J. Mar. Biol. Ass. U.K. (2002), **82**, 583–588
Printed in the United Kingdom

Orientation of *Chelonibia patula* (Crustacea: Cirripedia) on the carapace of its crab host is determined by the feeding mechanism of the adult barnacles

Zohar Pasternak*‡, Avigdor Abelson† and Yair Achituv*

*Faculty of Life Sciences, Bar Ilan University, Ramat Gan 52900, Israel. †Institute for Nature Conservation Research,
Tel Aviv University, Tel Aviv 69978, Israel. ‡E-mail: zpast@yahoo.com

The location and orientation of epizooic barnacles on the surface of their host is crucially important to the survival and growth of the animal and is determined at the time of settlement by the cyprid larva. The present study examines the location and orientation of *Chelonibia patula* barnacles on the upper surface of the carapace of the crab *Portunus pelagicus* from the Mediterrannean coast of Israel. Cirral activity behaviour patterns, such as turning angles of the cirral fan, types of cirral motion, and beat duration were determined with respect to the angular deviation of the rostro-carinal axis (RCA) of the barnacles from the direction of the incoming flow. While small barnacles (up to 1 cm rostro-carinal length) perform normal feeding beats and turn the cirral fan towards the incoming flow at all angles up to 180°, larger barnacles (>1 cm rostro-carinal length) do not extend their cirri when oriented at RCA angles exceeding 120°. Nearly all the sampled barnacles are oriented on the carapace at RCA angles of no more than 120° with respect to the anterior margin of the host crab, which is the predominant direction of incoming flow and food. It is concluded that larval choice of orientation at settlement is determined according to the direction of the current and the anticipated food-gathering ability of the adult barnacle.

INTRODUCTION

Barnacles are sessile, filter-feeding crustaceans that attach to a variety of marine substrata, including whales, turtles, crabs and inanimate objects. In order to obtain food particles they spread their thoracic appendages to form a fan. The concave, cup-shaped cirral fan faces upstream toward the incoming flow, and after it has gathered food particles, the extended cirri withdraw into the mantle cavity within the shell for transfer of trapped particles to the mouth (Crisp & Southward, 1961). Barnacles have been found to reorient their cirral fan to face the coming water upstream (e.g. Trager et al., 1992). In order to ameliorate the efficiency of particle capture, settling barnacle larvae attach themselves to the substratum so the rostrum becomes directed toward the prevailing current, making the extended fans of the adult face the direction of the current (Ayling, 1976). Barnacles inhabiting whales and turtles are exposed to uni-directional currents due to the nature of the locomotion of the host, but those that live on crabs may experience currents coming from different directions, depending on their location on the body of the crab and on the movement direction of the crab.

The behaviour of epizooic cirripedes is hardly known, but some examples do exist: *Cryptolepas rhachianechi*, embedded in the skin of the California grey whale, *Eschrichtius robustus*, is attached to the surface of the whale with its rostral plates directed approximately toward the anterior end of the whale, and the cirral fan toward the water current (Kasuya & Rice, 1970). Achituv (1998) found in *C. rhachianechi* a difference in the behaviour of barnacles of different ages. Adult animals in still water and in different types of flow beat continuously in the rostro-carinal direction and do not turn the cirral fan in response to water flow direction. In contrast to adults, juvenile animals exposed to carino-rostral currents or to oscillating waves respond to changes in current direction by turning their cirri in the carinal direction. The ability to respond to water current direction by twisting the body is lost in the adult animals. *Coronula diadema*, however, also epizoic on whales, exhibits prolonged cirral extension in response to water flow (Crisp & Stubbings, 1957). *Balanus crenatus* is a free-living barnacle that is found also on crabs. Heath (1976) studied the orientation of *B. crenatus* on the carapace of the crab *Carcinus maenas*, where the barnacles are attached so the cirral net faces backwards. This pattern originates from the settling cyprids' habit of orienting themselves toward the water currents generated by respiratory currents that flow forward over the carapace of the host.

