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AN INVASIVE CRAB IN THE WESTERN ATLANTIC

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## LIFE HISTORY, LARVAL DESCRIPTION, AND NATURAL HISTORY OF *CHARYBDIS HELLERII* (DECAPODA, BRACHYURA, PORTUNIDAE), AN INVASIVE CRAB IN THE WESTERN ATLANTIC

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### A B S T R A C T

This study provides descriptive information on the natural history and life history of an invasive population of *Charybdis hellerii*, which is native to the Indo-West Pacific region, and which invaded the western Atlantic Ocean in the late 1980s. In this study, sampling at 27 sites along the Indian River Lagoon, Florida, during 1995-1999 showed that this crab is established in structured habitats (riprap of jetties, coralline ledges, mangrove roots, and dense algae) near inlets of the central and southern portions of the lagoon. It was not found at sites away from inlets, nor from apparently suitable structured habitats at an inlet to the north of Cape Canaveral. Although crab abundances were low, the broad size structure of the population indicates sustained recruitment into the population. Data on life history features and formal larval descriptions were derived from a cohort of larvae reared in the laboratory, including egg incubation and hatching, complete larval development, early crab instars, juvenile growth to sexual maturity, and brood production. Larval descriptions include detailed drawings of all appendages, as well as the carapaces, abdomens, and telsons for all 6 zoeal stages, and a photograph of the megalopa. *Charybdis hellerii* possesses numerous life history traits and natural history characteristics that are adaptive for invasion of new geographic regions, including: (1) a relatively long larval life (44 days), which facilitates dispersal; (2) rapid growth and maturation within about one year, contributing to a short generation time, which promotes rapid population growth; (3) the ability to store sperm and to produce multiple broods of high fecundity in rapid succession, which favors rapid expansion of founder populations; (4) generalized carnivorous diet, which allows opportunistic exploitation of a variety of food resources; (5) ability to use a diversity of structured habitats, which provides opportunity to exploit a range of habitats, but also suggests that its secretive or cryptic behavior may serve to protect it from visual predators.

The portunid crab *Charybdis hellerii* (A. Milne Edwards, 1867) is native to the Indo-West Pacific Ocean. It has been reported widely from: the Red Sea (Rüppell, 1830); Djibouti (Nobili, 1906); Somalia (Guinot, 1962); South Africa (Stebbing, 1908); Madagascar (Crosnier, 1962); Persian Gulf (Stephensen, 1945); Pakistan, Andaman Islands, Hong Kong, and Singapore (Alcock, 1899); Ceylon and India (Henderson, 1893); Mergui Archipelago (De Man, 1887); China (Dai *et al.*, 1986; Dai and Yang, 1991); Japan (Urita, 1926); Indonesia (De Man, 1883); Australia (Miers, 1884); and New Caledonia (A. Milne Edwards, 1867). In its native range,

this crab is reported to prefer soft bottom substrates, but it is also found in rocky bottoms and among live coral from the intertidal zone to a depth of 51 m (Stephenson *et al.*, 1957; Crosnier, 1962).

This species is also introduced widely into non-native regions. It has invaded the eastern Mediterranean Sea along the coast of Israel as a lessepsian migrant through the Suez Canal (Monod, 1930; Galil, 1992). In the late 1980s it was also introduced into the western Atlantic Ocean, probably via larval transport in ballast water of ships arriving to the southwestern Caribbean basin. It quickly spread southward and northward, with

records from: Colombia in 1987 and 1988 (Campos and Türkay, 1989); Venezuela in 1987 (Hernández and Bolaños, 1995); Cuba in 1987 (Gómez and Martínez-Inglesias, 1990); and Brazil in 1995 (Cristina and Calado, 1996). In 1995 this invasive crab was recorded from the Indian River Lagoon, Florida, U.S.A. (Lemaitre, 1995). This rapid spread in the western Atlantic is thought to have occurred by larval dispersal, perhaps assisted by further ballast-water transport.

Despite the probable role of larval transport and dispersal in the invasion biology of this species, little is known about its life history in its introduced range, and its larval development has not been described. There are published larval descriptions of several other species of *Charybdis* (Yatsuzuka, 1952; Hashmi, 1969; Kurata and Omi, 1969; Kurata, 1975; Kurata and Nishina, 1975; Motoh and Villaluz, 1976; Greenwood and Fielder, 1980; Fielder *et al.*, 1984). However, complete larval development is available for only two species of *Charybdis* (Kurata and Omi, 1969; Greenwood and Fielder, 1980), and none of the previous studies includes information about other life stages, which are important for understanding life history development in brachyurans (Hines, 1986). Little is published about this species' natural history, especially in the western Atlantic. Some aspects of life history, natural history, and ecology are known for other *Charybdis* species (Stephenson *et al.*, 1957; Stephenson, 1962; Sumpton, 1990; Galil, 1992).

The present study provides basic information on the life history and natural history of *Charybdis hellerii*, with four main objectives: (1) to summarize natural history information on distribution, habitat use, abundance, and population structure during the initial phase of this crab's invasion within the Indian River Lagoon, Florida; (2) to provide data on the duration, age and size for larval development and juvenile growth to adult stages; (3) to describe larval development of *C. hellerii* in the laboratory, including detailed formal descriptions of all six zoeal stages, a general description of the megalopa, and carapace outlines of the first three crab instars; (4) to provide color photographs of key life history stages of this species in order to facilitate documentation of this species' invasion of other areas.

## MATERIALS AND METHODS

### Natural History Sampling

We conducted collecting surveys sporadically during 1995–1999 at 27 sites along the Indian River Lagoon from Ponce Inlet north of Cape Canaveral to St. Lucie Inlet at the southern end of the lagoon, as well as further south to Boca Raton Inlet (Fig. 1). Collecting methods included traps (polyvinyl chloride (pvc) pipe of 15-cm diameter and 50-cm long with wire mesh cones in the ends: cubical wire traps of 3-cm and 12-mm mesh); 3-m otter trawls pulled in 3–6-m deep water over soft bottom for 1-km distance; and hand collection in the intertidal zone during low tides and by snorkeling in the shallow (< 2 m) subtidal zone. Traps were set for 24-h, while trawling and hand collections were conducted during daylight. A variety of habitats were sampled, including mangroves (*Rhizophora mangle* Linnaeus), oyster reefs, concrete rubble, dredged channels with soft bottoms and with carbonate rock ledges. For all specimens of *Charybdis hellerii* collected, we recorded habitat, body size (carapace width in mm), and sex, including maturity and ovigerous condition for females. We also recorded the collecting effort as trap days, standard 1-km trawls, and person-hours of hand collecting.

### Life History Description

A description of the complete life history cycle, including larval development and growth to maturity and egg production, was based primarily upon rearing a cohort of crabs hatched from a brood of eggs produced by a female *Charybdis hellerii*. The female was captured during April 1995 by trap in the turning basin of Fort Pierce Inlet, Indian River Lagoon, Florida, U.S.A. Supplemental life history information was derived from additional field collections. The adult female specimen was transported to the Smithsonian Marine Station, where she was held in a recirculating sea water system at 24°C and 34–36 ppt. and fed *ad libitum* with fresh clams (*Mercuria mercenaria* Linnacus, 1758). The female was held in isolation until she became ovigerous and her eggs hatched during September 1995. Upon hatching, the larvae were collected from the tank and reared individually in compartmented plastic boxes at 24°C, 32-ppt salinity. Salinity for the larval cultures was lowered to 32 ppt to compensate for potential evaporation in the relatively small volumes (about 75 ml) of water used in the compartmentalized rearing trays. Early zoeal stages were fed rotifers (*Brachionas plicatilis* Müller), while later stages were fed a mixed diet of rotifers and newly hatched brine shrimp (*Artemia franciscana* Kellogg, 1906) nauplii (Sulkin, 1978; Sulkin *et al.*, 1980). Megalopas initially were fed adult brine shrimp. Because this food source was readily ingested, the brine shrimp diet was supplemented with small pieces of clam siphon muscle. This mixed diet also proved adequate for initial crab stages. Penicillin G and Streptomycin sulfate were used as antibiotics in the culture water, but no anti-fungal agent was used. Water and food were changed daily, and fresh antibiotic was applied. Initial crab stages were held individually in compartmented plastic boxes with the same temperature, salinity, and food conditions as megalopae. On 30 November 1995, 13 juvenile crabs (9 Second Instar Stage C2 and 4 Third Instar Stage C3) were transferred to a common tank, where they were maintained at 24°C, 32-

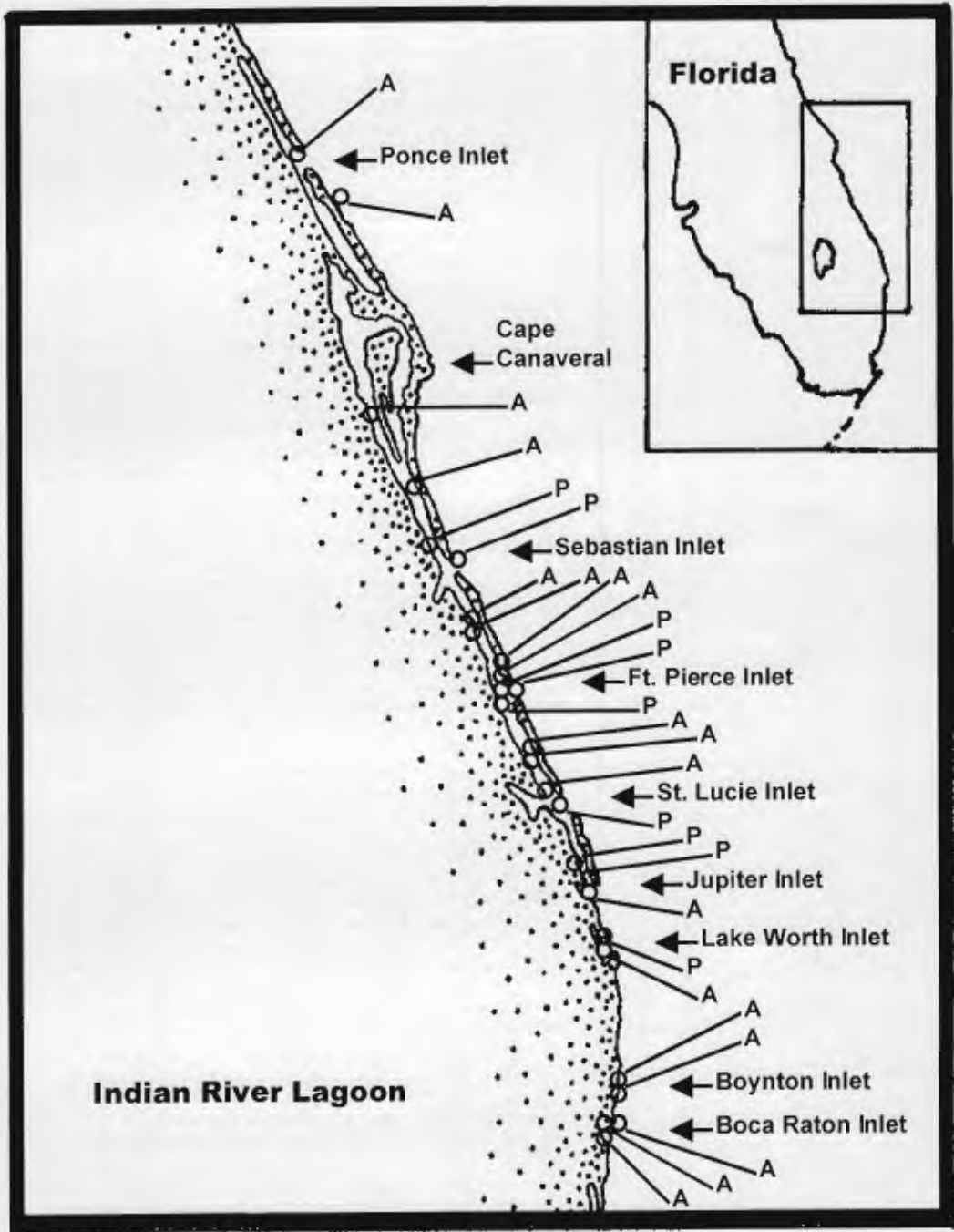


Fig. 1. The 17 collecting sites along the Indian River Lagoon, Florida. P = sampling sites where *Charybdis hellerii* was present; A = sampling sites where *C. hellerii* was not found.

ppt salinity and fed minced clam siphon muscle. After several days, salinity for rearing juveniles was raised to 34–36 ppt. Growing juveniles and a surviving adult had voracious appetites and readily ate a variety of invertebrates provided at about daily intervals. A single surviv-

ing adult female was kept in isolation in an aquarium with filtered, aerated sea water (changed approximately every 10 d) and provided with structured habitat. Her sequence of brood production also was recorded.

### Larval Specimen Preparation and Description

Appendages were dissected under a Wild M5 binocular microscope with a 2 $\times$  supplementary lens. Specimens were not stained but were cleared by mounting in Polyvinyl lactophenol. Cover slips were sealed with clear fingernail varnish, and the appendages were drawn using an Olympus BH-2 microscope equipped with Nomarski interference contrast and attached *camera lucida*. The long plumose natatory setae of the first and second maxilliped, and the antennal aesthetascs were drawn truncated. A total of 13 first stage zoeas, 8 second stage zoeas, 5 third stage zoeas, 2 fourth stage zoeas, 2 fifth stage zoeas, and 2 sixth stage zoeas were examined. The sequence of the zocal description (see Clark *et al.*, 1998) is based on the malacostracan somite plan and described from anterior to posterior. Setal armature on appendages is described from proximal to distal segments and in order of endopod to exopod. The spent female and some larval stages were deposited in the United States National Museum, and the slides were deposited in the Natural History Museum, London.

## RESULTS

### Natural History

During 1995–1999, we sampled 27 locations between Ponce Inlet in the north and St. Lucie Inlet in the south of the Indian River Lagoon and further south to Boca Raton Inlet. *Charybdis hellerii* was collected only in the vicinity of the 3 inlets of the central and southern portion of the lagoon (Sebastian Inlet, Fort Pierce Inlet, and St. Lucie Inlet) and in Lake Worth Inlet immediately to the south (Fig. 1). No *C. hellerii* were collected north of Sebastian Inlet, including at Ponce Inlet north of Cape Canaveral, nor were they collected further south in the vicinity of Boyton Inlet and Boca Raton Inlet. Individuals were collected from the low intertidal zone (–0.3 m) to shallow subtidal water (3.5-m depth). They appeared to be closely associated with habitat structure of both hard substrates and some plant structures. Crabs were collected in the following habitats associated with hard substrates: subtidal coralline rock and ledges (pipe traps at Fort Pierce Inlet turning basin); intertidal and subtidal rock rip-rap of jetties (hand collecting at Fort Pierce Inlet, Sebastian Inlet); subtidal rock and concrete rubble and bulkhead (snorkling and hand collecting at Bessie Cove, near St. Lucie Inlet). In these hard-substrate habitats, the crabs often were found under rocks and rubble or nestled in crevices and corners. We also collected specimens associated with plant structures, including subtidal mangrove prop roots (pipe traps near Fort Pierce Inlet) and dense patches of subtidal algae (trawls near Sebastian Inlet).

