



## Diverse life strategies in two coral-inhabiting barnacles (Pyrgomatidae) occupying the same host (*Cyphastrea chalcidicum*), in the northern Gulf of Eilat

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### ABSTRACT

Barnacles are one of the most common and well-studied groups in marine ecology. In the Gulf of Eilat, the barnacle assemblages in the subtidal zone are dominated by epibionts, inhabiting stony corals, hydrozoans and sponges. Pyrgomatidae barnacles are obligatory symbionts of scleractinian corals and hydrozoans. For many organisms there is a relationship between life strategies, as predicted by the r–K selection theory, and degree of habitat specialization. Earlier studies have suggested that coral-inhabiting barnacles exhibit a tendency towards the r-endpoint. In the present research we studied the life strategy of two pyrgomatidae: *Trevathana sarae*, a host specialist; and *Cantellius pallidus*, considered a host generalist, both of which occur on the same coral host, *Cyphastrea chalcidicum*. Our results indicate that the two species of barnacles present two different life strategies. *T. sarae* fits more into the K-strategy model: a slow development, late maturity (2 years), long life span (6 years), large embryos 440 μ, and a low number of propagules (ca. 40). In contrast, *C. pallidus* exhibits the r-selected traits: a fast development, early maturity (1 year), short life span (2 years), small embryos 270 μ, and a high number of propagules (ca. 300). These findings support the hypothesis that associates the tendency of a species strategy towards the r-or K-endpoint with the degree of habitat specialization. Furthermore, the results highlight the diversity of life strategies existing in the Pyrgomatidae.

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### 1. Introduction

Living corals offer potential symbionts not only food but also substrata, thus allowing a greater diversity of symbiotic modes of life than do many other types of hosts (Patton, 1976). The coral-inhabiting barnacles of the sub-family Pyrgomatinae are obligatory symbionts of scleractinian corals in the Indo-Pacific. There are more than 70 nominal species of coral-inhabiting barnacles in the family Pyrgomatidae (Ross and Newman, 2003); a number that is now rising due to use of modern research technologies such as resolution morphology techniques (SEM) and molecular analysis (Mokady et al., 1999; Mokady and Brickner, 2001; Simon-Blecher et al., 2007; Achituv et al., 2009; Chan et al., 2009). The study of life-history strategies integrates physiological, morphological, and behavioral traits in order to explain how different mechanisms allocate finite resources to maintenance, growth and reproduction, under both predictable and unpredictable environments. The r–K concept provides a valuable framework for classifying history traits. It suggests a continuum between two endpoints along which species can be positioned. Organisms found at the r-endpoint represent the optimal strategy for allocation of energy to reproduction and producing as many offspring

as possible. At the K-endpoint organisms allocate energy to competition ability and enhanced survival of organisms (Pianka, 1970, 1972; Quadros et al., 2009). Quadros et al. (2009) stated that “the tendency of a species strategy towards the r- or K-endpoint may be related to the degree of habitat specialization, as it characterizes reproduction and growth rates and, ultimately, a species’ colonizing ability.” Habitat specialists often show K-selection traits while habitat generalists show r-selected traits (Mckinney, 1997; Quadros et al., 2009). Coral-inhabiting barnacles show different degrees of host specificity (Hiro, 1938; Ogawa and Matsuzaki, 1992) and are consequently expected to demonstrate a variety of life strategies. However the number of ecological field studies on coral-inhabiting barnacles is limited and cannot as yet support this assumption. Hiro’s (1938) work is the only paper to date on this topic. Focusing on the drawbacks of living on live substratum, he noted that there is antagonism between the life strategy of the barnacle and that of its host. In order to feed, barnacles must keep their orifice open. However the continuous growth of the coral might eventually cover the shell-opening of the barnacle and entomb it within the coral skeleton. The growth of the basal part of the cirriped shell pushes it up, keeping pace with growth of the coral. Ross and Newman (1973) suggested that pyrgomatid barnacles are able to inhibit coral skeleton deposition over their shell plates and that their lateral growth slows down rather early, with the barnacles reaching their maximal diameter at a relatively early stage. Anderson (1992) found that the cirral activity

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and movement of the fringes of the mantle keep the orifice clear of coral tissue and skeleton.