Barnacles of the genus *Chelonibia* occur on the carapace and appendages of pelagic crabs, as well as on sea-turtles and inanimate floating objects. The orientation of the turtle barnacle *C. testudinaria* on the shield of *Caretta caretta* was studied by Meischner (2001), who found that the barnacles settle on the shield of the turtle so that the rostrum faces the oncoming current. In contrast, however, Key et al. (1997) studied the orientation of *Chelonibia patula* on the carapace of the crab *Callinectes sapidus* from Beaufort, North Carolina, and found no preferred orientation. In the present study we examined the location and orientation of *Chelonibia patula* on the carapace of their crab host *Portunus pelagicus* from the Mediterrannean coast of Israel. In addition, various cirral activity behaviour patterns such as the turning angles of the cirral fan, types

Figure 1. A *Portunus pelagicus* crab from the Mediterranean coast of Israel, bearing *Chelonibia patula* barnacles on its carapace.

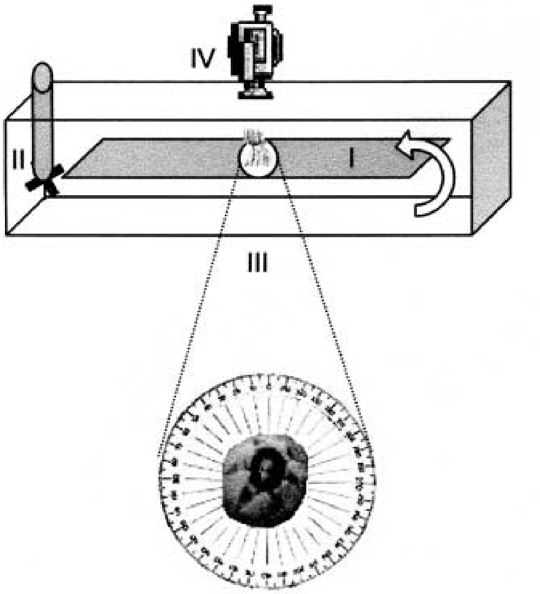

Figure 2. Outline of the flow tank, including (I) platform; (II) propeller; (III) protractor and barnacle (also shown enlarged); and (IV) video camera. Arrow indicates water direction.

of cirral motion, and beat duration were determined and correlated with the rostro-carinal axis (RCA) angle of the barnacles to the oncoming flow.

MATERIALS AND METHODS

Animals

Specimens of the pelagic crab *Portunus pelagicus* bearing *Chelonibia patula* barnacles on their carapace (Figure 1) were obtained from fishermen and fishmongers along the Mediterranean coast of Israel. Crabs with live barnacles were transferred to the laboratory in seawater. Barnacles were measured for rostro-carinal (RC) length and subsequently divided into two size groups, <1 cm and >1 cm, which we referred to as small and large, respectively. All specimens were carefully removed from their host by cutting the host carapace around them, and kept in running seawater at room temperature.

Cirral behaviour

All experiments took place within a week after collection of the animals. The cirral activity experiments were conducted in a modification of the Vogel & LaBarbera (1978) recirculating flow tank, as described by Trager et al. (1990; Figure 2). Unidirectional flow was generated using a motor-driven propeller immersed in the flow tank. The barnacles were attached to a small, rotating, circular platform that was placed in the flow tank (Figure 2). A 360° protractor was attached to the platform, showing the position of the RCA of the barnacle in relation to the direction of the flow. At the beginning of each experiment, the platform was placed at 0°, i.e. the RCA was parallel to the flow direction with flow from rostrum to carina. Flow velocity was $6\,\mathrm{cm\,s^{-1}}$; this flow velocity was chosen since it is the speed in which these barnacles are most active. Flow velocity was determined by videotaping the movement of ten free-floating, neutrally-buoyant particles in the water ~0.5 cm above the barnacles, and analysing the speed of the particles. White fibre-optic light was used for illumination. The behaviour of the animals was recorded using a Sony CCD V700E Hi8 PAL system camcorder with a close-up lens, positioned above the tank. The platform was rotated periodically, in order to examine the chosen behavioural parameters at different angles of RCA deviation from the flow direction. At each angle, at least ten small and ten large animals were observed, each specimen for at least three minutes. Videotapes were downloaded into a computer and analysed with frame-by-frame tracing using ATI Video Editor 6.2.

