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Monograph

Behavioral adaptations in larvae of brachyuran crabs: A review

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ABSTRACT

Larval development in brachyuran crabs includes a number of zoeal stages followed by a single megalopal stage. Zoeae and megalopae are relatively strong swimmers, and movement up or down in the water column takes advantage of vertical shear in ambient currents with consequent transport in the horizontal dimension. For some species, this process is important in controlling the dispersal of early-stage larvae away from spawning sites and in maintaining the supply of late-stage larvae to juvenile nursery habitat. For other species it enables retention near spawning sites throughout the larval period. Vertical position in the water column also modulates predator-prey interactions, which impact growth and survival of larvae. Swimming behavior in larval crabs is regulated by both external cues detected in the water column and endogenous rhythms entrained by external oscillators. Gravity, hydrostatic pressure, and light are the primary external cues because of their predictability in the environment. Light is also the most common external oscillator entraining swimming rhythms. Secondary cues include salinity, temperature, turbulent kinetic energy, and feeding state. Crab larvae also respond to chemical and tactile cues that facilitate settlement in juvenile habitat. This paper presents a review of the physical and chemical characteristics of these cues, the behavioral responses of crab larvae to the cues, and the patterns of larval transport that emanate from these responses.

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1. Introduction

Studies of swimming behavior in brachyuran crab larvae date back to the second half of the 20th century, and the total repertoire of papers is extensive. Larval development in crabs usually occurs within the plankton and includes a number of zoeal stages followed by a single megalopal stage (Fig. 1). Zoeae and megalopae are relatively strong swimmers, and movement up or down in the water column takes advantage of vertical shear in ambient currents with consequent transport in the horizontal dimension (Forward et al., 2003a). This process is important in controlling dispersal of early-stage larvae away from spawning sites and in maintaining the supply of late-stage larvae to juvenile nursery habitat (Queiroga and Blanton, 2005). Vertical position in the water column also modulates predator-prey interactions, which impact growth and survival of larvae (Cohen and Forward, 2009). Swimming behavior in larval crabs is regulated by external cues detected in the water column. Gravity, hydrostatic pressure, and light, are the primary cues and interact with a suite of secondary cues with consequent effect on behavior (Naylor, 2006). Crab larvae also respond to chemical and tactile cues that facilitate settlement and metamorphosis in juvenile habitat (Forward et al., 2001). Continuing interest in the behavior of crab larvae stems from a growing appreciation of the role of larval recruitment in practical issues such as: inter-annual variation in fishery yields (Ogburn et al., 2012); invasion of alien habitat by non-indigenous species (Tilburg et al., 2011); and response of ecosystems to climate change (Steneck and Wahle, 2013).

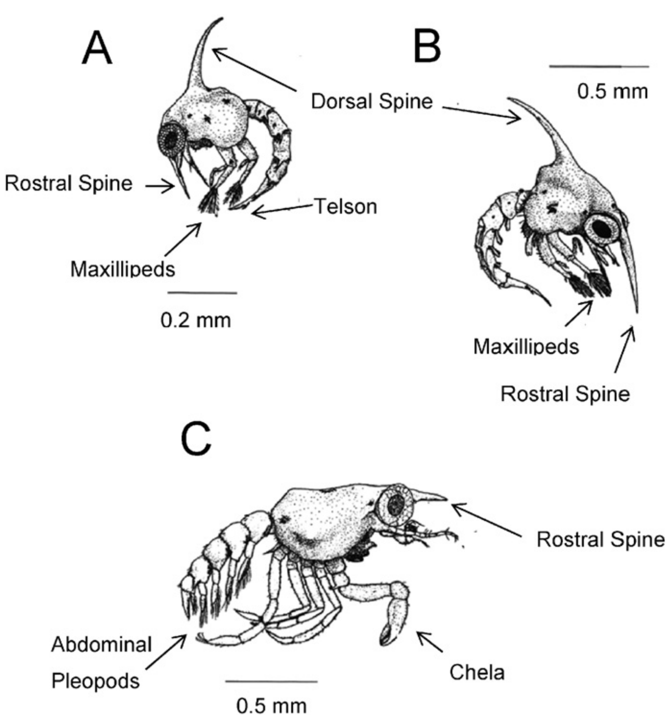

Fig. 1. Examples of the external anatomy of the larval stages of a typical brachyuran crab. (A) Early zoeal stage. (B) Advanced zoeal stage. (C) Megalopal stage. Modified from Costlow and Bookhout, 1959.

In the following sections of this review, orientation and swimming responses of decapod larvae to physical cues in the water column are discussed in detail. In some cases, a brief tutorial is provided concerning the characteristics and distribution of cues and the ways in which larvae perceive them. In an additional section, the role of swimming behavior in modulating dispersal is reviewed, along with the effects of behavioral parameters on the outcomes of model simulations of larval transport. This is followed by a section that concerns the chemical and tactile cues associated with appropriate juvenile habitat. A final section provides an integrative summary and conclusions.

2. Larval responses to external cues

2.1. General aspects

Locomotory behavior in brachyuran crab larvae mediates vertical distribution and predator-prey interactions, among other processes, and is commonly regulated by external (exogenous) cues detected in the water column. Such cues are most valuable when they are predictable and constant within the environment. Accordingly, gravity, hydrostatic pressure, and light are the three central external cues affecting larval behavior (see reviews by Thorson, 1964; Forward, 1976, 1988; Naylor, 2006; Cohen and Forward, 2009). These cues are reviewed here, both in terms of the physical nature of the cue in the water column and the morphology/physiology of the sensory structures detecting them. This discussion provides a conceptual framework for understanding the studies that have been done on behavioral responses to gravity, hydrostatic pressure, and light in larvae of brachyuran crabs. The section concludes with an analogous discussion of the responses of brachyuran larvae to variation in salinity and temperature in both the horizontal and vertical dimensions.

2.2. Nature and detection of gravity, hydrostatic pressure, and light

2.2.1. Gravity and hydrostatic pressure

For a larva in the water column, the gravitational field is uniform across depth with acceleration toward the center of the Earth. In contrast, hydrostatic pressure exists as a gradient that increases with depth as a function of water column mass. Both are highly predictable stimuli detected in brachyurans by a statocyst organ, which functions in providing feedback to motor systems in order to maintain equilibrium. The statocyst also stabilizes the body (appendages, eyes, etc.) and monitors angular acceleration (Fraser and Macdonald, 1994; Fraser, 2001; Fraser et al., 2004). In brachyurans, statocysts are tube-like