EPIBIONTS OF SYMPATRIC SPECIES OF *CANCER* CRABS IN BARKLEY SOUND, BRITISH COLUMBIA

Iain J. McGaw

Department of Biological Sciences, University of Nevada, 4505 Maryland Parkway,
Las Vegas, Nevada 89154-4004, USA. Tel. 702 895 1285, Fax 702 895 3956,
(imcgaw@ccmail.nevada.edu); and Bamfield Marine Station, Bamfield, British Columbia, Canada VOR 1BO

A B S T R A C T

The diversity, abundance and spatial distribution of macro-epibionts colonizing the graceful crab, *Cancer gracilis*, the red rock crab, *Cancer productus*, and the Dungeness crab *Cancer magister* were examined. These three crab species were common in Barkley Sound, British Columbia, occurring sympatrically across much of their range. Twenty nine epibiont species, representing ten different phyla were found. Thirty three percent of *Cancer gracilis*, 49% of *Cancer magister* and 68% of *Cancer productus* possessed one or more epibiont species. *Cancer gracilis* was the least speciose, while *Cancer productus* exhibited the greatest diversity of epibiont species. Male crabs were larger than females and had a greater species richness and diversity of epibionts. Epibionts were largely absent on juvenile crabs; in adult crabs, occurrence increased with crab size. Barnacles were the most common epibiont; the majority were *Balanus crenatus*, which predominated on the dorsal surfaces of the cephalothorax of each crab species. Green, red and brown algae were also common, the majority of which (>80%) were found on the antennae of the crabs. Tube-dwelling polychaete worms were less abundant, showing a preference for the ventral surfaces of the crabs. Hydrozoan colonies were found on only 7% of all the crabs examined, mostly settling on the ventral surfaces and limbs. Bryozoans were only found on *Cancer productus* and *Cancer magister*. The majority were the encrusting *Membranipora membranacea*. Unlike the above taxa, bryozoans showed no clear preference for a specific area of the carapace. Organisms in the phyla Urochordata, Mollusca and Porifera were only found on a few individual *Cancer magister* and *Cancer productus*. The distribution of each epibiont species is discussed in relation to larval settlement patterns and ecological, morphological and behavioural differences among the three host species.

INTRODUCTION

In coastal marine environments, sessile benthic organisms often compete for limited space (Connell and Keough, 1985). In areas where competition is high, living material such as algae and the hard bodies of other organisms may become sites for newly settling larvae (Seed, 1985; Wahl, 1989). The exoskeletons of decapod crustaceans are a well-known surface for epibiont settlement (Heath, 1976; Abello et al., 1990; Abello and Macpherson, 1992; Giri and Wicksten, 1992; Shields, 1992; Gili et al., 1993; Negreiros-Fransozo et al., 1995; Abello and Corbera, 1996; Becker, 1996; Dick et al., 1998; Key et al., 1997, 1999). Since many of the epibiont species are suspension feeders, this settlement location is advantageous because the movement of the crabs and their feeding activities will guarantee the arrival of food (Jorgensen, 1966; Heath, 1976). The epibionts may also be protected by the activities of the crustacean host (Key et al., 1997). Nevertheless, crustaceans moult the carapace, thus this temporary surface is only suitable for organisms with a short life cycle and/or a rapid growth phase (Gili et al., 1993). Epibionts may also be damaged by the host as it moves around its habitat or buries in the sediment (Negreiros-Fransozo et al., 1995).

Epibionts may impart benefits and costs to their host. Crabs in the family Majidae use epibionts for camouflage. This occurs not only due to passive settlement of organisms, but also by active masking behaviour (Parapar et al., 1997). In smaller crustaceans the added weight of heavy fouling can be metabolically costly (Overstreet, 1983; Dick et al., 1998) and increase predation risk (Willey et al., 1990, Key et al., 1997).

Three host species of crabs were examined for external epibionts: the graceful crab, *Cancer gracilis* (Dana, 1852), the red rock crab, *Cancer productus* (Randall, 1839), and the Dungeness crab, *Cancer magister* (Dana, 1853). All three crab species occur commonly in Barkley Sound, British Columbia. Although the habitat of each species differs, there is an overlap in their distribution, such that they co-occur in many areas (Orensanz and Galluci, 1988).

Epibiont characteristics can give important data on growth, moulting, and behaviour of the host (Botton and Ropes, 1988; Abello et al., 1990; Dick et al., 1998). Because *Cancer magister* and *Cancer productus* are commercially important and data for commercial species is limited (Key et al., 1997; Dick et al., 1998) the present study was undertaken to 1) survey the species of non-parasitic macro-epibionts, 2) describe their prevalence and 3) determine the spatial distribution of each epibiont species on the three species of crab.

MATERIAL AND METHODS

Male and female graceful crabs, *Cancer gracilis*, Dungeness crabs, *Cancer magister* and red rock crabs, *Cancer productus*, were collected at various locations in Barkley Sound, British Columbia (Fig. 1). Collections were made during April through September, 1998 to 2004. The crabs were collected using baited net traps (100 cm diameter × 25 cm deep) set at depths ranging between 5 to 50 m, with most trapping between 8–12 m. In addition, crabs were collected in the intertidal and shallow subtidal zone by hand.

