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Effect of an exotic prey on the feeding pattern of a predatory snail

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Abstract

The mussel *Brachidontes pharaonis*, which invaded the Mediterranean from the Red Sea about 120 years ago, has recently become abundant in many midlittoral and some infralittoral rocky habitats along the Israeli rocky shore. We investigated the influence of *B. pharaonis*, as a novel prey, on the foraging patterns of the large whelk *Stramonita haemastoma* in the field, and examined food preferences in the laboratory. *S. haemastoma* has shifted from indigenous species to feeding on the novel mussel when abundant. The whelk prefers to prey upon the invasive mussel over all indigenous species offered (e.g. barnacles and mussels), probably due to its larger size. In the midlittoral zone, the foraging activity of *S. haemastoma* is considerably low even where refuges are readily available (incisioned-rocks) and food density is high (mainly *B. pharaonis*). Higher proportions of whelks are actively foraging in the infralittoral zone but usually on smaller prey, mostly barnacles. We suggest that this differential foraging activity in the two zones is related to the degree of exposure to wave action. The midlittoral is inherently more exposed to wave action than the infralittoral, where sea conditions are more benign and the whelks may enjoy longer activity periods.

Keywords: Benthic ecology; Effects-community; Feeding strategy; Rocky shore; Gastropods; Mussels; *Stramonita haemastoma*; *Brachidontes pharaonis*; Introduced species; Eastern Mediterranean

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1. Introduction

Biological invasions (Carlton, 1989) can often result in loss of the local biotic uniqueness and in the homogenization of the earth's biota (Carlton, 1987; Lodge, 1993). Non-indigenous invaders can also act as keystone predators and dramatically reduce local prey populations (Carlton, 1996; Grosholz & Ruiz, 1996; Grosholz, Ruiz, Dean, Shirley, Maron, & Connors, 2000; Shiganova, 1998). However, the impact of most non-indigenous species remains unknown, and the predictability of their direct and indirect effects remains uncertain (Ruiz, Carlton, Grosholz, & Hines, 1997). One such impact can be a change in the feeding patterns of indigenous predators with the establishment of a profitable, potential prey.

The migration of Red Sea species into the Mediterranean through the Suez Canal (Lessepsian migration, sensu Por, 1978) is a well-documented case of an invasion process caused by past human activity. Since the opening of the canal in 1869, which removed a geographical barrier between the two seas, more than 200 species have migrated from the Red Sea into the Mediterranean (e.g. Golani, 1998; Lotan, & Fine, Ben-Hillel, 1994; Safriel & Ritte, 1986; Spanier & Galil, 1991). Nevertheless, the ecological impact of these invasions on indigenous populations is still little understood. Massive establishment of the Red Sea mussel *Brachidontes pharaonis* along the Israeli Mediterranean coast was recently reported (Rilov, 1999). Studies in the 1970s in the eastern Mediterranean describe this Lessepsian invader as rare and found "singly or in small groups dispersed within *Mytilaster minimus*" (the indigenous counterpart) along the rocky shores of Israel (Safriel, Gilboa, & Felsenburg, 1980; Safriel & Sasson-Frosting, 1988). *Brachidontes pharaonis* has now formed extensive beds in many rocky midlittoral sites, and also appears in patches in the infralittoral (=subtidal), usually on vertical surfaces among barnacles (Rilov, Benayahu, & Gasith, 2001). This mussel is 2–3 times larger than the indigenous one (Rilov, 1999; Safriel & Sasson-Frosting, 1988), indicating it may constitute a profitable prey for local predators including muricid gastropods.

Seventeen muricid gastropods are known to exist along the Israeli and northern Sinai shores (Barash & Danin, 1982), among the most abundant species is the relatively large species (up to 76 mm shell length) *Stramonita haemastoma* (family Thaidae; Kool, 1987). In the rocky intertidal zone *S. haemastoma* mainly inhabits locations where shelter is available, and in the shallow infralittoral zone, it mainly inhabits vertical surfaces (Rilov, Gasith, & Benayahu, 1996; Rilov et al., 2001). Its distribution thus overlaps that of *Brachidontes pharaonis*.

