ePublishing

ΕΘΝΙΚΟ ΚΕΝΤΡΟ ΤΕΚΜΗΡΙΩΣΗΣ
EKT
NATIONAL DOCUMENTATION CENTRE

Mediterranean Marine Science

Vol 13, No 1 (2012)

Biological aspects and ecological effects of a bed of the invasive non-indigenous mussel Brachidontes pharaonis (Fischer P., 1870) in Malta

L. BONNICI, J. EVANS, J.A. BORG, P.J. J. SCHEMBRI

doi: 10.12681/mms.32

To cite this article:

BONNICI, L., EVANS, J., BORG, J., & SCHEMBRI, P. J. (2012). Biological aspects and ecological effects of a bed of the invasive non-indigenous mussel Brachidontes pharaonis (Fischer P., 1870) in Malta. *Mediterranean Marine Science*, *13*(1), 153-161. https://doi.org/10.12681/mms.32

https://epublishing.ekt.gr | **e-Publisher:** EKT | **Downloaded at:** 06/09/2026 00:16:44

Research Article

Mediteranean Marine Science
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
The journal is available on line at http://www.medit-mar-sc.net

Biological aspects and ecological effects of a bed of the invasive non-indigenous mussel *Brachidontes pharaonis* (Fischer P., 1870) in Malta

L. BONNICI[1], J. EVANS[1,2], J.A. BORG[1] and P.J. SCHEMBRI[1]

[1] Department of Biology, University of Malta, Msida MSD2080, Malta
[2] Marine Biology and Ecology Research Centre, University of Plymouth, Plymouth PL4 8AA, UK

Corresponding author: patrick.j.schembri@um.edu.mt

Received: 9 January 2012; Accepted: 4 May 2012; Published on line: 6 June 2012

Abstract

No mussel beds were known to occur in the Maltese Islands previous to 2009, when a single bed of the Lessepsian immigrant *Brachidontes pharaonis*, first recorded from the islands in 1970, was discovered in Birzebbugia Bay. The population structure of *B. pharaonis* was investigated to assess its potential to spread and colonise new shores, while the biotic community at the mussel bed was compared to that present on uncolonised substratum to determine the effects of mussel bed establishment on the associated biota. Results indicate a lower species richness and slightly different community structure with greater small-scale heterogeneity at the mussel bed site compared to the adjacent rocky shore where mussels are present but where there is no bed formation. The *B. pharaonis* population had a peak density of 16550 ± 2051 ind.m^{-2} within the mussel bed and included recent recruits. These data suggest that the *B. pharaonis* population has the potential to expand. Establishment of extensive beds by this invasive mussel could change the structure of native rocky shore assemblages around the Maltese Islands and elsewhere in the Mediterranean.

Keywords*:* Mussel bed, rocky shore, alien species, ecosystem engineer, Central Mediterranean.

Introduction

The Red Sea mussel *Brachidontes pharaonis* (Fischer P., 1870) was one of the first Lessepsian migrants (*sensu* POR, 1978) to invade the Mediterranean Sea, having been recorded by Fuchs at Port Said in Egypt just seven years after the opening of the Suez Canal in 1869. Since then it colonised the eastern Mediterranean shores and spread north-westwards (Zenetos *et al*., 2004 and references therein), eventually invading the western Mediterranean (Gianguzza *et al*., 1997) and reaching as far as the northern Tyrrhenian Sea (Sarà & De Pirro, 2011). In favourable conditions, both the Red Sea and Mediterranean populations of *B. pharaonis* can attain very high densities on midlittoral hard substrata, resulting in the formation of mytilid beds (Safriel *et al*., 1980; Rilov *et al*., 2004; Sarà *et al*., 2006). Such mussel beds create a secondary substratum that can be colonised epizoically by species excluded from the rock surface (Lohse, 1993), while the complex multi-layered mussel matrix (Commito & Rusignuolo, 2000) can also support a rich infaunal assemblage, thereby increasing the species richness compared to patches of 'bare' rock (Tokeshi & Romero, 1995; Borthagaray & Carranza, 2007). However, establishment of extensive beds could result in biotic homogenisation, subsequently lowering species diversity on a regional scale (Carlton, 1987; Lodge, 1993). Furthermore, in the Mediterranean *B. pharaonis* competes directly with the native bed-forming mussel *Mytilaster minimus* (Safriel & Sasson-Frostig, 1988) as shown for the Israeli coast where a population increase of the invasive mussel, aided by a shift in habitat conditions in certain areas, has resulted in *B. pharaonis* becoming the numerically dominant mytilid (Rilov *et al*., 2004).

The occurrence of *B. pharaonis* in the Maltese Islands was first noted in October 1970, and this mussel is now present at various localities around the islands (Cachia *et al*., 2004). It generally occurs as solitary individuals found sporadically on rocky shores with the exception of Birzebbugia Bay, within Marsaxlokk Harbour (Fig. 1) where dense clusters have given rise to a mussel bed (Mifsud & Cilia, 2009). Since no mytilid beds were previously known from Malta, this represents the first and only such habitat type on the islands. Given that bed formation by *B. pharaonis* appears to depend on the presence of optimal habitat conditions and abundance of recruits (Safriel & Sasson-Frostig, 1988; Rilov *et al*., 2004) the first aim of this study was to investigate the popula-

