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Larval development, sensory mechanisms and physiological adaptations in acorn barnacles with special reference to *Balanus amphitrite*

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ABSTRACT

Barnacles have drawn the attention of many naturalists and often dominate fouling communities. *Balanus amphitrite*, is a shallow water acorn barnacle capable of inhabiting expanses from supralittoral to subtidal levels, and as an epibiont. Its potential to survive and successfully establish local population is endorsed by various physiological adaptations and larval sensory perceptions. The larval life cycle of this species has both planktrotrophic naupliar and non-feeding cyprid stages. The naupliar energetics has a bearing on the capabilities of cypris larvae to explore surfaces for settlement and also the recruitment success of juveniles. The most complete nervous system in the barnacles is established in the cypris larva. Although there has been considerable research with reference to their settlement and metamorphosis, not much is known about the olfactory, photo and auditory sensory mechanisms with respect to settlement and metamorphosis, which need further attention. Understanding the response of most sensitive life stages of barnacles to environmental changes in intertidal habitats can also serve as important models for understanding the effect of climate change on species distribution.

1. Introduction

Barnacles are one of the most dominant fouling organisms and an important component of the intertidal community. Among the barnacles, *Balanus amphitrite* is utilized as a candidate organism in antifouling research and hard substratum benthic ecology study, owing to well established rearing techniques. Darwin (1854) classified *B. amphitrite* complex into nine varieties namely *communis*, *venustus*, *pallidus*, *niveus*, *modestus*, *stutsburi*, *obscurus*, *variegatus* and *cirratus*. Since none of the original varieties had type specimen, a revised nomenclature was proposed by Harding (1962) by assigning lectotypes for the varieties of Darwin's dried specimens. He divided Darwin's nine varieties into four separate species: *B. amphitrite*, *B. pallidus*, *B. venustus* and *B. variegates. Balanus amphitrite communis* was placed into *B. amphitrite* var. *amphitrite*. The varieties *pallidus* and *stutsburi* were placed into species *pallidus*. Darwin's varieties *venustus*, *niveus*, *modestus* and *obscurus* were placed in the species *venustus*; the varieties *variegatus* and *cirratus* were placed under the species *variegatus*. He also synonymized Broch's (1927) variety *denticulata* with *B. amphitrite amphitrite*. It was revealed by Utinomi (1967) and further verified by Southward (1975) that Darwin had placed two species of *B. amphitrite* under the same taxa; *B. amphitrite* and *B. reticulatus*. Advancement in the understanding of the taxonomy of *B. amphitrite* group came through an extensive study of their morphology by Henry and McLaughin (1975) and it was concluded that only two subspecies exist, *B. amphitrite amphitrite* and *B. amphitrite saltonensis*. Based on genetic analysis, Flowerdew (1985), argued for placing *amphitrite* variety *saltonensis* in synonymy with the variety *amphitrite*. Pitombo (2004) carried out a major phylogenetic revision of Balanidae that resulted in a new family Amphibalanidae. As a consequence, *B. amphitrite* was renamed as *Amphibalanus amphitrite*. Recently, Clare and Hoeg (2008) suggested that the introduction of *Amphibalanus* would seriously confuse the naming of a barnacle that is at the centre of experimental research and suggested retention of the earlier nomenclature or adoption of a compromise nomenclature. However, in a reply to this suggestion Carlton and Newman (2009) stated that the new name, *Amphibalanus amphitrite* was proposed in accordance with the International Code of Zoological Nomenclature. They also pointed out that the criticism offered by Clare and Hoeg (2008) had no scientifically valid reason to return to the earlier nomenclature of this or any other well-known species of barnacle. In view of this, though we have used *B. amphitrite* in this paper, we wish to state that it is without any prejudice to the debated taxonomic status. This review provides an overview of the research carried out in relation to larval development, cyprid energetics, sensory mechanisms and physiological adaptations in acorn barnacles with special reference to *B. amphitrite*.