In the Gulf of Mexico large *S. haemastoma* prey on natural and cultivated oysters, barnacles, and epizoic mussels on oysters (Butler, 1985), whereas young whelks feed mainly on bivalve spat and bryozoans. Observations on shell drill-holes in the western Mediterranean and Crete suggest that the whelks *Murex* (*Hexaplex*) *trunculus* and *S. haemastoma* feed on 18 different gastropods and bivalves (including cannibalism, Basedow, 1994, 1996). *S. haemastoma* also "readily preys upon the Mediterranean mytilids" (i.e. *Mytilaster minimus*, Safriel et al., 1980). *Brachidontes pharaonis*, barnacles, limpets and vermetid gastropods are also potential prey in the eastern Mediterranean (Rilov et al., 2001).

Preference and feeding rate of macroinvertebrate predators are influenced by the size and abundance of prey and predator, prey value, and environmental factors. Prey size is usually correlated with predator size, although very large food items may sometimes escape predation (Barbeau & Scheibling, 1994; Brown & Richardson, 1987; Dye, 1991; Fairweather & Underwood, 1991a, 1991b; Gosselin & Chia, 1994). Foraging activity depends on the density of preferred prey and on the availability of shelter (e.g. Fairweather, 1985, 1988; Moran, 1985). Ingestive conditioning (past predation experience) can also influence prey choice. Whelks habituated to a particular prey often prefer it to other food items (e.g. Dunkin & Hughes, 1984; Hughes & Dunkin, 1984; West, 1986). Choice can also be affected by wave action, as in *S. haemastoma,* which feeds on smaller prey when exposed to intense wave action (Richardson & Brown, 1990). *S. haemastoma* were most active at water temperature of 30 °C, and ceased feeding when temperature was artificially lowered to 10 °C (Garton & Stickle, 1980). This correlates with studies indicating lower density and activity of the whelks *S. haemastoma* and *Nucella lapillus* in winter (Menge, 1978; Richardson & Brown, 1990; Rilov et al., 2001). Palmer (1983, 1984) suggested that predatory thaidids forage optimally by selecting prey that maximize individual growth rate.

Prey choice integrates several factors, including abundance, energy content, and handling time required by the predator (all determine the ‘‘food value’’). Selecting optimum-sized prey has considerable benefit because it can impact scope for growth (Garton, 1986).

Adopting the optimal foraging concept, we hypothesized that *S. haemastoma* would modify its feeding patterns and thus profit from the larger novel prey. In this study we examined the feeding patterns of *S. haemastoma* and its interaction with the novel prey *Brachidontes pharaonis*. We experimentally tested whether large *S. haemastoma* prefer *Brachidontes pharaonis* over indigenous prey. We additionally tested whether ingestive conditioning influences prey choice and, therefore, whether whelks in habitats predominated by barnacles would prefer barnacles over the novel mussel.

2. Methods

2.1. Feeding patterns—field observations

We studied the proportion of individuals *S. haemastoma* foraging, and the frequencies of the different prey types in the diet of the whelk at seven sites along the Israeli Mediterranean coast (Fig. 1), where whelks are relatively abundant (average density >0.2 individuals per m^2; Rilov et al., 2001). We conducted all observations in 1995, during September–October (a period of maximum feeding activity, Rilov et al., 2001) with calm sea conditions (water temperatures, 27–29 °C). In midlittoral sites (an incisioned-rock habitat in Akhziv, platform habitat in HaBonim and a beach-rock in Tel-Baruch; Fig. 1) the survey was carried out on foot, and in infralittoral habitats (i.e. platform walls and boulders below 1 m depth), by SCUBA. An incisioned-rock is a term we use for a rough horizontal flat with many incisions and holes (see Rilov et al., 2001). Survey length was 30–45 min (depending on whelk

