. acheronensis* populations (5.6–5.8 %) at specific level. Nevertheless, in the current paper *A. acheronensis* is still considered as a separate species since numerous species have been described with much lower divergence rates (e.g., Jesse et al. 2011). Furthermore, the delimitation of this species is considered precocious since the revision of the genus is still not completed. Taking into consideration the Balkan Peninsula and the Middle East are hot spot areas for the biodiversity and the cryptic speciation characterising the genus it is highly possible that more species within the genus *Atyaephyra* await discovery (Christodoulou et al. 2012; Christodoulou 2014; García Muñoz et al. 2014). Already preliminary results show a significant differentiation in a population from Lake Skadar in the boarders of Montenegro and Albania (Christodoulou, unpublished data, Jabłońska et al. 2015), in populations from Peloponnesus, Greece (Christodoulou 2014), and from the Middle East (Christodoulou et al. 2012; Christodoulou, unpublished data). The species *A. mesopotamica* Al-Adhub acknowledged by García Muñoz et al. (2014) is not included in the current paper because it is part of *A. orientalis* species complex which currently is under revision where most likely more than two species are involved (Christodoulou, unpublished data).

7.7.2.2 *Troglocaris* Aggr. *Anophthalmus*

The cave-dwelling *Troglocaris anophthalmus* species complex comprises a number of morphologically similar but geographically well-separated clades (Jugovic et al. 2011, 2012; Sket and Zakšek 2009; Table 7.3). First evidence for cryptic speciation was given by an allozyme study of morphologically similar populations of *T. anophthalmus* from Italian Karst which discovered a number of different lineages some of which were found in syntopy (Cobolli Sbordoni et al. 1990). Zakšek et al. (2009) studied the *T. anophthalmus* complex and found four independent evolutionary lineages (western Slovenia, eastern Slovenia, Adriatic, Soča) that probably represent four valid species (Zakšek et al. 2009) together with a putative fifth lineage from Istria, which co-occur in syntopy with the West Slovenia lineage. Nevertheless, only two species could be recognized according to the biological species concept, *T. planinensis* (corresponding to West Slovenia), and *Troglocaris anophthalmus* (consisted of all other lineages).

Although knowledge of freshwater shrimp biodiversity in the broader Mediterranean region is improving large gaps remain, especially for cave dwelling species from karst areas. The southern European Peninsulas (including Asia Minor and the Caucasus) are biodiversity hotspots. Only the shrimp faunas of the underground waters of Dinaric karst have been well studied and other underground systems are still largely unexplored (Cincotta et al. 2000; Kryštufek and Reed 2004; Sket and Zakšek 2009; Hewitt 2011). A number of authors have raised questions about the actual number of species of Caucasian freshwater cave shrimps, and further molecular and morphological analyses studies are needed from all populations before this diversity can be properly described (Birštein 1939, 1948; Juzbaš'jan 1940, 1947, 1951; Sket and Zakšek 2009; Jugovic et al. 2012; Marin and Sokolova 2014).

7.7.2.3 Palaemon

A large part of the history of the freshwater palaemonid shrimps is based on the genus *Palaemonetes* (De Grave and Ashelby 2013). Heller (1869) established *Palaemonetes* to distinguish freshwater shrimps from marine species of the genus *Palaemon*, but a recent phylogenetic study on the subfamily Palaemoninae

Table 7.3 A list of valid species and subspecies of *T.* aggr. *anophtalmus* ("*Anophthalmus*" lineage sensu Zakšek et al. 2007)

C	*Species/subspecies*	PG	Species delimit. criteria			GSC	EP	Currently known distribution
			HE	MM	C			
1	*Troglocaris (Troglocaris) planinensis*	W-Slo	•	•	•	A		SW Slovenia, NE Italy (Carso), Istria (SLO, CRO)
2	*Troglocaris (Troglocaris) anophthalmus*		•	•	•			
2.1	*T. a. anophthalmus*	E-Slo	•	•	•	B		SE Slovenia (NW Dolenjska, Suha Krajina)
2.2	*T. a. ocellata*						•	Bela Krajina SE from Dolenjska (SLO) and Kukuruzovića špilja near Rakovica (CRO)
2.3	*T. a. intermedia*							Mikašinovića pećina near Ogulin in central NW Croatia (maybe also wider Ogulin area)
2.4	*T. a. periadriatica*	Adriatic	•	•	•	C		Contiguous wide area along the Adriatic coast, approx. from Otočac in Lika (CRO) in NW to SE of Trebinje (BIH) in SE; probably absent from the Velebit mountains (CRO) but present in the detached peninsula Pelješac and some Adriatic islands: Brač, Ugljan (CRO)
2.5	*T. a. sontica*	Soča	•		•	D		Four caves in Soča/Isonzo-Vipava/Vipacco river system NW from *T. planinensis* (SLO, IT). These two taxa might be sympatric in the Italian Carso/Kras
2.6	*T. a. legovici*	Istra	•			?		Four caves from W and E coast of central Istra peninsula, and from S tip of peninsula (CRO), S from rivers Raša and Mirna. In E coast of Istria in syntopy with *T. planinensis*

Clades (C) 1 and 2 are recognized as separate biological species. The monophyly of five major phylogroups (PG) is supported by COI and ITS2, but populations from Istra are supported only by ITS2 (Zakšek et al. 2009). Dots denote when different species delimitation criteria are met (*sensu* Zakšek et al. 2009) (HE: haplotype exclusivity, MM: mutual monophyly, C: concordance (mitochondrial vs. nuclear DNA). Phylogroups recognized as different species according to the genealogical species concept (GSC) are denoted with different letters (Zakšek et al. 2009); inconclusive case is denoted by a question mark (?). No obvious morphological peculiarities have been recorded for these taxa except that *T. a. ocellata* (Jugovic et al. 2012) has a pigment in its eye rudiments (EP > 90 % of analysed specimens). Distribution data are based on Jugovic et al. (2012)

SLO Slovenia; *CRO* Croatia; *BIH* Bosnia and Herzegovina; *IT* Italy discovered significant paraphyly of *Palaemon* and *Palaemonetes* (Ashelby et al. 2012) and the genus *Palaemonetes* was considered to be junior synonym of *Palaemon* (De Grave and Ashelby 2013).

In the broader Mediterranean region only some species of *Palaemon*, such as *P. varians* or *P. antennarius*, have been studied extensively (e.g., De Grave 1999; Gottstein Matočec et al. 2006; Anastasiadou et al. 2009, 2014). Nevertheless key questions about the diversity of the genus in this region and the phylogenetic relationships between its species remain unanswered, as does its colonization of fresh water in relation to the paleogeography of the region. Even basic knowledge of the diversity of the broader Mediterranean taxa is not available due to insufficient primary descriptions of some taxa and this has resulted in taxonomic confusion within this group (Tzomos and Koukouras 2015). For example, the recent descriptions of *P. minos* from Crete and *P. colossus* from Rhodes (Tzomos and Koukouras 2015) were based on samples from populations that had been previously misidentified as *P. antennarius* which is widespread throughout the broader Mediterranean region (Holthuis 1961). The redescription of *P. antennarius* and a more comprehensive morphological analysis was a crucial step towards the resolvment of these longstanding taxonomic issues (Tzomos and Koukouras 2015). For instance, Greek populations of *P. antennarius* have a shallowly bilobed maxillular palp while Italian populations have a deeply bilobed palp, and north Italian populations have two setiform processes (instead of one) on their maxillular palp. Preliminary results based on 16S and COI sequences indicate that Greek, Croatian, and Italian populations of *P. antennarius* may belong to more than one species, and higher-resolution morphological methods (e.g., microtomography) combined with an extensive genetic analysis using more samples and more markers could confirm the existence of different taxa within the current *P. antennarius* s.l. (Tzomos 2014). It is clear that there is a need for a detailed taxonomic revision of the freshwater shrimp of the Mediterranean region using both molecular and morphological methods together with a much broader and in depth geographical and taxonomic sampling.

7.8 Conclusions

Although the inventory of the freshwater shrimps from the broader Mediterranean is still incomplete, this region harbours most of the Palaearctic shrimp species that belong to 11 genera and three families. Since these shrimps inhabit water habitats that are indispensable for the human well-being they face numerous threats and many are highly endangered. An immediate, coordinated effort to assess freshwater biodiversity in the region should be launched together with an ongoing development of strategies for the conservation and management of freshwater biodiversity.

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Chapter 8
Freshwater Decapod Diversity and Conservation in Mexico

Fernando Alvarez and José Luis Villalobos

Abstract The diversity, distribution, and conservation status of the 172 species of freshwater decapod crustaceans of Mexico is presented. These freshwater crustaceans are classified in eight families: Atyidae, Palaemonidae, Alpheidae, Cambaridae, Parastacidae, Pseudothelphusidae, Trichodactylidae, and Glyptograpsidae. The Mexican fauna is composed of Neotropical and Neartic lineages that occupy lowland areas near the coast as well as mountain rivers, high altitude lakes, and underground caves. Pseudothelphusid crabs and cambarid crayfish are the most diverse groups, followed by palaemonid and atyid shrimps, while trichodactylid crabs are represented by only five species, and alpheids, glyptograpsids, and parastacids by one species each. The conservation status of the Mexican species have been assessed using the IUCN Red List protocols and comprises 30 % least concern, 4 % near threatened, 14 % vulnerable, 5 % endangered, 5 % critically endangered, and 1 % extinct, while the largest number of species (41 %) are data deficient, and too poorly known to assess. The Cambaridae have the most threatened species, while the Atyidae and Palaemonidae have the highest proportion of species of least concern. Overexploitation of freshwater resources for agricultural and urban use together with the impact of introduced species are the most important threats to Mexico's freshwater decapod fauna.

Keywords Atyidae · Palaemonidae · Alpheidae · Cambaridae · Parastacidae · Pseudothelphusidae · Trichodactylidae · Glyptograpsidae

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8.1 Introduction

Fresh water in general is a scarce resource (representing only 2.5 % of all water on the planet) and occupies only 1.2 % of the earth's surface, but freshwater habitats are home to an exceptionally diverse fauna including 25 % of all vertebrates and more than 126,000 species of other animal groups (Balian et al. 2008). Freshwater habitats are also the most threatened ecosystems in the world due to pressure from human activities through urban development, agriculture, and industrial practices that have polluted ecosystems, with additional threats from introduced alien species.

Mexico is a large North American country (2 million km^2) that has about 0.1 % of the world's fresh water (Gleick 2014). Two thirds of this country is high land above 800 m asl, and there are more than 320 different hydrological basins. Surface fresh waters and groundwater habitats are present in the coastal states along both the Pacific Ocean and the Gulf of Mexico, and ground waters are also found in the arid northern parts of the country and in the Yucatan Peninsula. Most fresh water in Mexico is found in the rivers (68 %), followed by dams (18 %), ground water (12 %), and lakes and lagoons (2 %) (Centro del Tercer Mundo para el Manejo del Agua 2003). Most freshwater (80 %) is found from sea level to 500 m asl, and the amount declines with altitude to 15 % between 500 and 2000 m asl, and to 5 % above 2000 m asl.

The freshwater decapods are a highly diverse group of species that occupy a very spatially limited resource. For example, the 1300 species of primary freshwater crabs are the most diverse group of freshwater decapods worldwide, and comprise about 20 % of all brachyurans, but their distribution is restricted to about 1.2 % of the surface waters in the tropical and subtropical areas of the world (Cumberlidge et al. 2009). There are about 800 species (23 %) of freshwater caridean shrimps (out of 3500 species in all aquatic habitats) (De Grave et al. 2015); and about 590 species of crayfish in freshwater habitats in North America, Central and South America, Europe, Madagascar, eastern Asia, and Australia (but none in continental Africa or western or southern Asia) (Richman et al. 2015).

In Mexico freshwater decapods are distributed throughout most of the country with species hotspots along the Trans Mexican Volcanic Belt (TMVB) and the Gulf of Mexico slope, but these crustaceans are absent from the arid central zone (such as in the State of Aguascalientes) where there is little superficial water (Alvarez et al. 2012). In the arid Baja California Peninsula freshwater decapods are restricted to the eastern coastal region where they live in oases and springs (Hernández et al. 2007). Decapods are also not abundant in the State of Sonora along the Pacific slope perhaps because this is where the palaemonid shrimps of the genus *Macrobrachium* and pseudothelphusid crabs have reached the northern limits of their distributional ranges. South of this, beginning in the State of Sinaloa, the numbers of species of shrimps (Atyidae, Palaemonidae), crayfish (Cambaridae) and freshwater crabs (Pseudothelphusidae) increases and these decapods are found in the rivers and lakes associated with the Sierra Madre Occidental as far south as the border with Guatemala. The coastal plains and mountain rivers that descend from the Sierra Madre Oriental along the Gulf of Mexico are home to species of palaemonid and atyid shrimps, while the central plateau traversed by the TMVB has rich cambarid, pseudothelphusid and trichodactylid faunas. The Yucatan Peninsula has very few epigean bodies of freshwater and these are dominated by cambarid crayfish, while the Yucatan's subterranean waters are dominated by atyid and palaemonid shrimps (Alvarez et al. 2015).

8.2 Studies on Mexican Freshwater Decapods: A Historical Perspective

The first studies of Mexican freshwater decapods were based on collections made by foreign explorers during the 19th century who sent their specimens to the natural history museums in Europe and US Natural History Museum (later the Smithsonian Institution) in Washington DC in the USA.

The first freshwater decapod species to be described from Mexico was the freshwater shrimp *Atys scaber* Leach 1815 (=*Atya scabra* Leach 1815) (Atyidae) from Veracruz (Hobbs and Hart 1982). Over forty years later another species of freshwater shrimp, *Caridina mexicana* De Saussure 1857 [=*Potimirim mexicana* (De Saussure 1857a)] (Atyidae) was described from Veracruz (De Saussure 1857a; Villalobos 1960).

The first Mexican species of freshwater prawns to be described from Mexico were *Macrobrachium acanthurus* (Wiegmann 1836) and *M. carcinus* (Linnaeus 1758) (Palaemonidae) from Veracruz (that were originally described as *Palaemon mexicanus* and *P. montezumae* (De Saussure 1857b; Holthuis 1952).

The first crayfish to be described from Mexico were *Astacus* (*Cambarus*) *weigmanni* and *Astacus* (*Cambarus*) *mexicanus* (Cambaridae) (Erichson 1846). Shortly after that De Saussure (1857b) described *Cambarus montezumae* from Chapultepec in Mexico City and *Cambarus aztecus* from Veracruz. Bouvier (1897) then described *Cambarus* (*Procambarus*) *digueti* from Jalisco, and Faxon (1898) described two subspecies of crayfish (*Cambarus montezumae dugesi* and *C. m. occidentalis*) from Guanajuato and Mazatlán, Sinaloa, and *Cambarus chapalanus* from Lake Chapala, Jalisco. In the middle of the 20th century Villalobos (1955, 1983) described the crayfish fauna of that country, including a major monograph on the Mexican cambarid crayfish.

The first pseudothelphusid freshwater crabs to be described were all placed in the genus *Pseudothelphusa* by De Saussure (1857a). In the early 20th century Ortmann (1902) and Rathbun (1905) published the first monographs on the freshwater crabs of the Americas. In the mid to late 20th century several authors (R. Bott, G. Pretzmann, A.E. Smalley, and G. Rodríguez) each contributed a significant series of taxonomic publications and monographs, including the establishment of the modern systematics of the group by Rodríguez (1982). The first species of trichodactylid freshwater crab to be described from Mexico was *Trichodactylus constrictus* Pearse

1911 [=*Avotrichodactylus constrictus* (Pearse 1911)], from Veracruz, while the other four species of Mexican trichodactylids were described much later between the 1960s and the 1980s (Rodríguez 1992).

The first species of Mexican glyptograpsid crab was *Platychirograpsus typicus* from Tabasco (Rathbun 1914), which was later synonymized with *P. spectabilis* from West Africa by Buitendijk (1950), thereby recognizing an amphi-Atlantic distribution for this species. Schubart et al. (2002) revised the genera *Platychirograpsus* and *Glyptograpsus* and assigned them both to the family Glyptograpsidae.

8.3 Regional Diversity

All decapod species that either live permanently in fresh water or that require fresh water to complete their life cycle are considered here to be freshwater species (following De Grave et al. 2015). A total of 172 species belonging to the families: Atyidae (11), Palaemonidae (35), Alpheidae (1), Cambaridae (57), Parastacidae (1), Pseudothelphusidae (61), Trichodactylidae (5), and Glyptograpsidae (1) have been recorded from freshwater habitats in Mexico (Table 9.1). A brief account on the diversity of each of these families in Mexican freshwaters is provided below.

8.3.1 Family Atyidae

The Atyidae is represented in Mexico by 4 genera and 11 species, which is a small number of species given that the total diversity of this family is about 450 species worldwide (De Grave et al. 2009). The genera *Atya* and *Potimirim* are composed of epigean species that are distributed on both the Pacific and the Gulf of Mexico-Caribbean slopes of that country (Fig. 8.1). Some species, such as the shrimp *Jonga serrei* are associated with anchialine caves in Quintana Roo, and their distribution extends along the Caribbean coast to include Central America (Alvarez and Iliffe 2008). There are four endemic species of the stygobitic shrimp in the genus *Typhlatya* in the Yucatan Peninsula, whose congeners are also distributed in the Atlantic Ocean and the Mediterranean Sea, and there is one (questionable) species in the Galapagos islands (Botello et al. 2013).

8.3.2 Family Palaemonidae

This diverse family includes marine and freshwater taxa, and Mexico hosts 35 species in six genera that are either strictly freshwater, or mostly freshwater with an estuarine phase (Fig. 8.1). *Macrobrachium* (20 species) is the most species rich

Fig. 8.1 Localities sampled for freshwater decapods (shrimps) in Mexico, families Alpheidae, Atyidae and Palaemonidae. Information of records obtained from the National Crustacean Collection (CNCR), Institute of Biology, UNAM

genus of freshwater shrimps in Mexico. This genus includes several widely distributed and seasonally abundant species that are commercially exploited (*M. acanthurus*, *M. carcinus*, *M. tenellum*, *M. americanum*), other species that are rare endemics restricted to small areas (*M. tuxtlaense*, *M. totonacum*), and others that are stygobitic (*M. sbordonii*, *M. villalobosi*).

The genus *Palaemon* (previously placed in *Palaemonetes* by De Grave and Ashelby 2013) has Neartic zoogeographic affinities and includes freshwater, estuarine, and marine representatives, but its six Mexican species are strictly freshwater and are all restricted to the northern parts of the country (Alvarez et al. 2014a).

There are three stygobitic shrimp genera: *Creaseria morleyi* from the Yucatan Peninsula, *Neopalaemon nahuatlus* from northern Oaxaca, and *Troglomexicanus* (3 species) from caves in Sierra del Abra in San Luis Potosi and Tamaulipas (Villalobos et al. 1999). Other species of Mexican shrimps [*Cryphiops* (*Bythinops*), 4 species] are found in Chiapas and are associated with caves as well as open waters (Villalobos et al. 1989; Alvarez et al. 2011).

8.3.3 Family Alpheidae

Almost all species of alpheid shrimps are marine, except for a few freshwater species in the circumtropical genera *Potamalpheops* and *Alpheus* (Yeo and Ng 1996) including one Mexican freshwater species (*P. stygicola* Hobbs, 1973b) from two caves in northern Oaxaca (Fig. 8.1) (Sánchez et al. 2007a).

8.3.4 Family Cambaridae

There are 57 species and three genera of cambarid crayfish in Mexico: *Cambarellus*, *Orconectes* and *Procambarus*. Of these, 11 species in the genus *Cambarellus (Cambarellus*) are found in northern Mexico (Chihuahua and Coahuila), western Mexico (Sinaloa, Nayarit and Jalisco), and throughout the central plateau along the TMVB (Michoacán, Guanajuato, Querétaro, México, Tlaxcala and Puebla) (Fig. 8.2). Notably, *Cambarellus montezumae* has a wide distribution throughout the TMVB from Nayarit in the west to Puebla in the east (Rojas et al. 2002), while *C. zempoalensis* has the highest altitudinal distribution of all Mexican freshwater decapods occurring above 3000 m asl in Morelos. There is only one species of *Orconectes* found in Mexico (*O. virilis*, which is native to the Midwest of the United States) and was introduced into Chihuahua State via the Río San Pedro and has now been recorded from Cuauhtemoc near the City of Chihuahua (Campos and Contreras 1985).

The most species-rich genus of cambarid is *Procambarus* (180 species in total) with 15 subgenera, nine of which are found in Mexico. Several subgenera of *Procambarus* are endemic to Mexico: *P.* (*Mexicambarus*) and *P.* (*Procambarus*) (one species each) from Michoacán, *P.* (*Paracambarus*) (two species) from Puebla, and *P.* (*Villalobosus*) (12 species) from Puebla, Hidalgo, and Veracruz. Two other subgenera of *Procambarus* are *P.* (*Girardiella*) and *P.* (*Pennides*) each have only one species in Mexico and the rest of the species in these subgenera distributed in the United States. Similarly, *P.* (*Ortmannicus*) (59 species) is distributed mainly in

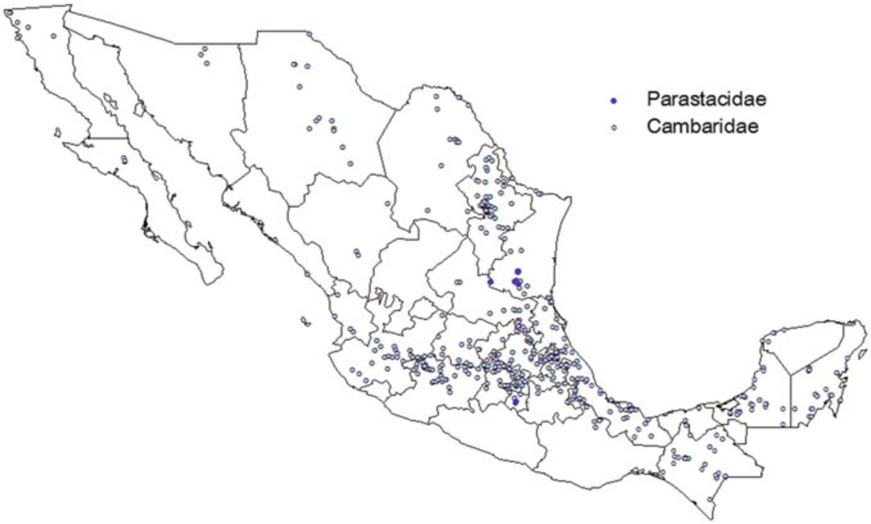

Fig. 8.2 Localities sampled for freshwater decapods (crayfish) in Mexico, families Parastacidae and Cambaridae. Information of records obtained from the National Crustacean Collection (CNCR), Institute of Biology, UNAM

the southeastern United States, but there are seven species that occur in Mexico. There are two species of crayfish whose native distribution includes both the United States and Mexico, one of which is the well-known invasive species *P.* (*Scapulicambarus*) *clarkii* (Hernández et al. 2008). The most diverse subgenus of *Procambarus* in Mexico is *P.* (*Austrocambarus*) (18 species) most of which are found along the Gulf of Mexico slope, while 3 species of this subgenus occur in Cuba and another one in Guatemala and Honduras.

8.3.5 Family Parastacidae

The southern hemisphere family Parastacidae is not found naturally in Mexico but the Australian redclaw crayfish, *Cherax quadricarinatus* has escaped from commercial aquaculture facilities and has recently established wild populations in Morelos (in 2000) and in Tamaulipas (in 2005) (Bortolini et al. 2007) (Fig. 8.2). Since then other populations of the redclaw crayfish have been found in southern Tamaulipas (from the same river basin that was previously studied) and from La Media Luna Lagoon in San Luis Potosi (Alvarez et al. 2014b).

8.3.6 Family Pseudothelphusidae

The freshwater crab family Pseudothelphusidae comprises 264 species in 34 genera and is distributed from Sonora in northern Mexico south through Central America to Peru and the southern part of the Amazon basin in Brazil (Villalobos and Alvarez 2008; Cumberlidge et al. 2014). This family comprises two subfamilies: the Epilobocerinae distributed in the Greater Antilles, and the Pseudothelphusinae distributed in continental America from Mexico to Brazil. The Pseudothelphusinae in turn is divided into five tribes, three of which occur in Mexico: Hypolobocerini, Potamocarcinini, and Pseudothelphusini.

The Hypolobocerini includes three genera from Mexico: *Lobithelphusa* (1 species) from Veracruz, *Spirothelphusa*, (1 species) from Chiapas, and *Phrygiopilus* (2 Mexican species from Chiapas) with the genus extending as far south as Guatemala (Alvarez and Villalobos 1998). The genus *Ehecatusa* (2 species) has been reported to occur in Mexico but is considered to be *incertae sedis* (Villalobos and Alvarez 2008).

The Potamocarcinini are distributed from southern Mexico to Central America, with 7 genera from Mexico. *Typhlopseudothelphusa* has two stygobitic species from Chiapas and others from Guatemala and Belize and *Villalobosius* has two stygobitic species one from Veracruz (the most northerly limit of the tribe) and one from Oaxaca (Rodríguez and Hobbs 1989). *Sylvathelphusa* has two species from Chiapas, one from a cave the other from a humid forest (Villalobos and Alvarez 2013), while *Zilchia* has two species from Chiapas, with a genus range that extends into Belize and Honduras (Pretzmann 1968a). *Odontothelphusa* has seven species from southern Mexico most of which are found in Chiapas, with *O. maxillipes* ranging from Chiapas to Veracruz (Alvarez et al. 2011). *Potamocarcinus* is widely distributed from southern Mexico to Central America, and Colombia in South America, and includes three Mexican species (Alvarez et al. 2011). *Raddaus* ranges from Mexico to Nicaragua and includes two Mexican species one from Chiapas and one from the border area with Guatemala (Villalobos and Alvarez 2008).

The Pseudothelphusini is endemic to central and northwestern Mexico and comprises 4 genera: the highly diverse *Pseudothelphusa* (26 species), *Tehuana* (8 species) *Disparithelphusa* (1 species) from northern Oaxaca, and *Smalleyus* (1 species) from Veracruz (Villalobos and Alvarez 2010).

8.3.7 Family Trichodactylidae

The 51 species of trichodactylid freshwater crabs are distributed mainly in South America and there are only five Mexican species in two genera, *Avotrichodactylus* (3 species) from Veracruz, Tabasco, and Chiapas, and *Rodriguezia* (2 species) from Chiapas (Ojeda et al. 2013) (Fig. 8.3).

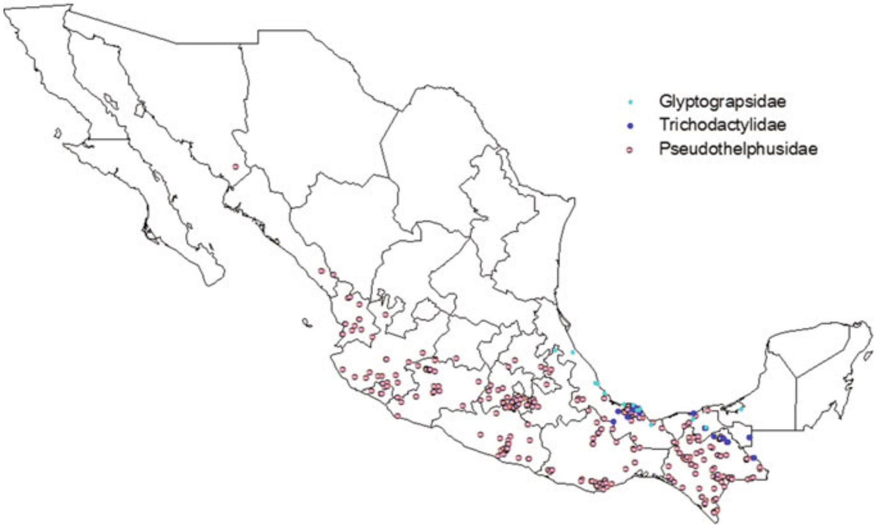

Fig. 8.3 Localities sampled for freshwater decapods (crabs) in Mexico, families Glyptograpsidae, Pseudothelphusidae and Trichodactylidae. Information of records obtained from the National Crustacean Collection (CNCR), Institute of Biology, UNAM

8.3.8 Family Glyptograpsidae

This family includes only one Mexican species, *Platychirograpsus spectabilis* that depends on estuaries to complete its life cycle and is distributed along the slopes of the Gulf of Mexico where its juveniles and adults are found in lowland rivers hundreds of kilometers from the coast (Rathbun 1918) (Fig. 8.3).

8.4 Distribution and Zoogeography

The Mexican freshwater decapods have high numbers of endemic species: four out of 12 species of Atyidae, 21 out of 83 species (25 %) of Palaemonidae, one species of Alpheidae, 55 out of 57 species of Cambaridae, and all species of freshwater crabs (Trichodactylidae and Pseudothephusidae) (Alvarez et al. 2014c). Many endemic species have a very restricted distribution and in many cases are known only from between one and five localities. In contrast, there are several species of freshwater shrimps in the genus *Macrobrachium* found in Mexico that have a very wide distributional range throughout tropical America.

Mexico lies in a transition zone between the Neartic and the Neotropical biogeographic regions and its fauna includes aquatic and terrestrial epicontinental organisms from both regions (Huidobro et al. 2006). Freshwater decapods from Mexico that have Neotropical affinities are also found mainly in tropical America, while those that have Nearctic affinities are also found mainly in North America (Canada, the United States, and Mexico).

8.4.1 Family Atyidae

Atyid shrimps have a circumtropical distribution in lowland areas close to coastlines. The genera *Atya* and *Potimirim* have clear Neotropical affinities because other species of both genera occur in Central and South America (Villalobos 1982; Hobbs and Hart 1982). The genus *Jonga* has its northernmost limits in southern Quintana Roo, and is also found in several Caribbean islands and Central America (Alvarez et al. 2015). Species of *Typhlatya* are all restricted to anchialine habitats in Mexico and have a wide global distribution, with the main lineage occurring in the Atlantic-Mediterranean basins, and there is one questionable species in the Galapagos Islands (Botello et al. 2013).

8.4.2 Family Palaemonidae

The Mexican freshwater Palaemonidae includes both tropical-subtropical and temperate lineages. The freshwater species of *Palaemon* have a Neartic affinity, with several species occurring throughout the United States (Strenth 1976) and six species from Mexico that follow a strict Neartic distribution and reach as far south as San Luis Potosi (Rodríguez-Almaraz and Muñiz 2008). The stygobitic and monotypic *Creaseria* from the north of the Yucatan Peninsula, and *Neopalaemon* from northern Oaxaca are both morphologically similar and probably derive from the same invasion of freshwater because both show a very early phylogenetic split from *Macrobrachium* (Botello and Alvarez 2013). *Troglomexicanus* (related to the Cuban *Troglocubanus*) represents another independent invasion of freshwater in the Sierra del Abra from the border between Tamaulipas and San Luis Potosi (Villalobos et al. 1999; Botello and Alvarez 2013).

Cryphiops exhibits a disjunct distribution with some species found in South America and some in Mexico. Species from Peru and Chile are assigned to *Cryphiops* (*Cryphiops*) *caementarius*, while species from Brazil and the four species from Mexico are assigned to *Cryphiops* (*Bythinops*) (Villalobos et al. 1989). *Cryphiops* is closely related to *Macrobrachium tuxltaense* from Veracruz (which has abbreviated development) suggesting that these Mexican taxa invaded freshwater independently at a different time from the South American species of *Cryphiops* (Botello and Alvarez 2013).

The zoogeography of *Macrobrachium* in the American continent is a complex one with groups of species with an amphiamerican distribution (on both the Atlantic and Pacific slopes) that inhabit inland bodies of water without contact with coastal waters (Acuña et al. 2013; Pileggi et al. 2014). Species with estuarine-dependent larval stages have extended larval development and a wide distributional range, while species inhabiting inland bodies of water have abbreviated larval development, a reduced distributional range, and limited dispersal capabilities. In Mexico, two species of *Macrobrachium* have an amphiamerican distribution, four occur along the Atlantic slope, four along the Pacific slope, and ten species that have an abbreviated development are found in inland waters. The *Macrobrachium* species that have abbreviated development are all endemic to Mexico (Acuña et al. 2013). Species of *Macrobrachium* that occur in lowland areas associated with estuaries are common with a wide distributional range that includes Mexico, the US states along the Gulf of Mexico, and South America.

8.4.3 Family Alpheidae

Potamalpheops includes 14 species and the genus has a wide distribution in West and Central Africa (Senegal, Cameroon, Congo), the Indo-West Pacific (Australia, Indonesia, Malaysia, New Caledonia, Philippines, Singapore, Sri Lanka), and North and South America (Brazil, Mexico) (Soledade et al. 2014). In Mexico, *Potamalpheops stygicola* from Oaxaca, together with five other species, are all strict freshwater taxa. Bruce (1991) suggested that the worldwide distribution of this genus was the result of an earlier radiation from a widespread ancestral stock living in the Tethys Sea.

8.4.4 Family Cambaridae

Cambarid crayfish originated in the Nearctic region in the southeastern United States and subsequently dispersed northward and southward (Hobbs 1984). The Mexican cambarid species are the product of two main invasions from the USA: one group includes several lineages of *Procambarus* that spread south along the Gulf of Mexico slope, and another group (*Cambarellus*) that spread south into north central Mexico via paleo-lakes that have since dried up (Pedraza-Lara et al. 2012).

The patterns of distribution shown by the different subgenera of *Procambarus* in Mexico reflect the southern spread of the genus in a series of geographic steps. *Procambarus* (*Ortmannicus*) from the central United States reached northern Veracruz, *P.* (*Villalobosus*) and *P.* (*Paracambarus*) reached central Veracruz and Hidalgo, *P.* (*Procambarus*) and *P.* (*Mexicambarus*) reached central western Mexico in the central lake district of Michoacán, and *P.* (*Austrocambarus*) reached central Veracruz and spread southward through Mexico to Guatemala and Honduras (Hobbs 1972; Villalobos 1983). *Cambarellus* (*Cambarellus*) has a disjunct distribution in central Mexico with one group in the states of Chihuahua, Coahuila, Sinaloa, Nayarit, and Jalisco and the other in the volcanic lakes of eastern Puebla east of the TMVB.

8.4.5 Family Parastacidae

Cherax quadricarinatus is a recently introduced species in Mexico so its distribution pattern has no biogeographic meaning. Its present distributional range that includes the lower Tamesi River basin in southern Tamaulipas is likely to expand south to the Balsas basin from Morelos in the Yautepec River to the Amacuzac River, and eventually it could occupy the entire Balsas River basin. The presence of *C. quadricarinatus* in the closed basin of the Media Luna Lagoon in San Luis Potosi is essentially confined and is not expected to expand to occupy a larger area (Alvarez et al. 2014b).

8.4.6 Family Pseudothelphusidae

Several hypotheses have been proposed to explain the distribution pattern shown by pseudothelphusid crabs. Bott (1972) proposed multiple invasions of fresh water by a widely distributed ancestral stock in the proto-Caribbean basin that gave rise to the different groups of species in South America, the Antilles, and Mexico. Rodríguez (1982) considered that the center of origin of the whole family was in the Antilles, with a secondary center of radiation in the border region between Colombia and Venezuela, and proposed nine migration routes to explain the radiation of the different lineages in South and Central America, Mexico, and the Antilles. Rodríguez (1986) refined his earlier hypothesis by adding vicariance events due to past continental plate movements as causal agents of distributional patterns, but did not explain the rapid evolution of the Central American and Mexican pseudothelphusid fauna following the closing of the Isthmus of Panama, or how the ancestral Antillean stock reached the mainland.

Alvarez and Villalobos (1994a) and Villalobos and Alvarez (2010) proposed that there were two centres of radiation for the pseudothelphusids, one in Colombia and one in the Isthmus of Tehuantepec in southern Mexico. This was based on the overlap of species belonging to the three different pseudothelphusid tribes in southern Mexico, and on the presence of several monotypic genera that have an aberrant gonopod morphology. For example, the Isthmus of Tehuantepec has the largest concentration of genera (14) within the entire range of the family. In the Cretaceous the ancestral pseudothelphusid stock originally evolved on the single American landmass and was subsequently split vicariantly, isolating populations in South America from populations in Central America and Mexico. More recently (3.1 mya) the formation of the Isthmus of Panama connected Central America with South America, allowing pseudothelphusids to migrate north into Central America and Mexico from what is now Colombia and Panama and others to migrate south from what is now northern Mexico (Knowlton and Weigt 1998).

8.4.7 Family Trichodactylidae

There are only five species of trichodactylid freshwater crabs in Mexico and one species in Nicaragua, otherwise all other species in this family are found in lowland rivers and lakes in South America (Rodríguez 1992). Several authors have proposed a Cretaceous origin for the family in order to explain its disjunct distribution with separate centers in Mexico, Central, and South America (Rodríguez 1986; Morrone 2003).

The five species from Mexico are classified in two genera: *Avotrichodactylus* with three epigean species in Veracruz, Tabasco, and Chiapas, and *Rodriguezia*, with two species in Chiapas that are associated with caves and rivers (Rodríguez 1992). Four out of the five species have a reduced distributional range usually restricted to two to five localities, while the fifth species (*Avotrichodactylus constrictus*) is distributed from Veracruz, to Tabasco, to northern Chiapas. A morphological analysis of *A. constrictus* sampled from throughout its range showed no significant differences in carapace or gonopod morphology between the different populations suggesting that the episodic flooding of the coastal lowlands in these three states may serve to connect the different populations, allow gene flow, and conserve a homogenous morphology (Ojeda et al. 2013).

8.4.8 Family Glyptograpsidae

The single representative of this family in freshwaters from Mexico is the endemic saber crab *Platychirograpsus spectabilis*. This species was described from specimens first collected in Veracruz and other were later collected in Tabasco and Campeche. *Platychirograpsus spectabilis* has been introduced into Tampa, Florida in the United States (Alvarez et al. 2014c).

8.5 Conservation Status

The conservation status of all freshwater decapods from Mexico has been assessed using IUCN protocols except for the glyptograpsid crab *Platychirograpsus spectabilis* and the recently described species of Palaemonidae and Pseudothelphusidae. Only 12 species (7 %) of freshwater decapods appear on the Mexican Red List (the Nom-059-Semarnat-2010) that were evaluated using the “Risk Evaluation Method” (MER in Spanish) (Sánchez et al. 2007b).

The IUCN Red List of Threatened Species includes 172 species of Mexican freshwater decapods of which 70 (40.7 %) are data deficient (DD), 52 (30.2 %) are least concern (LC), seven (4 %) are near threatened (NT), 22 (12.8 %) are vulnerable (VU), nine (5.2 %) are endangered (EN), nine (5.2 %) are critically endangered (CR), two (1.2 %) are extinct (EX), and two have not been assessed (Table 8.1; Fig. 8.4). The majority of the species of Atyidae (64 %) are classified as LC and have a wide distributional range in lowland areas close to the coastline, while the 9 % of species in the NT category and the 18 % of the species in the VU category include the stygobitic *Typhlatya dzilamensis*, *Atya ortmannioides* and *Jonga serrei* that all have a very limited distributional range in Mexico. Only one species of atyid shrimp (*Potimirim mexicana*) was assessed as DD (Fig. 8.5).

Nineteen species (54 %) of Mexican palaemonids are least concern (LC), most of which are in the genus *Macrobrachium* and these have an extended larval development and a large distributional range at a continental scale. One fourth (26 %) of the Mexican palaemonids are DD, a number that includes recently described species and rare stygobitic species in the genus *Troglomexicanus*. One Mexican species (*Macrobrachium occidentale*) is NT due to its overexploitation as

Table 8.1 Freshwater decapods from Mexico with conservation status using IUCN protocols (IUCN) and the official Mexican Red List (NOM-59) (Nom-059-Semarnat-2010)

	IUCN	NOM-059
Family Atyidae		
Atya crassa (Smith, 1871)	LC	
Atya ortmannioides Villalobos, 1956	VU	
Atya scabra (Leach, 1815)	LC	
Atya margaritacea A. Milne-Edwards, 1866	LC	
Jonga serrei (Bouvier, 1909)[a]	na	
Potimirim glabra (Kingsley, 1878)	LC	
Potimirim mexicana (De Saussure, 1857b)	DD	
Typhlatya campecheae Hobbs and Hobbs, 1976	LC	P
Typhlatya mitchelli Hobbs and Hobbs, 1976	LC	A
Typhlatya pearsei Creaser, 1936	LC	A
Typhlatya dzilamensis Alvarez, Iliffe and Villalobos, 2005	NT	
Family Palaemonidae		
Creaseria morleyi (Pearse, Creaser, 1936)	LC	A
Cryphiops (*Bythinops*) *luscus* (Holthuis, 1973)	CR	
Cryphiops (*Bythinops*) *perspicax* (Holthuis, 1973)	LC	
Cryphiops (*Bythinops*) *sbordonii* Baldari, Mejía and López, 2010	DD	
Cryphiops (*Bythinops*) *villalobosi* Villalobos, Nates & Cantú, 1993	DD	
Macrobrachium acanthurus (Wiegmann, 1836)	LC	
Macrobrachium acherontium Holthuis, 1977	VU	P
Macrobrachium americanum Bate, 1868	LC	
Macrobrachium carcinus (Linnaeus, 1758)	LC	
Macrobrachium cosolapaense Mejía-Ortiz and López-Mejía, 2011	DD	
Macrobrachium crenulatum Holthuis, 1950	LC	
Macrobrachium digueti Bouvier, 1895	LC	
Macrobrachium heterochirus (Wiegmann, 1836)	LC	
Macrobrachium hobbsi Villalobos and Nates, 1990	LC	
Macrobrachium jacatepecense Mejía-Ortiz and López-Mejía, 2011	DD	
Macrobrachium mazatecum Mejía-Ortiz and López-Mejía, 2011	LC	
Macrobrachium oaxacae Mejía-Ortiz and López-Mejía, 2011	DD	
Macrobrachium occidentale Holthuis, 1950	NT	
Macrobrachium olfersii (Wiegmann, 1836)	LC	
Macrobrachium sbordonii Mejía, Baldari and López, 2008	LC	
Macrobrachium tenellum (Smith, 1871)	LC	
Macrobrachium totonacum Mejía, Alvarez and Hartnoll, 2003	LC	
Macrobrachium tuxtlaense Villalobos and Alvarez, 1999	VU	
Macrobrachium vicconi Román, Ortega and Mejía, 2000	LC	
Macrobrachium villalobosi Hobbs, 1973b	LC	A
Neopalaemon nahuatlus Hobbs, 1973b	DD	P

(continued)

Table 8.1 (continued)

	IUCN	NOM-059
Palaemon hobbsi (Strenth, 1994)	LC	
Palaemon kadiakensis (Rathbun, 1902)	LC	
Palaemon lindsayi (Villalobos and Hobbs, 1974)	CR	
Palaemon mexicanus (Strenth, 1976)	CR	
Palaemon paludosus (Gibbes, 1850)	LC	
Palaemon suttkusi (Smalley, 1964)	EN	
Troglomexicanus huastecae Villalobos, Alvareze and Iliffe, 1999	DD	
Troglomexicanus perezfarfantae (Villalobos, 1971)	DD	P
Troglomexicanus tamaulipasensis Villalobos, Alvareze and Iliffe, 1999	DD	
Family Alpheidae		
Potamalpheops stygicola (Hobbs, 1973a)	LC	P
Family Cambaridae		
Cambarellus (*Cambarellus*) *alvarezi* (Villalobos, 1952)	EX	
Cambarellus (*Cambarellus*) *areolatus* (Faxon, 1885)	CR	
Cambarellus (*Cambarellus*) *chapalanus* (Faxon, 1898)	NT	
Cambarellus (*Cambarellus*) *chihuahuae* Hobbs, 1980)	EX	
Cambarellus (*Cambarellus*) *lermensis* Villalobos, 1943	VU	
Cambarellus (*Cambarellus*) *montezumae* (De Saussure, 1857b)	LC	
Cambarellus (*Cambarellus*) *occidentalis* (Faxon, 1898)	LC	
Cambarellus (*Cambarellus*) *patzcuarensis* Villalobos, 1943	EN	
Cambarellus (*Cambarellus*) *prolixus* Villalobos and Hobbs, 1981	CR	
Cambarellus (*Cambarellus*) *zacapuensis* Pedraza-Lara and Doadrio, 2015[b]	na	
Cambarellus (*Cambarellus*) *zempoalensis* Villalobos, 1943	LC	
Orconectes (*Gremicambarus*) *virilis* (Hagen, 1870)[c]	LC	
Procambarus (*Austrocambarus*) *acanthophorus* Villalobos, 1948	LC	
Procambarus (*Austrocambarus*) *catemacoensis* Rojas, Alvarez and Villalobos, 2000	CR	
Procambarus (*Austrocambarus*) *cavernicola* Mejía-Ortíz, Hartnoll and Viccon, 2003	VU	
Procambarus (*Austrocambarus*) *citlaltepetl* Rojas, Alvarez and Villalobos, 1999	VU	
Procambarus (*Austrocambarus*) *llamasi* Villalobos, 1954b	LC	
Procambarus (*Austrocambarus*) *maya* Alvarez, López and Villalobos, 2007	DD	
Procambarus (*Austrocambarus*) *mexicanus* (Erichson, 1846)	DD	
Procambarus (*Austrocambarus*) *mirandai* Villalobos, 1954b	LC	
Procambarus (*Austrocambarus*) *oaxacae* Hobbs, 1973a	VU	
Procambarus (*Austrocambarus*) *reddelli* Hobbs, 1973a	VU	
Procambarus (*Austrocambarus*) *olmecorum* Hobbs, 1987	LC	
Procambarus (*Austrocambarus*) *pilosimanus* (Ortmann, 1906)	DD	

(continued)

Table 8.1 (continued)

	IUCN	NOM-059
Procambarus (*Austrocambarus*) *rodriguezi* Hobbs, 1943	DD	
Procambarus (*Austrocambarus*) *ruthveni* (Pearse, 1911)	VU	
Procambarus (*Austrocambarus*) *sbordonii* Hobbs, 1977b	DD	
Procambarus (*Austrocambarus*) *vazquezae* Villalobos, 1954b	NT	
Procambarus (*Austrocambarus*) *veracruzanus* Villalobos, 1954b	DD	
Procambarus (*Austrocambarus*) *zapoapensis* Villalobos,1954b	NT	
Procambarus (*Girardiella*) *regiomontanus* Villalobos, 1954a	CR	P
Procambarus (*Mexicambarus*) *bouvieri* (Ortmann, 1909)	EN	
Procambarus (*Ortmannicus*) *cuevachicae* (Hobbs, 1941)	LC	
Procambarus (*Ortmannicus*) *caballeroi* Villalobos, 1944b	LC	
Procambarus (*Ortmannicus*) *gonopodocristatus* Villalobos, 1958	DD	
Procambarus (*Ortmannicus*) *hidalgoensis* López-Mejía and Alvarez, 2005	LC	
Procambarus (*Ortmannicus*) *toltecae* Hobbs, 1943	LC	
Procambarus (*Ortmannicus*) *villalobosi* Hobbs, 1969	DD	
Procambarus (*Ortmannicus*) *xilitlae* Hobbs and Grubbs, 1982	DD	
Procambarus (*Paracambarus*) *ortmannii* (Villalobos, 1949)	CR	
Procambarus (*Paracambarus*) *paradoxus* (Ortmann, 1906)	CR	
Procambarus (*Pennides*) *roberti* Villalobos and Hobbs, 1974	EN	
Procambarus (*Procambarus*) *digueti* (Bouvier, 1897)	EN	
Procambarus (*Scapulicambarus*) *clarkii* (Girard, 1852)[d]	LC	
Procambarus (*Scapulicambarus*) *strenthi* Hobbs, 1977a	DD	
Procambarus (*Villalobosus*) *achilli* López-Mejía, Alvarez and Mejía, 2003	LC	
Procambarus (*Villalobosus*) *contrerasi* (Creaser, 1931)	EN	
Procambarus (*Villalobosus*) *chacalli* López-Mejía, Alvarez and Mejía, 2003	DD	
Procambarus (*Villalobosus*) *cuetzalanae* Hobbs, 1982	NT	
Procambarus (*Villalobosus*) *erichsoni* Villalobos, 1950	DD	
Procambarus (*Villalobosus*) *hoffmanni* (Villalobos, 1944a)	DD	
Procambarus (*Villalobosus*) *hortonhobbsi* Villalobos, 1950	EN	
Procambarus (*Villalobosus*) *riojai* (Villalobos, 1944a)	DD	
Procambarus (*Villalobosus*) *teziutlanensis* (Villalobos, 1947)	DD	
Procambarus (*Villalobosus*) *tlapacoyanensis* (Villalobos, 1947)	DD	
Procambarus (*Villalobosus*) *xochitlanae* Hobbs, 1975	DD	
Procambarus (*Villalobosus*) *zihuateutlensis* Villalobos, 1950	EN	
Family Parastacidae		
Cherax quadricarinatus Von Martens, 1868[c]	na	
Family Pseudothelphusidae		
Disparithelphusa pecki Smalley and Adkison, 1984	DD	
Ehecathusa chiapensis (Rodríguez and Smalley, 1969)	DD	

(continued)

Table 8.1 (continued)

	IUCN	NOM-059
Ehecathusa mixtepensis (Rodríguez and Smalley, 1969)	DD	
Lobithelphusa mexicana Rodríguez, 1982	DD	
Odontothelphusa apicpac Villalobos, García and Velázquez, 2010	DD	
Odontothelphusa lacandona Alvarez and Villalobos, 1998	DD	
Odontothelphusa lacanjaensis Alvarez and Villalobos, 1998	DD	
Odontothelphusa maxillipes (Rathbun, 1898)	NT	
Odontothelphusa monodontis (Rodríguez and Hobbs, 1989)	DD	
Odontothelphusa palenquensis Alvarez and Villalobos, 1998	DD	
Odontothelphusa toninae Alvarez and Villalobos, 1991	DD	
Phrygiopilus montebelloensis Alvarez and Villalobos, 1998	DD	
Phrygiopilus yoshibensis Alvarez and Villalobos, 1998	DD	
Potamocarcinus chajulensis Alvarez and Villalobos, 1998	DD	
Potamocarcinus hartmanni Pretzmann, 1975	VU	
Potamocarcinus magnus (Rathbun, 1895)	LC	
Pseudothelphusa americana de Saussure, 1857a	LC	
Pseudothelphusa belliana Rathbun, 1898	LC	
Pseudothelphusa dilatata Rathbun, 1898	LC	
Pseudothelphusa doenitzi Bott, 1968	DD	
Pseudothelphusa digueti Rathbun, 1898	LC	
Pseudothelphusa dugesi Rathbun, 1898	VU	P
Pseudothelphusa galloi Alvarez and Villalobos, 1990	DD	
Pseudothelphusa granatensis Rodríguez and Smalley, 1969	DD	
Pseudothelphusa guerreroensis Rathbun, 1933	DD	
Pseudothelphusa hoffmannae Alvarez and Villalobos, 1996	DD	
Pseudothelphusa jouyi Rathbun, 1893	LC	
Pseudothelphusa leiophrys Rodríguez and Smalley, 1969	DD	
Pseudothelphusa lophophallus Rodríguez and Smalley, 1969	DD	
Pseudothelphusa mexicana Alvarez, 1987	DD	
Pseudothelphusa morelosis Pretzmann, 1968a	LC	
Pseudothelphusa nayaritae Alvarez and Villalobos, 1994b	DD	
Pseudothelphusa nelsoni Rathbun, 1905	DD	
Pseudothelphusa parabelliana Alvarez, 1989	DD	
Pseudothelphusa peyotensis Rodríguez and Smalley, 1969	DD	
Pseudothelphusa rechingeri Pretzmann, 1965	DD	
Pseudothelphusa seiferti Hobbs, 1980	DD	
Pseudothelphusa sonorensis Miles, 1967	DD	
Pseudothelphusa sulcifrons Rathbun, 1898	DD	
Pseudothelphusa terrestris Rathbun, 1893	DD	
Pseudothelphusa zongolicae Alvarez, Villalobos and Moreno, (2012)	DD	
Raddaus bocourti (A. Milne Edwards, 1866)	LC	

(continued)

Table 8.1 (continued)

	IUCN	NOM-059
Raddaus tuberculatus (Rathbun, 1897)	DD	
Smalleyus tricristatus Alvarez, 1989	DD	
Spirothelphusa verticalis (Rathbun, 1893)	DD	
Sylvathelphusa cavernicola Villalobos and Alvarez, 2013	VU	
Sylvathelphusa kalebi Villalobos and Alvarez, 2013	VU	
Tehuana complanata (Rathbun, 1905)	DD	
Tehuana chontalpaensis Villalobos and Alvarez, 2003	DD	
Tehuana diabolis Pretzmann, 1968b	DD	
Tehuana jacatepecensis Villalobos and Alvarez, 2003	DD	
Tehuana lamellifrons (Rathbun, 1898)	DD	
Tehuana lamothei Alvarez and Villalobos, 1994b	VU	
Tehuana poglayenorum Pretzmann, 1968b	DD	
Tehuana veracruzana Rodríguez and Smalley, 1969	VU	
Typhlopseudothelphusa hyba Rodriguez and Hobbs, 1989	EN	
Typhlopseudothelphusa mociñoi Rioja, 1952	VU	P
Villalobosius leptomelus (Rodríguez and Hobbs, 1989)	VU	
Villalobosius lopezformenti Alvarez and Villalobos, 1991	VU	
Zilchia aspoekorum (Pretzmann, 1968a)	VU	
Zilchia poglayeneuwalli (Pretzmann, 1968a)	DD	
Family Trichodactylidae		
Avotrichodactylus bidens (Bott, 1969)	VU	
Avotrichodactylus constrictus (Pearse, 1911)	LC	
Avotrichodactylus oaxensis Rodríguez, 1992	DD	
Rodriguezia mensabak (Cottarelli and Argano, 1977)	VU	
Rodriguezia villalobosi (Rodríguez and Manrique, 1967)	DD	
Family Glyptograpsidae		
Platychirograpsus spectabilis De Man, 1896	na	

DD Data deficient; *LC* Least concern; *NT* Near threatened; *VU* Vulnerable; *EN* Endangered; *CR* Critically endangered; *EX* Extinct; *na* not assessed. Abbreviations used in the Mexican Red List classification: A, threatened; P, critically endangered

[a] Species recently collected in Mexico; assessed in its previously known range

[b] Species recently described

[c] Introduced species; assessed in its native range

[d] Conservation status in its native range LC, but also an introduced species in western and southern Mexico

a species of economic importance. Six Mexican palaemonid species have a reduced distributional range and are threatened with extinction: two species are VU (*M. tuxtlaense*, with abbreviated larval development, and *M. acherontium* a stygobiont), three species are EN (all *Palaemon*), and one species is CR (*Cryphiops luscus*).

