Host use pattern of the pea crab *Afropinnotheres monodi*: potential effects on its reproductive success and geographical expansion

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ABSTRACT: The successful settlement of the African pea crab *Afropinnotheres monodi* in the Bay of Cadiz was analysed to gain new insights into the evolution of pea crab parasite life history traits. The pea crab lives symbiotically and with high prevalence in the bivalves *Cerastoderma glaucum* and *Mytilus galloprovincialis*, and with low prevalence in *Scrobicularia plana*. A remarkable monopolisation of the host (1 crab per bivalve) occurred irrespective of host species and crab demographic categories (males, hard females, soft females), probably as an optimisation of resources in small hosts. However, there was a clear asymmetry in host use by the different crab categories. A 1:1 sex ratio was found in crabs harboured by *C. glaucum* and *S. plana*, with most of the female crabs being small and hard specimens, whereas crabs inhabiting *M. galloprovincialis* were primarily large reproductive females. Ovigerous females were found throughout the year in *M. galloprovincialis*, and there was a strong correlation between female size and fecundity, suggesting that the females harboured by this host were the major contributors to the reproductive effort of the studied population. Conversely, most of the new crabs recruiting to the population were harboured by the remaining 2 host species. We hypothesise that such a generalist but asymmetrical usage of bivalve hosts by pea crabs may have clear benefits for species such as *A. monodi*, that are undergoing geographical expansion, facilitating their dispersal to new locations and their successful settlement in sheltered systems, such as the Bay of Cadiz.

KEY WORDS: Symbiotic crabs · Multiple hosts · Life cycle · *Afropinnotheres monodi* · *Cerastoderma glaucum* · *Mytilus galloprovincialis* · *Scrobicularia plana*

INTRODUCTION

As a result of natural cycles and human activity, boundaries of the geographic distribution of species are dynamic (Brown et al. 1996, Parmesan 2006, Doney et al. 2012, Jones et al. 2013). The successful settlement of species at a new location depends on a suitable mechanism of dispersal and on the ability to find appropriate habitats there (Bradbury & Snelgrove 2001). In the case of symbiotic lifestyles (in its etymological sense, i.e. including parasitism, commensalism and mutualism), this means that the invasive stage of symbionts must arrive at the new location and find a stable population of its original host and/or of a new suitable host. A symbiont that is not host-specific is expected to be more successful in colonising new areas than strict host specialists. Furthermore, the use of more than one host species may increase the fitness of symbiotic species: symbionts may sequentially infest different hosts in order to

optimise the use of resources (De Bruyn et al. 2010). In the long term, this can lead to a more complex life cycle; however, the initial and transitory step of the adaptation (facultative use of additional hosts) may favour the geographical expansion of the symbiotic guests.

Partnerships in marine symbiosis often include species of different sizes and lifestyles: commonly, one small mobile species (symbiotic guest) associated with a more sedentary species (symbiotic host). Due to the diverse morphology and lifestyle of hosts, there is also a wide diversity of social groups among guests: in large and morphologically complex hosts, several individuals of the smaller symbiotic guest generally share the same host, whereas in hosts with small body size and/or low morphological complexity, the symbiotic partner usually lives alone (De Bruyn et al. 2009, Baeza & Díaz-Valdés 2011). Since the smaller symbiotic guest obtains essentially refuge and food from its larger host, the adoption of a solitary lifestyle may respond to the optimisation of resources provided by small-size hosts (Baeza & Thiel 2003, 2007). However, such solitary lifestyles force reproductive males and/or females to temporarily leave their hosts for mating. Mating may take place inside the host of the female symbiont, or in the water column, with a consequent increase in the risk of predation on guests (Asama & Yamaoka 2009, Trottier & Jeffs 2012). Moreover, such mating-related migrations confer further complexity to the symbiont life cycle.

Among marine symbionts, pinnotherid pea crabs display a wide diversity of host–guest interactions. Pinnotherids may live as endo- or ectosymbionts of different taxonomic groups of invertebrates, mainly in the mantle cavity of molluscs, burrows of polychaetes, the integument of echinoids and the branchial sac of tunicates (Schmitt et al. 1973, Grove & Woodin 1996, Baeza & Díaz-Valdés 2011, Subida et al. 2011, Jossart et al. 2013). As for most brachyurans, pinnotherids have a complex free-living larval cycle, which represents the dispersive phase of the species (Scheltema 1986). After the settlement of megalopae, pinnotherids usually show a facultative free-living stage in both sexes (males and hard females). Thereafter, reproductive females have a last obligate symbiotic stage, during which soft females live in their host (Silas & Alagarswami 1967, Soong 1997, Becker & Türkay 2010). In symbiotic pea crabs with a solitary lifestyle (1 crab host^{-1}), males usually maximize their reproductive success by roaming among host individuals in search of receptive sedentary females (the 'pure-search polygy-

nandry of sedentary females' model proposed by Baeza & Thiel 2007). Thus, the spatio-temporal distribution of receptive females becomes crucial in determining the distribution of the remaining demographic categories (De Bruyn et al. 2009, Ocampo et al. 2012). For all of the above-mentioned reasons, pea crabs are considered an exceptionally interesting group to explore the different types of behavioural, phenotypic and genetic adaptations of symbionts during the evolution toward complex parasitic cycles (Grove et al. 2000, Jossart et al. 2013). Despite the increasing interest in host use and mating behaviour of pinnotherids in recent years (De Bruyn et al. 2009, 2010, Hernández et al. 2012, Ocampo et al. 2012, Jossart et al. 2013, Peiró et al. 2013), several aspects of their complex lifestyle are still unknown (Becker & Türkay 2010).

In the current scenario of rising seawater temperatures in southern Europe (Sanderson et al. 2011), new records and/or abundance increments of several African marine species in the Iberian Peninsula have been related to the warmer environmental conditions (Cabral et al. 2001, Castañeda & Drake 2008, Subida et al. 2011). According to the very scarce information available, this could also be the case for the African pea crab *Afropinnotheres monodi* Manning, 1993, which currently shows its northernmost populations in southern Europe (Subida et al. 2011). No information on hosts is available for the earliest African records, but European populations have been recorded living in the shell cavity of several bivalves (Subida et al. 2011). Thus, the arrival of *A. monodi* in the Gulf of Cadiz could be either due to accidental transport of pea crabs in ship-fouling species, i.e. in mussels (Apte et al. 2000), or to larval dispersal from the North African populations. Regardless of the mechanism behind the introduction of *A. monodi* in Europe, it is reasonable to assume that the northernmost populations are probably in the process of adapting to the newly colonised environments. Thus, the apparently fast and undoubtedly successful settlement of the pea crab *A. monodi* in the Bay of Cadiz offers a unique opportunity to gain new insights into the evolution of pea crab symbiotic life history traits.

