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Developmental changes in the mouthparts of juvenile Caribbean spiny lobster, *Panulirus argus*: Implications for aquaculture

Serena L. Cox [a,b,*], Andrew G. Jeffs [c], Megan Davis [a]

[a] Aquaculture Division, Harbor Branch Oceanographic Institute at Florida Atlantic University, 5600 US 1 North, Fort Pierce, Florida 34946, USA
[b] National Institute of Water and Atmospheric Research, Private Bag 14901, Kilbirnie, Wellington 6241, New Zealand
[c] Leigh Marine Laboratory, University of Auckland, P.O. Box 349, Warkworth 0941, New Zealand

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ABSTRACT

Light microscopy and video analysis were used to examine the mouthpart morphology and feeding behaviour of the Caribbean spiny lobster from puerulus (megalopal stage) (5–8 mm carapace length, CL) to adult (85 mm CL). Upon settlement the pueruli did not possess fully functional mouthparts, however, efficient feeding appendages appeared in the first instar juvenile (after the first moult from puerulus). From this stage the density, robustness and complexity of setation on the mouthparts, together with the size and calcification of the mouthparts increased progressively with the size of the lobster. The changes correlated well with previously observed ontogenetic changes in natural prey, from small and soft prey in early juveniles to large and well-armoured molluscs, crustaceans and echinoderms in late juveniles and adults. The efficiency of shredding and tearing food items, mostly with the second maxillipeds, increased concomitantly with lobster size, as did the ability of the mandibles to grind and process food. Based on morphological and behavioural observations it is recommended that formulated feeds for first instar juvenile lobsters should be small (1–2 mm in diameter), soft and pulpy in texture to maximise feed intake. For large juvenile lobsters (45–80 mm CL), food items should increase to 5–10 mm in diameter and be of firmer consistency. Differences in feeding behaviour between spiny lobster species suggest that formulated diets developed to be efficient in one species may not be directly transferable to other species.

1. Introduction

The Caribbean spiny lobster, *Panulirus argus*, is an excellent candidate for commercial aquaculture because of rapid growth and straightforward husbandry (Lellis, 1991; Booth and Kittaka, 2000; Jeffs and Davis, 2003). However, the development of a formulated feed for this spiny lobster species remains a significant impediment to its commercial aquaculture despite some initial research (Jeffs and Davis, 2003; Williams, 2007). There is an underlying lack of knowledge of the feeding capabilities and behaviour of spiny lobsters, including for the Caribbean lobster. Recent reviews of the nutrition of spiny lobsters in culture concluded that understanding the feeding capabilities and the corresponding format of formulated feeds are critical for advancing the development of formulated feeds for spiny lobster aquaculture, by maximising intake and reducing feed wastage (Nelson et al., 2006; Williams, 2007). For example, up to 50% of formulated feed pellets fed to juveniles of the spiny lobster, *Jasus edwardsii*, were wasted through inefficient handling by lobsters, and simple changes in pellet dimensions were found to reduce waste by as much as 19% (Sheppard et al., 2002).

Investigations of species-specific feeding behaviour and functional morphology, as well as digestive capabilities, over a range of life-history stages is an effective means of identifying ontogenetic changes in dietary capabilities (Cox and Johnston, 2004). This approach has been used successfully in a wide range of crustaceans and in many instances leading to advances in the design and method of delivery of formulated feeds for aquaculture. This approach has already been used with considerable success for larval spiny lobsters (Cox and Johnston, 2003), as well as slipper lobsters (Suthers and Anderson, 1981; Johnston and Alexander, 1999), blue crabs (McConaugha, 2002), and shrimp (Alexander and Hindley, 1985). While the feeding morphology and behaviour of adult spiny lobsters has been described (Mikami and Takashima, 1994), it is not well known in the puerulus (megalopal stage which is often incorrectly called the "postlarva" — Williamson, 1982) and the subsequent juvenile, which frequently undergo marked ontogenetic changes in habitat and diet (Butler et al., 2006). For example, the puerulus of the Caribbean lobster settles and remains within dense inshore macroalgal beds. Once it has molted to the first instar juvenile it begins to feed, mostly on small resident crustaceans and molluscs, before emerging at >15 mm carapace length (CL) to seek

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* Corresponding author. National Institute of Water and Atmospheric Research, Private Bag 14901, Kilbirnie, Wellington 6241, New Zealand. Tel.: +64 4 386 0300; fax: +64 4 386 2153.
E-mail address: s.cox@niwa.co.nz (S.L. Cox).

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shelter in nearby crevices and begin feeding locally on larger prey (Andrée, 1981; Marx and Herrnkind, 1985; Lalana et al., 1987). Larger juveniles then move offshore, particularly around reefs, and are more mobile, ranging across an array of habitats in search of a much wider variety of prey (Cox et al., 1997; Briones-Fourzán et al., 2003).

Therefore, the aim of this research was to describe the morphology and functioning of the mouthparts in the Caribbean spiny lobster from puerulus to young adult to determine the changes in feeding capabilities that could lead to improvements in the design of formulated feeds for aquaculture.

