E. V. Radhakrishnan · Bruce F. Phillips
Gopalakrishnan Achamveetil *Editors*

# Lobsters: Biology, Fisheries and Aquaculture

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# Foreword

This book is a welcome addition to the knowledge of lobster research. The book complements other books published on lobster research and management as it focuses on Indian lobster fisheries and aquaculture developments where there have been nearly 350 research papers and reports and 19 PhD awards. The book has 15 chapters covering many aspects of the biology of a number of spiny and slipper lobster species occurring in India and the status of lobster fisheries and aquaculture in India. The lobster fisheries in the Indian Ocean Rim countries and lobster aquaculture developments in Vietnam and Indonesia are also examined. The final chapter provides some perspectives and future directions of research.

The book is timely as the Second International Indian Ocean Expedition (IIOE) is currently underway (2015–2020), 50 years after the original IIOE (1959–1965), with some of the original lobster research on the biology and distribution of phyllosoma larvae being undertaken on the plankton samples collected during the first IIOE.

Many of the chapters are contributed by the authors from the Central Marine Fisheries Research Institute (ICAR-CMFRI) which has been collecting fishery and biological data on lobsters since 1950 when lobster fishing began on a subsistence scale, followed by some industrial fishing for lobsters in different parts of India. Unfortunately the development of some of these lobster fisheries was followed by overfishing due to lack of enforcement of regulations. Therefore it is important that these cases are documented and lessons learnt from them. CMFRI also initiated aquaculture research on lobsters in 1975 with the establishment of a field laboratory in Chennai. The book provides a valuable addition to our knowledge of the biology, fisheries and aquaculture of spiny and slipper lobsters.

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# Preface

Lobster is one of the most important commercially harvested marine resources in the world because of its higher economic importance. The high-value crustaceans support some of the most profitable fisheries in many countries of the world. World capture fisheries production of lobsters touched an all-time high of 0.3 million tonnes in 2016 with an additional 2000 tonnes from aquaculture. The major lobster-producing countries are Canada, USA, UK, Australia, Indonesia, Cuba, Brazil and Mexico. With over 260 species of extant lobsters under 54 genera identified till date, they constitute one of the prominent groups under the suborder Macrura Reptantia, owing to their large size and reasonably dense population forming commercially important fisheries in many parts of the world. Apart from their economic importance, they play a key role in maintaining and balancing the marine ecosystem, acting both as a benthic predator and as a prey. The world trade in lobsters grew substantially from 110,000 tonnes in 2001 to 170,000 tonnes in 2014 valued at US$3.3 billion. The scientific investigation on clawed and spiny lobsters gained importance as their fisheries became more profitable and the need for management of the resource more inevitable. Biological research on scyllarid lobsters was on a low key as they are not as commercially important as the nephropid and palinurid lobsters. However, failure of spiny lobster fisheries in some parts of the world due to overexploitation and poor management triggered commercial interest shifting towards the scyllarids. They form an important by-product in trawl fisheries, and wherever they are directly targeted, their volume has declined sharply and the fishery collapsed with no sign of recovery even after many years.

Lobsters were known to humans since the seventeenth century, with the first recorded lobster catch in 1605. The first scientific publication (monograph) on clawed lobster biology was compiled and published by Francis Hobart Herrick in 1895. Bruce F. Phillips and J. Stanley Cobb organized the First International Workshop on Lobster and Rock Lobster Ecology and Physiology (ICWL) in 1977 in Perth, Australia, which was followed by ten international workshops in different countries. The conference proceedings were published in several journals. The first comprehensive book (*The Biology and Management of Lobsters*) devoted to clawed and spiny lobsters (two volumes) edited by J.S. Cobb and B.F. Phillips was published by Academic Press in 1980. However, there was a big gap after the publication of this book, and in 1994 B.F. Phillips, J.S. Cobb and J. Kittaka edited and published a book focusing mainly on *Spiny Lobster Biology, Aquaculture and Management*. This volume was followed by a book on *Biology of the Lobster: Homarus americanus* (edited by Jan Robert Factor), and in 2000, B.F. Phillips and J. Kittaka updated an earlier volume published on spiny lobster fisheries and culture. Then in 2006, B.F. Phillips edited and published a book entitled *Lobsters: Biology, Management, Aquaculture and Fisheries*. The second edition of the book by B.F. Phillips, *Lobsters: Biology, Management, Aquaculture and Fisheries*, was published in 2013. In general, clawed and spiny lobsters received the maximum attention in these books. In 2007, Kari Lavalli and Ehud Spanier edited and published the first multi-authored book, *The Biology and Fisheries of the Slipper Lobster*, focusing on scyllarid lobster biology and fisheries. Two chapters, 'Global Review of Spiny Lobster Aquaculture' and 'Slipper Lobsters', published in the book *Recent Advances and New Species in Aquaculture* in 2011 and edited by Ravi Fotedar and B.F. Phillips, provide additional information on aquaculture of lobsters.

Lobster research in India probably dates back to the late nineteenth century when Alcock and Anderson (1894) documented the first report on deep sea crustaceans from the Bay of Bengal and Laccadive Sea (Lakshadweep), based on the collections by the exploratory cruise, H.M. Indian marine survey steamer 'Investigator'. A series of papers on the biology and distribution of phyllosoma larvae were published based on the plankton samples collected from the Indian Ocean by the DANA Expedition and the International Indian Ocean Expedition (IIOE). The Central Marine Fisheries Research Institute (CMFRI) under the Indian Council of Agricultural Research has been collecting fishery and biological data on lobsters since 1950 and is the only statistical database on lobsters in India. Lobster fishing, which began on a subsistence scale in the 1950s, flourished with the establishment of seafood processing plants along the southwest coast of India and export. In Kanyakumari district of Tamil Nadu, on the southwest coast of India, once the largest producer of lobsters in India, the catch has declined dramatically due to uncontrolled exploitation. With the expansion of trawl fishing, the northwestern states of Maharashtra and Gujarat became the leading lobster producers. However, landing in this part of the coast has also declined due to overharvesting, in the absence of any specific fishing regulations. Research investigation on the biology, fishery and population dynamics of lobsters from the southern (1960s) and the Bombay (Mumbai) coast (late 1980s and early 1990s) provide a volume of information on the stock position of lobsters. On the recommendation of CMFRI, Minimum Legal Size (MLS) for export of four species of lobsters was notified by the Ministry of Commerce and Industry, Government of India. However, in the absence of strict enforcement of fishing regulations by the state governments, the resource is facing extreme fishing pressure.

Lobster aquaculture research, specifically in Australia, is on the threshold of a phenomenal breakthrough with success in commercial-level hatchery production of the spiny lobster *Panulirus ornatus* and slipper lobsters of the genus *Thenus.* In India, aquaculture research on lobsters was initiated by ICAR-Central Marine

Fisheries Research Institute (CMFRI), Cochin in 1975 with the establishment of a Field Laboratory at Kovalam, Chennai. The centre has been conducting research on physiology, breeding, puerulus settlement, reproductive biology, feeding and growth of tropical spiny and slipper lobsters since then. Captive maturation and breeding of the spiny lobster *P. homarus homarus* and the slipper lobster *T. unimaculatus* have been achieved with successful seed production of the latter. The technical and economic feasibility of Lobster culture in indoor system were tested. Sea cage culture for value addition to lobsters, incidentally caught during fishing operations, on the southern and northwestern coasts involving local fishermen had a positive impact on the livelihood of coastal impoverished fishermen. Apart from CMFRI, lobster research has also been carried out by the Tamil Nadu Veterinary and Animal Sciences University and National Institute of Ocean Technology.