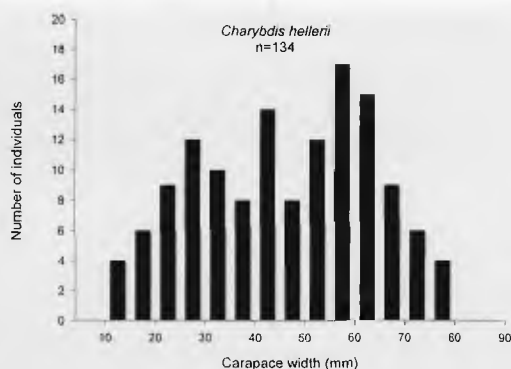


Fig. 2. *Charybdis hellerii*. Size-frequency distribution of crabs in collections from the Indian River Lagoon, Florida, 1995–1998.

In all cases, we collected *C. hellerii* only at high salinities (> 28 ppt) near inlets (Fig. 1). Exuvia from newly molted crabs were found occasionally in association with rock rip-rap at Sebastian Inlet and Fort Pierce Inlet. Our collections did not allow us to discern diurnal activity patterns, although observations during daytime snorkeling showed most (80%) crabs were found in or under structure, while others (20%) were observed partly exposed in crevices of concrete and wood bulkheads.

We derived estimates of population abundance and size structure from our collections. Abundances of crabs in our collections were not high, with a total of 134 crabs in our combined collections. The maximum number of crabs per unit of collection effort was: one crab per trap per day; 3 crabs per 1-km trawl; and 12 crabs per hour of collecting by hand in intertidal and subtidal rocks. Population size structure spanned 14–79 mm carapace width but included no clear size or age classes of crabs (Fig. 2). The sex ratio was approximately balanced with 65 females and 69 males, without apparent differences in size by gender. Maximum size for males (79 mm) was similar to that for females (77 mm). Oviparous females ( $n = 4$ ) were not common in the collection and ranged from 72–77-mm carapace width.

### Life History

A summary of life history development is provided in Table 1. A mature female (CW = 78 mm) collected in April 1995 produced a brood of bright orange eggs on 13 Septem-

Table 1. *Charybdis hellerii*. Life history characteristics for developmental stages reared in the laboratory. For each life stage, the following variables are given: Average Duration (with minimum time in parentheses); Average Age after hatching (with minimum age in parentheses); and Average Size (with size range in parentheses). Sizes are for diameter of eggs, carapace length for zoeal stages and megalopa, and carapace width for crab stages.

Life stage	Average duration (minimum)	Average age (minimum) post-hatching	Average size (range)
Egg (brood incubation) ( <i>n</i> = 20 from each of 6 crabs)	13 d		293 $\mu$ m (286–303 $\mu$ m)
Zoea I ( <i>n</i> = 5)	8 d (7 d)	0 d	310 $\mu$ m (300–330 $\mu$ m)
Zoea II ( <i>n</i> = 4)	7 d (6 d)	8 d	340 $\mu$ m (310–370 $\mu$ m)
Zoea III ( <i>n</i> = 3)	7 d (6 d)	15 d	470 $\mu$ m (430–500 $\mu$ m)
Zoea IV ( <i>n</i> = 3)	6 d (5 d)	22 d	640 $\mu$ m (600–680 $\mu$ m)
Zoea V ( <i>n</i> = 3)	6 d (5 d)	28 d	780 $\mu$ m (730–820 $\mu$ m)
Zoea VI ( <i>n</i> = 3)	6 d (5 d)	34 d (31 d)	910 $\mu$ m (900–920 $\mu$ m)
Megalopa ( <i>n</i> = 18)	14.1 d (8 d)	40.2 d (34 d)	1.8 mm (1.7–1.9 mm)
Crab 1 ( <i>n</i> = 16)	7.7 d (5 d)	44.3 d (42 d)	2.9 mm (2.6–3.2 mm)
Crab 2 ( <i>n</i> = 12)	8.2 d (6 d)	52.0 d (48 d)	3.3 mm (2.8–4.0 mm)
Crab 3 ( <i>n</i> = 5)		60.2 d (54 d)	5.1 mm (4.9–5.5 mm)
Crab 4 ( <i>n</i> = 2)			6.5 mm (6.0–7.0 mm)
Juvenile crab ( <i>n</i> = 2)		3 mo	18 mm
Juvenile crab ( <i>n</i> = 1)		6 mo	35 mm
Prepubertal instar (female) ( <i>n</i> = 1)		9 mo	55 mm
Maturation (female) ( <i>n</i> = 1)		12 mo	67 mm
1st Brood produced		6 Nov 1996	
2nd Brood produced		27 Nov 1996	
3rd Brood produced		28 Dec 1996	
4th Brood produced		8 May 1997	
5th Brood produced		29 May 1997	
6th Brood produced		28 Aug 1997	
Death		23.5 mo	77 mm
Largest crab collected			79 mm

ber 1995. This holding interval clearly demonstrates that *C. hellerii* can store viable sperm for at least five months. Brood incubation lasted 13 d, and hatching occurred on 26 September 1995. Duration of zoeal development averaged 40 d, and the megalopa stage (Fig. 3) lasted another 4 d, for a total average larval period of 44 d. Juvenile growth in the laboratory was rapid, and sexual maturity of a single female was attained at a size of 77 mm in about 12 months. This virgin female produced a series of 6 non-fertile broods over the period from November 1996 to August 1997. The irregular interval of brood production ranged from about 3 weeks to 5 months. The female evidently molted once after reaching maturity at 67 mm, and this female crab died in the laboratory of unknown causes at the age of about 2 years old at a size (77 mm) near the maximum of crabs collected in the field (79 mm).

#### LARVAL DESCRIPTIONS

Morphological features of Zoea I–VI of *Charybdis hellerii* are illustrated (Figs. 4–23), with descriptions of the carapace spination,

appendages, abdomen, and telson provided below for each zoeal stage.

#### Zoea I

**Carapace** (Fig. 4a).—Dorsal spine long, distally curved, spinulation absent; rostral spine slightly shorter than dorsal spine, approximately equal in length to protopod of antenna, spinulation absent; lateral spines present, much shorter than rostral, straight, not spinulate; anterodorsal setae absent; 1 pair of posterodorsal setae; each ventral margin without setae; eyes sessile.

**Antennule** (Fig. 7a).—Uniramous, endopod absent; exopod unsegmented, with 1 broad, long, 2 slender terminal aesthetascs and 1 terminal seta.

**Antenna** (Fig. 8a).—Protopodal process distally spinulate, approximately equal in length to rostral spine; endopod absent; exopod unsegmented, with 1 long terminal seta.

**Mandible**.—Mandibular palp absent.

**Maxillule** (Fig. 10a).—Coxal endite with 7 setae; basal endite with 5 setal processes and

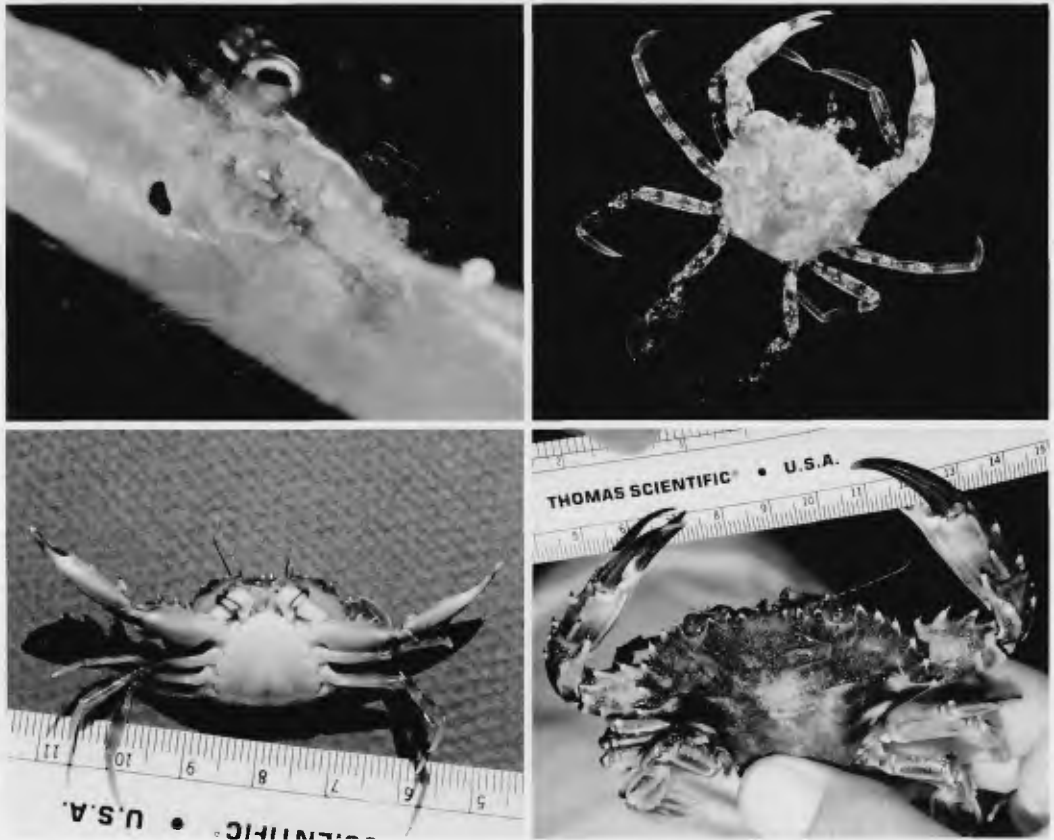


Fig. 3. *Charybdis hellerii*. Photographs of four life stages of crabs reared in the laboratory: (a, top left) megalopa on sea grass blade; (b, top right) first crab stage; (c, lower left) juvenile female at age 6 mos.; (d, lower right) mature female at age 12 mos.

2 small teeth; endopod 2-segmented, proximal segment with 1 seta; distal segment with 6 (2 subterminal + 4 terminal) setae; exopod seta absent.

*Maxilla* (Fig. 12a).—Coxal endite bilobed with 3 + 3 setae + 1 spine on distal lobe; basal endite bilobed, with 4 + 4 setae; endopod bilobed, with 2 + 4 setae; exopod (scaphognathite) margin with 4 setae and 1 long, distal, stout process.

*First Maxilliped* (Fig. 14a).—Coxa with 1 seta; basis with 10 setae arranged 2,2,3,3; endopod 5-segmented, with 2,2,0,2,5 (1 subterminal and 4 terminal) setae respectively; exopod 2-segmented, distal segment with 4 long, terminal, plumose natatory setae.

*Second Maxilliped* (Fig. 16c).—Coxa without setae; basis with 4 setae; endopod 3-segmented, with 1,1,5 (3 subterminal and 2 ter-

minal) setae respectively; exopod 2-segmented, distal segment with 4 long, terminal, plumose natatory setae.

*Third Maxilliped*.—Absent.

*Pereiopods*.—Absent.

*Abdomen* (Figs. 18, 20a).—5 somites; somite 2 with 1 pair of dorsolateral processes directed anteriorly; somite 3 with 1 pair of dorsolateral processes directed posteriorly; somites 1–2 with short, rounded and 3–5 with posterolateral spinous processes rudimentary; somites 2–5 with 1 pair of posterodorsal setae; pleopod buds absent.

*Telson* (Figs. 18a, 20a, 22a).—Each fork long, gradually curved, not spinulated; 1 pair of lateral spines and 1 pair of setae; 1 pair of dorsal medial spines; posterior margin with 3 pairs of stout spinulate setae.

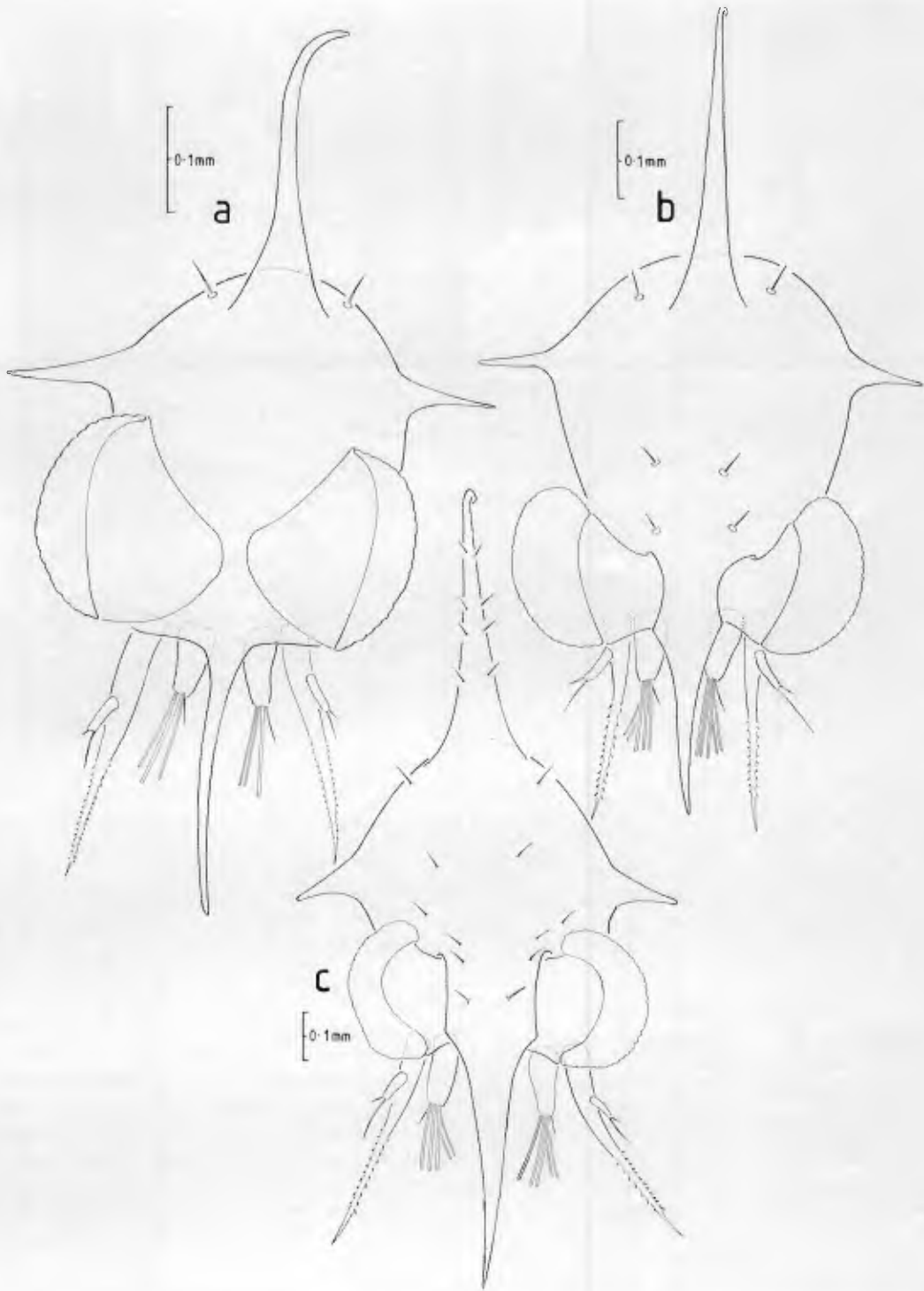


Fig. 4. *Charybdis hellerii*: anterior view of carapace; a. first stage zoea; b. second stage zoea; c. third stage zoea.



