CHAPTER 71-6

LARVAL DEVELOPMENT AND BEHAVIOUR STRATEGIES IN BRACHYURA

BY

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INTRODUCTION

Most benthic marine, as well as many limnic, invertebrates pass through complex (or biphasic) life cycles comprising a benthic juvenile-adult phase and an extended pelagic phase of embryonic and/or larval development (Pechenik, 1999; McEdward, 2000). It is generally accepted that biphasic life histories represent the ancestral pattern, while an abbreviated, or completely lacking, pelagic phase is considered as phylogenetically derived (see Jägersten, 1972; Nielsen, 1998, 2009; Wowor et al., 2009; but for a contrary view see Pereira & García, 1995).

Among decapod Crustacea, only species belonging to Dendrobranchiata release fertilized eggs into the water column where all embryonic and larval development takes place. By contrast, all so-called “higher” Decapoda (Pleocyemata, including Brachyura), carry their developing eggs under the female pleon, where the embryos are maternally brooded until hatching occurs (Meusy & Payen, 1988; Thiel, 2003; Fernandez et al., 2006; Hartnoll, 2006). The subsequent larval phase is typically pelagic (for exceptions, see below), comprising various stages that develop through extended periods (several weeks or months) in the plankton. However, numerous decapod taxa also show an abbreviated or even direct mode of development (Rabalais & Gore, 1985; Anger, 2001, 2006; Vogt, 2013).

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In the first section of this chapter, by Klaus Anger, the patterns of extended, abbreviated and direct development in brachyuran crabs are briefly reviewed, and the putative adaptive significance of the differing developmental strategies is discussed. Such considerations are particularly important in relation to biogeographic patterns, the dispersal capacities of so-called “invasive” species, and evolutionary processes that have led to the colonization of limnic and terrestrial environments. Particular attention is paid to abbreviated patterns of larval development, briefly updating the information provided in previous reviews (Rabalais & Gore, 1985; Anger, 2001; Vogt, 2013). Extended or “regular” patterns are considered to a lesser extent, as they are reviewed in the next section and in several previous works (Gurney, 1942; Costlow, 1968; Williamson, 1982; Rice, 1983; Gore, 1985; Ingle, 1992, 1998; Anger, 2001, 2006; Martin, 2014). Similarly, terminology and historical aspects of the subject have also been extensively discussed in these aforementioned works.

In the second section, the main patterns of larval dispersal in the marine environment are reviewed by Henrique Queiroga and Ricardo Calado. Their review focuses on estuarine and coastal species from the tropical and temperate regions, which usually show extended development (Ingle, 1998; Anger, 2001; see also Chapter 71-17 in this volume). The exposure to mortality factors during the extended larval phase implies very high rates of larval loss, which are also reviewed. Larval behaviour has a key role in the control of dispersal and in the avoidance of mortality factors (Queiroga & Blanton, 2005), and this section therefore emphasizes the behavioural adaptations that underpin the mechanisms of dispersal and recruitment.

**PATTERNS OF LARVAL DEVELOPMENT**

**Extended (“regular”) patterns of larval development**

About 80% of the 6900 described species of Brachyura pass through biphasic life cycles (Anger, 2001; Ng et al., 2008; De Grave et al., 2009). Internal fertilization is followed by embryogenesis inside a semipermeable egg membrane (Anderson, 1982; Wenner & Kuris, 1991; see also Chapter 71-4 of this volume). Hatching typically occurs as a free-swimming planktotrophic zoea (for terminology of larval stages based on functional morphology criteria, see Williamson, 1969, 1982; Ingle, 1992; Anger, 2001; Martin, 2014; see also Chapter 71-17 in this volume), or occasionally as a non-feeding and morphologically retarded prezoea (Hong, 1988). The latter, however, is generally not considered as a true larval stage but as a late embryo that may prematurely be released after rupture of the egg membrane, especially under stressful conditions (Williamson, 1982; Nagao et al., 1999).

**Zoeal phase**

Following hatching, crab larvae join the planktonic community and grow through several morphologically similar zoeal stages, each stage showing an increase in the number and complexity of swimming and feeding appendages. The number of stages may vary between species, but higher taxonomic groupings typically show characteristic