2. Methods and materials

2.1. Animal collection and husbandry

Approximately 100 newly settled *P. argus* pueruli were collected from 10 Witham collectors (Witham et al., 1968) moored in surface waters in the Florida Keys, following the new moon in March and April 2005. Newly settled pueruli were sorted from more advanced developmental stages on the basis of well-established staging criteria (Lewis et al., 1952). The pueruli were transported in seawater to the Harbor Branch Oceanographic Institute at Florida Atlantic University in Fort Pierce, Florida, and placed into holding tanks which included a selection of natural macroalgal (*Caulerpa* sp.) and artificial refuges. The lobsters were fed frozen brine shrimp, *Artemia salina* and wild food items (i.e., worms, amphipods, and other various small crustaceans, as well as frozen natural seafood items). Lobsters were held at 14:10 light–dark cycle, at 28±1 °C and salinity maintained at 30±2‰. Ten transparent pueruli (<5 days after settling) were used for mouthpart analysis immediately upon arrival at the laboratory, and remaining individuals were on-grown in the tanks until they subsequently reached the required developmental stage of early juveniles (10–15 mm CL), juvenile (15–44 mm CL), late juvenile–adult (45–80 mm CL) for video analysis of feeding behaviour and mouthpart morphology.

2.2. Mouthpart morphology and video analysis

For each size range of lobsters, five individuals were tethered with cyanoacrylic adhesive to fine wire (0.25 mm diameter), at the mid-section of the dorsal surface of the cephalothorax and then placed into a glass evaporating dish containing fresh seawater. Experimental temperature was maintained at 28±1 °C and light levels were kept constant at 2 lx. Feeding responses and mouthpart movements were induced by placing frozen *A. salina* or fresh clam tissue (*Mercenaria mercinaria*) within the oral field of the tethered lobster. The mouthpart movements and function during food capture, manipulation and mastication were observed using an inverted Meiji EM28TR compound microscope (Martin Microscope Company, USA) with fibre optic illumination and Sony Digital Handycam, which recorded directly onto DVD for later analysis. After recording was completed, the five individual lobsters were euthanized by rapid cooling in an ice slurry and the mouthparts dissected out, photographed and then drawn. In the following descriptions, the terminology of Paterson (1968) and Nishida et al. (1990) is used for the mouthparts and that of Factor (1978) is used to describe the setae.

3. Results

3.1. Puerulus (<9 mm CL)

The mandibles, maxillae and maxillipeds of the puerulus were small in size, lacked calcification, and had only a limited number of setae. Microscopic examination of the mouthparts and the gut confirmed that the puerulus stage is non-feeding by the inadequacy of the mouthparts and the absence of any food in the gut.

The oesophagus was not fully formed and the opening into the oesophagus appeared to be covered by a fleshy membrane. The overlying mandibles and maxillae were fleshy, soft structures which did not move, even when physically stimulated. The mandibles were asymmetrical and simplified, with an unsegmented, laterally attached mandibular palp which was partially covered posteriorly by the paragnaths (Fig. 1A). The left mandible incisor process consisted of an undeveloped single, blunt tooth. The first maxillae were flattened, with a spinose exopod and epipod, and a rudimentary endopod, together forming three flat lobes (Fig. 1B). The second maxilla gave rise to an elongated scaphognathite-like epipod, divided into proximal and distal endites, and a smaller lobe-like endopod (Fig. 1C). A fringe of setae was present along the distal edges of the exopod and a small tuft of simple spinose setae on the proximal endite. The distal and proximal endites are much reduced in the first maxilliped, with the endopod fused to the elongated exopod (Fig. 1D). A distal flagellum was present on the anterior tip of the exopod. The epipod resembled a flattened and membranous plate. Setae were present along the distal margins of both the exopod and endopod. The second and third maxillipeds were more elongated compared with the maxilla or first maxilliped (Fig. 1E and F). The endopods consisted of five segments each. The exopod on the second maxilliped was elongated with four segments, whereas the exopod on the third maxilliped was much reduced and only had two segments. Setae were present along the inner margin of the endopod dactyl and carpus of the third maxilliped.

Among the five individuals examined for feeding behaviour, there was consistency in their mouthpart morphology and movement, including the absence of any feeding behaviour. Close observations of untethered pueruli in the tanks indicated that the lack of feeding behaviour was not a response to the experimental tethering treatment.

3.2. Early juvenile (10–15 mm CL)

The relative position of the six pairs of mouthparts (mandibles, maxillae I and II, and maxillipeds I, II and III) as well as the labrum, paired paragnaths, and the posterioventral fleshy lobe (membranous lobe), remained constant between the puerulus and all subsequent juvenile stages, including early juveniles. The main changes between the puerulus and first instar juveniles were the development of additional setae and spines, increased mouthpart robustness (i.e., calcification), an immediate transition to fully functional mouthparts, and almost doubling in the overall dimensions of the mouthparts. In the first instar juvenile, the mandibular palps had developed simple setae on the proximal tips and had become segmented. The incisor process had also become more defined, bearing a more prominent groove in the molar process. The epipod, endopod and exopod of the first maxilla all bear setae and spines (Fig. 2A). The distal and proximal endites of the epipod of the second maxilla both bear setae. The exopod and the endopod have a fringe of setae along the lateral edges. The first maxilliped is similar in structure to the puerulus, however, the distal flagellum is elongated and the interior edge of the endopod is flatter and broader. The major difference between the second and third maxilliped in the early juveniles is the development of setation along the inner margin of the dactyl, propodus, merus and basis (Fig. 2B and C). Segmentation develops between the basis and coxa of the third maxilliped (Fig. 2C). The exopod is elongated and the distal segment also bears setae. Among the five individuals examined, there was consistency in their mouthpart morphology with mouthparts increasing in proportion to changes in body size. The mouth aperture was approximately 300 μm diameter, however, soft, fleshy food particles ranging from 1–2 mm and whole juvenile *A. salina* (up to 2 mm total length) were observed being pushed between the mandibles by the maxillae. Early juvenile lobsters were capable of efficiently shredding fleshy clam tissue and adult *A. salina* into small (1–3 mm) pieces.