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ORIGINAL ARTICLE

Biology and interspecific interactions of the alien crab *Percnon gibbesi* in the Maltese Islands

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Abstract

Spatial and bathymetric distribution, population density, habitat preferences, fecundity, breeding season and interspecific interactions of the alien grapsoid crab *Percnon gibbesi* (H. Milne-Edwards, 1853) from the Maltese Islands (Malta and Gozo) are compared among localities in the Mediterranean where established populations have been reported since 1999. In the Maltese Islands, habitat preferences and bathymetric distribution were similar to those in other Mediterranean localities. Spatial distribution was found to be limited by the availability of the boulder habitat in which this crab nearly always occurs. Fecundity was higher in the Maltese Islands than in Linosa and Lampedusa, the breeding season lasting from the end of May until September. On Maltese shores the habitat of the alien overlapped with that of the native grapsid *Pachygrapsus marmoratus* (Fabricius, 1787) (Crustacea: Brachyura: Grapsoidea) and, to a lesser extent, that of the native xanthid *Eriphia verrucosa* (Forskål, 1775). Laboratory studies to assess the possible interactions of the alien species with *P. marmoratus* suggest that the latter shows a competitive advantage over *P. gibbesi*, since 80.8% of encounters between the two species were initiated by *P. marmoratus*, and in 80% of the encounters it prevailed. This suggests that *P. marmoratus* is unlikely to be excluded from its natural habitat by the alien species, and that significant spatial resource partitioning on the part of *P. marmoratus* is unlikely to occur.

Key words: Interspecific interactions, Maltese Islands, *Pachygrapsus marmoratus*, *Percnon gibbesi*, population density

Introduction

Increased trade and tourism associated with globalization have facilitated one of the least reversible human-induced global changes: the homogenization of the Earth's biota through the establishment and spread of alien species (Kolar & Lodge 2002). The crab *Percnon gibbesi* (H. Milne Edwards, 1853), a grapsoid (superfamily Grapsoidea) of uncertain familial assignment (Schubart et al. 2000), has a wide natural latitudinal and temperature range that extends from Baja California to Chile on the eastern Pacific coast (Hendrickx 1995). On the western Atlantic coast its range extends from Florida to Brazil. Along the eastern Atlantic coast its range includes Madeira, the Azores, the Cape Verde Islands and the coast of Africa from Morocco to Ghana and offshore islands in the Gulf of Guinea (Manning & Holthius 1981; Relini et al. 2000). This species has recently been reported from the Mediterranean Sea,

where in 1999 it appeared concurrently in Ibiza, Spain (Muller 2001) and two locations in Italy: Linosa Island in the Straits of Sicily (Relini et al. 2000) and Capo Passero in southern Sicily (Mori & Vacchi 2002). Since that time, *P. gibbesi* has continued to spread rapidly throughout the Mediterranean basin. Other reports from Italy include Pantelleria and western Sicily (San Vito, Capo Gallo and Ustica) (Pipitone et al. 2001), the northern and Ionian coasts of Sicily, the Tyrrhenian coast of Calabria, the islands of Ischia and Ponza, southern Sardinia, Isola delle Femmine (northwest Sicily) (Cannicci et al. 2004), the central Tyrrhenian extending from the coasts of Cilento to the Pontine Islands, and the Gulf of Naples (Russo & Villani 2005). Reports from Spain include Dragonera and Es Pantaleu islands southwest of Mallorca (Deudero et al. 2005). Reports from Greece include: Xerocampos and the Gulf of Messiniakos (Crete), Antikythira Island and Rhodes Island (Cannicci et al.

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2006; Thessalou-Legaki et al. 2006). Reports from Turkey include Uc Adalar and Kas-Antalya (Yokes & Galil 2006). *Percnon gibbesi* was first recorded from Malta in 2001 (Borg & Attard-Montalto 2002).

Numerous mechanisms for the introduction and spread of *P. gibbesi* in the Mediterranean have been proposed. These include natural range expansion by adult migration or larval drift with Atlantic surface currents that enter the Mediterranean via the Strait of Gibraltar, favoured by a climatic change towards warmer waters (Pipitone et al. 2001); transport in the ballast tanks of vessels (Cannicci et al. 2006; Yokes & Galil 2006), or with fouling and boring communities on ship hulls (Mori & Vacchi 2002); and intentional release or accidental escape from aquaria (Borg & Attard-Montalto 2002). Whatever the mechanism of introduction, this species has established breeding populations in all Mediterranean localities where it has been reported. The remarkable success of this alien to colonize and establish itself in the Mediterranean has been linked to several attributes of *P. gibbesi* itself and the recipient communities, including favourable local environmental factors such as seawater temperature and absence of competitors (Pipitone et al. 2001); availability of unoccupied niches (Cannicci et al. 2004; Fanelli & Azzurro 2004); the crab's ability to rapidly adapt to different types of habitats (Pipitone et al. 2001); its flexible feeding habits (Cannicci et al. 2004); its long reproductive period (Fanelli & Azzurro 2004); its ability to produce several clutches of eggs each year (Mori & Vacchi 2002); and its long planktonic larval stage (Pipitone et al. 2001).

Even if the biology of a species in its native range is known, the consequences of an invasion are often not easily predicted (Ruiz et al. 1997) since various checks and balances that would normally limit population growth of the invader might be different or non-existent in the new environment. For example, the absence of predators and competitors for the alien ctenophore *Mnemiopsis* in the Black Sea, contrary to in its native habitat, had severe impacts on the Black Sea ecosystem in the late 1980s and early 1990s. The reduction in zooplanktivorous fish populations in the Black Sea due to overfishing prior to the ctenophore outbreak, combined with predation by *Mnemiopsis* on fish eggs, contributed to the success of *Mnemiopsis* in the Black Sea and subsequent reductions in fish populations (Purcell et al. 2001). The appearance of yet another invasive ctenophore (*Beroe*) – that preyed on *Mnemiopsis* – promoted recovery of the Black Sea ecosystem from effects of the *Mnemiopsis* invasion (Shiganova et al. 2001). Invasions may thus be regarded as ecological 'experiments' that could provide information on the structure (Crooks & Khim

1999) and resistance (Stachowicz et al. 1999) of natural communities, or on perturbations caused by the sudden arrival of new species into the system (Lambert et al. 1992; McDonald et al. 2001; Walton et al. 2002; Occhipinti-Ambrogi & Savini 2003; Branch & Steffani 2004).