MATERIALS AND METHODS

Study site and distribution of the bivalve hosts

All host individuals were collected within the Bay of Cadiz (southwestern Spain), an area that was originally part of the Guadalete River estuary but is now

a marine marsh system as a consequence of sedimentary processes and dams. The Río San Pedro inlet, a sinuous seawater channel characterized by semidiurnal mesotides (tidal range 1 to 3.5 m), runs through the northeastern area of the marsh. The tidal current from the bay flows along the inlet, whereas the freshwater inflow is insignificant except during periods of heavy rain. The inlet has a soft muddy bed at the inner zone and a muddy sand bed close to the river mouth (Fig. 1).

A stable population of the clam *Scrobicularia plana* inhabits the intertidal mud flats of the Río San Pedro inlet, where clams burrow relatively deep into the sediment of the high tide zone. Conversely, a very high density of the cockle *Cerastoderma glaucum* was observed for some years in the muddy sand flats located at the mouth of the Río San Pedro inlet, where cockles may be found lightly burrowed (in the first ~5 cm of sediment) in the mid-tidal zone; massive cockle mortality has been recorded in some summers and/or after rainy periods (P. Drake et al. unpubl.). Crowded patches of the mussel *Mytilus galloprovincialis* can be found all around the Bay of Cadiz, attached to artificial hard structures, such as bridge pillars and concrete blocks used to protect harbour walls; as mussels usually settle at the middle-low tidal level, they remain emerged for shorter periods of time during each tidal cycle than clams and cockles.
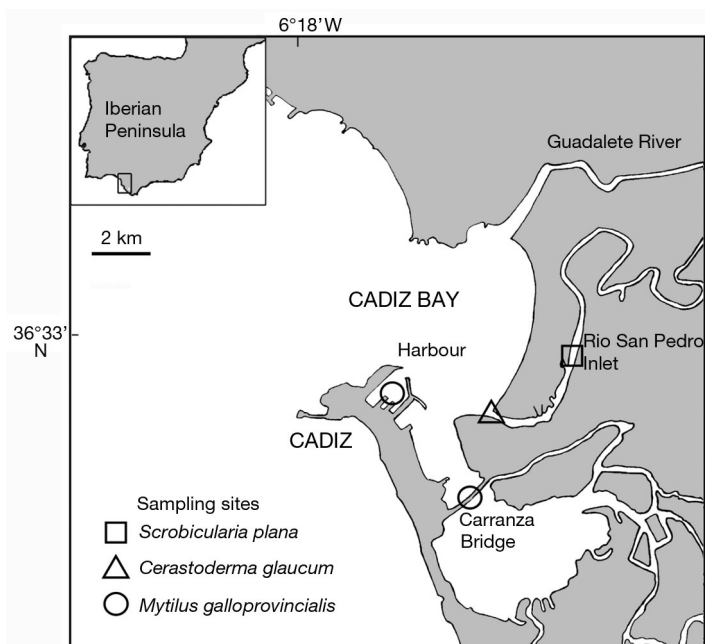

Fig. 1. Sampling sites of the bivalve host populations harbouring the pea crab *Afropinnotheres monodi* in the Bay of Cadiz (SW Iberian Peninsula)

Collection of hosts and crabs

Scrobicularia plana clams were sampled monthly over 2 yr (June 2010 to May 2012). Although an occasional presence of the cockle *Cerastoderma glaucum* was recorded at the mouth of the Río San Pedro inlet during the first sampling year, a crowded population of cockles inhabited the study area from May 2011 to September 2012. During this period, monthly samples of cockles were collected on the same dates as clams. The remarkably low abundance of pea crab reproductive females in clams and cockles, together with the concomitant high prevalence of non-reproductive pea crabs in the latter host, led us to search for an additional bivalve host in the area. In the Bay of Cadiz, *Afropinnotheres monodi* has also been collected in the bivalves *Chamelea gallina*, *Donax trunculus*, *Mactra stultorum*, *Mytilus galloprovincialis*, *Spisula solida* and *Venerupis decussatus* (P. Drake et al. unpubl.). Since reproductive females were only found in the mussel beds of *M. galloprovincialis*, this species was sampled monthly from June 2012 to May 2013. Mussel individuals were collected within the Bay of Cadiz from bridge pillars and concrete blocks; the demographic characteristics of the harboured pea crabs were similar at both sampling locations. During this last annual cycle, monthly samples of cockles were collected on the same dates that mussel sampling took place, until the disappearance of the cockle population in October 2012; *S. plana* clams were also occasionally sampled to corroborate that pea crab reproductive females were still extremely rare in this host.

In order to facilitate the collection of the 3 host bivalves in their respective habitats, clams, cockles and mussels were haphazardly sampled during the low tide of spring tides (full moon). *Scrobicularia plana* clams were collected by hand digging in the fine muddy sediment; *Cerastoderma glaucum* cockles were dug up from the sediment with a rake and then collected by hand; mussels were removed from the hard substrates using a knife.

Host use pattern

The collected living bivalves were quickly taken to the laboratory; no crabs were observed leaving their hosts during transportation. In the laboratory, the shell length (SL = maximum distance along the anterior–posterior axis of the shell) of each host bivalve was measured to the nearest 0.1 mm with a dial calliper (Tesa Cal IP65). Afterwards hosts were

opened and carefully inspected for the presence of symbiotic crabs.

Due to differences in shell morphology among the 3 studied hosts, the empty volume of the shell cavity can be very different, for the same SL, among species. Thus, for each bivalve species, the empty volume of the shell cavity was estimated in a subsample of the collected individuals, as follows. After host dissection and retrieval of crabs, the soft tissues of the bivalves were placed back into the shell and each valve was filled with water. The empty volume of the shell cavity was measured as the total volume of water retained within the valves. These data were further used to construct, for each host species, the best-fitting regression models between SL and the free volume of the shell cavity. Since volume data did not meet statistical assumptions of a parametric ANOVA, interspecific differences in mean empty volume of host individuals harbouring *Afropinnotheres monodi* were assessed by using the non-parametric Kruskal Wallis *H*-test.

All pea crabs found within each host individual were killed by freezing at −20°C and then preserved and stored in ethanol (80%) for further demographic observations. The carapace width (CW = maximum cephalothorax width) of each pea crab was measured to the nearest 0.01 mm under a stereomicroscope equipped with a calibrated ocular micrometer. Crabs were sexed on the basis of the presence (male) or absence (female) of gonopods. Furthermore, each female crab was classified either as hard or soft taking into account abdomen morphology, cephalothorax consistence and shape, and pleopod morphology: hard females show a flattened and quadrangular cephalothorax and swimming legs, whereas the body of soft females is mostly spherical and lacks swim-

ming legs. Lastly, soft females carrying eggs (embryos) were classified as ovigerous females.