Although several books on biology, fisheries, management and aquaculture have been published on lobsters with scientific contributions from international experts, only little attention has been given to Indian lobster fisheries and aquaculture developments. The Indian authors have published nearly 350 research papers and reports and 19 researchers have been awarded PhD by various Universities. One of us (EVR) is most fortunate to have been mentored by the pre-eminent researchers who pioneered research on lobsters. We believe that it is time to compile and review available biological information and bring out a volume with focus on research carried out in India. Earlier books have brought out a large volume of information on biology, ecology, fisheries, management and aquaculture of lobsters. The book opens with a brief introduction, general biology and life history of nephropid, palinurid and scyllarid lobsters followed by an updated taxonomy of world's marine lobsters, molecular phylogeny, a checklist of Indian lobster fauna and global distribution of palinurid lobsters. The book also reviews the status of lobster fisheries in India with a brief description of fisheries and management in Indian Ocean Rim countries. The global status and future challenges for managing major lobster fisheries has also been discussed. The chapters on Reproductive biology, Lobster mariculture, Health management in aquaculture, Larval culture of scyllarid lobsters and Aquaculture developments in Vietnam and Indonesia provide insights into aquaculture prospects of lobsters. Post harvest handling, processing, marketing and export of lobsters is covered in the following chapter. The last chapter discusses on prospects and challenges and future directions on research of this valuable resource. A bibliography of publications on lobsters has been included at the end. Since this volume is the most recent addition to a series of books published, the new developments in taxonomy, phylogeny, aquaculture and future challenges to major lobster fisheries across the globe have also been included.

We the Indian editors (EVR and AG) especially would like to thank Bruce Phillips of Curtin University, the doyen of lobster research in the world and editor of several books on lobsters, for joining as one of the editors of this book and providing guidance and support. The first editor (EVR) would like to thank Bruce Phillips, Tin Yam Chan, Clive Jones and Kaori Wakabayashi for contributing their expertise and vast knowledge in their respective fields. Thanks are also due to all the authors who immensely supported and contributed their vast experience in chapters

authored by them. We also thank the Central Marine Fisheries Research Institute for its support in the publication of this book.

It is our earnest hope that this volume will spur greater research interest amongst scientists and graduate research students in better understanding of lobster life history, physiology, genetics and pathology.

Cochin, Kerala, India — E. V. Radhakrishnan
Perth, WA, Australia — Bruce F. Phillips
Cochin, Kerala, India — Gopalakrishnan Achamveetil

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# About the Editors

**E. V. Radhakrishnan** joined the Central Marine Fisheries Research Institute, Kochi, under the Indian Council of Agricultural Research as scientist in 1976, after completing his post-graduate studies in marine biology from the University of Kerala. Throughout his scientific career spanning for more than 35 years, he has been studying lobster biology, physiology, ecology and fisheries and exploring the possibilities of aquaculture of lobsters. He has been instrumental in developing aquaculture laboratories at regional and research centres of CMFRI. He held the position of Head of the Crustacean Fisheries Division for 10 years and as Emeritus Scientist of ICAR for 2 years. He was the principal investigator of two World Bank-funded projects, 'Mud Crab Breeding and Seed Production' and 'A Value Chain on Oceanic Tuna Fisheries in Lakshadweep Sea'.

Dr. Radhakrishnan organized a series of stakeholder awareness workshops on lobster conservation in the maritime states of Tamil Nadu, Maharashtra and Gujarat under a participatory management project. The Ministry of Commerce issued a notification on minimum legal size for export of lobsters based on his studies and recommendation by CMFRI.

Dr. Radhakrishnan has been the co-editor of the *Handbook of Marine Prawns of India* and editor of research manuals and handbooks including contribution of chapters to several national and international books on lobsters. He has authored more than 200 peer-reviewed publications and technical reports.

**Bruce F. Phillips** was a scientist studying spiny lobsters with CSIRO for 28 years, before spending 3 years as the chief scientist for the Australian Fisheries Management Authority in Canberra.

Since 1996 he has been a research fellow and later an adjunct professor at Curtin University, in Western Australia. He is currently in the School of Molecular and Life Sciences and associated with several research projects developing spiny lobster aquaculture and enhancement.

Dr. Phillips has been the editor of 12 books on rock (spiny) lobster biology, management and aquaculture, including the contribution of many of the chapters in these volumes. He has also edited two books on eco-labelling in fisheries. In 2017 he published a two-volume book on *Climate Change Impacts on Fisheries and Aquaculture: A Global Analysis*.

**Gopalakrishnan Achamveetil** is a conservation geneticist with 29 years of research experience in the field of genetic characterization and gene banking of marine fauna. He started his career as scientist at the National Bureau of Fish Genetic Resources (NBFGR), Lucknow, in 1989 and later served as head of NBFGR Kochi Unit. Since 2013, he has been holding the position of director of CMFRI, Kochi. Dr. Gopalakrishnan has also served as the vice chairman of the Indian branch of the Asian Fisheries Society, the chairman of Genetics and Biodiversity – of the E – Consultation of Task Force (TF) Members for Development of the Network of Aquaculture Centres in Asia-Pacific (NACA) and a member of the Indo-Norwegian Working Group for Fisheries and Animal Sciences.

His areas of specialization include genetic stock identification of fishes using DNA markers, DNA barcoding of fishes using mtDNA markers, development of protocol for cryopreservation of milt of indigenous fishes for conservation, captive breeding of indigenous fishes, fish reproduction and fish genetic stock identification. He developed milt cryopreservation and captive breeding protocols of six threatened fish species and was instrumental in the development of six fish cell lines that will be of use in viral studies.

He has won several accolades during his service including a Fellowship of the National Academy of Agricultural Sciences, the DBT-CREST Award and the Asian Fisheries Society Gold Medal Award. He has authored more than 150 peer-reviewed articles and technical reports and 9 books.

# Introduction to Lobsters: Biology, Fisheries and Aquaculture

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E. V. Radhakrishnan, Joe K. Kizhakudan,
and Bruce F. Phillips

**Abstract**

Marine lobsters are high-valued crustaceans occupying a variety of habitats in tropical, subtropical and temperate oceans, from continental shelves and slopes to deep sea ridges, remote seamounts, lagoons and even estuaries. The highly diverse form and size are suited to their wide distribution in a range of shallow coastal and oceanic habitats. They are economically important, forming sustained profitable fisheries in many countries. In 2016, world capture production was 3,08,926 t, with an additional 2000 t from aquaculture. Apart from their economic importance, they are an important component of the marine ecosystems, playing pivotal roles as a prey and a predator. Lobster has been one of the most extensively studied group, and literature search has yielded more than 15,000 entries including research papers, technical reports and popular articles on taxonomy, biology, physiology, ecology, fisheries and aquaculture of clawed, spiny and slipper lobsters. The knowledge base created on individual species is critical in our understanding of the life history strategies and ecology of larvae, juveniles and adults. Advances in molecular techniques have been instrumental in resolving the conflicting hypotheses of evolutionary relationships among different taxa. Recent success in breeding and seed production has prompted researchers to develop commercially viable technologies for aquaculture of a few species, which is expected to relieve the mounting pressure on the natural resource. Lobster has been subjected to intensive exploitation due to high price in the international markets and except in a few countries where impeccable management strategies have ensured sustained production, the resource has been under heavy

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pressure due to poor enforcement of fishing and marketing regulations. The need to develop alternate management strategies, including co-management, is emphasised so that the resource could be conserved and their sustainability ensured. This volume attempts to present available information on biology, fisheries and aquaculture of lobsters with special focus on lobster research in India.