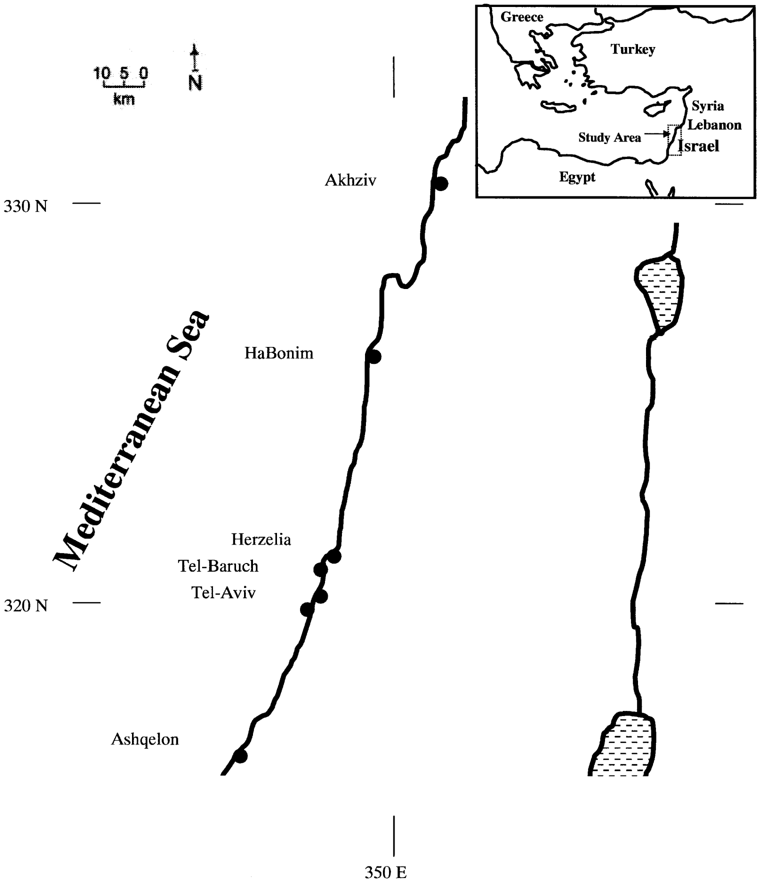

Fig. 1. Study area (upper right corner) and selected study sites along the Mediterranean Israeli coast.

abundance), and for every whelk encountered during a survey we recorded whether it was feeding and what was its prey. Feeding was determined by removing the whelks from the substrate and checking for an extended proboscis or drilling signs on the prey shell, or for empty or partially empty prey shells.

We examined effects of change in food availability on the feeding of *S. haemastoma* on the infralittoral boulders of the Herzelia marina breakwater (seaward side at depths of 2–4 m). These observations were conducted in October 1995, when *Brachidontes pharaonis* was rare, and in November 1998, when large patches of *Brachidontes pharaonis* were present at a depth of 1–3.5 m.

2.2. Prey selection—lab experiments

2.2.1. Comparison of predation rates

Whelks were collected for laboratory tests of prey choice from the intertidal zone at Akhziv and Tel-Baruch. At both sites mussels *Brachidontes pharaonis* and *Mytilaster* *minimus*, limpets *Patella caerulea*, and barnacles, mainly *Chthamalus stellatus* (mid-littoral) and *Balanus perforatus* (shallow infralittoral), were present. Fouling organisms were removed from the shells. Whelks were acclimated in 8-l aquaria containing artificial seawater for 10–14 days without feeding (Garton & Stickle, 1980). Acclimation temperature 24–26 °C, was that measured during maximum *S. haemastoma* density observed in the field (Rilov et al., 2001) and that resulted in maximum feeding rates in the lab (Rilov, 1999). Salinity 38–39‰ was of ambient seawater at the Israeli coast. Five types of experiments were conducted. In each experiment two types of prey were offered to a single snail in a pair-wise combination in an 8-l aquarium. The number of replicates for each experiment varied between 5 and 12 (Table 1). Two experiments were aimed to examine influence of the predator and prey sizes on prey selection: *Brachidontes pharaonis* of different size range (25–30 and 7–12 mm) were offered to large (55–65 mm) and medium-size (30–35 mm) whelks (small whelks were not found in the field during the study period; Rilov et al., 2001). The other three experiments aimed to examine preference of *Brachidontes pharaonis* versus other potential prey species: the indigenous mussel *M. minimus* (of different and similar sizes), the barnacles *Balanus perforatus* and the limpet *Patella caerulea*. Because *S. haemastoma* was rarely seen preying on small *Brachidontes pharaonis* or on *M. minimus* in the field, we conducted controls exposing large whelks to these types of prey (Table 1). Five individuals of each prey type were offered to a single whelk, except for barnacles, of which 20–25 individuals on a small rock were presented. We repeated twice the experiment exposing *S. haemastoma* to *Brachidontes pharaonis* and *M. minimus* of the same size. Because we observed a clear difference in prey choice in this experiment (see Section 3) we compared biomass of the two mussel species measuring dry weight of 10 mm individuals ($n = 4$, dry weight; oven, 70 °C for 48 h). The feeding response of *S. haemastoma* was recorded for 30–40 days (in 1–2 day intervals) during March–April (1997) and

