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Branching out: mapping the spatial expansion of the lessepsian invader mytilid *Brachidontes pharaonis* around the Maltese Islands

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One of the several lessepsian species colonizing areas of the Mediterranean is Brachidontes pharaonis*, a bivalve with the ability to form dense mytilid mats over a range of different mediolittoral substrata. Since its initial observation from the Maltese Islands in the early 1970s, the species has consolidated its presence all over the archipelago. Close examination of the entire length of the Maltese shoreline was conducted to collect quantitative and qualitative data on the mytilid and on dominant accompanying macrofaunal and macrofloral species, in what represents the first comprehensive mapping of an allochthonous species within an island territory.* Brachidontes pharaonis *was found to have colonized most of the northern and eastern coastal stretches of the island of Malta, preferring limestone substrata in inlets with limited wave exposure and affected by high marine concentrations of hydrocarbons and other pollutants, where it reached individual abundances exceeding 1000 individuals per square metre.*

Keywords: mapping, spatial expansion, lessepsian invader mytilid, *Brachidontes pharaonis*, Malta

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INTRODUCTION

The invasion of Red Sea species into the eastern basin of the Mediterranean through the Suez Canal is known as 'lessepsian migration' (Por, 1978). According to Zenetos *et al.* (2010), who give an updated list of alien marine species recorded to date from the Mediterranean Sea, a total of 955 alien marine species have been recorded from the Mediterranean, the vast majority of which (718) having being introduced in the Eastern Mediterranean and are thus, presumably, of lessepsian origin.

The taxonomy of the species discussed in this paper is in a state of flux, as until more genetic studies become available it is difficult to group or split the several *Brachidontes* morphological variants into one or more valid taxa.

On one hand, several geographical forms including *Brachidontes pharaonis* (Fischer, 1870) are considered by some authors (Lamy, 1936; Huber, 2010) to be variants of *Brachidontes ustulatus* (Lamarck, 1819). This is an Indo-Pacific mytilid with a highly variable shell first described as *Mytilus ustulatus*, with Lamarck's *locus typicus* for the type series being Brazil. Lamarck's description was based on specimens collected by the French explorer Nicolas Baudin, presumably during his voyage to Australia spanning from 1800 to 1803. For this reason, Lamy (1936) argues that the *locus typicus* is incorrect and the type series is actually from the Indo-Pacific area. According to Huber (2010), the variability of this species has led to the propagation of several synonyms such as *Brachidontes semistriatus* Krauss, 1848, *Mytilus variabilis* Krauss, 1848, (and hence *Brachidontes variabilis*), *Mytilus pharaonis* Fischer, 1870 and *Mytilus arabicus* Jousseaume in Lamy (1919). Lamy reassessed his 1919 opinion in 1936, synonymizing *M. arabicus*, *M. pharaonis*, and *M. variabilis* with their senior synonym *B. ustulatus*. Huber (2010) reiterates Lamy's view and groups several forms into one vast '*ustulatus*-complex' spreading from the Red Sea (and the westward invasion, cf. Sarà *et al.*, 2000) to Japan, individuals of which complex show a high degree of morphological plasticity.

On the other hand, molecular studies like that of Sirna Terranova *et al.* (2007) discover genetic divergence between separate geographical populations that are 'substantially higher' than those between species of other congeners of other mytilid genera such as *Mytilus* Linné, 1758. According to Sirna Terranova *et al.* (2007), *B. variabilis* actually consists of three species—*B. pharaonis* '*sensu lato*' (to which the Red Sea and Mediterranean populations belong), an Indian Ocean *B. variabilis* and a Pacific Ocean *B. 'variabilis'*.

In this paper, the authors adhere to the name *Brachidontes pharaonis* (Fischer, 1870) for the sake of geographical specificity and clarity.

