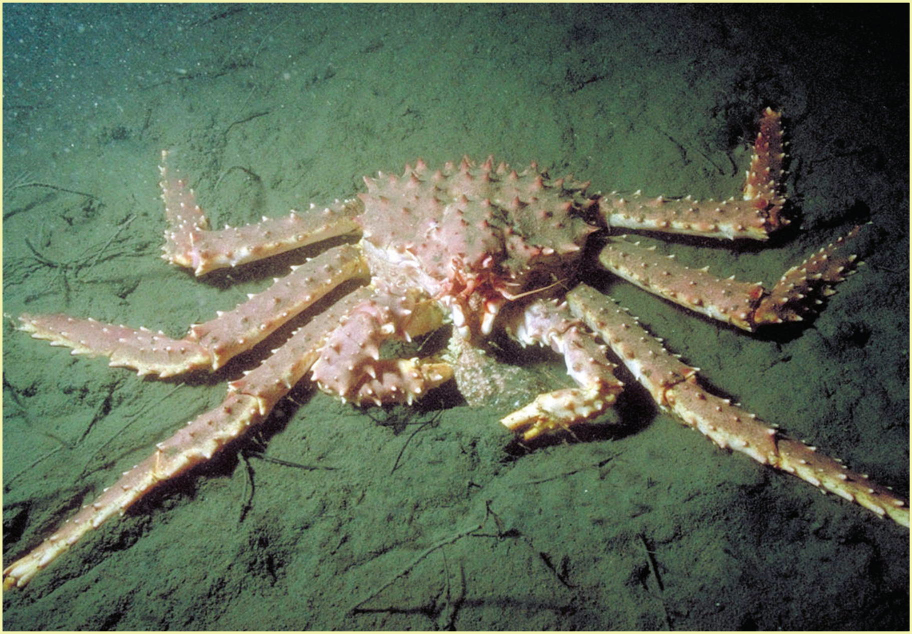
KING CRABS of the WORLD

Biology and Fisheries Management



Edited by

BRADLEY G. STEVENS

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This book is dedicated to

Guy Powell (Alaska Department of Fish and Game, retired), a pioneer of king crab research, and

Jiro Kittaka (Kitasato University, retired), who inspired a new generation of king crab scientists.

Contents

Preface: The King of Crabs

The king crab is truly the king of crabs. In terms of size, it is the largest crab that we routinely catch and eat, and in terms of value, it commands the highest price of any crab in the global marketplace. The throne on which it rests is augmented by the public interest in television shows such as *Deadliest Catch*, whose captains and crews have become the twenty-first-century equivalent of the American cowboy—iconic, independent, and isolated practitioners of a difficult and sometimes deadly undertaking that pits man against nature in a head-on, winner-take-all contest of will and endurance, fitting for the favor of a king.

Despite its lofty status, one might still ask: What, exactly, is a king crab? The question sparks a continuous debate, as described by Patsy McLaughlin in Chapter 2, and is nested within the encompassing question: What, exactly, is a crab? Though we might think we know crab and king crab on sight, our first impressions may be misleading and are qualified by many caveats. Let us start with the name—many morphologically similar crustaceans go by similar names, including the unfortunately mislabeled "Puget Sound king crab" *Lopholithodes mandti*, whose closest relative is the brown box crab *Lopholithodes foraminatus*. Related, yes, but not quite a king crab. From another perspective, if all species within the brachyura are deemed *short-tailed* crabs, then are all anomurans necessarily crabs also? It would only be fair. However, that group includes other presumably closely related organisms such as the galatheids, which go by names such as *red crab* and *squat lobster*, the mole crabs (family Hippidae), as well as all of the hermit crabs (families Diogenidae, Coenobitidae, Paguridae, Parapaguridae, and Pylochelidae). Any group of decapods that includes crabs, lobsters, moles, and hermits is truly confusing and challenges our sense of systematic orderliness.

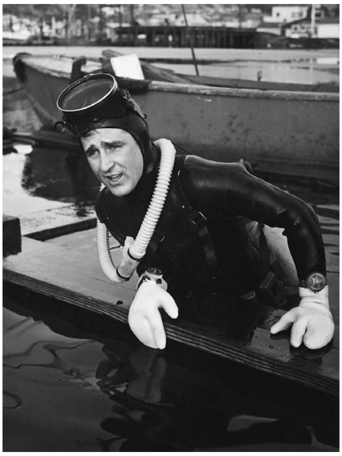
Therefore, within the context of this book, we will try to limit our definition of *king crabs* first to a particular family (the Lithodidae), and within that, to two genera containing species of commercial importance, *Lithodes* and *Paralithodes*. In doing so, we exclude several genera that are commonly not considered to be king crabs, including *Phyllolithodes*, *Rhinolithodes*, *Sculptolithodes*, *Glyptolithodes*, *Cryptolithodes*, and *Lopholithodes*, along with *Neolithodes*, which could arguably be considered a king crab by virtue of its familial resemblance, but we give passing reference to the genus *Paralomis*, which, although distinctly morphologically different, has potential as a commercially valuable species, despite its deep, remote habitat and lack of public familiarity. Fortunately, the latter genus has not yet gained acceptance in the marketplace, which would require a user-friendly common name—as a purist, I would propose something catchy and distinct like *spiny crab* but would probably be shoved aside by market forces wielding a more familiar sounding name like *Antarctic king crab*—that would throw the whole arrangement into disarray, and our reasoning likewise.

How else can we define king crabs? They are crabs whose genera and species are distributed in the polar regions of the world, as shown by Stevens and Lovrich in Chapter 1. Although their phylogeny is contentious, different authors having suggested that either they evolved from hermit-crab-like ancestors or vice versa, all king crab species have distinct developmental and systematic relationships (see McLaughlin, Chapter 2). North Pacific king crabs have unique and identifiable genomes that bear witness to postglacial recolonization (Grant et al., Chapter 3); they also have a particular body shape with asymmetric and cryptic appendages (Donaldson and Byersdorfer, Chapter 4). Most species of king crab undergo a similar series of developmental stages both within the egg case (Stevens, Chapter 7) and after one of the most extended hatching periods of any crab known. Species of the genera *Lithodes* and *Paralithodes* have distinctive larval forms and biology (Stevens, Chapter 8), whether feeding or not. Juvenile king crabs have specific growth patterns (Stevens and Jewett, Chapter 11) and are dependent on structurally complex habitats for settlement (Stevens, Chapter 9). Adults have relatively simple reproductive strategies but complex mating relationships (Webb, Chapter 10). King crabs have pathologies that are both unique and common to other crabs (Morado et al., Chapter 6). King crab fisheries have a typical history of exploitation (Otto, Chapter 5), encompassing regulations and management that are based on well-developed models of life history (Zheng and Kruse, Chapter 17). King crab populations are subject to the vagaries of nature via oceanographic effects on recruitment (Loher, Chapter 18). King crabs are caught, discarded, recaptured, and subject to a variety of mortality and bycatch issues (Stevens, Chapter 12). They have relatives at the antipodes that are both similar and different in life history (Lovrich and Tapella, Chapter 14). Red king crabs are both an introduced and an invasive species and the source of major fisheries (Sundet, Chapter 15). Their exoskeletons are host to many particular epibiota (Dvoretsky and Dvoretsky, Chapter 16). Depleted populations of king crabs are now the subject of intensive research on cultivation and enhancement (Stevens et al., Chapter 13).

So, what is a king crab? It is what we call it, and that can change as we will. Until then, it is still the king of crabs.

Acknowledgments

The creation of this book was one of the most difficult tasks I have ever undertaken. Writing, editing, coercing authors and reviewers, and dealing with the myriad details necessary to complete it occupied major portions of my life for over two years. I am indebted to all the authors, reviewers, and providers of miscellaneous material that contributed to its completion. All of these are named in the individual chapter acknowledgments, so I will not repeat them here. Mostly I am happy to have engaged the thoughts and memories of the most influential scientists who have ever studied king crabs. Many of them will soon retire, or have already done so, and their knowledge would be lost were it not encapsulated in this tome. The knowledge of that ensuing eventuality was a primary motivation behind this project. I only wish I had started earlier in order to include a few other authors who are no longer available or interested. I owe a great deal of thanks to my production editor Christine Selvan, and many others at CRC Press, for their encouragement, enthusiasm, and attention to detail. They caught many errors that evaded myself and other authors.



Finally, I wish to dedicate this book to two persons who have been extremely influential in the world of king crabs. Guy Powell spent most of his professional career studying king crabs in Kodiak, Alaska, and authored or coauthored many early publications on all aspects of king crab biology. In Kodiak, he was known as “Mr. King Crab” for many years, and he still lives there in retirement. Although my career in *king-crabology* began as his was ending, his shadow looms large. Guy generously made his extensive collection of underwater photographs available to me, and I regret that I could only include a few of them in this book.

The second dedication goes to Dr. Jiro Kittaka. Although he is less well known in the king crab community, he was a great influence to me personally. Most of Kittaka-sensei’s career was dedicated to the study of shrimp and lobster aquaculture at Tokyo Science University (now defunct), but in 1994 he began working in Nemuro, Hokkaido, on king crab cultivation. In 1995–1996, I spent a year working in his laboratory learning king crab cultivation techniques. His patience, knowledge, wisdom, and gentle guidance helped me to develop the skills needed to bring king crab aquaculture to the United States, changing my career entirely and providing the seeds for expansive growth of this research field. His mentorship enabled me to transfer his knowledge and skills to a new location (Alaska) and a new generation of younger scientists (e.g., Ben Daly, Celeste LeRoux, Sara Persselin, Jodi Pirtle, Kathy Swiney, Jim Swingle, and others), who are now leading the way. In a generational sense, Kittaka-san is the godfather of king crab cultivation. (Jiro Kittaka died in 2013 as this volume was being completed.)

To these, and many other advisors and mentors that I have met along the path, I say thank you; you have given us great shoulders on which to stand.

Bradley G. Stevens
Princess Anne, Maryland

Editor

Dr. Bradley G. Stevens received his PhD in fisheries science from the University of Washington School of Fisheries (now known as the School of Aquatic and Fisheries Sciences) in 1982. From 1984 to 2006, he worked for the National Marine Fisheries Service in Kodiak, Alaska, where he studied ecology and reproductive biology of commercial crab species, including king, Tanner, and snow crabs. In Alaska, he pioneered the use of submersibles and remotely operated vehicles (ROVs) for the study of crab ecology and behavior. In 1996, he spent a year in Japan studying aquaculture of king crabs, and after returning to Alaska, he began research on aquaculture and stock enhancement of red and blue king crabs; this research program eventually became the Alaska King Crab Research Rehabilitation and Biology Program sponsored by the University of Alaska Sea Grant Program. He left Alaska in 2006 to become an associate professor at the University of Massachusetts Dartmouth, where he studied the impact of epizootic shell disease on American lobsters. In 2009, he accepted a position as professor of marine science at the University of Maryland Eastern Shore, where he now serves as distinguished research scientist for the NOAA-funded Living Marine Resources Cooperative Science Center.

Dr. Stevens' research interests are the ecology and early life history of crustaceans and molluscs, with an emphasis on reproductive biology and postlarval processes. He has authored or coauthored over 50 peer-reviewed articles as well as numerous conference and technical reports on the subjects of ecology, behavior, reproductive biology, and fishery impacts on decapod crustaceans. He often uses in situ technology such as submersibles and ROVs and has built six video camera sleds for undersea research. He led two cruises to explore Gulf of Alaska seamounts with the submersible *Alvin* in 1999 and 2002. In 2003–2004, he discovered and surveyed the wreck of the Russian Barque Kad'yak, which sank in 1860; it is the only shipwreck from the Russian colonial period ever found and the oldest known wreck site in Alaska. When not working, he spends as much time as possible sailing, kayaking, or fishing.

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Overview of This Book

Bradley G. Stevens

This book can be divided roughly into three parts: Chapters 1 through 6 are largely descriptive of king crabs and their place in the physical world; Chapters 7 through 11 describe the life history and biology of various king crab species; and Chapters 12 through 18 discuss human and environmental interactions with king crabs through fisheries, management, and ecosystems.

We start our exploration of the world of king crabs from a global perspective in order to address the questions: What are king crabs, and where do they occur on planet Earth? In Chapter 1, Bradley Stevens and Gustavo Lovrich provide an introduction to the primary objects of this book, those species of king crabs for which there have been directed commercial fisheries. For six of those species, general descriptions are provided, and their geographic distribution, depth, and temperature ranges are described, along with maps of their known habitat. Several additional species are discussed that are either widely distributed or often observed but for which comprehensive biological or geographic information is unavailable.

In Chapter 2, the late Pat McLaughlin addresses the issue of where king crabs fit into our systematic structure of life. In doing so, she describes the intricate phylogenetic relationships between crabs of the family Lithodidae, including the king and hermit crabs. Always known for her lively and sometimes controversial work, she addresses the question of king crab evolution in a typically direct manner: Did the king arise from a hermit, or vice versa? This chapter, written just before she died, summarizes much of the output from her later years and can be rightly considered a capstone of her highly influential career.

We next ask the question: Where did king crabs come from, and how did they get to where they are now? In Chapter 3, William Stewart Grant, Daria A. Zelenina, and Nikolai S. Mugue address the more recent evolutionary history of red king crabs in the North Pacific. Using molecular techniques to unlock the secrets of their past history, they lead us to a new understanding of the phylogeography of the species and show that populations that appear to be close neighbors are actually quite distantly related.

Now, we look more closely at the organism and its structure. In Chapter 4, Bill Donaldson and Susie Byersdorfer describe the internal and external anatomy of king crabs with highly informative figures. These should enable any scientist, student, or fisher to easily identify the crab and its parts from their descriptions. These serve as a basis for all later chapters by defining correct terminology and vocabulary in order to facilitate a language of common understanding.

At this point, we step back from our close-up inspection with a historical account of the development of North Pacific king crab fisheries. Chapter 5 was written by Bob Otto, a scientist who studied and worked with king crabs for three decades and whose personal experience gives him a perspective that few other scientists can claim. His description of the boom and bust years of the Alaskan king crab fishery sets the stage for later discussions of these historical fluctuations. Though this chapter may seem out of order at first, many following chapters refer back to it with discussions of potential causative factors.

Continuing our descriptive study of king crabs, we drill down to cellular and suborganismal levels. In Chapter 6, authors Frank Morado, Christie Shavey, Tatyana Ryazanova, and Vanessa C. White provide a comprehensive overview of the diseases, parasites, symbionts, epibionts, and other anomalies of king crabs and their kin. The pathology caused by each member of this rogue's gallery is presented with a goal of understanding what impacts they may have had on king crab populations, but none appear to be a major source of mortality for any king crab population.

Chapter 7 begins our study of the life history and biology of king crabs. In this chapter, Bradley Stevens describes the embryonic development of king crabs and the effects of various environmental factors on development. These have direct consequences for the impacts of climate change, and are also useful for manipulating development for aquaculture or stock enhancement. King crabs have the longest embryonic development of any known crustacean, and the adaptive and evolutionary consequences of this take up the latter part of the chapter.

Chapter 8 discusses the next phase in king crab life history, the development and biology of larvae. Research on this subject began almost a century ago, and it is probably the most well-studied aspect of king crab biology, but we still have much to learn. Descriptions of larval stages are just detailed enough to distinguish the species without including the exhaustive detail of the original publications.

Chapter 9 deals with the ecology and biology of the juvenile stages. Following some early field studies on distribution, this area was largely neglected for many years. In the last decade, however, a new generation of scientists has made great inroads into the behavior and ecology of postlarval and postsettlement stages. Consequently, this chapter was updated constantly as new research was published, and it may become rapidly outdated.

In Chapter 10, Joel Webb discusses reproductive strategies of seven fished species of king crabs. Despite the presence of many conservative features, lifetime reproductive output can vary by two orders of magnitude among those species. His comparative approach illustrates many other remarkable similarities and differences, and how king crabs have adapted to their habitat with ontogenetic and seasonal migrations to facilitate reproductive success.

Chapter 11 by Bradley Stevens and Steve Jewett combines the topics of growth and feeding, which are inextricably related, with trophic ecology in general, including predation on king crabs. King crabs may be generalist predators, but their feeding has significant ecological impacts, as demonstrated in Norway where king crabs are an invasive species. And contrary to popular opinion, predation by Pacific cod *Gadus macrocephalus* probably has only a minor impact on king crab populations.

Chapter 12 begins the final portion of the book with a discussion of the impacts of fishing on king crabs, including bycatch, handling, and discard mortality. Although bycatch-related mortality has been named as a potential factor in crab population declines, it has been devilishly difficult to estimate, and despite some exceptional situations, probably represents only a small fraction of overall king crab mortality. Nonetheless, many efforts have been made to reduce or mitigate bycatch, and a whole industry has developed to observe and measure it.

Chapter 13 addresses king crab aquaculture and stock enhancement, which probably represents the epitome of human–crab interaction and manipulation. This chapter was written by an international team of contributors, including Bradley Stevens, Anya Dunham, Jiro Kittaka, Nikolina Kovatcheva, Sara Persselin, and Gro van der Meeren. After a slow start, renewed interest by American and Russian scientists since 2000 spawned a flurry of research to develop cultivation methods. This effort has produced more publications on the biology of king crab larvae and juveniles in the last decade than at in any previous time. Nonetheless, successful stock enhancement of king crabs is still far in the future.

In Chapter 14, Gustavo A. Lovrich and Federico Tapella discuss the biology of the southern king crab, *Lithodes santolla*, and other related lithodids in Southern Hemisphere waters, including various species of *Paralomis*. Though both types of crab support relatively small fisheries, they are important within their local economies and provide stimulating contrast to the biology of Northern Hemisphere king crabs. In addition, expansion of lithodid crab populations into Antarctica brings king crabs to the forefront of research on the impacts of global warming.

In Chapter 15, Jan Sundet looks at Barents Sea king crabs from an entirely different perspective. This population not only has the characteristics and consequences of an invasive species, but during the early years of its establishment it exhibited the characteristics of an unfished *virgin stock* as well. Those traits make this population unique and have led to the creation of two radically different management approaches; in the east, it is managed with quotas to ensure sustainability, whereas in the west, a free-for-all fishery was created with the singular intention of eradicating it.

Chapter 16, coauthored by Vladimir and Alexander Dvoretsky, discusses the king crab in Russia, including both the natural Pacific coast population and the introduced Barents Sea population. The second half of the chapter discusses epibiotic fouling of king crabs, a topic that is applicable to king crabs around the world.

We now leave the physical and biological world of king crabs and enter the digital world. In Chapter 17, Jie Zheng and Gordon Kruse discuss the assessment and management of king crab populations in Alaska.

Both authors have been instrumental in developing population assessments using length-based models, which helped bring king crab management from an era of *guesstimation* to one based on solid scientific principles and data.

Finally, we pull our perspective back to an ecosystem scale. In Chapter 18, Tim Loher discusses fisheries oceanography and the impacts of crab behavior, fishing, and current patterns on larval dispersal and recruitment. Though last in order, this topic synthesizes many previously discussed aspects of king crab biology and thus is one of the most important chapters in the book.

The last chapter of the book is an epilogue containing the personal perspective of Bradley Stevens on the future of king crab research, populations, and fisheries.

