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HERE AND THERE: A PRELIMINARY NOTE ON THE PREVALENCE OF AN ALIEN RHIZOCEPHALAN PARASITE AT THE SOUTHERN AND NORTHERN LIMITS OF ITS INTRODUCED RANGE

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ABSTRACT: The Erythrean invasive swimming crab *Charybdis longicollis* established dense populations in the Levantine Basin of the Mediterranean Sea in the mid 20th century. The crabs were subsequently parasitized by the rhizocephalan *Heterosaccus dollfusi*, itself an Erythrean alien. In May 2008, the crab populations were sampled at the southern (Israel) and northern (Turkey) limits of its introduced range. The prevalence of infection was 3 times as high, and multiple externae-bearing hosts more than 4 times as many, in Israeli waters as in Turkey. It seems that off the Israeli coast, the water temperature permits the synchronous ontogenetic development of both host and parasite, ensuring the availability of plentiful young, recently-molted, prospective hosts for infection by the short-lived parasite cypris. It is possible that the lower water temperature off Antalya (Turkey) may affect the timing of ontogenetic development of one species or the other, or increase the mortality of infected hosts, resulting in drastically reduced parasite prevalence.

Absence of natural enemies, be it competitors, predators, pathogens, or parasites, is one of the explanations given for the success of alien biota (Wolfe, 2002; Torchin et al., 2003). Diminished parasitization of alien species has been attributed to uninfected life history stages of the originator inoculum, the small numbers of the founding population, the absence of intermediate hosts in the new locale, host-specificity of native parasites, or some combination of these factors, that forestalls infection of alien hosts. However, although parasite species richness may be lower in alien hosts in their new range, the prevalence of infection may be many times higher (Galil and Lützen, 1995; Hines et al., 1997; Kruse and Hare, 2007). Invasive species management benefits from higher infection values by using parasites from the host's home range to reduce the host population densities (Hoddle, 2004). Indeed, Kuris (1997) proposed the use of rhizocephalan parasites as control agents for invasive marine decapod crustaceans, since they inflict reproductive death on their host and thus may serve as important regulators of host population density (but see Innocenti and Galil, 2007).

The Levantine populations of the Erythrean invasive swimming crab *Charybdis longicollis* Leene, 1938, have been parasitized by the sacculinid rhizocephalan *Heterosaccus dollfusi* Boschma, 1960, itself an Erythrean alien (Galil and Lützen, 1995) (Fig. 1). *Charybdis longicollis* was first recorded in the Mediterranean in 1954 from the Bay of Mersin, Turkey, and in 1961 from Tel Aviv, Israel (Lewinsohn and Holthuis, 1964). *Heterosaccus dollfusi* was first collected in the Mediterranean off the central Israeli coast in 1992 (Galil and Lützen, 1995), and in 1994 off the southeastern coast of Turkey (Øksnebjerg et al., 1997; Øksnebjerg, 2000). Since 1995, no data have been available on its prevalence of infection in the Turkish populations of *C. longicollis*.

Data on marine obligate host–parasite associations when both host and parasite are aliens are exceedingly rare (Torchin et al., 2002) but can be particularly instructive concerning the plasticity of their life history characteristics and population dynamics. An earlier study that examined the temporal variability of *H. dollfusi* prevalence at Palmahim, Israel, a site at the southern end of its introduced range, found that despite the high prevalence of the parasite and its injurious impact on the host, there was ''no noticeable reduction in the host population'' (Innocenti and Galil, 2007). We sought, therefore, to examine the spatial variability of the parasite's prevalence along a latitudinal gradient within its introduced range in order to study its impact on the crab population. To that end, we sampled the crab populations off Palmahim (Israel) and Antalya (Turkey) in May 2008.

MATERIALS AND METHODS

The Israeli material was collected within the framework of a monitoring program off the coast of Palmahim. The material was collected by the R/V *Shikmona* using a 1.15-m wide beam-trawl, with 5-mm mesh at the cod end, at depth of 30–37 m, during 22–23 May 2008. The sample consisted of 12 trawls of 20 min duration. The material from all trawls was pooled. The Turkish material was collected off Antalya, Turkey. The material was collected by the F/V *Zeytinoğlu.2* using an 8-m wide trawl, with 15-mm mesh at the cod end, at depth of 20–40 m, during 23 May 2008. The sample consisted of 2 trawls of 90 min duration. The material from the trawls was pooled. Examination of the host included determination of sex, size (carapace width [CW], distance between tips of lateral spines of the carapace to nearest mm), presence of parasite, and number of externae. The presence of the parasite in non–externae-bearing hosts was determined by the modification of the shape of the abdomen and abdominal appendages (Galil and Lützen, 1995). Data were analyzed with a G-test and with ANOVA; a SNK test was used as for post-hoc multiple comparison, with significance level set at $P < 0.05$.