Table 1
Experimental design of the long-term prey choice experiments

Experiment	Date	*n*	Predator size (mm)	Prey I		Prey II	
				Sp.	Size (mm)	Sp.	Size (mm)
1	March–April 1997	12	30–35	Bp	25–35	Bp	5–10
2	March–April 1997	7	55–65	Bp	25–35	Bp	5–10
3a	March 1997	7	55–65	Bp	5–10	Mm	5–10
3b	April 1997	7	55–65	Bp	5–10	Mm	5–10
4	October 1996	7	55–65	Bp	25–35	Bpe	4–8
5	October 1997	7	55–65	Bp	25–35	Pc	20–30
Control 1	March 1997	5	55–65	Bp	5–10		
Control 2	March 1997	5	55–65			Mm	5–10

In each experiment a single *Stramonita haemastoma* snail was offered a choice of two prey types indicated as prey I and prey II. Bp = *Brachidontes pharaonis*, Mm = *Mytilaster minimus*, Bpe = *Balanus perforatus*, Pc = *Patella caerulea*. *n* = number of replicates. Five individuals of each prey type were offered to the whelk except for barnacles, of which 20–25 individuals on a small rock were presented.

October (1996 and 1997), periods of maximum activity observed in the field (Rilov et al., 2001). In most days, intervals between observations ranged between 4 and 12 h. Consumed prey were replenished by fresh ones. Every other day, one third of the water was replenished with fresh artificial sea water to limit the buildup of waste products. The predation rate of *S. haemastoma* on the different prey types was measured. Predation preference index (PPI) was calculated as a ratio of the predation rate (i.e. the number of prey items eaten per day) of *Brachidontes pharaonis* divided by the predation rate of the other food item. PPI is significant when the difference in predation rate is significant, using a paired *t*-test (Peterson & Renaud, 1989). We did not directly measure handling time in this study, but frequent observations conducted several times along the experiment period allowed us to estimate its range.

2.2.2. *Effect of past experience on prey choice*

We examined whether whelks collected from infralittoral habitats dominated by the barnacle *Balanus perforatus* preferred mussels *Brachidontes pharaonis* or barnacles. To test this, a short-term Y-maze experiment recorded *S. haemastoma* choice of prey. The Y-shaped maze, made of white PVC, with each arm 20 cm in length, was filled with 3 l of artificial seawater (38–39‰, 24–26 °C). An air-stone was placed at the distal end of each arm to facilitate water circulation. Water movement in the maze was tested by following a drop of methylene blue dye applied near the airstone in one of the arms. The dye spread to the junction of the Y maze within 6.2 ± 0.8 s and to the far end of the maze arms within 19.6 ± 2.7 s ($n = 5$ measurements). A single mussel was placed next to the airstone of one arm. A small rock covered by 10–15 barnacles was placed near the airstone of the other arm, and a whelk was placed at the end of the third arm near the airstone. The location of prey was switched between arms to avoid possible bias of arm-specific condition. In October 1997, 15 large whelks (55–65 mm shell height) were collected from barnacle-dominated infralittoral rocks at Akhziv, and acclimated first in aquaria as described in the predation rate experiment. All runs were conducted simultaneously. The prey of choice was determined after 24–48 h (depending on the time it took the snail to initiate feeding). Prey choice was tested using a G-test for significance (H_0 was ratio of choice of mussel to barnacle = 1:1).