**Keywords**
External morphology · Life cycle · Biology · Spawning · Nephropid · Palinurid · Scyllarid lobsters

## 1.1 Introduction

Lobsters are an ecologically and commercially valuable marine crustacean resource harvested by many countries in the world. It contributes significantly to the economy of at least a few countries. Few invertebrates have attracted as much attention as lobsters due to their commercial importance and the growing research interest in the fundamental and applied biology of this unique group of crustaceans (Radhakrishnan 1989; Poore 2004). For the past seven decades, lobsters have been the subject of physiological, biochemical and molecular research and more than 15,000 research papers have been published on lobster biology, ecology, physiology, fisheries and aquaculture during the previous and current century. In fact, the clawed American lobster, *Homarus americanus*, was the most intensively studied species. The beginning of the twenty-first century witnessed an upsurge in molecular research, and these studies have redrawn the phylogenetic relationships among the different groups of lobsters (Tsang et al. 2008; Karasawa et al. 2013; Lavery et al. 2014).

Although many research findings on lobsters have been published in various journals, the first comprehensive book on lobsters was published in 1980 (*The Biology and Management of Lobsters*, Vol. 1 & 2, Edited by J.S. Cobb and B.F. Phillips, Academic Press). Austin Williams published *Lobsters of the World – An Illustrated Guide* in 1988, which was followed by L.B. Holthuis' invaluable *Marine Lobsters of the World: An Annotated and Illustrated Catalogue of the Species of Interest to Fisheries Known to Date*, FAO Species Catalogue No. 125, Vol. 13 in 1991. A series of books with almost a 14-year gap were published (*Spiny Lobster Management,* B.F. Phillips, J.S. Cobb and Jiro Kittaka, Fishing News Books, 1994; *The Biology of the Lobster Homarus americanus* by Jan Robert Factor, Academic Press, 1995; the second edition of spiny mobster management entitled *Spiny Lobsters: Fisheries and Culture* by B.F. Phillips & Jiro Kittaka, 2000; *Lobsters: Biology, Management, Fisheries and Aquaculture* by B.F. Phillips, Oxford, Blackwell, 2006; the first book on slipper lobsters, *The Biology and Fisheries of Slipper Lobsters*, Kari Lavalli & Ehud Spanier, Taylor & Francis, 2007 and the second edition of the earlier book, *Lobsters: Biology, Management, Aquaculture and Fisheries* by B.F. Phillips in 2013, Wiley-Blackwell).

Apart from publication of these books, lobster scientists from across the globe decided to meet every 3 or 4 years in different locations around the world to review the research carried out during the previous 3 years and develop strategies to meet the new challenges confronting lobster fisheries across the world. So far, 11 International Conferences and Workshops on Lobster Biology and Management (ICWL) were held from 1977 onwards though the second workshop was held only after 8 years. The first Workshop held at Perth, Australia, in 1977 was attended by 34 scientists from 6 countries who discussed issues on lobster ecology and physiology. The aims of the ICWL are to review recent advances in biology, ecology, fisheries and aquaculture of clawed, spiny and slipper lobsters to identify gaps in current knowledge and future research priorities and to encourage collaborative studies for future research (Briones-Fourzan and Lozano-Alvarez 2015). After Perth, subsequent ICWLs were held in Saint Andrews, Canada (1985), La Habana, Cuba (1990), Sanriku, Japan (1993), Queenstown, New Zealand (1997), Key West, USA (2000), Hobart, Australia (2004), Charlottetown, Canada (2007), Bergen, Norway (2011), Cancun, Mexico (2014) and Maine, USA (2017). The 12th Conference will be held at Perth, Australia, in 2020, the birth place of the first lobster conference. An interim workshop was held at Chennai, India, in 2010. The proceedings of some of these conferences were published as special volumes in international scientific journals (e.g., *Canadian Journal of Aquatic and Fisheries Sciences*, Volume 43, *Crustaceana,* Volume 66, *Marine and Freshwater Research*, Volume 48 (8) and 52 (8) and the *New Zealand Journal of Marine and Freshwater Research*, Volume, 39). The papers presented at the Chennai workshop were published in *Journal of Marine Biological Association of India*, Volume 52. Three reviews and 23 selected papers presented in the 10th ICWL at Mexico were published in the *ICES Journal of Marine Science*, *Journal du Conseil*, Volume 72 (Supplement 1), 2015. Significant advances in lobster research have happened since the publication of the last book in 2013, especially in taxonomy with additions of new species and changes in phylogenetic relationships based on molecular research. Further, new information on larval diets, feeding and pathogens has been generated, which helped in improvements in breeding and hatchery production technology of tropical lobsters. Seed production and farming of slipper lobsters have gained momentum with advancement of technologies and prospects for commercial farming of a few tropical species have emerged.

The Indian Ocean (FAO area 51 and 57) is one of the most productive ecosystems inhabited by lobsters representing almost all the groups: nephropid, palinurid and slipper lobsters. The fishers in countries bordering the Indian Ocean have been fishing for lobsters for more than 100 years, and research on ecology and biology of lobsters probably helped them to understand the behaviour and distribution pattern in relation to the ocean environment and their habitat. Lobster research in India dates back to the turn of the nineteenth century when R.I.M.S.S *Investigator* carried out coastal and deep sea surveys in the Bay of Bengal, Laccadive (Lakshadweep) Sea and the Andaman Sea. These resource surveys brought to light many new and interesting lobster fauna to science (Wood-Mason 1872; Alcock and Anderson 1894; Alcock 1901; Nobili 1903; Borradaile 1906; Balss 1925).

The Central Marine Fisheries Research Institute under the Indian Council of Agricultural Research has carried out pioneering work on biology, fisheries and aquaculture of lobsters. The institute has a strong database of gear and species-wise lobster landings across the country from 1950 onwards. The research information delivered in this volume, especially on the fisheries in India, is based on the institute's database. Nearly 350 research papers have been published on Indian lobster fauna in national and international journals and 19 theses were awarded PhDs by various universities. Kathirvel (2004) brought out a bibliography of Indian lobster fauna, compiling research papers, technical reports, popular articles and reports published by various agencies. An updated bibliography, mainly the research papers published by researchers on Indian lobster fauna and the titles of doctoral theses on lobsters, is listed in this book. However, a comprehensive book on lobsters reviewing the voluminous work carried out by lobster researchers in India has not been published. Therefore, this volume, apart from a special focus on lobster fisheries of India, also attempts to bring out the current taxonomic position of world fauna of lobsters and available information on molecular taxonomy, general biology, world distribution of palinurids, reproductive biology of spiny and slipper lobsters, diseases and recent developments in aquaculture from a global perspective.

The introductory chapter provides an outline of what is expected in this book and also from each chapter. It also deals with general biology, the external morphology of three major groups, homarid, palinurid and scyllarid lobsters, and the life cycle of homarid, spiny and slipper lobsters. Recent advances in molecular genetics have redefined phylogenetic relationships among different groups of marine lobsters. Several new species have been added after publication of an annotated checklist of marine lobsters with 248 valid species by Chan (2010). In Chap. 2, Tin Yam Chan presents the current taxonomic status and an updated checklist of global fauna of lobsters. The taxonomy and the distribution map of Indian lobster fauna are presented in Chap. 3. A review of molecular taxonomy and phylogenetics of lobsters with recent work carried out on Indian species is presented in Chap. 4. Chapter 5 deals with the ecology and distribution of world fauna of spiny lobsters, and Chap. 6 discusses the interrelationships of feeding, growth, reproduction and hormonal control of moulting and reproduction. Lobster fisheries and management in India and Indian Ocean Rim countries are presented in Chap. 7. Bruce Phillips and Monica Perez Ramirez deal with the current global status and challenges for management of lobster fisheries in Chap. 8. The large volume of work carried out on the reproductive biology of spiny and slipper lobsters with a special focus on Indian species is reviewed in Chap. 9. Lobster breeding and hatchery production is an exciting and at the same time a challenging field, spanning more than 100 years of research. The historical and recent developments in spiny and slipper lobster aquaculture with future challenges in making lobster farming a reality is discussed in Chap. 10. Identifying and developing a suitable feed for lobster larvae have been the greatest challenge for lobster aquaculturists. The art of culturing scyllarid lobster larvae by exclusively feeding on jellyfish is presented in Chap. 11. There have been two primary sectors of research and development on lobster aquaculture: (i) developing controlled breeding and hatchery production technology and (ii) utilising naturally settling lobster seed with a view on commercialising the sector. While the recent research outcome has revolutionised the hatchery-based aquaculture of spiny and slipper lobsters, Vietnam and Indonesia have embarked upon commercial aquaculture of lobsters using natural seed supply. The recent developments in lobster aquaculture in Vietnam and Indonesia and the future challenges are discussed in Chap. 12. The range of diseases found in aquaculture is one among the major problems faced by aquaculturists all over the world. Pathogens and disease management are part of aquaculture production systems and, therefore, health management in lobster aquaculture is given special focus in Chap. 13. The postharvest processing, value addition and marketing of lobsters are considered in Chap. 14 and the perspectives and future directions in lobster research in Chap. 15.

