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

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

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

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## 5.1 Introduction

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

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

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

## 5.2 Physiological Adaptation to Non-marine Conditions: Osmoregulate

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

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

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

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

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

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

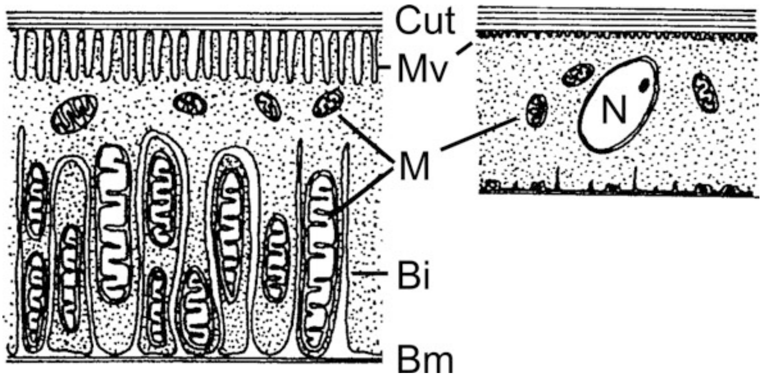

**Fig. 5.1** Ultrastructure of a ionocyte (*left*) compared to a regular epidermal cell (*right*). *Cut* cuticle; *Mv* Microvilli; *M* mitrochondria; *Bi* basal infoldings; *Bm* basal membrane; *N* nucleus (schematic drawings, after Cieluch 2004 with permission of the author)

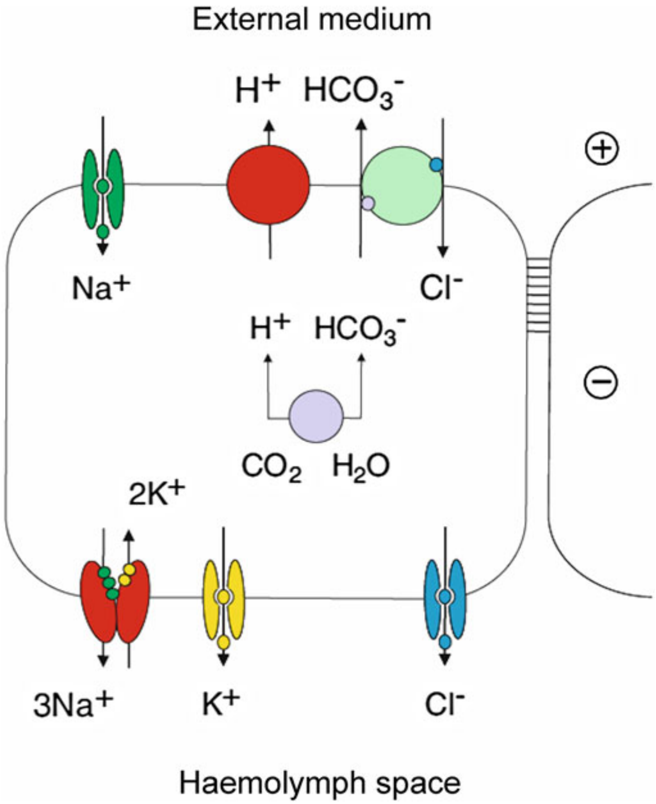

**Fig. 5.2** Schematic illustration of the principal processes of extracellular hyper-osmoregulate (from McNamara and Faria 2012 with permission of Springer Science + Business Media). As a net result, $Na^+$ and $Cl^-$ ions are taken up from the diluted external medium and transported against strong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