One of the earliest recorded and most successful lessepsian migrants in the Mediterranean Sea is indeed *B. pharaonis* (cf. Zenetos *et al.*, 2010), having established large and stable populations within the basin. The species hails from the Indo-Pacific, and by 1976 it spread as far west as the Red

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Sea forming mytilid clusters (Gilboa, 1976; Safriel *et al.*, 1980). The bivalve was first recorded in the Mediterranean Sea at Port Said just seven years after the opening of the Suez Canal in 1869, and has to date spread from the Israeli coastline, where a study covering the extent of colonization was carried out by Rilov *et al.* (2004), to the western coast of Sicily (Sarà *et al.*, 2008), establishing stable populations even in the north Adriatic (De Min & Vio, 1997). Records from the Aegean Sea are sporadic (e.g. Tenekides, 1989; Dogan *et al.*, 2007). Sarà *et al.* (2000) have predicted that the species will continue its westward spread from Sicily to North Africa and Gibraltar.

The first publications mentioning *Brachidontes pharaonis* for the Maltese Islands (as *Brachidontes variabilis* (Krauss)) were those by Cachia (1975) and Lanfranco (1975); however, records of the species from October 1970, in Qawra and Baħar iċ-Ċagħaq, exist, together with 1973 records from St Julian's, Kalkara, St Thomas' Bay and Birżebbuġa Bay (C. Cachia, personal communication). Most of these rare finds consisted of disarticulated valves, others of which occurred in 1985 in Marsaskala Bay (C. Mifsud, personal communication) (see Table 1 and Figure 1 for historical and unpublished records). Subsequent checklists (Cachia *et al.*, 1993; Cachia, 1999; Cachia *et al.*, 2004; Sciberras & Schembri, 2007) mention the species with the taxon now amended to *Brachidontes pharaonis* (P. Fischer, 1870). In Cachia *et al.* (2004) it is noted that the species occurs as 'few individuals living at the lower mediolittoral, often embedded in moss-like algae'. Mifsud & Cilia (2009) reported the first significant colonies with a mytilid cluster habitus from Birżebbuġa.

Brachidontes pharaonis displays several features that are typical of invading species (Sarà *et al.*, 2003), such as high fecundity and tolerance to variable environmental conditions, including high levels of pollution, according to Morton (1988) and Shefer (2003). The proliferation of *B. pharaonis* within the Mediterranean Sea, the ease with which it can be sampled and the evident displacement of indigenous species of *Mytilaster* Monterosato, 1883 it causes (Felsenburg & Safriel, 1974; Safriel & Sasson-Frostig, 1988; Rilov *et al.*, 2002) have fuelled physiological (e. g. Sarà, 2006) and even genetic (Shefer *et al.*, 2004; Sirna Terranova *et al.*, 2006, 2007) studies on the species. The latter investigations have disclosed a lack of genetic structure *within* the Mediterranean populations for the species, suggesting a relative lack of genetic differentiation between such populations.

The mapping of a species' distribution and the documentation of shifts in such an occurrence have fascinated biologists for decades, ever more so with the ascent of invasion biology. This study represents one of the first comprehensive attempts at mapping the distribution of a non-indigenous species (*B. pharaonis*) conducted over the entire extent of a national territory—that of the Maltese Islands—with one other similar study being that of Rilov *et al.* (2004), conducted in Israel. Supplementary information on the density of the mytilid and on the ecological and physical characteristics of each of the sampling sites is also compiled.

MATERIALS AND METHODS

A series of observations on local shores was carried out between 2009 and 2011 by the authors. A stretch of coastline at a time was explored and the presence or absence of *B. pharaonis* was noted. The entire extent of the low-lying coastline of the Maltese archipelago was investigated in this way, with only coastal stretches having a significant slope value (>10 degrees; e.g. the cliffs along the western coastline of Malta and Gozo) not being sampled.

In the case of positive results, a measurement of the population density was carried out using three randomly-positioned 0.01 m^2 replicates, about 1 m above mean sea level (as demarcated by *Cystoseira* spp. populations), with subsequent extrapolation to a value for one square metre. Locations with very small, scattered numbers of specimens were listed as containing 'isolated individuals'. The mytilids were not scraped off the rocks prior to counting, therefore the densities observed and reported in this study are an underestimate, consisting exclusively of superficially visible adults. Using on-site observations and maps (Government of Malta, 1993; Google Maps, 2011) the type of substratum colonized by *B. pharaonis* was recorded and coordinates of each sampling location were extracted. Predominant supralittoral to sublittoral macrofloral and macrofaunal species, in close proximity to the *B. pharaonis* populations or specimens, were identified, at least to generic level.

