Biologia (2020) 75:2239–2249
https://doi.org/10.2478/s11756-020-00479-x

ORIGINAL ARTICLE

Population structure and dynamics of the invasive crab *Charybdis longicollis* parasitised by the rhizocephalan *Heterosaccus dollfusi* along the Mediterranean coast of Turkey

Mehmet Cengiz Deval[1]

Received: 13 June 2019 / Accepted: 26 March 2020 / Published online: 4 May 2020
© Institute of Zoology, Slovak Academy of Sciences 2020

Abstract

The invasive crab *Charybdis longicollis* was first reported in Mersin Bay (Mediterranean Sea/Turkey) in 1954, and since the early 1990s, its populations have been heavily parasitised by the alien rhizocephalan *Heterosaccus dollfusi.* In Antalya Bay, 46.6% of the trawled catch is constituted by *C. longicollis*. Monthly biomass values fluctuated between 67 kg km^{-2} (June) and 704 kg km^{-2} (October), with a mean of 260 kg km^{-2}. The percentage of change in females ranged from 29% in October to 53% in January. The mean carapace width of uninfected crabs was significantly larger in males (35.1 mm) than females (30.6 mm). Male crabs (34.3%) were more heavily parasitised than females (12.1%). The reduction in size of the chela and broadening of the abdomen are two characteristic modifications of infected males. The size at first maturity was estimated at CW = 24.7 mm. Ovigerous females were found all year-round but were more abundant in spring. Male and female individuals of *C. longicollis* displayed a maximum of three and one modal groups per year, respectively. Natural mortality (*M*) was estimated as 1.1 year^{-1} for male crabs.

Keywords Invasive species · Catch · Rhizocephalan · Decapod · Bottom trawl

Introduction

The invasive crab *Charybdis longicollis* Leene, 1938 is native to the Indian Ocean, the Persian Gulf, and the Red Sea, and was first recorded in the Mediterranean Sea in Mersin Bay in 1954 (Holthuis 1961), from which the population spread to Egypt and Greece in the south-eastern Mediterranean and soon dominated the sandy-mud bottoms to a depth of 25 to 80 m (Innocenti and Galil 2011).

Since the early 1990s, the populations of *C. longicollis* in Israel (Galil and Lützen 1995) and Turkey (Øksnebjerg et al. 1997) have been heavily parasitised by the alien rhizocephalan barnacle *Heterosaccus dollfusi* Boschma, 1960. Infections in the females cause loss of swimmerets, while infected males acquire mobility of segments that are normally fused in unparasitised males; in addition, the copulatory appendages are lost or heavily reduced and the abdomen broadens to such a degree that it closely resembles that of a normal female (Galil and Lützen 1995; Innocenti and Galil 2007). Due to the negative impact of rhizocephalan parasites on decapod crustaceans, several researchers suggested the use of these species as control agents to reduce population densities of invasive species (Hoddle 2004; Kuris 1997). This hypothesis is not supported by *C. longicollis* populations along Levantine coasts because the population has consistently increased in recent decades (Innocenti and Galil 2007; Innocenti et al. 1998, 2009, 2017).

Charybdis longicollis prefers infaunal and slow-moving prey, and the most frequent food items are molluscs, crustaceans, and fishes. Since the species is extremely abundant in Levantine littoral and sublittoral zones, it is likely to impact the local biota (Stasolla et al. 2015). There are increasing complaints from both small-scale and trawl fisheries in Antalya Bay concerning the large amount of *C. longicollis* in fishing nets (fishermen, personal communications, 2010). Although the structure of the population of *C. longicollis* in Israel was studied in detail (Galil and Innocenti 1999; Galil and Lützen 1995; Innocenti and Galil 2007; Innocenti et al. 2017), only a few studies are available regarding populations distributed along the Turkish coastline (Innocenti et al. 2009; Özcan and Katağan 2016).

✉ Mehmet Cengiz Deval
deval@akdeniz.edu.tr

[1] Faculty of Fisheries, Akdeniz University, Dumlupınar Bulvarı 07058 Kampüs, Antalya, Türkiye

The aim of the present study was: *i*) to investigate the prevalence and impact of the alien rhizocephalan barnacle *H. dollfusi* on its host and *ii*) to provide scientific data on the population pattern of the host crab *C. longicollis* along the Turkish Mediterranean coast. Moreover, the survey data obtained in the present study was compared to populations of *C. longicollis* located in different parts of the Levant Sea.

Material and methods

Monthly field surveys were carried out during 2010 aboard the R/V "*Akdeniz Su*" at night in the trawling grounds of Antalya Bay (between 20 and 41 m) in the eastern Mediterranean (Fig. 1). After each haul, *C. longicollis* were separated from the rest of the catch and weighed. Subsamples of ~10 kg were randomly selected, placed in cold storage, and transported to the laboratory for analysis. According to sea surface temperature (SST) data obtained from the Turkish General Directorate of Meteorology, the monthly average SST value in 2010 fluctuated between 16.0 °C in February and 29.4 °C in August, with an annual average of 22.7 ± 4.7 °C.

In total, 15,451 specimens of *C. longicollis*, with a total weight of 121.2 kg, were analysed in the laboratory. The first step was determination of sex by observing the sexual opening (vulva) (Fig. 2a2). Seven different types of crabs were classified: *i*) apparently uninfected (UI) females (Fig. 2a) and *ii*) UI males (Fig. 2el, e2), *iii*) Ovigerous females (OvF) with the presence of eggs attached to pleopods (Fig. 2d), *iv*) infected and morphologically-modified (MM) females without pleopods (Fig. 2b1, b2), *v*) the presence of externally parasitised (EP) females (Fig. 2c), *vi*) infected and MM males with modification of abdomenal shape (Fig. 2f1) and without gonopods (copulatory appendages) (Fig. 2f2), and *vii*) the presence of EP males (Fig. 2g1, g2).

In the next step, the carapace width (CW) was measured with a digital Vernier calliper to the nearest 0.1 mm. In addition, the chela length (ChL), the maximum width of the fifth abdominal segment (5AW), and the number of externae recorded in the 600 individuals randomly selected each climatic season were measured. Physically damaged specimens were discarded.

Morphometric relationships were determined using the linear regression formula for both sexes: $\log Y = a + \log X * b$. To test the difference in slopes (b) among the equations, the series CW versus ChL and 5AW were subjected to multicomparison analysis of covariance (ANACOVA). The temporal relationship of SST with the incidence of parasitised crabs (Lafferty and Holt 2003) was investigated using correlations analysis. The degree of modifications of ChL and 5AW, according to infection status in crabs, were calculated using two ratios: CH ratio (ChL: CW) and AW ratio (5AW: CW). Data analysis was carried out using IBM SPSS 21.0 (one-way analyses, correlations, and regressions) and MATLAB version 7.0 (MathWorks®) ANACOVA. In those instances where data did not meet the prerequisites of the parametric tests (normality, homogeneity of variance), nonparametric tests were applied. All post hoc tests were corrected for multiple comparisons (Kristensen et al. 2012).

