Biological Invasions **6:** 347–364, 2004.

Prolonged lag in population outbreak of an invasive mussel: a shifting-habitat model

Gil Rilov[1,3,*], Yehuda Benayahu[2] & Avital Gasith[1]
[1]*Institute for Nature Conservation Research,* [2]*Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Ramat-Aviv, Tel Aviv 69978, Israel;* [3]*Current Address: School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 1, New Zealand;*
[*]*Author for correspondence (e-mail: gil.rilov@canterbury.ac.nz; fax: +64-3-3642024)*

Received 28 May 2002; accepted in revised form 9 December 2003

Key words: bioinvasions, *Brachidontes pharaonis*, Israel, lag-time, Lessepsian migration, Mediterranean Sea, mussel, rocky shore

Abstract

Biological invasions pose a great threat to the integrity of natural communities. Some invasive species demonstrate a population explosion shortly after arrival while in other cases a prolonged lag between arrival and population outbreak is evident. This paper describes a case of a prolonged lag and explores the possible mechanism for this lag. The Red Sea mussel *Brachidontes pharaonis*, a Lessepsian migrant, was first recorded in the Mediterranean seven years after the opening of the Suez Canal in 1869. Since then it spread along the Israeli coast and as far northwest as Sicily. Studies conducted in the late 1970s, when *B. pharaonis* was still rare, predicted that it would not establish dense populations along the Israeli coast and would not outcompete the indigenous mussel *Mytilaster minimus*, although it has strong negative effects on survival and growth of the native species. It was attributed to the invader's low intrinsic rate of increase relative to that of the native species, and to strong density-independent mortality generated by exposure to high wave action and sedimentation. In contrast to these predictions, we found massive formations of *B. pharaonis* beds after lag of about 120 years. We looked for distributional patterns that may explain this lag and found no south–north gradient but a strong habitat-dependent colonization. Most apparent are dense *B. pharaonis* mussel beds (density >300 per $100\,\text{cm}^2$) on rocky platforms where mussel beds were absent in the past. These platforms lack the vermetid rim that is typical to this formation. In platforms protected by a biogenic rim, sediment accumulation is high and perennial algae flourish. None of the mussel species form beds in such habitats. We suggest that the delayed formation of *B. pharaonis* beds along the Israeli coast is a consequence of a recent shift in habitat conditions on some platforms. It is possible that receding of the biogenic rim at the edge of these platforms allowed more effective washing, reduced sediment accumulation, and reduced perennial algae cover making platforms more suitable for the mussels. Lower density-independent mortality allowed *B. pharaonis* to dominate on such platforms over the indigenous species. On beachrock, a habitat previously dominated by *M. minimus*, we recorded a rapid shift in numerical domination to *B. pharaonis* (from 1 : 7 to 1.4 : 1 *Brachidontes/Mytilaster* individuals) over a period of 4 years (1995–1999). This is probably a result of saturation of the habitat by *B. pharaonis* recruits originating from the established populations on platforms. Salinity changes and a potential genetic shift may also have contributed to the invasive mussel outbreak.

Introduction

Biological invasions often result in homogenization of the earth's biota (Carlton 1987, 1989; Lodge 1993). They pose a great threat to the integrity of natural communities and to the preservation of endangered species by changing biotic interactions such as competition with and predation on native species

(Carlton and Geller 1993; Byers 2000; Grosholz et al. 2000; Grosholz 2002). Crooks and Soule' (1999) reviewed the dynamics of biological invasions and stated that during the early stages of invasion, the rates of population growth and range expansion of an alien species can vary markedly. Some species exhibit a rapid rate of population growth while others appear to have long time lags between initial introduction and subsequent population explosions. So far, the biological factors that operate during the early stages of invasions are not well understood (Crooks and Soule' 1999). Crooks and Soule' (1999) recognized three categories of time lags during population expansion of an invasive species: (1) inherent lags caused by the nature of population growth and range expansion; (2) environmental lags caused by changes in ecological conditions to those favored by the alien; and (3) genetic lags caused by the relative lack of fitness of the alien in a novel environment. In contrast to terrestrial ecosystems, long-term studies of marine invasions are scarce, and among those there are very few examples of long lags periods of population explosion of invaders (reviewed in Crooks and Soule' 1999; Grosholz 2002). In this paper, we present a case study of a Red Sea mussel invader with a prolonged lag in its population explosion after a relatively long period of range expansion, and using the revealed patterns propose hypotheses regarding the possible mechanisms that caused this temporal pattern.

The migration of Red Sea species into the Mediterranean Sea through the Suez Canal (Lessepsian migration, Por 1978) is a well-documented case of range expansion caused by human activity. Since the opening of the Canal in 1869, which removed a geographical barrier between the 2 seas, more than 200 species of various taxonomic groups, including numerous mollusks, have migrated from the Red Sea into the Mediterranean (e.g. Safriel and Ritte 1986; Spanier and Galil 1991; Barash and Denin 1992; Lotan et al. 1994; Golani 1998; Galil 2000). Nevertheless, only some studies deal with the dynamics of invader establishment in the new area or their effects on native species (for review, Galil 2000). For example, the rapid displacement of the indigenous K-selected (low fecundity, crawl-away larvae) Mediterranean gastropod *Cerithium repestre* by its r-selected (high fecundity, planktonic larvae) Red Sea congeneric *Cerithium scabridum* was studied in detail (Ayal 1978; Safriel and Ritte 1986; Ayal and Safriel 1989). In contrast, Safriel and Ritte (1986) suggested that the small, r-strategy, indigenous mussel *Mytilaster minimus* (Poli), is faster in monopolizing newly created patches in the highly wave-exposed Israeli Mediterranean rocky intertidal than the larger invasive Red Sea mussel *Brachidontes pharaonis* (Fischer 1870) = *B. variabilis* (Krauss 1848). Although the invader grows well under eastern Mediterranean conditions and can adversely affect (via interference) the recruitment of the native species, the native species numerically dominates rocky habitats along the Israeli coast (Safriel and Sasson-Frostig 1988).

Safriel and Sasson-Frostig (1988) suggested that the conditions prevailing along the Israeli Mediterranean coast allow coexistence of the two species in 'extinction-immigration competition equilibrium', in which newly opened patches are competed for by recruits of both species. *M. minimus* dominates due to its r-selected features, but in wave-protected habitats *B. pharaonis* has the potential to achieve dominance by its strong interference effect (the mechanism of this interference is not described). The authors predicted that in wave-exposed sites, the domination of the native species would persist due to a combination of density-independent mortality caused by wave action and periodical covering by sand and by the lower recruitment rate of the invader. Notably, in the Safriel and Sasson-Frostig (1988) study, recruitment of *B. pharaonis* was extremely low.

In the 1970s, Safriel et al. (1980a) conducted an extensive survey along the Israeli Mediterranean coast to describe the distribution patterns of mussel beds in the region. They characterized two major types of rock formations: soft sedimentary rocks that form horizontal eolianite platforms in exposed areas, and seaward dipping slabs of conglomerate beachrock. They also described three types of mussel distribution patterns: continuous 'beds', dispersed patches, and solitary individuals. They further stated that mussel beds or patches were associated only with beachrock, and were located in the lower and middle sections of the midlittoral. *M. minimus*, the numerically dominant species at that time, was found in high densities on beachrock in southern, central, and northern regions of the Israeli coast (Safriel et al. 1980a). Finally, they added that 'the southern site [Palmachim] is the only coast where eolianite platforms are devoid of [the vermetid gastropods] *Vermetus triquetus* and lack the seaward *Dendropoma* rim' (see also Tzur and Safriel 1978). Furthermore, 'these platforms [without rims] have a "*Mytilaster* bed", whereas all others [with no rim] do not'. Safriel et al. (1980a) suggested that sediment that is often trapped on the flat of platforms with rims prevents the development of mussel beds.

The Red Sea mussel *B. pharaonis* was first recorded near the Mediterranean exit of the Suez Canal seven years after its opening (Safriel et al. 1980a). Since then it spread northwest, reaching Sicily by the late 1960s (Sara et al. 2000). Dense beds were found in 1974 in the middle of the Suez Canal (Safriel et al. 1980a), but at that time it never formed 'beds' in the eastern Mediterranean, and 'is singly or in small groups dispersed within *M. minimus*'. In its native environment, *B. pharaonis* forms dense beds mainly in mid-midlittoral rocky habitats (Barash and Danin, 1982; Safriel et al. 1980b). The mussel's densities there varied between 4 and 10 individuals per 50 cm^2, while at the same time in the Mediterranean its density was more than 4-fold lower. In the 1970s, the density ratio between *B. pharaonis* and *M. minimus* in mixed beds in Israel was 1 : 90 (Lavee 1981).

In early 1994 we conducted a preliminary assessment of mussel distribution in the rocky shore along the Israeli Mediterranean coast and found that the invader established extensive beds in many wave-exposed habitats, notably also on platform formations in central and northern sites (Rilov et al. 1996). These findings contradicted the prediction of Safriel and Sasson-Frostig (1988) of continued domination of *M. minimus* in wave-exposed sites. It is possible that either (1) the above prediction was wrong, or (2) this is an extreme case of a prolonged lag in population explosion of a marine invader. As in other cases, changes in the 'receiving environment' may have facilitated the delayed population explosion (Lodge 1993; Crooks and Soule' 1999).