The host use patterns of *Afropinnotheres monodi* were assessed by describing the characteristics of the crab population inside each host species, the seasonal and host-size related structure of these populations and the mean prevalence of the pea crabs in each host species. The mean prevalence of crabs was estimated as the average prevalence values found on each sampling date. Mean carapace width of pea crab males and females from different hosts were compared using 1-way ANOVA (on log-transformed data), or the Kruskal Wallis *H*-test when data did not meet statistical assumptions of the parametric test.

The relationship between host size (SL) and crab size (CW) was assessed by means of a linear correlation analysis; the significance of the estimated Pearson correlation coefficient was used to measure the strength of this relationship. Additionally, the observed crab prevalence in each host size class was compared with the expected prevalence in the random Poisson distribution. Similarly, to test whether pea crabs tend to live solitarily, in pairs or aggregated in higher numbers inside the host, the frequency of occurrence of hosts without crabs and with different numbers of crabs was compared with the expected frequencies under a random distribution. For each host species, the observed sexual composition of pairs of crabs sharing a single host individual were compared with the expected frequencies of heterosexual and homosexual pairs in a random distribution. Also, the observed proportion of males to females was tested for deviation from a 1:1 sex ratio. In both cases, significant differences between the observed and the expected values were assessed using chi-squared tests (Zar 2010).

Table 1. Mean prevalence of the pea crab *Afropinnotheres monodi* in the bivalves *Scrobicularia plana*, *Cerastoderma glaucum* and *Mytilus galloprovincialis*. For each host species and demographic crab category, host shell length (SL) range (shell cavity volume range in brackets), mean crab carapace width (CW; range in brackets) and Pearson correlation coefficient between CW and the host SL are presented; ns, p > 0.05; *p < 0.05; **p < 0.01

Host	Prevalence (%) [no. of hosts examined]	Host SL (mm) [volume (ml)]			Crab CW (mm) [range]			CW–SL correlation		
		Male	Hard female	Soft female	Male	Hard female	Soft female	Male	Hard female	Soft female
Scrobicularia plana	4.1 [9441]	22.0–37.5 [1.0–4.0]	17.1–36.8 [0.5–3.8]	27.0–35.5 [1.7–3.5]	2.93 [1.80–3.80]	2.88 [1.39–4.65]	4.41 [3.70–5.53]	0.1 ns	0.21 ns	0.04 ns
Cerastoderma glaucum	41.1 [2661]	15.1–36.4 [0.8–7.2]	14.1–35.1 [0.7–6.6]	21.8–35.2 [2.0–6.6]	2.88 [1.35–7.33]	2.78 [0.65–6.83]	5.61 [3.77–8.67]	0.2*	0.04 ns	0.34*
Mytilus galloprovincialis [868]	45.9	14.0–44.3 [1.3–24.5]	13.1–37.2 [1.1–16.7]	14.6–49.8 [1.4–35.5]	4.66 [2.01–9.83]	3.29 [2.27–5.50]	9.29 [3.33–13.67]	0.3*	0.18 ns	0.63**

The fecundity of *Afropinnotheres monodi* was determined by counting all eggs carried by 108 ovigerous females. Eggs were extracted from the incubation chamber by immersing females for 5 min in an aqueous solution of sodium hypochlorite (10 g of active chlorine l^{-1}) followed by a soft agitation (adapted from Góes et al. 2005). Due to the extremely low prevalence of pea crab reproductive females in clams and cockles, most ovigerous females used for estimating fecundity were retrieved from mussels; only 3 females were retrieved from *Scrobicularia plana* and 11 from *Cerastoderma glaucum* cockles, whereas the remaining 94 ovigerous females were retrieved from the mussel *Mytilus galloprovincialis*. The relationship between CW and the number of embryos per female was fit to a power model by regression analysis. Since there was a significant effect of female size on the number of embryos, seasonal and host differences in fecundity were tested with an analysis of covariance (ANCOVA, covariate: log-transformed female CW; factors: season and host species) using the Student-Newman-Keuls *a posteriori* test.

Although a 5% significance level (p = 0.05) was considered for all statistical tests, in the multiple correlation analyses between host and crab sizes, the Bonferroni correction was used to avoid a spurious increase of significant correlations; in this case, a p of 0.005 was considered equivalent to a corrected p of 0.05 (Zar 2010).

RESULTS

Crab populations in different hosts

In total, 1557 pea crabs were collected during this study, distributed as follows: 225 in 9441 *Scrobicularia plana*, 920 in 2661 *Cerastoderma glaucum* and 412 in 868 *Mytilus galloprovincialis*. The mean prevalence of pea crabs was considerably higher in mussels (45.9%) and cockles (41.1%) than in clams (4.1%). No megalopae of *Afropinnotheres monodi* were found in the 3 studied hosts. The youngest stage observed, the first crab (first stage after larval metamorphosis with CW ≤ 1 mm), was occasionally found in cockles (Table 1). The remaining ontogenetic stages of the pea crab were present in the 3 studied hosts, but their proportion and mean size differed among hosts (Table 1, Fig. 2). The proportion of soft females was extremely low among the female crabs retrieved from *S. plana* (13.3%) and *C. glaucum* (13.1%) but extremely high in those retrieved
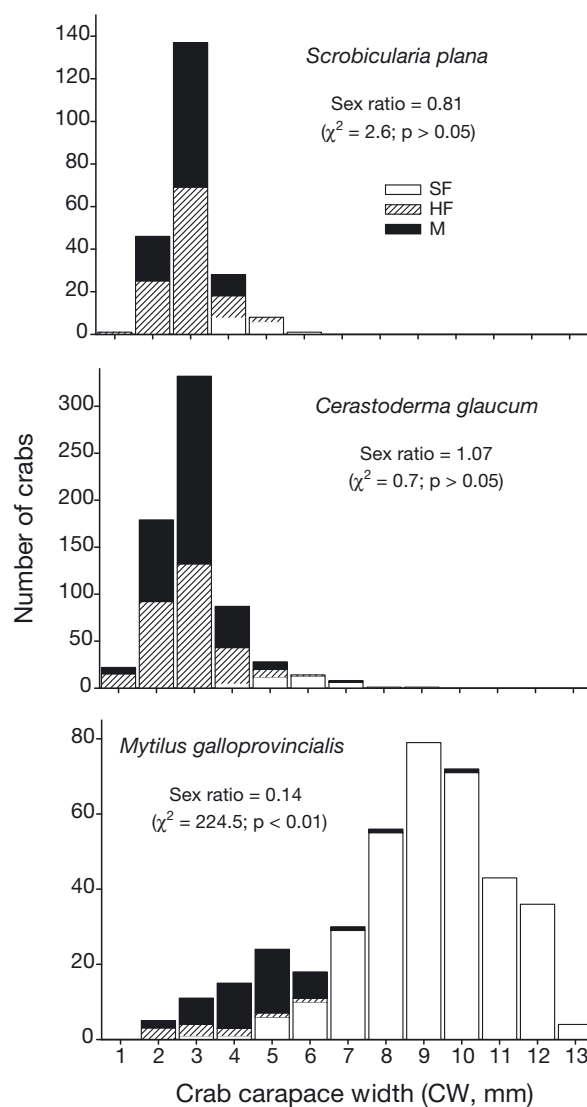