Information on the biology and ecology of *P. gibbesi* in the Mediterranean is steadily accumulating and indicates that this crab species interacts with its environment differently in different localities where it has been established. In this study we report field observations on the distribution, density and biology of *P. gibbesi* in the Maltese Islands. We also report results of a laboratory-based study to investigate the competitive advantage in one-on-one interspecific interactions between the alien species and the native syntopic grapsid, *Pachygrapsus marmoratus* (Fabricius, 1787), with which the alien was observed to share habitat and interact with during field observations.

Material and methods

Species studied in the Maltese Islands were identified by comparing crabs collected in the field with characteristics of *Percnon gibbesi* detailed in Schmitt (1939) and Williams (1984). All specimens examined were typical *P. gibbesi*.

Field investigation

Field surveys to assess the bathymetric distribution, habitat preferences and interaction with other species were carried out between July and October 2004 at 23 sites around the Maltese Islands (Figure 1). Observations were made and samples collected from Malta and Gozo – two of the islands that make up the Maltese archipelago. At 20 of the sites investigated, the population density between the 2 m depth contour and the shore was determined as the number of crabs in replicate virtual quadrats, in habitats where *P. gibbesi* was observed. The number of replicates varied from 5 to 49 (see Table II) based on size of the area investigated. Bottom areas of approximately 1 m² were estimated visually using landmarks. At Cirkewwa (Site 1 in Figure 1), St. Julians (Site 8), Marsascala (Site 10) and Hondoq ir-Rummien (Site 19), changes in crab population density with depth were studied for two depth strata: within 2 m and from 2 to 4 m, during the morning (10.00–12.00 h). At Pembroke (Site 7 in Figure 1), changes in crab population density with time of day were studied on six consecutive days by conducting quadrat counts between 11.00 and 14.00 h and then again between 17.00 and 19.30 h.

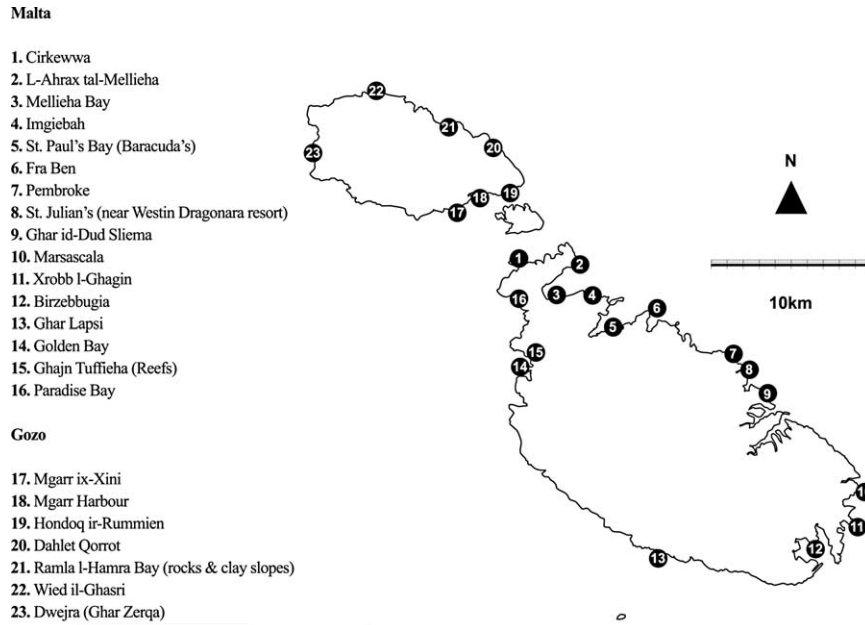


Figure 1. Map of the Maltese Islands showing the location of the 23 sites investigated.

Reproductive condition of female crabs was examined at weekly intervals between July and October 2004, and at monthly intervals between November 2004 and May 2005, with the exception of April 2005 when no samples were collected. Sexual maturity of the crabs was assessed based on abdominal morphology. Females with domed abdomens were considered mature; those with suboval abdomens were considered immature. Males with abdomens closely apposed to the thoracic sternites that could not be easily pried open with a dissecting needle, were considered immature. Maturity status (whether immature or mature) and fecundity status of females (whether females carry eggs or not) were determined using a sample of 270 crabs, of which 158 were male and 112 were female crabs. To investigate the relationship between number of eggs and size (measured as the maximum carapace length, CL), egg masses from 30 ovigerous females collected from the field were fixed in 70% alcohol and weighed; subsamples of eggs were then removed, weighed and the number of eggs in each was counted using a stereomicroscope. Prior to weighing, all egg samples were cleared of setules and other adhering debris. The total number of eggs in the egg mass was then calculated by simple proportion.

