BULLETIN OF MARINE SCIENCE, 64(3): 451–463, 1999

RHIZOCEPHALAN *HETEROSACCUS DOLLFUSI* BOSCHMA, OFF THE MEDITERRANEAN COAST OF ISRAEL

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ABSTRACT

The Levantine population of *Charybdis longicollis,* a Lessepsian migrant, has been parasitized recently by the sacculinid rhizocephalan, *Heterosaccus dollfusi.* Incidence of infestation, its effects on host's size, sex ratio and multiple infestation are examined. We recorded 77% infection rate with up to 57.6% of infested hosts bearing more than one externa. The rapid spread and the high prevalence of *H. dollfusi* can be ascribed to the dense population of the host and the year-round reproduction of the parasite promoting recurrent re-infection. As heavily-infested populations are presumably maintained by immigration, it is likely that the Levantine population of *C. longicollis* will suffer drastic perturbations, as it is doubtful whether immigration of non-infested crabs through the Suez Canal suffices for population renewal.

The defining feature of the fauna off the Mediterranean coast of Israel has been the mass establishment of migrant species from the Red Sea that entered through the Suez Canal. Of the approximately 300 species that have been identified as Lessepsian migrants, 40 are decapod crustaceans (Galil, 1992).

Charybdis longicollis Leene, found in the Red Sea (Leene, 1938), the Persian Gulf (Stephensen, 1946) and Madagascar (Guinot, 1966), was first recorded in the Mediterranean in 1954 from the Bay of Mersin, Turkey (Holthuis, 1961). Since then, it has been recorded all along the Levant coast, from Egypt to the south coast of Turkey (Lewinsohn and Holthuis, 1986). Off the Israeli coast, *C. longicollis* is common on sandy-mud bottoms at 25–60 m and occasionally deeper, to a record of 135 m (Galil, 1992).

Of the thousands of specimens of *C. longicollis* collected off the Israeli coast in over three decades, none were parasitized until 1992. Among the *C. longicollis* collected off Palmahim in October of 1992, a few had bulging yellow protuberances carried beneath the abdomen. Those protrusions were identified as the externae of a sacculinid rhizocephalan, *Heterosaccus dollfusi* Boschma, previously known only from a few specimens from the Gulf of Suez (Galil and Lützen, 1995), the first reported instance of Lessepsian migration by a rhizocephalan. Subsequent collections at the same site in October 1993, and May and November 1994, confirmed its presence (Galil and Lützen, 1995). In March 1995, *H. dollfusi* was found infesting *C. longicollis* on the easternmost part of the Anatolian coast (Enzenross, pers. comm.). It seems that although the host crab had immigrated to the Mediterranean over forty years ago, the parasite has appeared only recently and is spreading rapidly.

This study reports the incidence and some effects of parasitism of *H. dollfusi* on populations of *C. longicollis* off the Mediterranean coast of Israel. Infection levels are related to coastal topography, and the occurrence of multiple infection is discussed.

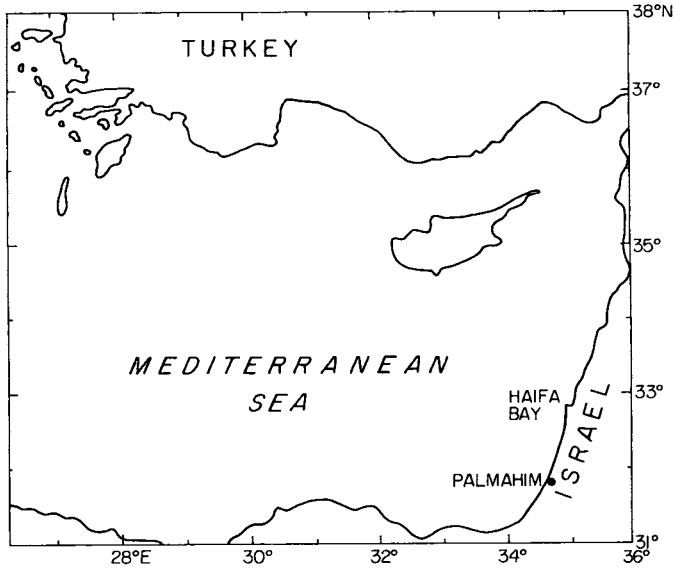

Figure 1. Map of the Levant basin with the collecting sites, Palmahim and Haifa Bay.

METHODS

The coast of Israel, at the southeastern corner of the Mediterranean, forms a smoothly curving arc except for the indentation of Haifa Bay (Fig. 1). Nile sediments produce a broad continental shelf along the southern coast, which narrows northward. At Haifa Bay, the sandy zone extending from the shoreline to a depth of 15–17 m is separated from the seaward plain by four submerged sandstone ridges. The ridges, ranged parallel to shore, crest at 10–20 m depth (Hall, 1976; Nir, 1980).

