THE EARLY LIFE HISTORY OF DRUPELLA CORNUS

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INTRODUCTION.

Many marine invertebrates exhibit population outbreaks at irregular intervals (Coe, 1956). Although population fluctuations may arise because of varying mortality or survival at any of the stages in the life cycle of the organism concerned, Thorson (1950) suggested that these fluctuations may be primarily attributable to processes affecting the early life cycle stages. It is likely, therefore, that an understanding of the early life history of Drupella cornus will contribute towards an explanation for the recent increase in the numbers of this snail along Ningaloo Reef.

MATERIALS AND METHODS.

Larval Rearing.

Reproductively mature D. cornus are maintained in covered 2.5L plastic aquaria. Each aquarium is supplied with aeration and running, non-recirculated seawater at 20°-26°C, which approximates the temperatures recorded in the natural habitat at the time the snails are collected.

Larvae are reared either in the laboratory or using in situ larval culturing equipment anchored on the reef at Coral Bay (see Olson, 1985, 1987; Olson et al., 1987, 1988). In the laboratory, larvae are reared in 4ml or 3000ml containers at an average density of 1-2 larvae/ml, and are fed a 1:1:1 mixture of Isochrysis galbana (Tahitian strain), Chaetoceros gracilis and Pavlova lutheri at a final concentration of 10,000 cells/ml, in 105um filtered natural seawater.

Larvae are tested for metamorphic competence by exposing them to small pieces of live coral species, coralline algae encrusted dead coral, or a solution of 20mM KCl which has been shown to induce metamorphosis in a number of marine invertebrates (Yool et al., 1986).

The spatial and temporal distribution of juvenile D. cornus along Ningaloo Reef.

Live coral colonies were collected from reef flat and back reef edge sites at Bundegi Reef, Neds Camp, Bloodwood, and Coral Bay in June/July 1990, October/November 1990 and January/February 1991, and examined for the presence of juvenile (<1cm shell length) D. cornus.

RESULTS.

Copulation and spawning have been observed in both the laboratory and the field. In the laboratory, egg capsules are attached to the sides, floors or lids of the aquaria, or inside the outlet pipes. In the field, D. cornus have been observed spawning capsules within small crevices in the rock substratum and dead bases of corals, and in shells. It is not known whether the females are gregarious. Gregarious spawning behaviour has, however, been documented for a number of muricids. There is no evidence of capsule protection by D. cornus, as the females move away from the spawn mass once a period of spawning has been completed.

Under laboratory conditions, spawning, which predominantly occurs at night-time, often continues for several days - one female was observed to produce a total of 115 capsules over 16 days. The capsules from each spawning event are generally deposited in discrete, close-packed clusters. The capsules are kidney-shaped in cross-section with distinct concave and convex sides, and average 2.8x3.2x1.8mm in size (n=25). The egg capsules are orientated so that the convex side of one capsule is aligned with, and in close proximity to, the concave side of the adjacent capsule. Capsules are generally attached directly to the substratum by a flattened base, and joined to adjacent capsules by a confluent basal membrane. There is no evidence of a basal attachment stalk. Each capsule has a sealed, oval exit pore (0.7x0.5mm in size), situated approximately one-third of the way down the concave side of the capsule, through which the veligers leave the capsule at hatching.

Each capsule contains between 300-1400 embryos (n=50). The eggs are spherical, pale creamy white in colour, 170µm in diameter (n=200), and embedded in a gel-like substance within the capsules. The general patterns of cleavage, gastrulation and early development of the veligers is essentially the same as described for other indirectly developing prosobranch gastropods (e.g. D'Asaro, 1966; Kumé & Dan, 1968). D. cornus does not appear to produce food or nurse eggs, and there is no evidence that cannibalism occurs within the capsules spawned in the laboratory. The development time appears to be temperature dependent - veligers hatch in 27-37 days at 21.5°C and in 20-29 days at 25.5°C. Newly hatched veligers have dextrally coiled shells, with $1^1/_3$-$1^1/_2$ whorls, and an average size of 265x215µm (n=75). They are characterised by the presence of a well developed bilobed, ciliated velum, a foot and an operculum, prominent eye-spots, and a darkly pigmented anal gland. Characteristic features of the shell include the larval beak, which is a prolongation of the outer edge of the shell aperture extending over the shell opening, between the velar lobes. There is a concentration of red/brown pigmentation at the growing edge of the shell, in the region of the larval beak and the developing shell columella. Feeding and shell growth appear to begin very soon after hatching (see Figure 1). A distinct demarcation is evident between the shell growth that occurs