1

King Crabs of the World: Species and Distributions

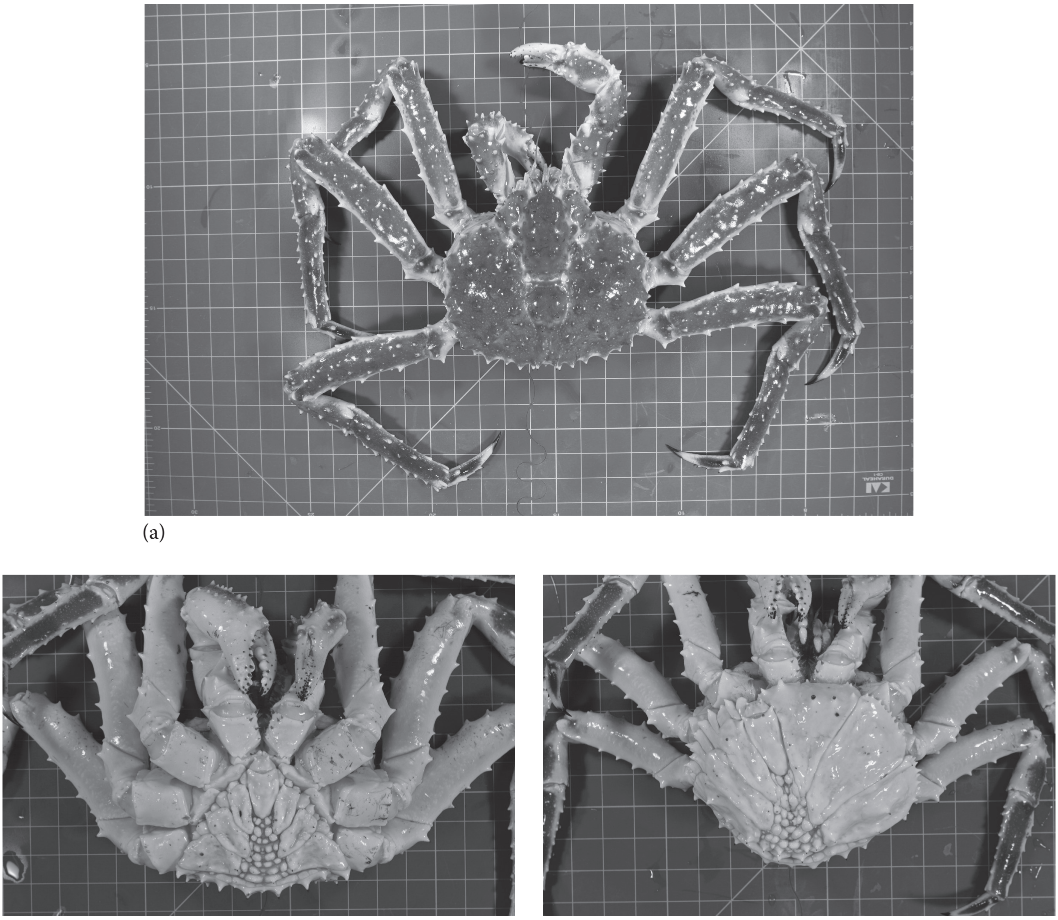
Bradley G. Stevens and Gustavo A. Lovrich

CONTENTS

1.1 Introduction

When used generically, or in relation to abundance, "king crab" typically brings to mind a single species, the red king crab (RKC) *Paralithodes camtschaticus* (Plate I). Historically and commercially, the name "king crab" has been applied to a number of species, including the blue king crab (BKC) *P. platypus*, the Hanasaki king crab *P. brevipes*, the golden and scarlet king crabs, *Lithodes aequispinus* and *L. couesi*, respectively, and the southern king crab *Lithodes santolla*. All of these belong to the family Lithodidae, subfamily Lithodinae, which included 79 species in 1985 (Dawson and Yaldwyn, 1985), but as of this publication includes 121 species in 10 genera, including *Lithodes* (29 species), *Paralithodes* (5 species), *Cryptolithodes* (3 species), *Paralomis* (66 species), *Lopholithodes* (2 species), *Neolithodes* (12 species), and *Phyllolithodes*, *Rhinolithodes*, *Sculptolithodes*, and *Glyptolithodes* with only 1 species each (McLaughlin, Chapter 2). The family originated in the North Pacific, where lithodid diversity is highest, and ~70% of known species occur (Zaklan, 2002). Lithodids underwent tropical submergence during their southward radiation along the Pacific coast of the Americas (Bouvier, 1896; Hall and Thatje, 2009b). Otto (Chapter 5) relates the historical usage of the term "king crab" within the seafood industry. For most of this book, we will concentrate on the six major commercial species within the genera *Paralithodes* and *Lithodes*, with occasional references to *Paralomis* spp. since they are of little commercial interest, tend to occupy deep water, and there is not enough biological information on them to support a dedicated treatise at this time.

A complete description of the various species of king crabs and keys to their identification can be found in Dawson and Yaldwyn (1985), and specific characteristics of the major king crab families are provided in McLaughlin (Chapter 2). Rather than including all of this previously published information,



(a)

(b)

(c)

PLATE I (See color insert.) Red king crab, *Paralithodes camtschaticus*: (a) male, dorsal view; (b) male, ventral view; and (c) female, ventral view. Grid spacing is 2.54 cm. (Photos by Brad Stevens.)

only that material relevant to the commercial species is included in the following text. King crabs can be identified by several major features (Dawson and Yaldwyn, 1985), including the following:

- Four apparent pairs of walking legs (including the chelipeds); the fifth pair is reduced in size and tucked up within the gill chambers.
- The first pair of legs (chelipeds) are unequal in size; in almost all cases, the right (“crusher”) chela is larger than the left (“cutter”), but exceptions occur (see later).
- Flattened “crab-like” appearance with triangular shape.
- A flattened abdomen that is only partially calcified and bent forward, without uropods; it is symmetrical in males and asymmetrical in females, curving to the right.
- The body and appendages are covered with sharp spines, requiring careful handling.
- Males lack pleopods, whereas females have four or five on the left side of the abdomen and one on the right.
- Antennae are external to the eyestalks, unlike those of true crabs (Brachyura).
- Adult crabs are generally large (>10 cm in carapace width [CW] or length [CL]) and do not live in mollusk shells (thus excluding hermit crabs and other small lithodids).

A more complete and detailed synopsis of the family Lithodidae is included in McLaughlin, Chapter 2. A comprehensive list of lithodid species distributions including latitudes, longitudes, depths, sizes, and life history traits can be found in Zaklan (2002), from which certain details have been cited. See Otto (Chapter 5) for a history of the fishery, crab abundance, and landings in the North Pacific. This chapter provides general descriptions and distributions of the most common species. Descriptions of king crabs in this chapter are meant to distinguish the principal species and may not be complete. A key to the four Alaskan species of king crabs is included in Donaldson and Byersdorfer (2005).

1.2 Red King Crab *Paralithodes camtschaticus* (Tilesius, 1815)

RKCs *Paralithodes camtschaticus* are one of the most widely distributed and best known of all king crabs, ranging from British Columbia north through the Bering Sea, and southwest to Korea. US fishermen targeted RKC around Kodiak Island since the 1940s. This species is what most people imagine when they think about king crabs.

RKCs are the largest of the king crabs. Historically, crabs with CLs exceeding 20 cm were common, though few crabs now exceed 17 cm. On a large crab, leg span could reach 1.8 m tip to tip (measured between the dactyls of the third longest pair of legs). The largest king crabs on record (in Alaska)* were a female weighing 4.8 kg (10.5 lb) and a male weighing 10.9 kg (24 lb). For comparison, the average size of male RKCs landed by the fishery in the eastern Bering Sea (EBS) today is about 2.9 kg (6.5 lb). The maximum recorded size of a male RKC was 22.7 cm measured front to back (CL), and 28.3 cm side to side (CW); maximum size for a female was 19.5 cm CL and 21.3 cm CW (Zaklan, 2002).

RKCs can be identified by their color, ranging from reddish brown to burgundy. Their shells are oval shaped. They have a short, slightly upcurved rostrum with a single point, a medial spine on top, and a pair of small dorsal spines near the base (though numbers of spinelets vary). The center of the carapace has anterior and posterior mounds defining the gastric and cardiac regions (see Donaldson and Byersdorfer, Chapter 4), which bear four and three pairs of small spines, respectively. Other spines are distributed across the carapace, which is bordered by 24–30 spines at intervals. Spines also cover the tops and sides of the legs and chelae. The ventral side of the crab is white and bears no spines, except for the last three segments of each leg, which are pigmented on the top and the bottom. Like all other king crabs, RKCs are asymmetrical, with the largest chela usually on the right side, and the largest abdominal plates (in females) on the left side. Occasionally, this asymmetry is reversed, resulting in left-handed ("southclaw") individuals, as observed in RKC (B. Stevens, pers. observ.), *Lithodes maja* (Zaklan, 2000), and *Lopholithodes foraminatus* (Duguid, 2010), and in extremely rare individuals, entire segments are missing (Stevens and Munk, 1990). In the genus *Paralithodes*, the first abdominal segment is mostly hidden beneath the carapace, but the second abdominal segment (the main one observed in posterior view) is divided into five plates, including a pair of marginals, a pair of laterals, and a median plate (Dawson and Yaldwyn, 1985).

The type specimen for RKC was collected off the Kamchatka Peninsula in 1812 and named *Lithodes camtschatica* (Tilesius, 1815); it was later determined that it belonged to the genus *Paralithodes*, and around 1990, the species name was corrected to *P. camtschaticus* in order to maintain Latin consistency. In the North Pacific Ocean, the distribution of RKC can be defined in three large regional groups (see Grant, Chapter 3), which roughly correspond with large marine ecosystems (LMEs) (Maps 1.1 and 1.2). Note that the original maps of RKC distribution used in this chapter were included in a large format Atlas of maps published by NOAA (NWAFC, 1990) and later converted to digital files; they have been modified slightly and extended to include the Western North Pacific. The southernmost group of RKC occupies the Gulf of Alaska (GOA) LME. RKCs exist throughout the fjords and channels of British Columbia and Southeast Alaska, where small fisheries exist. They have been captured as far south as Prince Rupert and Kitkatla Inlet, British Columbia, at approximately 54°N, and a few specimens were captured in Boundary Bay, British Columbia, in 1956, and near Bellingham, Washington, in 1960. It is likely, however, that crabs found at the latter two locations were accidental releases from aquaria or

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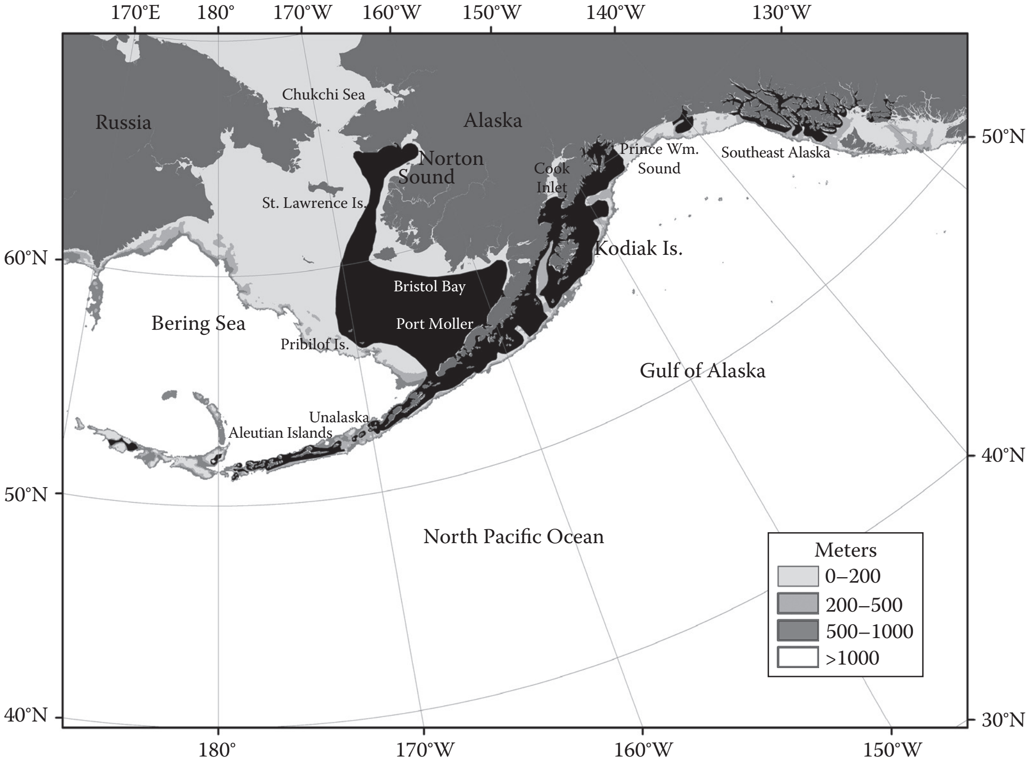
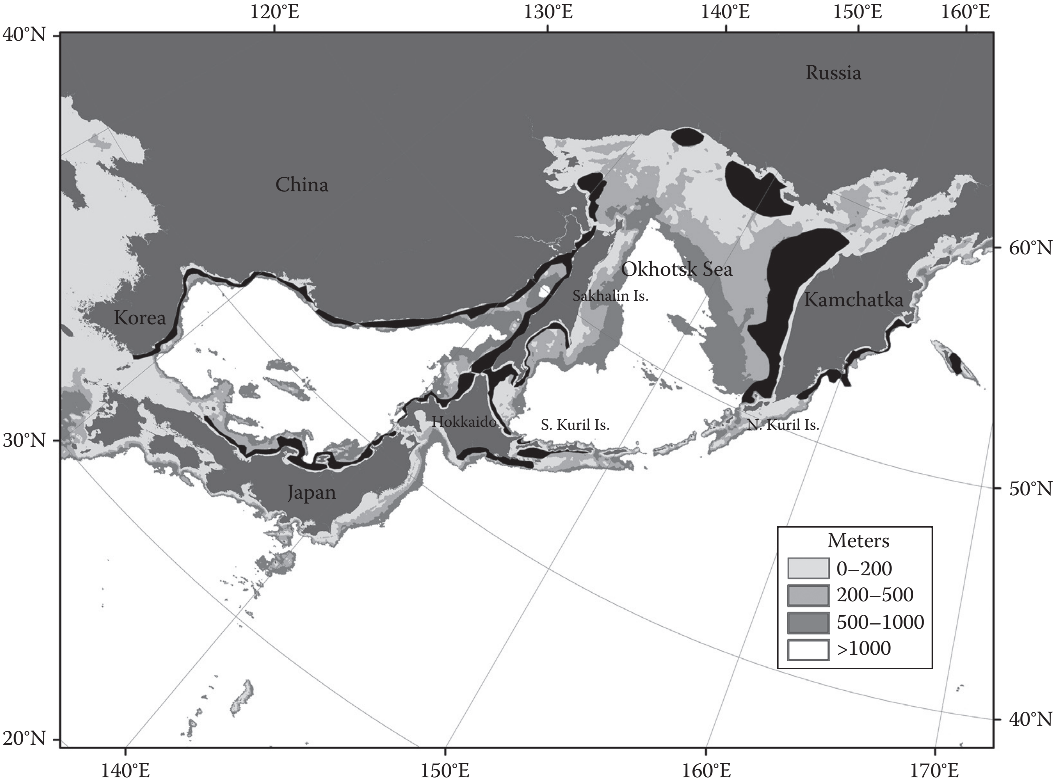
* http://www.adfg.alaska.gov/index.cfm?adfg=redkingcrab.main.



MAP 1.1 Distribution of red king crab *Paralithodes camtschaticus* in the eastern North Pacific Ocean and Bering Sea. All areas where crabs have been found are included. (Data from NWAFC, *West Coast of North America Strategic Assessment Data Atlas: Invertebrates and Fish*, Northwest and Alaska Fisheries Center, National Oceanic and Atmospheric Administration, Rockville, MD, 1990, p. 112.)

fishing boats (Butler and Hart, 1962). In the north of Juneau, Alaska, RKCs are loosely scattered along the narrow continental shelf, which serves as a geographic barrier between Southeast Alaska and the Southwest Alaskan fjords of Prince William Sound and Cook Inlet. Population density increases around the archipelago of Kodiak Island, where RKC was once extremely abundant in the bays and fjords of Chiniak Bay, Ugak Bay, and Alitak Bay. The second geographic group, occupying the EBS LME, occurs along the shelf and among the bays and islands on the south side of the Alaska Peninsula, and at lower densities in the bays of the easternmost Aleutian Islands (AIS), including Unalaska Island. RKCs reach their greatest abundance on the broad, shallow continental shelf of the EBS, where they range from Unimak Pass and the Port Moller region north to the Kvichak River in Bristol Bay. This group of RKC extends northwest of Bristol Bay as discontinuous, scattered individuals. One small population exists around St. Paul Island in the Pribilof Islands, and another slightly larger population exists in Norton Sound near Nome and King Island. These populations may be genetically distinct (see Grant, Chapter 3) and have different sizes at maturity, generally decreasing with increasing latitude, from Kodiak to Norton Sound (see Webb, Chapter 10). The third group (West Bering Sea LME) extends north from Norton Sound into the Chukchi Sea as scattered individuals (Natcher et al., 1996; Feder et al., 2005), southwest along the coast of Kamchatka, Russia, into the Sea of Okhotsk, where another large population exists, and southward along the Kuril Islands to Hokkaido in Northern Japan, and the east coast of Korea (Nakazawa, 1912). Abe (1992) indicated the presence of RKC along the western coasts of Sakhalin and Hokkaido, and isolated populations in the northern Sea of Okhotsk, separate from the West Kamchatka population, but his description was not detailed, so their exact distribution is unknown. In Map 1.2, the presence of RKC is shown out to the 200 m contour, although they probably do not occupy all of that range, and some may exist at greater depths.



MAP 1.2 Distribution of red king crab *Paralithodes camtschaticus* in the western North Pacific Ocean, Sea of Okhotsk, and Sea of Japan. All areas where crabs have been found are included. Distribution is shown out to the 200 m isobaths in those areas where it is present.

Although the native range of RKC extends only around the North Pacific, there is now a fourth population existing in the Barents Sea north of Murmansk, Russia, having been transplanted there in the 1960s (Orlov and Ivanov, 1978). This population has grown significantly since 1990 and now constitutes a large invasive population extending around and among the fjords of Finnmark in northern Norway. The ramifications of this growing population and newly established fishery are discussed by Sundet in Chapter 15, and its biological characteristics are discussed by Dvoretsky and Dvoretsky in Chapter 16.

Throughout their range, RKCs can be found from the intertidal region to the continental slope. Data from NOAA summer trawl surveys* for 1982–2011 show that RKC were captured in depths ranging from 9 to 460 m (Table 1.1); the following statistics were calculated using tow depths and are not weighted by catch numbers. Mean depths of tows where RKC were caught were 52 m in the EBS (Figure 1.1a), which is mostly shallow shelf; 123 m in the GOA, which includes shelf and slope stations; and 156 m in the Aleutian Islands–Bering Sea slope region (AIS), which mostly consists of deeper rocky slope stations. Over 95% of trawls with RKC occurred in <100 m of water (Figure 1.1c). In Kodiak, juveniles are rarely found in the intertidal (B. Stevens, pers. observ.), whereas in Juneau, Alaska, young of the year commonly occur under rocks in the intertidal (Tom Shirley, Univ. of Alaska, pers. commun.). RKCs were found in water temperatures ranging from −1.8°C to 12.8°C, with mean temperatures of 5.5°C in the GOA, 3.2°C in the EBS, and 4.4°C in the AIS (Table 1.2; Figure 1.1b). Note, however, that these data were collected in May–July, so may not represent the full range of occupied depths and temperatures.

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* http://www.afsc.noaa.gov/RACE/groundfish/survey_data/default.htm.

TABLE 1.1

Depth (m) Distribution of King Crabs in the GOA, EBS, and AIS Regions

Species	Region	n	Min	Max	Mean	sd
Red kings	GOA	50	31	360	122.9	87.6
	EBS	273	9	112	51.7	17.7
	AIS	111	73	461	155.8	75.1
Blue kings	EBS	1387	15	166	76.7	21.1
Golden kings	GOA	1206	73	1200	308.9	139.7
	EBS	19	123	201	158.4	17.7
	AIS	104	47	571	298.3	104.3
	Seamounts	103	152	931	485	187
Scarlet kings	GOA	16	119	954	669.1	218.2
	AIS	120	221	1200	793.2	207.9
	Seamounts	67	234	1633	681	254

Source: Data (except seamounts) from NOAA/NMFS Groundfish surveys, 1982–2011, http://www.afsc.noaa.gov/RACE/groundfish/survey_data/default.htm.

Note: Number of trawls with data indicated by n.