We aim to (1) test the state of coexistence of *B. pharaonis* and *M. minimus* along the Israeli coast, (2) uncover possible temporal changes in dominance of the two mussel species, and (3) look for possible spatial patterns and/or habitat-related differential establishment of *B. pharaonis* populations. For that, we investigated the distribution pattern of *B. pharaonis* at different habitat types along the coast; recorded the density and biomass relationships of the two mussel species in different habitats; and looked for spatial–temporal changes in size structure. Our preliminary surveys reviled that many of the central and northern platforms, which according to Safriel et al. (1980a) had well-developed *Dendropoma* rims in the 1970s, now lacked them. Therefore, we paid special attention to the structure of rocky habitats where beds of *B. pharaonis* were present or absent along the coast in relation to platform size and the presence or absence of the *Dendropoma* rims at the edge of platforms.

Methods

Study sites and habitats

Between 1995 and 1999 we surveyed rocky sites along ca 90 km of the Israeli shore from Akhziv in the north to Ashqelon in the south (Figure 1). We selected 13 sites (Table 1), representing all formation types of rocky habitats in the Israeli coast. These formations were:

a) *Platforms*: Eolianite, sand- or limestone structures projected seaward at approximately mean sea level. We have classified them into four sub-categories based on their shape, size, topography, and biotic cover, all of which vary considerably along the shore: (1) 'Narrow platform' (Figure 2a) is no more than 10–20 m on the axis parallel to the shore, and extends 10–50 m seaward. Algae cover these platforms seasonally and intensive flushing of the rock surface limits sand accumulation to large depressions and holes. (2) 'Intermediate platform' is 30–100 m wide along the shore and 15–30 m long seaward. It is usually covered by several centimeters of water at low tide, enabling growth of perennial algae and the deposition of sand. Both the narrow and intermediate platforms generally resemble the 'mature platform' formation described by Safriel (1966), except that at the time of our study the biogenic rim formed by the vermetid gastropod *Dendropoma petraeum* was underdeveloped or even completely absent. (3) 'Offshore platform' (Figure 2b) usually a small formation, which is located 50–100 m offshore and usually has an underdeveloped vermetid rim. (4) 'Horizontal vermetid ledge' (Safriel 1966) platform (Figure 2c) which extends 10–20 m seaward and usually runs for 10–100 m on the axis parallel to the shore. This type of platform has a well-developed *Dendropoma* rim at its seaward edge. The rim encloses shallow basins, which usually hold water on the platform's flat during period of low tides and calm sea, and are covered by sand (depth to 4 cm) and perennial algae (covering up to 90% of the rock surface).

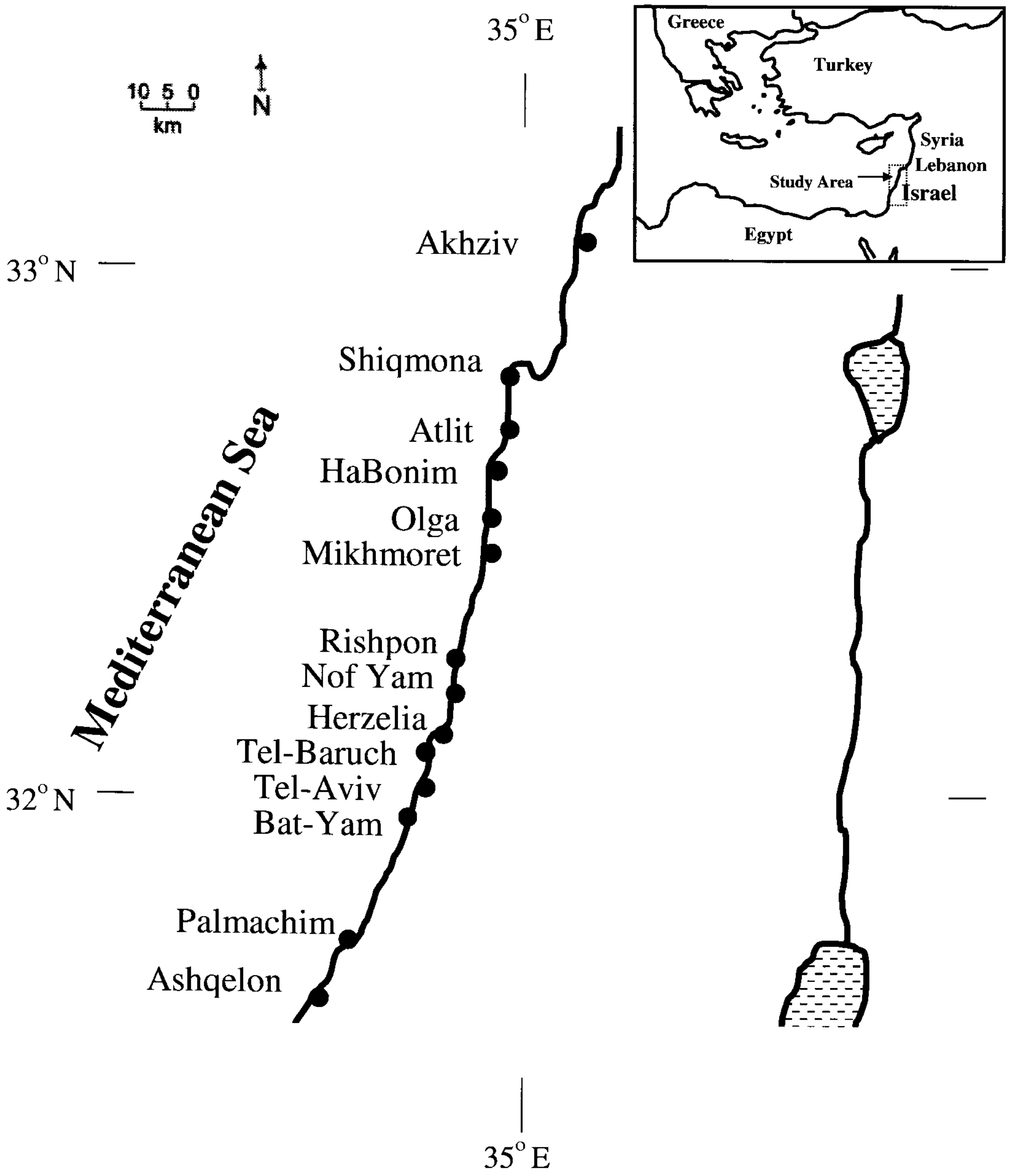

Figure 1. The studied region (upper right insert) and study sites along the Israeli Mediterranean coast.

Water depth near the platforms varies between 1 and 7 m. The subtidal walls of all the platforms described above are often covered by red algae or by barnacles and encrusting sponges, bryozoans, and hydrozoans in more shaded areas. Underwater boulders and man-made concrete blocks of breakwaters that were also surveyed are characterized by the same benthic cover. The bedrocks (horizontal rocks at 1–4 m of depth) that surround platforms at several locations are usually covered by sand and algae (Figure 2c).

b) *Incisioned-rocks (Figure 2d)*: A sandstone or eolianite rocky bench that is structurally highly heterogeneous, its surface is usually several centimeters below the level of platforms, and is usually only 5–10 m long seaward. It is characterized by abundant holes and crevices, which may, at times, be partially filled with sand.

Table 1. Study sites along the coast from north to south with type of habitat surveyed.

	Habitat	Platforms				Incisioned-rocks	Beachrock	Boulders	Intertidal walls
	Site	Narrow	Intermediate	Horizontal vermetid ledge	Small off-shore				
North	Akhziv	×				×	×[a]	×[b]	×
	Shiqmona		×						
	Atlit		×						
	HaBonim			×[c]	×[d]	×			×
	Olga							×	
	Mikhmoret		×[e]						
	Rishpon						×		
	Nof Yam							×	
	Herzelia Marina breakwater							×[f]	
	Tel-Baruch				×		×[g]	×	
	Tel-Aviv Marina breakwater							×[f]	
↓	Bat-Yam	×			×				
South	Palmachim	×					×		

× marks where a specific habitat was surveyed.

[a] Slabs with smooth surface.

[b] Only subtidal.

[c] Run, with several interruptions, for ca 4 km along the shore.

[d] Located ca 50 m from the ledge.

[e] Reduced vermetid rim and a pronounced algal cover.

[f] The marina breakwater and breakwaters to the north and south.

[g] 15 m from the shoreline.

Areas of bare rock are also found in this formation. The incisioned-rock reaches depths of 0.5–1.5 m underwater.

c) *Beachrock (Figure 2e)*: Eolianite rocky bench, 5–10 m wide and slightly tilted seaward. In some areas it forms 'smooth rocky slabs', in others a more complex topography. Areas bare of sessile macroinvertebrates and perennial algae are common. Strong storms can result in partial cover of the beachrock by sand for a period of days to weeks. The beachrock usually reaches depths of 0.5–1 m.

d) *Boulders (Figure 2f)*: Eolianite boulders 1–4 m high, found at depths of 1–7 m.

e) *Intertidal walls*: Rocky structures that are part of the eolianite ridge that usually forms platforms or incisioned-rocks but in this case the rocks extend diagonally from the supralittoral zone, 1–2 m above sea level, into the water and do not form a platform. They are sometimes characterized by a gradual, irregular descent of the rocky structure towards the midlittoral, creating narrow upper-midlittoral ledges (10–30 cm) with depressions and crevices. Areas bare of sessile macroinvertebrates and perennial algae are common.

The tidal range along the Israeli Mediterranean is relatively small (up to 40 cm) and low tides are often concealed by wave action.