Laboratory investigation

Specimens of *Pachygrapsus marmoratus* and *Percnon gibbesi* were collected by hand between December 2004 and March 2005. *Pachygrapsus marmoratus* were collected from rock pools, beneath boulders

and within rock crevices at Pembroke (Site 7 in Figure 1). *Percnon gibbesi* were collected from Pembroke (Site 7 in Figure 1) and Marsascula (Site 10 in Figure 1) depending on weather and sea conditions. In the laboratory, each crab was sexed and measures taken of its carapace length (CL), carapace width (CW), chela length (total propodus length, TPL) and chela width (total propodus width, TPW) using vernier callipers (accurate to ± 0.1 mm). The crabs were held in plastic aquaria (31.5 cm \times 19.5 cm \times 19.5 cm deep) supplied with aerated seawater at 20°C. They were left to acclimate to laboratory conditions for a period of 7 days prior to behavioural observations. During these experiments the crabs were not fed to motivate aggressive behaviour between the two crab species. To ensure competitiveness in behavioural observations, only crabs were used that had no missing chelipeds or recently regenerated chelipeds and hard exoskeletons (Sneddon et al. 1997).

Individuals of both species were grouped into three size classes; large (L) with CL greater than 30 mm, medium (M) with CL between 20 and 30 mm and small (S) with CL smaller than 20 mm. In total, nine size combinations were investigated (Table I). A minimum of 10 one-on-one interspecific encounters were staged for each size combination by placing the two crabs in a plastic aquarium (length 29.5 cm \times width 20 cm \times depth 19 cm). The bottom of the test aquarium was layered with gravel and filled with aerated seawater at 20°C. The crabs were allowed a settling time of 30 min in isolation; keeping the two individuals separate with an opaque vertical partition across the test aquarium, after

Table I. The size combinations investigated in interspecific interactions between *Pachygrapsus marmoratus* and *Percnon gibbesi* (the number of replicate trials for each size combination tested is also given).

Size combination	<i>Pachygrapsus marmoratus</i>	<i>Percnon gibbesi</i>	Number of replicate trials
LL	Large	Large	10
LM	Large	Medium	12
LS	Large	Small	10
ML	Medium	Large	12
MM	Medium	Medium	13
MS	Medium	Small	12
SL	Small	Large	11
SM	Small	Medium	12
SS	Small	Small	11

Large (L) indicates crabs with CL larger than 30 mm, medium (M) indicates crabs with CL between 20 and 30 mm, and small (S) indicates crabs with CL smaller than 20 mm.

which, the partition was raised gently to initiate the encounter. To reduce the possibility of chemical communication, the air pump was switched off during the settling and observation period to minimize mixing. Each encounter lasted for a maximum of 1 h or until the contest was ended by one crab injuring its opponent. The actions of both crabs were recorded for subsequent analysis, using a video camera.

Results

Percnon gibbesi was found at all 23 sites investigated during this study. This species showed a preference for boulder fields (boulder size: 30 cm up to 1 m or more in maximum diameter) with surfaces either bare of sessile macrobenthic organisms but covered with a microalgal film; covered with encrusting algae or algal turf; or with a moderate cover of erect macroalgae (see Table II). Occasionally, crabs were also present on wide bare rock ledges or in crevices on vertical rock walls with minimal vegetation cover (see Table II). However, this species was never observed on sandy bottoms, homogeneous rocky sea beds, bottoms with sparse and widely scattered boulders, or in seagrass meadows.

In the Maltese Islands, *P. gibbesi* is strictly subtidal and limited to the uppermost reaches of the infralittoral zone. The bathymetry at the sites studied ranged from 0.05 to 4 m (Table II), 4 m being the lower depth limit with significant accumulation of boulders. However, the possibility that individual crabs occurred in slightly deeper water cannot be excluded for four of these sites, namely Cirkewwa; Hondoq ir-Rummien; Wied il-Ghasri; and Dwejra (Ghar Zerqa) – where the boulder habitat favoured by this species extended to depths greater than 4 m, making observations of these well-camouflaged crabs in dark spaces amongst boulders at these depths difficult. Observation became more proble-

matic due to the agility with which the crabs retreated at the slightest disturbance or movement. However, in most localities, the boulder habitat gradually merged into a homogeneous rocky or sandy bottom at depths less than 4 m; here no crabs were observed beyond the boulder zone.

For the 20 localities where population counts were made, the mean population density of *P. gibbesi* ranged from 1.6 ± 0.5 to 11.9 ± 7.1 crabs m^{-2} (Table II). Population density was significantly different between sites (Kruskal–Wallis H-test; $P < 0.05$); the highest records were for Marsascala, Hondoq ir-Rummien and Dahlet Qorrot, possibly because at these localities, the favoured boulder bottoms extended as a band for relatively long distances along the shore rather than being restricted to small patches. Conversely, a lower population density was obtained at sites such as Ghajn Tuffieha, Birzebbugia, Fra Ben and Mgarr ix-Xini, where availability of adequate habitat was limited. At Ghajn Tuffieha, the crabs were restricted to a small patch of boulders surrounded by a sandy bottom. At Birzebbugia, boulders and crevices favoured by *P. gibbesi* were absent within the first 2–3 m from shore, while at Fra Ben and Mgarr ix-Xini, the majority of boulders were heavily covered by macroalgae.

The mean population density changed significantly with depth at sites where *P. gibbesi* occurred, both above and below 2 m depth (Mann–Whitney U-test; $P < 0.05$) (Figure 2). Higher mean population densities were obtained at depths smaller than 2 m compared to those obtained at 2 to 4 m depths. A two-fold increase in the mean population density between morning (before 13.30 h; 5.2 ± 3.4 crabs m^{-2}) and late afternoon (after 16.00 h; 10.1 ± 5.7 crabs m^{-2}) suggests that *P. gibbesi* becomes most active towards dusk (Mann–Whitney U-test; $P < 0.05$). The difference in population density between morning and evening counts is not related to tides since the average tidal range for

Table II. The mean population density, depth range, general habitat and microhabitat of *Percnon gibbesi* at 23 sites in the Maltese Islands.