The only freshwater species of alpheid shrimp in Mexico (*Potamalpheops stygicola*) is found in three caves in northern Oaxaca and is assessed as LC due to the lack of identified threats (Sánchez et al. 2007a).

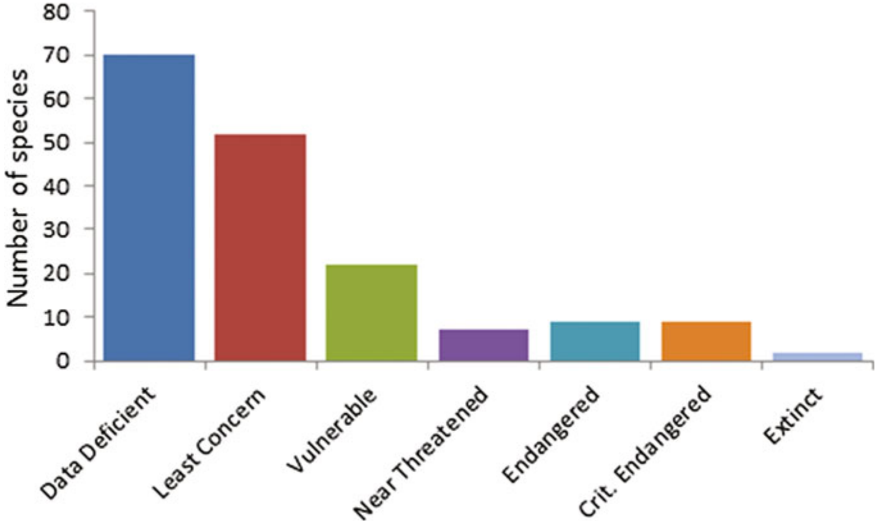

Fig. 8.4 Number of species of freshwater decapods from Mexico in each of the IUCN Red List categories

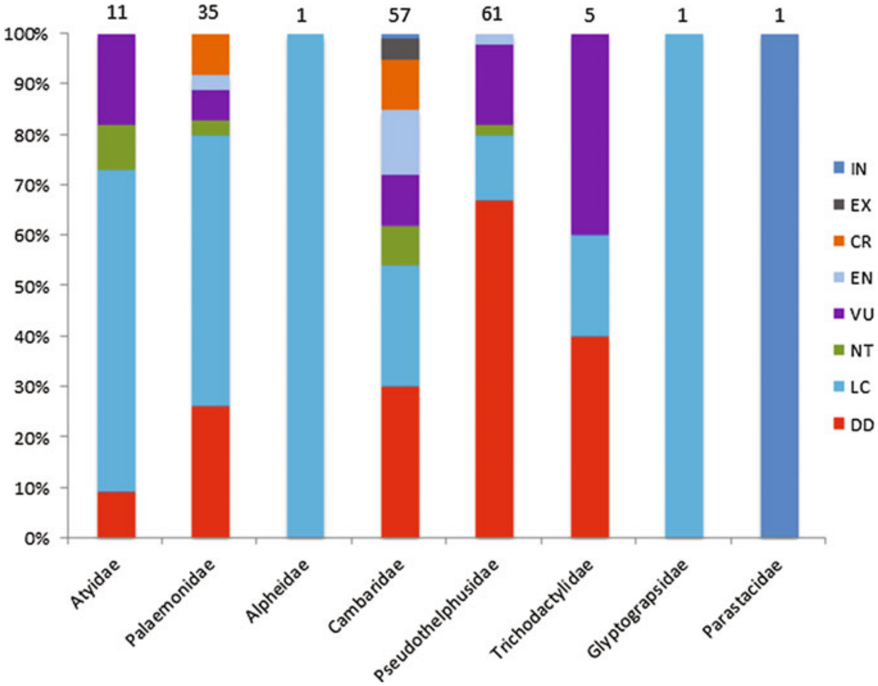

Fig. 8.5 Percentage of species by family of freshwater decapods from Mexico included in each of the seven threat categories of the IUCN Red List and introduced species

Cambarid crayfish are a diverse group with 56 Mexican species, excluding *Orconectes virilis*, assigned to seven of the eight IUCN Red List categories (Fig. 8.5). Seventeen (30 %) species are DD because they are only known from their original description and have not been collected again. Fourteen species (25 %) (e.g., *Cambarellus montezumae*, *Procambarus acanthophorus,* and *P. llamasi*) are LC and are widely distributed in rural areas and they have no identified threats. Five species are assessed as NT and VU (*Cambarellus chapalanus* and *Procambarus vazquezae* from Chapala and Catemaco Lakes, and *P. cavernicola*, *P. oaxacae* and *P. reddelli*) that are found in caves in river basins that might become developed in the near future. Seven species are assessed as EN: *C. patzcuarensis*, *P. bouvieri* and *P. digueti* (from the central lake district in Michoacan that is experiencing rapid development and pollution), *P. roberti* (from the endorreic Media Luna Lagoon in San Luis Potosi), and *P. contrerasi*, *P. hortonhobbsi* and *P. zihuateutlensis* (from either one or a few localities in northern Puebla). Five cambarids are critically endangered (CR); *C. areolatus* and *C. prolixus* (which have not been collected in many years), *P. catemacoensis* (from a small section of Lake Catemaco in Veracruz), *P. regiomontanus* (from the metropolitan area of the City of Monterrey in Nuevo Leon), and *P. ortmanni* and *P. paradoxus* (from two small creeks in northern Puebla). Two species of cambarids that were endemic to springs that no longer exist are now assessed as extinct (EX): *Cambarellus alvarezi* from southern Nuevo Leon, and *Cambarellus chihuahuae* from northern central Chihuahua (Rodríguez-Almaraz and Muñiz 2008).

Some 41 out of 61 species (67 %) of pseudothelphusids are data deficient (DD), are known only from the type specimen, and have not been collected a second time. Eight species (13 %) are LC because they have a wide distributional range in large river basins. One species, *Odontothelphusa maxillipes*, occurs from Veracruz to Chiapas but is classified as NT because most of the localities in its range lie in rapidly developing areas. Stygobitic species of *Typhlopseudothelphusa* and *Villalobosius* are classified as VU because they are known only from a single cave, as well as other VU species that occur near urban areas (e.g., *P. dugesi*) or agricultural districts (e.g., *P. hartmanni*). The stygobitic *Typhlopseudothelphusa hyba* is EN because it is only found only in one cave in Chiapas that is highly impacted with a disturbed habitat.

Two species (*Avotrichodactylus oaxensis* and *Rodriguezia villalobosi*) out of the five species of Mexican trichodactylid freshwater crabs are DD, while *A. constrictus* has a wide distributional range and is assessed as LC. Two other cave-dwelling species, *A. bidens* (Tabasco) and *Rodriguezia mensabak* (Chiapas) are assessed as VU because they live in highly disturbed cave habitat.

The glyptograpsid crab *Platychirograpsus spectabilis* is widely distributed in several Mexican states along the Gulf of Mexico and its conservation status has not been assessed, but it would probably be assessed as LC because it has no identified immediate threats.

8.6 Threats and Conservation Issues

The main threat to freshwater decapods in Mexico is the increasing demand for water from large-scale human activities such as agriculture (76.5 % of the total water extraction), urban supplies (14.5 %), industrial use (4 %), and thermoelectric power generation (5 %) (Torregrosa et al. 2015). The National Commission for the Study and Use of Biodiversity (CONABIO) has identified 110 Priority Hydrological Regions (RHP) for the study and conservation of biodiversity (Arriaga et al. 2000). It is estimated that 75 % of the RHP are rich in biodiversity, and that 70 % of these have serious conservation threats, while 26 % lack information on their conservation status (Arriaga et al. 2000). Overexploitation of groundwater for agriculture, and pollution of water bodies with agrochemicals are probably the most important problems.

Incomplete conservation assessments of species represent a serious hindrance to the protection of the freshwater decapod fauna in Mexico. The Nom-059-Semarnat-2010 (the official Mexican Red List of threatened species) includes only 12 of the 79 species of freshwater decapods, and this lack of knowledge hampers the implementation of special protection programs for the country's critically endangered species.

Introduced species in Mexican freshwater ecosystems represent a growing threat for the native freshwater decapod fauna. For example, the common carp *Cyprinus carpio*, that is native to China is now found in Mexico along the TMVB where it impacts populations of *Cambarellus montezumae*. Although carp are mainly herbivores they displace crayfish by modifying water quality through the removal of the macrophyte cover (except for floating plants), and by re-suspending sediments and increasing the turbidity (Hinojosa-Garro and Zambrano 2004). This is of concern because these carp are becoming established in a large number of water bodies elsewhere in Mexico, where their effect on native decapod species is unknown.

The Australian redclaw crayfish *Cherax quadricarinatus* represents another significant threat to native species in Mexico because it has spread rapidly following its accidental release in Tamaulipas and Morelos in the early 2000s (Alvarez et al. 2014b). There is no current evidence that *C. quadricarinatus* is affecting native decapod populations, however, these crayfish are known to transmit viruses, protists, and helminthes that may impact local populations in the future (Mendoza-Alfaro et al. 2011).

The red swamp crayfish *Procambarus clarkii* is native to northern Mexico and the southeastern United States (Campos and Rodríguez-Almaraz 1992) but it is also an introduced species in northwestern and southern Mexico (Hernández et al. 2008; Torres and Alvarez 2012). Introduced populations of *Procambarus clarkii* may soon have an impact in two areas of high native biodiversity where it is expanding its range: the Cuatro Ciénegas Valley in Coahuila and near to the City of Comitán in central Chiapas.

Two decapod species that have been introduced into Mexico but have not had an impact on the native fauna are the Malaysian river prawn *Macrobrachium rosenbergii* and the virile crayfish *Orconectes virilis. Macrobrachium rosenbergii* has been cultivated in many regions in Mexico but so far has not been reported to have escaped from aquaculture farms or to have established wild populations. *Orconectes virilis* has been captured over the years in the same restricted area in central Chihuahua and does not seem to be expanding its distributional range or to be interacting with any of the native species in the area.

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Chapter 9
Freshwater Decapod Diversity and Conservation in Central America and the Caribbean

Ingo S. Wehrtmann, Alonso Ramírez and Omar Pérez-Reyes

Abstract This chapter provides an overview of the species diversity and conservation status of the freshwater decapods in Central America and the Caribbean islands that date back to the late 1800s in both areas. The majority of the early studies were on taxonomy but our knowledge of freshwater decapod ecology (especially of freshwater shrimps from some Caribbean islands) has increased substantially over the last four decades. Currently, 86 species of freshwater decapods are known from Central America and the Caribbean. Here the decapod fauna comprises two families of primary freshwater crabs (Pseudothelphusidae and Trichodactylidae), three families of freshwater shrimps (Atyidae, Palaemonidae and Xiphocarididae), and one family of crayfish (Cambaridae). Several species have been introduced to this region for aquaculture and have now established wild populations. We also provide a list of Central American and Caribbean freshwater decapods that host parasites. To date, the conservation status of 43 % of all freshwater decapods in the region has been assessed using the IUCN Red List protocols; 5 % of these species are endangered or Critically Endangered, and two species (*Cambarellus alvarezi* and *C. chihuahuae*) are likely extinct. Cuba is the country with the most Vulnerable species (7 spp.), while Bermuda (2 spp.) and

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Barbados (1 sp.) have Critically Endangered species. The biodiversity of the freshwater decapod fauna of this region is still incompletely known despite recent efforts, and much more data need to be collected on species that are already known to be threatened with extinction, and on species that are too poorly known to assess. The high diversity of amphidromus caridean shrimps makes them especially vulnerable to threats from the modification of natural river systems such as the construction of dams for hydroelectric power or for water supply.

Keywords Latin America · Neotropics · Isthmus · Biodiversity · Conservation assessment · Decapoda

9.1 Introduction

Studies on the freshwater decapods of Central America and the Caribbean date back to the late 1800s. As in most areas of scientific research in Latin America, initial studies were carried out by scientists based outside of the region who relied museum specimens and material submitted to them by local naturalists. Today, in both regions, locally based researchers are leading the way.

9.1.1 Freshwater Decapod Research in Central America

Mary Jane Rathbun was the first author to describe species of freshwater crabs from Central America (Rathbun 1893), based on material from Nicaragua, Costa Rica, and Cuba, and specimens deposited in the collections of the United States National Museum. Rathbun (1896) revised the freshwater crabs of America and described two species of pseudothelphusid crabs from Costa Rica, which were sent to her by Mr. José Fidel Tristan from the Museo Nacional de Costa Rica. Rathbun (1898) concluded in the section about the distribution of Pseudothelphusinae: "Costa Rica has yielded the greatest number of species of any one region. This is due not to the superabundance of species in this State, but to the diligence of collectors, Mr. J. Fid Tristan and his colleagues of the National Museum of Costa Rica, at San José, and Mr. H. Pittier, of the Physical-Geographic Institute of Costa Rica, also in San José." During this early phase of exploration, Pesta (1931) published the results of the Austrian expedition to Costa Rica, which was carried out between March and September 1930, that included freshwater crabs and two freshwater shrimps (one palaemonid and one atyid) (Pesta 1931).

After this early period, decades passed by with no published information on freshwater decapods in the region. The second period of freshwater decapod research started with the description of a new genus of the family Atyidae by Alejandro Villalobos F. (Mexico) who obtained specimens from Dr. Fenner A. Chace of the Smithsonian Institution, and described *Archaeatya chacei* from Isla del Coco, an island located roughly 500 km off the Pacific coast of Costa Rica (Villalobos 1959). A few years later, Alfred E. Smalley (1963) from Tulane University, New Orleans, Louisiana, U.S.A., revised the genus *Potimirim* (Decapoda: Atyidae) from Central America and examined specimens from Nicaragua, Costa Rica, and Jamaica. Smalley (1964a, b) revised the freshwater crabs of Costa Rica (Pseudothelphusidae) and described their gonopods (Smalley 1964a); he also described two river crabs from Nicaragua (Smalley 1964b). Later, Smalley (1970) erected a new genus (*Phrygiopilus*) from Guatemala to accommodate two new species and provided an identification key for the Central American pseudothelphusids (Smalley 1970).

Important contributions on the river crabs of Central America were published by Richard Bott from the Forschungsinstitut Senckenberg, Frankfurt a.M., Germany. Bott (1956) revised material collected by A. Zilcher during his expedition to El Salvador in 1951 together with specimens from El Salvador and Honduras. Bott (1967, 1968) revised the pseudothelphusids of eastern Central America (including Costa Rica) based on material deposited in several European museums.

Gerhard Pretzmann of the Naurhistorisches Museum in Vienna, Austria published a great deal on the freshwater crabs of Central America. Pretzmann (1975) revised the genus *Pomatocarcinus* based on material from Guatemala, Nicaragua, and Panama. Pretzmann (1978, 1980) later revised the freshwater crabs of Central America and Mexico based on specimens collected by Ivo Poglayen-Neuwall from Costa Rica, Guatemala, Honduras, Nicaragua, and Panama. In the 1980s, other authors published studies of freshwater decapods: Abele and Kim (1984) described the endemic freshwater shrimp species *Macrobrachium cocoensis* and five other species of river shrimps from the Isla del Coco.

The decapod fauna of the subterranean waters of Central America was studied by Horton H. Hobbs III (Wittenberg University, Ohio, U.S.A., and the Smithsonian Institution, Washington D.C., U.S.A.) and Gilberto Rodríguez (Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela). These carcinologists described species inhabiting Central American caves in Belize (Hobbs Jr 1986), Costa Rica (Hobbs III 1991), and Guatemala (Rodríguez and Hobbs 1989, 1990). Reviews of troglobitic decapod crustaceans and their biogeography in the Americas were published by Hobbs et al. (1977) and Hobbs III (1994).

While all the above-mentioned studies were carried out by colleagues from the U.S.A. or Europe, Carlos R. Villalobos from the Escuela de Biología, Universidad de Costa Rica, was the first carcinologist from Central America to publish on freshwater decapods when he described two freshwater crabs from Costa Rica, *Ptychophallus costaricensis* and *Potamocarcinus nicaraguensis* (=*Potamocarcinus nicaraguensis* Rathbun 1893) (Villalobos 1974; Villalobos and Burgos 1975).

The study of freshwater decapods from Central America during the past few decades has expanded from taxonomic works to now including ecological and molecular studies. In 2010 a new species of pseudothelphusid (*Allacanthos yawi* Magalhães et al. 2010) was described from southern Costa Rica, Lara et al. (2013) studied the species diversity and distribution of river crabs inhabiting the basin of the río Grande de Térraba on the Pacific slope of Costa Rica, and Wehrtmann et al.

(2010) provided information on reproduction in pseudothelphusid crabs. A number of publications have focused on freshwater shrimps from the region: Alvarez Ruiz et al. (1996) and Lara and Wehrtmann (2009) described the reproduction in *Macrobrachium carcinus* from Costa Rica, and provided information on the diversity, abundance, and distribution of river shrimps in the largest river basin of Costa Rica (Lara and Wehrtmann 2011). Recently, Pileggi et al. (2014) presented a molecular perspective on the transisthmian *Macrobrachium* species and concluded that all sibling species studied by them were valid taxonomic entities, but not all sibling pairs formed natural groups.

9.1.2 Freshwater Decapod Research in the Caribbean

Research on freshwater decapods in the Caribbean dates back to the 1800s that were followed by major faunistic studies in the mid-1900s. The early reports included partial lists of freshwater decapods for Puerto Rico (Gundlach 1887–1894) and Dominica (Pocock 1889). The decapod fauna of the other islands remained poorly studied until the mid- 1900s when Curacao was included in the work by Chace and Holthuis (1948). Chace and Hobbs (1969) provided the first comprehensive review of freshwater decapods in the Caribbean, with particular emphasis on Dominica, and this study remains a valuable source of information for carcinologists interested in the decapod fauna of all islands.

Research on the biology and ecology of freshwater decapods in the Caribbean has increased rapidly during recent years, with several studies describing their role in aquatic ecosystems, as part of food webs and in processing organic matter. One of the most studied locations is El Yunque National Forest in Puerto Rico, with research focusing on ecological interactions among decapod and non-decapod species (Pringle et al. 1993; Crowl and Covich 1994; Pringle 1996; March et al. 1998, 2002; Johnson and Covich 2000; Cook et al. 2008a, b; Covich et al. 2009; Hein et al. 2011), the effects of natural and anthropogenic disturbances on the populations (Covich et al. 1991, 1996, 2003, 2006; March et al. 1998, 2003; Benstead et al. 1999; 2000; Greathouse et al. 2005; 2006; Hein et al. 2011), and nutrient recycling (Covich and McDowell 1996; Pyron et al. 1999; Crowl et al. 2001, 2006; March et al. 2001; March and Pringle 2003; Wright and Covich 2005; Cross et al. 2008; Benstead et al. 2010). All species of freshwater shrimps are amphidromous and their migratory behavior in the Caribbean has been studied in detail in Puerto Rico (Benstead et al. 1999) and Guadeloupe (Fièvet et al. 1999).

Caribbean freshwater decapods are widespread and many species are found living sympatrically. Recent genetic studies have assessed several aspects of decapod biology. Taxon cycling with sequential expansions and contractions of distributional ranges was supported by studies with *Atya* (Atyidae) in Puerto Rico, where most species studied undergo regional population expansions. Genetic studies (Cook et al. 2008a) on the Puerto Rican freshwater crab *Epilobocera sinuatifrons* (Pseudothelphusidae), a non-migratory species, suggested shallow but significant genetic isolation among populations, which were intermediate between highly divergent populations (e.g., terrestrial specialists) and highly connected populations (e.g., migratory shrimp; Cook et al. 2008b).

9.2 Regional Diversity of Freshwater Decapods

Three groups of freshwater decapods are found in the region: crayfish, shrimps, and crabs. Freshwater crayfish species are represented in the Neotropics by two families: Cambaridae (48 spp.) and Parastacidae (16 spp.) (Crandall and Buhay 2008). Representatives of five (sub) families of caridean shrimps have been reported to occur in the Neotropics (De Grave et al. 2008): Alpheidae (1 sp.), Atyidae (19 spp.), Palaemonidae (83 spp.), Euryrhynchinae (4 spp.), and Xiphocarididae (2 spp.). There are 312 species of primary freshwater crabs in the Neotropics in two families: Pseudothelphusidae (262 species) and Trichodactylidae (51 species) (Yeo et al. 2008). Cumberlidge et al. (2014) updated the available information about the biodiversity of freshwater crabs in the Neotropics and concluded that there are 313 species of pseudothelphusid and trichodactylid freshwater crabs. Overall, the Neotropics harbor a total of 485 freshwater decapods, which makes this region one of the most diverse areas, especially considering the biodiversity of freshwater crabs.

9.2.1 Central American Freshwater Decapod Diversity

Our knowledge of freshwater decapods inhabiting the Central American region stems principally from studies in Costa Rica, Guatemala, and Panama, although some information on freshwater crabs is available from other countries in the region (see this Sect. 9.1.1). Overall, the Central American region has 86 species of freshwater decapods, while the Caribbean has 61 species (Fig. 9.1).

Astacidea. Roughly 10 % of the 638 currently known freshwater crayfish species occur in the Neotropics (Crandall and Buhay 2008). However, reports of crayfish from Central America are scarce (Table 9.1) (Alvarez and Villalobos 2016): *Procambarus (Austrocambarus) pilosimanus* has been reported to occur in northern Guatemala and Belize by Villalobos-Figueroa (1955, 1983), Villalobos (1982), Hobbs (1989), and Alvarez and Villalobos (2015). *Procambarus* (*A.*) *williamsoni* is known to occur in Guatemala and Honduras (Alvarez and Villalobos 2016), and *P.* (*A.*) *llamasi* is found in northern Guatemala (Alvarez et al. 2007; Barba-Macías et al. 2015). Considering the similarities of these species, a closer examination of the morphology and the genetics of the material reported for Central America is highly recommended (JL Villalobos pers. comm.). A fourth species, *Procambarus* (*Scapulicambarus*) *clarkii* was introduced into Costa Rica in 1966 (Huner 1977). Torres and Álvarez (2012) compared the genetic variability of the

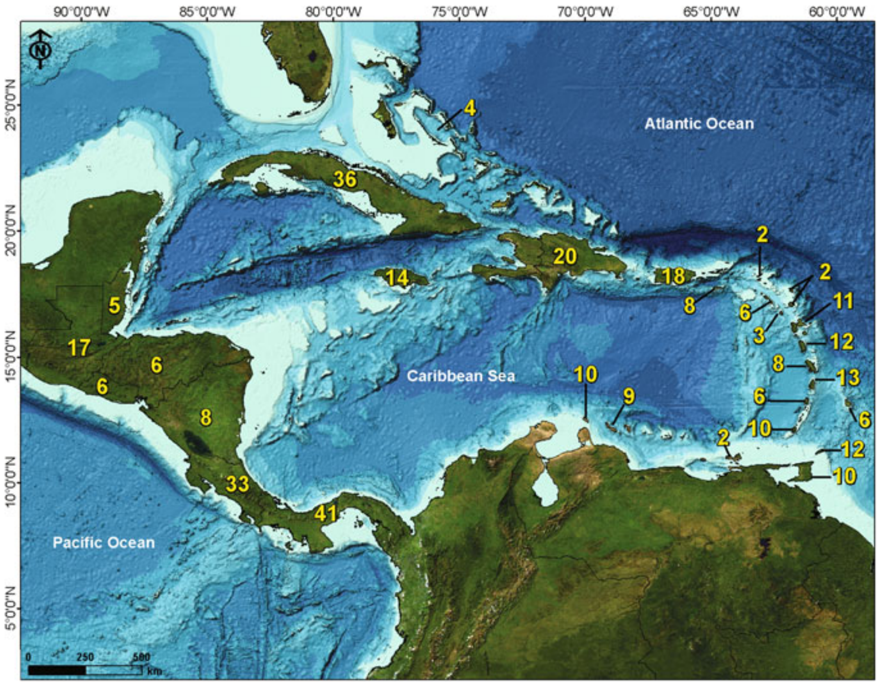

Fig. 9.1 Geographical distribution of the freshwater decapods from Central America from Belize to Panama (Astacidea, Atyidae, Palaemonidae, Pseudothelphusidae, and Trichodactylidae) and from the Caribbean to the Greater and Lesser Antilles (Atyidae, Astacidea, Grapsidae, Palaemonidae, Pseudothelphusidae, Trichodactylidae, and Xiphocarididae). *Numbers* represent the number of species per island/region. (*Background map source* The GEBCO_2014 Grid, version 20150318, http://www.gebco.net)

Costa Rican *P.* (*S.*) *clarkii* population with that of specimens of this species living in Mexico and concluded that the genetic variation of the native and introduced populations was equally low in both. *Cherax quadricarinatus* is also present in Costa Rica in the northwestern Pacific drainage near Guanacaste (RL Lara, pers. comm.). This species is native to freshwater habitats in northern Australia and Papua New Guinea and has been translocated worldwide due to its suitability for aquaculture (Ahyong and Yeo 2007).

Atyidae. According to a recent global assessment of freshwater shrimps (De Grave et al. 2015), atyid shrimps comprise 443 species (58.1 % of all the freshwater shrimp fauna) of which 37 % of atyid species are threatened with extinction. Atyid shrimps are widely distributed in Central America and are a common element of the freshwater decapod fauna (Table 9.1) (Smalley 1963; Hobbs and Hart 1982). The Atyidae in the region are represented by six genera (*Atya*, *Jonga*, *Micratya*, *Neorhynchoplax*, *Potimirim* and *Typhlatya*) with eleven species. The most speciose genera in Central America are *Atya* (*A. crassa*, *A. innocuous*, *A. margaritacea*, *A. scabra*) and *Potimirim* (*P. americana*, *P. glabra*, *P. poeyi* and *P. potimirim*).

Table 9.1 Presence/absence of freshwater decapod families in Central America and the Caribbean

Country/decapod family		Atyidae	Astacidea	Palaemonidae	Pseudothelphusidae	Trichodactylidae	Xiphocarididae	Selected references
Central America	Nicaragua	X	–	X	X	X	–	Rathbun (1893); Smalley (1964c); Pretzmann (1980); Rodriguez (1982); Magalhães and Türkay (2008)
	Honduras	X	X	X	X	–	–	Pretzmann (1980); Rodriguez (1982); Alvarez et al. (2005); Alvarez and Villalobos (2016)
	Guatemala	X	X	X	X	–	–	Pretzmann (1980); Rodriguez (1982)
	Panama	X	–	X	X	X	–	Rathbun (1893); Rathbun (1912); Pretzmann (1980); Rodriguez (1982); Magalhães and Türkay (1996, 2008); Magalhães et al. (2013)
	Costa Rica	X	X	X	X	–	–	Hobbs Jr (1986); Magalhães et al. (2015)
	Belize	X	X	X	X	–	–	Rathbun (1893); Rodriguez (1982); Hobbs Jr (1986); Magalhães and Türkay (1996, 2008)
	El Salvador	X	–	X	X	X	–	Holthuis (1954); Bott (1956); Rodriguez (1982)
Greater Antilles	Cuba	X	X	X	X	–	X	Chace and Hobbs (1969); Holthuis (1977); Rodriguez (1982); Hobbs (1984); Navarro-Pacheco et al. (1998); Juarrero (1993; 1999); Capolongo and Pretzmann (2002); Capolongo (2003); Rodríguez and Magalhães (2005)
	Hispaniola	X	–	X	X	–	X	Rodriguez (1982); Rodríguez and Williams (1995); Pérez-Gelabert (2008)
	Bahamas	X	–	X	–	–	–	Alvarez et al. (2005)
	Jamaica	X	–	X	–	–	X	Hart (1961); Schubart and Koller (2005)
	Puerto Rico	X	–	X	X	–	X	Chace and Hobbs (1969); Karge et al. (2013); Pérez-Reyes et al. (2013)

(continued)

Table 9.1 (continued)

Country/decapod family		Atyidae	Astacidea	Palaemonidae	Pseudothelphusidae	Trichodactylidae	Xiphocarididae	Selected references
Lesser Antilles	Trinidad	X	–	X	X	X	X	Rodríguez (1992); Rodríguez and López (2003)
	Guadeloupe	X	–	X	X	–	X	Rodriguez (1982); Fièvet et al. (1999)
	Martinique	X	–	X	X	–		Rodríguez and López (2003)
	Margarita	–	–	–	X	–	–	Rodríguez and López (2003)
	Dominica	X	–	X	X	–	X	Chace and Hobbs (1969); Rodriguez (1982); Rodríguez and López (2003); Bass (2004a, 2007)
	Saint Lucia	X	–	X	X	–	X	Barnish (1984); Thorpe and Lloyd (1999); Rodríguez and López (2003)
	Curacao	X	–	X	–	–	X	Debrot (2003)
	Antigua and Barbuda	X	–	X	–	–	–	Bass (2005)
	Barbados	X	X	X	X	–	–	Hobbs and Hart (1982); Felix (1991); Bass (2003a)
	Grenada	X	–	X	X	–	X	Hobbs and Hart (1982); Bass (2004b)
	U.S. Virgin Islands	X	–	X	X	–	X	Chace and Hobbs (1969); Hobbs and Hart (1982); Nemeth and Platenberg (2007)
	St. Vincent	X	–	X	X	–	X	Hobbs and Hart (1982); Rodriguez (1982); Rodríguez and López (2003);
	Tobago	X	–	X	X	–	X	Hynes (1971); Maitland et al. (2002); Bass (2003b)
	Saint Kitts and Nevis	X	–	X	–	–	X	Chace and Hobbs (1969); Bass (2006)
	Montserrat	X	–	X	–	–	–	Hobbs and Hart (1982)

Three species of *Atya* (*A. crassa*, *A. innocuous* and *A. scabra*) are found on both the Pacific and Atlantic coasts of Central America, while the fourth species (*A. margaritacea*) is restricted to the Pacific slope from Baja California southward to Peru (Hobbs and Hart 1982; Snyder et al. 2011). *Neorhynchoplax kempi* is native to Iraq, and may have been introduced into the Panama Canal along with an exotic aquarium plant (Abele 1972). The only reported troglobitic species from Central America is *Typhlatya utilaensis* from Utila Island, Honduras (Alvarez et al. 2005). Recently, Torati et al. (2011) surveyed 17 locations on several islands of the Bocas del Toro archipelago and the adjacent mainland of Panama, and provided information of the distribution of freshwater shrimps on a more regional scale. These authors documented the variability of the color pattern of five atyid species encountered in their study area (*A. scabra*, *J. serrei*, *M. poeyi*, *P. glabra*, and *P. potimirim*), and noted the extremely high color variability in *P. glabra*. The molecular phylogeny of shrimps of the genus *Potimirim* was studied by Torati and Mantelatto (2012) based on several atyid species from Central America (*J. serrei*, *M. poeyi*, *P. americana*, *P. glabra*, *P. potimirim*) and revealed *P. americana* to be the most basal species.

Palaemonidae. This family is one of the two dominant freshwater shrimp families worldwide and comprises 300 species (39.3 % of all currently known freshwater shrimp species), and 14.8 % of species of palaemonid freshwater shrimps are threatened with extinction (De Grave et al. 2015). In Central America (Table 9.1), several palaemonid species live in brackish water. For example, Lara and Wehrtmann (2011) reported the presence of *Palaemon gracilis* and *P. hancocki* from the estuarine zone at the mouth of the river Grande de Térraba on the Pacific slope of Costa Rica. Only palaemonid species of the genus *Macrobrachium* are widely distributed in the freshwater habitats of the region. Although the highest diversity of *Macrobrachium* is located in the Indo-Pacific region, more than 55 valid species out of the currently recognized 300 species (De Grave et al. 2015) are found in The Americas, which highlights the geographical importance of this region for the Palaemonidae (Holthuis 1952; Pileggi et al. 2014). So far, 13 species of *Macrobrachium* have been reported from Central America (Holthuis 1952; Lara and Wehrtmann 2011): *M. acanthurus*, *M. americanum*, *M. carcinus*, *M. cocoense*, *M. crenulatum*, *M. digueti*, *M. hancocki*, *M. heterochirus*, *M. occidentale*, *M. olfersi*, *M. panamense*, *M. rathbunae*, and *P. tenellum*. An additional species, *M. amazonicum*, has been reported to occur in Nicaragua and Costa Rica, but so far no specimens have been deposited in collections (Vergamini et al. 2011). In addition, *M. rosenbergii* has been introduced in Costa Rica for aquaculture (I.S. Wehrtmann, pers. commun.), but wild populations of this species have not yet been found. The only endemic species of freshwater shrimps in Costa Rica is *M. cocoense* from the Pacific island of Isla de Coco (Abele and Kim 1984). The geographic distribution of the genus *Macrobrachium* is generally confined to the Pacific or Caribbean slopes of Central America (Valencia and Campos 2007), with eight species on the Pacific slope (*M. digueti*, *M. hancocki*, *M. occidentale*, *M. olfersi*, *M. panamense*, *M. rathbunae*, *P. tenellum*, and *M. cocoense* from Isla del Coco), and five species on the Caribbean slope (*M. acanthurus*, *M. carcinus*, *M. crenulatum*, *M. heterochirus*, and *M. olfersi*). If confirmed, *M. amazonicum* would be the sixth species known from the Caribbean slope. Only *M. olfersii* has been reported from both the Pacific and Caribbean slopes of Central America (Anger 2013; Pileggi et al. 2014). The raising of the Isthmus of Panama about 3.1 million years ago (Keigwin 1978; Coates et al. 1992; Coates and Obando 1996; Anger 2013) has thus contributed to the formation of two distinct species groups on both sides of the landbridge (see Lessios 2008). However, despite of the geographic separation, some of the species on different sides of the country are extremely difficult to tell apart and were called "sibling species" by Knowlton (1993). Holthuis (1952) also referred to similar-looking pairs of species of *Macrobrachium* from the Caribbean and Pacific slopes as "sister species". Pileggi et al. (2014) assessed the relationship among the transisthmian sister species of *Macrobrachium* in a molecular phylogenetic context and confirmed all species to be valid, and that the following pairs of sibling species formed natural monophyletic groups (the first species is from the Pacific drainage, the second from the Caribbean slope): *Macrobrachium occidentale* – *M. heterochirus*, *M. americanum* – *M. carcinus*, *M. digueti* – *M. olfersii*, *M. hancocki* – *M. crenulatum*, and *M. tenellum* – *M. acanthurus*. Many *Macrobrachium* species are known for their amphidromous migrations (Bauer 2013) with larval development occurring in estuarine waters, while the adults inhabit freshwater habitats. Other *Macrobrachium* species are hololimnetic inland species, and their life cycle includes an abbreviated and lecithotrophic mode of larval development (Anger 2013; Bauer 2013). In Central America, all *Macrobrachium* species have an extended larval development, and their larvae need estuarine waters for successful development (Anger 2013). As far as we know, hololimnetic inland species are absent in Central America.

Pseudothelphusidae and Trichodactylidae. There are five families of primary freshwater crabs worldwide (Cumberlidge and Ng 2009) with more than 1306 species (Yeo et al. 2008; Cumberlidge 2015). Two of these families, the Trichodactylidae (51 species) and the Pseudothelphusidae (278 species) are endemic to the Neotropics. Representatives of both these primary freshwater crab families occur in Central America (Table 9.1) (Yeo et al. 2008; Cumberlidge et al. 2014), making a total of 50 species for this region (Pseudothelphusidae, 47 species) and Trichodactylidae (3 species) (Magalhães et al. 2015; C. Magalhães, unpubl. data). Central American pseudothelphusids belong to 12 genera. The most speciose genus is *Ptychopallus* (13 species from Costa Rica and Panama), followed by *Potamocarcinus* (8 species from Costa Rica, Guatemala, El Salvador, Honduras, Nicaragua, and Panama), and *Zilchia* (5 species from Belize, Guatemala and Honduras). Several genera are known only from either one or two countries: *Achlidon* (Costa Rica), *Camptophallus* (Nicaragua), *Spirocarcinus* (Panama), *Allacanthos* (Costa Rica and Panama), *Hypolobocera* (Panama and South America), and *Phrygiopilus* (Guatemala and Mexico). Panama (18 species) and Costa Rica (12 species) harbor the most diverse freshwater crab fauna in the region. However, the freshwater decapod fauna of these countries is the most studied in Central America, and future surveys in the other countries of the region are likely to discover several more new species (Yeo et al. 2008). The three species of trichodactylids from the region are *Trichodactylus quinquedentatus* and *Poppiana dentata* from Nicaragua, and *Melocarcinus meekei* from Panama (Magalhães and Türkay 2008; Magalhães et al. 2013).

Xiphocarididae. *Xiphocaris elongata* is widely distributed in the Caribbean (Chace and Hobbs 1969; also: see Sect. 9.2.2.) but has not been reported to occur in Central America (Table 9.1).

9.2.2 Caribbean Freshwater Decapod Diversity

Many species of Caribbean freshwater decapods live exclusively in freshwater and are completely independent of the marine environment, while other species (usually carideans) are tolerant of high salinities and have larval stages that need to develop in sea water (Bauer 2011a, b, 2013). These life cycle strategies add to the complexity of explaining how (and when) freshwater species reached the islands they are found on today. The more than 61 species of freshwater decapods found in the Antilles belong to seven families: Atyidae, Cambaridae, Grapsidae, Palaemonidae, Xiphocarididae Pseudothelphusidae, and Trichodactylidae (Table 9.1) (Chace and Hobbs 1969; Crandall and Buhay 2008; Cumberlidge et al. 2014). More species are found in the Greater Antilles than the Lesser Antilles probably because the wider variety of aquatic habitats in the Greater Antilles has resulted in more diversification (Fig. 9.1) (Pérez-Reyes et al. 2013). The islands in the Caribbean are classified in three categories: volcanic or coral origin islands with sediment uplift. These islands include: the Greater Antilles (Cuba, Hispaniola, Puerto Rico, Jamaica), and the Lesser Antilles (Dominica, Montserrat, Saint Lucia, Saint Thomas, Saint John, Tortola, Grenada, Saint Vincent, Guadeloupe, Martinique, Nevis, and Saint Kitts). Islands of volcanic or coral origin have a steep topography with elevations that range from as high as 3000 m (Pico Duarte, Dominican Republic) to 45 m below sea level (Enriquillo Lake, Dominican Republic, Hispaniola) (Kennedy et al. 2006). These island of volcanic or coral origin are forested and receive abundant rainfall, especially at higher elevations and during the rainy season (May–November) (Heartsill-Scalley et al. 2007). The streams and rivers of these islands typically have rocky substrates that increases the diversity of habitats (Smith et al. 2003). Trinidad and Tobago are continental islands on the continental shelf that belong to the northwestern South American transitional zone (Weeks et al. 1971, Morrone 2006). Other Caribbean islands (Aruba, Bonaire, Curaçao, Guadeloupe's Grand Terre, Antigua, Barbuda, Saint Martin, Anguilla, Barbados, Cayman Islands, and Saint Croix) have been formed by sediment uplift and have a flat low-lying topography, lack lush dense forests, and rainfall is low (Bass 2003b). Here the streams are intermittent or ephemeral and streambeds are typically composed by mud and silt (Bass 2003b).

Freshwater decapods are diverse and very common in both the island streams as well as in the coastal continental creeks and rivers. Streams on islands are dominated by species of freshwater decapods that fill the same ecological roles as the insects, amphipods, or isopods that dominate continental and temperate streams (Boulton et al. 2008). Freshwater shrimps found in streams and rivers on Caribbean islands live in all parts from river mouths to high altitude headwater streams. They have complex life cycles, and those species whose larval stages need to develop in marine or estuarine environments have migratory behavior (Bauer 2011a, b; Bauer 2013). Adult amphidromous shrimp mature and reproduce in freshwater, and females release larvae that move downstream to estuaries where they develop further and migrate back upstream as juveniles. The larvae of marine species of decapods are transported over wide areas by oceanic surface currents (Cook et al. 2008b, 2009; Page et al. 2008), and represents a stock for streams in Caribbean islands. Molecular and phylogenic analyses of species of freshwater shrimps from the Antilles and Central America (Cook et al. 2008b, 2009, 2012; Page et al. 2008, 2013) indicate that the amphidromous species of shrimp in the Caribbean share a common genetic pool.

Astacidea. All species of crayfish found in the Greater Antilles are endemic to their islands, and probably reached there by overseas dispersal on floating logs from Central America to the Greater Antilles (Hobbs 1984; Hobbs III 1994; Crandall and Buhay 2008). This is supported by experimental evidence that indicates that some species of crayfish are tolerant to changes in salinity and to drought (surviving for long periods buried in soil) (McClain and Romaire 2007). Three species of crayfish are found in the Greater Antilles: *Procambarus atkinsoni*, *P. cubensis* (with 2 subspecies), and *P. niveus*, and all are endemic to Cuba (Hobbs 1984; Sinclair et al. 2004). *Procambarus cubensis cubensis* has a widespread distribution in Cuba, *P. cubensis rivalis* is found in the western part of the island, *P. atkinsoni* is restricted to Isla de Pinos, and *Procabarus niveus* is a troglobitic species with a limited distribution in the western provinces. Several species of crayfishes have been introduced for aquaculture to Jamaica (*Cherax quadricarinata*), the Bahamas (*C. quadricarinata*), Hispaniola (Haiti and Dominican Republic), (*Procambarus clarkii*, *Pacifastacus leniusculus*), to Puerto Rico (*C. quadricarinatus*), and to islands in the Lesser Antilles (Williams et al. 2001; Kairo et al. 2003; Neal et al. 2009; Pienkowski et al. 2015).