RESULTS

Figure 1 gives the current distribution of *B. pharaonis* in the Maltese Islands as reported by the present study. Table 1 lists all the previous records of *B. pharaonis* from the Maltese Islands, whilst Table 2 lists the findings at each individual sampling site adopted in the present study.

Table 1. Historical and unpublished records of *Brachidontes pharaonis* (Fischer, 1870) in the Maltese Islands.

Date of record	Location	Number on map	Comments	Communication
X.1970	Qawra	1	NA	Charles Cachia
	Baħar iċ-Ċagħaq	2		
1973	St Julian's	3		
	Kalkara Creek	5		
	St Thomas' Bay	7		
	Birżebbuġa Bay	9		
VIII.1990	Miġer Ilma, below Dingli Cliffs	10	Live attached to rocks at waterline	Constantine Mifsud
IX.1985	Marsaskala Bay	6	In detritus from −4 m	
IX.2004	Baħar iċ-Ċagħaq	2	Juveniles from tidepool	
24.VI.2007	Qajjenza, Marsaxlokk Bay	8	On fish farm nets	
III.2010	Rinella Bay	4	On old tyre near shore	

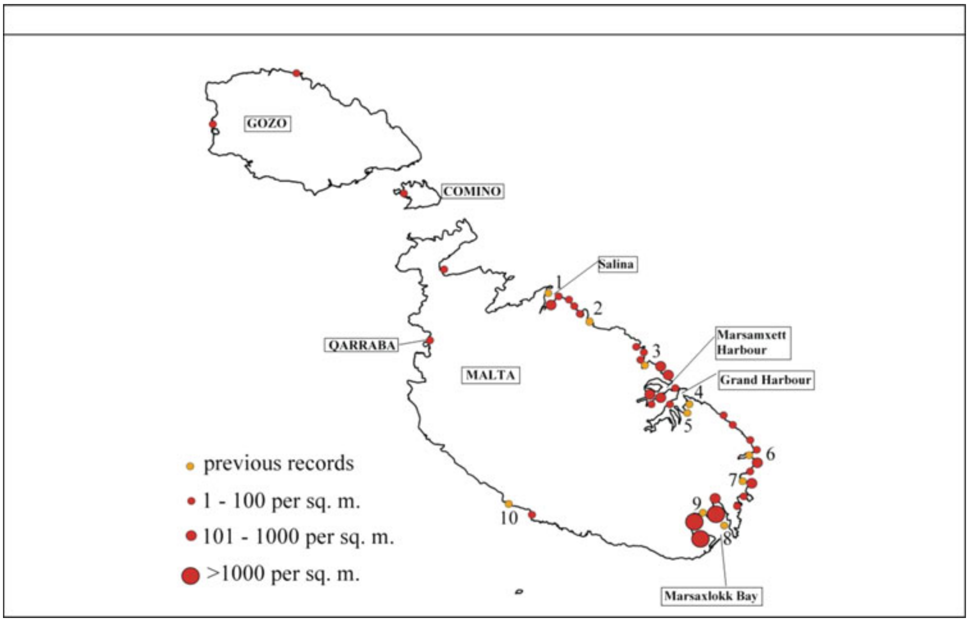

Fig. 1. Previous and current records, with the latter including population densities, for *Brachidontes pharaonis* (Fischer, 1870) around the Maltese Islands. Named coastal zones indicate embayments where the highest densities of *B. pharaonis* were recorded or where interesting observations about the species were made. Refer to Table 1 for the numbered records.