Site	N ^a	Mean population density \pm SD (crabs m ⁻²)	Depth range (m)	Habitat description ^b	Microhabitat preference ^c
Cirkezza	19	3.4 \pm 2.2	0.6–4.0	1; 2; 4	a; b; c; d
L-Ahrax tal-Mellicha	21	5.5 \pm 3.5	1.4–3.0	2	a; b; c
Mellicha Bay	14	4.8 \pm 3.0	0.3–0.6	3	a; b
Imgiebah	16	4.5 \pm 2.2	3.0	2	a; b
St. Paul's Bay	10	4.3 \pm 2.0	1.5–2.5	2	b; c
Fra Ben	7	3.9 \pm 2.4	0.5–1.5	2	a; c; d
Pembroke	43	5.4 \pm 3.9	0.6–2.6	2	a; b; c
St. Julians	32	2.4 \pm 1.7	1.2–3.0	2	a; b; c
Ghar id-Dud	43	5.2 \pm 2.4	1.5–4.0	2	a; b; c; e
Marsascula	21	11.9 \pm 7.1	0.3–4.0	2	a; b; c
Xrobb l-Ghagin	29	5.5 \pm 2.5	0.5–2.0	2	a; e
Birzebbugia	6	4.5 \pm 3.3	0.3–0.6	1; 2	b; c; d
Ghar Lapsi	17	5.7 \pm 5.2	0.1–3.0	2	a; b; c; d
Golden Bay	8	4.6 \pm 3.1	1.5–2.0	3	a; b; c
Ghajn Tuffieha	5	1.6 \pm 0.6	2.0	3	a; b
Paradise Bay	25	5.8 \pm 2.5	0.3–2.0	3	a; b; c
Mgarr ix-Xini	9	3.7 \pm 2.1	0.6	1; 2	a; b; c; d
Mgarr Harbour	12	3.3 \pm 2.6	1.0–1.5	2	a; b
Hondoq ir-Rummien	20	10.0 \pm 6.0	0.6–3.6	2	a; b; c; d
Dahlet Qorrot	49	8.9 \pm 5.2	0.05–2.0	2	a; b; c
Ramla l-Hamra Bay	–	–	–	3	a; b
Wied il-Ghasri	–	–	–	4	a; b; c
Dwejra (Ghar Zerqa)	–	–	–	4	b; c

^aN is the number of replicate quadrats used for estimation of population density. No population counts were made at Ramla l-Hamra Bay, Wied il-Ghasri and Dwejra (Ghar Zerqa) due to high water turbidity and poor visibility at the time of observation.

^bKey to general habitat types: 1 = vertical rock faces with crevices that merge into a rocky bottom with dense cover of macroalgae at depths less than 4 m; 2 = boulder field which merges into a bare rocky bottom covered by dense macroalgae or seagrass meadows at depths less than 4 m; 3 = boulder field which merges into a sandy bottom at depths less than 4 m; 4 = boulder field which extends beyond a depth of 4 m.

^cKey to microhabitats in which *Percnon gibbesi* were observed: a = boulders with surface bare of sessile macrobenthos, but with a cover of microalgae; b = boulders covered by encrusting algae or algal turf; c = boulders with a moderate cover of erect macroalgae; d = rock ledges or crevices in rock faces which are either bare of vegetation or have a cover of encrusting algae or algal turf; e = vertical rock faces bare of sessile macrobenthos but with a cover of microalgae.

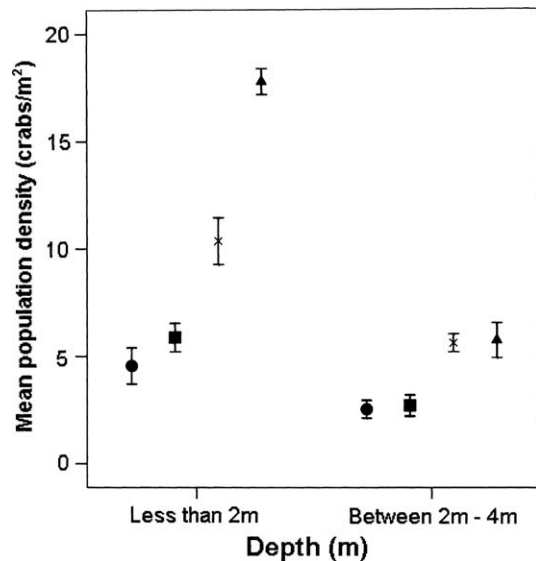


Figure 2. Mean population density (individuals per m²) of *Percnon gibbesi* at depths above 2 m and between 2 and 4 m, at St Julians (●), Cirkezza (■), Hondoq ir-Rummien (×) and Marsascula (▲). The population density was estimated between 10.30 and 13.30 h. Error bars represent the 95% confidence interval above and below the mean.

the Maltese Islands is 6 cm, with a spring tide maximum of 20 cm.

Carapace length (CL) of crabs collected from the field ranged from 6.3 to 37.2 mm (the largest male collected). The largest female had a carapace length of 35.6 mm. During July to October, crabs with CL between 21 and 35 mm constituted 79% of the sample, whereas crabs with CL less than 21 mm and more than 35 mm made up 19 and 2% of the sample, respectively (Figure 3).