3. Results

3.1. *Feeding patterns*

Comparing the proportion of feeding individuals in the midlittoral and infralittoral habitats during September October (1995 and 1998), we found higher percentage of the population active and feeding in the infralittoral than in the midlittoral (71.3 ± 10.2 and $29.9 \pm 8.9\%$, respectively, $t_{df=8} = -5.4$, $P < 0.001$, *t*-test after arcsine transformation, Fig. 2). In the midlittoral, non-feeding individuals were observed only in holes and crevices, whereas in the infralittoral non-feeding individuals were found out of shelters. Where the mussel *Brachidontes pharaonis*

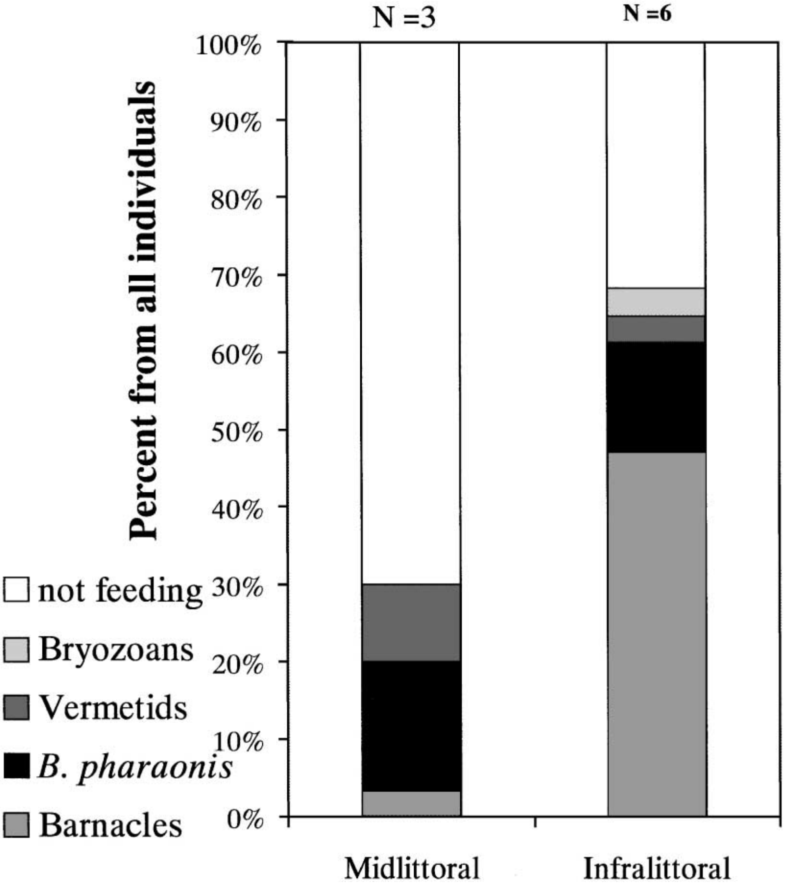

Fig. 2. Mean proportion of whelks observed feeding on the different prey items in the midlittoral and infralittoral zones. N = number of site. Whelk density in surveys of all sites is >0.2 m^2.

formed beds (e.g. two midlittoral sites, Akhziv and Tel-Baruch, and one infralittoral site, Ashqelon), whelks fed almost exclusively on the novel mussel. In habitats where *Brachidontes pharaonis* was relatively rare, the whelks primarily fed on other abundant prey items such as *Vermetus triquater* (HaBonim midlittoral site) or barnacles (in most infralittoral habitats). *S. haemastoma* was also observed feeding on encrusting bryozoans in the infralittoral. When *Brachidontes pharaonis* constituted $>25\%$ of the available prey (calculated from data in Rilov, 1999; Rilov et al., 2001) it was the major food item in the whelk's diet (Fig. 3) except for the Bat-Yam infralittoral site. In the three sites where the proportion of *Brachidontes pharaonis* in diet is well above the trend line, the mussel appeared in beds and the whelks were mainly found on them. In Bat Yam and the breakwater of the Herzelia Marina in 1998 (the two points with *Brachidontes pharaonis* densities $>50\%$ and below the trend line) *Brachidontes pharaonis* was mainly distributed in small patches.