Most of our knowledge on the life strategy of coral-inhabiting barnacles is based on examination of museum specimens or a short field study. Hiro (1938), based on a comparison of the depth of the barnacle basis and the growth rings of the host coral, concluded that the life span of *Creusia* is five years. Lewis (1992) conducted a short field study on the balanid *Megabalanus stultus* (Darwin) living on *Millepora complanata* Lamarck, revealing that the growth rate of this barnacle is higher than that of free-living balanids. Ross and Newman (1973) and Foster (1987) noted that the growth rate of commensal barnacles is high, they reach maturity fast, and their life span is short.

Barnacles are hermaphrodites and there is usually cross-fertilization between neighbors. The fertilized eggs are packed in protein membrane and stored as egg lamellae in the mantle cavity till first-stage nauplii are discharged into the water. Due to the presence of egg lamellae it is easy to follow the reproduction cycle of barnacles, and Hines (1978) identified five types of such cycles. In boreo-Arctic barnacles like *Balanus balanus* L., *Semibalanus balanoides* L., and *Chirona hameri* (Ascanius), there is a single synchronized clutch during the winter which is incubated within the mantle cavity, and the nauplii are released into the water in the spring. In *Balanus glandula* Darwin and *Verruca stroemia* Rauh & Razaf there is one main clutch during the winter and additional non-synchronized breeding events during the spring and summer. In warm-water barnacles there is a continuous production of small clutches during the summer. *Tetraclita squamosa* Bruguiere presents the fourth reproductive pattern, with three clutches during the late summer. In *Elminius modestus* Darwin and *Megabalanus pacificus* (Pilsbry) there is no seasonality in breeding, and these barnacles reach sexual maturity shortly after settlement and reproduce continuously. Likewise, in the coral reef in Eilat it was found that *Wanella milleporae* (Darwin), which inhabits the hydrocoral *Millepora dichotoma* Forskal, breeds throughout the year, with two peaks in the spring and summer (Vago, 1989).

Patton (1976), reviewing the life history of the fauna associated with corals, pointed out that the settling larvae need to avoid predation by the coral as well as undergo morphological and physiological adaptations to life on living corals. Data concerning the settlement of coral-inhabiting barnacles are limited. Utinomi (1943) described the growth of juveniles barnacles of *Creusia spinolusa* Leach settling on *Leptastrea purpurea* (Dana). Moyse (1971) found in the laboratory that cyprids of *Megatrema anglicum* (Sowerby) settle at the perimeter of the polyp or on adult barnacles of the solitary coral *Caryophyllia smithi* Stokes and Broderip.

Colonization of the host coral must involve some special attribute of the cyprid enabling it to penetrate the coral tissue and resist its immune action, allowing the cyprid to metamorphose within the tissue and at a later stage to fuse its calcifying basis with the corallite. Mechanisms for resisting the immune response of the coral tissues may be linked to mechanisms of host recognition (Foster, 1987). Regarding host specificity, Hiro (1935, 1938) concluded that pyrgamotids with more modified shell and opercular valves (*Nobia*, *Savignium* and *Pyrgoma*) are more host-specific than the more balanid-like pyrgamotids (*Creusia* and *Cantellius*), i.e. the more peculiar the morphological characteristics of the barnacle, the more host-specific it is (Ross and Newman, 1973).

