

## **Skeletal Modifications in Stony Corals Caused by Indwelling Crabs: Hydrodynamical Advantages for Crab Feeding**

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### **Abstract**

Two crab species of the family Cryptochiridae, dwelling within corals, have the ability to modify coral morphology in their vicinity, by affecting coral growth. Two basic skeletal modifications caused by these crabs have been observed: depressions in massive corals ("pits"), and flattened spheres made of two valves in branching corals ("galls"). The effects of "galls" and "pits" on water flow pattern were tested in the field and laboratory using a flow tank. Ambient water currents are altered in distinct ways by the two different morphologies. Consequently, the supply of nutritional particles strongly differs between these skeletal modifications. We suggest that such modifications provide advantages to the crabs in gaining food particles, in addition to providing shelter. Moreover, our results revealed two distinct feeding mechanisms which are likely to be tied very closely to the effects of skeletal modifications on ambient flow: suspension feeding in "galls" and deposit feeding in "pits"

Keywords: reef corals, gall crabs, hydrodynamics, suspension feeding, deposit feeding

## 1. Introduction

Stony corals are common hosts for a wide variety of organisms which live on the coral colony surface or within its skeleton. In most cases, the sessile coral associates are suspension feeders (Patton, 1976). Suspension feeders can be divided into two categories according to the source of energy which drives currents passing their feeding structures: (1) active suspension feeders — those animals in which metabolic energy is used to drive the feeding currents, and (2) passive suspension feeders — animals that depend exclusively on ambient water currents to drive water past their filtering structures (LaBarbera, 1984). Usually, surface coral associates are passive filter feeders that must have the ability to project their filtering devices into the flow, while indwellers are mostly active filter feeders that can live within the skeleton, due to their ability to produce currents past their hidden filters.

This study deals with cryptochirid crabs, commonly known as "gall crabs", which have the ability to modify coral morphology by affecting the skeletal growth of the coral (Semper, 1881; Patton, 1976). Until recently "gall crabs" have been considered to be filter feeders (Patton, 1976). Kropp (1986) refuted this long standing hypothesis by reporting the feeding behavior and mouthpart morphology of three cryptochirid crabs that feed on mucus, debris and pieces of coral tissue.

Despite the potential importance of a hydrodynamic environment in sessile animal feeding (e.g. Patterson, 1984; Okamura, 1987; Johnson, 1988), the effects of skeletal modifications on flow pattern and particle behavior was ignored in studies dealing with "gall crabs". Skeletal modifications may locally alter current regime and particle behavior. Consequently, feeding ability could be affected by skeletal modifications to an extent that a feeding mechanism could be elicited.

In this preliminary study, we call attention to the effects of skeletal modifications on ambient currents and particle behavior. The specific hypothesis is that the coral skeletal modifications affect ambient flow in a way that can be related to food acquisition by the crabs. Moreover, we believe that the specialized cryptic mode of life of "gall crabs" is made possible by these effects of skeletal modifications.

The following questions are addressed in this study: (1) In what way do coral skeletal modifications influence ambient flow? (2) How does the affected ambient flow change the particle behavior? (3) What are the feeding mechanisms of the two crab species? (4) What are the correlations between the crabs' feeding mechanisms and ambient flow patterns?