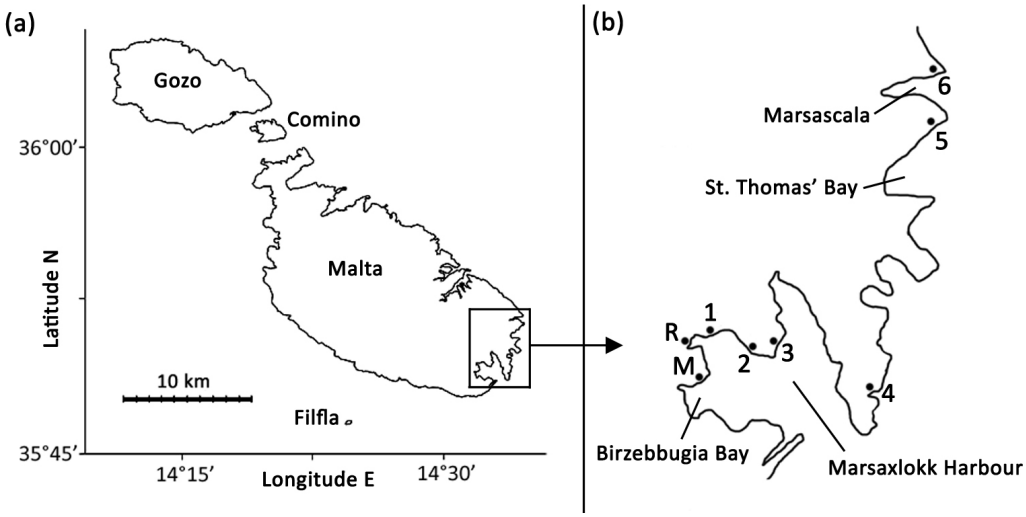

Fig. 1: **(a)** Map of the Maltese Islands showing the location of Marsaxlokk Harbour and Birzebbugia Bay; **(b)** Position of the eight sites investigated, including the 'mussel bed' (**M**) and 'reference' (**R**) sites within Birzebbugia Bay where most of this study was carried out, and six other sites (**1 – 6**) where surveys for *Brachidontes pharaonis* were made.

tion biology of the mussel at an established bed, as well as the physical features of the underlying substratum, and compare these to nearby sites to determine whether *B. pharaonis* has potential to establish new beds. Since very little attention has been paid to the biotic assemblage associated with *B. pharaonis* beds in the Mediterranean, the second aim of this study was to investigate the effect of this ecosystem engineer on the Mediterranean rocky shore community.

Material and Methods

Study sites and sample collection

An initial reconnaissance survey of the occurrence of *Brachidontes pharaonis* was made at different sites around Malta. Mussel beds were only found within Marsaxlokk Harbour and more detailed investigations were made there and on the low-lying shores to the east of it (only cliff shores occur west of the harbour). The distribution of *B. pharaonis* at five sites within Marsaxlokk Harbour and at another three on the shores east of it was surveyed (Fig. 1). Based on these field observations, two sites were chosen for further study: one in Birzebbugia Bay, highlighted by Mifsud & Cilia (2009) as the location of a main bed (hereafter 'mussel bed' site; Site M in Fig. 1) and another site located about 600 m away which lacked a mytilid bed (hereafter 'reference' site; Site R in Fig. 1). At these two locations, the shore consists of gently sloping (≈15°) Globigerina limestone bedrock forming a narrow platform at sea level, thus resulting in a mediolittoral zone of approximately 2 m, which is comparatively wider than that typically found along most of Malta's coastline.

Two shore-normal transects were laid at each of the mussel bed and reference sites; the position of transects within each site was chosen randomly, but the two transects were placed 10 m apart. Sampling was carried out using 10x10 cm quadrats laid contiguously along the transects, starting 0.5 m below the low water mark (LWM) and ending 3 m above it (measured as distance along the shore), such that each transect had a total of 35 quadrats. No *B. pharaonis* individuals were located outside this zone, which extended from the upper infralittoral to the start of the supralittoral. The biota present in each quadrat were collected by scraping off from the substratum and preserved in 70% ethanol. A surface profiler was used to characterise the microtopography of each transect, using an index of roughness (IR) given by the ratio of the measured profile length and the straight-line distance between the start and end points (for a perfectly smooth surface, IR = 1). The shore slope angle (shore gradient, SG) was also estimated for each transect, while the exposure to wave action (exposure index, EI) at each site was estimated using the method outlined by Thomas (1986). All fieldwork was carried out between 28 June and 3 September 2010.

Population parameters and biomass

The number of live *B. pharaonis* and empty shells of this species present in each quadrat was counted to estimate population abundance; mean abundance of live and dead mussels for the two sites was plotted against distance from LWM. The shell length (SL; mm) of each individual was subsequently obtained by measuring the greatest anterior-posterior axis to the nearest 0.01 mm using a digital caliper, while the shells were emptied of cavity water and weighed to the nearest 1 mg to obtain their total wet biomass (TB; g). Plots of mean abundance of live mussels, segregated into five size-classes

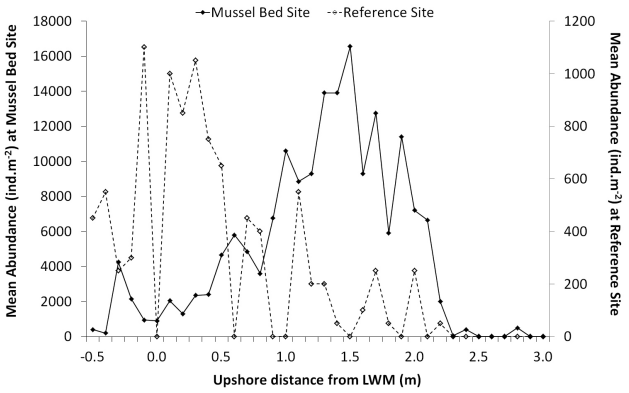

Fig. 2: Mean abundance (ind.m^{-2}) of live *Brachidontes pharaonis* at the 'mussel bed' and 'reference' sites with increasing upshore distance from low water mark (LWM).