## 1.2 What Are Lobsters?

'Lobsters' generally refers to the clawed lobsters of the Family Nephropidae, though there are other related groups, the spiny/rock lobsters, slipper lobsters, reef lobsters and the blind lobsters, which all come under the Suborder Macrura Reptantia of Order Decapoda under Class Malacostraca of Subphylum Crustacea and Phylum Arthropoda. Currently, 260 valid species (including 4 valid subspecies) of extant marine lobsters in 6 families and 54 genera are recognised (Chan, Chap. 2 in this book). The clawed lobsters are more related to the reef lobsters and have a sister relationship with the three families of freshwater crayfish (Crandall et al. 2000; Porter et al. 2005; Tsang et al. 2008; Toon et al. 2009). Spiny lobsters play an important role, both as prey and predator, serving as prey for sharks, finfish and other marine species and as a keystone predator of a diverse assemblage of benthic and infaunal species (Lipcius and Cobb 1994; Toller 2003). Indiscriminate and unregulated fishing due to high demand for this special seafood has led to stock collapse in some countries. There are some well-managed fisheries in the world due to enforcement of strict regulatory measures and those fisheries are sustainable.

Lobsters are marine animals and are generally poikilosmotic (Philipps et al. 1980) over their tolerated salinity range and very few enter brackish waters. For example, the mudspiny lobster *P. polyphagus* can tolerate wide ranges of salinity 17–50 ppt (Kasim 1986). Lobsters can stay outside water for a prolonged period if their gills are sufficiently moistened, and this advantage is exploited by the live lobster export trade to transport lobsters to long distances. While some species are solitary in nature, others are gregarious. *H. gammarus* is typically found on rocky substrates but may also burrow into cohesive mud or form depressions in sand. *N. norvegicus* spends much of its time inside burrows constructed in muddy substrates. Some of the species attain large sizes. The American lobster, *H. americanus*, attains a total body length of 64 cm and weighs more than 20 kg and the Southern rock lobster, *Sagmariasus* (*Jasus*) *verreauxi*, also grows to a total length of 60 cm. The smallest lobsters are in the Family Scyllaridae. An adult specimen of *Eduarctus* (*Scyllarus*) *martensii* measures a total body length of 2.5 cm (Holthuis 1991).

The world annual production of lobsters from capture fisheries is an average 2,73,051 t, excluding a small volume of 'mud shrimps' and 'ghost shrimps', which are not currently considered as lobsters (2005–2015) (FAO 2016). The global market for lobsters is over US$4 billion a year with the Asia-Pacific region contributing about 75% of the total revenue (Musa Aman 2012). Among the 260 extant species (including four subspecies) of marine lobsters distributed worldwide, only three families are commercially important: the Nephropidae (clawed lobsters), Palinuridae (spiny or rock lobsters) and Scyllaridae (slipper lobsters). The clawed lobster fishery is supported by four genera: *Homarus*, *Nephrops*, *Metanephrops* and *Nephrospsis*. In 2015, while the American lobster, *H. americanus*, constituted 49% of the total world production, the Norwegian lobster, *N. norvegicus*, contributed 15%, the Caribbean spiny lobster, *P. argus*, 12% and others, 24% of the total production. Generally known as 'rock', 'spiny' or 'crayfishes', depending upon local or regional trade requirements, palinurid lobsters support valuable seafood trade and exports in many countries. Among the 63 species (59 species + 4 subspecies) of palinurids under the 12 genera, 34 species under 6 genera (*Jasus, Projasus, Sagmariasus, Panulirus, Palinurus* and *Puerulus*), contribute to lobster fisheries. Lobsters, of the genus *Panulirus*, support the largest fisheries. The scyllarid lobsters also have several different names, 'slipper', 'shovel-nosed', 'sand' and 'Moreton Bay bug' as in Australia, and they are found throughout the tropical and temperate world oceans. Generally, they form incidental catch in commercial trawl fisheries and are rarely targeted, except for some species valuable in the aquarium trade. Occasionally, they constitute a subsistence gillnet fishery in some areas. The commercially valuable scyllarid genera are *Thenus*, *Scyllarides* and *Ibacus.*

## 1.3 The Life Cycle of Homarid, Spiny and Slipper Lobsters

Nephropid lobsters exhibit an abbreviated larval development. The prelarva is followed by three larval stages and the fourth stage termed as the postlarva is planktonic and soon settles at the bottom and changes to a benthic lifestyle. The larval phase is completed within 3 weeks. On the other hand, spiny and slipper lobsters have a prolonged larval phase lasting several months. Lobsters undergo five different phases in their life history (Philipps et al. 1980): adult, egg, larva (phyllosoma), postlarva (puerulus or nisto) and juvenile. The juvenile phase has recently been divided into an early benthic phase and an older juvenile phase (subadults), occupying almost similar adult habitats (Herrnkind and Butler 1986). The sexes are mostly separate and some are hermaphrodites, whereas abnormal development (psuedohermaphroditism) has also been also reported (Radhakrishnan et al. 1990). Larval behaviour and the ecology of many species are still not clearly understood though fairly good information is available on recruitment processes and the environmental influences on these processes of some shallow water species (Booth and Phillips 1994). Information on larval distribution patterns is essential to understand the recruitment processes (Booth et al. 2005).

### 1.3.1 Spawning–Hatching Cycle of Nephropid Lobsters

In nephropids, the male deposits the spermatophore in the thelycum or the seminal receptacle on the ventral side of the newly moulted female (Aiken and Waddy 1980). Most observations support that fertilisation is external in nephropid lobsters (Talbot and Helluy 1995; see review by Aiken and Waddy 1980; Phillips et al. 1980; Aiken et al. 2004) except that of Farmer (1974) who thought it may be internal in

*H. gammarus.* In general, the nephropids have a 2-year reproductive cycle, spawning in early autumn, hatching the eggs the next year in summer, and then moulting (and probably mating) in late summer or early autumn (Ennis 1980, 1984; Campbell 1983; Comeau and Savoie 2002; Agnalt et al. 2007). However, deviation from the normal cycle has also been reported (Aiken and Waddy 1982; Comeau and Savoie 2002). In *H. americanus* from southern St. Lawrence, Canada, 20% of multiparous females ranging between 65 and 109 mm CL have been observed to spawn in successive years instead of the generally accepted 2-year cycle, and some could even moult and spawn during the same summer. Similarly, up to 20% of primiparous females could also moult and spawn (for the first time) in the same year instead of spawning the following year. The European lobster, *H. gammarus*, also has a pluri-annual reproductive cycle similar to *H. americanus*, spawning every 2 or 3 years (Aiken and Waddy 1986). The Norwegian lobster, *N. norvegicus*, reproduces biannually, spawning in summer and the eggs hatching out either in late winter or early summer. The incubation period varies from 6 months in the Mediterranean population to 10 months in Icelandic lobsters (Sarda 1995).