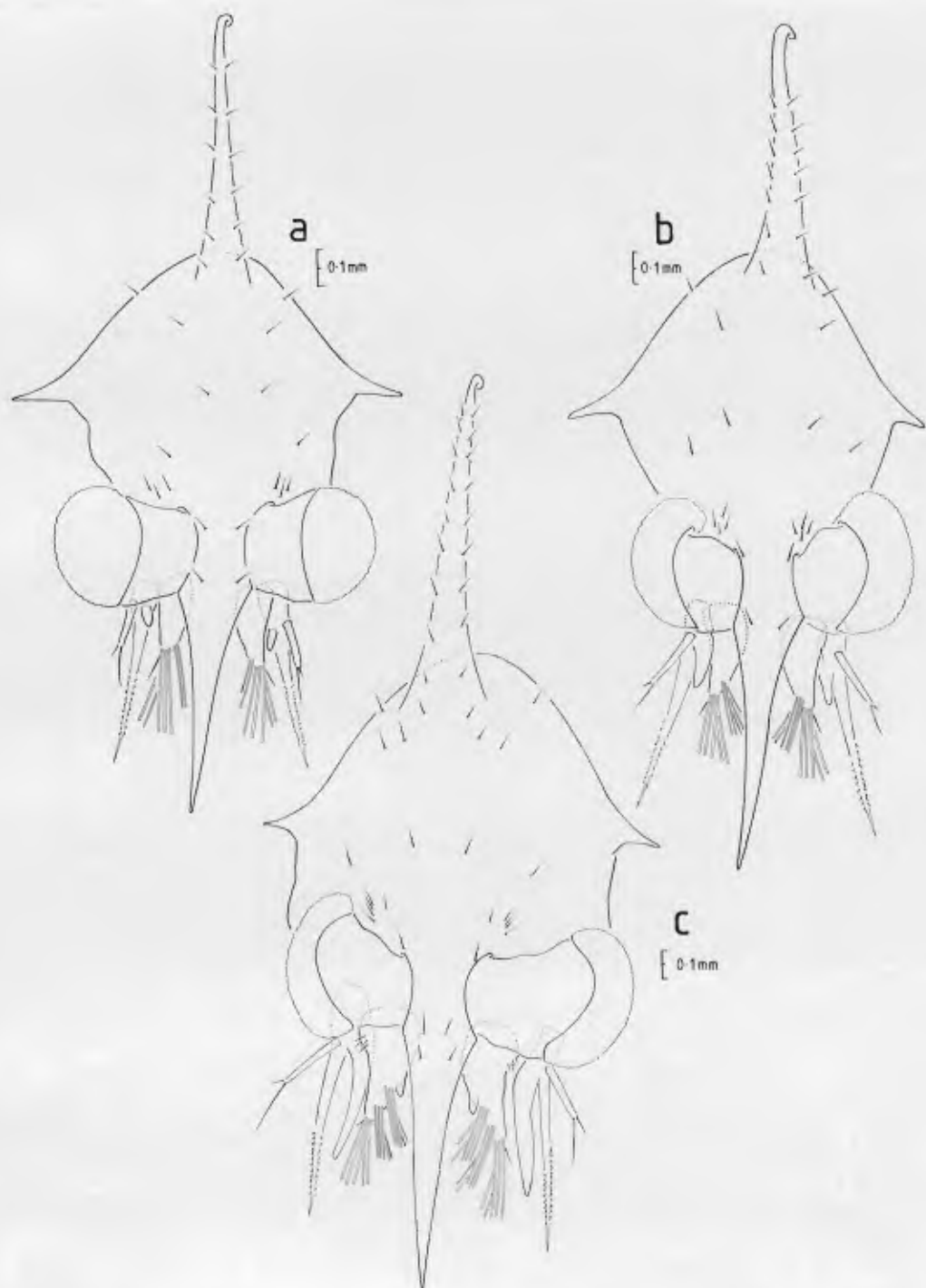


Fig. 5. *Charybdis hellerii*: anterior view of carapace; a. fourth stage zoea; b. fifth stage zoea; c. sixth stage zoea.

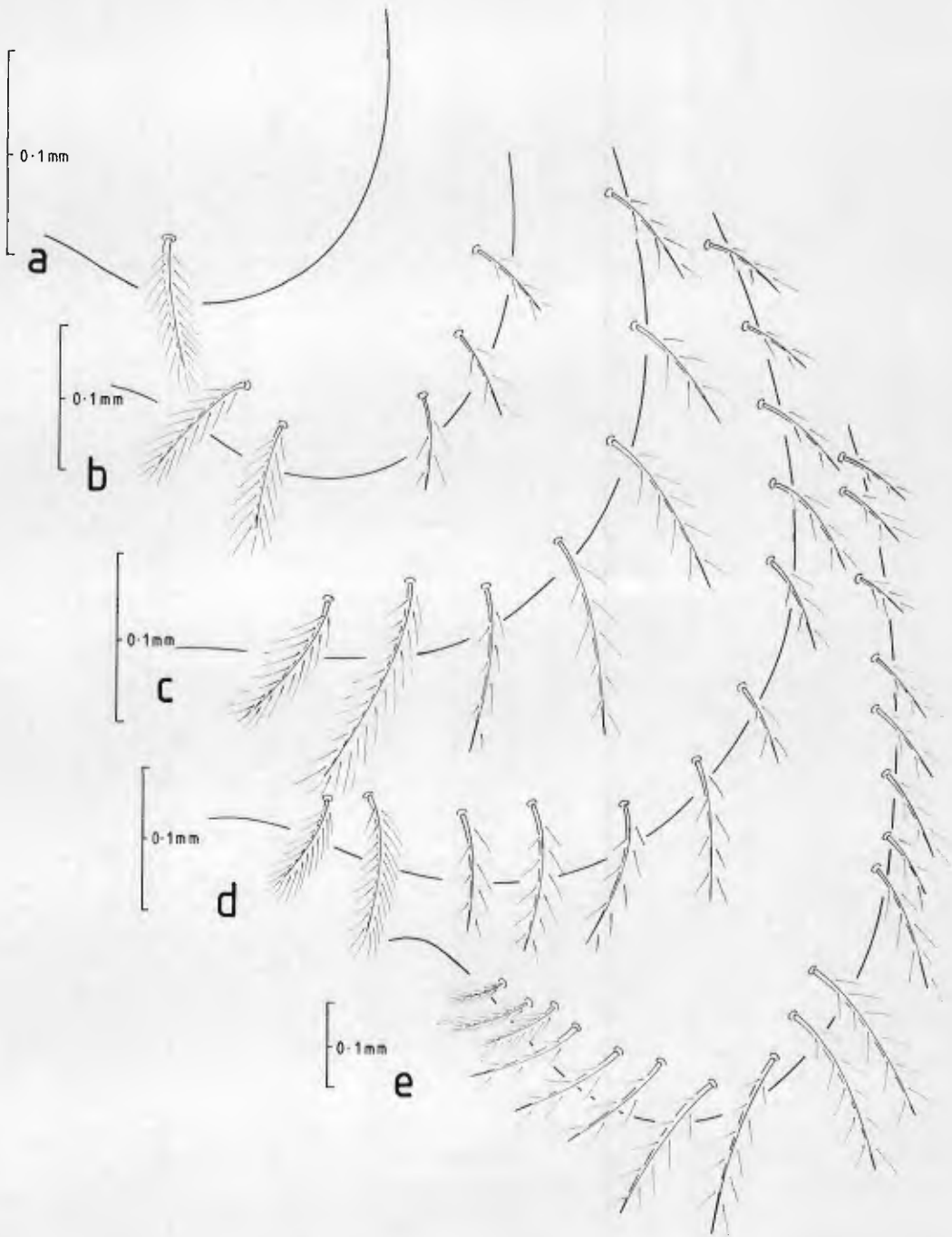


Fig. 6. *Charybdis hellerii*: chaetotaxy of ventral carapace margin; a. second stage zoea; b. third stage zoea; c. fourth stage zoea; d. fifth stage zoea; e. sixth stage zoea.

#### Zoea II

*Carapace* (Figs. 4b, 6a).—2 pairs of anterodorsal setae; each ventral margin with 1 plumose anterior seta; eyes stalked; otherwise unchanged.

*Antennule* (Fig. 5b).—Exopod now with 3 broad and 2 slender long aesthetascs; otherwise unchanged.

*Antenna* (Fig. 8b).—Unchanged.

*Mandible*.—Unchanged.

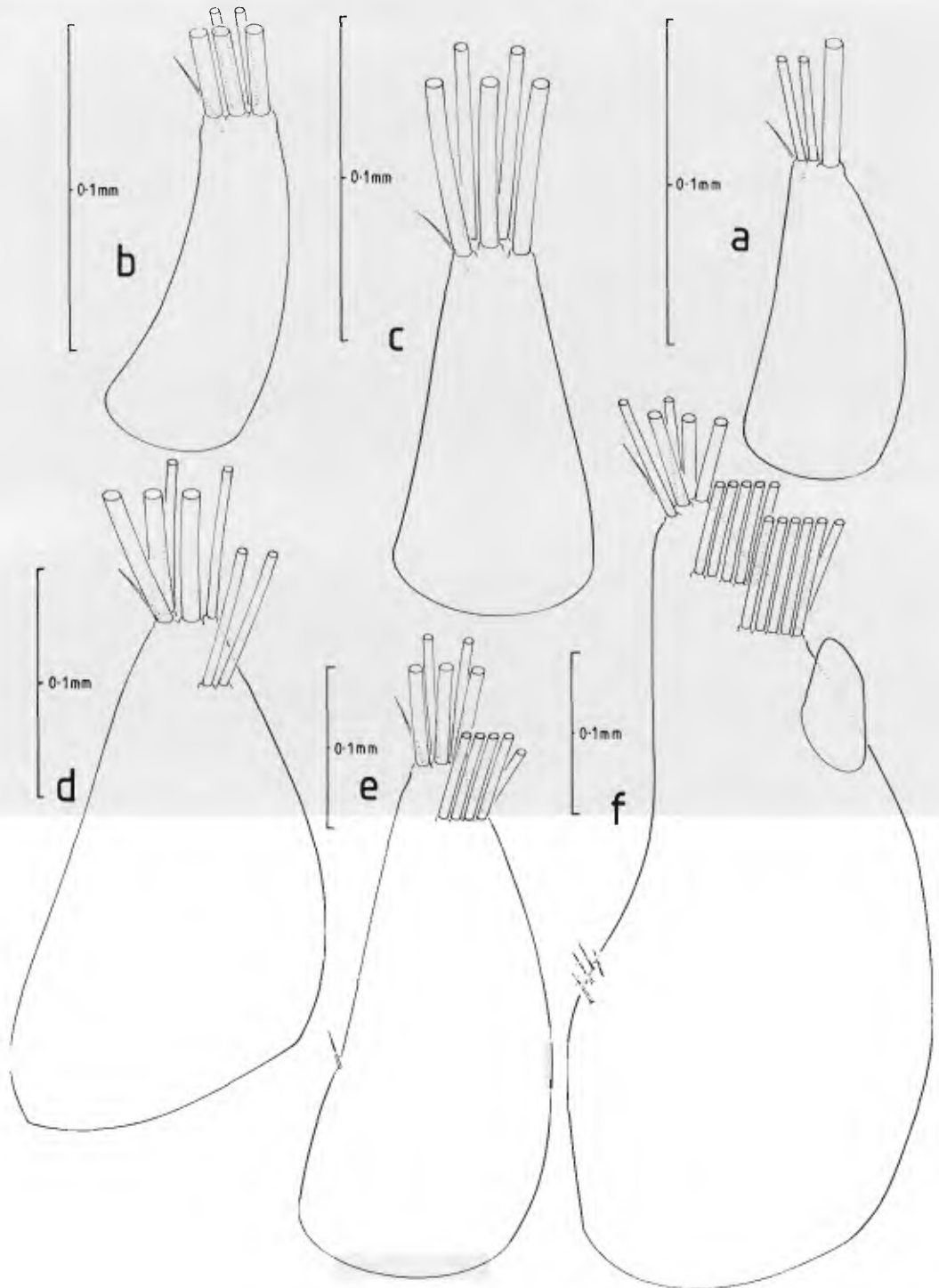


Fig. 7. *Charybdis hellerii*: antennule; a. first stage zoea; b. second stage zoea; c. third stage zoea; d. fourth stage zoea; e. fifth stage zoea; f. sixth stage zoea.

