

THE NATURAL HISTORY OF THE CRUSTACEA



# Life Histories

VOLUME

5

EDITED BY

Gary A. Wellborn

Martin Thiel



# Life Histories

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# Life Histories

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The Natural History of the Crustacea  
Volume 5

EDITED BY GARY A. WELLBORN AND MARTIN THIEL

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## PREFACE

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*Life Histories* is the fifth volume of a ten-volume series titled *The Natural History of the Crustacea*. It follows *Volume 1: Functional Morphology and Diversity*, *Volume 2: Lifestyles and Feeding Biology*, *Volume 3: Nervous Systems and Control of Behavior*, and *Volume 4: Physiology*. The remaining five volumes will explore additional aspects of crustacean natural history, including behavioral ecology, reproduction, development, evolution and biogeography, fisheries and aquaculture, and ecology and conservation biology.

Chapters in this volume synthesize our current understanding of diverse topics in crustacean life histories. Two central themes unite the chapters: (1) an underlying cost-benefit perspective to illuminate the evolution and ecology of life histories and behaviors and (2) exploration of this perspective across the breathtaking variety of crustacean ecologies, morphologies, life cycles, habitats, and taxonomic diversity.

In this volume, Olesen examines the diversity of crustacean life cycles from the perspective of environmental adaptation, and Baeza, Ocampo, and Luppi consider the specialized life cycles of symbiotic crustaceans. Strathmann describes constraints and adaptations shaping offspring developmental strategies. Several chapters review and synthesize current literature on fundamental life history traits. Glazier discovers interesting patterns in an analysis of body size scaling relationships of clutch mass, offspring mass, and clutch size across several crustacean groups, and Maszczyk and Brzeziński review current science on ecological determinants of body size, maturation size, and growth rate. Varpe and Ejsmond integrate theoretical and empirical research on semelparity and iteroparity in crustaceans. San Vicente organizes and explores patterns of voltinism, and Vogt brings together disparate sources of research on aging and life span in crustaceans. Predation, a powerful agent of life history evolution, is the central theme of three chapters. Weiss and Tollrian provide a current and comprehensive review of predator-induced defenses, Wellborn discusses the manifold antipredator adaptations of prey species, and Bleakley presents the evolutionary and ecological consequences of cannibalism. Several chapters provide life history perspectives on salient behavioral topics. Bauer examines the often-remarkable seasonal and life cycle migrations of crustaceans, and Dawidowicz and Pijanowska review and synthesize current science on diel vertical migrations of planktonic crustaceans. Laidre considers the evolutionary ecology of construction and defense of burrows, and Hughes and Heuring review territoriality in crustaceans. Finally, Walsh and coauthors present the topic of ecoevolutionary dynamics.

Collectively, these 16 chapters provide a thorough exposition of present knowledge across the major themes in crustacean life histories. We expect this volume will be valuable to scholars and students of both life histories and crustaceans, and we also hope its syntheses and thoughtful ideas spur new avenues of research on life histories within the Crustacea and beyond.



## ACKNOWLEDGMENTS

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We thank our contributors for graciously sharing their time, energy, knowledge, and insights to make this volume possible—it has been both a pleasure and honor to work with each of them. Our editorial assistants, Annie Mejaes, Mika Tan, Tim Kiessling, and Miles Abadilla were impeccably skilled and organized, and they always kept us moving forward. We thank our external reviewers for their valuable and generous feedback. Finally, we express our appreciation to our publisher, Oxford University Press, for its commitment to this project.

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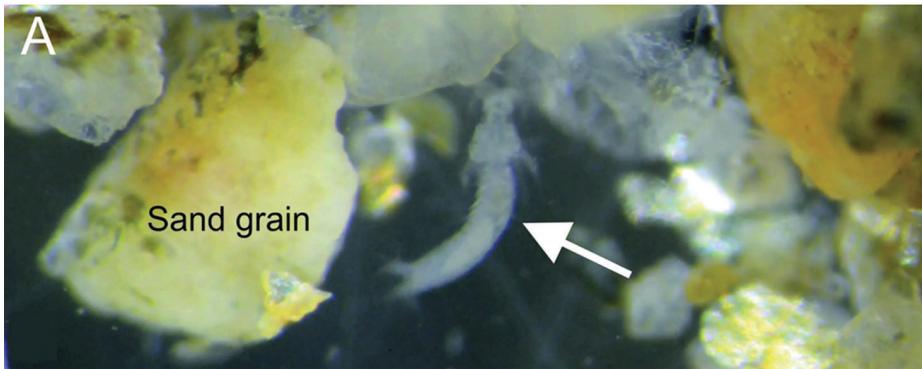


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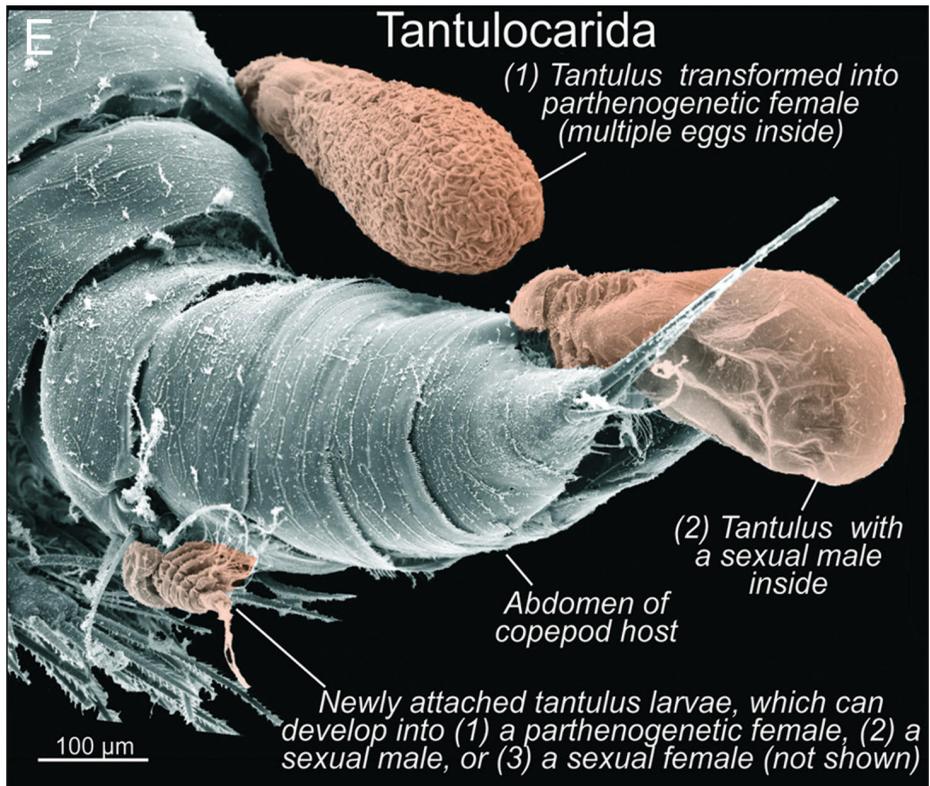
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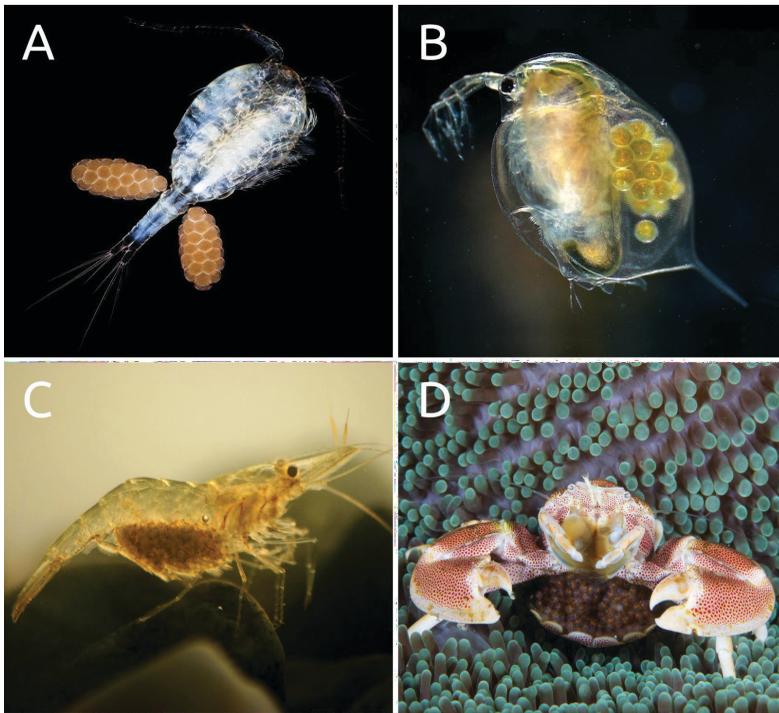
**Fig. 1.3**  
Life cycle and larval stages of Mystacocarida and Branchiopoda. (A) Adult *Derocheilocaris remanei* (Mystacocarida) among sand grains from beach at Canet Plage near Perpignan, France.

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**Fig. 1.9**

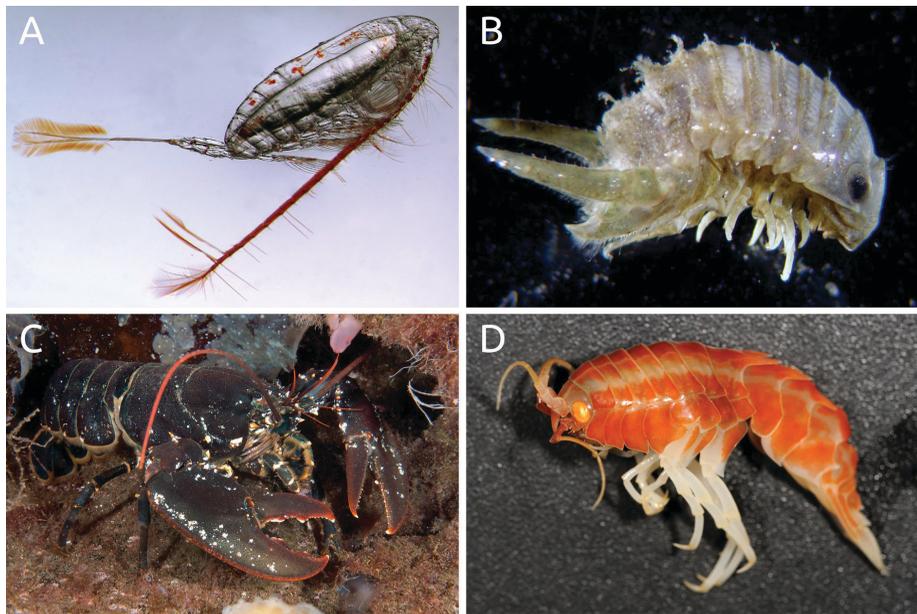
Life cycle and developmental stages of Cirripedia and Tantulocarida. (E) Three life stages of *Arcticotantulus kristensenii* (Tantulocarida) attached to hind body of copepod host (tantulocarids shaded in red).



**Fig. 3.2**

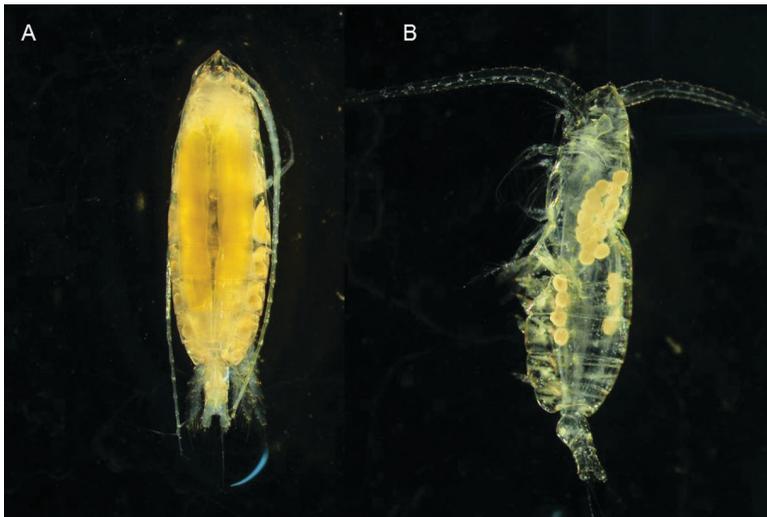
Photographs of egg-bearing crustaceans in the classes Maxillipoda (A), Branchiopoda (B) and Malacostraca (C, D). (A) Copepod with egg sacs in a sample from Surrey Bend Regional Park (British Columbia, Canada). Photograph by Waldo Nell ©, <https://www.flickr.com/photos/pwnell/16119409481/>. (B) Female cladoceran (*Daphnia magna*) with eggs. Photograph by Hajime Watanabe, under Creative Commons license (BY), doi:10.1371/image.pgen.v07.i03. (C) Decapod shrimp (*Palaemonetes pugio*) carrying eggs. Photograph by Brian Gratwicke, under Creative Commons license (BY), [https://commons.wikimedia.org/wiki/File:Palaemonetes\\_pugio.jpg](https://commons.wikimedia.org/wiki/File:Palaemonetes_pugio.jpg). (D) Berried porcelain crab (Decapoda: *Neopetrolisthes maculatus*). Photograph by Klaus Stiefel, under Creative Commons license (BY-NC), <https://www.flickr.com/photos/pacificklaus/17369531096/>.