(SL of 0-5.00, 5.01-10.00, 10.01-15.00, 15.01-20.00 or 20.01-30.00 mm), were produced for each site to investigate any changes in population size structure with increasing distance along the transects. Differences in size structure between mussel bed and reference sites were tested using a chi-square (χ^2) test based on the mean abundance of each size class at each site. To examine scaling effects on the body-size to mass ratio, SL and TB data were fitted to an allometric equation ($TB = aSL^b$; La Barbera, 1989). Following Sarà *et al*. (2006), natural log transformed data were used to estimate the value of the scaling exponents and coefficients via linear regression.

Ecological Impact

Samples collected by scraping were sorted in the laboratory, and all the biota present were identified to the lowest possible taxon. The abundance of macrofauna (animals retained by a 0.5 mm sieve) was recorded in a species by sample matrix. In order to assess the effects of the presence of the mussel bed, subsequent analysis was based on quadrats collected between 1 m above LMW and 2 m above LMW, where the highest abundance of mussels was recorded (see Results). The taxon richness of both algae and macrofauna and the mean total macrofaunal abundance were estimated for each site. Multivariate analyses, consisting of group-average hierarchical cluster analysis with similarity profile (SIMPROF) permutation tests, non-metric multidimensional scaling (nMDS) and the similarity percentages (SIMPER) routine, were subsequently carried out to compare the biotic communities at the two sites. The analyses were based on a Bray-Curtis similarity resemblance matrix constructed using presence/absence transformed data of both algal and faunal species. Multivariate analyses were carried out using the PRIMER 6 software package (Clarke & Gorley, 2006).

Results

Distribution, population parameters and biomass

Individuals of *Brachidontes pharaonis* were present on many Maltese low-lying rocky shores with a medium to low exposure, however, no beds occurred outside Marsaxlokk Harbour and even within the harbour, developed beds were only found in a very circumscribed area. Amongst the sites located in Birzebbugia Bay, the mussel bed site (Site M) had the highest peak densities while the reference site (Site R) had the lowest ones, hence these two were selected for comparison of population parameters of *B. pharaonis* and associated assemblages between shores having mussel beds and those lacking beds.

A total of 3473 live *B. pharaonis* individuals and 382 dead shells were collected from the mussel bed site (Site M), compared to 190 live and 88 dead specimens from the reference site (Site R), with a total area of 0.72m^2 sampled at each site. Within the mussel bed site, over 70% of the individuals were recorded from the zone between 1 m and 2 m above LWM, with the mean (± SD) population density peaking at 16550 ± 2051 ind.m^{-2} at 1.5 m above LWM. On the other hand, over 81% of the mussels present at the reference site were located between LWM and 1 m above it, while the highest mean (± SD) population density of 1100 ± 441 ind.m^{-2} was recorded close to the LWM; for comparison, the mean density recorded near the LWM in the mussel bed site reached 2050 ± 1909 ind.m^{-2}. In both sites, the abundance of mussels was lowest beyond 2 m above LWM (Fig. 2). Macroalgae occupied most of the rock surface at and just above the LWM, and mussels in this zone at both sites were found in small clusters intermixed with the macroalgae. On the other hand, the mussels were the main occupiers of space in the zone beyond 1 m above LWM in the mussel bed site, where they occurred in patches within depressions in the rock surface and thus had an aggregated distribution. However, the high densities within the 1-2 m above LWM zone meant that a network of interconnected mussel clumps were present in this region, while discrete patches occurred beyond 2 m above LWM (Fig. 3).

Overall, there were no differences in the along-shore distribution of individuals belonging to the four size-classes with SL <20 mm recorded at both sites (Fig. 4). On the other hand, no apparent trend in abundance of mussels having SL ≥20 mm was evident at the mussel bed site, while such large individuals were not present at the reference site. The mean abundance of mussels in each size-class differed significantly ($\chi^2 = 121.40$, $p < 0.001$) between the two sites. This was mainly due to the prevalence of larger individuals at the mussel bed site, where 47% of the specimens exceeded 15 mm in length, compared to 13% at the reference site. In contrast, only 3% of the individuals recorded from the mussel bed site belonged to the smallest size-class (SL <5 mm), whilst these comprised 17% of the individuals present at the

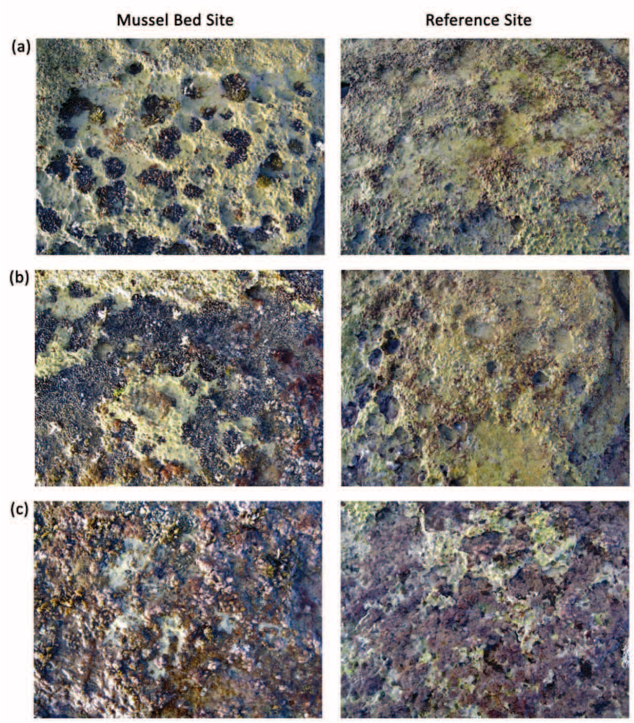

Fig. 3: Comparison of mussel dispersion pattern at the 'mussel bed' and 'reference' sites; each frame represents an area of approximately 80x60 cm. **(a)** Zone beyond 2 m above the low water mark (LWM); **(b)** Zone between 1m and 2m above LWM; **(c)** Zone spanning from 0.5 m below LWM to 0.5 m above it.