## 2. Materials and Methods

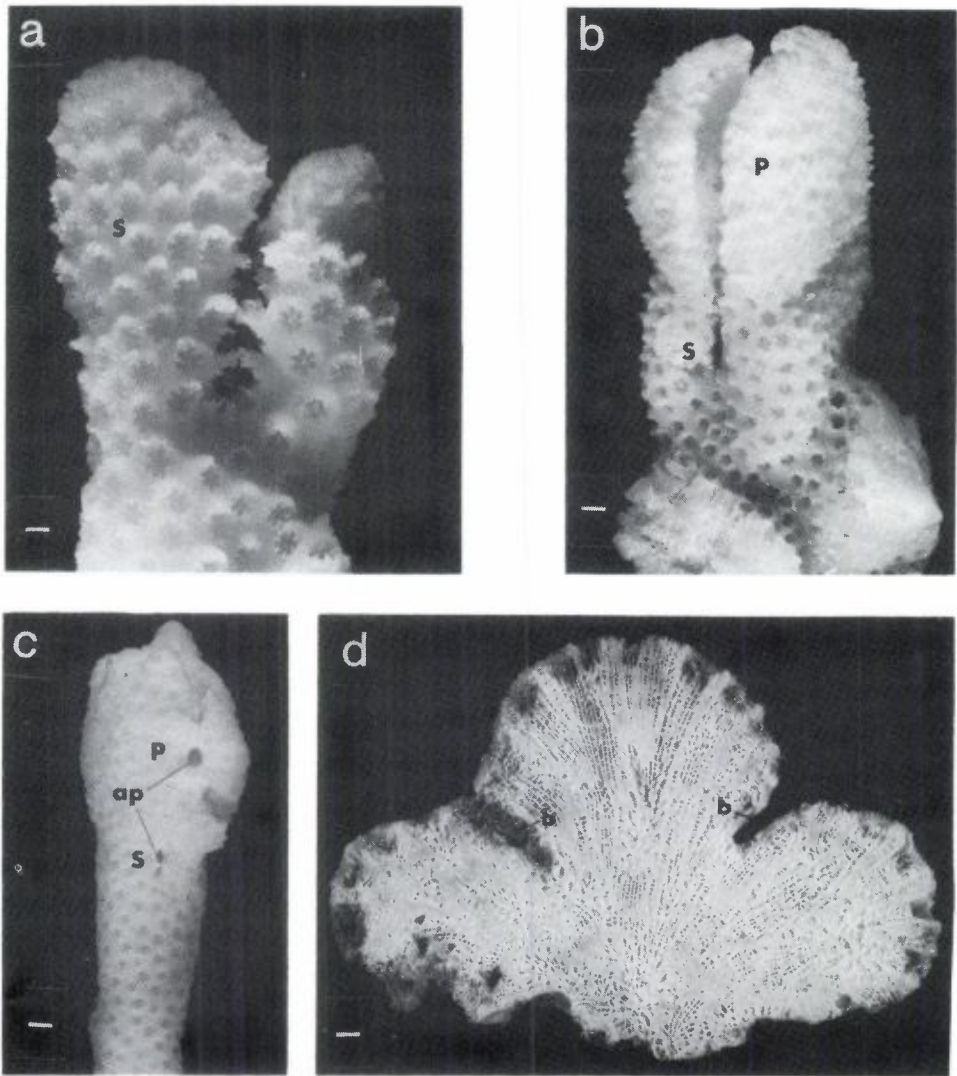
Field sampling and observations were conducted in the coral reef of Eilat, Gulf of Eilat, Red Sea. Two species of cryptochirid crabs were studied: *Hapalocarcinus marsupialis* Stimpson, which induces formation of galls in branching corals (Fig. 1a-c), termed in this paper as "gall crabs" and *Cryptochirus coralliodytes* Heller, which induces formation of pits in massive corals (Fig. 1d) termed in this paper as "pit crabs". The two species are common in the coral reefs of the Gulf of Eilat. *Hapalocarcinus marsupialis* dwells in pocilloporid corals, and specimens for this study were collected from *Stylophora pistillata*. *Cryptochirus coralliodytes* dwells in faviid corals, and specimens were collected from *Favia fava*. Host colonies were found in a wide range of zones ranging from the reef flat to a depth of 30 m.

### *Flow visualizations*

To visualize the streamlines in the vicinity of the galls and the pits, fluorescein dye was released upstream of natural structures and models. The course of dye in the field was video-taped using a video camera (SONY, CCD-V90) in an underwater housing (Amphibico Inc., Canada). The flow was analyzed using a frame by frame video screen. Particle behavior was visualized by detecting two types of particles, Pliolite VT (Goodyear Co.) and *Artemia* cysts, suspended in given concentrations within the tank or released upstream of the skeletal modifications in the field. The Pliolite VT particles density is 1.026 g/cm<sup>3</sup> and fall velocity in freshwater of 0.07-0.11 cm/s (size range chosen for this study was 200-350  $\mu$  in diameter). Fall velocity of *Artemia* cysts in freshwater ranges from 0.125-0.250 cm/s. The size range of the *Artemia* cysts was 200-240  $\mu$  in diameter.

