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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). Moyses (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 Achituv 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 μ) and 50 mg/ml ampicillin. Temperature was 22 \pm 2 $^{\circ}$ 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 Achituv, 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 (Aquamend, USA), at 5 m depth in front of the IUI. This allowed enough time

for the coral tissue to regenerate over the removed barnacles' bore holes, before the new barnacle settlements began (December, 1989). Recruitment of barnacles was recorded over a year, covering two seasons of settlement (1989–1990), at one month intervals. New recruits were detected under a dissecting microscope.

3. Results

3.1. Distribution

Cyphastrea chalcidicum is a common Favaiid coral in the shallow water down to 20 m depth in the coral reefs of Eilat. The abundance of *C. chalcidicum* in front of the IUI and its percentage of occupation by the barnacles are presented in Fig. 1. *C. chalcidicum* comprises about 5% of the total number of coral colonies down to 10 m depth. At 20 m its abundance is lower and reaches only 1% of the colonies total number. No *C. chalcidicum* colony was found at 1 m or at 30 m depth. The rate of *C. chalcidicum* colonies hosting barnacles was found to be high, up to 97% of the corals at 5 m depth.

Comparison of barnacle distribution on *C. chalcidicum* colonies at two depths, 3 m and 20 m, is presented in Fig. 2. *T. sarae* was more abundant than *C. pallidus*, and all those were infested by *T. sarae*. 80% of the corals from 3 m depth and 89% of the corals from 20 m depth were inhabited by *C. pallidus*. In 89% of the colonies the number of specimens of *T. sarae* was higher than that of *C. pallidus*. *T. sarae* was found to be more abundant in the shallow water than at 30 m depth. In shallow water the highest number of *T. sarae* was 105 per standard colony (see Materials and methods section), while that of *C. pallidus* was 4. At 20 m depth the maximum number of *C. pallidus* per examined colony was 28, in comparison to 72 *T. sarae* barnacles found on the same colony.

3.2. Age structure and growth

The *C. chalcidicum* colonies are hemispherical in shape. Mean annual diametric growth rate of 20 colonies of the coral *C. chalcidicum*, as measured by the Alizarin method, was $2.5 \pm 0.4 \text{ year}^{-1}$. This enables estimation of the age of its inhabiting barnacles (Fig. 3). The maximal age of *T. sarae* was found to be 6 years while that of *C. pallidus* was only 2 years. The average age of *C. pallidus* was $1.5 \pm 0.5 \text{ years}$ ($n = 10$). The average age of *T. sarae* was $2.3 \pm 1.2 \text{ years}$ ($n = 148$), with 84% being less than 3 years old.

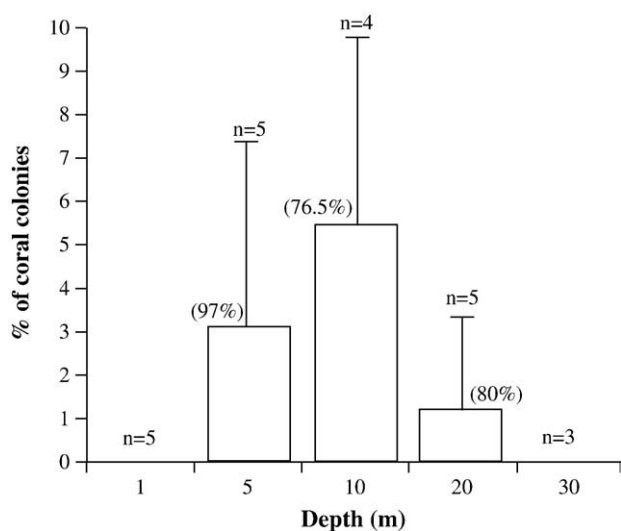


Fig. 1. Abundance of *Cyphastrea chalcidicum* colonies compared to all the stony coral colonies at different depths across from the IUI. Numbers in parentheses represent the proportion of *C. chalcidicum* colonies inhabited by barnacles.