Atyidae. Nineteen species of atyid shrimps are found in Antillean islands, 11 of which are endemic to these Caribbean islands: *Atya lanipes*, *A. brachyrhinus*, *Typhlatya garciai*, *T. monae*, *T. consobrina*, *T. elenae*, *T. garciadebrasi*, *T. iliffei*, *T. taina*, *T. kakuki*, and *Micratya cooki*. Eight species are found in freshwater streams and rivers in both Central America and the Caribbean islands: *Atya innocuous*, *A. scabra*, *Jonga serrei*, *Micratya poeyi*, *Potimirim americana*, *P. mexicana*, *P. potimirim*, and *P. glabra* (Bass 2003a, b, 2004a, b, 2005, 2006, 2007; Pérez-Reyes et al. 2013). *Atya lanipes* is the most basal and morphologically less specialized species of the *Atya* in the region and is found in Cuba, Jamaica, La Hispaniola, Puerto Rico and U.S. Virgin Islands (Hobbs and Hart 1982). The troglobitic genus *Typhlatya* is represented in the Antilles by seven species, five of which are endemic to Cuba (*T. garciai*, *T. consobrina*, *T. elenae*, *T. garciadebrasi*, and *T. taina*), one (*T. iliffei*) is endemic to Bermuda (Hunter et al. 2008), and one (*T. monae*) is found in Puerto Rico, Curacao, Hispaniola, and Barbuda (Botello et al.

2013). In addition, *Typhlatya kakuki*, from the Bahamas was described by Alvarez et al. (2005) (which closely resembles species from Cuba). Other taxa of freshwater shrimps from the region include *Micratya cooki* from Puerto Rico (Karge et al. 2013), and a potential new species of *Potimirim* sp. from Puerto Rico that is currently being described (F. L. Mantelatto pers. com.).

Pseudothelphusidae and Trichodactylidae. The freshwater crabs of the Caribbean belong to two families: Pseudothelphusidae and Trichodactylidae. The pseudothelphusids generally prefer higher altitude streams, but in this region these crabs are found in low altitude rivers throughout the aquatic ecosystems up to headwater streams at 3000 m above sea level, and most species can breathe air and are semiterrestrial in habit (Rodríguez 1992; Rodríguez and Magalhães 2005). Five genera of pseudothelphusids (out of 40) belonging to 15 species are found in the Caribbean (*Epilobocera*, *Neoepilobocera* *Rodriguezus*, *Guinotia*, and *Pseudothelphusa*) (Cumberlidge et al. 2014). Cuba has the highest diversity of pseudothelphusids in the region with two genera (*Epilobocera* and *Neoepilobocera*) and nine species (Capolongo 2003; 2005). Hispaniola (Haiti and Dominican Republic) has two species, *Epilobocera haytensis* (which has a wide distribution in the Dominican Republic and Haiti,) and *E. wetherbeei* (which is restricted to high altitude localities up to 2300 m above sea level in the island). *Epilobocera sinuatifrons* is found in Puerto Rico and Saint Croix (Chace and Hobbs 1969; Cook et al. 2008a), and this distribution implies a common origin on the Puerto Rico Bank (at a time when Puerto Rico and Saint Croix were part of a single land mass), that became separated recently when sea levels rose following the end of the most recent Ice Age about 10000 years ago (Larue 1994). The most recent status about the populations of *E. sinuatifrons* in Puerto Rico was described by Cook et al. (2008a) who reported genetic divergence in the populations from different rivers in the island, but their isolation may be recent because this species has not experienced a population expansion or a bottleneck. Trinidad and Tobago have two species of pseudothelphusids, the South American continental species *Rodriguezus garmani* and the endemic species *Microthelphusa odaelkae* (Cumberlidge et al. 2014).

The trichodactylid freshwater crabs live in lakes and lowland streams in tropical South America, but a few species are found in Mexico and Central America (Nicaragua), and the range of one mainland species (*Poppiana dentata*) extends to Trinidad (Rodríguez 1992), which is the only trichodactylid found on any Caribbean island (Cumberlidge et al. 2014).

Palaemonidae. The 16 species of Caribbean palaemonid freshwater shrimps live in fresh water and brackish water, and 12 species are found in West Indian freshwater habitats. The troglobitic genus *Troglocubanus* is endemic to Cuba (*Troglocubanus calcis*, *T. eigenmanni*, *T. gibarensis*, and *T. inermis*) and to Jamaica (*T. jamaicensis*) (Hobbs III 1994; Hobbs et al. 1994). The troglobitic species *Macrobrachium lucifugum* is found in caves and sinkholes in Cuba, Hispaniola, Barbados, Curacao, and Jamaica (Juarrero 1999; Debrot 2003; Anger 2013), and the range of the continental species *Macrobrachium jelskii* includes Trinidad and Tobago (Bass 2003b, 2004b), islands that are closest to the continent. In South America *M. jelskii* is found in Suriname, Venezuela, Brazil, Peru

Paraguay, and Argentina, Five species of *Macrobrachium (M. acanthurus*, *M. carcinus*, *M. crenulatum*, *M. heterochirus*, and *M. faustinum)* are distributed throughout Central America and the Caribbean Islands (Pérez-Reyes et al. 2013). *Palaemon pandaliformis* is common in brackish waters in Cuba, Saint Kitts and Nevis, Tobago, Saint Lucia, Puerto Rico, and Barbados (Pérez-Reyes et al. 2013). The presence of the Asian species *Macrobrachium rosenbergii* in several Caribbean islands is likely the result of the introduction of this species for aquaculture and its subsequent release or escape (Anger 2013).

Xiphocarididae. Caribbean freshwaters are inhabited by two species of xiphocarids: *Xiphocaris gomezi* and *X. elongata*, that are distinguished by their retention of primitive characters of the exopods of their pereiopods (Chace and Hobbs 1969). *Xiphocaris gomezi* is endemic to Cuba and is known from shallow pools with a high density of organic matter at three high altitude localities (600 m above sea level) where it lives sympatrically with *X. elongata*, *A. lanipes*, and species of *Macrobrachium* (Juarrero 1993; Navarro-Pacheco et al. 1998; De Grave 2013). *Xiphocaris elongata* has a widespread distribution in the Antilles and occurs in large numbers in streams and rivers draining into low-altitude valleys near river mouths, where they tolerate daily fluctuations in salinity. Populations of *X. elongata* that live in headwaters are predated by palaemonid shrimp, pseudothephusid crabs, and freshwater fishes. Populations of *X. elongata* that are heavily predated by fish have evolved a longer rostrum (>5 mm) that presumably deters attacks by predators (Ocasio-Torres et al. 2014, 2015).

9.2.3 Species that Are Vectors of Parasites

In many regions of the Caribbean and Central America freshwater decapods are not only an important component of the stream ecosystem (Covich and McDowell 1996), they are also part of the diet of the local human communities (Wehrtmann et al. 2014). The potential for the spread of parasites and diseases increases along with increasing aquaculture of decapods with the introduction of non-native freshwater organisms. For example, when bopyrids infect juvenile shrimp it slows their growth, while trematodes such as *Paragonimus*, the human lung fluke, infect mammal definitive hosts that feed on freshwater crabs.

Paragonimiasis. Paragonimiasis is a foodborne parasitic zoonosis caused by lung flukes of the genus *Paragonimus* (Fürst et al. 2012). Species of *Paragonimus* are parasites of wild carnivores, domestic carnivores, and humans. Carnivores and humans acquire the disease when they eat uncooked/undercooked crustaceans that are infected with lung fluke metacercariae. Once the parasite has been ingested it migrates from the intestine to the lungs where it develops into encysted resident adult worms (Acha and Szyfres 2003). Humans with paragonimiasis can develop additional medical complications if parasites migrate to different organs besides the lungs, including the brain (Procop 2009). *Paragonimus* species are highly evolved parasites with a complex life cycle that involves three hosts: a snail, a crustacean, and a mammal (Doanh et al. 2013). *Paragonimus mexicanus*, reported from Colima, Mexico, and *P. caliensis* from Colombia are important pathogens in Central and South America (Brenes et al. 1985; Calvopiña et al. 2014). Freshwater crabs serve as the second intermediate host of *Paragonimus* and are infected by cercariae that then develop inside crabs into metacercariae, the most infective stage for mammals. *Paragonimus mexicanus* has been found in 14 out of the 278 species of Pseudothelphusidae (Lamothe-Argimedo 1995), while *P. caliensis* has been found in four species of freshwater crabs (Rodríguez and Magalhães 2005) (Table 9.2). The incidence of *P. mexicanus* in endemic areas of the parasite from Mexico to Panama is very high and 85 % of the studied crabs (*Ptychophalus tristani*) were infected with *Paragonimus* metacercariae (Monge et al. 1985).

The life cycle of *Paragonimus* requires two intermediate hosts (one snail, one crustacean), and a final definitive host (a mammal) (Calvopiña et al. 2014). Eggs of the adult parasites are released by the mammal host into a freshwater body where they hatch after 2–3 weeks and release a miracidium that infects a snail. Inside the snail the miracidia develop into cercariae that are then released into the water where crabs (and crayfish) become infected (Calvopiña et al. 2014).

In Latin America, *Paragonimus* infections in humans are associated with the ingestion of raw or undercooked freshwater crabs in traditional dishes such as the locally called "ceviche", where crabs are marinated in citrus juice that does not kill the parasites (Blair et al. 2008). The spread of the parasite in Central America is enabled by commercial or artisanal fishermen who import crabs from areas where the parasite is endemic.

Bopyrids. Epicaridean isopods (bopyrids) are ectoparasites of other crustaceans that live in the gill chambers of their crustacean hosts where they gain entry to the body and either sterilize them completely, or reduce the rate of gametogenesis (Beck 1980) and reduce the rate of respiration and the metabolic rate in general (Chaplin-Ebanks and Curran 2007). In the Caribbean and Central America the isopod *Probopyrus pandalicola* infects freshwater shrimps of the genera *Macrobrachium* and *Palaemon* (Kensley and Schotte 1989; Bunkley-Williams and Williams 1998) (Table 9.2). *Probopyrus pandalicola* hatches as an epicaridium larva that swims and attaches to a copepod (the intermediate host) where the larva molt and metamorphosize into an infective stage (cryptoniscus) that leaves the copepod host and infects the final host (a shrimp) (Cash and Bauer 1993). Inside the shrimp the first larval parasite stage (cryptoniscus) is a female that then develops into a dwarf male that lives attached to a female. The parasite then increases in size until it compresses and atrophies the gills and internal organs (Schuldt and Rodrigues-Capítulo 1985). These infections end in the production of thousands of bopyrid larvae and the death of the crustacean host that failed to reach maturity.

The effect of bopyrids varies from species to species. Female parasites feed on host haemolymph by piercing a blood sinus usually on the inside wall of the gill chamber where the parasite consumes up to 25 % of the host's haemolymph in a day (Lester 2005). As a result of this blood removal, the parasite sequesters the host's energy intake and lowers the host's egg production (Anderson 1977). Parasitized shrimps have less energy to capture food and migrate to breeding sites

Table 9.2 Species of freshwater decapods from Central America and the Caribbean that host parasites

	Parasite	Host	Localities	Reference
Crustacea: Isopoda	*Probopyrus pandalicola* (Packard, 1879)	*Macrobrachium acanthurus* *Macrobrachium amazonicum* *Macrobrachium boneli* *Macrobrachium carcinus* *Macrobrachium faustinum* *Macrobrachium ohione* *Macrobrachium olfersii* *Macrobrachium surinamicum* *Palaemon pandaliformis*	Cuba, La Hispaniola, Puerto Rico, Virgin Islands, Panama, Costa Rica, Nicaragua, Martinique, Curacao	Bunkley-Williams and Williams (1998) Kensley and Schotte (1989)
Platyhelminthes: Trematoda	*Paragonimus mexicanus* Miyazaki and Ishii, 1968	*Odonotelphusa maxillipes* *Potamocarcinus magnus* *Pseudothelphusa belliana* *Pseudothelphusa dilatata* *Pseudothelphusa nayaritae* *Pseudothelphusa propinqua* *Pseudothelphusa terrestris* *Ptychophalus coclensis* *Ptychophalus costaricensis* *Ptychophalus richmondi* *Ptychophalus tristani* *Ptychophalus tumimanus* *Raddaus bocourti* *Raddaus tuberculatus*	Mexico, Costa Rica, Guatemala, Panama, Honduras, Nicaragua	Brenes et al. (1985) Calvopiña et al. (2014) Lamothe-Argimedo (1995) Monge et al. (1985) Rodríguez and Magalhães (2005) Vélez et al. (2003)
Platyhelminthes: Trematoda	*Paragonimus caliensis*	*Pseudothelphusa dilatata* *Potamocarcinus magnus* *Ptychophalus exilipes* *Ptychophalus tristani*	Costa Rica, Panama	Rodríguez and Magalhães (2005)

(Somers and Kirkwood 1991) and suffer reductions in their fecundity and structural changes in their appendages (Anderson 1977; Calado et al. 2008; Williams and Boyko 2012).

Bopyrids cause castrations, stunting, the lack of development of secondary sexual characteristics, and increased mortality to their shrimp and crab hosts, and have direct and indirect effects on crustacean fisheries (De Castro 1985). A high prevalence of bopyrids in commercial species results in financial losses from stunting and mortality of crabs and shrimps.

9.3 Conservation Status

A total of 130 decapod species have been reported from freshwater ecosystems in Central America (86 spp.) and the Caribbean (61 spp.). Most species are still poorly studied beyond their taxonomy and distribution. According to the IUCN Red List, the conservation status of only 53.8 % of all decapod species in the region is known (Table 9.3), and the remaining species (46.2 %) are too poorly known to assess (Data Deficient). Three species (*Atya brachyrhinus*, *Procaris chacei*, *Typhlatya iliffei*) are threatened with extinction (Critically Endangered), two species (*Macrobrachium occidentale*, *Troglocubanus eigenmanni*) are Near Threatened, and none are extinct.

The number of threatened species (Vulnerable (VU) and Critically Endangered (CR)) varies among countries. Bermuda has two species that are CR and Barbados has one species that is CR. The highest number of VU species are found in Cuba (7 species), Guatemala (4 species), and Costa Rica (2 species). *Thyphlatya* has 5 species of threatened species, *Troglocubanus* has 4 species, and *Epilobocera* has 2 species. The remaining genera are represented by single threatened species. Cuba, El Salvador, Guatemala, and Margarita all have one species that is assessed as not currently threatened (Near-Threatened NT), but that may become threatened in the future if threat levels were to increase.

Almost half (46.2 %) of the freshwater decapods from Central America and the Caribbean are too poorly known to assess (Data Deficient) (Table 9.3). On a global scale, the level of data deficiency of freshwater shrimps is 37.0 % (De Grave et al. 2015), 49.1 % for freshwater crabs (Cumberlidge et al. 2009), and 21.2 % for

Table 9.3 Conservation status of the 130 freshwater decapod species so far reported for Central America and the Caribbean

Status	%
Not evaluated	22.0
Data Deficient	24.2
Least Concern	38.6
Vulnerable	11.4
Endangered	0.0
Critically Endangered	2.3
Near Threatened	1.5
Extinct	0.0

crayfish (Richman et al. 2015). Clearly, more studies are needed to fill these knowledge gaps and to provide sufficient information for a more complete assessment of the extinction risks of the freshwater decapod fauna in Central America and the Caribbean.

9.4 Threats and Conservation Issues

Like all freshwater fauna, decapods face a series of threats associated with changes in their environment. Here we focus on three major impacts from the large diversity of anthropogenic activities that result in ecosystem degradation and loss of fauna. First, loss of access to the ocean for freshwater species is important for island and coastal decapod populations; second, changes in land use cover (including urbanization) have led to the degradation of freshwater ecosystems, and third, fishing has had a major impact on decapod populations.

9.4.1 Loss of Ocean Connectivity

Connectivity with the oceans is a key aspect of ecosystem integrity for freshwater ecosystems. Hydrologic connectivity refers to the water-mediated movement of matter, energy, or organisms among components of the landscape (Pringle 2001). For stream and river ecosystems longitudinal connectivity joins downstream ecosystems including estuaries with upstream ecosystems. The free movement of decapods up and down stream networks is a key factor in conserving the long-term stability of populations of freshwater decapods in Central America and the Caribbean because it allows for the completion of life cycles in migratory species and facilitates genetic exchange between populations. Although there are primary freshwater species in the region, a number of species of decapods are secondary freshwater (amphidromous) species whose adult populations live in freshwater ecosystems but whose eggs and larval stages require salt or brackish water to develop into juveniles. Newly hatched larvae migrate downstream to marine environments where they grow into juveniles, which then migrate back into freshwater to complete their life cycle.

River damming is one of the main drivers of longitudinal connectivity loss in rivers. In temperate regions the negative effects of dams on species such as anadromous fish like salmon that migrate annually upstream to spawn are well known, and has both economic and conservation importance (Zabel and Williams 2002). In tropical areas, less is known about the effects of dams and other in-channel structures on freshwater organisms, despite the fact that many decapods and over 200 species of fish are diadromous (Milton 2009). Builders of dams across tropical rivers that include fish ladders for migratory fish to navigate the obstruction base their design on the needs of anadromous fish such as salmon, that are often still impassable for many other native freshwater species (McCully 1996). Dams block the downstream movement of the larvae of amphidromous tropical decapods, and the reservoir and water intakes become a major source of larval mortality (Benstead et al. 1999). Similarly, juvenile shrimps migrating upstream are able to climb over waterfalls and small dams with water flowing over vertical walls, but large dams are impervious migratory barriers for juvenile shrimps.

Connectivity of freshwater ecosystems with the ocean creates a particularly complex conservation problem, because most protected areas are not designed to protect entire watersheds. In Puerto Rico protected areas are either located on the upper parts of the mountains (e.g., El Yunque National Forest) or in the lowlands (e.g., Guánica State Forest). The importance of these reserves for the conservation of native decapods will depend on the location of the large dams that are built downstream from them, because of dams, reserves only partially protect decapod populations. All watersheds with a large dam on them (dam wall of >30 m) lack native fish and shrimp in their upper reaches (Holmquist et al. 1998; Cooney and Kwak 2013). Although large dams have drastic effects on amphidromous decapod populations, small dams and water intakes are a major conservation threat due to the high incidence of larval mortality.

El Yunque National Forest is one of the best-protected areas in Puerto Rico. The upper parts of El Yunque had been under some type of protection for over 200 years because the Spanish Crown set aside the mountains as a source of wood. The lowlands in Puerto Rico are heavily urbanized, but most rivers lack major dams. However, the rivers draining El Yunque are important sources of water for human consumption and at least 60 % of the runoff is diverted toward municipal facilities to be used as drinking water (Crook et al. 2007). Studies of migratory shrimp larvae show a clear nocturnal migration by the shrimp and that there is a high larval mortality due to water abstraction. Water abstraction in one of the main watersheds draining El Yunque accounts for between 30 and 60 % of decapod larval mortality, depending on the amount of water extracted (Benstead et al. 1999). Given the preference for shrimps to migrate at night, larval mortality could be greatly reduced by simple management practices that could include stopping water extraction for a few hours each night.

9.4.2 Land Cover and Land Use

A major cause of ecosystem degradation and a threat to decapod conservation is the conversion of land use from natural vegetation to agricultural use or urban development. Changing land use alters the water physicochemistry and habitat characteristics of freshwater ecosystems and creates new conditions that are often adverse for native biota. The sediment delivery rates of streams affect channel morphology and substrate composition (Chin 2006), the physicochemical characteristics of the stream water are often affected by nutrient loads from nearby agricultural activities (Herlihy et al. 1998; Jones et al. 2001). Urbanization is perhaps the most extreme type of land use conversion because urban freshwaters often carry large solute loads, have altered geomorphologies, and are often inhabited by exotic species (Walsh et al. 2005). The effects of changes in land cover use on freshwater decapod populations clearly can follow complex pathways, with numerous indirect effects and unknown mechanisms.

Freshwater macroinvertebrate assemblages change their abundance and species composition in response to changes introduced by inland use (Maloney and Weller 2011), but decapods do not seem to follow this general response. In Puerto Rico, shrimp assemblages are abundant and diverse in forested, agricultural, and urban streams and do not show evidence of assemblage degradation (Kwak et al. 2007). Comparisons of shrimp assemblages in watersheds with different levels of urbanization in Puerto Rico showed similar decapod species composition and densities, and appeared to unaffected by watershed land use (Pérez-Reyes et al. 2016). The loss of species richness and abundance of freshwater shrimps (*Atya lanipes*, *A. innocous*, *A. scabra*, *Macrobrachium carcinus*) in urban streams on tropical islands such as Puerto Rico is the result of a series of human stressors that have degraded decapod habitat (Pérez-Reyes et al. 2016).

The migratory behavior and the vulnerability of decapod populations to the loss of connectivity of their home streams with the ocean are more important than land use changes when explaining the presence of decapods at a particular location. Urban streams that keep a connection with the ocean maintain their shrimp assemblages (Pérez-Reyes et al. 2016) but both urban and forest streams above large dams are likely to be either completely devoid of shrimps or only have relic populations (Fig. 9.2).

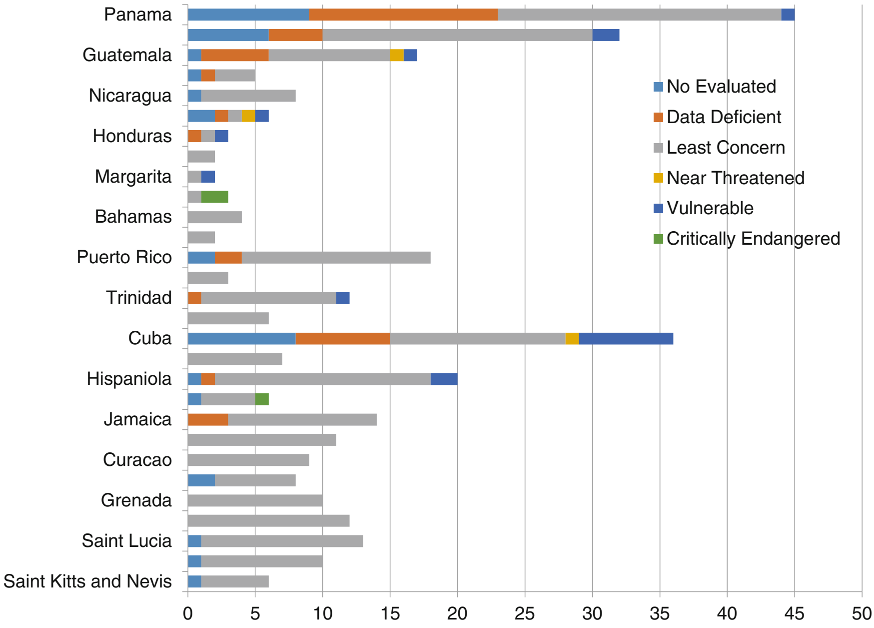

Fig. 9.2 Percentage of freshwater decapod species in each of the IUCN Red List categories (Least Concern, Near Threatened, Vulnerable, and Critically Endangered) for Central America and Caribbean countries

9.4.3 Fishery Impacts

In Central America as well as in the Caribbean freshwater decapods are an important source of protein for humans, and the harvesting of these crustaceans is a common practice, making overharvesting an important conservation issue. Traditional harvesting techniques involve either the use of traps, or snorkeling and harpooning of individuals. The almost complete lack of fishery data is a major problem when trying to assess the impact of the exploitation of shrimps and crabs inhabiting freshwater habitats. Shrimps (*Macrobrachium* spp.) are the main targets of recreational fisheries in the region (Figs. 9.3 and 9.4) and in rural areas are harvested for personal consumption and for restaurants (I. S. Wehrtmann, pers. obs. in Costa Rica). The impacts of the recreational fisheries on populations of *M. olfersi* in lowland Neotropical streams in Costa Rica revealed a sharp decline (87 %) in relative abundance between recent and historical data, and one possible explanation for the observed decrease was direct harvesting of adult shrimps (Snyder et al. 2013). An assessment of the recreational fishery of freshwater shrimps is urgently needed in order to develop adequate management protocols and to obtain a better understanding of the impact and sustainability of local fishing activities on the populations of freshwater shrimps and crabs.

Fig. 9.3 Typical bamboo trap for *Macrobrachium* used in an artisanal fishery in northern Costa Rica (Photo courtesy of R. L. Lara)

Fig. 9.4 Wooden container for maintaining live specimens of *Macrobrachium carcinus* caught in northern Costa Rica (Photo courtesy of R. L. Lara)

Harvesting of freshwater shrimp in Costa Rica may include the illegal poisoning of river sections with chlorine bleach or even stronger chemicals, which kill not only shrimps and other macroinvertebrates but also smaller fishes; the consumption of these fishes may lead to serious health consequences, especially for children (Greathouse et al. 2005; J. Picado, pers. comm. from Costa Rica). Studies on the impacts of these illegal chemical releases on ecosystems are scarce. Greathouse et al. (2005) documented ecosystem structure, function, and biotic interactions three months after a chlorine bleach poisoning event in a stream in Puerto Rico, and found a rapid recovery of the habitat and the organisms in it. Shrimp abundances after three months were either unchanged or even greater, but the effect of repeated poisoning of the same stream is unknown, and may have severe impacts on the ecosystem and the abundance of the shrimps and other organisms living there.

9.5 Perspectives

A series of recent publications have addressed the diversity, conservation status, threats, and conservation actions on a global scale for freshwater crabs (Cumberlidge et al. 2009, 2014), crayfish (Richman et al. 2015), and freshwater shrimps (De Grave et al. 2015). Here we provide a regional view of the diversity and conservation of freshwater decapods in Central America and the Caribbean, which is certainly not completed and needs to be continued. For example, the freshwater decapods in Honduras and Nicaragua in Central America and in Haiti/Dominican Republic in the Caribbean are still poorly studied, and intensive biotic surveys in these areas are needed to extend our knowledge on the decapod fauna. Species discovery rates over time of freshwater shrimps (De Grave et al. 2008) and freshwater crabs (Yeo et al. 2008) are still climbing steeply and show no sign of flattening out (except perhaps for the trichodactylid freshwater crabs), and additional sampling will provide valuable data on the distribution of known species, and discover a number of new species. For example the freshwater crab *Allacanthos yawi* (Magalhães et al. 2010) was recently described from the Pacific slope of Costa Rica whose freshwater decapod fauna is relatively well-studied (Magalhães et al. 2015).

An improved assessment of the freshwater decapod fauna in Central America and the Caribbean faces a major obstacle given the current lack of experienced taxonomists (Pearson et al. 2011). It is necessary therefore to increase our efforts to train more students in the identification of freshwater decapods, to establish collaborations with experienced taxonomists outside the region, and to organize regional workshops to bring together young scientists and students interested in the topic.

Support to regional museums is also critical. Collected material needs to be deposited in official museum-based collections, preferably located directly in the region. Museum collections are cornerstones of traditional taxonomy and systematics and they also play a critical role in studies of the effects of environmental changes on organisms over time. However, these contributions have been widely unappreciated by decision makers, resulting in insufficient financial support for their maintenance and improvement (Suarez and Tsutsui 2004). Not surprisingly, only a few countries in Central America and the Caribbean have museums with zoological collections maintained by a curator and technical staff (Alonso-Eguíalis et al. 2014a). As a consequence many valuable specimens are simply stored in laboratories and offices and are inaccessible to taxonomists which impedes biodiversity studies in the region. There is clearly a need to develop a regional plan for the inclusion and curation of all preserved specimens of freshwater decapods currently in unofficial collections.

Our understanding of the true diversity of the freshwater decapod fauna of Central America and the Caribbean would be greatly enhanced by studies that combine taxonomic and molecular techniques. Several widespread freshwater species in Central America and the Caribbean include morphologically variable specimens from different parts of the range but species boundaries are difficult to identify (Pileggi et al. 2014) and these taxa may prove to represent species complexes comprising one or more cryptic species.

Pollution, climate change, human disturbance, invasive species, modification of natural ecosystems, and mining represent the greatest threats to species of caridean shrimps from Central America and the Caribbean that are threatened with extinction (De Grave et al. 2015). In addition, the modification of natural river systems by

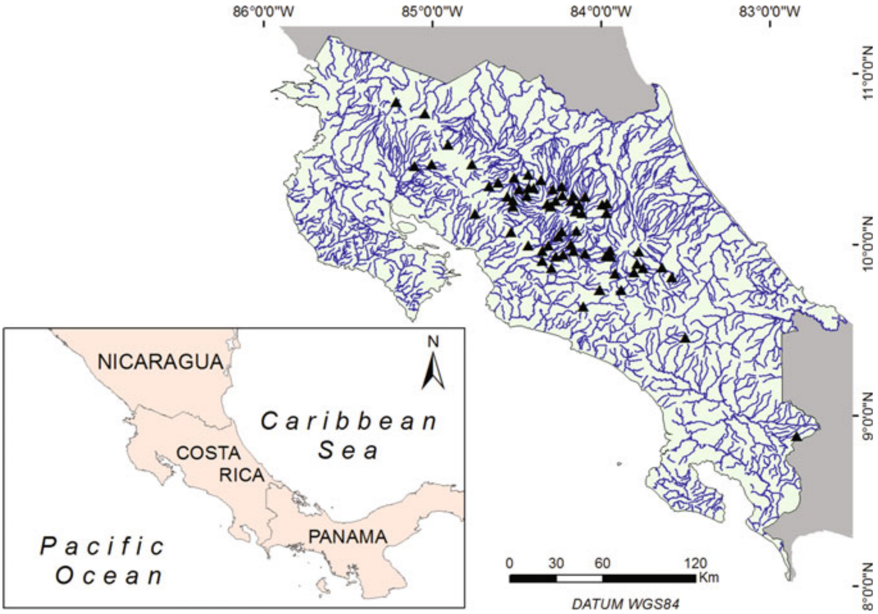

Fig. 9.5 Location of existing hydroelectric plants in Costa Rica (excluding those under construction or at the planning stage).

constructing dams across rivers to either generate hydroelectric power or to create a reservoir is a serious problem for migratory amphidromous decapods such as species of *Macrobrachium* and species of atyids. Figure 9.5 shows the distribution of 75 hydroelectric projects in Costa Rica, excluding those which are under construction and/or in progress. The dams block the migratory routes of migratory amphidromous shrimps, and represent a major threat to these freshwater decapods (March et al. 2003; Lara and Wehrtmann 2011; De Grave et al. 2015). In México the construction of small permanent barriers across waterways has been shown to have had a negative impact on the upstream movement of the migratory freshwater shrimp *M. tenellum* (Rodríguez-Uribe et al. 2014). It is known that the construction of dams and reservoirs blocks migratory pathways of freshwater animals and significantly alters their distribution and abundance in many parts of the world; the impact of such barriers on freshwater decapods of Central America and the Caribbean is still poorly understood (Holmquist et al. 1998; March et al. 2003; Rodríguez-Uribe et al. 2014). There is clearly a need to develop research projects aimed at obtaining a better understanding of the migratory patterns of palaemonid and atyid shrimps in Central America and the Caribbean and to develop protocols that can mitigate this problem (De Grave et al. 2015). There is also a need for a closer interaction between scientists and decision makers to ensure that the threats to migratory species of amphidromous shrimps are taken into account in management plans.

The literature on freshwater decapods in Central America and the Caribbean is dominated by taxonomic studies, while their ecology and physiology is poorly understood. There is a need for more studies on the impact of climate change on freshwater ecosystems and the organisms that live there, because climate change has been identified as a significant threat with a potentially high impact (De Grave et al. 2015). Such studies should also include monitoring programs to detect medium and long-term changes in the populations of freshwater decapods (Snyder et al. 2013).

Finally, we strongly recommend network building among scientists in Central America and the Caribbean and elsewhere (such as the Mesoamerican network for freshwater macroinvertebrates) aimed at facilitating the exchange of information and development of joint projects (Alonso-EguíaLis et al. 2014b). Also needed is an open-access library with a database that includes unpublished data from environmental impact studies, and more international and/or regional conferences, small meetings, and training workshops that provide opportunities to discuss current problems and possible collaborations.

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Chapter 10
Diversity, Distribution and Conservation of Freshwater Crabs and Shrimps in South America

Célio Magalhães, Martha R. Campos, Pablo A. Collins and Fernando L. Mantelatto

Abstract South America has a huge diversity of freshwater decapods that occupy a variety of ecosystems including major rivers, lakes, wetlands, and mountain streams. Although large areas of the continent's freshwater ecosystem are still pristine and well preserved, many decapod species are increasingly impacted by different anthropogenic threats. This chapter focuses on the warm-water freshwater decapods found in the tropical and subtropical regions of South America that include the freshwater crabs (2 families, 34 genera, 209 species) and the freshwater shrimps (5 families, 11 genera, 88 species). The most species rich country for freshwater crabs is Colombia (105 species), followed by Brazil (49 species), and Venezuela (46 species), while the most species rich-country for freshwater shrimps is Venezuela (36 species), followed by Brazil (35 species), and Colombia (30 species). IUCN Red List conservation assessments have been carried out recently on a global scale for both freshwater crabs and shrimps, but national level assessments have so far only been made for the 76 species of Brazilian decapods, which found no threatened species in that country, and only one shrimp, *Atya scabra*, to be Near Threatened. Comparisons of national and regional assessments

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with the IUCN global assessments in some South American countries are made, and recommendations for freshwater decapod research in the region are offered.

Keywords Brachyura · Caridea · Dendrobranchiata · Decapoda · Conservation assessment · Diversity · Endemism · IUCN · Neotropical region · Threatened species

10.1 Introduction

The freshwater crab and shrimp fauna of the Neotropics are the second most diverse of all of the world's biogeographic regions, with the greatest species richness in South America (Cox 2001; Yeo et al. 2008; Cumberlidge et al. 2014; De Grave et al. 2015). The continent's complex geological history has produced a variety of landscapes dominated by the Andes Mountains, the Precambrian Guyana and Central Brazilian Shields, and some of the world's largest river systems. Over time, South America's decapod fauna has colonized almost all of the freshwater habitats available and in the process has become remarkably diverse (Collins et al. 2011a).

This chapter focuses on the diversity, distribution, and conservation of South America's freshwater crab and shrimp fauna; the crayfish (Parastacidae) and anomuran freshwater crabs (Aeglidae) are treated elsewhere in this volume (Almerão et al. 2015; Bueno et al. Chap. 2 this volume; Kawai and Crandall Chap. 3 this volume). The IUCN Red List currently provides the conservation status of freshwater crabs and shrimps globally, including all species from the Neotropical region (Cumberlidge et al. 2009, 2014; De Grave et al. 2015). However, at the regional and national levels, conservation assessments of freshwater decapods using the IUCN Red List protocols have only been carried out for the Brazilian fauna (IUCN 2003; Magris et al. 2010). The results of these two studies are compared, and the conservation status of new species described since these assessments were carried out are discussed.

10.2 Regional Diversity and Distribution

At the family level the freshwater crab and shrimp fauna of South America is similar to that of Central and North America and the Caribbean. The primary freshwater crabs (Pseudothelphusidae and Trichodactylidae), and freshwater shrimps (Caridea: Atyidae, Euryrhynchidae, Palaemonidae, Xiphocarididae, and Dendrobranchiata: Sergestidae) are found throughout the Neotropics, but their distributional ranges vary (Holthuis 1952; Chace and Hobbs 1969; Rodríguez 1982, 1992; Magalhães and Türkay 1996; Campos 2005, 2014; Valencia and Campos 2007; De Grave and Fransen 2011; Cumberlidge et al. 2014). For example, freshwater shrimp of the families Sergestidae (Omori 1975; D'Incao and Martins

2000; Collins et al. 2007; Valencia and Campos 2010) and Euryrhynchidae (Holthuis 1951; Tiefenbacher 1978; De Grave 2007; Valencia and Campos 2010) are only found in some of the large South American river basins.

10.2.1 Primary Freshwater Crabs

Primary freshwater crabs are found in almost all countries in South America, although the two families are not uniformly distributed throughout the continent. The pseudothelphusids are a tropical group and the southern limit of their range is about 12–13°S, and they are not found beyond the southern boundaries of the Amazon basin (Magalhães 2003; Rodríguez and Suárez 2004). Pseudothelphusid freshwater crabs are present in the Pacific and Atlantic slopes of the continent where their eastern limits are as far as the Brazilian state of Ceará (Magalhães et al. 2005a) (Fig. 10.1), but are absent from Bolivia, Uruguay, Paraguay, southern Argentina, and Chile. The trichodactylids have a much wider distribution in South America reaching as far south as 33–34°S in temperate zones as far south as the tributaries of Río de La Plata close to Buenos Aires in Argentina. Trichodactylid freshwater crabs do not occur in the river basins of the Pacific slope and are not found in Chile (Fig. 10.2). The diversity and distribution of freshwater crabs in South America is still underexplored and the number of species and the range of many described species are sure to increase with future exploration. For example, the distributional ranges of trichodactylid species previously only known from the Amazon basin

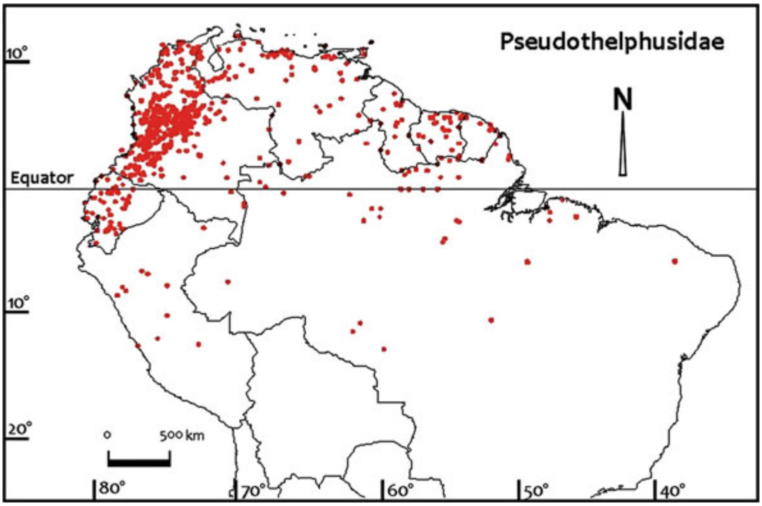

Fig. 10.1 Distribution of Pseudothelphusidae in South America (modified from Cumberlidge et al. 2014: Fig. 1)

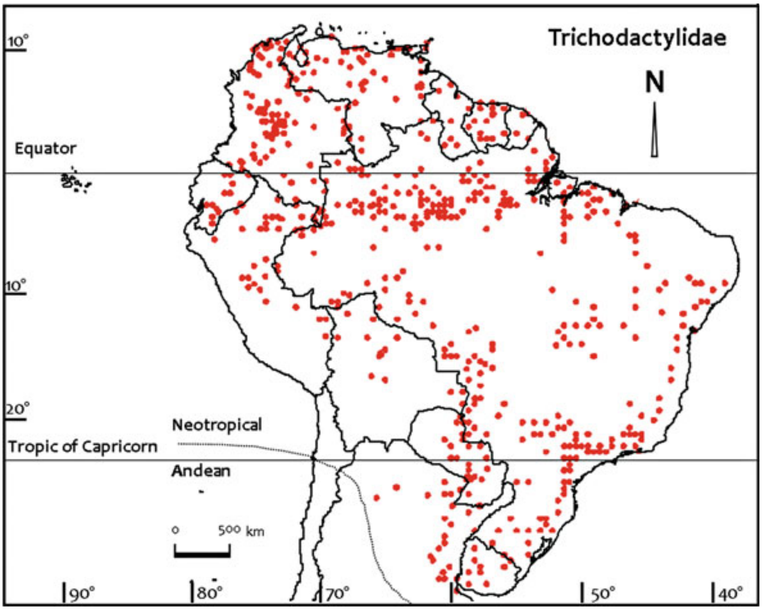

Fig. 10.2 Distribution of Trichodactylidae in South America (modified from Cumberlidge et al. 2014: Fig. 2)

(*Dilocarcinus septemdentatus*, *Sylviocarcinus pictus*, and *Zilchiopsis oronensis*) or from the northern part of the Paraná River basin (*Sylviocarcinus australis* and *Z. oronensis*) have all been extended southwardly (Collins et al. 2002, 2009). The latter two species have taken advantage of the extension of Brazilian tropical conditions south to Argentina through the Paraná River, and this is a potential pathway for the southern spread of other warm-water species (although only a few range expansions have so far been recorded). Prolonged dry seasons such as those brought about occasionally by the El Niño-Southern (ENSO) phenomenon that causes dissolved oxygen levels to fall and the levels of nutrients and toxins from nitrogenous animal excretion to rise, intensify interspecific and intraspecific interactions between freshwater decapods, and this causes their populations to fall (Ezcurra de Drago et al. 2007; Carvalho et al. unpublished data). The 2008–2009 ENSO phenomenon reduced freshwater crab populations dramatically (some of which have not yet recovered), and there are still only three species remaining in some areas today (*T. borellianus*, *D. pagei*, and *Z. collastinensis*) (Collins unpublished data).

Both families of freshwater crabs have marked differences regarding latitudinal and ecological distributions. Rodríguez (1981) divided the South American freshwater decapod fauna into two elements, the pseudothelphusids were considered to be a montane fauna because the majority of species are found between elevations of 300 and 3000 masl in small mountain streams and semi-terrestrial habitats, where most species use their highly developed air-breathing capacity (Díaz and Rodríguez 1977). In the Amazon region there are a few pseudothelphusid species found below

300 masl where they live in shaded forest streams draining terra firme forest, which is never inundated by the periodical floods of the main Amazonian rivers (Magalhães 2003).

The second element, the trichodactylids, was considered to be a lowland fauna because the majority of these species are found below 300 masl, and have widespread distributions throughout the periodically flooded plains in the large South American hydrographic basins such as the Orinoco, Amazon and Paraguay/Paraná river systems. However, a few species are found between 600 to 1000 masl in the foothills of the Eastern Cordillera of Colombia. Examples include *Moreirocarcinus emarginatus* and *Valdivia serrata* (see Campos 2005), *Trichodactylus kensleyi* at 600 masl (Collins 2005), *Zilchiopsis collastinensis* at 600 masl in Cadillal Lake (26° 37′S, 65° 11′W) (Collins, unpublished data), *T. fluviatilis* at 1100 masl in southern Brazil (Magalhães 1999; Mantelatto, unpublished data), and *Sylviocarcinus devillei* in the eastern slopes of the Ecuadorian Andes (Magalhães 2005).

In the Neotropical region, the pseudothelphusids (34 genera and 264 species) are far more diverse than the trichodactylids (15 genera and 47 species) (Cumberlidge et al. 2014). Since that publication, one new genus and ten new species of pseudothelphusids have been described (Campos and Magalhães 2014; Magalhães et al. 2014; Pedraza and Tavares 2014; Pedraza et al. 2015; Suárez 2015). In South America, there are 22 genera of Pseudothelphusidae and 12 genera of Trichodactylidae, with the pseudothelphusids (168 species) being four times as species-rich as the trichodactylids (41 species). The great diversity of the pseudothelphusids is associated with their widespread occurrence throughout the Andes mountains and highland massifs of northern and central South America and their disjunct isolation in freshwater systems after a series of complex past geologic events, episodes of tectonic movements, and headwater captures and separations (Rodríguez 1982; Yeo et al. 2008; Collins et al. 2011a).

The distribution of the freshwater crab taxa among the South American countries reflects the high diversity of the pseudothelphusids in the Andes. For example, Colombia has more genera (24) and species (105) of both families combined than any other country (Table 10.1). Brazil has the second largest number of freshwater crab species (49 species in two families) but this number is significantly lower than Colombia because the species-poor trichodactylids dominate most of the lowland areas of the South American river basins in Brazil. The high diversity and high species richness of the freshwater crabs in South America is concentrated along the northwestern part of the continent in Colombia, Venezuela, and Ecuador. The majority of the pseudothelphusid species occur in these three countries, many of which have restricted distributions, and many of these are endemic species (Table 10.1).

Our present knowledge of the number of species and distributional patterns of freshwater crabs in South America (Table 10.1) is poor when we consider the vast areas of the countries in this region, together with the different research attention that has been invested in different countries over the years. This means that the real diversity of the freshwater crabs of South America is likely to be higher than the numbers presented in Table 10.1. Our updates of the cumulative number of species

Table 10.1 Number of genera and species (total and endemics) of freshwater crabs of the families Pseudothelphusidae and Trichodactylidae in the South America countries

	Pseudothelphusidae				Trichodactylidae				Total			
	Genera		Species		Genera		Species		Genera		Species	
	Total	Endemic	Total	Endemic	Total	Endemic	Total	Endemic	Total	Endemic(%)	Total	Endemic(%)
Argentina	0	0	0	0	6	0	11	1	6	0	11	1 (9.0)
Bolívia	0	0	0	0	6	0	10	1	6	0	10	1 (10)
Brazil	5	1	20	11	10	0	29	8	15	1 (6.6)	49	19 (38.7)
Colombia	15	6	90	85	9	0	15	1	24	6 (25)	105	86 (81.9)
Ecuador	3	0	18	15	5	0	6	0	8	0	24	15 (62.5)
F. Guiana	2	0	3	0	4	0	4	0	6	0	7	0
Guyana	4	1	8	4	3	0	3	0	7	1 (14.3)	11	4 (36.4)
Paraguay	0	0	0	0	5	0	6	0	5	0	6	0
Peru	4	0	7	5	10	0	15	2	14	0	22	7 (31.8)
Suriname	2	0	5	1	3	0	3	0	5	0	8	1 12.5)
Trinidad	2	0	2	1	1	0	1	0	3	0	3	1 (33.3)
Uruguay	0	0	0	0	1	0	2	0	1	0	2	0
Venezuela	11	2	37	29	6	0	8	0	17	2 (11.7)	45	29 (64.4)

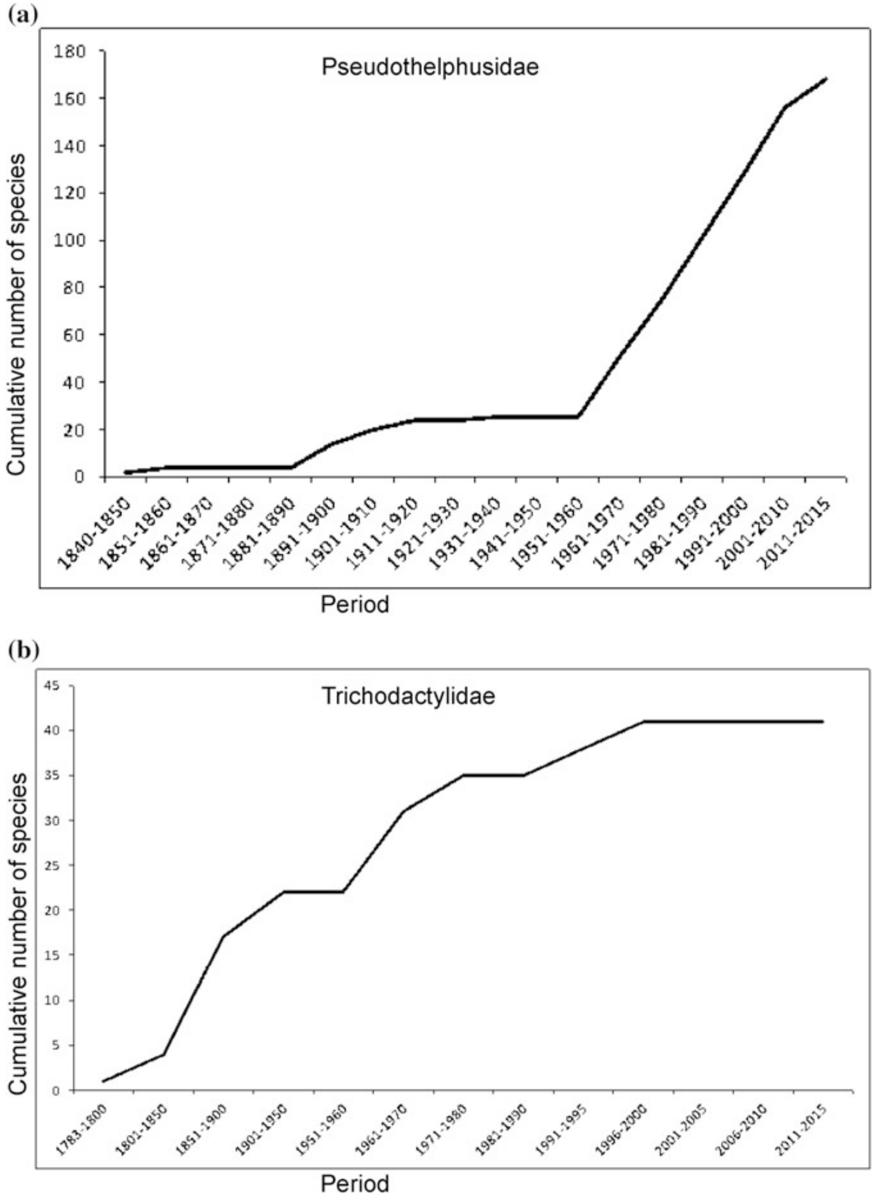

Fig. 10.3 Cumulative number of South American species of: **a** Pseudothelphusidae described since 1840; **b** Trichodactylidae described since 1783

described over time by Yeo et al. (2008) corroborate their conclusions for South America that the diversity of the Pseudothelphusidae will continue to increase, while the Trichodactylidae will plateau (Fig. 10.3). Nevertheless, we consider it probable that there are still a number of trichodactylid species to be discovered, particularly in the genera *Trichodactylus* and *Valdivia*, where molecular studies are likely to reveal cryptic species. For example, current research underway in Brazil (using morphological and molecular analyses) to examine species complexes for cryptic taxa is expected to reveal the presence of new taxa (Souza de Carvalho 2013). In addition, the large gaps on the maps in Figs. 10.1 and 10.2 reveal vast areas of the Amazon basin that are still either very poorly surveyed or completely unexplored for decapods where exploration for new species potentially is most productive.