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**Fig. 4.1**

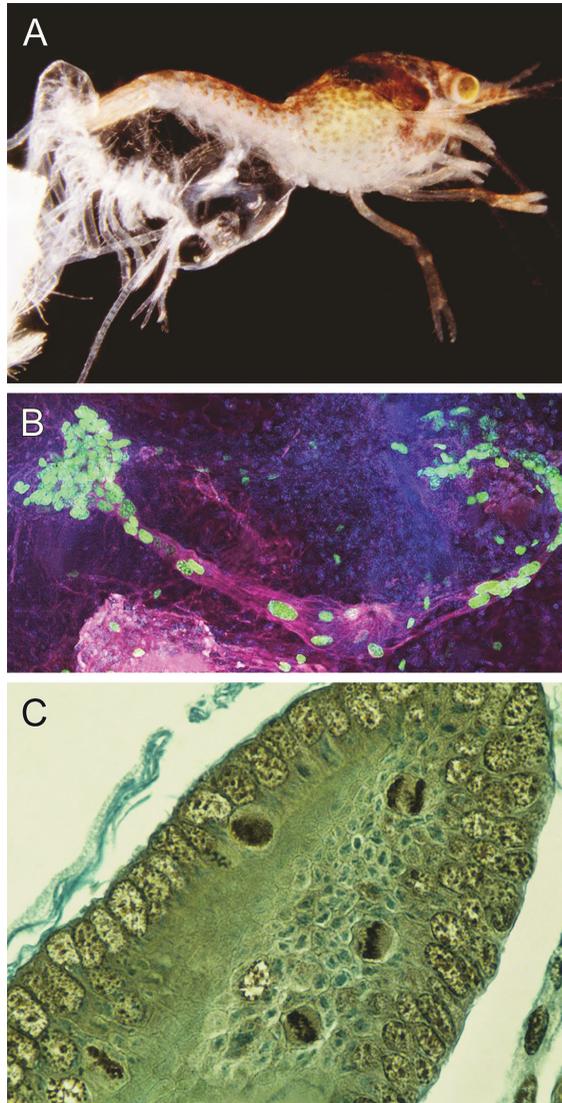
Photos of crustacean representatives with life history strategies ranging from strict semelparity to long-lived species with iteroparity. See Fig. 4.3 for a schematic representation of the parity continuum. (A) Semelparous copepods of the genus *Neocalanus* spp., here represented by *Neocalanus plumchrus*. These copepods do not develop feeding appendices in their mature stage and rely on energy reserves for reproduction, with death following reproduction (see also Fig. 4.4). Note the well filled oil sac, a large energy reserve. Photograph by Ross Hopcroft ©. (B) In the isopod *Paracerceis sculpta* the females are strictly semelparous and die after one reproductive event, whereas males mate with multiple females and live longer. Depicted here is an “alpha” male known to attract and guard females from other males. Photograph by Alice Lodola ©. (C) Many lobsters and crabs, here represented by *Homarus gammarus*, are iteroparous. In these taxa iteroparity is often combined with indeterminate growth and long lifespans. Fecundity then typically increases with age and body size. Photograph by Erling Svensen/UWPhoto ©. (D) Many amphipods are semelparous, but some also represent the very iteroparous side of the continuum. *Eurythenes gryllus* is such an example of a long-lived, indeterminate growing, and iteroparous amphipod. Photograph by Armin Rose ©.



**Fig. 4.4**

Two female individuals of the calanoid copepod *Neocalanus cristatus* in different reproductive stages. Individual (A) represents an early stage full of energy reserves and with some of the early eggs seen. Individual (B) is almost fully spent with only a few eggs left to be released, and little more than the exoskeleton remains (e.g., Miller et al. 1984). In this species the mature female stage does not develop feeding appendages and is unable to feed. Egg production is therefore fully based on capital breeding through stores gathered near the surface the previous summer and brought to depth where the female later develop and release eggs, and then die. For a semelparous organism it is adaptive to use all available resources for the single reproductive event, as illustrated by the spent stage in this copepod. In general, knowing that a given species cannot regain strength after reproduction (for instance because of the inability to feed) represents strong evidence for semelparity. Photographs by Toru Kobari ©.

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**Fig. 7.5**

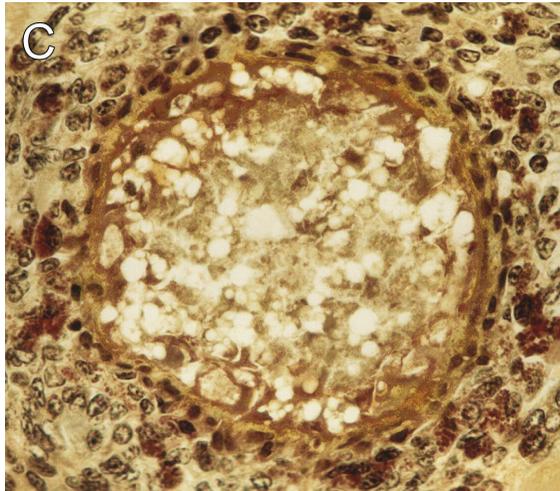
Anti-aging mechanisms in Decapoda. (A) Prevention of mechanical aging by molting in marbled crayfish, *Procambarus virginalis* (see Fig. 7.5A). (B–C) Activity of adult stem cells: (B) Neurogenic system in brain of red swamp crayfish, *Procambarus clarkii* (see Fig. 7.5F). (C) Stem cell niche in hepatopancreas of marbled crayfish (see Fig. 7.5D).

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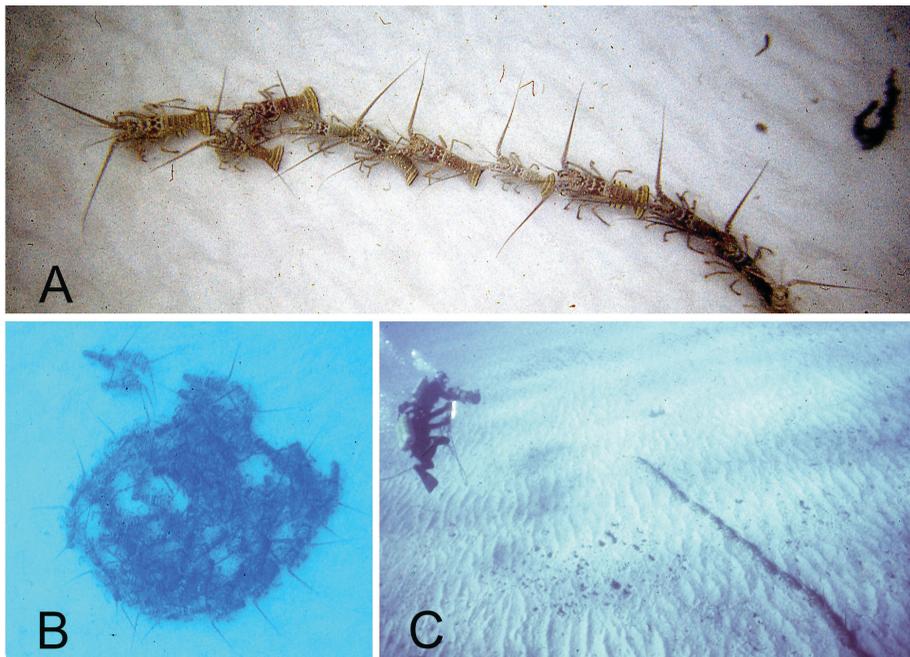


**Fig. 7.6**

(D) Lysosomal detoxification of environmental copper in the hepatopancreas of giant tiger prawn, *Penaeus monodon*.



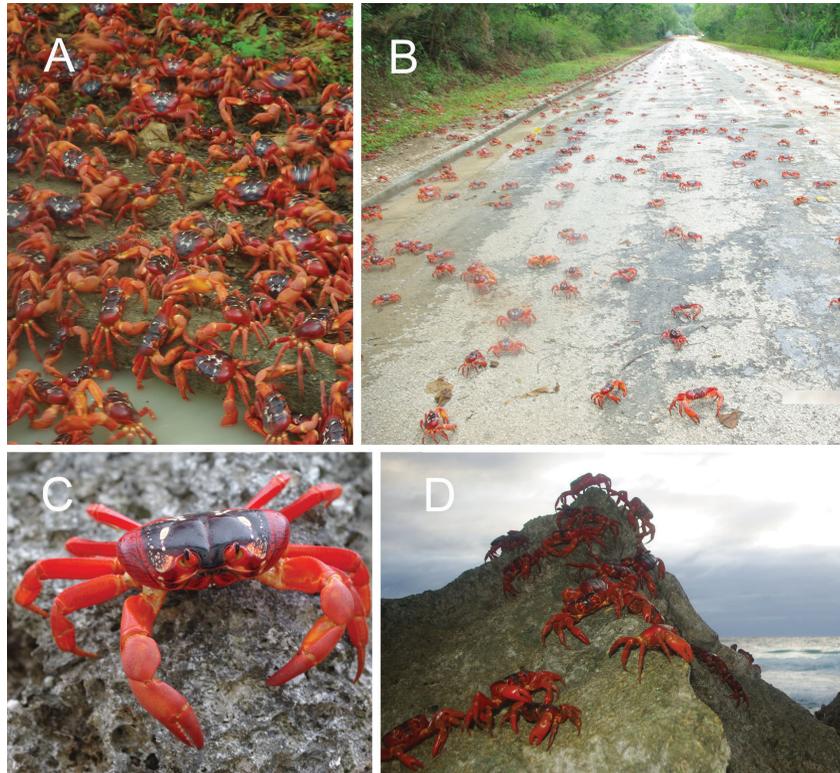
**Fig. 7.7**  
(C) Immune defense against bacterial infection in noble crayfish, *Astacus astacus*.



**Fig 8.5**

Spiny lobster (*Panulirus argus*) migration queues. (A) Close-up of a queue showing the head-to-tail single-file formation of the migrating lobsters. (B) Defensive rosette or spiral formed by a queue when threatened by a predator. (C) Migratory queue moving over a soft bottom; diver included for perspective. Original photographs courtesy of William Herrkind ©.

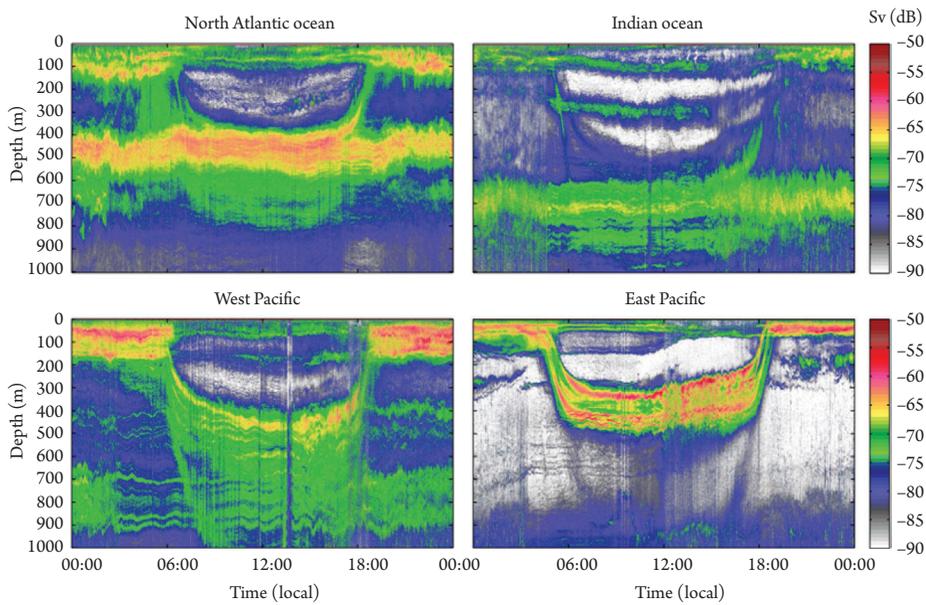
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**Fig 8.9**

Reproductive migrations by the red crab *Gecarcoidea natalis* on Christmas Island (Indo-Pacific). (A) Mass migration of red crabs towards the coast. (B) Red crabs crossing a road during migration. (C) Red crab portrait. (D) Females descending rocky sea cliffs to hatch out larvae. Photographs courtesy of Allison Shaw ©, from a research project funded by the National Geographic Society/Waite Grants program.