RESULTS

Prevalence of parasites

In May 2008, some 1,308 specimens of *C. longicollis* were collected off Palmahim, Israel, and 944 off Antalya, Turkey. Of these specimens, 822 (62.8%) and 183 (19.4%), respectively, were either externae-bearing or morphologically-modified crabs. The prevalence of infection in Palmahim waters was, therefore, more than 3 times higher than off Antalya (Table I).

Effect of parasites on host size

Examination of CW measurements of uninfected *C. longicollis* indicated that the average, and maximal, size of males were significantly larger than females in both locations (ANOVA, $F =$

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FIGURE 1. *Charybdis longicollis* parasitized by 6 *Heterosaccus dollfusi*, collected off Palmahim (Israel).

133.1542, df = 2, 245, $P < 0.0001$), but the maximal size of both sexes was greater in the Antalya material (Table II). A post-hoc SNK test revealed that the uninfected males were significantly larger than either uninfected females (F and F OV), externae-bearing (ME, FE) or morphologically-modified crabs (MI, FI) of either sex in both locations, while the uninfected crabs from Antalya were significantly larger than those collected off Palmahim (t = 2.021, df = 1, 245, $P < 0.05$). The average and maximal sizes of externae-bearing crabs of both sexes were nearly identical in the Israeli and Antalya material. The average and maximal sizes of externae-bearing females were significantly greater than uninfected females in both localities (externae-bearing females vs. uninfected females from Palmahim: t = 7.014, df = 481, $P < 0.01$; from Antalya: t = 2.473, df = 348, $P < 0.02$).

Examination of the size (CW) frequency distribution of *C. longicollis* indicated that a much larger fraction of the Palmahim population were between 35- and 40-mm wide, and that many more in this size range were infected (Fig. 2a) than in Antalya (Fig. 2b). Larger male crabs (CW > 50 mm off Palmahim; CW > 45 mm off Antalya) were not infected, and their fraction was smaller off Palmahim.

TABLE I. Prevalence of parasitization in *Charybdis longicollis* off Palmahim, Israel, and Antalya, Turkey. M, F, and F OV, respectively, uninfected males, females, and ovigerous females; MI and FI, males and females with internal infection; ME and FE, externae-bearing males and females.

	Palmahim, 22–23 May		Antalya, 23 May	
	N	%	N	%
M	264	20.2	481	51.0
F	62	4.7	41	4.3
F OV	160	12.2	239	25.3
MI	96	7.3	20	2.1
ME	409	31.3	82	8.7
FI	56	4.3	11	1.2
FE	261	20.0	70	7.4
Total	**1308**		**944**	
Total not infected		486		761
Total infected		822		183
% Infection		62.8		19.4

TABLE II. Effects of parasitization on host size (carapace width, in mm). M, F, and F OV, respectively, uninfected males, females, and ovigerous females; MI and FI, males and females with internal infection; ME and FE, externae-bearing males and females.

	Palmahim, 22–23 May			Antalya, 23 May		
	Average size	SD	Range	Average size	SD	Range
M	42.47	7.8	18.1–56.9	41.76	7.9	21.6–63.5
F	31.72	4.1	21.3–41.3	32.44	4.3	24.6–37.7
F OV	33.80	3.1	28.1–41.8	35.21	3.3	27.1–46.7
MI	33.15	4.2	23.5–46.8	34.28	5.9	27.1–53.4
FI	32.64	4.6	19.7–42.8	30.33	3.9	25.3–39.0
ME	35.85	4.9	23.3–49.3	36.68	4.6	26.3–54.7
FE	35.56	4.0	24.4–49.4	36.03	4.2	25.8–43.9

Multiple infections

Multiple infections were common in the Palmahim population of *C. longicollis*, i.e., over half of the externae-bearing hosts harbored more than 1 externa, and nearly 20% bore 3 or more. In contrast, most of the externae-bearing hosts (84.2%) collected off Antalya bore a single externa, and only 4.5% bore 3 or more (G = 67.100, df = 4, $P < 0.001$) (Table III).