Fig. 2. *Afropinnotheres monodi.* Population structure (size and demographic category) of pea crabs in the 3 studied hosts. SF: soft female; HF: hard female; M: male. Sex ratio of pea crabs harboured by the mussel *Mytilus galloprovincialis* was significantly different from 1:1

from *M. galloprovincialis* (97.4%). Moreover, the maximal size and hence the mean size of soft females was also significantly higher in crabs inhabiting mussels (F = 190.3, p < 0.01). In contrast, hard females represented almost 50% of the pea crabs retrieved from clams and cockles and were seldom found inside mussels; differences in the size of hard females retrieved in different hosts were small (F = 2.0, p > 0.05). The sex ratio of pea crabs collected in *S. plana* (0.81) and *C. glaucum* (1.07) did not significantly differ from 1:1 (χ^2 = 2.6 and 1.07, respectively, p > 0.05), but a significantly higher number of females was
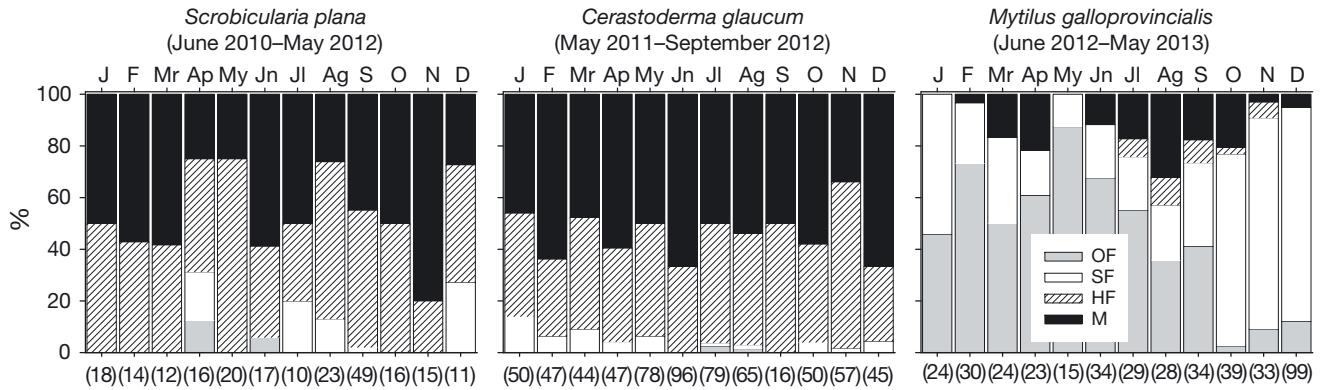
Fig. 3. *Afropinnotheres monodi*. Seasonal pattern in the occurrence of each demographic category of the pea crab in the 3 host species. OF: ovigerous soft female; SF: non-ovigerous soft female; HF: hard female; M: male. Dates below host species names (in parentheses): sampling periods of the corresponding host. Numbers on *x*-axis (in parentheses): numbers of pea crabs collected
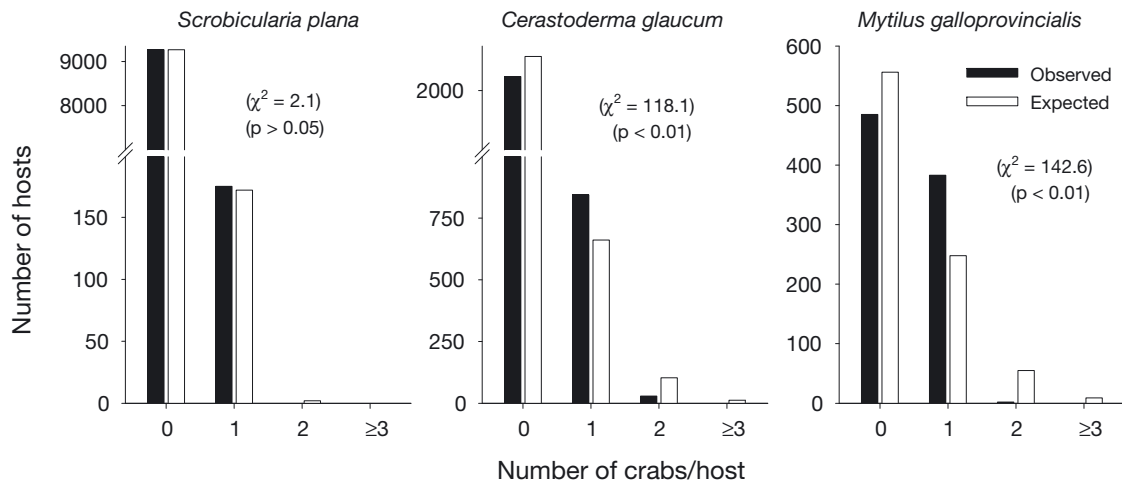

Fig. 4. *Afropinnotheres monodi*. Population distribution of pea crabs in the 3 host species. Observed frequency of occurrence of crabs in *Cerastoderma edule* and *Mytilus galloprovincialis* differed significantly from expected in a random distribution

observed in crabs obtained from *M. galloprovincialis* (sex ratio = 0.14; χ^2 = 224.5, p < 0.01) (Fig. 2). Moreover, the maximal size and hence the mean size of males was significantly higher in crabs retrieved from mussels (H = 80.6, p < 0.01).

The above mentioned differences in the proportion of ontogenetic stages among hosts occurred all year round, although moderate seasonal changes could be observed (Fig. 3). Minimal seasonal changes were observed for the pea crab population inhabiting cockles. The pea crab population in clams displayed monthly changes in the sex ratio that lacked a clear seasonal pattern. Although ovigerous crab females could be found all year inside mussels, their proportion in autumn (October to December) was relatively low compared with the rest of the year. The occa-

sional record of ovigerous females inside clams (April and June) and cockles (July and August) occurred during the period of higher reproductive activity (higher number of ovigerous females in mussels) of the pea crab (Fig. 3).