DISCUSSION

Findings from the present study seem to suggest that *B. pharaonis* has a predilection for sedimentary substrates (limestone), in particular Globigerina Limestone, on which it reaches the highest densities. In fact, the species occurs only as small clusters or as isolated individuals on other types of limestone, such as Upper Coralline or Lower Coralline Limestone. Besides limestone substrates, *B. pharaonis* exhibited a high degree of environmental plasticity in that it was also recorded in the present survey from concrete, wood, a discarded seaborne tyre and even from within vermetid (*Dendropoma petraeum* (Monterosato, 1884) and *Vermetus* sp.) reefs. In the westernmost record for the island of Malta, within the Qarraba area (Figure 1), the species was even observed inhabiting empty boreholes of *Lithophaga lithophaga* (Linné, 1758).

Although surveys conducted by malacologists since 1970 in the Maltese Islands were not systematic ones but just snapshot studies restricted to point locations only, such that *B. pharaonis* might have been under-reported in the past, findings of the present study suggest that this species has greatly expanded its range in the archipelago in recent years, reaching, in some areas, the same densities reported, for example, from a hyperhaline saltpan in western Sicily (Sarà, 2006; Sarà *et al.*, 2008).

The first record of *B. pharaonis* in the Maltese Islands was at Qawra (point 1 in Figure 1), made in 1970—since then, the species has expanded its range within the archipelago, being recorded also in small densities from the islands of Comino and Gozo (Figure 1). On these two islands, *B. pharaonis* is restricted mainly to concrete jetties, suggesting that vessels are acting as vectors, at least in initial stages, in proliferating the species.

Displacement of the native Mediterranean mytilid *Mytilaster minimus* (Poli, 1795) is an often-cited effect of invasion of *B. pharaonis* (e.g. Safriel & Sasson-Frostig, 1988; Rilov *et al.*, 2004). In many of the sampled localities, an absence of *M. minimus* was noted; in a small number of localities, like Baħar iċ-Ċagħaq, Balluta and some areas in Valletta (Table 2), a degree of sympatry betwen the two species was observed; however, the density of *M. minimus* was always much lower than that of the invasive species and on no occasion was a dense cluster of *M. minimus* observed. It is impossible to accurately define the extent of displacement of *B. pharaonis* over *M. minimus* simply because there are no previous studies on the latter's population densities on the Maltese coastline. However, shell sizes exceeding the 10 mm normally attained by *M. minimus* were very rarely observed in areas where both species were present. Safriel & Sasson-Frostig (1988) hypothesize that the two species are able to coexist due to different environmental preferences and an extinction–immigration continuum. Juvenile specimens of another mytilid species, *Mytilus galloprovincialis* Lamarck, 1819, were encountered within the St Thomas' Bay community.

In a few places, like Spinola Bay, Manoel Island and the Msida marina (Table 1), high populations of *Ostreola stentina* (Payraudeau, 1826) seem to inhibit clustering of *B. pharaonis*, creating 'breaks' in what would otherwise be a complete stretch of *Brachidontes*-colonized coast. A wooden boat observed at the Spinola inlet yielded a vast population of *O. stentina* yet only a single, mature, individual of *B. pharaonis*. Two main reasons are postulated for this competitive exclusion—the size and complex nature of *O. stentina* clusters make it more difficult for larva of *B. pharaonis* to settle on the substratum, while their larger and more extensive filter-feeding apparatus may competitively inhibit the invasive species from obtaining the required nutrition. In addition, *O. stentina* is seemingly less selective as regards substratum (colonizing concrete walls more frequently) and is probably much more resistant to polluted water, such as in the innermost parts of the Msida marina, where it reaches very high population densities. In Sliema, areas containing juveniles of another lessepsian migrant bivalve *Pinctada radiata* (Leach, 1814) lacked any specimens of the mytilid.

Table 2. Populations of *Brachidontes pharaonis* (Fischer, 1870) in the Maltese Islands as discovered during the present research. Records are sorted clockwise beginning from Dwejra, Gozo.