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**Fig. 9.1**

Examples of deep see echograms covering 24 hours periods, from different geographic regions in the mesopelagic zone of the North Atlantic ocean (upper left), Indian ocean (upper right), East Pacific (lower left), and West Pacific (lower right). Diel vertical displacements of pelagic animals forming sonic scattering layers (SSC) is evident in all areas, although proportion of migrating backscatter varies between ~20% in the Indian Ocean to ~90% in the Eastern Pacific. Most of this variability can be explained by physical properties of water masses in the localities, such as oxygen concentration, turbidity and temperature. From Klevjer (2016).



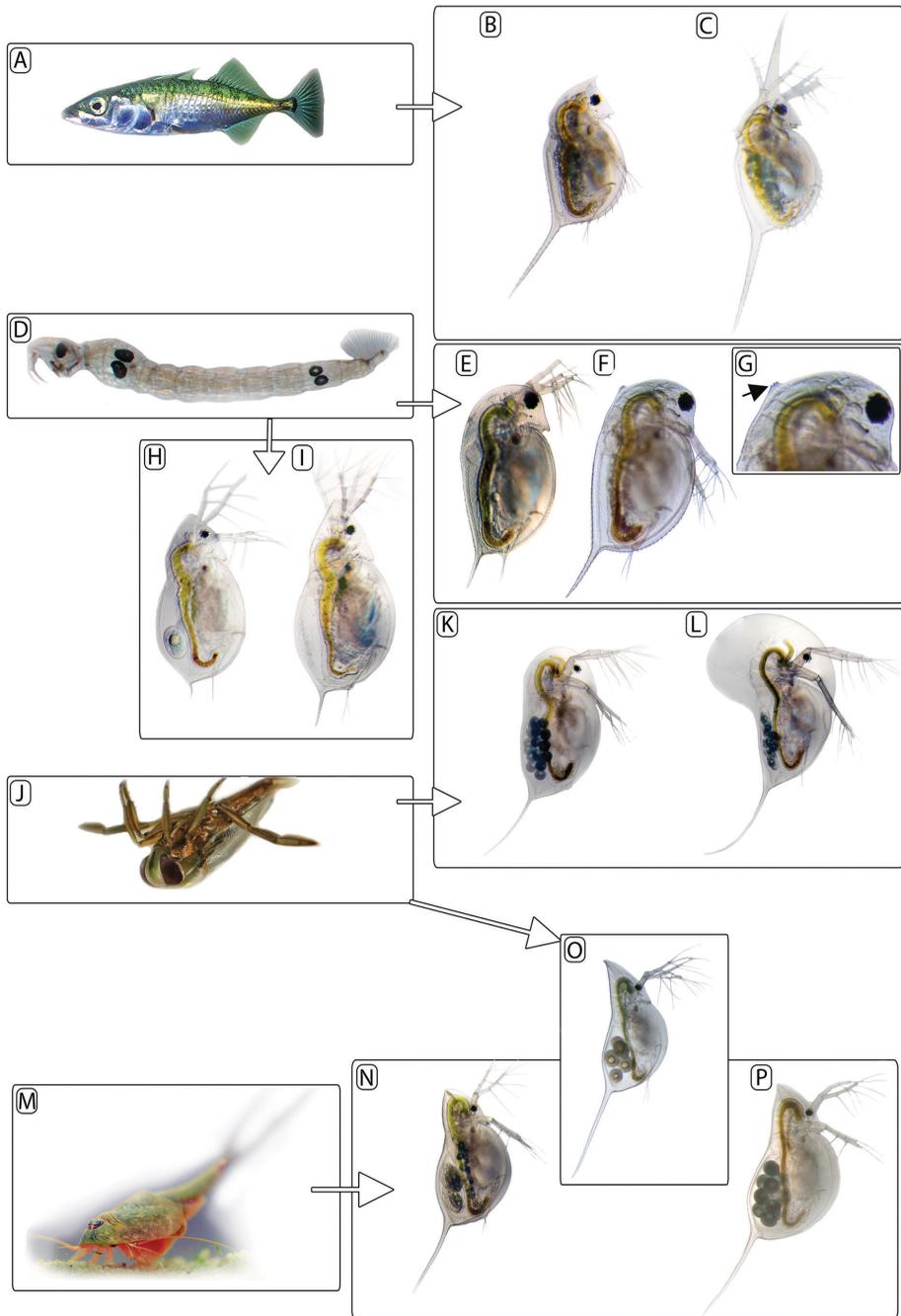
**Fig. 11.1**

(A) Burrow of a coconut crab (*Birgus latro*) carved into the ground beneath the roots of a coconut tree (*Cocos nucifera*) in the Chagos Archipelago. Burrow owner is at entrance. Note substantial coconut husk located at mouth of burrow in front of owner.



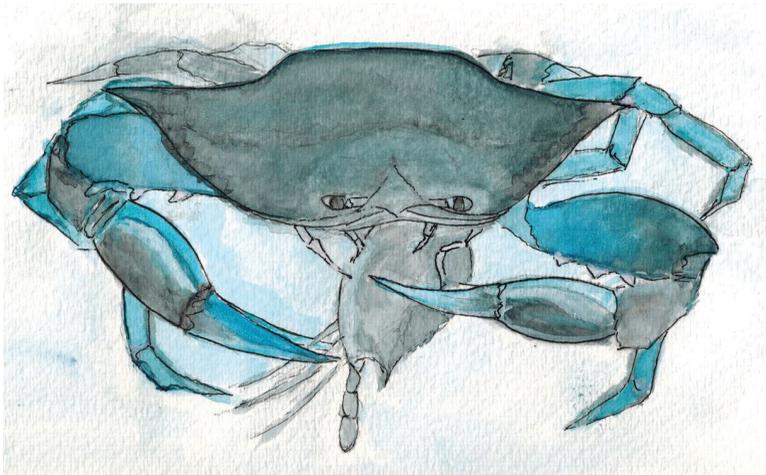
**Fig. 11.4**

Transportable burrow: a shell (*Nerita scabricosta*) carved out by terrestrial hermit crabs (*Coenobita compressus*). Left shows before excavation (unremodeled) and right shows after excavation (fully remodeled). The shell interior has been completely hollowed out by the crab, which has eliminated the shell columella.



**Fig. 12.2**

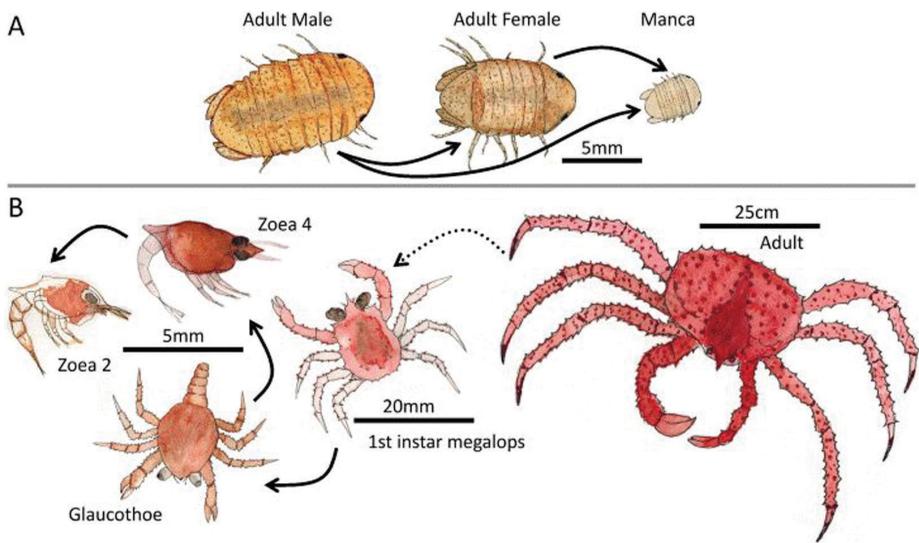
Predator induced defenses in different *Daphnia* species. (A) Predator *Gasterosteus aculeatus* (three-spined stickleback) that induces helmets in *D. lumholtzi*. (B) Undefended *D. lumholtzi*. (C) Defended *D. lumholtzi* with remarkably elongated head and tail-spines. (D) The invertebrate predator *Chaoborus obscuripes* commonly described to induce defenses in *D. pulex*. (E) Undefended *D. pulex* compared to (F) defended *D. pulex* carrying neckteeth in the dorsal head region. (G) Insert shows magnification of neckteeth displayed in (F). Likewise, *Chaoborus* induces helmet development in *D. cucullata*: (H) Undefended *D. cucullata* (I) Defended *D. cucullata* with helmet and elongated tail spine. (J) The backswimmer *Notonecta glauca* induces morphological defenses in *D. longicephala*. (K) The undefended *D. longicephala* morphotype is small and inconspicuous in comparison to the defended morphotype. (L) Defended *D. longicephala* grow large crests as well as elongated tail spines. (M) The ancient predator *Triops cancriformis* that induces defenses in *D. barbata*. (N) *D. barbata* (here: undefended form) develops defense modalities adapted to the predation regime. (O) *Notonecta*-defended *D. barbata* develop larger and straight helmets in comparison to (N) and to (P) the *Triops*-defended morphotype which has larger and backwards-bending helmets and tail-spines. Illustrated by Linda C. Weiss (2016) ©.



**Fig. 14.1**

Intraspecific predation. An adult blue crab, *Callinectes sapidus*, kills and consumes a juvenile blue crab. Based on Smithsonian Environmental Research Center 2014. Illustrated by Bronwyn H. Bleakley ©.

---



**Fig. 14.3**

Size asymmetry and profitability of prey influence the incidence of cannibalism. (A) Cannibalism in Socorro isopods (*Thermosphaeroma thermophilum*), which display size-structured cannibalism. Any smaller individual is at risk, although manca (direct developing juveniles) and small females are at greatest risk of depredation. (B) Effects of size-asymmetry and profitability on cannibalism in red king crabs (*Paralithodes camtschaticus*). Smaller individuals within a developmental cohort and across close developmental classes are susceptible to cannibalism; however, adults likely do not eat larvae because extreme size differences reduce the profitability of cannibalism among those classes. Solid lines indicate common direction of attack. Dotted line indicates direction of attack when the size difference between the aggressor and victim is small enough to make the attack profitable. Illustrated by Bronwyn H. Bleakley ©.

# 1

## CRUSTACEAN LIFE CYCLES—DEVELOPMENTAL STRATEGIES AND ENVIRONMENTAL ADAPTATIONS

---

Jørgen Olesen

### Abstract

Crustacea (or Pancrustacea) have explored virtually all possible milieus in different parts of their life cycle, including freshwater, marine, and terrestrial habitats, and even the air (pterygote insects). Many crustacean taxa display complex life cycles that involve prominent shifts in environment, lifestyle, or both. In this chapter, the overwhelming diversity of crustacean life cycles will be explored by focusing on *changes* in the life cycles, and on how different phases in a life cycle are adapted to their environment. Shifts in crustacean life cycles may be dramatic such as those seen in numerous decapods and barnacles where the development involves a change from a pelagic larval phase to an adult benthic phase. Also, taxa remaining in the same environment during development, such as holoplanktonic Copepoda, Euphausiacea, and Dendrobranchiata, undergo many profound changes in feeding and swimming strategies. Numerous taxa shift from an early larval naupliar (anterior limbs) feeding/swimming system using only cephalic appendages to a juvenile/adult system relying almost exclusively on more posterior appendages. The chapter focuses mainly on nondecapods and is structured around a number of developmental concepts such as anamorphosis, metamorphosis, and epimorphosis. It is argued that few crustacean taxa can be characterized as entirely anamorphic and none as entirely metamorphic. Many taxa show a combination of the two, even sometimes with two distinct metamorphoses (e.g., in barnacles), or being essentially anamorphic but with several distinct jumps in morphology during development (e.g., Euphausiacea and Dendrobranchiata). Within the Metazoa the Crustacea are practically unrivalled in diversity of lifestyles involving, in many taxa, significant changes in milieu (pelagic versus benthic, marine versus terrestrial) or in feeding mode. Probably such complex life cycles are among the key factors in the evolutionary success of Crustacea.