Interactions between crabs

The number of pea crabs per host varied between 0 and 1 in clams and between 0 and 2 in mussels and cockles; 100% of the clams, 99.5% of the mussels and 96.6% of the cockles harboured a single crab (Fig. 4). Thus, crab distribution among hosts did not display a random pattern: there were more bivalves harbouring 1 crab and fewer bivalves without crabs
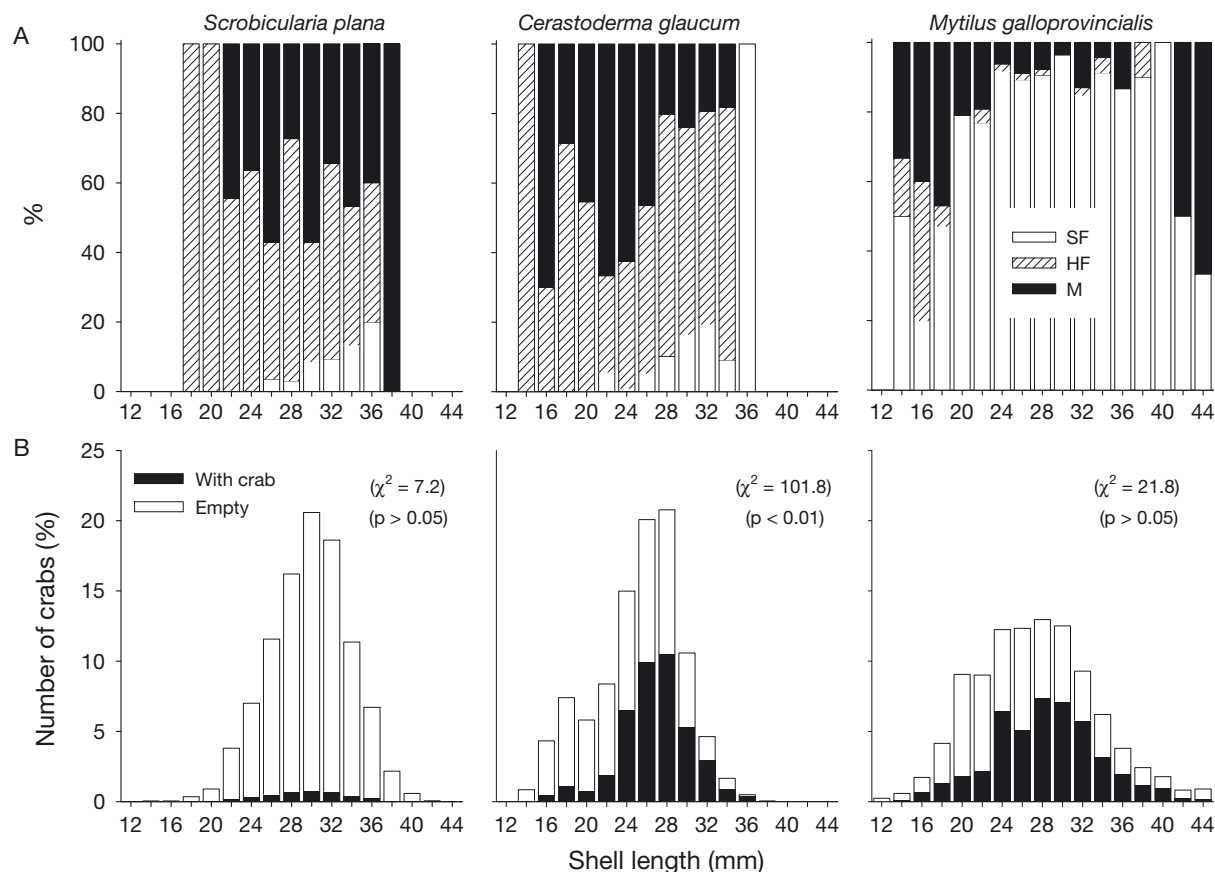
Fig. 5. *Afropinnotheres monodi.* (A) Percentage of occurrence of each demographic category of pea crabs in each host size class, and (B) frequency distribution of pea crabs in the different size classes of each host species *Scrobicularia plana*, *Cerastoderma edule* and *Mytilus galloprovincialis*

or harbouring >1 crab, than those expected by chance alone. The observed departure from a random pattern was statistically significant (χ^2 test, p < 0.01) only for the 2 host species with high prevalence of pea crabs, viz. mussels and cockles (Fig. 4).

A total of 31 *Cerastoderma glaucum* harboured pairs of crabs, of which 17 (54.8%) pairs were heterosexual (15 with 1 hard female and 1 male and 2 with 1 soft female and 1 male) and 14 were homosexual (10 with 2 males and 4 with 2 hard females). In mussels, of the 5 pairs of crabs sharing the same host individual, 4 were heterosexual (with 1 soft female and 1 male) and a single pair was homosexual with 1 soft and 1 hard female. Taking into account the different sex ratio observed in both hosts (Fig. 2), the sexual composition of the crab pairs in cockles did not differ significantly from that expected by chance alone (χ^2 = 2.0; p > 0.05); whereas in mussels there were fewer female-female pairs than expected by chance alone (χ^2 = 10.1; p < 0.05). However, due to the extremely low number of crab pairs found in mussels, the latter should be considered with caution.

Host size effects

The frequency distributions of crabs in host size classes were relatively similar for the 3 bivalves, with a mean host size of 26.8 mm in *Cerastoderma glaucum*, 27.3 mm in *Mytilus galloprovincialis* and 29.8 mm in *Scrobicularia plana* (Fig. 5). In contrast, the corresponding empty volume of the shell cavity was significantly different among hosts: 3.3 ml in *C. glaucum*, 7.4 ml in *M. galloprovincialis* and 2.2 ml in *S. plana* (H = 649.3, p < 0.01). Furthermore, 100% of the clams and 92.2% of the cockles harbouring crabs were individuals with an empty volume in the shell cavity lower than 5 ml, whereas only 20.8% of mussels followed this pattern (Fig. 6).