### *Flow tank study*

Gall-shape and pit-shape skeletal modifications as well as Polyester and clay models, were planted in a recirculating freshwater flow tank similar to that described by Vogel and LaBarbera (1978). The models we used were exact copies of skeletal modifications, created by using inverse molds of silicone rubber (RTV 630, General Electric Co.) into which Polyester was injected for the gall models, and clay was stamped for the pit models. Since velocity gradients, characterized by the shear velocity ( $u^*$ ), experienced by different crab specimens varies considerably, we set up the  $u^*$  to be in the order of a tenth the mainstream velocity, as in many boundary layer flows (Denny, 1988).



**Figure 1.** Skeletal modifications in stony corals induced by "gall crabs". Galls (side view) in the branching coral *S. pistillata* induced by *Hapalocarcinus marsupialis* (a-c), and pits in the massive coral *F. favus* induced by *Cryptochirus coralliodytes* (d). (a) First-stage of gall development — creation of the secondary chamber. Bar = 1 mm. (b) Mid-stage of gall development (open gall) — creation of primary chamber. Bar = 1.7 mm. (c) Final-stage of gall development (closed gall) — the valves of primary chamber converged, leaving only small apertures. Bar = 2.5 mm. (d) Vertical cross section of *F. favus* illustrating two pits with a burrow in their center. Bar = 6 mm. p- primary chamber. s- secondary chamber. ap- aperture. b- burrow

Velocity gradients across the tank were adjusted by determining different profiles of flow collimators. Velocity gradients were measured with thermistor flowmeter (LaBarbera and Vogel, 1976) and by timing the rate of movement of Pliolite VT particles at different heights above the bottom. Three flow velocities were created in the flow tank: a slow flow (1–2 cm/s), an intermediate flow (4–5 cm/s) and a fast flow (8–9 cm/s). The three velocities roughly represent the range of unidirectional boundary flow velocities in the study site.

#### *Particle trapping experiments*

Flow tank experiments were conducted to test whether skeletal modifications (galls and pits) are likely to enhance particle entrapment as compared with other coral structures. Two types of galls, closed and open (Fig. 1b–c), were compared with a tube model mimicking a branch with a burrow. Two pit models of different sizes were compared with dome models. The flow tank contained a suspension of Pliolite VT particles or *Artemia* cysts. Particle concentrations were set by adding appropriate volumes of stock concentrations to a known volume of water in the flow tank. Only one velocity was set in these experiments (5 cm/s). Trapped particles were counted under a dissecting microscope. Transparent tubes, of the same diameter as coral branches, were connected to the gall base, and falling particles within the tube were counted.

#### *Scanning electron microscopy*

Mouth parts were carefully removed using a dissecting microscope, mounted on stubs, dried and coated with carbon and gold-paladium in preparation for examination with scanning electron microscope (JEOL 1200-EX).

#### *Feeding behavior*

The crabs' feeding behavior was observed under a dissecting microscope. The skeletal structures were cut vertically to enable observations without removing the crabs. Particles of fine marine sediment were used to observe particle behavior, water motions and feeding reactions. Feeding behavior was observed during day and night in seawater jars.

### 3. Observations and Results

#### *Particle behavior and flow path visualization*

##### *Gall*

Field and flow tank observations, using Fluorescein dye and Pliolite VT particles, have shown that the gall morphology induces flow through the gall, with water entering the upstream apertures and leaving through the upper and downstream apertures (Figs. 2,3).

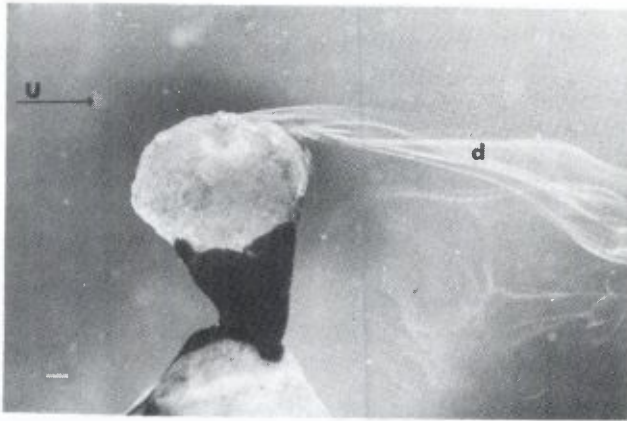


Figure 2. The path of water flowing out of a gall model (traced by fluorescein dye). Arrows indicate flow direction. Main flow speed is (U) 9 cm/sec. Bar = 3 mm. d-dye.