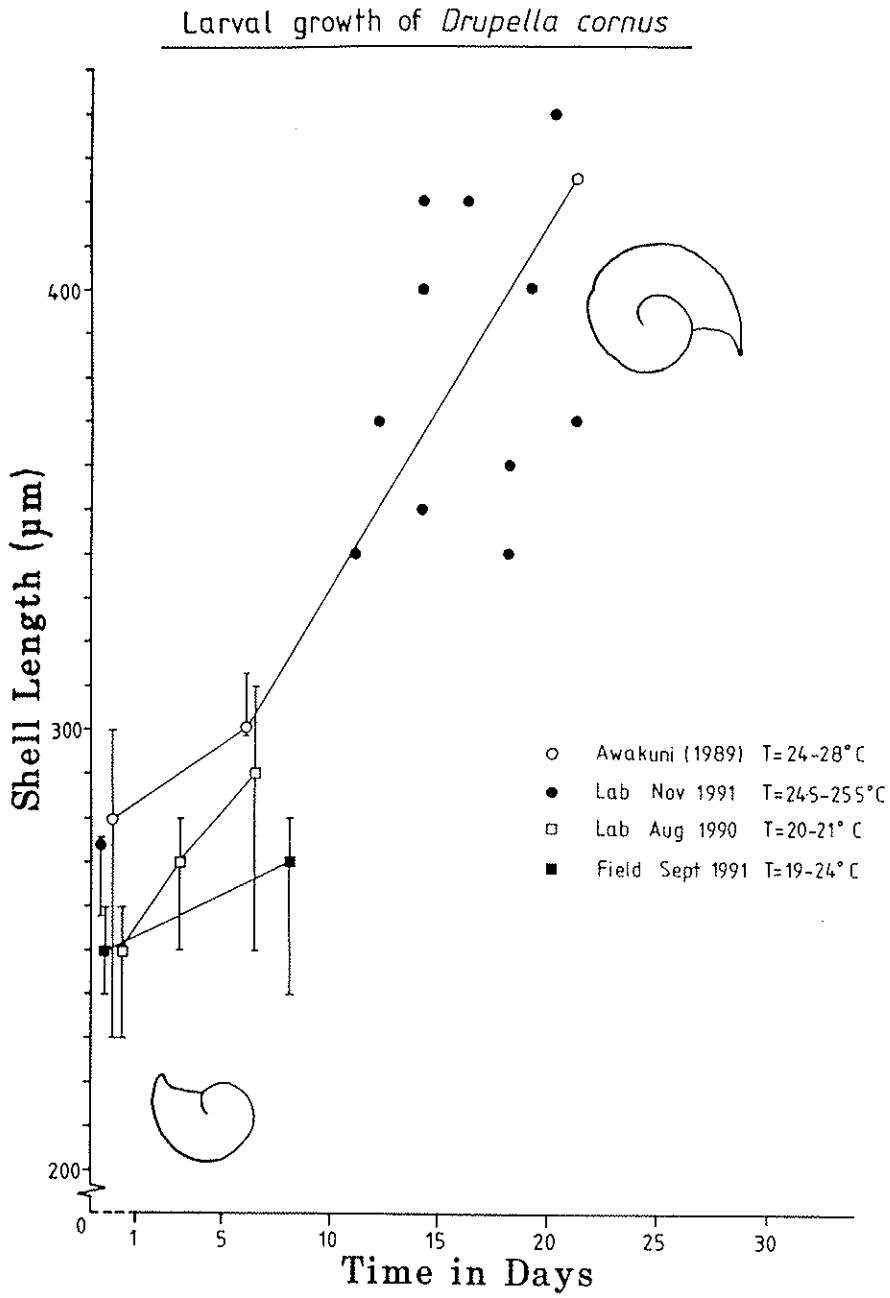

FIGURE 1 : Larval growth of Drupella cornus veligers in the laboratory (August 1990 and November 1991), the field (September 1991) and in a study by Awakuni (1989). Mean shell length and range in length are shown.

August 1990 : larvae reared in 3 litre-volume chambers. (n=11 at hatching; n=9 at 4 days after hatching; n=16 at 7 days after hatching).
November 1991 : larvae reared in 4 ml-volume chambers. (n=10 at hatching; each point thereafter represents the size of individual larvae).
September 1991 : larvae reared in 3 litre-volume chambers. (n=7 at hatching and at 9 days after hatching).
Awakuni (1989) : larvae reared in 2 litre-volume beakers (n=23 at hatching; n=17 at 7 days after hatching; n=1 at 22 days after hatching).

within the egg capsule before hatching (the protoconch I), and the shell that is grown during the planktonic larval period after hatching (the protoconch II).

