S. Afr. J. mar. Sci. 22: 177–183
2000

DETERMINATION OF MOULT STAGE IN THE SOUTH AFRICAN WEST COAST ROCK LOBSTER *JASUS LALANDII* (H. MILNE EDWARDS) (CRUSTACEA: DECAPODA)

G. ISAACS, A. C. COCKCROFT†, M. J. GIBBONS* and C. J. DE VILLIERS**

Nine stages and substages of post-, inter- and premoult were distinguished in the West Coast rock lobster *Jasus lalandii* by microscopic examination of the cuticle, epidermal retraction and setal development in the pleopods. The postmoult condition is characterized by progressive thickening of the setal walls and cuticle through to intermoult. Premoult commences with apolysis (Stage D_0), followed by setal development (Stage D_1', D_1", D_1'") and culminates with cuticle deposition (Stage D_2). The diagnostic features of the stages are generally similar to those of other decapod crustaceans.

Most decapods spend their lives in a continuous cycle of moult-related events (Aiken 1980). Based on integumental changes, Drach (1939 as cited by Chan *et al*. 1988) first divided the crustacean moult cycle into four phases: metecdysis (subdivided into Stages A and B), the period immediately following ecdysis; anecdysis (Stage C), a period of tissue growth and accumulation of food reserves; proecdysis (Stage D), a period of active morphological and physiological change in preparation for the next moult; and ecdysis (Stage E), the shedding of the old cuticle.

Macroscopic changes in exoskeletal condition (shell state) or colour have been used to "stage" the moult cycle of lobsters (Heydorn 1969, Silberbauer 1971, Aiken 1980). The "hardness" or "softness" of the carapace usually enables classification into broad categories (e.g. "soft new" defines a newly moulted stage and "hard old" an intermoult stage), but the grouping does not allow for exact identification of the moult stage. These macroscopic changes also lack the resolution needed to identify the transition from intermoult to premoult, a key point within the moult cycle (Aiken 1980).

Because of differences in the onset and rate of completion of different premoult events, reliability can only be achieved by basing subdivisions on changes in a single developing system (Aiken 1980). The system that has proved to be the most convenient and reliable is the state of setal development, and changes associated with this have been used for moult staging in various crustacean species (Aiken 1973, Peebles 1977, Van Herp and Bellon-Humbert 1978, Lyle and MacDonald 1983, Chan *et al*. 1988). This method uses internal changes in the morphology of the developing setae of such appendages as pleopods, together with exoskeletal changes in order to assess moult stage (Lyle and MacDonald 1983). The general details of setal development are similar for a variety of crustaceans (Turnbull 1989).

Jasus lalandii is distributed from about 23°S, just north of Walvis Bay in Namibia, to about 28°S, near East London on the east coast of South Africa. Commercial densities are restricted to the area between 25°S (southern Namibia) and Cape Point in South Africa (Pollock 1986). The South African fishery is managed mainly by means of Total Allowable Catch (*TAC*), size limits, closed seasons and specified fishing areas. A coastwide decrease in the somatic growth rate of *J. lalandii* over the past decade (Cockcroft and Goosen 1995) has been part of the reason for decreased catches and ultimately a decrease in the *TAC* for the species. Subsequent studies on aspects of lobster growth identified the lack of detailed information on moult stages as a major drawback in the interpretation of field and laboratory data (Cockcroft 1997). An accurate reassessment of the moult stages would allow: (1) detailed comparison of the moult cycles between various areas; (2) more accurate interpretation of commercial catch data on an area and monthly basis; (3) better interpretation of behaviour and physiology (both laboratory and in the field), including biochemical changes during the moult cycle; and (4) comparison with the currently used moult-staging method, using exoskeletal condition.

The aim of this study is to detail the stages in the moult cycle of *Jasus lalandii*, using epidermal retraction and the degree of setal development in the pleopods as the basis for determination.