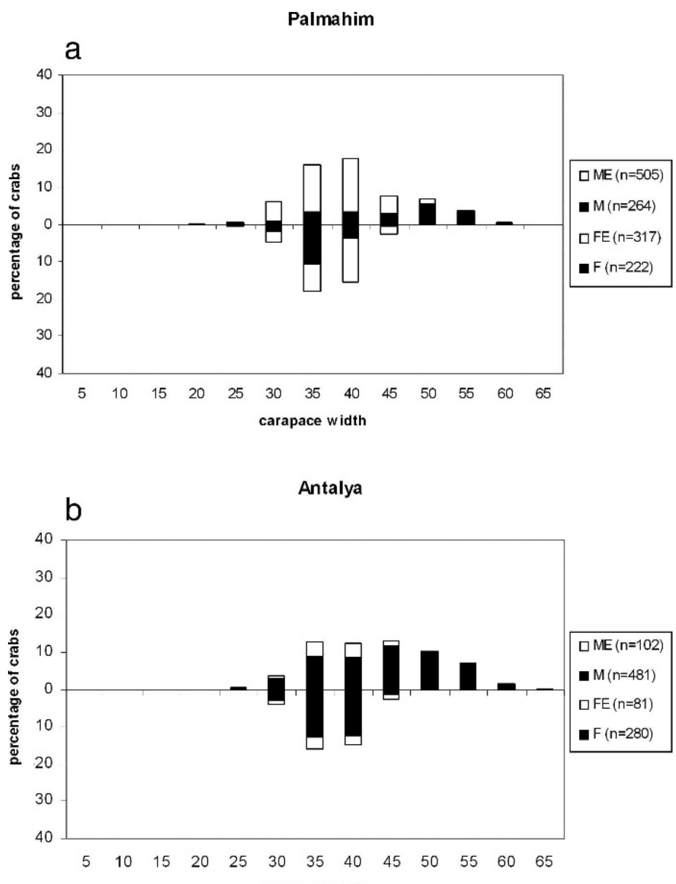

FIGURE 2. (**a**) Size (CW) frequency distribution of *C. longicollis* of the Palmahim population. (**b**) Size (CW) frequency distribution of *C. longicollis* of the Antalya population.

TABLE III. Prevalence of multiple externae in *Charybdis longicollis* off Palmahim, Israel, and Antalya, Turkey.

No. of externa	Palmahim n	Palmahim %	Antalya n	Antalya %
1	329	49.1	128	84.2
2	208	31.0	17	11.2
3	97	14.5	5	3.3
4	22	3.3	1	0.7
>5	14	2.1	1	0.7
Total externae-bearing crabs	670	100	152	100

DISCUSSION

Charybdis longicollis has been recorded in the Mediterranean since the mid 1950s (Lewinsohn and Holthuis, 1964). Already early on it was ". . .found to be quite frequent on the Turkish south coast" near Antalya and Mersin (Holthuis, 1961), and observers noted ". . .a steady rise in the population sizes" on the Turkish Mediterranean coast (Øksnebjerg et al., 1997). Similarly, scientists reported that the ". . .species became so abundant in southern Israel coastal waters that it now must be considered a true pest, the fishermen complain that their nets are filled with these crabs" (Lewinsohn and Holthuis, 1964). Its introduced range extends from Egypt to the Levantine coast of Turkey, Cyprus, and Rhodes I., Greece (Galil et al., 2002; Ozcan et al., 2007), and it was recently reported from the southern Turkish coast of the Aegean Sea (Yokes et al., 2007). In the Mediterranean, it inhabits depths of 10 to 135 m. It is particularly common on sandy-mud bottoms at depths of 25–60 m, where it is the most abundant trawl-caught decapod crustacean and may constitute as much as 70% of the benthic biomass (Galil, 1986; Ozcan et al., 2005).

Heterosaccus dollfusi was collected almost concurrently off the Israeli and the southeastern coast of Turkey in the early 1990s (Galil and Lützen, 1995; Øksnebjerg et al., 1997). Of the thousands of specimens of the host, *C. longicollis*, collected off the Israeli coast and studied by one of us (B. S. Galil, pers. obs.), none bore a rhizocephalan parasite before 1992. Similarly, off the Turkish coast, where the host is common trawl by-catch "no parasites have ever been observed" (Galil and Lützen, 1995), and "[u]ntil the spring of 1994, none of the specimens [of *C. longicollis*] were parasitized by rhizocephalans" (Øksnebjerg et al., 1997). The parasite has not been observed to infect other portunid crabs co-occurring with *C. longicollis*, neither the aliens *Charybdis helleri* (Milne Edwards, 1867) and *Portunus pelagicus* (Linnaeus, 1758), nor the native *Portunus hastatus* (Linnaeus, 1767). The parasite causes sterilization, morphological and behavioral feminization, and cessation of molting in its host (Galil and Lützen, 1995; Innocenti et al., 1998; Galil and Innocenti, 1999; Innocenti and Galil, 2007).