During the period of maximum reproductive activity (April and May), Ov and UI females were evaluated to determine size at first maturity ($CW_{50\%}$). The maturity probabilities were modelled by means of logistic curves: $r(l) = [\exp(v_1 + v_2.l)/1 + \exp.(v_1 + v_2.l)]$, using the software CC2000 (ConStat 1995), where $r(l)$ is the probability of reproductive individuals for each 2-mm size class (l), and v_1 and v_2 are regression parameters to be estimated.

From the monthly size frequency distribution (CWFD) of *C. longicollis* for both sexes, the growth parameters (L_∞ and K) were estimated using the ELEFAN I method by means of the FiSAT II software (Gayalino et al. 2002). The instantaneous M coefficient was computed using the empirical model

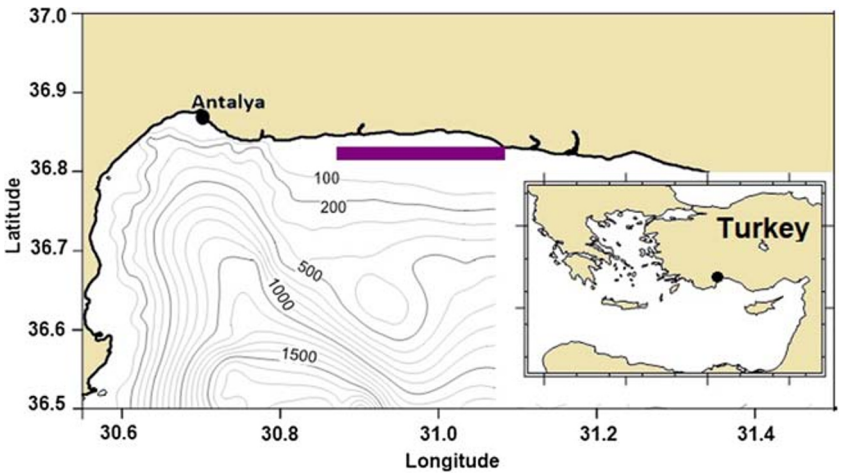


Fig. 1 Study area and sampling stations in Antalya Bay, Turkey

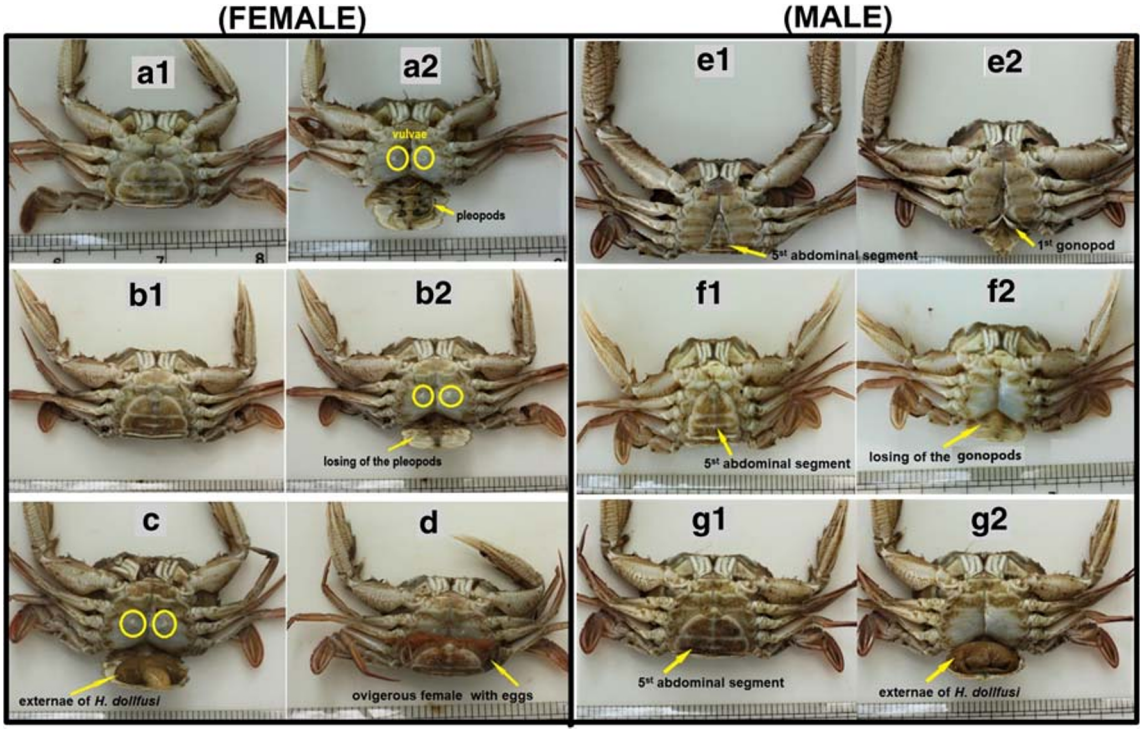


Fig. 2 Morphological features of *C. longicollis* relative to infection status. Ventral view of uninfected females (**a1** and **a2**) and males (**e1** and **e2**), infected and morphologically modified female with missing pleopods (**b1** and **b2**), externally parasitised female (**c**), ovigerous female with attached eggs on pleopods (**d**), infected and morphologically-modified male with modification of the shape of the abdomen (**f1**) and the gonopods (**f2**), and externally parasitised male (**g1** and **g2**)

of Pauly (1980): $\ln M = -0.0066 - 0.279 \ln L_\infty + 0.6543 \ln K + 0.463 \ln T$, where T is the mean SST in degrees centigrade (22.7 °C).

Results

During the survey, a total of 820.1 kg of *C. longicollis* were caught in a total trawling time of 39.2 h. Of the trawled biomass, 46.6% was constituted by *C. longicollis* (Table 1). The monthly percentage of females in the population varied between 29% (October) and 53% (January). The chi-square test showed a significant difference in the sex ratio (SR) from the 1:1 expectation ($X^2 = 7.626$, $p < 0.05$). The monthly CPUE (catch per unit effort) values fluctuated between 5.9 kg h^{-1} (April) and 60.6 kg h^{-1} (October), with a mean of 22.6 ± 16.9 kg h^{-1}. Seasons had a statistically significant effect on the CPUE (H-test, $X^2 = 244.609$; $p = 0.000$).

Prevalence of infestation

The percentage of infected *C. longicollis* by *H. dollfusi* in the total population varied significantly (chi-square test, $X^2 = 44.013$; $p = 0.000$) between 7.3% (January) and 43.1% (December) with a mean of 25.3 ± 11.6 (Table 1). There was also a significant difference according to SST (chi-square test, F = 44.013; $p = 0.000$) and season (H-test; $X^2 = 93.789$, $p = 0.000$), which were positively related to both variables (Spearman's rho, r = 0.706, $p = 0.010$, and r = 0.490, $p = 0.000$, respectively). Male crabs (34.3% ± 19.2) were infected more often than females (12.1% ± 5.1) (*t*-test, $t = -4.513$; $p = 0.001$).

