Alternative feeding mechanisms in megalopae of the blue crab *Callinectes sapidus*  

**Abstract** The apparent mismatch between the energy requirements for planktotrophic growth and prey availability has long been paradoxical. One hypothesis to explain this paradox is that planktotrophic larvae display plasticity in feeding mechanisms in response to variable prey types and concentrations. This hypothesis was tested by videotaping megalopae of the brachyuran crab *Callinectes sapidus* Rathbun feeding on various-sized prey. Frame-by-frame analysis of the videotapes indicated that *C. sapidus* megalopae used both raptorial and suspension feeding to capture prey while in the water column. Raptorial feeding was used to capture macrozooplankton, including copepods. The swimming form of suspension feeding was based on a modified fling-and-clap mechanism using the chelipeds. Suspension feeding while at rest utilized a weak current generated by the mouthparts to direct prey to the mouth. Both suspension-feeding mechanisms resulted in the efficient capture of rotifer-sized particles. The energy/handling time ratios for all three feeding mechanisms are very similar (\(E/H\) range 0.016–0.019 \(\mu\)g \(\text{C s}^{-1}\)) for the natural prey tested. These results support the hypothesis that feeding in brachyuran larvae is plastic and includes mechanisms of both raptorial and suspension feeding. The ability to suspension feed at rest is adaptive, since megalopae use selective tidal transport to re-invoke an estuary and may spend up to 18 h day\(^{-1}\) clinging to a benthic substrate.  

Electronic supplementary material to this paper can be obtained by using the Springer LINK server located at http://dx.doi.org/10.1007/s00227-002-0781-1.

**Introduction**  

A long-standing paradox in the study of planktotrophic invertebrates is the apparent mismatch between prey availability and estimates of larval energetic requirements. Based on this mismatch Thorson (1950) hypothesized that starvation was a major ecological factor in determining recruitment success in benthic invertebrate populations. Despite considerable efforts by ecologists during the last century (Hjort 1914; Thorson 1950; Strathmann 1987; Olson and Olson 1989), the role of larval nutrition as a factor in recruitment remains poorly understood.

Predator–prey interactions are complex, multi-component processes. Successful interactions are determined by encounter rate, attack and capture success, and the ability to consume prey after the initial capture. The encounter rate between predator and prey has been hypothesized as the key factor in determining feeding success (Gerritsen and Strickler 1977; Rothschild and Osborn 1988). An alternative, or supporting, hypothesis accounting for increased feeding success is the evolution of developmental plasticity that allows larvae to use several feeding strategies to enhance their overall feeding efficiency. Developmental plasticity includes morphological adaptations that increase larval size and feeding success during periods of low food concentration (Strathmann et al. 1993; Fenaux et al. 1994). Both meroplankton and holoplankton species have behavioral responses that allow them to utilize different feeding mechanisms to capture a broad range of prey sizes (Lonsdale et al. 1979; Paffenholz and Harris 1979; Barshaw and Bryant-Rich 1988; Lavalli and Barshaw 1989; Strathmann and Bone 1997). A broad spectrum of prey types and increased capture efficiency may compensate for low prey densities, thus reducing the risk of larval starvation. While we have modified the questions and methodologies to include physiological, metabolic, and biochemical parameters, the type, quantity, and quality of prey required for growth of planktonic larvae...
and the mechanisms used to capture them are still being studied.

Basic knowledge of brachyuran larval feeding and nutrition has generally been obtained from studies designed to improve laboratory culture techniques (reviewed by McConaugha 1985). Larvae fed natural mesozooplankton (Rust and Carlson 1960) or Artemia spp. nauplii (Costlow and Bookhout 1960) had good survival and development rates to metamorphosis. Based on these studies the concept that brachyuran larvae and megalopae are size dependent, raptorial predators with limited hunting ability became the accepted paradigm (McConaugha 1985; Strathmann 1987). While the paradigm was generally accepted, anecdotal (Costlow and Bookhout 1960; Rust and Carlson 1960) and experimental evidence (Robertson 1983; Factor and Dexter 1993; Lehto et al. 1998; Crain 1999) have shown that brachyuran larvae can ingest phytoplankton and ciliates. We hypothesized that as brachyuran larvae molted and grew larger the proportion of small prey in the diet would be reduced because of mechanical handling costs and the need to capture higher energy prey. This hypothesis was tested and rejected using zoeae and megalopae of the blue crab Callinectes sapidus (McConaugha et al. 1991, and unpublished data). In fact, late-stage zoeae and megalopae very efficiently removed small prey, often ingesting all of the small prey even when they were offered in conjunction with larger prey items. Feeding mechanisms that allow brachyuran larvae and megalopae to ingest prey ranging in size from 5 to 750 μm have not been previously demonstrated.

