

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.

Wakkanai, Japan
Marquette, USA
May 2016

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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 (Aeglididae) 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 potamidids 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

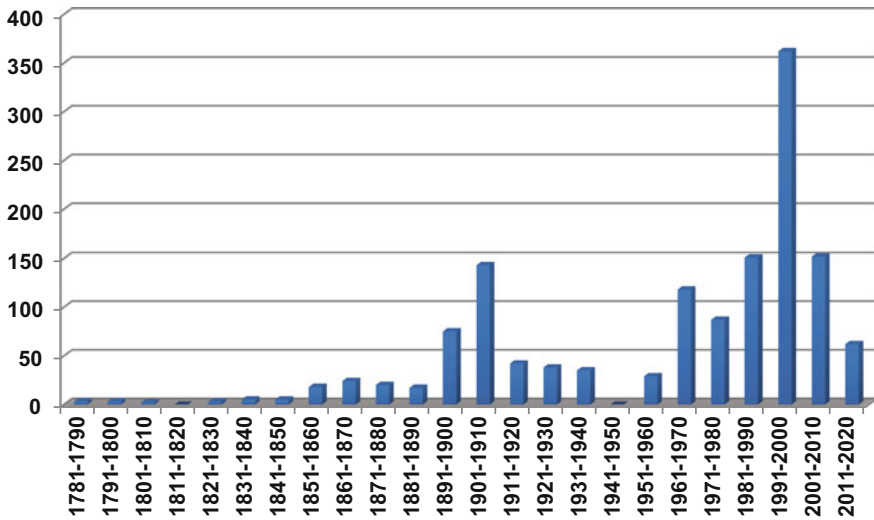


Fig. 1.1 Record of the number of species of freshwater crabs described per decade around the world from 1783 until the present day (*vertical axis*). All five families of primary brachyuran freshwater crabs are included. The *horizontal axis* shows time in ten-year blocks beginning with the discovery 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/km²) 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 Palearctic, 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 depressus* (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 sesarimid 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 habitats (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 (Cumberlidge 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 phytotelm. 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