The mean CW of UI male crabs was significantly larger (35.1 ± 8.3 mm) than the UI females (30.6 ± 3.5 mm) (U-test, Z = −18.137; $p = 0.000$), and the CWFD was found to be significantly different between the sexes (Kolmogorov-Smirnov test, $D_{obs} = 0.427 > D_{crt} = 0.045$; $p < 0.001$).

Evaluation of infestation in relation to CWFD of *C. longicollis* revealed that the infestation exceeded 50%, especially in small size classes (18–27 mm) of male crabs and negatively related to size ($r^2 = -0.930$, $p = 0.000$) (Fig. 3a); while larger male crabs (CW > 55 mm) were free of infestation. The mean CW of the MM crabs (28.1 ± 5.1 mm) was significantly lower than the UI (38.7 ± 8.3 mm) and EP (39.1 ± 4.5 mm) males (Tukey HSD test, $p = 0.000$). In contrast, the infestation was extremely low in small (20–32 mm CW) females and showed a positive correlation with size ($r^2 = 0.847$, $p = 0.000$) (Fig. 3b). The mean CW (31.8 ± 3.9 mm) of UI crabs was statistically different from both MM (35.8 ± 3.4 mm) and EP (37.2 ± 4.1 mm) female crabs (Tukey HSD test, $p = 0.000$). In both sexes, an increase in CW in infected individuals continued uninterrupted until the individuals suffered from the external parasites. The per-cent infestation

Table 1 Trawling time (TT, hours), monthly average sea surface temperatures between January and December 2010 (SST) and percentage of infected *C. longicollis* (*Cl*) sampled from Antalya Bay

Month	TT	SST	CPUE	*Cl*	IR	SR	Male			Female			
							IR	MM	EP	IR	MM	EP	Ov
Jan	3.3	17.8	17.0	57.5	7.3	0.53	10.1	9.2	0.9	4.7	1.2	3.5	28.9
Feb	3.3	16.0	10.4	38.8	15.1	0.34	14.4	8.1	6.8	15.6	2.7	12.9	42.0
Mar	4.2	16.2	13.6	54.1	16.3	0.49	22.0	13.6	8.4	10.2	2.8	7.4	67.6
Apr	3.5	18.1	5.9	16.3	20.0	0.43	21.9	7.2	14.7	17.5	2.7	14.8	61.5
May	3.0	20.3	6.4	15.7	24.9	0.34	29.6	17.1	12.5	15.9	4.0	11.9	69.1
Jun	3.0	23.8	5.9	9.4	24.8	0.43	28.9	5.0	23.9	19.3	10.3	9.0	27.8
Jul	3.3	27.3	19.6	36.9	32.4	0.29	40.0	34.7	5.3	13.5	3.6	10.0	36.3
Aug	3.2	29.4	25.8	44.4	33.3	0.37	45.0	40.0	5.0	13.4	3.1	10.3	45.8
Sep	3.2	28.4	43.7	51.1	28.8	0.41	42.1	35.4	6.6	9.4	1.3	8.2	53.6
Oct	3.2	25.4	60.6	87.9	36.3	0.27	47.6	45.2	2.5	5.6	1.7	3.9	46.6
Nov	3.0	22.8	32.0	83.1	32.8	0.39	48.6	43.3	5.3	7.9	3.4	4.6	39.3
Dec	3.0	20.8	30.1	63.9	43.1	0.47	69.7	61.8	7.9	12.9	3.5	9.4	21.3
Mean ± SD		**22.7 ± 4.7**	**22.6 ± 16.9**	**46.6 ± 25.1**	**25.4 ± 11.6**	**0.40 ± 0.8**	**34.3 ± 19.2**	**26.7 ± 18.9**	**8.3 ± 6.2**	**12.1 ± 5.1**	**3.4 ± 2.2**	**8.6 ± 3.5**	**45.0 ± 15.6**
N		–	–	–	–	–	5821	2173	743	2547	199	519	2697

CPUE: kg h^{-1}; SR: sex ratio; IR: % prevalence of all infected crabs; Ov: % ovigerous crabs; MM: % prevalence of morphological modified crabs; EP: % prevalence of externa-bearing crabs; N: number of individuals

(%IR) for both sexes was predicted using the following regression models:

Male: %IR = 56.612–0.708 * CW (mm), (r^2 = 0.834; F = 104.5, $p < 0.01$).
Female: %IR = 31.220 + 0.155 * CW (mm), (r^2 = 0.966; F = 224.2, $p < 0.01$).

Feminisation effect on hosts

The reduction in size of the chela and broadening of the abdomen are characteristic of infected *C. longicollis*. In healthy crabs, the mean ChL of males (31.4 mm) were 50% larger than in females (21.2 mm) (U-test, Z = 18.082; $p = 0.000$), while the mean 5AW of males (5.4 mm) (Fig. 2e1) was 62% narrower than females (14.1 mm) (Fig. 2a1) (Z = −29.930; $p = 0.000$) because each sex has a unique abdominal shape. Through the feminisation progress of the secondary sex characteristics, the ChL of infected males decreased, while the 5AW widened (Fig. 2f1). The ChL of externally-infected males (27.7 mm) decreased to the mean value of infected females (26.1 mm) (U-test, Z = 4.697; $p = 0.000$). Concurrently, the mean 5AW of externally-infected males (15.5 mm) (Fig. 2g1) increased 200%, reaching the size of infected females (15.6 mm) (U-test, Z = 1.707; $p = 0.088$) (Table 2).

Comparison of regression lines—ChL versus CW by infection status for male and female crabs—are shown in Fig. 4. The ChL of MM and EP male crabs decreased linearly with CW (Fig. 4a). ANACOVA analyses revealed statistically significant differences among the slopes for three values of infection status at the 99% confidence level (F = 140.70; $p = 0.000$). The MM and EP male crabs have slopes significantly different from UI males ($p < 0.01$) (Fig. 4b).

Following infection for two infected (MM and EP) groups of crabs (Fig. 4c), the width of 5AW of males increased linearly with CW and there is a statistically significant difference among slopes (ANACOVA, F = 3229.27; $p = 0.000$). Multicomparison analyses showed that all three male groups have slopes (Fig. 4d) significantly different from each other ($p < 0.01$). Results suggest a significantly higher rate in males than in the MM and EP female groups. However, two infected female groups did not exhibit reduction in size of chela (Fig. 4e) or broadening of 5AW (Fig. 4g). ANACOVA analyses showed no significant differences in the ChL and 5AW versus CW ratio between UI and MM, EP female crabs ($p > 0.05$) (Fig. 4f, h).