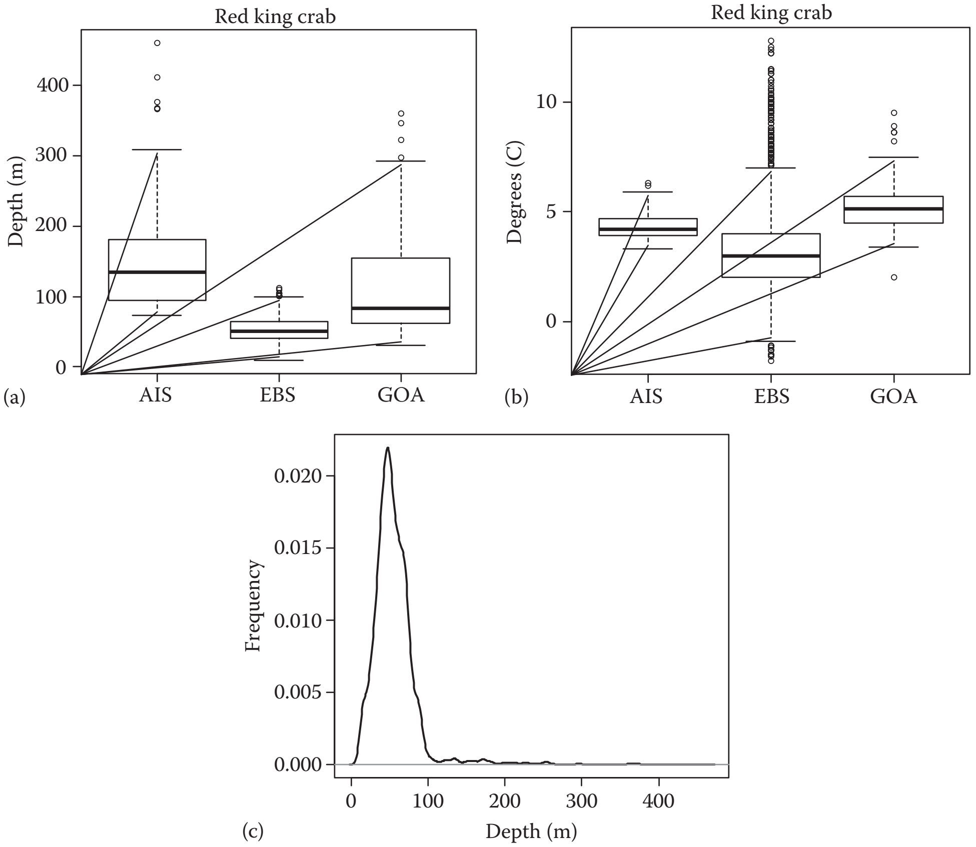


FIGURE 1.1 Depth and temperature distribution of red king crab *Paralithodes camtschaticus* in the AIS, EBS, and GOA. Boxplots of distribution by (a) depth and (b) temperature. Boxes enclose central 50% of data; horizontal line is median; vertical bars delimit observations within 1.5 box lengths, whereas circles represent data beyond that limit. (c) Frequency distribution of depth for all data.

TABLE 1.2

Temperature (°C) Distribution of King Crabs in the GOA, EBS, and AIS Regions

Species	Region	n	Min	Max	Mean	sd
Red kings	GOA	30	2	9.5	5.5	1.7
	EBS	2610	−1.8	12.8	3.2	1.9
	AIS	83	3.3	6.3	4.4	0.6
Blue kings	EBS	1297	−2.1	11.8	1.5	1.8
Golden kings	GOA	1086	2	5.8	3.9	0.4
	EBS	18	1.7	4.2	2.8	0.7
	AIS	91	3.8	6.2	4.8	0.6
	Seamounts	103			3.5	0.3
Scarlet kings	GOA	14	3.0	4.6	3.8	0.5
	AIS	116	2.3	4.3	3.1	0.3
	Seamounts	67			3.5	0.4

Source: Data (except seamounts) from NMFS surveys, 1982–2011.

1.3 Blue King Crab *Paralithodes platypus* (Brandt, 1850)

BKCs *Paralithodes platypus* are generally smaller than RKCs, and their color ranges from bluish brown to a distinct sky blue on the merus of the chelae (Plate II). They have a short single-point rostrum with two small spines on top, as opposed to the single spine of RKCs. The cardiac and gastric regions of the carapace each bear three and two pairs of spines, respectively (one pair less than RKCs in each region). Ten to twelve spines are distributed across the top of the carapace, and there is a distinct border consisting of about 30 spines spaced around the edge of the carapace like a crown. Spines also cover the tops and sides of the legs and chelae. Pigmentation on the ventral side is white, except for a few dark bands on the distal leg segments.

The distribution of BKC in the eastern North Pacific is limited to a few small, distinct populations in the EBS and GOA that are associated with islands or bays and fjords (Map 1.3). In the Bering Sea, one population extends from Norton Sound into the Bering Strait, around St. Lawrence Island, and into the northern Chukchi Sea (Natcher et al., 1996; Feder et al., 2005). Another, possibly separate, population exists around St. Matthew Island and the Pribilof Islands, and scattered individuals occur between these locations. BKCs at these two locations have slightly different characteristics and are currently managed as separate stocks, although there is no evidence of genetic dissimilarity, so they are shown as a single, large, contiguous population in Map 1.3. Small populations of BKC occur in Herendeen Bay on the north side of the Alaska Peninsula, and in Olga Bay on Kodiak Island, both of which are deep bays (>75 m) surrounded by relatively shallow shelf areas (<25 m). In Southeast Alaska, small populations exist in Russell Fjord, Glacier Bay, Endicott Arm, and Lynn Canal, near Juneau. In the Northwest Pacific (Eastern Hemisphere), BKCs are scattered from the Bering Straits southward along the Chukotsk Peninsula and through the Anadyr Gulf, are relatively common along the Koryak Coast and in Karaginsky Bay and Olyutorski Bay (Slizkin, 1974), along the Kamchatka Peninsula and into the Sea of Okhotsk, and are common among the Kuril Islands, around Sakhalin Island, and the northeastern parts of Hokkaido. Abe (1992) indicated the presence of BKC around the southeast coast of Hokkaido, among the Habomai Islands off the Nemuro Peninsula, and around the most Northern and Southern Kuril Islands, but not among the central Kuril Islands. Although Abe (1992) did not provide a detailed description, BKC may also be present along the northern coast of Hokkaido and southern Sakhalin Island. In Map 1.4, the presence of BKC is shown out to the 200 m contour, although they probably do not occupy all of that range, and some may exist at greater depths.

Although the distribution of BKC overlaps somewhat with that of RKC, they are usually not found immediately adjacent to each other. Somerton (1985) suggested that the disjunct distribution of BKCs represented relict populations that resulted from the contraction of a much larger population during

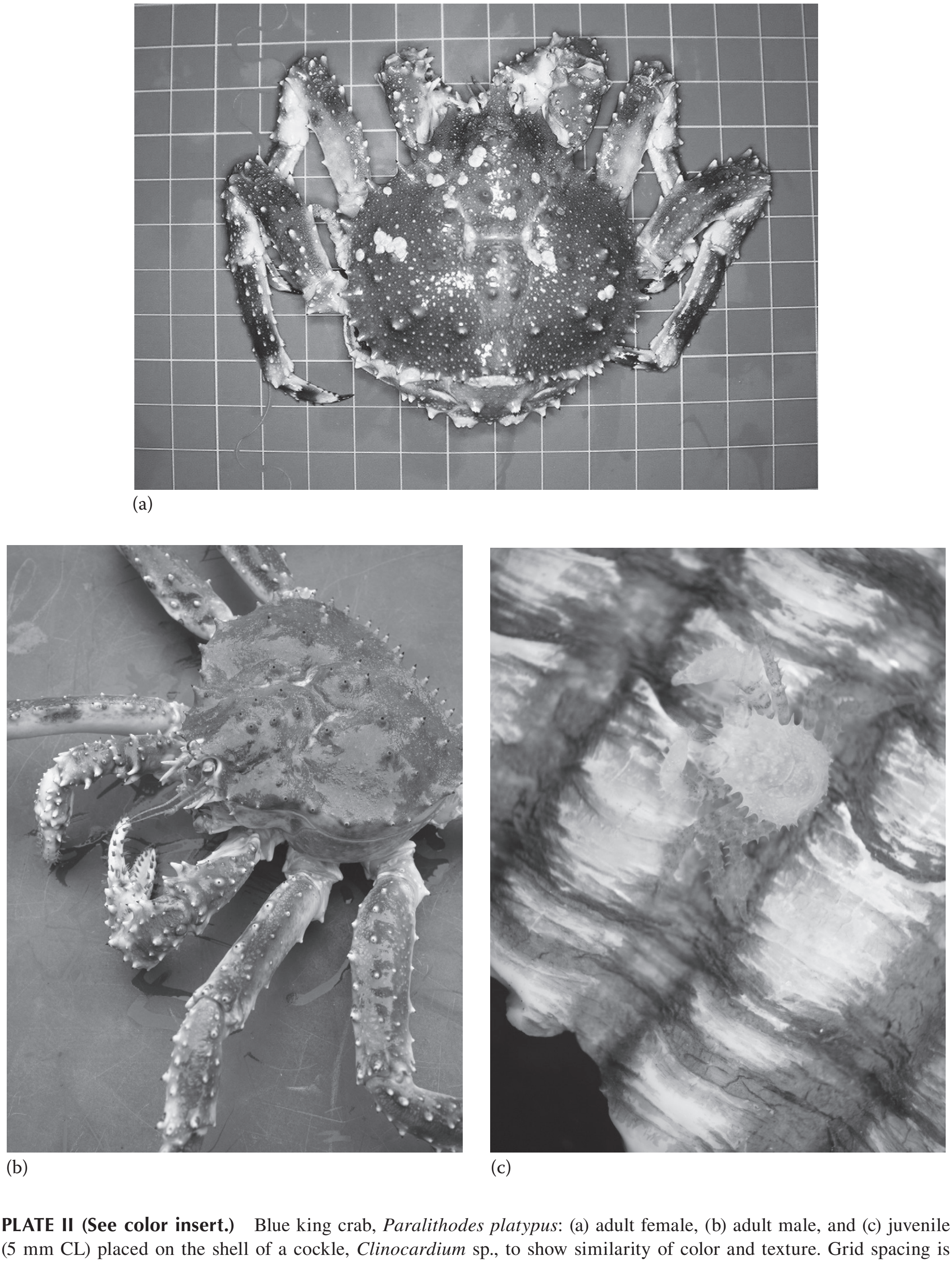
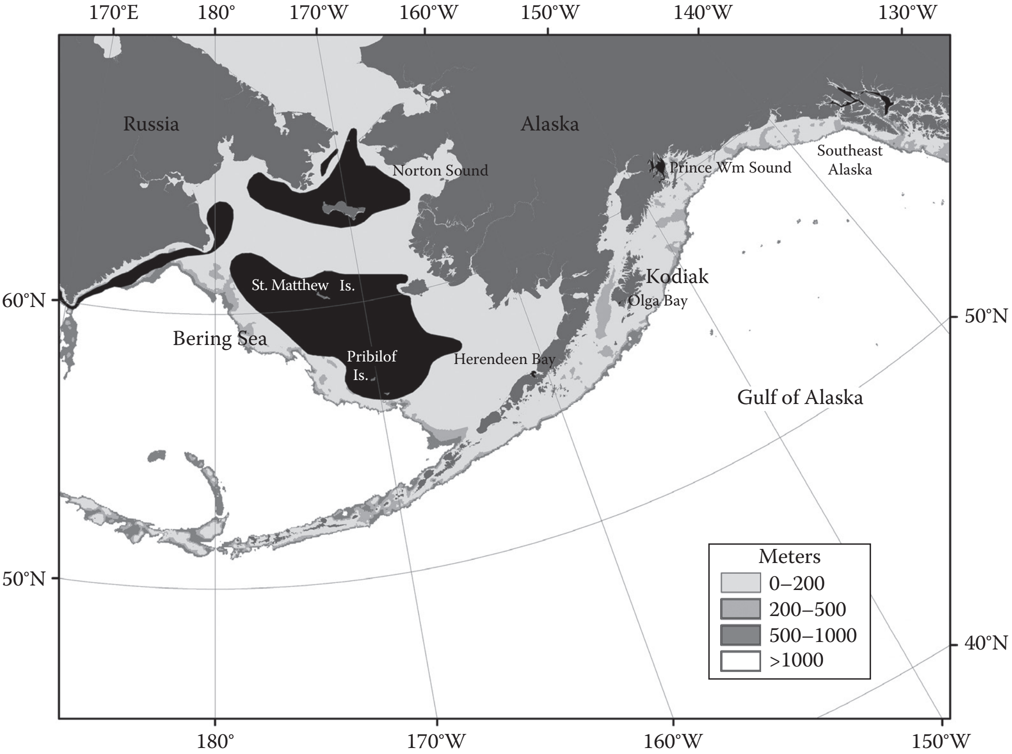


PLATE II (See color insert.) Blue king crab, *Paralithodes platypus*: (a) adult female, (b) adult male, and (c) juvenile (5 mm CL) placed on the shell of a cockle, *Clinocardium* sp., to show similarity of color and texture. Grid spacing is 2.54 cm. (Photos by Brad Stevens.)

glacial epochs. As the glaciers melted and temperatures warmed, RKC expanded their range, while BKC retreated into deeper, colder refuges. Somerton (1985) also suggested that the separation of RKC and BKC was most likely due to competitive exclusion of RKC from BKC habitat. In the EBS, BKCs tend to occupy waters that are deeper than those occupied by RKC (76 *vs.* 52 m, respectively) and colder (mean 1.5°C *vs.* 3.2°C, respectively) (Tables 1.1 and 1.2; Figure 1.2a and b). In the EBS, depths where BKCs were



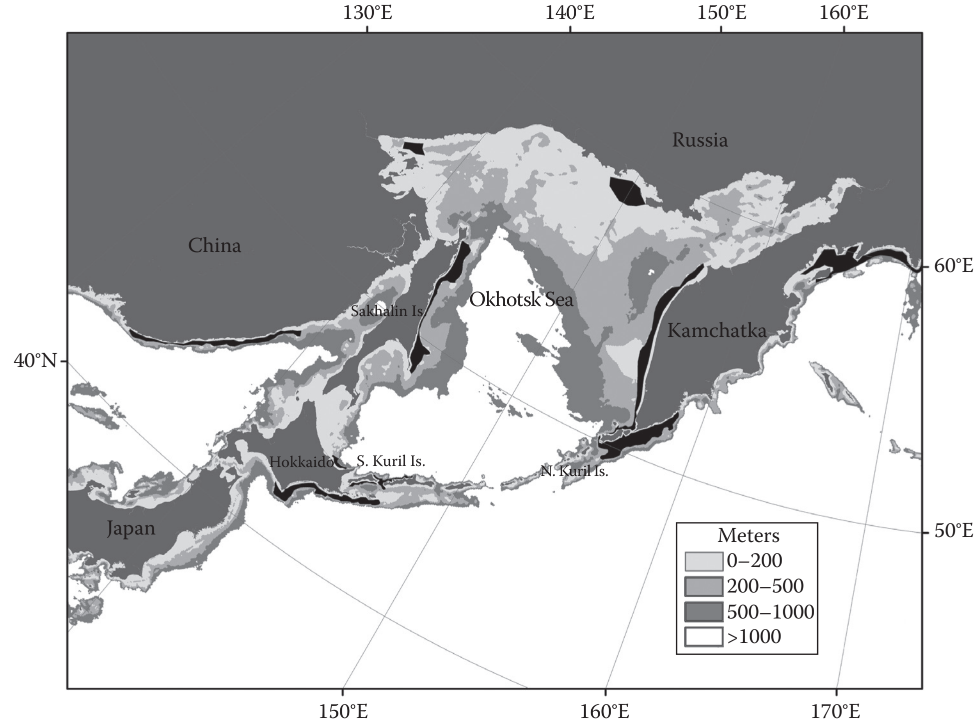
MAP 1.3 Distribution of blue king crab *Paralithodes platypus* in the eastern North Pacific Ocean and Bering Sea. All areas where crabs have been found are included. Note small pockets in Olga Bay, Herendeen Bay, and SE Alaska. Distribution is shown out to the 200 m isobath in those areas where it is present. (Data from NWAFC, *West Coast of North America Strategic Assessment Data Atlas: Invertebrates and Fish*, Northwest and Alaska Fisheries Center, National Oceanic and Atmospheric Administration, Rockville, MD, 1990, p. 112.)

found formed a bimodal distribution with peaks at 75 m (representing catches near the Pribilof Islands) and 100 m (representing catches near St. Matthew Is.; Figure 1.2c).

1.4 Golden King Crab *Lithodes aequispinus* (Benedict, 1895)

Golden king crabs (GKCs) *Lithodes aequispinus* are somewhat smaller than RKCs and BKCs (Plate IIIa). They are a uniform golden-brown all over (though shade varies from light to dark), and unlike RKCs and BKCs, their coloration extends to the ventral sides of the legs, so these can be distinguished even after cooking. They appear to be "spinier" than either RKCs or BKCs, having spines that are both larger and more numerous. The rostrum is bifurcate, unlike *Paralithodes* spp., and bears four lateral spines and two dorsal spines; in addition, it has a single, downward-pointing ventral spine (Butler and Hart, 1962). On top of the carapace, they have four and three pairs of major spines on their gastric and cardiac regions, respectively, plus additional spines between and around these. In the genus *Lithodes*, the second abdominal segment is either entire (i.e., intact as a single plate) or divided into three plates (Dawson and Yaldwyn, 1985). Diagrams of the rostrum and second abdominal segment, showing the difference between *Paralithodes* spp. and *Lithodes* spp., are included in Donaldson and Byersdorfer (2005).

GKCs range across the margins of the North Pacific from British Columbia to Japan (Maps 1.5 and 1.6). The southernmost records are of a few scattered individuals caught off of Vancouver Island, and in Queen Charlotte Sound, British Columbia (Jamieson and Sloan, 1985), but these are not included in Map 1.5. In Canada and Southeast Alaska, they occur in steep, narrow fjords including the Portland Inlet system



MAP 1.4 Distribution of blue king crab *Paralithodes platypus* in the western North Pacific Ocean, Sea of Okhotsk, and Kuril Islands. All areas where crabs have been found are included. Small populations in North and Northeast Okhotsk Sea are of unknown extent. Distribution is shown out to the 200 m isobath in those areas where it is present.