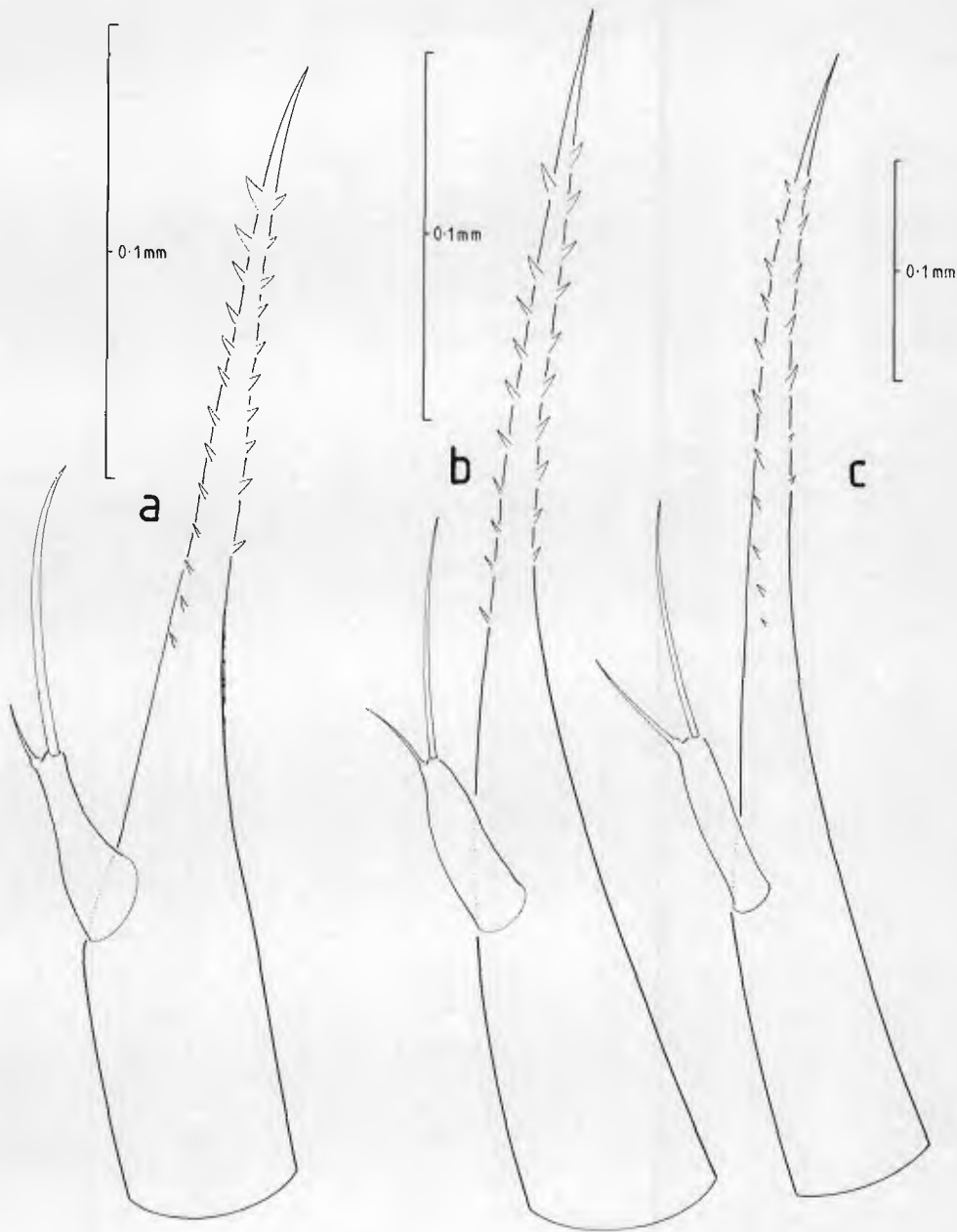


Fig. 8. *Charybdis hellerii*: antenna: a. first stage zoea; b. second stage zoea; c. third stage zoea.

*Maxillule* (Fig. 10b).—Coxal endite unchanged; basal endite with 7 setal processes, inner margin with teeth no longer prominent; endopod unchanged; exopod seta present.

*Maxilla* (Fig. 12b).—Coxal endites unchanged; basal endite with an additional spine on proximal lobe; endopod bilobed, unchanged; exopod (scaphognathite) margin

with 8 setae including reduced long distal stout process.

*First Maxilliped* (Fig. 14d).—Exopod distal segment with 6 long, terminal, plumose natatory setae; otherwise unchanged.

*Second Maxilliped* (Fig. 15b).—Exopod distal segment with 6 (occasionally 7) long, ter-



Fig. 9. *Charybdis hellerii*: antenna; a. fourth stage zoea; b. fifth stage zoea; c. sixth stage zoea.

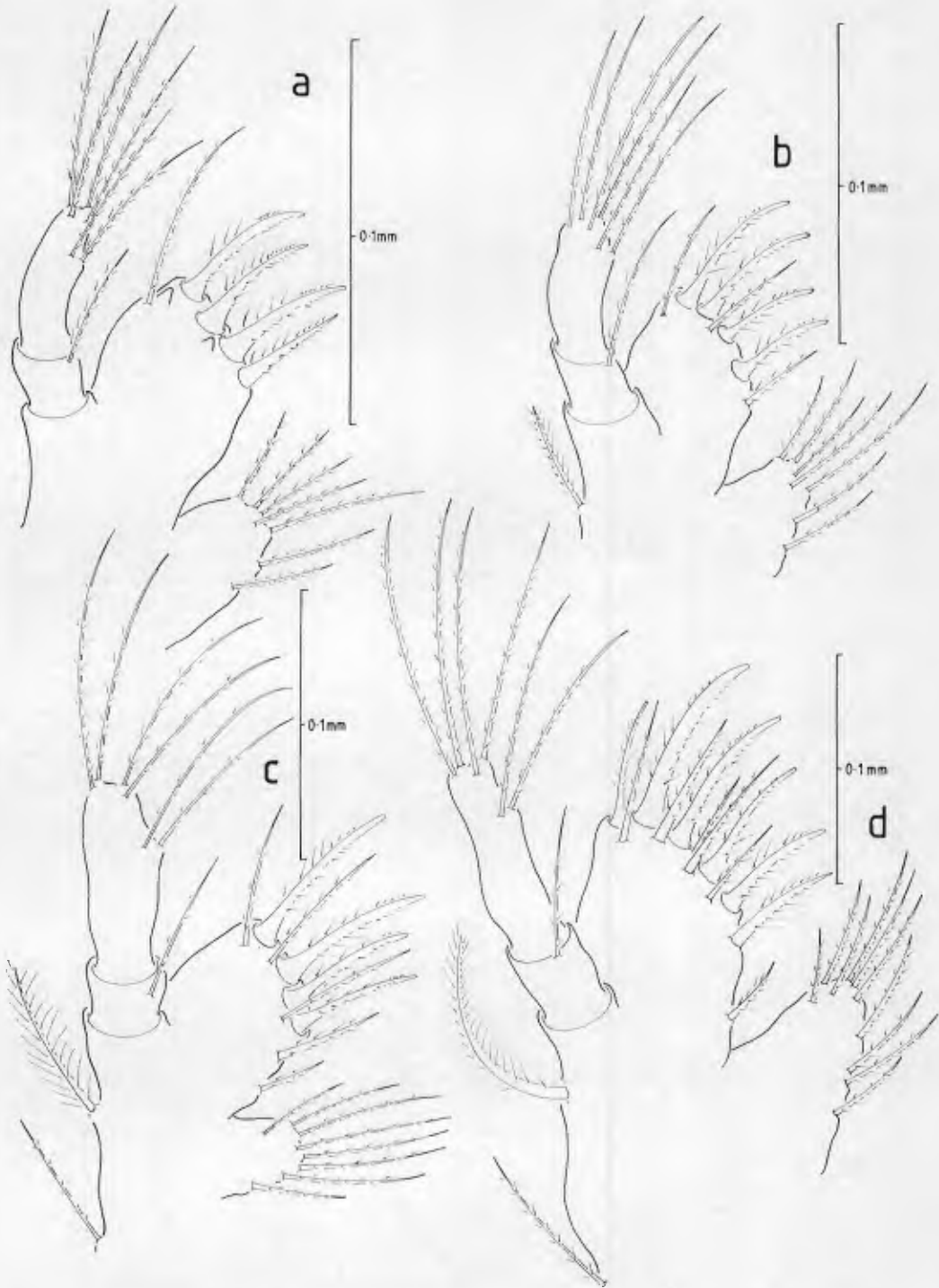


Fig. 10. *Charybdis hellerii*: maxillule; a. first stage zoea; b. second stage zoea; c. third stage zoea; d. fourth stage zoea.

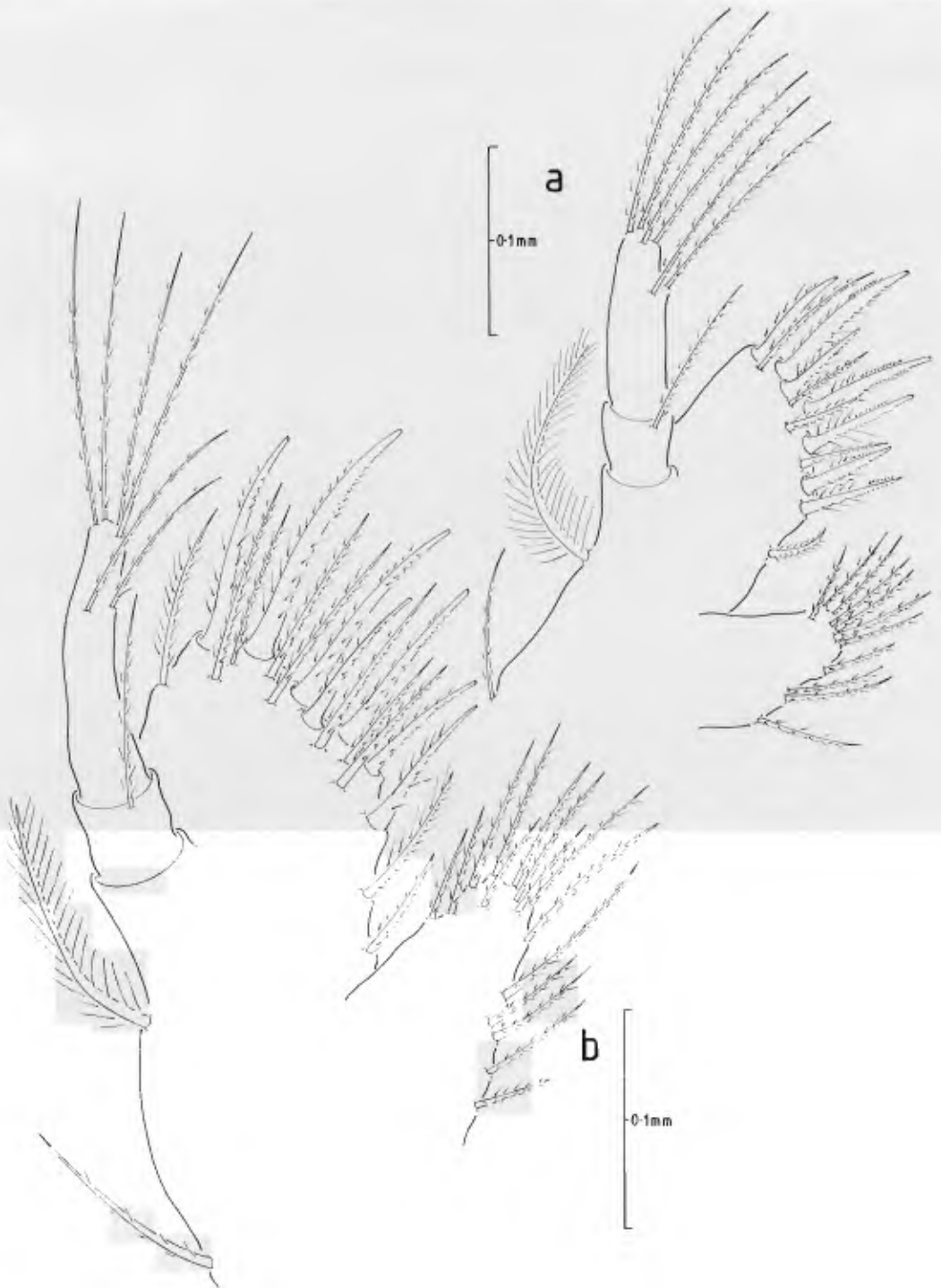


Fig. 11. *Charybdis hellerii*: maxillule: a. fifth stage zoea; b. sixth stage zoea.

minal, plumose natatory setae; otherwise unchanged.

*Third Maxilliped*.—Absent.

*Pereiopods*.—Absent.

*Abdomen* (Figs. 18b, 20b).—Somites 3–5 with posterolateral spinous processes more developed; otherwise unchanged.

*Telson* (Figs. 18b, 20b).—Posterior margin with additional pair of medial setae; otherwise unchanged.

### Zoea III

*Carapace* (Figs. 4c, 6b).—Dorsal spine with 4 pairs of setae; 5 pairs of anterodorsal setae; each ventral margin with 5 setae (1 plumose anterior seta and 4 posterior setae); otherwise unchanged.

*Antennule* (Fig. 7c).—Unchanged.

*Antenna* (Fig. 8c).—Unchanged.

*Mandible*.—Unchanged.

*Maxillule* (Fig. 10c).—Coxal endite with 8 setae; basal endite with 9 setal processes; epipod present; otherwise unchanged.

*Maxilla* (Fig. 12c).—Coxal endite with 3 + 4 setae, spine on distal lobe now absent; basal endite bilobed with 5 + 5 setae, spine on proximal lobe absent; endopod unchanged; exopod (scaphognathite) margin with 10 marginal setae.

*First Maxilliped* (Fig. 14c).—Exopod distal segment with 10 long, terminal, plumose natatory setae; otherwise unchanged.

*Second Maxilliped* (Fig. 16a).—Exopod distal segment with 10 long, terminal, plumose natatory setae; otherwise unchanged.

*Third Maxilliped*.—Absent.

*Pereiopods*.—Absent.

*Abdomen* (Figs. 18c, 20c).—6 segmented; somites 3–5 with posterolateral spinous processes more pronounced and extended posteriorly; somite 1 with 1 seta; somite 6 with 1 pair of posterodorsal setae, without posterolateral spinous processes; otherwise unchanged.

*Telson* (Figs. 18c, 20c, 22c).—Unchanged.

### Zoea IV

*Carapace* (Figs. 5a, 6c).—Dorsal spine with 6 pairs of setae; 8 pairs of anterodorsal setae; each ventral margin with 7 setae (1 plumose anterior seta and 6 posterior setae); otherwise unchanged.

*Antennule* (Fig. 7d).—Exopod now with 2 additional slender subterminal aesthetascs; terminal aesthetascs unchanged.

*Antenna* (Fig. 9a).—Endopod present; otherwise unchanged.

*Mandible*.—Unchanged.

*Maxillule* (Fig. 10d).—Coxal endite with 10 setae; basal endite with 12 setal processes; otherwise unchanged.

*Maxilla* (Fig. 12d).—Coxal endite bilobed, with 3 + 5 setae; basal endite bilobed, with 6 + 6 setae; endopod unchanged; exopod (scaphognathite) margin with 23 setae.

*First Maxilliped* (Fig. 14d).—Coxa now with 2 setae; endopod 5-segmented, with 2,2,1,2,5 (1 subterminal and 4 terminal) setae respectively; exopod distal segment with 12 long, terminal, plumose natatory setae.

*Second Maxilliped* (Fig. 16b).—Exopod distal segment with 12 long terminal plumose natatory setae; otherwise unchanged.

*Third Maxilliped*.—Unchanged.

*Pereiopods*.—Unchanged.

*Abdomen* (Figs. 19a, 21a).—Somite 1 with 1 pair of dorsomedial setae; somite 2–4 with 1 pair of dorsomedial setae; otherwise unchanged.

*Telson* (Figs. 19a, 21a, 23a).—Posterior margin now with 3 medial setae; otherwise unchanged.

### Zoea V

*Carapace* (Figs. 5b, 6d).—Dorsal spine with 7 pairs of setae; 9 pairs of anterodorsal setae; each ventral margin with 12 setae (1 plumose anterior seta and 11 posterior setae); otherwise unchanged.

*Antennule* (Fig. 7e).—Exopod now with 1 proximal seta; 5 slender subterminal aesthetascs; terminal aesthetascs unchanged.