10.2.2 Freshwater Shrimps

The caridean shrimps represent a very diverse group within the decapod crustaceans, with more than 3500 species currently known (De Grave and Fransen 2011). Of these, approximately 800 species live in freshwater and related continental waters, representing about a fifth of global shrimp diversity. The families Atyidae and Palaemonidae comprise 97.4 % of all freshwater shrimp species worldwide (De Grave et al. 2015). In South America the freshwater shrimp fauna is dominated by these two families (Atyidae, 10 species; Palaemonidae, 53 species), followed by the Euryrhynchidae (5 species), Sergestidae (2 species) and Xiphocarididae (1 species). The distribution patterns and species diversity of freshwater shrimps are similar to those described for freshwater crabs, and encompasses almost all countries, with most species in Brazil, Colombia, Venezuela, and French Guiana, and fewest species in Chile (Mantelatto et al., unpublished data).

Worldwide, the Atyidae (42 genera, 469 species) has the highest diversity of species of freshwater shrimps (De Grave and Fransen 2011), but there are only four genera in South America: *Atya* (6 species), *Potimirim* (2 species), *Jonga* and *Micratya* (each with only one species) (Melo 2003; Torati and Mantelatto 2012; Mantelatto et al., unpublished data). Most of these shrimps are associated with low altitude coastal and estuarine river habitats in Brazil and Venezuela (up to 150 masl). *Jonga*, *Micratya* and *Potimirim* are all restricted to the western Atlantic slope, the latter being the one with the southernmost distribution in the Brazilian state of Santa Catarina (27°S); whereas *Atya* occurs in both the Pacific and Atlantic slopes as far south as 30°S in the state of Rio Grande do Sul (*Atya*).

The Palaemonidae (130 genera, 981 species worldwide), the most speciose of the five families in South America (De Grave and Fransen 2011), is widely distributed in a number of different habitats, and are commonly found in low altitude habitats (up to 250 masl) in both the Atlantic and Pacific drainages. The large genus *Macrobrachium* (246 species worldwide) is the most widespread shrimp genus globally, and includes about 40 species found in the tropical and subtropical freshwaters of South America (Mantelatto et al. 2008; Valencia and Campos 2007; De Grave and Fransen 2011; Pileggi and Mantelatto 2010, 2012; De Grave and Ashelby 2013; Pileggi et al. 2014). Other South American genera include

Palaemon (84 species worldwide, 4 freshwater species) (De Grave and Ashelby 2013; Carvalho et al. 2014), *Pseudopalaemon* (7 freshwater species) all restricted to South America, and *Cryphiops* (2 freshwater species, 1 in Brazil and 1 in Chile) (Kensley and Walker 1982; García-Dávila and Magalhães 2003).

In South America the Euryrhynchidae is represented by the genus *Euryrhynchus* (5 freshwater species) (De Grave and Fransen 2011) all in the northern part of the continent. The freshwater members of the family Sergestidae in South America belong to the genus *Acetes* (2 species) (D'Incao and Martins 2000; Melo 2003). The Xiphocarididae is represented by the genus *Xiphocaris* by a single species from Venezuela and Trinidad and Tobago (De Grave 2013).

Venezuela (36 species), Brazil (35 species), and Colombia (30 species) are the most species-rich countries (De Grave et al. 2015: Appendix S1) where freshwater shrimps inhabit lowland habitats in the two major South American river systems, the Amazon and the Orinoco basins.

10.3 Conservation Status/IUCN Red List Status

The conservation status of the freshwater crabs and shrimps has been recently assessed on a global scale (Cumberlidge et al. 2009; De Grave et al. 2015, respectively) and the results are shown on the IUCN Red List website (http://www.iucnredlist.org). However, regional or national conservation assessments of the South American decapod fauna are only available for Brazil (Magris et al. 2010). Conservation assessments using the IUCN Red List criteria and categories of 255 species of Brazilian crustaceans were made at regional and national levels during three workshops held in 2010 and 2013 (IUCN 2003). In total, 76 species of freshwater decapods (mostly freshwater crabs and shrimps) were included that represented the entire Brazilian faunas for these groups (ICMBio 2011). The lack of population data for most species from Brazil hampered statements of population size and population trends, and most assessments were therefore based mainly on distributional and abundance data.

10.3.1 Freshwater Crabs

Twenty-eight species of Brazilian trichodactylid freshwater crabs were assessed at national level as Least Concern, although two species (*Trichodactylus crassus* and *Valdivia cururuensis*) were not assessed because of their questionable taxonomic status. Thirteen species of pseudothelphusid freshwater crabs were assessed at national level as Least Concern and five species (*Brasiliothelphusa dardanelosensis*, *Fredius ykaa*, *Kingsleya gustavoi*, *K. junki*, and *Microthelphusa somanni*) were assessed as Data Deficient due the lack of adequate information on their distribution and/or population status. The national level assessments are mostly in agreement with the IUCN global freshwater crab assessments (Cumberlidge et al. 2009) but there were some conclusions that differed. For example, the difference between the conservation status of *T. crassus* from Brazil in the two studies (EN, global and LC, national) arises from taxonomic concerns because this species may actually prove to be part of a species complex currently identified as *T. fluviatilis* (see Souza de Carvalho 2013). Similarly, *Brasiliothelphusa tapajoense*, *Kingsleya besti*, *K. gustavoi*, *K. junki*, and *Microthelphusa somanni* were listed as DD (global) but as LC (national) and two species (*B. dardanelosensis* and *F. ykaa*) were not included in the IUCN global assessment because they were described after 2009, and so had their conservation status assessed for the first time (DD).

Colombia (105 species) is the most species-richest country for freshwater crabs in South America and also has the highest degree of endemism at the species level (81.9 %), followed by Venezuela (64.4 %), and Ecuador (62.5 %) (Table 10.1). The high number of species of pseudothelphusids in Colombia reflects the high diversity of these crabs in the Andes mountains. Colombia also has the highest endemism at the genus level (25 %) in South America, followed by Guyana (14.3 %), and Venezuela (11.8 %) (Table 10.1). The recent IUCN Red List conservation assessments of the whole Neotropical freshwater crab fauna by Cumberlidge et al. (2014) reported that Colombia (VU: 13, CR: 1), Venezuela (VU: 7), and Ecuador (VU: 5) had the highest numbers of species in a threatened category, but that almost half of this fauna (148 species: Colombia, 41, Venezuela, 11, and Ecuador, 8) was Data Deficient because there was too little information to carry out an evaluation according to the IUCN Red List protocols (see Cumberlidge et al. 2014: Figs. 10.3 and 10.4; Tables 10.5 and 10.6).

10.3.2 Freshwater Shrimps

The national conservation assessment of the Brazilian crustacean species held in 2013 evaluated all freshwater shrimp species belonging to the five families found in that country. The freshwater shrimp global assessment (IUCN 2015), prepared in part during regional workshops in 2011 and 2012, listed 21 South America species in threatened and near threatened categories (CR, EN, VU, NT) and 103 species as either LC or DD (De Grave et al. 2015: Table 10.1). *Macrobrachium denticulatum* from Brazil was assessed as Critically Endangered due to its restricted distribution in a single river system, imminent threats to its habitat (from dams, siltation, and sewage pollution), and the time since the collection of the last specimen (1995). However, the 2013 freshwater Brazilian crustacean assessment assessed this species as Data Deficient. *Atya scabra* was assessed globally as Least Concern due to its wide amphi-Atlantic distribution (from Mexico southwards to Brazil, most Caribbean islands and Africa) and abundance in some regions. However, the 2013 freshwater Brazilian crustacean assessment assessed this species as Near Threatened (NT) due to existing threats in Brazil (exploitation for economic resources in some regions and sewage pollution). Despite these differences in conservation assessments, both species need to be monitored, especially the little known *M. denticulatum*, which is endemic to Brazil.

10.4 Threats and Conservation Issues

10.4.1 Freshwater Crabs

The Brazilian conservation assessment did not find any species of freshwater crabs found in that country to belong to any of the IUCN threatened categories. Factors that might account for such situation are as follows. The majority of species of freshwater crabs found in Brazil occur in the Amazon basin where large areas are still in pristine condition or relatively well-preserved and most species have a very wide distribution that extends to more than one country. In addition, crabs live in the lowlands of river systems where the habitat is homogeneous, with no significant long-term threats, and where their relatively small size, low abundance, and cryptic habits make them unattractive for commercial fisheries (although freshwater crabs are consumed by Yanomami Indians in the northern Amazon of Brazil) (Magalhães et al. 2006). Five species of Brazilian freshwater crabs (all pseudothelphusids) were found to be Data Deficient (DD) because they are only known from just a few specimens and with a restricted recorded distribution in remote areas of the Amazon basin.

There are very few studies on the population dynamics of any species of trichodactylid in Brazil. Alarcon et al. (2002) presented preliminary results on the population structure of *Trichodactylus fluviatilis* in Ubatuba (SP), verifying a sex ratio of 1:1, with a normal distribution of the population size classes. Recently, Davanso et al. (2013) studied the population dynamics of *Dilocarcinus pagei* in the Marimbondo-Furnas hydroelectric dam reservoir in the Grande River (state of São Paulo) where the species had been introduced by human activities (Magalhães et al. 2005b). Davanso et al. (2013) found seasonal reproduction in *D. pagei* with the largest number of reproductive individuals recorded during the winter and spring months, with hatching taking place in spring, and an intense recruitment of juveniles in the summer months coinciding with the period of heaviest rain. Rosa et al. (2009) studied the distribution of three species (*Dilocarcinus pagei*, *Poppiana argentiniana*, and *Valdivia camerani*) in the wetlands of the Pantanal mato-grossense during the flooding period and found an average density of 0.63 individuals/m^2, most of which were juveniles. Collins et al. (2006) studied the population dynamics of *Trichodactylus borellianus* in the alluvial valley of the Paraná River in relation to the hydro-sedimentological cycle and seasonal changes in aquatic vegetation, whilst Williner et al. (2011) and Torres et al. (2014) investigated the relationship between the population profiles of *T. borellianus*, *D. pagei*, and *Zilchiopsis collastinensis*, measuring the interchange rates among populations in the alluvial valley of Paraná River in relation to the seasonal variation of the hydro-sedimentological cycle. The feeding ecology of trichodactylid freshwater crabs from the floodplain of the Parana River was studied by Williner and Collins (2002, 2011) and Williner et al. (2014), but there are no similar studies for any of the pseudothelphusid species in South America, other than an investigation of the fecundity and parental care in three species from the Amazon basin and Central America (Wehrtmann et al. 2010). *Dilocarcinus pagei* has been introduced into the upper Paraná River basin (a non-native area for this species) where it has adapted well and its population size is increasing (Magalhães et al. 2005b).

There is little information about possible threats to species of Trichodactylidae. In the Pantanal mato-grossense in Brazil, *D. pagei* is heavily fished for live bait for game fishing but there are no studies on the impact of this on the population of this species (Moraes and Espinoza 2001). *Trichodactylus fluviatilis* is used as a food source by traditional village communities in Pedra Branca in Bahia state in Brazil (Costa Neto 2007). In southern Brazil, Uruguay, and Argentina, *Trichodactylus panoplus* and *T. kensleyi* are found in areas subjected to intense agricultural activity where its populations may be affected by pollution from agricultural pesticides. In the Pampas region in southern South America studies of the effects of pollutants such as agrochemicals, heavy metals, and petroleum products on crabs (e.g. *T. borellianus*, *Z. collastinensis*, *D. pagei*) and shrimps (e.g. *Palaemon argentinus*, *Macrobrachium borellii*), found that crabs could resist higher concentrations of pollutants than shrimps (Williner and Collins 2003; Montagna and Collins 2005; Collins et al. 2011b; Negro et al. 2011). This difference may be attributed to the enclosed carapace and gill chambers of the freshwater crabs compared to the more exposed respiratory systems of shrimps. Sub-lethal concentrations of pollutants do not produce immediate consequences for the populations, but do affect growth (Montagna and Collins 2007), metabolism (Montagna and Collins 2008; Negro et al. 2012a, b), reproduction (Negro et al. 2014; Negro et al. 2015), and trophic activities via changes in the frequencies of cell types in the hepatopancreas (Collins and Cappello 2006; Collins 2010). The large volumes of water in the major rivers buffer and dilute the impact of pollutants to undetectable levels and have little impact on the decapods living there, but animals living in the smaller tributary streams draining cultivated areas are more likely to be affected. In addition, pollutants in the sediments could be ingested by decapods when they are feeding or building their shelters. The Brazilian Atlantic Forests are currently heavily impacted by anthropogenic activities and decapods that are found there (such as *T. fluviatilis*, *T. petropolitanus* and *T. dentatus*) might be threatened by pollution, habitat degradation, or habitat loss, but there is no information on population declines for any of these species. Crabs and shrimps found in remote areas or in protected areas such as the parks and reserves along the Serra do Mar in Brazil were all assessed as Least Concern because of the lack of threats and stable population levels that are not likely to be in decline.

Colombia is the most species-rich South American country for freshwater crabs (Cumberlidge et al. 2009, 2014) with 105 species (trichodacylids and pseudothelphusids combined), of which 45 species are LC, one species is NT, 13 species are

VU, none are EN, and one species is CR, making a total of 14 species (13.3 % of the fauna) that are threatened. The latest figures indicate that Colombia has 15 species of trichodactylid freshwater crabs of which 12 are least concern (LC), two are vulnerable (VU) (*Bottiella cucutensis* and *B. medemi*), and one that is newly recorded (*F. raddai*) and has not yet been assessed (Arias-Pineda et al. 2015). The threatened conservation status of *Bottiella medemi* should be revised in the light of information from new material from new localities in the San Jorge River basin, which may warrant a status of Least Concern (LC) for this species (Cumberlidge et al. 2014; Campos 2014). Similarly, the conservation status of *B. niceforei*, needs to be revised from its current status as Least Concern (LC) given the lack of information on its distribution and the population levels that might justify Near Threatened (NT) status.

To date, Colombia has 90 species of pseudothelphusids species including the newly described taxa, *Colombiathelphusa culmarcuata* and *Eidocamptophallus chacei* (see Campos and Magalhães 2014). The high number of species of pseudothelphusids reflects the high diversity of habitats found in the Colombian Andes and the high rate of endemism in that country (81.9 %) that reflects the ease of genetic isolation in these crabs. According to Cumberlidge et al. (2014), 12 species of pseudothelphusids and 2 species of trichodactylids are threatened with extinction (VU or CR), while 41 species were too poorly known to be assessed and were listed as Data Deficient. Most of the DD species are found in areas that are either too difficult to access, or that live in highly disturbed habitats where their status cannot be properly evaluated.

Eleven species of freshwater crabs from Colombia were listed in the IUCN global assessment as DD: *Martiana clausa*, *Moritschus narinnensis*, *Neostrengeria libradensis*, *N. macarenae*, *Phallangothelphusa juansei*, *Potamocarcinus colombiensis*, *Strengeriana bolivarensis*, *S. flagellata*, *S. florenciae*, *S. foresti*, and *S. huilensis*. Since that study new data are available that allow conservation assessments using the IUCN Red List protocols, and the results of this suggest that these taxa should now all be considered as Vulnerable (VU). The new studies also indicate that *Chaceus ibiricensis*, *Hypolobocera andagoensis*, *Hypolobocera rodundilobata*, *Lindacatalina sumacensis* and *Moritschus altaquerensis* listed by the IUCN as Vulnerable (VU) should now be listed as DD. Two other species (*Eudaniela casanarensis* and *Potamocarcinus pinzoni*) that are currently listed by the IUCN as DD, should probably be listed as LC, in the light of new studies which increased their distributional range (Campos 2014). *Neostrengeria macropa* appears on the IUCN Red List as LC, but this species should probably be listed as VU (Campos 2007), which is its classification in the Red Book of Terrestrial Invertebrates of Colombia. This vulnerable species faces immediate extinction threats from ecosystem degradation and indiscriminate capture for commercial markets, but no conservation actions have yet been taken by the Colombian Ministry of the Environment. A national assessment of the conservation status of the Colombian freshwater crabs of the family Pseudothelphusidae is currently underway using the IUCN Red List protocols (Campos and Lasso, unpublished data).

10.4.2 Freshwater Shrimps

The Brazilian conservation assessment of freshwater shrimps found only two species (*Atya gabonensis* and *Macrobrachium carcinus*) to be threatened with extinction. Conservation action plans are being developed for these species in three Brazilian regions as part of the "Plano de Ação Nacional para a Conservação das Espécies Aquáticas Ameaçadas de Extinção da Bacia do Rio Paraíba do Sul (São Paulo, Rio de Janeiro and Minas Gerais)" proposed by ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade), and the "Plano de Ação Nacional para a Conservação dos Manguezais", under preparation by ICMBio. These action plans were proposed because these two species were included in previous lists of endangered species in Brazil (Instrução Normativa MMA nr 5, 21 May 2004), but were excluded in a recent reassessment (Portaria MMA nr 445, 17 December 2014). Nevertheless, conservation monitoring of *A. gabonensis* and *M. carcinus* has been implemented in view of the threat status of these species in 2014 based on population decreases in recent years and immediate threats from local fishermen (Carvalho et al., unpublished data).

The reason for the low number of threatened species of freshwater shrimps in Brazil may be due to the fact that most species occur, either partially or totally, in areas of the Amazon basin or Atlantic forest streams that are still in pristine condition and relatively well preserved with no long-term threats, that are difficult to access. In addition, many species of *Macrobrachium* live in lowland river systems with homogenous habitats where they are abundant (with populations comprising all size classes), have a small body size (making them unattractive for commercial or artisanal fisheries) or have a wide distribution spanning more than one country.

There are a few abundant species of freshwater shrimps that can support commercial harvesting and these are being studied as potential species for large scale aquaculture (carcinoculture) because they have continuous year-round reproduction, continuous recruitment of new individuals into the population and extended larval development which permits wide dispersal. However, the life history strategies and ecological preferences are not uniform for all species of freshwater shrimps from different parts of the continent, and there are many for which there is little or no information. This overall promising outlook for freshwater shrimps in South America is offset by the potential for anthropogenic threats to many species and by the high number of species classified as DD. Our experience gained from working with freshwater shrimps and crabs in South America over the years leads us to state that the most important long-term threats to these crustaceans are from the impacts of anthropogenic activities such as pollution, habitat degradation, or habitat loss.

10.4.3 Conservation Actions

In Brazil (and the rest of South America) there are no conservation actions that are directed specifically at any species of freshwater crabs, and only a few that are directed at shrimps. It is encouraging that large numbers of species of these freshwater decapods occur within the boundaries of protected areas, such as reserves, ecological stations, and national parks. It is recommended that joint efforts by governmental and non-governmental organizations be developed and aimed at monitoring threatened species, with an emphasis on the preservation of their habitats and the mitigation of threats. As pointed out by Cumberlidge et al. (2009), the risk of extinction of endemic species of freshwater crabs can be minimized by a compromise between developmental activities and protection of their habitats, and the same practices are also valid for freshwater shrimps.

10.5 Perspectives

Our capacity to carry out more accurate evaluations of the conservation status of the South American decapod fauna and our abilities to propose adequate conservation strategies require quality data and sound scientific information (Cumberlidge et al. 2009, 2014; De Grave et al. 2015; IUCN 2015). We recommend that further studies be carried out, aimed at protecting the threatened species of Neotropical decapods, as well as studying the large number of Data Deficient species. These include:

1. Biodiversity inventories in the large areas of South America which are still very poorly explored for decapods, especially in the Amazon Basin, the Guyana and Central Brazilian Shields, and the extensive areas along the Andes mountains.
2. Improved taxonomic, systematic, and zoogeographic expertise is needed for these biodiversity inventories, including distribution patterns and phylogenetic relationships.
3. Improved monitoring of threatened and little known species to provide good quality data on their habitats, natural history, physiology, population trends and threats. These data are all essential for adequate threat assessments and for the development of conservation action plans, especially for those species that are under the most intense threats from anthropogenic factors.

The conservation of freshwater decapods in South America involves the mitigation of threats from anthropogenic actions arising from pollution by biocides and heavy metal, as well as the overexploitation of land resulting in habitat fragmentation. These conservation actions will not only protect the current, rich decapod diversity, but will also promote the sustainable use of natural resources long into the future.

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Chapter 11
Biotechnology, Biocontrol and Conservation: Potential Approaches—Harnessing RNAi-Based Sex-Differentiation Manipulations in Decapods

Amit Savaya-Alkalay and Amir Sagi

Abstract Invasive species of various taxa, including crustaceans and snails, are harmful to freshwater ecosystems, inflicting a reduction in biodiversity, vast losses for agriculture, alterations in natural ecosystems, and even some human health issues (such as bilharzia). We describe here some destructive invasive species of crustaceans and snails that can be controlled using biotechnological solutions. Specifically, we propose the use of sexually manipulated non-breeding all-male decapod crustacean populations generated through novel techniques that use temporal gene silencing via RNA interference (RNAi), namely, non-genetically modified organisms (non GMO), to control invasive species. The first part of the chapter deals with the control of invasive and destructive freshwater snails using snail-eating freshwater prawns; specifically we propose the use of all-male prawn populations to act as non-invasive and sustainable biocontrol agents. Freshwater prawns have already been shown to act as voracious predators of a few freshwater snail species. Since male prawns grow faster, reach larger size and do not migrate like females, it is likely that they will act as efficient biocontrol agents over snails. The second part of the chapter deals with the proposed control of invasive crustaceans by skewing the sex ratio of the invasive populations by repetitive releases into the invasive populations of neo-females, which bear 100 % male progeny. Since RNAi is becoming widely used and since the commercial use of RNAi-based biotechnologies for the production of neo-females and all-male prawn populations has already been implemented, our proposed solution is readily available for eco-protection applications.

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11.1 Introduction

The science of conservation biology was born in reaction to the global biodiversity crisis that has been unfolding over the past 100 years, driven mostly by human activities. A key concern in conservation biology is the damage to habitats and native species caused by deliberate or accidental human-mediated introductions of non-native invasive species (NIS) (Sala et al. 2000). Most introduced species fail to become established in their new environments and do not become troublesome invasive species. However, a minority of non-native invasive species do succeed in their new environments, and some of these have become serious threats to global biodiversity and ecosystem stability (Kolar and Lodge 2001). In the present chapter, we discuss some decapod crustaceans and snails—that have become devastating invasive species in freshwater ecosystems. Compared to terrestrial ecosystems, such ecosystems are particularly vulnerable to non-native invasive species due to water-related anthropogenic activities, such as transportation and recreation. The vulnerability of freshwater ecosystems is further exacerbated by the dispersion tendency of freshwater organisms and the relative geographic isolation of some lakes and streams, leading in some cases to location-specific adaptations of indigenous species (Lodge et al. 1998; Gherardi 2000; Sala et al. 2000; Beisel 2001; Gherardi 2006).

Freshwater decapods, such as crayfish, crabs, and shrimps, are among the largest and most long-lived invertebrates, and some act as keystone species due to their diverse diet, on the one hand, and their role as prey for other species, on the other hand (Moyle and Light 1996; Nyström et al. 1996). Non-native decapod crustaceans can have a significant effect on freshwater ecosystems due to their predation activity (Degerman et al. 2001) and their ability to change the physical conditions of the habitat (Anastacio et al. 2005b, c), thereby causing considerable environmental and economic damage (Guan and Wiles 1997). The introduction of freshwater decapods into non-native ecosystems may thus result in irreparable shifts in species diversity (Hobbs et al. 1989). This chapter focuses on invasive crustaceans that have negative impacts on freshwater ecosystems containing these keystone species and suggests that the introduction of non-breeding decapod populations could contribute to the solution of this problem. We describe several potential applications of an RNA interference (RNAi)-based sex-differentiation manipulation in decapods as novel and sustainable approaches to address environmental threats of the type described above. The proposed crustacean biocontrol agents can be applied to challenge invasive snails and crustaceans, thereby reducing the negative impact of the invasive species on freshwater ecosystems.

11.2 Production of All-Male Crustacean Populations for Aquaculture and for Biocontrol of Unwanted Species

All male populations of crustaceans are produced in a two-step procedure that involves sex-reversal of males to neo-females, namely, functional phenotypic females with a masculine genotype (as described in detail below), followed by mating of these neo-females with normal males. The resulting offspring will be male, due to the homogametic sex chromosomes of male malacostracans (Katakura 1989; Sagi et al. 1997; Jiang and Qiu 2013). The main advantage for aquaculture of all-male populations lies in increased commercial yields by virtue of the fact that that male prawns grow faster and are larger than females (Nair et al. 2006). An additional advantage of such monosex populations is that they are non-breeding and thus do not pose a threat to the environment. They can therefore be exploited as competitive species for biocontrol of native or invasive undesirable species. These two applications—aquaculture and biocontrol—are discussed below.

11.2.1 Production of All-Male Populations via Androgenic Gland Manipulation or RNAi-Based Biotechnology for Aquaculture

Sexual differentiation in crustaceans is governed by the presence or absence of the androgenic gland (AG), an endocrine organ that is unique to males (Charniaux-Cotton 1954; Sagi and Cohen 1990; Sagi et al. 1997) and that controls masculine traits (Touir 1977; Taketomi et al. 1990; Manor et al. 2004). In the commercially important species of freshwater prawn *Macrobrachium rosenbergii*, microsurgical removal of the AG resulted in the production of female characters (Nagamine et al. 1980) and in sex-reversal from males to neo-females. This finding was applied by our group for the commercial production of all-male populations of *M. rosenbergii* (Aflalo et al. 2006). However, microsurgery has a low success rate (~ 1.3 %), so alternative technologies were sought with the aim to improve the efficiency of the approach (Aflalo et al. 2006). One such technology to produce all-male populations—temporal gene silencing by RNAi (Fire et al. 1998)—exploited the discovery by our group of the main secretory product of the decapod AG, the insulin-like androgenic gland hormone (IAG). This hormone was first discovered in the crayfish *Cherax quadricarinatus* (Manor et al. 2007) and later in other decapods (Ventura and Sagi 2012) (Table 11.1), including a number of economically important species (Manor et al. 2007; Ventura et al. 2009; Chung et al. 2011; Mareddy et al. 2011; Savaya-Alkalay et al. 2014; Vázquez-Islas et al. 2014).

Table 11.1 Accession numbers of published IAGs of decapod crustaceans

Species	Type	Accession number
Macrobrachium rosenbergii	Prawn	FJ409645
Portunus pelagicus	Crab	HM459854
Cherax quadricarinatus	Crayfish	DQ851163
Fenneropenaeus chinensis	Shrimp	JQ388277.1
Macrobrachium nipponense	Prawn	KC460325.1
Penaeus monodon	Shrimp	GU208677.1
Callinectes sapidus	Crab	HM594945.1
Marsupenaeus japonicus	Shrimp	AB598415
Palaemon paucidens	Shrimp	AB588013.1
Palaemon pacificus	Shrimp	AB588014
Macrobrachium lar	Prawn	AB579012.1
Cherax destructor	Crayfish	EU718788
Jasus edwardsii	Lobster	AIM55892.1
Scylla paramamosain	Crab	AIF30295.1
Sagmariasus verreauxi	Lobster	AHY99679.1
Macrobrachium vollenhovenii	Prawn	KJ524578.1

Since the seminal study on "genetic interference by double-stranded RNA" of Fire et al. (1998), the "biology, mechanisms and applications" of RNAi have been studied in a variety of plant (Agrawal et al. 2003; Qi and Hannon 2005; Sagi et al. 2013) and metazoan species (e.g., Agrawal et al. 2003; Qi and Hannon 2005; Sagi et al. 2013), including crustaceans (Agrawal et al. 2003; Qi and Hannon 2005; Sagi et al. 2013). The strength of RNAi in biological applications lies in the fact that the administration of double-stranded RNA (dsRNA) does not cause genomic modifications [namely, it does not produce genetically modified organisms (GMO)], and therefore it can be applied for aquaculture purposes (Ventura et al. 2012). The first commercial use of temporal gene silencing in aquaculture was demonstrated by our research group (Ventura et al. 2012), with the production of all-male populations of *M. rosenbergii*, without the need for microsurgery (Ventura et al. 2012). In our study, juvenile male prawns were manipulated using dsRNA injections, causing a full and functional sex reversal from males into neo-females that produced 100 % male progeny (Ventura et al. 2012; Ventura and Sagi 2012). This RNAi-based non-GMO biotechnology does not involve hormonal or chemical intervention (Fire et al. 1998; Lezer et al. 2015), rather it relies on a safe temporal intervention at the IAG gene transcriptome level that does not modify the organism's genome (Lezer et al. 2015). The non-breeding monosex populations that are produced with this technology are suitable for both aquaculture and, as elaborated in the next section, sustainable environmental applications (Aflalo and Sagi 2014).

11.2.2 All-Male Populations as Sustainable Biocontrol Agents

The above-described RNAi-based biotechnology to produce all-male crustacean populations was initially developed to meet the needs of the aquaculture sector. However, recently we suggested a novel approach using such all-male populations as non-invasive biocontrol agents (Savaya-Alkalay et al. 2014). It has been demonstrated under laboratory conditions that freshwater prawns of the genus *Macrobrachium* act as efficient predators of species of freshwater snails that serve as vectors for human diseases (Lee et al. 1982; Roberts and Kuris 1990; Sokolow et al. 2013). Preliminary predation studies under laboratory conditions suggest that *M. rosenbergii* prawns are voracious consumers of species of *Pomacea* freshwater snails (Savaya-Alkalay, personal communication). Therefore, we propose that all-male prawn populations should be tested as biocontrol agents—that do not carry the risk of becoming invasive species—against snails in both endemic and exotic habitats.

There are three advantages to using all-male populations of *Macrobrachium* as efficient and sustainable biocontrol agents (Savaya-Alkalay et al. 2014):

(a) Large size and fast growth. Male prawns grow faster and reach a larger body size than females and consume larger quantities of food (or prey) (Sagi et al. 1986), thereby offering both ecological and economic (aquaculture) advantages.
(b) Non-migratory behavior. All-male populations of *Macrobrachium* (vs. populations with a 50:50 male:female sex ratio) are preferable as agents for snail control because males do not migrate (while females of *Macrobrachium* spp. must swim downstream to release their larvae in brackish estuarine water) (Bauer 2011).
(c) Reproductive sterility. All-male populations of *Macrobrachium* cannot reproduce and thus cannot become invasive species following introduction into a new habitat. In addition, if in the long term the all-male prawn populations were found to cause more damage than benefit, they could easily be removed at any time by refraining from restocking.

11.3 Controlling Invasive Species by Using Non-reproductive Crustacean Agents

Two different ‘problematic’ groups of species can be controlled by RNAi-manipulated crustaceans: (1) explosive populations of invasive freshwater snails that can be controlled by prawn predation, and (2) explosive populations of invasive crustaceans that can be controlled by changing the sex ratio of these populations towards maleness until the invasive population collapses.

11.3.1 Invasive and ‘Problematic’ Species of Freshwater Snails

Freshwater snails are distributed worldwide, with negative effects on biodiversity, agriculture, and human health being caused by a number of non-native invasive species. Snails are often overlooked as agricultural pests in the scientific literature, even though they cause major losses for different crops around the globe (Barker 2002). We present here two case studies of invasive and damaging snails from different families for which there is potential for biological control by crustacean species.

11.3.1.1 Apple Snails (Ampullariidae)

Apple snails, the largest freshwater gastropods (reaching a shell height of 155 mm), are distributed mainly in humid tropical and subtropical habitats in South and Central America, Africa, and Southeast Asia (Pain 1960; Burky 1974). Many species of apple snail are amphibious, having both a gill and a lung, and are therefore able to spend long periods of time out of the water—a trait that challenges efforts to control these snails (Prashad 1925; Burky et al. 1972). Apple snails are not only agricultural pests (Naylor 1996), but they are also ecologically destructive and have the potential to alter wetland ecosystems via the impact of their omnivorous diet, their large size, and their amphibious capabilities that help them evade control measures (Naylor 1996; Kwong et al. 2009).

There are a few reports of apple snails causing damage to crops (mostly rice in paddies) in their native habitats, but the major crop damage is caused by apple snails introduced outside of their natural habitats; apple snails have therefore been categorized as one of the world’s 100 worst invasive species (Lowe et al. 2000; Horgan et al. 2014). The global spread of apple snails was triggered by two major commercial activities, namely, the food industry and the aquarium trade (Perera 1996). Apple snails, which are native to South America, were first introduced to Hawaii (in the 1960s) and then to a number of Asian countries (in the 1970s and 1980s) as food items. However, the economic potential of this sector was overestimated, and the market failed due to lack of demand (Naylor 1996; Vitousek et al. 1996). In East Asia, apple snails that either escaped or were released from captivity established themselves as invasive populations. It appears, however, that the aquarium trade market bears the major responsibility for the wide-spread establishment of alien populations of apple snails the world over—Cambodia, Chile, China, Dominican Republic, Egypt, Guam, India, Indonesia, Israel, Japan, Laos, Malaysia, Myanmar, Papua New Guinea, Pakistan, Philippines, Russia, Singapore, South Africa, South Korea, Spain, Sri-Lanka, Taiwan, Thailand, and the USA (Roll et al. 2009; Horgan et al. 2014).

An illustrative case study of invasive apple snails is that of the establishment of the golden apple snail *Pomacea canaliculata* in the delta of the Ebro river in Spain, first observed in 2009 (López et al. 2010). Since then, none of the efforts to control the snails has been successful. The dominant agricultural crop in the Ebro River delta is rice, whose production has been dramatically reduced since the apple snail invasion. The snails reach high densities, with a biomass of 1 kg m^{-2}, and produce more than 5 egg masses m^{-2}.

The first introduction of apple snails in Asia caused enormous damage to agricultural production (mostly rice) as well as to natural ecosystems and even to human health (Naylor 1996). Agricultural damage depends on the density and size of the snails as well as on the age of the crop, with losses varying between 20 % (at a density of 1 snail m^{-2}) and 90 % (at a density of 8 snails m^{-2}) (Hirai 1988; Basilio 1991). In Japan, damage due to apple snails caused major reductions to crops such as rice, water spinach, lotus, taro, and mat rush (Mochida 1991), in addition to damage to ecosystems and to humans from the intensive use of molluscicides and insecticides (Laughlin and Lindén 1985; Clark et al. 1988; Hoch 2001). Furthermore, *Pomacea canaliculata* snails act as intermediate hosts for the parasitic worm *Angiostrongylus cantonensis*, which causes human eosinophilic meningitis if not destroyed by sufficient cooking of the snails (Lv et al. 2009). Dozens of cases of human eosinophilic meningitis were detected in 2006 in southern China, where infected apple snails were found to be on sale in markets and restaurants (Lv et al. 2009).

The predation potential of biocontrol agents over populations of *Pomacea* snails was investigated in southern Japan, where 46 species were tested under laboratory conditions as predators of these snails (Yusa et al. 2006). Under these conditions, ducks, rats, turtles and carp were found to be efficient predators of adult *Pomacea canaliculata* snails, and a few species of crustaceans could act as efficient predators of small- to medium-sized snails. However, the only species of *Macrobrachium* tested (*M. formosense*) was a small species (2.4 g average weight), which is significantly smaller than *M. rosenbergii,* suggested here as a biocontrol agent.

11.3.1.2 Snail Hosts of *Schistosoma*

Schistosomiasis (bilharzia), a debilitating chronic disease that infects more than 240 million people around the world, is caused by parasitic flatworms of the genus *Schistosoma* (WHO 2013a). These parasitic worms require two hosts to complete their life cycle, a freshwater snail intermediate host (a species of *Biomphalaria* or *Bulinus*) and a vertebrate definitive host (usually a mammal) (WHO 2013a). The distribution of schistosomiasis is intimately linked to the distribution and abundance of the snail hosts, and control efforts are focusing on snail distribution as a major target in breaking the disease cycle.

A few species of crustaceans have been tested as potential biocontrol agents for snails that transmit parasitic diseases to humans (Mkoji et al. 1999; Sokolow et al. 2013). Until recently, the invasive crayfish *Procambarus clarkii* was the only species that has been studied under field conditions (Hofkin et al. 1991a, b; Ibrahim et al. 1995; Mkoji et al. 1999; Lodge et al. 2005). Later studies with

M. vollenhovenii are discussed below. We review here two different parts of Africa where schistosomiasis affects large numbers of people: firstly, Kenya (East Africa), where more than 25 % of the population (more than 11 million people) is in danger. Secondly, the Senegal River basin (West Africa), in northern Senegal, whose damming has been associated with the fastest recorded spread of human schistosomiasis; more than 30 % of Senegal's population (about 4 million people) requires preventive chemotherapy against the disease (Southgate 1997; Southgate et al. 2001; Sow et al. 2002; WHO 2013b).

In Kenya, the North American crayfish or red swamp crayfish *Procambarus clarkii* was originally introduced for aquaculture (Oluoch 1990), but escaped crayfish have now spread out, and *Procambarus clarkii* has become a well-established invasive species with a significant impact on native ecosystems (Mkoji et al. 1999). Scientists have examined the efficiency of *Procambarus clarkii* as a biocontrol agent of snails infected with *Schistosoma* under field conditions (Mkoji et al. 1999) following laboratory experiments that supported the hypothesis that these crayfish could decrease the prevalence of schistosomiasis in human populations (Hofkin et al. 1991a, 1992). Indeed, under certain environmental conditions, the introduction of *Procambarus clarkii* significantly reduced the abundance of *Schistosoma*-infected snails and the rate of infection among human residents of the study area (Mkoji et al. 1999). However, the impact of *Procambarus clarkii* on aquatic ecosystems is an issue of major concern from a conservation point of view, because the appetite of these crayfish for aquatic plants is large enough to alter the biotic and physical conditions of the invaded habitats (see Sect. 3.2.2). Therefore, it is essential to carefully consider the environmental costs and benefits of using an invasive crustacean species as a biocontrol agent to reduce populations of damaging invasive snails.

Another conservation approach has been to reintroduce endemic species that have been extirpated from their natural environment by anthropogenic environmental changes. For example, the man-made Diama dam on the Senegal River created favorable conditions for freshwater snails but unfavorable conditions for its natural predator, the freshwater African river prawn *M. vollenhovenii* (Savaya-Alkalay et al. 2014). The females of *M. vollenhovenii*, being catadromous, need to migrate down the Senegal River to release their larvae in saltwater habitats, but they are prevented from so doing by the Diama dam downstream on the river. As a result, the present distributional range and population levels of *M. vollenhovenii* are greatly reduced from their former sizes, and the reduction of this predator has coincided with a population explosion of freshwater snails, which are vectors of schistosomiasis. Reintroduction of *M. vollenhovenii* to the Senegal River is an appealing idea but would require careful management, because its sustainability is dependent on a constant prawn stocking strategy together with the building of ‘fish ladder’ channels (Gowans et al. 1999) at the dam to allow the prawns to navigate the river upstream and downstream. A recent field study in the Senegal River basin demonstrated that African river prawns as biological control agents had a significant effect on snail density and hence on human infection rates and disease burden (Sokolow et al. 2015). These findings provide support for the suggested solution of using all-male African river prawns as sustainable and efficient biocontrol agents (Savaya-Alkalay et al. 2014).

11.3.2 *Invasive Crustaceans as a Conservation Challenge*

Decapod crustaceans are successful invaders of freshwater ecosystems due to their efficient adaptive behavior. Factors that contribute to the high adaptability of crustaceans that are invasive species include a high reproductive rate, a tolerance to environmental fluctuations, and a diverse diet (Gherardi 2006). All these characteristics result in high fitness and contribute to the successful invasion of new habitats, especially in combination with opportunistic behavior. The presence of invading species impacts the habitat through alterations of vegetation patterns and food resources that may increase the vulnerability of endemic species to extinction. In addition to their negative impact on natural ecosystems, invasive species also frequently cause damage to the agricultural and aquaculture sectors (Anastacio et al. 2005a, b, d).

Biological control via altering the reproductive success of a species has been widely utilized by the agricultural sector to manage insect pests (Dyck et al. 2005). The technique is based on releasing sterilized males that compete with normal males for females, which eventually decreases fecundity through unsuccessful mating. Here, we propose that this concept be exploited in a novel technique that relies on RNAi-based biotechnological approaches to eradicate invasive crustacean species by creating and releasing neo-females that produce all-male offspring. This approach is based on the premise that successive releases of neo-females would compete with the population of normal females for mates; the all-male progeny of the neo-females would skew the sex ratio of the population towards males, with the obvious consequent reduction in the population size.

The proposed technique could be applied for controlling invasive shrimps, crayfish and prawns, as discussed below. Examples of crustacean pests are the burrowing shrimps *Neotrypaea californiensis* and *Upogebia pugettensis*, whose activities soften the intertidal substrate where oysters are grown. The soft sediment particles clog up the oysters' filter-feeding and respiratory channels, leading to oyster mortality and consequent economic losses to the oyster industry (Dumbauld et al. 2006). Controlling sexual differentiation in shrimp populations such as these could pave the way for safely skewing their sex ratio, thereby controlling the size of the populations and hence minimizing their negative effect.

Crayfish are probably the most dangerous crustaceans in terms of invasion impacts due to their high densities, relatively long life spans, and large size (Gherardi 2006). Crayfish are keystone species due to their dominant role in the food chain and thus invasions by crayfish species may cause significant alterations to freshwater food webs (Lodge et al. 1998; Covich et al. 1999). Crayfish invasions reduce biomass and the species richness of the organisms comprising their diet, and this causes an accompanying reduction in the recruitment of commercial fish species (Lodge and Lorman 1987; Nyström 1999). One of the most damaging invasive crustacean species is the North American red swamp crayfish *Procambarus clarkii*, which has been commercially cultured since the 1950s in a number of southern US states. The species is endemic from northeastern Mexico to the south-central USA but is now found in every continent, excluding Australia and Antarctica (Huner 2002). The success of *P. clarkii* as an invasive species lies in a number of biological characteristics that aid its colonization of new habitats. This species exhibits an *R*-selected reproductive strategy (producing large numbers of offspring), a small body size, early sexual maturity, a fast growth rate, and the ability to incubate eggs all year round (Lindqvist and Huner 1999; Paglianti and Gherardi 2004). In addition, *P. clarkii* has a very high tolerance to extreme environmental conditions, such as polluted habitats and temporary streams that dry up seasonally (Gherardi et al. 2000). Another important aspect of *P. clarkii's* survival potential is its ability to carry but not be infected by the pathogenic fungus *Aphanomyces astaci*, which causes crayfish plague in native species (Dieguez-Uribeondo and Söderhäll 1993). Additional ecological damage is caused by *P. clarkii*'s burrowing activities, which alter water quality and sediment characteristics and may hence severely affect the agricultural and aquaculture sectors (Souty-Grosset 2006). One solution to the problem would be to release neo-female crayfish into the invaded habitats so that sex-ratios would be skewed toward males and the invading population would be extirpated over a few generations.

A few years ago, invasive populations of the Asian freshwater prawn *M. rosenbergii* were found in freshwaters in northern Brazil. *M. rosenbergii* was originally introduced into northern Brazil for aquaculture in the late 1970s, and its escape from captivity has resulted in the establishment of wild breeding populations in a number of locations, including three in which the presence of berried *M. rosenbergii* females has been reported (Silva-Oliveira et al. 2011). The invasion potential of this prawn is high due to its high reproductive rate, its adaptive behavior, and its omnivorous diet. It is therefore an urgent challenge to halt the prawn invasions before they spread further, and one way that this could be done would be by introducing neo-females of this species to skew the sex ratio towards all male populations.

11.4 Epilogue

The rapid development of genomic and transcriptomic sequencing techniques has the potential for the discovery of thousands of new crustacean genes; from these it would be possible to select candidates to be used as conservation tools to fight invasive species by applying RNAi-based or similar biotechnologies. One major drawback of current RNAi biotechnologies is that non-GMO delivery mechanisms are currently based on microinjection methods that are labor intensive and require the professional training and special equipment that are not available in low-tech facilities. Another disadvantage of RNAi is the high price of the gene silencing agents. However, applying RNAi treatments at the brood stock level (Ventura and Sagi 2012; Aflalo and Sagi 2014), where each treated animal produces thousands of offspring, makes the price of dsRNA more acceptable. In contrast, when RNAi is considered as a treatment to be utilized on an entire population of an invasive or problematic species (for vaccination, environmental manipulations, or as a growth promoter), the price might indeed be a limiting factor. A global research effort is thus needed to address the above challenges by focusing on a more efficient delivery method (preferably a non-invasive technique to be delivered orally as a food supplement) and on a more cost effective dsRNA production method. Such developments would enable the establishment of more elegant solutions to addressing the problems associated with invasive species; these solutions could then be applied by conservationists in their fight against the ever-increasing loss of global biodiversity.