Along the central Israeli coast, parasite prevalence in host populations has been fairly high and exhibited long-term (13 yr) temporal stability (May 1994, 62.6%; June 1996, 67.4%; May 2002, 58.6%; May 2004, 44.4%; May 2005, 65.9%; May 2006, 58.1%; May 2007, 69.8%) (Galil and Innocenti, 1999; Innocenti and Galil, 2007, 2010), similar in value to the result obtained in the present study (62.8%). In the sole record of the parasite from Turkey, in April 1995, the prevalence of infection was reportedly 90% (of the 39 specimens collected) between Fener Burnu and Karatas and 50–60% to the east of Karatas, but "no infected specimens have been recorded at all" elsewhere (Øksnebjerg et al., 1997; Øksnebjerg, 2000).

The results of our sampling show that though the crabs had established prolific populations in the Levant in the middle 20th century, that parasite colonization occurred in the last decade of the century, and that prevalence of infection differed markedly between the southern and northern locales in its introduced range.

The size modification of parasitized *C. longicollis* is pronounced. The average and maximal sizes of uninfected males are larger than externae-bearing males, whereas uninfected females are often smaller than externae-bearing females. The maximal size of uninfected males collected off Antalya (63.5 mm) is similar to that of uninfected males collected off Palmahim in May 1994 and June 1996, but not encountered since (Galil and Innocenti, 1999; Innocenti and Galil, 2007; this study). Innocenti and Galil (2009) noted that multiple externae are related to prevalence of infestation, since the parasite avoids settling on an already infected host and does so only when the chances of encountering an uninfected host are diminished. The pattern that emerges from the percentage of externae-bearing hosts bearing more than a single externa (May 1994, 52%; June 1996, 55%; May 2002, 47.6%; May 2004, 37%; May 2005, 58%; May 2006, 52%; May 2007, 61%; May 2008, 51%) is that it increases sharply when the prevalence of infection rises above 50%. There is a small percentage of externae-bearing hosts bearing more than a single externa off Antalya (15.8%), though the density of the host population is high, which is further evidence that parasite recruitment off Antalya is indeed a fraction of that in Palmahim and not a fortuity of the sampling.

The prevalence of rhizocephalans, e.g., in *Sacculina carcini*, Thompson 1836, often present wide local variations, even when populations are observed over short distances (e.g., Werner, 2001). While this phenomenon has for the most part been poorly studied, factors such as host sex, size, molting frequency, molt stage, and migratory behavior, as well as environmental factors such as temperature, salinity, and depth, may presumably affect parasite recruitment (see Boone et al., 2004). Also, host defenses, including an immune response to counteract cypris settlement, are presumed to control prevalence. What then could constrain the parasitization of *C. longicollis* in the northern part of its introduced range? Physical dispersal barriers are unlikely to have been responsible for the reduced parasite prevalence since the spread of the host, and then the parasite, throughout the Levant was rapid.

Could it be a biological response of a thermophilic alien to a latitudinal gradient in temperature? Sea surface temperature in May at Palmahim is approximately 20.5 C, and near bottom at a depth of 30 m, 18 C (N. Kress, pers. comm.), whereas off Antalya, spring surface water temperature is no higher than 17.6 C, and at 30 m, 16.6 C (Eryilmaz and Eryilmaz, 2008). As in other species of rhizocephalans, *H. dollfusi* passes through a succession of stages starting with the infection of the vulnerable soft-shell juvenile host by a female cypris larva. Data from the population off the Israeli coast suggest that this critical stage is present in spring (Galil and Lützen, 1995). Off the Israeli coast, the water temperature permits the synchronous ontogenetic development of both host and parasite, ensuring availability of plentiful young and recently-molted prospective hosts to the short-lived parasite cypris. The lower water temperature off Antalya may affect the timing of ontogenetic stages of one or the other, or increase the mortality of infected hosts, resulting in a sharply reduced infection success.

We are mostly ignorant of the mechanisms through which climate translates into ecologically important changes in populations, but it is likely that temperature has a significant influence on the establishment and distribution of a thermophilic parasite through its impact on a suite of population characteristics (reproduction, survival) that determines interspecific interactions and, therefore, the prevalence patterns of both host and parasite species. It is proposed that the differential rhizocephalan parasitization of the southern and northern populations of *C. longicollis* reflects a latitudinal gradient of temperature that resulted in a temporal mismatch between parasite and host.

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