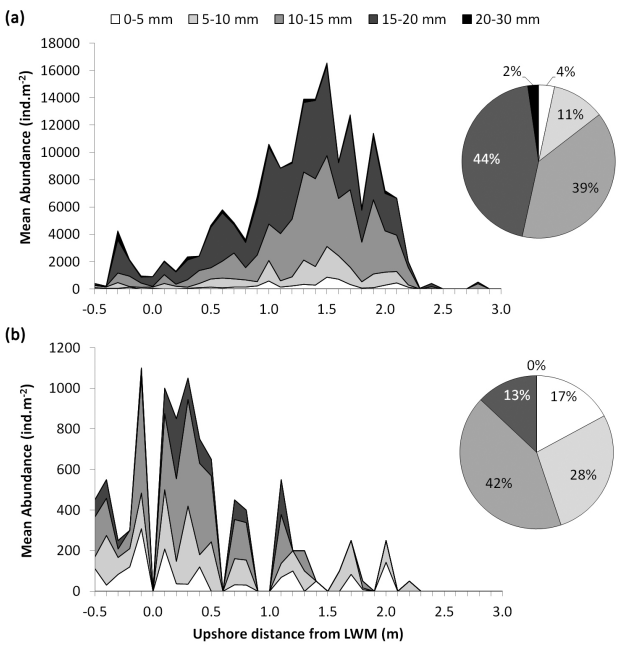

Fig. 4: Stacked graphs of variation in mean abundance of *Brachidontes pharaonis* individuals in each of five size-classes with increasing upshore distance from low water mark (LWM) together with the percentage frequency of shells belonging to each size-class for **(a)** the 'mussel bed' site, and **(b)** the 'reference' site.

Table 1. Shell length (SL) to total wet biomass (TB) scaling regression equations based on natural log transformed data (lnTB = lna + b*lnSL) of mussels collected from the 'mussel bed' and 'reference' site.

Site	ln*a* ± SE	*b* ± SE	R^2	*p*
Mussel Bed	-8.73 ± 0.05	2.87 ± 0.02	0.892	< 0.001
Reference	-9.65 ± 0.18	3.18 ± 0.09	0.877	< 0.001

Table 2. Mean values for shore gradient (SG), index of roughness (IR; see text for estimation) and exposure index (EI; calculated according to Thomas [1986]) for the 'mussel bed' and 'reference' sites.

Site	SG ± SD (°)	IR ± SD	EI
Mussel Bed	13.5 ± 0.7	1.067 ± 0.016	2.044
Reference	17.5 ± 0.7	1.041 ± 0.022	2.238

reference site. However, in terms of absolute number of individuals, the density of mussels having SL <5 mm recorded from the mussel bed site was over 2.5 times that recorded from the reference site (Fig. 4). The results of body-size and mass scaling regressions are shown in Table 1. Overall, similar scaling exponents were obtained for mussels collected from the two sites, which were close to the value of 3.0 that would be expected for isometric growth ($TB \propto SL^3$).

Physical characteristics of study sites

Values of shore gradient, surface roughness and exposure to wave action for the mussel bed and reference sites are summarised in Table 2. Both sites were characterised by a gently sloping (SG = 13-18°) rocky shore having relatively smooth surface microtopography (IR only marginally >1). Since the two sites are both located within the sheltered Birzebbugia Bay, both are only slightly exposed to wave action (EI = 2-2.5; compare with EI ≈25 for highly exposed locations in the Maltese Islands). Thus, overall, only minor differences in physical features were recorded between the two sites, with the reference site having a slightly steeper gradient and being marginally more exposed than the mussel bed site.

Biotic assemblages of study sites

Macroscopic algae were nearly entirely absent from the mussel bed site, while an average of almost two species per quadrat was recorded from the reference site in the zone between 1 m and 2 m above LWM. In the case of macrofauna, taxon richness was also higher at the reference site, although the difference was not as marked as in the case of algal species, while the total abundance of macrofauna was, on average, approximately 4 times higher at the reference site (Table 3). The dendrogram

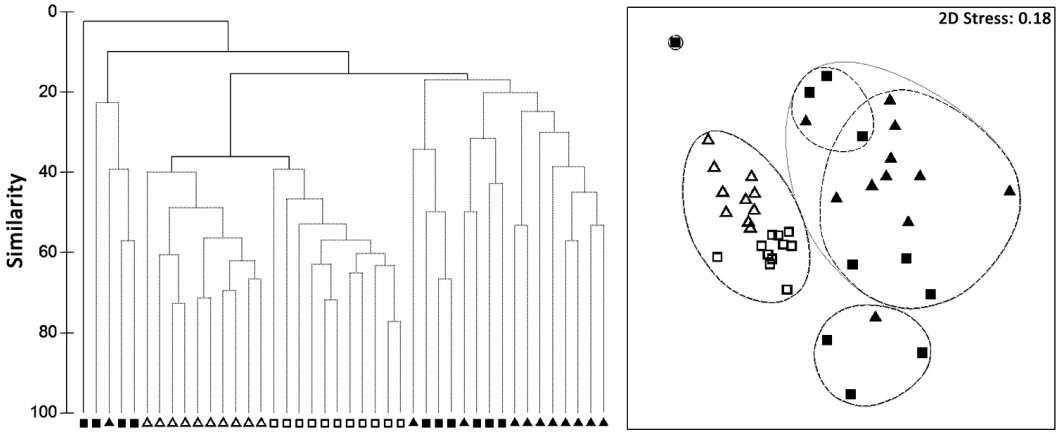

Fig. 5: Group-average hierarchical cluster analysis dendrogram and nMDS plot based on Bray-Curtis resemblances produced using presence/absence-transformed macroalgal and macrofaunal species occurrence data recorded from quadrats found between 1 m and 2 m above the low water mark at the 'mussel bed' (Transect 1:▲; Transect 2:■) and 'reference' (Transect 1:△; Transect 2:□) sites.

produced by group-average hierarchical cluster analysis resulted in distinct clusters of quadrats from the two reference site transects, which were more similar to one another than to the mussel bed quadrats; the latter were mainly grouped into a single cluster containing quadrat samples from both mussel bed transects (Fig. 5).