Figure 5 shows the relationship between CH and AW ratios versus infection status and sex. The mean CH ratio decreased from 0.797 ± 0.09 to 0.698 ± 0.06 (12.4%) when the UI males have been externally parasitised. However, the AW ratio of UI males (0.143 ± 0.01) increased 178% to 0.397 ± 0.03 for males carrying external parasites. A Kruskal-Wallis (K-W) test showed that there was a statistically significant difference

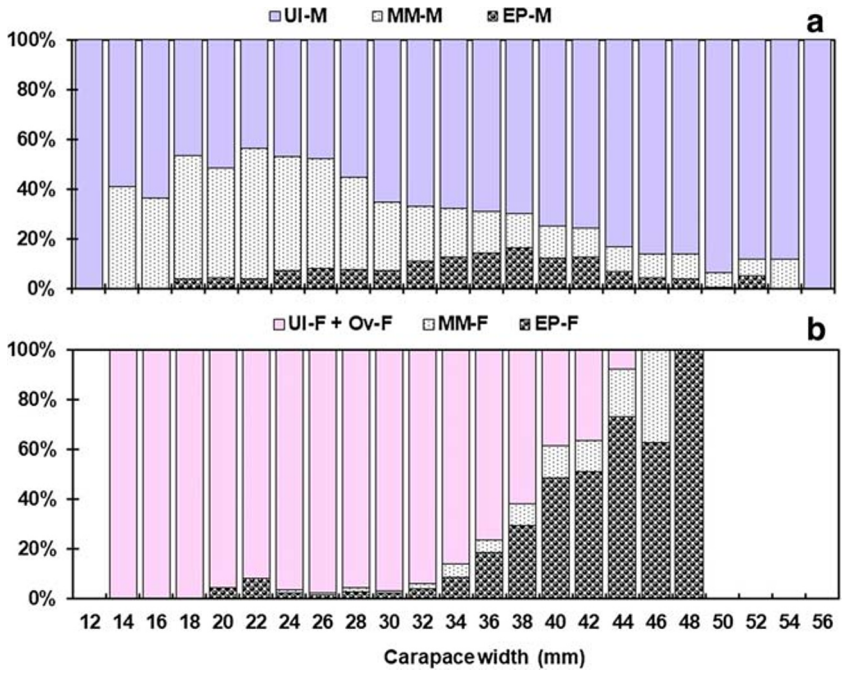


Fig. 3 Size (CW) frequency distribution of *C. longicollis* sampled in Antalya Bay: **a** male, **b** female. UI-M: uninfected male; MM-M: morphological modified male; EP-M: externally parasitised male; UI-F: uninfected non ovigerous female; OvF: ovigerous female; MM-F: morphologically modified female; EP-F: externally parasitised female

between the three infection statuses (UI, MM, EP) for both CH ($X^2 = 577.88$, $p < 0.0005$; Tamhane post hoc test, $p < 0.0005$) and AW indices ($X^2 = 339.81$, $p < 0.0005$; Tamhane post hoc test, $p < 0.0005$) (Fig. 5a). The abdomen of male crabs with external parasites were broad like females to provide the same degree of protection for the parasite as is normally offered to the brood. Moreover, CH of EP female individuals (0.69 ± 0.05) was significantly larger than UI (0.66 ± 0.05) individuals (*t*-test, F = 72.393, $p = 0.000$), while the AW ratio of EP females (0.41 ± 0.03) was significantly smaller than UI (0.44 ± 0.05) crabs (*t*-test = 95.760, $p = 0.000$) (Fig. 5b).

Multiple infections

Three hundred thirty-three EP male and 321 EP female individuals of *C. longicollis* were examined for the existence of external parasites. Multiple infections were not common in the population of *C. longicollis* in Antalya Bay. For both sexes combined, 91.1% of individuals with external parasites showed only one externa, five individuals had three externae, and one male specimen had five. One-way ANOVA indicated that sex was a significant factor on the number of externae in *C. longicollis* (F = 5.025, $p < 0.05$), with males more prone to infection.

Reproduction of *C. longicollis*

While individual OvF were encountered throughout the year, the percentage fluctuated between 24.5% in December and 82.2% in May, with a mean of 51.4%, but proportions of OvF in excess of 50% of the total female population occurred between March and May, and in September (Table 1, Fig. 6). The only factor that had a significant effect on both SR and the proportion of OvF ($p < 0.05$) was the season. There was a not significant correlation between OvF and SST (r = −0.378, $p = 0.226$). The CW of OvF ranged from 20 to 45 mm, with a mean 31.7 ± 3.4 mm ($n = 2697$). The fitted logistic curve revealed a CW at first maturity ($CW_{50\%}$) of 24.7 mm (Fig. 7). Also, the CW/5AW relationships of the UI female crabs

Table 2 The mean values (±standard deviation) of the biometric measurements (in mm) according to sex and infection status in the population of *C. longicollis*

Infection status	Male			Female		
	CW	ChL	5AW	CW	ChL	5AW
UI	38.7 ± 8.3	31.4 ± 9.2	5.5 ± 1.0	31.8 ± 3.9	21.2 ± 2.9	14.1 ±
MM	28.1 ± 5.1	18.2 ± 4.4	7.4 ± 2.9	35.8 ± 3.4	25.0 ± 2.8	14.4 ±
EP	39.1 ± 4.5	27.7 ± 4.0	15.5 ± 2.1	37.2 ± 4.1	26.1 ± 3.6	15.6 ±
Ov	–	–	–	31.7 ± 3.4	–	–

UI: Uninfected; MM: morphological modified; EP: externally infected; Ov: ovigerous; CW: carapace width; ChL: the chela length; 5AW: maximum width of the 5th abdominal segment