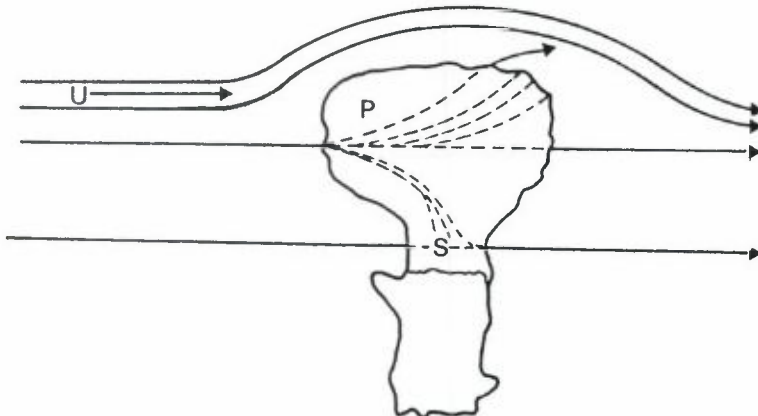


Figure 3. Diagram of flow pattern over and within a gall. Arrows and dashed lines indicate flow paths. p- primary chamber. s- secondary chamber. (see text for details).

### *Pit*

Streamlines close to the coral surface have been observed to separate from the wall, corresponding to backflow formation and creation of a vortical flow within the pit (Fig. 4). Particles were entrapped within the vortex created by the pit. Of these particles, some were seen to leave the vortex, falling into the pit (Fig. 4), while others were carried away.

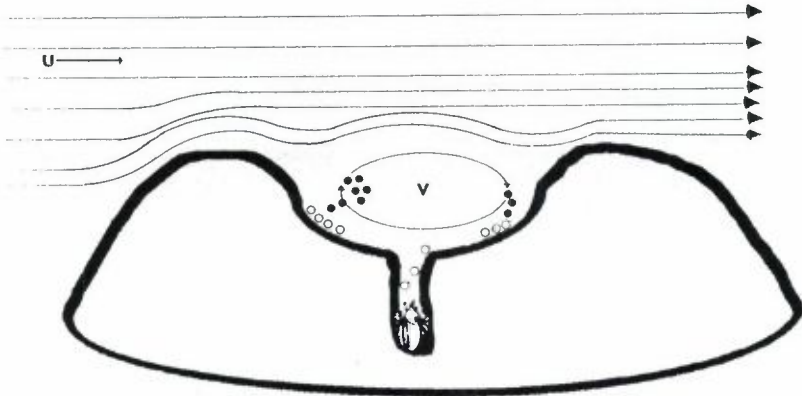


Figure 4. Diagram of flow path over and within a pit. Arrows indicate flow paths; empty dots indicate settled particles and black dots indicate suspended particles. U- mainstream. V- vortex. (see text for details).

### *Particle trapping experiments*

#### *Gall*

The experiments were conducted with individual galls and models immersed in suspension of *Artemia* cysts (11.5 cysts/ml) and Pliolite VT particles (5 particles/ml) recirculated in a freshwater flow tank. The results showed a significant increase in particle entrapment within both types of galls compared to a hypothetical branch with a burrow (Fig. 5) (one way ANOVA,  $p < 0.01$ ). Particle trapping rate in an open gall, although much higher, could not be statistically distinguished from a closed gall (t-test,  $p > 0.05$ ).