Mussel distribution, density, and size structure

We visited each study site at least four times during the study period, usually in different seasons (during 1994–1999). We qualitatively described the cover of the mussels *B. pharaonis* and *M. minimus* within each habitat type as follows: 'beds' (large dense formations continuously covering areas $>1\,\text{m}^2$), 'patches' (small dense formations covering areas $<1\,\text{m}^2$), and 'solitary' mussels. We measured density and relative abundance of the mussels within beds or within patches and determined their size frequency distribution on different dates in the following habitats: narrow and intermediate platforms (Palmachim, Bat-Yam, Mikhmoret, and Akhziv), horizontal vermetid ledge platform (HaBonim), beachrocks (Tel-Baruch), incisioned-rocks (Akhziv), and subtidal boulders (Herzelia Marina breakwater) (Figure 1). We estimated mussel density in $10 \times 10\,\text{cm}^2$ quadrats ($n = 3$–5) by scraping mussels from the substrate using

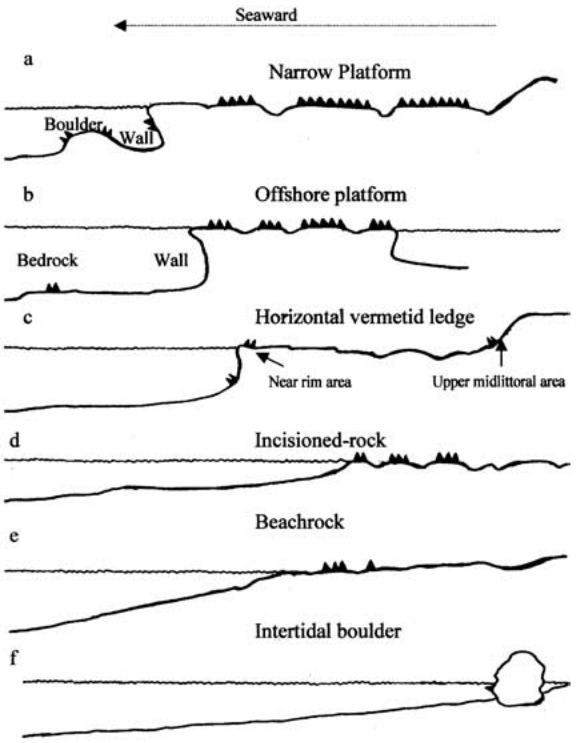

Figure 2. Profiles of different types of rocky habitats along the Israeli coast (not to scale). The location of mussel beds or patches is illustrated by small black triangles (▲▲▲).

a 5-cm wide spatula and analyzing the samples in the lab. We had to limit our density estimates to rare periods of calm sea conditions (Rilov et al., in preparation), to minimize loss of material while scraping. This limited our ability to sample different sites in the same period. We preserved the mussels in 70% alcohol, and in the lab we spread the samples (which usually consisted of several hundreds of individuals) uniformly in a 15-cm diameter petri dish and divided them into 4 equal sub-samples. Preliminary counts of 10 samples showed that the coefficient of variation among the 4 sub-samples was small (<15%). Thereafter, we randomly selected a single sub-sample for sorting to species and mussel size. We counted the mussels and estimated their shell length using section paper (± 0.5 mm). The values obtained for a sub-sample were multiplied by four to get an estimate of the sample's density. We calculated the numerical ratio between *B. pharaonis* and *M. minimus* in each sample and averaged them for each habitat within a site on each sampling date. Differences in the size structure of the two mussel species may suggest differences in habitat quality, detect temporal trends in recruitment rates and population growth, or a change in competitive dominance between the species.

In sites or habitats where mussel density was low we determined the relative abundance of both mussel species by direct field counts using either $10 \times 10\,\text{cm}^2$ quadrats placed along a line at 1-m intervals (in the margins of the horizontal vermetid ledge habitat), or by counting eight such quadrats randomly chosen within a $1 \times 1\,\text{m}^2$ area that was divided into 100 smaller quadrats (in the intermediate-platform formation). The latter method was repeated 16 times (because of high observed patchiness) by tossing the $1 \times 1\,\text{m}^2$ quadrat haphazardly on the platform. In the horizontal vermetid ledge habitat, density was determined (except in mussel patches on the flat itself, see above) in the upper-midlittoral at the back of the ledge at 10 and 20 cm above the platform flat ($n = 45$ quadrats per height), and at the seaward edge of the ledge near the *Dendropoma* rim ($n = 30$).

Mussel cover and biomass

To minimize possible bias of comparative estimates of mussel cover, biomass, and density and size structure in different habitats, we compared these features in different habitats within the same site at a given sampling date. During November 1997, we measured cover and took samples from 4 habitat types (narrow platform, incisioned-rock, upper-midlittoral ledge, and smooth rocky slabs) all located within a coastal stretch of 150 m at the Akhziv site. Because perennial algae may compete for space with mussels, we compared the percent cover of mussels and algae at the different habitats within this site by placing a $1 \times 1\,\text{m}^2$ quadrat (divided by lines into smaller sub-quadrats), 1 m away from the seaward edge of the rocks. The presence of mussels and/or algae found under each of 100 junctions created by the lines dividing the quadrat and the 2 sides of the quadrat (uniform point sampling technique) were recorded ($n = 10$ for each habitat). We measured cover on the Akhziv platform (Figure 1) that had almost a rectangular shape, in the southern, northern, and western faces, as well as the center of this platform (3–4 m from the seaward edge).

Summation of the weight of the individual mussels gave the total biomass per $10 \times 10\,\text{cm}^2$ area of bed or patch. We calculated this from data of mussel density, mussel size, and the relationship between size and biomass (oven dry tissue weight, 70 °C for 48 h). We measured biomass for each size class, which were separated by 2-mm increments (4–6 individuals for each size class of each species, CV < 25%).

Results

Distribution of mussels

There was no south–north spatial trend in the appearance of *B. pharaonis* beds along the coast, and beds dominated by this species were found from Palmachim in the south to Akhziv in the north (Table 2). Similar densities of *B. pharaonis* within beds or patches on these platforms were found in different sites (Table 3, comparison of samples taken in 1997 from Palmachim, Bat-Yam, HaBonim, and Akhziv, one-way ANOVA, $F = 2.4$, $P = 0.11$). There were, however, distinctive habitat-related patterns in the distribution of the invasive mussel. We found extensive beds of *B. pharaonis* on horizontal and relatively narrow rocky habitats where the *Dendropoma* rim was underdeveloped, and sand and perennial algal coverage was low (i.e. on narrow and offshore platforms, and on incisioned-rocks, Table 2). *B. pharaonis* beds covered 40%–80% of the rock surface on the narrow platforms, peaking near the middle and decreasing towards the shoreward or seaward sides of the platforms. For example, 60% of the total surface area of the narrow platform in Bat-Yam ($220\,\mathrm{m}^2$) was covered by *B. pharaonis* mussel bed in 1995, and most of the surface bare of mussels was on the shore side. Beds of *B. pharaonis* covered the entire surface of most small ($< 50\,\mathrm{m}^2$) offshore platforms

Table 2. A qualitative comparison of the distributional pattern of *Brachidontes pharaonis* and *Mytilaster minimus* in different habitat types.

Habitat type	Location*	Presence	Distributional pattern
Narrow and offshore platforms	North: Akhziv Center: HaBonim, Bat-Yam South: Palmachim	*B. pharaonis* found in large numbers including large individuals. A few *M. minimus* found among *B. pharaonis*	Mostly in beds and occasionally in patches Beds' size declined shoreward on large platforms
Horizontal vermetid ledge	Center: HaBonim	Mussels rare, except for marginal areas to the lee and seaward sides of the platform, and in areas of high flushing	Solitary or in small patches inside depressions in the upper-midlittoral (up to 20 cm above the platform) and near or on the *Dendropoma* rim Patches are rare
Intermediate platform	North: Shiqmona, Atlit Center: Mikhmoret	Both mussels relatively rare	Solitary, or in small patches
Incisioned-rock	North: Akhziv	*B. pharaonis* found in large numbers including large individuals. A few *M. minimus* found among *B. pharaonis*	Beds and patches
Beachrock	North: Akhziv Center: Rishpon, Tel-Baruch South: Palmachim	Both mussels present where the topography is complex or on elevated horizontal surfaces	Patches of various sizes, or small patches inside crevices or depressions
Intertidal walls	North: Akhziv Central: HaBonim	Both mussels present on upper-midlittoral ledges	Patches of various sizes, or small patches inside crevices or depressions
Intertidal boulders	Central: Olga, Nof-Yam	Both mussels relatively rare	Small patches inside depressions
Subtidal platform walls and boulders	All locations	Present to a depth of 3–4 m *B. pharaonis* found in large numbers including large individuals. A few *M. minimus* found among *B. pharaonis*	Small but dense patches; usually in shaded areas amongst barnacles
Subtidal bedrock	North: Akhziv Center: Bat-Yam South: Palmachim	Both mussels rare	Patches can be found in places with almost no sand and algal cover

*Location depicts the studies sites where these habitat types were studied along the Israeli coast.

Table 3. Mean density per 100 cm^2 (±SD) of *Brachidontes pharaonis* and *Mytilaster minimus* and their ratio in different habitat types along the Israeli Mediterranean coast (n = number of samples).