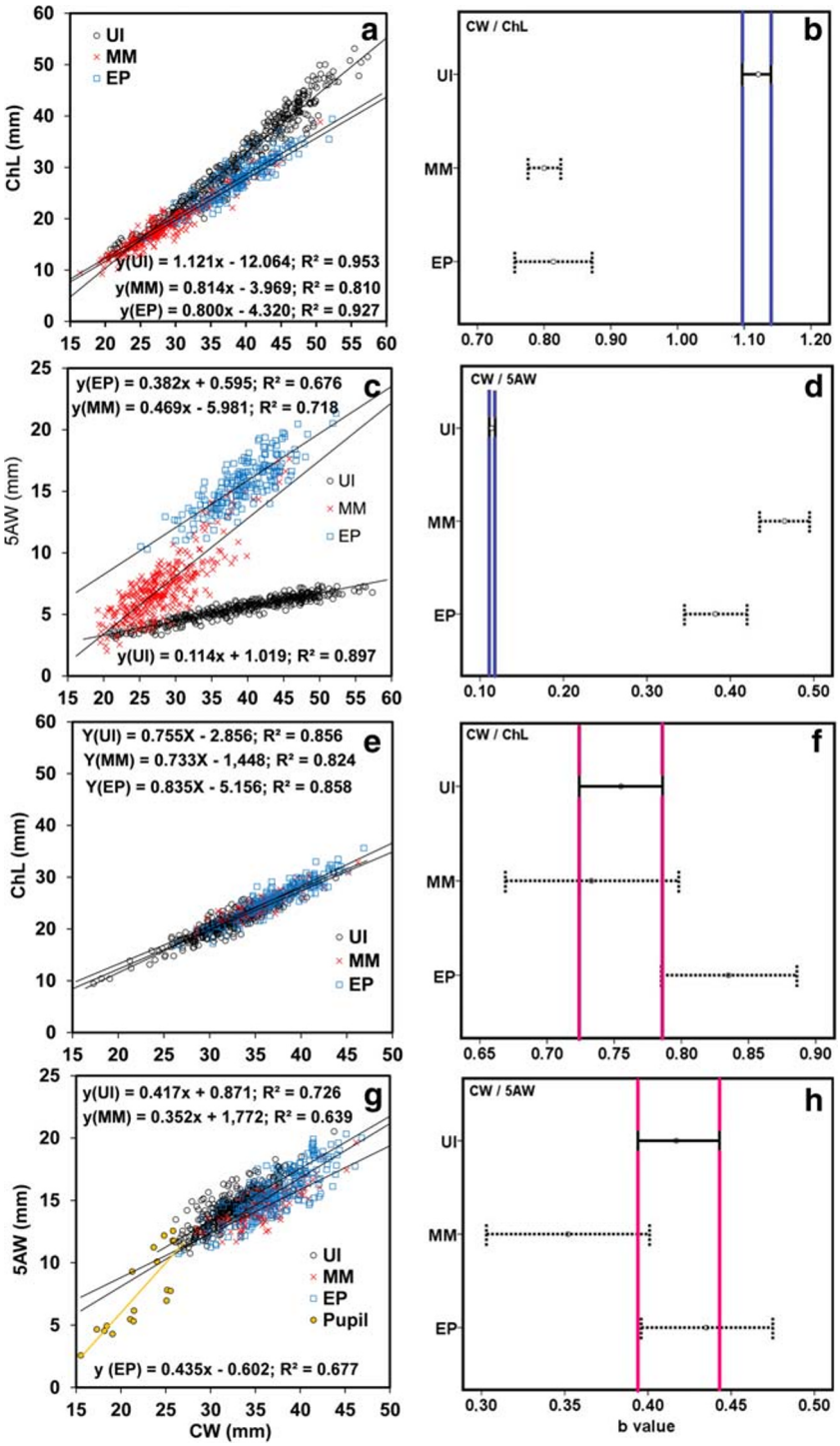


Fig. 4 Dimensions of chela length (ChL) and maximum width of fifth abdominal segment (5AW) as a function of carapace width (CW) of uninfected and infected *C. longicollis* specimens (circle; uninfected (UI), square; morphologically-modified (MM), cross; externally parasitised (EP), yellow circle; pupil). The CW/ChL relationship of male (**a**) and female (**e**), The CW/5AW relationship for male (**c**) and female (**g**). Multiple comparison using one-way ANACOVA results to determine which biometric relationships (slope: b value) are significant. Dashed vertical lines denote statistical confidence limits for multiple comparisons of both sexes. Male (**b** and **d**); female (**f** and **h**)

showed that crabs above 24–25 mm CW tended to have larger abdominal segments (Fig. 4g).

Age and growth

In both sexes, the pooled (infected and UI) CWFD (Fig. 8) were used for the analysis. Identification by age group (modal group) showed that males of *C. longicollis* exhibited a maximum of three modal size groups per year, while females exhibited only one. Due to the small number of female cohorts identified, exploitation and mortality were analysed only for males. The ELEFAN analysis yielded an optimised von Bertalanffy growth curve with the following parameters: $L_\infty = 58.8$ mm and $K = 0.72$ year^{-1} for males. The mean CW per year in males, using the parameters of the von Bertalanffy growth models,

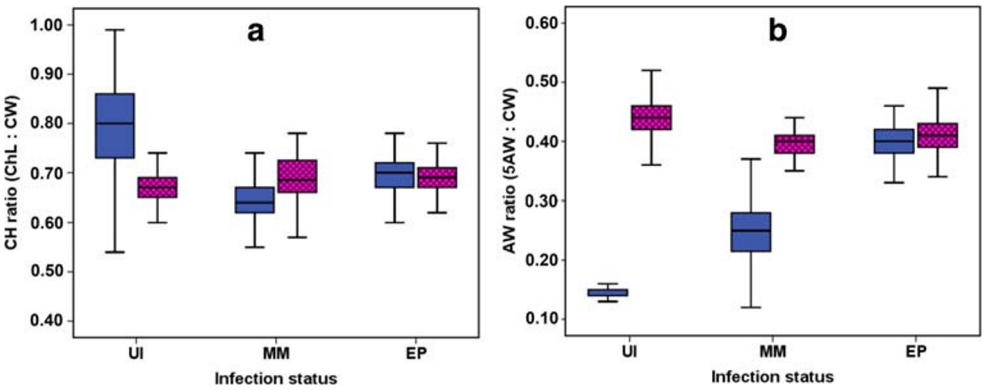


Fig. 5 Box plot (median, range of quarters, low, high and outliers) graphs of CH (**a**) and AW (**b**) ratios according to infection status and sex in *C. longicollis*. Uninfected (UI), morphologically modified (MM), externally parasitised (EP), male (blue), and female (diamond-pink)

were: 25, 42, 51, and 55 mm. The *M* values were estimated as 1.08 year^{-1} for male crabs.

Discussion

Some swimming crabs belonging to the genus *Charybdis* De Haan, 1833 have proven to be highly invasive, spreading outside their original range of distribution via shipping and the Suez Canal (Froglia 2012). Until now, the presence of six species of this genus have been identified in the Mediterranean (Kondylatos et al. 2017).

Charybdis longicollis is the most abundant (70%) trawl-caught decapod crustacean (Galil 1986) along the coast of Israel. With 22.6 kg h^{-1} CPUE and 47.2% of the trawled biomass, *C. longicollis* is the most abundant species in Antalya Bay. Although the species was not in the main catch in 1983 along the İskenderun Bay, abundance of the species increased to 5% with 1.9 kg h^{-1} CPUE value in 1984. In the following years (2002–2003), abundance of this species was reported as 9.7% of the total catch with a CPUE value of 2.6 kg h^{-1} (Çiçek et al. 2014). Moreover, surveys carried out between 2009 and 2013 reported an average CPUE value of 2.1 kg h^{-1}, and the species constituted 12.5% of the total biomass in Mersin Bay (Gökçe et al. 2016).

Previous studies (Table 3) indicated that, even though the population of *C. longicollis* settled in the Levant Sea in the second half of the twentieth century, infected populations of the species have only been observed in the last decade. Moreover, in terms of the infection characteristics, significant differentiation with latitude (between lower (Israel) and upper (Turkey)) have been reported. Although, no infection was reported in the population of *C. longicollis* distributed along the Israeli coast until 1992; in subsequent years, infestation rates were reported to increase: 35.5% in 1993–94 (Galil and Lützen 1995), 60.5% in 2005–07 (Innocenti and Galil 2011), 62.8% in May 2008 (Innocenti et al. 2009), and 89% in 2008–12 (Innocenti et al. 2017). Similar to the southern part of Levant, no infection by *H. dollfusi* was observed along the Turkish shoreline until the spring of 1994 (Galil and Lützen 1995; Øksnebjerg et al. 1997). Çiçek et al. (2014) reported a 23.3% infestation in 1120 individuals from Iskenderun Bay examined in 2002 and 2003. In May 2008, the infestation rate was reported to be 19.2% ($n = 944$) in Antalya Bay (Innocenti et al. 2009). In this study, the infestation rate detected was 25% in May and the annual infestation rate was 26.3%. Nevertheless, even in limited distribution areas, the