#### *Pit*

The experiments tested settlement of particles within pits, which are assumed to enhance particle settlement on coral surfaces. In addition, we also tested particle entrapment within burrows, since the particles available for the crabs are apparently those entrapped in the burrows. The experiments were conducted on individual pit and dome models immersed in *Artemia* or

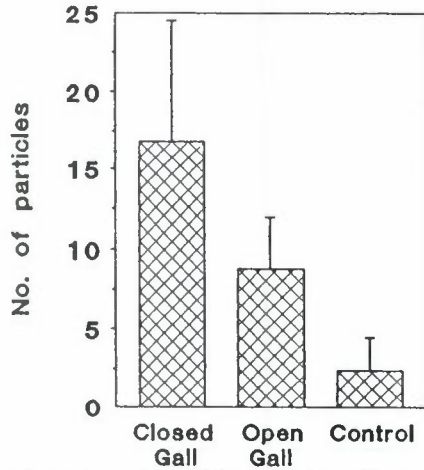


Figure 5. Mean number of entrapped particles within galls and a tube (control) per one minute.  $n = 5$  in each test.

Pliolite VT suspension with the same concentrations described above. The results of the experiments with Pliolite VT particles showed no significant difference in the number of settling particles between the two pit models (t test,  $p > 0.05$ ) (Fig. 6). However, a significantly higher number of settled particles

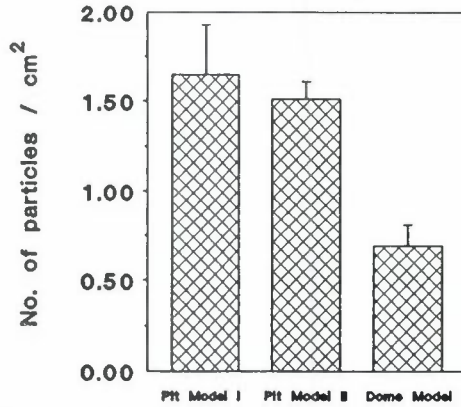


Figure 6. Mean number of settled Pliolite particles in models of pits and dome per cm<sup>2</sup> per three minutes.  $n = 4$  in each test.

was recorded in the pit models as compared with the dome model (one-way ANOVA,  $p < 0.01$ ). In another experiment, with *Artemia* cysts, the pattern recurred, but with much greater numbers of settled particles. Experiments of particle settlement in burrows located within pits and domes have shown



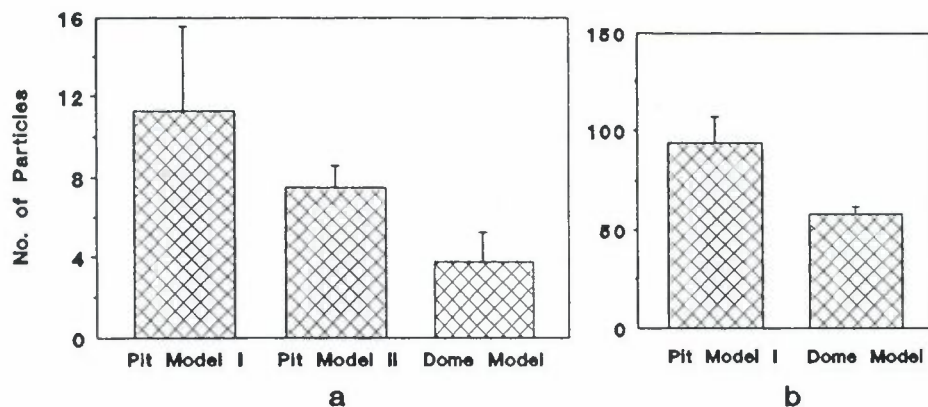


Figure 7. Mean number of settled particles in burrows located in the pits and domes per three minutes.

(a) Pliolite particles.  $n = 4$  in each test.

(b) *Artemia* cysts.  $n = 4$  in each test.

increased settlement of Pliolite VT particles (Fig. 7a) (one-way ANOVA,  $p < 0.05$ ) and *Artemia* cysts (Fig. 7b) (t-test,  $p < 0.01$ ) within pits as compared with domes.

#### *Morphology of feeding structures*

##### *H. marsupialis* ("gall crab")

Chela smooth, nearly glabrous, surface with few short setae (Fig. 8a). Ischium of third maxilliped greatly dilated, nearly glabrous (Fig. 8c). Inner margin of ischium of third maxilliped fringed with long setae, distally set with two parallel rows of spinules on interior margin, and distally on dactyl. Carpus and propodus with long, comb-like setae distally on interior margin. Endopod of second maxilliped with acuminate, comb-like setae exteriorly on two last segments. Exopod of second maxilliped distally with a row of nearly thirty long plumose setae (Fig. 8e).