Date of record	Location	Coordinates	Density	Substrate
09.VI.2011	Dwejra, Gozo	36°03′13″N 14°11′29″E	Isolated individuals	Weathered/eroded concrete platform
09.VI.2011	Qbajjar Bay, Marsalforn, Gozo	36°04′37″N 14°15′07″E	$\sim$10 m^{-2}	Lower and Middle Globigerina Limestone
13.VI.2011	Blue Lagoon, Comino	36°00′51″N 14°19′28″E	Isolated individuals	Upper Globigerina Limestone coastline
18.V.2011	Għadira, Mellieħa	35°58′07″N 14°21′08″E	Isolated individuals	Upper Coralline Limestone
06.VI.2011	Baħar iċ-Ċagħaq–Salini stretch	35°57′14″N 14°26′16″E	None	Lower Coralline Limestone coastline
	06.VI.2011	35°57′06″N 14°26′37″E	None	
	06.VI.2011	35°56′52″N 14°26′47″E	Isolated individuals	
	06.VI.2011	35°56′41″N 14°26′57″E	$\sim$10 m^{-2}	
	06.VI.2011	35°56′40″N 14°27′09″E	Isolated individuals	
	06.VI.2011	35°56′37″N 14°27′19″E	None	
06.VI.2011	35°56′25″N 14°27′25″E	$\sim$100 m^{-2}	Upper Globigerina Limestone coastline	
05.XII.2010	Pembroke	35°56′14″N 14°28′24″E	None	Lower Coralline Limestone coastline
05.XII.2010		35°56′13″N 14°28′40″E	None	
05.XII.2010		35°56′10″N 14°28′53″E	None	Vermetid reef on Lower Coralline Limestone
05.XII.2010		35°55′53″N 14°29′14″E	None	Lower Coralline Limestone coastline
30.VI.2011	St George's Bay area, St Julian's	35°55′35″N 14°29′16″E	Isolated individuals	Artificially modified Lower Coralline Limestone coastline
30.VI.2011		35°55′34″N 14°29′25″E	Isolated individuals	Lower Coralline Limestone coastline with concrete patches
30.VI.2011		35°55′32″N 14°29′16″E	None	Sand
30.VI.2011	Spinola Bay area, Sliema	35°55′25″N 14°29′37″E	Isolated individuals	Lower Coralline Limestone coastline
30.VI.2011		35°55′22″N 14°29′44″E	Isolated individuals	
30.VI.2011		35°55′13″N 14°29′43″E	Isolated individuals	
21.IX.2010		35°55′10″N 14°29′25″E	<10 m^{-2}	Wooden fishing boat
21.IX.2010	Balluta	35°54′56″N 14°29′49″E	<10 m^{-2}	Concrete wall
21.IX.2010	Sliema Seafront, Sliema	35°54′55″N 14°30′24″E	$\sim$50 m^{-2}	Lower Globigerina Limestone coastline
26.III.2011	Qui-si-sana, Sliema	35°54′41″N 14°30′29″E	$\sim$10 m^{-2}	Lower Globigerina Limestone coastline
26.III.2011		35°54′41″N 14°30′26″E	$\sim$10 m^{-2}	
26.III.2011		35°54′40″N 14°30′35″E	$\sim$100 m^{-2}	
26.III.2011		35°54′40″N 14°30′32″E	$\sim$10 m^{-2}	
26.III.2011		35°54′37″N 14°30′38″E	$\sim$100 m^{-2}	
26.III.2011		35°54′34″N 14°30′40″E	$\sim$100 m^{-2}	
26.III.2011	Tignè Point, Sliema	35°54′32″N 14°30′41″E	$\sim$100 m^{-2}	Lower Globigerina Limestone coastline
26.III.2011		35°54′31″N 14°30′43″E	$\sim$10 m^{-2}	
26.III.2011	35°54′22″N 14°30′34″E	Not observed	Concrete wall	
26.III.2011		35°54′21″N 14°30′38″E	$\sim$10 m^{-2}	
26.III.2011		35°54′20″N 14°30′40″E	None	Lower Globigerina Limestone coastline
26.III.2011	35°54′19″N 14°30′42″E to 35°54′30″N 14°30′43″E	Not observed	Mostly Lower Globigerina Limestone coastline with concrete areas	
26.III.2011		35°54′30″N 14°30′43″E	$\sim$10 m^{-2}	Lower Globigerina Limestone coastline
23.XII.2011	Sliema Creek area	35°54′31″N 14°30′13″E	None	Concrete steps
23.XII.2011		35°54′27″N 14°29′58″E	Not observed	Concrete wall
23.XII.2011	35°54′15″N 14°29′45″E	None	Concrete and boulders	
23.XII.2011		35°54′10″N 14°29′44″E	None	
23.XII.2011	Ta' Xbiex	35°54′02″N 14°29′52″E	None	Concrete wall