Host size did not significantly affect the prevalence of crabs in *Scrobicularia plana*, with a higher number of crabs collected in the most frequent size classes. In contrast, a smaller crab prevalence than expected from a random distribution was observed in the smallest individuals of *Cerastoderma glaucum* and *Mytilus galloprovincialis*; however, such host size-
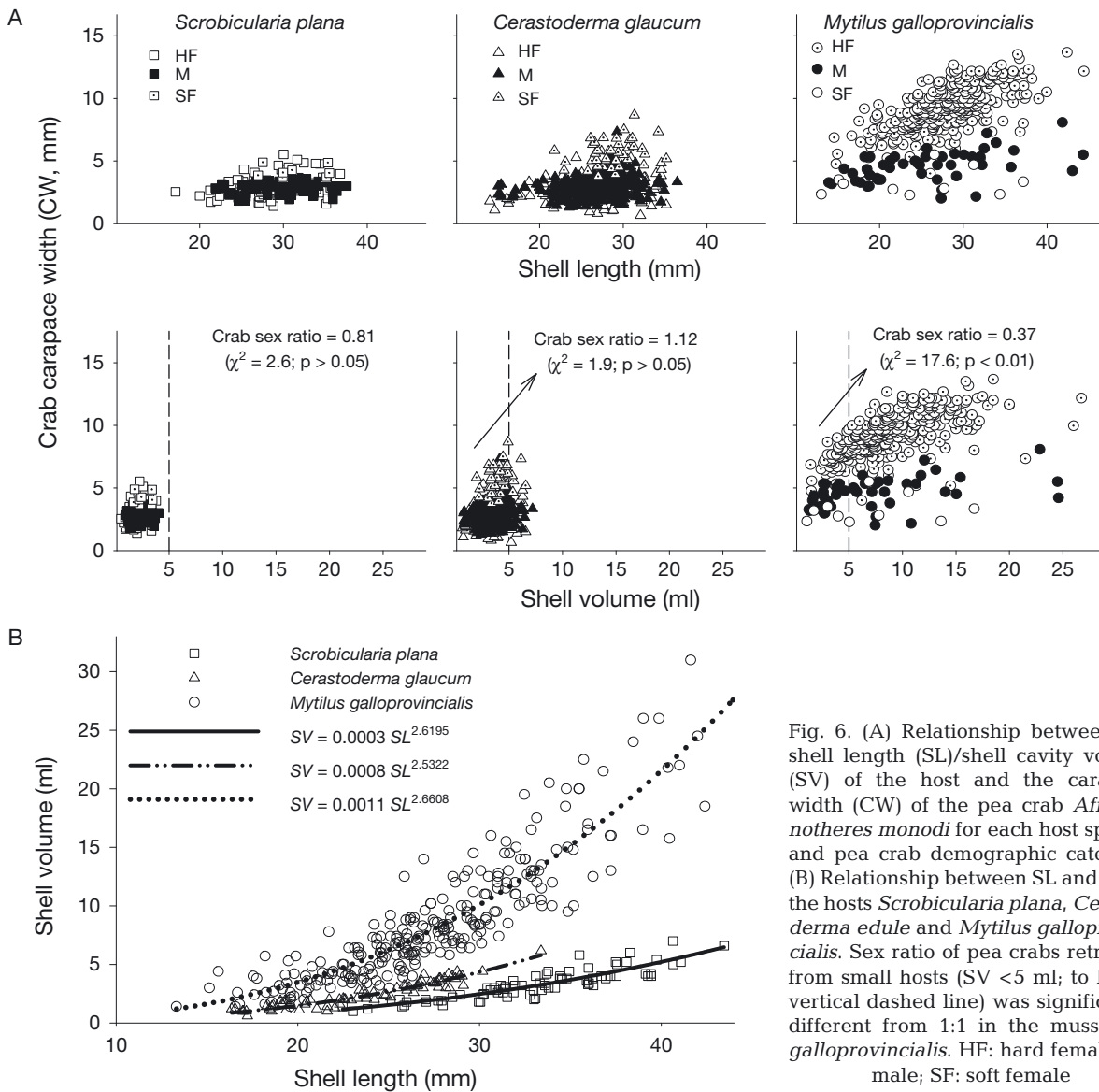
Fig. 6. (A) Relationship between the shell length (SL)/shell cavity volume (SV) of the host and the carapace width (CW) of the pea crab *Afropinnotheres monodi* for each host species and pea crab demographic category. (B) Relationship between SL and SV of the hosts *Scrobicularia plana*, *Cerastoderma edule* and *Mytilus galloprovincialis*. Sex ratio of pea crabs retrieved from small hosts (SV <5 ml; to left of vertical dashed line) was significantly different from 1:1 in the mussel *M. galloprovincialis*. HF: hard female; M: male; SF: soft female

related bias was only statistically significant in cockles (Table 1, Fig. 5).

Regardless of the host species, no clear host size-related distribution pattern of males and hard females of *Afropinnotheres monodi* was observed, although soft females were more frequent in larger host individuals. Nevertheless, when restricting the analysis to crabs collected inside bivalves with similar empty volume in the shell cavity (volume <5 ml), the estimated sex ratio of crabs retrieved from mussels proved to be significantly different from 1:1, with a higher prevalence of females (Fig. 6).

The size of soft females showed a highly significant positive correlation with mussel size and a moderate positive correlation with cockle size. No significant relationship was observed between host size and the size of hard female crabs, regardless of the host species. A moderate positive correlation was also found for host size and the size of males retrieved from cockles and mussels (Table 1, Fig. 6).

The fecundity of *Afropinnotheres monodi* increased significantly with female size regardless of host species (ANCOVA, $F_{1,101}$ = 283.2, p < 0.01; Fig. 7). After removing the effect of female size, fecundity did not differ significantly between seasons (ANCOVA, $F_{3,101}$ = 2.4, p > 0.05), but the host effect was significant (ANCOVA, $F_{2,101}$ = 19.0, p < 0.01), due to the lower number of eggs female^{-1} in crabs retrieved from clams (Student-Newman-Keuls test; p < 0.01).
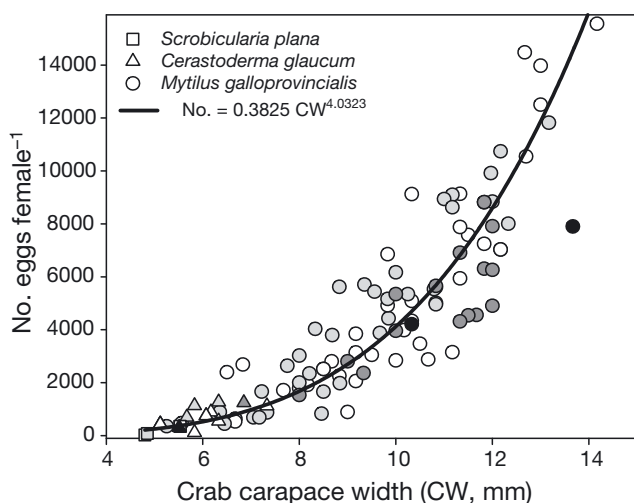
Fig. 7. *Afropinnotheres monodi*. Relationship between the crab carapace width (CW) and the number of eggs (No.) carried by ovigerous female *Afropinnotheres monodi* retrieved from the bivalves *Scrobicularia plana*, *Cerastoderma edule* and *Mytilus galloprovincialis*. Symbol colour indicates the season of host and pea crab collection (open: spring; light grey: summer; black: autumn; dark grey: winter)