The present study is based on six years of observations (1989–1994) on the barnacles of the stony coral *Cyphastrea chalcidicum* Forskal in the northern Gulf of Eilat (Aqaba) Red Sea (Brickner, 1994). This coral hosts two species of barnacles, *Trevathana sarae* Brickner and Aчитuv known only from *Cyphastrea* (Brickner et al., 2010), and *Cantellius pallidus* (Broch). These two barnacles show different degrees of host specificity. *T. sarae* (formerly assigned to *T. dentata*) (Brickner et al., 2010) is restricted to a limited number of hosts (mainly of the family Faviidae). *Cantellius pallidus* in contrast, is found

on a wide spectrum of coral genera (*Acroporidae*, *Pocilloporidae*, *Agaricidae*, *Fungiidae*, *Poritidae*, *Caryophyllidae*, *Faviidae*). Recently, molecular studies have indicated an even higher host specificity in *T. sarae* (Brickner et al., 2010).

The objective of the present study was to compare the life strategies of two sympatric barnacle species, *C. pallidus* and *T. sarae*, occurring on the same coral host *Cyphastrea chalcidicum*, in the northern Gulf of Eilat (Aqaba) Red Sea.

## 2. Materials and methods

The distribution of the coral *C. chalcidicum* and the presence of inhabiting barnacles were studied during 1991 in front of the Interuniversity Institute in Eilat (IUI), using SCUBA gear. The abundance of *C. chalcidicum* relative to the total numbers of coral colonies, and the degree of presence of inhabiting barnacles on it were recorded using the 10 m line transect method (Loya and Slobodkin, 1971). Five line transects were deployed at each depth, at 1, 5, 10, 20 and 30 m, parallel to the seashore. Coral colonies with at least one barnacle were identified as inhabited.

To estimate the quantity of barnacles on inhabited colonies of *C. chalcidicum*, eight colonies from 3 m depth and nine colonies from 20 m depth, 5 cm in diameter were collected using a hammer and chisel. The barnacles on these corals were identified and counted.

For age structure and growth rate of *C. chalcidicum* we used the Alizarin staining method (Lamberts, 1978). Twenty colonies, were enclosed in transparent plastic bags *in situ*, at 3 m to 5 m water depth, during day time, with Alizarin Red-S (15 ppm in sea water; 12 h), staining was repeated several times during two years. After two years these corals were removed from the sea, dried and sliced, deposits of coral aragonite appeared as white zones above the red lines, the coral linear growth was than estimated from sliced corals. In each colony the intervals between the stained layers or between the last stained layer and the surface were measured at 10 points of the slice. Mean radial increment of the colonies was calculated. Barnacle age and growth were estimated from comparison of the depth of its basis and related it to the annual growth of the coral as estimated by the Alizarin method. A monthly sample of three *C. chalcidicum* colonies was collected at 3 m depth in front of the IUI. The barnacles on these corals were counted and the carino-rostral diameter was measured under a dissecting binocular using a calibrated eyepiece. Following removal of the shell plates and prosoma using a pointed knife and fine forceps, the depth of the basis was measured using a Varnier calipers with a fine depth probe. The age of the barnacle was estimated by relating the depth of the basis to the mean radial annual growth of *C. chalcidicum*.

Breeding season was determined by the presence of egg lamellae in the mantle cavity of the monthly-collected colonies. The egg lamellae were suctioned from the cavity using a Pasteur pipette, and the number of embryos, their stage of development and size of more than 300 larvae from each species were recorded. The egg lamellae were taken to the laboratory and kept in 5 ml tissue culture cells until hatched. After hatching the larvae were relocated to beakers with 80 ml filtered sea water (1  $\mu$ ) and 50 mg/ml ampicillin. Temperature was 22 + 2 °C, with 13 h light and 11 h dark cycle; water was replaced daily; food was not added. Embryonic development duration is defined as being from the one cell stage to hatching; larval development duration is determined from hatching to the cyprid stage. Embryos' long axis and larval length from the frontal margins to the tip of the caudal spine were measured (Barnes and Aчитuv, 1981).

Barnacle recruitment experiments were conducted on four coral colonies during 1989–1990. In August 1989 the coral colonies were detached from the reef, and all barnacles were removed from them, under a dissecting binocular, using tweezers. The corals were then attached to an artificial substratum, using underwater glue (Aqua-Mend, USA), at 5 m depth in front of the IUI. This allowed enough time

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