Habitat type	Site	Date	Density		Ratio $B:M$	n
			B. pharaonis	*M. minimus*		
Narrow platform[a]	Palmachim	April 96	216 ± 54	87 ± 72	3.1 ± 1.4	5
		November 96	164 ± 30	36 ± 40	9.2 ± 7.8	5
		January 97	161 ± 21	19 ± 4	8.8 ± 1.9	5
		April 97	180 ± 36	15 ± 4	13.0 ± 4.8	5
	Bat-Yam	November 97	221 ± 37	59 ± 17	4.4 ± 1.0	5
	Akhziv	January 95	153 ± 53	1 ± 2	128.0*	5
		December 95	271 ± 74	23 ± 12	13 ± 4.5	5
		November 97	261 ± 68	21 ± 11	12.9 ± 4.0	5
Offshore platform[a]	HaBonim	November 97	225	20	11.2	1
Horizontal vermetid ledge[a]	HaBonim	November 97	220 ± 36	22 ± 4	9.8 ± 1.3	5
Upper-midlittoral, 20 cm above horizontal vermetid ledge[b]	HaBonim	May 95	1.2 ± 2.2	7.2 ± 9.6	0.17*	45
Upper-midlittoral, 10 cm above horizontal vermetid ledge[b]	HaBonim	May 95	0.4 ± 1.8	2.7 ± 5.9	0.15*	45
Edge of horizontal vermetid ledge[b]	HaBonim	May 95	1.1 ± 2.3	2.9 ± 8.2	0.38*	30
Intermediate-platform formation[b]	Mikhmoret	May 95	0.1 ± 0.6	0.7 ± 1.7	0.14*	128
Incisioned-rock[a]	Akhziv	June 96	154 ± 56	100 ± 43	1.6 ± 0.6	5
		November 97	356 ± 93	81 ± 30	4.7 ± 1.2	5
		November 99	198 ± 64	7.5 ± 0.7	26.3	2
Beachrock[a]	Tel-Baruch	November 95	90 ± 58	881 ± 31	0.17 ± 0.09	5
		November 96	316 ± 120	604 ± 114	0.53 ± 0.19	3
		November 97	333 ± 15	352 ± 15	0.98 ± 0.13	5
		November 98	299 ± 42	382 ± 18	0.78 ± 0.09	5
		November 99	196 ± 52	156 ± 69	1.43 ± 0.66	6
Upper-midlittoral ledge[a]	Akhziv	November 97	168 ± 58	394 ± 158	0.53 ± 0.32	5
Smooth rocky slabs[a]	Akhziv	November 97	8	368	0.02	1
Infralittoral boulders[a]	Herzelia	November 98	315 ± 11	12 ± 3	28 ± 8.0	5

*Ratio calculated by dividing the density means and not by averaging the ratios of samples. Only in cases where *M. minimus* was absent in at lease one of the samples.

[a] Habitats where density was measured only from samples within beds.

[b] Habitats where density was measured directly on the rocks.

(e.g. HaBonim, Tel-Baruch, and Bat-Yam). We found mixed patches of both *B. pharaonis* and *M. minimus* (similar density within patch) mainly on beachrocks and upper-midlittoral ledges of intertidal walls. There, mussel patches were found usually in and around grooves and crevices, whereas the rest of the rock surface was mostly bare (Table 2). Mussel patches on vertical subtidal surfaces (i.e. platform walls and boulders) were composed mainly of *B. pharaonis* distributed among barnacles and perennial algae.

Mussels were rare on horizontal surfaces of either vermetid ledge platforms or subtidal bedrocks, except for confined areas of these habitats where water movement was strong. There, mixed-species or *B. pharaonis*-dominated patches were present. We found solitary mussels or small patches of both species inside depressions on beachrocks, intermediate-platform formations, smooth lower-midlittoral beachrock, slabs, and intertidal boulders. Solitary mussels or mussels in patches were also found at the margins of the horizontal vermetid ledge platform, in the upper-midlittoral and at the edge of the platform flat near or on the *Dendropoma* rim (Table 2). *M. minimus* did not substantially spatially dominate any habitat investigated along the shore.

Density and relative abundance

The mean density of *B. pharaonis* and of the indigenous mussel *M. minimus* varied considerably among habitats (Table 3). Mussel beds with >150 individuals per 100 cm^2 of *B. pharaonis* were consistently recorded on narrow platforms and offshore platforms and in the incisioned-rock habitats. We recorded similar densities in the few mussel patches on the horizontal vermetid ledge, beachrock (except for 1995), upper-midlittoral ledge, and subtidal boulder habitats. On the margins of the horizontal vermetid ledge platform (upper-midlittoral and near the platform's edge), on the intermediate platforms and on smooth rocky beachrock areas the density of *B. pharaonis* was about two orders of magnitude lower than in the above beds and patches (Table 3). *M. minimus* attained densities > 350 individuals per $100\,\mathrm{cm}^2$ within mixed mussel patches in intertidal habitats (beachrocks, the upper-midlittoral ledge of intertidal walls, and smooth rocky slabs). These patches were separated by relatively large areas bare of other sessile macroinvertebrates or perennial algae. In mixed mussel beds found on narrow and offshore platforms, and in the incisioned-rock habitat the density of *M. minimus* was about four-fold lower than on beachrocks, the upper-midlittoral ledge of intertidal walls and smooth rocky slabs (Table 3). At the margins of the horizontal vermetid ledge and on intermediate platforms only a few individuals of *M. minimus* per $100\,\mathrm{cm}^2$ were found (Table 3).

The numerical dominance of either mussel species is portrayed by their density ratios (indicated in Table 3). *B. pharaonis* dominated in beds found on platforms (density ratio > 3), in incisioned-rock habitats (ratio > 1.6), and in mussel patches on subtidal surfaces (ratio $= 28$, Table 3). We observed an increase in the numerical dominance of *B. pharaonis* at certain sites. For example, at a platform site in the south (Palmachim) the density ratio increased by 4-fold in 1 year, and at the incisioned-rock habitat (Akhziv) by 16-fold over a period of 3 years (Table 3). *M. minimus* was the dominant mussel on beachrock, upper-midlittoral ledge, marginal areas of horizontal vermetid ledge, intermediate-platform formations, and smooth rocky slabs (Table 3). At a beachrock habitat (Tel-Baruch) the dominance shifted from that of *M. minimus* to that of *B. pharaonis* over the course of 4 years (from density ratio of 1 : 7 *B. pharaonis* to *M. minimus* in 1995 to 1.4 : 1 in 1999). This change in dominance was a result of a progressive 2-fold increase in the density of *B. pharaonis* and more than a 5-fold decrease in the density of *M. minimus* (Table 3, regression of density ratio with time: $r^2 = 0.85$; $F = 27.5$, $P < 0.05$).

Table 4. Effect of habitat type (narrow platform, incisioned-rock, and beachrock) and species (*Brachidontes pharaonis* and *Mytilaster minimus*) on mussel density, Akhziv (November 1997).

Effect	SS	d*f*	MS	*F*	*P*
Habitat	95 720	2	47 860	5.5	0.0105
Species	81 641	1	81 641	9.4	0.0052
Habitat ∗ species	417 331	2	208 665	24.1	<0.0001
Error	207 653	24	8652		

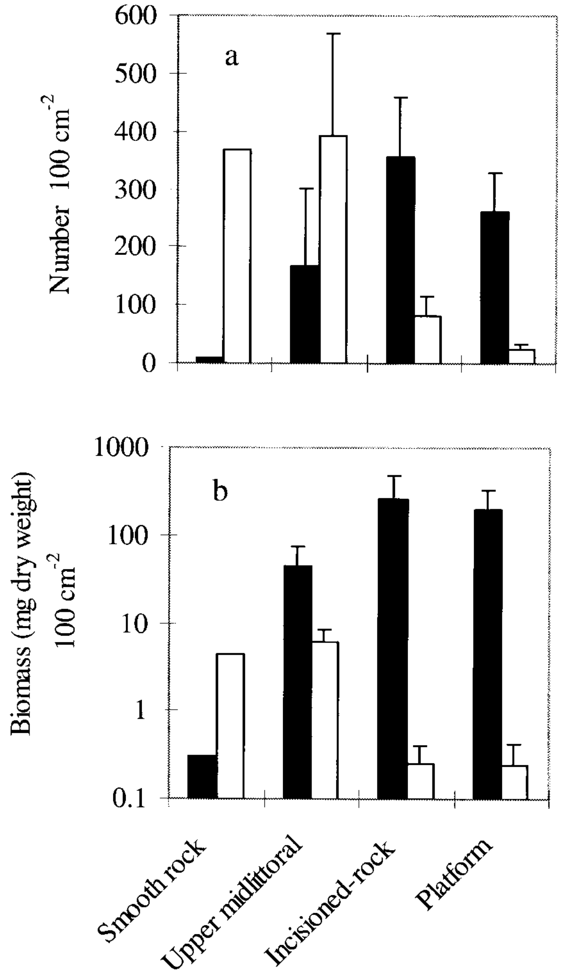

Figure 3. Comparison of (a) mean density (±SD) and (b) biomass (log scale) of *Brachidontes pharaonis* (dark bars) and *Mytilaster minimus* (empty bars) within mussel beds or patches in four different rocky habitats within one site (Akhziv, November 1997). $n = 1$ at the smooth rock and $n = 5$ in the other 3 habitats.

We recorded differences in mean densities of *M. minimus* and of *B. pharaonis* among habitats and between species in four adjacent habitats of one site (Akhziv, Table 4; Figure 3a). Only one small clump in the smooth rocky slab habitat almost exclusively consisted of *M. minimus* (thus not included in the analysis). In the upper-midlittoral habitat, the density of *M. minimus* was about two-fold higher than that of *B. pharaonis*. In contrast, *B. pharaonis* dominated the incisioned-rock and narrow and offshore platform habitats, where its mean densities were

4.5- and 10-fold higher, respectively, than that of *M. minimus*.

