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RESEARCH ARTICLE

Gil Rilov · Avital Gasith · Yehuda Benayahu

Effect of disturbance on foraging: whelk activity on wave-exposed rocky shores with minimal tidal range

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Abstract For slow-moving rocky intertidal predators such as whelks, frequent stress can be detrimental. Most studies on the foraging behavior of whelks have been conducted in regions where tidal amplitude is >1 m and on relatively small species. We studied the effects of wave action, desiccation, and water temperature on the foraging behavior of a large (approximately 80 mm) rocky shore whelk, *Stramonita haemastoma*, at the small-tide (<40 cm) but wave-exposed Israeli Mediterranean coast. We hypothesized that in such conditions foraging activity of this large predator will be greatly limited. Field observations show that when wave height exceeds 0.5 m, activity of whelks decreases by at least threefold relative to that seen under calm-sea conditions, and most whelks remain inside shelters. Wave height data from offshore moorings demonstrate that such conditions occur along the coast $>85\%$ of the time. Whelks move into shelters or completely disappear when exposed to prolonged desiccation conditions that can last for days along the shore during spring and autumn. Foraging activity is greater at night than in daytime and might be related to lighter winds and calmer sea conditions at night. Laboratory experiments show that elevated water temperatures during winter do not result in increased predation rates relative to those measured during spring. This indicates that a seasonal endogenous biological rhythm may exist. Our findings demonstrate that the foraging activity of large whelks can be extremely constrained by high rates of disturbance, that is, frequent wave action, and less frequent desiccation. We claim that high rates of disturbance in the eastern Mediterranean explain why large whelks are scarce in intertidal habitats where food is plentiful but suitable shelter is rare.

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G. Rilov (✉) · A. Gasith
Institute for Nature Conservation Research,
George S. Wise Faculty of Life Sciences,
Tel-Aviv University, Ramat-Aviv,
69978 Tel-Aviv, Israel
E-mail: gil.rilov@gmail.com

Y. Benayahu
Department of Zoology,
George S. Wise Faculty of Life Sciences,
Tel-Aviv University, Ramat-Aviv,
69978 Tel-Aviv, Israel

Present address: G. Rilov
School of Biological Sciences,
University of Canterbury, Private Bag 4800,
Christchurch 1, New Zealand

Introduction

Consumer-stress models in littoral systems predict that predators are more susceptible to abiotic stresses while actively foraging than are sessile prey (Menge and Olson 1990). Predation is expected to become an effective regulator of community structure (e.g. prey abundance) when environmental stresses are relatively low (Menge and Sutherland 1987). Accordingly, whelks, which can be important predators in the intertidal zone (Moran 1985; Berlow 1997), are more likely to influence prey abundance on rocky shores when local conditions allow safe foraging (Menge 1978a, 1978b; Hughes and Burrows 1993). Stresses that affect whelk distribution and temporal foraging patterns include tidal fluctuations (Moran 1985), desiccation (Moran 1985), and exposure to wave action (Menge 1991; Hughes and Burrows 1994; Dahlhoff et al. 2001).

Unlike fish and crabs that are highly mobile and effective intertidal predators on wave-exposed shores (G. Rilov and D.R. Schiel, unpublished manuscript), and unlike seastars that have a very high ratio of adhesion surface to body height to help withstand the battering of waves, whelks are relatively slow and have a lower adhesion-surface to body-height ratio. Therefore, in shallow littoral habitats, benthic predators like whelks face a high risk of dislodgment (Denny 1988). Among marine gastropods, whelks are more susceptible to dislodgment than less mobile and squatter gastropods such as limpets (Denny 1985). Denny et al. (1985) demonstrated that muricid gastropods *Thais* spp. (now *Nucella* spp.) have much lower adhesion tenacity than limpets and therefore are more susceptible to dislodgment, especially during locomotion in water velocities >5 m/s. Moreover, mobile individuals of the same species are at greater risk than those that are stationary (Denny 1985; Denny et al. 1985). On wave-swept shores, whelks are typically confined to refuges and forage mostly at times of calm sea conditions ("mechanically safe" environment, Menge 1978a, 1978b; Moran 1985; Burrows and Hughes 1989). The availability of shelter in the intertidal zone can thus play a major role in determining predatory whelk distribution and activity (Fairweather 1988a, 1988b; Gosselin and Bourget 1989; Johnson et al. 1998).

The observed density and the activity of whelks in shallow intertidal habitats fluctuate seasonally; they tend to become more cryptic and appear less abundant and less active during the colder, stormy winter months (Menge 1978a, 1978b; Richardson and Brown 1990; Rilov et al. 2001). Lower activity during winter could be attributed to low seawater temperature decreasing the whelk's metabolism and reducing its feeding rate (Garton and Stickle 1980) as well as to higher wave activity.