## INTRODUCTION

Crustaceans only rarely employ the same lifestyle during their entire life span and stay in the same general habitat (e.g., benthic, planktonic, parasitic). In most crustacean taxa, there is a shift (or more shifts) in environment and/or lifestyle that play a prominent role in the life cycle. The unfolding of animal life as discrete developmental phases that exhibit contrasting morphological, physiological, behavioral, or ecological attributes has been termed *complex life cycles* (see Moran 1994). This chapter explores crustacean life cycles with particular focus on smaller or larger changes in lifestyle (e.g., in locomotion and feeding) during development and their link to shifts in environment (e.g., from pelagic to benthic or from free-living to parasitic).

Classical examples of dramatic life cycle shifts are seen in numerous decapods (e.g., crabs, lobsters), where development involves a change from a pelagic larval phase to a benthic phase with bottom-associated, typically crawling adults (Felder et al. 1985, Charmantier et al. 1991, Anger 2001, Rötzer and Haug 2015), or in barnacles where the adults settle irreversibly (Glenner and Høeg 1993, Anderson 1994, Høeg and Møller 2006, Maruzzo et al. 2012). Other examples of spectacular shifts in environment during development are seen in river-inhabiting amphidromous caridean shrimps, the life cycle of which often involves upstream hatching followed by river drift of larvae to the sea, again followed by larval/juvenile upstream migration (crawling/swimming along banks at night) to the adult habitat (Bauer 2011, 2013; see Chapter 8 in this volume). The life cycle of taxa such as terrestrial hermit crabs and land crabs even requires a shift from a marine larval phase to a terrestrial adult phase (Bliss 1968, Greenaway 2003, Wang et al. 2007). The most spectacular changes in morphology and lifestyle during the life span are unarguably seen in the parasitic barnacles (Rhizocephala) and tantulocarids, where development includes complicated shifts in lifestyle involving, for example, larval stages specialized for settling and adults modified for absorbing nutrients from mostly crustacean hosts (Huys et al. 1993, Høeg 1995, Glenner et al. 2000).

Crustacean life cycles may also involve changes that are less dramatic but still important. Taxa staying roughly in the same environment during their entire life cycle may undergo many changes in feeding/swimming strategy. Numerous taxa shift from an early larval naupliar feeding/swimming system using only cephalic appendages to a juvenile/adult system relying almost exclusively on more posterior appendages. Examples are large branchiopods such as fairy shrimps (Anostraca) and tadpole shrimps (Notostraca), where early larvae exclusively use naupliar appendages for both feeding and locomotion, while these functions are fully shifted to more posterior appendages during further development (Fryer 1983, 1988, Schrehardt 1987). Other taxa such as the interstitial/benthic cephalocarids, mystacocarids, and harpacticoid copepods start with a naupliar feeding and locomotory system that is basically maintained during development, also in adults, but supplemented by a posterior system resulting in the two systems operating concomitantly from late larvae into the adult (Sanders 1963, Walossek 1993, Olesen 2001). In yet other taxa, the early developmental phase is characterized by the complete absence of feeding (lecithotrophy). This is the case in the naupliar phase of both euphausiids (krill) and dendrobranchiate shrimps, the only two taxa within Malacostraca where development involves a naupliar phase (Martin and Gómez-Gutiérrez 2014, Martin et al. 2014a, Akhter et al. 2015), but also in the entire naupliar phase of parasitic barnacles (Rhizocephala; Walossek et al. 1996), Remipedia (Koeneemann et al. 2009), and in the earliest naupliar stages of some branchiopods and copepods (Anderson 1967, Dahms 1989, Olesen 2004, Ivanenko et al. 2007). In many cases, the nonfeeding phase in the early part of crustacean life cycles has been taken to an extreme in which free-living larvae have been skipped completely. Instead, larvae are brooded in various types of brooding chambers or are attached to

specialized limbs of the female (e.g., peracarid malacostracans, cladoceromorph branchiopods, ascothoracican thecostracans, or astacid decapods; Martin et al. 2014b).

This chapter takes a broad look at crustacean life cycles. The subject is large, because a life cycle in biology can be broadly defined as a series of changes in form that an organism undergoes, returning to the starting state in the next generation, implying that virtually any aspects of the life history of a given species can be relevant. Here, the overwhelming diversity of crustacean life cycles will be explored by focusing on *changes* in the life cycles, and on how different phases in a life cycle are adapted to their environment, and, to narrow the scope, most focus has been on nondecapods (for decapod larval biology, see Volume 7 of this series). All imaginable adaptations in the life cycle to dispersal, settling, infesting, and swimming/feeding are necessarily intimately linked to the distinct and sometimes peculiar morphology of many crustacean larval types. Hence, familiarity with some of the unique larval types, both their names and morphology, is unavoidable. Therefore, at various places in this chapter short overviews of general crustacean types of development are given, spanning from the more gradual (anamorphic) type, involving a long series of stages changing only slightly during development (e.g., fairy shrimps in temporary ponds, and the “living fossils,” cephalocarids), to the more modified types of development involving abrupt, metamorphic changes with distinct larval types sometimes adapted for specific functions such as locating a host and settling in cirripedes and tantulocarids (cyprid and tantulus larvae).

For a full understanding of crustacean life cycle specializations, it is important to note that a given life cycle also is the result of its ancestry, meaning that it is best interpreted by implementing not only ecological but also evolutionary interpretations. Moran (1994) pointed out that the description of complex life cycles of animals is divided into two largely discrete bodies of literature with different foci: (1) ecologically oriented studies emphasizing ecological reasons behind the diversification of life cycles into discrete phases, and (2) developmentally oriented studies more concerned with evolutionary and phylogenetic explanations focused on the relative degree of conservatism in aspects of various life cycle stages. In reality, these two different ways of understanding life cycle adaptations are not in conflict but rather are relevant at two different time scales. Whereas the ecological approach seeks shorter-term explanations, such as food availability, for particular adaptations (e.g., a certain feeding behavior), an evolutionary/developmental approach operates at much longer evolutionary scales using shared ancestry as a tool for understanding the sometimes profound conservatism of particular developmental phases in the life cycle. One key question when dealing with Crustacea, many groups of which have complex life cycles, is the extent to which different development phases are evolutionarily linked to each other. For example, to what degree are larvae and adults free to evolve independently of one another? Or, as many developmental biologists have been concerned with, are early stages of ontogeny more conserved than late stages? These and many other aspects will be integrated into the following treatment of crustacean life cycles.

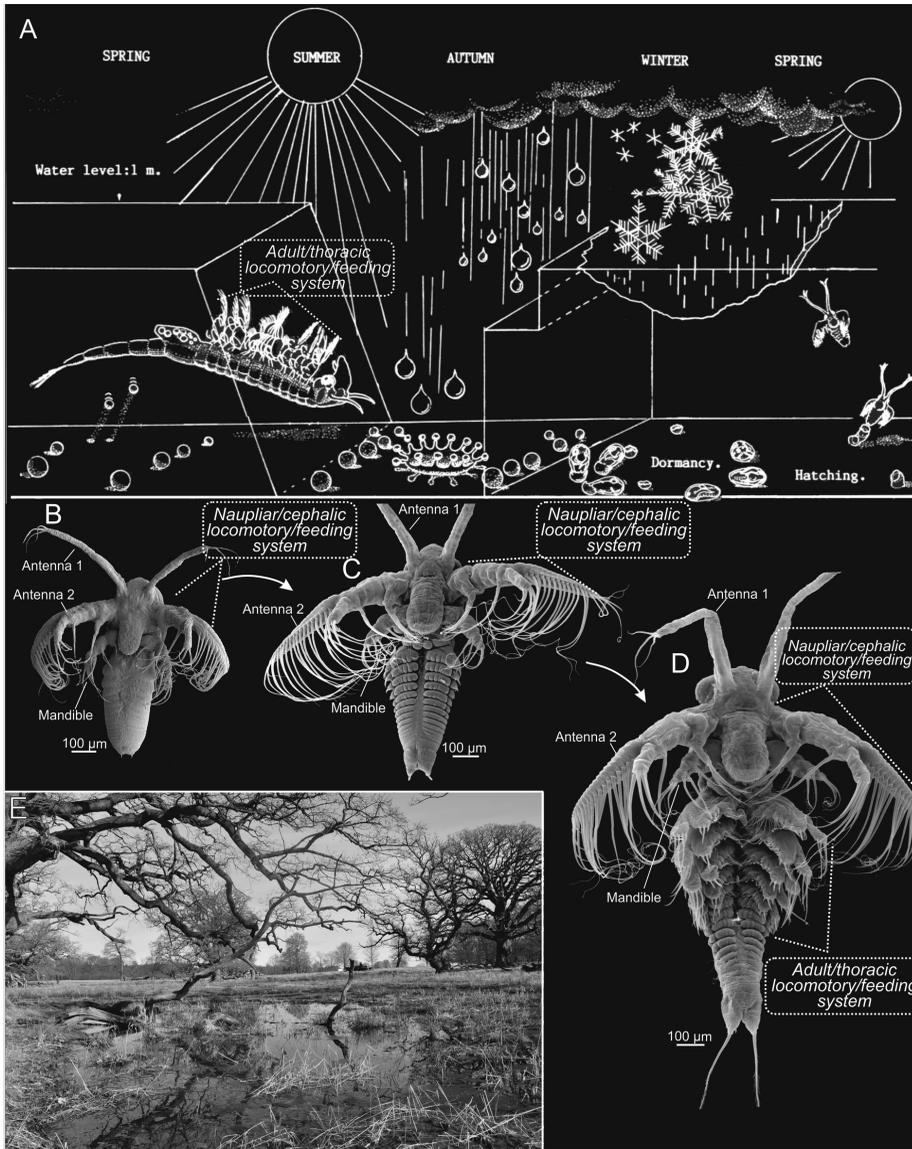
Due to the long and successful evolution of Crustacea, a multitude of developmental types and life cycles exist, and these are accompanied by a likewise diverse and not always straightforward terminology. Much terminology was defined in the *Atlas of Crustacean Larvae* (Martin et al. 2014b), but due to the complicated nature of the subject, and because definition of terms is an ongoing process that goes hand in hand with an increased understanding of homologies and phylogeny, some definitions will be repeated or modified in this chapter. A number of developmental concepts (anamorphosis, metamorphosis, epimorphosis) and their interrelationships are of particular importance, and consequently the chapter is structured around these concepts, with each section beginning with a more precise definition and discussion followed by examples from various crustacean taxa.

## GRADUAL (ANAMORPHIC) DEVELOPMENT—ANCESTRAL OR ADAPTATION TO STABLE ENVIRONMENT?

Anamorphosis, or anamorphic development, is defined by Martin et al. (2014b) as “a type of indirect development in which a hatchling or larva with few segments develops into the adult gradually, via a series of small stepwise changes in body morphology, with progressively more segments and appendages added during morphogenesis.” This type of development, where a nauplius-type larva develops into the adult, is seen in some Branchiopoda (e.g., Anostraca) (Fig. 1.1) and Cephalocarida (Fig. 1.2H–L) and was already present early in crustacean evolution, as evidenced by the Cambrian *Rehbachella kinnekullensis* (Walossek 1993). As many as 25 preadult stages have been reported for *Artemia salina* (Anostraca; Benesch 1969; also see Walossek 1993), and Fryer (1983) identified 20 instars of *Branchinecta ferox* before a full complement of functional trunk limbs was acquired. Common for these “classic” anamorphically developing taxa is that no profound changes in morphology and locomotion/feeding take place between 2 consecutive stages during the development (no metamorphosis). All major changes are stepwise and involve multiple instars. The development starts with a naupliar (cephalic) locomotory/feeding system that gradually develops into an adult thoracic one. The two systems operate concomitantly (e.g., in late anostracan larva in Fig. 1.1D) across many intermediate stages of all three taxa (Cephalocarida, Anostraca, *Rehbachella*). In adult anostracans, the thoracic system has taken over both functions entirely (except for the coxal part of the mandible, which is obviously still involved in feeding; Barlow and Sleight 1980, Fryer 1983, Olesen and Møller 2014), while in both Cephalocarida and *Rehbachella kinnekullensis*, the “naupliar two” second antennae maintain a role in locomotion (Sanders 1963, Walossek 1993) alongside a fully functional adult thoracopodal system. In accordance with a number of previous authors (Sanders 1963, Fryer 1983, Walossek 1993, Haug and Haug 2015), I view this specific type of strict anamorphic development, starting with a nauplius-type larva to which somites and functional limbs are added gradually posteriorly, as the most likely candidate for an ancestral type of crustacean development. However, in addition to being ancestral, the anamorphic development may also be an adaptation to stable environments, which, in the case of most anostracans are found in the water phase of small freshwater temporary pools, and in the case of cephalocarids as bottom dwellers both as larvae and adults (Sanders 1963). Some constancy in environment is probably a prerequisite for anamorphic development.