2. Larval development

Most of the balanomorph barnacles are simultaneous hermaphrodites (Charnov, 1987), for which obligate internal cross-fertilization

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is the norm. However, incidences of self-fertilization have also been reported (Barnes and Crisp, 1956; Furman and Yule, 1990; El-Komi and Kajihara, 1991; Desai et al., 2006). Experiments with *B. amphitrite* indicated that egg production was high with brood intervals of 5–8 days per brood compared to boreo-arctic species which usually produce a single brood per year (Crisp and Davis, 1955; El-Komi and Kajihara, 1991). Temperature and nutritional conditions also influence breeding and molting processes in this species. Field observations in a tropical coastal environment influenced by monsoon also point out a positive relationship between gonad development of *B. amphitrite* and chlorophyll *a* concentration (Desai et al., 2006). Documenting reproductive hotspots along the Oregon Coast (USA), Leslie et al. (2005) pointed out that the intertidal barnacle *Balanus glandula* population in the region of higher primary productivity produced almost five times more offspring than those in the regions of lower productivity. Barnes and Barnes (1958) concluded that availability of the 'right' food type is of fundamental importance in the development of planktonic larvae with high metabolic rates and suggested that food may interact with and compensate for the effect of temperature. It was pointed out that, when starved adults of *Semibalanus balanoides* retain egg masses beyond the 'normal' hatching time, egg metabolism occurs largely at the expense of remaining lipid reserves (Lucas and Crisp, 1987). In general, eggs of marine species use lipids as their main energy source followed by proteins and carbohydrates (Pandian, 1969, 1970). Thus, the ability of adults to postpone hatching may have important implications for the energy reserves and viability of newly hatched nauplii. Whenever retention period is reasonably short, each newly hatched larva appears to possess enough energy to start the pelagic life (Lucas and Crisp, 1987). Experiments with the nauplii of *B. amphitrite*, that were hatched from adults collected during different seasons indicated that larvae obtained during late autumn to early spring had poor capability to develop when compared to larvae collected during the summer months. It was pointed out that generally, during late autumn to early spring, less food is available for adults; hence, retention of egg mass within the adult would be at the cost of its nutritional status (Anil et al., 1995). Thus, in balanomorph barnacles energy metabolism of eggs has a vital role in their larval ecology.

Olson and Olson (1989) assessed food limitation of planktotrophic invertebrate larvae and concluded that larval starvation is likely to be important to recruitment success in cirripedes. Studies on the specific mechanisms effecting starvation sensitivity in the larval development of decapod crustaceans suggested a positive interaction between food availability and endogenous hormonal control of development (Anger, 1987). Furthermore, when an early larva is starved beyond a certain point, its feeding ability decreases and it eventually experiences irreversible damage, probably to the mitochondria and hepatopancreas system (Storch and Anger, 1983). Scheltema and Williams (1982) proposed that reduced feeding efficiency of *B. eburneus* nauplii reared at low experimental temperature can be compensated by increased algal cell concentration. *B. amphitrite* larval development is euryhaline and observations revealed that the temperature influence is greatest on the instar II nauplii (Anil et al., 1995). It was further observed that food availability and temperature jointly determine energy allocation for development and the influence varied with naupliar instars. The influence of salinity (15, 25 and 30) at a given food concentration (0.5, 1 and 2×10^5 cells ml^{-1} of *Skeletonema costatum*) on instar IV, V, VI and total naupliar duration was negligible at 20 °C, while at 30 °C there was a marked decrease in duration with increasing salinity (Anil, 1991; Anil and Kurian, 1996).