Most studies on the foraging behavior of whelks have been conducted where tidal amplitude is >1 m and on relatively small (<40 mm) whelks (e.g., Moran 1985; Burrows and Hughes 1989). In locations where the tidal amplitude is large, whelks on exposed coasts can forage with low risk of dislodgment either underwater at high tide or exposed on the rocks during low tide when the wave height is smaller than the tidal amplitude and when the risk of desiccation is low. On wave-exposed coasts with very small tidal amplitude, intertidal predators are expected to be at greater risk of dislodgment by waves even during low tides.

The Israeli Mediterranean coastline is relatively straight and exposed to the prevailing westerly winds. The tidal amplitude is small (up to 42 cm), irregular, and often obscured by wave action (Safriel 1966). Recently, we presented evidence that food availability (barnacles, mussels, vermetids, limpets) is a poor predictor for density of the large whelk *Stramonita haemastoma* (Kool 1987, shell length up to 76 mm) in midlittoral rocky habitats along this shore (Rilov et al. 2001). *S. haemastoma* is rare (density <0.1 individuals per m^2) on rocky platforms, but it is more common on nearby bench-like rocks (incisioned-rock habitat, Rilov at al. 2001). Food (mussel beds) is plentiful in both habitats and both sites are equally exposed to waves. The sites do differ greatly in shelter availability; appropriate shelters for a large whelk such as *S. haemastoma* (small and medium-sized holes) are scarce on platforms but are readily found in the incisioned-rock habitat. We suggested that, along the Israeli coast, shelter availability and risk of dislodgment by waves influences the distribution and abundance of large whelks.

In this study we hypothesized that in a region where tidal amplitude is small and the rocky shore is exposed to the prevailing winds, large whelks have only a narrow window of opportunity for safe foraging even where shelter is ample. To test this hypothesis we (1) assessed the degree of wave action at the Israeli coast using existing data on wave heights; (2) determined whelk observed abundance and foraging activity in relation to wave action and desiccation; and (3) assessed the influence of low winter temperatures on whelk foraging activity.

Materials and methods

Study site

A bench-like sedimentary incisioned-rock site in Akhziv (Rilov et al. 2001) was chosen for study. It is almost constantly exposed to the prevailing winds and to wave action but provides both ample shelter and dense beds of mussels (mainly *Brachidontes pharaonis*) available as prey for *Stramonita haemastoma*, whose densities there are the highest along the Israeli Mediterranean coast (mean of 4 to 7 whelks per m^2 during spring–autumn). The size range of *S. haemastoma* in this site during the study period was 40–75 mm and the mean varied between 57 and 63 mm, depending on year (see Rilov et al. 2001).

Degree of waviness

Along the Israeli Mediterranean coast northwesterly to southwesterly winds prevail most of the year, from late morning (around 0900 hours) to sunset (approximately 1500 to 1900 hours; data from the Israeli Meteorological Service, IMS). During summer and autumn, night winds (approximately 2100 to 0700 hours) are weaker (below 12 km/h), so that more than 60% of the time their velocity is below the response threshold of the instruments. In winter, strong southerly storms may occasionally occur. To determine the frequency of biologically meaningful (as determined from the observations on whelk activity described below) wave action along the shore we used IMS records on maximum-wave-height data (waviness, sensu Denny 1995) that were taken from two buoys located about 2 km offshore, one opposite Haifa, about 15 km south of the study site, and the other opposite Ashdod, about 155 km south of the study site. Data were obtained at intervals of 3 h, for 15 min each time, and the highest value obtained was designated as the maximum wave height. We used maximum wave heights as a proxy for a biologically meaningful degree of waviness in the region, following Gaines and Denny (1993). A total of 5,510 measurements were recorded in Haifa (1995–1996) and 7,275 in Ashdod (1995–1997). To test the effect of time of the year (month) and time of day (hour) on wave height, we applied a three-way analysis of variance (site treated as a random factor) on the data with years, and days in the month used as replicates.