Size frequency distribution

The two mussels differ considerably in size. *B. pharaonis* is about 3 times larger than *M. minimus* (maximal size, 33 and 13 mm, respectively). The size frequency of the two mussel species differed among habitats within and among sites. The largest individuals of *B. pharaonis* recorded in this study (> 30 mm) were found in the narrow and intermediate platforms (Akhziv, Palmachim, Bat-Yam sites, Figures 4a and 5d–g) and in the incisioned-rock habitat

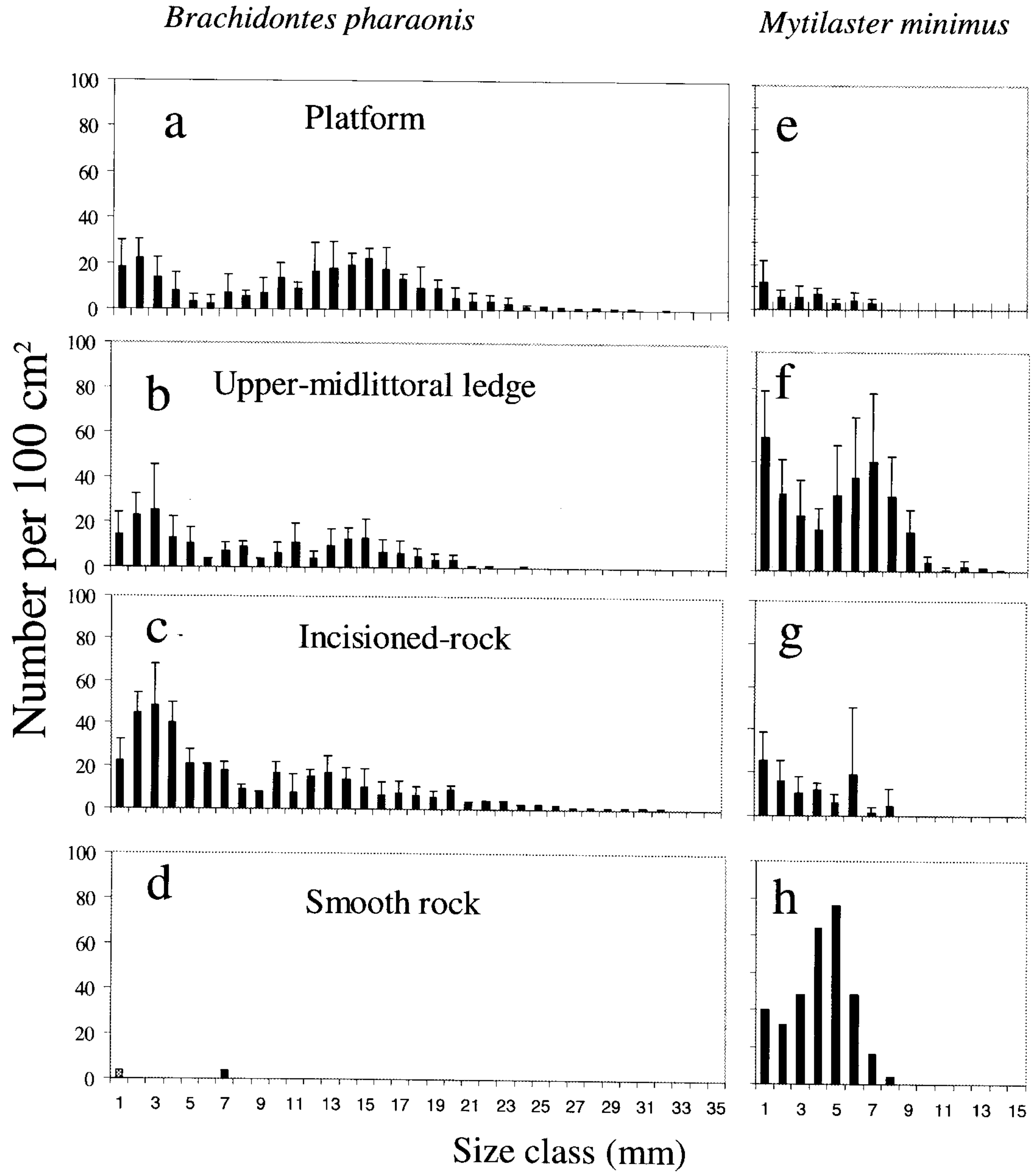

Figure 4. Size structure of *Brachidontes pharaonis* and *Mytilaster minimus* assemblages within mussel-beds and patches in 4 rocky habitat types in Akhziv in November 1997 (mean + SD, $n = 5$ for a–c, e–g).

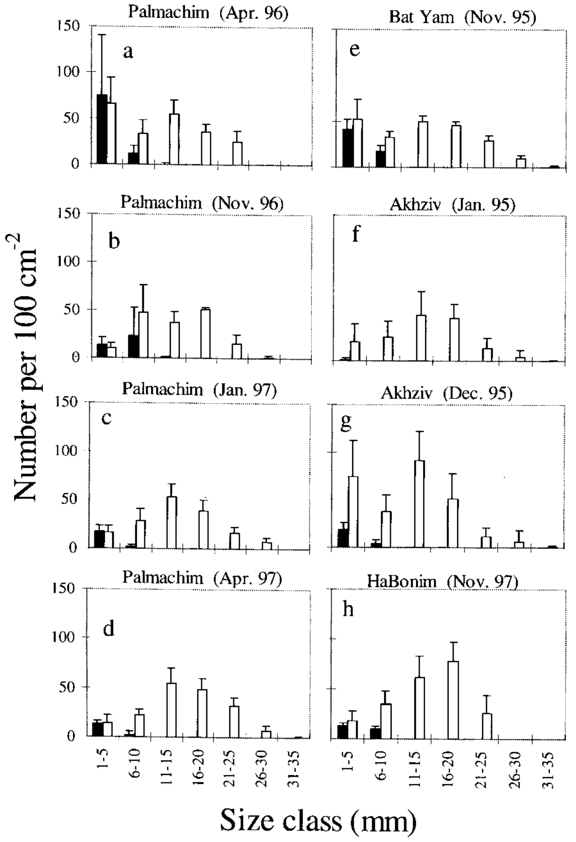

Figure 5. Mytilaster minimus (dark bars) and *Brachidontes pharaonis* (empty bars) population size structure of within mussel beds on selected rocky platforms along the Israeli coast (mean + SD, $n = 5$).

(Akhziv, Figure 4c). The largest *B. pharaonis* did not exceed 25 mm in the upper-midlittoral ledge (Akhziv site, Figure 4b) and the horizontal vermetid ledge (HaBonim, Figure 5h).

The largest individuals of *M. minimus* (10–13 mm) were found on the upper-midlittoral ledge (Akhziv, Figure 4f) and beachrock habitats (Tel-Baruch, Figure 6), whereas on incisioned-rocks and platforms individuals > 5 mm were rare (Figures 4e, g and 5). *M. minimus* > 7 mm were absent or rare in all but the upper-midlittoral ledge in Akhziv (Figure 4f).

Analysis of the size structure of the mussels on rocky platforms at different sites revealed that already in 1995 relatively large individuals of *B. pharaonis* (> 20 mm) were present on the central (Bat-Yam) and northern (Akhziv) platforms (Figures 5e–g, respectively) and accounted for about 15% of the total number of individuals in mussel bed samples of this species. Large individuals of *B. pharaonis* were rare on the horizontal vermetid ledge platform in 1997 (HaBonim, Figure 5h). On a platform at a southern site (Palmachim) the distribution of the mussels changed over one-year period (1996–1997). The number of recruits of *M. minimus* declined whereas that of individuals of *B. pharaonis* > 15 mm increased (Figures 5a–d). A similar trend was observed over a four-year period on beachrock in a central site (Tel-Baruch, Figure 6). The density of individuals of *B. pharaonis* > 15 mm progressively increased from 1995 to 1998 at this site (regression of density with time: $r^2 = 0.94$, $F = 29.5$, $P < 0.05$).

Mussel biomass

We determined the following relationship between the mussel biomass (dry weight) and size: *M. minimus* weight (g) $= 2.94L - 2.6$ ($r^2 = 0.99$), and for *B. pharaonis* weight (g) $= 0.39L^{2.7}$ ($r^2 = 0.99$), where L is the shell length in millimeters. Using this relationship, we calculated the respective biomass from density and size data. The biomass of *B. pharaonis* per unit area of mussel bed or patch was higher than that of *M. minimus* in all but the one clump from the smooth rock habitat at the northern site (Akhziv, Figure 3b). In the upper-midlittoral of this site the biomass of *B. pharaonis* was 7.2-fold higher than that of *M. minimus*, and at both the incisioned-rock and platform habitats it was higher by about four orders of magnitude (Figure 3b). The biomass of both *M. minimus* and *B. pharaonis* differed significantly among the 4 studied habitats within the Akhziv site (Kruskal–Wallis non-parametric ANOVA, $H_{3,16} = 10.8$, $P = 0.01$, and $H_{3,16} = 8.4$, $P = 0.04$, respectively). Highest biomass per $10 \times 10\,\text{cm}^2$ patch area of *B. pharaonis* was found on the platforms and those of *M. minimus* on the upper-midlittoral rocks.