The body was divided into sections (Figure 2, modified from Gili, et al., 1993). The dorsal surface of the carapace was divided into 3 areas: the anterior cephalothorax, which was defined as the portion anterior to the widest area of the cephalothorax and the posterior area behind and a third area which encompassed the eyes and antennae. The ventral surface of the
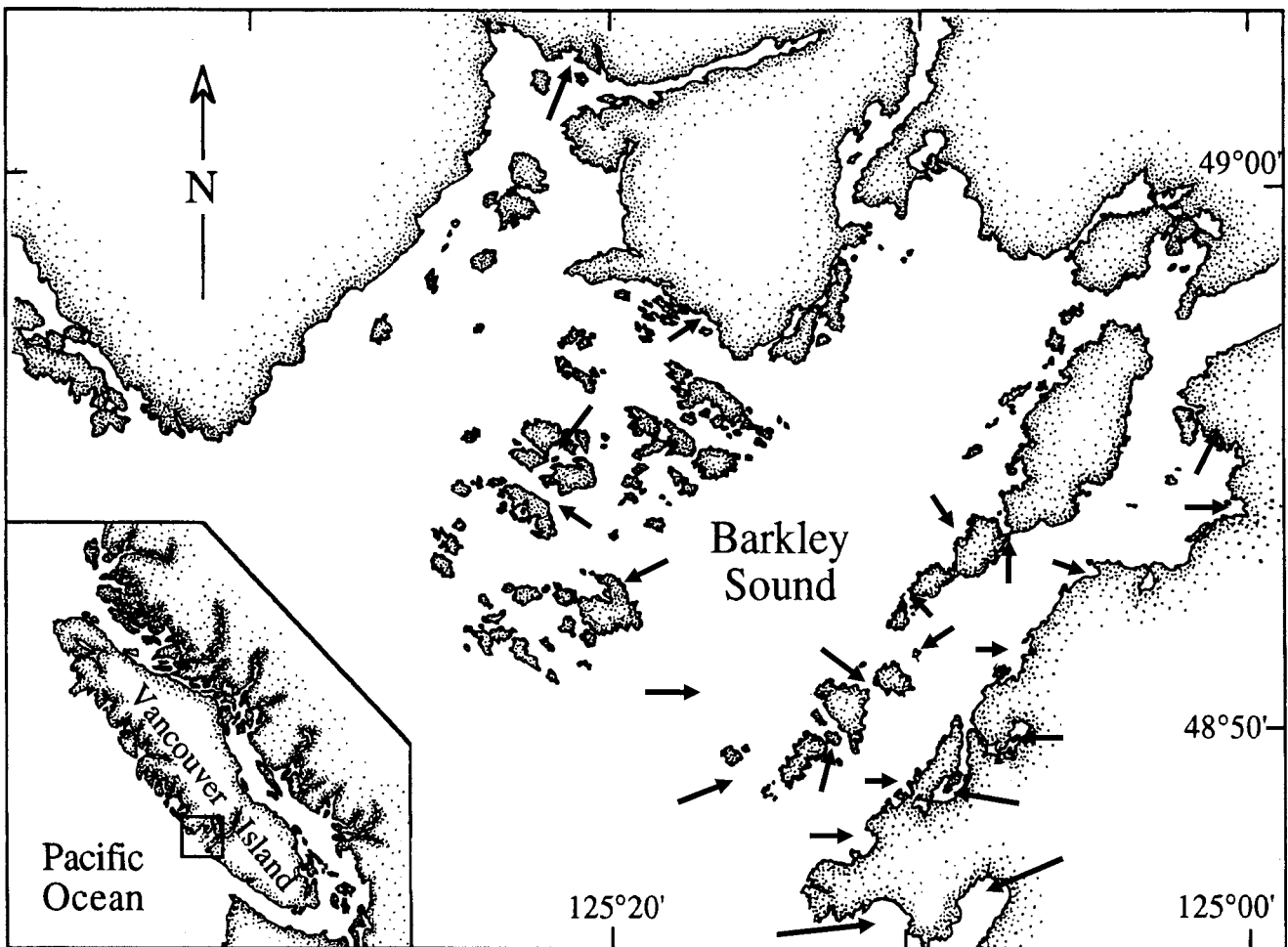
Fig. 1. Map of Barkley Sound, British Columbia showing areas (arrows) where crabs were collected.

body was also divided into three areas. The first area included the underside of the carapace, thorax, abdomen and palps. The legs, and the chelae comprised the second and third areas. The designated areas represented surfaces that would most often come into contact with sediment, or areas that could be groomed by the crabs (McGaw et al., 1999; McGaw 2005). The number of live or dead individuals of each macro-epibiont taxa were recorded on each of the areas of carapace. For colonial organisms, the percentage cover was estimated. Crab size was measured across the width of the carapace, which was the widest distance between the anterolateral spines. Sex and missing appendages were also recorded. The influence of seasonality, environmental factors or habitat structure on epibiont settlement was not investigated.

Size differences between crabs with and without epibionts were examined using Mann-Whitney rank sum tests (P < 0.01). The relationship between epibiont species and location on the carapace was investigated using Pearson chi-square tests (P < 0.01).

RESULTS

Size Range

A total of 553 *Cancer gracilis* were collected, of which 171 (30.8%) were female. *Cancer gracilis* ranged in size from 27 mm to 126 mm with a mean size of 86.4 mm ± 18.1 mm (SD). One hundred and fifty three crabs (32.7%) had one or more species of epibiont growing on the carapace. Of the total number, 59 (10.5%) *Cancer gracilis* had one or both chelae missing. Nine hundred and fifty nine *Cancer magister* were collected, of which 364 (38%) were females. *Cancer*

magister ranged in size from 27 mm to 202 mm with a mean size of 151.4 mm ± 22.3 mm. Of these, 465 (48.5%) possessed one or more species of epibiont. Sixty nine *Cancer magister* (7.2%) had missing chelae. A total of 1227 *Cancer productus* were collected, of which 259 (21.1%) were females. *Cancer productus* ranged in size from 20 mm to 184 mm with a mean size of 138 mm ± 26.3 mm. *Cancer productus* exhibited the highest prevalence of epibionts, with 833 (67.8%) infested hosts. One hundred and nineteen *Cancer productus* (9.7%) had one or both chelae missing.

The size of each host species with epibionts was significantly greater than those without epibionts (Table 1). Epibionts were not found on the smallest size classes of crab (<50 mm) and were rarely found on crabs that were not sexually mature (Fig. 3a–c). Female crabs were significantly smaller (Table 1) and did not reach the larger size classes of their male counterparts (Fig. 3a–c). There was no clear pattern among the host species with regard to the percentage of male and female crabs possessing epibionts.

Epibiont Species

A variety of epibionts were found on each crab species (Table 2). *Cancer gracilis* had the lowest diversity of epibiont species, while *Cancer productus* had the greatest
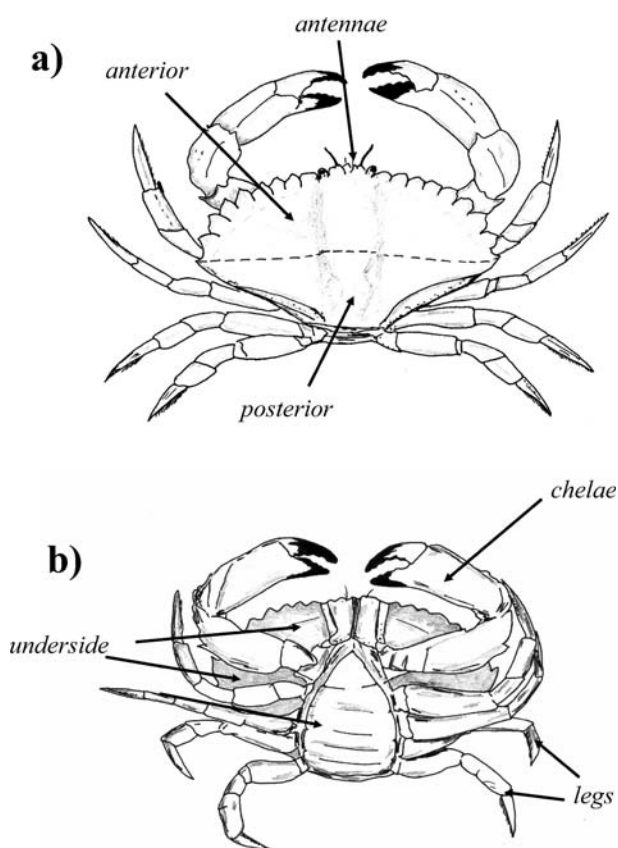
Fig. 2. Divisions of the carapace assigned to study settlement of epibionts: a) dorsal surface, b) ventral surface.