Foraging and sheltering patterns

To determine the conditions most suitable for *S. haemastoma* foraging activity, we recorded in Akhziv the activity of the whelks (feeding or non-feeding) and their position (exposed on the rock surface or sheltered in holes and crevices) within a 10×1-m marked plot with the long axis positioned from north to south along the rocky bench. The plot was located approximately 1 m away from the seaward edge of the bench and divided into ten quadrats. On each observation the activity and position of whelks were recorded. A whelk was designated as feeding if it was found holding to the mussel bed or clinging to an individual mussel while inside a hole or crevice shelter and non-feeding if it was found on the bare rock. Because in most cases we did not want to interrupt the whelks' activity, we did not move or remove them to verify that the proboscis was protruded. Data were obtained during 1995–1997 under different sea and weather conditions. We conducted overall 21 daytime observations during April–June and October–December, when the whelks are most active (Rilov et al. 2001). On each date, we scored the sea condition according to four arbitrary categories: (0) hot and dry weather with easterly (seaward) winds and calm sea (a weather condition known locally as "Hamsin"); (1) no detectable air movement to slight westerly or northwesterly winds, wave height <0.5 m; (2) moderate westerly to northwesterly winds, wave height 0.5–1 m; and (3) relatively strong westerly to northwesterly winds, wave height 1–1.5 m. In category 0 rock surface was exposed to the air except for holes deeper than about 10 cm; in category 1 the rock surface was gently washed by water; in category 2 strong currents intermittently washed the rocks; and in category 3 the rocks were continuously under relatively strong wave action. When the rocks were washed by waves we used a mask to look for snails. Whelk activity could not be examined under rough seas stronger than category 3. During each observation we also recorded seawater and air temperature. We tested the effect of sea conditions on the proportion of the number of individuals in the plot feeding and exposed on rocks using the non-parametric Kruskal–Wallis test. A non-parametric test was chosen because of the different sample sizes of the different sea condition categories and because of heteroscedastic variances. Because the measured sea and air temperatures were not categorical predictors we tested for potential correlation between them and the whelk activity using regression analysis. To test if whelks feed while sitting in their refuge we examined whether the proportion of individuals feeding was higher than the proportion exposed on rocks using the Wilcoxon matched pairs test on the pairs of proportions from all observations. We assessed a possible diurnal pattern of foraging activity of the whelks by recording their activity during the morning (0900–1000 hours) and at night (midnight to 0200 hours, using a flashlight) on 18–21 October 1996 and on 17–20 September 1997.

Effect of water temperature and seasonality on predation rates

We exposed whelks collected in different seasons, including winter, when they are rarely observed active in the field, and spring–summer when they are most active (Rilov et al. 2001), to late spring water temperatures. Our working hypothesis was that if feeding rate is mainly regulated by temperature, then whelks collected at different times of the year but kept at a given similar temperature would portray similar feeding activity. Rejecting this hypothesis would mean that foraging activity is mainly regulated by something other than temperature, possibly innate seasonal clues. Six to ten snails (55–60 mm shell length) were collected in January and April 1996, and in January, March, and August 1997 from intertidal rocks near Tel Aviv. In January (winter), and during March and April (spring) the ambient seawater temperature is 16–17°C. In August (summer), the ambient temperature reaches 29°C. For two weeks the snails were kept individually, each in an 8-l aquarium without food, and were acclimated to the test temperature. Test temperatures were 24–25°C in the January, March, and April experiments, and 25–27°C in the August experiment. Light–dark cycle was kept at 12:12 h in all experiments. After the 2-week acclimation period, five individuals of the mussel *Brachidontes pharaonis* (25–30 mm shell length) were offered to each snail. This mussel has been shown to be preferred prey of *S. haemastoma* (Rilov et al. 2002). The daily mussel consumption was recorded for 40 days in the January experiments, and for 30 days in the March, April, and August experiments. One-third of the water in the aquaria was replaced with fresh seawater every other day. Food was continuously replenished so that the availability of prey remained constant. We recorded the time elapsed until commencement of feeding, the feeding rate as number of mussels eaten per whelk per day, and length of intervals between successive predation events. We calculated predation rates only for the time period after the initial feeding event. To test differences among seasons the non-parametric Kruskal–Wallis test was used. To determine whether the snails are dormant during winter we recorded the daily location of each snail in the aquarium in the January 1996 experiment. We calculated the proportion of cases in which the snails changed location ($n=76$ observations).

Results

Degree of waviness

A high degree of waviness was found for the nearshore waters of the Israeli Mediterranean coast. Out of 5,510 measurements in Haifa, 94% had a maximum wave height of >0.5 m, and 57% had a wave height of >1 m. Of 7,275 measurements in Ashdod, 88% had a maximum wave height of >0.5 m, and 50% had a wave height of >1 m. Because wave height usually increases by up to 60% as the wave shoals when the bottom depth is below 10 m (Denny 1995), measurements taken 2 km offshore may in fact underestimate the real wave heights that wash the rocky intertidal. Mean maximum wave height usually exceeded 1 m and was highest in January–April and lowest in May, but wave height at the two sites behaved differently, mostly during winter (notice the drop during February in Haifa that is missing in Ashdod), resulting in a strong Site×Month interaction (Fig. 1, Table 1). A diurnal pattern in wave height appears to exist, mainly during late summer and autumn (August–October) when wave height was lowest during the late night and the early morning hours, resulting in a strong Month×Hour interaction (Table 1). Hour also interacted with site, indicating that diurnal patterns were somewhat different between sites.

