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A host, a parasite, and a predator: the dynamics of successive invasions in the eastern Mediterranean

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Abstract

The eastern Mediterranean shelf ecosystem has been profoundly disrupted by the influx of invasive alien species introduced through the Suez Canal. Yet, the role of retaining or shedding co-evolved parasitofauna in the success of the invading biota has been scarcely monitored, with the exception of the lesser swimming crab *Charybdis* (*Archias*) *longicollis* Leene, 1938 parasitized by the rhizocephalan *Heterosaccus dollfusi* Boschma, 1960. Host size, sex ratio, prevalence of ovigerous females, parasitization, and multiple parasitization, were studied over 30 years to determine long-term host-parasite variation. Our results reveal that *C. longicollis* crabs have shifted their temporal activity pattern shortly following the domination of their preferred depth niche by the invasive diurnal predator, the silver-cheeked toadfish *Lagocephalus sceleratus* (Gmelin, 1789), which preferentially feeds on *C. longicollis* locally. A unique set of predator-host-parasite interactions among three successive Erythraean invasive aliens is considered herein.

Key words: invasive alien species, Mediterranean Sea, diel activity shift, *Charybdis* (*Archias*) *longicollis*, *Heterosaccus dollfusi*, *Lagocephalus sceleratus*

Introduction

The Levantine Basin, Mediterranean Sea, has endured an extraordinarily high influx of Erythraean biota ever since the opening of the Suez Canal in late 19th Century (Galil 2023). The realization that marine biological invasions profoundly disrupt native ecosystems came early to those who witnessed them firsthand (W. Steinitz 1919; H. Steinitz 1970). Yet, the role of 'parasite escape', the shedding of co-evolved parasitofauna, in the success of the Erythraean biota invading the Mediterranean Sea received little attention (Paperna 1972; Diamant 2010).

The lesser swimming crab *Charybdis* (*Archias*) *longicollis* Leene, 1938 is native to the Red Sea, Arabian (Persian) Gulf, Gulf of Oman, off East Africa and off northwestern Madagascar (Türkay & Spiridonov 2006; Naderloo 2017). It was first collected along the Mediterranean Israeli coast in 1961, where already it occurred in great numbers (Lewinsohn & Holthuis 1964), and subsequently spread throughout the Levant, from Egypt to Greece (Galil & Kevrekidis 2002). Following a temporary parasite escape, the parasitic barnacle *Heterosaccus dollfusi* Boschma, 1960, an Erythraean alien as well, were discovered parasitizing a few specimens of *C. longicollis* in 1992 (Galil & Lützen 1995). *H. dollfusi* was described from five specimens of *C. longicollis,* identified as *C.* (*Goniohellenus*) *hoplites* (Wood-Mason, 1877), collected in the Gulf of Suez in 1928 by Dr. R. Ph. Dollfus (Monod 1938; Boschma 1960). Since then, interestingly, no more *H. dollfusi* specimens were described from its presumed native range. The introduction and spread of *H. dollfusi* in recently "naïve" host populations outside its native range offer a natural test of the potential effects of interaction on the host's ecology. Its impact on the host is extreme. *H. dollfusi* causes sterilization, morphological and behavioral feminization, curtailment of molting and mortality induced by nutrient extraction. By reducing recruitment, biomass, growth and survival of its host, and its considerable prevalence, *H. dollfusi* was expected to reduce its host population (Galil & Lützen 1995; Innocenti *et al.* 1998; Galil & Innocenti 1999; Innocenti & Galil 2007). Though *H. dollfusi* had been recorded as reaching prevalence exceeding 80%, it did

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not seem to impact its host's abundance (Innocenti *et al*. 2017). In the early 1990s *C. longicollis* was singled out as the main crustacean discarded by Israeli trawl fishers (Edelist *et al*. 2011), and in Spring 2021 it had still dominated nocturnal and diurnal trawl hauls at 40 m depth, constituting 96% of the total abundance (N. Stern, pers. comm.).

Parasites may increase vulnerability of infected hosts to predation, thus predation pressure that reduces both host and parasite populations is supposed to keep infection rates relatively low (Lopez & Duffy 2021). It so happened that the Erythraean silver-cheeked toadfish *Lagocephalus sceleratus* (Gmelin, 1789), first collected off the Israeli coast in 2004 (Golani & Levy 2005), established abundant populations in the 18–45 m depth niche (Chaikin *et al*. 2023; Frid *et al*. 2023). Analysis of its gut contents revealed that *C. longicollis*, is by far the most frequent prey item (relative abundance 0.465) *L. sceleratus* feeds on, constituting 49% of the Erythraean alien prey items (Chaikin *et al*. 2023).

Here the effects of three successive Erythraean aliens are studied: the lesser swimming crab *C. longicollis*, host to the castrating rhizocephalan *H. dollfusi*, both preyed upon by the pufferfish *L. sceleratus*. The recent host size, sex ratio, ovigerous females, prevalence of parasitization, and multiple parasitization are compared with earlier data (2008 to 2011) to determine long-term variation as well as the apparent shift in temporal activity .