diversity of epibionts. For each species, male crabs had a greater species richness and diversity of epibionts compared with females. Both male and female crabs showed a high community dominance index (CDI). The most common epibionts were barnacles, over 90% of which were *Balanus crenatus* (Brugiere, 1789). Algae were also a dominant epibiont. Green algae (primarily *Enteromorpha*), predominated on *Cancer gracilis* and *Cancer magister*, whereas various genera of red algae were the dominant seaweed phylum on *Cancer productus*. A number of the larger seaweed specimens were identified to the level of genus (Table 2). However, in most cases, due to their small size, seaweeds could only be identified to the level of phylum. Polychaete worms were present on both *Cancer magister* and *Cancer productus*. In *Cancer productus*, the calcareous serpulid and spirorbid tube worms were the most abundant. In *Cancer magister*, the predominant species was the tube-dwelling worm, *Dipolydora socialis* (Schmarda, 1861). Only a few of these worms were found on the other two crab species (Table 2). Bryozoans were found on *Cancer magister* and *Cancer productus*, the majority of which were the encrusting bryozoan *Membranipora membranacea* (Linnaeus, 1767). Hydrozoans were found in lesser numbers on each crab species. The most common species was *Sertularella turgida* (Trask, 1857), which formed dense mats on each host species. The hydrozoan *Obelia* spp. (Pallas, 1766) was rare and only found on two *Cancer productus*. Organisms in the phyla, Urochordata, Mollusca

and Porifera were found on a few individual *Cancer magister* and *Cancer productus* (Table 2).

Colonization Areas

Statistical analysis was performed by recording the presence of an epibiont within a designated area, independent of the number of individuals. This was considered to be more valid than using number of individuals per section of the carapace. The colonizable surface area of each section was not equal, there was considerable variation in the size range of crabs and the presence of a larger individual epibiont would reduce available space for other individuals. Since the sex ratio of each species was skewed towards males, which also reached a larger body size, the crabs were not separated by sex.

Each epibiont species colonized specific areas of the crab carapace in a non-random pattern (Pearson Chi-Square, $P < 0.001$) and these areas were consistent across each of the three host species (Table 3a–c). Barnacles were most abundant on the dorsal surface of the cephalothorax and the chelae. There appeared to be a preference for areas with surface irregularities such as the grooves along the edges of the gastric and cardiac regions, but this was not quantitatively examined (Fig. 4a). They were less abundant on the underside and legs. No barnacles were found on the eyestalks or antennae. In contrast, algal species were predominately (>80%) found growing on the antennae of each species of crab (Fig. 4b, c). Green algae occasionally colonized the anterior edge of the cephalothorax and the upper surfaces of the chelae and legs. However, red and brown algae were almost always (>90%) found on the antennae.

Polychaete worms also exhibited preference for specific areas of the carapace (Chi-Square $P < 0.001$). *Dipolydora socialis* was only found on the underside of the crabs (Table 3a–c). On *Cancer productus* the majority of polychaetes also colonized the underside of the body (73.3%) and the ventral surface of the chelae (14.5%). Only a few spirorbid and serpulid worms were found on the anterior surface of the carapace, with a small individual growing on the antenna of one *Cancer productus* (Table 3c).

On each crab species, the greatest percentage of hydrozoans, as well as the larger sized colonies, were found on the ventral surfaces of the carapace (38% to 100%; Table 3a–c). Hydrozoan species were absent from the dorsal surface of the cephalothorax. Several smaller colonies were found on the antennae of *Cancer magister* and *Cancer productus* (Table 3b,c). Hydrozoan colonies were relatively common on the legs (14.7%) and chelae (29.4%) of *Cancer magister*, whereas they were absent or infrequently found in these areas on *Cancer gracilis* and *Cancer productus*.

In contrast to the other epibiont species, Bryozoa exhibited no common pattern of distribution among the crab species. On *Cancer magister*, most bryozoans (76.9%) were found as small colonies (5 mm^2 to 2 cm^2) on the legs (Table 3b). On *Cancer productus* (Table 3c), the majority of bryozoans were found on the ventral surface (72%). These colonies were larger (1 cm–5 cm^2) than those found on *Cancer magister*. Bryozoans also colonized the anterior surface of the *Cancer productus* carapace fairly frequently

Table 1. Size class data and statistical analysis for female and male *Cancer gracilis*, *Cancer magister* and *Cancer productus* with and without epibionts.

	Female		Male	
	Uninfested	Epibonts	Uninfested	Epibonts
Cancer gracilis				
Percentage	76.2%	23.8%	66.8%	33.2%
Mean (±SD)	66.2 ± 14.0 mm	78.0 ± 9.4 mm	92.3 ± 15.6 mm	98.1 ± 12.0 mm
Median	68 mm	78 mm	95 mm	98 mm
Mann-Whitney	$P < 0.001$		$P < 0.01$	
Cancer magister				
Percentage	63.1%	36.9%	43.8%	56.2%
Mean (±SD)	137.4 ± 17.1 mm	145.6 ± 14.3 mm	153.8 ± 29.2 mm	162.3 ± 14.9 mm
Median	140 mm	146 mm	160 mm	163 mm
Mann-Whitney	$P < 0.001$		$P < 0.001$	
Cancer productus				
Percentage	23.6%	76.4%	32.3%	66.7%
Mean (±SD)	105 ± 26.3 mm	119.1 ± 11.7 mm	135.5 ± 32.2 mm	147.1 ± 19.8 mm
Median	112 mm	118 mm	142.5 mm	150 mm
Mann-Whitney	$P < 0.001$		$P < 0.001$	

(17.3% of individuals) and to a lesser extent on the legs and chelae. Tunicates, molluscs and sponges were only found on a few individual crabs (Table 3b,c), therefore, distribution patterns were not evident.