C. longicollis specimens were collected at Palmahim in 1977 and 1987 as part of a baseline survey in preparation for a marine sewage outlet. The material was collected by the R/V SHIKMONA with a 1.15 m wide beam trawl, at depths of 30–45 m and preserved in the zoological collections of Tel Aviv University. A continuing monitoring program of the sewage outlet at Palmahim made possible repeated sampling in October 1993, May and November 1994 (Galil and Lützen, 1995) and June 1996. The samples were again collected by the R/V SHIKMONA with a 1.15 m wide beam trawl, at depths of 31–36 m. Each sample was made up of 16 trawls of identical duration, taken within a limited area. The material from all trawls was pooled.

In Haifa Bay *C. longicollis* specimens were collected in November 1995 by a commercial trawler at depths of 15–20 m.

A total of 5792 specimens were examined. Carapace width (CW—distance between tips of lateral spines to nearest mm), sex, presence of parasite, number and wet weight of externae (to nearest 0.01 g) and presence of epizoids were noted.

RESULTS

INCIDENCE OF INFESTATION.—During October 1993, May and November 1994, November 1995, and June 1996, 5470 specimens of *C. longicollis* were collected. Among these, 1946 were externae-bearing crabs and 1722 were morphologically modified pre-external infections. The incidence of infection varied among the samples (Table 1), from an overall infection of 23.9% in October 1993 to 77.0% in November 1995.

EFFECTS OF INFESTATION ON THE SIZE OF *C. LONGICOLLIS*.—A sample taken from the pre-infested population of Palmahim, shows that males of *C. longicollis* were significantly larger than females (Table 2). Examination of the post-infestation samples indicates an increase in the average size of infested and non-infested crabs of both sexes, males remaining significantly larger than females. The dif-

Table 1. The state of infection between sexes in *Charybdis longicollis* collected in Palmahim and Haifa Bay. M and F: normal males and females, MI and FI: males and females with internal infection, ME and FE: males and females with externa. SR: sex ratio.

	1993, October Palmahim		1994, May Palmahim		1994, November Palmahim		1996, June Palmahim		1995, November Haifa Bay	
	tot	%	tot	%	tot	%	tot	%	tot	%
NORMAL										
M	186	31.8	47	13.6	65	34.9	213	18.3	503	15.7
F	258	44.2	82	23.8	51	27.4	165	14.2	232	7.3
tot	**444**		**129**		**116**		**378**		**735**	
SR normal	*41.9*		*36.4*		*56.0*		*56.3*		*68.4*	
PARASITIZED										
MI	11	1.9	30	8.7	14	7.5	71	6.1	1,300	40.7
ME	67	11.5	94	27.2	36	19.4	441	38.0	559	17.5
FI	5	0.9	16	4.6	5	2.7	19	1.6	251	7.9
FE	57	9.8	76	22.0	15	8.1	252	21.7	349	10.9
tot	**140**		**216**		**70**		**783**		**2,459**	
SR parasitized	*55.7*		*57.4*		*71.4*		*65.4*		*75.6*	
Parasite ratio (parasite/tot)	**23.9**		**62.6**		**37.6**		**67.4**		**77.0**	
G-TEST = 675.660, df = 4 P < 0.001										
SR normal vs. SR parasitized										
G-Test	*8.15*		*14.280*		*4.427*		*8.792*		*14.645*	
P<	*0.01*		*0.001*		*0.05*		*0.1*		*0.001*	
Total males	264		171		115		725		2,362	
Total females	320		174		71		436		832	
tot	**584**		345		186		1,161		3,194	
SR tot	***45.2***		***49.6***		***61.8***		***62.4***		***74.0***	

Table 2. CW average and range size in pre-infestation and post-infestion *Charybdis longicollis* collected in Palmahim and Haifa Bay. The sizes are expressed in mm [ME and FE: males and females with externae].

	Palmahim, June 1797			
	Average size	n	SD	Range
M	26.5	90	7.8	12.8–45.1
F	24.1	89	4.6	12.2–36.6
	$t = 2.592$, df = 177, $P < 0.01$			

	Palmahim, October 1993				Palmahim June 1996				Haifa November 1995			
	Average size	n	SD	Range	Average size	n	SD	Range	Average size	n	SD	Range
M	44.1	186	7.3	23.0–59.0	46	213	11.0	19.3–63.8	29.1	503	5.8	12.6–53.8
F	36.7	258	3.8	26.0–46.0	34.9	165	5.0	23.5–45.2	26.7	232	4.7	14.6–43.1
	$t = 14.85$, df = 519, $P < 0.01$				$t = 12.079$, df = 376, $P < 0.01$				$t = 5.461$, df = 733, $P < 0.01$			
ME	40.1	67	5.1	26.0–52.0	37.5	441	5.5	23.1–51.0	34.2	559	3.7	18.9–48.9
FE	39	57	3.2	31.0–46.0	36.2	252	5.3	22.4–49.5	32.7	349	3.3	18.4–47.0
	$t = 1.348$, df = 115, ns				$t = 3.004$, df = 691, $P < 0.01$				$t = 6.455$, df = 906, $P < 0.01$			

ference in average size among the non-infested male and female crabs is bigger than among externae-bearing male and female crabs.