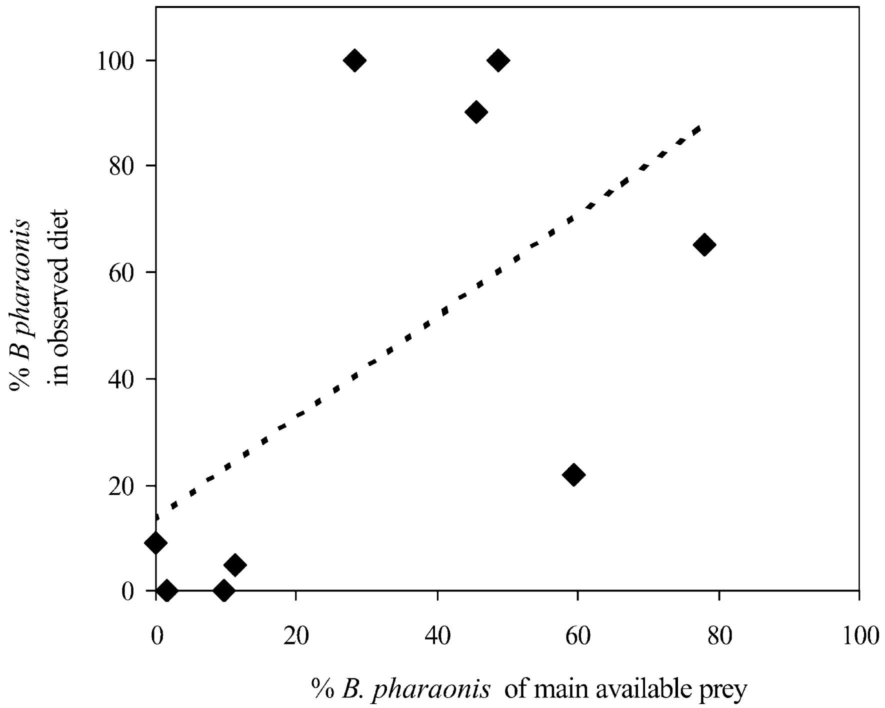

Fig. 3. Relationship between the percentage of *Brachidontes pharaonis* in the array of available prey and in the diet of *Stramonita haemastoma*. Each point represents a site/habitat examined during the 1995 survey. A logarithmic trend line is shown.

In a new marina site in Herzelia we also observed a shift in feeding of the whelks from the indigenous species to *Brachidontes pharaonis* as the novel mussel became more abundant. In 1995 barnacles predominated the macrobenthic community on the breaker of this marina and constituted the main food source of the whelks (80% of feeding whelk foraged on barnacles); three years later, when *Brachidontes pharaonis* was abundant at this site, the majority of whelks fed on this mussel (60%).

3.2. Prey selection

In predation rate experiments, large *S. haemastoma* preferred large *Brachidontes pharaonis* to small ones (PPI = 4), whereas medium-sized whelks showed no such preference (Table 2). Moreover, unlike the larger whelks, the medium-sized ones often left uneaten tissue when preying on large mussels. The predation rate of large *S. haemastoma* on large *Brachidontes pharaonis* was at least an order of magnitude higher than on *Balanus perforatus* or *Patella caerulea* (PPI > 10, Table 2). Judging from our observations, handling times appeared to range between 3 and 16 h on large *Brachidontes pharaonis* and < 4 h on the barnacles. When *Brachidontes pharaonis* and mussels *Mytilaster minimus* of the same size were paired, the whelks consumed twice as many *Brachidontes pharaonis* (Table 2). When the same prey types were