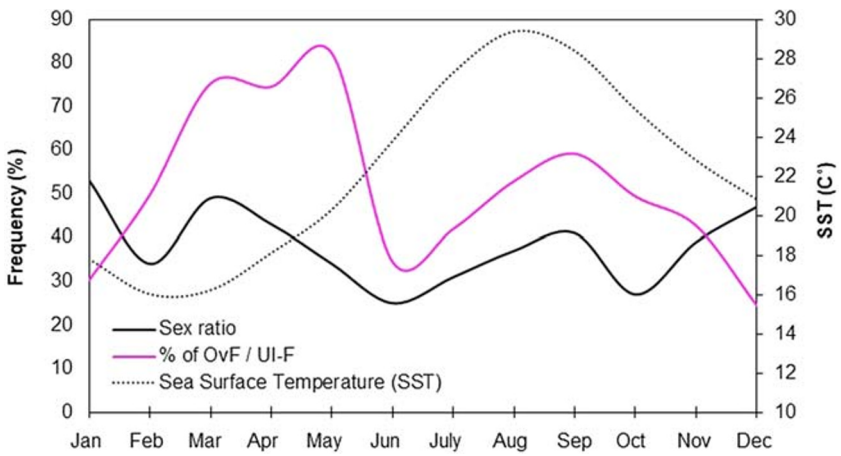


Fig. 6 Temporal variation in relative abundance of ovigerous females (OvF) among uninfected female (UI-F) individuals, sex ratio of *C. longicollis*, and monthly mean sea surface temperature (SST) in the Antalya Bay during the study period

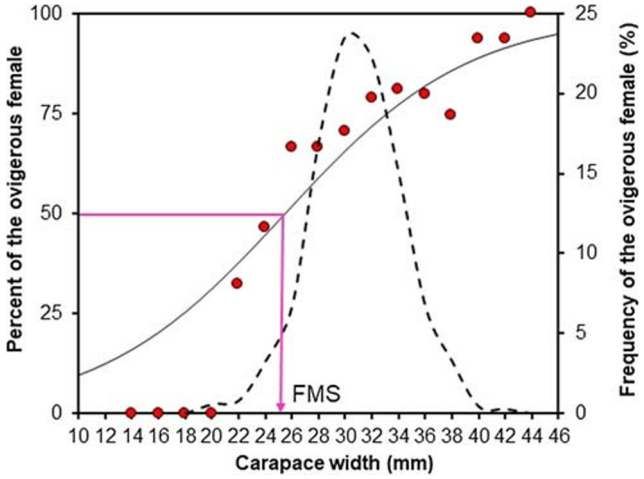


Fig. 7 Expected (logistic line) and observed percentage of mature specimens, related to overall size and size at first maturity (FMS) of *C. longicollis* sampled in Antalya Bay

prevalence of the parasite displayed local variations (Innocenti et al. 2009; Werner 2011). Boone et al. (2004) identified several factors (host sex, size, molting frequency, molt stage, and migratory behavior) that affect parasite recruitment. In this study, the percentage of infected males (35.0%) was much higher than infected females (12.2%); this result is in accordance with those reported in other studies in Israel (Galil and Innocenti 1999; Galil and Lützen 1995; Innocenti et al. 2009; Innocenti and Galil 2011), which found that males constituted the majority of infected crabs.

The reduction in chela size, broadening of the abdomen, and degeneration of pleopods are the most common morphological modifications in male crabs infected with the rhizocephalan parasite (Kristensen et al. 2012). These modifications also occur in other brachyurans (Yamaguchi and Aratake 1997) and anomurans. The present study clearly demonstrates that

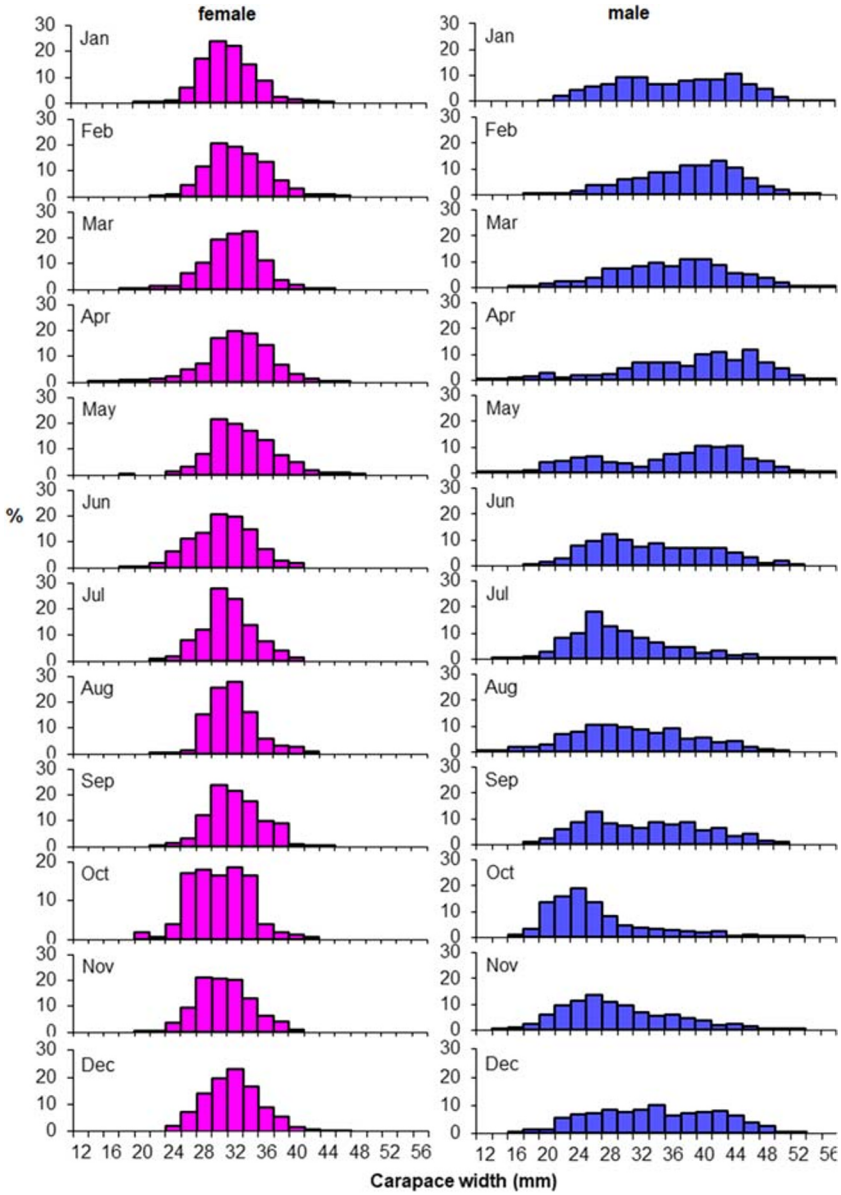


Fig. 8 Monthly changes in the chela width frequency standardised distribution (CWFSD) of *C. longicollis* in Antalya Bay between January and December 2010

Table 3 Current knowledge related to biological parameters of *C. longicollis* obtained by various authors in the Mediterranean Sea