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

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

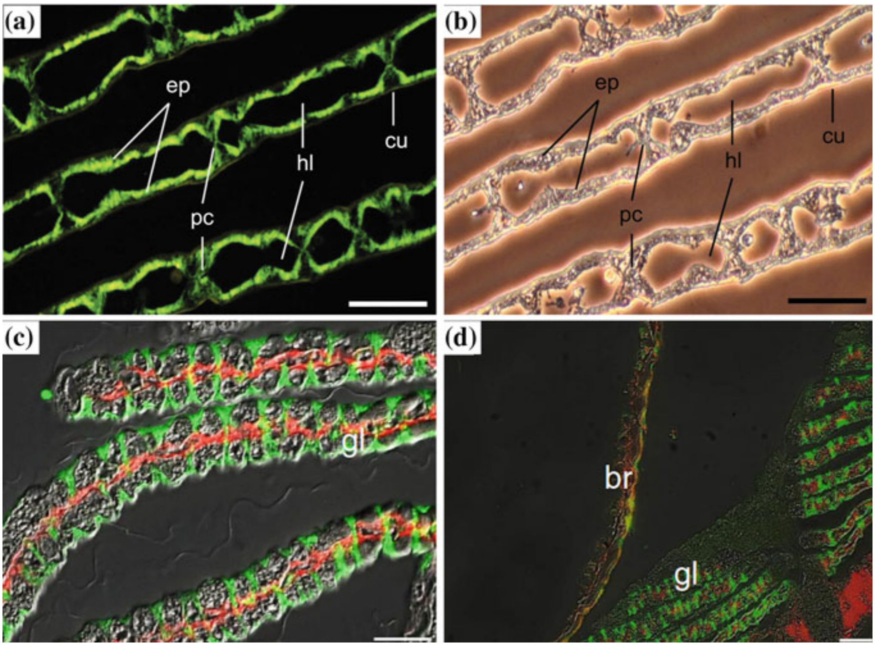

**Fig. 5.3** Immunohistochemical localization of two key enzymes involved in osmoregulate; *upper pictures* posterior gills of a juvenile euryhaline crab, *Carcinus maenas* (from Cieluch et al. 2004); **a** fluorescent micrograph, showing $Na^+$–$K^+$-ATPase; **b** corresponding phase-contrast micrograph;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

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

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

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

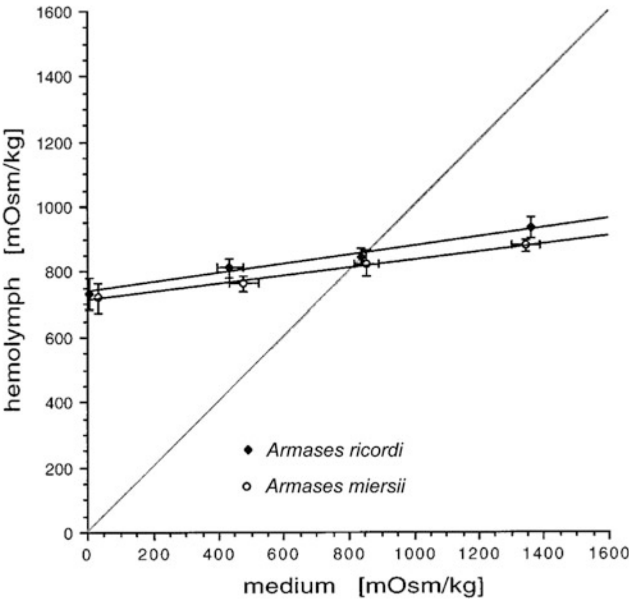

**Fig. 5.4** Haemolhymph osmolality plotted against the osmolality in the external medium in two strong hyper-hypo-osmoregulators, the semiterrestrial sesarmid crabs *Armases ricordi* and *A. miersii* (from Schubart and Diesel 1998, with permission of Bulletin of Marine Science; slightly modified); *straight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

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

## 5.3 Principal Life-History Patterns in Decapod Crustaceans

### *5.3.1 Extended Larval Development*

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

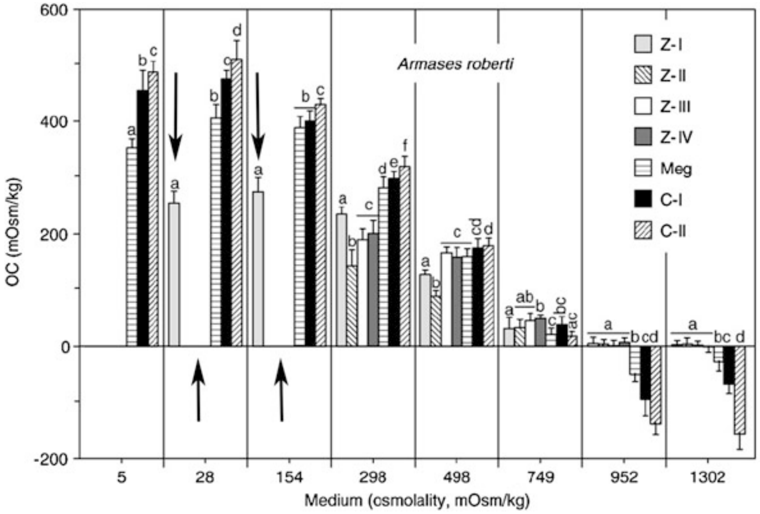

**Fig. 5.5** *Armases roberti*. Variations of osmoregulatory capacity (*OC*) in different ontogenetic stages (zoeal stages I–IV; megalopa; crab stages I and II) in relation to the osmolality of the external medium; note that the megalopa is a strong hyper-osmoregulator in fresh water (5 m Osm/kg), showing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