Continued

Table 2. Continued

Date of record	Location	Coordinates	Density	Substrate
23.XII.2011	35°53′58″N 14°30′02″E	~100 m^{-2}	Lower Globigerina Limestone coastline	
23.XII.2011		35°53′50″N 14°30′00″E	~100 m^{-2}	
23.XII.2011		35°53′47″N 14°30′00″E	Less than 10 m^{-2}	
23.XII.2011	Msida Marina, Msida	35°53′47″N 14°29′50″E	None	Concrete wall
23.XII.2011		35°53′47″N 14°29′29″E	None	
23.XII.2011		35°53′45″N 14°29′38″E	None	
23.XII.2011		35°53′44″N 14°29′25″E	None	
23.XII.2011	Pietà Seafront	35°53′36″N 14°29′49″E	<10 m^{-2}	Concrete wall
23.I.2011	Xatt it-Tiben, Sa Maison	35°53′35″N 14°29′51″E	~50 m^{-2}	Concrete slope
02.IV.2011	Fort St Elmo area (Marsamxett), Valletta	35°54′12″N 14°31′08″E	None	Lower Globigerina Limestone coastline
02.IV.2011		35°54′12″N 14°31′05″E	~10 m^{-2}	
02.IV.2011		35°54′11″N 14°31′13″E	None	
02.IV.2011		35°54′11″N 14°31′01″E	None	
02.IV.2011		35°54′10″N 14°31′14″E	None	Artificially modified Lower Globigerina Limestone coastline
02.IV.2011		35°54′05″N 14°30′55″E	~10 m^{-2}	Lower Globigerina Limestone coastline
02.IV.2011		35°54′06″N 14°30′52″E	~100 m^{-2}	
02.IV.2011	Fort St Elmo area (Grand Harbour), Valletta	35°54′07″N 14°31′11″E	None	Lower Globigerina Limestone coastline
02.IV.2011		35°54′05″N 14°31′10″E	None	
02.IV.2011		35°53′56″N 14°31′06″E	None	
02.IV.2011	Ta' Liesse area, Valletta	35°53′48″N 14°31′01″E	None	Concrete wall
02.IV.2011		35°53′47″N 14°30′56″E	~10 m^{-2}	Isolated Lower Globigerina Limestone patch
02.IV.2011		35°53′45″N 14°30′51″E	None	
02.IV.2011		35°53′40″N 14°30′48″E	None	Concrete wall
02.IV.2011		35°53′37″N 14°30′46″E	None	
02.IV.2011	Grand Harbour, Valletta Waterfront, Floriana	35°53′26″N 14°30′33″E	None	Concrete wall
02.IV.2011		35°53′20″N 14°30′26″E	None	
14.VI.2011	Xgħajra–Marsaskala stretch	35°53′07″N 14°33′10″E	10 m^{-2} to 100 m^{-2}	Lower Globigerina Limestone coastline
14.VI.2011		35°53′00″N 14°33′22″E	10 m^{-2}	
14.VI.2011		35°52′52″N 14°33′27″E	None	
14.VI.2011		35°52′49″N 14°33′40″E	None	
14.VI.2011		35°52′41″N 14°33′52″E	None	
14.VI.2011		35°52′30″N 14°34′03″E	None	
14.VI.2011		35°52′22″N 14°34′14″E	Isolated individuals	
13.V.2011		35°52′10″N 14°34′21″E	None	
13.V.2011		35°52′01″N 14°34′20″E	~10 m^{-2}	
13.V.2011		35°51′56″N 14°33′58″E	Scattered individuals	Weathered/eroded concrete platform
13.V.2011		35°51′49″N 14°33′55″E	None	Vertical concrete wall
13.V.2011		35°51′46″N 14°34′24″E	~100 m^{-2}	Lower Globigerina Limestone coastline
13.V.2011		35°51′35″N 14°34′24″E	~10 m^{-2}	
13.V.2011	Tal-Miġnuna Cliffs, Marsaskala	35°51′25″N 14°34′13″E	10 m^{-2} to 100 m^{-2}	Middle Globigerina Limestone coastline
01.V.2009	St. Thomas' Bay area, Birżebbuġa	35°49′32″N 14°31′55″E	>1000 m^{-2}	Middle/Lower Globigerina Limestone coastline
01.V.2009		35°49′31″N 14°31′52″E	~100 m^{-2}	Concrete wall
01.V.2009		35°49′27″N 14°31′46″E	~10 m^{-2}	Sand
01.V.2009		35°49′24″N 14°31′45″E	>1000 m^{-2}	Middle/Lower Globigerina Limestone coastline
01.V.2009		35°49′22″N 14°31′46″E	>1000 m^{-2}	
01.V.2009		35°49′21″N 14°31′46″E	>1000 m^{-2}	
01.V.2009		35°49′20″N 14°31′47″E	>1000 m^{-2}	
01.V.2009		35°49′17″N 14°31′49″E	~100 m^{-2}	
01.V.2009		35°49′15″N 14°31′49″E	~100 m^{-2}	
01.V.2009		35°49′12″N 14°31′50″E	~100 m^{-2}	