In *H. americanus*, hatching and release of eggs occur after 9–12 months incubation by the ovigerous female. Ovigerous females migrate to deeper water (>200 m) during the winter months (Campbell and Stasko 1986). Egg-bearing females return to shallow water during the following summer to hatch their eggs. Hatching takes place from late May through September. Observations made on spawning in *H. americanus* in the Massachusetts State Lobster Hatchery for 10 years show that the lowest temperature at which hatching occurs was at 12.2 °C, but usually hatching takes place at temperatures between 15 and 20 °C (Hughes and Matthiessen 1962).

The eggs hatch at night and the larvae swim to the surface of the ocean and drift away along with the currents, feeding on zooplankton. *H. gammarus* hatches out as prelarva and attaches to the maternal pleopods after hatching (Mehrtens 2011). The prelarva on release undergoes three moults before settling as postlarva on the benthic substratum (Rotzer and Haug 2015). The larval phase lasts for 15–35 days. The larva of *H. americanus* hatches out at the prelarval stage and undergoes a series of four moults before metamorphosing into the postlarval stage (Ennis 1975). Stage 1 larva is approximately 8 mm long and Stage II is 9 mm and closely resembles Stage 1. The main difference between Stage 1 and Stage II larvae is the presence of four pairs of pleopods on the second to fifth abdominal segments. Stage III larvae is 11 mm long and the prominent feature is the complete tail fan with uropods. The final postlarva (Stage IV) resembles a miniature adult and is marked by the transition from a pelagic to a benthic life style.

In *H. americanus*, the duration of postlarval stage is about 11 days at 22 °C. The settling behaviour starts 2–6 days after moulting to the postlarval stage (Cobb et al. 1989). The postlarvae prefer substrates with crevices and macroalgal cover and if suitable substratum is found, they may even settle one day after moulting to the postlarva and burrows within 34 h (Botero and Atema 1982). The shelter-restricted juvenile measures 4–14 mm CL. Usually one lobster is seen in a shelter. Sometimes, more numbers of juveniles with in a contiguous shelter space may also be found (Lawton and Lavalli 1995). The emergent juvenile stage (15-mm CL) lobsters are mostly with limited movements outside the shelter. The vagile juvenile stage

(25–40 mm CL) is the size at which they attain physiological maturity and are still found in shallower benthic environment. More extensive movements outside the shelter and foraging for food were observed. The adolescent stage is reached when the lobster measures an average 50 mm CL but is still to reach functional maturity. The lobster attains adult stage at a carapace length more than 50 mm CL and is mostly nocturnal. Seasonal reproductively mediated movements from shallow to deeper waters were observed in sexually mature lobsters (Lawton and Lavalli 1995).

Postlarval *H. gammarus* spends nearly 2 years in burrows. Their preferred habitat is gravels ranging from coarse sand to fine shingle, though juveniles have also been known to form burrows in cohesive mud. They feed on marine worms, small crabs, urchins and gastropods as well as retaining the ability to filter-feed on plankton. They leave their burrows for crevices in rocky substrate at about 15 mm CL to begin life as an adult.

### 1.3.2 Spawning and Hatching in Palinurid Lobsters

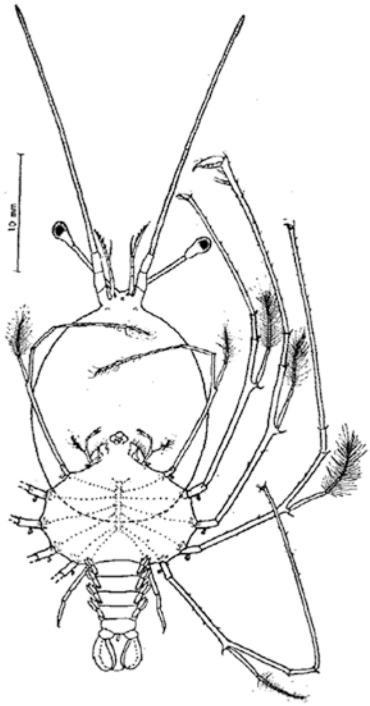
Palinurids reproduce every year after attaining sexual maturity and may even spawn several times in a year. The Caribbean spiny lobster, *P. argus*, breeds year round with peak spawning activity during the spring (March–June) followed by a smaller peak during the autumn months (September–October) (Briones-Fourzan et al. 2008). Berry (1970) observed four broods/year in *P. homarus rubellus* from eastern Africa. *P. homarus* in Oman waters follows the general pattern of breeding by the tropical palinurids that they either breed throughout the year or had an extended spawning period with multiple spawning (Al-Marzouqi et al. 2008). Laboratory-held adult females of *P. cygnus* breed continuously, averaging six spawnings in a year, when held at a constant temperature of 25 °C and given abundant food (Chittleborough 1976). *P. penicillatus* in Solomon Islands is estimated to produce at least four broods per year and even as many as 11 broods per year in the most active size class (95–105 mm CL) (Prescott 1988). Vijayakumaran et al. (2005) report an average four broods per year with a maximum of seven spawnings in a year by a single *P. homarus homarus* lobster under captive conditions. Although egg-bearing lobsters are found throughout the year, peak spawning activity has been reported in certain months. While some species such as *P. homarus homarus* spawn in shallow coastal waters, species such as *P. ornatus* in Torres Strait was reported to migrate to long distances across the Gulf of Papua and breed in certain specific breeding grounds at the eastern limit of the Gulf (Moore and MacFarlane 1984). Mass movement of lobsters to specific breeding grounds has also been recorded for *P. argus* (Herrnkind 1980), *P. cygnus* (Phillips 1983) and (*Jasus*) *Sagmariasus verreauxi* (Booth 1984, 1997). On attaining maturity, adults of *P. argus* in Cuban waters are believed to migrate to deeper offshore reefs to breed (Cruz et al. 1986; Davis and Dodrill 1980). In palinurid lobsters, fertilization is external. In Stridentes subgroup of palinuridae, males deposit the spermatophore as a sticky mass on the thoracic sternal plate of the females, which hardens on contact with seawater, whereas in the Silentes subgroup, the gelatinous spermatophore sticks to the sternum of the female temporarily and falls off rapidly (Berry 1970; Berry and Heydorn 1970; MacDiarmid 1989; George 2005). Sexually mature females release the ova, which get fertilised on contact with the sperms released from the spermatophore. Females carry the fertilised eggs on the pleonal pleopods during which the embryonic development takes place. The newly deposited eggs in palinurids are bright orange in colour, which turn into coral red and then finally to brown just before hatching. The eyespot of the larva is visible through the transparent egg shell at this stage.

There is a close relationship between egg size and fecundity, with higher fecundity in females producing smaller eggs. Adult females of the same size have higher fecundity when the eggs are smaller and vice versa, presumably an adaptation to offset high larval loss during their prolonged developmental phase in oceanic waters (Sekiguchi et al. 2007). In tropical palinurids, specifically in the genus *Panulirus*, fecundity is high and the eggs are smaller whereas in temperate species, eggs are few and larger. In many species under the genus *Panulirus*, the larvae hatch out directly as the phyllosoma larvae, which are free swimming. Sometimes these larvae of spiny lobster have also been described as 'naupliosoma', 'prenaupliosoma' and 'prephyllosoma' (Phillips and Sastry 1980). In some species of palinurids such as those under the genus *Jasus*, the larva hatches out as naupliosoma. In *Jasus edwardsii*, the larva hatches out as a nonfeeding naupliosoma stage lasting 0.5–1 h, before metamorphosing into Stage 1 phyllosoma (Tong et al. 2000). The naupliosoma is round in shape and the first three pairs of thoracic limbs are folded under ventrally (Batham, 1967). Capture of naupliosoma stage of *J. edwardsii* in the plankton suggests that this is a normal stage in this species (MacDiarmid 1985). In *P. homarus*, the larva in most instances hatched out as the free-swimming phyllosoma stage (Radhakrishnan and Vijayakumaran 1995). Though there are instances of larvae hatching out as naupliosoma as in *P. homarus* under laboratory conditions, it was believed to be due to handling/transportation stress (Vijayakumaran et al. 2014). The naupliosoma had their pereipods wrinkled so that they were unable to swim freely and settled to the bottom of the tank and died (Radhakrishnan, personal observation). In *J. lalandii*, Silberbaur (1971) observed the naupliosoma after 8–12 h of hatching settling at the bottom of the tank and moulting into the first phyllosoma stage after 5–20 min.