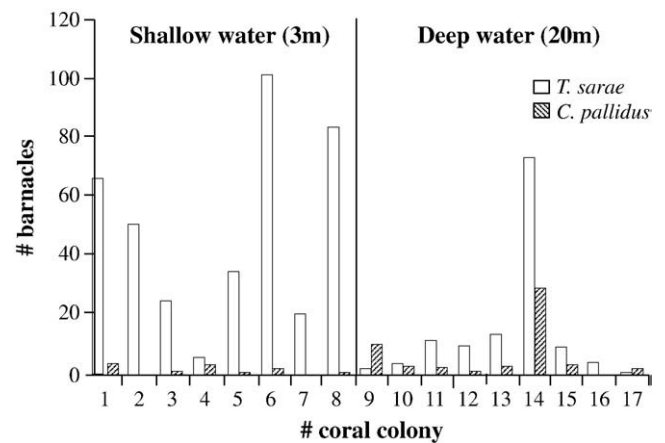


Fig. 2. The distribution of *Trevathana sarae* and *Cantellius pallidus* occurring on 17 colonies of *Cyphastrea chalcidicum* at two depths, 3 m and 20 m.

3.3. Breeding

The percentage of barnacles containing egg lamellae is presented in Fig. 4. The breeding season of *T. sarae* started in November and lasted three months, with the percentage of animals possessing egg lamellae never exceeding 17%. In *C. pallidus* egg lamellae were found only in December, when 54% of the animals contained these in their mantle cavity. Fig. 5 presents the age groups of barnacles in which egg lamellae were found during the breeding season of 1989–1990. One-year-old *C. pallidus* already possessed egg lamellae while in *T. sarae* such were found only in animals aged two years. In one-year-old *T. sarae* the ovaries were not discernable. In *T. sarae* the penis degenerates after the breeding season and eventually disappears in April. In *C. pallidus* the penis is present throughout the year.

The egg lamellae of *C. pallidus* are found under the prosoma filling the mantle cavity. In *T. sarae* the egg lamellae are small, separated, and found on both sides of the prosoma. Table 1 summarizes the differences in size and number of eggs, and sizes of different stages of embryos of the two species. *T. sarae* produces a smaller number of eggs than *C. pallidus*, but the eggs themselves are larger. Larvae of both species were kept in culture, but only the nauplii of *T. sarae* reached the cypris stage. Food was not added to the culture, indicating that

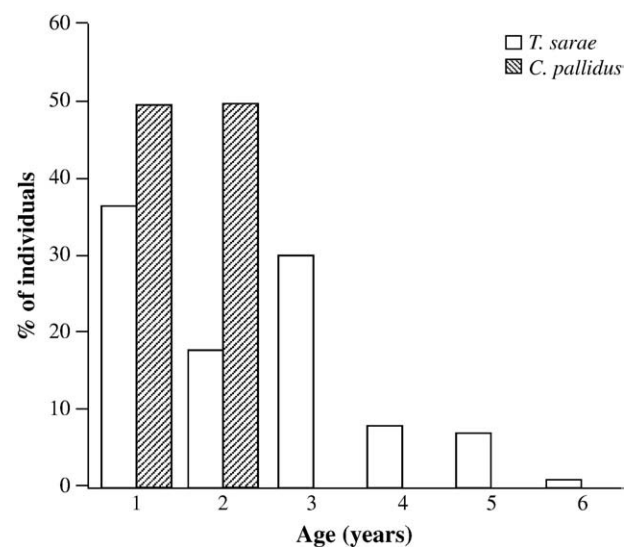


Fig. 3. Age distribution of *Trevathana sarae* ($n = 148$) and *C. pallidus* ($n = 20$) on a single coral colony of *C. chalcidicum*. The barnacles' age was inferred from a comparison of the depth of their basis to the annual growth rate of the coral host as measured by the Alizarin Red method ($2.5 \pm 0.4 \text{ year}^{-1}$).