* Zoology Department, University of the Western Cape, Private Bag X17, Bellville 7535, South Africa
† Marine & Coastal Management, Private Bag X2, Rogge Bay 8012, South Africa. E-mail: cockcrof@sfri.wcape.gov.za

Manuscript received September 1999; accepted April 2000

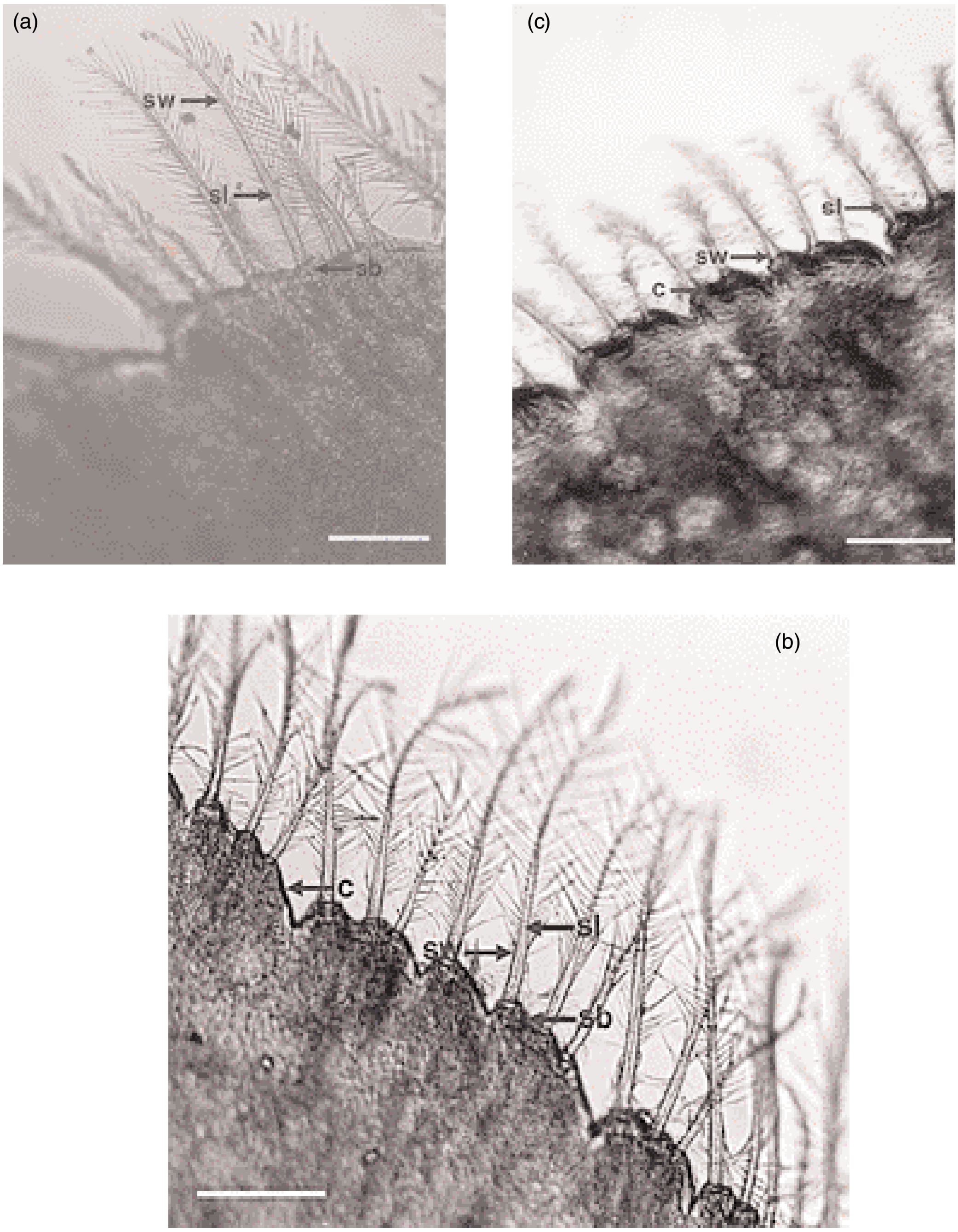

Fig. 1: Post- and intermoult stages of *Jasus lalandii* – (a) Stage A, with thin setal walls (sw), poorly defined setal bases (sb) and wide, grainy setal lumen (sl); (b) Stage B, with thicker setal walls, well defined setal bases, narrower, less grainy setal lumen and thin cuticle; (c); Stage C, with thick setal walls, narrow setal lumen and thick cuticle. Scale bar = 100µm

MATERIAL AND METHODS

Juvenile lobsters were collected monthly using SCUBA at Green Point and from the Cape Town Harbour Wall during the period February 1996–February 1997. The exoskeletal condition (shell state) was determined using the method of Heydorn (1969), and individuals considered to be in premoult or in intermoult (20–45 mm carapace length, *CL*) were retained for further observation.