It has also been observed that *B. amphitrite* naupliar swimming rate significantly increases with increasing temperature (Yule, 1984). He hypothesized that, if the larvae swim faster due to an increase in temperature, a greater percentage of their available energy may go into swimming, and the ability of the larvae to replace that energy becomes a limiting factor for continued larval development. Podolsky (1994) manipulated sea water viscosity at various temperatures, to distinguish the physiological and mechanical effects of temperature on suspension feeding by ciliated echinoderm larvae and found that the increased viscosity alone accounted for half of the decline in feeding rate at lower temperatures. High viscosity shifted ingestion towards larger particles, which suggests that viscosity affects particle capture and rates of water processing (Podolsky, 1994). Laboratory studies on the nauplii of *Balanus improvisus*, revealed that total starvation suppressed molting beyond stage II; 50% mortality occurred in approximately 4 days at both 15 and 21 °C, while the longest survival time was 7 days at 15 °C and 6 days at 21 °C (Lang and Marcy, 1982). Susceptibility of *B. amphitrite* nauplii to starvation varied significantly with the rearing temperature. Nauplii starved at 5 °C had Ultimate Recovery Point (URP) of 204 h (URP, denotes the starvation point in hours at the end of which a larva can recover and continue development). The URP reduced to 60 and 24 h when the nauplii were starved at 15 and 24 °C respectively (Desai and Anil, 2000).

In nature, larvae fulfill their energy demands from a soup of available food material, while those reared in the laboratory are typically provided with a suitable diet. In order to understand the variations between laboratory and field reared larvae, instar II nauplii of *B. amphitrite* were reared in the field using micro enclosures (1 liter capacity PVC bottles, which were cut at the sides as well as the bottom, sealing the cut portion with 100 µm mesh using glue, and ensuring that they are leak proof). The micro enclosures were suspended in the water column from the jetty at a depth of 1 m below the lowest low tide mark. After every 24 h, nauplii were washed into glass beakers and about 25 nauplii were siphoned out and the larval size and stage was recorded and were measured for RNA and DNA content. Results from this study showed that larvae reared in the laboratory had approximately 1.7 times higher RNA: DNA ratio (as a nutritional status indicator) than those raised at a comparable temperature in the field. Naupliar duration for laboratory reared larva was two days shorter (Desai and Anil, 2002). Chlorophyll *a* values during field rearing ranged from 1.9 to 4 µg l^{-1}, whereas chlorophyll *a* content of food provided in the laboratory (1×10^5 cells l^{-1} of *S. costatum*) was 60 µg l^{-1}. Even at the lowest laboratory rearing concentrations, the chlorophyll *a* content was 15 times higher than the maximum value found in the field. It is also to be noted that the natural phytoplankton population includes forms, which are of no value as cirripede larval feed. Owing to such differences, the status of the larvae in the field and those raised in the laboratory can be widely different.

Another important factor that influences larval development is the naupliar feeding mechanism. Interpretation of cirripede naupliar feeding mechanism is largely based on anatomy and limb motions during swimming and grooming rather than direct observations of particle capture. Studies show that the gnathobases of the second antennae are used to ingest particles, but a variety of mechanisms are involved in the concentration of particles and in transporting them to mouth (Strathmann, 1987; Vargas et al., 2006). Food clearance rate in feeding is proportional to the length of ciliated band (Strathmann, 1971; Strathmann et al., 1972), which commonly increases with increasing larval body length (Strathmann and Bonar, 1976; McEdward, 1984). It was pointed out that intersetular distance of cirripede nauplii is likely to increase with successive molts (Stone, 1986, 1988). This increase in mesh size can influence the size of food particles that larvae capture (Stone, 1988). Thus grazing rate would vary ontogenetically and with food type. Exemplifying this, it has been found that early naupliar instars of *B. amphitrite* had higher grazing rates when fed with single cell diatom *Cheatoceros calcitrans* (4–6 µm) whereas in the case of advanced instars it was chain forming *S. costatum* (4–12 µm in diameter). Early instar larvae recovered better from starvation when fed with *C. calcitrans* whereas advanced instars recovered better when fed with *S. costatum* (Desai and Anil, 2004).