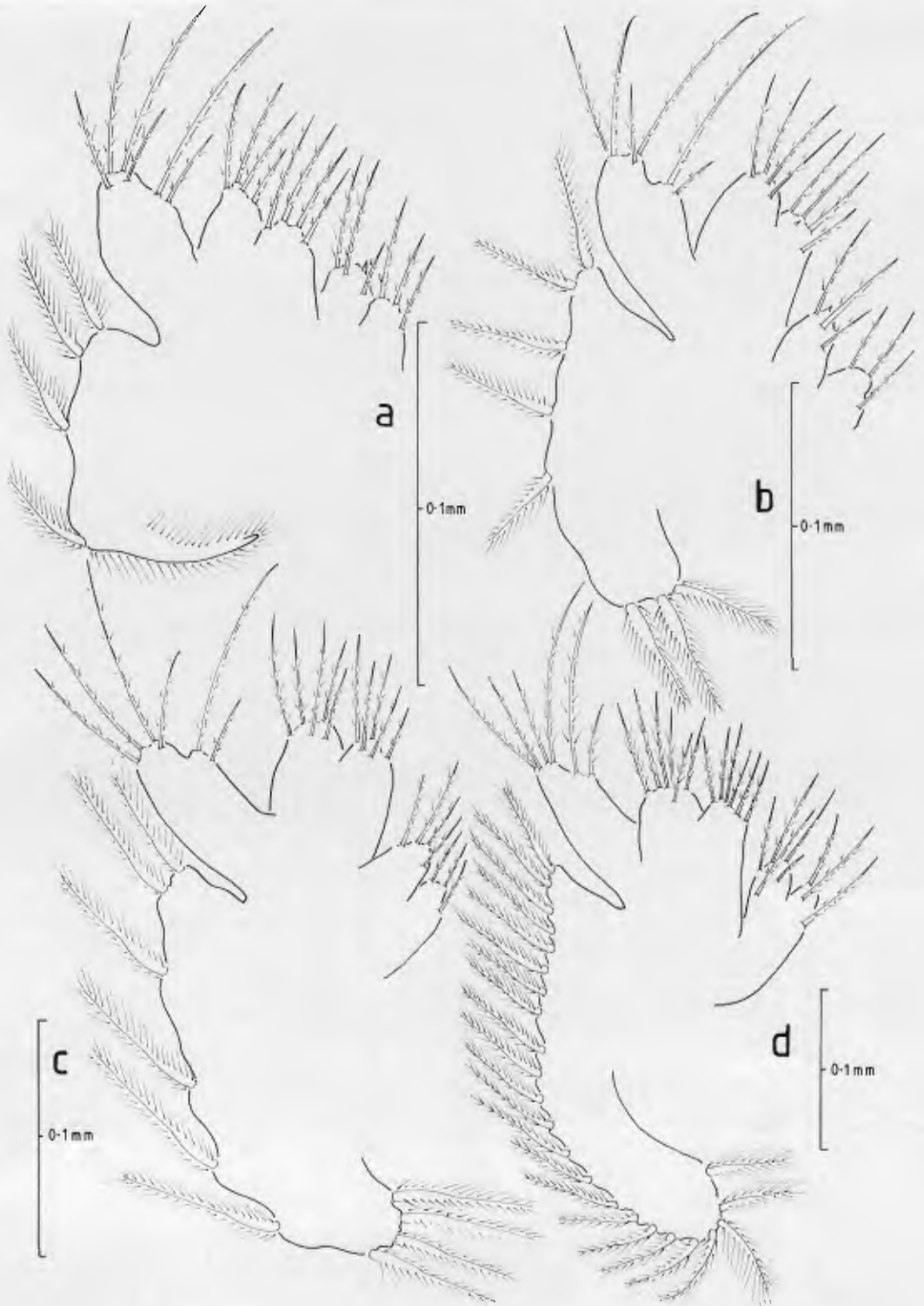


Fig. 12. *Charybdis hellerii*: maxilla; a. first stage zoea; b. second stage zoea; c. third stage zoea; d. fourth stage zoea.

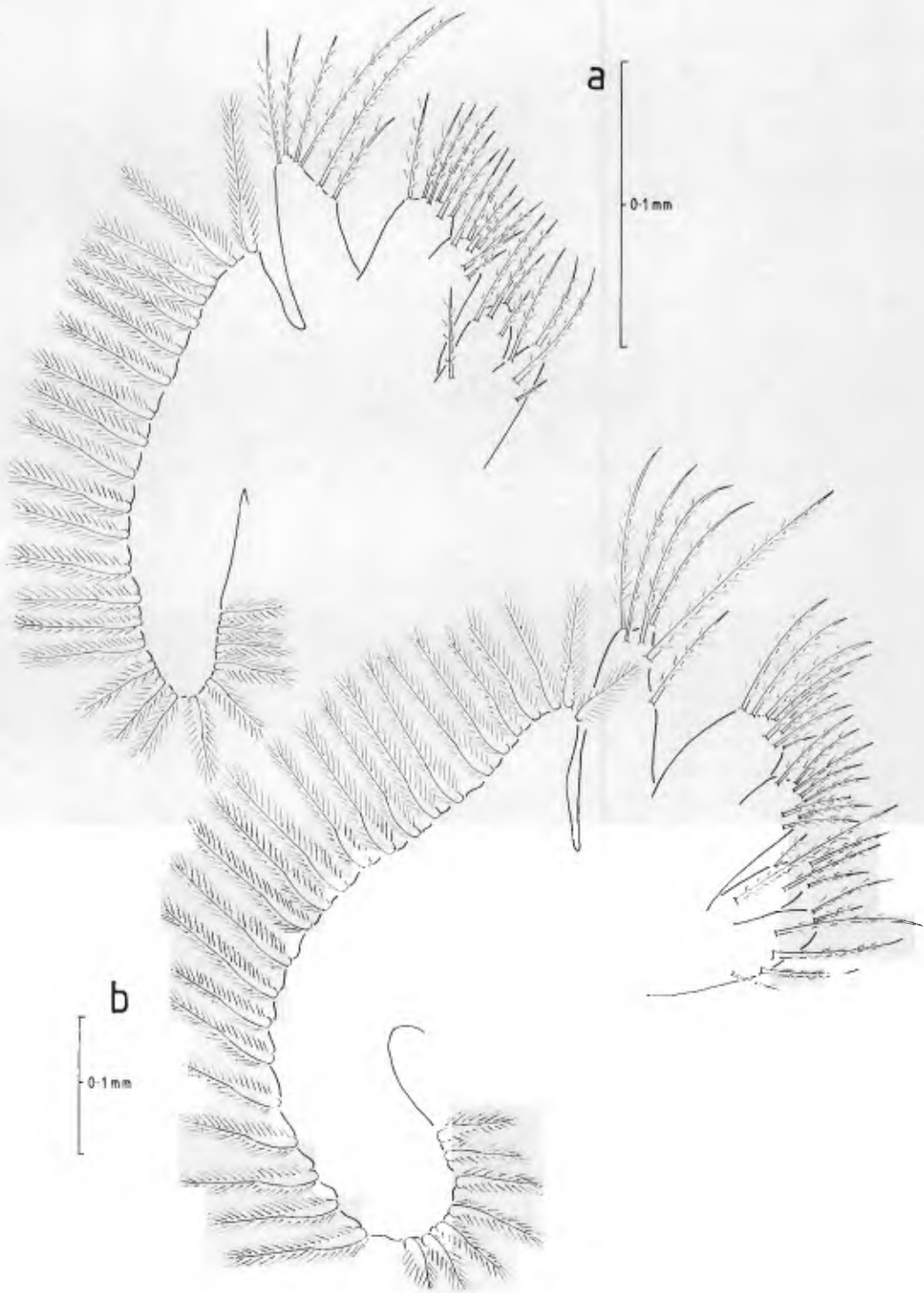


Fig. 13. *Charybdis hellerii*: maxilla; a. fifth stage zoea; b. sixth stage zoea.

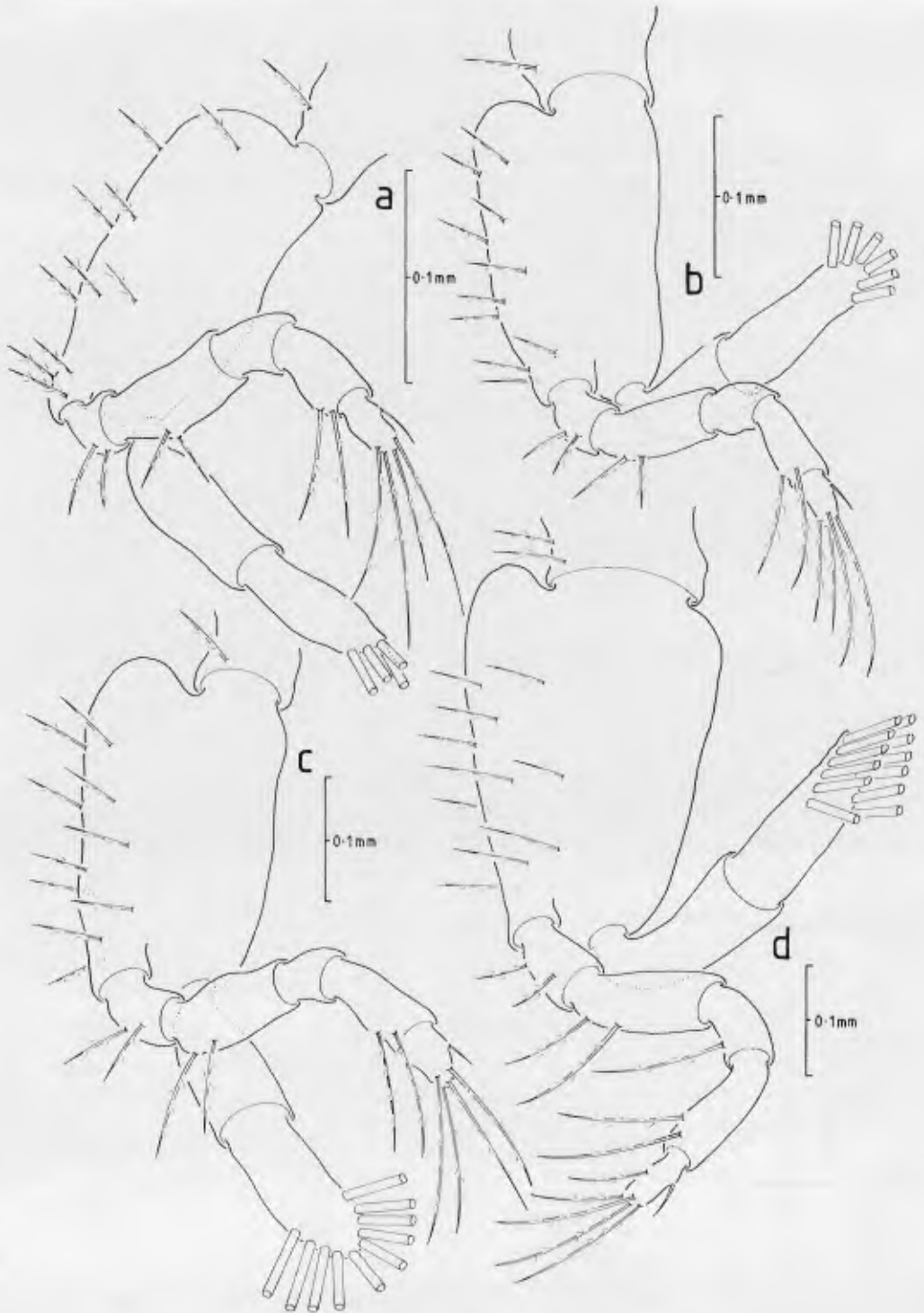


Fig. 14. *Charybdis hellerii*: first maxilliped; a. first stage zoea; b. second stage zoea; c. third stage zoea; d. fourth stage zoea.

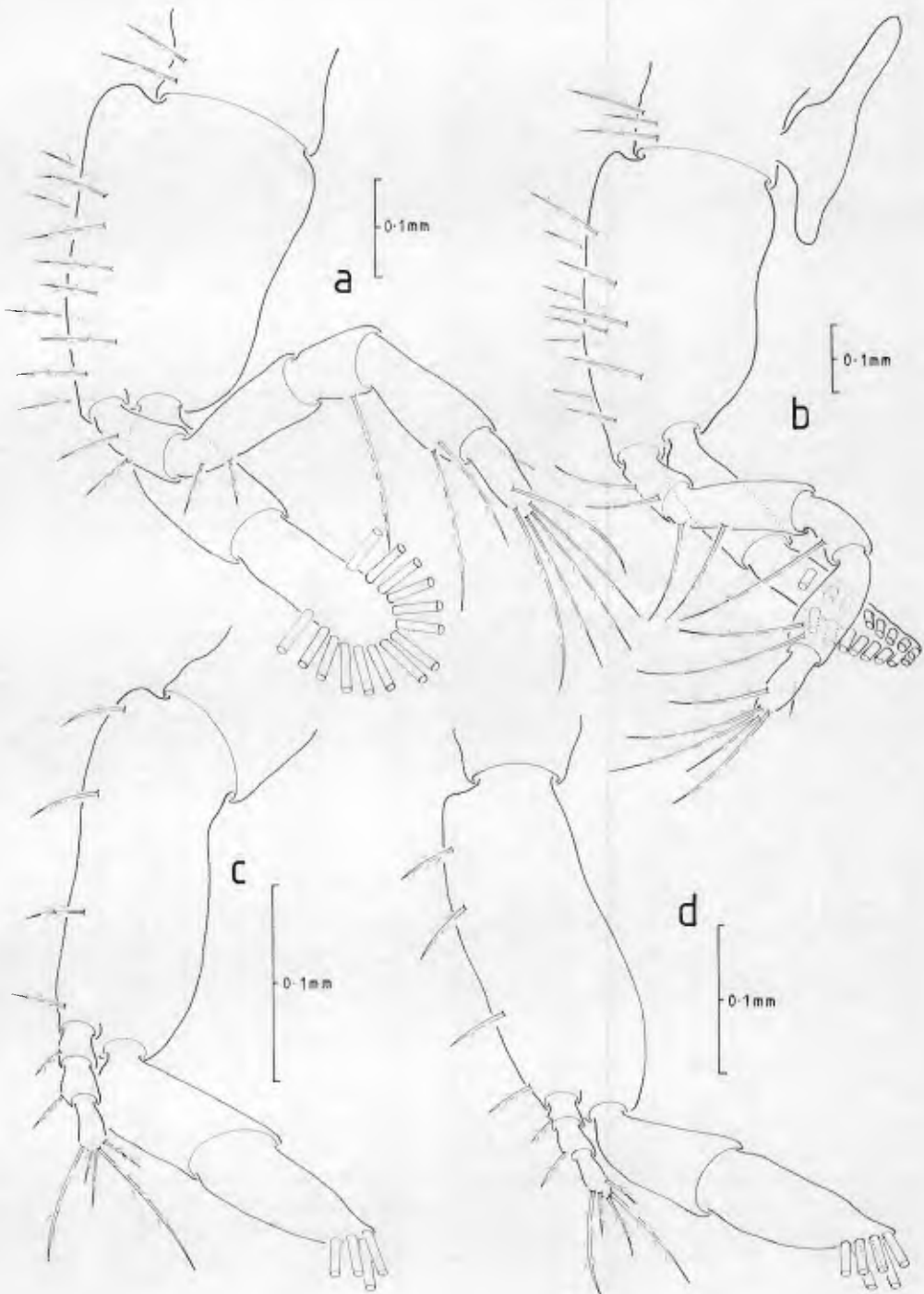


Fig. 15. *Charybdis hellerii*: first maxilliped; a. fifth stage zoea; b. sixth stage zoea; second maxilliped; c. first stage zoea; d. second stage zoea.