Materials and methods

The lesser swimming crabs were collected off Ashdod, Israel, between November 2021 and November 2022. Sampling was carried out onboard the 240 hp bottom-trawler '*Moti*', using an otter trawl with a distance of 70 m between otter boards, vertical and horizontal openings of 2 and 12 m, respectively, 20 m long from opening to cod-end, 40 mm diamond shaped cod-end mesh. Each cruise consisted of nocturnal trawling along two isobaths, each repeated twice. Each tow lasted 90 minutes, at an average speed of 2.8 knots, covering an estimated swept area of 90,000 m². Samples were taken along the 40 m isobath (November 2021, 2022), and along the 60 m isobath (December 2021, May 2022, November 2022) (Tab. 1). The entire catch was transported to the laboratory and sorted. As few specimens were collected during daytime hauls, the material examined consists of the night trawl hauls only. Crab specimens were examined, their sex noted, the carapace width (CW, i.e. distance between tips of lateral spines of the carapace to nearest mm) was measured, and the presence of the parasite and number of externae (external part of the rhizocephalan parasite) were observed. The presence of the parasite in non-externa bearing hosts was visually recognized by the modification of the shape of the abdomen, lack of the abdominal appendages and by the position of gonopores (Galil & Lützen 1995).

TABLE 1. Hauls during the years 2021–2022. Total number of collected *Charybdis longicollis*.

Date	Depth (m)	GPS_Start_N	GPS_Start_E	Start_time	GPS_End_N	GPS_End_E	End_Time	N	NetID
30/11/2021	40	31°51.976 N	34°34.588 E	-	31°47.713 N	34°31.739 E	-	96	5
14/12/2021	60	31°49.255 N	34°29.913 E	10:30:00 PM	31°45.309 N	34°27.163 E	12:00:00 AM	254	7
15/12/2021	60	31°45.198 N	34°27.054 E	12:40:00 AM	31°49.416 N	34°30.090 E	2:10:00 AM	204	8
31/5/2022	60	31°50.130 N	34°30.550 E	0:55:00	31°46.300 N	34°27.800 E	2:25:00	530	7
31/5/2022	60	31°46.200 N	34°27.600 E	3:10:00	31°50.300 N	34°31.000 E	4:40:00	215	8
14/11/2022	40	31°51.500 N	34°34.000 E	6:15:00 PM	31°47.450 N	34°31.330 E	7:45:00 PM	585	5
14/11/2022	40	31°47.400 N	34°31.400 E	8:25:00 PM	31°51.660 N	34°34.100 E	9:55:00 PM	911	6
22/11/2022	60	31°45.700 N	34°27.200 E	12:30:00 AM	31°49.800 N	34°30.300 E	2:00:00 AM	1171	8

The same vessel, equipment and procedure was utilized in 2008–2011 surveys off Ashdod (Innocenti *et al*. 2017). The number of surveys and their timing were constrained by funding, weather and the availability of the fishing vessel engaged for the task. Surveys antedating 2008 were carried out off Palmahim (31°46'N 34°27'E, 12 km north of Ashdod) at 29–37 m depth, aboard the RV 'Shikmona' using a 1.15 m wide beam trawl, with a cod end mesh size of 22 mm. Each sample consisted of 12 hauls, lasting 20 min each, at an average speed of 2.2 knots, pooled. The samples were fixed in 10% formaldehyde seawater before being transferred to 70% EtOH for storage.

The carapace width data obtained between 2008 and 2021 were analyzed using a series of Generalized Additive Models (GLMs) with gaussian distribution after visually confirming the distribution of the data with histograms using the *glm* function of the MASS R package (Ripley *et al*. 2013). Carapace widths were analyzed as a function of the following predictors: 'year', 'depth' [two levels; 40 m, 60 m] at which samples were obtained, 'sex' [two levels; male, female], 'parasitization' [two levels; yes, no], and the 'number of externa' [multiple levels; 0=no parasites; 1=1 externa; >1=2-8 externa]. We further specified our analysis of male and female individuals separately, across the two periods (periods: 2008–2011; 2020–2022), and regarding the degree of parasitization (not parasitized, internally parasitized, specimens with externae) using Analyses of Variance (ANOVA). The level of significance set at $p < 0.05$. All analyses were performed using R version 4.2.3 (RCore Team 2022).

Results

Host size. Examination of CW measurements of unparasitized *C. longicollis* collected at 40 m (November 2021, 2022) indicated that average and median size of males was markedly higher than females (F=8.585, df=1857, P<0.001), and the larger size classes were unparasitized (Figs. 1, 2). The gap was reduced or reversed at 60 m (December 2021; May, November 2022) (F=5.561, df=1186, P<0.001). The internally parasitized males and females were significantly smaller than externae-bearing males and females throughout (means respectively 27.7 and 33.0; F=15.49, df=2778, P<0.001). Externae-bearing females were significantly larger than unparasitized females throughout (means respectively 28.6 and 33.2; F=37.248, df=785, P<0.001) (Tab. 2).