DISCUSSION

A total of 29 species representing 10 phyla may be a conservative estimate of the species richness of epibionts found on cancrid crabs in Barkley Sound, since this figure doesn't take into account the abundant micro-epibiont fauna (Becker, 1976; Fernandez-Leborans et al., 1997; Fernandez-Leborans, 2001). Notwithstanding, the diversity of macro-epibionts was comparatively limited (Table 2) compared with fouling communities occurring on rocks and man-made structures in Barkley Sound, which are dominated by the Cnidaria, Mollusca and Porifera (personal observation). Crab carapaces are only temporary surfaces, therefore they are unlikely to reach the climax communities of more permanent structures (Gili et al., 1993; Key et al., 1999). In addition, permanent structures vary in topography, surface roughness, chemical attractants and bacterial biofilms that are instrumental in larval settlement (Crisp, 1974; Rodriguez et al., 1993).
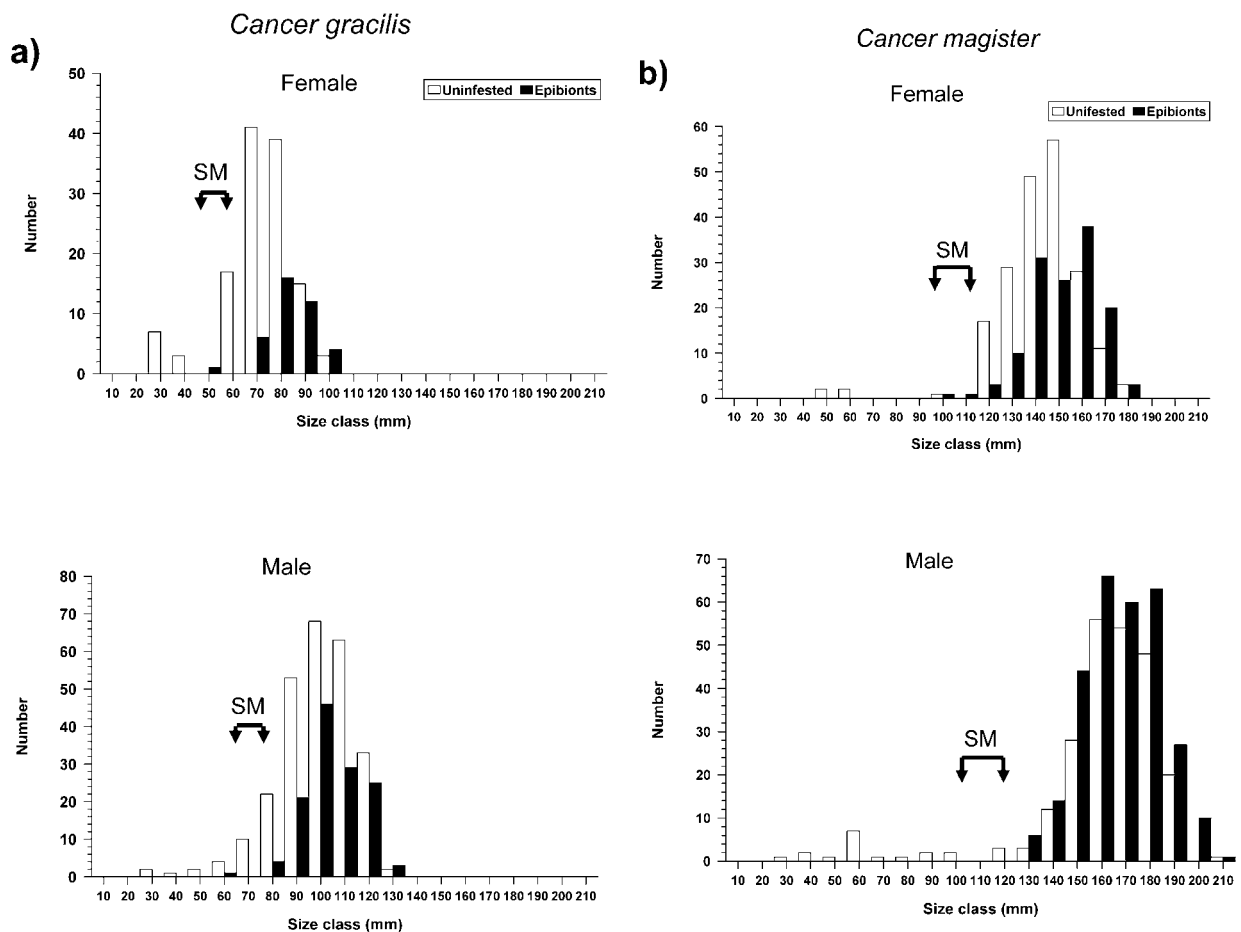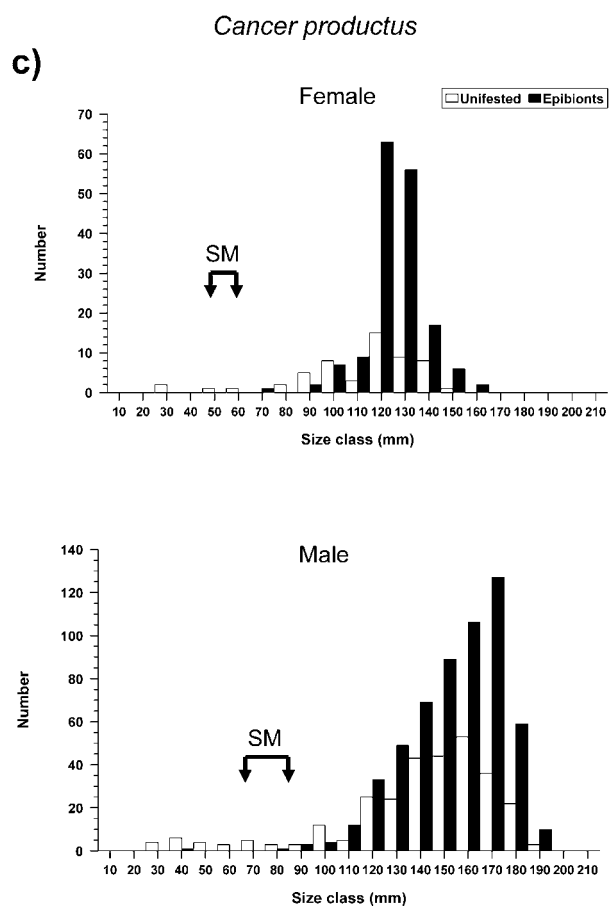

Fig. 3. Number of female and male crabs (per 10 mm size class) with (shaded bars) and without epibionts (open bars). a) *Cancer gracilis* b) *Cancer magister* c) *Cancer productus*. The size range at which each species becomes sexually mature (SM) is indicated on each of the graphs following data of Orensanz and Galluci (1988), Wainwright and Armstrong, (1993).

c)

Cancer productus

Female charts and Male charts showing Number vs Size class (mm), with Unifested and Epibonts bars. SM markers indicated.