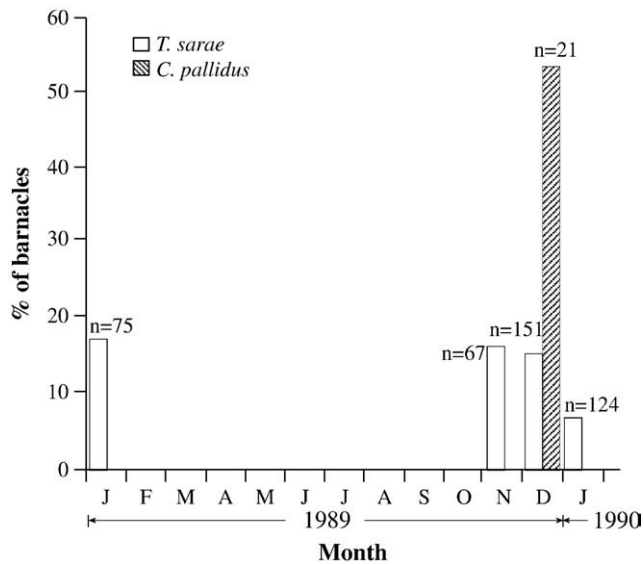


Fig. 4. Reproduction season of *Trevathana sarae* and *Cantellius pallidus*, according to the percentage of barnacles containing egg lamellae between the years 1989–1990. Three colonies were studied every month. (n) The number of examined barnacles.

these larvae are lecithotrophic. The nauplii of *C. pallidus* did not reach the third naupliar stage.

3.4. Recruitment

The dynamics of recruitment of the two barnacles on four *C. chalcidicum* colonies is presented in Fig. 6. Although the breeding season of the two species of barnacles, as revealed from presence of egg lamellae, overlapped, settlement on the host corals occurred at different periods. Settlement of *T. sarae* was detected in November 1989; however these were not counted, due to their fragility, and therefore not presented in Fig. 6, next recruits of *T. sarae* settlers could be observed in December 1990, which coincident with the breeding season. The first recruitment of *C. pallidus* (dotted bars) was noticed at the end of March, 1990. The number of recruits of *T. sarae* on the four coral colonies was much higher than that of *C. pallidus*. The barnacles settled on the live tissue of the coral, and spats of *T. sarae* were found on the external septa of the coral polyps (costae). In many cases several spats were found around a single polyp. The settling stages penetrate the coral tissue and their presence is initially hard to detect. During these stages the barnacles are loosely attached to the septa of the coral, their basis is discernable and is not embedded in the coral skeleton, as it is in mature barnacles. The basis is thin, conical, and the

Table 1

Comparison of characters of embryos and different larval stages of *Trevathana sarae* and of *Cantellius pallidus* from the Gulf of Eilat, Red Sea. Embryonic development duration defined from one cell stage to hatching, larval development duration is determined from hatching to cyprid stage.

	<i>Trevateana sarae</i>	<i>Cantellius pallidus</i>
Number of egg masses examined	15	8
Number of eggs in egg lamella	38 ± 16	290 ± 39
Size (length) of embryos and of larval stages (μ)		
Single cell embryo	320–330	190–210
Multiple cells embryo	360–370	240
Limb buds and eyes visible	400–440	270
Nauplii Stage I	470–500	470
Nauplii Stage II	470–500	500
Cypris	420–440	–
Duration of embryonic development, Days	9–12	–
Duration of larval development, Days	12–19	–

single shell plate is also conical. *C. pallidus* settles among the polyps in areas where the coral tissue is thin, and its basis is flat and strongly attached to the coral skeleton.

3.5. Growth

Fig. 7 presents the growth of the two barnacles over the course of the first two years post-recruitment. The data were collected from the four coral colonies presented in Fig. 6. In the first eight months after *C. pallidus* settlement there was no size difference between the two species ($p > 0.05$). From November on a significant difference could be seen in the size of the barnacles ($p < 0.05$). At that stage there was no change in the carino-rostral diameter, indicating slow growth rate of the two barnacle species. After two years the average size of *C. pallidus* was 3.5 ± 0.35 mm and that of *T. sarae* 2.5 ± 0.22 mm. Despite their slowed growth rate, *T. sarae* adults continue to grow during the third year of their life.