Ovigerous females occurred between the end of May and September; 73.2% of mature females collected from July to October carried eggs, whereas 98% of the females collected between November and March were mature but not ovigerous, suggesting that the crab breeds during the summer months. Brood size produced by mature ovigerous females ranged between 254 eggs (total number of eggs in the smallest egg mass) and 32,040 \pm 281 eggs (estimated from three sub-samples taken from the largest egg mass) per brood. There was a significant positive correlation between log number of eggs per brood and the log carapace length of ovigerous

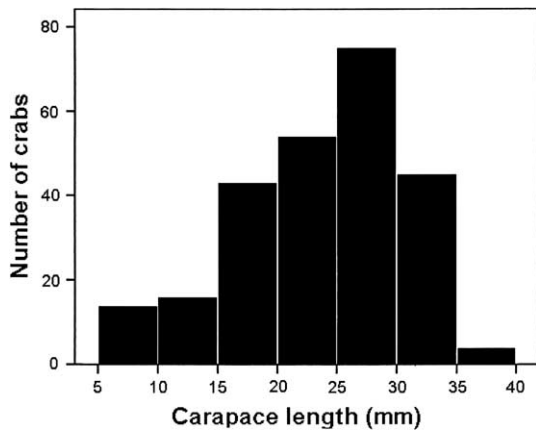


Figure 3. The size-frequency distribution of *Percnon gibbesi* collected from sites around the Maltese Islands during the period July to October 2004. The total sample consisted of 251 crabs.

females (Pearson product-moment correlation; $r = 0.82$, $P < 0.001$). Juveniles (crabs with CL less than 15 mm) were first observed at the end of September and continued to appear throughout the winter months until at least March; this suggests that recruitment into the population occurred during this period, however, given the low number of crabs observed (very small *Percnon* seek shelter deep in crevices during rough weather) it could also indicate sampling bias.

Analysis of abdomen morphology suggested that female *P. gibbesi* reach sexual maturity at a CL of 15.0–16.0 mm; this was supported by the fact that the smallest ovigerous female sampled had a CL of 16.1 mm. Assessment of size at sexual maturity using abdomen morphology gave identical results for males and females. All crabs studied were homochelate at all sizes (apart from individuals with injuries or regenerating chelae). A morphometric change indicated by an upward inflection in male

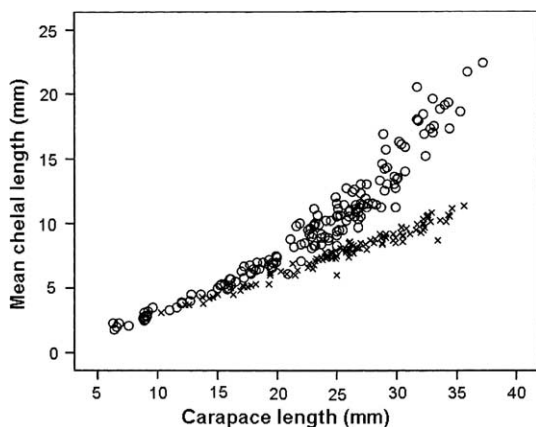


Figure 4. Biplot of mean chelae length with carapace length for male (O, $n = 157$) and female (x, $n = 113$) *Percnon gibbesi*. Only crabs with both chelae intact and no sign of regeneration were used in this analysis.

chelae length at CLs of 12–13 mm was not seen in females (Figure 4).

Field observations of *P. gibbesi* suggested that this species feeds using a combination of microphagy and macrophagy. They used their chelipeds to scoop the biofilm or detritus from the surfaces of boulders; they also used their chelae to either grasp pieces of macroalgae that floated past in the water current – when these came within striking distance – or to tear off pieces of macroalgae attached to boulders. In the field, *P. gibbesi* were observed to feed on the following algae: *Stypocaulon (Halopteris) scoparium*, *Hypnea musciformis*, *Liagora viscida*, *Gelidium crinale*, *Sphacelaria* sp., *Caulerpa racemosa*, *Fania rubens*, *Padina pavonica* and *Dictyopteris polypodioides*. On one occasion, a large male was observed to emerge from its shelter and grasp a jellyfish that was floating just above the bottom. The crab dragged it back into its shelter where it presumably ate it.

In the field, *P. gibbesi* was observed to overlap in habitat with the native grapsid, *Pachygrapsus marmoratus*, and to a lesser degree with the native xanthid, *Eriphia verrucosa* (Forskål, 1775); on several occasions during the population density counts, either or both of these decapods were observed within the same 1 m² virtual quadrat as *P. gibbesi* (Table III). Although interactions between *P. gibbesi* and *P. marmoratus* were rarely observed in the field, when *P. gibbesi* was surrounded by *P. marmoratus* – some of which were larger than the alien and were within 10 cm of its hiding place – *P. gibbesi* remained confined to its shelter. When the alien was surrounded by *P. marmoratus* that were smaller than it, both species foraged independently of each other. When *P. gibbesi* touched one of the native crabs with its pereopods, however, the latter was observed to advance quickly towards the intruder, which would then retreat to a distance of ca. 20 cm away from the aggressor. No interactions between *P. gibbesi* and *E. verrucosa* were observed in the field.

Laboratory investigation

Interspecific interactions were recorded as a series of discrete action patterns (acts), described in Table IV.

The initiator of an encounter was defined as the first crab to move towards its opponent or to make physical contact with its opponent. *Pachygrapsus marmoratus* initiated 80.8% of the interactions for all size combinations investigated; the remaining interactions were initiated by *Percnon gibbesi* (Figure 5).

The winner of an encounter was the individual that elicited repeated retreats from the other, or successfully caught its opponent inflicting damage, or even consuming it. Encounters with no winner

Table III. Co-occurrence density (individuals of *Percnon gibbesi*, *Pachygrapsus marmoratus* and *Eriphia verrucosa* in the same m² quadrat) at the 11 locations where spatial overlap was observed.

Site	Density (individuals m ⁻²)		
	<i>Percnon gibbesi</i>	<i>Pachygrapsus marmoratus</i>	<i>Eriphia verrucosa</i>
Cirkewwa	4	1	
L-Ahrax tal-Mellieha	9	1	
Mellieha Bay	7	1	
Pembroke	26	1	
	22	1	
	10	1	
Ghar id-Dud	8	1	
Marsascala	1	5	
Xrobb l-Ghagin	3	2	
Birzebbugia	1	2	
Ghar Lapsi	3	4	
Mgarr ix-Xini	6	1	
	1	4	
	1	1	
Dahlet Qorrot	11	1	
	19	1	
St. Paul's Bay	1		1
Birzebbugia	3		1
Ghar Lapsi	22		1
Paradise Bay	3		1
Dahlet Qorrot	22		1
Mellieha Bay	7	1	1
Xrobb l-Ghagin	3	5	1
Ghar Lapsi	3	4	1

occurred when one crab moved towards its opponent but no reaction was elicited from the opponent, or when the two crabs showed an equal number of

Table IV. Action patterns used during interspecific encounters between *Percnon gibbesi* and *Pachygrapsus marmoratus* in the laboratory.