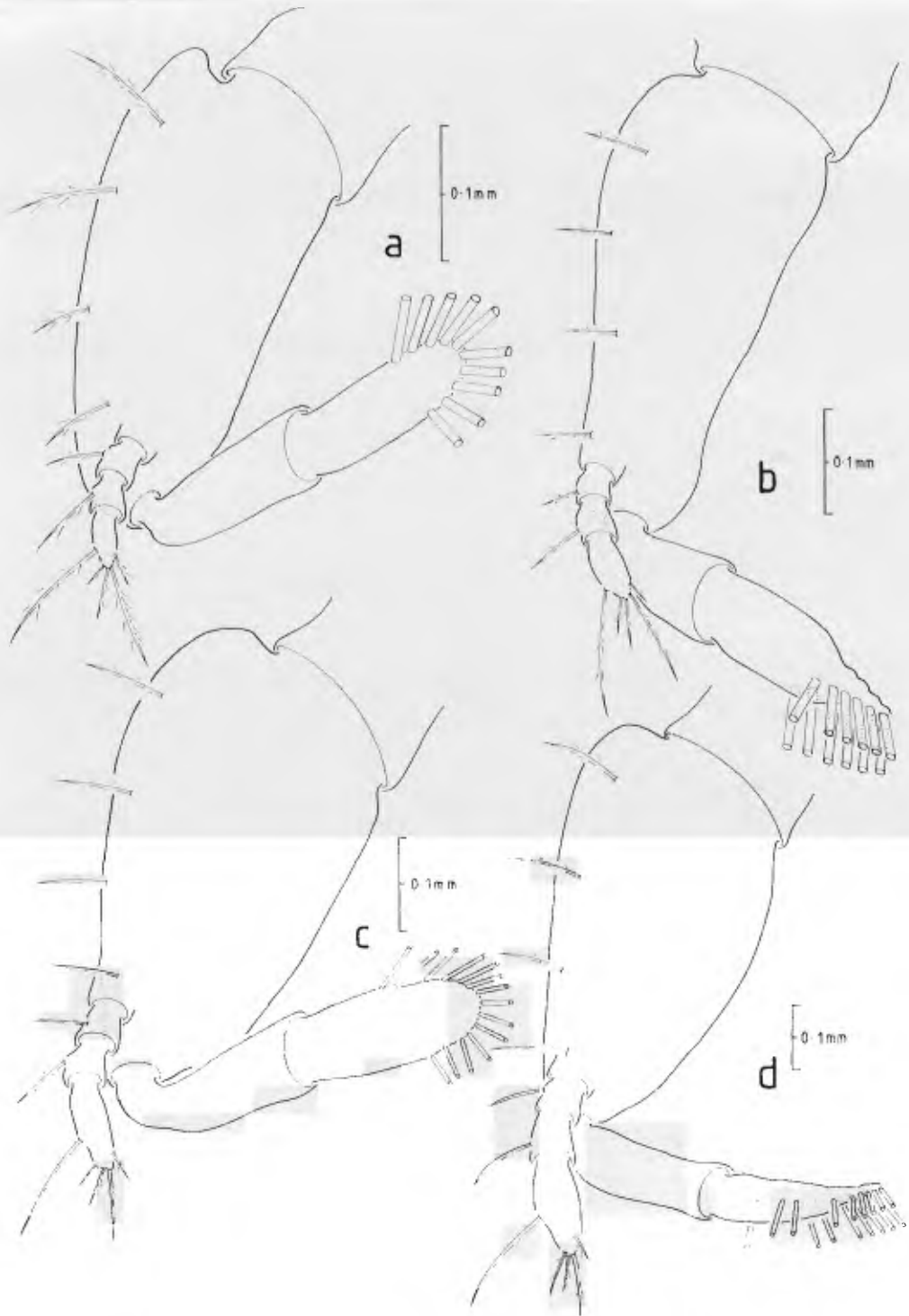


Fig. 16. *Charybdis hellerii*: second maxilliped; a. third stage zoea; b. fourth stage zoea; c. fifth stage zoea; d. sixth stage zoea.

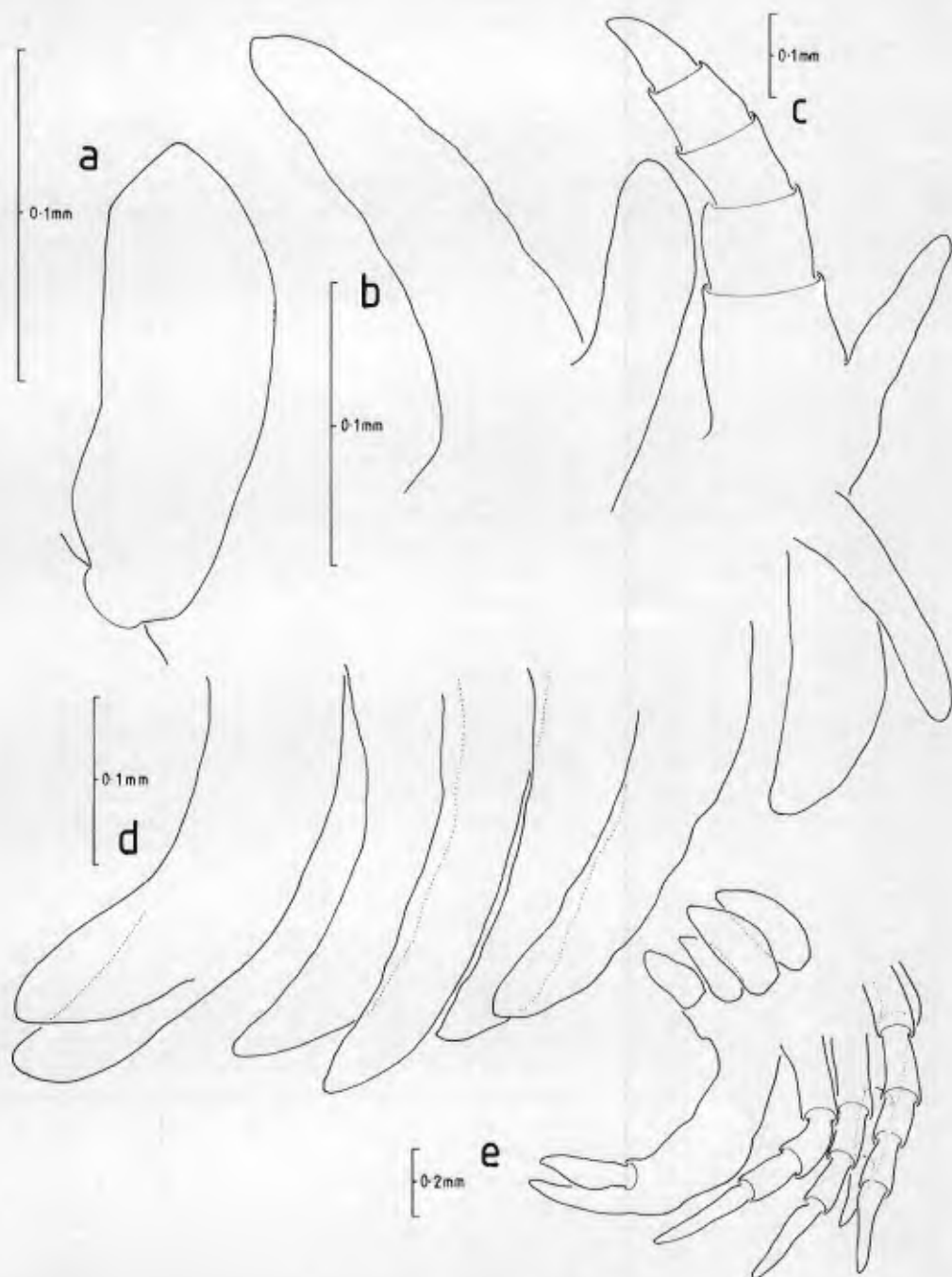


Fig. 17. *Charybdis hellerii*: mandibular palp; a. fifth stage zoea; third maxilliped; b. fifth stage zoea; c. sixth stage zoea; pereiopods; d. fifth stage zoea; e. sixth stage zoea.

*Antenna* (Fig. 9b).—Endopod developing; otherwise unchanged.

*Mandible*.—Unchanged.

*Maxillule* (Fig. 11a).—Coxal endite with 11 setae; otherwise unchanged.

*Maxilla* (Fig. 13a).—Coxal endite with 4 + 5 setae; basal endite bilobed, with 7 + 6 setae; endopod unchanged; exopod (scaphognathite) margin with 25 setae.

*First Maxilliped* (Fig. 15a).—Coxa unchanged; endopod 5-segmented, with

2,2,1,2,6 (2 subterminal and 4 terminal) setae respectively; exopod distal segment with 14 long, terminal, plumose natatory setae.

*Second Maxilliped* (Fig. 16c).—Exopod distal segment with 14 long, terminal, plumose natatory setae; otherwise unchanged.

*Third Maxilliped* (Fig. 17b).—Present, biramous, endopod longer than exopod.

*Pereiopods* (Fig. 17d).—Present, cheliped bilobed.

*Abdomen* (Figs. 19b, 21b).—Somite 1 with 3 dorsomedial setae; pleopods present, but endopods absent; otherwise unchanged.

*Telson* (Figs. 19b, 21b, 23b).—1 pair of dorsomedial setae; otherwise unchanged.

#### Zoea VI

*Carapace* (Figs. 5c, 6e).—Dorsal spine with 10 pairs of setae; 12 pairs of anterodorsal setae; each ventral margin with 18 setae (1 plumose anterior seta and 17 posterior setae); otherwise unchanged.

*Antennule* (Fig. 7e).—Biramous; endopod present, exopod now with 4 proximal setae; 5 + 5 slender subterminal aesthetascs; terminal aesthetascs unchanged.

*Antenna* (Fig. 9b).—Endopod approximately  $\frac{2}{3}$  length of spinous process; otherwise unchanged.

*Mandible* (Fig. 17a).—Mandibular palp present.

*Maxillule* (Fig. 11b).—Coxal endite with 15 setae; basal endite with 17 setal processes, otherwise unchanged.

*Maxilla* (Fig. 13b).—Coxal endite now with 6 + 5 setae; basal endite bilobed, with 8 + 8 setae; endopod unchanged; exopod (scaphognathite) margin with 31 setae.

*First Maxilliped* (Fig. 14d).—Coxa with 3 setae and epipod; endopod unchanged; exopod distal segment with 16 long, terminal, plumose natatory setae.

*Second Maxilliped* (Fig. 16d).—Exopod distal segment with 16 long, terminal, plumose natatory setae; otherwise unchanged.

*Third Maxilliped* (Fig. 17c).—Present, biramous, endopod segmented and longer than

exopod; epipod and arthrobranch gill present.

*Pereiopods* (Fig. 17d).—Developing and segmented, gills present.

*Abdomen* (Figs. 19c, 21c).—Somite 1 with 5 dorsomedial setae; somites 2–5 with 1 pair of dorsomedial setae; pleopods developing, with endopods present; otherwise unchanged.

*Telson* (Figs. 19c, 21c, 23c).—Unchanged.

#### Megalopa

Insufficient prepared specimens were available and no detailed morphological description is provided here. However, general features of the megalopa are evident in the photograph of life history stages (Fig. 3a).

#### Crab Instars 1, 2, 3

Carapaces of the first three crab instars (Fig. 24a, b, c) are rectangular in shape, and the number of lateral spines increases from 4 in the first crab to 5 in the third crab instar.

#### DISCUSSION

*Charybdis hellerii* appears to be well established within the central and southern portions of the Indian River Lagoon and immediately to the south at Lake Worth Inlet. Although we did not collect specimens of *C. hellerii* further south at Boyton and Boca Raton Inlets, they are reported from shallow nearshore reefs at Boca Raton, Florida (W. Lee, Smithsonian Marine Station, personal communication). We did not find the species in apparently suitable structured habitat near Ponce Inlet north of the biogeographic break at Cape Canaveral. The invasive population in Florida is closely associated with structured habitats near inlets, whereas in its native range and in the introduced population in the eastern Mediterranean, it is reported from soft-bottom habitats as well as rocky and coral bottoms (Lemaitre, 1995).

While the abundance of *C. hellerii* in the Indian River was relatively low, it is not clear if its cryptic behavior masks a population that was actually larger than it appeared in our limited collections. It is also not clear if the presently low population abundance may be a prelude to substantial increases in crab densities as the population becomes further established. Although abundances of the crab were variably low at each location where we collected it, the population size structure in-

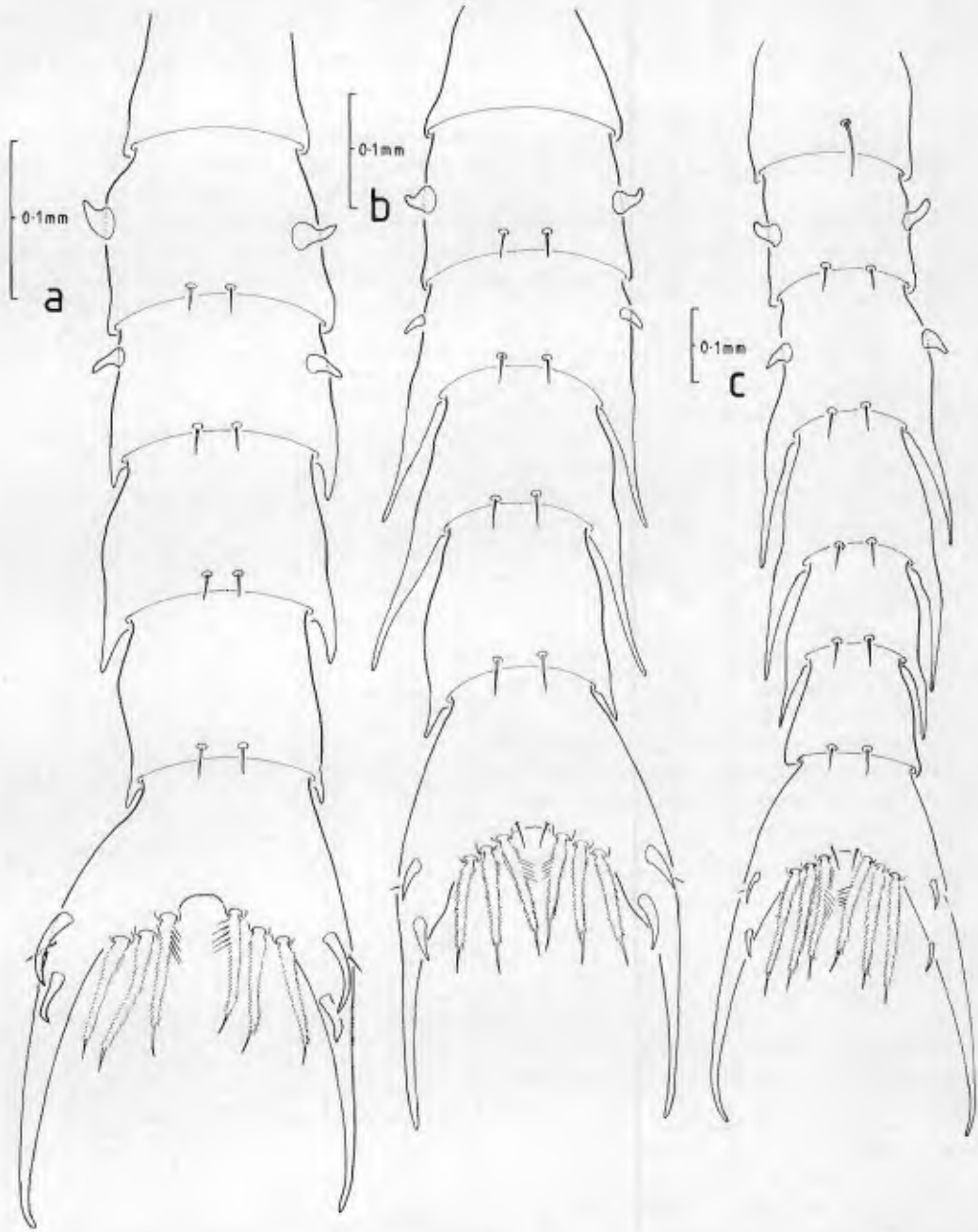


Fig. 18. *Charybdis hellerii*: dorsal view of abdomen; a. first stage zoea; b. second stage zoea; c. third stage zoea.

cluded the full range of juvenile to adult sizes, clearly indicating sustained recruitment to the population.