Fig. 8 presents the correlation between the carino-rostral diameter of the shell and the depth of the basis, which in *T. sarae* represent the age of the barnacle. The data are based on 148 barnacles from a colony whose growth was monitored (2.5 ± 0.4 year⁻¹). It was found that growth ceases at the age of about three years; the difference in size of barnacles from different age cohorts was significant ($p < 0.05$, variance analysis with different samples), and size of five-year-old barnacles was 3.55 ± 0.23 mm.

Scanning electron microscopy study of the shells revealed that calcium carbonate deposition over the shell of *T. sarae* is low (Fig. 9). The radial projections over the shell plate that resemble the sclerosepta of

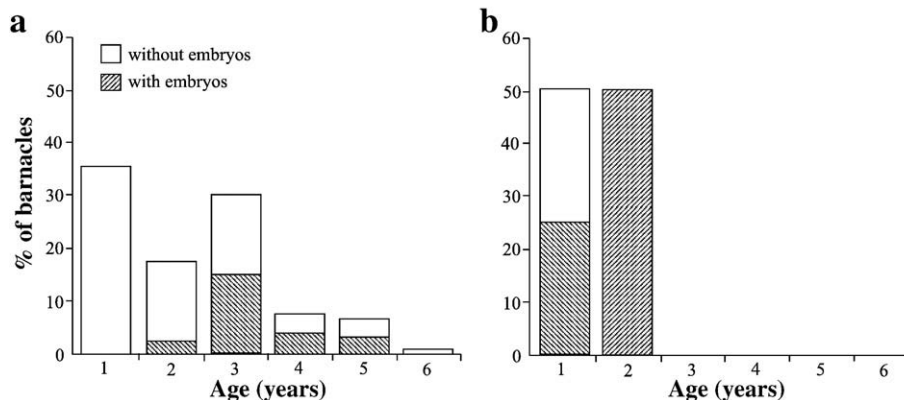


Fig. 5. Distribution of reproductive barnacles according to age groups between the years 1989–1990. a. *Trevathana sarae* (n = 417). b. *Cantellius pallidus*. (n = 21).

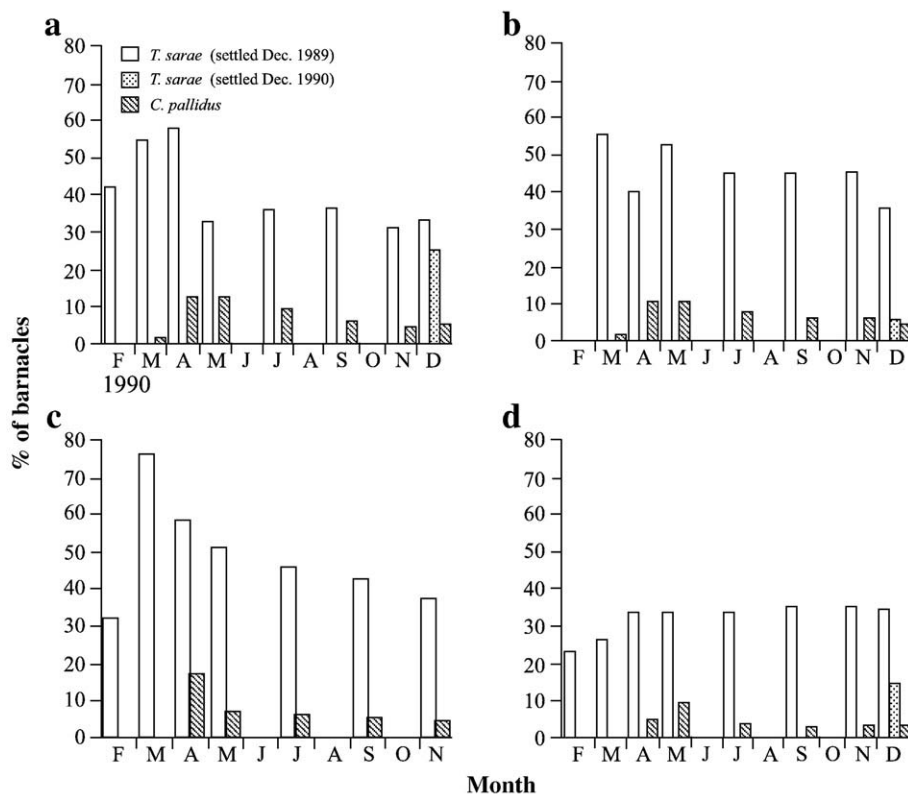


Fig. 6. Recruitment of *Trevathana sarae* and *Cantellius pallidus* on four colonies of *C. chalcidicum* during 1990; bars present the number of young barnacles.