The average size of non-infested crabs taken at Haifa Bay is much smaller than that of non-infested crabs of the post-infestation samples taken at Palmahim ($t = 38.501$, $df = 1183$, $P < 0.01$). Moreover, the average size of externae-bearing male crabs taken at Haifa Bay is larger than non-infested male crabs in that sample ($t = 17.245$, $df = 1060$, $P < 0.01$).

In all samples and for both sexes, as crab size (CW) increases the relative proportion of infestation decreases. This trend is more pronounced in males, where larger size classes are free of infestation (Fig. 2).

SEX RATIO.—The overall sex ratio of both pre-infestation samples collected in Palmahim in 1977 and 1987 was about equal (Fig. 3). In October 1993, 41.9% of the 444 non-infested crabs collected in Palmahim were male, whereas among the 140 infested crabs 55.7% were male. In the sample collected a year later, in November 1994, 56.0% of the non-infested crabs were males as compared with 71.4% of infested crabs. With the increasing incidence of infestation there is a concurrent rise in the number of males in the population, to a maximum of 75.6% in infested crabs in the November 1995 sample (Table 1).

MULTIPLE INFESTATION.—Multiple infestation is common in *C. longicollis,* with up to 57.6% of infested hosts bearing more than one externa (Table 3).

Multiple infections are much more common in spring samples than in fall; however, the number of multiple infections rises with increased incidence of infestation. Thus, in the sample collected at Palmahim in May 1994 incidence of infestation is 62.6% and percentage of multiple infestation is 52% vs 67.4% and 57.6% in the sample collected in June 1996. Similarly, in Haifa Bay (November, 1995) incidence of infestation is 77.0% and percentage of multiple infestation 36.7%, whereas in Palmahim (November, 1994) the corresponding values are 37.6% and 23.5% (Table 3).

Five and six externae were recorded only from small crabs (max. CW 31.2 mm), whereas two and three externae were recorded for nearly the whole size range (Fig. 4). In the June 1996 Palmahim sample the average CW of both male and female multiple-infected crabs decreases with the increase in number of externae, while in the November 1995 Haifa sample the average CW of multiple-infected crabs increases slightly with increasing number of externae (Table 3).

SIZE OF EXTERNAE.—The average weight of an individually-occurring externa is greater than the average weight of each externa in a multiple-infested host, the average weight decreasing with increasing number of externae per host. However, the average total weight of multiple externae was greater than that of an individually-occurring externa, except in the case of five or more externae per host (Table 3).

There is a positive relation between size of host (CW) and total wet weight of externae, a larger host bearing a greater mass, whether a single or multiple externae (Fig. 5).

DISCUSSION

INCIDENCE OF INFESTATION.—Distinct morphological modification of the host crabs by *H. dollfusi* is evident even in internally infested individuals (Galil and Lützen, 1995), enabling us to detect infection not solely on the presence of externae, thus reducing underestimation of infestation.

Prevalence of rhizocephalan infection is usually low (Lützen, 1984; Hochberg et al., 1992; Shields, 1992), but isolated cases of high infestation have been re-