The anamorphosis concept, however, is considerably more complex than implied previously. Closer scrutiny provides several examples of types of gradual development that do not apply strictly to the definition. For example, in some taxa the degree of anamorphosis depends on which part of the body is considered (i.e., body somites, limbs, or internal anatomy). When comparing anostracan and cephalocaridan development, the latter has an essentially gradual development of body somites but shows a considerable “delay” in the appearance of limbs and their further differentiation (Olesen et al. 2011, Haug and Haug 2015) (Fig. 1.2H–L). Also, because crustaceans molt their external cuticle during development, the development is stepwise externally but gradual internally. Complicating things even further is the concept of complex life cycles where more than one phase of gradual development can be present during the entire course of development, separated by one or more smaller or larger, nongradual jumps in morphology, or metamorphoses, between 2 stages in the series. Well-known examples are copepods in which two anamorphic phases (naupliar and copepodite) are separated by a metamorphic shift in morphology, and dendrobranchiate decapods, where more anamorphic phases (naupliar, protozoal, and mysis phases) are separated by profound jumps in morphology (both treated in detail below).

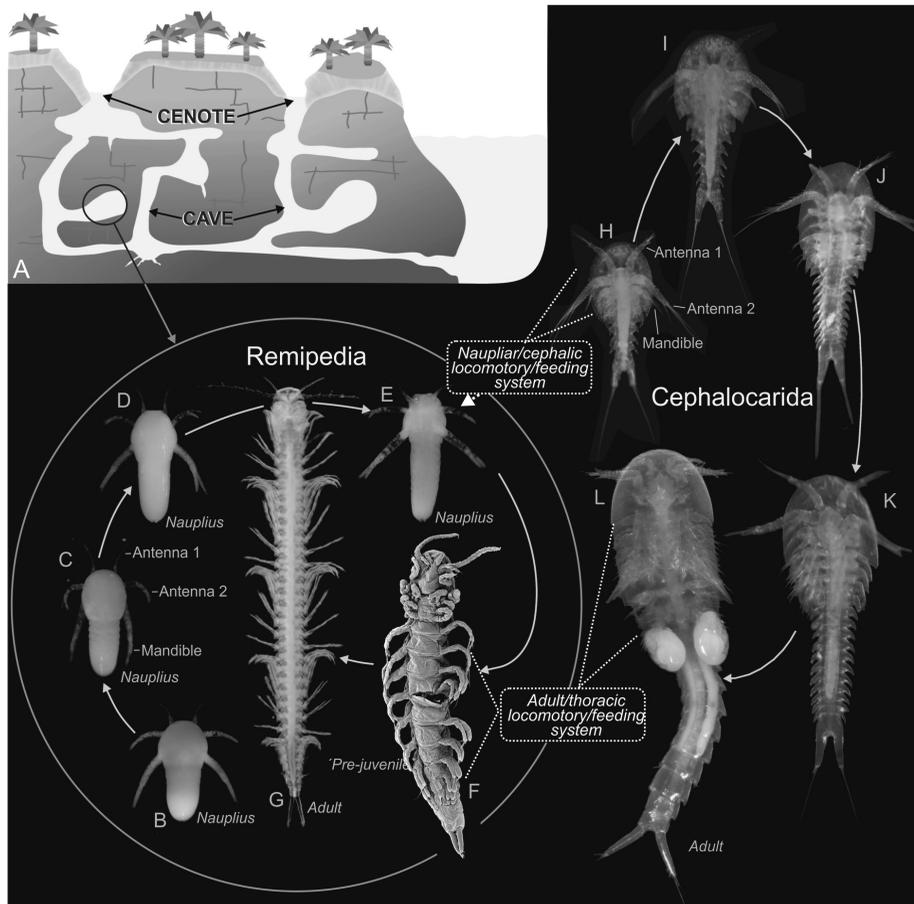
Used in the strict sense of the definition above, anamorphic development applies to only a few taxa such as certain branchiopods (anostracans), cephalocarids, perhaps remipedes, and certain Cambrian “Orsten” fossils such as *Rehbachella kinnekullensis*, that all start with an orthonauplius



**Fig. 1.1.**

Life cycle and larvae of anamorphically developing fairy shrimps (Branchiopoda: Anostraca). (A) Schematized year cycle from spring to spring of *Eubranchipus grubii* in ephemeral pool followed from hatching of resting eggs to adult. Modified from Mossin (1986), with permission from Oxford University Press. (B–D) Three larval stages of *E. grubii*, and early stage, an intermediate stage, and a late stage. Modified from Møller et al. (2004), from Springer. (E) Ephemeral pool in Denmark inhabited by *E. grubii*. Photograph by Jørgen Olesen ©.

that during development adds one or few somites in each molt until adulthood. Such strict definition is unpractical for Crustacea, which display many other types of gradual development not involving clear addition of somites. Therefore, in this chapter, “anamorphic development” is applied in a broader sense, essentially as a synonym for gradual development. This implies that anamorphic development in Crustacea does not necessarily concern the entire development but often



**Fig. 1.2.**

Life cycles of anamorphically developing Remipedia and Cephalocarida. (A) Schematized representation of typical remipede-inhabited anchialine cave system at the Yucatan Peninsula, Mexico. Illustrated by Tim Kiessling and Jørgen Olesen, under Creative Commons license (BY). (B–E) Four early lecithotrophic nauplius larvae of *Pleomothra apretocheles* (Remipedia). (F) Late larval/early juvenile of *P. apretocheles* (Remipedia). (G) Adult of *Xibalbanus tulumensis* (Remipedia) from “Cenote Crustacea,” Yucatan Peninsula, Mexico. Photograph by Jørgen Olesen ©. (H–K) Four larval stages of *Hutchinioniella macracantha* (Cephalocarida). (L) Adult of *H. macracantha* (Cephalocarida). (B–F) Modified from Koenemann et al. (2009), with permission from Springer. (H–L) Modified from Olesen et al. (2014c), with permission from Johns Hopkins University Press.

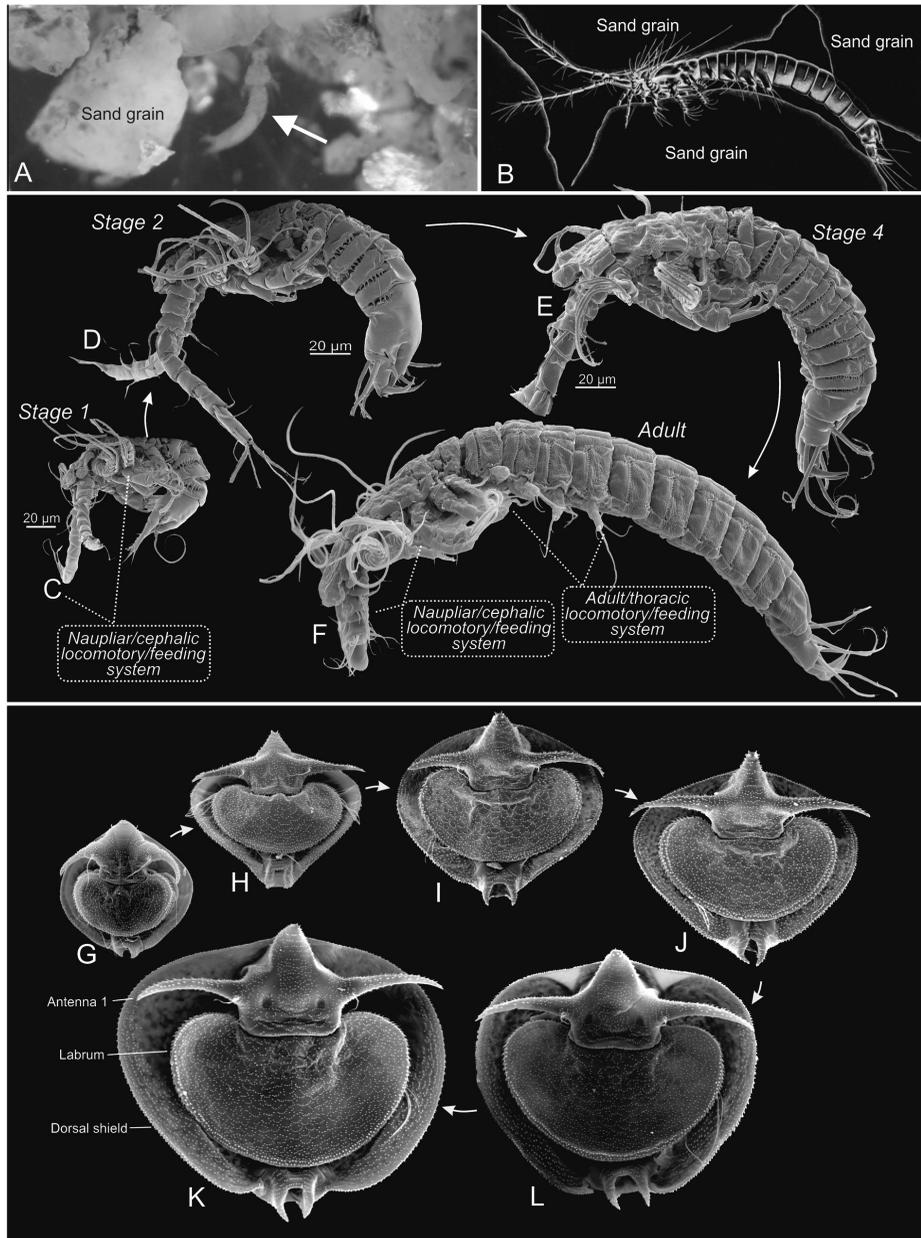
only parts (e.g., only the naupliar phase in cirripedes), and that it can concern a broad spectrum of body parts not all of which develop at the same speed. Hence, a development is anamorphic if one or more of the following applies: (1) somites are added gradually (one or few somites per molt); (2) appendages are added gradually; (3) appendages gradually become more developed; (4) internal structures such as anlagen to somite or appendages gradually appear despite not being clearly indicated externally; (5) gradual addition of setation, spines, or scales; and (6) general enlargement of body or its parts.

Within branchiopods, at least some anostracan branchiopods are strictly anamorphic during their entire development (Fig. 1.1; Fryer 1983, Schrehardt 1987). However, the larval development of branchiopods such as laevicaudatan and spinicaudatan clam shrimps can also be

characterized as anamorphic despite their lack of a clear addition of externally identifiable somites (Fig. 1.3G–L; Olesen and Grygier 2004, Olesen 2005). The hatchling of *Lynceus brachyurus* (Laevicaudata) is a peculiar dorsoventrally flattened “UFO”-shaped larva, consisting of a large, rounded dorsal shield dorsally and an almost as large ventral labrum, between which the swimming antennae and mandibles are concealed (except when swimming; Fig. 1.3G). The ensuing larvae are very similar and essentially only enlarge and change shape slightly during development (Olesen 2005). The last larva in this series is followed by a juvenile very different from the larvae (metamorphosis). Development in the larval phase in the Spinicaudata is characterized by larger morphological modifications than in the Laevicaudata. The development of notostracans (tadpole shrimps) is essentially gradual during its entire development, although there are significant jumps in morphology during certain stages (but none metamorphic) (Møller et al. 2003, Olesen and Møller 2014). As a whole, the development of Branchiopoda can be characterized as anamorphic, but with important exceptions in clam shrimps and cladoceromorphans (Cycletherida and Cladocera), which are described below. The predominantly anamorphic development in branchiopods as seen in recent anostracans may be inherited from ancestral crustaceans because much evidence suggests anamorphic development was already present in the Cambrian, around 500 Ma (Walossek 1993, Haug and Haug 2015). It was retained in branchiopods because of an early successful colonization of inland ephemeral pools, which, despite their fluctuating nature, seem to have been a very constant environment present since the Devonian, around 400 Ma (Scourfield 1926, Gueriau et al. 2016, Strullu-Derrien et al. 2016).