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Chapter 12
Quantitative Habitat Models for the Conservation of the Endangered European Crayfish *Austropotamobius pallipes* Complex (Astacoidea: Astacidae)

Paolo Vezza, Daniela Ghia and Gianluca Fea

Abstract Crayfish are the largest mobile freshwater invertebrates and are keystone species in European aquatic ecosystems particularly in small streams and rivers. The white-clawed crayfish *Austropotamobius pallipes* (a species complex) is currently classified by the IUCN Red List as an endangered species (EN), because its populations have decreased significantly over the last decades in a number of European countries including Italy, due mainly to habitat modifications and the introduction and spread of alien species. Data on the ecological requirements of *A. pallipes* are needed to quantify the effects of habitat alteration, to simulate restoration scenarios, and to implement effective conservation measures for this species. We describe here a new methodology for modelling the habitat requirements for this endangered crayfish using the mesohabitat scale approach based on data from crayfish living in small streams draining the Italian foothills of the Alps (Lombardy region) and in streams in the mountainous areas of the Gran Sasso and Monti della Laga National Park (Abruzzo region). Data from seven morphologically different streams were used to train and validate the habitat models. The Random Forests algorithm was used to identify the best and most parsimonious habitat model, and to define the lowest number of variables to be surveyed in the future. The best habitat models were applied to each stream and used to classify each mesohabitat into suitability categories. Habitat flow-rating curves were developed to analyze spatio-temporal variation of habitat availability, and habitat time series analysis were used to define detailed management schemes for environmental river management. Flow releases and water

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temperature regimes were assessed for individual water diversions in order (1) to represent how physical habitat changes through time, and (2) to identify stress conditions for *A. pallipes* created by the persistent limitation of habitat availability. Results indicated that the kind of substrate in the stream bed (such as the proportion of fine-grained substrates), the water depth (whether shallow or deep), and the available cover (such as the presence of boulders, woody debris, and undercut banks) were all significant factors governing the occurrence of crayfish. The habitat models performed well in both calibration and validation phases (with accuracy ranging from 71 to 79 % in training and from 69 to 73 % in validation) and can be considered to be a valuable tool to predict the distribution of *A. pallipes* over a wide range of stream types. An example of how to establish environmental standards for small streams is presented. The proposed habitat model provides a useful tool that can be applied even when other commonly used methodologies are unsuitable. As such, this habitat model can be used to develop regional rules for the conservation of the endangered crayfish *A. pallipes* complex and for defining more site-specific management criteria.

Keywords Endangered crayfish · Mesohabitat · MesoHABSIM · *Austropotamobius pallipes* · Crayfish conservation

12.1 Introduction

The white-clawed crayfish, *Austropotamobius pallipes* (Lereboullet 1858) species complex, is indigenous to European freshwater ecosystems (Fig. 12.1) and it is considered a “flagship species”, rather than indicative of good water quality (Füreder and Reynolds 2003).

Fig. 12.1 The white-clawed crayfish, *Austropotamobius pallipes* complex

Populations of *A. pallipes* complex have undergone a remarkable decline, and the extent of occurrence of this species in Europe has contracted sharply over the last 50 years (Souty-Grosset et al. 2006). In Italy declines in both crayfish numbers (down by 74 %), and in the distributional range have been reported over the last 10 years (Holdich et al. 2009). This has led to the species being listed in the EU Directive 92/43/EEC (Habitats Directive) as 'a species of community interest whose conservation requires the designation of special areas of conservation', and 'whose exploitation may be subject to management measures' (Annexes II and V, 92/43/EEC). This species is also listed as endangered (EN) by the IUCN (Füreder et al. 2010) due to habitat alteration, water diversion, water pollution, and the introduction of competitive North American freshwater crayfish species (*Procambarus clarkii* and *Orconectes limosus*) which are also carriers of the organism that causes the crayfish plague (the oomycete *Aphanomyces astaci* Schikora 1906) (Aquiloni et al. 2011). Habitat fragmentation has led to the geographic and genetic isolation of the remaining populations which are now confined to small streams in the headwaters of hydrographic basins (Nardi et al. 2004). In addition to the present threats, several hundred applications for new small hydropower plants (SHP) have been made across the whole Alpine and Apennine area (CIPRA 2010; CIRF 2014), and most of these are located in the small high gradient streams and headwaters which constitute the remaining unaltered habitat of the residual populations of *A. pallipes* complex.

Different management projects have been undertaken to prevent the extinction of native crayfish populations in European countries (Bernardo et al. 1997; Diéguez-Uribeondo et al. 1997; Holdich and Rogers 1997; Whitehouse et al. 2009; Berger and Füreder 2013; Ghia et al. 2015); but quantitative, predictive models and tools that can support the implementation of crayfish conservation actions are currently underdeveloped (Ghia et al. 2013). The prediction of crayfish distribution and abundance in relation to the stream habitat characteristics has multiple uses such as (1) planning reintroduction programmes, (2) assessing environmental flow releases from dams, and (3) evaluating and designing habitat restoration measures (Parasiewicz et al. 2012). Habitat simulation models are common tools used to perform stream habitat analyses and to demonstrate the effectiveness of the ecological management of watercourses (Maddock et al. 2013). These models use simulations of the spatio-temporal variation of habitat characteristics. The models aim to find the optimal hydro-morphological conditions needed to preserve aquatic communities and thereby avoid the decline of a selected group of target species beyond a determined conservation level. The meso-scale (or mesohabitat) approach is currently being used to model habitat changes in small high gradient streams in the Italian Alps and Apennine mountain ranges (Vezza et al. 2014a, b). These mesohabitats often correspond in size and location to hydro-morphological units (HMUs) such as pools, riffles, and rapids (Parasiewicz et al. 2013). Compared to the traditional micro-scale approach (e.g., Bovee 1982; Jorde et al. 2001) the mesohabitat scale allows for the surveying of longer portions of watercourses and involves a larger range of habitat descriptors in the analysis. As such it can be used to represent and model the complex morphology of high gradient mountain streams

(Vezza et al. 2012a). In addition, traditional modeling approaches are mainly focused on the use of fish as indicator species, because fish have important touristic and economic benefits for the surrounding human population. However, fish are often absent from the small mountain streams where crayfish populations do well, so these crustaceans can be used as the target species for restoration actions. Currently no comprehensive methodology has been presented in the literature to model the habitat for crayfish. A few case studies (Foster 1995; Clavero et al. 2009; Favaro et al. 2011) have described the habitat preferences of *A. pallipes* at different spatial scales, but this has not been integrated into habitat simulation tools (e.g., CASiMiR, Jorde et al. 2001; MesoHABSIM; Parasiewicz 2007a) and remains unexploited for environmental flow assessment and the design of habitat restoration measures.

Hydro-morphological and biological data from seven reference mountain streams in Italy have been used to develop a comprehensive habitat simulation methodology to describe and predict habitat requirements for the endangered crayfish *A. pallipes* complex. Streams were selected based on (1) the natural conditions of the habitat, (2) the absence of water abstraction, and (3) the presence of a native crayfish population with a well-structured age-class composition (Ghia et al. 2015). The Mesohabitat Simulation Model—MesoHABSIM (Parasiewicz et al. 2013) describes the natural spatio-temporal variation of habitat characteristics analyzed under reference conditions and quantifies habitat alteration, assesses environmental flow releases from existing and new water abstractions, and proposes habitat restoration measures for *A. pallipes* complex.

12.2 Study Area

The study was carried out in seven small streams, five of them were in the foothills of the Italian Alps in the Po River basin (Lombardy region, northern Italy), and two of them in the mountainous areas of the Gran Sasso and Monti della Laga National Park (Abruzzo region, central Italy) in the Saline and Tordino River basins (Fig. 12.2).

Each study stream has a stable population of white-clawed crayfish (*A. pallipes* complex), a moderate current velocity, generally high inorganic substrate heterogeneity, and woody debris, leaves, and detritus are all present. These study sites are located in the altitudinal range typical for *A. pallipes* complex (Fea et al. 2006) and each has the optimal value for the annual mean water temperature of the species (Souty-Grosset et al. 2006). Moreover, these streams were chosen within European protected sites (Natura 2000) and are surrounded by woodland in order to minimize anthropic disturbance including the poaching of crayfish. Each high-gradient stream site was characterized by a different morphological type (ranging from cascade, to step-pool, to plane bed type) (Montgomery and Buffington 1997; Vezza et al. 2014b). The length of the analyzed stretch was from 15 to 30 times the width of the stream, so that the hydro-morphological unit of distribution in small mountain

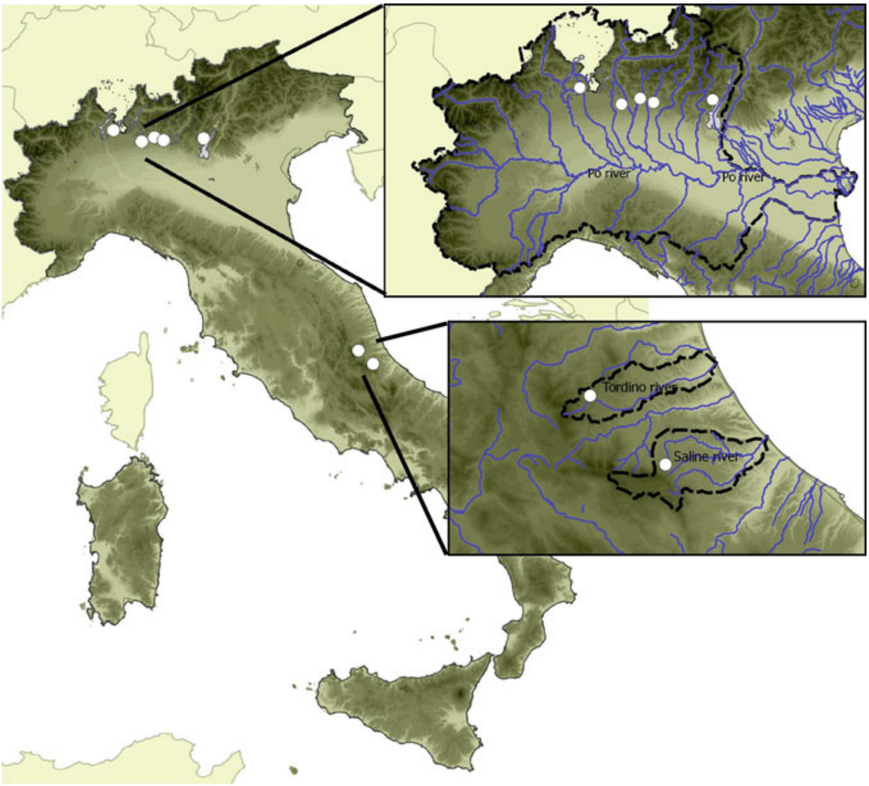

Fig. 12.2 Study sites selected in reference streams in the foothills of the Italian Alps in the Po River basin (Lombardy region, northern Italy) and in the Gran Sasso and Monti della Laga National Park (Abruzzo region, central Italy)

watercourses could be described (as mentioned in the system for morphological unit classification published by the Italian National Institute for Environmental Protection and Research, Rinaldi et al. 2015).

12.3 A Mesohabitat Simulation Model for the Endangered *A. pallipes* Complex

12.3.1 Habitat Description

Vezza et al. (2014b) described the changes in mesohabitat distribution over a selected range of stream discharges. The survey of mesohabitat characteristics was carried out with a rangefinder (Trupulse 360B, Laser Technology, Centennial, Colorado, USA) and a rugged field computer (e.g., Nomad TDS [tripod data system], Field Environmental Instruments, Sunnyvale, California, USA) along with a global positioning system [GPS]. The GPS was used to capture the starting point of the survey, defined as a nearby opening with good satellite coverage, or from a clearly identifiable ground control point. The HMU polygons were delineated using the rangefinder and both mesohabitat-scale features (e.g., HMU type, gradient, cover sources). Random samples of water depth, flow velocity, and substrate composition were recorded for each of the mapped mesohabitats. In particular for each HMU we collected from 7 to 30 mean water column velocity values (by using the flowmeter Marsh—McBirney Flo-Mate; Hach Company, Loveland, Colorado, USA), and carried out depth measurements and substrate estimates in order to describe the frequency distribution of these physical variables and to describe the entire HMU area. Flow velocity, water depth, and substrate type were then divided into frequency classes as a percentage of the random samples. The complete list of habitat descriptors collected during a habitat survey for crayfish is reported in Table 12.1. This HMU survey was repeated over a range of flows, between the minimum low flows and the medium/high flows that would be expected on these watercourses.

Table 12.1 Physical habitat attributes used to describe hydro-morphological units for *A. pallipes* complex

Variable name	Unit	Classes	Categories/description
Hydro-morphological unit (HMUs)	Yes/no	12	Photole, pool, plunge pool, glide, rock glide, riffle, rapid, cascade, step, waterfall, backwater pool, dune system
HMU length	m	1	Longitudinal length of the HMU
HMU width	m	1	Mean width of the HMU
HMU gradient	%	1	Longitudinal mean slope of the water surface
Cover	Yes/no	8	Boulders; canopy shading; woody debris; overhanging Vegetation; submerged vegetation; emergent vegetation; undercut bank, exposed tree roots
Flow velocity	Percentage of at least 7 random samples	9	Classes in 15-cm increments (range 0–120 cm and above)
Water depth	Percentage of at least 7 random samples	9	Classes in 15-cm/s increments (range 0–120 cm/s and above)
Substrate	Percentage of at least 7	12	Gigalithal (roks); Megalithal (>40 cm); Macrolithal (20–40 cm); Mesolithal (6–20 cm); Microlithal

(continued)

Table 12.1 (continued)

Variable name	Unit	Classes	Categories/description
	random samples		(2–6 cm); Akal (gravel); Psammal (sand); Pelal (silt, clay), Detritus (organic matter); Xylal (woody debris, roots); Sapropel (dark anoxic mud); Phytal (submerged plants)
Froude number	(flow velocity)/(9.81 depth)^0.5	1	Average value over the HMU area
Flow velocity standard deviation (SD)	cm/s	1	Flow velocity SD over the HMU area

12.3.2 Biological Data Collection

Crayfish (*A. pallipes*) were collected in each stream at night when these animals are most active in order to define the habitat requirements and to build mesohabitat suitability models (Barbaresi and Gherardi 2001). During summer 2012 and 2013 crayfish were quantitatively sampled by hand by walking upstream in each previously mapped HMU (Smith et al. 1996; Ghia et al. 2015). The gender of each crayfish was recorded. The cephalothorax length (CL = from the tip of the rostrum to the posterior median edge of the cephalothorax) was measured using digital calipers. CL was used as a reliable measurement of length due to the rigid structure of the cephalothorax. All crayfish that either lacked a rostrum or had a mutated rostrum were excluded from the length-frequency distributions. Wet weight was determined using a handy spring balance and any morphological mutilations were recorded. After measurement, crayfish were returned to the same sampled HMU part of the stream. Then, each crayfish was classified as adults or juveniles using size-frequency distributions to estimate the age composition (Ghia et al. 2015).

12.3.3 Defining Mesohabitat Suitability Criteria for A. pallipes Complex

Data from five reference streams in the foothills of the Italian Alps, which comprised 130 sampled HMUs, were used for *A. pallipes* model training. An independent dataset was collected in the two reference streams in the Gran Sasso and Monti della Laga National Park (65 HMUs, 50 % of the training data-set) and was used for model validation. In terms of crayfish presence the proportion of occurrence (i.e., model prevalence) of adult *A. pallipes* was 0.49 in training, and 0.46 in validation, whereas the proportion of occurrence of juveniles was 0.56 in training and 0.34 in validation. Abundance thresholds for crayfish were assessed as

1.5 ind/m^2 for adults and as 2.0 ind/m^2 for juveniles, whereas the presence/abundance model prevalence in training was 0.21 for adults and 0.28 for juveniles. The low density values of crayfish found in the validation sites (<0.8 ind/m^2) meant that only absence/presence models could be validated using an independent dataset.

To find effective mesohabitat suitability criteria the relationship between habitat variables and crayfish distribution was explored by Random Forests (Breiman 2001) as implemented in R (Liaw and Wiener 2002). RF is an ensemble learning technique based on the combination of a large set of decision trees (i.e., Classification and Regression Trees—CART, Breiman et al. 1984).

In RF, each tree is trained by selecting a random bootstrap subset Xi (i = bootstrap iteration which ranges from 1 to t, maximum number of trees) of the original dataset X and a random set of predictive variables (Liaw and Wiener 2002). Breiman (2001) provides details of the algorithm for growing a RF of decision trees. Following the MesoHABSIM approach two binary models were built as follows: a suitable habitat model (to distinguish between the absence and presence of crayfish) and an optimal habitat model (to distinguish between the presence and abundance of crayfish). The cutoff value for low and high abundance was determined as the inflection point of the envelope curve of the crayfish density histograms (Vezza et al. 2014b). As the response variable was categorical (crayfish absence/presence and presence/abundance), we therefore confined our attention to classification RF models.

To improve model parsimony the minimum number of variables was identified by the Model Improvement Ratio (MIR, Murphy et al. 2010) technique. The improvement ratio was calculated as [In/Imax], where In is the importance of a given variable and Imax is the maximum variable importance. To carry out this analysis the conditional variable importance was used to avoid RF bias towards correlated predictor variables (see, Strobl et al. 2008). Starting from MIR = 0, we then iterated through MIR thresholds (i.e., 0.02 increments), with all variables above the threshold retained for each model. Models corresponding to different subsets were compared and the model exhibiting the minimum EOOB and the lowest maximum EClass (j) was selected. Lastly, to avoid collinearity effects on the model performance, the correlation among the selected variables was tested using a correlation matrix. Crayfish habitat models were developed for both adults and juveniles.

The performance of the predictive models was evaluated using six performance metrics, i.e., accuracy, sensitivity, specificity, Cohen's kappa (k), area under Receiver Operating Characteristic (ROC) curve (AUC), and true skill statistic (TSS), which are commonly used in ecological modelling (Vezza et al. 2015). The partial dependence plots provided a way to visualize the marginal effect of the selected independent variables on the probability of crayfish presence or abundance. Specifically, these plots can be used to characterize graphically the relationship between habitat variables and the predicted probabilities of fish presence obtained by RF (Cutler et al. 2007).

12.3.4 Modelling Spatio-temporal Variation of Habitat Availability

The obtained mesohabitat suitability criteria were then applied to all HMUs mapped at each flow to calculate the probability of presence and high abundance and to classify mesohabitat into suitability categories (not suitable, suitable, or optimal). A probability equal to 0.5 is commonly used by RF to define the probability threshold and to determine the best separation of not-suitable/suitable (or suitable/optimal) habitat units. To develop habitat-flow rating curves, the area of HMUs with suitable and optimal habitats was summarized for every site by weighting suitable habitat area by 25 % and optimal habitat area by 75 %, and was plotted against the wetted area at the highest measured flow (Parasiewicz 2007a). To represent the habitat rating curve, the habitat values were interpolated using a mathematical spline function for the target species and the considered life stages (Vezza et al. 2014b).

In addition to habitat-flow rating curves, the definition of the reference habitat time series is an important final element needed for the full determination of environmental standards for watercourses (Milhous et al. 1990). The MesoHABSIM model emphasizes the temporal scale by statistically analysing habitat time series to detect stress periods due to limited habitat availability. This analysis is based on the assumption that habitat availability is a limiting factor, and events occurring rarely in nature create stress to aquatic fauna and shape the community. The identification of periods of stress has to not only consider the magnitude of a possible impact (i.e., the amount of diverted water), but also needs to provide a means of quantitatively measuring duration and frequency of stress events.

The habitat time series is calculated by converting the stream flow time series using the habitat flow rating curve (Milhous et al. 1990). Unfortunately, hydrological information and the stream flow time series are usually not available for small mountain streams. Therefore, the water levels and water temperatures of streams were continuously measured using HOBO © pressure transducers (Onset Computer Corporation, Bourne, Massachusetts, USA) and the mean daily discharge was calculated using discharge versus stage curves calibrated in stable regular cross-sections. The obtained habitat time series was then statistically analyzed using the uniform continuous under thresholds (UCUTs) methodology. The UCUT-curves are considered projected contours of a habitat surface area in the three dimensional space of duration, frequency, and habitat quantity (Vezza et al. 2012b). They are defined as the sum length of all events of the same duration, computed as a ratio of a total duration of the considered bioperiod, where proportions are plotted as a cumulative frequency. This procedure is repeated for an entire set of possible thresholds (e.g., from 2 % to the maximum value of available habitat). The UCUTs for very low frequency are located in the bottom left corner of the UCUT graph (Fig. 15.5). As habitat level continues to increase, this pattern of UCUTs rapidly changes and the distance between the curves increases. The highest curve is usually selected in the rare-event group of curves, as the rare-event level threshold. The distance between the lines after exceeding the rare-event level are usually greater than in the previous group, but are still close to each other. The next outstanding curve, demarcating a rapid change in the frequency of events (i.e., an increase in distance between curves), is assumed to mark the stage at which the common under-threshold events begin (Parasiewicz 2007b).

This analysis helps to identify the longest period that under-threshold events are allowed to continue before reaching catastrophic conditions (Parasiewicz et al. 2013). The results of habitat and water temperature time series analyses were used to define natural conditions and environmental standards, aimed at reducing or excluding continuous duration of events that are stressful for *A. pallipes*.

12.4 The Application of the Results to the Mesohabitat Suitability Models

A total of 1033 crayfish (538 females and 495 males) were collected at both of the locations used here (the model training and validation sites). Using the cross-validation procedure embedded in RF, model training performances were found to be high for both adult and juvenile crayfish absence/presence models (Table 12.2). In model training the lower value for accuracy was 0.71, 0.76 for AUC, and 0.46 for TSS.

Table 12.2 Performance metrics of the mesohabitat suitability models for both adult (Ad.) and juvenile (Juv.) *A. pallipes* complex. Two binary classification models were built: the absence/presence model and the presence/abundance model. Only the absence/presence model was validated using an independent data sets due to low density values in the validation sites

	Model training		Model validation	
	Ad. *A. pallipes*	Juv. *A. pallipes*	Ad. *A. pallipes*	Juv. *A. pallipes*
Absence/presence model				
Accuracy	0.75	0.75	0.69	0.73
Sensitivity	0.75	0.73	0.80	0.83
Specificity	0.74	0.76	0.61	0.67
Cohen's kappa	0.51	0.49	0.39	0.47
Area under ROC curve	0.76	0.82	0.71	0.75
True skill statistics	0.49	0.49	0.41	0.50
Prevalence	0.49	0.56	0.45	0.34
Presence/abundance model				
Accuracy	0.79	0.71		
Sensitivity	0.77	0.75		
Specificity	0.79	0.71		
Cohen's kappa	0.47	0.39		
Area under ROC curve	0.83	0.82		
True skill statistics	0.56	0.46		
Prevalence	0.21	0.28		

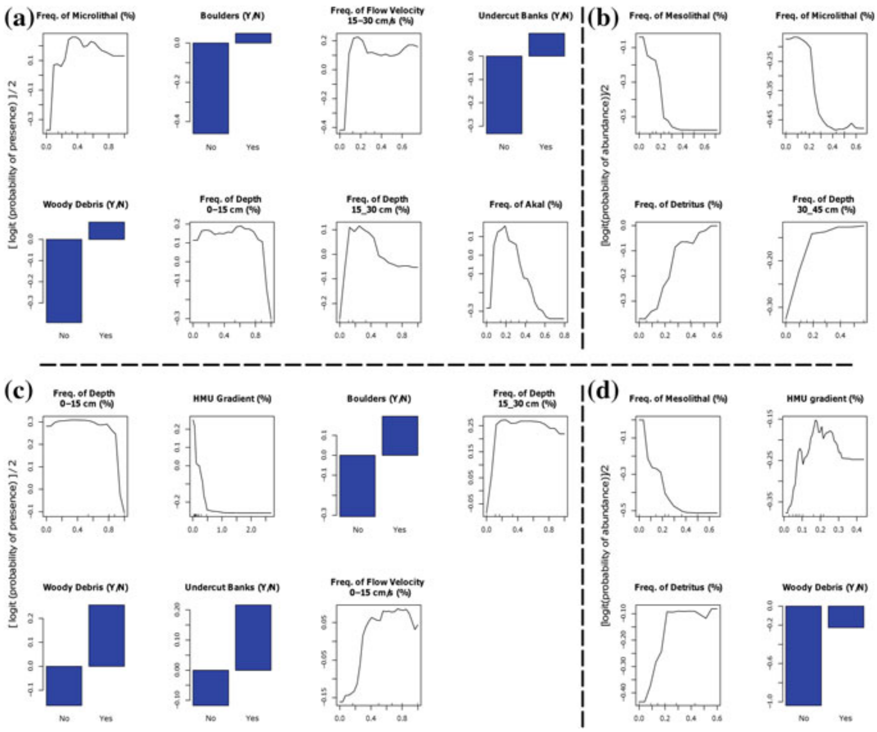

Fig. 12.3 Random forest model for crayfish to predict **a** adult presence, **b** adult abundance, **c** juvenile presence and **d** juvenile abundance. Selected variables are reported in order of importance. A detailed description of considered habitat attributes is reported in Table 12.1 and in Vezza et al. (2014b). The relationship between variables and probability is shown using partial dependence plots to investigate the marginal effect of the selected independent variable on the predicted probability of crayfish presence

Mesohabitat characteristics significantly affected the presence of crayfish ($\chi^2 = 43.582$, df = 9, $p = 0.000$). Crayfish occurred mostly in pools (58.1 %), riffles (14.3 %), and plunge-pools (13.1 %), and rarely in backwaters (1.5 %), shallow margins (0.5 %), and steps and waterfalls (0.3 %). The partial dependence plots (Fig. 12.3) indicated that the mesohabitat models provided similar sets for adults and juveniles although variables were ranked differently. Specifically, a microlithal substratum (grain size: 2–6 cm), akal (gravel), water depth up to 30 cm, and flow velocity up to 30 cm/s were selected as important for the presence of both adult and juvenile *A. pallipes*. In addition, mesohabitat features such as type of cover (boulders, woody debris and undercut banks) were important to these crayfish, and the presence of the cover positively correlates with the probability of presence.

Where crayfish was found as present, *A. pallipes* abundance models were calibrated. Low proportion of mesolithal, and high occurrence of detritus were selected

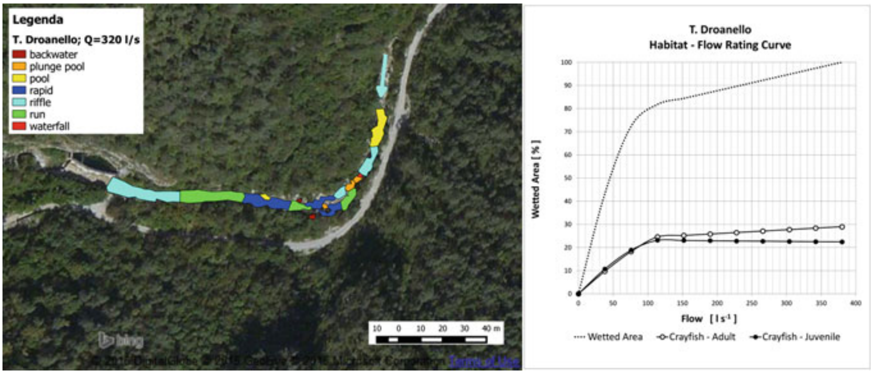

Fig. 12.4 The study site on the Droanello Creek (in the foothills of the Italian Alps, Lombardy region). MesoHABSIM model application to build habitat-flow rating curves for *A. pallipes* (adult and juvenile crayfish). Details of field data collection and model application are reported in Vezza et al. (2014b)

as important habitat characteristics for *A. pallipes* abundance. Furthermore for adults, high proportion of water depth between 30 and 45 cm are also positively correlated with the probability of abundance. Mesohabitat suitability models predicting crayfish presence and abundance are reported in Fig. 12.3 for both adults and juveniles.

Habitat-flow rate curves for both adult and juvenile *A. pallipes* were built by applying mesohabitat suitability models to mapped HMUs (Fig. 12.4). These curves define the habitat variation at the selected range of flows and are plotted together with the wetted area curve. The distance between the wetted area and the habitat curves represents the amount of river channel that is not available for *A. pallipes* complex.

Flow and water temperature data collected at the study sites were used to generate the reference habitat and water temperature time series and to calculate the uniform continuous under threshold (UCUT) curves for the spring/summer period (May–July, Figs. 12.5 and 12.6). This period was the most critical bioperiod for crayfish due to flow recession, low flow occurrence, and increased water temperatures. Each curve on the diagram represents the cumulative duration of under-threshold events (ranging between 2 and 30 % of the channel area for habitat availability, and from 10 to 19 °C for water temperature). The reduction in slope, as well as the increase of spacing between the two curves, indicate the increase in the frequency of under-threshold events (Parasiewicz 2007b). Thresholds that identify rare under-threshold events (i.e., habitat availability equal to 16 % of the channel area and water temperature equal to 13 °C) and common under-threshold events (26 % of the channel area and 18 °C for water temperature) were selected and used to demarcate the references for the frequency and duration of events that were allowable (green area), critical (yellow area), or catastrophic and not allowable (red area) in the Droanello Creek.

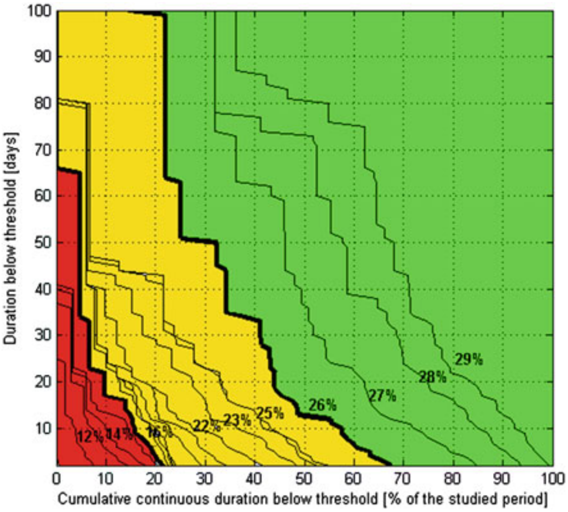

Fig. 12.5 The application of uniform continuous under threshold (UCUT) curves for Droanello Creek, Lombardy, Italy, to determine habitat stressor thresholds. Events between 2 and 29 % of channel area available for *A. pallipes* were analyzed referring to spring/summer low-flow periods (1 May–31 July). Increase of spacing between two curves, indicate an increase in the frequency of under-threshold events and rare (16 %) and common (26 %) habitat thresholds were selected and used to demarcate associated allowable (*green*), critical (*yellow*) and catastrophic (*red*) frequency-durations areas in the graph

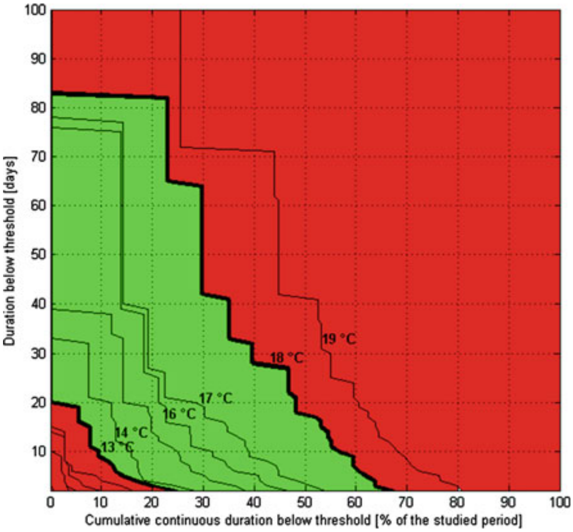

Fig. 12.6 The application of uniform continuous under threshold (UCUT) curves for Droanello Creek, Lombardy, Italy, to determine water temperature stressor thresholds during spring/summer (1 May–31 July). Events between 8 and 19 °C were analyzed. As for habitat availability, rare (13 °C) and common (18 °C) temperature thresholds were selected and used to demarcate associated allowable (*green*) and catastrophic (*red*) frequency-durations areas in the graph

12.5 Discussion

To date habitat simulation models have been mostly built to identify the habitat characteristics used by target fish species (Vezza et al. 2014b). The research presented here provides a comprehensive methodology to model habitat for freshwater crayfish in small, high gradient mountain streams. Specifically, the mesohabitat scale was used to link in-stream environmental conditions to crayfish presence and abundance. The mesohabitat scale adapts well to the description of crayfish habitat use and distribution, and demonstrates great potential for the environmental management of watercourses (Fig. 12.7).

Mesohabitats as reference units for the analyses are useful ways to capture the confounding effects of different environmental variables (i.e., channel geometry, cover availability, flow velocity, water depth, substrate composition), focussing on how crayfish interact with the spatial arrangement of habitat characteristics. Random Forests (RF) was also effective in predicting the probability of crayfish presence and abundance in response to habitat variables. The conditional variable importance (Strobl et al. 2008) was used together with the Model Improvement Ratio (MIR) technique (Murphy et al. 2010) and the procedure allowed us to minimize noise and to improve model performance. RF is robust to overfitting when the number of noise variables increases and, together with the MIR procedure, is appropriate for parsimonious model construction (Vezza et al. 2015). A balanced species prevalence (i.e., presence, or abundance, frequency equal to 50 %) was not used to build mesohabitat suitability models due to its negligible

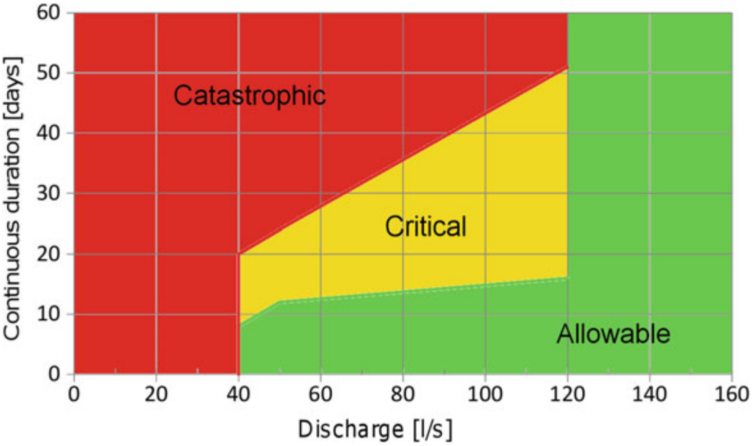

Fig. 12.7 E-flow scheme for the Droanello Creek, Lombardy, Italy. A possible e-flow option would be to allow hydropower generation with environmental flow release in the bypass section of 50 l/s with two-day interruptions every three weeks (catastrophic duration, *red area* in the graph). Once the inflow drops below this discharge value, the operation would cease until there is an increase to 120 l/s for two consecutive days. This conservative scenario, which aims to avoid subsistence flow, is one of the available options

influence on RF results (Freeman et al. 2012). All models developed for crayfish showed high accuracy, high sensitivity/specificity values, and strong Cohen's kappa statistics, indicating a very good to excellent model performance (Allouche et al. 2006). The area under ROC curve (AUC) and the true skill statistic (TSS), which are considered independent of prevalence (Vaughan and Ormerod 2005), also suggested low cross-classification errors and reliable predictions of crayfish distribution.

The high preference of *A. pallipes* for pools is in accordance with the findings of Englund and Krupa (2000) and Clavero et al. (2009). Crayfish were also found in mesohabitats characterized by moderate flow velocity (e.g., plunge-pools and riffles with velocity values of up to 40 cm/s). All the selected habitat variables in the models are features already reported to be important for microhabitat use by white-clawed crayfish in Mediterranean streams (Benvenuto et al. 2008; Clavero et al. 2009). Specifically, deep water plays an important role in decreasing the risk of predation by terrestrial and aquatic predators (Smith et al. 1996). Adult crayfish were found in deep pools with a water depth up to 50 cm. In addition, the availability of shelters for the crayfish reduces the risk of predation. In areas where crayfish density was high, crayfish often shifted towards shallow water if there was abundant cover, which served to reduce cannibalism after moult among adult crayfish (Ackerfors 1996). In the mesohabitat suitability models developed here (Fig. 12.3), the presence of refuges (mostly boulders, undercut banks and woody debris) was found to be a crucial factor that allows this species to inhabit a stream. This is confirmed by previous research (Foster 1993), in which the size of hidden crayfish was shown to be positively correlated to the size of the shelter stones. Woody debris and detritus also represent the main sources of energy and proteins available for *A. pallipes* which mostly acts as a detritus consumer (Gherardi et al. 2004). The fine-grained sediment (microlithal and akal) is the most suitable medium for macroinvertebrates and for the growth of the periphyton that constitutes the main food source for the white-clawed crayfish (Foster 1995; Naura and Robinson 1998). It is important to note that in this study we collected crayfish during the night because that is when they showed the most foraging activity (Barbaresi and Gherardi 2001; Gherardi et al. 2001). This nocturnal behavior can be considered one of the main reasons why the presence of woody debris and detritus significantly affects the presence of *A. pallipes*.

The high model performance in validation (Table 12.2) demonstrated the ecological relevance of the selected variables in predicting crayfish presence. As reported in Vezza et al. (2015), the use of independent data for validation is not a common procedure and it is often omitted when researchers build predictive models of species distribution (Elith and Leathwick 2009). Current practice usually involves testing predictive performance using data resampling (e.g., split-sample or cross-validation procedures, Favaro et al. 2011). Testing modelled crayfish-habitat relationships with independent data collected in different regions with different environmental conditions can provide valuable insights into model effectiveness and transferability (Bennett et al. 2013). Although we did not validate our presence/abundance models our results showed that absence/presence data would be promising, and future model validation tests are already planned.

The influence of different habitat variables (which can be either categorical or continuous) was captured by the modeling technique used here, which uses an ecologically relevant spatial scale. Indeed, the present approach substantially differs from traditional and more commonly used micro-scale analyses (Bovee 1982; Jorde et al. 2001) which are limited in including a large range of habitat variables (Vezza et al. 2012a), and when working on mountain streams that have a complex morphology and high gradient (Vezza et al. 2014b). In addition, collecting observational data across large spatial extents (e.g., several streams each with different morpho-climatic characteristics) is more useful when investigating the effect of habitat variables (Vezza et al. 2015). Apart from its ecological relevance, our regional predictive model builds in reference conditions based on reference variables that can be objectively measured and used as references for the effective environmental management of watercourses.

A recent guidance published by the European Union (Petitguyot et al. 2015) stressed the urgent need to better address over abstraction of water, the second most common pressure on the ecological status of rivers in the EU. The guidance identified possible methods that should be used to calculate ecological flows for the implementation of the European Water Framework Directive (WFD, 2000/60/CEE). The proposed mesohabitat modeling approach is recognized by the EU guidance as a reference method to achieve the WFD's environmental objectives, and as a specific application for crayfish.

The case study of crayfish from the Droanello Creek described here used the habitat time series analysis as a key component for the definition of environmental flows. This analysis demonstrates how physical habitat changes through time, and identifies stress conditions created by persistent limitation in habitat availability. The reference habitat time series uses UCUT curves to establish frequency and duration of events that characterized natural habitat conditions (Fig. 15.5). These highly informative diagrams allow the approximation of an envelope of typically occurring habitat events that are harmless to the fauna, so any environmental flows recommended for specific water abstractions should fall within this envelope. Catastrophically low habitat quantity can be identified by this method and although these events occur under natural conditions, they are not common. Consequently, environmental flow management offers one way to avoid increasing the frequency of such disturbances (Vezza et al. 2014b).

UCUTs help to identify the longest period that a habitat event is allowed to continue before reaching catastrophic/not allowable conditions (Parasiewicz et al. 2013). Once the allowable duration of released flow is exceeded the strategy calls for the release of water for a few consecutive days so that the amount of habitat increases and the continuous stress is stopped. This strategy can be summarized in operational rules and used for individual hydropower facilities. Figure 15.7 simplifies and summarizes the UCUT graph reported in Fig. 12.5.

Using the Droanello Creek as an example of a mountain stream in northern Italy it may be possible to allow hydropower generation in May–July (i.e., the flow

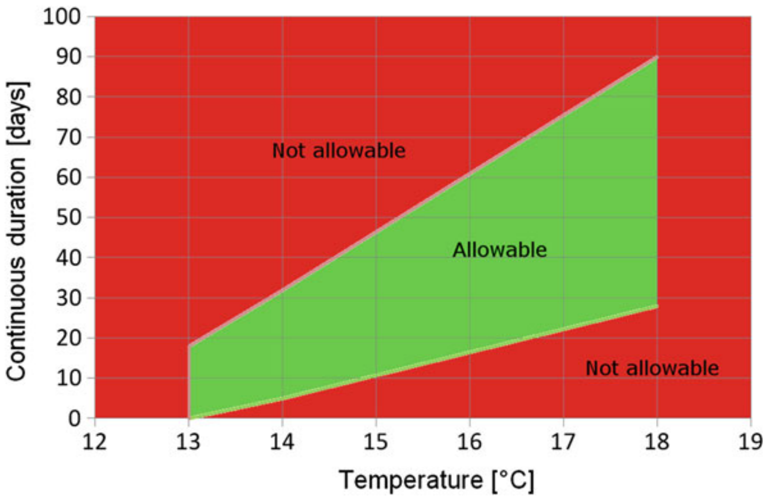

Fig. 12.8 Water temperature reference scheme for the Droanello Creek, Lombardy, Italy. The increase in temperature from 13 to 18 °C should be maintained in the spring/summer period. In July the water temperature is commonly below 18 °C, whereas the trend in increasing water temperatures can be maintained by following the continuous duration under-threshold (represented by the *green area* in the graph)

recession and low flow period) by releasing 50 l/s as e-flows in the bypass section with two-day interruptions every three weeks. Once the inflow drops below 50 l/s, the operation would cease until there is an increase to at least 120 l/s for two consecutive days. This conservative scenario aims to avoid continuously constant subsistence flow and continuous low habitat availability. The same concept can be used to define natural reference conditions for the water temperature. The results of this UCUT analysis are reported in Figs. 12.6 and 12.8.

The natural water temperature in May–July typically increases from 13 to 18 °C and this would not be affected by water abstractions. In July, it is common for water temperature to stay below 19 °C, and increases in the frequency and duration of these warm water events may lead to catastrophic changes in the composition of local crayfish populations. It is important to say that the trend in naturally increasing water temperatures between spring and summer should be maintained by respecting the continuous duration under-thresholds scheme reported in Fig. 15.8 (green area). For example, water temperatures of less than or equal to 14 °C cannot be maintained in the stream for more than one month (30 days). If the period started on May 1st, then June temperatures would be maintained higher than this value.

The methodological approach described here for Italian mountain streams can support e-flow implementation and habitat restoration actions and is critically needed to (1) protect local populations of endangered species of crayfish, (2) implement recent water laws, such as the European Water Framework Directive, and (3) address the present lack of intervention methods. Specific negative impacts on

A. pallipes can be detected before modifying the hydrological regime or morphological conditions. For existing water abstractions different restoration strategies can be compared using the proposed approach, and cost-effectiveness analyses can be carried out by decision makers to select the best restoration alternative.

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Chapter 13
Conservation First: Strategic Planning to Save the Critically Endangered Singapore Freshwater Crab, *Johora singaporensis*

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Abstract The critically endangered Singapore freshwater crab, *Johora singaporensis,* is among the 100 most threatened species in the world. The species is endemic to Singapore and known from only a few hill stream localities. Conservation approaches so far have largely focused on basic descriptive research into the animal's taxonomy, autecology and distribution, and on in situ site conservation and management. In an effort to enhance and ensure the long-term survival of this flagship aquatic invertebrate, a conservation strategy was recently developed along International Union for Conservation of Nature (IUCN) guidelines to integrate efforts and approaches into a cohesive action plan. This article outlines the background, development processes (including analysis of threats), and follow-up that have led to publication of the Singapore freshwater crab species conservation strategy, which is to our knowledge, the first for a single invertebrate species.

Keywords Aquatic · Brachyura · Decapoda · Invertebrate · Potamidae · Southeast Asia · Stream · Threatened species

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13.1 Introduction

13.1.1 Freshwater Crabs at Risk

Primary freshwater crabs (Pseudothelphusidae, Potamidae, Potamonautidae, Gecarcinucidae, and Trichodactylidae) are a group of wholly freshwater families (Yeo et al. 2008a, 2014; Cumberlidge and Ng 2009). In the first-ever global conservation assessment of the primary freshwater crabs, Cumberlidge et al. (2009) found a significant proportion (one-sixth) of the world's close to 1300 species to be threatened with extinction, and a larger proportion (about half) to lack sufficient data to even be evaluated in the first place; they identified various threats facing this group of animals, and called for strategies to be developed to safeguard the world's threatened freshwater crabs.

Citing various sources (Ng 2008; Yeo et al. 2008b), Cumberlidge et al. (2009) highlighted the Singapore freshwater crab, *Johora singaporensis* Ng 1986 (Fig. 13.1) as a case study of an environmentally-sensitive species teetering on the edge of extinction, which, while protected, remained highly restricted spatially, and prone to sudden, random events that could possibly lead to extinction. Locally, the status of the Singapore freshwater crab had long been recognised and conservation

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Fig. 13.1 The Singapore freshwater crab (*Johora singaporensis*). Photo DJJN

efforts begun (Ng 2008; Yeo et al. 2008b), but since then, *Johora singaporensis* has now also come to represent a flagship and an international focal point for concerted conservation efforts (Chua 2014; Khew 2015; Ng et al. 2015a).

13.1.2 The Singapore Freshwater Crab, **Johora singaporensis** *Ng 1986*

Johora singaporensis (family Potamidae) was described relatively recently from Singapore by Ng (1986). The species is the only member of *Johora* to be found in Singapore, with the remaining members of the genus distributed through the rest of the Malay Peninsula up to southern Thailand (Ng 1988; Yeo et al. 2007). While belonging to the same phylogenetic clade and being geographically closest to species found in the state of Johor (e.g., *J. johorensis* and *J. murphyi*) just north of Singapore (Yeo et al. 2007), *J. singaporensis* is nevertheless a distinct species based on differentiation in its male first pleopod morphology (Ng 1988) and 16S rRNA, COI, and H3 genes (Yeo et al. 2007). This means that the species is entirely restricted to the island of Singapore, and this endemicity carries with it important implications for conservation.

Johora singaporensis is one of three freshwater crab species that are endemic to Singapore island—the other two being *Irmengardia johnsoni* Ng and Yang, and *Parathelphusa reticulata* Ng (both Gecarcinucidae) (Yeo et al. 2008b; Yeo and Lim 2010). It is also one of only four primary freshwater crab species known from the city-state; the fourth species is *Parathelphusa maculata* (Gecarcinucidae), a fairly abundant and widespread species found in lowland forest streams in Singapore, southern Peninsular Malaysia, and southern Sumatra (Ng 1988).

As one of the very few endemic species known from Singapore, *J. singaporensis,* is regarded as an icon of both Singapore's national as well as natural heritage (Tan et al. 2010; Yeo and Lim 2010), having been featured as such in local media, on postage stamps, and in various biodiversity awareness events. Unfortunately, however, as mentioned earlier, *J. singaporensis* is also an icon of threatened aquatic biodiversity. As a freshwater decapod crustacean, it belongs to one of the three aquatic faunal groups (freshwater fishes, freshwater decapod crustaceans, and amphibians) to have experienced the highest rates of extinctions in Singapore, mostly owing to loss of forest habitat (Brook et al. 2003).

Johora singaporensis is particularly at risk. Prior to 2008, it was known to exist in only three small, isolated hill-stream drainages on Singapore Island, which are fragmented from one another. Of these, one site (the type locality) was within a nature reserve and under strict protection; the protection afforded to this site lead to the species being categorized as Endangered in a national conservation assessment (Yeo et al. 2008b). Soon after, however, it was discovered that, despite being protected, the population at the type locality had severely declined to the point of extirpation, possibly as a result of anthropogenic acidification (Ng 2008). Accordingly, as part of a global assessment, the threat status of *J. singaporensis* was re-evaluated and upgraded to Critically Endangered (Esser et al. 2008), making it the only member out of the 15 species of *Johora* to be categorized as such. As mentioned earlier, this prompted Cumberlidge et al. (2009) to feature the species as a case study. Subsequently, the plight of the species received international recognition when the Zoological Society of London in collaboration with IUCN subsequently listed *J. singaporensis* as one of the world's 100 most threatened species (Baillie and Butcher 2012).

Despite concern for its threatened status, little, apart from taxonomy and systematics and some anecdotal information on autecology and distribution, was known about the ecology and biology (especially quantitative aspects) of *J. singaporensis.* This is in part down its small size (about 30 mm carapace width), cryptic behaviour, and challenging habitat sites (e.g., hill streams with water flowing between/under large immovable granite boulders; or location within gazetted military areas).