Act	Description
Advance	The crab moves towards the other
Retreat	The crab retreats (moves away) from the approaching opponent
Touch	Any physical contact by means of the pereopods or chelae between the two interacting individuals
Low-intensity merus display	The 'neutral' posture of a crab where the body is held close to the substratum with the chelae folded inwards
Medium-intensity merus display	The body is raised up a little off the substratum by the ambulatory legs and the chelae are partly spread laterally
High-intensity merus display	The crab stands on the tips of the dactyls of the walking legs with the body well off the substratum and chelae fully spread laterally
Attack in high-intensity merus display	The crab moves towards its opponent on the tips of the dactyls and snaps the chelipeds from an open to a closed position in an attempt to trap and grasp its adversary
Chelae wave display	The crab raises the chelipeds up and down simultaneously or in an alternative fashion in front of its opponent

submissive (retreat or low merus display) and aggressive (medium or high merus display, attack, or chelae wave display) reactions. *Pachygrapsus marmoratus* won 80% of the trials within most size combinations investigated (Figure 6). *Percnon gibbesi* won encounters in only 3% of the trials, and only when matched with a smaller *P. marmoratus* (Figure 6). In 13 out of 22 encounters between a large or medium *P. marmoratus* and a small *P. gibbesi*, *P. marmoratus* deliberately attacked *P. gibbesi* and killed it. A large or medium-sized *P. gibbesi*, on the other hand, was never observed to inflict injury or kill a smaller-sized *P. marmoratus*.

Percnon gibbesi, the 'loser' in most encounters, performed more acts of retreat than *P. marmoratus*. Acts of retreat performed by *P. gibbesi* constituted 92% of all observed acts of retreat (Figure 7). Conversely, acts of aggression performed by *P. marmoratus* constituted 95% of all observed acts of aggression (Figure 7).

Cheliped displays were good predictors of which species was likely to win an encounter; such displays were used as indicators of the relative aggressive 'drive state' of the animal to claim a limited resource (Hazlett & Bossert 1965). *Pachygrapsus marmoratus* made extensive use of cheliped displays compared to *P. gibbesi* (Figure 8). When *P. marmoratus* was equal in size to *P. gibbesi* (LL, MM, SS), *P. marmoratus* performed more cheliped displays than *P. gibbesi*.

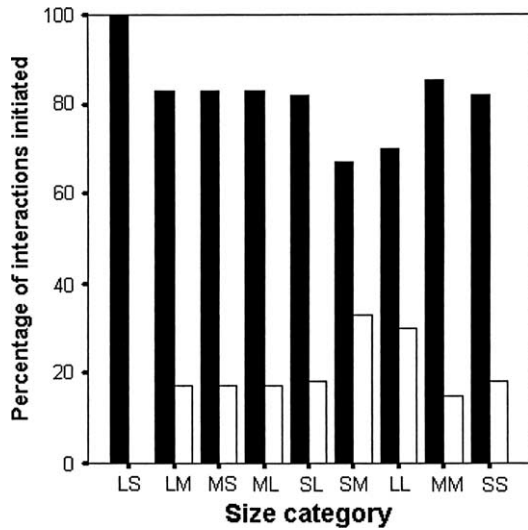


Figure 5. The percentage of interactions initiated by each crab species in each of the nine size combinations (refer to Table I for abbreviations). Black bars represent the percentage interactions initiated by *Pachygrapsus marmoratus*, white bars represent the percentage initiated by *Percnon gibbesi*.

When *P. gibbesi* was smaller than *P. marmoratus* (LS, LM, MS) it did not perform any cheliped displays. When a small *P. marmoratus* was matched with a large *P. gibbesi* (SL) the two performed almost the same number of cheliped displays (Figure 8).

Discussion

The basin-wide distribution of breeding populations of the alien grapsoid *Percnon gibbesi*, since its

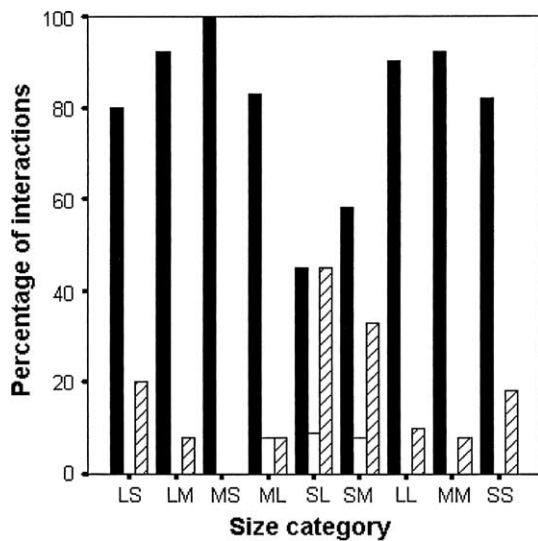


Figure 6. The percentage of interactions won by each crab species in each of the nine size combinations (refer to Table I for abbreviations). Black bars represent the percentage interactions won by *Pachygrapsus marmoratus*, white bars represent the percentage won by *Percnon gibbesi* and hatched bars represent the percentage of interactions with 'no winner'.