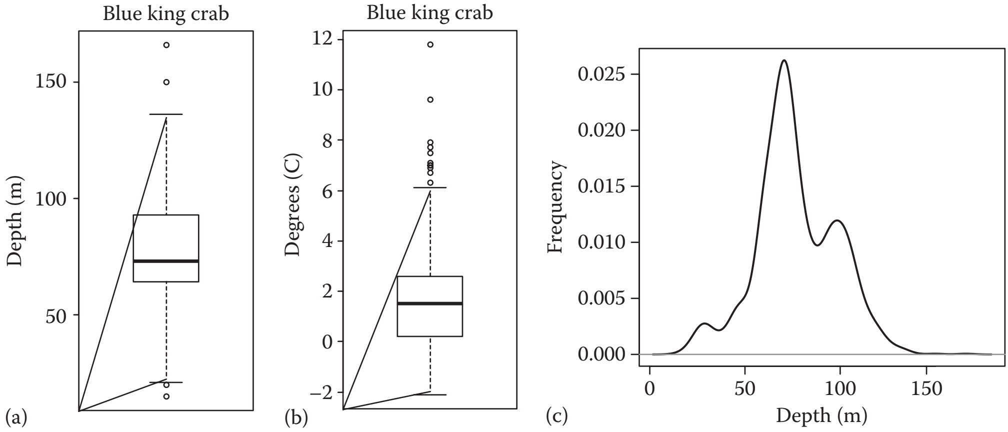


FIGURE 1.2 Depth and temperature distribution of blue king crab *Paralithodes platypus* in the EBS. Boxplots (as in Figure 1.1) of distribution by (a) depth and (b) temperature. (c) Frequency distribution of depth for all data.

at the border of Alaska and British Columbia (at 54° 40′N lat.) (Sloan, 1984; Jewett et al., 1985). They occur along the upper edge of the continental shelf slope through Shelikof Strait, the Shumagin Islands southwest of Kodiak, and into Prince William Sound*; GKCs are common along the Aleutian Islands and Bering Sea shelf slope near the Pribilof Islands (Somerton and Otto, 1986) and also occur on isolated seamounts in the GOA (Hughes, 1981; Alton, 1986; Hoff and Stevens, 2005). GKCs also occur along

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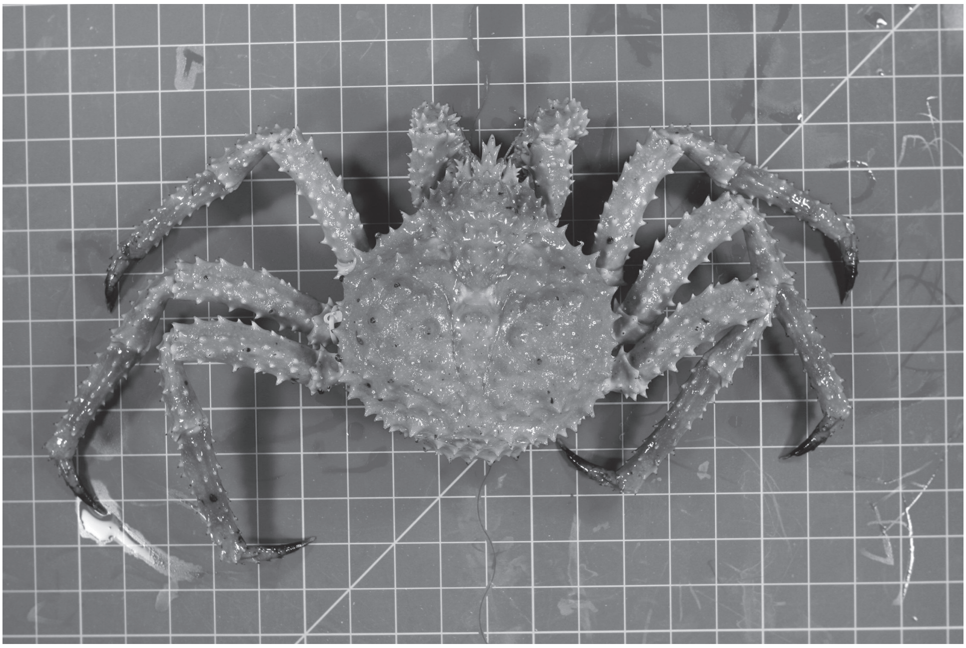
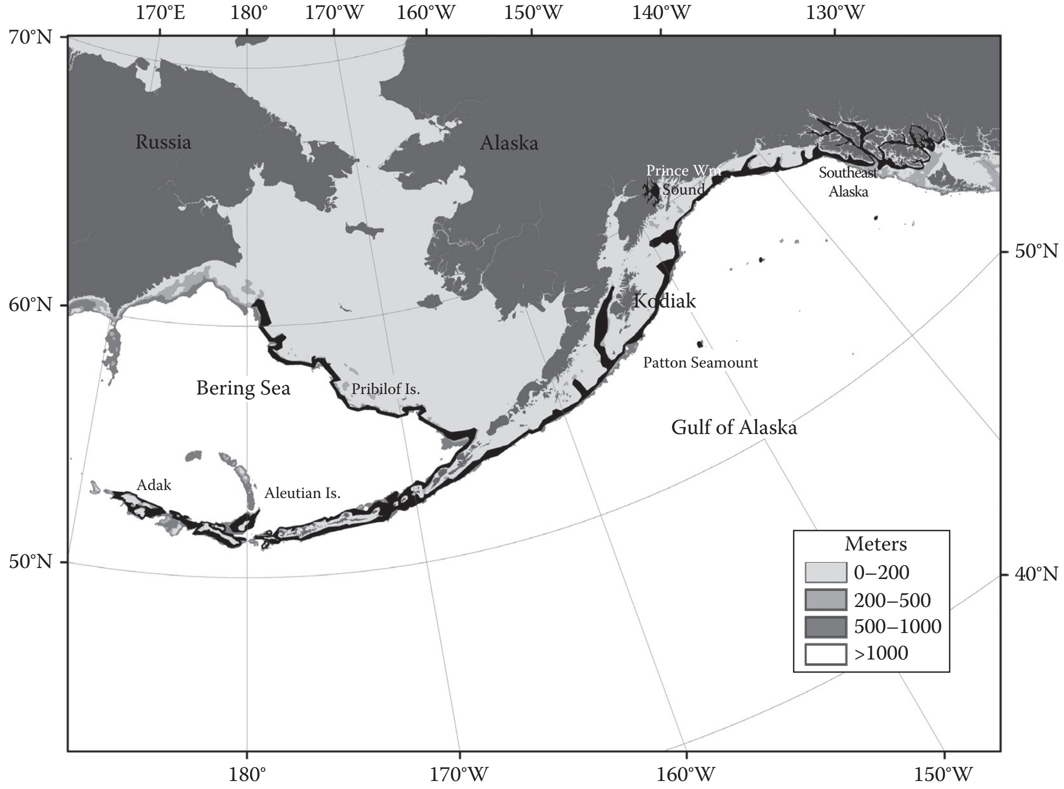
* http://www.adfg.alaska.gov/index.cfm?adfg=goldenkingcrab.main.



(a)

(b)

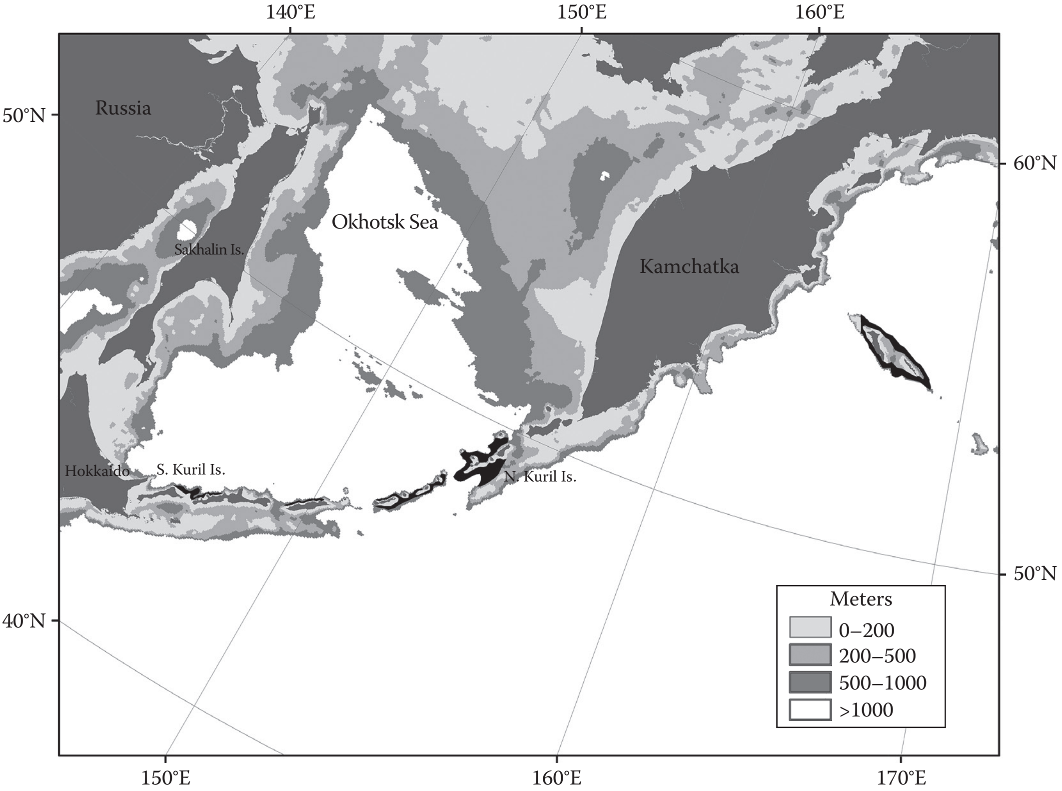
PLATE III (See color insert.) (a) Golden king crab, *Lithodes aequispinus* female, with plastic tag around left third pereiopods. (b) Scarlet king crab, *Lithodes couesi*. (Photos by Brad Stevens.)



MAP 1.5 Distribution of golden king crab *Lithodes aequispinus* in the eastern North Pacific Ocean and Bering Sea. All areas where crabs have been found are included. Distribution is shown between the 200 and 500 m isobaths in those areas where it is present. (Data from NWAFC, *West Coast of North America Strategic Assessment Data Atlas: Invertebrates and Fish*, Northwest and Alaska Fisheries Center, National Oceanic and Atmospheric Administration, Rockville, MD, 1990, p. 112.)

Bowers Bank at 180°W lat. and were commonly fished there by Japanese vessels in the 1970s (McBride et al., 1982). In the Eastern Hemisphere, GKCs occur along the Kamchatka Peninsula, Sakhalin Island, and northern Hokkaido Island, Japan (Rodin, 1970), and reach their southernmost extent at 35°N lat. in Suruga Bay (Suzuki and Sawada, 1978). Note that Map 1.6 does not include these locations due to the lack of more specific details. In Sagami Bay and off Boso Peninsula in Central Japan, adult GKCs predominated from 400 to 600 m depth, whereas juveniles were more abundant below 600 m (Hiramoto and Sato, 1970; Hiramoto, 1985). Along the West Kamchatka shelf, juveniles predominated north of 55°N–57°N lat., and adults predominated from 53°N to 55°N lat. (Rodin, 1970). GKCs live throughout the Kuril Islands including a 440 km expanse in the central Kurils that is not occupied by RKCs or BKCs (Klitin and Nizyayev, 1999). The narrow, steep continental shelf and strong currents in this area prevent colonization from coastal stocks of RKCs and BKCs, but allow retention of the demersal, lecithotrophic larvae of GKC (Klitin and Nizyayev, 1999).

GKCs live at greater depths than RKCs or BKCs, and tend to occur mostly on steep rocky substrata. In the Aleutian Islands and along the Bering Sea shelf slope, GKCs were caught from 73 to 1200 m, with a mean capture depth of 308.9 ± 139.7 m (mean ± SD; Table 1.1, Figure 1.3), though this is probably more a function of the distribution of survey trawls than of the crabs. They were caught at a mean bottom temperature of 3.9°C ± 0.4°C (range 2.0°C–5.8°C). The depth distribution of GKC is bimodal with peaks at 250 and 400 m, probably due to different depth regimes in the GOA and AIS, respectively. During a series of dives with the DSV *Alvin* on the Patton-Murray seamount complex in 1999 and 2002, 103 GKCs were observed at depths from 152 to 931 m, with a mean depth of 485 ± 187 m and



MAP 1.6 Distribution of golden king crab *Lithodes aequispinus* in the western North Pacific Ocean and Kuril Islands. All areas where crabs have been found are included. Distribution is shown between the 200 and 500 m isobaths in those areas where it is present.

at a mean temperature of 3.5°C ± 0.3°C (B. Stevens and T. Shirley, unpublished data). However, this distribution was markedly bimodal because adult crabs live at shallower depths than juveniles. Almost all adults were observed in the depth range of 250–400 m, whereas >50 juveniles were observed in a narrow depth zone between 583 and 623 m (B. Stevens and T. Shirley, unpublished data). In contrast, the vertical distribution of GKC in fjords of British Columbia, Canada, was reversed; juveniles (defined as anything < 114 mm CL) were most abundant from 50 to 100 m, adult males were most common from 50 to 150 m with a peak at 100 m, and adult females were most abundant below 150 m (Sloan, 1985). In Maps 1.5 and 1.6, the distribution of GKC is shown primarily between the depths of 200 and 500 m throughout their range, in order to prevent exaggerating their distribution.

1.5 Scarlet King Crab *Lithodes couesi* (Benedict, 1895)

As their name implies, scarlet king crabs *Lithodes couesi* are deep red in color, which is an advantage for life in the deep sea (Plate IIIb). Red light does not penetrate to the depths where these crabs live, so they would appear black or otherwise inconspicuous to predators. They have relatively smaller bodies and thinner legs than either RKCs or GKCs (see later) and live at greater depths.

Scarlet king crabs live even deeper than GKCs. Few of them are caught by NOAA surveys because they live at depths that are infrequently sampled and in rocky habitats that are not amenable to sampling by trawls. In the Aleutian Islands and the Bering Sea shelf slope, scarlet king crabs were caught from 221 to 1200 m and have a unimodal depth distribution with a mean depth of 793.2 ± 207.9 m (mean ± SD; Table 1.1; Figure 1.4). They are found at bottom temperatures of 3.1°C ± 0.3°C (range 2.3°C–4.3°C,

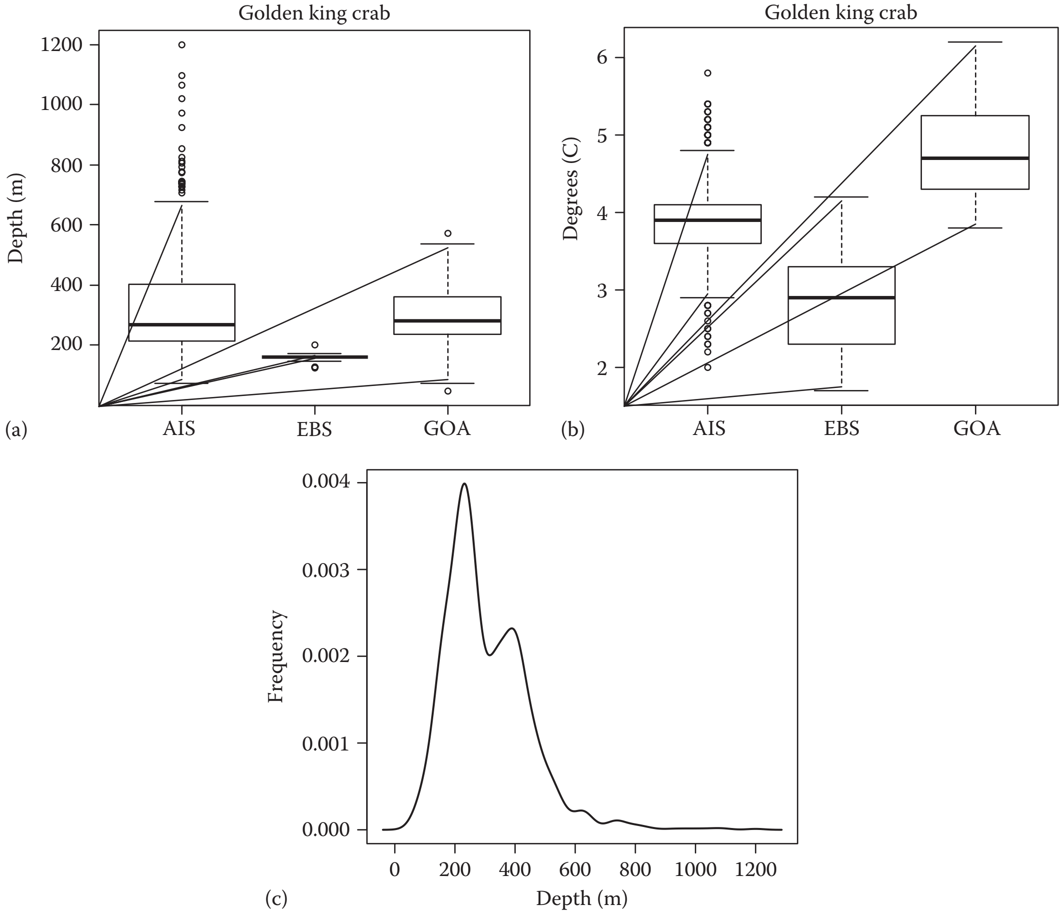


FIGURE 1.3 Depth and temperature distribution of golden king crab *Lithodes aequispinus* in the AIS, EBS, and GOA. Boxplots (as in Figure 1.1) of distribution by (a) depth and (b) temperature. (c) Frequency distribution of depth for all data.

Table 1.2). Somerton (1981) captured scarlet king crabs on GOA seamounts using traps at depths from 380 to 850 m. During a series of *Alvin* dives on GOA seamounts in 1999 and 2002, 67 scarlet king crabs were observed at depths from 234 to 1633 m, with a mean depth of 681 ± 254 m and a mean temperature of 3.1°C ± 0.4°C (B. Stevens and T. Shirley, unpublished data). Somerton (1981) noted that scarlet king crabs occurred at shallower depths on seamounts than on continental slopes, possibly due to the absence of some predators and subsequent competitive release. Although typically found in cold deep waters, specimens of *L. couesi* have been identified off of central-Southern California (no depth or location supplied, Wicksten, 1989), and Martin et al. (1997) collected 22 specimens as far south as Bahia Tortugas, Baja California Sur, at 27° 22.5′N lat., from a depth of 740 m, of which 12 (55%) were infested by the rhizocephalan *Briarosaccus callosus* (Boschma, 1962). All parasitized individuals were identified as females, which could be the result of parasitic feminization (Martin et al., 1997). Due to the rather scarce and anecdotal nature of scarlet king crab observations, a map of their distribution is not included.