Unlike the short larval phase of nephropid lobsters, the life cycle of *Panulirus* species is complex and includes a prolonged oceanic larval phase, lasting several months before metamorphosing into the postlarva (puerulus). The life history of a generalised palinurid is depicted in Fig. 1.1. The egg-bearing lobsters move to deeper breeding grounds and the eggs hatch out releasing the phyllosoma larvae. The larvae carried away by the currents to oceanic waters undergo final metamorphosis to the postlarva (puerulus) and return to the coastal areas for settlement. In the western rock lobster *Panulirus cygnus*, the larval phase lasts for 9–11 months (Phillips et al. 1979) and in *Panulirus ornatus*, the larval phase is estimated to be only 4–7 months (Dennis et al. 2001) though it is still shorter under laboratory rearing conditions (refer Chap. 10). The phyllosoma larva of *Panulirus* sp. is transparent with a dorsoventrally flattened bilobed body and several plumose appendages, morphologically adapted for a prolonged planktonic existence (Fig. 1.2). The dispersive ability of phyllosoma larvae is


**Fig. 1.1** Life cycle of a palinurid lobster. (Sketch by: Joe K Kizhakudan, CMFRI)

**Fig. 1.2** Diagrammatic sketch of late-stage phyllosoma larva of *Panulirus gracilis* (from Johnson 1971). (Reproduced from FAO, 1991 Fig.13). FAO Species catalogue, Vol.13. Marine Lobsters of the world. FAO Fisheries Synopsis No. 125, Vol.13



evident from the estimated duration of nearly 24 months in *J. edwardsii*, probably the longest for a crustacean larva (Booth 1994). In the laboratory, the phyllosoma larvae of *J. edwardsii* have been reared to settlement in 212–274 days (Kittaka et al. 2005). The shorter larval duration in culture was possible due to sustained elevated water temperature of the rearing water and the availability of unrestricted amount of live feed (Ritar 2001). The larval phase of palinurids varies between 65 and 359 days depending upon species, and this information was available only after completion of the larval phase in the laboratory (Kittaka, 1994). Earlier information on phyllosoma larva morphology and their distribution was mainly based on descriptions of larvae from plankton collections (Gurney 1936; Prasad and Tampi 1959, 1965, 1966; Johnson 1971a, b; Berry 1974; Prasad et al. 1975; Kathirvel 1989). Assignment of larvae to a particular species and also to a specific stage in development was based on the presence or absence of certain appendages or spines and sometimes resulted in incorrect identifications. For example, the Stage I larvae described as that of *P. polyphagus* by Deshmukh (1968) belong to the *P. homarus–P. ornatus–P. versicolor* group, as the author's figure had subexopodal spines on leg 4 (Berry 1974), which was proved to be absent in later investigations (Prasad et al. 1975). The early stage larvae of almost all tropical *Panulirus* species of lobsters look morphologically similar whereas in *Palinurus* species, such as *P. elephas* and *P. delagoae*, the larvae hatch in an advanced stage of development. Identification of planktonic phyllosoma specimens from planktonic collections is very difficult due to the morphological similarity between species and difference within species (Konishi et al. 2006). Several lobster species share similar distribution ranges (Holthuis 1991), and their long-lived teleplanic larvae (Chittleborough and Thomas 1969) may be transported to oceanic waters far away from the adult distributional range. However, recent advances in molecular phylogeny have significantly improved species identification of lobster phyllosoma larvae. Silberman and Walsh (1992), using restriction fragment length polymorphism (RFLP) analysis based on polymerase chain reaction (PCR) amplification of 28S rDNA, successfully discriminated between phyllosoma larvae of two northwestern Atlantic *Panulirus* species, *P. argus* and *P. guttatus*. Ptacek et al. (2001) analysed partial nucleotide sequences of two mitochondrial DNA segments (cytochrome oxidase subunit I and 16S ribosomal DNA) of almost all lobster species in the genus *Panulirus*. Yamauchi et al. (2002) reported the nucleotide sequence of the entire mitochondrial DNA of the Japanese spiny lobster *P. japonicus*. Chow et al. (2006) applied nucleotide sequence analysis for *Panulirus* phyllosoma samples collected in the Japanese waters and successfully showed the samples to comprise eight species. Konishi et al. (2006) identified a late stage larvae of the spiny lobster *P. echinatus* collected from Atlantic Ocean using nucleotide sequence analysis of mitochondrial 16S rDNA.

The larval size at hatching varies between different species. The first instar of *Panulirus* species of lobsters measures a mean 1.7 mm body length and the final instar, an average 29.4 mm (Matsuda et al. 2006; Goldstein et al. 2008). Among the palinurids, the first instars of *Palinurus elephas* and *P. delagoae* are larger in size, measuring 2.8–3.9 mm in total length (TL) (Berry 1974; Williamson 1983; Kittaka and Ikegami 1988). The larger size at hatching and shorter time to metamorphose into puerulus is characteristic of these species (Kittaka and Ikegami 1988). The first-stage larva of *P. penicillatus* has a pair of unsegmented eyes, a long cephalothorax, a very short abdomen and three pairs of pereiopods and measures 1.75–1.80 mm in TL, whereas final stage larvae measure 27.0–33.6 mm TL (Matsuda et al. 2006). The phyllosoma larvae of all palinurid lobsters, except *Jasus*, *Sagmariasus* and possibly *Projasus*, have a biramous (both exopod and endopod) third maxilliped whereas *Jasus, Sagmariasus* and *Projasus* have a uniramous third maxilliped (exopod absent) (Baisre 1994). Immediately after hatching, phyllosoma larvae are highly positively phototactic whereas late-stage larvae exhibit negative phototaxis (Goldstein et al. 2008).

After hatching, the free-swimming phyllosoma larvae of palinurids pass through several metamorphic moults and finally metamorphose into the pelagic postlarva, 'puerulus', in offshore waters. The transparent puerulus is the postlarval transitional stage between the planktonic phyllosoma and the benthic juvenile and resembles the adult in morphology but lacks pigments, sculpturing, pubescence and spination of the carapace of the adult (Booth and Phillips 1994; McWilliam 1995). The first instar of *Panulirus* species of lobsters measure a mean 1.7 mm body length and the final instar, an average 29.4 mm (Matsuda et al. 2006; Goldstein et al. 2008). The puerulus swims towards the shore and settles on to the seaweeds or rocks. The non-feeding puerulus metamorphoses into juveniles within 8–12.8 days depending upon the temperature (Lemmens 1994). The puerulus survive on the energy reserves stored in the hepatopancreas during the final phyllosoma stage, which is crucial for their moulting to the postpuerulus stage and survival.