The individual fecundity of female D. cornus may be high. Considerable numbers of capsules may be deposited, each containing several hundred small eggs, all of which appear to develop into veliger larvae. The life-time fecundity of D. cornus will be determined by their adult life-span, the age at which sexual maturity is attained, and the frequency of spawning.

Larvae from laboratory or field-spawned capsules reared in situ at Coral Bay all died within a few days of hatching. There was no evidence of larval feeding and growth was either absent or reduced (see Figure 1). The low survivorship of larvae in the field experiments may have arisen because the larvae were food-limited. Chlorophyll a values for water samples collected adjacent to the larval rearing equipment were very low - 0.09µg Chl a/l (range = 0-0.3µg Chl a/l) (Lucas (1982) cited average values of 0.2-0.5µg Chl a/l for West Pacific coral reefs). It is known from the laboratory studies that phytoplankton are a suitable food source for D. cornus larvae, but this does not necessarily imply that this is the only food source utilised. Bacteria, dissolved organic compounds, detritus etc. are all potential food sources. However, none of these are quantified by chlorophyll a measurements. There is considerable controversy over the extent to which planktonic larvae may be food limited in the wild (e.g. Lucas, 1982; Paulay et al., 1985; Bell, 1987; Olson, 1987; Olson et al., 1987; Uchida & Nomura, 1987).

No larvae have so far been successfully reared through to settlement. However, a relatively extended planktonic life (probably of several weeks) can be inferred since hatching occurs at an early veliger stage, when the shell has approximately $1^1/_2$ whorls, and the protoconchs of juvenile D. cornus collected in the field are between 3-4 whorls in size, and between 0.7-0.95mm (n=47) in length. The well defined apertural beak is also characteristic of most long-term planktotrophic prosobranch veligers (D'Asaro, 1966).

Juvenile D. cornus were recorded at all the sites examined, with the exception of Bundegi Reef, and in greatest numbers at the back reef edge site at Coral Bay (mean density = $6/m^2$, range = $0-33/m^2$). There was a peak in the abundance of very small D. cornus (0.1-0.7mm shell length) in February 1991, with lower numbers being recorded in November 1990. In June 1990 slightly larger juveniles (0.4-1.3mm) were more prevalent. Nardi (1991), in a study of the gametogenic cycle of D. cornus, recorded a peak in the spawning activity of the Coral Bay population in late spring/early summer of 1989 and 1990. The temporal variation in the size distributions of the juveniles recorded in the present study may reflect this seasonal reproductive activity. 84% of all the juveniles recorded in the present study were found on the corymbose/caespitose growth forms of Acropora, in particular on A. verweyi, A. nasuta and

A. cerealis (coral identification confirmed by Dr J.E.N. Veron). Lower numbers were found on other growth forms of Acropora, and other coral species (e.g. Pocillopora damicornis, Seriatopora caliendrum, Cyphastrea serailia, Montipora species). Juveniles were also generally, but not exclusively, found in coral colonies with larger D. cornus individuals present. Whether this is the result of an aggregative settlement behaviour in response to the presence of adult conspecifics per se, or whether the larvae are settling in response to damaged coral resulting from the feeding activities of the adults, is as yet undetermined.

DISCUSSION.

The presence of a relatively long-term (>1 week) free-swimming planktonic veliger stage in the life cycle of D. cornus is in contrast to many other species of muricid gastropods which undergo direct development (see Spight, 1975, 1976). Thorson (1950) has suggested that species with long planktonic larval lives (2 weeks - 3 months) are the most likely to undergo large fluctuations in numbers from year to year, because of the vagaries of a planktonic existence. Species with relatively constant populations have either very short planktonic stages (hours or days) in their life cycles, or undergo direct development. Results from the laboratory observations indicate that female D. cornus are potentially very fecund, thus, small changes in the rate of mortality of the early stages may be reflected in relatively large changes in the absolute numbers of recruits into the post-settlement adult populations. Because of the low survivorship of the planktonic stages of many marine invertebrates, subtle shifts in the balance of factors affecting larval development and survival can have a significant effect on the numbers recruiting into the population, and thus on the dynamics of the population as a whole. Mortalities occurring during the planktonic larval stages in the life cycle of many species may represent a major source of mortality for the population as a whole (Thorson, 1950). Many factors (including the abundance and quality of the available food resources, water temperature, the availability of suitable settlement surfaces, transport by currents away from recruitment sites, and predation) may directly affect larval development, growth and survival, and may also have a significant indirect effect by prolonging larval residence time in the plankton with concomitant effects on their survival. Occasionally optimal conditions for survival may occur, resulting in increased recruitment into the adult population. However, any explanation of the D. cornus outbreaks at Ningaloo must also be able to account for the fact that there are no reports of outbreaks of other reef invertebrates with planktonic stages in their life cycles.

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