Both scarlet king crabs and GKCs have several adaptations to life in deep water with less oxygen (Somerton, 1981). In the GOA, the depth range from 200 to 800 m is the oxygen minimum zone, where dissolved O_2 falls to <0.5 ppm or about 5% of surface levels, and both species live within this zone (B. Stevens, unpublished data). Compared to RKCs and BKCs, both scarlet king crabs and GKCs have relatively inflated gill chambers, which allow for greater surface area of gill lamellae; they also have larger excurrent apertures and scaphognathites, flap-like extensions of the third maxillipeds used for pumping water over the gills. In addition, they both have relatively thin walking legs; according to Somerton

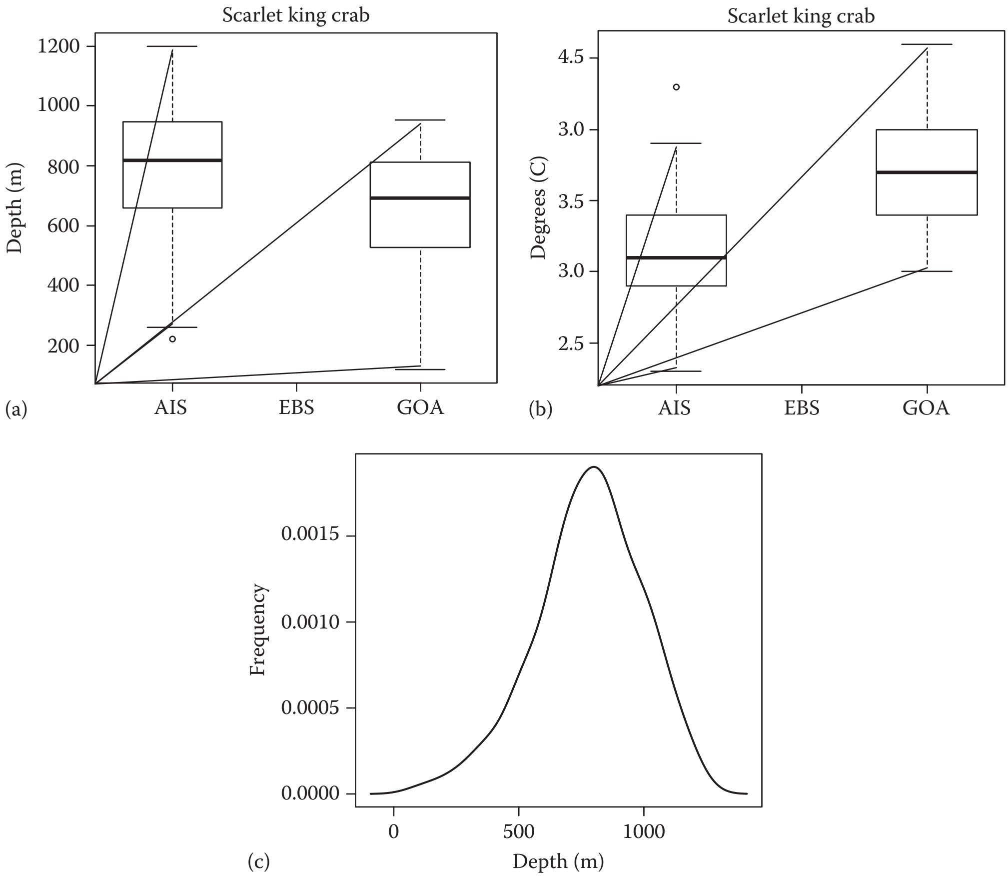
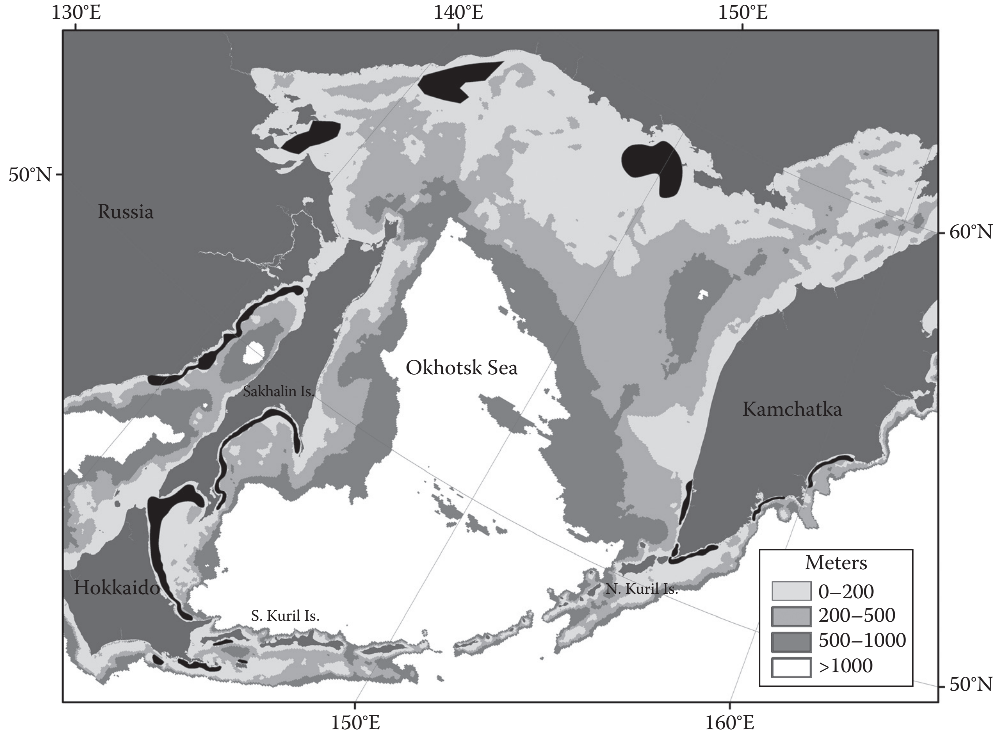


FIGURE 1.4 Distribution of scarlet king crab *Lithodes couesi* in the AIS, EBS, and GOA. Boxplots (as in Figure 1.1) of distribution by (a) depth and (b) temperature. (c) Frequency distribution of depth for all data.

(1981), the ratio of merus width to length for GKCs is less than that for RKCs and is lower yet for scarlet king crabs, which live at the greatest depths. The adaptive advantage of slender legs may be that they are relatively less energetically expensive, while allowing for greater stride length with lower effort than shorter legs (Somerton, 1981); this, in turn, allows them to search large areas in the deep ocean for scarce food resources. Finally, aseasonal reproduction and lecithotrophic larval development are characteristics of *L. aequispinus* and probably *L. couesi* as well (see Stevens, Chapter 8, and Webb, Chapter 10).

1.6 Hanasaki or Spiny King Crab *Paralithodes brevipes* (Milne Edwards and Lucas, 1841)

The spiny king crab *Paralithodes brevipes* (Milne Edwards and Lucas, 1841) is primarily restricted to the Pacific coastal area around northeast Hokkaido, Japan, the Kuril Islands, the Sea of Okhotsk (Miyake, 1982), the island of Sakhalin, the south of Kamchatka, and the southwest Bering Sea, from the intertidal to depths of 50 m (Komai and Yakovlev, 2000) (Map 1.7). In Japan, spiny king crabs are known as “Hanasaki-gani” and have been commercially exploited by Japanese and Russian fishing vessels that land much of their catch in the port of Hanasaki, thus the eponymous name. Generally smaller than RKC, the coloration of spiny king crab is mottled, having a dark red background with lighter brown to beige patches on the carapace and legs, and the claws tend to be lighter red to orange in color (Plate IVa). The rostrum is thicker and more blunt than that of RKCs or BKCs, with a single vestigial dorsal spine, and tends to curve downward and back up (Abe, 1992). Compared to other species of king crabs, spiny



MAP 1.7 Distribution of Hanasaki king crab *Paralithodes brevipes*. All areas where crabs have been found are included. Distribution is shown out to the 100 m isobath in those areas where it is present. Populations in the Northern Okhotsk Sea are of unknown extent and are shown within their depth range.

king crabs have a relatively restricted geographic distribution. Their westernmost limit is in the Northern Sea of Japan, along the Russian coast in the Strait of Tartary, west of Sakhalin Island, and along the western coast of the Sea of Okhotsk (Abe, 1992). In Japan, it occurs at the eastern tip of Hokkaido, along the south (Pacific) side of the Nemuro Peninsula and among the Habomai Islands, and the southernmost Kuril Islands of Kunashiri, Shikotan, and Etorofu. They do not continue through the Kuril Islands, but do occur around the southern tip of the Kamchatka Peninsula, on both the Okhotsk and Pacific coasts (Abe, 1992). Juvenile crabs (<75 mm CL) live in shallow water of <10 m depth, mature females and larger males occur from 20 to 35 m, and large mature males >100 mm CL live at depths >40 m (Abe, 1992). Their habitat includes areas of sand, pebbles, shells, rocks, and seaweed. Spiny king crabs have a spring breeding season, and a male-only fishery occurs from the port of Hamanaka, in eastern Hokkaido, from April through July (Sato and Goshima, 2006). The fishery began in the 1950s and was always small, with landings between 1000 and 2000 tons, until 1976. In 1977, Russia claimed the waters around the Kuril Islands to within 3 miles of the Nemuro coastline, and fishing by Japanese boats in the area was banned, after which landings declined to <100 tons (Abe, 1992). Although their distribution overlaps with that of RKC, their relatively shallow depth range prevents competition and is a form of habitat partitioning.

1.7 Distribution of Southern King Crab and Other Lithodids off South America

A total of 34 species of lithodids belonging to 4 genera are distributed around South America (23 *Paralomis* spp., 7 *Lithodes* spp., 3 *Neolithodes* spp., and 1 *Glyptolithodes* sp.; Figure 1.5). These four genera originated from deep waters and have expanded into waters outside their area of origin (Hall and Thatje, 2009b). Species richness decreases southward, with 13 species occurring off Central America down to 10°S, at the Panamic biogeographic province (sensu Boschi, 2000) (Figure 1.5; Map 1.8)

(a)

(b)

PLATE IV (See color insert.) (a) Spiny king crab, *Paralithodes brevipes*. (Photo by Brad Stevens.) (b) Northern stone crab, *Lithodes maja*. (Photo by Alastair Brown.)

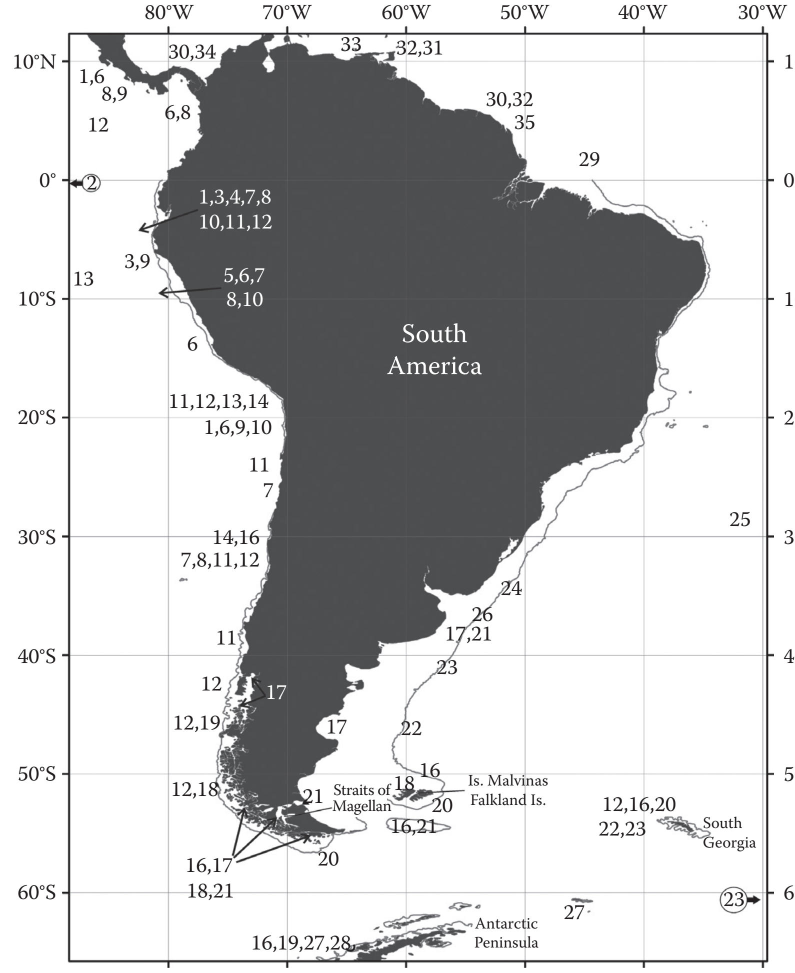
Reference in Map	Species	Panamic 23°N–10°S	Peru-Chilean 10°S–41°S	Magellanic–Pacific 10°N–52°S	Magellanic–Tip SA 52°S–55°S	Magellanic Atlantic 55°S–34°S	South Georgia 55°S	Antarctica South 60°S	Brazilian–Caribbean 5°S–20°N
1	*Lithodes wiracocha*	■	■						
2	*Lithodes galapagensis*	■							
3	*Paralomis inca*	■							
4	*Paralomis phrixa*	■							
5	*Paralomis inca*	■							
6	*Paralomis diomedeae*	■	■						
7	*Glyptolithodes cristatipes*	■	■						
8	*Lithodes panamensis*	■	■						
9	*Paralomis papillata*	■	■						
10	*Paralomis aspera*	■	■				1	1	
11	*Paralomis otsuae*	■	■	■					
12	*Neolithodes diomedeae*	■	■	■			■		
13	*Paralomis longipes*	■	■						
14	*Paralomis chilensis*		■						
15	*Paralomis sonne*		■						
16	*Lithodes turkayi*		■		■	■	■ 1	■ 1	
17	*Lithodes santolla*			■	■	■			
18	*Paralomis granulosa*			■	■	■			
19	*Paralomis tuberipes*			■				■	
20	*Paralomis spinosissima*		?		■	■	■		
21	*Lithodes confundens*				■	■			
22	*Paralomis anamerae*					■	■		
23	*Paralomis formosa*					■	■	■	
24	*Paralomis longidactylus*					■			
25	*Paralomis shinkaimaruae*					■			
26	*Paralomis birsteini*							■	
27	*Neolithodes yaldwyni*							■	
28	*Paralomis cubensis*								■
29	*Neolithodes agassizii*								■
30	*Paralomis arethusa*								■
31	*Lithodes manningi*								■
32	*Paralomis pectinata*								■
33	*Paralomis serrata*								■
34	*Paralomis grossmani*								■

FIGURE 1.5 Distribution of lithodids around South America at different biogeographic provinces as defined by Boschi (2000). The Magellanic Province which surrounds the southern tip of South America, was divided into Pacific and Atlantic Sides and a mixed area that includes the Straits of Magellan, Beagle Channel, and system of fjords and channels. Numbers in the first column correspond to species numbers shown on the distribution Map 1.1 references: 1—reported as *L. murrayi* (Klages et al., 1995; Purves et al., 2003); ?—species not confirmed (Bahamonde and Leiva, 2003). *Literature sources*: (Haig, 1974; Solar, 1981; Báez et al., 1986; Macpherson, 1988b, 1992, 2004; Lopez-Abellan and Balguerias, 1994; Arana and Retamal, 1999; Brito, 2002; Zaklan, 2002; Bahamonde and Leiva, 2003; Thatje and Arntz, 2004; Guzmán, 2009; GBIF, 2012; Retamal, 2000; Retamal and Moyano, 2011; Smith et al., 2011; Sotelano et al., 2013).

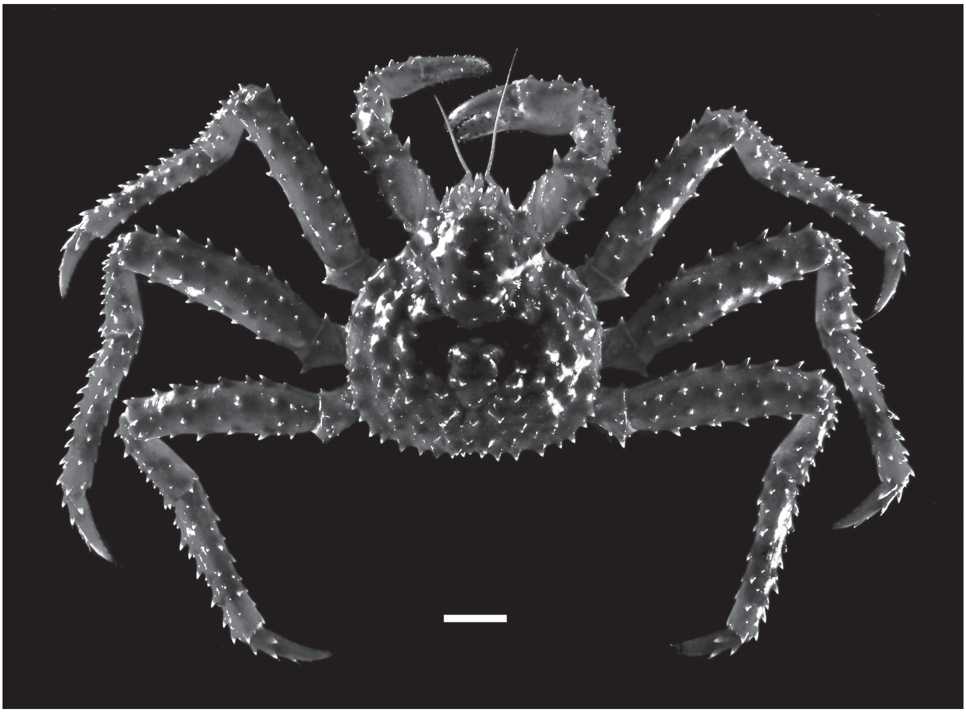
(Haig, 1974; Hall and Thatje, 2009a; Macpherson and Wehrtmann, 2010; GBIF, 2012). Some of the species occurring in South America are known only by the few specimens used for taxonomic descriptions (e.g., *Lithodes galapagensis*, *P. tuberipes*). Notwithstanding, exploration for new fisheries is expanding the knowledge of lithodid distribution in South America (e.g., Bahamonde and Leiva, 2003).

N. diomedeae is the lithodid species with the broadest latitudinal range in the world occurring in both the Northern and Southern Hemispheres. Its distribution extends from Baja California (26°N) down to the Antarctic convergence, occurring along the SE coast of South America. Its southernmost occurrence on the Pacific coast is about 53°S, and it reemerges on the continental slope of the SW Atlantic and off South Georgia (Map 1.8) (Macpherson, 1988a; GBIF, 2012). Other species occurring in both hemispheres are *Paralomis multispina* occurring off Indonesia and in the Bering Sea and the tropical *Lithodes tropicalis*, *L. turritus*, *L. ferox*, *P. hirtella*, and *P. diomedeae*, all at >400 m depth (GBIF, 2012). Moreover, *N. diomedeae* is abundant in the fishing pots used off Central Chile (ca. 30°S) and constitutes a potential fishery (Brito, 2002; Bahamonde and Leiva, 2003).

Seven of the species of the Panamic province extend their distribution southward and occur in the Peru-Chilean biogeographic province (Figure 1.5), and six other newly identified species occur in this



MAP 1.8 Distribution of *L. santolla* and other lithodid crabs around South America. Numbers correspond to species listed in Figure 1.5. Line corresponds to the 200 m isobath. Numbers encircled with an arrow indicate the latitude at which species occur, but at a longitude outside of the map.



(a)

(b)

PLATE V (See color insert.) (a) Southern king crab, *Lithodes santolla*, from the Beagle Channel and (b) southern stone crab, *Paralomis granulosa*. Scale bar is 30 mm. (Photos by Gustavo Lovrich.)

province, which has the highest species richness (Map 1.8) (Haig, 1974; Báez et al., 1986; Wilson, 1990; Macpherson, 1992; Retamal, 2000; Brito, 2002; Retamal and Moyano, 2011). Two species, *N. diomedeae* and *P. otsuae* also occur in the Magellanic Province. Two species *L. santolla* (Plate Va) and *P. granulosa* (Plate Vb) are known to be representative of this latter province (Haig, 1974) and occur in great abundance in the coastal waters of the Southern tip of South America south to 40°S, where they support profitable fisheries with annual landings of 3000 tons (see Lovrich and Tapella, Chapter 14). The distribution of *L. turkayi* at approximately 35°S is within the Magellanic Province, and it also occurs in South Georgia and Antarctica (Campodonico and Guzmán, 1972; Vinuesa et al., 1999; Thatje and Arntz, 2004). This species is easily confounded with and occasionally reported as *L. murrayi*, which apparently occurs only in the eastern Pacific and Indian Oceans (Macpherson, 1988a; Zaklan, 2002; GBIF, 2012). On the Pacific side of the Magellanic Province, a single occurrence of *P. tuberipes* was recorded (Macpherson, 1988b). In coastal waters of the Islas Malvinas/Falkland Islands, the only reported species is *Paralomis granulosa* (Hoggarth, 1993).

In the Antarctic sector near South America, lithodids are present only in the lower continental slope of the Western Peninsula. They are absent from the cold mass waters that are on the continental shelves, including that of the Weddell Sea (Hall and Thatje, 2011). On the Antarctic convergence, South Georgia represents an ecotone area for decapods, with lithodids such as *N. diomedeae*, *L. turkayi*, *P. spinosissima*, *P. formosa*, *and P. anamerae*, which also occur in the Magellanic Province (Macpherson, 2004; Thatje and Arntz, 2004; Lovrich et al., 2005). Some of these species also occur in Antarctica, along with the exclusive Antarctic lithodids *P. birsteini* and *N. yaldwyni* (Arana and Retamal, 1999; Thatje and Arntz, 2004; Smith et al., 2011). The range of *P. formosa* extends further south, occurring off the South Sandwich and South Orkney Islands—but not reaching further south—and northerly on the Atlantic continental slope to 40°S (Map 1.8) (Lopez-Abellan and Balguerias, 1994; GBIF, 2012). Some species occurring in Antarctica such as *P. tuberipes* or *L. turkayi* also occur as far north as 45°S and 31°S, respectively (Map 1.8). Furthermore, *P. spinosissima* apparently extends its distribution further north on the Pacific coast, since specimens of a similar species were reported at >1300 m depth in fishing surveys off central Chile at 30°S (Bahamonde and Leiva, 2003).

On the Atlantic side of South America, *L. confundens* and *L. santolla* are very abundant in coastal areas, and these and other species such as *P. formosa*, *P. anamerae*, and *P. longidactyla* occur northerly on the continental shelf. *P. shinkaimaruae* has a single record in the Atlantic at approximately 30°S (Map 1.8). Northerly in the Western Atlantic, there is an apparent gap in lithodid distribution between 30°S and the Equator. In the Caribbean Sea, there are seven species (Figure 1.5) (GBIF, 2012), which do not coincide with any of the species present in the SW Atlantic nor Eastern Pacific (Macpherson, 1988a). Nevertheless, knowledge of the distribution of lithodids in the Caribbean Sea is scarce and fragmentary.