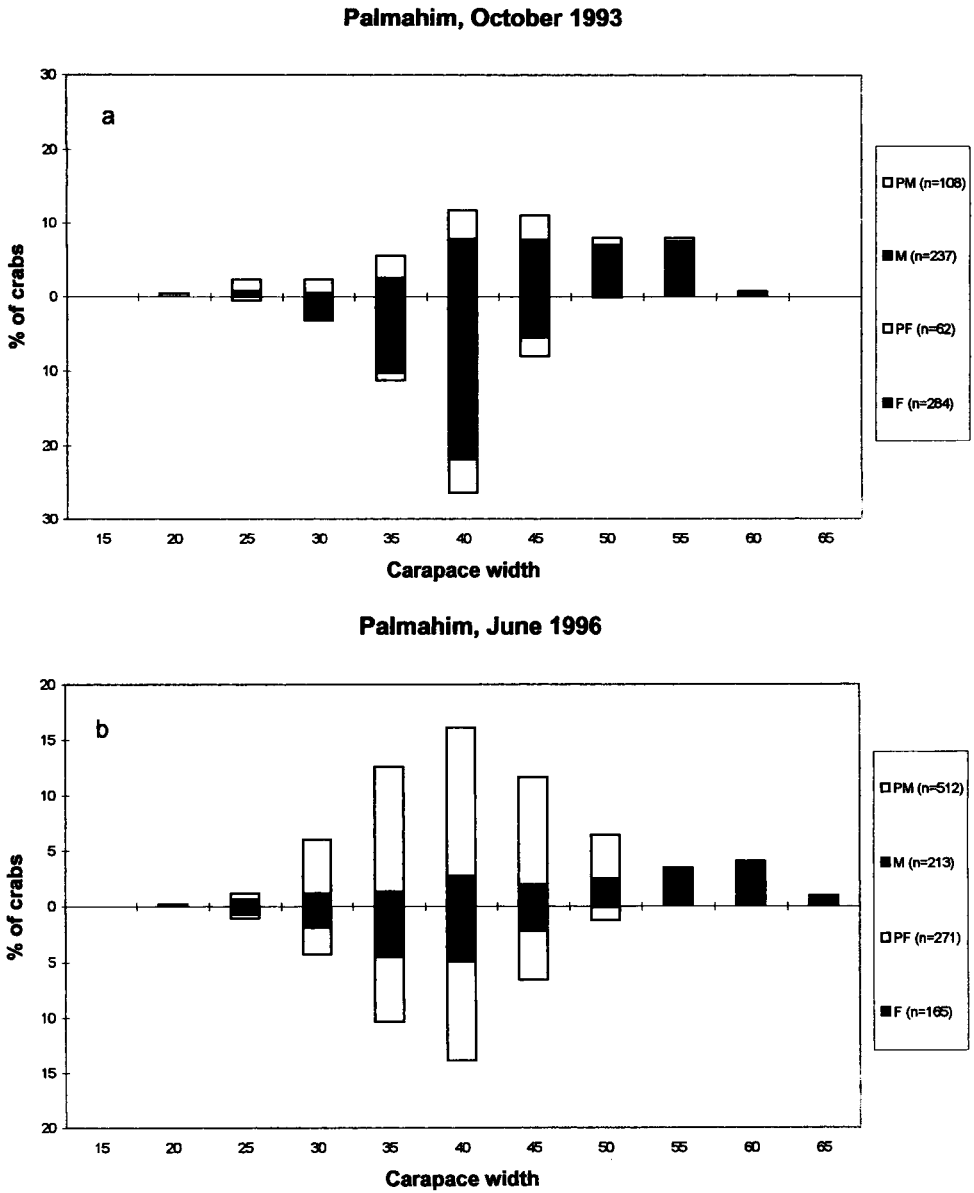

Figure 2. Size (CW) frequency distribution of *Charybdis longicollis* from Palmahim a) October 1993, b) June 1996, and Haifa Bay c) November 1995. Non-infected crabs represented by solid bars, infected crabs by open bars.

corded with a local percentage of infection as high as 90% (Veillet, 1945) and 95% (Hoeg, 1995). Hines et al. (see also Alvarez et al., 1995) reported that the Rhode River population of *Rhithropanopaeus harrisii* was first infected with *Loxothylacus panopaei* in 1989 and two years later, 72% were infected. However, the 77% infection rate recorded from Haifa Bay is very high compared with levels reported from other infected portunid hosts. Incidence of infection in the commercially valuable sand crab, *Portunus pelagicus,* infected by *Sacculina granifera,*

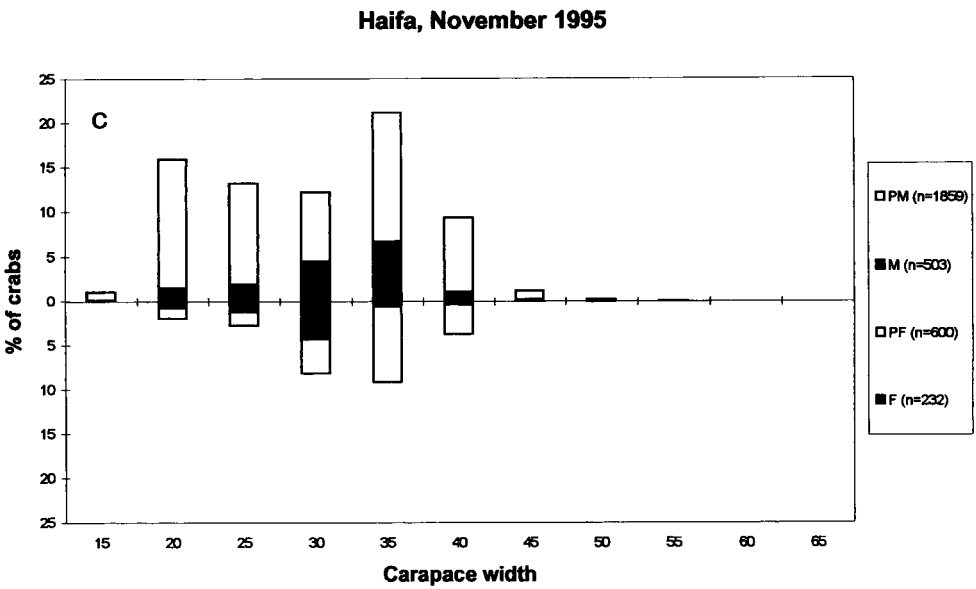

Figure 2. Continued.

may be as high as 29% (Thomson, 1951), though usually much lower (Phillips and Cannon, 1978; Weng, 1987). Pillai and Thomas (1972) found that 12.2% of *Neptunus pelagicus* from the Gulf of Manaar were infected by *Heterosaccus indicus*. In Lake Pulicat, 17.5% of *Portunus sanguinolentus* were infected by *H. ruginosus* (Srinivasagam, 1982; cf. Galil and Lützen, 1995). Lazaro-Chavez et al. (1996) recorded that up to 51.5% of the blue crab, *Callinectes sapidus,* in the Gulf of Mexico were infested by *Loxothylacus texanus.*