Location and orientation

The orientation of the RCA of each barnacle on the carapace of the crab was determined using a 360° protractor, with 0° being the direction of the anterior end of the host. Location on the host carapace was determined by generating a 'carapace grid': the X-axis being the connecting line between the tips of the two prominent anterolateral carapace spines, and the Y-axis being the median line, i.e. the perpendicular line running from the median anterior notch on the face of the crab to the posterior end of the carapace at the border with the first abdominal segment (Figure 4). Location measurements were standardized for *P. pelagicus* mean body size, and density distribution diagrams were calculated for barnacle location on the rows and columns of the grid.

Host behaviour

In order to assess the directions of water flow to which *C. patula* are exposed, the behaviour of three adult *Portunus pelagicus* crabs was examined in a recirculating flow tank. The testing area of the flow tank was 25×100 cm, which allowed free movement for the crabs. The bottom of the tank was covered with 10 cm of sand, in which the crabs could burrow. Each crab was observed for one hour in

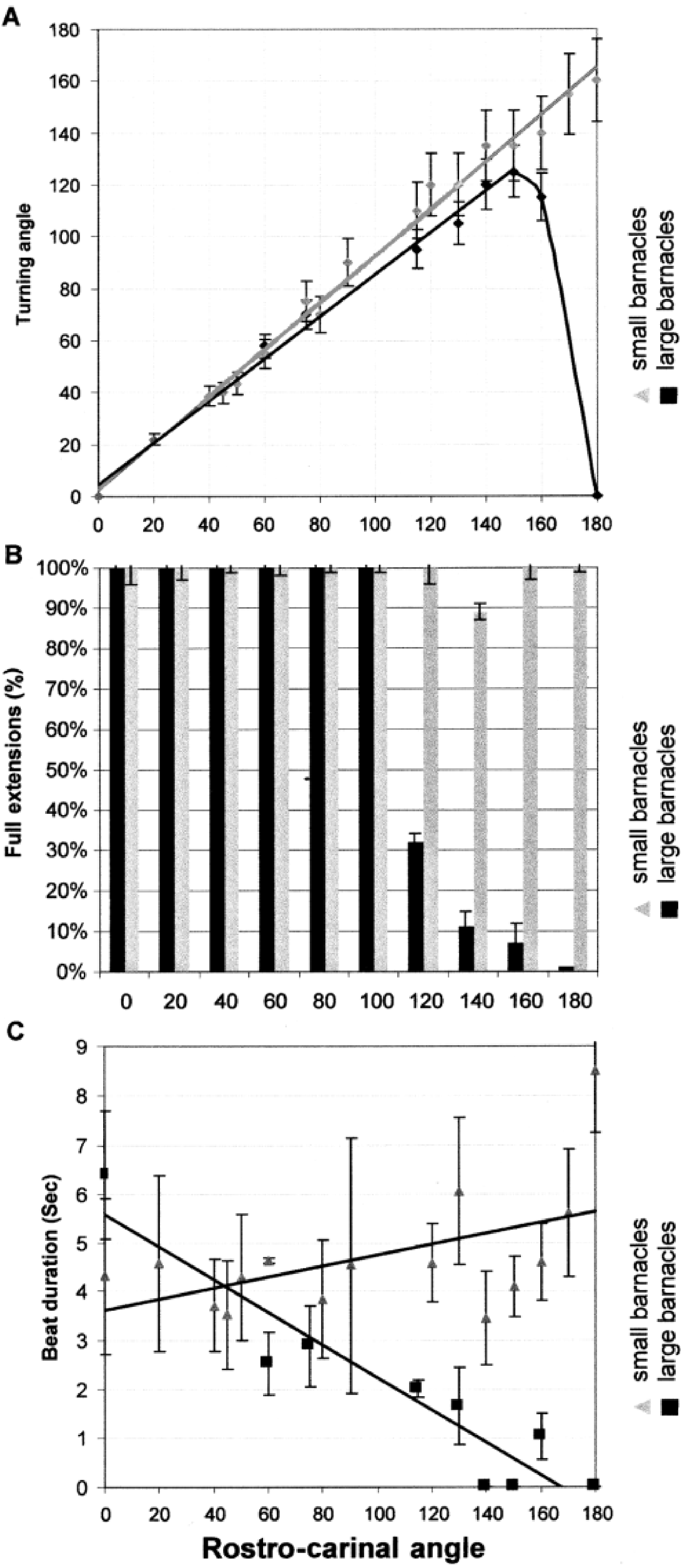

Figure 3. Behavioural parameters of cirral beating (mean ±1 standard deviation) in large (black) and small (grey) *Chelonibia patula*: (A) cirral fan turning angles at different rostro-carinal axis (RCA) angles to the flow (at RCA=0°, the RCA is parallel to the flow and the rostrum is facing upstream). Linear regressions are given for small barnacles at 0°–180° and for large barnacles at 0°–150°; (B) percentage of normal beats (beats comprising full cirral extension) out of the total number of beats at different RCA angles to the flow; (C) beat duration at different RCA angles to the flow.