This population size structure did not appear to reflect year classes, which is consistent with the apparent 1 to 2 year life span indicated by the few individuals we reared

in the laboratory. This broad population size structure is similar to those reported for collections of parasitized and non-parasitized *Charybdis longicollis* Leene, 1938, in the Mediterranean Sea (Galil and Lützen, 1995) and from a trap fishery for *C. natator* Herbst in Australia (Sumpton, 1990). Although we



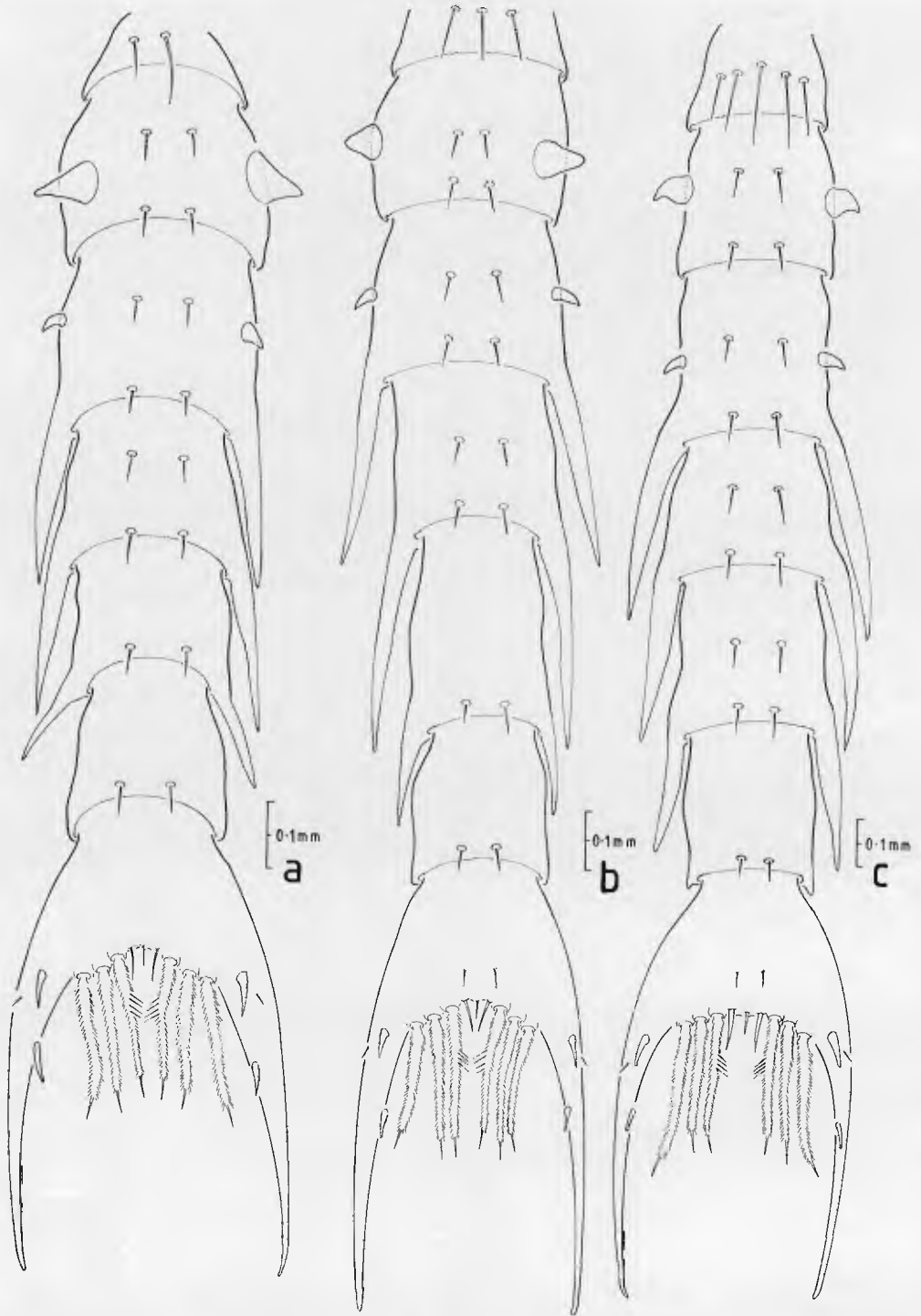


Fig. 19. *Charybdis hellerii*: dorsal view of abdomen; a. fourth stage zoea; b. fifth stage zoea; c. sixth stage zoea.

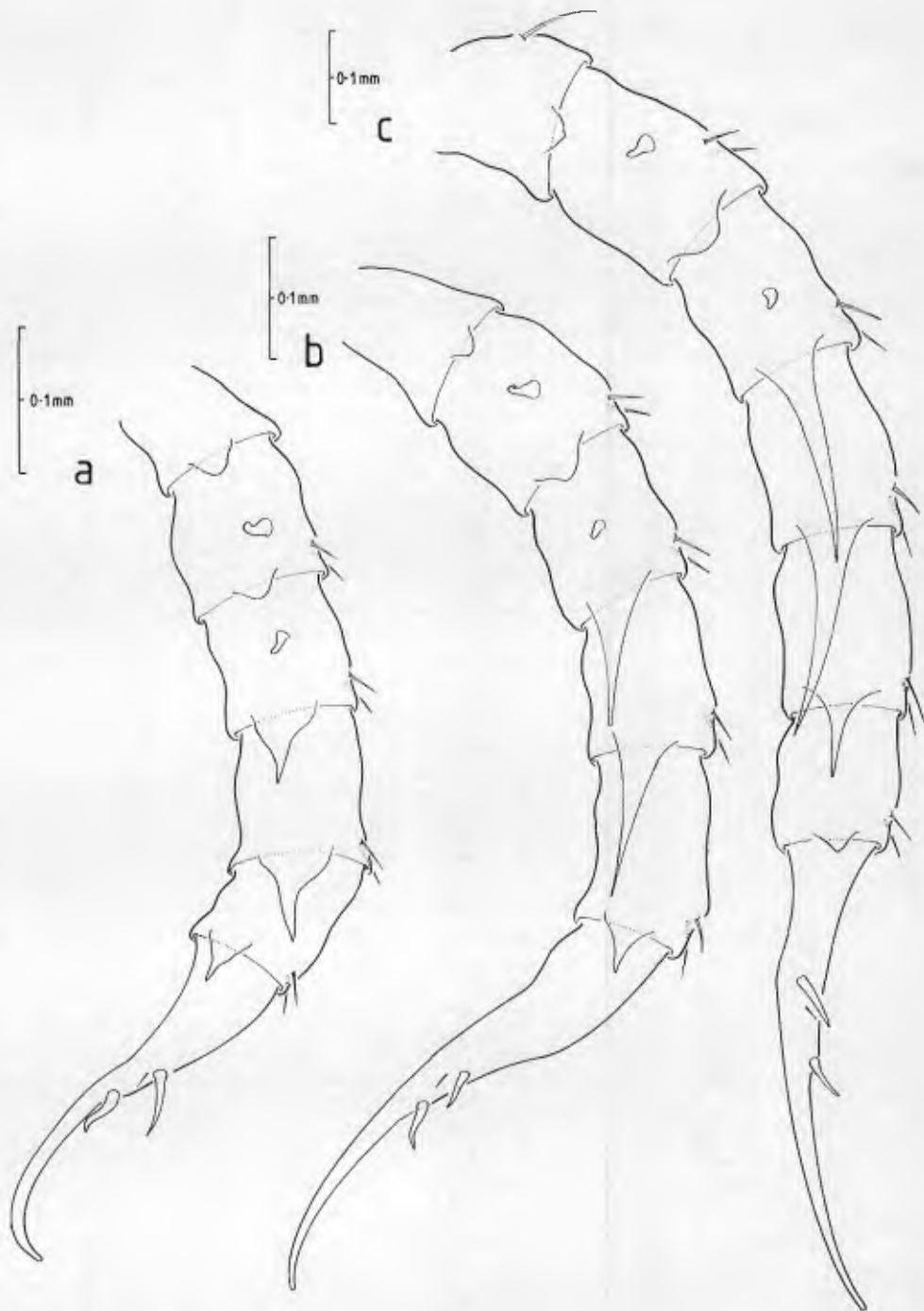


Fig. 20. *Charybdis hellerii*: lateral view of abdomen: a. first stage zoea; b. second stage zoea; c. third stage zoea.

collected ovigerous females during the spring (April-June), our collections were not adequate to consider seasonal aspects of reproduction in the field. The single female that we

maintained at room temperature in the laboratory produced broods throughout much of the year (with a possible hiatus in winter), whereas *C. natator* exhibits two distinct peaks

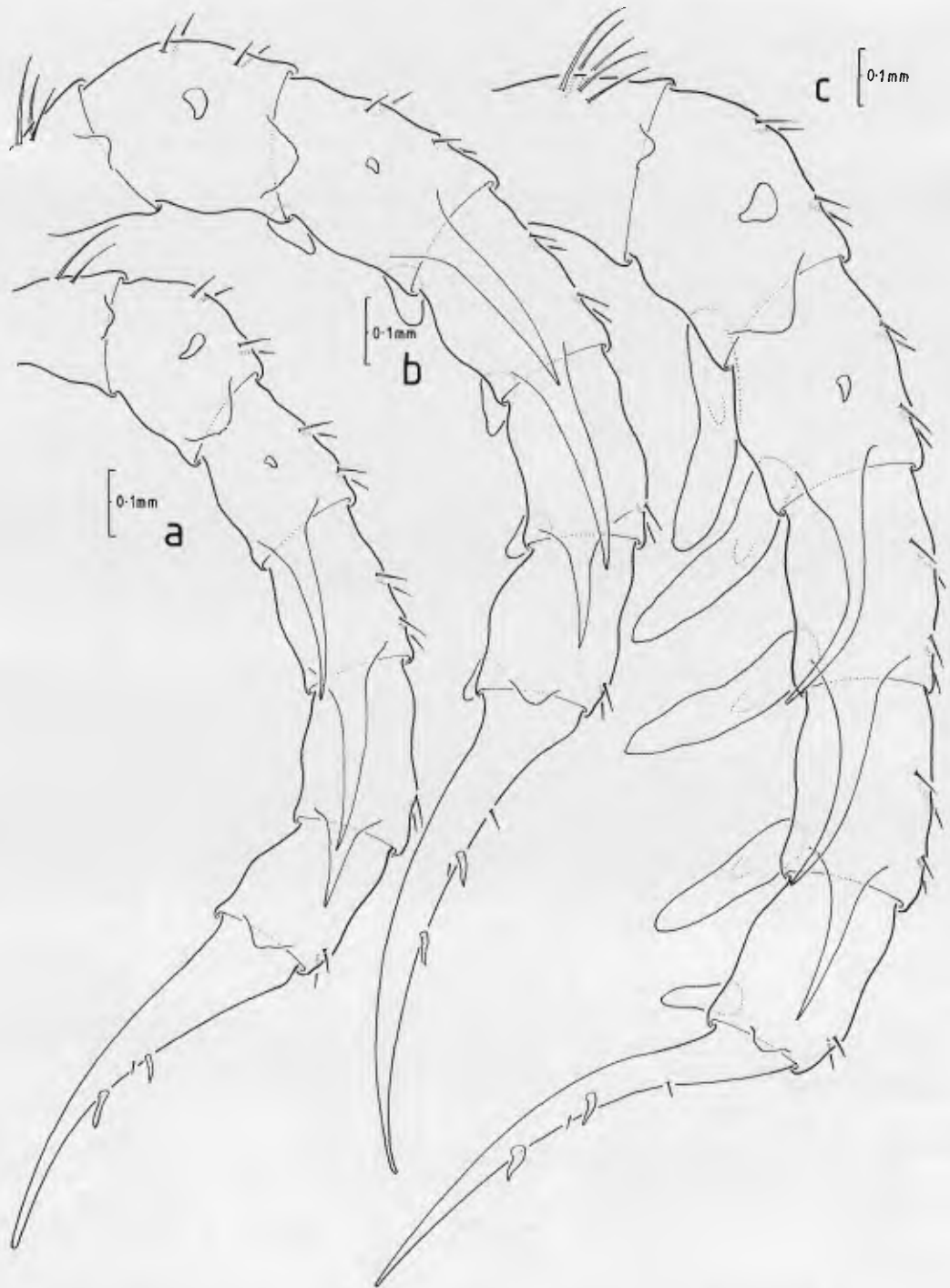


Fig. 21. *Charybdis hellerii*: lateral view of abdomen; a. fourth stage zoea; b. fifth stage zoea; c. sixth stage zoea.