The greater number of remarkably high prevalence of rhizocephalan infestation takes place in enclosed bodies of water, be it a bay, a fjord or a lagoon (Hartnoll, 1967; Sloan, 1984; Hawkes et al., 1986; Yamaguchi et al., 1994). Thus, Veillet (1945) observed high infestation in populations isolated within inlets of the Etang de Thau, a brackish water lagoon in southeast France, Srinivasagam (1982) in a brackish lagoon in southeast India; Hawkes et al. (1986) in inlets of Glacier Bay, Alaska; Hines et al. (see Alvarez et al., 1995) in Rhode River, Chesapeake Bay, Maryland; Yamaguchi et al. (1994) in sheltered bays around Amakusa Islands, Japan; Lazaro-Chavez et al. (1996) in brackish Tamiahua Lagoon, and Alvarez and Calderon (1996) in Sontecomaoan Lagoon, both in Mexico.

Sheltered bays or lagoons allow the short-lived nauplii to remain within its environment and afford favorable conditions for settlement on host. As about 85% of mature externae of *H. dollfusi* were ovigerous both spring and fall (Galil and Lützen, 1995), the year-round release of parasite larvae in the relatively enclosed Haifa Bay may have promoted heavier self infection than in Palmahim, on the open coast.

Effects of Infestation on Size of *C. longicollis*.—Sacculinid-infected crabs are undersized compared with non-infected ones (Hoeg, 1995). Phillips and Cannon (1978) attribute the stunted size to molt-inhibition by the parasite, whereas O'Brien and Van Wyk (1985) ascribe it to reduction in the number of molts and Hawkes et al. (1987) to diminished molt increments. Hoeg (1995) considers that