Relationship between mussels and algae

Perennial algae (e.g. *Jania rubens*) were found in horizontal vermetid ledge, intermediate-platform formation, and to a lesser degree in narrow platform habitats. Algae like *Ulva lactuca* and *Enteromorpha* sp. usually cover midlittoral rocky habitats seasonally. We observed an inverse relationship between mussel and algal cover on platform and incisioned-rocks at the northern site (Akhziv, November 1997, Figure 7). Mostly *B. pharaonis* covered $> 80\%$ of the area where algae were absent (e.g. the incisioned-rock and on

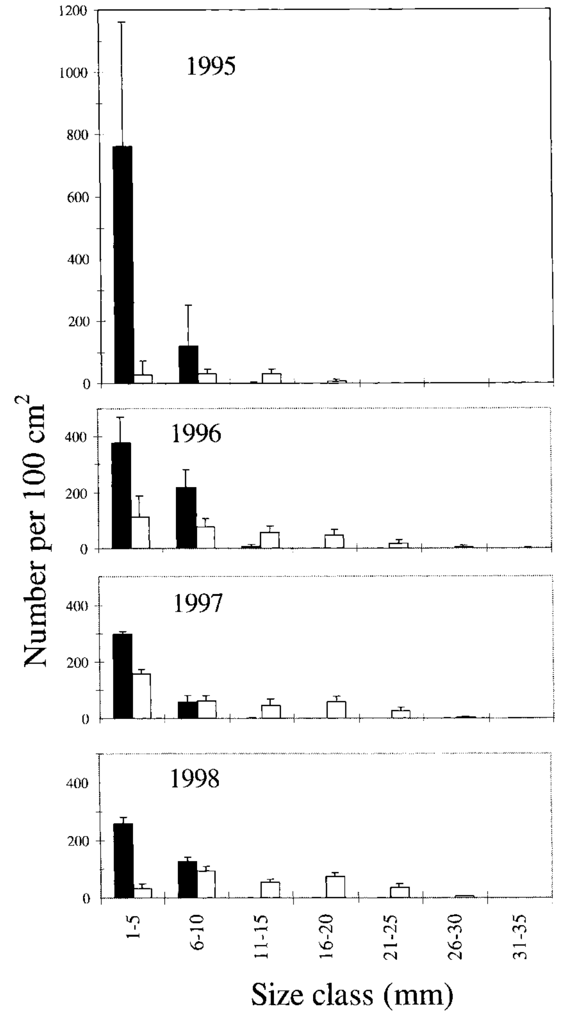

Figure 6. Mytilaster minimus (dark bars) and *Brachidontes pharaonis* (blank bars) population size structure of within mussel patches on the beachrock habitat in Tel-Baruch (mean + SD, $n = 5$) during 1995–1998.

the north, south and central areas of the platform in Akhziv) and were rare where algae were abundant (e.g. smooth rocky slabs, Figure 7). About 60% of the surface of the Akhziv platform facing westward was covered by perennial red algae and 15% by *B. pharaonis* (Figure 7). At the upper-midlittoral ledge of the intertidal wall the cover of both mussels and algae was low (about 5%) and the rest of the surface was bare rock. *B. pharaonis* and *M. minimus* were patchily distributed in a beachrock habitat at a central site (Tel-Baruch) (14 ± 7 SD, 9 ± 2, and 16 ± 12% area cover in November 1996, February, and April 1997, respectively).

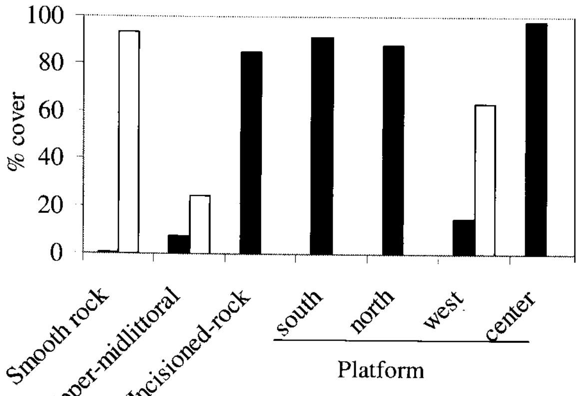

Figure 7. Percent coverage of algae (blank bars) and mussel (dark bars) in different habitats in Akhziv (November 1997).

Discussion

The invasion of the Red Sea mussel, *B. pharaonis*, to the Israeli Mediterranean coast presents a clear case of a prolonged lag (>120 years) in the outbreak of an alien species. Three major findings are highlighted in our investigation: (1) Mussel beds in general have recently expanded their distribution along the Israeli coast, and now appear on many platforms in the central and northern part of the country where no mussels (neither *B. pharaonis* nor *M. minimus*) used to prevail; (2) there is no evidence for a south–north geographical pattern of distribution of mussels on platforms along the Israeli coast, but there is a clear habitat-dependant presence of mussel beds on platforms; (3) a shift in numerical dominance has occurred from prevalence of the smaller, indigenous mussel *M. minimus* to that of the Red Sea invader *B. pharaonis* in habitats (beachrock) where the former used to prevail. Based on these findings, we suggest a probable mechanism that can explain the shift in mussel abundance along the Israeli coast. Specifically, we propose that a shift in the fine topography (receding biogenic rim) of some platforms made them suitable for mussel colonization, and that due to the interference effect of *B. pharaonis* on recruits of the indigenous mussel *M. minimus* (Safriel and Sasson-Frostig 1988), the Red Sea invader became the dominant species in the mussel beds on such platforms.

The shift in mussel dominance

Comparison of mussel density in beds and patches along the Israeli coast between the 1970s (Safriel et al. 1980a) and the 1990s (our study) demonstrates a shift in numerical dominance from *M. minimus* to *B. pharaonis*. For example, on beachrock there was a 12-fold increase in the ratio of *B. pharaonis* to *M. minimus* from 1 : 90 measured in the 1970s (Shave Ziyyon, Lavee 1981) to 1 : 7 in 1995 (Tel-Baruch site, this study), and a 14-fold increase by 1999 (ratio = 1.4 : 1), this study. On the southern platforms at Palmachim the density ratio changed from 1 : 170 in the late 1970s (Safriel and Sasson-Frostig 1988), to 3.1 : 1 in 1996, and a year later to 13 : 1. In the Palmachim case we have evidence that indicates that changes in mussel density resulted not only because of an increase in *B. pharaonis* numbers but also as a result of a decline in *M. minimus* from ca 600 individuals per 100 cm^2 in autumn 1973 (Safriel et al. 1980a) to 36 in autumn 1997 (this study). The decline of *M. minimus* may be attributed to the interference effect imposed by the larger *B. pharaonis* on *M. minimus* recruits (Safriel and Sasson-Frostig 1988). On some platforms that were never covered by mussel beds (i.e. narrow-shaped or small offshore eolianite platforms and subtidal rocks) the 1990s density ratio between the immigrant and indigenous mussel attains values of up to 128 : 1. Furthermore, *B. pharaonis*, which earlier was restricted only to the midlittoral (Lavee 1981), now extends its distribution to depths of 2–3 m. *M. minimus* maintains numerical dominance over the invasive species only in habitats where both species are found in relatively small numbers and form small patches, such as in depressions and crevices on walls or rims. It appears that after a lag of 120 years *B. pharaonis* is progressively increasing its population (both range and size) in the eastern Mediterranean, and is gradually excluding its native counterpart *M. minimus* in most habitats where the latter used to prevail. These observations contradict earlier predictions of continuous domination of *M. minimus* in exposed rocky sites along the Israeli coast (Safriel and Sasson-Frostig 1988).

Shifting-habitats model: a potential explanation for the outbreak of B. pharaonis

Our findings raise the question as to why *B. pharaonis* formed beds in rocky habitats along the Israeli shore only after approximately 120 years from its first appearance in the Mediterranean. This question is particularly intriguing in light of the fact that this mussel species had already spread as far north as Beirut and as far west as Sicily by the middle of the 20th century (Safriel et al. 1980a). The wide gaps in data on *B. pharaonis* densities make it impossible to calculate the intrinsic rate of increase (r) from first establishment along the Israeli coast, or to determine if it deviates from an inherent lag duration in the colonization process of a population (Crooks and Soule' 1999). Nevertheless, circumstantial evidence suggests that the prolonged lag is not a consequence of progressive range expansion (Crooks and Soule' 1999). Large beds were noticed in Sicily already in the 1960s (Safriel et al. 1980a). It is also not a taxa-related lag. Other mussels have demonstrated a much shorter lag-time, notably, the zebra mussel in North America, which exploded in numbers only several years after its first arrival (Ram and McMahon 1996). One possible explanation for the difference in population dynamics from the case mentioned above is an influence of environmental changes that facilitated the population explosion of *B. pharaonis*.

Safriel and Sasson-Frostig (1988) claimed that the two mussels coexist on beachrock due to density-independent mortality caused by wave action; an explanation that corresponds to the intermediate disturbance effect (*sensu* Connell 1979). They predicted that *B. pharaonis* would therefore never dominate highly wave-exposed habitats. We found this conclusion to be false and have shown that *B. pharaonis* can form dense beds on wave-exposed rocks (platforms). In fact, it has been shown that mussel beds usually dominate temperate wave-exposed rocky shores (for review, Menge and Branch 2001). Therefore, it is unlikely that wave action limits the establishment of mussel beds on platforms. Alternatively, we suggest that sediment cover is responsible for limiting mussel bed development on platforms. Platforms that hold sediment either due to their sheer size, or due to the existence of developed biogenic rims do not support mussel beds of any species, as was evident in investigations in the 1970s (Safriel et al. 1980a, Safriel and Sasson-Frostig 1988). The negative effects of heavy sedimentation on *B. pharaonis* in the Suez Canal have also been suggested by Mohammed (1997), and were demonstrated for other rocky intertidal mussels (e.g. *Mytilus californianus* in southern California, Littler et al. 1983). Furthermore, perennial algae that are abundant on large or rimmed platforms may negatively affect the mussels either directly by outcompeting them, or indirectly by facilitating sediment accumulation on platforms. In contrast to descriptions of platforms along the shore in the 1960s and 1970s (Safriel 1966, Safriel et al. 1980a) many platforms studied in our investigation lacked developed *Dendropoma* rims, and those that are narrow were covered by dense *Brachidontes* beds.