the polyps are part of the barnacle shell and not part of the coral. Over these projections there is a thin deposition of an amorphous layer of calcite, which is deposited by the barnacle. (IR analysis by the late H. Lowenstam, unpublished). In a preliminary experiment *T. sarae* barnacles were sacrificed using a needle, without damaging the coral tissue covering the barnacle shells, and left *in situ*. A month later it was found that the dead barnacle shells were covered with a thick layer of calcareous deposition (Fig. 9), deposited by the coral.

The shell of *Cantellius* is composed of four compartments with sutures between them, enabling expansion of the shell. Field observations revealed that by the time that *C. pallidus* reaches the age of one year its shell is completely covered by the calcium carbonate that initially covered the perimeter of the shell where the shell plates interlock with the basis (Fig. 9). In some extreme cases

polyps of the coral were found on the shell of the barnacle, which constrained the vertical growth of the latter.

4. Discussion

Our results indicate that the two species of barnacle present two different life strategies. MacArthur and Wilson (1967) identified two basic life strategies, r- and K-selected species. r-selected species maximize their reproductive efforts and allocate most of their resources to reproduction; these organisms are usually small, short-lived and opportunistic. K-selected species increase their probability of survival and allocate energy to larger and longer living adults, and less energy to reproduction. There are many intermediate types between the extremes of these two strategies. The characteristics of the life strategies of the two barnacles hosted by *Cyphastrea* corals are summarized in Table 2. A population is classified as an r- or K-strategist by comparing it to other populations that are found on other positions on the r-k scale (Pianka, 1970). The two barnacle species discussed here living on the same host coral present two different life strategies. *C. pallidus* fits more into the r-strategy mode while *T. sarae* is a K-strategist. *T. sarae* shows a slow development, late maturity, long life span, large embryos, and low number of propagules. *C. pallidus*, in contrast, shows a different life strategy. These findings agree with the hypothesis relating the tendency of a species' strategy towards the r- or K-endpoint to its degree of habitat specialization. Usually, habitat specialists show K-selected traits, while habitat generalists show r-selected traits (Bengtsson and Baur, 1993; McKinney, 1997; Purvis et al., 2000; Quadros et al., 2009). The generalist barnacle *C. pallidus* confirms this hypothesis, in occupying a wide spectrum of host corals. In the Table compiled by Ogawa and Matsuzaki (1992) this coral was recorded from 37 species of corals. We suggest that the life strategy exhibited by *C. pallidus* enables it to adapt to a wide range of host corals. In contrast, Mokady et al. (1999) and Brickner et al. (2010) reveal the high degree of host specificity existing in the genus *Trevathana*.

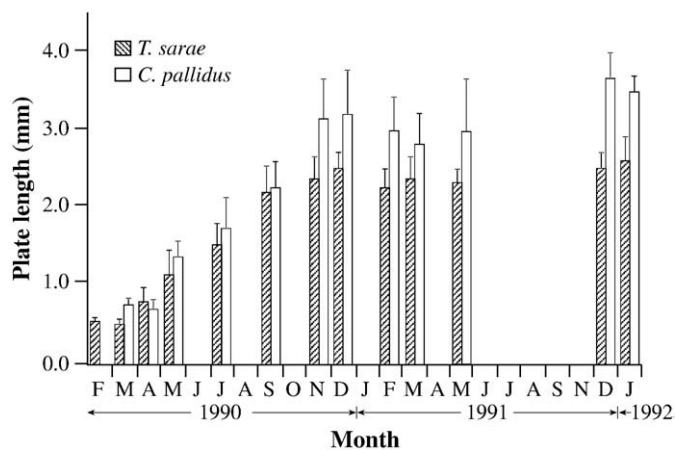


Fig. 7. Monthly average size (carino-rostral shell diameter) of *Trevathana sarae* and *C. pallidus* between the years 1990–1992. The barnacles settled on the corals during winter 1989 and March 1990, respectively. The data were collected from the experiment represented in Fig. 6.