Information on the pueulus and early juvenile morphology of several species of the genera, *Panulirus*, *Palinurus*, *Jasus* and *Projasus*, is known (Bouvier 1913, 1914; Santucci 1926; Orton and Ford 1933; Caroli 1946; Gordon 1953; Berry 1974; Deshmukh 1966; Nishida et al. 1990; Briones-Fourzán and McWilliam 1997; Kittaka et al. 1997; Hunter 1999; Báez and Ruiz 2000). Wild-caught pueruli of spiny lobster measure 7.0–9.9 mm in carapace length. Pueruli obtained from laboratory-reared phyllosoma larvae of *P. penicillatus* and *P. japonicus* are slightly smaller in size compared to wild specimens whereas laboratory-reared pueruli of *P. argus* are comparatively larger than the wild-caught ones (Table 1.1). Briones-Fourzan and McWilliam (1997) compared the morphological features of the pueruli of *P. guttatus* and *P. argus*, the sympatric species distributed in the Caribbean Sea, and found the former larger in size with a more specialised form and, hence, is presumably of a recent evolutionary origin. McWilliam (1995) proposed an evolutionary sequence of four species groups (P1–P4) in the larval and puerulus phases of *Panulirus*. Groups P1 and P2 pueruli have a tapered antennal flagellum and no posterolateral sternal spines and those in Groups P3 and P4 have a spatulate or semispatulate antennal flagellum and posteriorly directed posterolateral sternal spine. The puerulus of *P. guttatus* falls in Groups P3 and P4 but has a relatively short exopod on the third maxilliped (characteristic of Group P2) and a long exopod, with a nonannulate flagellum on the second maxilliped (as in Groups P1 and P2) and, therefore, puerulus of *P. guttatus* was given a special status 'Group P2B'. *P. argus* falls in Group P1.

**Table 1.1** Body length measurements of wild-caught and laboratory-reared pueruli of palinurid lobsters

| Species | Wild/laboratory reared | Carapace length (mm) | Total length (mm) | Location | Authors |
|---|---|---|---|---|---|
| *Panulirus homarus* | Wild | 7.78 ± 1.16 (mean) | 20.83 ± 1.77 | Tuticorin, east coast of India | Dharani et al. (2009) |
| *Panulirus polyphagus* | Wild | 9.0 | 23.2 | Chennai, east coast of India | Girijavallabhan and Devarajan (1978) |
| *Panulirus ornatus* | Wild | 7.0–8.0 | – | Vietnam | |
| *Panulirus penicillatus* | Wild | – | 26.0–27.9 | Japan | Tanaka et al. (1984) |
| | | | 28.5–29.3 | Pacific equatorial | Michel (1971) |
| | Laboratory | 9.08 | 23.08 | Japan | Matsuda et al. (2006) |
| *Panulirus japonicus* | Wild | 7.0–9.9 | 20.2–26.8 | Japan | Nakamura (1994), Nonaka et al. (1958) |
| | Laboratory | 6.0–8.0 | 17.3 | Japan | Kittaka and Kimura (1989), Yamakawa et al. (1989), Sekine et al. (2000) |
| *Panulirus mauritanicus* | Wild | 8.8–9.0 | 23.3–24.0 | Western Mediterranean | Guerao et al. (2006) |
| *Palinurus elephas* | Wild | – | 21.0 | Mediterranean | Hunter (1999) |
| | Wild | 7.5–8.0 | – | Western Mediterranean | Goni and Latrouite (2005) |
| | | | – | | |
| | Wild | 7.0–8.0 | | | Diaz et al. (2001) |
| | Laboratory | 10.0 | – | Japan | Kittaka (2000), Ceccaldi and Latrouite (2000) |
| *Panulirus cygnus* | Wild | 7.0–8.0 | | Western Australia | Booth and Kittaka (2000) |
| *Panulirus guttatus* | Wild | 10.0–10.5 | 27–28 | Western Central Atlantic coast | Sharp et al. (1997), Briones-Fourzan and McWilliam (1997), Robertson and Butler (2003) |
| *Panulirus argus* | Wild | 5.4–6.5 | 16–19 | Western Central Atlantic coast | Briones-Fourzan and McWilliam (1997) |
| *Panulirus argus* | Laboratory | 6.2–6.75 | 15.7–17.9 | | Goldstein et al. (2008) |

### 1.3.3 Spawning and Hatching in Scyllarid Lobsters

The majority of temperate species of scyllarids exhibits a seasonal reproductive cycle with a clear peak spawning activity during spring and summer (Oliveira et al. 2008). Most species of the genus *Scyllarides* spawn multiple broods during the reproductive season (Spanier and Lavalli 2006). Unlike most of the tropical palinurids, which breed throughout the year, *T. unimaculatus* from Mumbai waters exhibits a well-defined breeding season from October to January (Radhakrishnan et al. 2005). Successive spawning within a season is believed to occur in *T. orientalis* and *T. indicus* (Jones 1988), *S. latus* (Spanier and Lavalli 1998), *S. nodifer* and *S. depressus* (Lyons 1970).

In a few scyllarids, absence of spermatophore on the sternum of egg-bearing females has led to speculation that fertilization may be internal (Lavalli et al. 2007). In other species, although the spermatophore is deposited on the sternal plate, it rapidly breaks down in seawater, and, therefore, is seen only occasionally (Kizhakudan 2014).

Generally, eggs of scyllarid lobsters hatch out into phyllosoma, though there are exceptions. In the laboratory, *Ibacus ciliatus* and *I. novemdentatus* hatch as phyllosoma larvae (Wakabayashi et al. 2012, 2016). Larvae of some species such as *Scyllarides latus* hatch out as the nonfeeding naupliosoma (Aktas et al. 2011). The naupliosoma, as in palinurid lobsters, remains only for a few hours and moults into first-stage phyllosoma. Earlier information on phyllosoma larvae of scyllarid lobsters was also from descriptions of larvae from plankton samples (Prasad and Tampi 1957, 1960, 1965, 1968; Johnson 1971a, b; Berry 1974; Kathirvel 1990; Inoue and Sekiguchi 2005). The duration of the larval phase of some species of scyllarids has been estimated from laboratory culture (see Chap. 10) and is, in general, shorter (17–192 days) than the palinurid lobsters. The number of instars varies among species from 4 to 13. 'Giant phyllosomas' (75–80 mm TL) have been recorded from Atlantic, Pacific and Indian Oceans (Richters 1873; Johnson 1971b; Robertson 1968; Prasad et al. 1975; Yoneyama and Takeda 1998), which were assigned to the scyllarid *Parribacus antarcticus*. Palero et al. (2014) confirmed by morphological identification and DNA-barcoding techniques that the 'giant phyllosoma' larvae, collected from Coral Sea near Osprey Reef and earlier from various oceanic regions, belong to *P. antarcticus.* The first larval instar of laboratory-reared phyllosoma of *T. orientalis* measures an average 3.89 mm TL and the final instar (Stage IV instar), 18.22 mm TL (Mikami and Greenwood 1997). The first instar of phyllosoma larva of *T. australiensis* is larger (TL 4.03 mm) (Wakabayashi and Phillips 2016). The scyllarid phyllosoma larvae have a uniramous third maxilliped unlike the majority of palinurid lobster phyllosoma larvae. The cephalic shield of phyllosoma larvae of scyllarid lobsters is wide rather than long (CW: CL ratio >1) whereas in palinurid larvae, it is longer than wide (<1). While no difference in the cephalic shield (CW:CL) ratio (1.2) between Stage I and Stage IV phyllosoma was observed in *T. orientalis*, for phyllosoma reared in the laboratory (Mikami and Greenwood 1997), the CW:CL ratio of Stage X larva (0. 0.57) was lower than Stage I (0.78) of laboratory-reared *P. argus* phyllosoma larvae (Goldstein et al. 2008). Gradual


**Fig. 1.3** Life cycle of a generalised scyllarid lobster. (Sketch by: Joe K Kizhakudan, CMFRI)

reduction in CL: CW ratio was observed until Stage III (Stage I, 0.78 and Stage III, 0.60) beyond which it was stable (0.51–0.55) throughout until the final Stage X.