The lobsters were kept in aquaria supplied with running seawater at a temperature of 12–14°C, temperatures broadly similar to those experienced by lobsters along the west coast of South Africa. The lobsters in intermoult were fed three times a week on a diet of fish and various invertebrates. Pre-moult lobsters did not require feeding (Silberbauer 1971, Pollock 1973). Pleopods from animals in premoult were removed on alternate days to determine changes in premoult stage, whereas those of postmoult individuals were removed daily, whenever possible. Lobsters in intermoult were sampled on an *ad hoc* basis, until they entered premoult.

In all, 1 450 pleopods were cut at their base and frozen for later examination. After thawing, the pleopod was placed in an aquaculture slide in water and examined at 63, 100 and 160× magnification using a Zeiss IM35 inverted, phase-contrast photo-microscope. The pleopods were photographed and then used to describe the various moult stages. Freezing and thawing of pleopods did not influence the accuracy of staging (Lyle and MacDonald 1983).

DESCRIPTION OF MOULT STAGES

Nine stages and substages, based on the development of setae and the degree of epidermal retraction in the pleopods, are described.

Postmoult

Stage A (Fig. 1a) – The setal walls show little or no thickening and the internal walls appear wavy. The setal bases are not well defined compared to those of Stage B. The setal lumen is wide and granular. The entire exoskeleton is extremely soft.

Stage B (Fig. 1b) – The setal walls begin to thicken. The setal lumen is narrower and less grainy, and the setal bases are well defined. The cuticle is relatively thin compared to Stage C. The exoskeleton starts to harden.

Intermoult

Stage C can be divided into four substages, based on shell rigidity (Aiken 1980), with the fourth stage (C_4) usually referred to as the intermoult phase.

Stage C_4 (Fig. 1c) – The setal walls become thick. The setal lumen is narrow and sometimes nonexistent owing to the thick setal walls. The cuticle is thick and the epidermis lies close to it. The exoskeleton is hard throughout this stage.

Premoult

The onset of premoult is often associated with a change in colour of the abdominal flesh from pink to a dark brown/black. However, the absence of a colour change does not necessarily mean that an individual has not entered the premoult stage.

Stage D_0 (Fig. 2a) – This stage is characterized by apolysis, or the retraction of the epidermis from the cuticle of the pleopod, which results in a transparent gap between the two tissues. Retraction starts at the apical tip of the pleopod and continues laterally.

Stage D_1' (Fig. 2b) – The tips of the new setae become visible in the zone of retraction, as flaccid wisps of tissue, which are small and irregular in appearance.

Stage D_1'' (Fig. 2c) – This stage commences with the invagination of the setae.

Stage D_1''' (Fig. 2d) – Appearance of barbules along the setal axes. The proximal ends of the setae are poorly defined. There is no epicuticle deposition.

Stage D_2 (Fig. 2e) – The proximal ends of the setae appear bifurcate and deposition of the new epicuticle has begun.

Stage D_3 (Fig. 2f) – The new exoskeleton has foldings to accommodate subsequent growth. The proximal ends appear blunt (but not clear in Fig. 2f).

No further changes appeared to be visible in the pleopods until ecdysis/moult. A diagrammatic representation of moult Stages A–D_3 is given in Figure 3.