Table 2
Average (±SD) number of food items eaten per day by large (55–65 mm) and medium size (32–37 mm) *Stramonita haemastoma*

Experiment/ Snail size	Prey item					PPI	*t*	*P*	df
	Large Bp	Small Bp	Mm	Bpe	Pc				
1 Medium	0.30±0.16	0.32±0.19				0.9	−0.6	0.54 ns	6
2 Large	0.25±0.01	0.06±0.05				4.2	13.4	<0.001	11
3a Large		0.22±0.05	0.12±0.08			1.8	2.9	=0.02	6
3b Large		0.24±0.02	0.11±0.07			2.3	3.9	<0.01	6
4 Large	0.34±0.25			0.03±0.08		11.0	2.75	=0.03	6
5 Large	0.14±0.08				0.01±0.02	14.0	4.25	<0.001	6
Controls									
Large		0.43±0.16							
Large			0.40±0.17						

PPI = predation preference index (ratio between the first and second predation rate). Bp = *Brachidontes pharaonis*, Mm = *Mytilaster minimus*, Bpe = *Balanus perforatus*, Pc = *Patella caerulea*. Controls include only one prey species (only for small *Brachidontes pharaonis* and for *M. minimus*). Paired *t*-test was used to determine prey preference. Each individual snail was tested once.

presented separately (controls) *S. haemastoma* predation rate was comparable to the combined rates in the experiments (Table 2). The dry-weight flesh biomass of 10 mm *Brachidontes pharaonis* was greater by a factor of 1.6 than that of *M. minimus* of the same shell length (15.5±3.1 and 9.4±0.3 mg respectively, $n=4$ for each species, one-way ANOVA, $P<0.05$). Handling time of small mussels appeared to be similar for both species and less than 4 h because the snail was never seen on the same individual on two consecutive observations. During our observations we noticed that in order to feed on limpets, *S. haemastoma* usually detached them from the aquarium glass using the edge of its shell.

In 15 Y maze tests, *S. haemastoma* from barnacle-covered infralittoral walls, chose and fed on mussels in 11 tests, on barnacles in three tests, and one snail did not move to either direction (*Brachidontes pharaonis*: barnacle ratio = 3.6:1, Fc = 3.4, $F=4.85$, $P<0.05$, G-test).

4. Discussion

4.1. Feeding patterns and prey selection

Prior to the establishment of dense beds of the invading mussel *Brachidontes pharaonis* along the Israeli Mediterranean coast, the indigenous species, i.e. barnacles, small mussels, vermetid gastropods and limpets formed the main potential food of *S. haemastoma*. Our results show that in sites where the novel mussel *Brachidontes pharaonis* is abundant, it constitutes the main food of *S. haemastoma*. During the course of the study, in a site where *Brachidontes pharaonis* was rare in 1995 and become abundant in 1998, we were able to depict a marked shift in the foraging patterns of *S. haemastoma* from feeding on small indigenous species to feeding on the invasive mussel. When *Brachidontes pharaonis* constituted $>25\%$ of the available prey it usually was the major prey of the whelk. When *Brachidontes pharaonis* is less abundant energetic limitation (search "efforts" versus energetic gain) apparently "force" the predator to prey on the more abundant, but probably less profitable prey. Interestingly, when *Brachidontes pharaonis* is relatively abundant but is distributed in small patches, it constitutes less than expected part of the *S. haemastoma* diet. This may suggest that search time plays an important role in the whelk's consideration of profitability, but this subject still deserves a closer investigation in future studies.