##### *C. coralliodytes* ("pit crab")

Chela proximally tuberculate on upper surface, with long setae on carpus and merus (Fig. 8b). Ischium and merus of third maxilliped greatly dilated, tuberculate (Fig. 8d). Inner margin of ischium of third maxilliped with few short serrate setae. Carpus, propodus and dactyl with long comb-like setae on interior margin. Exopod of second maxilliped distally with a row of four long

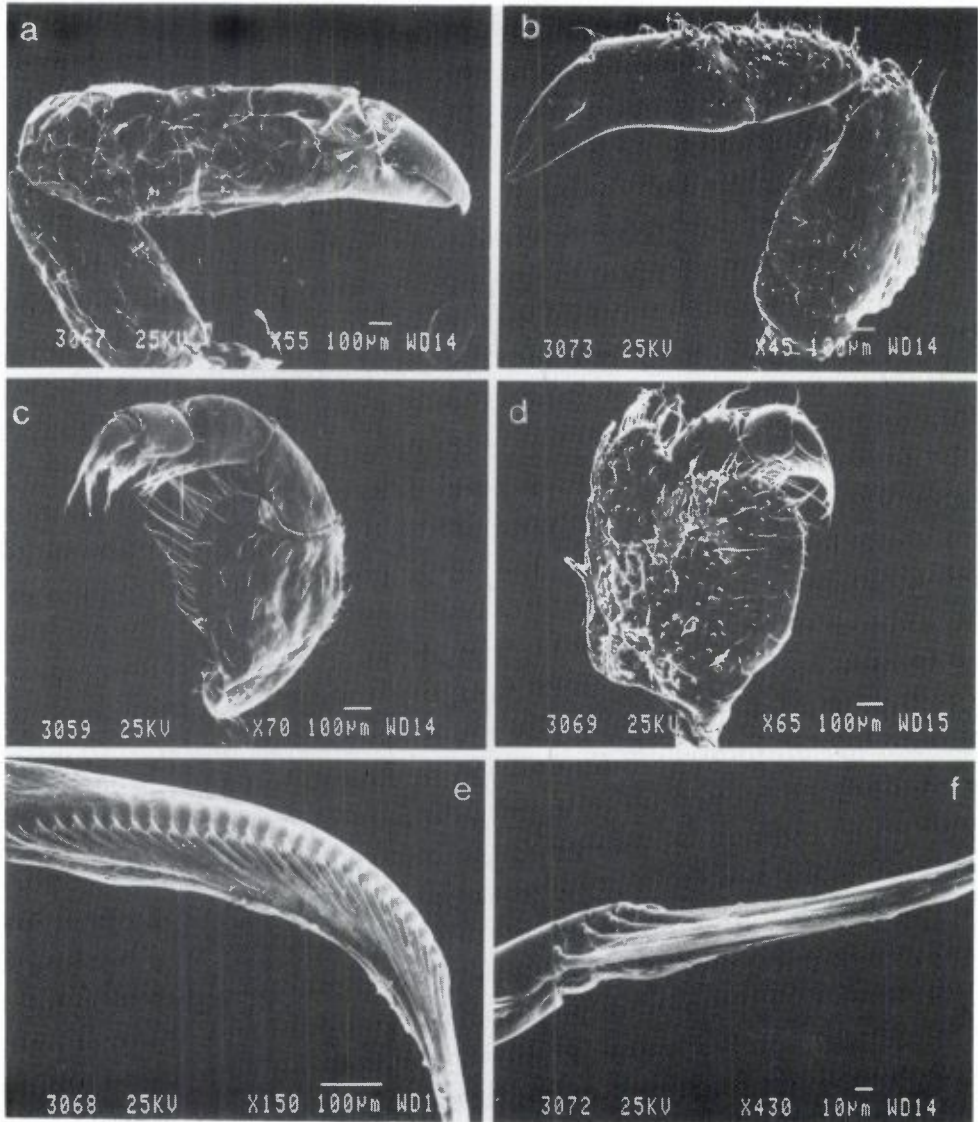


Figure 8. Feeding appendages of *Hapalocarcinus marsupialis* (a,c,e) and *Cryptochirus coraliodytes* (b,d,f). (a-b) Chela. (c-d) Third maxilliped. (e-f) Distal portion of exopod of second maxilliped. (see text for details).

plumose setae (Fig. 8f). Endopod of second maxilliped with long spoon-tipped serrate setae exteriorly on dactyl and propodus. Shafts of the spoon-shaped setae bear slender, tooth-like spines.