The similarity in biotic composition among quadrats collected from a given transect was much higher for the reference site than for the mussel bed site (Fig. 5). This was corroborated by the results of the SIMPER analysis, which showed much higher average similarity within the two reference site transects (average similarity transect 1: 57%; transect 2: 56%) than within mussel bed transects (average similarity transect 1: 32%; transect 2: 16%), suggesting greater homogeneity of biotic assemblage structure within the reference site. Only five taxa contributed more than 5% to the dissimilarity between the two sites, with another eight taxa contributing at least 2% each (Table 4). While these 13 taxa together accounted for nearly 70% of the differences between the two sites, in eleven cases this was due to the taxon having a higher abundance at the reference site.

Discussion

In the Mediterranean Sea, *Brachidontes pharaonis* occurs in the mediolittoral zone attached by its byssus to hard substrata (e.g. Safriel *et al*., 1980), where it has the potential to form extensive mytilid beds (e.g. Rilov *et al*., 2004; this study), a characteristic it shares with the indigenous mytilids *Mytilaster minimus* and *Mytilus galloprovincialis*, both of which form beds in nearby Sicily (Riggio *et al*., 1992). However, although all three species occur in the Maltese Islands, these generally only occur as solitary individuals (Cachia *et al*., 2004) and no mussel beds were known to exist in Malta prior to 2009, when a single *B. pharaonis* bed was discovered in Birzebbugia (Mifsud & Cilia, 2009) after a lag of 40 years

Table 3. Mean taxon richness of macroscopic algae (S_{algae}) and macrofauna (S_{fauna}) and mean total abundance of fauna (TA_{fauna}; ind.m^{-2}) (excluding *Brachidontes pharaonis*) for quadrats collected from between 1 m and 2 m above the low water mark, together with the overall taxon richness (S_{max}) recorded from this zone at the 'mussel bed' and 'reference' sites.

Site	Transect	S_{algae} ± SD	S_{fauna} ± SD	TA_{fauna} ± SD
Mussel Bed	1	0.1 ± 0.3	7.1 ± 3.7	3164 ± 2392
	2	0.1 ± 0.3	4.3 ± 1.9	800 ± 579
	Total (S_{max})	2	42	n/a
Reference	1	1.8 ± 0.8	8.5 ± 4.0	6420 ± 2291
	2	1.8 ± 1.3	14.9 ± 5.6	12364 ± 6684
	Total (S_{max})	9	48	n/a

Table 4. Mean total abundance (TA; ind.m^{-2}) of taxa contributing most to dissimilarity in biotic assemblages found between 1 m and 2 m above the low water mark at the 'mussel bed' and 'reference' sites, together with the percentage contribution of each taxon; only taxa contributing >2% dissimilarity are shown.

Species	Mussel Bed TA	Reference TA	Contribution %	Cumulative %
Bittium spp.	19.65	40.04	13.88	13.88
Tanaidae sp.	1.43	38.4	11.5	25.38
Rissoa sp.	0.48	29.1	11.05	36.43
Hyale sp.	1.3	19.27	6.38	42.8
Elasmopus sp.	1.97	18	5.19	47.99
Dynamene sp.	5.11	16.1	4.44	52.43
Acanthochitona sp.	1.9	8.59	2.65	55.08
Gibberula spp.	0	5.34	2.49	57.57
Osilinus turbinatus	6.34	0	2.34	59.91
Nereis ?rava	5.98	0.48	2.21	62.12
Amphitoe sp.	2.38	6.64	2.19	64.32
Maera sp.	0	7.43	2.06	66.38
Gibbula spp.	0	6.54	2.04	68.42

since this non-indigenous species was first recorded from the islands. A similar situation occurred in Israel, where *B. pharaonis* started to form dense beds after a lag of 120 years since its initial introduction (Rilov *et al*., 2004).

Although studies carried out in the late 1970s along the Israeli coast, when *B. pharaonis* had not yet formed extensive beds, indicated that the species could not outcompete the indigenous bed-forming mytilid *Mytilaster minimus* at exposed sites (Safriel & Sasson-Frostig, 1988), it has now become the numerically dominant bivalve, possibly outcompeting the native species by saturating the habitat with recruits originating from populations established in more favourable sites (Rilov *et al*., 2004). The density of *B. pharaonis* recorded at the mussel bed site during the present study was slightly lower than that found along the Israeli coast (15,000 – 35,000 ind.m^{-2}; Rilov *et al*., 2004), but similar to that present in Western Sicily (10,000 – 25,000 ind.m^{-2}; Sarà *et al*., 2006), whilst the source population in the Red Sea reaches lower densities of up to 7,000 ind.m^{-2} (Safriel *et al*., 1980). It is not clear whether the mussel density in Birzebbugia Bay is on the increase because Mifsud & Cilia (2009) did not provide estimates of the density present when these mussel beds were initially discovered.