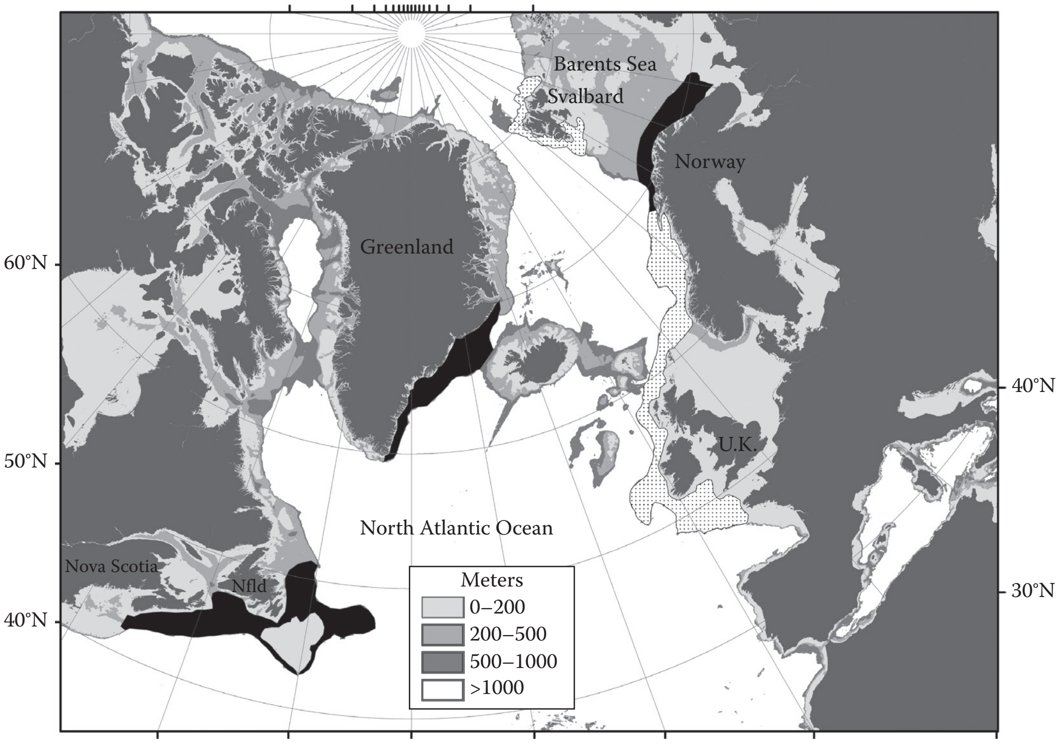
Lithodids are predominately cold water inhabitants. Their low tolerance to temperatures higher than 13°C–15°C has constrained their radiation and their present distribution, especially in tropical and subtropical areas (Hall and Thatje, 2009b, 2011). All species occurring north of 40°S, including those occurring in the Caribbean and Panamic provinces, are distributed deeper than 200 m, typically below 400 m, at the continental slopes, where water temperatures are below 10°C (Hall and Thatje, 2011 and references therein). They emerge to shallow waters where temperature permits, for example, in coastal waters and continental shelves of Southern South America, where the thermal regime is between 5°C and 10°C. Optimal levels of growth and survival during larval development occur at this temperature range in laboratory-reared species (Anger et al., 2003; Jørgensen and Nilssen, 2011). Hence, this temperature tolerance window restrains lithodids from occurring at shallow waters in tropical and subtropical areas and in the coldest waters of the world that occur in the Antarctic continental shelves (Hall and Thatje, 2009b, 2011).

1.8 Other Lithodids

Many other species of lithodid crabs are found throughout the world ocean. Most of these do not occur in great enough numbers or at shallow enough depths to support commercial fisheries. The species listed in the following text, while not exhaustive, are those that are commonly encountered and for which reliable records are obtainable.

1.8.1 *Lithodes maja* (or *maia*) (Linnaeus, 1758)

This species, commonly called stone crab or northern stone crab, was one of the first decapods recognized by Linnaeus. Originally called *Cancer maja*, it is still commonly referred to as *Lithodes maia* Smith, 1879, or *Lithodes maya*, which are simply misspellings of the original species name (McLaughlin et al., 2010). In Norway, it is known by the colorful common name of trollkrabbe. Coloration is orange-red to brown; spines are longer than those of RKC, with the longest spines arrayed around the perimeter of the carapace (Plate IVb). The species is common to the Barents and White Seas (Dvoretsky and Dvoretsky, 2008) and extends southward in the Northeast Atlantic along the coast of Norway to the Faroe-Icelandic threshold, though some are occasionally seen in the northern British Isles (Sokolov, 2006). It was reported from as far north as Svalbard by Dyer et al. (1984), who thought its presence was an indication of warming seawater temperatures, but more recent surveys did not find it in Spitsbergen fjords (Hop et al., 2002). In the western Atlantic, it is found along the eastern and southern coasts of Greenland and along the Labrador coast south to Nova Scotia and the Gulf of Maine, and in the deep waters (>400 m) of the St. Lawrence Estuary (Map 1.9). A test fishery conducted in southeast Greenland in 1995–1996 captured specimens on the continental slope at depths of 300–700 m, with the greatest concentration from 400 to 500 m, at temperatures of 4°C–5°C (Woll and Burmeister, 2002). Specimens from 14 to 155 mm CW have been collected along the southern and western shores of Newfoundland (DFO, 2000), along the continental slope of Nova Scotia (Markle et al., 1988), along the edge of the Laurentian Channel and the Scotian Shelf, and in the mouth of the Bay of Fundy (Tremblay et al., 2007). There, they occur in temperatures of 0°C–11°C (mean 4°C–8°C) and depths from 25 to 660 m, with the majority greater than 100 m. Specimens have been found in the stomachs of wolffish *Anarhichas lupus* from the Scotian Shelf (Templeman, 1985; Markle et al., 1988).



MAP 1.9 Distribution of northern stone crab *Lithodes maja* in the North Atlantic Ocean. All areas where crabs have been found are included. Distribution is shown between the 100 and 500 m isobaths in those areas where it is present. Populations along Nova Scotia, Greenland, and northern Norway are known (shown in black); those around Svalbard, the east coast of Norway, and the British Isles are suspected from anecdotal observations (shown as stippled).

The southern limit in the western Atlantic was thought to be Sandy Hook, New Jersey, but Williams (1988) observed a single female from the Johnson Sea-Link submersible between 171 and 381 m depth in the Baltimore Canyon at 38° 09′N, 73° 51′W, thus extending its range to the Maryland–Virginia border. Specimens have been captured off the coast of Ireland, including a 10 cm CL individual caught from 50 m of water in 1975 (O'Riordan, 1975) and an 8.7 cm CL specimen in 1986 (O'Riordan, 1986), both caught in County Kerry; although these were considered rare, the author noted that the latter specimen was the eighth of this species recorded from that area. In Map 1.9, the distribution of *L. maja* is depicted as "known" along the Scotian Shelf, the SE coast of Greenland, and Northern Norway, and as "probable" around Svalbard, southern Norway, and the British Isles, between the depths of 100 and 1000 m.

1.8.2 *Paralithodes californiensis* and *Paralithodes rathbuni* (Benedict, 1895)

Two species of king crabs, *Paralithodes californiensis* and *Paralithodes rathbuni*, are both commonly referred to as California king crab. While some authors treat them as separate species, others suggest that they may be synonymous. Both were originally placed in the genus *Lithodes* by Benedict (1895) based on two females of the former, and one male of the latter. The type specimen of *P. californiensis* was collected from 283 m off Santa Cruz Island, California, and that of *P. rathbuni* from 386 m off San Simeon Bay, both during the Albatross expedition of 1912–1913 (Schmidt, 1921). Schmidt (1921) expressed doubts about the differences between these two species, and their status is still unresolved (R. Lemaitre, pers. commun., November 2012; McLaughlin et al., 2010). Wicksten (2011) considered them to be unique species and provided a key to distinguish them:

> 11. Rostrum bifid, anterior lateral spines of rostrum reaching to apex of bifurcation of rostrum………. *Paralithodes rathbuni*
> – Rostrum simply bifid or split, anterior lateral spines of rostrum not reaching half way to bases of terminal spines……….. *Paralithodes californiensis*

Wicksten's (2011) descriptions lead to the comparisons shown in Table 1.3.

Both species were also collected by the M/V *N. B. Scofield* from 150 m near Pismo Beach, California, in 1950 (Goodwin, 1952). They are occasionally observed in the deeper waters of Southern California, such as along oil pipelines (Love and York, 2005). Specimens attributed to *P. rathbuni* were captured from depths of 170–320 m, from Baja California at 28° 12′N lat to Cordell Bank, north of San Francisco, at 38° 00′N lat (Wicksten, 1987). Their range probably overlaps significantly and is shown in Map 1.10 extending from San Francisco Bay south to Baja California between the depths of 100 and 500 m.

1.8.3 Other King Crabs

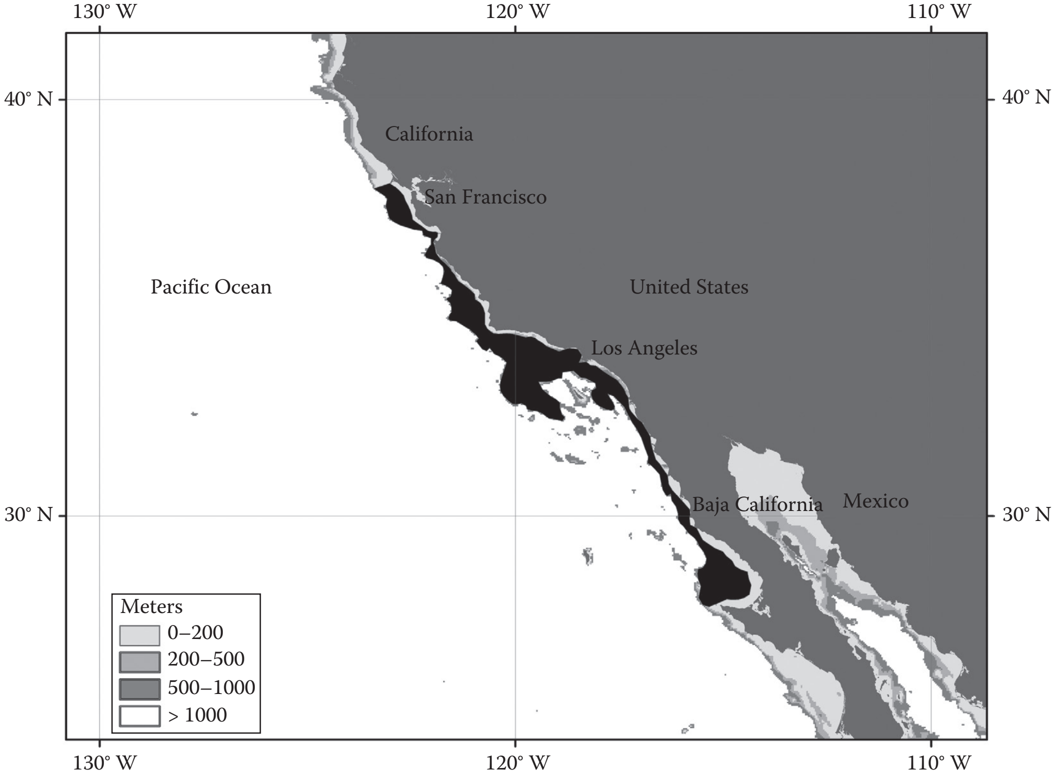
A number of other species in the family Lithodidae are discussed elsewhere in this treatise, with a few exceptions that should not go unmentioned. *Neolithodes agassizii* (Smith, 1882) occurs on the continental

TABLE 1.3

Comparison of Characteristics Reported for *Paralithodes californiensis* and *P. rathbuni*

Character	*P. californiensis*	*P. rathbuni*
Carapace	Longer than wide	Wider than long
Rostrum	Bifid	Upward pointing
Rostral spines	Subrostral, to end of cornea	Flanking terminal point
Color	Orange with bluish-white spines	Pale orange
Habitat	Mud or rocks	Sand, mud, or rock
Depth	145–300 m	92–380 m
Range	Pismo Beach to San Diego, CA	Cordell Bank to Baja California

Source: Wicksten, M.K., *Decapod Crustacea of the Californian and Oregonian Zoogeographic Provinces*, Scripps Institution of Oceanography Library, Scripps Institution of Oceanography, La Jolla, CA, 2011.



MAP 1.10 Distribution of California king crabs *Paralithodes californiensis* and *P. rathbuni* along the west coast of the United States and Mexico. All areas where crabs have been found are included. Distribution is shown between the 100 and 500 m isobaths in those areas where they are present.

shelf of the Northeast Atlantic from south of Cape Hatteras, North Carolina, through the Gulf of Mexico to Guyana, South America (Zaklan, 2002). *L. manningi* (Macpherson, 1988a) occurs in the Caribbean and Gulf of Mexico. Macpherson (1994) recovered a 15 mm juvenile from 1236 m, near Barbados, at 11° 14′N, 59° 22′W. *Lithodes panamensis* Faxon 1893 occurs from Panama to Peru (Wicksten, 1989). In recent years, additional species of lithodids have been found and identified in the Antarctic. Whether this is the result of increased scrutiny of the Antarctic ecosystem, or warming of Antarctic waters allowing expanded ranges, is unknown. New species identified there include *Neolithodes capensis* (Garcıa-Raso et al., 2005) and *Neolithodes brodiei* (Macpherson, 2001). Macpherson (2004) captured and described a new species, *Neolithodes duhameli*, from a depth of 1500 m near Crozet Island at 46° 18′S, 51° 14′E. In the GOA, *Paralomis multispina* and *P. verillii* occur on the continental slope and seamounts, but their distribution is poorly documented. During *Alvin* dives on Patton Seamount in the GOA in 1999 and 2002, both species were observed and verified by captured specimens, but the two species could not be distinguished on videotapes; their distributions overlapped considerably, ranging from 933 to 2008 m, with a mean depth of 1303 ± 315 m (mean ± SD), and the mean temperature where they were observed was 2.25°C ± 0.24°C (B. Stevens and T. Shirley, unpublished data).

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2

Systematics of King Crabs

Patsy A. McLaughlin†

CONTENTS

2.1 Introduction

The common name, king crab, is most frequently associated with the commercially important "red," "golden," "southern," "false," and "spiny" lithodid crabs of the genera *Paralithodes*, *Lithodes*, and *Paralomis*, some of the largest crabs in the infraorder Anomura. However, these are but a very few of the 129 species included in the 15 genera presently assigned to the two families in the superfamily Lithodoidea. The currently recognized valid genera and species are listed in Table 2.1. This list has been taken from McLaughlin et al. (2010), and further information regarding primary synonyms and sources of original descriptions may be found in that publication.

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† Deceased, April 4, 2011.

TABLE 2.1

Extant Families and Genera of the Lithodoidea

- **SUPERFAMILY LITHODOIDEA** Samouelle, 1819
  - **Family Hapalogastridae** Brandt, 1850
    - *Acantholithodes* Holmes, 1895
      - *Acantholithodes hispidus* (Stimpson, 1860)
    - *Dermaturus* Brandt, 1850
      - *Dermaturus mandtii* Brandt, 1850
    - *Hapalogaster* Brandt, 1850
      - *Hapalogaster cavicauda* Stimpson, 1859
      - *Hapalogaster dentata* (De Haan, 1849)
      - *Hapalogaster grebnitzkii* Schalfeew, 1892
      - *Hapalogaster mertensii* Brandt, 1850
    - *Oedignathus* Benedict, 1895
      - *Oedignathus inermis* (Stimpson, 1860)
    - *Placetron* Schalfeew, 1892
      - *Placetron wosnessenskii* Schalfeew, 1892
  - **Family Lithodidae** Samouelle, 1819
    - *Cryptolithodes* Brandt, 1848
      - *Cryptolithodes expansus* Miers, 1879
      - *Cryptolithodes sitchensis* Brandt, 1853
      - *Cryptolithodes typicus* Brandt, 1848
    - *Glyptolithodes* Faxon, 1895
      - *Glyptolithodes cristatipes* (Faxon, 1893)
    - *Lithodes* Latreille, 1806
      - *Lithodes aequispinus* Benedict, 1895
      - *Lithodes aotearoa* Ahyong, 2010
      - *Lithodes australiensis* Ahyong, 2010
      - *Lithodes ceramensis* Takeda & Nagai, 2004
      - *Lithodes chaddertoni* Ahyong, 2010
      - *Lithodes confundens* Macpherson, 1988
      - *Lithodes couesi* Benedict, 1895
      - *Lithodes ferox* Filhol, 1885
      - *Lithodes formosae* Ahyong & Chan, 2010
      - *Lithodes galapagensis* Hall & Thatje, 2009
      - *Lithodes jessica* Ahyong, 2010
      - *Lithodes longispina* Sakai, 1971
      - *Lithodes macquariae* Ahyong, 2010
      - *Lithodes maja* (Linnaeus, 1758)
      - *Lithodes mamillifer* Macpherson, 1988
      - *Lithodes manningi* Macpherson, 1988
      - *Lithodes megacantha* Macpherson, 1991
      - *Lithodes murrayi* Henderson, 1888
      - *Lithodes nintokuae* Sakai, 1978
      - *Lithodes panamensis* Faxon, 1893
      - *Lithodes paulayi* Macpherson & Chan, 2008
      - *Lithodes rachelae* Ahyong, 2010
      - *Lithodes richeri* Macpherson, 1990
      - *Lithodes robertsoni* Ahyong, 2010
      - *Lithodes santolla* (Molina, 1782)
      - *Lithodes turkayi* Macpherson, 1988
      - *Lithodes turritus* Ortmann, 1892
      - *Lithodes unicornis* Macpherson, 1984
      - *Lithodes wiracocha* Haig, 1974
    - *Lopholithodes* Brandt, 1848
      - *Lopholithodes foraminatus* (Stimpson, 1859)
      - *Lopholithodes mandtii* Brandt, 1848
    - *Neolithodes* A. Milne-Edwards & Bouvier, 1894
      - *Neolithodes agassizii* (Smith, 1882)
      - *Neolithodes asperrimus* Barnard, 1947
      - *Neolithodes brodiei* Dawson & Yaldwyn, 1970
      - *Neolithodes bronwynae* Ahyong, 2010
      - *Neolithodes capensis* Stebbing, 1905
      - *Neolithodes diomedeae* (Benedict, 1895)
      - *Neolithodes duhameli* Macpherson, 2004
      - *Neolithodes flindersi* Ahyong, 2010
      - *Neolithodes grimaldii* (A. Milne-Edwards & Bouvier, 1894)
      - *Neolithodes nipponensis* Sakai, 1971
      - *Neolithodes vinogradovi* Macpherson, 1988
      - *Neolithodes yaldwyni* Ahyong & Dawson, 2006
    - *Paralithodes* Brandt, 1848
      - *Paralithodes brevipes* (H. Milne Edwards & Lucas, 1841)
      - *Paralithodes californiensis* (Benedict, 1895)
      - *Paralithodes camtschaticus* (Tilesius, 1815)
      - *Paralithodes platypus* (Brandt, 1850)
      - *Paralithodes rathbuni* (Benedict, 1895)
    - *Paralomis* White, 1856
      - *Paralomis aculeata* Henderson, 1888
      - *Paralomis africana* Macpherson, 1982
      - *Paralomis alcockiana* Hall & Thatje, 2009
      - *Paralomis anamerae* Macpherson, 1988
      - *Paralomis arae* Macpherson, 2001
      - *Paralomis arethusa* Macpherson, 1994
      - *Paralomis aspera* Faxon, 1893
      - *Paralomis birsteini* Macpherson, 1988
      - *Paralomis bouvieri* Hansen, 1908
      - *Paralomis ceres* Macpherson, 1989
      - *Paralomis chilensis* Andrade, 1980
      - *Paralomis cristata* Takeda & Ohta, 1979
      - *Paralomis cristulata* Macpherson, 1988
      - *Paralomis cubensis* Chace, 1939
      - *Paralomis danida* Takeda & Bussarawit, 2007
      - *Paralomis dawsoni* Macpherson, 2001
      - *Paralomis diomedeae* (Faxon, 1893)
      - *Paralomis dofleini* Balss, 1911
      - *Paralomis echidna* Ahyong, 2010
      - *Paralomis elongata* Spiridonov, Türkay, Arntz & Thatje, 2006