Area	Date	Sex	N	Depth	SR	CW	Average CW			%			Max	
						range	UI	MM	EP	IR	MM	EP	externa	
Palmahim/Israel	1993–94	♂	555	31–36	0.46	22–51	–	–	–	45.0	9.9	35.5	–	Galil and Lützen (1995); Galil and Innocenti (1999)
		♀	565		0.54	22–51	–	–	–	30.8	4.6	26.2	–	
		♂♀	1120			22–51	–	–	–	**35.5**	–	–	5	
Iskenderun/Turkey		♂	425	4–50	–	??-67	–	–	–	–	–	–	–	Özcan and Katağan (2016)
		♀	432		–	19-??	–	–	–	47.6	–	–	–	
		♂♀	857			19–67	–	–	–	**23.3**	–	–	4	
Antalya/Turkey	May 2008	♂	583	20–40	0.62	22–63	41.8	34.3	36.7	17.5	3.4	14.1	–	Innocenti et al. (2009)
		♀	361		0.38	25–47	32.4	30.3	30.6	22.4	3.0	19.4	–	
		♂♀	944			22–63	–	–	–	**19.4**	–	–	>5	
Ashdod/Israel	May 2008	♂	769	30–37	0.59	18–57	42.5	33.1	35.8	65.7	12.5	53.2	–	
		♀	539		0.41	20–49	31.7	32.6	35.6	58.8	10.4	48.4	–	
		♂♀	1308			18–57	–	–	–	**62.8**	–	–	>5	
Palmahim/Israel	2005–07	♂	3552	30–40	0.59	–	–	–	–	67.5	–	–	–	Innocenti and Galil (2011)
		♀	2486		0.41	–	–	–	–	50.4	–	–	–	
		♂♀	6038			–	–	–	–	**60.5**	–	–	8	
Ashdod/Israel	2008–12	♂♀	11,849	40–250	–	6–65	–	–	–	**89–50**		56.1–26.5	7	Innocenti et al. (2017)
Antalya/Turkey	2010	♂	9131	20–50	0.59	12–56	35.4	29.2	34.6	35.0	26.7	8.3	4	This study
		♀	6320		0.41	14–48	30.9	34.8	35.2	12.2	3.4	8.6	3	
		♂♀	15,454			12–56	–	–	–	**26.3**	–	–	4	

N: number of specimens; SR: sex ratio; CW: carapace width in mm; UI: uninfected; MM: morphologically modified; EP: externally infected

broadening of the abdomen and reduction in the size of the chela are the two characteristic modifications of the secondary sex character of infected males of *C. longicollis* (Figs. 4 and 5; Table 2).

Although more than 80 species of *Charybdis* are known, few comparative data on their life histories are available. There is no reported information on lifespan and growth of the *C. longicollis* in the literature. Four species of the genus have life spans of about one year in *Charybdis bimaculata* Miers, 1886 (Doi et al. 2008), two to four years in *Charybdis japonica* A. Milne-Edwards, 1861 (Kim 2001; Ogawa 1997), one year in *Charybdis smithii* MacLeay, 1838 (Van Couwelaar et al. 1997), and three cohorts in *Charybdis feriata* Linnaeus, 1758 (Dash et al. 2014). In the present study, the *C. longicollis* population showed two to three cohorts.

In all previous studies, the sex ratio (0.38–0.41) differed from the expected 1:1 ratio in northern and southern parts of the Levant Sea (Table 3). There was a clear surplus of male individuals in the populations. No previously reported values on the reproduction and instantaneous natural mortality of *C. longicollis* were found in the literature.

Conclusion

Despite the high prevalence of infection by *H. dollfusi* and its potential negative impact on *C. longicollis* (fecundity, larval dispersal and juvenile recruitment, growth, mortality) (Galil and Lützen 1995; Innocenti and Galil 2007; Innocenti et al. 1998), populations of *C. longicollis* are not decreasing in the region. The reason is crucial and two explanations are suggested: *i)* overpopulation of C. longicollis can be ascribed to the density of ovigerous and parasite-free individuals with high fecundity and the ability to spawn year-round (24.5% in December and 82.2% in May) and *ii*) Chondrichthyan species (especially Raja clavata Linnaeus, 1758 and Dasyatis pastinaca Linnaeus, 1758)—the top predators of C. longicollis (Yeldan et al. 2009)—are susceptible to fishing pressure and have been decimated by injurious fishery practices over the years (Çiçek et al. 2014; Innocenti et al. 2017). The prohibition of fishing for 11 cartilaginous species including *R. clavata* and two *Rhinobatos* species (*Rhinobatos rhinobatos* Linnaeus, 1758 and *Rhinobatos cemiculus* Geoffroy Saint-Hilaire, 1817) in Turkish Seas in April 2018 confirm the decline in top predators and need for protection.

Acknowledgements I would like to acknowledge graduate students Gökçe Özgen and İsmet Saygu for laboratory support, and the captain and crew of the R/V "*Akdeniz Su*" for professional and diligent work at sea. This study was partially presented orally at the 4th International Symposium on EuroAsian Biodiversity (SEAB2018) in Kyiv (Ukraine), and I would like to thank the Akdeniz University Scientific Research Fund (FYS-2017-1959) for financial support to attend symposia.

Compliance with ethical standards

Ethics approval No ethical approvals are required.

Conflict of interest The author declare that they have no conflicts of interest.

References

Boone E, Boettcher AA, Sherman TD, O'Brien JJ (2004) What constrains the geographic and host range of the rhizocephalan *Loxothylacus texanus* in the wild? J Exp Mar Biol Ecol 309(2):129–139. https://doi.org/10.1016/j.jembe.2004.03.013

Çiçek E, Karataş M, Avşar D, Moradi M (2014) Catch composition of the bottom trawl fishery along the coasts of Karataş-Adana (North-Eastern Mediterranean Sea). Int J Aquat Biol 2(5):229–237

ConStat (1995) CC selectivity, Granspaettevej 10, DK-9800 Hjjlarring, Denmark

Dash G, Dash SS, Koya M, Sreenath K, Thangavelu R, Mojjada SK, Zala M (2014) Analysis of fishery and stock of the portunid crab, *Charybdis feriata* (Linnaeus, 1758) from Veraval waters, north-west coast of India. Indian J Fish 61(4):1–9

Doi W, Yokota M, Strüssmann CA, Watanabe S (2008) Growth and reproduction of the portunid crab *Charybdis bimaculata* (Decapoda: Brachyura) in Tokyo Bay. J Crustacean Biol 28(4): 641–651. https://doi.org/10.1651/07-2964.1

Froglia C (2012) First record of *Charybdis japonica* (Crustacea: Decapoda: Portunidae) in the Mediterranean Sea. Mar Biodivers Rec 5:E33. https://doi.org/10.1017/S1755267212000140

Galil BS (1986) Red Sea decapods along the Mediterranean coast of Israel, ecology and distribution. In: Dubinsky Z, Steinberger Y (eds) Environmental quality and ecosystem stability, Vol. III/a. Bar Ilan Univ Press, Israel, pp 179-183