Also the cave-dwelling Remipedia, one of the classical candidates as “primitive” crustaceans because of their long, homonomous bodies (Schram 1983, Brusca and Brusca 1990), but now finding a phylogenetic position close to the Hexapoda (Regier et al. 2010, von Reumont et al. 2012, Lozano-Fernandez et al. 2016), seemingly undergo anamorphic development (Fig. 1.2A–G). The development is only known for one species (*Pleomothra apretocheles*), and all that is known is based on 14 specimens, which were individually collected by cave divers (by hand) in an anchialine cave in the Bahamas (Koenemann et al. 2007, 2009). The fact that the limited number of larvae found to date represents as many as 9 different developmental stages suggests that more stages remain to be found. It appears that a very long part of remipede development is nonfeeding/lecithotrophic, starting with yolk-containing nauplius-type larvae that gradually add limb buds and increase in size (Fig. 1.2B–E). Among the few specimens collected was a late specimen (termed *prejuvenile* by Olesen et al. 2014a), in which the antennae and mandibles had atrophied or become modified and no longer act in locomotion, a function transferred to the about 10 trunk limbs that are developed at this stage (Fig. 1.2F). Most likely, the transfer from a naupliar locomotory system to a “thoracic” system is gradual as in the Anostraca/Cephalocarida/*Rehbachella* system, but the limited specimens so far collected do not allow for a firm conclusion. Certainly an important difference is that the anterior naupliar system in Remipedia is used for locomotion only (not feeding), which is in contrast to the combined locomotory/feeding function in Anostraca/Cephalocarida/*Rehbachella*. Probably, the presence of anamorphic development in Remipedia is facilitated by the relatively stable environment of anchialine caves. The long phase of lecithotrophy is certainly derived and may be an adaptation to poor nutrition in many anchialine caves.

Yet another group that essentially undergoes anamorphic development (but with few species studied), are the Mystacocarida, a species-poor group of tiny (< 1 mm) crustaceans that undergo their entire life cycle interstitially, for example, among sand grains just a dozen centimeters below the surface of sandy Mediterranean beaches (e.g., southern France; Fig. 1.3A–F). As above, their anamorphic development (lack of metamorphoses) may be linked to the lack of shift in environment during their life cycle. As in Anostraca/Cephalocarida/*Rehbachella*, the hatchling in *Derocheilocaris remanei* and *D. typica* (Olesen 2001, Haug et al. 2011) is a naupliar-type larva (metanauplius), with three pairs of naupliar appendages (and weakly developed maxillules; Fig. 1.3C). The naupliar



**Fig. 1.3.**

Life cycle and larval stages of Mystacocarida and Branchiopoda. (A) Adult *Derocheilocaris remanei* (Mystacocarida) among sand grains from beach at Canet Plage near Perpignan, France. Photograph by Jørgen Olesen ©. (B) *Derocheilocaris typica* (Mystacocarida) crawling in interstitium between sand grains. Modified from Lombardi and Ruppert (1982), with permission from Springer. (C–F) Developmental sequence of *D. typica* (Mystacocarida). Modified from Olesen (2001), with permission from The Royal Danish Academy of Sciences and Letters. (G–L) Anamorphic development of larval sequence of *Lynceus brachyurus* (Branchiopoda: Laevicaudata). Modified from Olesen (2005), with permission from John Wiley and Sons. See color version of figure part 1.3A in the centerfold.

locomotion/feeding apparatus (biramous mandibles and antennae) is retained into adulthood in mystacocarids, which has often been assumed to indicate a neotenic origin (e.g., Hessler and Newman 1975, Hessler 1992), but may be interpreted more simply as retained primitive features similar to that seen in the Cephalocarida. Many other aspects of the type of anamorphosis seen in *D. remanei* and *D. typica* (Olesen 2001, Haug et al. 2011) are rather different from the assumed ancestral type in Anostraca/Cephalocarida/*Rehbachella*, such as the fact that the hatchling is rather “advanced” (with three somites), body development is “speeded up” with mostly two somites added per molt (Olesen and Haug 2014, Haug and Haug 2015), and trunk limbs are modified to four pairs of setose lobes in adults (Fig. 1.3B, F), the latter being a clear adaptation to interstitial life among sand grains.

What most of these anamorphically developing taxa have in common is the lack of abrupt changes in environment during their development. Of the taxa mentioned above, large branchiopods such as most anostracans and laevidaucatans undertake their entire life cycle in the water phase of small temporary freshwater pools, remipedes develop in the marine water phase of anchialine caves, cephalocarid larvae and adults are associated to marine sediments, and mystacocarids are interstitial in sandy beaches for their entire life. Hence, the presence of a constant environment during development seems to be a prerequisite for anamorphic development. But there is no inverse relation. Pelagic copepods, for example, despite developing in a constant environment (the pelagic water phase) are known to have a distinct metamorphosis in their development (see the following section). It is striking that most of the anamorphically developing taxa are archaic-looking for a number of other reasons than their gradual development, most notably the anostracans and cephalocarids, which have stayed morphologically constant since the Cambrian. Therefore, the type of anamorphic development seen in these taxa seems to be evolutionarily very old, possibly without any particular adaptive value. In other cases, however, the extended anamorphic phases in a number of pelagic crustaceans such as copepods, krill, and dendrobranchiate shrimps may be adaptations to dispersal, while at the same time having old evolutionary roots.

## CRUSTACEAN METAMORPHOSES, DEVELOPMENTAL “JUMPS,” AND THEIR RELATION TO LIFE HISTORY

### On “Metamorphosis” Within Crustacea

In only a few crustaceans, such as anostracans, is development strictly anamorphic, that is, gradual across their entire development. Instead, in many taxa, such as thecostracans, branchiurans, and malacostracans, development can be characterized as predominantly anamorphic but interrupted by molts between two instars that involve significant changes in morphology or lifestyle. Often the term *metamorphosis* is applied to these abrupt changes (e.g., Haug and Haug 2013). Well-known examples of crustaceans that undergo metamorphic changes during their development include, among many others, the shift from a naupliar phase to the cyprid (a settling stage) in most cirripedes, and the characteristic shift from a zoeal phase to the decapodid (e.g., megalopa in *Brachyura*), a transitional stage between the planktonic and benthic phase in the life cycle.

The balance between anamorphic and metamorphic development will be scrutinized in a number of crustacean examples. The possible adaptive value of metamorphosis in particular taxa will also be evaluated. But first it is worth considering what is actually meant by *metamorphosis*. Martin et al. (2014b) broadly referred to it as a “profound change in morphology (typically accompanied by behavioral and functional changes) during the life cycle of an organism.” This definition wisely does not address the very pertinent question: Exactly *how* profound should

the change in morphology be to be characterized as a metamorphosis? It also does not address a challenge specific for arthropods that relates to their molting nature. Specifically, the internal anatomical development may be more gradual than what is expressed in the external cuticle (e.g., when internal changes begin well ahead of an eventual metamorphic molt and continue afterward).

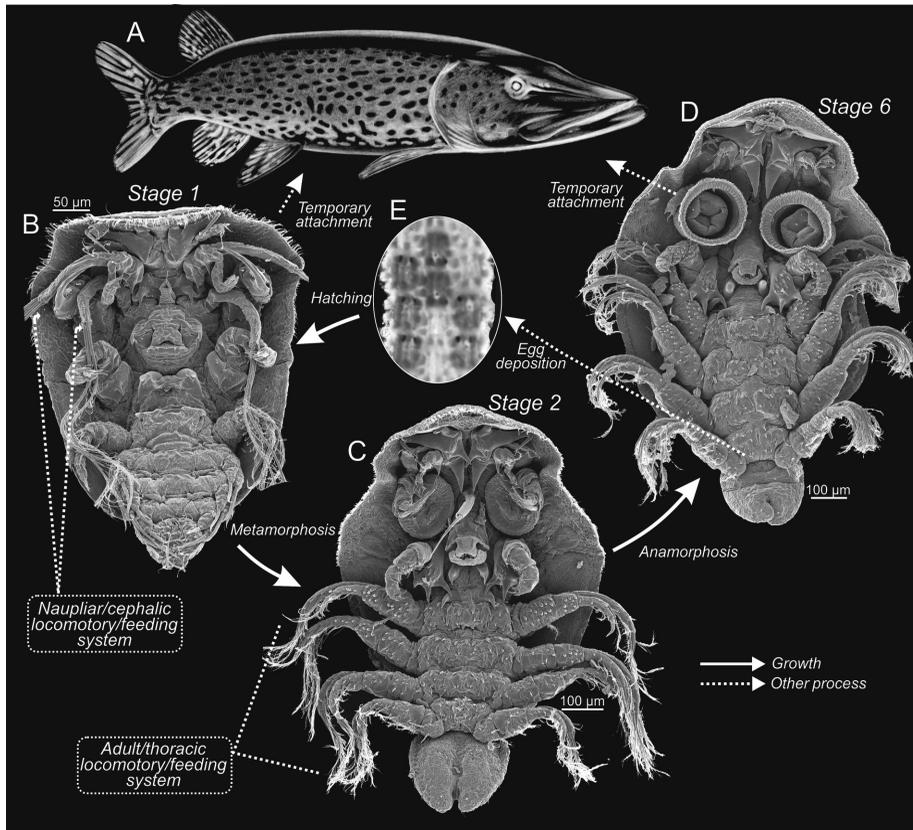
Here, for practical reasons, the term *metamorphosis* is suggested to be primarily applied on the basis of changes in the external cuticle. Cuticular information is simpler to obtain than information on internal anatomy and is available for a large assemblage of crustaceans in the literature. Furthermore, it is suggested that the type of “profound change in morphology” that qualifies to be termed “a metamorphosis” should involve an abrupt shift from one stage to another (or within a few stages) regarding which appendages specifically are involved in feeding or locomotion. Other types of smaller changes that only involve adding more somites, appendages, and so on, between two molts, or accelerating or delaying the development of some morphological aspects but not others (heterochrony), but which do not involve any major shifts in feeding or locomotion, can, if they are significant over a short period, be regarded as “developmental jumps.”

### The Branchiura Life Cycle: A Combination of Anamorphic and Metamorphic Development

The Branchiura, ectoparasites on mainly freshwater fish, use in most species spectacular suction disks (modified first maxillae) for temporary attachment to the fish surface (Fig. 1.4). Their development combines anamorphic and metamorphic development (Møller et al. 2007, Olesen and Møller 2014). In some species, for example *Argulus foliaceus*, the hatchling is very different from the following stages and the separating molt can be called a metamorphosis because it involves a significant shift in which appendages are used for locomotion (Fig. 1.4B,C). The *A. foliaceus* hatchling has a naupliar type of swimming using exopods of second antennae and mandibles (Møller et al. 2007; Fig. 1.4B), but in the following stage the mode of swimming changes completely. The naupliar exopods have atrophied significantly (Møller and Olesen 2014) and play no role in swimming, a function taken over by the more posteriorly placed trunk limbs, which are directed laterally as four pairs of large oars similar to the situation in the adults (Fig. 1.4C,D). Clearly, one result of this metamorphic transfer of locomotion from naupliar appendages to trunk limbs is enhanced swimming speeds and thereby more efficient host location. Feeding apparently does not change markedly during development and is accomplished by a mouth cone consisting of modified mouthparts (Martin 1932, Gresty et al. 1993), which is in contrast to many other crustaceans where structures of the more anteriorly positioned antennae 2 are involved in feeding during early development. Branchiurans deviate much from other crustaceans, but it is interesting to note that the naupliar-style of locomotion (using antennae and mandibles) in the hatchling of *A. foliaceus* and a few other species (Møller et al. 2007) is an ancestral (plesiomorphic) characteristic, providing a link to many other crustaceans starting their development with nauplii that use a similar form of locomotion. In the majority of branchiurans, however, the naupliar-style–swimming hatchling has been lost so that the development starts with a more advanced stage, basically like the second stage of *A. foliaceus*.