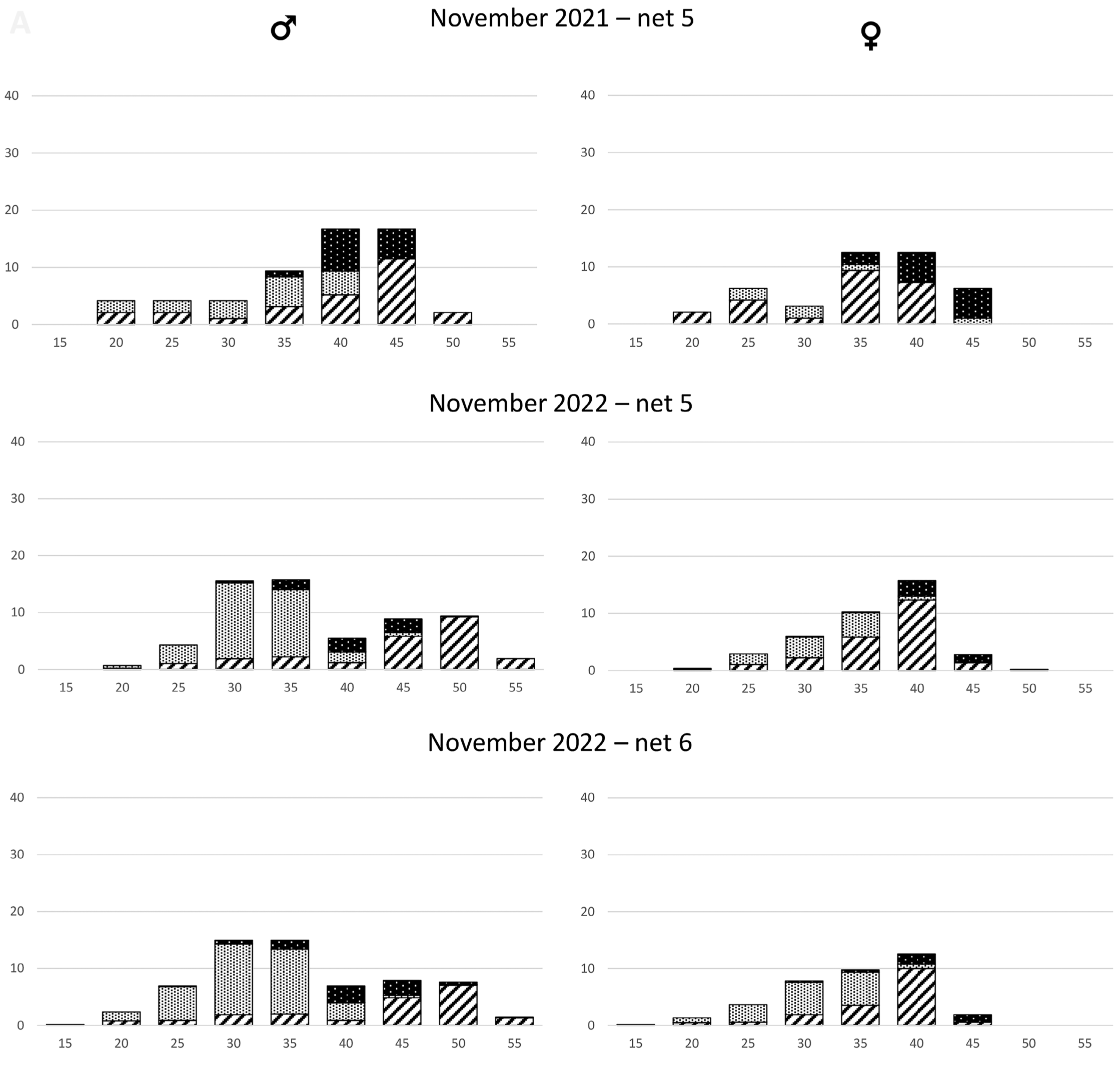

FIGURE 1. Carapace width of *Charybdis longicollis* collected off Ashdod, Israel, at 40 m depth. Legend: stripes—unparasitized crabs; black dots—internally parasitized crabs; white dots—externa-bearing crabs; males on the left, females on the right.