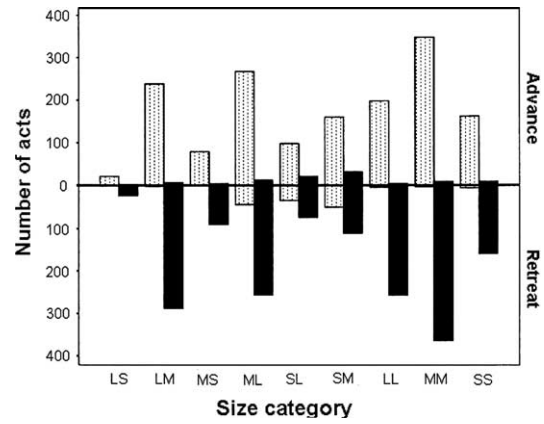


Figure 7. The number of retreat and advance acts by *Pachygrapsus marmoratus* (dotted bars) and *Percnon gibbesi* (black bars) in each of the nine size combinations (refer to Table I for abbreviations).

introduction in the Mediterranean Sea, suggests that abiotic and biotic conditions favour establishment and expansion of this alien. One critical aspect of predicting the impact of introduced species is to determine the range of habitats that are likely to be occupied. In Mediterranean sites studied to date, including the Maltese Islands, *P. gibbesi* indicates a preference for the infralittoral zone – amongst boulders with surfaces almost devoid of sessile macrobenthic organisms (Pipitone et al. 2001; present study) but covered by thin algal felts, or amongst mostly bare boulder surfaces with limited macroalgal cover (Cannicci et al. 2004; Deudero et al. 2005; present study). The high affinity of *P. gibbesi* for boulder bottoms may be due to

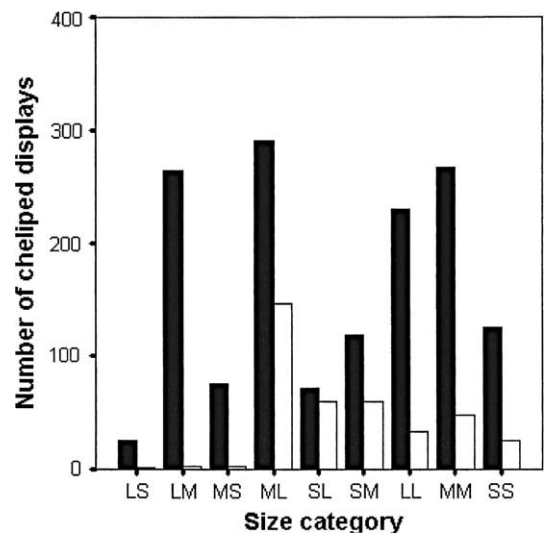


Figure 8. The number of cheliped displays, including medium and high-intensity merus displays, attack in high merus display, and chelae wave display, by each crab species (black bars represent *Pachygrapsus marmoratus*, white bars represent *Percnon gibbesi*) in each of the nine size combinations (refer to Table I for abbreviations).

increased protection from predators, and a readily available food supply which includes small algae and epibenthic organisms (Pipitone et al. 2001), as well as the algal turf and sparse macroalgae growing on the boulder surfaces (as observed in the present study).

In the Maltese Islands, it appears that *P. gibbesi*'s spatial and bathymetric distribution are controlled by factors such as habitat type and availability; the absence of this species from habitats other than boulder fields, and its high abundance in areas where boulder fields cover large areas along the shore, supports this theory. Sites where *P. gibbesi* was observed were typically characterized by boulder scree, such as Ghajn Tuffieha, Golden Bay, Imgiebah, Paradise Bay, Dahlet Qorrot and Hondoq ir-Rummien, or characterized by shores at the bottom of cliffs such as L-Ahrax tal-Mellieha, or at valley mouths such as Mgarr ix-Xini and Wied il-Ghasri. As suggested by Deudero et al. (2005), variability in abundance of *P. gibbesi* between replicate quadrats within the same site may be explained in terms of a patchy distribution within a heterogeneous habitat. During this study, no partitioning of crab size with depth as reported in Deudero et al. (2005) was observed, since crabs with a CL less than 10 mm were recorded at depths shallower than 2 m as well as between 2 and 4 m depth, 4 m being the lower depth limit for the crab at the sites studied here. The maximum depth range of *P. gibbesi* in the Maltese Islands (7 m) reported by Borg & Attard-Montalto (2002) falls within the limits reported in other studies in the Mediterranean (Müller 2001; Deudero et al. 2005), but is far less than that reported in its native range: 29 m (Mori & Vacchi 2002). At sites investigated in Spain, Deudero et al. (2005) contend that bathymetric distribution is restricted to the upper metres to avoid predation by macrocarnivorous feeders such as groupers *Epinephelus* spp. or bass *Serranus* spp. However, within its native range *P. gibbesi* has been reported from dense algal canopies (Mori & Vacchi 2002), which would presumably furnish shelter and protection from predators, thus enabling it to inhabit deeper waters. The mean population densities of *P. gibbesi* in the Maltese localities studied (Table II) are larger than those reported by Deudero et al. (2005) for Balearic waters (0.22–7.66 individuals per 200 m² at Dragoneira Island and Es Pantaleu; 3 individuals per m² along the southwest of Mallorca). However, these two estimates of population density are not comparable, since our samples are taken in patches of the preferred habitat (boulder bottoms) whereas samples taken by Deudero et al. (2005) were from the entire seabed including habitats not preferred. No data on the proportion of bottoms consisting of

fields of boulders are provided by Deudero et al. (2005), so we cannot estimate whether the population densities of *P. gibbesi* in its preferred habitat are comparable between the Balearics, Spain and the Maltese Islands. Apart from the present study, that by Deudero et al. (2005) is the only one that has reported population densities of *P. gibbesi* in the Mediterranean. Population density during evening hours was on average twice that for morning counts, suggesting that *P. gibbesi* becomes more active towards dusk, presumably to avoid diurnal predators. Similarly, observations by Cannicci et al. (2004) at Capo Gallo, Isola delle Femmine, show that the crab is most active during dusk and at night when light intensity is low.