TABLE 2.1 (continued)

Extant Families and Genera of the Lithodoidea

- *Paralomis erinacea* Macpherson, 1988
- *Paralomis formosa* Henderson, 1888
- *Paralomis gowlettholmes* Ahyong, 2010
- *Paralomis granulosa* (Hombron & Jacquinot, 1846)
- *Paralomis grossmani* Macpherson, 1988
- *Paralomis haigae* Eldredge, 1976
- *Paralomis hirtella* de Saint Laurent & Macpherson, 1997
- *Paralomis histrix* (De Haan, 1849)
- *Paralomis hystrixoides* Sakai, 1980
- *Paralomis inca* Haig, 1974
- *Paralomis indica* Alcock & Anderson, 1899
- *Paralomis investigatoris* Alcock & Anderson, 1899
- *Paralomis jamsteci* Takeda & Hashimoto, 1990
- *Paralomis japonicus* Balss, 1911
- *Paralomis kyushupalauensis* Takeda, 1985
- *Paralomis longidactylus* Birstein & Vinogradov, 1972 {14}
- *Paralomis longipes* Faxon, 1893
- *Paralomis macphersoni* Mũnoz & García-Isarch, 2013
- *Paralomis makarovi* Hall & Thatje, 2009
- *Paralomis manningi* Williams, Smith & Baco, 2000
- *Paralomis medipacifica* Takeda, 1974
- *Paralomis mendagnai* Macpherson, 2003
- *Paralomis microps* Filhol, 1884
- *Paralomis multispina* (Benedict, 1895)
- *Paralomis nivosa* Hall & Thatje, 2009
- *Paralomis ochthodes* Macpherson, 1988
- *Paralomis odawarai* (Sakai, 1980)
- *Paralomis otsuae* Wilson, 1990
- *Paralomis pacifica* Sakai, 1978
- *Paralomis papillata* (Benedict, 1895)
- *Paralomis pectinata* Macpherson, 1988
- *Paralomis phrixa* Macpherson, 1992
- *Paralomis poorei* Ahyong, 2010
- *Paralomis roeleveldae* Kensley, 1981
- *Paralomis seagranti* Eldredge, 1976
- *Paralomis serrata* Macpherson, 1988
- *Paralomis spectabilis* Hansen, 1908
- *Paralomis spinosissima* Birstein & Vinogradov, 1972
- *Paralomis staplesi* Ahyong, 2010
- *Paralomis stella* Macpherson, 1988
- *Paralomis stevensi* Ahyong & Dawson 2006
- *Paralomis taylorae* Ahyong, 2010
- *Paralomis truncatispinosa* Takeda & Miyake, 1980
- *Paralomis tuberipes* Macpherson, 1988
- *Paralomis verrilli* (Benedict, 1895)
- *Paralomis webberi* Ahyong, 2010
- *Paralomis zealandica* Dawson & Yaldwyn, 1971

Phyllolithodes Brandt, 1848
- *Phyllolithodes papillosus* Brandt, 1848

Rhinolithodes Brandt, 1848
- *Rhinolithodes wosnessenskii* Brandt, 1848

Sculptolithodes Makarov, 1934
- *Sculptolithodes derjugini* Makarov, 1934

2.2 Systematics

2.2.1 General Crustacean Systematics

The term systematics as applied to modern crustacean research has been expanded considerably since the days of the early naturalists. Whereas systematics at one time was primarily restricted to the typological interpretation of morphological attributes of the single "type" of the species under study, even that alpha-level taxonomy has been broadened to include observable variations and sexual dimorphism. However, systematics of the twenty-first century is no longer concerned with only taxon descriptions, but the broader "landscape" of phylogenetic relationships among taxa. Although descriptive morphology still remains the cornerstone of crustacean systematic research, its development has been significantly complemented by studies of behavior and biogeography, spermatological investigations, statistical and cladistic methodologies, and most recently by molecular analyses enhanced by the applications of computerized tools and models (see Grant et al., Chapter 3).

2.2.2 Lithodoid Systematics

As pointed out by McLaughlin et al. (2010), the classification of the Hapalogastridae has been somewhat controversial. Rathbun (1904), Schmitt (1921), Hart (1982), Williams et al. (1989), McLaughlin et al. (2005), De Graves et al. (2009), and McLaughlin et al. (2010) all have included Holmes' (1895) *Acantholithodes* in the family, whereas authors such as Makarov (1938, 1962), Dawson and Yaldwyn (1985), Macpherson (1988a), and Dawson (1989) considered *Acantholithodes* only a synonym of *Dermaturus*. It would appear from the most recent classifications and checklists that *Acantholithodes* has been accepted as a distinct and valid genus.

The generic composition of the Lithodidae has not changed much in more than a century. Only the genus *Sculptolithodes* was added by Makarov (1934); all previous genera were proposed in the nineteenth century. The diagnostic characters defining these genera principally remain those of the pleonal tergites and carapacial spines; however, a recently recognized deep longitudinal fissure present medianly on the sternite of the chelipeds will immediately separate *Lithodes* and *Neolithodes* from the remaining genera. The recognition of a multitude of recent new taxa in the species-rich genera *Lithodes*, *Neolithodes*, and *Paralomis* has made it necessary to supplement descriptive morphology at the specific level with morphometrics of the chelipeds and walking legs (Ahyong 2010b).

2.3 Classification

2.3.1 Early History of Lithodid Classification

The family Lithodidae has been included in the infraorder Anomura (or Anomala) since its placement there by Henri Milne Edwards (1837), but not without conflict. Specifically, *Cancer maja* was one of the two anomuran decapods included by Linnaeus (1758) in his 10th edition of *Systema Naturae*, the starting point of zoology's binominal nomenclature. *C. maja* was subsequently transferred to the genus *Lithodes* by Latreille (1806) as its type species, but renamed *Lithodes arctica*. However, prior to Latreille's assignment of *C. maja* to *Lithodes*, Lamarck (1801) proposed the name *Maja eriocheles* for the type species of his brachyuran genus *Maja*. It would appear that Lamarck selected the name *M. eriocheles* as a replacement name for Linnaeus' *C. maja*. The two type species, despite the changes in their names, were identical, with *Lithodes* being the junior objective synonym of *Maja*. Nonetheless, *Lithodes* was in common use as a genus of anomuran crabs, while *Maja* was in similar common use as a genus of brachyuran crabs, and both were type genera for their respective families. A petition to address this nomenclatorial dilemma finally was submitted to the International Commission for Zoological Nomenclature (ICZN) requesting the use of its plenary powers (Holthuis 1956) to resolve this ambiguity. In ICZN Opinion 511 (1958), the commission set aside all prior type species designations for the genus *Maja* and designated *C. squinado* as the type species for this brachyuran genus. *C. maja* was placed on the Official List of Specific Names in Zoology as the type species of the anomuran genus *Lithodes*, whereas *L. arctica* was placed on the Official Index of Rejected and Invalid Specific Names in Zoology.

Anomuran classifications have at one time or another included a broad assortment of decapods (see McLaughlin et al. 2007 for specifics). De Haan (1841), for example, restricted his anomurans to the Galatheidea, Porcellanidea, Hippidea, Paguridea, and Lithodeacea (Lithodidae). In contrast, Boas (1880b) consolidated these five major taxa into three groups, the first being "Paguroiderne," including *Pagurus*, *Coenobita*, and *Birgus* and also *Lithodes* and its relatives. Although Brandt (1848, 1850) had proposed generic rank for the several lithodid taxa he described, Boas (1880b) in his reference to the relatives of *Lithodes* apparently was only aware of the two genera proposed by White (1848). These Boas (1880b) reduced to subgeneric rank under *Lithodes*. Henderson's (1888) classification was patterned after Boas' (1880b), but the latter's sectional rankings were expanded to families. As Henderson was dealing just with taxa collected during the *Challenger* expedition, only the genera *Lithodes* and *Paralomis* were included in his family Lithodidae. The "Tribe Paguridea" of Borradaile (1906) was divided into families by Bouvier (1940), who, like Henderson (1888), also recognized the distinctness of the family Lithodidae.

2.3.2 Recent Interpretations of Lithodid Classification

Although the thread of a close pagurid–lithodid relationship had been woven into the earliest of formal classifications, a major shift in interpretation was introduced by MacDonald et al. (1957). In a larval study of 10 British anomuran species, namely, 1 diogenid, 8 pagurids, and 1 lithodid, to which

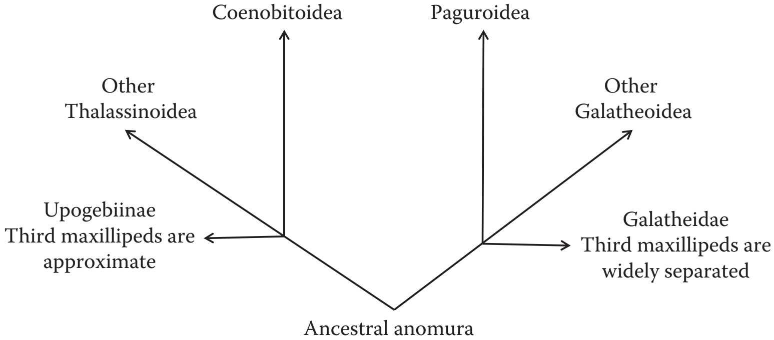

FIGURE 2.1 Hypothetical evolution of the Paguroidea of MacDonald et al. (1957). (Modified from McLaughlin, P.A., *J. Crust. Biol.*, 3, 608, 1983.)

were added data gleaned from the literature for 9 more pagurids and 11 diogenids, these authors reported differences in larval development that suggested a major division in the evolution of the Anomura (Figure 2.1). Thus, MacDonald et al. determined that these major taxa should not be simply separated into distinct families, but into distinct superfamilies. Their Coenobitoidea contained the families Pylochelidae, Diogenidae, Coenobitidae, and Lomisidae, while the Paguroidea consisted only of the Paguridae (including parapagurids) and the Lithodidae. At that time, many carcinologists still considered the Thalassinidae to be included in the Anomura, and the Coenobitoidea of MacDonald et al. was simply an offshoot of the Thalassinoidea, while their Paguroidea arose from a galatheid-like ancestral lineage. McLaughlin (1983) argued strongly against this interpretation; however, not until Martin and Davis's (2001) publication of an Updated Classification of Recent Crustacea did McLaughlin's proposed suppression of the Coenobitoidea receive recognition. Nonetheless, the Lithodidae remained a family within the superfamily Paguroidea, until McLaughlin et al. (2007) formally removed the family to its own superfamily with families Lithodidae and Hapalogastridae, a removal not accepted by all carcinologists.

2.4 Descriptive Taxonomy

2.4.1 General Overview of King Crab External Morphology

The body shape in both hapalogastrids and lithodids is very crablike with the carapace generally well calcified, albeit less so in some hapalogastrids, and covering the entire cephalothorax. Regions of the dorsal carapace, indicative of the internal organs beneath, are usually moderately well delineated by shallow grooves and identified accordingly (Figure 2.2). The integument is provided with spines, tubercles, and/or granules except in *Cryptolithodes*, where the carapace is smooth and broadened to entirely conceal the ambulatory legs when retracted against the body. The rostrum is typically spiniform except in *Cryptolithodes* and is variable in length and armature, but always present; external orbital spines (cf. Macpherson 1988a; Ahyong 2010b) may be well developed or not. The ocular peduncles generally are short but may be provided with small granules or spinules; the pigmented corneas are distoventral on the peduncles; no ocular acicles are developed. The antennular peduncles often are as long as or longer than the antennal peduncles. The antennal peduncles exhibit supernumerary segmentation, and the antennal acicles may be well developed, reduced, or absent. The third maxillipeds are pediform and widely separated basally; the ischium has a well-developed crista dentata and accessory tooth. The gills are phylobranchiate, 11 on each side: five pairs of arthrobranchs are present on the arthrodial membranes of the third maxillipeds, chelipeds, and pereiopods 2–4; one pleurobranch is developed on the body wall above each fourth pereiopod. Internally, male and female reproductive organs, together with other principal organ systems, are located in the cephalothorax as they are in brachyuran crabs.

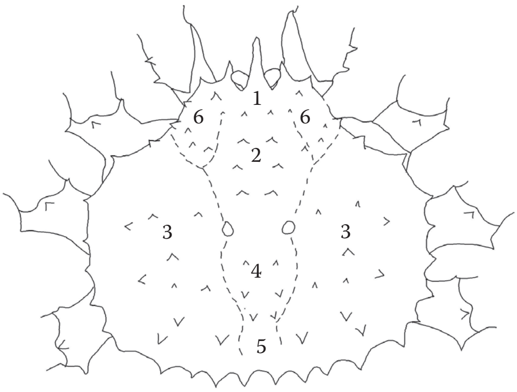

FIGURE 2.2 Diagrammatic lithodid showing general regions of the dorsal carapace: (Modified from Makarov, 1962.) (1) Frontal region, (2) gastric region, (3) branchial region, (4) cardiac region, (5) intestinal region, and (6) hepatic region. (Figure by B. Stevens.)

Chelipeds (pereiopods 1) usually, but not always, are markedly unequal, with the right largest. Pereiopods 2–4 are developed as walking legs; pereiopod 5 is reduced and most frequently carried dorsally under the carapace. The gonopores are paired in both sexes, the female gonopores open on the coxae of the third pereiopods, and the male gonopores open on the coxae of the fifth pereiopods.

The pleon is short, weakly to firmly bent under the cephalothorax and sexually dimorphic, symmetrical in males, asymmetrical in females with the plates of the left side increasing in size with maturity. The tergites of the first and second pleomeres may be distinct or fused; the second is provided with 5, 3, or 1 plate(s), or nodules, distinct or fused, in place of the actual calcified plates; tergites 3–5 are primarily membranous in males of the Hapalogastridae, variable in females, with those of the left side often having some calcification. The pleonal tergal plates are incompletely to completely calcified in the Lithodidae. Adult males lack pleopods completely, whereas females each are provided with a pair of small pleopods developed on the first pleonal segment; segments 2–5 each have an unpaired, left uniramous pleopod. Uropods are entirely absent in adults of both sexes. The telson is reduced to a small calcified plate.

The terminology applied to the pleonal tergites has the potential for serious confusion. If Macpherson's (1988a) monograph of Atlantic lithodids is taken as the basic reference, emphasis in his Figure 2.1 is placed on the subdivision of the second tergite into five distinct plates, a single median plate and paired lateral and paired marginal plates. Two examples of tergites 3–6 are provided, one with the median plates each represented by a cluster of nodules and the other by calcified median plates; paired lateral plates are present in both diagrams, while the marginal plates are contiguous with all three tergites (3–5) in one or only incompletely present in the other. A pair of median accessory plates is present only in those pleons with complete median plate calcification. This terminology also was utilized by Macpherson (1988b, 1989), McLaughlin and Lemaitre (2000), McLaughlin (2003), and McLaughlin et al. (2004) and implied by Takeda and Bussarawit (2007). Ahyong and Dawson (2006) described the pleon of *P. birsteini* and *P. stevensi* as consisting of median, lateral, and marginal plates, but those of *Neolithodes yaldwyni* as composed of a single median, paired submedian, and paired lateral plates. Ahyong and Chan (2010) also referred to these plates as median, submedian, and lateral, whereas Ahyong (2010a,b) and Ahyong et al. (2010) cited the plates as median, submedian, and marginal. There is developmental evidence (discussed in Section 2.5.2) that provides the rationale for the original Macpherson (1988a) terminology of median, lateral, and marginal plates.

2.4.2 Specific Characters Utilized in Defining Genera and Species

As implied earlier, the calcification of the third to fifth tergites of the pleon, or lack thereof, immediately distinguishes members of the two families; however, within each family, the division of the second pleonal tergite, or similarly lack thereof, is of primary importance.

2.4.2.1 Hapalogastridae

Characters diagnostic for the genera of the Hapalogastridae include the presence or absence of a median plate or nodules on the second pleonal tergite, amount of setation on the carapace and appendages, carapace armature, and/or ornamentation and the general symmetry of the chelipeds. All hapalogastrid genera, except *Hapalogaster*, are monotypic; therefore, characters diagnostic for the genera apply equally to the species. The number of spines on the carapace and armament of the chelipeds are characters used to differentiate among the four species of *Hapalogaster*.

2.4.2.2 Lithodidae

Characters diagnostic for genera of the Lithodidae include carapace shape and sculpturing; the shape and armature of the rostrum, including the presence or absence of paired lateral spines; and the development of the antennal acicle (scaphocerite), pattern of spines on the dorsal surface of the carapace, and most importantly the composition of the pleonal tergites. Other characters diagnostic for the family include the second tergite consisting of five, three, or only one plate; representation of tergites 3–5 as entirely scattered calcified nodules in males, at least left lateral plates of female entire; median plates of tergites 3–5 composed of nodules; and median, lateral, and marginal plates of tergites 3–5 all as calcified plates. Within lithodid genera, positions and abundance of carapacial spines are important, as are the segmental lengths and widths of the ambulatory legs. The overall lengths of these appendages measured on the dorsal (extensor) and ventral (flexor) margins may also be informatory, but must be used with care as these are influenced by sex and animal size. Although spine presence and lengths of the walking legs, rostrum, and carapace are subject to allometry, they can be of significance in species identifications. Cheliped asymmetry has been considered a defining adult character of all lithodoids; however, a recently described species of *Lithodes* from New Zealand reportedly has symmetrical chelipeds in both sexes (Ahyong 2010b).

2.5 Theories of Lithodoid Evolution

2.5.1 "From Hermit to King"

Although a close relationship between the hermit crab genus *Pagurus* and the lithodid genus *Lithodes* was proposed by Henri Milne Edwards as early in carcinological history as 1837, the phrase "from hermit to king" was first coined by Cunningham et al. (1992) with the publication of the authors' results of the first application of a molecular analysis to hermit/lithodid phylogeny. However, the first morphological evidences for this evolution had been put forward in the late nineteenth century by Boas (1880a,b) and by Bouvier (1894, 1895, 1897).