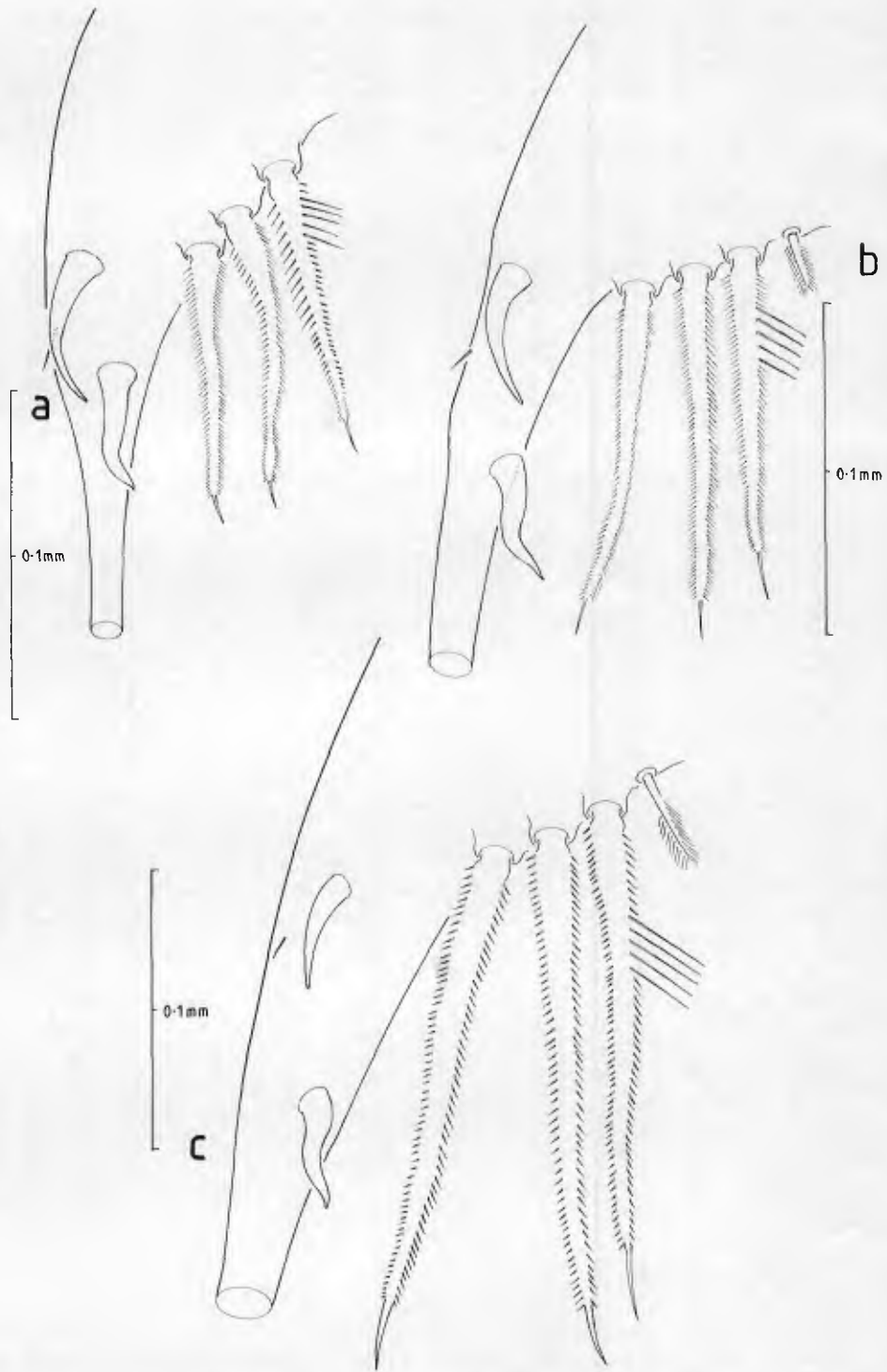


Fig. 22. *Charybdis hellerii*: dorsal view of telson; a. first stage zoea; b. second stage zoea; c. third stage zoea.

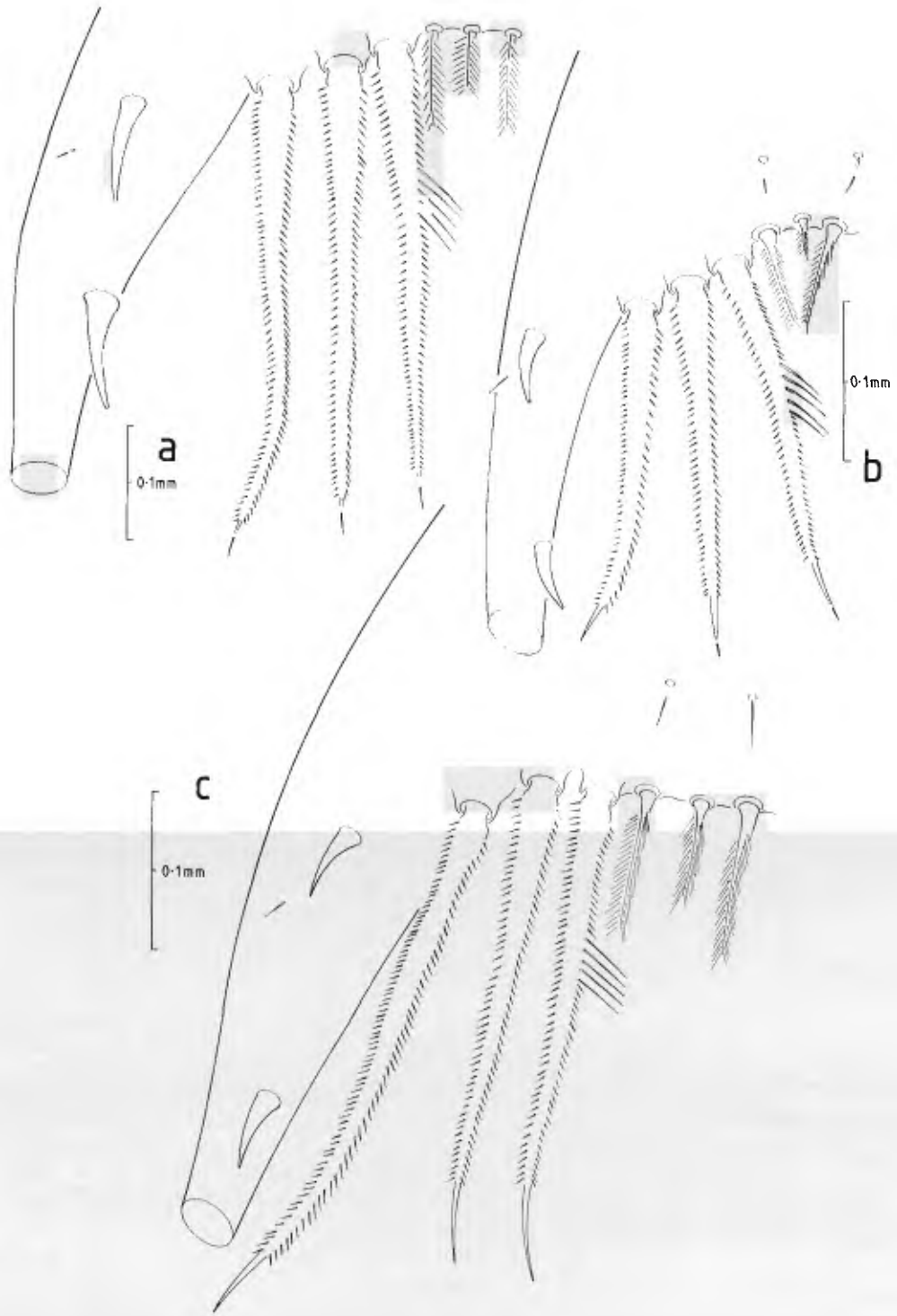


Fig. 23. *Charybdis hellerii*: dorsal view of telson; a. fourth stage zoea; b. fifth stage zoea; c. sixth stage zoea.

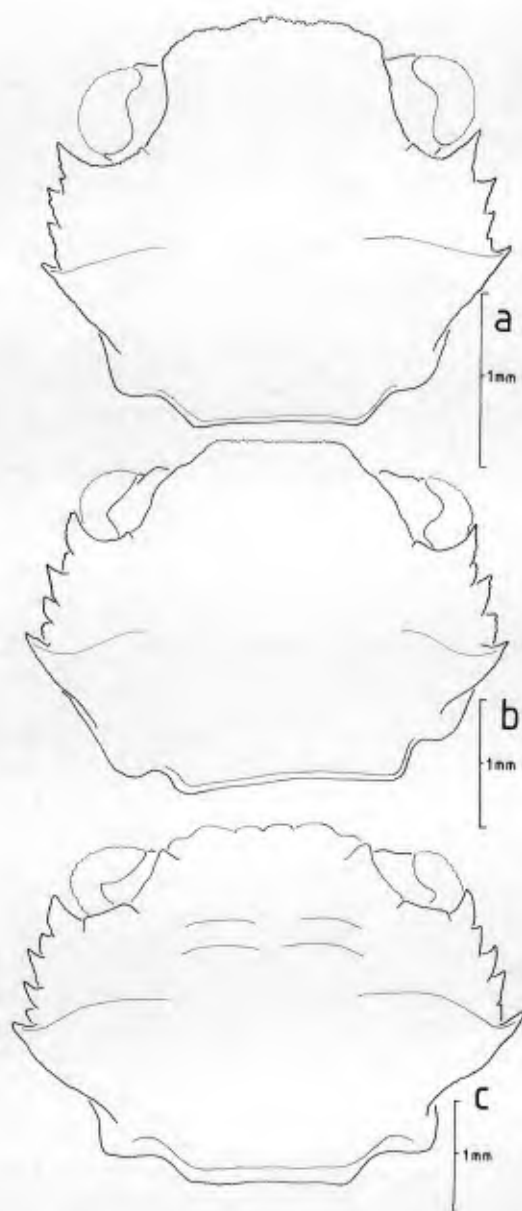


Fig. 24. *Charybdis hellerii*: dorsal view of carapace of (a) first, (b) second, and (c) third instar crabs.

of spawning activity per year (Sumpton, 1990). A balanced sex ratio characterized our *C. hellerii* collections without clear evidence of size dimorphism, although males predominate in larger sizes of *C. natator* (Sumpton, 1990).

Although more than 30 species of *Charybdis* are known from the Indo-West Pacific region (Stephenson, 1962), few comparative data are available for life histories of other

species of this genus. Swarming and mating behavior is reported for *C. edwardsii* Leene and Buitendijk, 1949 (see Daniel and Chakraphay, 1983) and mating in *C. feriatus* Linnaeus (see Campbell, 1984), but such behavior was not observed by us in *C. hellerii*. *Charybdis hellerii* appears to mature at a size that is 10–20 mm smaller than *C. natator*, and both species are capable of producing a series of multiple broods per year: three for *C. natator* (Sumpton, 1990) and at least six for *C. hellerii*. Fecundity in *C. hellerii* is high and ranges from 22,550 eggs to 3,200,000 eggs per brood depending on size of the female (Sumpton, 1990; Siddiqui and Ahmed, 1992; Lemaitre, 1995). On the coast of India, *C. cruciata* (Herbst) and *C. hopilites pusilla* Alcock also produced multiple broods throughout the year with a peak season of brooding (Pillai and Nair, 1976). There are few documented reports in the literature of brood production in crabs in the absence of copulation, as we observed in our isolated, virgin female *C. hellerii*.

There are published larval descriptions of several other species of *Charybdis*, but complete larval descriptions exist for only two other species. Kurata and Omi (1969) described the larval development of *C. acuta* A. Milne-Edwards, including six zoeal stages and a megalopa; Greenwood and Fielder (1980) observed that *C. callianassa* Herbst larval development had only five zoeal stages and a megalopa. Zoeal development through six stages in about 40 days in *C. hellerii* was more than twice as long as the 15 days reported for *C. callianassa* (Greenwood and Fielder, 1980) and the 23 days for *C. acuta* (Kurata and Omi, 1969). Total larval development time to first crab in *C. hellerii* at about 44 days was also longer than the 30-day larval period for *C. acuta* (Kurata and Omi, 1969). The longer development time for *C. hellerii* could be due to a lower rearing temperature. For example, larvae of both *C. acuta* and *C. callianassa* were reared at 26°C (Kurata and Omi, 1969; Greenwood and Fielder, 1980), whereas larvae of *C. hellerii* were reared at 24°C (present study). Substantial differences in development time resulted when larvae of *C. acuta* were reared at various temperature regimes (Kurata and Omi, 1969).

Descriptions of part of the larval development have been published for a few other

*Charybdis* species. For *C. japonica* A. Milne Edwards, 1861, Kurata and Nishina (1975) described only the first four zoeal stages and compared them with those of *Portunus hastatoides* Fabricius. Kurata (1975) provided a key to *C. bimaculata* Miers (zoeal stages I–IV only), *C. truncata* Fabricius (zoeal stages I–III only), *C. miles* De Haan (zoea I only), and other Japanese species of *Charybdis*. However, these earlier published larval descriptions lack sufficient detail for close morphological comparison with the descriptions provided here for *C. hellerii*. This much finer resolution of morphological detail is needed to distinguish species (Clark *et al.*, 1998), and earlier workers encountered similar difficulty with inadequate detail of morphology (e.g., Greenwood and Fielder, 1980).

*Charybdis hellerii* possesses numerous life history traits and natural history characteristics that are adaptive for invasion of new geographic regions. A relatively long larval life enhances larval transport and dispersal, and the 44-day larval period in *C. hellerii* is comparatively long for a tropical crab (Hines, 1986). This larval period is more than twice as long as the three-week transit time of modern ships carrying ballast water from the eastern Mediterranean Sea to coastal waters of the western Atlantic Ocean, clearly accounting for its long-distance dispersal. Reproductive features of *C. hellerii*, including the ability to store sperm and to produce multiple broods of high fecundity in rapid succession, favor rapid expansion of these founder populations. Establishment of founder populations also is enhanced by short generation time, as exhibited by the rapid growth and maturation within about one year for *C. hellerii*. The generalized carnivorous diet of our *C. hellerii* held in the laboratory indicates that it can exploit opportunistically a variety of food resources. Similarly, *C. hellerii* in the Indian River Lagoon exploited a diversity of structured habitats, providing opportunity to use a range of habitats, but also suggesting that its secretive or cryptic behavior may serve to protect it from daytime visual predators. If it is more active at crepuscular or nocturnal periods, then this too would reduce predation from visual predators, such as many species of fish in the Indian River Lagoon. These features of the life history and natural history of *C. hellerii* are similar to those of *Carcinus maenas* Linnaeus, 1758, another

portunid species that has invaded numerous locations around the world (Cohen *et al.*, 1995; Grosholz and Ruiz, 1996).

The impact of this introduced species on native communities in Florida is difficult to determine in the absence of controlled experiments or studies comparing communities before and after its establishment in a new site (Ruiz *et al.*, 1999). We encourage further analysis of this invasion, and we anticipate that the present report will assist others to detect the inevitable spread of this invasive species, both in regions adjacent to the Indian River Lagoon and in distant sites.

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