The life cycle of a generalised scyllarid is depicted in Fig. 1.3. The phyllosoma larvae on hatching out are carried away by oceanic currents and after final metamorphosis settles as the nectonic 'nisto' in coastal habitats. The 'nisto' is an intermediate stage between the phyllosoma larva and the adult stage, characteristic of Achelata. The duration of nisto varies between 5 and 24 days, depending upon the species. It is a non-feeding post-larval stage similar to the puerulus of spiny lobsters. The carapace length of nistos of species from different subfamilies vary: Arctidinae (CL: 9–15 mm), Ibacinae (CL: 11–21 mm), Scyllarinae (CL: 3.5–8 mm) and Theninae (CL: 7–9 mm) (Sekiguchi et al. 2007).

For detailed information on the early life history of spiny lobsters, refer Booth and Phillips (1994), and for the slipper lobsters, Sekiguchi et al. (2007).

## 1.4 External Morphology of Nephropid, Palinurid and Scyllarid Lobsters

Lobsters, in general, have a typical crustacean anatomy with the body bilaterally symmetrical with paired appendages on each segment. The body consists of 19 somites or segments, which is covered by the hard exoskeleton (Fig. 1.4). The body is divided into two parts: an anterior sub-cylindrical cephalothorax (1–13 all fused) and the posterior pleon (14–19 all unfused) (Wahle et al. 2012). Each of the 19 somites bears a pair of appendages, except somite 14 in palinurids. Schram and

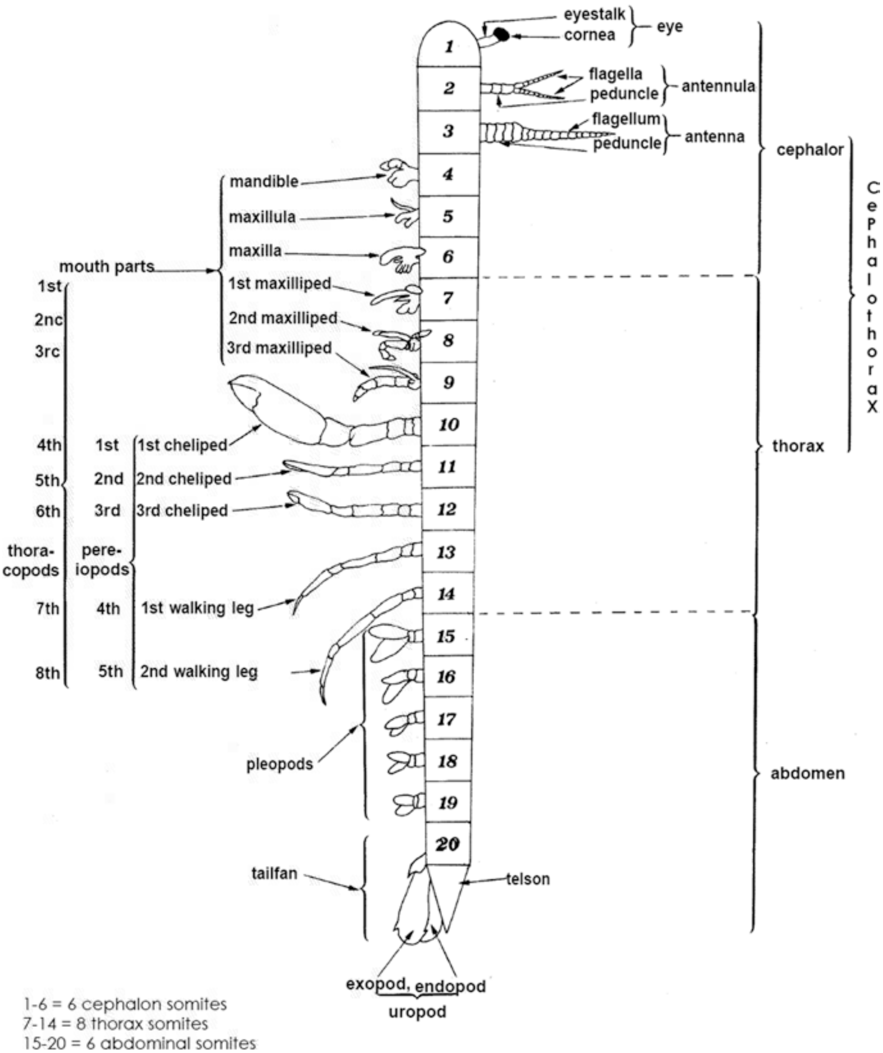



**Fig. 1.4** Schematic illustration of the body and appendages of a nephropid lobster. (Reproduced from FAO, 1991 Fig.2). FAO Species catalogue, Vol. 13. Marine Lobsters of the world. FAO Fisheries Synopsis No. 125, Vol.13

Koenemann (2004) suggested that 'pleon' is the most appropriate term for the posterior tagmata of malacostracans and is not just an equal or interchangeable alternative for the term abdomen, as the pleon of malacostracans and the abdomen of other crustaceans exhibit fundamentally different developmental pathways. The cephalon bears the sensory and feeding appendages: the eyes, antennules, antennae, mandibles, maxillules (first maxillae) and maxillae (second maxillae). The thorax bears the feeding appendages (first, second and third maxillipeds), the first pereiopods and walking legs (the remaining pereiopods). The pleon bears the pleopods (swimmerets) and, posteriorly, the tail fan (Wahle et al. 2012). The appendages may be either uniramous (exopod only) or biramous with both exopod and endopod.

### 1.4.1 Cephalothorax

On the dorsal side, the cephalothorax is covered by the carapace, which is formed by the fusion of five somites of cephalon with eight somites of the thorax in homarid, palinurid and scyllarid lobsters (Wahle et al. 2012). The carapace is either subcylindrical as in nephropids, palinurids and some scyllarids or dorsoventrally flattened as in the genus *Thenus* (Holthuis 1991). Laterally, the carapace extends up to the legs and covers the branchial chamber. In nephropids, the carapace bears a rostrum, the median extension of the anterior part of the carapace, in between the eyes (Figs. 1.5a, 1.5b and 1.5c). The carapace is divided into distinct regions with carinae, grooves and spines, which have taxonomic implications. In some groups, such as the palinurids, a part of the antennular somites forms the so-called antennular plate which bears spines; the number and arrangement are of taxonomic importance (Holthuis 1991). In some genera of palinuridae, the lateral margins of the antennular plate is ridge-like, forming a stridulating organ which produces a rasping sound when the inner margin of the antennal peduncle rubs over the ridge. Those without a stridulating organ fall in the Silentes group. Palinurids possess elongated and spiny antennae, a pair of frontal horns over the eyes, whip-like antennules which are sensory and a sub-chela on the fifth pereiopod of females (Fig. 1.6). The Scyllarids have highly modified, broad, flattened antennae, blunted nodules on carapace and

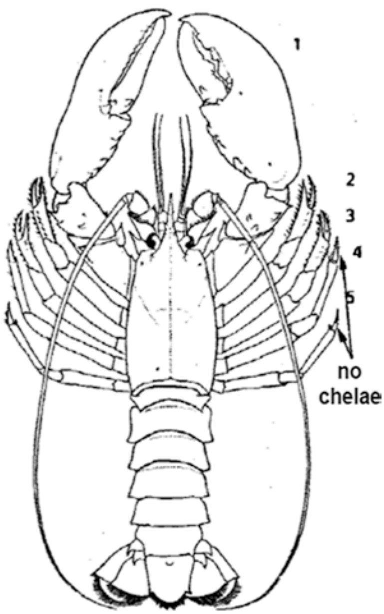



**Fig. 1.5a** Schematic sketch of *Homarus americanus*. (Reproduced from FAO, 1991 Fig.18). FAO Species catalogue, Vol.13. Marine Lobsters of the world. FAO Fisheries Synopsis No. 125, Vol.13