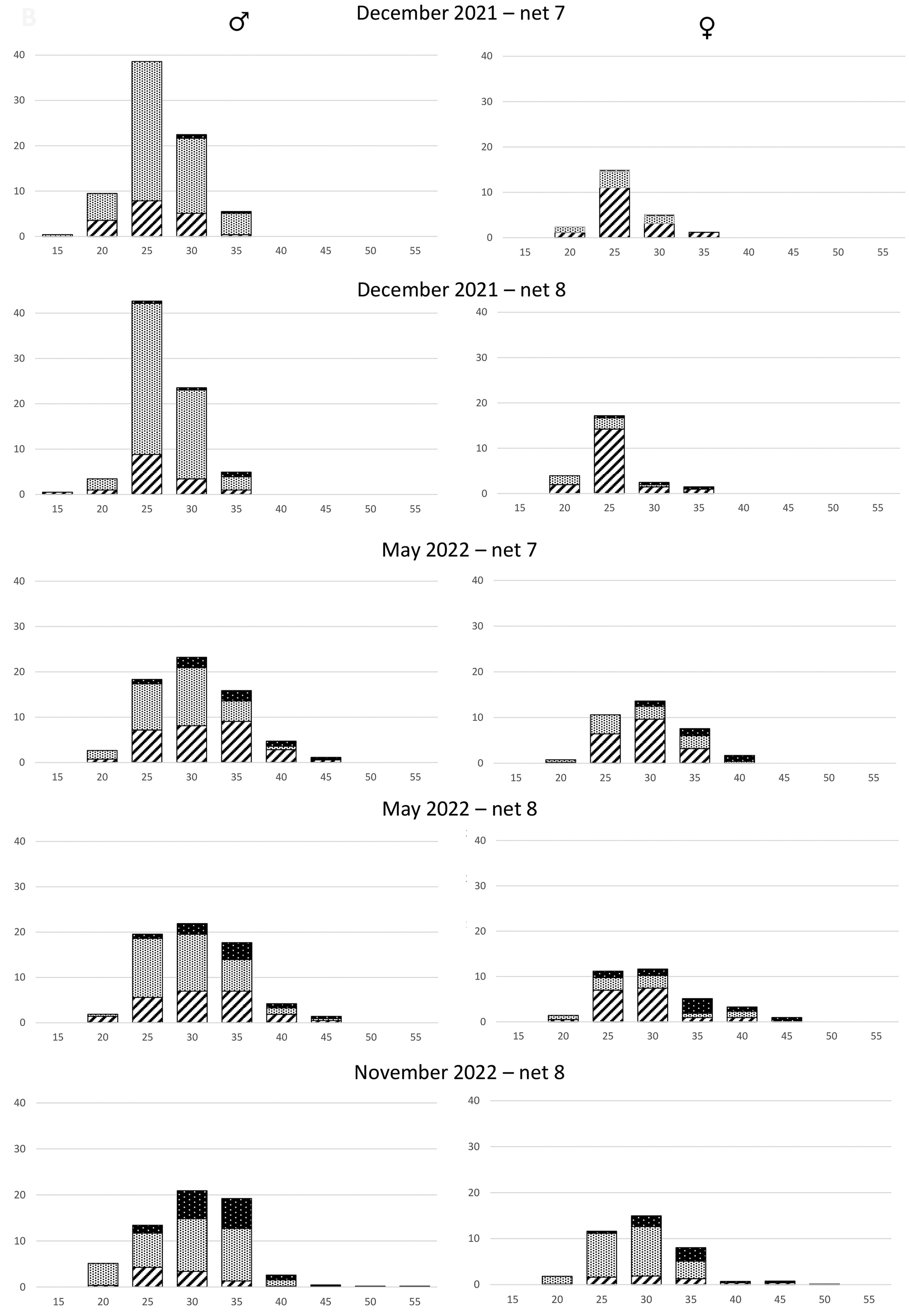

FIGURE 2. Carapace width of *Charybdis longicollis* collected off Ashdod at 60 m depth. Legend: stripes—unparasitized crabs; black dots—internally parasitized crabs; white dots—externa-bearing crabs; males on the left, females on the right.

TABLE 2. Total number of collected *Charybdis longicollis*, M UP, unparasitized males, F UP, unparasitized females, M IP, internally parasitized males, F IP, internally parasitized females, M EB, externa bearing males, F EB, externa bearing females. Sex ratio, UP, unparasitized crabs, P, parasitized crabs; %P, percentage of parasitized crabs, %E, percentage of externa bearing crabs. CW, carapace width, SD, standard deviation.

Date, depth (m)		**N**	**CW Av**	**median**	**SD**	**CW range**	**%P**	**%E**
November 2021								
40	M UP	26	36.6	39.9	2.0	17.3–46.3		
Net 5	F UP	23	30.8	33.1	6.0	18.8–38.3		
	M IP	16	29.7	31.6	6.3	18.3–36.7	16.7	
	F IP	6	28.7	26.2	7.3	22.0–42.5	6.3	
	M EB	13	39.0	39.7	2.0	35.0–41.3	13.5	
	F EB	12	38.4	38.9	3.5	32.7–43.9	12.5	
total		**96**					49.0	53.2
Sex Ratio	UP	53.1						
	P	61.7						
December 2021								
60	M UP	43	23.5	23.2	3.7	17.2–31.5		
Net 7	F UP	42	23.6	22.9	3.4	16.0–32.0		
	M IP	148	24.4	24.3	3.5	14.3–34.7	58.3	
	F IP	16	23.0	23.6	2.5	17.2–26.6	6.3	
	M EB	3	27.7	26.8	2.5	25.8–36.6	1.2	
	F EB	2	26.8	26.8	3.8	24.5–29.8	0.8	
total		**254**					66.5	3.0
Sex Ratio	UP	50.6						
	P	89.3						
December 2021								
60	M UP	30	23.7	23.6	4.1	11.4–34.0		
Net 8	F UP	38	23.0	22.5	3.3	17.1–34.0		
	M IP	119	24.6	24.6	3.0	21.9–33.3	58.3	
	F IP	10	22.1	22.0	4.0	24.6–33.0	4.9	
	M EB	4	28.2	28.9	5.1	15.6–34.8	2.0	
	F EB	3	29.0	29.5	4.2	17.1–29.8	1.5	
total		**204**					66.7	5.1
Sex Ratio	UP	44.1						
	P	90.4						

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TABLE 2. (Continued)

Date, depth (m)		N	CW Av	median	SD	CW range	%P	%E
May 2022								
60	M UP	151	28.7	29.0	5.2	28.7–44.3		
Net 7	F UP	103	26.6	26.6	3.6	15.5–34.5		
	M IP	161	26.3	26.1	4.3	16.6–42.8	30.4	
	F IP	57	27.0	26.0	4.8	16.8–38.9	10.8	
	M EB	37	30.8	30.6	5.3	20.7–43.7	7.0	
	F EB	21	32.2	32.1	3.8	26.3–37.1	4.0	
total		**530**					52.1	21.0
Sex Ratio	UP	59.4						
	P	71.7						
May 2022								
60	M UP	50	28.7	28.2	5.2	19.4–40.9		
Net 8	F UP	36	26.2	25.4	3.8	19.6–36.4		
	M IP	75	27.3	27.0	4.8	18.5–40.7	34.9	
	F IP	19	26.7	26.1	5.3	19.4–36.7	8.8	
	M EB	18	31.0	30.7	5.1	21.4–40.2	8.4	
	F EB	17	31.8	31.2	5.8	23.6–43.6	7.9	
total		**215**					60.0	27.1
Sex Ratio	UP	58.1						
	P	72.1						
November 2022								
40	M UP	137	41.8	44.7	8.2	17.3–54.8		
Net 5	F UP	134	35.0	36.3	4.6	17.9–43.1		
	M IP	184	29.8	29.9	4.3	18.7–44.2	31.5	
	F IP	63	29.5	29.1	4.8	17.5–40.8	10.8	
	M EB	41	38.0	38.7	4.8	28.7–45.4	7.0	
	F EB	26	38.8	38.8	3.5	28.8–45.2	4.4	
total		**585**					53.7	21.3
Sex Ratio	UP	50.6						
	P	77.1						

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TABLE 2. (Continued)