Given the high population density of *B. pharaonis* recorded in this study, it is plausible that massive recruitment akin to that observed in Israel could occur in the Maltese Islands, leading this invasive mussel to establish populations and form mytilid beds on shores adjacent to the present bed within Birzebbugia Bay, and possibly elsewhere outside of the bay. However, two pre-requisites are necessary for this to occur: (i) that the source population is stable, healthy, and actively reproducing, and (ii) that the pelagic larvae reach habitats suitable for successful settlement and recruitment.

The results obtained during the present study suggest that the first condition is satisfied in spite of the fact that Malta is nearly at the westernmost edge of the geographical range of *B. pharaonis* as presently known. This is not surprising given that this mussel has a high physiological plasticity and can tolerate a wide range of temperature and salinity conditions (Sarà *et al*., 2008). The allometric growth equations yielded a scaling exponent value of 2.9, comparable to the value of 2.7 obtained by both Sarà *et al*. (2006) and Rilov *et al*. (2004), while the population size structure of the mussel bed at Birzebbugia (modal size-class SL = 15-20 mm) was intermediate between those present in western Sicily (modal size class SL = 21-24 mm; Sarà *et al*., 2006) and Israel (modal size classes SL = 1-4 mm and 12-15 mm; Rilov *et al*., 2004). Finally, the density of recent recruits (taken as mussels with SL < 5 mm) recorded at Birzebbugia Bay was within the range of densities of recruits (1,000-10,000 ind.m^{-2}) recorded by Rilov *et al*. (2004) at various sites in Israel. Despite this, recruitment in such large numbers has not yet occurred at sites close to the mussel bed location at the time of sampling. For instance, the reference site used in this study is located just 600 m away from the mussel bed and has similar physical features (shore gradient, surface rugosity, wave exposure), yet the population density of recent recruits was less than half that present at the mussel bed site. Similarly, peak densities of mussels at the other sites within Birzebbugia Bay were much lower than those recorded from the mussel bed site. Although no data on water current strength are available, it is unlikely that strong currents are preventing mussel larvae

from reaching these sites, since they are all very close to the mussel bed and located in a sheltered area. However, the biology of larval settlement may play an important role in determining recruitment densities. For instance, initial settlement of mussels may occur preferentially on filamentous substrata such as bryozoans, hydrozoans and filamentous algae, with subsequent secondary recruitment on existing mussel beds or hard substrata (Bayne, 1964; Lane *et al*., 1985) and thus, the presence of such filamentous substrata would stimulate larval settlement, resulting in a higher likelihood of mussel bed formation in the vicinity.

Direct recruitment of larvae onto existing mussel beds has also been observed (McGrath *et al*., 1988; Lasiak & Barnard, 1995). The presence of shells and byssal threads probably stimulates larval settlement into mussel beds (Bayne, 1976). Indeed, Mohammed (1992) found very few individuals (0.02 ind.m^{-2}) of *B. pharaonis* in samples taken 15 m outside the boundary of a mussel bed in the Suez Canal, whereas samples collected 15 m within the bed contained numerous juveniles (153 ind.m^{-2} with SL <6 mm), while in four species of mussels, including *Brachidontes erosus* and *Brachidontes rostratus*, larvae have been shown to settle preferentially on conspecific byssus threads (Ompi, 2010). This might explain why a higher density of recent recruits was observed at the mussel bed site during the present study. However, it also suggests that once a large enough cohort of individuals settle at a given site, these will result in intraspecific facilitation of further recruitment, progressively leading to the formation of a mussel bed. Thus, it appears that given enough time, *B. pharaonis* has the potential to establish dense mussel beds at other locations around the Maltese Islands.

Extensive mussel bed formation by *B. pharaonis* in the Maltese Islands could be a cause for concern since this can have a profound effect on the native communities. The impact of a recently established mussel bed was investigated during this study; however, no data on the biotic community present at the 'mussel bed' site prior to the establishment of the mussel bed itself are available. Thus, the only comparisons that can be made are with similar sites on adjacent shores which presumably have similar biological characteristics to those that used to be present at the mussel bed site. The results indicate three main differences between the mussel bed and the reference site: (i) *B. pharaonis* appears to have outcompeted nearly all the algal species normally present on mediolittoral shores; (ii) the mussel bed community was characterised by a marginally lower faunal species richness and had a lower abundance of associated fauna; and (iii) the faunal composition of mussel bed quadrats was not as homogenous as that at the reference site.

Bed-forming mussels are competitively dominant species that, given the opportunity, form extensive monocultures occupying all the space available on the primary substratum at the expense of other species (e.g. Paine, 1974; Paine & Levin, 1971; Seed, 1976), which accounts for the near absence of macroalgae within the *B. pharaonis* bed at Birzebbugia Bay. However, the mussel shells themselves provide a colonisable secondary substratum (Lohse, 1993) which often results in higher macrofaunal species richness and abundance within mussel beds compared to adjacent patches lacking beds (Mohammed, 1992; Tokeshi & Romero, 1995; Crooks, 1998; Borthagaray & Carranza, 2007). Physical and architectural effects, such as the increase in surface area and structural complexity of the habitat and the accumulation of sediment and detritus as a result of mussel bed formation (Suchanek, 1985; Commito & Rusignuolo, 2000) appear to play a greater role than biological effects of the living mussels in facilitating settlement of other organisms (Crooks & Khim, 1999).