DISCUSSION

Lyle and MacDonald (1983) grouped Stages A and B of postmoult together in *Panulirus marginatus*, whereas these stages were separate for *Panulirus ornatus* (Turnbull 1989) as well as for *J. lalandii* in the current study. The key features of the postmoult stages are the thickening of the setal walls and the wide diameter of the setal lumen, which is filled with a granular protoplasm. The postmoult stages of *J. la-*

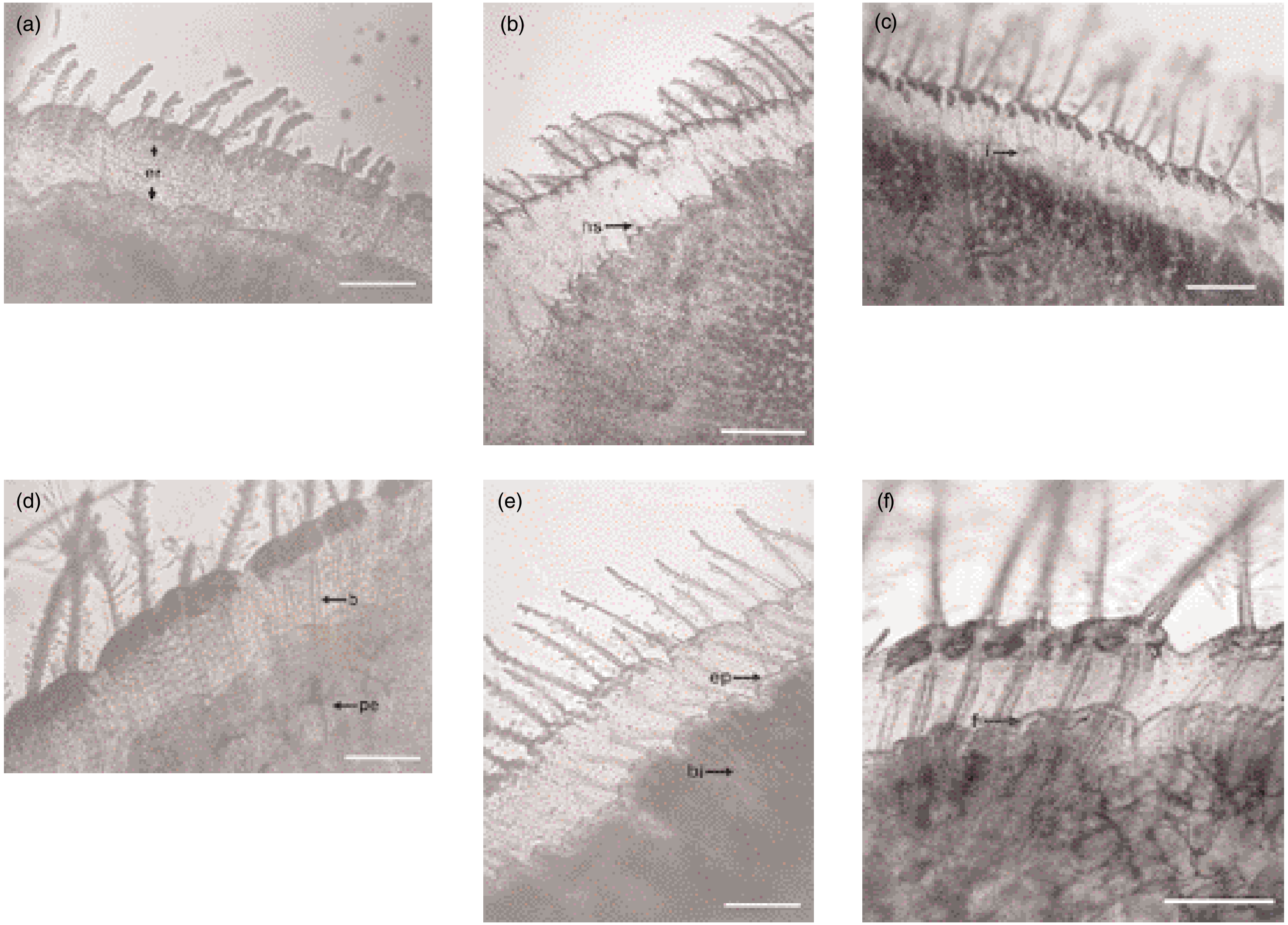

Fig. 2: (a) Stage D_0, showing epidermal retraction (er); (b) Stage D_1', with new setae (ns) visible in the retracted zone; (c) Stage D_1'', showing invagination (i) of the new setae; (d) Stage D_1''', with barbules (b) along the setal axes and poorly defined proximal ends (pe); (e) Stage D_2, showing bifurcate (bi) proximal ends of the setae and with new epicuticle deposition (ep); (f) Stage D_3, showing folding (f) of new exoskeleton. Scale bar = 100µm