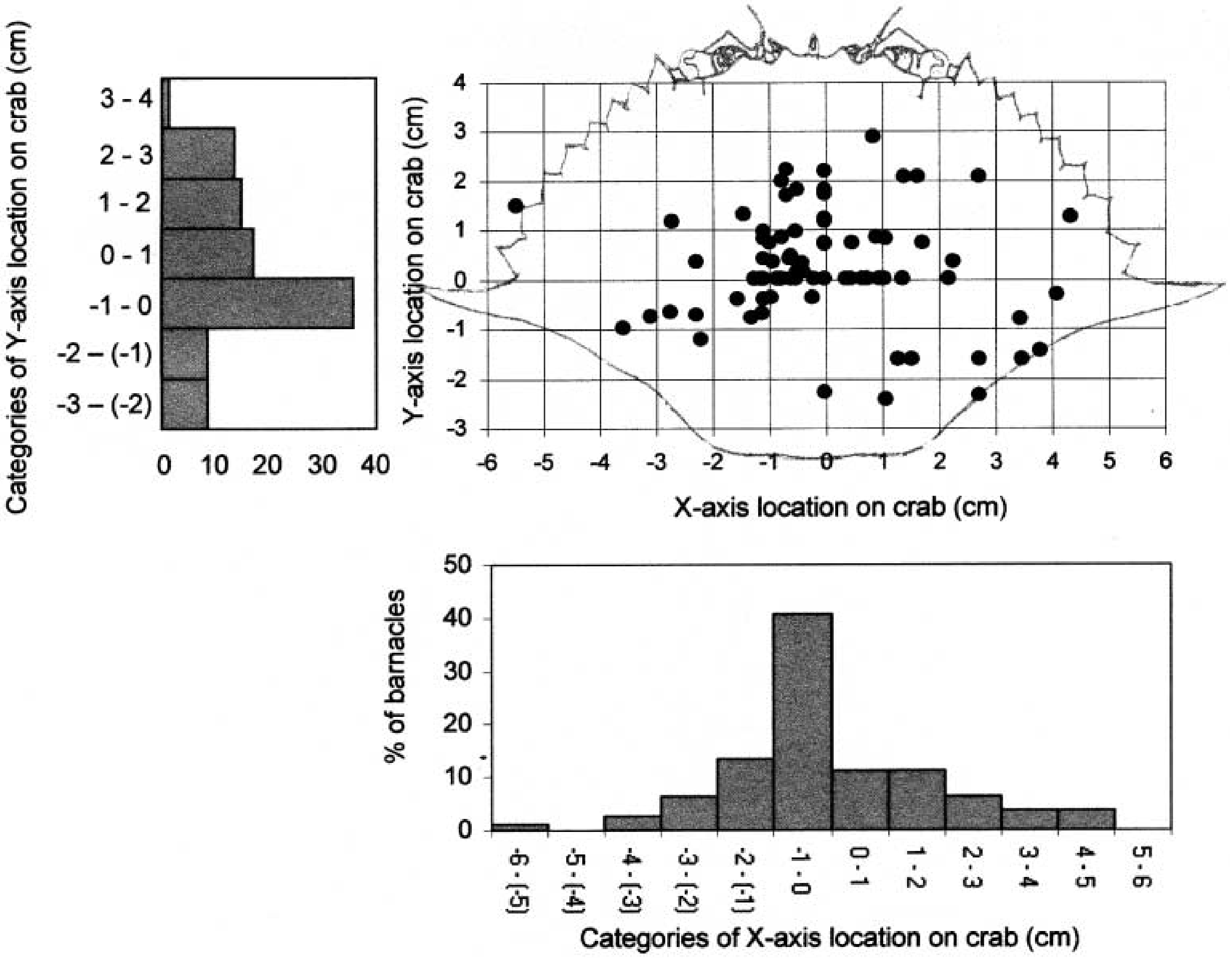

Figure 4. Location of barnacles (N=81) on carapace of crab hosts, based on cumulative data from 26 crabs. 'Carapace grid' is generated so that the X-axis is the connecting line between the tips of the two prominent anterolateral carapace spines and the Y-axis is the median line running from the median anterior notch on the crab's face to the posterior end at the first abdominal segment. Location measurements are standardized for *Portunus pelagicus* mean body size and density distribution diagrams are calculated for rows and columns on the carapace grid. Density in histograms is presented as percentages.

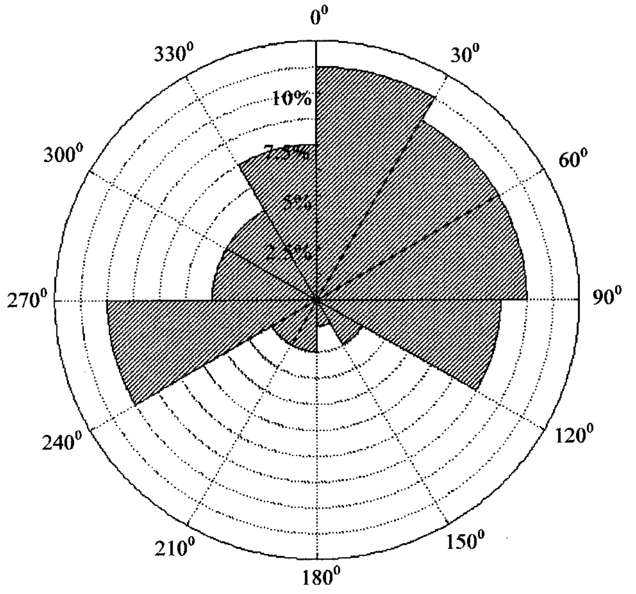

Figure 5. Density distribution (N=81) of barnacle orientation on carapace of crab hosts (N=26). The RCA angle of 0° is parallel to the median line of the carapace grid, with the rostrum at the direction of the anterior end of the host.

still water and one hour in a flow velocity of 5 cm s^{-1}. Crab behaviour was divided into three categories: swimming, walking, and immobile, and the percentages of time spent at each flow direction (=angle) was recorded for each behavioural category. The angles of the crabs were determined as described above, with accordance to the direction of the flow, e.g. 0° denoting that the water is flowing from the anterior end of the crab to the posterior end (either when it is moving forward or when it is static and facing directly upstream).