This question was investigated using field-collected C. sapidus megalopae fed a broad range of prey types. Megalopae were videotaped feeding on prey items including rotifers, Branchionus plicatus (50–150 μm), Artemia spp. nauplii (250–300 μm), Uca spp. first-stage zoeae (250–300 μm effective length), and copepodites of Acartia tonsa (450–750 μm), an estuarine-coastal holoplankton species.

Materials and methods

Callinectes sapidus Rathbun megalopae used in the study were collected at Sand Shoal Inlet on the eastern shore of Virginia, USA, during August and September 1996. Megalopae were attracted to a light suspended in the water and collected with a hand-held dip-net and placed in glass fiber-filtered (nominally 1.0 μm) seawater (salinity 30–32). Megalopae were held unfed for 12–36 h prior to testing. To restrict the range of movement, megalopae were tethered by attaching a short length of 2 pound test fishing line to the dorsal carapace with cyanoacrylic glue. Megalopae were then suspended in a 2.5×2.5×0.5 cm Plexiglas container. While this limited the distance a megalopa could swim, it did not prohibit the megalopa from vigorously swimming using the abdominal pleopods for periods of 1–5 min.

Individual megalopae were observed for 10–15 min while being offered a single prey type. Prey items were added to the observation chamber by pipette. Each megalopa was tested only once with a single prey type. Following the observation period the megalopa was removed and the chamber flushed with filtered seawater to remove any remaining prey. A white light from a dissecting microscope light was used for observing and videotaping. Light intensity was greater in a 1.5 cm diameter circle around the tethered megalopa. This caused prey to aggregate in the higher illumination, increasing the effective prey concentration within the swimming range of the tethered megalopa. Since prey densities could not be accurately determined, prey concentrations are not reported. Four prey species, copepodite stages (IV-VI) of Acartia tonsa (five to six added per test), freshly hatched (12–18 h) Artemia spp. nauplii (~50), Uca spp. first-stage zoeae (8–10), and the rotifer Branchionus plicatus (~100) were tested as prey. Sample sizes for individual prey types were 13, 15, 8, and 15 megalopae, respectively. A. tonsa copepodites and Uca spp. zoeae were collected from plankton tows taken with a 333 μm mesh net. Artemia spp. were hatched from cysts daily. B. plicatus were cultured in the laboratory. Observations were made at room temperature (22–25°C). Ambient seawater temperature was 23–26°C during the study period.

Feeding was observed and video-taped at 30 frames s⁻¹ through a Wild M-8 dissecting microscope with an Ikegami high-resolution, black-and-white video camera attached to a phototube. Tapes were analyzed on a Sony videotape editor with individual frame capabilities. Estimates of feeding duration and prey handling times were determined by measuring the number of frames between the beginning and end of a feeding event.

Results

Observations of Callinectes sapidus megalopae indicate that they utilize two distinct feeding methods depending on prey size: raptorial and suspension feeding. Large prey (>200 μm) were captured by the chelipeds and manipulated by the mouthparts before being ingested. An Artemia spp. nauplius, 250–300 μm, was grasped by a cheliped and rapidly transferred to the mouthparts. The mouthparts (mandibles, maxilla, and maxillipeds) were capable of controlling the prey while manipulating it into a head-first position (video electronic supplement JRM_Art). Nauplii were ingested whole. Megalopae quickly captured another prey with the chelipeds after transferring a nauplius to the mouthparts. At high prey densities, megalopae often had one Artemia spp. nauplius in the mouthparts and one in each cheliped. Megalopae could consume eight to ten Artemia spp. nauplii in 1–2 min.

First-stage Uca spp. zoeae were presented to eight megalopae, resulting in 20 captures/feeding events. Total zoal length was 450–500 μm from the base of the rostrum to the caudal furca. Because of the swimming position of zoeae the effective prey size is the length of the carapace (250–300 μm). Initial capture of the zoeal was similar to that of Artemia spp. nauplii. C. sapidus megalopae used a single cheliped to capture a zoea, and the prey was immediately transferred to the mouthparts, where it was manipulated into a tail-first position and consumed. Unlike Artemia spp., zoeae were not consumed whole but were masticated by the mouthparts. Subsequent zoal captures were held in the cheliped until the first prey was ingested. Successful ingestion occurred in only 44% of the captures. In several instances the zoea escaped from the cheliped before being transferred to the mouth. In other cases it appeared that the zoea