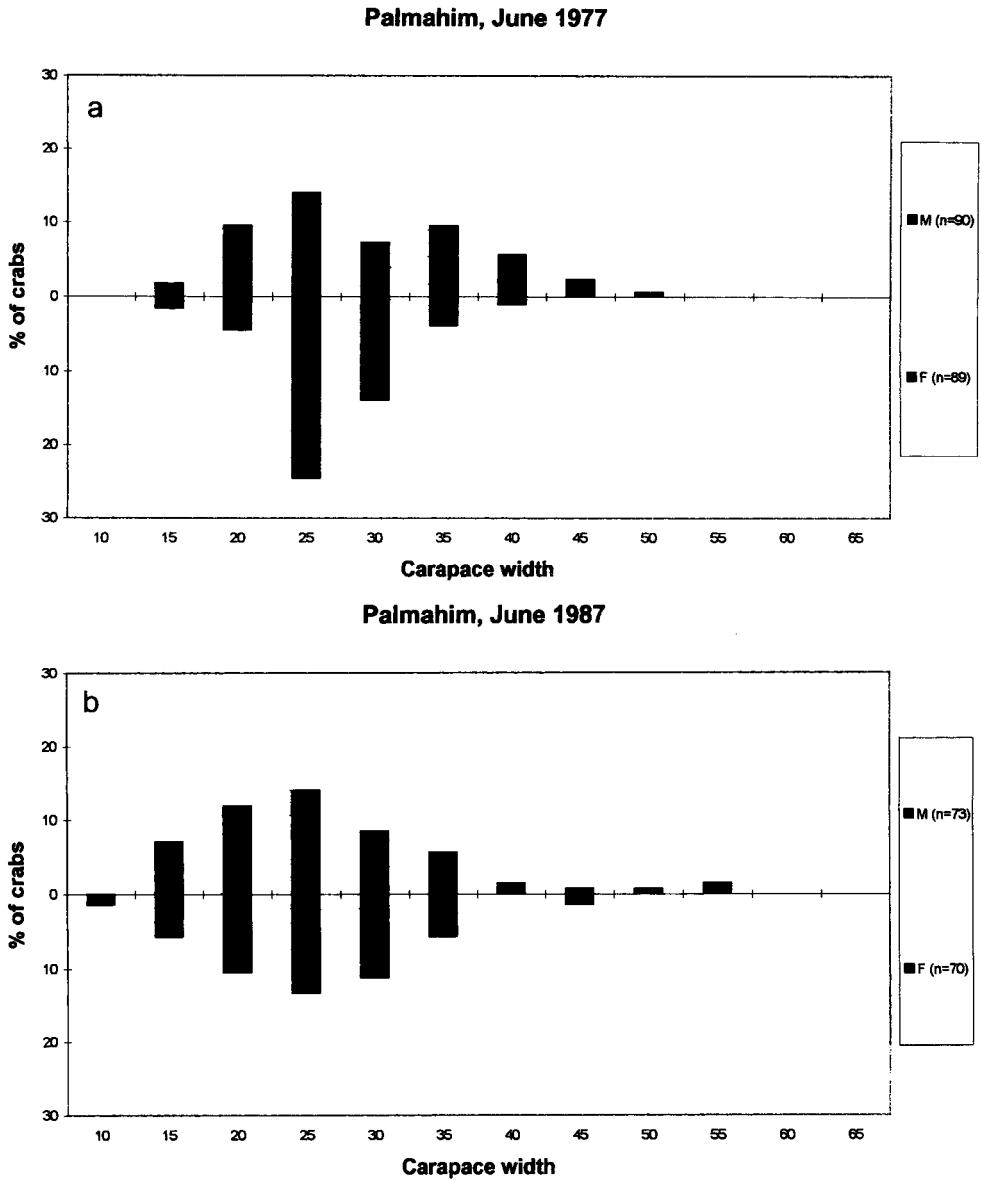

Figure 3. Size (CW) frequency distribution of *Charybdis longicollis* from Palmahim a) June 1977, b) June 1987.

the rhizocephalans' effect on their hosts' size may also be related to size or sex-dependent survival.

Galil and Lützen (1995) noted that crabs bearing old externae and scars commonly bore an epizoic serpulid worm, *Hydroides operculatus,* a Lessepsian migrant itself. Phillips and Cannon (1978) and Weng (1987) observed that infested crabs bore more epibionts on their carapace than non-infested ones, indicating molt inhibition. However, epibiont accumulation may also suggest inhibition or curtailment of cleaning behavior by infested crabs (Ritchie and Hoeg, 1981).

Table 3. Wet weight (g) of mature single or multiple externae of *Heterosaccus dollfusi* and CW (mm) of externally infected *Charybdis longicollis*.

			Individual externae		Total externae		Males			Females		
	N. externa per host	N	Range	Average	Range	Average	CW range size	CW average size	n	CW range size	CW average size	n
Palmahim	May 1994											
	1	42	0.22–1.65	0.84								
	2	24	0.06–1.17	0.51	0.30–1.96	1.02						
	3	11	0.11–0.74	0.34	0.35–1.58	1.02						
	4 or 5	11	0.06–0.63	0.24	0.31–1.54	0.98						
Palmahim	November 1994											
	1	31	0.18–1.13	0.60								
	2	7	0.11–0.63	0.42	0.64–1.04	0.84						
	3 or 4	4	0.05–0.62	0.24	0.44–1.05	0.77						
Palmahim	June 1996											
	1	263	0.28–2.51	0.96			27.4–49.5	39.8	165	23.8–49.2	37.5	98
	2	199	0.25–1.56	0.58	0.38–2.46	1.27	23.1–51.0	35.6	129	22.4–46.2	36.1	70
	3	125	0.13–1.32	0.62	0.24–2.50	1.23	25.3–49.0	34.4	79	23.6–46.0	33.6	46
	4	26	0.10–1.12	0.48	0.40–3.00	1.06	28.8–41.2	32.5	20	25.7–42.4	32.0	6
	5 or 6	8	0.05–0.38	0.21	0.55–0.89	0.7	26.2–31.2	28.8	6	26.5–28.6	27.6	2
Haifa Bay	November 1995											
	1	345	0.11–0.94	0.38			24.8–48.9	34.0	214	25.5–38.0	31.8	131
	2	136	0.02–0.57	0.24	0.12–1.00	0.47	24.5–43.3	33.9	82	26.3–38.1	32.3	54
	3	50	0.02–0.39	0.15	0.19–0.94	0.46	26.2–42.0	33.2	30	28.5–36.8	32.5	20
	4	14	0.02–0.32	0.12	0.19–0.82	0.48	25.5–40.1	34.5	13	33.8	33.8	1