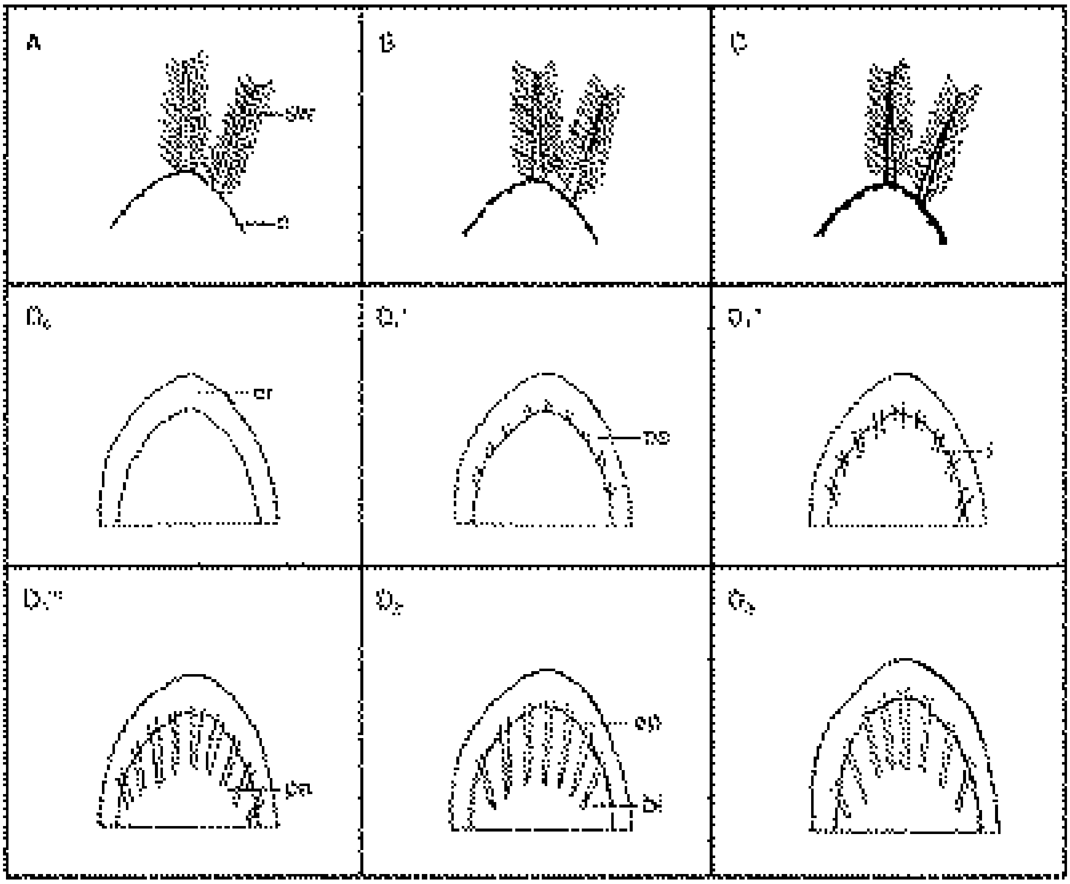

Fig. 3: Diagrammatic representation of moult Stages A–D_3. Stages A–C show progressive thickening of the setal walls (sw) and cuticular (c) thickening; Stage D_0 shows epidermal retraction (er); and Stages D_1'–D_3 show the various stages of setal development (new setae = ns, invagination = i, proximal end = pe, bifurcate end = bi, epicuticle = ep)

landii are characterized here by a progressive thickening of the setal walls through to intermoult. Turnbull (1989) determined the same for *P. ornatus*, and he noted that the setal walls of individuals at Stage A were wavy and that the setal lumen was filled with a granular protoplasm. Van Herp and Bellon-Humbert (1978) described the setae in *Astacus leptodactylus* as being filled with a fibrillar protoplasm during moult Stage A, and then by a homogenous protoplasm in Stage B. Mills and Lake (1975) attributed these changes in the setal lumen of *Parastacoides tasmanicus* to the development of an internal matrix in the setae.