The fauna associated with mussel beds are influenced by the age of the bed: in Japan, mussel patches consisting predominantly of young *Mytilus edulis* supported a lower species richness and abundance of associated fauna, which also had a different species composition when compared to patches of larger, older mussels; this was related to the lower amounts of shell fragments, byssal threads and organic detritus in younger patches (Tsuchiya & Nishihira, 1986). The *B. pharaonis* bed in Malta, which consisted mainly of intermediate-sized mussels, was only recently established and had a low proportion of dead mussel shells (<11%), suggesting that at the time of sampling, the associated fauna had a lower abundance and slightly lower richness than that present at the reference site because of the bed's relatively young age. In an older mussel bed, the increased complexity of the mussel matrix due to addition of more mussel shells forming a multi-layered structure, and the ensuing accumulation of sediment, shell fragments and detritus, could lead to further colonisation of the bed (especially given the longer time period for invasion and settlement) and thus a greater richness and abundance of associated fauna than recorded in the present study. The complex matrix also provides shelter for interstitial fauna such as errant polychaetes, which can attain much higher abundances in mussel beds (Borthagaray & Carranza, 2007) and may even be restricted to this habitat on exposed shores (Tokeshi & Romero, 1995). The *B. pharaonis* population at Birzebbugia Bay may already be having such an effect given the significantly higher abundance of *Nereis* ?*rava* recorded from the mussel bed site.

One factor which does not appear to have been investigated in detail is the effect of mytilid beds on the small-scale variation in associated biota. The results of the present study indicate that the *B. pharaonis* bed caused an increase in heterogeneity of faunal attributes, since the dissimilarity among samples collected from this site was greater than that among the reference site samples. However, given that our results also suggest that changes in

the faunal composition and abundance may occur with increasing age of the mussel bed, it is not clear whether this enhanced spatial variation only features in young mussel beds, which may represent a transient condition between no mussel beds and developed ones, or if such higher small-scale variation would be present within mytilid beds that have been established for a longer time.

Conclusion

Based on this study, it appears that the *Brachidontes pharaonis* population in Birzebbugia Bay shows no signs of being stressed and is actively reproducing, and therefore has the potential to establish mussel beds in new locations. As has happened in Birzebbugia Bay, mussel bed formation will lead to competitive exclusion of other species from the primary substratum, resulting in a decrease in faunal species richness and abundance, and modified species composition compared with the composition of the typical native biotic assemblage. Thus, through its ecological effects as a habitat engineer, *B. pharaonis* can be a threat to the native shore biotic community. However, ecosystem engineers can have positive effects on diversity if they provide conditions that are not present elsewhere; since the native mediolittoral bivalve *Mytilaster minimus* does not form mytilid beds in the Maltese Islands, contrary to the situation in other Mediterranean countries, formation of *B. pharaonis* beds in Malta will not occur at the expense of local bed-forming species but actually represents the creation of a novel habitat. On the other hand, given the previous absence of mussel beds, it is unlikely that species that are restricted to this habitat exist in the Maltese Islands. Given that *B. pharaonis* is an invasive species and can undergo exponential growth, rapidly colonising new habitats (e.g. Rilov *et al*., 2004), it ought to be a priority for marine conservation managers to control the population of this alien species, lest it undergoes massive recruitment and establishes extensive mussel beds. This could jeopardise the state of Malta's native mediolittoral communities, including those found in marine protected areas, and may also have direct negative effects on protected species such as the reef-forming vermetid *Dendropoma petraeum* (Milazzo *et al*., 2009).

Acknowledgements

We are grateful to Mr Edwin Lanfranco (University of Malta) for identification of algae, to Prof Renato Chemello (University of Palermo) for supplying us with some hard to find literature, and to two anonymous referees for their helpful comments on a previous version of this paper.

References

Bayne, B.L., 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *Journal of Animal Ecology*, 33 (3): 513-523.

Bayne, B.L., 1976. The biology of mussel larvae. p. 81-121. In: *Marine mussels: their ecology and physiology*. Bayne, B.L. (Ed). Cambridge, Cambridge University Press.

Borthagaray, A.I. & Carranza, A., 2007. Mussels as ecosystem engineers: their contribution to species richness in a rocky littoral community. *Acta Oecologica*, 31: 243-250.

Cachia, C., Mifsud, C. & Sammut, P., 2004. *The Marine Mollusca of the Maltese Islands. Part 4: Caudofoveata, Solenogastres, Bivalvia, Scaphopoda and Cephalopoda*. Leiden, Backhuys Publishers, 270 pp.

Carlton, J.T., 1987. Patterns of transoceanic marine biological invasions in the Pacific Ocean. *Bulletin of Marine Science*, 41 (2): 452-465.

Clarke, K.R. & Gorley, R.N., 2006. *PRIMER v.6: User Manual/Tutorial*. Plymouth, PRIMER-E, 190 pp.

Commito, J.A. & Rusignolo, B.R., 2000. Structural complexity in mussel beds: the fractal geometry of surface topography. *Journal of Experimental Marine Biology & Ecology*, 255 (2): 133-152.

Crooks, J.A., 1998. Habitat alteration and community-level effects of an exotic mussel, *Musculista senhousia*. *Marine Ecology Progress Series*, 162: 137-152.

Crooks, J.A. & Khim, H.S., 1999. Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. *Journal of Experimental Marine Biology & Ecology*, 240 (1): 53-75.

Gianguzza, P., Chemello, R. & Riggio, S., 1997. Segnalazione di *Brachidontes pharaonis* (P. Fischer, 1870) (Bivalvia, Mytilidae) nella salina di Marsala e considerazioni sulla distribuzione della specie in Mediterraneo. *Bollettino Malacologico*, 33 (9-12): 169-172.

La Barbera, M., 1989. Analyzing body size as a factor in ecology and evolution. *Annual Review of Ecology & Systematics*, 20: 97-117.

Lane, D.J.W., Beaumont, A.R. & Hunter, J.R., 1985. Byssus drifting and the drifting threads of the young post-larval mussel *Mytilus edulis*. *Marine Biology*, 84 (3): 301-308.