13.1.3 Johora singaporensis *Conservation to Date*

Recognising the precarious situation of *J. singaporensis,* and especially in light of the loss of the population in the protected nature reserve (Ng 2008), collaborative efforts have been ongoing between the National Parks Board, Singapore (NParks), National University of Singapore (NUS), and Wildlife Reserves Singapore (WRS), in cooperation with other government agencies, to protect the populations from further decline. The priorities of initial immediate efforts focused on the gathering of more data on the distribution and ecology of the species through intensive stream surveys and monitoring (Ee 2013), and on protection and management of existing sites, i.e., in situ conservation approach. A positive result from these early efforts was the discovery after the 2008 study of another site within the protected nature reserve with a healthy population of *J. singaporensis* (see Ng et al. 2015b). Several other findings stemming from this aspect (research and monitoring) of the conservation effort have since been published. These include an overview of the conservation challenges and actions taken (Ng et al. 2015c), expansion of the distribution of the species through discovery of new populations/sites (Ng et al. 2015b; Li et al. 2015); observations on feeding and reproduction (Ng and Yeo 2013; Chua et al. 2014); and a study of the characteristics of the hill stream habitats of *J. singaporensis* (see Chua et al. 2015).

Preliminary captive breeding was also attempted as a form of ex situ conservation. This was somewhat limited and ad hoc in nature owing to logistic constraints and lack of prior experience with freshwater crab breeding, but has been expanded and developed now into a dedicated breeding programme supported by a purpose-built facility at WRS (Chua 2014). However, it would take more than just publications and facilities, or the individual efforts of carcinologists and site managers, for the applied conservation of *J. singaporensis* to be successful.

What was still lacking at the beginning was a specific, encompassing and cohesive conservation strategy or plan, which would include many other stakeholders and integrate all aspects of the conservation effort, e.g., research and monitoring; site protection and management; captive breeding and husbandry; and outreach, education and awareness. Therefore, in 2014, steps were taken to develop a formal conservation strategy for *J. singaporensis* based on the guidelines and framework of the IUCN Species Conservation Planning Sub-Committee (IUCN/SSC 2008a, b). While earlier IUCN Action Plans had been previously developed for vertebrates (e.g., Asian elephant—Santiapillai et al. 1990; cetaceans—Reeves et al. 2003), and invertebrates (e.g., swallowtail butterflies—New et al. 1991; dragonflies—Moore 1997), the conservation strategy for *J. singaporensis,* which was completed in June 2015 (Ng et al. 2015a), is one of the first strategies to be developed and published using a more inclusive and participatory approach called for by the IUCN/SSC (2008b: 3); it is also the first conservation strategy for a single invertebrate species. What follows is a description of the process and follow-up that led to the development of this strategy.

13.2 Conservation Planning

13.2.1 Freshwater Crab Conservation Round Table (FCCRT)

The first critical step to developing the conservation strategy for *J. singaporensis* was to bring together the most relevant parties and/or experts with stakes or interests in the survival of the crab and the preservation/protection of its immediate habitats (and surrounding environments) to discuss and provide input to the process. This was achieved through a Freshwater Crab Conservation Round Table (FCCRT) co-organised by NParks, NUS, and WRS, in cooperation with the IUCN-Species Survival Commission (IUCN-SSC).

The FCCRT brought together for the first time all the key stakeholders and experts with specific and/or general interests and priorities related to the conservation of *J. singaporensis* and its habitats. More than 40 people participated in the FCCRT, with representatives from: the co-organisers (NUS, WRS, NParks); IUCN-SSC [specifically, the Species Conservation Planning Sub-Committee (SCPSC), and Freshwater Crab and Crayfish Specialist Group (FCSG)]; several sister agencies to NParks that have stakes in ownership, protection, and/or management of the land through which the *J. singaporensis* streams drain or of the actual as well as nearby or connected water bodies/waterways; and local and international non-governmental organisations (NGOs), as well as experts in freshwater crab breeding and husbandry.

The FCCRT was conducted over three days, with closed-door discussions during the first two days, and culminating in a public forum on the third day. In summary, the FCCRT Programme ran as follows:

1. Background
    (a) Freshwater crab overview and research
    (b) In situ conservation work
    (c) Role of ex situ conservation and communications
2. Conservation planning
    (a) Setting Vision and Goals
    (b) Identifying Objectives and specifying Actions
    (c) Follow-up and implementation
3. Public forum

The first part of the two days of discussions involved consolidation of and updates on existing background information and conservation efforts for *J. singaporensis*. Specifically, the following topics were covered:

- Historical overview of freshwater crabs in Singapore
- Current and future threats to *Johora singaporensis*
- Current conservation management and policy with regards to *Johora singaporensis*
- Current research and status of *Johora singaporensis*.

This was followed by discussion of additional/new approaches and perspectives applicable to *J. singaporensis* conservation, which largely centred on the roles of ex situ conservation (specifically, sharing of expert views and experiences on freshwater crab husbandry and captive breeding) and communication and outreach. These aspects had up till then (March 2014) been less emphasised on because the priorities had been to urgently learn as much as possible about the crab and its existing distribution (research and monitoring), and to immediately manage/protect the existing sites and their in situ population from further decline (in situ conservation). However, in order to have viable long-term success in protecting *J. singaporensis*, inclusion and development of ex situ conservation and communication/outreach aspects for a more comprehensive and integrated conservation strategy was also needed.

13.2.2 Developing the Strategy

After the baseline was laid out, the meeting moved on to the crux of the FCCRT—the planning and development of a conservation strategy that all the stakeholders present would be able to support, i.e., one that would balance the biological/conservation needs of the species with the various human/societal needs and interests of people. This section was facilitated by the SCPSC representative, who introduced the concepts and framework of conservation strategy planning based on best practices recommended by the IUCN SCPSC (IUCN/SSC 2008a, b).

The conservation strategy essentially encompasses a hierarchical series of statements that will provide direction/guidance for conservation efforts at different levels and in various areas, with each successive and more specific level being driven by the previous level (Fig. 13.2). The strategy begins with a Vision statement that provides overarching guidance. This is followed by one or more Goals that will help to realise the Vision. At the next, more specific level, a set of Objectives outlines how the Goals will be met. And finally at the lowest level, specific Actions describe activities to be carried out in order for the Objectives to be achieved.

The FCCRT was divided into four focus groups concentrating on the following broad aspects relevant to *J. singaporensis* conservation: ecological research; site management (in situ conservation); captive breeding (ex situ conservation); and education and communication. The Vision and Goals were then crafted through a process of brainstorming, first within and then among, the four focus groups bearing in mind that the Vison is the long term or ultimate target for the particular strategy, and the Goals articulate, in practical terms, just what are needed in order to achieve the Vision. This exercise resulted in a Vision statement for *J. singaporensis* that encapsulates the FCCRT's hopes for the species and for the conservation effort as a whole (Fig. 13.3). Building on that, the FCCRT then agreed upon two broad

Fig. 13.2 Conservation strategy. Smaller number of broad statements at higher-levels (e.g., goals) drives larger number of more specific statements at lower levels (e.g., objectives, actions)

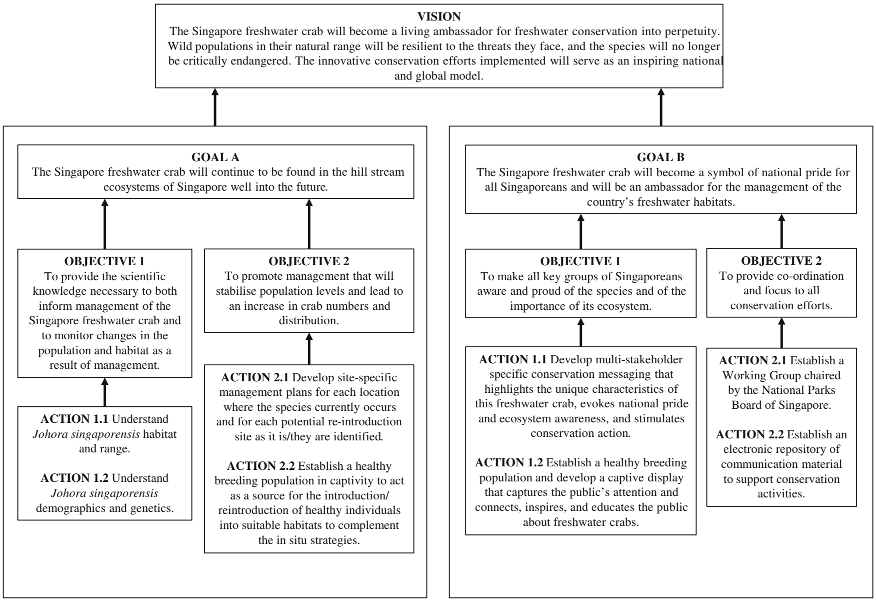

Fig. 13.3 Vision, goals, objectives and actions of the conservation strategy for *J. singaporensis* (after Ng et al. 2015a)

but practical Goals with different but complementary implications, which it felt were the key to realising the Vision (Fig. 13.3).

13.2.2.1 *What Ails* Johora singaporensis?

The next step was to identify pertinent Objectives that would essentially outline how the Vision and Goals will be turned into reality. This was done through a problem (threat) analysis, which was carried out in order to: (1) assess the various key threats facing *J. singaporensis* and the major constraints on the responses to overcoming these threats; and (2) understand the drivers of the threats in order to develop an integrated and practical way forward that maximises the species' survival chances. Brainstorming was again carried out, with participants once more divided into focal groups for more comprehensive coverage. In the discussions, stakeholders were asked to consider their respective association with the threat(s) and their potential to contribute to alleviating the threat(s).

The top few global threats to aquatic biodiversity, e.g., habitat loss or modification, pollution (including siltation), alien species, and over-exploitation (Wilcove et al. 1998), are similarly prevalent in Singapore (Yeo et al. 2011). These are manifested in various specific threats to *J. singaporensis,* some of which (loss of forest cover, habitat degradation and modification including stream acidification, reduction in water table, stream flow, and suitable habitats; aquatic pollution) have previously been cited in local and global Red List assessments (Yeo et al. 2008b; Esser et al. 2008). The problem analysis for *J. singaporensis* identified these as well as other current threats relating to various aspects including habitat, biology, and human interactions. Below are just some examples of current key threats or constraints (to addressing the threats):

- Rarity of hill stream habitat (coupled with apparent habitat specificity of the crab)—The hill streams that *J. singaporensis* are restricted to, are themselves a rare habitat type in Singapore to begin with. Existing hill streams are restricted to a small hilly part of central Singapore; while some of these hill streams are in protected areas, others are not necessarily so. The streams are potentially under threat from loss or modification (e.g., deviation or canalization), while some of the land or watershed of these streams are at risk of being developed for alternate land use (e.g., housing) or vector control (e.g., canalization to prevent mosquito breeding). Singapore's nature reserves do have natural forest streams capable of supporting native aquatic species including freshwater crabs (Yeo and Lim 2011). Few of these streams, however, possess the characteristics associated with *J. singaporensis* occurrence, viz., typically moderately elevated (about 50–60 m asl), with slightly acidic to neutral pH (6.3–7.2) (but see Li et al. 2015) and relatively high dissolved oxygen (81–87 %), and relatively low organic substrate cover (10–15 %) (see Chua et al. 2015); most of Singapore's forest streams are instead low-lying and relatively more acidic (pH 5.5–6) (Yeo and Lim 2011).
- Stream acidification—one of the hill streams that *J. singaporensis* has disappeared from was found to have become more acidic compared to 15 years ago (pH 4 or lower vs pH 5–6 in the 1990s—Ng et al. 2015a, b, c; unpublished data) and in comparison to other nearby streams that still support *J. singaporensis* (pH 5 or higher—Li et al. 2015; Ng et al. 2015a, b, c; Chua et al. 2015; unpublished data). It has been postulated that the acid precipitation may have been a factor in the stream acidification (Ng et al. 2015c) but further investigation is needed to verify this. In any case, given the typically less acidic nature of streams where *J. singaporensis* does occur, stream acidification—from any source—would be a threat.
- Small population/limited distribution—*Johora singaporensis* suffers from having a very small population (a few hundred mature individuals; Ng et al. 2015a) and a very limited distribution, with an Extent of Occurrence of less than 5 km^2 and an Area of Occupancy of less than 0.5 km^2, which makes the species highly vulnerable to random catastrophic events that could lead extinction.
- Isolated populations and limited dispersal ability—Despite the small Extent of Occurrence, the five stream sites where *J. singaporensis* are currently found are independent drainages found in separate land fragments. Hence, coupled with the limited dispersal ability of these crabs, the populations are also threatened by likely absence of recruitment and gene flow among the five sites (Khew 2015).
- Lack of formal protection—Three of the five known hill stream localities where *J. singaporensis* is found, and the species itself, lack any specific formal or legal

protection. Only two sites are within a designated nature reserve. This lack of formal protection has in turn lead to a perception of lack of ownership of the problem. NParks, however, by taking responsibility for *J. singaporensis* conservation, has clearly demonstrated its ownership of the problem among government agencies. The real issue here lies in unclear ownership over the various streams situated in locations with differing legal statuses under different jurisdictions (i.e. too many official owners/stakeholders).

Associations among these and other threats/constraints were illustrated in a network analysis of problems that are ultimately driving the immediate problem of population decline of *J. singaporensis* (Ng et al. 2015a: Fig. 3). In addition, several potential threats that may become cause for concern in the future were also identified. These include for example:

- Invasive species—Singapore has numerous aquatic alien species, including freshwater decapod crustaceans, some of which could potentially be competitors or predators of *J. singaporensis* (see Yeo 2010; Yeo and Chia 2010). The likelihood of this threat, however, is low owing to the relatively inaccessible hill stream habitat of *J. singaporensis,* and the fact that most aquatic invasive species in Singapore are found in more open, artificial habitats like reservoirs, ponds, and canals (Yeo and Chia 2010; Yeo and Lim 2011). Nevertheless, the prevalence of aquatic alien species in Singapore means that this should not be ignored.
- Human interference—A potential concern for *J. singaporensis* is the potential disturbance of their habitats by humans for a variety of possible reasons ranging from poaching for pets to over-enthusiastic nature-lovers keen to see the species or explore the habitat first-hand.

The problem analysis allowed the FCCRT to then plan various Actions (Fig. 13.3) for the conservation strategy. These Actions essentially describe discrete activities to be undertaken to achieve each Objective. The Goals, Objectives and Actions, were as a whole designed to be SMART (Specific, Measurable, Attainable, Relevant, and Time-bound). Therefore, as far as possible, the Actions in particular referred to specific activities that were time-bound.

13.2.3 Forum and Feedback

The final day of the FCCRT was dedicated to outreach and dissemination of information to the public, and soliciting of feedback and views, through a public forum. The day's programme began with presentations of background information, including an introduction of the FCCRT and explanation of its importance to freshwater crab conservation, and a historical overview of freshwater crabs in Singapore. The preliminary outcomes from the previous two days of closed-door meetings of the FCCRT were summarised and presented, and this was followed by presentation of conservation management and policy relating to *J. singaporensis.* The programme concluded with a question and answer session-panel discussion, with representative panel members from IUCN/SSC-SCPSC, IUCN/SSC-FCSG, NParks, NUS, and WRS.

13.3 Conclusions

13.3.1 Outcomes and Maintaining Momentum

Following up from the FCCRT, one of the important outcomes was the formation of a Singapore Freshwater Crab Working Group (SFCWG) soon after in 2014. The SFCWG is chaired by NParks, and also includes representatives from NUS and WRS. Other stakeholders and participants of the FCCRT, e.g., IUCN-SSC (SCPSC and FCSG) and other government agencies, are consulted and updated regularly or as and when necessary. This working group, which meets regularly (and communicates frequently), is the main channel through which subsequent discussions, decisions, actions and recommendations pertaining to the *J. singaporensis* arising from the strategy conservation are followed up on.

The SFCWG has also been responsible for initiating/driving the elaboration and implementation of specific actions. The following are some examples:

- For example, monitoring to better understand the population demographics and dynamics and research into the genetics of *J. singaporensis* is now ongoing (Ng et al. in prep.) (Under Goal A, Objective 1, Actions 1.1 and 1.2; see Fig. 13.3).
- Facilities for maintaining captive populations of *J. singaporensis* for ex situ breeding are established and running (Khew 2015); at the same time, preliminary translocation trials into new suitable habitats are ongoing (Ng et al. in prep.) (Under Goal A, Objective 2, Action 2.2; see Fig. 13.3).
- The SFCWG has reached out at various opportunities (e.g., Singapore Festival of Biodiversity) to the general public as well as to decision-makers to enhance awareness of the issues surrounding *J. singaporensis* and the conservation strategy (under Goal B, Objective 1, Action 1.1; see Fig. 13.3).

A significant outcome and milestone has been the drafting, refining, finalizing, and publication of the *J. singaporensis* conservation strategy in June 2015 (Ng et al. 2015a; Khew 2015).

13.3.2 Broader Conservation Implications

There have been some encouraging developments in the situation of *J. singaporensis,* such as the release of and publicity surrounding the formal conservation strategy (Ng et al. 2015a; Khew 2015), and the discovery of new freshwater hill stream locations with populations of *J. singaporensis* (Ng et al. 2015b; Li et al. 2015). These have served to enhance awareness and interest and galvanise efforts, not only for *J. singaporensis* conservation, but, significantly, more broadly for freshwater stream conservation in Singapore.

The *J. singaporensis* conservation strategy also has important broader, global implications beyond Singapore. It can serve as an example of what can be done, even in a highly urbanized country with multiple competing economic and land use priorities, first and foremost for other similarly threatened freshwater crab species (Cumberlidge et al. 2009), but also for other iconic or flagship invertebrate species, which are underrepresented when it comes to specific conservation strategies (http://www.iucn.org/about/work/programmes/species/publications/species_actions_plans/).

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Chapter 14
Biodiversity Assessment of Freshwater Shrimps and Crabs in the Nee Soon Swamp Forest, Singapore

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Abstract The Nee Soon Swamp Forest (NSSF) (87 ha) in Singapore houses a rich diversity of fauna and is the only area of primary freshwater swamp left on that island. The current study investigates the diversity and population changes of the freshwater decapod fauna of the NSSF with the aim of facilitating future conservation actions. Surveys were carried out by hand sampling and trap sampling from February 2013 to May 2014 in 12 sites in the NSSF that represent different microhabitats from the outskirts to the lower, middle, and upper reaches of the streams draining the swamp forest. Stream water parameters (temperature, pH, DO, and TDS) and stream profile characters (substrates, cross section, canopy cover, and riparian vegetation) were recorded. Species richness and Shannon-Wiener's index (H′) were calculated and compared for all sites over 10 sampling cycles. The length-frequency relationships of species of freshwater shrimps (*Caridina malayensis*, *Macrobrachium malayanum*, *M. sundaicum*, *M. platycheles*) and freshwater crabs (*Parathelphusa maculata* and *P. reticulata*) were investigated. The highest species diversity was found to occur in the middle and lower reaches of the stream, followed by the upper reaches of the stream, then the outskirts of the swamp. The distribution patterns of the freshwater decapods of the NSSF are discussed and their conservation status is updated.

Keywords Biodiversity · Crab · Freshwater · Nee Soon Swamp Forest · Population · Shrimp · Singapore

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14.1 Introduction

The 87 ha Nee Soon Swamp Forest (NSSF, Fig. 14.1) is the only primary freshwater swamp left in Singapore and is critical to the retention of a large number of Red Listed plant and animal species that are threatened with extinction, including two endemic species of freshwater crabs. Over the last 200 years urban development in Singapore has reclaimed 98% of that country's swamps and if the Nee Soon swamp is lost or compromised the island is facing the loss of almost 50% of its freshwater fish, 70% of its amphibians, 25% of its reptiles, and hundreds of species of plants, insects, birds and mammals (Ng and Lim 1992). The NSSF represents the remaining section of a larger swamp forest that once existed between Upper Seletar Reservoir and Mandai Road in Singapore (Corner 1978; Turner 1996) and is now threatened by the expansion of a dam to create a freshwater reservoir in the Lower Seletar area. The streams in the NSSF drain into the Lower Seletar reservoir and the dam forms a barrier between the swamp (which lies less than 10 m above the mean sea level) and the sea (Taylor et al. 2001). The streams in the NSSF are shaded and have shallow waters flowing over clay, sand, or mud, and their pH is more acidic than other forest streams due to the decomposition of accumulated leaf litter and woody debris. The soil in the NSSF is anaerobic and unstable due to periodic flooding. All these factors have resulted in a diverse flora and fauna that are adapted to these unusual conditions. However, this also means that these habitat specialists are sensitive to environmental disturbances such as changes in the drainage system, introduction of non-indigenous species, soil erosion, and disturbances from development.

Freshwater shrimps and crabs are involved in many important ecological processes and influence primary production, leaf-litter breakdown, and the composition of benthic stream communities (Yam and Dudgeon 2006). Furthermore, the study of the population dynamics of invertebrates that are sensitive to changes in microhabitat and microclimate provides a good indicator of ecological variations (Sodhi et al. 2010). However, to date most studies of the freshwater shrimps and crabs have been taxonomic accounts and there is very little available data on their distribution and abundance in the NSSF. Nine of the sixteen species of freshwater shrimps found in Singapore have been recorded to occur in the NSSF. Five of these species (*Macrobrachium sundaicum* (as *M. trompii* in Ng 1997), *M. idae, M. neglectum, M. platycheles* and *Caridina malayensis*) were found only in NSSF (Ng 1997; Ou and Yeo 1995; Wowor et al. 2004; Cai et al. 2007). Recent studies added *Macrobrachium nipponense* and *Potamalpheops amnicus* into NSSF fauna (Sun 2011; Soh 2011). *Macrobrachium nipponense* is likely to be accidentally introduced into local streams due to high ornamental trading activities in Singapore (Chong et al. 1987). Conversely, *P. amnicus* is believed to be native, but they might be overlooked by earlier researchers due to its small size. No sufficient data have been collected to determine if *Caridina malayensis* is native or introduced. Ng (1997) listed four species of crabs found in the NSSF, including *Parathelphusa reticulata* (which was initially thought to be a variation of *P. maculata*) (Ng 1990a). It is of concern that a recent study on the freshwater crabs of the NSSF by Khoo (2010) did not record *P. reticulata* and it

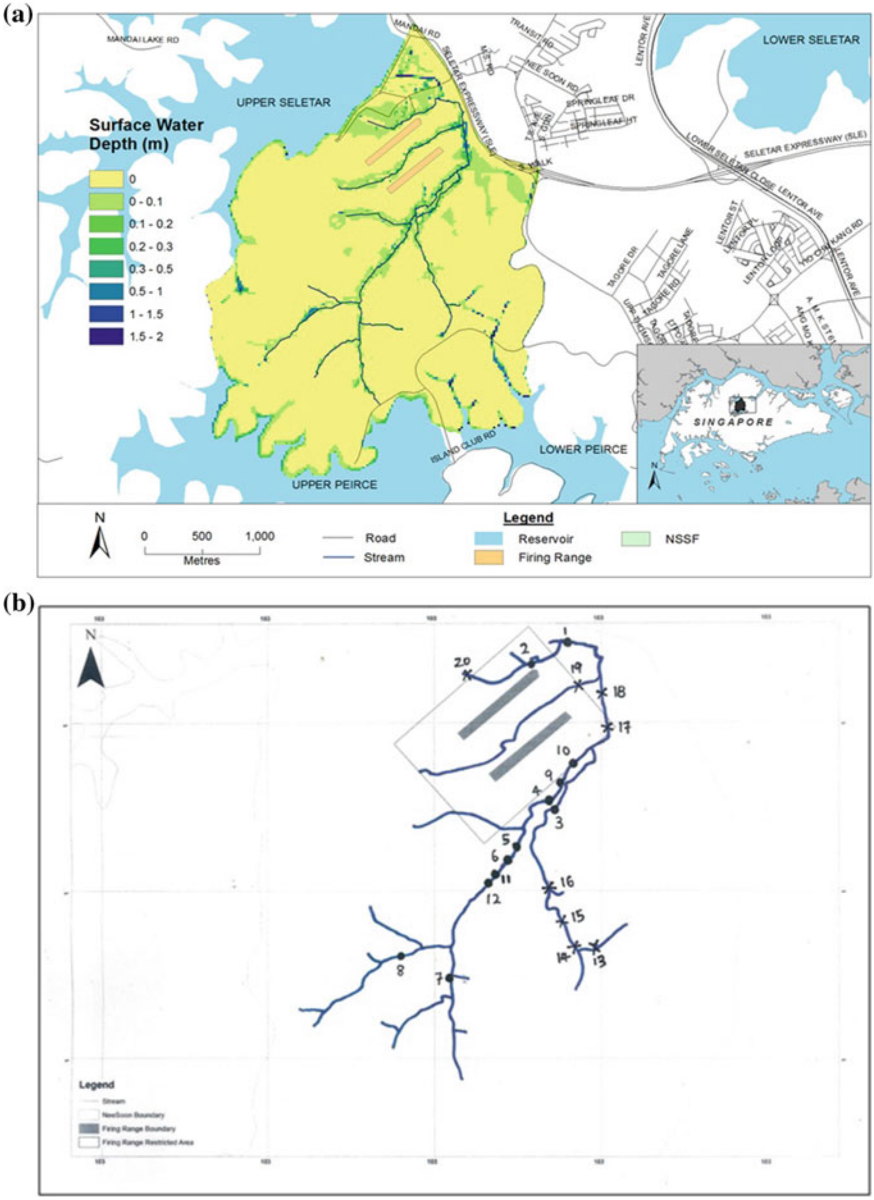

Fig. 14.1 **a** Map of the Nee Soon Swamp Forest (NSSF) in Singapore; **b** Map of the sampling sites located in the NSSF

is possible that this species has been affected by a period of dry weather that caused water bodies in the NSSF to shrink.

Swings in the hydrology and ecology of the NSSF over the last few decades have made it difficult to determine the conservation actions that are needed to ensure the long-term sustainability of this freshwater swamp ecosystem. Both the forest and the surface waters of the NSSF have changed considerably over the last two decades, with stream banks experiencing raised water levels in some parts and drying up in others, and a shifting of the boundaries between the swamps and dry land forests. Baseline studies assessing the biodiversity of the freshwater shrimps in the NSSF were carried out in 2011 from February to April (Sun 2011) and from May to July (Soh 2011). Here we report on current population levels of the freshwater decapod fauna of the NSSF and update the conservation status of species. The aim is to highlight the challenges facing the implementation of species conservation actions in this area, and to evaluate sampling protocols that would be suitable for a long-term monitoring program of the threatened NSSF freshwater ecosystem and its fauna.

14.2 Survey Sites

Surveys were conducted at 20 sites: quantitative sampling was carried out at 12 sites (1–12), and qualitative sampling was carried out at 8 sites (13–20). Sites 1–8 were surveyed 8 times (between February and March 2013, and between September 2013 and May 2014), while sites 9–12 were surveyed 4 times from September 2013 to May 2014.

Upper Seletar Reservoir (USR) sites 1 and 2 (Fig. 14.1b) are situated on the boundary of the NSSF close to urban areas and are influenced by human activities. The stream at USR 1 has moderately low vegetation cover (Fig. 14.2a) and its water levels vary greatly depending on the amount of water released from the nearby reservoir. On hot days when water is not released from the reservoir the water depth of USR 1 is at knee level and water flow is moderately slow, while on wet days when water is released from the reservoir the water depth at this site increases by 2–3 times. The stream at USR 2 has knee-deep water, a moderately slow flow, banks lined with sparse vegetation, and shade from the thick canopy cover of the forest (Fig. 14.2b).

Mainpond sites 1 and 2 (sites 3 and 4 in Fig. 14.1b) are located along a pipeline maintenance path inside the forest and are relatively open and unshaded. For Mainpond 1, part of the stream consists of a deep pond lined by short vegetation, while the rest of the stream has knee-deep water with moderate flow that is shaded by the forest canopy along the stream (Fig. 14.2c). Mainpond 2 is on a relatively open stream lined with moderate vegetation along one bank and thick vegetation on the other bank, and water from knee deep to chest deep, while water flow is moderately fast and the stream bed sandy (Fig. 14.2d).

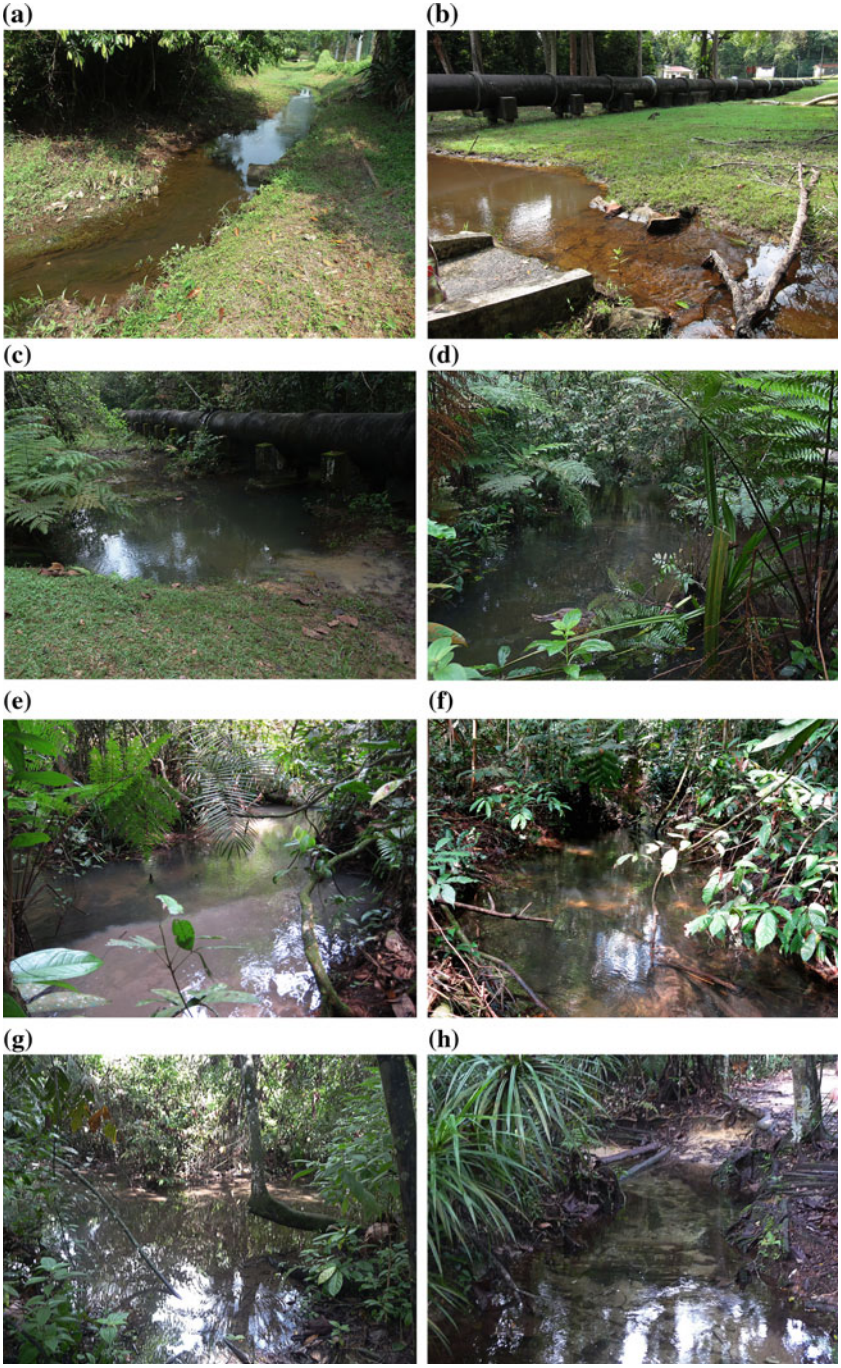

Fig. 14.2 a–h Photographs of the streams at sites USR 1, USR 2, Mainpond 1, Mainpond 2, Midpoint 1, Midpoint 2, WCT 1 and WCT 2, respectively

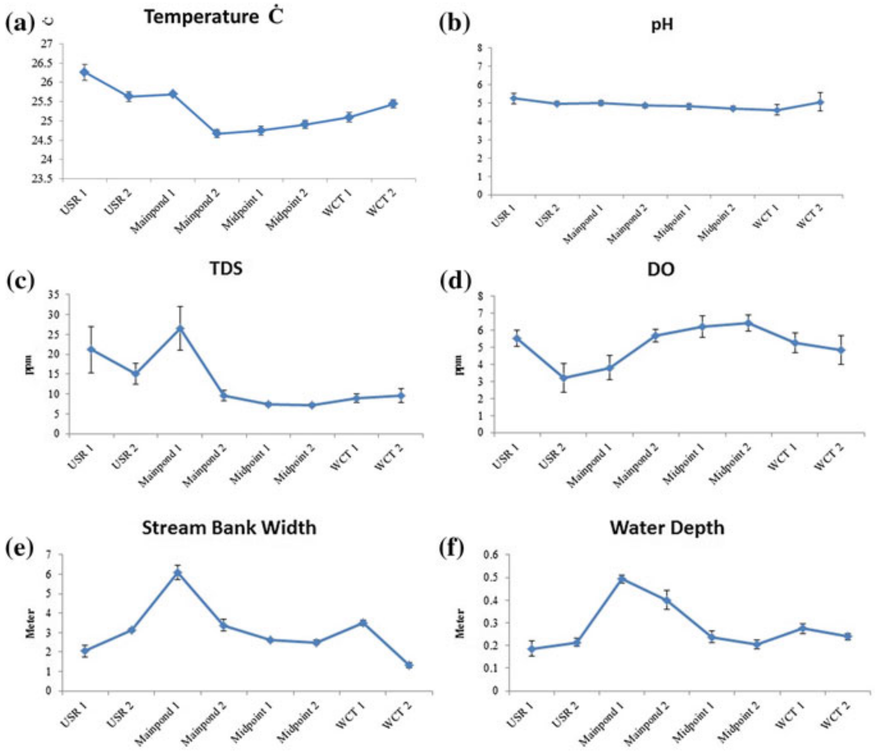

Fig. 14.3 Water parameters and stream profiles of the sampling sites (see text for abbreviations)

Midpoint sites 1 and 2 (sites 5 and 6 in Fig. 14.1b) are relatively undisturbed and lie deep inside the NSSF. Both sites are shaded by the dense forest canopy, the water is waist deep, the water flow is moderately fast, and the stream bed consists of a mixture of sand and clay (Figs. 14.2e, f).

Woodcutter’s Trail (WCT) sites 1 and 2 (sites 7 and 8 in Fig. 14.1b) are located along a forested trail that is closed to public access. WCT 1 consists partly of an open exposed pond lined by tall vegetation, and partly of a stream with knee deep water shaded by forest canopy that has a moderately slow water flow (Fig. 14.2g). The stream at WCT 2 is partly exposed and partly shaded by the forest canopy, and the water is knee deep with a fast flow rate (Fig. 14.2h).

Sites 9 and 10 are in the lower swamp forest area where the stream is shaded by the forest canopy, has slow flowing water and a very muddy bed. Sites 11 and 12 are part of the upper swamp forest and the stream here has fast flowing water, a bed of sand and clay, and shade from the forest canopy. Sites 13–16 are all along a small, narrow stream that leads to the pond at site 3, while sites 17–20 are close to the Nee Soon military firing range.

At each site the temperature, pH, TDS, and DO of the water were recorded using a hand-held pH meter or HANNA 9829 Multiparameter, and stream profiles were measured (Fig. 14.3). The streams within the NSSF (Mainpond, Midpoint, and WCT sites) are slightly acidic (pH from 4.40 to 6.54), while the pH of the water at the USR sites on the outskirts of the NSSF is less acidic. The temperature of the streams is influenced by the amount of vegetation cover and unshaded sites have a higher water temperature than shaded sites. TDS levels at site 3 were higher than all of the other sites due to the wider and deeper stream profiles and slow flowing waters that tend to deposit more solid particles. The high TDS levels at USR 1 may be partly due to periodic flooding, while the relatively low DO levels at sites 2 and 3 may be due to slow water flow rates.

14.3 Methodology

14.3.1 Quantitative Surveys: Hand Sampling

Shrimps and crabs were caught manually using a 60 cm by 40 cm tray net and hand nets (mesh size 0.5 cm). At each site consistent uniform sweeps were made along 20 meter length of stream moving from downstream to upstream for thirty minutes. The tray net also sampled mud, leaf litter, trailing roots and fallen branches where shrimps and crabs may be found. Other aquatic organisms and associated stream material collected during the study were released to minimise habitat disturbance.

14.3.2 Quantitative Surveys: Trap Sampling

Plastic minnow traps were laid along streams at each sampling site and were baited with similar amounts of pig liver and kuning fish (*Selaroides leptolepis*). Traps were positioned in the stream so that shrimps or crabs could crawl into them, and were fully submerged with their openings pointing downstream and touching the streambed. A two-kilogram weight held the trap to the bottom of the stream and prevented it from being washed away by the current (Fig. 14.4). Traps were placed overnight and the catch collected the following day to minimize fatalities.

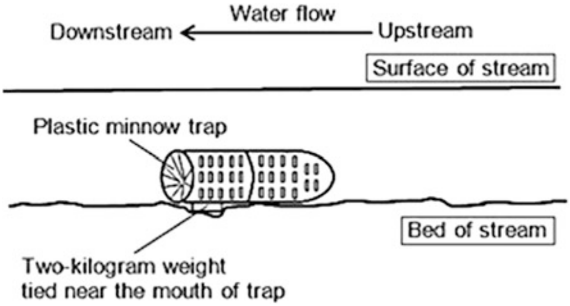

Fig. 14.4 Placement of the plastic minnow trap

14.3.3 Species Identification

Identification and measurements were made in the field by direct examination after which most specimens were released. If specimens could not be identified then two live specimens were brought to the laboratory for further analysis. Juveniles of *Parathelphusa maculata* and *P. reticulata* that were too small to be identified (CL < 0.4 cm) were listed as '*Parathelphusa* spp.'.

14.3.4 Measurements

Measurements (in centimeters (cm)) of carapace length (CL) (for *Macrobrachium* and all freshwater crabs) and body length (BL) (for *Caridina*) were made with digital vernier calipers. The CL of *Macrobrachium* was measured from the postorbital margin to the posterior margin of the carapace, while the CL of freshwater crabs was measured from the widest length of the carapace. Because of their small size, measurements of *Caridina* species were taken as the entire body length (BL) from the postorbital margin to the tip of the telson. *Macrobrachium malayanum* were so abundant that the number of specimens with a CL < 0.6 cm was recorded, rather than measuring the CL of individual specimens. The majority of shrimps and crabs were released following identification and measurement to ensure minimal disruption to the environment.

14.3.5 Qualitative Surveys

Qualitative surveys were performed once at sites 13–20 and other *ad hoc* areas in the NSSF using the same hand and/or trap sampling techniques as the quantitative surveys except that the duration of the hand sampling was not timed. Specimens were released following identification and measurement, and these qualitative data allowed a more thorough coverage of the distribution of freshwater decapod crustaceans in the NSSF.

14.3.6 Data Analysis

Sites 1 to 8 were surveyed for a total of 10 cycles so data analysis was only carried out for these 8 sites. Significant differences in the abundance of each decapod species between sites and between sampling cycles were detected using one-way analysis of variance (ANOVA) to give an overview of decapod crustacean populations in the NSSF on spatial and temporal scales. Mean population densities of shrimps and crabs captured at each survey site were graphed and changes in the mean population abundance between the 10 cycles were analysed to detect seasonal trends. Species diversity at each site was calculated using the Shannon-Weiner index (H′):

$$H' = -\Sigma(\mathrm{Pilog}[\mathrm{Pi}]),$$

where Pi = number of individual species/total number of individuals.

The shrimps and crabs were assigned to different class-sizes according to carapace and body length measurements and were graphed according to site and sampling cycle to analyse their population dynamics.

14.4 Results

14.4.1 Species Accounts

Nine species of freshwater decapod crustaceans (5 species of shrimps and 4 species of crabs) were recorded to occur in the NSSF.

Family Atyidae

Caridina malayensis Cai et al., 2007 (Fig. 14.5).

This species is identifiable by its small size (BL 18 mm), its short, small chela with tufts of setae at the tips, a short rostrum, non-protruding eyes, and grey-black spots on a translucent body. *Caridina malayensis* lives in black water peat swamps and in the lower-middle reaches of slightly acidic forest streams that have slow-flowing water. This species clings to trailing roots and hides in leaf litter and submerged vegetation, feeds on organic debris, and gravid females carry large, circular eggs

Fig. 14.5 Live specimen of *Caridina malayensis*

under their abdomen. *Caridina malayensis* is a gregarious species whose females are larger than the males. In Singapore this species is found only in the NSSF, while elsewhere its distribution includes the southern Malay Peninsula and the Riau Islands. Its global conservation status according to the IUCN Red List is least concern (De Grave and Cai 2013).

Family Palaemonidae

Macrobrachium malayanum (Roux, 1934) (Fig. 14.6).

This is the most abundant species at all the sites surveyed and grows up to CL 20 mm. Its morphological characteristics include a straight, blade-like rostrum, a chela covered with short, fine setae, and cheliped fingers that are longer than the merus. Males have one cheliped larger than the other, but females have chelipeds of equal sizes. The body color ranges from orange-red to blue-grey depending on age, environment, and even time of day, and serves as camouflage from predators. Fertilized eggs range in colour from yellow to orange-brown. *Macrobrachium malayanum* is an omnivore, feeding mostly on plant debris, organic matter, and small invertebrates. This species lives in slightly acidic forest streams that have either fast or slow-flowing water that is either shaded or open, and the streambed is variable. In Singapore this species is found in the Central Catchment Nature Reserve, Bukit Timah Nature Reserve, and other forested nature areas, while its wider range includes the Malay Peninsula, Sumatra, and Borneo and its global conservation status according to the IUCN Red List is least concern (De Grave et al. 2013).

Macrobrachium sundaicum (De Man, 1898) (Fig. 14.7).

This species is found in low numbers at all the survey sites in this study, but nowhere was it common, especially gravid females. This species is characterized by medium body size (up to CL 21 mm), black tiger stripes on its body (but otherwise

Fig. 14.6 Live specimen of *Macrobrachium malayanum*

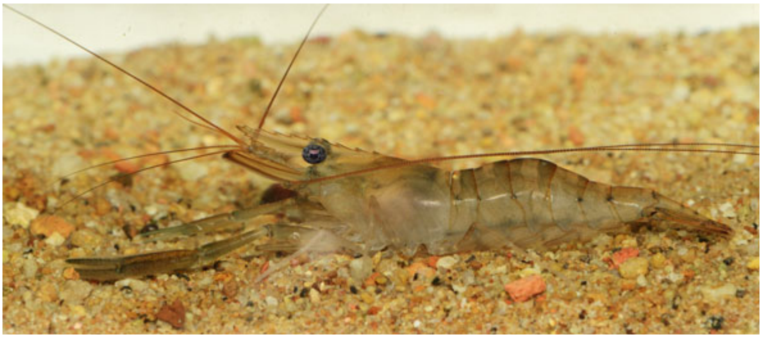

Fig. 14.7 Live specimen of *Macrobrachium sundaicum*

its colours are variable), an upward-curving rostrum (especially in juveniles), and an elongated thin cylindrical tube-like carpus on the cheliped. *Macrobrachium sundaicum* is a fast-swimming omnivore that feeds on organic debris and small invertebrates, and is found in shaded, acidic forest streams with dense aquatic vegetation, trailing roots, and plenty of leaf litter. In Singapore this species is uncommon within the NSSF but is found in the Central Catchment Nature Reserve. *Macrobrachium sundaicum* has a wider distribution in the Malay Peninsula, Sumatra, and Borneo and its global conservation status according to the IUCN Red List is least concern (De Grave and Wowor 2013).

Macrobrachium platycheles Ou and Yeo, 1995 (Fig. 14.8).

This rare species is the smallest of all the *Macrobrachium* studied here (CL 12 mm), and is identified by an inflated merus and a laterally flattened chela with a

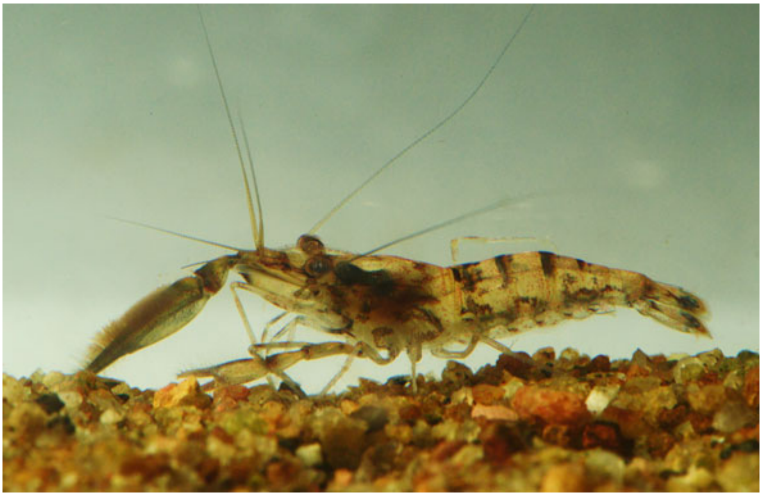

Fig. 14.8 Live specimen of *Macrobrachium platycheles*

dense covering of soft setae, and dark blue or black spots that disappear when shrimps are kept in the laboratory overnight, making them appear translucent. *Macrobrachium platycheles* lives in the upper and middle reaches of the stream in NSSF where it is found at the streambed over which rapid clear water flows. *Macrobrachium platycheles* feeds on small invertebrates and organic debris. In Singapore this species is only found in the NSSF and it is listed as critically endangered in the Singapore Red Data Book. When its wider distribution in the Malay Peninsula is taken into account its global conservation status according to the IUCN Red List is least concern (De Grave et al. 2013).

Macrobrachium nipponense (De Haan, 1849) (Fig. 14.9).

This medium sized species (CL 27 mm) is characterised by a moderately long rostrum, long and slender chelipeds with sparse setae, elongated chela with long cylindrical carpii and the second pair of pereiopods, orange bands on the joints of its chelipeds and walking legs, a translucent body with reddish-brown speckles in juveniles, and gravid females with visible greenish-yellow, circular ova. This species is typically found in open fast-flowing waters where it resides in dense aquatic vegetation (such as *Hydrilla*), and feeds on organic debris and small invertebrates. *Macrobrachium nipponense* is established in reservoirs in Singapore and has been found at one site in the NSSF (USR 1) that is a disturbed, slightly acidic stream. The native range of *M. nipponense* includes China, Japan, Korea, Taiwan, and Myanmar, but it has been introduced to Iran, Iraq, Malaysia, Laos, the Philippines, and Singapore and its global conservation status according to the IUCN Red List is least concern (De Grave 2013).

Fig. 14.9 Live specimen of *Macrobrachium nipponense*

Family Gecarcinucidae

Parathelphusa maculata De Man, 1879 (Fig. 14.10).

This species is the largest and most abundant species (CL 60 mm) of freshwater crab in Singapore and is found in Nee Soon Swamp Forest. The carapace of *P. maculata* is flat with a trapezoidal outline in adults and high with a square outline in juveniles (Ng 1988). There is a distinct epibranchial tooth on the anterolateral margin in line with the postfrontal crest, and adult males are heterochelous with larger chelae than females. The carapace and chelipeds of adult *P. maculata* are brown with dark spots (that may be due to the acid waters and soils in the NSSF) while the underside of the body and legs is light yellow to orange-brown, and juveniles are mottled all over (Ng 1988). *Parathelphusa maculata* tolerates a wide range of conditions but prefers lowland streams with abundant leaf litter where it feeds on organic debris, small invertebrates, and scavenged material. This lowland forest crab is very tolerant to poorly oxygenated water and is often found in stagnant pools (Ng 1988). Besides Singapore, *P. maculata* is distributed throughout the Malay Peninsula and in the southern part of Sumatra.