We suggest that community structure on platform habitats alternates between two steady states depending on the presence of a biogenic rim and the size of the platform. In the presence of a rim or on very large platforms, the community consists primarily of perennial algae. When the rim is absent on narrow platforms, mussel beds dominate. These two steady states or pathways are illustrated in Figure 8. Large platforms and small platforms with developed rims have reduced water flushing but sedimentation is higher and they also hold water even during low tide and calm seas. Conditions on narrow platforms with underdeveloped rims alternate between high flushing most of the time and desiccation, depending on sea and atmospheric conditions. Sediment accumulation and cover of perennial macroalgae on such platforms are generally low and food flux is expected to be high. Furthermore, the absence of a protective rim limits the holding of water on the platform during calm sea and during prolonged desiccation periods (common at times of high barometric pressure in spring and autumn, personal observations). These conditions favor mussel development (Littler et al. 1983; Menge and Farrell 1989), and can explain extensive continuous beds where *B. pharaonis* grows to its maximum size. As a result of competitive interference (Safriel and Sasson-Frostig 1988) *M. minimus* is displaced to marginal habitats where *B. pharaonis* is less likely to establish. The low density of the native mussel in this habitat, the fact that it does not grow to its maximum size (Figure 4), and probably does not reach sexual maturity (Safriel and Sasson-Frostig 1988), support the above conclusion.

We propose a shifting-habitat model in which, for some unknown reason, over the last two decades the *Dendropoma* rims on many platforms along the Israeli Mediterranean coast partially or completely eroded. Consequently, platforms that are small or narrow on the axis parallel to the shore could no longer hold water and trap sediment on their flat, or had reduced sediment residence time. These changes apparently reduced the survival of benthic fauna and flora on the platform (e.g. the gastropod *Vermetus triqueter* and the perennial alga *Laurencia papillosa*) that may compete for space with mussels. Indeed, we found low densities of *V. triqueter* and algae on such platforms (Rilov et al. 2001), where they previously prevailed (the Mikhmoret site (Figure 1); Lipkin and Safriel 1971). Thus, we hypothesize that reduced sedimentation and reduced cover of other space occupiers, together with higher food flux (plankton) in the absence of rims facilitated the establishment of mussel beds on such platforms.

Negative synergistic effects of sedimentation and wave action (as suggested by Safriel and Sasson-Frostig 1988) prevail in beachrock habitats, which border sandy bottoms more than most platforms. Indeed, mussel distribution on beachrock is patchy, the two mussel species still coexist and *B. pharaonis* does not achieve maximum size (Figure 6). However, even in this habitat changes in mussel domination do occur and are discussed below. Future investigation can test the alternative stable state hypothesis presented here by analyzing the response of *B. pharaonis* to manipulation of algal cover, or elimination of the biogenic rim in test plots on platforms. Furthermore, the reason for the decline of the biogenic (*Dendropoma*) rim is yet to be explained.

The progressive shift in numerical domination and increase in size of *B. pharaonis* on beachrock (Figure 6) can probably be explained by the 'intermediate recruitment hypothesis' presented by Dial and Roughgarden's (1998), and by the interference effect imposed by the invader mussel on the native one (Safriel and Sasson-Frostig 1988). Most likely, once *B. pharaonis* overtook the platform habitats, its larvae increased dramatically in numbers and overwhelmed less stable environments such as beachrock with recruits. Once there, the species can reduce the native's fitness as described above. Indeed, while the density of *B. pharaonis* increased markedly from 1995 to 1996 (Tel-Baruch site) and remained relatively high ever since, that of *M. minimus* decreased by six-fold over the same period (Table 3). Reduction in overall *M. minimus* densities along the coast seems to result in lower recruitment rates. In 1970 the density of *M. minimus* measured on the Mikhmoret platforms where no mussel beds occurred then and at present was about 16 per 100 cm^2 on the exposed flat of the platform (Table 6 in Safriel et al. 1980a), and declined to 0.1 in 1995 (present study). We expect that with the progressively increasing numbers of the new colonizer in rocky habitats along the Israeli coast (mostly platforms) the invader will eventually out-compete *M. minimus* in beachrock sites as well.

An alternative explanation for the decline of the indigenous mussel *M. minimus* is direct response to

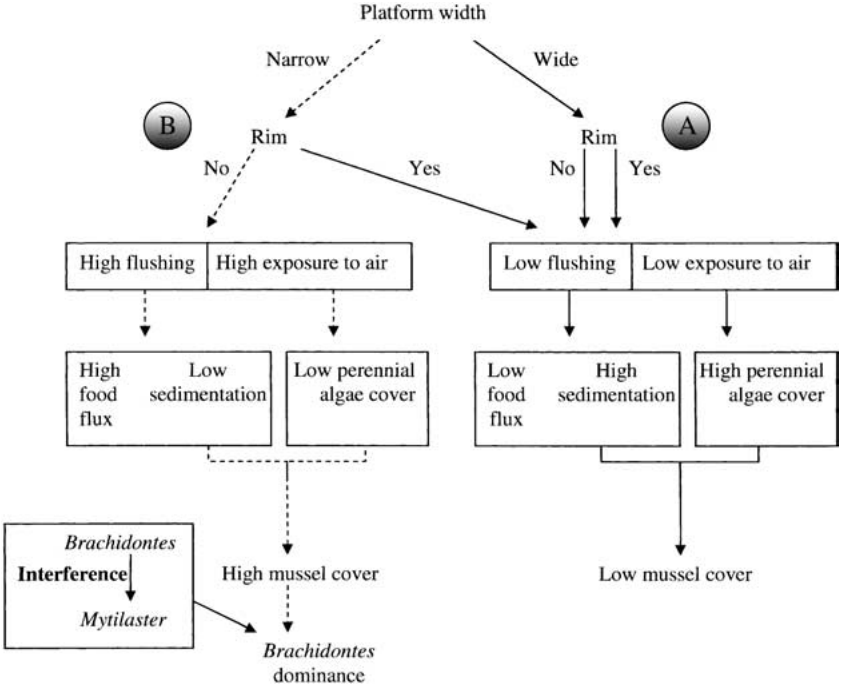

Figure 8. A conceptual model describing two potential pathways (A and B) resulting in the presence or absence of mussel beds on platform habitats. Pathway A (complete arrows) leads to low mussel cover on platforms. Pathway B (broken lines) leads to high mussel cover, and in conjunction with the biological interaction, to the dominance of *Brachidontes pharaonis* within mussel beds.

recent, yet unknown, environmental changes that reduced *M. minimus* fitness, which opened up space for the colonization of *B. pharaonis*. Even if that was the case, the fact that *B. pharaonis* massively colonizes areas that were not occupied previously by *M. minimus* suggests that negative environmental effect on the indigenous species is a less likely mechanism that can explain the outbreak of the invader populations.

Other potential mechanisms for the population outbreak

Salinity change. Another environmental change that may have contributed to the outbreak of *B. pharaonis* in the past several decades is the elimination of the seasonal salinity reduction during the flooding season (Fall) as a result of the damming of the Nile in 1964 (Oren and Komarovsky 1961; Hecht 1964; Sharaf El Din 1977). Histological work suggested that August–September is the period of reproduction of *B. pharaonis* in the Mediterranean (Felsenburg 1974) and the lower salinities then may have impaired its reproduction. Furthermore, the disappearance of the summer salinity decline may have enhanced survival of *B. pharaonis* by increasing its tolerance to the high summer temperatures (up to 31 °C) in the eastern Mediterranean (Stern and Achituv 1978). However, the species relatively high physiological plasticity at different salinities (Sara et al. 2000) suggest that the salinity changes are less likely to be a major factor that could have facilitated the population increase of *B. pharaonis*.

Genetic change. Crooks and Soule' (1999) claimed that ‘genetics remains the great unknown in the biological basis of lag effects and the causation of sudden, explosive growth and expansion of exotics’. Lavee (1981) noted that several rare alleles in the Mediterranean *B. pharaonis* populations were absent in the Red Sea ones. This finding may indicate natural selection towards alleles more suitable to the eastern Mediterranean conditions. Furthermore, the reproductive season of *B. pharaonis* shifted from winter in the Red Sea to spring and autumn in the Mediterranean (Felsenburg 1974), which corresponds with the reproductive season of the indigenous species *M. minimus*. On the platforms we found individuals of

B. pharaonis that were ca 30% larger than the largest individuals reported by Sasson (1981) for both the Red Sea and Mediterranean populations. This increase in size may be an indication of increased fitness and possibly a genetic drift. There is also a possibility that genotypes other than the Red Sea ones arrived in the Israeli coast through, for example, ballast water of ships. More genetic information is needed to test for either supporting or disproving a genetic shift in the eastern Mediterranean populations of *B. pharaonis*.

Conclusions

By now, *B. pharaonis* has dramatically changed the community structures on many platforms along the Israeli Mediterranean coast. At its current rate of spread and growth, it may soon attain massive populations all over the rocky intertidal and will likely have a significant impact on the unique platform habitats (Safriel 1974; Tzur and Safriel 1978). *B. pharaonis* is acting as a habitat-modifying species and can have serious effects on the trophic structure and interactions of the benthic community along the Israeli coast. Such an effect was demonstrated, for example, in the case of the zebra mussel that invaded freshwater ecosystems in North America (e.g. Strayer et al. 1988; Macisaac 1996) and the Asian marine mussel *Musculista senhousia* in the California coast (Crooks and Khim 1999). In the case of *B. pharaonis*, Rilov et al. (2002) already demonstrated a dramatic change in feeding habits of the predatory snail *Stramonita haemastoma* that shifted from feeding on native species to feeding on *B. pharaonis* in the Israeli Mediterranean.