The intermoult Stage C is characterized by thick setal walls, and a narrow, and sometimes occluded, setal lumen. The cuticle is thick. Turnbull (1989) described setae in this stage as having narrow lumen that had lost most of its grainy appearance, and also noted thick and smooth setal walls, and a thick cuticle that extended to below the setal bases. It is not known whether the appearance of the setal lumen is a result of a retraction of the cellular contents, but it appears to involve a thickening of the setal walls (Lyle and MacDonald 1983). As for *P. marginatus* (Lyle and MacDonald 1983), Stage C in *J. lalandii* could not be further subdivided on the basis of microscopic examination of the pleopods.

As reported for *Homarus americanus* (Aiken 1980) and *Jasus edwardsii* (R. Musgrove, South Australian Research and Development Institute [SARDI], pers. comm.), the absence of a blackened abdominal flesh colour in *J. lalandii* does not necessarily indicate that an individual is not in premoult. The premoult condition in *J. lalandii* has been divided into Stages D_0, D_1, D_2 and D_3. The onset of premoult (Stage D_0) in decapods is generally identified by the retraction of the epidermis from the exoskeleton (Kurup 1964, Aiken 1973, Mills and Lake 1975, Turnbull 1989), a condition known as apolysis (Jenkin and Hinton 1966). There appears to be considerable epidermal retraction in *J. lalandii* before the appearance of the new setae, indicating that the duration of this stage is relatively long. *P. ornatus* also has a relatively long Stage D_0 (Turnbull 1989), and Aiken (1973) described this stage as having a broad transitional phase between intermoult and premoult. However, this stage is very short in *J. edwardsii* (R. Musgrove, pers. comm.).

Stage D_1 can be divided into three substages in *J. lalandii*, as is generally the case for other lobsters. Substage D_1’ is characterized by the appearance of the tips of the new setae in the retracted zone. Early setal development is a common feature in many other decapods (Kurup 1964, Stevenson *et al.* 1968, Aiken 1973, Mills and Lake 1975, Van Herp and Bellon-Humbert 1978). Maximum epidermal retraction in *P. marginatus* is attained during D_1’, and the formation of the new setae is assigned to substage D_1”. Although substages D_1’ and D_1” in *P. ornatus* were grouped by Turnbull (1989), because maximal epidermal retraction and the appearance of new setae occur at approximately the same time, the substages are distinct in *J. lalandii*.

Progressive invagination of the new setae into the epidermis was characteristic of Stage D_1” in *J. lalandi,* as in other decapods (Aiken 1973, Mills and Lake 1975). However, this feature is sometimes obscure. For example, Lyle and MacDonald (1983) found the pleopods of *P. marginatus* to be heavily pigmented and opaque, which made identification difficult.

Stage D_1’” is characterized by the formation of barbules on the new setae in *J. lalandii*, as in *P. ornatus* (Turnbull 1989), *Astacus leptodactylus* (Van Herp and Bellon-Humbert 1978) and *Parastacoides tasmanicus* (Mills and Lake 1975), as well as for some stomatopods (Reaka 1975). However, this feature is not found in *P. marginatus* (Lyle and MacDonald 1983) or *Homarus americanus* (Aiken 1973), barbules only becoming apparent in those species at Stage D_2.

The deposition of the new cuticle is indicative of Stage D_2 in *J. lalandi* and the final stage that can be identified before ecdysis is Stage D_3. The blunting of the proximal ends of the setae in Stage D_3 is a feature that has been observed in *H. americanus* (Aiken 1973), but it appears to be absent in *J. edwardsii* (R. Musgrove pers. comm.), in which bifurcation is still present at Stage D_3.

ACKOWLEDGEMENTS

We thank Messrs M. Noffke and A. Hazell (University of the Western Cape) for their assistance in the field. Dr R. Musgrove (SARDI) is thanked for his assistance with staging methodology. The University of the Western Cape, the South African Network for Coastal and Oceanographic Research, and Marine & Coastal Management are acknowledged for financial and logistic support.