Parathelphusa reticulata Ng, 1990 (Fig. 14.11)

This medium-sized species (CL 40 mm) is recognized by the distinctive reticulated mottling pattern on its carapace which distinguishes it from *P. maculata* whose carapace has a spotted pattern. The carapace spots found on juvenile *P. reticulata* change into red-brown reticulations as crabs grow. The carapace of *P. reticulata* is high with a trapezoidal outline and has a distinct epibranchical tooth on the

Fig. 14.10 Live specimen of *Parathelphusa maculata*

Fig. 14.11 Live specimen of *Parathelphusa reticulata*

anterolateral margin in line with the postfrontal crest. This species is found in shaded streams with shallow, slow-flowing water and a streambed of mud and thick leaf litter. Crabs bury themselves in leaf litter during the day and emerge at night to forage on detritus and scavenged organic matter. *Parathelphusa reticulata* is endemic to Singapore where it is only found in the NSSF, and is listed as critically endangered on the IUCN Red List (Esser and Cumberlidge 2008a).

Irmengardia johnsoni Ng and Yang, 1985 (Fig. 14.12).

This small species (CL 18. 9 mm) is recognised by a carapace with a trapezoidal outline with a mottled or reticulated red-brown pattern and a small epibranchial tooth on the anterolateral margin. Adult males are heterochelous, with the major cheliped rounded and coloured orange-brown, while females have smaller less heterochelous chelipeds. This species prefers lowland secondary forest streams with shallow and acidic slow-flowing water with a streambed of mud and leaf litter in which crabs remain buried during the day and emerge at night, feeding in the stream and nearby land. Crabs feed on organic debris, leaf litter, and small invertebrates. *Irmengardia johnsoni* is endemic to Singapore where it is found in the NSSF, Bukit Timah Nature Reserve, and the Central Catchment Nature Reserve and is listed as vulnerable on the IUCN Red List (Esser and Cumberlidge 2008b).

Fig. 14.12 Live specimen of *Irmengardia johnsoni*

Family Sesarmidae

Geosesarma peraccae (Nobili, 1903) (Fig. 14.13).

This small species (CL 6.3 mm) is recognized by its almost square carapace outline, a carapace with red-brown patches on a dark grey-brown or red background

Fig. 14.13 Live specimen of *Geosesarma peraccae*

(Ng 1988), and chela that are either red-orange (males) or red-brown (females). *Geosesarma peraccae* is a semi-terrestrial species that spends a great deal of time out of water but still depends on aquatic habitats for osmoregulation and to avoid dehydration. Captured adult crabs held by their pincers shed their chelae to escape. When threatened juveniles stop moving and keep their legs close to their bodies making them difficult to detect amongst the leaf litter on the tray net, but they move if the leaf litter on the net is either disturbed or half submerged. *Geosesarma peraccae* was the least abundant species of crab encountered in the NSSF where it occurs in areas with decaying logs and dense leaf litter. Elsewhere in Singapore this species is found in the Central Catchment Nature Reserve and the Bukit Timah Nature Reserve, and it also occurs in the southern Malay Peninsula. The conservation status of this species has not yet been assessed.

14.4.2 *Distribution of Freshwater Shrimps and Crabs in the NSSF*

Quantitative surveys were carried out in 12 sampling sites (sites 1–12) while qualitative surveys were conducted at sites 13–20. The species of freshwater crustaceans found in each of these sites is summarized in Tables 14.1 and 14.2. Both *M. malayanum* and *M. sundaicum* were found at all the 12 quantitative sampling sites, with *M. malayanum* being the most commonly encountered species. *Macrobrachium platycheles* was rare and prefers the more acidic and fast-flowing waters found in upstream regions such as Mainpond 2, Midpoint 1 and 2, and WCT

Table 14.1 Distribution and Mean abundance of freshwater shrimps and crabs at quantitative sites 1–12. (Abbreviations: +++: Abundant (>15.00), ++: Common (5.01–15.00), +: Rare (0.10–5.00), -: Not Found at Site)

Species	**Sites**											
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Family Atyidae												
Caridina malayensis	-	+	+++	++	+	+	+	-	+	+	+	+
Family Palaemonidae												
Macrobrachium malayanum	+++	+++	+++	+++	+++	++	+++	+++	+++	+++	+++	+++
Macrobrachium nipponense	+++	-	-	-	-	-	-	-	-	-	-	-
Macrobrachium platycheles	-	-	+	+	++	++	+	+	+	++	++	+
Macrobrachium sundaicum	+	+	++	++	+++	++	++	++	+	++	++	+

(continued)

Table 14.1 (continued)

Species	Sites											
	1	2	3	4	5	6	7	8	9	10	11	12
Family Gecarcinucidae												
Irmengardi johnsoni	+	+	+	+	+	+	+	+	-	-	-	+
Parathelphusa maulata	+	+	+++	+++	+++	+++	+++	++	+++	++	+++	+++
Parathelphusa reticulata	-	+	+	+	++	+	+	-	+	+	+	+
Family Sesarmidae												
Geosesarma peraccae	-	+	+	-	-	+	+	+	+	-	-	-

Table 14.2 Distribution of freshwater shrimps and crabs at qualitative sites 13–20. (Abbreviations: +: Present, -: Absent)

Species	Sites							
	13	14	15	16	17	18	19	20
Family Atyidae								
Caridina malayensis	-	-	-	-	+	-	-	+
Family Palaemonidae	-	-	-	-	-	-	-	-
Macrobrachium malayanum	+	+	+	+	+	+	+	+
Macrobrachium nipponense	-	-	-	-	-	-	-	-
Macrobrachium platycheles	-	+	+	-	-	-	-	-
Macrobrachium sundaicum	-	+	+	-	+	+	-	-
Family Gecarcinucidae								
Irmengardi johnsoni	+	-	-	+	-	-	-	-
Parathelphusa maculata	+	+	-	-	+	+	+	+
Parathelphusa reticulata	-	-	-	-	-	-	+	+
Family Sesarmidae								
Geosesarma peraccae	-	+	-	+	-	-	-	-

1 and 2, while *M. nipponense* prefers less acidic, slow-flowing waters found at USR 1. *Caridina malayensis* was found in 10 of the 12 sites, was most abundant in the lower-middle part of the NSSF, and less abundant towards the extreme limits of the swamp. The freshwater crab *P. maculata* was found at all sites in the study and was by far the commonest of the four crab species included in this work. *Parathelphusa reticulata* was found only at the middle and lower reaches of the NSSF while *I. johnsoni* and *G. peraccae* were encountered at only a few sites in the upper and lower reaches of the NSSF.

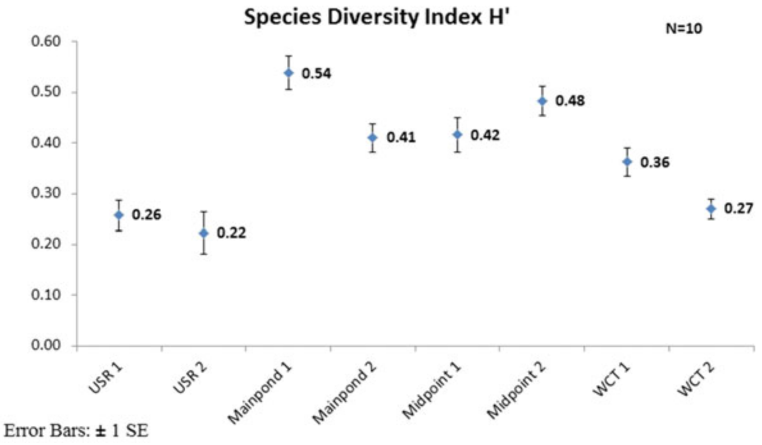

Fig. 14.14 Species diversity of freshwater decapods at 8 survey sites calculated using the Shannon-Wiener species diversity index (H′)

14.4.3 Diversity of Freshwater Shrimps and Crabs in the NSSF

The species diversity at each survey site was plotted using the Shannon-Wiener index (H′) (Fig. 14.14). Mainpond 1 (H′ value of 0.54) had the greatest species diversity among the sites surveyed, while USR 2 (H′ value of 0.22) had the lowest species diversity. Species richness graphs (Fig. 14.15) show the proportion of different species found at different sites (which is not shown by the Shannon-Wiener index). Species richness ranged from 3.0 to 5.8 species/site with the highest species richness at Mainpond 1 and the lowest at USR 2.

14.4.4 Population abundance of freshwater shrimps and crabs in the NSSF

The mean abundance of seven species of freshwater decapods (*M. sundaicum*, *M. platycheles*, *M. nipponense*, *C. malayensis*, *P maculata*, *P. reticulata* and *I. johnsoni*) was calculated using a one-way ANOVA and was found to be significantly different between the eight sites surveyed (Table 14.3). Two species (*M. malayanum* and *G. peraccae*) were not found to be significantly different between sites. When the abundance of freshwater decapods was analysed across 10

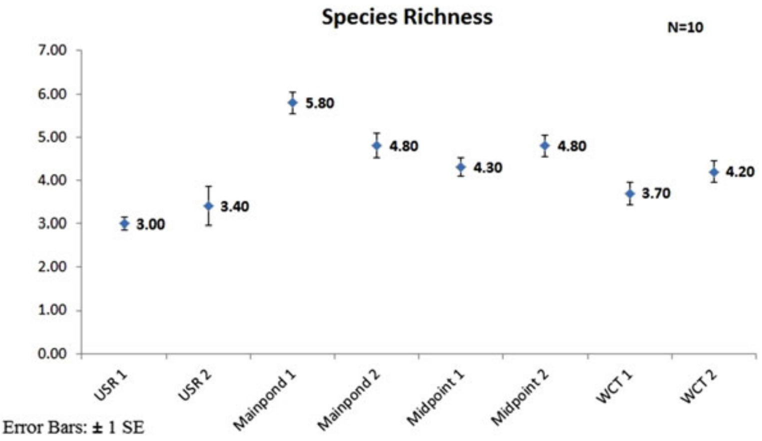

Fig. 14.15 Species richness graph of freshwater decapods at 8 survey sites in the NSSF

Table 14.3 Comparison between mean abundance of freshwater shrimps and crabs at the 8 survey sites, using one-way ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
M.malayanum	Between Groups	127766.888	7	18252.413	3.068	.007
	Within Groups	428307.100	72	5948.710		
	Total	556073.988	79			
M.sundaicum	Between Groups	1984.488	7	283.498	4.399	.000
	Within Groups	4639.700	72	64.440		
	Total	6624.188	79			
M.platycheles	Between Groups	385.350	7	55.050	12.944	.000
	Within Groups	306.200	72	4.253		
	Total	691.550	79			
M.nipponense	Between Groups	17405.150	7	2486.450	18.687	.000
	Within Groups	9580.400	72	133.061		
	Total	26985.550	79			
C.malayensis	Between Groups	5341.588	7	763.084	19.449	.000
	Within Groups	2824.900	72	39.235		
	Total	8166.488	79			
P.maculata	Between Groups	6737.788	7	962.541	16.741	.000
	Within Groups	4139.700	72	57.496		
	Total	10877.488	79			
P.reticulata	Between Groups	765.688	7	109.384	7.622	.000
	Within Groups	1033.300	72	14.351		
	Total	1798.988	79			
I.Johnsoni	Between Groups	104.350	7	14.907	2.266	.038
	Within Groups	473.600	72	6.578		
	Total	577.950	79			

(continued)

Table 14.3 (continued)

		Sum of Squares	df	Mean Square	F	Sig.
G.peraccae	Between Groups	.750	7	.107	1.134	.352
	Within Groups	6.800	72	.094		
	Total	7.550	79			

Table 14.4 Comparison between mean abundance of freshwater shrimps and crabs at the 10 survey cycles, using one-way ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
M. malayanum	Between Groups	60303.363	9	6700.374	.946	.492
	Within Groups	495770.625	70	7082.438		
	Total	556073.988	79			
M. sundaicum	Between Groups	527.563	9	58.618	.673	.730
	Within Groups	6096.625	70	87.095		
	Total	6624.188	79			
M. platycheles	Between Groups	60.550	9	6.728	.746	.665
	Within Groups	631.000	70	9.014		
	Total	691.550	79			
M. nipponense	Between Groups	1197.550	9	133.061	.361	.950
	Within Groups	25788.000	70	368.400		
	Total	26985.550	79			
C. malayensis	Between Groups	433.613	9	48.179	.436	.911
	Within Groups	7732.875	70	110.470		
	Total	8166.488	79			
P. maculata	Between Groups	719.863	9	79.985	.551	.832
	Within Groups	10157.625	70	145.109		
	Total	10877.488	79			
P. reticulata	Between Groups	145.113	9	16.124	.682	.722
	Within Groups	1653.875	70	23.627		
	Total	1798.988	79			
I. johnsoni	Between Groups	84.700	9	9.411	1.336	.235
	Within Groups	493.250	70	7.046		
	Total	577.950	79			
G. peraccae	Between Groups	1.300	9	.144	1.618	.127
	Within Groups	6.250	70	.089		
	Total	7.550	79			

sampling cycles no significant differences were observed in the mean abundance of all species (Table 14.4).

The spatial difference in mean abundance of shrimp in the NSSF was calculated and *M. malayanum* (Fig. 14.16) was found to be the most abundant species with a mean of 98.49 individuals per site per sampling cycle (ind/site), which is more than

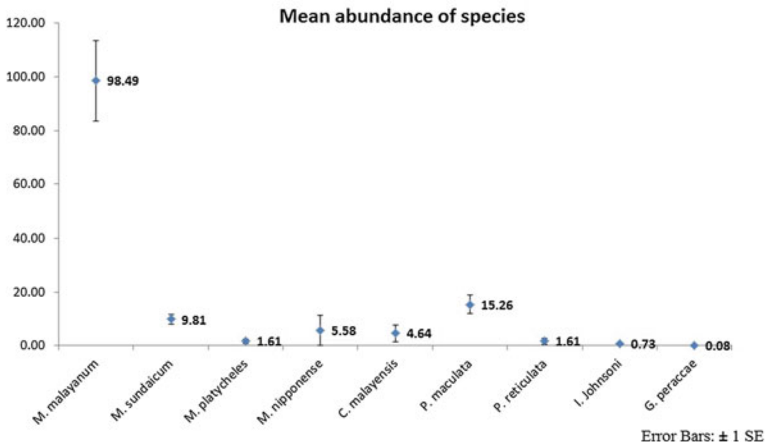

Fig. 14.16 Mean abundance graph of freshwater decapods (ind/site)

10 times that of the 2nd most abundant shrimp species *M. sundaicum* (9.81 ind/site). Both of these species of shrimp were found at all the survey sites (Fig. 14.17a, b). *Macrobrachium platycheles* was found at all sites (except USR 1 and 2) although it was much less abundant (1.61 ind/site) (Fig. 14.17c), while *M. nipponense* was abundant but was only found at one site (USR 1) (Fig. 14.17d). *Caridina malayensis* occurs in all sites (except USR 1) and is significantly abundant at Mainpond 1 (Fig. 14.17e).

Only the freshwater crab *P. maculata* (Fig. 14.18a) was found at all survey sites (mean abundance of 15.26 ind/site) and is by far the most common species of crabs in the NSSF. *Parathelphusa reticulata* (Fig. 14.18b) is the 2nd most abundant crab species, but its abundance is much lower (1.61 ind/site) and it is absent from USR 1 and WCT 2, while *I. johnsoni* is rare and is absent from USR 1, Midpoint 1 and 2 (Fig. 14.18c). *Geosesarma peraccae* was rarely encountered and was only found at USR 2, Midpoint 1, and WCT 2 (Fig. 14.18d).

14.4.5 Temporal Difference in Mean Abundance

The mean population abundance between the 10 cycles was analysed for changes in shrimp and crab abundance between cycles, but it did not indicate a seasonal trend. The mean abundance within each species of decapods over 10 cycles is shown in Figs. 14.19 and 14.20, and indicates that *M. malayanum*, *M. sundaicum*, and *M. nipponense*, all have the first mean abundance peak at cycle 3 (March 2013), and

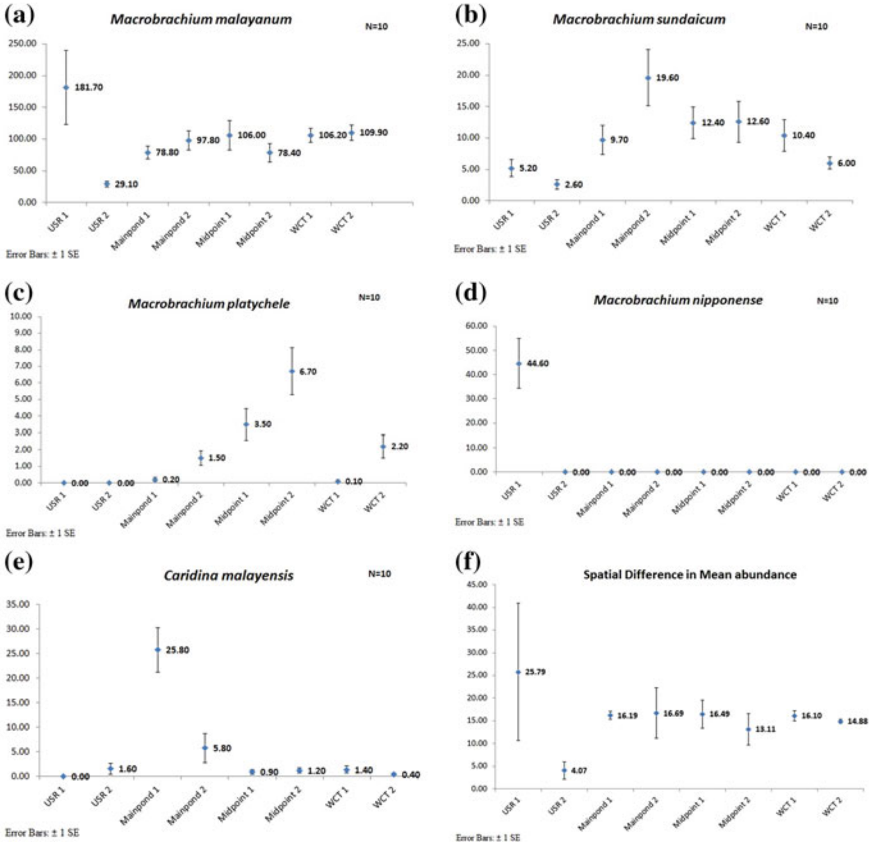

Fig. 14.17 Mean abundance of freshwater shrimps at 8 survey sites, over 10 survey cycles. **a** *Macrobrachium malayanum*, **b** *M. sundaicum*, **c** *M. platycheles*, **d** *M. nipponense*, **e** *Caridina malayensis,* and **f** sum of all species

the second and third peaks at cycles 5 (Sept. 2013) and 8 (March 2014) respectively. *Caridina malayensis* displays a similar abundance pattern but the third peak appears at cycle 9 (May 2014) instead of cycle 8. *Macrobrachium platycheles* has a slight increase in abundance between cycles 2 to 7, followed by a decrease to cycle 9 and an increase at cycle 10. The mean abundance of the two species of *Parathelphusa* over the 10 cycles also had the highest peak at cycle 2 (Feb. 2013) corresponding to the end of the northwest monsoon period with a fall in rainfall.

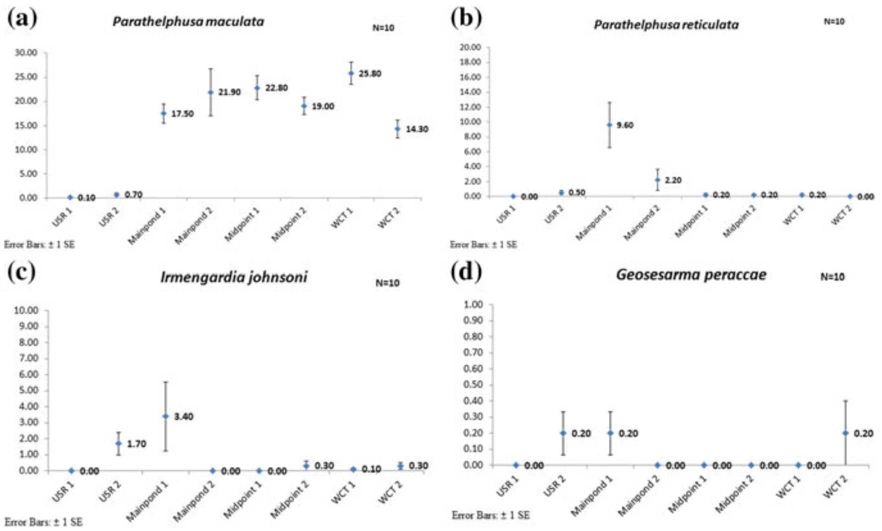

Fig. 14.18 Mean abundance of freshwater crabs at 8 survey sites over 10 survey cycles. **a** *Parathelphusa maculata*, **b** *P. reticulata*, **c** *Irmengardia johnsoni*, and **d** *Geosesarma peraccae*

14.4.6 Population Dynamics of Freshwater Shrimps and Crabs in the NSSF

The carapace and body length measurements for each species were grouped into eleven length classes and the frequencies of individuals in each length class were analyzed over 10 cycles. Those species with a high abundance and occurrence are analyzed further.

Macrobrachium malayanum

This species had the highest abundance and occurrence across all of the sampling cycles based on results from USR 1 (Fig. 14.21) and Midpoint 1 (Fig. 14.22). For the first 4 cycles there was a sharp decrease from the CL 0.6–0.7 cm group to the CL 0.71–0.75 cm group, with the other length groups forming two smooth peaks. The results suggest that from January to March 2014 the population of *M. malayanum* in USR 1 comprised two separate growth cohorts. In the first cohort, with length below 0.95 cm, there was a significant portion of gravid females. This supports the observation that gravid *M. malayanum* tends to be smaller in size

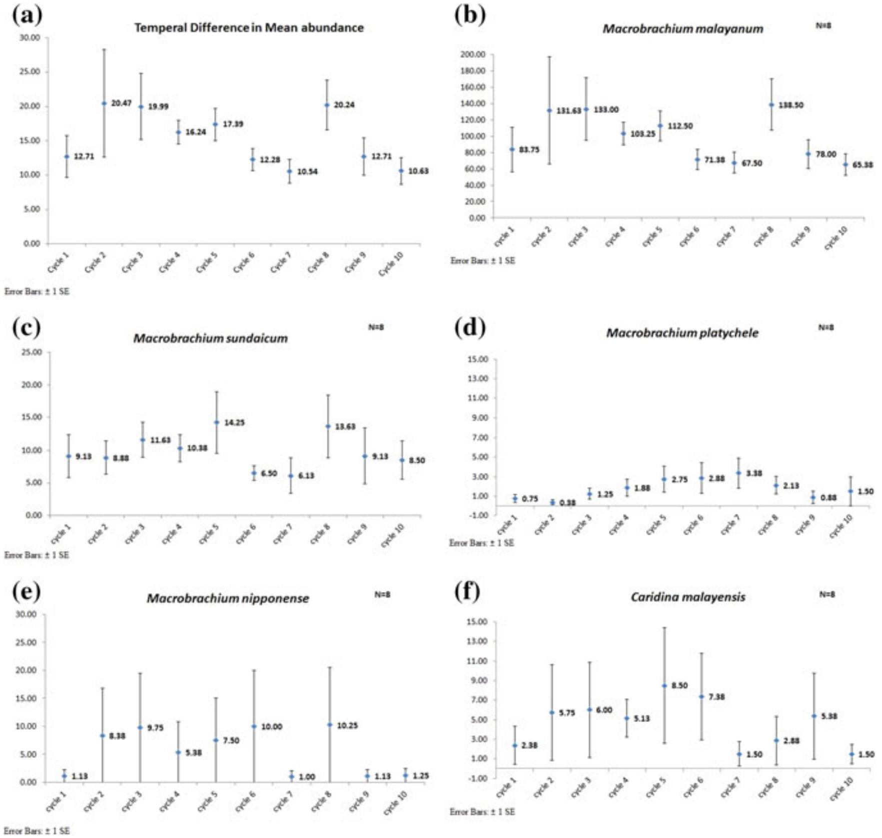

Fig. 14.19 Mean abundance of freshwater shrimps at 10 survey cycles over 8 sites. **a** Mean abundance of all species, **b** *Macrobrachium malayanum*, **c** *M. sundaicum*, **d** *M. platycheles*, **e** *M. nipponense*, and **f** *Caridina malayensis*

within its own species. At cycle 5 (Sept. 2013) there was a rise in the number of groups larger than CL 1.1 cm where the length-frequency changed significantly over the consecutive cycles and cohorts are similar to cycles 6 (Nov. 2014) to 10. The interval between these cycles was about two months and it is possible that this gap may be too long to monitor the population of *M. malayanum* effectively, especially because no gravid females were found at cycles 6, 7, and 10 that had a 2-month interval between them.

At Midpoint 1 *M. malayanum* (Fig. 14.22) had a large proportion of adults and the population displayed a distinct length-frequency pattern compared to that at

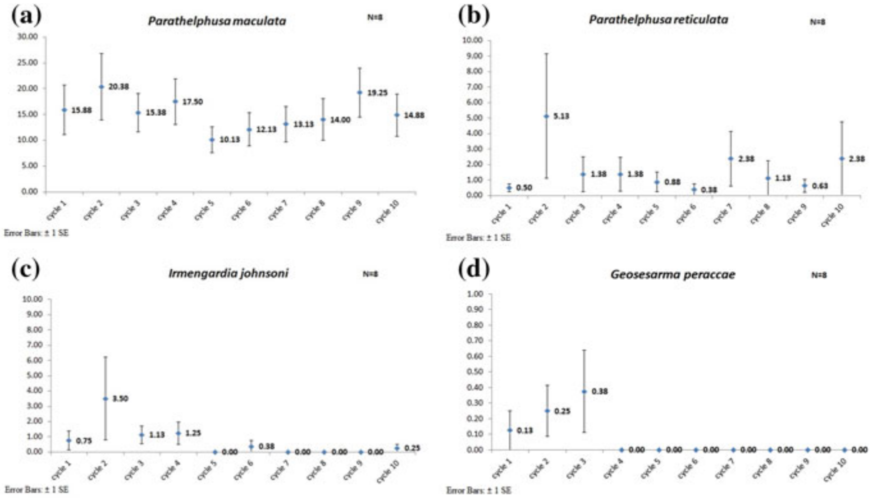

Fig. 14.20 Mean abundance of freshwater crabs at 10 survey cycles over 8 survey sites. **a** *Parathelphusa maculata*, **b** *P. reticulata*, **c** *Irmengardia johnsoni*, **d** *Geosesarma peraccae*

USR 1. Cycles 1–5 at Midpoint 1 showed a U-shaped distribution with the majority of the length size comprising mostly adults together with a significant proportion of juveniles (CL less than 0.75 cm). After cycle 7 this pattern changed to two small peaks. The microhabitat of *M. malayanum* at Midpoint 1 may be more stable, experience less interspecific competition, and offer more favorable conditions for growth in this species than does that at USR 1.

Macrobrachium sundaicum

The length-frequency profile of *M. sundaicum* at Mainpond 2 (Fig. 14.23) is influenced by its low abundance and in cycles 1, 3, and 5 there was only one central peak, while cycles 2, 4, 6 and 7 had very low numbers and no detectable pattern. Cycles 8, 9, 10 show two separate cohorts, the second of which is formed by adult specimens (including gravid females, but these were rarely encountered in this study).

Macrobrachium platycheles

This species was most abundant and most frequently captured at Midpoint 2 (Fig. 14.24). Cycles 1–4 produced only a few small specimens (all less than CL 0.75 cm), cycles 5 and 6 produced more specimens that were all small (CL 0.55–0.65 cm) including two small gravid females. In cycles 7 and 8 the length

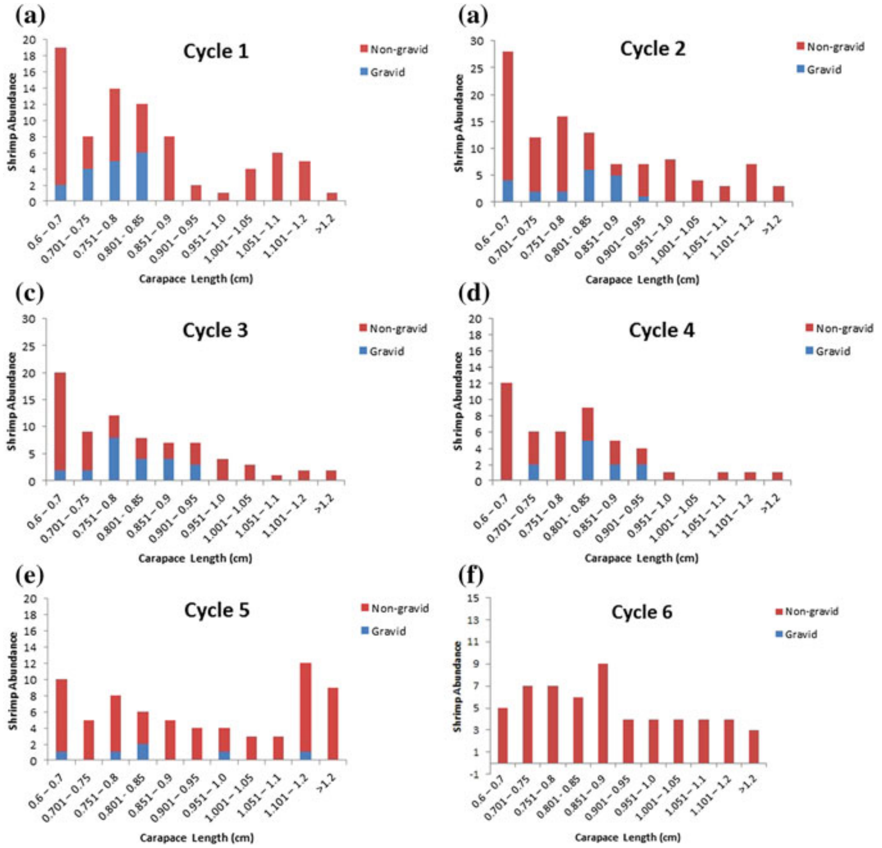

Fig. 14.21 **a**–**j** Length-frequency of *Macrobrachium malayanum* at USR 1 for Cycles 1–10 respectively

groups spread out with low numbers and produced only a few specimens, but did include gravid females (CL 0.60–0.75 cm). No gravid females were recorded in cycles 9 and 10.

Macrobrachium nipponense

This species was only found in the NSSF at USR 1 (Fig. 14.25). Cycles 1–4 showed a left-skewed distribution of length-frequency profiles, with most gravid females in the first 5 length groups. Cycles 5, 6, 7, 9, and 10 all had a low abundance, but cycle 8 had a high abundance with two peaks (one at CL 0.85–0.90 cm, the other at CL 1.1–1.2 cm) and a distinct recruitment group (CL 0.6–0.7 cm). Very few gravid females were found in length groups from CL 0.85 to

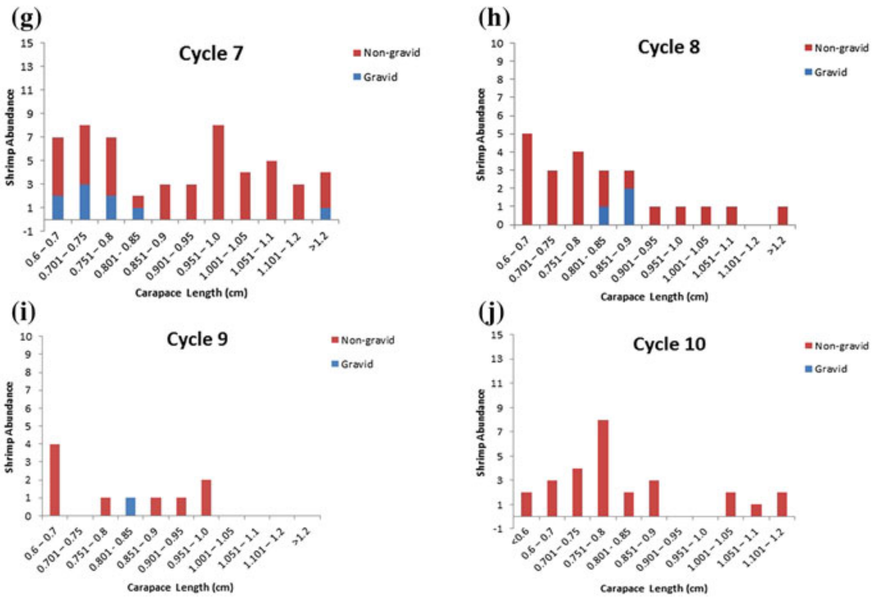

Fig. 14.21 (continued)

1.05 cm. This species is similar to *M. malayanum* in that at USR 1 both species experienced low abundance in cycles 7 and 9, but had a high abundance in cycle 8. This pattern may be due to a similar flow regime, rather than inter-species competition. *M. nipponense* in USR 1 seems to comprise a significant "migrants" from the reservoir. The site was directly connected to and frequently flooded with reservoir water especially during the monsoon seasons.

Caridina malayensis

The length-frequency data for this species are from hand sampling because *C. malayensis* is too small to be collected by trap sampling (Fig. 14.26). Cycles 1–7 had two cohorts with a distinct separation point at length groups between BL 1.0–1.2 cm, and with larger gravid females in the second cohort implying that female individuals of this species grow larger than males. However, these cohorts became less distinct in cycle 7, and by cycle 9 the second cohort had disappeared. In Mainpond 1 cycles 2–10 there was an increment in number of large-sized specimens (BL > 1.10 cm).

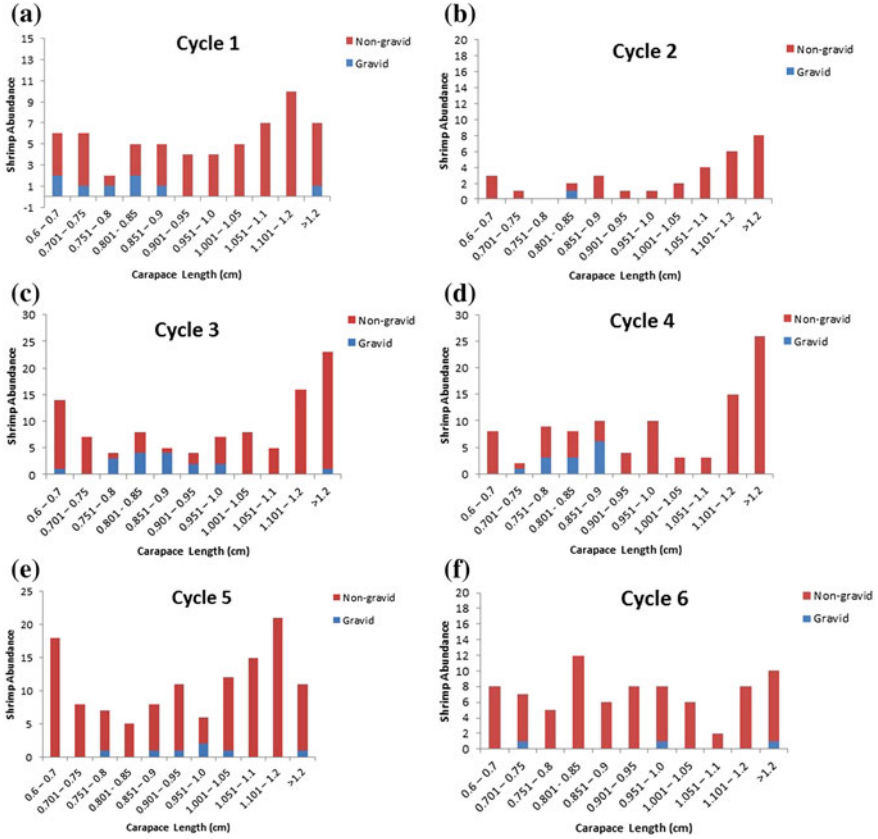

Fig. 14.22 **a–j** Length-frequency of *Macrobrachium malayanum* at Midpoint 1 for Cycles 1–10 respectively

Parathelphusa maculata

This species was most abundant at sites Midpoint 2 and WCT 1 in cycles 1–10 (Figs. 14.27 and 14.28). Two distinct length cohorts were found, one with relatively large numbers of young specimens, and the other with increasing numbers of adults. Gravid females were found in most of the cycles and only appeared in large size specimens. However, the combination of hand and trap sampling used to collect this species may have introduced sampling biases because hand sampling catches more young specimens, while trap sampling catches more large specimens.

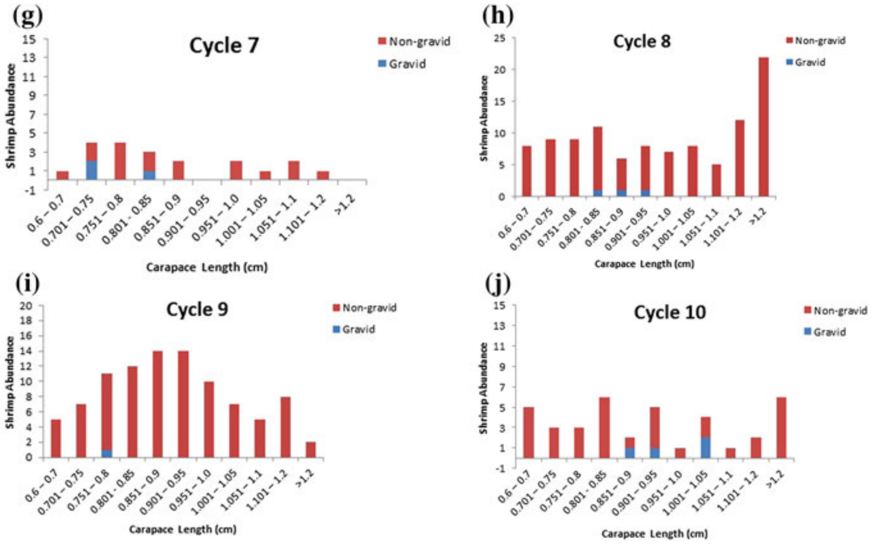

Fig. 14.22 (continued)

Parathelphusa reticulata
This species was most abundant at Mainpond 1 and was chosen for the length-frequency analysis (Fig. 14.29). However, very few specimens were caught during any of the 10 sampling cycles, but cycles 2, 8, and 10 caught the most specimens in two separate size cohorts, with small sized individuals were less abundant.

14.4.7 Evaluation of Hand Sampling and Trap Sampling Techniques

The effectiveness of the two different sampling techniques was assessed and the mean carapace length of shrimps and crabs caught from the first 4 cycles were graphed (Fig. 14.30). In general, trap sampling produced the larger sized shrimps and crabs. For *M. sundaicum* there was a large difference (CL 0.401 cm) between

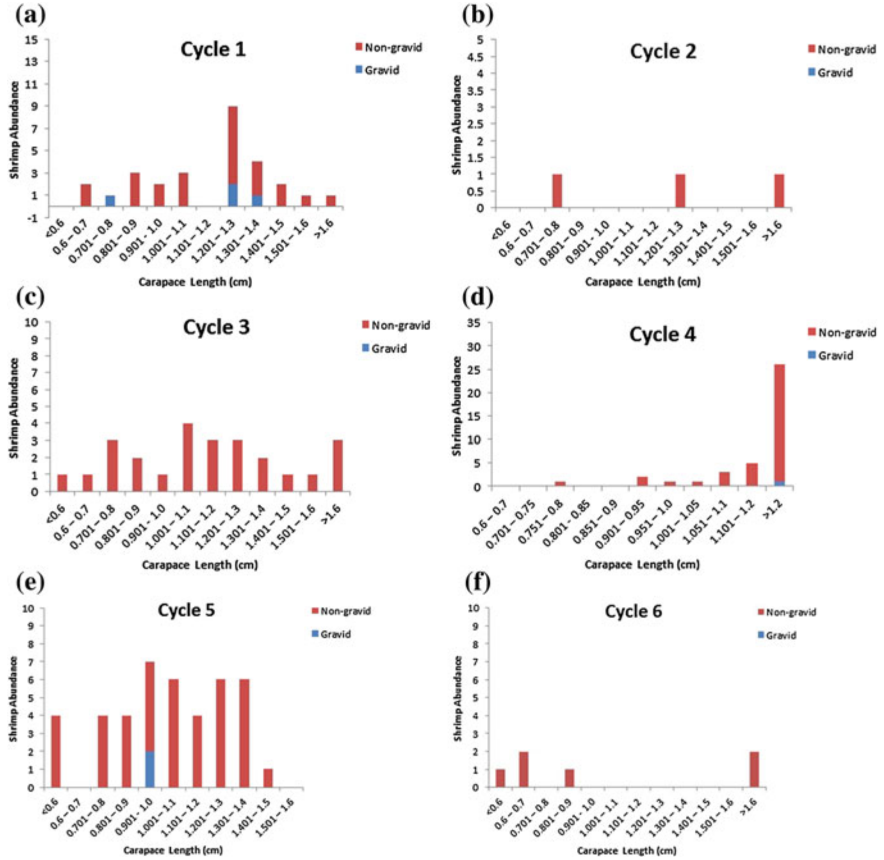

Fig. 14.23 **a–j** Length-frequency of *Macrobrachium sundaicum* at Mainpond 2 for Cycles 1–10 respectively

the mean CL of hand and trap sampled specimens, while for *M. platycheles* the difference between the mean CL of trap and hand sampled specimens was only CL 0.070 cm. For *P. maculata* there was a large difference between the mean CL of trap and hand sampled specimens (CL 2.082 cm), while for *I. johnsoni* the difference between the mean CL of trap and hand sampled specimens was only CL 0.024 cm.

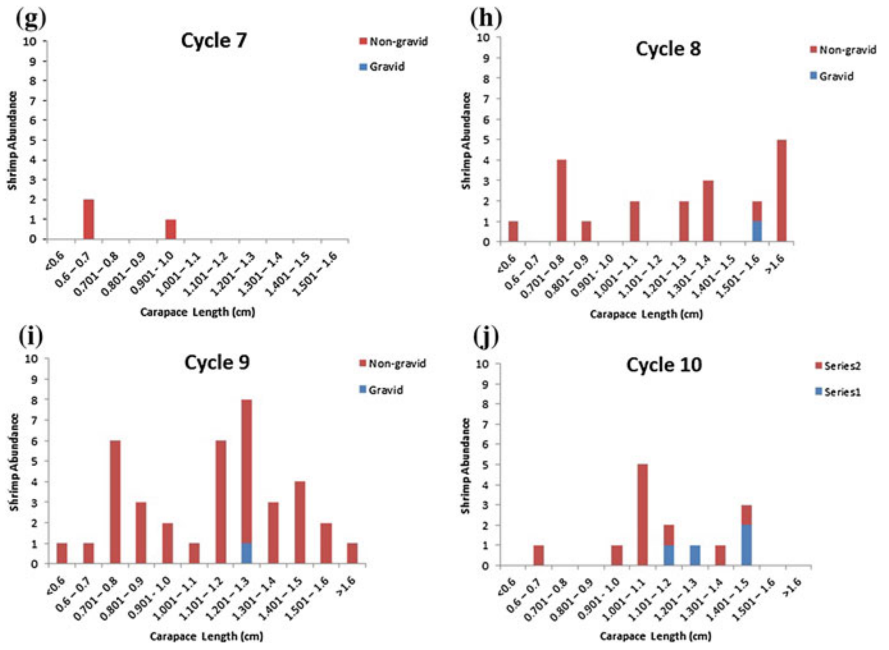

Fig. 14.23 (continued)

14.5 Discussion

14.5.1 *Distribution of Freshwater Shrimps and Crabs*

The environmental conditions throughout the NSSF are generally similar, but there are differences in the microhabitats at different locations that may influence species diversity and abundance. The freshwater decapod crustaceans studied here in the NSSF each have their own preferred habitat and their own optimal environmental conditions.

Macrobrachium malayanum was the commonest and most widespread species in the NSSF and was found at all sites surveyed. The wide distribution of *M. malayanum* may be due to its ability to adapt to harsh environmental conditions, including water with low oxygen, low pH (4.40–6.54), and low calcium levels (Chong and Khoo 1987). *Macrobrachium sundaicum* was also collected at all

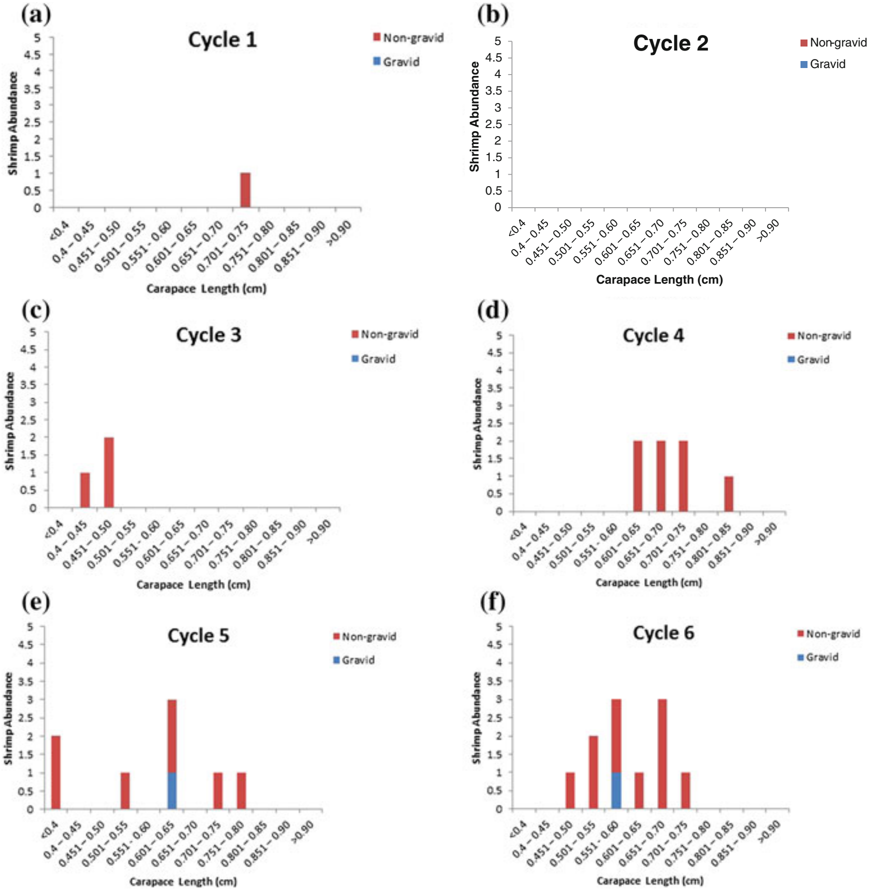

Fig. 14.24 **a**–**j** Length-frequency of *Macrobrachium platycheles* at Midpoint 2 for Cycles 1–10 respectively

quantitative sites surveyed but in much lower numbers than *M. malayanum*. In addition to the above abiotic factors the geographical distribution of shrimps is also affected by biotic factors such as predation, food availability, competition, and stress (Margules et al. 2002). The fact that sympatric populations of *M. malayanum* and *M. sundaicum* co-exist in the same water bodies (but at different abundances) suggests that there may be competition between these two species.

Several species (*M. platycheles*, *M. nipponense* and *C. malayensis*) were only found at specific sites in the NSSF where there are presumably different micro-habitat conditions that influence species distribution (Iwata et al. 2003). For

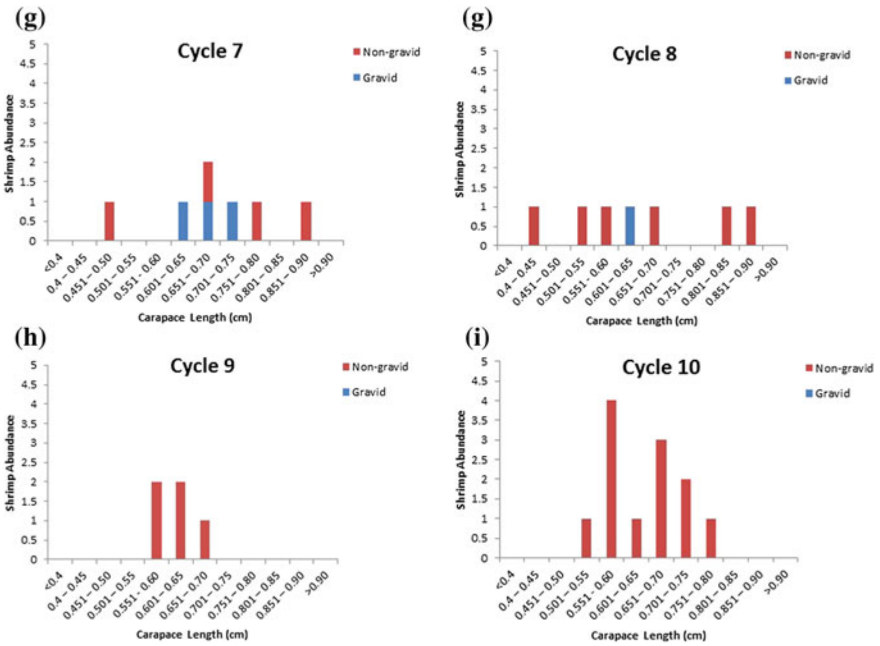

Fig. 14.24 (continued)

example, *M. platycheles* prefers acidic and fast-flowing water in the middle stream regions, while *M. nipponense* prefers the less acidic and more open waters of the streams in the outskirts of the NSSF.