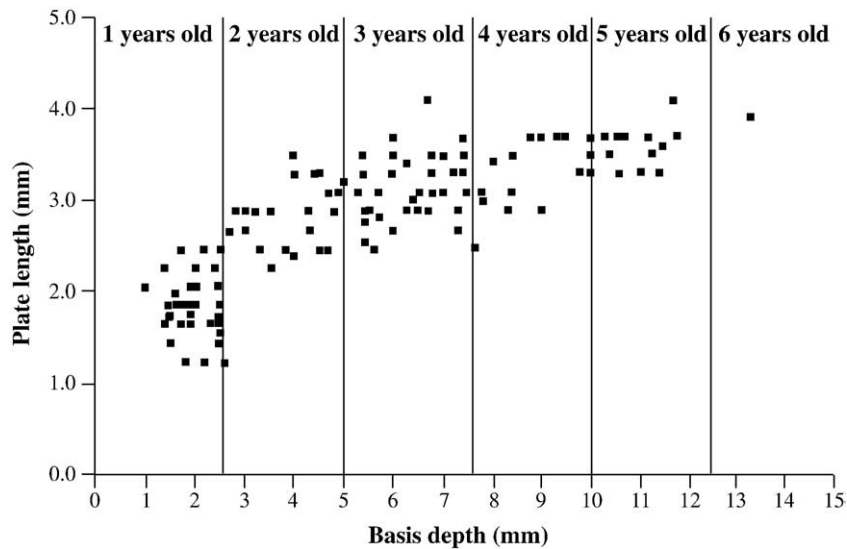


Fig. 8. Correlation between carino-rostral shell diameter (mm) and basis depth of *Trevathana sarae* ($n = 145$), on a single coral colony of *Cyphastrea chalcidicum*. The barnacle age group was based on coral annual grow rate ($2.5 \text{ mm a year}^{-1}$). A correlation of $r^2 = 0.75$ ($p = 0.001$) $y = -0.02 \times 2 + 0.43 \times = 1.17$.

Foster (1987) noted that commensal barnacles are characterized by high growth rate, early sexual maturity, and short life span. These traits are in agreement with the life strategy of *C. pallidus*. The life strategy of *T. sarae* differs from the expected life strategy of a commensal barnacle. The shell plate reaches its maximal size at the age of three years, with the fastest growth being in the first year post-settlement. These findings do not agree with previous studies suggesting that coral-inhabiting barnacles cease their growth shortly after settlement (Ross and Newman, 1973). The age of onset of reproduction is late, not only relative to *C. pallidus* but also to free-

living barnacles. Late reproduction age was found in large barnacles that attain a shell diameter of several centimeters, such as *Tetraclita*, which is found at high tide levels (Hines, 1978). The life span of *Trevathana sarae* agrees with the estimated life span proposed by Hiro (1938), which is a rather long life span for a barnacle. The embryos of *T. sarae* are large, reaching 400μ . This is one of the largest balanomorph embryos reported; and in culture the larvae grow and metamorphose to a spat without the addition of food, indicating lecithotrophy. Lecithotrophic larvae were found in *Tetraclita rufotincta* from the Gulf of Eilat (Barnes and Achituv, 1981), and those authors