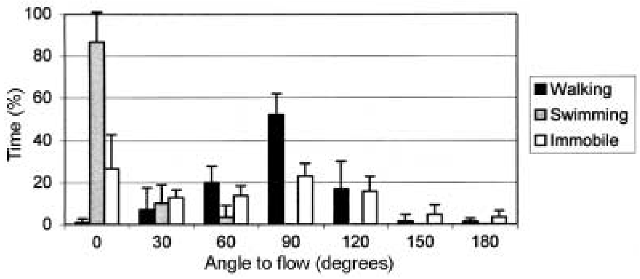

Figure 6. Time-percentage distribution of directions of water flow over the carapace of *Portunus pelagicus* crabs (N=3) at three behavioural categories: immobile (white), swimming (grey) and walking (black).

RESULTS

Cirral activity patterns

Figure 3 presents the behavioural responses of small and large *Chelonibia patula* to changes in current angle. Small barnacles exhibit a strikingly different cirral beat behaviour than that of large barnacles. Those differences were characterized using three parameters: turning angle of the cirral fan, percentage of beats with full extension of the cirral net, and beat duration.

When the RCA of the barnacle is turned away from the flow, the animals respond by turning the cirral fan back to an upstream-facing position (Figure 3A). This is a linear correlation for small barnacles at all turning angles, up to 180° ($r^2=0.99$, $P<0.05$), and for large ones at turning angles of up to 150° ($r^2=0.99$, $P<0.05$), when the RCA of the large barnacles is positioned at an angle greater than 160° to the incoming flow, however, no turning motion occurs and they continue to beat in the direction of the rostrum.

Cirral motion pattern differs between small and large barnacles at different RCA angles (Figure 3B). While small animals fully extend their cirral nets at almost every beat at all RCA angles, large barnacles do so only at RCA angles of less than 120°. Beyond 120°, the animals cease full cirral extension almost completely, and most of their activity thereafter comprises small testing beats.

Patterns of beat duration of small and large barnacles (Figure 3C) reveal that as the RCA angle of small ones is turned further from the incoming flow direction, the beat duration seems to increase, albeit not significantly ($r^2=0.26$, $P>0.05$). Contrarily, when the RCA of the large barnacles is turned away from the flow direction, the beat duration is linearly and significantly decreased ($r^2=0.88$, $P<0.05$).

Orientation and location

Location: barnacles were placed mostly on the central region of the carapace of the host. Over 50% of all barnacles were located between −1 cm and 1 cm along the X-axis, and over 50% were located between −1 cm and 1 cm along the Y-axis (Figure 4).

Orientation: 91% of the barnacles (N=81), both small and large, were oriented at RCA angles of no more than 120° with respect to the anterior margin of the host (Figure 5). The mean (±1 SD) deviation angle of the RCA of these barnacles from the anterior margin of the host was 55° ±32°.

Host behaviour

Figure 6 presents the prevailing directions of flow over the carapace of *Portunus pelagicus*. The percentages of time spent performing each of the three behavioural categories differed significantly between crabs, and between still water and flow (analysis of variance [ANOVA] test, $P>0.5$). However, the angles toward the flow direction at which they performed each activity did not differ significantly between the crabs or between the still water and flow experiments ($P<0.05$), and the results were therefore pooled. While either immobile, walking or swimming, the crabs spent well over 90% of their time directed so that flow passed their carapace at angles between 0° and 120°.

DISCUSSION

Based on the flow tank experiments, it is concluded that small *Chelonibia patula* extend their cirral fan so that it is oriented towards the incoming flow, regardless of the direction of the flow with respect to the RCA. Since the small barnacles turn at almost every beat and do not perform testing beats, nearly all of their beats are normal beats, i.e. include a full extension of the cirral fan—a trait which improves the efficiency of food intake. The small increase in beat duration which happens when the cirral fan turns at larger angles may be attributed to a requirement for more energy when turning at larger angles, so the animal needs to collect more food particles in order to compensate and make the beat energetically profitable.