Date, depth (m)		N	CW Av	median	SD	CW range	%P	%E
November 2022								
40	M UP	179	40.4	44.2	9.4	15.0–54.5		
Net 6	F UP	155	34.4	35.9	5.4	14.6–42.4		
	M IP	318	29.0	29.4	5.0	16.4–49.8	34.9	
	F IP	148	28.4	28.8	4.5	16.0–38.2	16.2	
	M EB	77	37.7	38.2	5.3	22.7–50.3	8.5	
	F EB	34	38.1	38.2	3.9	28.4–44.3	3.7	
total		**911**					63.3	19.2
Sex Ratio	UP	53.6						
	P	68.5						
November 2022								
60	M UP	117	27.1	25.5	6.7	18.4–59.2		
Net 8	F UP	67	29.1	27.6	5.7	20.0–43.2		
	M IP	428	27.2	27.3	5.2	15.8–40.3	36.5	
	F IP	304	25.8	25.6	3.9	17.8–41.8	26.0	
	M EB	182	29.9	30.1	4.1	22.7–44.7	15.5	
	F EB	73	30.8	30.8	4.7	21.9–46.9	6.2	
total		**1171**					84.3	25.8
Sex Ratio	UP	63.6						
	P	61.8						

Examination of the size (CW) frequency distribution of *C. longicollis* indicated that at 60 m (December 2021; May, November 2022) the largest number of male and female crabs were sized between 25–30 mm. The largest number of male and female crabs collected at 40 m in November 2021 were sized between 40–45, 35–40 mm, respectively; males collected at 40 m in November 2022 were bi-modally arrayed (30–35, 45–50 mm), whereas the largest number of females were sized between 35–40 mm (Figs. 1, 2).

Sex ratio. The overall sex ratio of unparasitized *C. longicollis* collected at 40 m was stable, with 53.1, 50.6, 53.6% males in November 2021 (Net 5) and November 2022 (Net 5 and Net 6) respectively, though among parasitized crabs the percentage of males was higher, 61.7, 77.1, 68.5% respectively. The sex ratio of unparasitized crabs collected at 60 m varied more (44.1–63.6%), and, among parasitized crabs, the percentage of males was higher, surpassing 90% among crabs collected at in December 2021 (Tab. 2).

Ovigerous females. No ovigerous females were identified among the specimens collected on November 2021 at 40 m and in December 2021 at 60 m, and only 2 and 4 ovigerous females were collected at 60 m in May and November 2022, respectively. At both 40 m samples in November 2022 ovigerous females constituted 12.3 and 9.8% of the total number of crabs.

Prevalence of parasitization. In November and December 2021 and May and November 2022, a total of 3966 specimens of *C. longicollis* were collected off Ashdod. The prevalence of the parasite varied from 49.0% in November 2021, to 84.3% in November 2022 (Tab. 2). The percentage of externa-bearing crabs varied from 53.2% in November 2021 to 3.9% in December 2021, where internally parasitized crabs dominated. More males than females were collected and males were more prone to the parasitization. Analysis of parasitization prevalence (internally parasitisized (IP) and externae-bearing (EB) individuals) in different host size groups shows a widespread presence of IP in the 15–35 mm size classes, while EB crabs are more frequent, even if in lower numbers respect to IP, in the 35–45 mm size classes for both sexes (Tab. 2, Figs. 1, 2).

Multiple parasitization. In the samples collected in November 2021 and November 2022, off Ashdod at 40 m depth, prevalence of external parasitization (i.e., externa-bearing crabs) was 26.0, 11.4, 12.2%, of which percentage of crabs bearing multiple externae (> 1 externa/host) was 44.0, 14.9, 26.1%, respectively. Prevalence of externae differed for males and females, being slightly significant (G=6.352, P<0.1), more common on male crabs (Tab. 2). The GLM analysis underscored the presence of the parasite and the number of externae had stronger effects on male specimens (Appendix 1). Multiple externae were generally confined to smaller-sized crabs, in November 2021 the average CW was 38.7 mm (SD=1.6; median=38.4) in males and 38.2 mm (SD=3.3; median=37.9) in females; in November 2022, net 5, the average CW was 34.1 mm (SD=5.1; median=31.5) in males and 37.4 mm (SD=1.1; median=37.4) in females; in net 6 the average CW was 33.8 mm (SD=5.6; median=33.6) in males and 36.2 mm (SD=4.7; median=38.2) in females; a male crab with CW of 28.9 mm bore 6 mature externa (Fig. 3). In November 2022, at 60 m depth, the smallest males bearing 4 and 5 externa were respectively 22.9 and 25.2 mm, the smallest females respectively 26.0 and 33.1 mm.

FIGURE 3. *Charybdis longicollis* collected off Ashdod, Israel, November 2022, at 40 m depth, male, CW 28.9 mm, bearing 6 mature externae (photo: Oz Rittner).

The applied GLM analysis found that all predictors (‘year’, ‘depth’, ‘sex’, ‘presence of the parasite’, and the ‘number of externa’) significantly affected the CW of the collected *C. longicollis*, both males and females (Supplementary material).

The applied ANOVAs to the entire set of data identified that *C. longicollis* collected in deeper depths are significantly smaller (40 m: 32.9 mm±8.75; 60 m: 28.3 mm±6.14), have a significantly higher parasitization ratio (40 m: 63.1%; 60 m: 72.6%), and a significantly higher number of externa (40 m: 0.965±1.02; 60 m: 1.04±0.982) (Suppementary material).