There was a greater species richness and diversity of epibionts on male crabs. This is the opposite to that reported for portunid crabs (Shields, 1992). Male crabs were significantly larger than female crabs. A greater occurrence of epibionts on larger crabs appears to be a common pattern in crustaceans (Key et al., 1999; Fig. 3). Not only do larger crabs make a larger target for settling larvae, but also, as they age, they moult less frequently. The appearance of epibionts correlates closely with the size at which crabs change from juvenile, which moult every 1–3 months, to adult, where moulting is an annual or bi-annual event (Orensanz and Galluci, 1988; Wainwright and Armstrong, 1993). Crabs were collected between April and September but moulting peaks between June and October (Orensanz and Galluci, 1988). Therefore, during April and May, the crabs should have reached maximum epibiont loading. Heavy fouling, covering the majority of the carapace, is evidence of terminal anecdysis (Abello et al., 1990). Although each *Cancer* species may undergo a terminal anecdysis (Orensanz and Galluci, 1988), the numbers of epibionts, even in the heaviest fouled individuals, were not very high compared to other crustacean species (Abello et al., 1990, Key et al., 1997) (Fig. 4a). Senescence occurs in the winter following the terminal moult (Orensanz and Galluci, 1988) and so animals were probably not captured the following year, when infestations were likely to be highest. Also it has been suggested that decapod crustaceans possess chemical anti-

fouling agents that may help deter settlement of some larval organisms (Becker, 1996).

The presence and size of certain epibiont species can be used to estimate intermoult period in crustaceans (Gili et al., 1993; Lovrich et al., 2003). However, because the exact time of larval settlement was unknown and epibiont growth rates can be affected by many factors (Crisp and Bourget, 1985), at best, epibiont settlement patterns will be a very rough estimate of intermoult duration in *Cancer* crabs.

There were noticeable differences in the amount and diversity of epibiont species on each of the crab species (Table 2). *Cancer gracilis*, had the least amount of epibionts. This species was significantly smaller than the other two; thus, the available surface area for colonization was lowest. It also had the most conserved distribution, being largely confined to shallow bays of fine mud and sand. This species spends a considerable amount of time buried in fine sediment (Orensanz and Galluci, 1988) in areas where the mud is anoxic (Bernatis et al., in review). Such conditions are unfavourable for both larval and adult epibionts alike (Becker, 1996).

Cancer productus exhibited the greatest species richness. Because they were substantially larger than *Cancer gracilis* this also gave more surface area for epibionts to colonize. *Cancer magister* is also a large crab, but it did not have as many epibionts compared to *Cancer productus*. When crabs bury, epibionts may be abraded from the carapace (Negreiros-Fransozo et al., 1995; Becker, 1996; Key et al., 1999). *Cancer productus* does not bury as frequently as the other two species (McGaw, 2005) and often inhabits rocky areas where burial is not possible. This may have accounted for the difference in epibionts between the two crab species (Becker, 1996).

More epibionts settled on the underside of *Cancer magister* compared with *Cancer gracilis* and *Cancer productus*. This species differs from the other two in that there are dense setae on the underside that may attract and offer protection for newly settling organisms (Crisp, 1974). Although the anterior surface of crabs was similar in appearance, the surface of the carapace was not at investigated at the microscopic level. This could also account for differences in settlement patterns among the three crab species (Heath, 1976; Patil and Anil, 2000).

The differences in epibiont distribution on each of the areas of the carapace (Table 3) most likely represents differences in larval settlement patterns. Barnacles prefer narrow grooves (Crisp, 1961; Heath, 1976) and most settlement occurred in the grooves surrounding the stomach, heart region, and the grooves around the margins of the cephalothorax (Fig. 4a). A similar settlement pattern is recorded for *Carcinus maenas* and *Cancer pagurus* (Heath, 1976). Over 60% of barnacles were found on the anterior surfaces of the cephalothorax and chelae, this occurs because barnacle cyprids exhibit photopositive behaviour during settlement (Crisp, 1974). It has been suggested that barnacles will not colonize recently moulted crabs because they do not possess a bacterial film, necessary for settlement (Gili et al., 1993). However, results from the present study suggest otherwise. A number of crabs with soft carapaces (2 weeks post-moult: O'Halloran and O'Dor, 1988) had several small *Balanus crenatus* grow-

Table 2. Epibiont species found on *Cancer gracilis*, *Cancer magister* and *Cancer productus*. The number of individual crabs of each species and sex infected with a particular epibiont is given. Each epibiont is also expressed as a percentage of the total number of each crab species with epibionts and is given in brackets. The species richness, diversity H′ (Shannon-Wiener Index) and a community dominance index (CDI) is shown at the bottom of the table.

Epibiont taxa	Cancer gracillis			Cancer magister			Cancer productus		
	Female	Male	Total	Female	Male	Total	Female	Male	Total
Sub-phylum Crustacea									
Class Cirripedia									
Balanus crenatus	4	58	62 (42.2%)	107	190	297 (63.8%)	107	514	656 (78.9%)
Balanus glandula	0	4	4 (2.7%)	0	3	3 (0.6%)	0	6	6 (0.7%)
Balanus nubilis	—	—	—	1	2	3 (0.6%)	4	2	6 (0.7%)
Phylum Annelida									
Class Polychaeta									
Spirorbis spp.	—	—	—	—	—	—	24	27	51 (6.1%)
Serpulid spp.	—	—	—	0	2	2 (0.4%	11	15	26 (3.1%)
Dipolydora socialis	0	3	3 (2.0%)	0	21	21 (4.5%)	2	4	6 (0.7%)
Phylum Cnidaria									
Class Hydrozoa									
Obela spp.	—	—	—	—	—	—	0	2	2 (0.2%)
Sertularella turgida	1	1	2 (1.4%)	5	16	21 (4.5%)	1	6	7 (0.9%)
Phylum Porifera									
Haliclona permollis	—	—	—	0	1	1 (0.22%)	1	0	1 (0.1%)
Phylum Mollusca									
Mytilus californiensis	—	—	—	1	2	3 (0.7%)	0	1	1 (0.1%)
Alia gausatata (eggs)	—	—	—	0	1	1 (0.2%)	—	—	—
Notoacmea scutum	—	—	—	—	—	—	0	1	1 (0.1%)
Phylum Bryozoa									
Membranipora membranacea	—	—	—	1	8	9 (1.9%)	22	37	59 (6.8%)
Schizoporella unicornis	—	—	—	0	4	4 (0.9%)	—	—	—
Flustrellidra corniculata	—	—	—	1	4	5 (1.1%)	0	2	2 (0.2%)
Phylum Urochordata									
Cnemidocarpa finmarkiensis	—	—	—	0	1	1 (0.2%)	1	5	6 (0.7%)
Ascidia callosa	—	—	—	0	1	1 (0.2%)	1	3	4 (0.5%)
Metandrocarpa taylori	—	—	—	—	—	—	0	2	2 (0.2%)
Phylum Chlorophyta	29	59	88 (59.9%)	44	83	127 (27.3%)	1	29	30 (3.6%)
Enteromorpha									
Ulva									
Percursaria									
Acrosiphonia									
Phylum Phaeophyta	1	8	9 (6.1%)	9	4	13 (2.8%)	10	86	96 (11.5%)
Laminaria									
Alaria									
Phylum Rhodophyta	2	11	13 (8.8%)	2	73	75 (16.1%)	39	164	203 (24.4%)
Callithamnion									
Polyneura									
Porphyra									
Platythamnion									
Polysiphonia									
Species Richness	11	15	15	14	25	25	18	26	27
CDI	0.89	0.81	0.83	0.88	0.66	0.72	0.70	0.75	0.74
Diversity H′	0.99	1.33	1.26	1.07	1.64	1.54	1.51	1.48	1.51