### Copepoda—Anamorphic Crustaceans with Distinct Metamorphosis

A treatment of crustacean life cycles is not complete without the Copepoda. In almost every measurable way, including habitats, lifestyles, morphological variation, and abundance, the Copepoda are among the most diverse groups of multicellular animals on Earth (Huys and Boxshall 1991, Huys 2014). Most significantly, copepods are dominant members of both the marine and freshwater holoplankton, but they have also colonized numerous interstitial habitats, and many forms are parasitic on a variety of other organisms. Despite their large diversity, the development of many groups

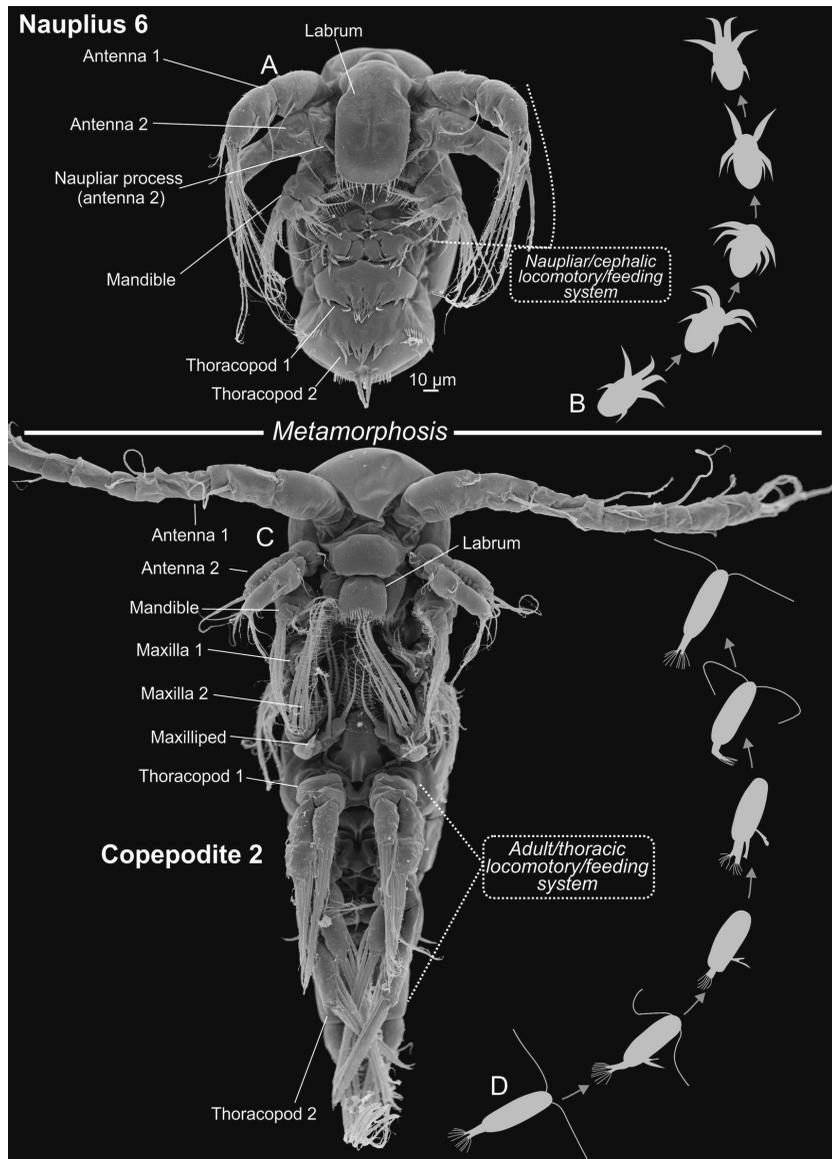


**Fig. 1.4.**

Life cycle and larval stages of Branchiura. (A) Pike, at typical fish host of *Argulus foliaceus* (Branchiura). Illustrated by Robin Woolnough ©. (B–D) Three developmental stages of *A. foliaceus* (Branchiura). (E) Close-up sediment-attached egg string of *A. foliaceus* (Branchiura). (B–E) Modified from Møller and Olesen (2014), with permission from Johns Hopkins University Press.

of copepods can be divided into an early naupliar phase and a later copepodite phase (leading to the adult), with, in many groups, a constant number of stages (six nauplii and five copepodites). However, there are numerous modifications of this general scheme, such as reductions in the number of nauplii, or brooding of the naupliar phase (see Ferrari and Dahms 2007, Huys 2014). The focus here is on a “standard” type of copepod development, with its two different developmental phases (naupliar and copepodite), and, with a few examples from the literature as background, I explore the extent to which development of copepods can be categorized as anamorphic, metamorphic, or a combination of these (example in Fig. 1.5). The focus will be on which significant changes in locomotion/feeding take place at the transition to naupliar and copepodite phases. Gurney (1942) stated that “the most complete example of metamorphosis is shown by the Copepoda.” This seems to be an exaggeration, however, considering, for example, the profound shift in morphology and lifestyle between the free-living nauplii and the settling cyprid in cirripedes and the almost as significant change in morphology between the planktonic zoea phase and the transitional (before settling) decapodids of decapods (see subsequent discussion).

Considering first the typical naupliar development as seen in many species, this phase is easily characterized as anamorphic. In the case of, for example, *Canuella perplexa* (Harpacticoida), the



**Fig. 1.5.**

Developmental phases and metamorphosis in Copepoda. (A) Late nauplius of *Acartia tonsa* (Copepoda). (B) Snapshots of swimming sequence of nauplius of *A. tonsa*. (C) Copepodite 2 of *A. tonsa*. (D) Snapshots of swimming sequence of copepodite/adult of *A. tonsa*. (A, C) Photograph by Jørgen Olesen © of cultured material (originally from Øresund, Denmark; specimens generously provided by Benni W. Hansen). (B, D) Illustrations created on basis of a video from Kiørboe et al. 2014, with permission from The National Academy of Sciences (PNAS).

hatchling is a short, ovoid, typical copepod-type nauplius, with only three pairs of appendages and no additional limb rudiments (Vincx and Heip 1979). See also the nauplius of *Acartia tonsa* in Fig. 1.5A), which is typical of many groups (Salvacion et al. 2004, Chullasorn et al. 2009, Moon et al. 2015). The further development is very gradual and involves primarily only general enlargement,

addition of setae on limbs, appearance of more setae/spines terminally at the hind body, and the addition of some postmandibular limb buds (starting in N<sub>2</sub> with the anlage of maxilla 1 as two long setae, and ending in N<sub>6</sub> with rather well-developed maxillae 1) and 3 additional limb buds. Because of the presence of postmandibular limb anlagen in N<sub>5</sub>–N<sub>6</sub>, these stages can, by definition, be called “metanauplii” as in Haug and Haug (2015). In some other taxa, there are no distinct postmandibular limb buds late in the naupliar phase (e.g., Carton 1968).

Naupliar swimming in calanoids has been categorized as comprising of at least 2 types (after Gauld 1959, van Duren and Videler 1995, Mauchline 1998, Andersen Borg et al. 2012): (1) slow gliding movement performed by antennae and mandibles (antennules in “resting” position), and (2) rapid, darting movements in which all three pairs of appendages sweep backward and forward rapidly in what is considered to be a metachronal rhythm (termed “fast swimming” or “relocation jumps” after Andersen Borg et al. 2012) (Fig. 1.5B). These 2 motility modes have since been confirmed in several studies, with calanoid nauplii exhibiting both types and cyclopoid nauplii only moving in the jerky mode (Bruno et al. 2012). In an early study, Storch (1928) observed two different modes of feeding: (1) nauplii of the calanoid *Diaptomus gracilis* creating a feeding current using the antennae and the mandibles, and (2) nauplii of the cyclopoid *Cyclops strenuus* grasping food particles. High-speed cinematography applied to the study of naupliar locomotion and feeding in 3 species of Calanoida (*Temora longicornis*, *Oithona davisae*, *Acartia tonsa*) clarified many details (Andersen Borg et al. 2012, Bruno et al. 2012). Fast swimming, involving fast metachronal movements of the naupliar appendages, was found in all three species, but in *A. tonsa* it was mainly caused by beats of antenna 1 (A<sub>1</sub>) and antenna 2 (A<sub>2</sub>) (mandible, Md, relatively immobile), in contrast to the other 2 species where all naupliar limbs are involved. Nauplii of two of the species (*T. longicornis* and *A. tonsa*) are ambush feeders that feed on motile prey during fast swimming, whereas one species (*O. davisae*) produces a feeding current while swimming slowly (“gliding”) using the antennae and mandibles (Bruno et al. 2012).

Between the naupliar phase and the following copepodite phase, there is a profound modification in morphology, involving a shift in mode of locomotion, which clearly can be categorized as a metamorphosis (as in the calanoid copepod *A. tonsa* in Fig. 1.5). Dahms (1992), who explored this metamorphic shift in copepod development in detail for a number of species of harpacticoid copepods, identified a suite of significant changes both at the general and more detailed level. Not least significantly, three thoracopods appear in one step, changing the mode of locomotion from a naupliar-based system to a thoracopod-based one (Fig. 1.5), which, as in adults, are responsible for the fast, jumping mode of swimming so typical of copepods (Fig. 1.5C,D). The evolutionary origin of this locomotory system has been suggested as one of the explanations for the great evolutionary success of copepods (Kiørboe 2011). The mode of swimming is essentially the same in early copepodites and the adult, but because more thoracopods appear gradually during development, the swimming speed is constantly increased in successive stages (Mauchline 1998). In the raptorial cyclopoids, swimming is almost exclusively by use of the thoracopods, the swimming legs (Strickler 1975, Alcaraz and Strickler 1988). In calanoids, the dominant way of locomotion is swimming at a constant speed by setting up a feeding/swimming current by “vibration” of mouthparts, but this is regularly broken up by escape reactions that consist of a series of power strokes of the thoracopods (swimming legs) (Alcaraz and Strickler 1988, Kiørboe et al. 2010).

In summary, based on a combination of morphological and functional criteria, it is clear that the shift between the naupliar and copepodid phase can be characterized as a metamorphosis. It is striking, however, that the copepod metamorphosis does not involve a shift in environment (e.g., from a planktonic to a benthic/parasitic phase), which is often coupled to metamorphic changes in other crustacean taxa. Many copepods, such as the calanoids focused on previously, are holoplanktonic and therefore essentially spend their entire life cycle in the same environment. Hence, it is not straightforward to explain the presence of metamorphosis in copepods. It is likely,

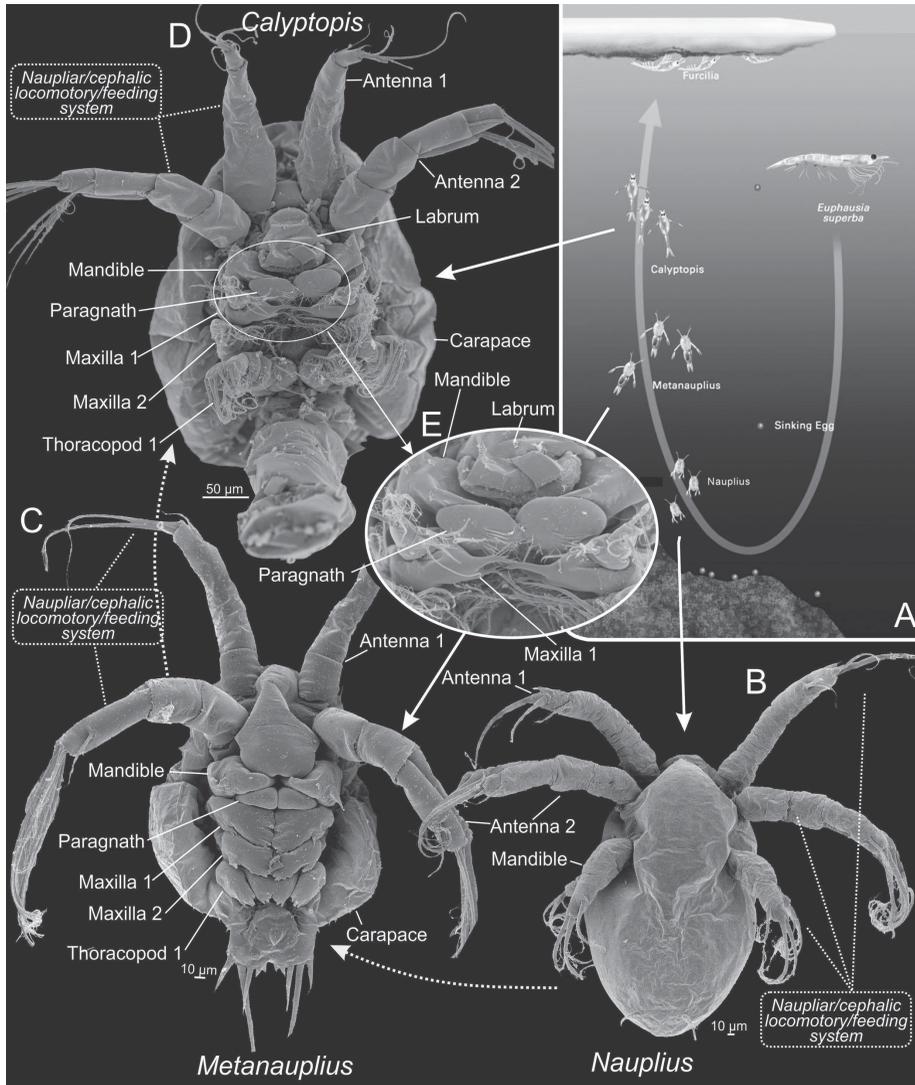
however, that its presence is linked to the profound differences in feeding and/or locomotion in the naupliar and copepodid phase, because these are the parts of the behavior that change significantly during metamorphosis. In a number of decapods with distinct metamorphoses such as scyllarids, fossil specimens that are intermediate between well-known developmental phases (larval and juvenile) have appeared in recent years (Haug and Haug 2013), indicating a gradual evolutionary appearance of a metamorphosis in these taxa. Despite absence of developmentally intermediate copepod fossil specimens (copepods fossilize poorly, Selden et al. 2010), it is likely that metamorphosis in copepods also has appeared gradually. This more anamorphic developmental series would have included stages that combined naupliar and adult locomotion/feeding, as is seen in intermediate stages of the Anostraca/Cephalocarida/*Rehbachella* type of development. It may be that such mechanically more complicated transitional stages, involving 2 different locomotory systems operating concomitantly, has been selected against. Favored instead are 2 distinctly different and better adapted phases (naupliar and copepodid phase).