Discussion

Studies of introductions of marine parasitic species have largely focused on their systematics, life history, and impact on native ‘novel’ hosts, in particular on those of commercial interest (Torchin *et al*. 2002; Feis *et al*. 2016; Goedknegt *et al*. 2016). Few studies have documented the population dynamics of rhizocephalans, highly modified parasites of crustaceans, and their hosts (Mouritsen *et al*. 2018; Al-Wazzan *et al*. 2021); fewer still described the population dynamics of introduced rhizocephalans. Two exceptional host-parasite histories of parasite 'spillover' without host-switching have been noted among rhizocephalans. *Loxothylacus panopaei* (Gissler, 1884), native to the Gulf of Mexico and southern Florida, was first noted in Chesapeake Bay in 1964, presumably introduced with infected panopeid crabs transplanted with oysters from the Gulf of Mexico (Van Engel *et al.* 1965). Transported to an area harboring naïve populations of the same host species as in its native region, *L. panopaei* was found to parasitize them (Hines *et al*. 1997; Tepolt *et al*. 2020). In the case of *H. dollfusi*, the parasite followed its native host, *C. longicollis*, into the Mediterranean Sea through the Suez Canal, affording the crab just a brief period of 'parasite escape' (Galil & Lützen 1995). The extreme physiological, morphological and behavioral manipulation of its host being apparent from the first (Galil & Lützen 1995; Innocenti *et al.* 1998, 2003), the temporal variability of host-parasite populations were periodically surveyed since the early 1990s to determine long-term modifications (Galil & Innocenti 1999; Innocenti & Galil 2007; Innocenti *et al.* 2009, 2017).

Host size. A sample collected in November 1987 from the pre-parasitized population off Palmahim, revealed that in the mature fall population, the CW of 45.7% of males were 45 mm or larger, and CW of 40.3% of males were 30–40 mm compared with 78.7% of the females in the same size classes (Innocenti & Galil 2011). In post-parasitization samples collected in October 1993 average CW of unparasitized males and females was 44.1 and 36.7 mm, respectively, and externa-bearing males, females 40.1, 39.0 mm, respectively (Galil & Innocenti 1999). By November 2009, average CW of unparasitized males, females collected at 40 m off Ashdod was reduced to 42.2, 33.7 mm, respectively, and externa-bearing males, females to 38.4, 36.1 mm, respectively. In November 2022, average CW of unparasitized and externa-bearing males was further reduced to 41.8, 38.0 mm, respectively, whereas the average CW of unparasitized and externa-bearing females increased to 35.0, 38.8 mm, respectively. Similarly, *Carcinus maenas* (Linnaeus, 1758) females parasitized by *Sacculina carcini* Thompson, 1836 were significantly larger than uninfected ones, whereas the opposite was the case for male crabs (Mouritsen *et al*. 2018).

The stunting of rhizocephalan-parasitized crabs has been conventionally attributed to moult inhibition, fewer molts, and smaller moult increments (Phillips & Cannon 1978; O'Brien & Van Wyk 1985; Hawkes *et al*. 1987; Hoeg 1995). Parasite-induced moult interruption however, fails to explain the size increase in parasitized female specimens. Since the fecundity of the parasite is related to externa size, and the latter is dependent on the size of the host, it is proposed that *H. dollfusi* regulates the host size to best endure the significant metabolic costs of the reproductive externa, and provide it with optimal physical protection (Innocenti & Galil 2007).

Epibionts. Of the 3966 specimens collected in November 2021 and 2022, only three crabs bore a single serpulid polychaete each on the carapace. The absence of epibionts was remarkable as both unparasitized and parasitized *C. longicollis* crabs have been noted to bear epibionts, more commonly on specimens bearing mature externae (Galil & Lützen 1995). The frequency of epibionts reached its apogee in fall 2007, when more than a third of the externae-bearing crabs were fouled with the serpentine calcareous tubes of the Erythraean alien serpulid polychaete, *Hydroides operculatus* (Treadwell, 1929) compared with only 1% of the unparasitized crabs (Innocenti & Galil 2011: fig. 9). It has been frequently commented that prevalence of fouling on rhizocephalan-parasitized crabs is higher than on unparasitized ones (Phillips & Cannon 1978; Lützen & Takahashi 1997; Isaeva *et al*. 2001; Gaddes & Sumpton 2004; Mouritsen & Jensen 2006; Lützen *et al*. 2018). The proliferation of epibionts on externally parasitized crabs has been variously ascribed to inhibited or curtailed moulting, reduced grooming and burying of the host, and energetic burden. It may be that the energetic cost of bearing epibionts along with large externa-mass is too great a burden and increases host mortality. In addition, the none too nimble doubly hampered individual is highly vulnerable to predation (Innocenti *et al*. 1998).

Host sex ratio. The sex ratio of *C. longicollis* pre-infestation samples collected off Palmahim in 1977 and 1987 was about equal (Galil & Innocenti 1999). Yet, post-infestation sex ratios diverged greatly both between non-parasitized and parasitized *C. longicollis*: in November 1994, at 40 m depth, male to female ratio was 56.1/43.9% among non-parasitized crabs, and 71.4/28.6% among parasitized crabs. In November 2021 and 2022, at 40 m depth, sex ratio was 53.1/46.9%, 50.6/49.4% and 53.6/46.4% among non-parasitized crabs, 61.7/38.3%, 77.1/22.9% and 68.5/31.5% among parasitized crabs. A decade earlier at 40 m depth, sex ratio was 45.1/54.9%, 67.5/32.5% and 55.7/44.3% among non-parasitized crabs, 59.5/40.5%, 73.3/26.6% and 69.3/30.7% among parasitized crabs in December 2008, November 2009 and 2010, respectively. Surveys carried in Antalya Bay, Turkey, revealed sex ratio 59/41% for the *C. longicollis* population (parasitized and non-parasitized) in November and December 2010 (Deval 2020). The rise in the number of males in the population did not parallel the increase in prevalence of parasitization. This is in stark contrast to results obtained from the study of *L. panopaei*-parasitized *Eurypanopeus depressus*

(SI Smith, 1869) populations in their native and introduced regions: a higher percentage females than males were recorded in the lower Chesapeake Bay, with sex ratios (F/M) of 1.5:1 and 2.2:1 in the unparasitized and parasitized populations, respectively; these ratios are prevalence dependent, with higher ratios of females to males reported from areas with higher levels of infection (Daugherty 1969; O'Shaughnessy *et al*. 2014a, b).