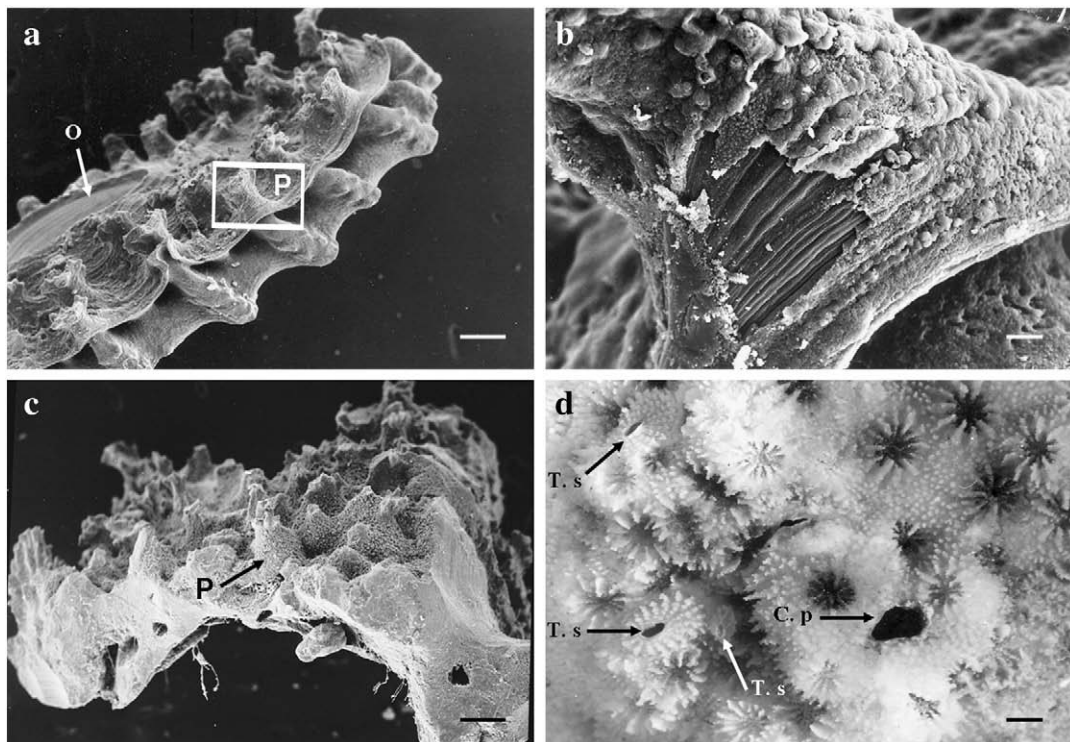


Fig. 9. *Cyphastrea chalcidicum* calcareous deposition over the shell of its inhabitant *Trevathana sarae*. a. External view of the shell of *T. sarae*. The internal frame reveals one of the projections (*p*). (*o*) Barnacle orifice. b. Barnacle projection in close-up. Note the shell growth rings, covered with a thin layer of coral calcareous deposition. c. External view of the shell of a dead *T. sarae*. The projections (*p*) and the area between are covered with a thick calcareous layer deposited by the coral host. d. *C. chalcidicum* skeleton with two barnacle species, *T. sarae* (*T.s*) clearly seen, and *C. pallidus* (*C.p*) covered by the coral skeleton, and identified only by the orifice. Note the polyps growing over the *C. pallidus* shell. Scale: a, c 200μ , b 20μ , d 1 mm.

Table 2

Comparison of life traits of *Trevathana sarae* and of *Cantellius pallidus* from the Gulf of Eilat, Red Sea.

	<i>Travethana sarae</i>	<i>Cantellius pallidus</i>
Proportion of coral colonies inhabited by barnacles	All colonies of <i>Cyphastrea</i>	Small proportion of colonies
Host specificity	Specialist, only on <i>Cyphastrea</i>	Generalist, on many hosts corals
Number of barnacles per host	High	Low
Max carino-rostral diameter (on <i>Cyphastrea</i>)	≈ 4 mm	≈ 4 mm
Calcium deposition on the shell	Minimal	Prominent
Life span	± 6 years	2 years
Age of maturation	2 years	1 year
Number of eggs in egg masses	Low	High
Mode of larval nutrition	Lecitotroph	Planktotroph
Larval competent period	Short, about 2 weeks	Long, about 2 months