Continued

Table 2. Continued

Date of record	Location	Coordinates	Density	Substrate
13.V.2011		35°51′17″N 14°34′00″E	~10 m^{-2}	
09.II.2011	Xrobb l-Għaġin, Delimara	35°50′26″N 14°34′07″E	Scattered individuals	Upper Globigerina Limestone, with occasional Middle and Lower Globigerina Limestone outcrops
09.II.2011		35°49′52″N 14°33′33″E	Scattered individuals	
09.II.2011	San Luċjan promontory, Qajjenza, Birżebbuġa	35°50′18″N 14°32′59″E	None	Middle Globigerina Limestone large cobbles/ stones/small boulders
09.II.2011		35°50′10″N 14°32′43″E	Scattered individuals	Concrete wall (relatively smooth)
09.II.2011		35°50′04″N 14°33′04″E	None	Concrete wharf/jetty—in ruins
09.II.2011		35°49′59″N 14°32′44″E	Scattered individuals	Upper Globigerina Limestone, with occasional Middle and Lower Globigerina Limestone outcrops
04.II.2011		35°49′55″N 14°32′21″E	>1000 m^{-2}	
04.II.2011		35°49′46″N 14°32′41″E	<10 m^{-2}	
09.II.2011		35°49′53″N 14°32′46″E	~100 m^{-2} to 1000 m^{-2}	Middle and Upper Globigerina Limestone platform
13.V.2011	Munxar Point, Birżebbuġa	35°51′00″N 14°34′13″E	~100 m^{-2}	Middle Globigerina Limestone coastline
13.V.2011		35°51′00″N 14°34′13″E	~100 m^{-2}	Middle/Lower Globigerina Limestone coastline
13.V.2011		35°51′00″N 14°34′02″E	~10 m^{-2}	Middle Globigerina Limestone coastline
13.V.2011		35°51′00″N 14°34′02″E	~10 m^{-2}	Middle/Lower Globigerina Limestone coastline
09.II.2011		35°50′14″N 14°33′48″E	Scattered individuals	
09.II.2011	St George's Bay, Qajjenza, Birżebbuġa	35°49′58″N 14°32′13″E	~10 m^{-2}	Upper Globigerina Limestone, with occasional Middle and Lower Globigerina Limestone outcrops
09.II.2011		35°49′57″N 14°32′17″E	>1000 m^{-2}	
09.II.2011		35°49′56″N 14°32′06″E	>1000 m^{-2}	
09.II.2011		35°49′56″N 14°32′00″E	~100 m^{-2}	
09.II.2011		35°49′56″N 14°31′57″E	~10 m^{-2}	
29.VI.2011	Magħlaq promontories	35°49′34″N 14°25′51″E	None	Lower Coralline Limestone coastline
29.VI.2011		35°49′33″N 14°25′53″E	None	
29.VI.2011		35°49′32″N 14°25′55″E	None	
13.V.2011	Għar Lapsi main area	35°49′38″N 14°25′25″E	~10 m^{-2}	Weathered/eroded concrete platform
29.I.2011	Fomm ir-Riħ – Anchor Bay stretch	35°54′48″N 14°20′15″E to 35°57′35″N 14°20′20″E	None	Isolated Upper, Middle and Lower Globigerina Limestone outcrops along extensive coastal stretch
05.III.2011	Għajn Tuffieħa to Il-Mixquqa area, Mellieħa	35°55′47″N 14°20′40″E	None	Upper Coralline Limestone boulders and pebbles
05.III.2011		35°55′43″N 14°20′40″E	None	Sand
05.III.2011		35°55′40″N 14°20′34″E	~10 m^{-2}	Upper Coralline Limestone boulders and pebbles
05.III.2011		35°55′34″N 14°20′27″E	None	