Ovigerous females. Among the specimens collected on December 2008, November 2009 and November 2010 at 40 m, ovigerous females constituted 4.0, 7.7 and 12.7% of the total number of crabs, similar to the prevalence identified among the specimens collected on November 2022, at 40 m. The cause for the absence of ovigerous females in 60 m in both 2021 and 2022, and at 40 m in 2021, is unclear.

Prevalence of parasitization. Prevalence of rhizocephalan infections in their native range is typically low, though cases of extreme outbreaks occur, mostly in enclosed bays and lagoons (Wardle & Tirpak 1991; Lázaro-Chávez *et al*. 1996; Brockerhoff *et al*. 2010; Waiho *et al*. 2017; Mouritsen *et al*. 2018).

It was observed that parasites co-introduced with invasive hosts may attain higher densities and generate epidemic-like outbreaks with or without 'spill over' to native hosts (Torchin *et al*. 2002; Goedknegt *et al*. 2016): *L. panopaei,* introduced into lower Chesapeake Bay in the early 1960s, reached by the end of that decade high prevalence in *E. depressus* (70%) and *Rhithropanopeus harrisii* (Gould, 1841) (87%), in marked contrast to moderate infection in its native region of the Indian River Lagoon, Florida (Daugherty 1969; Hines *et al*. 1997; Tepolt *et al*. 2020).

Similarly, *H. dollfusi*, considered rare in the Red Sea, since for nearly a century no specimens apart from the type series were recorded, proliferated in the Mediterranean Sea. The distinctive morphological modification of *C. longicollis* by *H. dollfusi* is evident even in internally infested individuals (Galil & Lützen 1995), enabling an accurate accounting of prevalence of parasitization. The percentage of externae-bearing and infected morphologically-modified crabs varied among the samples, 49.0, 53.7, 63.3% at 40 m depth in November 2021 and 2022, respectively, 66.5, 66.7, 84.3% at 60 m in December 2021 and November 2022, respectively (Tab. 2). It was noticeably lower a decade earlier, 54.0, 42, 47.1% at 40 m in December 2008, November 2009 and November 2010, respectively (Innocenti *et al*. 2017), and much lower at the start of the parasite outbreak, nearly three decades earlier: 23.9, 37.6% at 40 m in October 1993 and November 1994, respectively (Galil & Innocenti 1999). Nocturnal surveys carried out at depths between 20 and 41 m in Antalya Bay, Turkey, revealed 32.8% and 43.1% parasitization in *C. longicollis* in November and December 2010 (Deval 2020), congruent with an earlier study reporting prevalence of infection in Israeli waters was higher than in Antalya Bay (Innocenti *et al*. 2009).

Multiple parasitization. Multiple *H. dollfusi* externae have been regularly recorded in *C. longicollis* along the Israeli coast. In December 2008 and November 2010 samples collected off Ashdod at 40 m depth, prevalence of external parasitization was 29.6, 35.4% and percentage of multiple externae (> 1 externa/host) was 24.4, 24.6%, respectively (Innocenti *et al*. 2017). In November 1994 samples collected off Palmahim the corresponding values were 22.6% and 26.2%, (Galil & Innocenti 1999). Heavily parasitized host populations may induce higher rates of multiple externae due to the heavy 'propagule pressure' as parasite vermigons co-infest the same host or successively infest an already parasitized host (Galil & Innocenti 1999; Innocenti and Galil 2007). In samples collected in Antalya Bay, Turkey, in 2010, only 9% of the externa-bearing hosts had more than a single externa (Deval 2020).

The highest number of externae recorded in 2021–2022 material was six, borne by a male crab (CW 28.9 mm) collected in November 2022 at 40 m (Fig. 3). The occurrence of five and six externae per host is rare, and typically recorded from small-sized crabs (Galil & Lützen 1995; Galil & Innocenti 1999).

It seems that even in their native regions *Heterosaccus* spp. have a propensity for multiple externae: one of the five *Charybdis* hosts of the type series of *H. dollfusi* bore two externae (Boschma 1960: fig. 1d). Similarly, a specimen of *C. callianassa* (Herbst, 1789) bore the three paratypes of *H. lunatus* Phillips, 1978; a specimen of *C. truncata* (Fabricius, 1798) bore four paratypes of *H. multilacinensis* Phillips, 1978; 3% of *Portunus pelagicus* (Linnaeus, 1758) crabs with *H. indicus* Boschma, 1957 bore 2 or 3 externae; 13% of *C.* (*Charybdis*) *japonica* (A. Milne-Edwards, 1861) with *H. papillosus* (Boschma, 1933) externae bore 2 externae (Pillai & Thomas 1972; Phillips 1978; Kim & Hong 2002).

Predator-induced shift in diel activity. Top–down regulation by predators is a powerful process shaping ecological communities in myriad ways (Pinnegar *et al*. 2000). Predator–prey interactions are a primary structuring force in marine communities, and novel predators may significantly reduce the abundances of benthic invertebrates (Grosholz *et al*. 2000; Nõomaa *et al*. 2022).