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

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

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

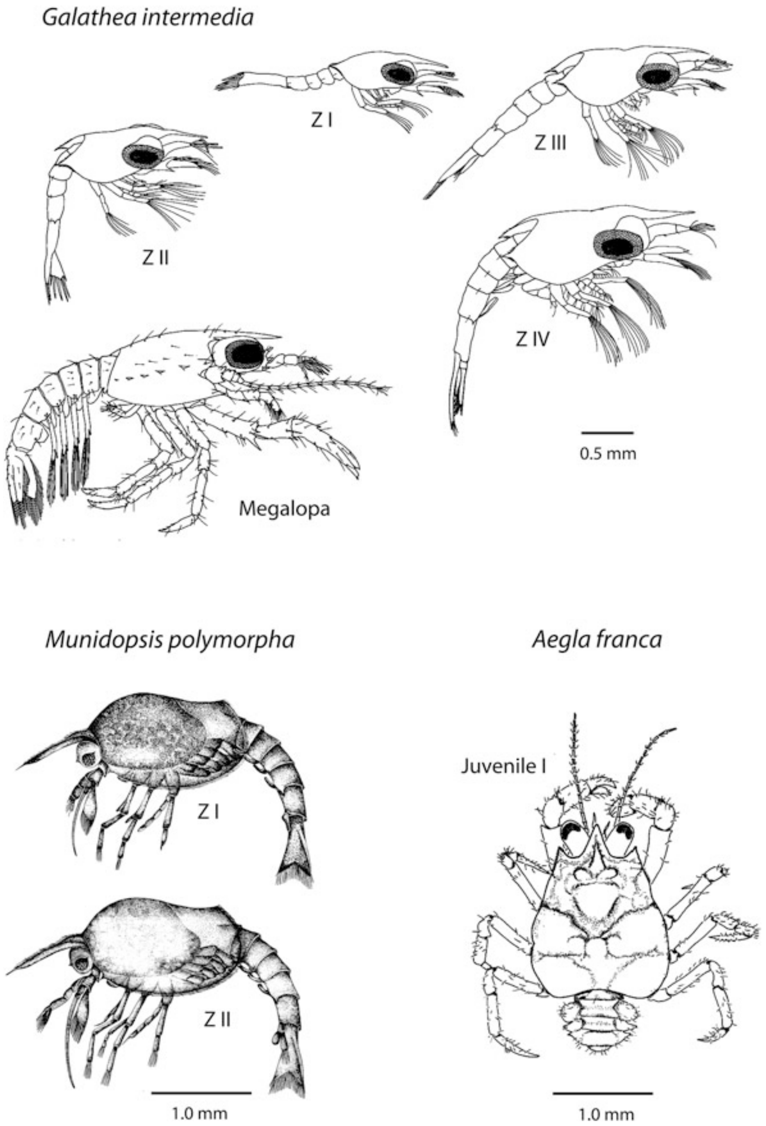

**Fig. 5.6** Developmental patterns in Galatheoidea (Decapoda, Anomura): extended larval development in the marine species *Galathea intermedia* (Galatheidae) (from Christiansen and Anger 1990); abbreviated larval development in *Munidopsis polymorpha* (Galatheidae) from anchialine caves (from Wilkens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

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

### 5.3.2 Abbreviated Larval Development

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

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

### 5.3.3 Direct Development

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

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

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

### *5.4.1 The "Freshwaterization" Paradigm*

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

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

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

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

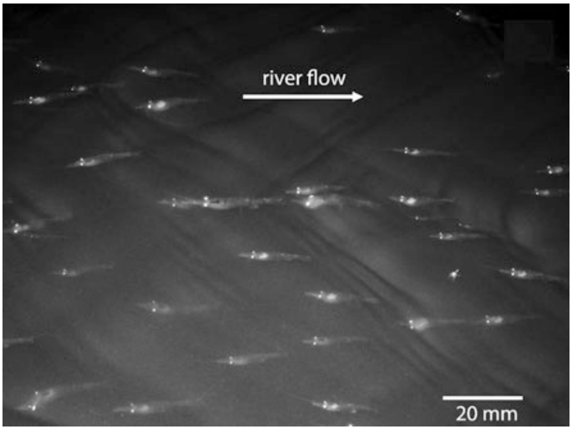

**Fig. 5.7** Diadromous upstream migration of juvenile palaemonid shrimps, *Macrobrachium ohione*; *scale bar* 20 mm (from Bauer and Delahoussaye 2008)

#### 5.4.2.1 Terminology: "Diadromous" Versus "Amphidromous"

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

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

#### 5.4.2.2 Breeding Migrations in Terrestrial Decapoda

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

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

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

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

#### 5.4.2.3 Diadromous Migrations in Freshwater-Inhabiting Decapoda

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

#### 5.4.3.1 Abbreviated Development in Terrestrial and Limnic Decapoda

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

## *5.4.5 Exceptions from the "Freshwaterization" Rule*

### 5.4.5.1 Abbreviated and Direct Development in the Sea

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

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

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

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

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

#### 5.4.5.2 Extended Larval Development in Fresh Water

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

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

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

## 5.5 Possible Colonization Routes to Non-marine Environments

### 5.5.1 Basic Considerations and Currently Proposed Routes

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

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

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

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

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

## *5.5.2 Alternative Hypotheses for Limnic Invasions*

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

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

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

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

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

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

#### 5.5.2.2 Land-Locked Transitional Environments as Putative Entrance Portals

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

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

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

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

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

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

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

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

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

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