### Malacostraca—Large Diversity in Life Cycles and Development

The diverse Malacostraca display numerous developmental types spanning from a mainly anamorphic type of development (but with metamorphosis-like jumps in morphology) with free larvae hatching at the nauplius stage in the mainly holoplanktonic taxa Euphausiacea (krill) and Dendrobranchiata (Decapoda), to strongly metamorphic development (but with anamorphic sequences) with distinct larval types in Stomatopoda and some pleocyematan decapods (Martin 2014; see the following section). Many taxa such as Leptostraca, Peracarida (e.g., Isopoda, Amphipoda, Thermosbaenacea), and some crayfish (Olesen and Walossek 2000, Scholtz and Kawai 2002, Vogt and Tolley 2004, Boyko and Wolff 2014, Wolff 2014, Olesen et al. 2014b, Goy 2014, Olesen et al. 2015) have skipped free larvae completely and development is epimorphic, or “direct,” with the part of the developmental phase corresponding to the free larval phase in other crustaceans passed inside an “egg” in various types of brood chambers (peracarids) or associated with various appendages of the female (see the following section). It has been discussed whether the presence of free-living nauplii in euphausiids and dendrobranchiates is an ancestral feature for the Malacostraca (see Akhter et al. 2015), retained in these 2 taxa, or whether the nauplii have become secondarily free-living again from “egg-nauplii,” as are those of many other malacostracans (see Scholtz 2000, Jirikowski et al. 2013). Here the former hypothesis (free nauplii as ancestral) has been favored (see arguments in Akhter et al. 2015). The following will show that euphausiids and dendrobranchiates occupy unique positions as morphological links between malacostracans and nonmalacostracans. In particular, the naupliar phase of these taxa has much resemblance with the early development of many nonmalacostracans, whereas stages in the later phases (e.g., calyptopis, furcilia, protozoa) have much resemblance to larval types found in some other malacostracans (Decapoda, Pleocyemata) in which the naupliar phase is lacking.

#### *Euphausiacea (Krill)—Life Cycle and Development*

The Euphausiacea (krill) are a relatively small (86 species) but ecologically important group of holoplanktonic crustaceans found in all world oceans and are important links between trophic levels (Boden et al. 1955, Mauchline 1980, Martin and Gómez-Gutiérrez 2014). The euphausiid life cycle (Fig. 1.6) is well known and comprises a short developmental phase of lecithotrophic nauplii (Fig. 1.6B), followed by a lecithotrophic metanauplius (Fig. 1.6C), again followed by a phase of more advanced feeding larvae, the calyptopis larvae (Fig. 1.6D,E), finally followed by a phase of stages called furcilia larvae during which the adult morphology is gradually reached (Sars 1898, Knight 1976, 1978, 1980, Marschall and Hirche 1984, Martin and Gómez-Gutiérrez 2014). However,



**Fig. 1.6.**

Life cycle and larval stages of Euphausiacea (Malacostraca). (A) Generalized life cycle of a euphausiacean. Modified from an illustration by Karen Carr, with permission from Sant Ocean Hall/Smithsonian Institution. (B) Nauplius of *Thysanoessa raschii* (Euphausiacea). (C) Metanauplius of *T. raschii*. (D) Calyptopis larva of *T. raschii*. (E) Closeup of mouth parts of calyptopis larva. (B–E) Modified from Akther et al. (2015).

variation to this pattern exists because some species are so-called sac spawners, meaning that they, instead of releasing their fertilized eggs into the free water, spawn into a sac attached to the posterior pairs of thoracic legs in which the early part of the development takes place (Gómez-Gutiérrez and Robinson 2005). These species are essentially brooders. Larvae are then released from the sac at a progressed stage (e.g., as a pseudometanauplius; Boden 1951, Martin and Gómez-Gutiérrez 2014). Most species spawn eggs directly into the water in which the embryos, during the sinking phase of the eggs, undergo considerable development before hatching. The hatched lecithotrophic nauplii are motile but clearly nonfeeding because they lack feeding structures (Fig. 1.6B). Mostly two

naupliar stages are reported in this developmental phase (Lebour 1926a, Macdonald 1928, Fraser 1936, Knight 1975, Suh et al. 1993, Jia et al. 2014), but Akther et al. (2015) found evidence for three nauplii in *Thysanoessa raschii* that differed from each other in only minute details. The development in this phase is anamorphic, because only minute changes take place. Swimming is accomplished by three pairs of naupliar appendages (antennae 1 and 2 and mandibles; Marschall 1984).

The metanauplius differs in significant ways from the preceding nauplius (Fig. 1.6C), including (1) loss of mandibular palp; (2) appearance of anlagen to paragnaths and three pairs of limbs (maxillae 1 and 2 and thoracopod 1); and (3) appearance of a dorsal shield, which is the precursor of the carapace (e.g., in *T. raschii*; see Akther et al. 2015). Swimming now takes place by the use of A1 and A2 only (Md palp reduced). Following the metanauplius are three feeding calyptopis larvae (Fig. 1.6D), characterized by the presence of compound eyes (but imperfectly developed), a more developed carapace and well-developed mouthparts (mandible, maxillae 1 and 2, thoracopod 1) being active in feeding (Marschall 1984, Martin and Gómez-Gutiérrez 2014). Based on general morphology of the calyptopis (Fig. 1.6D), it would seem that antennae 1 and 2 are the main propulsive organs, but locomotory functions need clarification based on studies of live specimens. After this comes a phase of 3–6 furcilia larvae (number is species-dependent), which are characterized by fully developed compound eyes, and during which the thoracopods and pleopods develop (Martin and Gómez-Gutiérrez 2014). In the first furcilia stages the antennae are still natatory, but in the later larvae of the phase this function is lost (Martin and Gómez-Gutiérrez 2014), and apparently it is gradually taken over by the thoracopod exopods and the pleopods. The last couple of furcilia stages were originally named *cyrtopia larvae* based on a reduction of the natatory function of the second antennae (Sars 1885, Macdonald 1928), but later authors have considered these changes too gradual to justify separate naming of two phases (Fraser 1936, Boden 1950, Silas and Mathew 1977, Martin and Gómez-Gutiérrez 2014). Pleopodal swimming begins in the furcilia phase and its significance is increased during furcilia development as more pleopods are added (number varies much between species, see Lebour 1926b), but is probably insignificant in furcilia 1–2 as the pleopods are only buds. In adult *Euphausia superba*, the thoracopodal exopods move independently of the endopods (which form the filter basket) and together with the pleopods are part of a metachronally moving limb series that serve for locomotion (pleopods) and possibly produce a feeding current (thoracopodal; Boyd et al. 1984). It is uncertain how early in the furcilia phase the thoracopodal exopods function as in adults, but this function is probably attained alongside with the development of the filtering chamber starting in furcilia 2 in *E. superba* (Marschall 1984).

The overall impression of the development of Euphausiacea as outlined above is that it is anamorphic. None of the changes between various larval types can be characterized as clearly metamorphic because no abrupt change in the mode of locomotion takes place. Naupliar type of locomotion (but with mandibular exopod already reduced in metanauplius) is kept until late in the furcilia phase but is then gradually taken over by the thoracopodal exopods and the pleopods, which is also the adult mode of locomotion (together with “escape” swimming). It is known that the Antarctic krill (*E. superba*) go through a characteristic vertical migration during their development (“ontogenetic migration”), which can take place over a time span of 2 years (Fig. 1.6A). Generally, gravid *E. superba* are found offshore in deeper water than the rest of the adult population, which, after spawning, ensures that the eggs are in suitable waters for their further development (Nicol 2006). Eggs of *E. superba* sink, but eggs of other species may float (Nicol 2006).

The embryos of *E. superba* hatch into nonfeeding, free-swimming larvae at depths of 700 to 1,000 meters (Fig. 1.6A). The larvae swim upward, developing as they swim, and reach the surface some 30 days after the eggs are laid. The first feeding stage (the first calyptopis) is reached after 30 days, and it is critical for survival that the larvae find food within six days (Nicol 2006). Late larval stages and juveniles spend a part of their development associated with sea ice and feed on ice algae (Nicol 2006) (Fig. 1.6A). A practical advantage of having the eggs and developing larvae

laid offshore from the main body of the krill population may be avoidance of cannibalism on larvae from the swarming adults, which are dominant consumers of suspended material (Nicol 2006).

Lecithotrophy is generally considered an adaptation to low or unpredictable food production as seen in, for example, the deep sea (Thorson 1961), and is congruent with lecithotrophy in the early phase of krill development (nauplii and metanauplius). Nicol (2006) remarked that there is an obvious need to better understand the early life history stages of krill. Locomotory and feeding mechanisms of a broad suite of developmental stages need more study, because this is important for a full understanding of the ecological roles of various krill species. Currently, only a rough picture can be put together based on scattered information from different sources. Larval locomotion is accomplished by the antennae 1 and 2 during the naupliar development, but after this phase locomotion is gradually transferred to the thoracopodal exopods and the pleopods. But how does this transition exactly take place? Feeding is known to start in the first calyptopis, and is accomplished by the mandibles, maxillae 1 and 2, and the thoracopods 1 apparently operating as a filtration system (Fig. 1.6D,E), for example, feeding on diatoms as shown by analyses of gut contents by Marschall (1984). According to Marschall (1984), the number of feeding appendages and their essential morphology remain relatively constant between the first calyptopis and first furcilia stages, and the feeding basket present in adults apparently becomes functional from second furcilia. But no detailed information on how the filtration system operates in calyptopis larvae seems available, and a complete understanding on how it transforms into the complex filtering basket in adults is lacking (see adult function in Boyd et al. 1984).

### *Dendrobranchiata—Life Cycle and Development*

Dendrobranchiata (Fig. 1.7), containing the economically important penaeoid and sergestoid shrimps, are commonly classified as sister group to all decapods (Richter and Scholtz 2001, Tavares and Martin 2010). They are widely thought to be the least derived of the extant Decapoda, for example, because they, as euphausiaceans, shed their eggs directly into the water from which nauplii hatch (except Luciferidae, which have a short brooding phase), and because the larval development overall is anamorphic (Tavares and Martin 2010, Martin et al. 2014b). Actually, as will be shown in the following, the development is in many ways more anamorphic than that of Euphausiacea to which many similarities exist. There are approximately 500 extant species, nearly all of which are marine with species from shallow tropical waters to depths of about 1,000 m on the continental slopes (Pérez Farfante and Kensley 1997, Tavares and Martin 2010, Martin et al. 2014c). Almost half of the known species are members of the Penaeidae, which inhabit shallow and inshore tropical and subtropical waters, some species of which form the basis of massive seafood industries. Other dendrobranchiate families are predominantly in deep water, while others again are either deep benthic dwellers, members of the meso- and bathypelagic fauna, or entirely planktonic. Most information on life cycles is available for coastal penaeids, but from what can be inferred from the few available studies on deep benthic or pelagic species, many aspects of the life cycles seem the same, such as duration of larval phases and feeding strategies (Martin et al. 2014c).

Development of dendrobranchiates can be divided into a number of phases, during each of which the larval stages in the series changes only relatively little (Fig. 1.7). These phases are (following Martin et al. 2014c): a phase of nonfeeding nauplii (five to eight stages), a protozoal phase (three stages), a mysis phase (variable number mentioned in literature), and a decapodid phase. Although practical, this division into distinctly named phases, reusing terms from nonmalacostracan (naupliar phase) and nondendrobranchiate decapod (postnaupliar phase) ontogenies, somewhat hides the gradual nature of dendrobranchiate development. The division into phases has traditionally been based on a combination of somite and limb development, and on limb functionality (as in other Crustacea), some details of which will be reviewed here. In the naupliar phase of species, such as *Metapenaeopsis*