ing on them. This is not unexpected; barnacle larvae are attracted to the molecule arthropodin, which is in highest concentrations in newly moulted crabs (Crisp, 1974).

Approximately 25% of all the crabs surveyed had one or more species of seaweed growing on the antennae and anterior margins of the cephalothorax. Newly settled seaweeds are susceptible to dislodgment (Granhag et al., 2004). Since the antennae and edges of the cephalothorax remain above the sediment when crabs bury (McGaw, 2005) it could be that these were the only algae able to survive scouring by the sand (Negreiros-Fransozo et al., 1995; Becker, 1996; Key et al., 1999). In contradiction of this hypothesis, when I suspended crabs for 2 months in the shallow subtidal zone in cages, algae did not grow elsewhere, suggesting that settlement may be dependent on other factors. Seaweed zoospores exhibit a clear chemotaxis to areas with a high nitrogen and phosphate content (Fukuhara et al., 2002) when settling. As crabs are messy feeders and the urinary openings are situated near the antennae, this may account for the settlement patterns.

Table 3. Percentage occurrence of each individual epibiont group on each of the six areas of the carapace: a) *Cancer gracilis* b) *Cancer magister* and c) *Cancer productus*.

	Anterior	Posterior	Antennae	Underside	Chelae	Legs
Cancer gracilis						
Barnacles	30.1%	26.2%	0%	8.7%	27.2%	7.8%
Green Algae	2.0%	1.0%	82.2%	7.9%	2.0%	4.9%
Red Algae	2%	0%	100%	0%	0%	0%
Brown Algae	0%	0%	90%	10%	0%	0%
Polychaetes	0%	0%	0%	100%	0%	0%
Hydrozoans	0%	0%	0%	100%	0%	0%
Cancer magister						
Barnacles	28.2%	30.0%	0%	18.0%	18.1%	5.7%
Green Algae	7.9%	3.9%	80.3%	0.7%	3.9%	3.3%
Red Algae	4.2%	0%	95.8%	0%	0%	0%
Brown Algae	0%	0%	92.9%	7.1%	0%	0%
Polychaetes	0%	0%	0%	100%	0%	0%
Hydrozoans	0%	0%	17.6%	38.2%	14.7%	29.4%
Bryozoans	0%	0%	0%	23.1%	0%	76.9%
Molluscs	0%	0%	0%	100%	0%	0%
Sponges	0%	0%	0%	0%	100%	0%
Urochrodates	0%	0%	0%	50%	50%	0%
Cancer productus						
Barnacles	30.4%	27.2%	0%	14.4%	24.7%	3.3%
Green Algae	21.1%	2.6%	60.5%	2.6%	13.2%	0%
Red Algae	1.4%	0%	95.8%	0.5%	2.3%	0%
Brown Algae	1%	0%	98.0%	0%	1%	0%
Polychaetes	10%	1.1%	1.1%	73.3%	14.5%	0%
Hydrozoans	0%	0%	11.1%	66.7%	22.2%	0%
Bryozoans	17.3%	0%	0%	72.0%	9.3%	1.3%
Molluscs	0%	0%	0%	100%	0%	0%
Sponges	0%	0%	0%	100%	0%	0%
Urochrodates	0%	0%	0%	100%	0%	0%

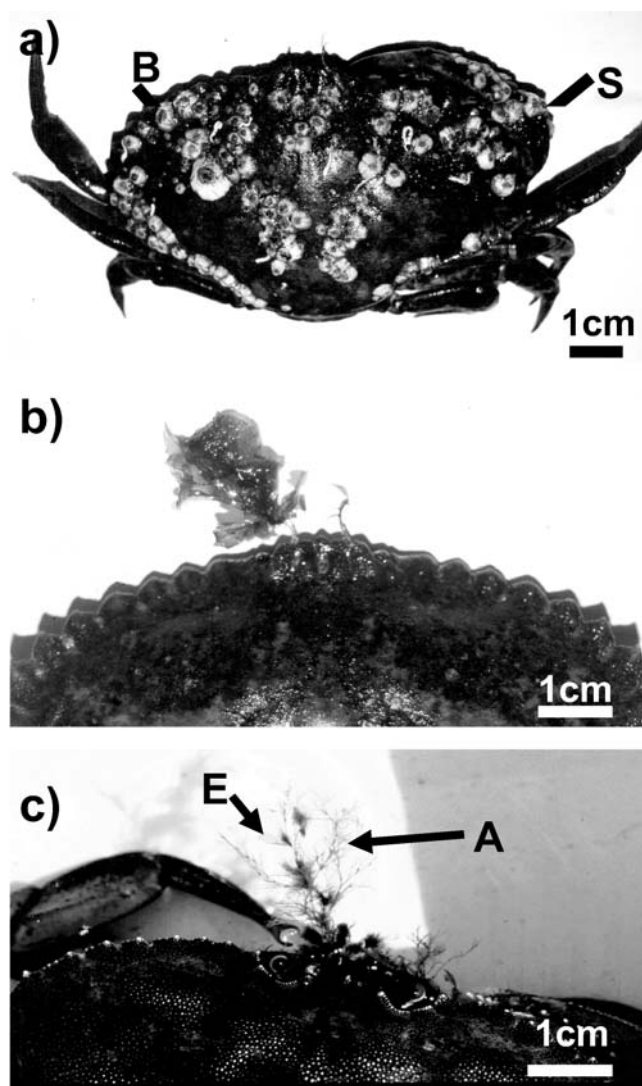Epibionts on body regions as a percentage of the total for each taxa.