Galil BS, Innocenti G (1999) Notes on the population structure of the portunid crab *Charybdis longicollis* Leene, parasitized by the rhizocephalan *Heterosaccus dollfusi* Boschma, off the Mediterranean coast of Israel. Bull Mar Sci 64(3):451–463

Galil BS, Lützen J (1995) Biological observations on *Heterosaccus dollfusi* Boschma (Cirripedia: Rhizocephala), a parasite of *Charybdis longicollis* Leene (Decapoda: Brachyura), a lessepsian migrant to the Mediterranean. J Crustacean Biol 15(4):659–670. https://doi.org/10.1163/193724095X00064

Gayalino FC, Sparre O, Pauly D (2002) The FAO-ICLARM stock assessment tools (FiSAT II) program package. FAO, Rome

Gökçe G, Saygu İ, Eryaşar AR (2016) Catch composition of trawl fisheries in Mersin Bay with emphasis on catch biodiversity. Turk J Zool 40:522–533. https://doi.org/10.3906/zoo-1505-35

Hoddle MS (2004) Restoring balance: using exotic species to control invasive exotic species. Conserv Biol 18(1):38–49. https://doi.org/10.1111/j.1523-1739.2004.00249.x

Holthuis LB (1961) Report on a collection of Crustacea Decapoda and Stomatopoda from Turkey and the Balkans. Zoologische Verhandelingen 47(1):1-67

Innocenti G, Galil BS (2007) Modus vivendi: invasive host/parasite relations—*Charybdis longicollis* Leene, 1938 (Brachyura: Portunidae) and *Heterosaccus dollfusi* Boschma, 1960 (Rhizocephala: Sacculinidae). Hydrobiologia 590(1):95–101. https://doi.org/10.1007/s10750-007-0761-z

Innocenti G, Galil BS (2011) Live and let live: invasive host, *Charybdis longicollis* (Decapoda: Brachyura: Portunidae), and invasive parasite, *Heterosaccus dollfusi* (Cirripedia: Rhizocephala: Sacculinidae). In: Galil B, Clark PF,Carlton JT (eds) In the wrong place - alien marine crustaceans: distribution, biology and impacts. Invading

Nature - Springer Series in Invasion Ecology, vol 6. Springer, Dordrecht, pp 583–605. https://doi.org/10.1007/978-94-007-0591-3_20

Innocenti G, Galil BS, Yokes MB, Diamant A, Goren M (2009) Here and there: a preliminary note on the prevalence of an alien rhizocephalan parasite at the southern and northern limits of its introduced range. J Parasitol 95(6):1387–1390. https://doi.org/10.1645/GE-2026.1

Innocenti G, Stasolla G, Goren M, Stern N, Levitt-Barmats Y, Diamant A, Galil BS (2017) Going down together: invasive host, *Charybdis longicollis* (Decapoda: Brachyura: Portunidae) and invasive parasite, *Heterosaccus dollfusi* (Cirripedia: Rhizocephala: Sacculinidae) on the upper slope off the Mediterranean coast of Israel. Mar Biol Res 13(2):229–236. https://doi.org/10.1080/17451000.2016.1240873

Innocenti G, Vannini M, Galil B (1998) Notes on the behaviour of the portunid crab *Charybdis longicollis* Leene parasitized by the rhizocephalan *Heterosaccus dollfusi* Boschma. J Nat Hist 32(10–11):1577–1585. https://doi.org/10.1080/00222939800771111

Kim K (2001) Growth and reproduction of *Charybdis japonica* (Milne-Edwards) (Decapoda: Portunidae) in Korean waters. (unpublished doctoral dissertation). Department of Marine Biology, Graduate School, Pukyong National University

Kondylatos G, Kampouris T, Kouloumperis V, Foka MC (2017) The indo-Pacific brachyuran *Charybdis paucidentatus* (Milne-Edwards, 1861) (Brachyura, Portunidae) in the Cyclades. Aegean Sea Turk J Zool 41(6):1118–1120. https://doi.org/10.3906/zoo-1612-48

Kristensen T, Nielsen AI, Jørgensen AI, Mouritsen KN, Glenner H, Christensen JT, Høeg JT (2012) The selective advantage of host feminization: a case study of the green crab *Carcinus maenas* and the parasitic barnacle *Sacculina carcini*. Mar Biol 159(9):2015–2023. https://doi.org/10.1007/s00227-012-1988-4

Kuris A M (1997) Conceptual framework for biocontrol of introduced marine pests. In: Ronald ET (ed) Proceedings of the first international workshop on the demography, Impacts and management of introduced populations of the European crab *Carcinus maenas,* CSIRO Marine Laboratories, Hobart/Tasmania, pp 66–68

Lafferty KD, Holt RD (2003) How should environmental stress affect the population dynamics of disease? Ecol Lett 6:654–664

Ogawa Y (1997) Population biology of *Charybdis japonica* in the area beyond Tajiri of Hiroshima prefecture. Reports of Seto-Inland Sea Stocks and Ocean Research Association 3:31–38

Øksnebjerg B, Enzenross R, Enzenross L (1997) First record of Rhizocephala (Crustacea: Cirripedia) from Turkish waters with notes on Lessepsian migration. Stuttg Beitr Naturkd A 557:1–7

Özcan T, Katağan T (2016) Prevalence of *Heterosaccus dollfusi* Boschma, 1960 (Rhizocephala: Sacculinidae) on *Charybdis longicollis* Leene, 1938 (Brachyura: Portunidae) from Iskenderun Bay, Turkey. J Black Sea/Medit Environ 22(2):128–136

Pauly D (1980) On the interrelationship between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J Conseil 39(2):175–192

Stasolla G, Innocenti G, Galil BS (2015) On the diet of the invasive crab *Charybdis longicollis* Leene, 1938 (Brachyura: Portunidae) in the eastern Mediterranean Sea. Isr J Ecol Evol 61(3–4):130–134. https://doi.org/10.1080/15659801.2015.1123362

Van Couwelaar M, Angel MV, Madin LP (1997) The distribution and biology of the swimming crab *Charybdis smithii* McLeay, 1838 (Crustacea; Brachyura; Portunidae) in the NW Indian Ocean. Deep-Sea Res Pt II 44(6–7):1251–1280. https://doi.org/10.1016/S0967-0645(97)00017-9

Werner M (2011) Prevalence of the parasite *Sacculina carcini* Thompson 1836 (Crustacea, Rhizocephala) on its host crab *Carcinus maenas* (L.) on the west coast of Sweden. Ophelia 55(2):101–110. https://doi.org/10.1080/00785236.2001.10409477

Yamaguchi T, Aratake H (1997) Morphological modifications caused by *Sacculina polygenea* in *Hemigrapsus sanguineus* (De Haan) (Brachyura: grapsidae). Crustac Res 26:125–145

Yeldan H, Avşar D, Manaşırlı M (2009) Age, growth and feeding of the common stingray (*Dasyatis pastinaca*, L., 1758) in the Cilician coastal basin, northeastern Mediterranean Sea. J Appl Ichthyol 25:98–102. https://doi.org/10.1111/j.1439-0426.2008.01075.x

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.