Since, contrary to the small barnacles, the large ones' cirral-fan turning is angle-dependent, they use an energy-cheap mechanism for sensing the flow direction, i.e. testing beats (see also Anderson & Southward, 1987). Indeed, the results show that when the angle between the flow and the RCA is between 0° and 100°, all the beats are normal, but when the angle increases, the percentage of normal beats drops rapidly and most of the activity of the barnacle consists of testing beats. This may be due either to a physical inability of the large barnacles to rotate their cirral fans at angles greater than 160°, or to an energetic strategy stating that wide-angle cirral rotations are so energetically expensive for the large animals, that the food particles gathered cannot possibly make the rotation worthwhile. Since we have observed some large barnacles performing 180° turns during copulation, we conclude that their turning strategy derives from energetic considerations rather than anatomical limitations (see also Achituv, 1998). Moreover, we can deduce that the energetic 'limit angle' for normal beating and food gathering in the large barnacles is around 120°, based on the observation that at greater RCA angles the barnacles hardly ever perform normal beats.

An alternative explanation for the differences in beating behaviour between small and large barnacles may involve the risk of predation that barnacles face every time the cirral fan is extended outside the protective shell. Small barnacles have a more pressing need for energy in order to grow and reach maturity as quickly as possible, and this need may result in a more 'adventurous' strategy, keeping the cirri outside for longer periods of time despite the increased risk of predation. The large barnacles, on the other hand, whose need for food uptake is less critical, may be able to decrease the time of cirral extension in order to reduce the risk of predation.

The orientation of barnacles on the crab carapace is probably designed to maximize their feeding capabilities, with the cirral net oriented perpendicular to the direction of the incoming flow (Ross & Jackson, 1972). The behavioural results suggest that the 'acceptable' range of deviation angle of the RCA of the large barnacles from the medio-anterior end of the crab is no more than 120°, and therefore it is not surprising that *C. patula* specimens were found to be oriented on the carapace at a maximal deviation angle of 120° to either side of the medio-anterior end of the host. The orientation of barnacles is in most cases determined at the larval settlement stage (Anderson, 1994), and there are two possibilities to account for the non-random orientation in *C. patula*: (1) the cyprids orient at random, metamorphose and grow to become small barnacles that can feed at all orientation angles (Figure 3), whereas later, only the large animals that happen to be 'correctly' angled survive, while the others die and fall off the carapace; (2) the cyprids choose their orientation according to the dominant flow direction at the time of settlement (Forbes et al., 1971). Our data support the hypothesis of larval angle selection, since we find that nearly all small barnacles, including ones as small as 1 mm RC length, are oriented exclusively at RCA deviation angles of no more than 120° with respect to the medio-anterior margin of the host.

Ross & Jackson (1972) found, based on qualitative observations, that *C. patula* barnacles fouling the carapace of *Callinectes sapidus* are attached with their RCA oriented towards the lateral ends of the crab. Their suggested explanation was that since *C. sapidus* spends a large portion of its time walking sideways, the dominant flow direction over its carapace is lateral (right-to-left or left-to-right), and it would be beneficial for a barnacle to be oriented towards those directions. Our observations indicate that on *Portunus pelagicus*, the barnacles are oriented mainly towards currents coming from the anterior end and from the right lateral and left lateral ends of the carapace (90° and 270°, respectively—see Figure 4). Our behavioural observations of *P. pelagicus* confirm that the dominant flow directions over its carapace are along the anterior–posterior axis when the crab is swimming, and from the lateral axes when the crab is walking.

Key et al. (1997) found significant location preference for *Chelonibia patula* barnacles on the carapace of *Callinectes sapidus*; the density of barnacles was higher on the lateral carapace sectors than on the medial sectors. They suggested that this distribution pattern is due to the burrowing activity of *C. sapidus* (e.g. Wilson et al., 1987), which results in the abrasion of barnacles and may have a greater impact on the topographically elevated medial sectors. Contrarily, in the present study we found that barnacles are concentrated on the central carapace region of *P. pelagicus*, a related crab species that also burrows in the sediment. As with orientation selection, we propose that location selection of the barnacles on the carapace is due to larval settlement choice rather than consequent abrasion of the adult animals: the cyprids not only choose their orientation of settlement but also their location, being attracted to the elevated central region since it offers greater net flow of water (see also Crisp & Barnes, 1954; Ayling, 1976; Heath, 1976).