Fig. 4. a) Photograph showing a heavily infested *Cancer productus*. The majority of epibionts were the barnacle, *Balanus crenatus* (B) and a few serpulid worms (S), b) Close-up of antennae of *Cancer productus* showing red algae of genus *Porphyra*, c) Close-up of *Cancer magister* antennae with green algae *Acrosiphonia* (A) and a small blade of *Enteromorpha* (E).

However, the antennae are important for osmoreception (Tazaki, 1975; Gleeson et al., 1997) and food detection (Rebach, 1996; Keller et al., 2003) and seaweed settlement could interfere with their function. Crabs actively clean the antennae with the mouthparts (McGaw et al., 1999), which would remove the seaweeds, but this did not occur here. It is possible that seaweeds are used as camouflage (Wicksten, 1993). When the crabs are deeply buried, the antennae are the only structures that protrude above the sand. They flick these to sense the environment (McGaw, 2005). Seaweed attachment could camouflage the antennae and prevent grazing by small fish and invertebrates.

Polychaete worms occurred fairly frequently on cancrid crabs. Many polychaete larvae are photonegative when settling (Knight-Jones et al., 1971). This would explain why the majority of individuals occurred on the underside of crabs. Like barnacles, polychaete larvae are gregarious settlers (Knight-Jones et al., 1971); however, they did not occur in the density observed for barnacles. Usually only 1 to 4 individuals were found on a crab. The highest density recorded was 35 serpulid and spirorbid worms on an individual *Cancer productus*. Even these were scattered over most areas of the carapace. Polychaete larvae prefer surfaces with a bacterial film (Williams, 1964), which can take several months to form on crabs (Gili et al., 1993) and polychaete worms were mainly found on the larger crabs which appeared to have been in intermoult for some time.

Bryozoans were found on *Cancer productus* and *Cancer magister*. Bryozoans are susceptible to sedimentation and did not occur on *Cancer gracilis*, which is confined to muddy areas (Orensanz and Galluci, 1988). Bryozoan larvae are photonegative when settling (Thorson, 1964). This may explain their location on *Cancer productus*, where the majority settled on the ventral surfaces. However, in *Cancer magister*, bryozoans were found more frequently on the legs, which offer little protection from light. *Membranipora membranacea* comprised most of the infestations on *Cancer magister*, and for *Membranipora membranacea* larval settlement is highly dependent on the characteristics of the surface, rather than light or gravity (Ryland and Stebbing, 1971).

Hydrozoans occur in high frequencies on some crabs species (Gili et al., 1993). They were only found on 7% of the crabs surveyed, although they were common in Barkley

sound (personal observation). Hydrozoans are very sensitive to sedimentation (Boero, 1984). Because all three crab species bury in the sediment (Orensanz and Galluci, 1988; McGaw, 2005), this may have restricted their numbers.

Colonizing mobile surfaces such as crustacean carapaces is beneficial for many epibiont species because it enhances food acquisition and affords them a degree of protection from predators (Wahl, 1989). This may offset the comparatively short life-span of the carapace (Key et al., 1999). The benefits and costs for the host species are less apparent. Although ectocommensal barnacles that attach to crab gills may impart a physiological cost for the host species (Gannon and Wheatly, 1992), the presence of epibionts on outer carapace of cancrid crabs (Table 2) probably does not benefit or harm the host. There is unlikely to be a substantial physiological cost to the crabs of carrying an extra load of external epibionts because the epibionts did not reach high densities and were also more prevalent on larger crabs (Overstreet, 1983; Dick et al., 1998). However, there is little evidence of a benefit for the host either; because the epibiont coverage was sparse it probably wouldn't act as camouflage for cancrid crabs, as it does for other crab species (Wicksten, 1993).

REFERENCES

Abello, P. R. Villanueva, and J. M. Gili. 1990. Epibiosis in deep sea crab populations as an indicator of biological and behavioural characteristics of the host.   Journal of the Marine Biological Association of the United Kingdom 70: 687-695.

Abello, P., and J. Corbera. 1996. Epibiont bryozoans (Bryozoa, Ctenostomatida) of the crab *Goneplax rhomboides* (Brachyura, Goneplacidae) off the Ebro delta (western Mediterranean). Miscelania Zoologica 19: 43-52.

———, and E. Macpherson. 1992. Epibiosis and rhizocephalan infestation patterns in relation to the reproductive biology of *Lithodes ferox* (Filhol, 1885) (Anomura: Lithodidae).   Journal of Crustacean Biology 12: 561-70.

Becker, K. 1996. Epibionts on carapaces of some malacostracans from the Gulf of Thailand.   Journal of Crustacean Biology 16: 92-104.

Bernatis, J. L., S. L. Gerstenberger, and I. J. McGaw (in review). Feeding and digestion in the Dungeness crab, *Cancer magister*, in hypoxic conditions. Marine Biology.

Boero, F. 1984. The ecology of marine hydroids and effects of environmental factors a review. P.S.Z.N.   Marine Ecology 5: 93-118.

Botton, M. L., and J. W. Ropes. 1988. An indirect method for estimating longevity of the horseshoe crab *Limulus polyphemus* based on epifaunal slipper shells *Crepidula fornicata*.   Journal of Shellfish Research 3: 407-412.

Connell, J. H., and M. J. Keough. 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrata. pp. 125-151. In, S. Pickett and P. White, eds. Ecology of natural disturbance and patch dynamics. Academic Press, San Diego.

Crisp, D. J. 1961. Territorial behaviour in barnacle settlement.   Journal of Experimental Biology 38: 429-446.

———. 1974. Factors influencing the settlement of marine invertebrate larvae. pp. 177–265. in Grant and Mackie, eds. Chemoreception in marine organisms Academic Press, London.

———, and E. Bourget. 1985. Growth in barnacles.   Advances in Marine Biology 22: 199-244.

Dick, M. H., W. E. Donaldson, and I. W. Vining. 1998. Epibionts of the tanner crab *Chionoecetes bairdi* in the region of Kodiak Island, Alaska.   Journal of Crustacean Biology 18: 519-528.

Fernandez-Leborans, G. 2001. A review of the species of protozoan epibionts on crustaceans. III Chonotrich ciliates.   Crustaceana 74: 581-607.

———, M. J. H. Cordoba, and P. G. delArco. 1997. Distribution of ciliate epibionts on the portunid crab *Liocarcinus depurator* (Decapoda: Brachyura).   Invertebrate Biology 116: 171-177.