Parasite-induced changes in morphological, physiological and behavioral traits, that may increase predation risk, have been observed and described for parasitized *C. longicollis* (Galil & Lützen 1995; Galil & Innocenti 1999; Innocenti *et al*. 1998, 2003). Parasitized male crabs are undersized compared with unparasitized ones—

both average and maximal CW of externa-bearing males are smaller than unparasitized males, and their chelae "feminized". Though unparasitized males' behavioral patterns had more aggressive elements than unparasitized females, agonistic encounters were much reduced among parasitized males. In addition, crabs lacking externae were prone to remain buried when inactive. The presence of externae was observed to modify digging and to inhibit burying behavior. It is likely the striking "feminization" of morphology and behavior in parasitized *C. longicollis*, particularly pronounced in externae-bearing individuals, increases their vulnerability and places them at heightened predation risk. Similar changes in behavioral patterns were recorded affecting other crab-sacculinid interactions: both male and female blue swimmer crabs *Portunus pelagicus* (Linnaeus, 1758) parasitized by *Sacculina granifera* Boschma, 1973, behaved like ovigerous females and exhibited only moderate diurnal activity, buried significantly slower than non-ovigerous crabs, and initiated and dominated fewer encounters than unparasitized individuals of similar size and sex (Bishop & Cannon 1979). Gehman & Byers (2017) reported that predators were associated with increased prevalence of parasitized *E. depressus*, and proposed that a positive correlation between predators and parasitized hosts could be driven by predator aggregation near areas of higher infection prevalence.

The breakout of the silver-cheeked toadfish, *L. sceleratus*, soon after its arrival along the Israeli coast raised the plausibility of a unique set of predator-host-parasite interactions among three successive Erythraean invasive aliens. Analysis of its gut contents revealed that *L. sceleratus* selectively feeds on *C. longicollis*, by far its most frequent prey item (relative abundance 0.465), constituting 49% of the Erythraean alien prey items (Chaikin *et al*. 2023). The aggressive, generalist benthophage fish has been recorded from the subtidal to 114 m depth, but a distinctly large population was observed in the 18–45 m depth niche (Chaikin *et al*. 2023; Frid *et al*. 2023), mirroring the densest *C. longicollis* population. Indeed, significant difference in size, parasitization ratio and load were noted between *C. longicollis* populations in 40 and 60 m, in line with the smaller population of the novel predator at 60 m, possibly allowing survival of smaller, more heavily parasitized crabs.

Species may mitigate risk by predator avoidance across space or time: retreat from predator-dominated habitats, or share habitats through temporal partitioning (Kronfeld-Schor & Dayan 2003). The present results call attention to the fact that *C. longicollis* crabs may have shifted their temporal activity pattern shortly following the proliferation of the diurnal predator *L. sceleratus* (Louisy 2015, *fide* Arndt & Evans 2022). The diurnal and nocturnal samples collected in December 2008 were the last hauls to comprise comparable numbers of *C. longicollis* crabs (day 931, night 1092). Later diurnal samples were greatly impoverished. These results raise the possibility that *C. longicollis* has been capable of shifting activity at short timescale into the nighttime following predator domination of its preferred habitat.

This study suggests that the invasion of dominant predators into the highly degraded Mediterranean shelf ecosystems may be associated with yet little-studied temporal alterations in the behavioral patterns of current residents—native and non-native—that deserve more attention.

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APPENDIX 1

GLM analysis of carapace width, crabs collected off Ashdod, November, December 2021, May 2022, November 2022, at 40 and 60 m depth.

Overall assessment of data over time

#	Year	mean_CW	sd_CW	parasite_count	mean_ext	sd_ext
1	2021	25.9	5.81	554	0.733	0.678
2	2022	30.3	7.01	3412	0.919	0.943

Male Model

```
Call: glm(formula = CW ~ Year + Depth + parasite + Extent, family = Gaussian(), data = Males

Deviance Residuals:
Min      1Q      Median  3Q      Max
-28.933  -5.810  -0.066  5.853   34.927

Coefficients:
                 Estimate        Std. Error      t value     Pr(>|t|)
(Intercept)      387.35126       45.11834        8.585       < 2e-16 ***
Year             -0.17110        0.02254         -7.590      3.76e-14 ***
Depth            -0.14551        0.01360         -10.700     < 2e-16 ***
Parasite         -10.12277       0.32816         -30.847     < 2e-16 ***
Nr of parasites  2.82506         0.15132         18.670      < 2e-16 ***
---
Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Gaussian family taken to be 66.158)
Null deviance: 452533 on 5438 degrees of freedom
Residual deviance: 359503 on 5434 degrees of freedom
AIC: 38243
Number of Fisher Scoring iterations: 2
```

Female Model

```
Call: glm(formula = CW ~ Year + Depth + parasite + Extent, family = Gaussian(), data = Females)

Deviance Residuals:
Min      1Q      Median  3Q      Max
-21.764  -3.525  0.218   3.753   19.844

Coefficients:
                 Estimate        Std. Error      t value     Pr(>|t|)
(Intercept)      440.96125       38.78943        11.368      < 2e-16 ***
Year             -0.19915        0.01938         -10.277     < 2e-16 ***
Depth            -0.18237        0.01255         -14.526     < 2e-16 ***
Parasite         -1.84443        0.33168         -5.561      2.93e-08 ***
Nr of parasites  1.62298         0.15465         10.495      < 2e-16 ***
---
Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
(Dispersion parameter for Gaussian family taken to be 30.51303)
Null deviance: 113092 on 2881 degrees of freedom
Residual deviance: 87786 on 2877 degrees of freedom
AIC: 18037
Number of Fisher Scoring iterations: 2
```