The authors would like to thank Mr Y. Chanin of the Fisheries Department of the Israel Ministry of Agriculture for collection of crabs, and Ms N. Shoshani for her tremendous assistance in obtaining the data required for this study. This work is part of a dissertation of Z. Pasternak towards his PhD degree.

REFERENCES

Achituv, Y., 1998. Cirral activity in the whale barnacle *Cryptolepas rhachianechi*. *Journal of the Marine Biological Association of the United Kingdom*, **78**, 1203–1213.

Anderson, D.T., 1994. *Barnacles: structure, function, development and evolution*. London: Chapman & Hall.

Anderson, D.T. & Southward, A.J., 1987. Cirral activity of barnacles. In *Barnacle biology* (ed. A.J. Southward), pp. 135–174. Rotterdam: A.A. Balkema.

Ayling, A.M., 1976. The strategy of orientation in the barnacle *Balanus trigonus*. *Marine Biology*, **36**, 335–342.

Crisp, D.J. & Barnes, H., 1954. The orientation and distribution of barnacles at settlement with particular reference to surface contour. *Journal of Animal Ecology*, **23**, 142–162.

Crisp, D.J. & Southward, A.J., 1961. Different types of cirral activity of barnacles. *Philosophical Transactions of the Royal Society* B, **243**, 271–308.

Crisp, D.J. & Stubbings, H.G., 1957. The orientation of barnacles to water currents. *Journal of Animal Ecology*, **26**, 179–196.

Forbes, L., Seward, M.J.B. & Crisp, D.J, 1971. Orientation to light and the shading response in barnacles. In *Proceedings of the Fourth European Marine Biology Symposium* (ed. D.J. Crisp). Cambridge: Cambridge University Press.

Heath, D.J., 1976. The distribution and orientation of epizoic barnacles on crabs. *Zoological Journal of the Linnean Society of London*, **59**, 59–67.

Kasuya, T. & Rice, D.W., 1970. Notes on baleen plates and on arrangement of parasitic barnacles of gray whale. *Scientific Reports of the Whale Research Institute*, **22**, 39–43.

Key, N.M., Volpe, J.W., Jeffries, W.B. & Voris, H.K., 1997. Barnacle fouling of the blue crab *Callinectes sapidus* at Beaufort, North Carolina. *Journal of Crustacean Biology*, **17**, 424–439.

Meischner, D., 2001. Seepocken auf einer Meeres Schidkröte, ein ökologisches Idyll. *Natur und Museum*, **131**, 1–7.

Ross, A. & Jackson, C.G., 1972. Barnacle fouling of the ornate diamondback terrapin *Malaclemys terrapin macrospilota*. *Crustaceana*, **22**, 203–205.

Trager, G.C., Coughlin, D., Genin, A., Achituv, Y. & Gangopadahyay, A., 1992. Foraging to the rhythm of ocean waves: porcelain crabs and barnacles synchronize feeding motions with oscillations. *Journal of Experimental Marine Biology and Ecology*, **164**, 73–86.

Trager, G.C., Hwang, J.S. & Strickler, J.R., 1990. Barnacle suspension-feeding in variable flow. *Marine Biology*, **105**, 117–127.

Vogel, S. & LaBarbera, M., 1978. Simple flow tank for research and teaching. *BioScience*, **28**, 638–643.

Wilson, K.A., Heck, K.L. & Able, K.W., 1987. Juvenile blue crab, *Callinectes sapidus*, survival: an evaluation of eelgrass, *Zostera marina*, as refuge. *Fisheries Bulletin of the United States*, **85**, 53–58.

Submitted 24 December 2001. Accepted 12 May 2002.