In the Mediterranean, *P. gibbesi* was described as strictly herbivorous by Puccio et al. (2006); others have reported that it feeds on both plant and animal matter (Cannicci et al. 2004; Deudero et al. 2005). Deudero et al. (2005) reported opportunistic feeding on algae, pagurids and polychaetes. Stomach analyses of crabs from northwest Sicily showed that animal matter, primarily gastropod and crustaceans, constituted 43.2% of the stomach contents (Cannicci et al. 2004). This flexibility in feeding is probably a key factor that has facilitated the spread of *P. gibbesi* in the Mediterranean. Field observations from the present study, and those by Muller (2001), suggest that plant material constitutes the bulk of the diet; however, *P. gibbesi* was observed to feed on a jellyfish. Stomach content analysis of *P. gibbesi* and laboratory feeding experiments are currently under way to determine the food preferences of *P. gibbesi*.

Puccio et al. (2003) hypothesized that the breeding season for *P. gibbesi* in the Mediterranean is likely to begin in April as it does in Madeira, since the surface temperature of seawater in the Mediterranean is similar, if not higher than that surrounding the archipelago at Madeira. Results from the present study do not support this hypothesis, since ovigerous females in the Maltese Islands were recorded between the end of May and September. The smallest ovigerous female recorded by Fanelli & Azzurro (2004) had a smaller carapace length (14 mm) than the smallest one collected in the Maltese Islands. This suggests that female crabs from the southern coast of Italy attain physiological maturity before those in the Maltese Islands. However, fecundity in the Maltese Islands was on average twice as high as that reported by Puccio et al. (2003) for specimens with the same carapace length collected in Linosa and Lampedusa during the same period of the year as for the Maltese Islands. Increased fecundity of *P. gibbesi* in the Maltese Islands may thus counterbalance the shorter breeding season, relative to Madeira, such that the species

maintains a high reproductive output; this is yet another factor that may have facilitated its rapid and successful spread. In the present study, juveniles (CL < 15 mm) were observed at the end of September/beginning of October, possibly suggesting that in the Maltese Islands, recruitment does not occur in early summer, as assumed by Deudero et al. (2005) for the western Mediterranean. This may explain why individuals with carapace length less than 16 mm made up only a small percentage of those collected between July and October (Figure 3).

Growth in the chelae of *P. gibbesi* shows a pattern similar to that of *Corystes cassivelaunus* (Pennant, 1777), *Eurynome aspera* (Pennant, 1777) and *Macropodia rostrata* (Linnaeus, 1761) reported by Hartnoll (1974), where male chela length has a much larger positive allometry than that of females, which show low positive allometry. In the Maltese population, sexual dimorphism seems to manifest at an early stage during the crab's life cycle; at CLs as small as 12–13 mm, male chela length showed an upward inflection relative to that of the female. The sexual dimorphism of the chelae may be a consequence of their use by the male in combat, display and courtship (cf. Hartnoll 1974).

Introductions of alien species have been identified as one of the leading causes of endangerment and extinction of native species (Czech & Krausman 1997; Mooney & Cleland 2001). Competition in particular is increasingly recognized as a major means through which non-indigenous species have an impact on native species (Nichols et al. 1990; Byers 2000). From this study and that by Muller (2001), it appears that *P. gibbesi* and *P. marmoratus* are potential competitors for space – and according to Muller (2001), also for food – since the two species have been observed to occur in close proximity. Whether or not the two species actually compete for food in the Maltese Islands remains a question at present; detailed studies on diet are currently under way.

What has been described on some Mediterranean shores as a vacant niche for *P. gibbesi*, that is, free of competition from other brachyuran species (Pipitone et al. 2001; Deudero et al. 2005), might actually be 'competition ground' for resources essential to both the alien and native species in the Maltese Islands. On Maltese shores, *P. marmoratus* normally occupies supralittoral rock crevices and rock pools. It also occupies rock crevices and boulders in the mediolittoral and uppermost infralittoral zones on most rocky shores (Paul Galea, unpublished dissertation, 1995), where it has been observed to overlap with *P. gibbesi* (present study, Table III). Spatial overlap with *Eriphia verrucosa* was

also observed, but to a lesser extent since on Maltese shores *E. verrucosa* typically inhabits deeper water in the upper infralittoral, only occasionally appearing in the uppermost regions of the infralittoral in calm weather (Schembri & Lanfranco 1984).

Laboratory experiments from the present study indicate that when competing for space, *P. marmoratus* dominates the interactions with *P. gibbesi*, irrespective of the size combination being investigated. The behaviour of the 'winner' and 'loser' differed considerably; the 'winner' (*P. marmoratus* in the majority of the agonistic interactions) performed more advance acts and cheliped displays, whereas the 'loser' (*P. gibbesi* on most occasions) showed more submissive behaviour – by retreating from, and avoiding contact with, its aggressor. According to game theory, contests should begin with energetically inexpensive movements, such as display acts, followed by more energetically demanding acts involving physical contact, and then on to injurious behaviour (Sneddon et al. 1997). In interactions between *P. marmoratus* and *P. gibbesi*, encounters consisted mainly of visual displays such as medium and high merus displays, attack in high merus display, and chelae wave displays; they seldom escalated into injurious fights. This suggests that the crabs assessed each other visually to decide the outcome of contests. The use of the chelipeds in visual displays indicates that chelae size may be the 'resource holding potential' (RHP) (Sneddon et al. 2000) by which the two crabs assessed each other's strength and likelihood of winning.

The laboratory results presented here suggest that *P. marmoratus* shows competitive advantage over *P. gibbesi*. Hence, *P. marmoratus* has a greater chance of winning a territorial dispute in the field. The native species is thus unlikely to be excluded from its natural habitat by the alien. It is also unlikely that significant spatial resource partitioning on the part of *P. marmoratus* will occur.

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