The physical conditions in the sheltered area near Manoel Island, which is lacking in *B. pharaonis*, are similar to others where large densities of the species may be found. The bivalve's absence may be due to the extensive populations of *Anemonia viridis* Forsskål, 1775 which may preclude the larvae from settling.

A gastropod which may actively inhibit the settlement of *B. pharaonis* larvae is the predatory *Pisania striata* (Gmelin, 1791), whose presence in the current study mostly coincided with the absence or a relative scarcity of the mytilid. On the other hand, *Osilinus turbinatus* (Born, 1778), *Muricopsis cristata* (Brocchi, 1814), *Cerithium lividulum* Risso, 1826, patellids, chitons, and *Chthamalus* spp. were very frequently observed inhabiting the same areas as *B. pharaonis*. Bonnici (unpublished data) reports the following molluscan species as being exclusively reported from *B. pharaonis* beds (i.e. these species were missing from reference locations where *B. pharaonis* was only present as sparse individuals and not as beds): *O. turbinatus*, *Ocinebrina edwardsii* (Payraudeau, 1826) and *Patella* spp., together with *Podocerus* sp., nereids, nemerteans and sabellids.

A variety of macrofloral species characterized shores with *B. pharaonis*, with the main dominant species being *Corallina elongata* Ellis & Solander, *Cladophora prolifera* (Roth) Kützing, *Ceramium ciliatum* (Ellis) Ducluzeau, *Ulva/Enteromorpha* spp. and *Jania rubens* (Linné) Lamouroux along sheltered and polluted shores, and *Cystoseira* spp., *Padina pavonica* (Linné) Thivy, *Sargassum vulgare* C. Agardh and *Dictyopteris polypodioides* (De Candolle) Lamouroux along more exposed shores.

Besides ecological interactions, tolerance to the prevailing physical conditions obviously shape the current distribution of *B. pharaonis*, with exposure to wave action and phytoplankton quantity seemingly being the most important distribution determinants for the species. In fact, according to CIESM (2003) 'its abundance seems to be negatively associated with wave exposure'. The main repositories of *B. pharaonis* individuals recorded in the current study were sheltered areas, mainly within large embayments (Marsaxlokk Bay, Grand Harbour, Marsamxett Harbour and Salina), characterized by significant levels of water pollution in view of their popularity for shipping and recreational vessel berthing. Large breaks in the distribution of *B. pharaonis* have been recorded along the most exposed shores of the island of Malta (e.g. Pembroke—refer to Table 2). This finding is consistent with that of Safriel & Sasson-Frostig (1988) but contradicts that reported by Rilov *et al.* (2004), who report extensive beds of *B. pharaonis* from wave-exposed stretches of the Israeli coastline. Bonnici (unpublished data) reports no significant variation between wave exposure values for locations with mussel beds formations and with sparse individuals.

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