DISCUSSION

From the 3 European species of pinnotherids currently accepted (Becker & Türkay 2010), *Pinnotheres petunculi* Hesse, 1872, *P. pisum* (Linnaeus, 1767) and *Nepinnotheres pinnotheres* (Linnaeus, 1758), only the latter 2 species have been occasionally collected in the Gulf of Cadiz (Zariquiey Álvarez 1968, González-Gordillo et al. 2001, 2003a, López de la Rosa et al. 2002). In addition to these European species, one small free-living specimen identified as *Afropinnotheres* sp., was collected in the Bay of Cadiz in 1995 (López de la Rosa et al. 2002) and, more recently, the presence of adult *A. monodi* was reported in 3 different bivalve hosts from the Gulf of Cadiz (Subida et al. 2011). A revision of larval pinnotherid specimens previously collected in the Río San Pedro inlet (July 1991 to June 1992; June 1998 to August 1998) and in the Guadalete estuary (in spring/summer of 2006 and 2007) demonstrated that zoeae and megalopae of this African pea crab were being misidentified as *N. pinnotheres* (Drake et al. 1998, González-Gordillo et al. 2003b, Olaguer-Feliú et al. 2010). In fact, neither *P. pisum* nor *N. pinnotheres* were collected during the present study, which indicates that *A. monodi* is currently the dominant symbiotic pinnotherid in intertidal bivalve populations of the Bay of Cadiz. The expansion of the distribution range of African marine species into

colder European waters is expected in the current scenario of rising seawater temperatures. Several other African crabs have their northward limit of distribution in the Gulf of Cadiz or on the Portuguese coast (García Raso & Manjón-Cabeza 1996, Drake et al. 1998). However, since at least one of the hosts of *A. monodi* is a fouling organism (i.e. mussel), its arrival to the European coasts could have occurred by accidental transport on ships (Apte et al. 2000). Regardless of the pathway through which species coming from warmer latitudes are introduced into northern habitats, the reproductive cycles of their northernmost populations are usually determined by temperature. The breeding periods of these species in the Gulf of Cadiz are usually shorter (falling in the warmest months) than in their African populations (González-Gordillo et al. 1990, Rodríguez et al. 1997). However, larval stages (Drake et al. 1998) and ovigerous females of *A. monodi* (this study) were found year round in the studied area, in contrast with the shorter (mainly in summer) reproductive activity of *N. pinnotheres* and *P. pisum* (Zariquiey Álvarez 1968, Becker 2010). Furthermore, the autumnal decrease of the reproductive activity of *A. monodi* observed in the studied area could disappear in the near future if the seawater temperature of the Mediterranean area keeps increasing (Sanderson et al. 2011). Likewise, *A. monodi* has an extended development, with 5 larval stages (E. Marco-Herrero et al. unpubl.), large enough to facilitate dispersal and colonisation of new areas (Abelló et al. 2003). Taken together, all of these features may have contributed to the quick and successful settlement of *A. monodi* in the Gulf of Cadiz, possibly to the detriment of *N. pinnotheres* and *P. pisum* populations.

Both males and females of *Afropinnotheres monodi* tend to live alone inside their host. Two hypotheses have been proposed to explain why this 1 crab host^{-1} relationship is recurrent among other pea crab species: (1) the crab releases a chemical cue that discourages conspecific guests from entering the same host; (2) a prior resident crab might show aggressive behaviour toward a later invading one (Bell 1984, Haines et al. 1994, Soong 1997, Takeda et al. 1997). Although some species of pea crab seem to show chemoreception (Stevens 1990, Ambrosio & Brooks 2011), when *A. monodi* individuals were retrieved from their hosts and immediately placed together in an aquarium in the presence of living hosts, multiple infestation by crabs was more frequent than in field observations (P. Drake et al. unpubl. data). This finding suggests that *A. monodi* crabs cannot detect the presence of conspecifics in the host, or, in some cir-

cumstances (i.e. more guests than available hosts) the presence of conspecifics is not a limiting factor. In addition, in the few pairs of crabs observed inside the studied hosts, heterosexual pairs were not more frequent than expected by chance alone. Thus, mating in this species might take place outside hosts or, if occurring inside hosts, might last a very short period of time, after which males abandon the temporarily shared host (Hamel et al. 1999, Ocampo et al. 2012, Peiró et al. 2013). That is, the dominance of solitary guest crabs in this population of *A. monodi* suggests that the selection of the host in this species tends to be random (opportunity-related) and, consequently, the occasional pairs observed inside hosts were accidental and transitory. This host monopolisation is an efficient adaptation (more benefits than costs) to hosts with small body size and/or low morphological complexity (Baeza & Thiel 2003, 2007, Hernández et al. 2012), such as the host bivalves in this study. In fact, mussels, the host that harboured mainly soft females, showed fewer female–female pairs than expected by chance. As males and hard females have significantly smaller body size (Figs. 2 & 6) and stronger swimming capacity than soft females, they may roam among hosts in search of empty hosts (both sexes) or receptive females (only males). In contrast, soft females seem to be totally adapted to a symbiotic lifestyle and never leave the host (De Bruyn et al. 2009, Becker et al. 2011, 2012). Thus, from the point of view of costs and benefits, host monopolisation could be more relevant for reproductive females than for the remaining demographic categories when host resources (space, food and oxygen) are limiting (Baeza et al. 2002, Narvarte & Saiz 2004, Baeza & Thiel 2007, De Bruyn et al. 2009).