Fukuhara, Y., H. Mizuta, and H. Yasui. 2002. Swimming activities of zoospores of *Laminaria japonica* (Phaeophyceae).   Fisheries Sciences 68: 1173-1181.

Gannon, A. T., and M. G. Wheatly. 1992. Physiological effects of an ectocommensal gill barnacle, *Octolasmis muelleri*, on gas exchange in the blue crab *Callinectes sapidus*.   Journal of Crustacean Biology 12: 11-18.

Gili, J. M., P. Abello, and R. Villanueva. 1993. Epibionts and intermoult duration in the crab *Bathynectes piperitus*.   Marine Ecology Progress Series 98: 107-113.

Giri, T., and M. K. Wicksten. 1992. Fouling of the caridean shrimp, *Lystama wurdemanni*, (Gibbes, 1850) by the barnacle *Balanus improvisus* Darwin 1854 and other epibionts.   Crustaceana 74: 1305-1314.

Gleeson, R. A., M. G. Wheatley, and C. L. Reiber. 1997. Perireceptor mechanisms sustaining olfaction at low salinities: insight from the euryhaline blue crab *Callinectes sapidus*.   Journal of Experimental Biology 200: 445-456.

Granhag, L. M., J. A. Finlay, P. R. Jonsson, J. A. Callow, and M. E. Callow. 2004. Roughness dependent removal of settled spores of the green alga *Ulva* (syn. *Enteromorpha*) exposed to hydrodynamic forces from a water jet.   Biofouling 20: 117-122.

Heath, D. J. 1976. The distribution and orientation of epizoic barnacles on crabs.   Zoological Journal of the Linnaen Society 59: 59-67.

Jorgensen, C. B. 1966. Biology of suspension feeding. Pergamon Press. Oxford.

Keller, T. A., I. Powell, and M. J. Weissburg. 2003. Role of olfactory appendages in chemically mediated orientation of blue crabs.   Marine Ecology Progress Series 261: 217-231.

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

———, J. E. Winston, J. W. Volpe, W. B. Jeffries, and H. K. Voris. 1999. Bryozoan fouling of the blue crab *Callinectes sapidus* at Beaufort, North Carolina.   Bulletin of Marine Science 64: 513-533.

Knight-Jones, E. W., J. H. Bailey, and M. S. Isaac. 1971. Choice of algae by larvae of *Spirorbis* especially *Spirorbis spirorbis*. pp. 89-104 in D. Crisp, ed. Fourth European Marine Biology Symposium. Cambridge University Press.

Lovrich, G. A., J. A. Calcagno, and B. D. Smith. 2003. The barnacle *Notobalanus flosculus* as an indicator of the intermoult period of the male lithodid crab *Paralomis granulosa*.   Marine Biology 143: 143-156.

McGaw, I. J. 2005. Burying behaviour of two sympatric crab species: *Cancer magister* and *Cancer productus*.   Scientia Marina 69: 375-381.

———, C. L. Reiber, and J. A. Guadagnoli. 1999. Behavioral physiology of four crab species in low salinity.   Biological Bulletin 196: 163-176.

Negreiros-Fransozo, M. L., T. M. Costa, and A. Fransozo. 1995. Epibiosis and molting in two species of *Callinectes* (Decapoda: Portunidae) from Brazil.   Review Biologica Tropica 43: 257-264.

O'Halloran, M. J., and R. K. O'Dor. 1988. Molt cycle of the male snow crab *Chionoecetes opilio*, from observations of external features, setal changes and feeding behaviour.   Journal of the Marine Biological Association of the United Kingdom 8: 164-176.

Orensanz, J. M., and V. F. Galluci. 1988. Comparative study of postlarval life-history schedules in four sympatric species of *Cancer* (Decapoda: Brachyura: Cancridae).   Journal of Crustacean Biology 8: 187-220.

Overstreet, R. M. 1983. Metazoan symbionts of crustaceans. pp 155-250. In, A. Provenzano, ed. Biology of Crustacea. Volume 6. Pathobiology. Academic Press, New York.

Parapar, J., L. Fernandez, E. Gonzalez-Gurriaran, and R. Muino. 1997. Epibiosis and masking material in the spider crab *Maja squinado* (Decapoda: Majidae) in the Ria de Arousa (Galicia, NW Spain).   Cahiers de Biologie Marine 38: 221-234.

Patil, J. S., and A. C. Anil. 2000. Epibiotic community of the horseshoe crab *Tachypleus gigas*.   Marine Biology 136: 699-713.

Rebach, S. 1996. Role of prey odor in food recognition by rock crabs *Cancer irroratus* Say.   Journal of Chemical Ecology 22: 2197-2207.

Rodriguez, S. R., F. P. Ojeda, and N. C. Inestrosa. 1993. Settlement of benthic marine invertebrates. Marine Ecology Progress Series 97: 193-207.

Ryland, J. S., and A. R. D. Stebbing. 1971. Settlement and orientated growth in epiphytic and epizoic bryozoans. pp. 105-126 in D. Crisp, ed. Fourth European Marine Biology Symposium. Cambridge University Press.

Seed, R. 1985. Ecology patterns in the epifaunal communities of coastal macroalgae. pp. 22-35. In, P. Moore and R. Seed, eds. Ecology of Rocky Coasts. Hodder and Stoughton, London.

Shields, J. D. 1992. Parasites and symbionts of the crab *Portunus pelagicus* from Moreton bay eastern Australia. Journal of Crustacean Biology 12: 94-100.

Tazaki, K. 1975. Sensory units responsive to osmotic stimuli in the antennae of the spiny lobster, *Panuliris japonicus*. Comparative Biochemistry and Physiology 51A: 647-653.

Thorson, G. 1964. Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. Ophelia 1: 67-208.

Wahl, M. 1989. Marine epibiosis. I Fouling and anti fouling: some basic aspects. Marine Ecology Progress Series 58: 175-189.

Wainwright, T. C., and D. A. Armstrong. 1993. Growth patterns in the Dungeness crab (*Cancer magister* Dana): Synthesis of data and comparison of models. Journal of Crustacean Biology 13: 36-50.

Wicksten, M. K. 1993. A review and model of decorating behavior in spider crabs. (Decapoda, Brachyura, Majidae). Crustaceana 52: 135-140.

Williams, G. B. 1964. The effects of extracts of *Fucus serratus* in promoting settlement of *Spirorbis spirorbis* (Polychaeta). Journal of the Marine Biological Association of the United Kingdom 44: 397-414.

Willey, R. L., P. A. Cantrell, and S. T. Threlkeld. 1990. Epibiotic flagellates increase the susceptibility of some zooplankton to fish predation. Limnology and Oceanography 35: 952-959.