#### *Crab feeding behavior*

##### *H. marsupialis ("gall crab")*

The crabs use the second maxillipeds to strain light particles out of the passing water. Rapid beating episodes of the exopodites of the second and first maxilliped were observed with the left and right sides used alternately. The crabs utilize the sharply pointed chelipedal dactyls to pick small particles off the coral surface. The young crabs' feeding behavior differs from that of the adults in the frequency of exopodite "beating" and dactyl utilization for particle grasping, which was much higher in adults.

##### *C. coralliodytes ("Pit crab")*

The crab was observed collecting particles and mucus off the substrate either selectively with its chelipedal dactyls or by brushing the chelipedal setae against the substrate. The collected material was transferred to the buccal area, where the third maxillipeds brushed it off. After organic material had been removed, the residue was spat out as a round pellet, by a strong vertical current created by the crab.

## 4. Discussion

### *Potential particle types available for crab feeding*

Location and morphology of skeletal modifications apparently determine the available particle types for crab feeding through physical parameters governing particle transport by moving fluid. In a given flow velocity, massive particles (relatively large and dense particles) tend to be carried very close to the bed as part of the "bed load" (Jumars and Nowell, 1984; Allen, 1985). These are the particles rolling or saltating only a few grain diameters above the bed, mainly as a result of lift forces. In contrast, smaller particles whose density is closer to water density, can be raised far above the sea bed. These particles, called "suspension load", are suspended in water due to turbulence (Allen, 1985).

Pits in massive corals, the host corals of *C. coralliodytes*, are likely to be in the pathway of "bed load" particles owing to the coral hemispherical morphology (Abelson and Loya, in prep.). Accordingly, an important source of

nutritive particles for *C. coralliodytes* are the relatively large and dense particles of mineral grains encrusted with edible matter. On the other hand, the chance of galls, built on the tips of coral branches, encountering "bed load" particles is likely to be low because of the thin elongated shape of the coral branches (Abelson and Loya, in prep.). However, they encounter suspended particles which include most of the biological particles (Strathmann, 1971).

*Physical description of water path, particle behavior and particle trapping  
Gall*

The morphology of galls induces a flow-through by means of pressure gradients that can be explained in terms of energy conservation (Bernoulli's principle). According to Bernoulli's equation there is an inverted relation between flow velocity and pressure, where high velocity means low pressure and vice versa (Vogel, 1981; White, 1986). The gall slows down the current on its upstream side because of the disturbance to water path. However, the flow accelerates when passing over the widest part of the gall because of the reduced cross section for water path. The differences in flow velocity give rise to pressure gradients which induce flow from upstream side of the gall to the upper and downstream side (Fig. 2).

Our observations indicated that water passing through the gall's apertures in a given velocity slowed down, presumably due to the expanding cross section within the gall. As a result, availability of particles increases due to enhanced residence time of particles within the gall. Furthermore, the ability of the flow to carry particles is reduced, leading to settlement of the heavier particles within the gall. At the same time, particle settlement may be enhanced by reducing turbulence intensity. Reduction in turbulence intensity, to a degree of a laminar flow, was observed and may be explained as a result of flow collimation by the gall apertures, or due to the entrance of a water flow to the gall, which is a narrow duct with a low Reynolds number.

*Pit*

There are some examples of enhanced particle deposition in soft bottom pits and burrows in the literature (Nowell et al., 1984; DePatra and Levin, 1989). These structures are built by a variety of organisms and described as traps of prey organisms and feeding particles. Our results indicate that particle deposition is enhanced in pits as well as in the burrows located within the pits.