LITERATURE CITED

AIKEN, D. E. 1973 — Proecdysis, setal development, and molt prediction in the American lobster (*Homarus americanus*). *J. Fish. Res. Bd Can.* **30**: 1337–1344.

AIKEN, D. E. 1980 — Molting and growth. In *The Biology and Management of Lobsters*. **1**. *Physiology and Behavior*. Cobb, J. S. and B. F. Phillips (Eds). New York; Academic Press: 91–163.

CHAN, S-M., RANKIN, S. M. and L. L. KEELEY 1988 — Characterization of the moult stages in *Penaeus vannamei*: setogenesis and hemolymph levels of total protein, ecdysteroids, and glucose. *Biol. Bull. mar. biol. Lab., Woods Hole* **175**: 185–192.

COCKCROFT, A. C. 1997 — Biochemical composition as a growth predictor in male West Coast rock lobster (*Jasus lalandii*). *Mar. Freshwat. Res.* **48**: 845–856.

COCKCROFT, A. C. and P. C. GOOSEN 1995 — Shrinkage at moulting in the rock lobster *Jasus lalandii* and associated changes in reproductive parameters. *S. Afr. J. mar. Sci.* **16**: 195–203.

HEYDORN, A. E. F. 1969 — The rock lobster of the South African west coast *Jasus lalandii* (H. Milne-Edwards). 2. Population studies, behaviour, reproduction, moulting, growth and migration. *Investl Rep. Div. Sea Fish. S. Afr.* **71**: 52 pp.

JENKIN, P. M. and H. E. HINTON 1966 — Apolysis in arthropod moulting cycles. *Nature, Lond.* **211**: p. 871.

KURUP, N. G. 1964 — The intermoult cycle of an anomuran, *Petrolisthes cinctipes* Randall (Crustacea – Decapoda). *Biol. Bull. mar. biol. Lab., Woods Hole* **127**: 97–107.

LYLE, W. G. and C. D. MACDONALD 1983 — Molt stage determination in the Hawaiian spiny lobster *Panulirus marginatus*. *J. crustacean Biol.* **3**: 208–216.

MILLS, B. J. and P. S. LAKE 1975 — Setal development and moult staging in the crayfish *Parastacoides tasmanicus* (Erichson), (Decapoda Parastacidae). *Aust. J. mar. Freshwat. Res.* **26**: 103–107.

PEEBLES, J. 1977 — A rapid technique for moult staging in live *Macrobrachium rosenbergii*. *Aquaculture* **12**: 173–180.

POLLOCK, D. E. 1973 — Growth of juvenile rock lobster *Jasus lalandii*. *Investl Rep. Sea Fish. Brch S. Afr.* **106**: 16 pp.

POLLOCK, D. E. 1986 — Review of the fishery for and biology of the Cape rock lobster *Jasus lalandii* with notes on larval recruitment. *Can. J. Fish. aquat. Sci.* **43**(11): 2107–2117.

REAKA, M. L. 1975 — Moulting in stomatopod crustaceans. 1. Stages of the moult cycle, setagenesis and morphology. *J. Morphology*. **146**: 55–80.

SILBERBAUER, B. I. 1971 — The biology of the South African rock lobster *Jasus lalandii* (H.Milne-Edwards). 2. The reproductive organs, mating and fertilisation. *Investl Rep. Div. Sea Fish. S. Afr.* **93**: 46 pp.

STEVENSON, J. R., GUCKERT, R. H. and J. D. COHEN 1968 — Lack of correlation of some proecdysial growth and developmental processes of the crayfish. *Biol. Bull. mar. biol. Lab., Woods Hole* **134**: 160–175.

TURNBULL, C. T. 1989 — Pleopod cuticular morphology as an index of moult stage in the ornate rock lobster, *Panulirus ornatus* (Fabricius 1789). *Aust. J. mar. Freshwat. Res.* **40**: 285–293.

VAN HERP, F. and C. BELLON-HUMBERT 1978 — Setal development and molt prediction in the larvae and adults of the crayfish, *Astacus leptodactylus* (Nordmann, 1842). *Aquaculture* **14**: 289–301.