suggested that lecithotrophy is an adaptation to life in oligotrophic waters such as of the Red Sea. Lecithotrophic larvae suggest a short planktonic stage and short dispersal distance (Scheltema, 1971). It was expected that in *T. sarae* the larvae would be limited to settlement in close vicinity to the original host colony; however, we showed that it takes two weeks for the larvae to reach the settlement stage, by which time larvae may be dispersed to a distance of tens of kilometers from the spot where they were released. In fact, the finding of newly-recruited young barnacles on the corals at the beginning of the breeding season indicates that the residence time and dispersal of *T. sarae* larvae are shorter than those found in the larvae maintained in culture (Table 1). A similar phenomenon was found in the lecithotrophic larvae of *Hliotis rubra* Leach: in this mollusk the dispersal range of the larvae did not exceed more than tens of meters, in spite of the fact that their residence in the plankton lasted several days (Prince et al., 1988). The short dispersal distance can be explained by the fact that the larvae reach their host coral (at an early developmental stage) as stage IV nauplii, and the development to stage V and VI as well as metamorphosis to the cypris stage take place on the host coral surface (Brickner and Høeg, this issue).

One of the basic assumptions in the ecological theories dealing with life strategies is that of the existence of selection of characters with the highest probability of fitness for survival. There is a tendency to predict what life strategies may be preferable under certain environmental conditions (Stearns, 1976, 1977). According to the r- and K-selection theory, K-characters are preferred in a stable environment with predictable conditions, while r-characters are preferable in unstable and unpredictable conditions. It might be assumed that two barnacle species that occupy the same niche would demonstrate the same life strategies; however, here we found that the two studied barnacles inhabiting the same coral exhibit two very different life strategies.

Based on Hiro's (1938) assumption, we suggest that growth of the coral host is the major factor affecting coral-inhabiting barnacles. The "growth race" between the host and the corals has resulted in a trade-off between different energetic demands. The existence of a trade-off system is an essential assumption in theories dealing with life strategies (Cody, 1966). Assuming that the energetic sources of an organism are limited, it will be impossible to invest all its energy, simultaneously, in two channels, like growth and reproduction, and that allocating resources to reproduction is done at the expense of growth or other physiological activities and vice versa. Our findings indicate that the two barnacles differ in their ability to withstand and

compete with the growth of the host coral. *T. sarae* is able to limit calcareous deposition on its shell: during the first stages of settlement most of its energy is directed to growth, first growth of the shell and at a later stage growth of the basis, which it must crucially grow at the same pace as the coral in order to avoid being entombed by the growing coral. During the first breeding season the barnacle produces only sperm which are energetically cheaper than oocytes. Sequential hermaphroditism is known in barnacles: in *Megabalanus nigrescens* (Lamarck) the young barnacles function as males while the mature barnacles are hermaphrodites (Harris, 1990). *C. pallidus*, in contrast, is limited in its race with the growing coral and the deposition of aragonite over its shell. Unlike the nearly flat shell of *T. sarae*, the shell of *C. pallidus* is conical and composed of four plates. Growth is achieved mainly by growth of the shell and not of the basis unlike in *T. sarae*. The basis of *C. pallidus* is wide and flat, a shape less adapted to matching the vertical growth of the coral. During the course of its life this barnacle's shell becomes thus covered by a layer of aragonite deposited by the coral. The deposition of aragonite in the sutures between the shell plates limits the barnacle's growth and might lead to its death. Lewis (1992) found that in *Megabalanus stultus*, which lives on the hydrocoral *Millepora complanata*, the barnacles are unable to avoid coverage of their shell by the growing hydrocoral.

Coral-inhabiting barnacles are very common in coral reefs and play an important role as a component in the coral holobiont. Understanding the life strategies of these barnacles may contribute to our overall knowledge of coral reefs. Only a few studies on the life strategy of coral-inhabiting barnacles have been conducted to date. It is possible that further investigations will reveal a variety of additional life strategies. The availability of a phylogenetic tree of coral-inhabiting barnacles (Simon-Blecher et al., 2007), together with the new data on the life strategies of these barnacles, will enable a study of this symbiosis from an evolutionary perspective.

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