The change in feeding patterns of *S. haemastoma* at the Israeli coast may be attributed to a higher profitability (energy gain relative to energy expenditure, Garton, 1986) of the novel mussel over the indigenous prey, and suggests the ability to assess prey value, regardless of their feeding history. Our Y maze experiment also supports this claim. When given the choice, individuals of *S. haemastoma* from infralittoral habitats prefer the mussel *Brachidontes pharaonis* over their regular food item, barnacles, suggesting ingestive conditioning is less significant than profitability. The ability of *S. haemastoma* to assess profitability was reported by Richardson and Brown (1990) and Brown (1997). The whelk *Nucella lamellosa* readily adds to its diet a prey that was equally profitable as that of the highest-quality indigenous prey (Carroll & Wethey, 1990). *N. lapillus* gains more energy by feeding on a few large size mussels than by feeding mainly on barnacles (Burrows & Hughes, 1991). Etter (1997) also observed a higher growth rate (greater profitability) of whelks feeding on mussels than that of those feeding on barnacles. Preference of large prey (e.g. Brown & Richardson, 1987; Hughes & Burrows, 1994; Palmer, 1984) suggests that prey size plays a more important role than handling time in determining profitability. This is also supported by our laboratory finding that whelks prefer large mussels over barnacles or small size mussel (*M. minimus*), despite an apparent longer handling time for the former. Moreover, large *S. haemastoma* individuals prefer large *Brachidontes pharaonis* over smaller ones as well as small *Brachidontes pharaonis* over the indigenous mussel *M. minimus* of equal shell length but with smaller biomass.

The size of the prey chosen is also determined by the predator's size. Juvenile *S. haemastoma* feed on small prey such as bryozoans, hydroids, barnacles and oyster spat, and as they grow, shift to larger prey (Garton, 1986). When small *S. haemastoma* from the Gulf of Mexico fed solitarily on large mussels, they demonstrated low feeding efficiency (Brown & Richardson, 1987). We found that large *S. haemastoma* preferred large mussels over small ones, whereas medium-sized whelks showed no preference. Moreover, large whelks completely consumed the soft tissue of large mussels, unlike medium-sized individuals.

4.2. Foraging activity

Along the Israeli coast, the frequency of feeding individuals of *S. haemastoma* in the infralittoral is higher than in the midlittoral, even where both food and shelter are abundant. This may be attributed to higher risk of dislodgment, caused by constant wave action in the midlittoral (e.g. Burrows & Hughes, 1989; Hughes & Burrows, 1993; Menge, 1978; Menge et al., 1997; Moran, 1985; Richardson & Brown, 1990). In rare calm sea conditions, when the midlittoral is exposed to high air temperature, the whelk also avoids this habitat (see Rilov, 1999). We suggest that the recent establishment of dense beds of a relatively large novel prey (*Brachidontes pharaonis*) in midlittoral habitats allows the whelks to gain more energy per unit time in short foraging bouts, although handling times may be somewhat longer.

Physical conditions that influence time available for prey handling may explain differences in feeding habit of whelks in different parts of the world. In the Azores, where tidal amplitudes are relatively large (up to 2 m, Nancy Hadley, personal communcation), *S. haemastoma* feeds mainly on limpets (Spence, Hawkins, & Santos, 1990). The latter are common in midlittoral habitats along the Israeli shore (Rilov et al., 2001), but only rarely consumed by *S. haemastoma*. In the laboratory we noticed that when *S. haemastoma* feeds on limpets, the limpet detaches from the substratum. In the eastern Mediterranean, where tidal amplitude is small and wave action is almost constant, detached limpets will probably be easily washed away and thus could not be efficiently handled by the whelks.

In this study we have demonstrated that *S. haemastoma* has switched to prey on the invasive Red Sea mussel *Brachidontes pharaonis* where the invader became abundant. From a community structure standpoint we might expect that this switch would regulate to some extent the mussel's colonization process. In the oyster beds of Louisiana, *S. haemastoma* is a major predator and even considered a pest on cultivated oysters. In the 1970s, Safriel et al. (1980) suggested that the density and distribution of the indigenous mussel *M. minimus* in some rocky habitats is regulated by *S. haemastoma*. The shift to feeding mainly on the novel invasive species should thus have reduced predation pressure on the populations of the indigenous mussel and potentially should have enabled their proliferation. However, *Brachidontes pharaonis* also competitively excludes *M. minimus* in habitats where the latter used to form large beds (mainly beachrocks, Rilov, 1999). The recent rapid establishment of *Brachidontes pharaonis* in some habitats may be attributed to a decline in *S. haemastoma* populations (Rilov et al., 2001), and thus the loss of an important predator.

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