2.5.1.1 Morphological Evidence

Boas (1880a,b) proposed a pathway that led to the evolution of a king crab from a pagurid-like hermit crab ancestor based on morphological similarities such as the structure of the mouthparts and gills, fusion of the first pleomere with the last thoracic somite, and reduction in pleonal tergites between pagurids and lithodids. Although Bouvier (1894, 1895, 1897) agreed with Boas on the structural similarities, he took his hypothesis a step further to propose a series of gradual and progressive stages in the transformation of the pagurid pleon into a typical lithodid (Figure 2.3). Specifically, the membranous pleon of the ancestral hermit crab was progressively invaded by calcified nodules, and during the course of evolution, these nodules ultimately fused to form calcified plates. Initially, this fusion was seen in the first and second tergites, with the third through fifth occupied by only calcified granules. As plate development continued, the granules of the third through fifth tergites increased in size, and their fusion initially formed the lateral and marginal plates. Ultimately, the median nodules also fused resulting in the entirely calcified plates seen in *Cryptolithodes* (McLaughlin and Lemaitre 2000). It was Bouvier's theory of transformation through calcification and fusion that gained acceptance in the carcinological community, and this

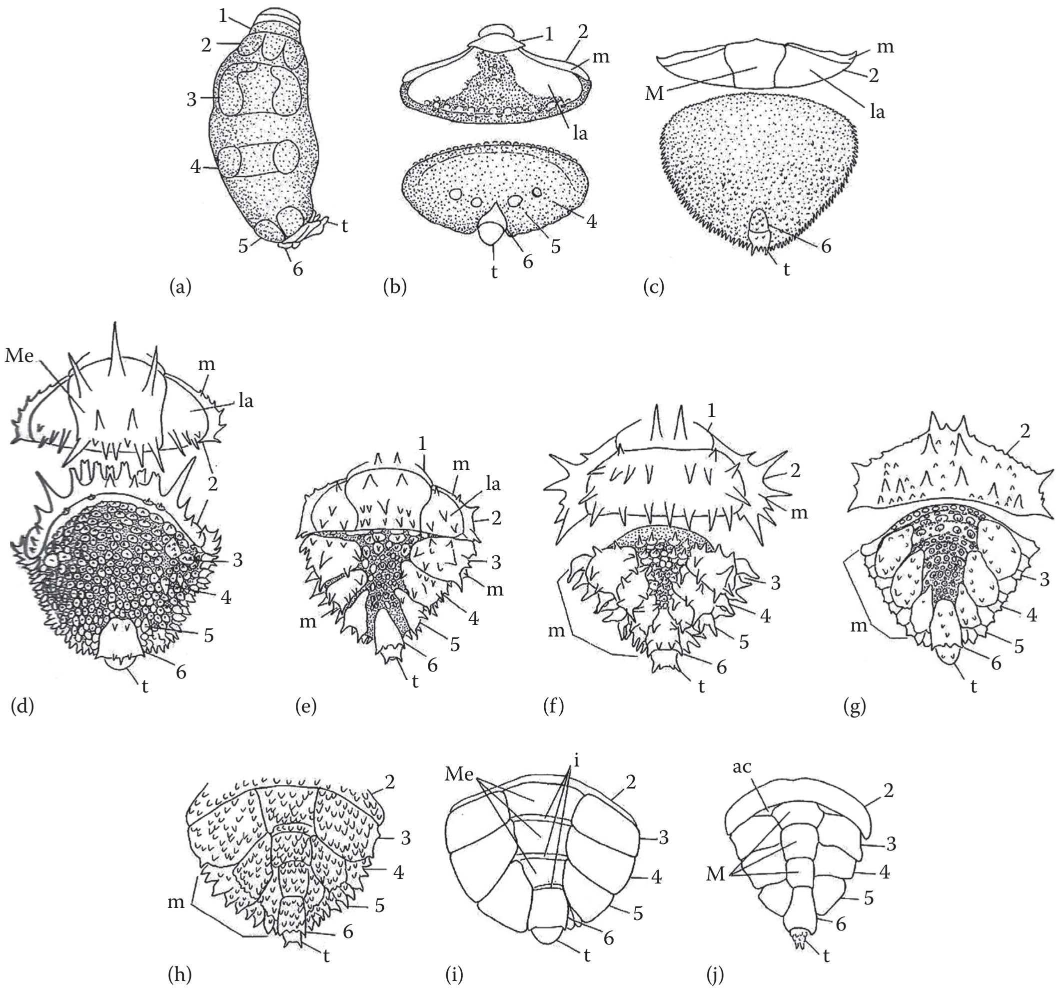

FIGURE 2.3 Bouvier's (1895, 1897) stages in the transformation of the pleon from a pagurid to a lithodid. (Modified from McLaughlin, P.A. and Lemaitre, R., *Contrib. Zool.*, 67, 79, 1997.) (a) Pagurid precursor; (b) *Haplogaster*, tergites 1 and 2 (upper), 3–6, and telson (lower); (c) *Dermaturus*, tergites 1 and 2 (upper), 3–6, and telson (lower); (d), *Neolithodes*, tergites 1 and 2 (upper), 3–6, and telson (lower); (e) *Paralithodes*, tergites 1 and 2 (upper), 3–6, and telson (lower); (f) *Lithodes*, tergites 1 and 2 (upper), 3–6, and telson (lower); (g) *Lopholithodes*, tergites 1 and 2 (upper), 3–6, and telson (lower); (h) Paralomis, tergites 1 and 2 (upper), 3–6, and telson (lower); (i) *Rhinolithodes*, tergites 1 and 2 (upper), 3–6, and telson (lower); and (j) *Cryptolithodes*, tergites 1 and 2 (upper), 3–6, and telson (lower). Abbreviations: ac, accessory plate; i, intercalary rods; la, lateral plates; m, paired marginal plates; Me, unpaired median plates; numbers indicate pleonal somites 1–6; and t, telson. Not to scale.

interpretation has been amplified by a number of more recent investigators. However, none has been as definitive as Bouvier in proposing pathways (e.g., Borradaile 1916; Wolff 1961; Richter and Scholtz 1994; Scholtz and Richter 1995; Tudge et al. 1998). Even when conflicting analytical results indicated a separation of lithodids from pagurids (Dixon et al. 2003), the authors' conclusion was that an inaccuracy occurred as a result of the remarkably derived form of the Lithodidae.

2.5.1.2 Evidence from Molecular Studies

Although the molecular results of Cunningham et al. (1992) were criticized because of the limited sample size in their investigation, theirs was the first attempt to analyze paguroid phylogeny using genetic tools. The "hermit to king" hypothesis gained support through the gene rearrangement study of Morrison et al. (2002) although the significance of their analysis was the demonstration of parallel evolution of the crablike body form. A few more recent studies of decapod phylogeny have included conclusions regarding pagurid/lithodid relationship, but none has been focused on that relationship exclusively. Ahyong and O'Meally (2004) used both morphological and molecular data and found disagreement between the results furnished by each. Tsang et al.'s (2008) emphasis was twofold: (1) to demonstrate the utility of nuclear protein-coding genes in phylogenetic inference in decapods and (2) to investigate the origin and evolution of reptant decapods. Only token attention by the latter authors was paid to pagurid/lithodid relationships. The most focused study is that of Ahyong et al. (2009), the results of which have further complicated interpretations of relationships. Ahyong et al. found the Lithodidae and Hapalogastridae nested within the Paguridae, theoretically corroborating the "hermit to king" hypothesis and casting doubt on the validity of the separate superfamily Lithodoidea as proposed by McLaughlin et al. (2007). But Ahyong et al. found polyphyly among the "asymmetrical" paguroids, as well as independence of the family Parapaguridae. As the authors noted, further research would be required using more taxa and more data to confirm or reject these results. In a more recent study, Ahyong et al. (2011) honed in on the evolution of various body forms in the Anomura, concluding that all anomuran body forms derived from symmetrical hermit crab ancestors, and thus entangling even more the relationships and possible classification of the various groups. According to their study, the asymmetrical hermit crabs evolved at least twice, one clade including the asymmetrical Parapaguridae together with the squat lobsters (Chirostylidae, Kiwaidae, and Aeglidae) and the crab-like Lomisidae, and another clade with the asymmetrical hermit crabs Diogenidae, Coenobitidae, and Paguridae, together with the crab-like Lithodidae or king crabs. The Hapalogastridae were not considered. Presumably, the king crabs are the only crablike anomurans derived from asymmetrical hermit crabs.

2.5.2 "From King to Hermit"

What has become a divisive hypothesis in lithodid phylogeny had an unintentional beginning. As a prelude to a symposium on carcinization in the Brachyura, McLaughlin and Lemaitre (1997) were asked to provide an overview of carcinization in the Anomura. During the course of their investigation, the authors came to the conclusion that carcinization as perceived to mean the evolution of a crablike body form from a shell-dwelling pagurid was incorrect. McLaughlin and Lemaitre countered the hypothesis of "hermit to king" with the proposition that through integumental calcium loss over time, the calcified pleons of lithodids evolved into the weakly calcified pleons found in hapalogastrids and ultimately to the membranous pleons identifiable with Recent pagurids, that is, from "king to hermit." However, like the molecular studies of the aforementioned authors, McLaughlin and Lemaitre's focal point was not king crab evolution, but the broader assessment of carcinization in anomurans.

2.5.2.1 Morphological Evidence

The first suggestion that the hypothesis of a close relationship between pagurids and lithodids was incorrect was that of Martin and Abele (1986), but these authors were evaluating phylogenetic relationships within the Aeglidae, with only comments upon overall anomuran phylogeny.

McLaughlin and Lemaitre (1997) reviewed in detail the morphological characters that first had prompted Boas (1880a,b) and subsequently modified his (Boas 1924) concept of pagurid/lithodid evolution, along with a similar hypothesis of their evolution by Bouvier (1894, 1895, 1897). Using 37 characters and an unconventional application of cladistic analysis, McLaughlin and Lemaitre generated a cladogram in which only a distant relationship between lithodids and pagurids exclusive of the Pylochelidae was indicated. In their analysis, this latter family was considered basal to all other anomurans because the authors were looking for pathways of carcinization, not phylogenetic relationships per se; pylochelids show little evidence of carcinization.

A second examination of anomuran phylogenetic relationships based on adult morphological characters was conducted by McLaughlin et al. (2007), this time utilizing 79 characters. The in-group consisted of the 15 anomuran families and the 2 subfamilies of the Lithodidae. The cladogram generated by the authors' results distinctly separated the two subfamilies of the Lithodidae from the Paguridae, suggesting instead a much closer relationship between these subfamilies and the Hippoidea. McLaughlin et al. elevated both subfamilies to familial rank in their own superfamily, Lithodoidea. However, these authors could find no synapomorphies shared by the Lithodoidea and Hippoidea.

2.5.2.2 Evidence from Larval Studies

Fortuitously, in the interim, the rearing studies of Crain and McLaughlin (2000a,b) provided these authors the opportunities not only to examine the complete larval development of one lithodid and one hapalogastrid species but to document the changes that took place in the lithodoid first and second crab stages that followed the megalopae. These data were supplemented by similar stages provided on loan from several colleagues, which allowed McLaughlin and Lemaitre (2000) to decisively refute Bouvier's hypothesis of pleon transformation as well as the evolutionary scenario proposed by Richter and Scholtz (1994). These latter authors reported that divided pleonal tergites similar to those of most pagurids occurred in the Lithodidae, and that in *L. maja*, these were secondarily connected by calcified nodules or in *P. granulosa* by median plates, which suggested a secondary evolution of hard and calcified plates not seen in megalopae. McLaughlin and Lemaitre's (2000) studies confirmed the chitinous integuments of some megalopae, three hapalogastrids and three lithodids, but found these six tergites to be at least weakly calcified in four other genera, one hapalogastrid and three lithodid. Evidence gleaned from the changes that began with the molt-to-crab stage 1 confirmed McLaughlin and Lemaitre's (1997) proposition that transformation resulted, at least initially with division in the individual plates rather than fusion, but these did not occur at the same rate among or within genera.

In *Lopholithodes mandtii* (Figure 2.4), for example, they found the megalopal pleon composed of six moderately well-calcified tergites, each with its own identifiable spines. With the molt-to-crab stage 1, tergites 3–5 developed incomplete to complete lateral sutures dividing each tergite into median and lateral plates. With the molt-to-crab stage 2, the first and second tergites fused partially or completely; tergite 3 was divided into one median, a pair of accessory plates, and two lateral plates, all separated by membranous areas. These same plates are similarly identified in adults. Another example of well-calcified megalopal tergites was found in *P. granulosa*. In this species, McLaughlin et al. (2003) were able to follow plate development through crab stage 5 (Figure 2.5). In crab stage 1, the first and second tergites varied from remaining entire and distinct or becoming partially to almost entirely fused; tergites 3–5 had developed partial to complete lateral sutures dividing each into one median and a pair of lateral plates. At crab stage 3, tergites 1 and 2 were usually partially or completely fused; the lateral plates of tergites 3–5 were entirely separated from the median plates. By crab stage 5, sexual dimorphism

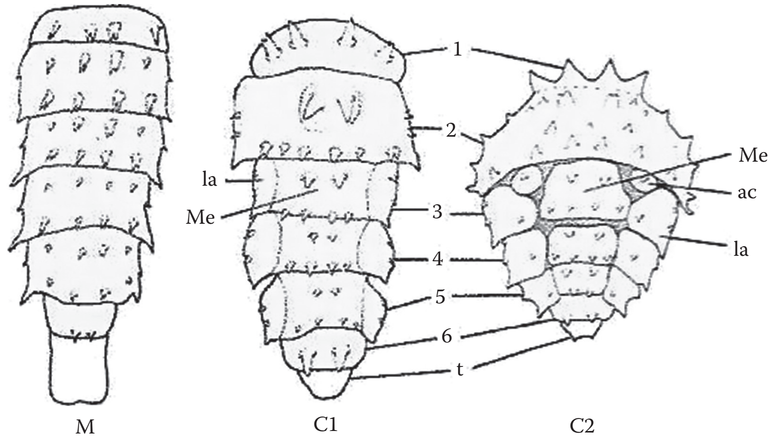

FIGURE 2.4 Megalopa (M), crab stage 1 (C1) and crab stage 2 (C2) of *Lopholithodes mandtii*. (From McLaughlin, P.A. et al., *Contrib. Zool.*, 73, 165, 2004.) Abbreviations as in Figure 2.3. Not to scale.

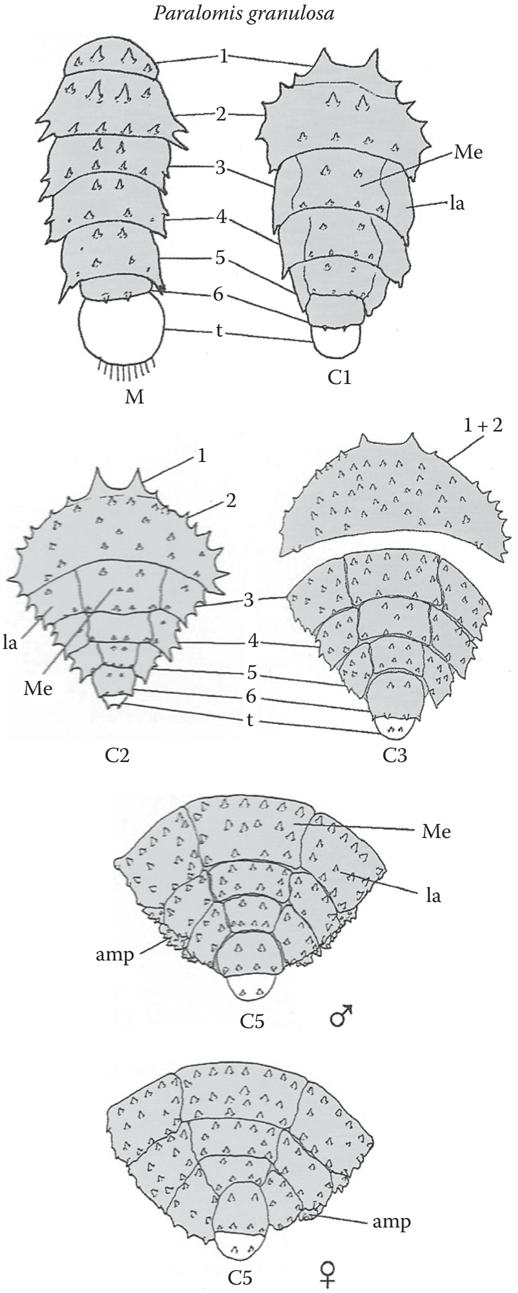

FIGURE 2.5 Megalopa, crab stage 1(C1), crab stage 2 (C2), crab stage 3 (C3), and crab stage 5 (C5) male and female of *P. granulosa*. (From McLaughlin, P.A. et al., *Contrib. Zool.*, 73, 165, 2004.) Abbreviations: amp, accessory marginal plates, remainder as in Figure 2.4. Not to scale.

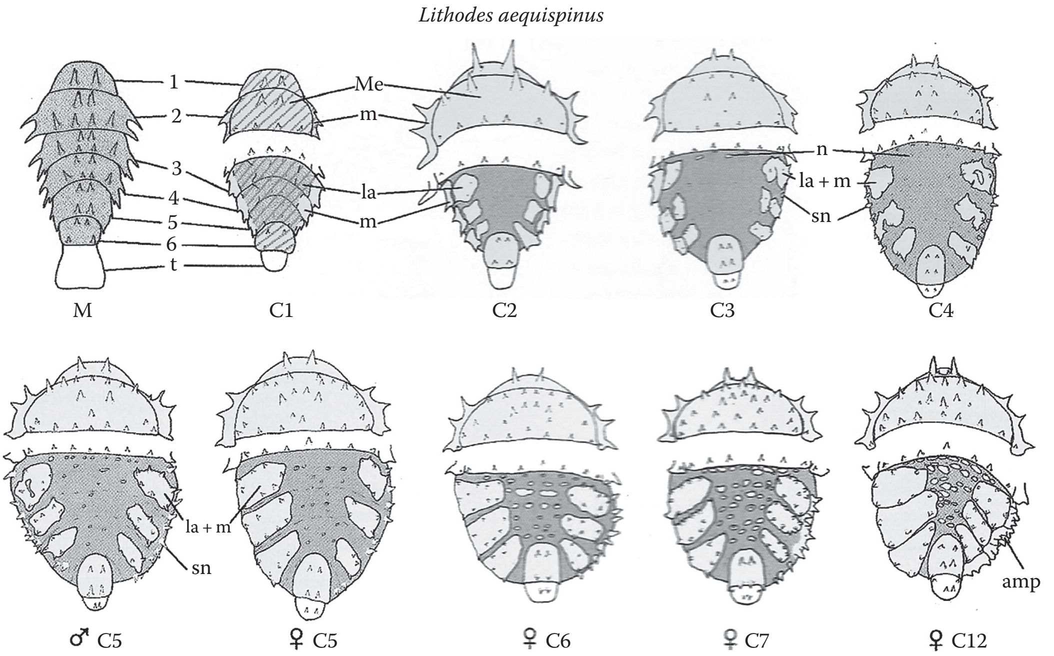

FIGURE 2.6 Megalopa, crab stages 1–4, sex indeterminate; crab stage 5 (C5, male and female); crab stages 6, 7, and 12 (female) of *L. aequispinus*. (From McLaughlin, P.A. et al., *Contrib. Zool.*, 73, 165, 2004.) Abbreviations as in Figure 2.3 with additions: n, calcified nodules; sn, spiniform nodules. Not to scale.

was apparent, with small but well-defined marginal plates present on the right sides of tergites 3–5 in females and on both left and right sides in males. Similarly, female lateral plate asymmetry was unmistakable, particularly on tergite 5. The most complete developmental series was provided for *L. aequispinus* by McLaughlin and Paul (2002). In this species (Figure 2.6), the megalopal tergites were chitinous, and tergites 1, 2, and 6 remained so or became weakly calcified with the molt-to-crab stage 1. Also in crab stage 1, the first tergite remained distinct and undivided, whereas the second and third through fifth tergites had weakly calcified, partially or entirely separated, marginal plates as could be identified by the marginal spines of the megalopa. Calcification of tergites 1, 2, and 6 increased in crab stage 2, as did calcification of the then clearly delineated lateral plates; the median areas of tergites 3–5 remained membranous. During crab stages 3 and 4, the lateral and marginal plates of the third through fifth tergites remained separated, contiguous, or partially rejoined; a few small nodules sometimes formed in the membranous integument of tergite 3. By crab stage 5, small nodules had formed in the median areas of tergites 3–5, sexual dimorphism had become apparent with enlargement of the completely rejoined marginal + lateral plates of females, and the small spiniform nodules that had developed in the margins of left tergites 3–5 in those females or both sides in males. Subsequent crab stages showed increases in nodular development in the median areas of tergites 3–5 and in the accessory marginal spines on these tergites (right only in females). By crab stage 12, these accessory marginal plates in the female had begun to fuse and form the “marginal plates” of the adult; in the male, this fusion was not yet as apparent. A similar developmental series was observed in *L. santolla*, although rearing studies were conducted only through crab stage 5 (McLaughlin et al. 2001). Clearly, information obtained through these studies of early juvenile development in lithodoids demonstrates that the hypotheses proposed on the basis of adult morphology were inaccurate. But what caused such a complicated transition? Two or three processes appeared to be involved: division, decalcification/dechitinization, and/or lack of calcium deposition. If these ontogenetic observations have a phylogenetic meaning, the conclusion must be that king crabs gave rise to hermit crabs rather than hermits to king crabs.