The distribution and abundance of species of freshwater crabs in the NSSF is influenced by the microhabitat and by the ability of the species to survive there (Iwata et al. 2003). Highly adapted species such as *P. maculata* were found in almost all sites studied in the NSSF that have a range of water pH and temperature. The conditions at USR 1 may be unsuitable for freshwater crabs because only one juvenile specimen of *P. maculata* was caught there throughout the study period. The water levels at USR 1 were high and the stream banks were tough and dry, and the water temperature was high due to a lack of forest cover. The streambed also lacked mud and leaves that typically provide hiding places for crabs. The abundant algal growth at USR 1 may be the result of fertilizer run-off from a nearby golf course, which is also a source of pesticide pollution in the NSSF.

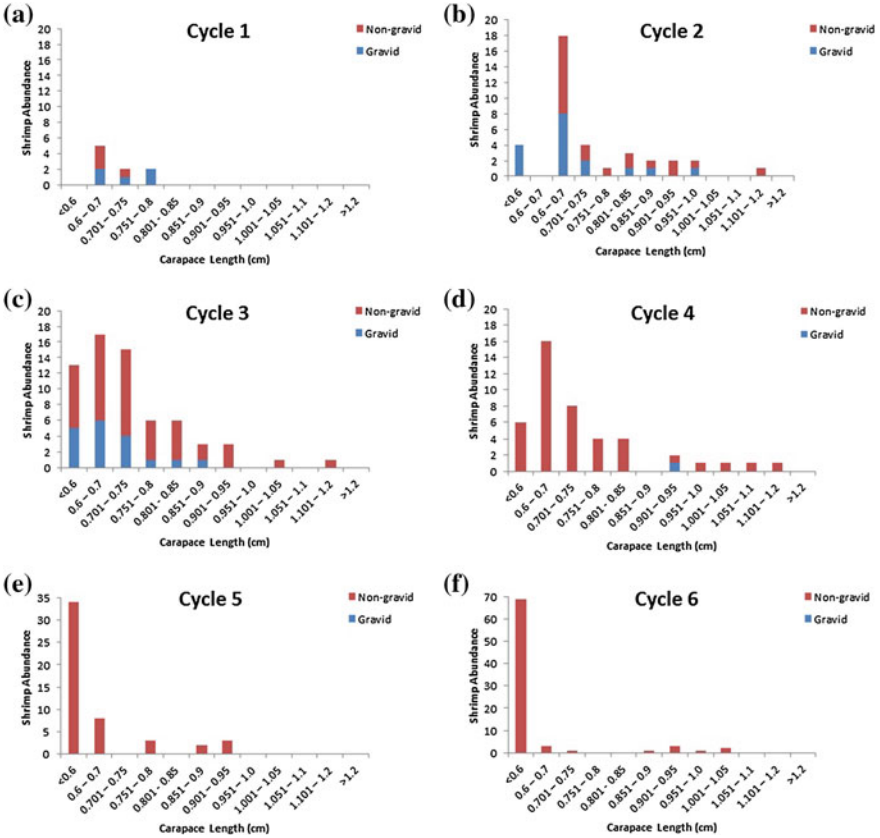

Fig. 14.25 **a–j** Length-frequency of *Macrobrachium nipponense* at USR 1 for Cycles 1–10 respectively

14.5.2 Diversity and Abundance of Freshwater Shrimps and Crabs

Species diversity and abundance are intrinsically linked to hydrological conditions and vegetation dynamics (Hansen et al. 2010). The varied vegetation found along the streams in Mainpond 1 (including trailing roots) provides a large selection of microhabitats for shrimps, and may contribute to their high diversity and species richness (e.g., *C. malayensis*). Sites USR 1 and 2 had the lowest species diversity and species richness. This may be due to the sparse vegetation cover and open and

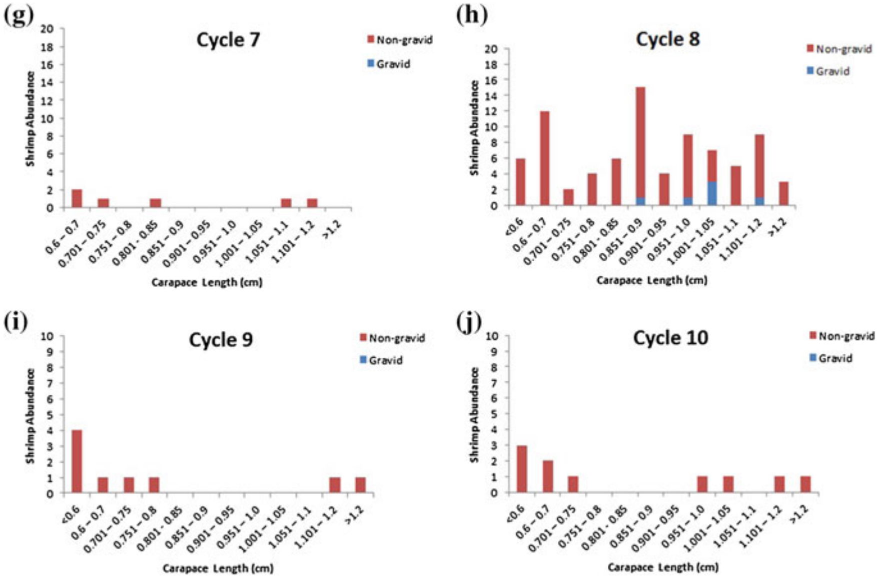

Fig. 14.25 (continued)

unshaded water, or to the water level fluctuations due to reservoir operation, or to increasing pollution, all of which make it uninhabitable for sensitive species such as *M. platycheles*.

Macrobrachium malayanum, *M. sundaicum* and *M. platycheles* were all abundant in cycles 3 and 4, possibly because of the lower water levels in March 2013 than in February 2013 (due to unseasonably low rainfall in March 2013). The reduced water body for shrimps to swim in during March 2013 increased their chances of capture and may explain the increased abundance in cycles 3 and 4. An increase in *C. malayensis* was seen at Mainpond 1 in cycles 2 and 3. High rainfall and fast flowing water washes nutrients downstream and affects the abundance of *Macrobrachium* and *Caridina* differently. *Caridina malayensis* normally clings to trailing roots near the banks in Mainpond 1, but it risks being washed away downstream due to its small body size. Mainpond 1 may have abundant *C. malayensis* because it acts as a collection site for shrimp that have been swept downstream by the fast flowing waters, where they remain until swimming back upstream to their original habitat. *Macrobrachium* species prefer to hide under substrate accumulations and are less affected than *Caridina* by changing water levels and rainfall patterns.

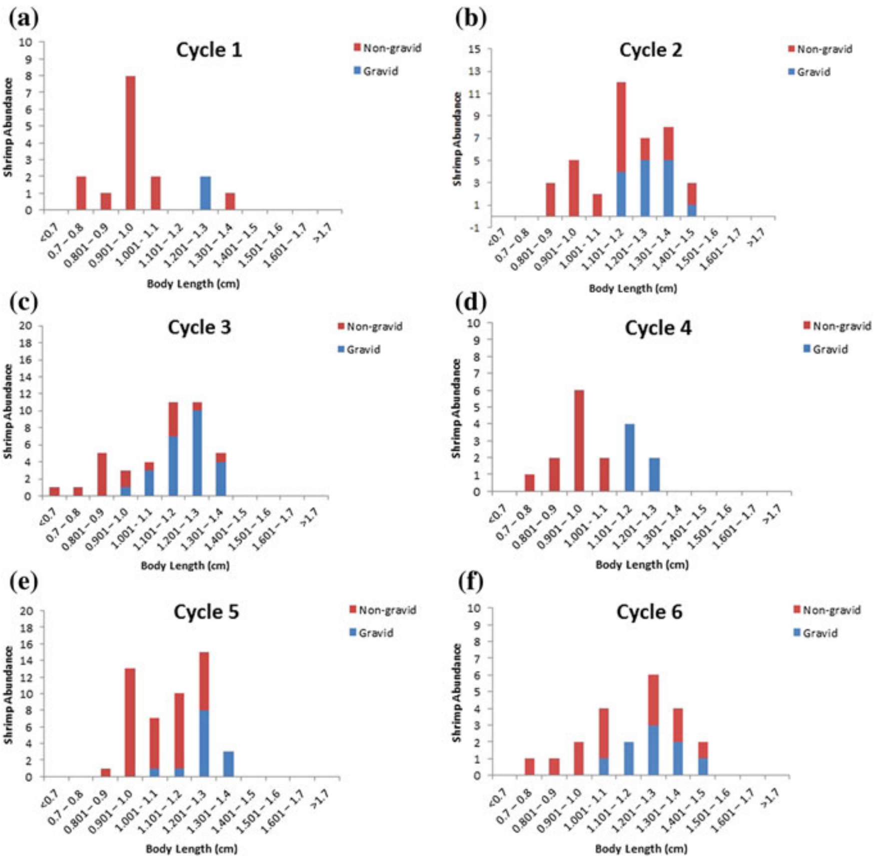

Fig. 14.26 a–j Length-frequency of *Caridina malayensis* at Mainpond 1 for Cycles 1–10 respectively

Parathelphusa maculata was the most abundant species of freshwater crab, followed by *P. reticulata,* the second most abundant species, then by *I. johnsoni* and *G. peraccae*. *Irmengardia johnsoni* was abundant in USR 2, Mainpond 1, WCT 1 and 2 where the stream flows through secondary forest. In addition, more *P. reticulata* were found in site 2 than *P. maculata. Parathelphusa reticulata* prefers sites with a low water level, while *P. maculata* prefers sites with a high water level. The fact that *G. peraccae* was rarely encountered during this study may be due to its semi-terrestrial habits compared to those of fully aquatic species (Ng 1988). The upstream microhabitat in Mainpond 1 (shallow, shaded water with a lot of leaf litter and mud) supported the highest species diversity of freshwater crabs.

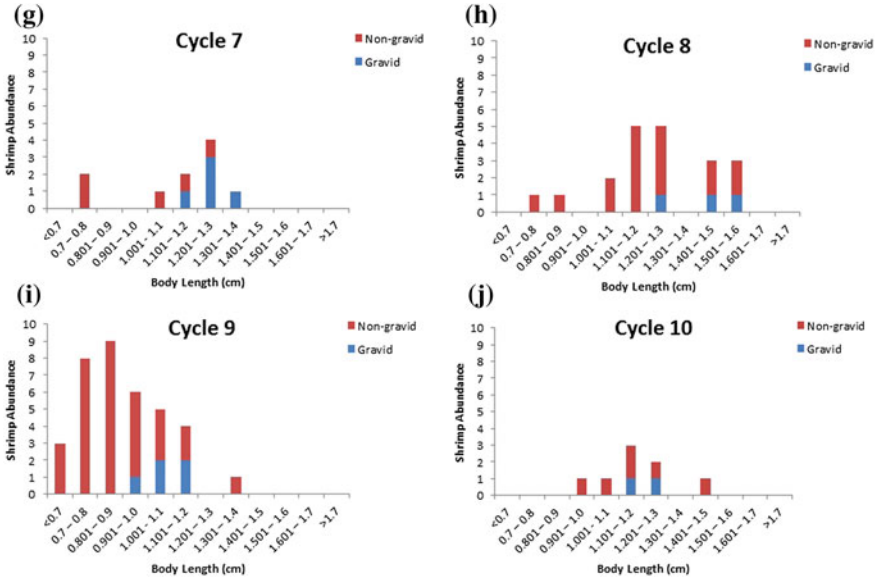

Fig. 14.26 (continued)

14.5.3 Population Dynamics of Freshwater Shrimps and Crabs

A distinct breeding season was not detected for most of the decapod species in the NSSF, and gravid females were caught in most places and during most sampling cycles. Short-term seasonal trends in length-frequency profiles in *C. malayensis* and *M. malayanum* display two cohorts, with the majority of gravid females in the second cohort. Gravid females of *M. malayanum* were smaller than gravid females of *M. sundaicum*. *M. nipponense* was only found in the NSSF at USR 1. There is a leftward-skewed distribution of the length-frequency profiles in the first four cycles, with the majority of gravid females falling in the five smaller length groups. A general trend was seen in the length-frequency profiles of *M. maculata* in only two of the sampling sites despite the underlying variation across cycles (due mostly to differences in abundance). *Parathelphusa maculata* showed two distinct length groups, one with young specimens and the other with adults. In the first group, the number of small specimens is high and decreases as body length increases, while in the second group there was an increase in the number of large specimens (including large gravid females). The two distinct size groups in the samples under discussion here may be due to different habitat preferences of medium sized specimens

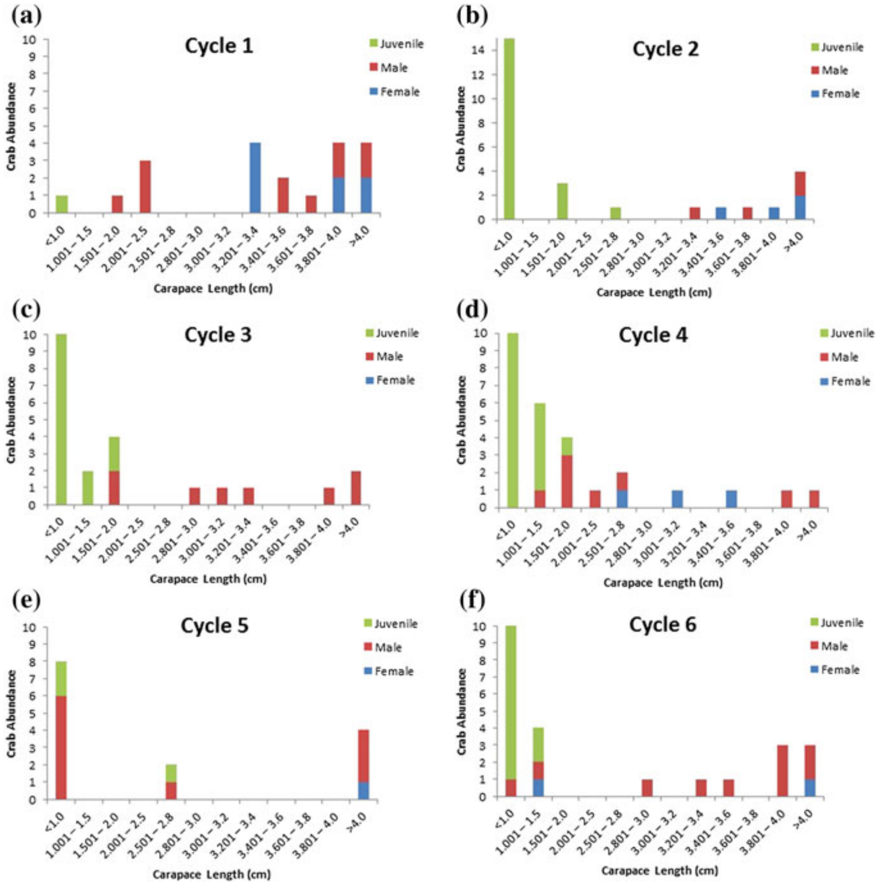

Fig. 14.27 **a–j** Length-frequency of *P. maculata* at Midpoint 2 for Cycles 1–10 respectively

compared to those of juveniles and adults, or it may be due to the limitations of the hand sampling and trap sampling methods that fail to catch medium sized animals.

14.5.4 Evaluation of Sampling Techniques

Hand sampling tends to collect small-sized *Macrobrachium* that hide underneath substrate accumulations during the day. In contrast, trap sampling tends to catch larger specimens from a wider area after they have emerged at night to feed (Reader et al. 2003) because they can swim against the current and feed further afield. A combination of hand and trap sampling provides a better coverage of the actual population of decapods in the NSSF.

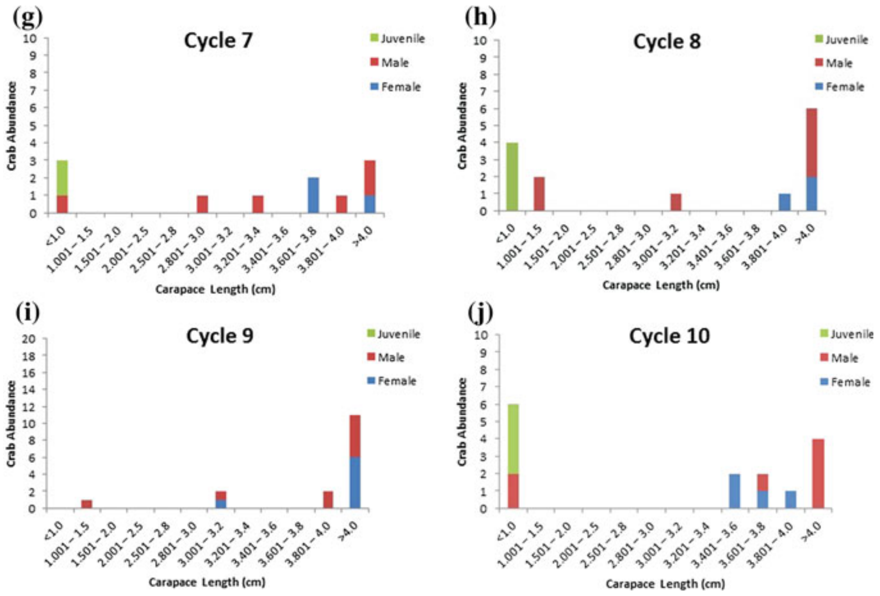

Fig. 14.27 (continued)

The long-term monitoring of shrimp and crab populations in the NSSF should take into account the limitations of the sampling techniques used here. For example, medium-sized crabs were not collected by either hand sampling or trap sampling, and small-sized shrimps were missed by the larger mesh hand nets. We recommend using finer-mesh nets for hand sampling to ensure that even the smallest *C. malayensis* can be caught. A drawback of trap sampling is that big fishes (such as catfish and snakeheads) that get trapped can kill many of the shrimps caught in the same trap thus affect the accuracy of the results.

14.5.5 Conservation Status of Freshwater Shrimps and Crabs in the NSSF

No new records of shrimp species were found in this study but the absence of *Macrobrachium idae, M. neglectum* and *Caridina gracilirostris* implies that these species may be extirpated from the NSSF. For example, in the 1980s *M. idae* and *M. neglectum* were commonly encountered on the outskirts of the NSSF but a huge reduction in their population levels was documented in 1997, and no specimens were collected in 2011 (Ng 1997; Soh 2011; Sun 2011). *Macrobrachium idae*,

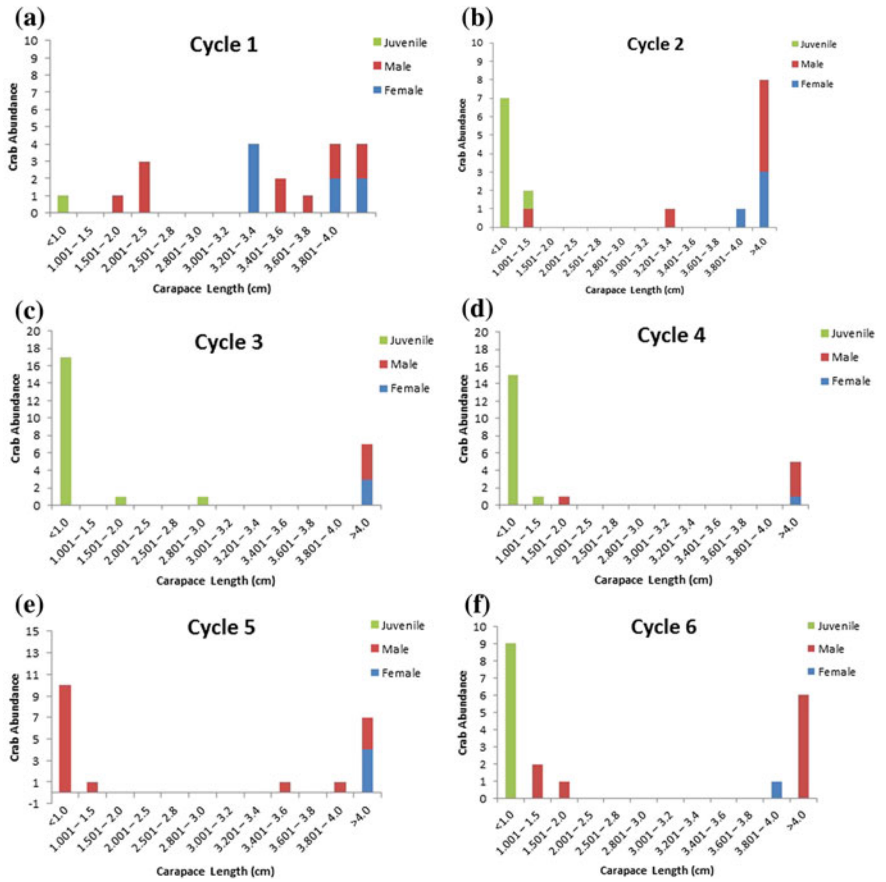

Fig. 14.28 a–j Length-frequency of *Parathelphusa maculata* at WCT 1 for Cycles 1–10 respectively

M. neglectum and *Caridina gracilirostris* all need brackish waters to complete the development of their larvae while *Macrobrachium* species found extant in the NSSF can complete their whole life cycles within the swamp forest. It is likely that the dam built to construct the Lower Seletar Reservoir in 1986 prevented the downstream breeding migrations of these three species and rendered them unable to complete their life cycles. Two female specimens of the rare and tiny (BL 6 mm) riverine apheid shrimp *Potamalpheops amnicus* were recorded from USR 1 in the NSSF in 2011 from a partly shaded slightly acidic forest stream with a clay-sandy streambed (Sun 2011; Cai pers. observ.). *Potamalpheops amnicus* is one of only a handful of freshwater species in the largely marine snapping shrimp family (Yeo and Ng 1997) and was previously only known to occur in Singapore in its type

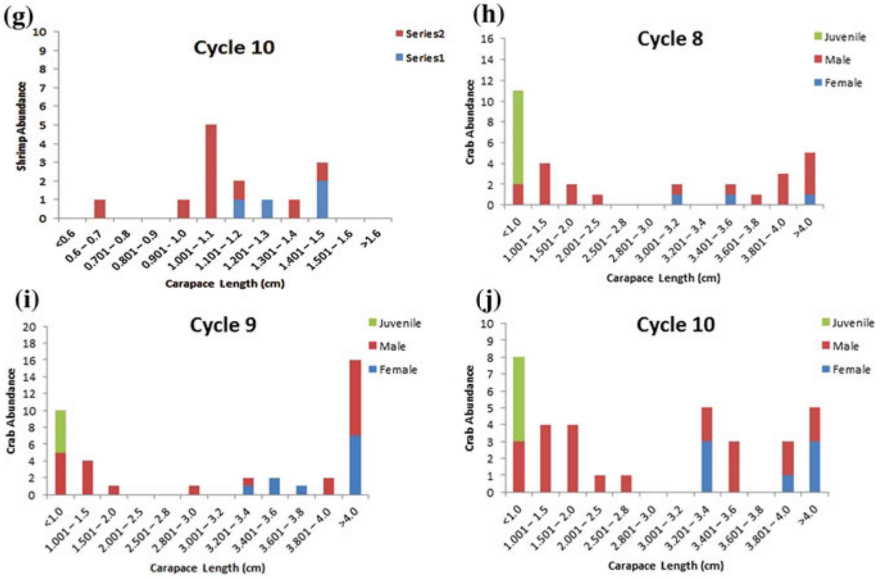

Fig. 14.28 (continued)

locality (Sime Road Forest). However, *P. amnicus* was not found in the NSSF during the current survey, and is listed as endangered in the Singapore Red Data Book. Besides Singapore, *P. amicus* also occurs in the Malay Peninsula and in Bintan, Indonesia. It would be premature to report that *P. amicus* has been extirpated from the NSSF because the sampling methods used here may have missed the presence of these tiny species.

The endemic swamp crab *Parathelphusa reticulata* is restricted to the NSSF and so has a small distributional range with its strict habitat requirements that make it highly susceptible to climate-caused changes in water flow and water acidity (Ng 1997). As a result this species is listed as critically endangered by the IUCN Red List because both its extent of occurrence and area of occupancy are less than 10 km^2, and because it is found in only one location where habitat quality is deteriorating (Esser and Cumberlidge 2008a). A total of 129 specimens of *P. reticulata* were encountered in this study in 12 of the 20 sites with the highest number (41) at cycle 2 and most of these specimens had a small body size. Yeo et al. (2008) listed the status of *P. reticulata* as ‘Endangered’ in the Singapore Red Data Book. However, according to the criteria of the categories of threat in Davison (2008) this species would be ‘critically endangered’ because less than 50 mature individuals were encountered in every cycle of sampling in this study. However, the data presented here are based on a small-scale study in the NSSF and more research that has a wider coverage throughout the NSSF is needed.

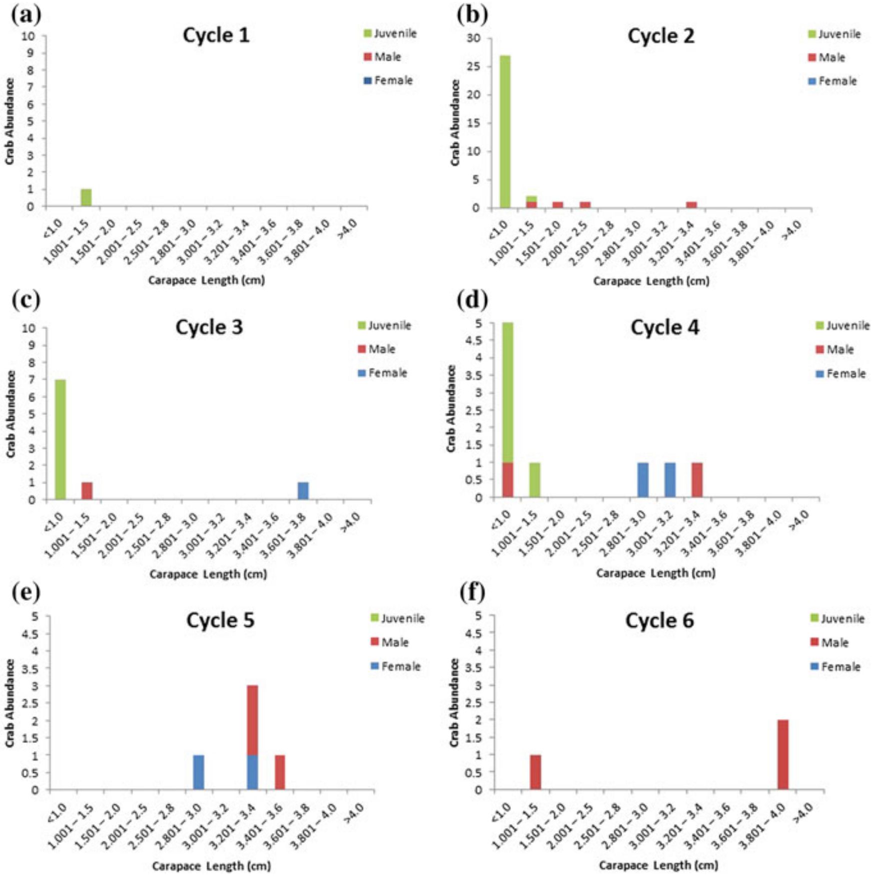

Fig. 14.29 **a–j** Length-frequency of *Parathelphusa reticulata* at Mainpond 1 for Cycles 1–10 respectively

Macrobrachium nipponense is native to China, Japan, and other East Asian countries, but it is not native in Singapore where it has been reported to occur in most of that island's reservoirs, the Sungei Seletar drainage, and the NSSF at USR 1 (Chong et al. 1987; Yeo 2010; Sun 2011, Cai pers. observ.). *Macrobrachium nipponense* could have reached the NSSF via connections with the Upper Seletar Reservoir and has become established because it thrives in disturbed and open habitats with less acidic water such as at USR 1 where the average pH of the water is 6.12) (Ng et al. 1993). *Macrobrachium nipponense* is not known to be a threat to the existence of the native freshwater decapods in Singapore (Ng 1990; Yeo 2010), but it could spread further via the streams draining the outskirts of the NSSF, and control measures should be considered to prevent its further range expansion.

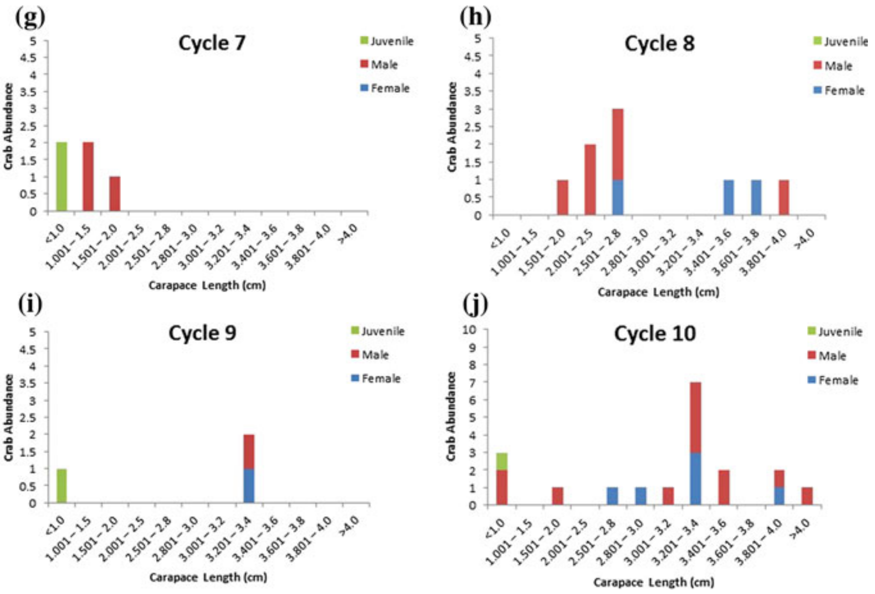

Fig. 14.29 (continued)

14.6 Conservation Management and Future Prospects

The NSSF is the only primary freshwater swamp habitat left in Singapore and much of its biodiversity, including the freshwater decapods, is severely threatened. Extirpation of a species from part of its range would represent a severe threat to the continued existence of that species elsewhere in its range. The continued survival of freshwater shrimps and crabs in the NSSF will require conservation actions at the local level as part of the on-going efforts aimed at sustaining forest biodiversity in the densely populated island of Singapore. These actions will require in-depth studies of the microhabitat-dependent distribution of freshwater shrimps and crabs as well as studies of their complex interactions with other species. Future conservation management actions include stream rehabilitation and enhancement, the reintroduction of native species to their original habitats, the formulation of long-term monitoring programmes, increased patrolling, and stricter enforcement of existing protection of the NSSF and its biodiversity.

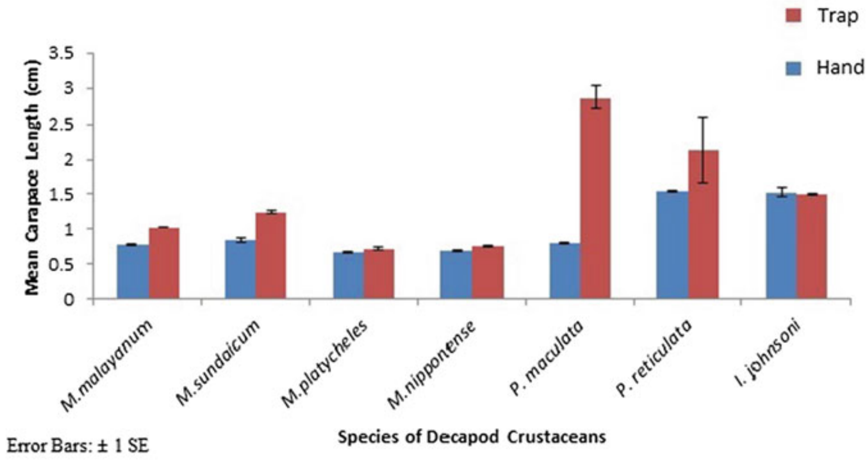

Fig. 14.30 Comparison of the mean carapace lengths of freshwater decapods collected using hand sampling and trap sampling

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Chapter 15
Concluding Remarks About Freshwater Decapod Conservation

Neil Cumberlidge and Tadashi Kawai

Abstract Invertebrates in general are the most species-rich group of organisms on the planet. At the same time invertebrates are the most poorly known and include the highest number of threatened species, and this is especially true for those species that live in freshwater habitats. The different aspects of freshwater decapod conservation covered in this book leave us in no doubt that a high proportion of this important group of organisms are threated with extinction, mainly from anthropogenic impacts. The IUCN Red List assessments quantify extinction threats for groups of organisms globally but the coverage, with only 3.4 % of all species represented, is far from complete, particularly invertebrates. For example, 61 % of vertebrate species are represented on the IUCN Red List compared to only 1.2 % of invertebrates. The current rate of description of new species of freshwater decapods is given, along with the recorded rates of species extinction, and future prospects are discussed.

Keywords *Aegla* · Conservation · Crab · Crayfish · Evolution · Shrimp

15.1 Introduction

The more than 3000 species of freshwater decapod crustaceans make up about one fifth of all known species of decapods (which number around 15,000 species) (De Grave et al. 2009). Freshwater crabs, freshwater shrimps, crayfish and aeglids all rely heavily on the inland freshwater habitats in continents and islands for their survival (De Grave et al. 2008; Yeo et al. 2008; Cumberlidge 2011, 2014a, b; Cumberlidge et al. 2011a, b; Cumberlidge et al. 2014). However, the rivers, streams,

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lakes, wetlands, and subterranean waters are highly discontinuous habitats and together comprise less than 3 % of the total water on the planet. Freshwater habitats offer a wide variety of small ecological niches to the animals that live in these fragmented water bodies, and this, together with the frequent occurrence of genetic isolation, may be responsible for the unusually high species-richness seen in all groups of freshwater decapods worldwide (Dudgeon et al. 2006).

The idea for this volume came about at the Summer Meeting of the Crustacean Society held in Costa Rica in 2013. The meeting was attended by specialists from all parts of the world who work on freshwater decapods, had both a first-hand knowledge of the threats facing these animals, and an interest in their conservation. Our objective was to produce an up-to-date work on the state of decapod crustacean conservation written by scientists currently working on the most threatened groups. To do this we planned to respond to the series of recent global conservation assessments of freshwater decapods that had all used the IUCN Red List criteria (Cumberlidge et al. 2009; De Grave et al. 2014; Richman et al. 2014), all of which indicated that all groups of freshwater decapods were facing high extinction threat levels in all parts of their ranges. As a response to the pressing need for worldwide conservation efforts we organized conservation symposia at two conferences in 2014: the 8th International Crustacean Congress (ICC8) in Frankfurt, Germany, and the joint meeting of the International Association of Astacologists and the Japanense Carcinological Society meeting in Sapporo, Japan. The result was the present volume—a selection of 15 studies on the current state of research on freshwater decapod conservation that were either presented by the authors at the above symposia, or were included here as invited contributions in order to provide balanced coverage of this topic.

This book includes general overviews of global diversity and conservation of freshwater decapods (Cumberlidge—freshwater crabs; Bueno—aeglids; and Kawai and Crandall—crayfish); chapters that deal with the history of freshwater crab research (Chap. 4 Tuerkay and Sonnewald) and life history strategies of freshwater decapods (Chap. 5 Anger—adaptation to life in fresh water; Chap. 6 Vogt—larval development in freshwater; and Chap. 7 Magdalini et al.—freshwater shrimp life history). Three other chapters focus on the conservation of freshwater decapods in Latin America (Chap. 8 Alvarez and Villalobos—Mexico; Chap. 9 Wehrtmann et al. —Central America and the Caribbean, and Chap. 10 Magalhaes et al.—South America); and four chapters deal with active conservation programs for threatened freshwater decapods (Chap. 11 Sagi—biotechnology and conservation; Chap. 12 Vezza—quantitative habitat modelling; Chap. 13 Yeo et al.—conservation planning and implementation; and Chap. 14 Cai et al.—biodiversity assessment of Nee Soon Swamp in Singapore).

Recent IUCN Red List conservation assessments of three groups of freshwater decapods focus a spotlight on the large numbers of species of freshwater crabs, crayfish, freshwater shrimp, and freshwater aeglids from all parts of the world that are threatened with extinction. There is clearly an urgent need for the effective development and implementation of conservation actions (see Chap. 13 by Yeo et al. present volume). Freshwater decapods are particularly vulnerable to the threat of extinction because all groups include endemic species with restricted distributions that are strongly affected by anthropogenic threats of various kinds that heavily impact freshwater habitats throughout the inland waters of the world.

15.2 Freshwater Decapod Diversity and Conservation

At 1.4 million published species, invertebrates make up over 80 % of the named and unnamed biodiversity (1.4 million and 10 million species respectively), meaning that most species of invertebrates are still unknown to science and have not yet been discovered. Indeed, the rate of species discovery of invertebrates is showing no signs of slowing down (Table 15.1). The estimated current rate of species discovery is between 16,000 and 20,000 new species per year, a figure that includes between 55 and 60 new species of freshwater decapods per year (Table 15.2).

Birds (~10,000 species) and mammals (~6,000 species) are by far the best-known groups, and include so few data deficient species that new species discoveries are a rarity that attract a great deal of attention. In contrast, most other vertebrate and invertebrate groups include large numbers of poorly known (data deficient) species, and it is here, the largest part of the world's biodiversity, where we expect the highest rates of new species discovery, and the highest rates of extinction losses (Collen et al. 2008; 2014).

Table 15.1 Estimated numbers of described and undiscovered species by group

	Described species	Estimated total species	Estimated species still undiscovered
Vertebrates	65,000	80,500	15,500
Invertebrates	1.4 million	8–10 million	6.6–8.6 million
Insects + spiders	1.1 million	5.6 million	4.5 million
Molluscs	85,000	200,000	115,000
Crustaceans	47,000	150,000	103,000
Nematodes	25,000	500,000–1 million	475,000–975,000

Table 15.2 Rate of description of new species of freshwater decapods since 2008

	2008	2014	New species since 2008	Rate/year
Primary FW crabs	1280	1370	90	16
Secondary FW crabs	170	220	50	8
Crayfish	569	638	59	10
FW shrimps	655	765	107	18
Aeglidae	68	85	17	3
Totals	2742	3078	336	+56

Most species of freshwater decapods reproduce by direct development and have no planktonic larval stages (Anger, Chap. 5 of this volume), which is an adaptation that equips them well for life in inland waters such as rivers, lakes, marshes, caves, trees, and the neighboring land. This adaptation may also be responsible for their restricted distributional ranges, their high rates of endemism, and their high species diversity. These biological characteristics also make these decapods more vulnerable to threats from changes to their habitat, pollution, exotic species, and overharvesting by humans.

These threats to freshwater decapods are mostly anthropogenic and are ultimately driven by the expanding human population (7.3 billion and counting) that is making demands on the environment that are driving habitat disruption. For example, activities such as deforestation, agriculture, mining, dams and water diversion all disrupt aquatic habitats, change water flow patterns, cause siltation and pollution from pesticide and fertilizer use. In addition, there are increasing threats from competition with invasive alien species and from overharvesting for food or the aquarium trade. Threats to freshwater decapods are highest for species that have a narrow distribution, that are semi-terrestrial air breathers which live in specialized habitats (burrows, caves, karsts, phytotelms), or in highlands, or on islands.

Although the IUCN Red List has a relatively patchy coverage of invertebrate groups as a whole, freshwater decapods are well represented (Tables 15.3, 15.4). The results indicate high levels of extinction threats for the species in most groups of freshwater decapods (crayfish 32 %, freshwater crabs 31 %, freshwater shrimps 27 %), as well as for marine lobsters (27 %) and marine reef-building corals (33 %) (Collen et al. 2008; Cumberlidge et al. 2009; Richman et al. 2014; De Grave et al. 2014). Only 12 species (4 crayfish, 8 freshwater shrimps) out of the more than

Table 15.3 Groups on the IUCN Red List that have been assessed globally

Group	No. global assessments	Year assessed
Birds	5	1988, 1994, 2000, 2004, 2008
Mammals	2	1996, 2008
Amphibians	2	1980, 2004
Reef-building corals	2	1996, 2008
Freshwater crabs	1	2009
Crayfishes	1	2010
Freshwater shrimps	1	2013
Aeglids	1	2016
Marine lobsters	1	2013
Octopuses	1	2014
Gymnosperms (cycads, conifers), mangroves, sea grasses	1	2015
Angelfish, billfishes, tunas, wrasses, butterfly fish, groupers, sharks, rays	1	2015
Crocodilians, marine turtles, sea snakes	1	2015

Table 15.4 IUCN Red List taxonomic coverage at the end of 2015

	No. species described	No. species red listed	Percent assessed (%)
All species	1.9 million	74,106	3.9
Vertebrates	62,000	37,927	61.0
Invertebrates	1.4 million	16,741	1.2

3,000 species of decapods on the IUCN Red List are known to be extinct (Tables 15.5 and 15.6).

The conservation of freshwater decapods requires that the IUCN Red List be updated at least every 10 years, and more frequently if possible, because sharp declines need to be detected and appropriate conservation action plans devised. The process of assessment is very labor intensive, however, because IUCN Red List

Table 15.5 Extinct organisms on IUCN Red List

2015	Extinct species	Total species by group
Extinct vertebrates	354	62,000
Extinct plants	134	300,000
Extinct invertebrates	409	1.4 million
Molluscs	324	85,000
Insects	58	1 million
Crustaceans	12	47,000
Arachnids	9	45,000
Annelids	1	10,000
Total extinctions	897	Extinction rate 3000/year (8/day)

Table 15.6 Extinct species of freshwater decapods and non-decapod freshwater shrimp

Extinct crayfish	Common name	Country
Cambarellus alvarezi		Mexico
Cambarellus chihuahuae	Chihuahua dwarf crayfish	Mexico
Pacifastacus nigrescens	Sooty crayfish	USA
Procambarus angustatus	Sandhills crayfish	USA
Extinct freshwater shrimp	**Common name**	**Country**
Syncaris pasadenae	Pasadena freshwater shrimp	USA
Afrocyclops pauliani	(Cyclopoida, Cyclopidae)	Madagascar
Austrogammarus australis (CR or EX)	Dandenong freshwater amphipod	Australia
Dexteria floridana	Florida fairy shrimp	USA
Namibocypris costata	(Ostracoda, Candonidae)	Namibia
Stygobromus lucifugus	Rubious cave amphipod	USA
Tropodiaptomus ctenopus	(Calanoida, Diaptomidae)	Madagascar
Liocypris grandis (EX or CR)	(Ostracoda. Cyprididae)	South Africa

protocols require that a great deal of basic biological information be collected on population levels and trends over time, as well as on habitat requirements, distributional ranges, and immediate and long term threats to the continued existence of a species.

15.3 Extinction of Freshwater Decapods

The IUCN Red List is the international gold standard for species threatened with extinction, and this plus thoughtful estimates of future trends, has led to the realization that there is now a biodiversity crisis, and that extinction rates are escalating. Estimates of the current extinction rate are alarming—we could be losing 3000 species a year (8 species every day), which is 100–1000 times faster than the 'natural' background extinction rate (Table 15.5). However, this high extinction rate is not reflected in the IUCN Red List because the protocols used for conservation assessments set the bar high for demonstrating that a species is actually extinct. For example, a species is probably extinct if surveys of its known habitat, at appropriate times, throughout its historic range, all fail to record any individuals, and it has not been encountered for the last 60 years. Of the 897 species on the IUCN Red List that are extinct, most (409) are invertebrates, followed by vertebrates (354), and plants (134). Invertebrates also make up the highest number of estimated (as yet undocumented) extinctions (Table 15.5). The extinction of large numbers of species of invertebrates is likely to disrupt the normal functioning of most on the world's ecosystems, with catastrophic impacts on human wellbeing. The leading conservationist E. O. Wilson wrote in 1987 that "If human beings were to disappear tomorrow, the world would go on with little change…. But if invertebrates were to disappear, I doubt that the human species could last more than a few months".

15.4 Conservation Actions

The Convention on Biological Diversity (2011–2020) established a number of targets to achieve by 2020 that included the conservation of 17 % of terrestrial and inland water areas and 10 % of marine and coastal areas (Aichi Target 11), and the prevention of the extinction of known threatened species and the improvement of their conservation status (Aichi Target 12). The data compiled by the IUCN Red List can provide a means of measuring whether these targets have been achieved.

The IUCN Red List identifies species that are threatened with extinction and has formalized the steps needed to implement conservation strategies aimed at saving species threatened with extinction. These steps bring together all of the stakeholders needed to develop a status review, vision, goals, objectives, and the actions to be taken to accomplish the objectives. The biological data that need to be collected in order to achieve conservation actions include biological inventories, distribution data (EOO & AOO), population monitoring, niche preferences, and threat identification. To be successful, conservation actions must inform the public and policymakers at all levels via education messages designed to raise awareness of the numbers of threatened freshwater invertebrates and the stresses on the habitats on which they depend, and of the benefits of invertebrate conservation and the high value of the ecosystem services that intact natural habitats provide. Ecosystems provide substantial benefits for species and people including provisioning services (that sustain human livelihoods), supporting and regulating services (that provide drinking water, hydroelectricity generation, transportation, pollutant removal), and cultural services (Cardoso et al. 2011).

Other approaches conservationists should take include promoting freshwater decapods as flagship species for the conservation of freshwater species and their threatened habitats. Flagship species should be selected for characteristics such as their massive size, their striking colors, their charismatic behavior, their key role in maintaining freshwater ecosystem health, and their sensitivity to detrimental environmental changes.

The development of new technological approaches to conservation is very promising, such as those outlined in Chap. 12 of this volume that propose the use of genetically engineered physiological measures to control invasive species that are threats to endangered species, and Chap. 13 of this volume that propose using quantitative habit models for the conservation of endangered European crayfish. Nearly all threats to freshwater decapods are anthropogenic in origin and the list includes climate change, competition from alien species, habitat disturbance from logging and agriculture, over harvesting, and pollution. Clearly, the conservation of freshwater decapods requires interventions that protect species from these threats. These in turn require educational outreach to the public and policymakers on all aspects, from the number of species threatened with extinction (IUCN Red List), to the detailed causes of species endangerment (Chap. 13 of this volume). Education is especially important for the younger generation, because conservationists need to implement long-term action plans that will take years to succeed (Goto and Kawai 2012).

It is conceded that it is unlikely that we will not be able to know the conservation status of all 1.9 million species that have already been described in the short time frame set by the increasing rates of species decline and extinction. However, it is possible to assess a representative sample of all biodiversity on Earth, selected to provide an estimate of the true numbers of species that are currently threatened with extinction le. The target for the representative number of species that would still need to be assessed is estimated to be 160,000 species (or 4 % of the total described diversity), and the shortfall between this target and the present level of knowledge (74,106 species assessed) is an additional 85,894 species that would need to be assessed. Stuart et al. (2010) estimated the cost of meeting the internationally agreed target for species conservation globally as being about US$60 million. An additional 28,563 species of invertebrates would need to be assessed to meet the target for a representative sample of the 1.4 million species of described invertebrates (45,344 species, 3.3 %) at an estimated cost of US$20 million. These targets can only be met if the resources the necessary taxonomic expertise were available.

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Index

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