Two mechanisms of particle trapping by pits are assumed to take place: trapping of massive particles and trapping of particles with similar density to the water. Both mechanisms are conditioned by vortical flow creation within the pit. Because of the depression in the substratum there is more cross sectional area for the flow to fill. Consequently, the flow slows down as it flows over and into the pit. Flow deceleration leads to an adverse pressure gradient that increases the pressure in downstream direction. Above a certain threshold of pressure gradient, the boundary layer will separate off the wall corresponding to backflow formation and creation of a vortical flow over and within the pit. The creation of vortical flow depends on steepness of walls (pit) and flow velocity (White, 1986).

In the first trapping mechanism, massive particles, owing to inertia, are unable to follow curvilinear flow and tend to continue along a straight path settling on the pit surface as the fluid curves (Fig. 4). This mechanism, called inertial impaction (Fuchs, 1964; Rubenstein and Koehl, 1977), depends on Stokes number, where higher values of Stokes number means higher intensity of inertial deposition. Stokes number is a dimensionless ratio of the stop distance of a particle to the characteristic dimension of the system (Fuchs, 1964). Based on Stokes number, index of intensity of particle deposition by inertial impaction was described for fibers and pores (Rubenstein and Koehl, 1977). According to this index, increase in particle density or radius, as well as increase in flow velocity, would increase the intensity of inertial deposition. Inertial impaction is considered unimportant for liquid-borne particles (Spielman, 1977) and described to be of minor importance for most suspension feeders, since most biological particles are close to the density of water (LaBarbera, 1984). Nevertheless, as discussed earlier, pits in massive corals are within the path of high density mineral particles. Moreover, pits situated in a vertical plane are very abundant in the coral reef of Eilat, and for such pits gravitational deposition can not be a potential mechanism for particle supply. Taking into account these points, we suggest that inertial impaction is likely to play an important role in providing feeding particles to *C. coralliodytes*.

The second trapping mechanism involves nearly neutrally-buoyant particles. Tooby et al. (1977) proposed a mechanism by which such particles, which follow the streamlines nearly instantaneously, can be retained in the vortex and tend to concentrate in the upstream side of the vortex. After a while, these particles spiral slowly out of the vortex due to inertial forces. Butman et al. (1986) described particle trapping by sediment traps based on this mechanism. According to their description, the particles that spiral out of the vortex are those settled within the traps. Similarly, nearly neutrally-buoyant particles can be trapped by pits (Fig. 4).

### *Feeding mechanisms of the crabs*

#### *H. marsupialis* ("gall crabs")

Behavioral and morphological observations have shown that *H. marsupialis* is a facultatively active suspension feeder. Although it creates local, temporary currents within the gall, it relies on ambient currents to bring particulate food into the gall. The ability to create local currents enables the crab to trap particles that are suspended within the gall. This ability is important chiefly when dealing with biological particles.

Another mode of obtaining particulate food was observed when these crabs selectively collected deposited particles with their chellae. We assume that this mode is of greater importance in closed galls, where the pressure gradients between apertures and gall center are greater, causing deposition of greater amounts of particles (Fig. 5).

#### *C. coralliodytes* ("Pit crabs")

*C. coralliodytes* is a deposit feeder, feeding on detritus containing inedible particles encrusted with edible organic matter. The spoon-tipped setae are understood as scraping devices to remove surface-bound organic material from inedible particles (Miller, 1961; Robertson and Newell, 1982; Maitland, 1990). The spit action in *C. coralliodytes* can be explained as the way these crabs reject particle remains of poor nutritive value.

## 5. Conclusions

The commonly accepted premise that "gall crabs" are filter feeders was refuted by Kropp (1986) whose observations have shown "gall crabs" to be detritus and mucus feeders. We have found, based on the crab feeding behavior and feeding appendages morphology that *H. marsupialis* and *C. coralliodytes* differ in their feeding mechanisms. *H. marsupialis* was observed to rely mainly on filter feeding, while *C. coralliodytes* was found to be a deposit feeder. The two distinct feeding modes are likely to be tied very closely to the effects of skeletal modifications on ambient flow. Our results indicate that host skeletal modifications can be utilized as a particle trapping device by the crabs, in addition to their role as shelter. We suggest that studies concerned with feeding mechanisms of "gall crabs" should take into account the ambient flow characteristics and resultant particle behavior.

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