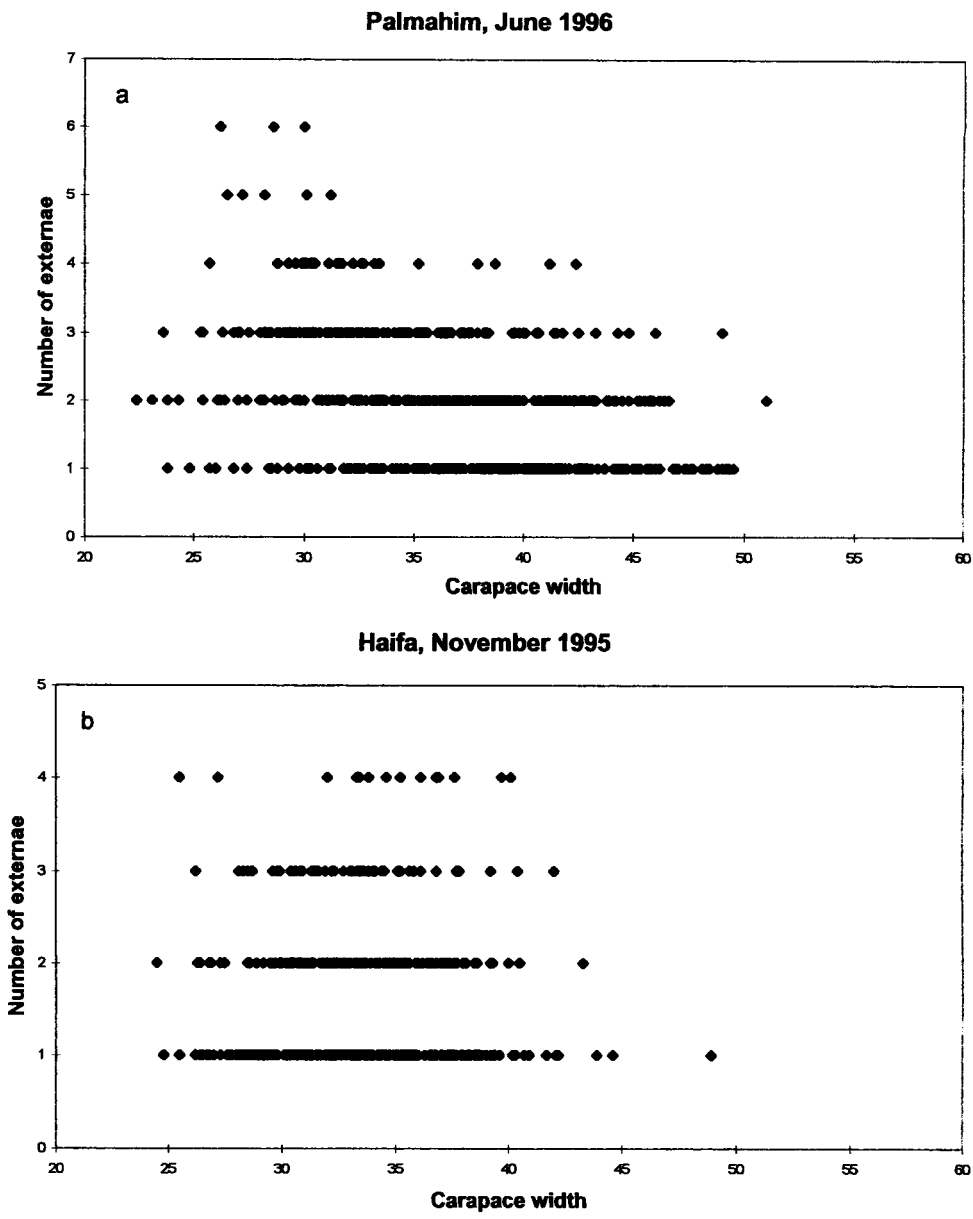

Figure 4. Size (CW) range of multiple-infected *Charybdis longicollis* from a) Palmahim, June 1996, b) Haifa, November, 1995.

Both the average and maximal size of non-infected males of *C. longicollis* in the post-infestation samples from Palmahim are larger than externa-bearing males. In female crabs, average and maximal size of non-infected ones are smaller than those bearing externa, while average and range size of ovigerous females nearly equal that of externa-bearing females. Weng (1987) explained a similar pattern in *P. pelagicus* parasitized by *S. granifera,* in that "the parasite matured when their hosts, whose gonad development was inhibited, reached the size of mature crabs."