Like the other pea crabs recorded on European coasts (Becker & Türkay 2010), *Afropinnotheres monodi* is not host-specific (Subida et al. 2011) and has been found in a high number of bivalve species, resembling the pattern shown by *Pinnotheres pisum*. Indeed, in the Bay of Cadiz, symbiotic males and females of this African species were found throughout the year inside the 3 studied hosts. However, there were clear differences in the global (total number of crabs) and specific (by demographic categories) prevalence of *A. monodi* in each host (Table 1, Fig. 2). Results of laboratory experiments, which aimed to assess host preferences in other species of pea crabs, did not always match the host preferences predicted from field observations of the same species (De Bruyn et al. 2010, Ocampo et al. 2012). Therefore, if we assume that in the field the *A. monodi* distribution on the different hosts

was random, the prevalence in each host should be proportional to the corresponding host accessibility and availability. From the 3 studied hosts, *Scrobicularia plana* clams are the host showing last accessibility to crab guests since they bury deeply in the sediment (more difficult to be reached by crabs) of the higher intertidal zone (more time emerged). In fact, *S. plana* was the host in which *A. monodi* showed the lowest prevalence. However, the varying habitat characteristics of the 3 hosts alone do not explain the asymmetrical host usage by each demographic category observed for the studied pea crab. Under the assumption that pea crabs are optimally adapted to the environment, their current performance must be determined by costs and benefits associated with the different behaviours (Baeza & Thiel 2007). In the case of *A. monodi*, we hypothesise that the different host uses observed could be triggered by an ontogenetic change in the swimming behaviours and habitat preferences of crabs. That is, if megalopae of this species tend to choose the soft sediment of sheltered sand-muddy flats for their benthic settlement (Olaguer-Feliú et al. 2010), immature males and females of *A. monodi* could be more likely to infest benthic species inhabiting the sediment, such as cockles and clams, which are small in size (small empty space in the shell cavity) but abundant and protected from predators. However, when the pea crabs grow, their swimming capability increases, favouring the adoption of a temporal free roaming behaviour (De Bruyn et al. 2009, Jossart et al. 2013). Although the risk of predation is higher for pea crabs out of their hosts, to obtain refuge in larger hosts such as mussels is a relevant benefit (increase of resources) for future ovigerous females. Assuming that males are able to distinguish between female stages (Diesel 1988, De Bruyn et al. 2009, Ambrosio & Brooks 2011), they could increase their mating opportunities by living near hosts infested with receptive females. Indeed, *A. monodi* males were found in the 1:1 sex ratio only on the 2 host species harbouring mainly hard/receptive females (clams and cockles), whereas soft females were found mainly in mussels. An analogous asymmetrical host usage by the different demographic categories has been reported for the pea crab *Fabia subquadrata* in the Puget Sound (Washington, USA) area (Garth & Abbott 1980). With the available information, the life history of *A. monodi* hypothesised herein is the most plausible to explain the results obtained in the Bay of Cadiz. However, in the absence of a fully simultaneous sampling of the studied hosts and of experimental

assays demonstrating the movement of pea crabs between hosts, the inferences concerning this aspect of the guest's autoecology should be considered with caution.

As for other pea crab species (Christensen & McDermott 1958, Soong 1997, Kane & Farley 2006, Ocampo et al. 2012), we found a strong correlation between host size and symbiotic ovigerous female size of *Afropinnotheres monodi*, which suggests that space availability within hosts is a relevant factor in determining the final size of this sedentary phase (soft females) of symbiotic crabs and, consequently, of its reproductive pattern. Similarly, a positive relationship between the fecundity and the body size of female pea crabs, previously reported for other species (Bell & Stancyk 1983, Baeza & Thiel 2000, De Bruyn et al. 2010), has been observed for *A. monodi*: large ovigerous females found inside mussels have much higher fecundity than the scarce and small ovigerous females inhabiting clams and cockles (Fig. 7). Nevertheless, when the body size of female crabs was taken into account, differences in size-specific fecundity were only observed between females inhabiting clams and those from the remaining 2 host species, suggesting that the flattened morphology of the shell of *Scrobicularia plana* makes this host rather unsuitable for the almost-spherical ovigerous female pea crabs. That is, the size of reproductive females that use cockles as a host is constrained by the relatively small size of this host, and crabs inhabiting clams also show a decrease in size-specific fecundity. Thus, even if all demographic categories of *A. monodi* could be observed inside the 3 studied hosts, the reproductive effort of this crab would still correspond mainly to females inhabiting mussels. Moreover, the fecundity of large ovigerous females of *A. monodi* was higher than (Bell & Stancyk 1983, Hamel et al. 1999, Baeza & Thiel 2000, De Bruyn et al. 2010) or similar to (Silas & Alagarswami 1967, Ocampo et al. 2012) other pea crab species. However, the input of new recruits to the adult population occurred mainly in clams and cockles, which convert these smaller-size hosts in a relevant step to the establishment of abundant and stable populations of *A. monodi* in the studied area. According to Debruyn et al. (2010), this type of asymmetrical usage of hosts by parasitic pea crabs may be comparable with the transitory stages predicted by models of evolution of complex parasite life cycles (Parker et al. 2003). Namely, the asymmetrical usage of clams, cockles and mussels by *A. monodi* in the Gulf of Cadiz resembles the transitional stage predicted by the 'downward incorporation' of a new host into the life cycle of this pea crab. In any case, the generalist but asymmetrical usage of bivalve hosts found in *A. monodi* may have clear benefits for species in geographical expansion: first, the presence of all demographic categories in the 3 hosts can facilitate the settlement of the species in new locations; second, the asymmetrical use of different hosts can lead to the settlement of copious and stable populations in some areas, such as complex estuarine habitats in the case of *A. monodi*, which act as a massive source of pelagic larvae with high capacity for dispersal. Thus, the use of >1 host species by symbiotic species may increase their fitness and, simultaneously, shape their life cycle and evolution (De Bruyn et al. 2010). Nevertheless, incorrect selection of the definitive host by females may become a disadvantage: after metamorphosis, reproductive females become too immobile to leave the host and/or reach and enter a new one. In fact, during the study, we collected dead mussels whose valves harboured large ovigerous females of *A. monodi* in unhealthy condition or even dead.

Several species of pinnotherids worldwide parasitize commercially exploited bivalves (Stauber 1945, Christensen & McDermott 1958, Silas & Alagarswami 1967, Sun et al. 2006). In shellfish farms, a significant loss of production has been observed even with low levels of pea crab infection (Trottier et al. 2012). Furthermore, pea crabs may rapidly colonise bivalves from a shellfish farm, and subsequently infect nearby shellfish farms (Trottier & Jeffs 2012). However, considering the asymmetrical use of different hosts by *Afropinnotheres monodi*, we expect that the strongest threats may be posed to shellfish farms located in sheltered waters (e.g. bays, inlets, rías, harbours), where populations of the different hosts used by this African species coexist. As the species seems to be in clear northward expansion, it may become, in the near future, a significant threat for European bivalve aquaculture. Thus, the confirmation of the hypotheses presented in this study, by experimental assays, is of high social and economic interest.

In conclusion, the symbiotic African pea crab *Afropinnotheres monodi* seems to be currently in geographical expansion. It shows a series of features in its life cycle (wide reproductive period, high fecundity, long planktonic phase, generalist and asymmetric host use) that facilitate its quick and successful settlement in new locations. Both characteristics make it particularly relevant to studying the evolution of pea crab symbiotic life history traits.

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