Lasiak, T.A. & Barnard, T.C.E., 1995. Recruitment of the brown mussel *Perna perna* onto natural substrata: a refutation of the primary /secondary settlement hypothesis. *Marine Ecology Progress Series*, 120: 147-153.

Lodge, D.M., 1993. Biological invasions: lessons for ecology. *Trends in Ecology & Evolution*, 8: 133-137.

Lohse, D.P., 1993. The importance of secondary substratum in a rocky intertidal community. *Journal of Experimental Marine Biology & Ecology*, 166 (1): 1-17.

McGrath, D., King, P.A. & Gosling, E.M., 1988. Evidence for the direct settlement of *Mytilus edulis* larvae on adult mussel beds. *Marine Ecology Progress Series*, 47: 103-106.

Mifsud, C. & Cilia, D.P., 2009. On the presence of a colony of *Brachidontes pharaonis* (P. Fischer, 1870) (Bivalvia: Mytilidae) in Maltese waters (Central Mediterranean). *Triton*, 20: 20-22.

Milazzo, M., Quattrocchi, F., Graziano, M., Badalamenti, F., Sarà, G. & Chemello, R., 2009. Invasive mussels directly threat intertidal vermetid reef: some evidences from a Si-

cilian MPA. p. 12. In: *Proceedings of the InterMED Workshop 9-10 March 2009*, *Palermo, Italy.*

Mohammed, S.Z., 1992. The interaction between adults and recruitments in the *Brachidontes variabilis* L. (Lamellibranchiata) bed in the Bitter Great Lake, Suez Canal. *Qatar University Science Journal*, 12: 228-232.

Ompi, M., 2010. Settlement behaviour of mussel larvae from the family Mytilidae (*Brachidontes erosus* (Lamarck, 1819), *Brachidontes rostratus* (Dunker, 1857), *Trichomya hirsutus* (Lamarck, 1819), and *Mytilus galloprovincialis* Lamarck, 1819). *Journal of Coastal Development*, 13 (3): 215-227.

Paine, R.T., 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, 15: 93-120.

Paine, R.T. & Levin, S.A., 1971. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological monographs*, 51: 145-178.

Por, F.D., 1978. *Lessepsian migration. The influx of Red Sea biota into the Mediterranean by way of the Suez Canal. Ecological studies No. 23*. Berlin, Springer-Verlag, 228 pp.

Riggio, S., D'Anna, G. & Pia Sparla, M., 1992. Coastal eutrophication and settlement of mussel beds in NW Sicily: remarks on their significance. p. 117-120. In: *Marine Eutrophication and Population Dynamics, Proceedings of the 25th European Marine Biology Symposium 10-15 September 1990, Ferrara, Italy*. Colombo G., Ferrari I., Ceccherelli V.U. & Rossi R. (Eds). Fredensborg, Denmark, Olsen & Olsen Publishers & Printers.

Rilov, G., Benayahu, Y. & Gasith, A., 2004. Prolonged lag in population outbreak of an invasive mussel: a shifting-habitat model. *Biological Invasions*, 6: 347-364.

Safriel, U.N., Gilboa, A. & Felsenburg, T., 1980. Distribution of rocky intertidal mussels in the Red Sea coasts of Sinai, the Suez Canal, and the Mediterranean coast of Israel, with special reference to recent colonizer. *Journal of Biogeography*, 7: 39-62.

Safriel, U.N. & Sasson-Frostig, Z., 1988. Can colonizing mussel outcompete indigenous mussel? *Journal of Experimental Marine Biology & Ecology*, 117 (3): 211-226.

Sarà, G. & De Pirro, M., 2011. Heart beat rate adaptations to varying salinity of two intertidal Mediterranean bivalves: the invasive *Brachidontes pharaonis* and the native *Mytilaster minimus*. *Italian Journal of Zoology*, 78 (2): 193-197.

Sarà, G., Romano, C. & Mazzola, A., 2006. A new Lessepsian species in the western Mediterranean (*Brachidontes pharaonis* Bivalvia: Mytilidae): density, resource allocation and biomass. *Marine Biodiversity Records*, 1: e8. doi:10.1017/S175526720600087X

Sarà, G., Romano, C., Widows, J. & Staff, F.J., 2008. Effect of salinity and temperature on feeding physiology and scope for growth of an invasive species (*Brachidontes pharaonis* - Mollusca: Bivalvia) within the Mediterranean Sea. *Journal of Experimental Marine Biology & Ecology*, 363 (1-2): 130-136.

Seed, R., 1976. Ecology. p. 13-65. In: *Marine mussels: their ecology and physiology*. Bayne, B.L. (Ed). Cambridge, Cambridge University Press.

Suchanek, T.H., 1985. Mussels and their role in structuring rocky shore communities. p. 70-96. In: *The Ecology of Rocky Coasts*. Moore, P.G. & Seed, R. (Eds). London, Hodder & Stoughton.

Thomas, M.L.H., 1986. A physically derived exposure index for marine shorelines. *Ophelia*, 25 (1): 1-13.

Tokeshi, M. & Romero, L., 1995. Filling a gap: dynamics of space occupancy on a mussel-dominated subtropical rocky shore. *Marine Ecology Progress Series*, 119: 167-176.

Tsuchiya, M. & Nishihira, M., 198. Islands of *Mytilus* as habitat for small intertidal animals: effect of *Mytilus* age structure on the species composition of the associated fauna and community organization. *Marine Ecology Progress Series*, 31: 171-178.

Zenetos, A., Gofas, S. Russo, G. & Templado, J., 2004. *CIESM atlas of exotic species in the Mediterranean, Vol.3 Molluscs*. Briand, F. (Ed). Monaco, CIESM Publishers, 376 pp. URL: http://www.ciesm.org/atlas/Brachidontespharaonis.html [visited on 29 November 2011].