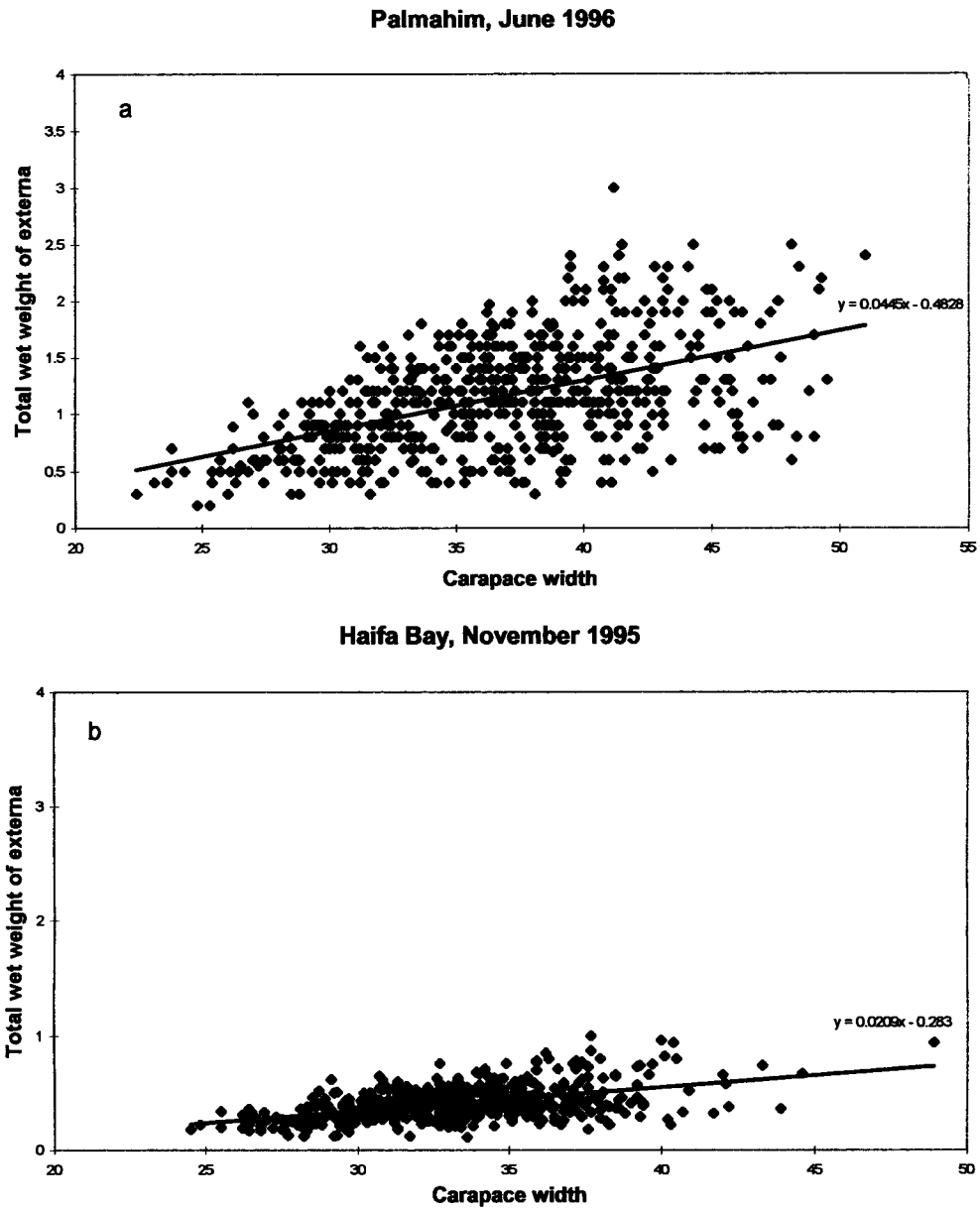

Figure 5. Linear relationships of total wet weight of externae of *Heterosaccus dollfusi* and size (CW) of *Charybdis longicollis* from a) Palmahim, June 1996, b) Haifa Bay, November 1995.

Hoeg (1995) maintains that stunted males are an indication of "feminization" of the hosts; would larger infected females be considered "masculinized"?

SEX RATIO.—Both sexes of *P. pelagicus* crabs in Moreton Bay, Australia, were found to be equally infected by *S. granifera* (Phillips and Cannon, 1978; Weng, 1987; Shields, 1992), though in the Gulf of Carpentaria, male crabs were infected more often than females (Weng, 1987). In the *C. sapidus* population of the Gulf of Mexico, females were infested more often than males even when the latter

were more abundant (Lazaro-Chavez et al., 1996). Similarily, in the *Paralithodes platypus* population of Glacier Bay, Alaska, females were prone to infestation by *Briarosaccus callosus* more than males (Hawkes et al., 1986).

Though in the first post-infestation samples taken at Palmahim (October 1993), 25% of the non-infested crabs were males, the percentage of non-infested males in subsequent samples (November 1994, November 1995) was significantly higher. In all samples, males constitute a majority of infected crabs, from 55.7% in October 1993, Palmahim, to 75.6% in November 1995, Haifa Bay. These results are in accordance with those reported by Lützen (1984), who found that though sex ratio for the entire population of *Carcinus maenas* in Isefjord, Denmark, was about even, males were more often infected by *S. carcini* and constituted 66–75% of all infected crabs.

MULTIPLE INFESTATION.—The occurrence of five and six externae per host is highly unusual and has been recorded only in few instances (Galil and Lützen, 1995).

Sloan (1984) noted that multiple infestation was more frequent in crowded populations and attributed it to higher rates of re-infection. Our results suggest that multiple infestation may be related to incidence of infestation, and occurs more frequently when the host population is heavily infested due to recurrent re-infection. Contagious distributions were noted in *Callinectes* populations in the Gulf of Mexico (Lazaro-Chavez, 1966; Alvarez and Calderon, 1966) and may be due to the aggregated pattern of distribution of the crabs (Hoeg, 1982).

The rapid spread and the high prevalence of *H. dollfusi* infestation can be ascribed to the dense population of the host and the year-round reproduction of the parasite, causing recurrent infection. As heavily-infested populations are presumably maintained by immigration (Kuris, 1974; Yamaguchi et al., 1994), it is likely that the Levantine population of *C. longicollis,* effectively isolated from its Indian Ocean source, will suffer drastic perturbations as it is doubtful immigration of non-infested crabs through the Suez Canal suffices for population renewal.

ACKNOWLEDGMENTS

G. I. stay in Israel was supported by the Israel Government scholarships, Ministry of Foreign Affairs.

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DATE SUBMITTED: November 10, 1996. DATE ACCEPTED: May 12, 1997.

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