In a rapidly human-mediated changing environment, and with limited monitoring efforts, significant changes in population of marine invaders can pass unnoticed for several critical years. This problem is especially true in the highly invaded, but yet little-studied eastern Mediterranean rocky shore (but see Ben Eliahu and Safriel 1982; Safriel and Ritte 1986; Fine 1988). For example, in a recent review on alien species in the Mediterranean Sea with special emphasis on Lessepsian migration, the invasion of the mussel *B. pharaonis* was completely ignored (Galil 2000). Our investigation of *B. pharaonis* is one of relatively few quantitative examples of massive population increase of an invader after an exceptionally long lag in which it was latent in its new environment. At this point of time the most probable explanation for the above response is the slow but progressive shift in habitat conditions on many of the platforms along the shore.

Acknowledgements

We thank Drs L. Crowder and B. Kirby Smith of Duke University for their useful comments on an earlier version of this manuscript. We thank T. Yacobovitch and M. Tenser for devoted assistance in the field and lab work and for creative ideas. We also thank the Akhziv Field School of the Nature Protection Society for accommodating us, and the Nature Reserves Authority for the permit to work in the nature reserves and collect animals for the lab work.

References

Ayal Y (1978) Geographical distribution, ecological niche and the strategy of reproduction of the colonizer *Cerithium scabridum* Phil. (Gastropoda: Prosobranchia) as compared with those of some other sympatric non-colonizing congeneric species. PhD dissertation. The Hebrew University of Jerusalem. Jerusalem, Israel [in Hebrew]

Ayal Y and Safriel UN (1989) Has the indopacific gastropod *Cerithium scabridum* partially outcompeted the Mediterranean *Cerithium repestre*? In: Spanier E, Steinberger Y and Luria M (eds) Environmental Quality and Ecosystem Stability, Vol IVb, pp 155–168. Jerusalem, Israel

Barash A and Danin Z (1982) Mediterranean mollusca of Israel and Sinai: composition and distribution. Israel Journal of Zoology 31: 86–118

Barash A and Danin Z (1992) Fauna Palestina, Mollusca I, Annotated List of Mediterranean Molluscs of Israel and Sinai. Keter Press Enterprises, Jerusalem

Ben Eliahu MN and Safriel UN (1982) A comparison between species diversities of polychaetes from tropical and temperate structurally similar rocky intertidal habitats. Journal of Biogeography 9: 371–390

Byers JE (2000) Competition between two estuarine snails: implications for invasion of exotic species. Ecology 81: 1225–1239

Carlton JT (1987) Patterns of transoceanic marine biological invasions in the Pacific Ocean. Bulletin of Marine Science 41: 452–465

Carlton JT (1989) Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. Conservation Biology 3: 256–273

Carlton JT and Geller JB (1993) Ecological roulette: the global transport of nonindigenous marine organisms. Science 261: 78–82

Connell JH (1979) Intermediate-disturbance hypothesis. Science 204: 1344–1345

Crooks JA and Khim HS (1999) Architectural vs biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. Journal of Experimental Marine Biology and Ecology 240: 53–75

Crooks JA and Soule' ME (1999) Lag times in population explosions of invasive species: causes and implications. In: Sandlund OT, Schei PJ and Viken A (eds) Invasive Species and Biodiversity Management, pp 103–125. Kluwer Academic Publishers, Dordrecht, The Netherlands, 431 pp

Dial R and Roughgarden J (1998) Theory of marine communities: the intermediate disturbance hypothesis. Ecology 79: 1412–1424

Felsenburg T (1974) *Brachidontes variabilis* as a successful colonizer – a preliminary survey. Thesis, Hebrew University, Jerusalem [in Hebrew]

Fine M (1998) The scleractinian coral *Oculina patagonica*: a new invader to the Mediterranean sea, biological and ecological aspects. MSc thesis, Tel-Aviv University, 59 pp

Galil BS (2000) A sea under siege – alien species in the Mediterranean. Biological Invasions 2: 77–186

Golani D (1998) Impact of Red Sea fish migrants through the Suez Canal on the aquatic environment of the Eastern Mediterranean. Bulletin of Yale School Frost Environmental Studies 103: 375–385

Grosholz E (2002) Ecological and evolutionary consequences of coastal invasions. Trends in Ecology and Evolution 17: 22–27

Grosholz ED, Ruiz GM, Dean CA, Shirley KA, Maron JL and Connors PG (2000) The impacts of a nonindigenous marine predator in a California bay. Ecology 81: 1206–1224

Hecht A (1964) On the turbulent diffusion of the water of the Nile floods in the Mediterranean sea. State of Israel Prime Minister's Office National Council of Research and Development Bulletin 36: 1–24

Lavee D (1981) Genetic variability in a Colonizatory system: comparison between the mussels *Brachidontes variabilis* and *Modiolus Auriculatus* (Bivalvia: Mytilidae). PhD dissertation. The Hebrew University of Jerusalem, Jerusalem, Israel, 80 pp

Lipkin Y and Safriel U (1971) Intertidal zonation on rocky shores at Mikhmoret (Mediterranean, Israel). Journal of Ecology 59: 1–30

Littler MM, Martz DR and Littler DS (1983) Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. Marine Ecology Progress Series 11: 129–139

Lodge DM (1993) Biological invasions – lessons from ecology. Trends in Ecology and Evolution 8: 133–137

Lotan A, Fine M and Ben-Hillel R (1994) Synchronization of the life cycle and dispersal pattern of the tropical invader scyphomedusan *Rhopilema nomadica* is temperature dependent. Marine Ecology Progress Series 109: 59–65

Macisaac HJ (1996) Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. American Naturalist 36: 287–299

Menge BA and Branch GM (2001) Rocky shore intertidal communities. In: Bertness MD, Gaines SD and Hay ME (eds) Marine Community Ecology, pp 221–251. Sinauer Associates, Sunderland, Massachusetts

Menge BA and Farrell TM (1989) Community structure and interaction webs in shallow marine hard-bottom communities: tests of an environmental stress model. Advances in Ecological Research 19: 189–262

Mohammed SZ (1997) Growth, survival and settlement of the mussel *Brachidontes variabilis* (Bivalvia: Mytilidae) in the epifaunal and infaunal substrates in the Suez Canal. Indian Journal of Marine Sciences 26: 350–355

Oren OH and Komarovsky B (1961) The influence of the Nile flood on the shore waters of Israel. Rapports et Proces-Verbaux des Reunions, Conseil International pour l'Exploration Scientifique de la Mer Medeterranee. Monaco 16: 655–659

Por FD (1978) Lessepsian Migration. The Influx of Red Sea Biota into the Mediterranean by Way of the Suez Canal. Springer-Verlag, Berlin, 228 pp

Ram JL and McMahon RF (1996) Introduction: the biology, ecology, and physiology of zebra mussels. American Zoologist 36: 239–243

Rilov G, Gasith A and Benayahu Y (1996) Selected aspects in the ecology of large predatory gastropods in rocky littoral habitats along the Israeli Mediterranean coast. In: Steinberger Y (ed) Preservation of Our World in the Wake of Change, Vol VI B, pp 608–613. ISEEQS Publications, Jerusalem, Israel

Rilov G, Benayahu Y and Gasith A (2001) Low abundance and skewed population structure of the whelk *Stramonita haemastoma* along the Israeli Mediterranean coast. Marine Ecology Progress Series 218: 189–202

Rilov G, Benayahu Y and Gasith A (2002) Effect of an exotic prey on the feeding pattern of a predatory snail. Marine Environmental Research 54: 85–98

Safriel UN (1966) Recent vermetid formation on the Mediterranean shore of Israel. Proceedings of the Malacological Society of London 37: 27–33

Safriel UN (1974) Vermetid gastropods and intertidal reefs in Israel and Bermuda. Science 186: 1113–1115

Safriel UN and Ritte U (1986) Population biology of Suez Canal migration – which way, what kind of species and why. In: Karlin S and Nevo E (eds) Evolution Processes and Theory, pp 561–581. Academic Press, New York

Safriel UN and Sasson-Frosting Z (1988) Can colonizing mussel outcompete indigenous mussel? Journal of Experimental Marine Biology and Ecology 117: 211–226

Safriel UN, Gilboa A and Felsenburg T (1980a) 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 UN, Felsenburg T and Gilboa A (1980b) The distribution of *Brachidontes variabilis* (Krauss) along the Red Sea coasts of Sinai. Argamon Israel Journal of Malacology 7: 31–43

Sara G, Romano M and Mazzola A (2000) The new Lessepsian entry *Brachidontes pharaonis* (Fischer P, 1870) (Bivalvia, Mytilidae) in the western Mediterranean: a physiological analysis under varying natural conditions. Journal of Shellfish Research 19: 967–977

Sasson Z (1981) Interspecific competition in a colonization system. MSc dissertation, Hebrew University of Jerusalem, Jerusalem, Israel

Sharaf El Din SH (1977) Effects of the Aswan High Dam on the Nile flood and on the estuarine and coastal circulation pattern along the Mediterranean Egyptian coast. Limnology and Oceanography 22: 194–207

Spanier E and Galil BS (1991) Lessepsian migration: a continuous biogeographical process. Endevor 15: 102–106

Stern S and Achituv Y (1978) Effects of temperature and salinity on the metabolism and byssal formation of *Brachidontes variabilis* Krauss (Bivalvia). Comparative Biochemistry and Physiology 59A: 101–105

Strayer DL, Smith LC and Hunter DC (1998) Effects of the zebra mussel (*Dreissena polymorpha*) invasion on the macrobenthos of the freshwater tidal Hudson River. Canadian Journal of Zoology 76: 419–425

Tzur Y and Safriel UN (1978) Vermetid platforms indicators of coastal movement. Israel Journal of Earth-Sciences 27: 124–127