Foraging and sheltering patterns

Water temperature varied between 18 and 28°C and air temperature between 16 and 32°C among our observations. Air and water temperature were poor predictors of the whelks' activity: for both the proportion of whelks exposed and the proportion feeding r^2 values were <0.01 and $P>0.9$, but sea conditions strongly affected it (Kruskal–Wallis test: $H_{(3,21)}=15.56$, $P=0.0014$ for proportion exposed; and $H_{(3,21)}=12.98$, $P=0.0047$ for proportion feeding). The highest proportion of whelks exposed on the rocks or engaged in feeding was recorded under calm sea conditions when the midlittoral incisioned rock was gently washed by water (Fig. 2, category 1). Desiccation (category 0), or when wave height exceeded 0.5 m (categories 2 and 3), reduced whelk activity relative to that observed under calm-sea conditions by at least threefold (Fig. 2). Although most whelks foraged on mussels that were attached to the exposed rock surface, some fed inside their shelter on mussels that were detached from the rock. This resulted in a higher proportion of whelks engaged in feeding than whelks found exposed on rocks (Fig. 2, Wilcoxon matched pairs test, $P=0.0002$, $n=26$).

During both October 1996 and September 1997 the proportion of whelks exposed on the rocks was greater at night, when the sea conditions were more moderate, than in daytime (Fig. 3, 23 ± 6 and 6 ± 3%, respectively, Kruskal–Wallis ANOVA, $P=0.02$, $n=13$). Also, more of the individuals fed at night than during the day (31 ± 10 and 14 ± 10%, respectively, $P=0.003$, $n=13$). By day, most of the whelks were sheltering. The maximum proportion of foraging whelks was 45%, on the night of 19 October 1996.

Water temperature and seasonality in predation rates

Individuals of *S. haemastoma* collected in winter but exposed to summer water temperature maintained their normal, low feeding activity (Fig. 4a). Whelks collected in spring (March and April), when the ambient water temperatures are still low (16–17°C), and exposed to similar summer temperatures exhibited the highest feeding rate (by a factor of 2–5 if the entire experimental period is considered, or 0.3–3, if the pre-feeding period is excluded from the analysis, Fig. 4a). Similar time intervals between successive predation events were found for the whelks collected on most dates, except for those collected in winter 1997, which exhibited significantly longer intervals than those collected in March and April (Fig. 4b). The whelks collected in March, April, and

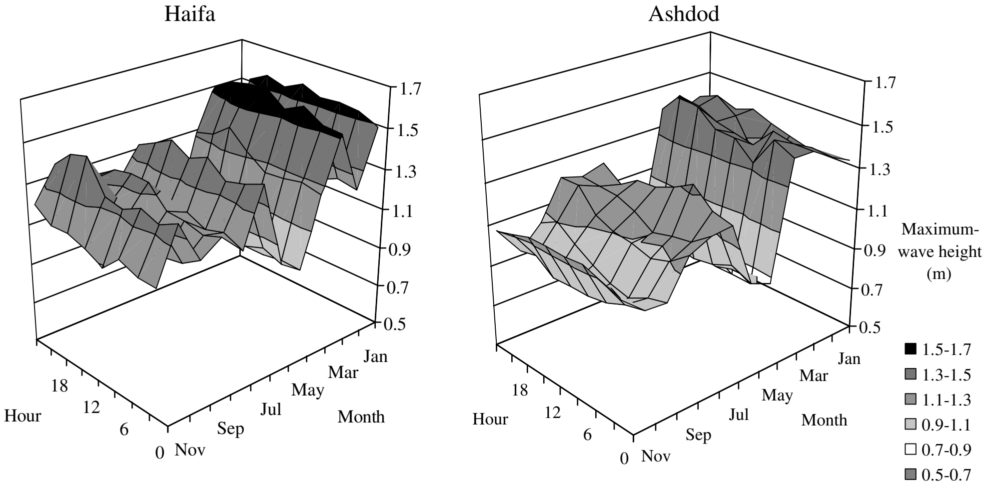

Fig. 1 Average maximum wave height as measured from buoys located 2 km offshore at two sites (Ashdod and Haifa). Data pooled for all years

Table 1 Three-way analysis of variance. The effects of site (random factor), time of year (month), and time of day (hour) on maximum wave height in Haifa and Ashdod (based on data derived from the Israeli Meteorological Service). Significant *P* values are indicated in bold

Source of variation	SS	*df*	MS	*F*	*P*
Site	35.6	1	35.58	6.5	**0.026**
Month	354.9	11	32.26	6.0	**0.003**
Hour	7.3	7	1.05	5.1	**0.023**
Site×Month	58.9	11	5.35	70.4	**<0.0001**
Site×Hour	1.4	7	0.20	2.6	**0.019**
Month×Hour	9.6	77	0.12	1.6	**0.016**
Site×Month×Hour	5.8	77	0.08	0.1	1.000
Error	8,132.2	12,592	0.65		

August commenced feeding within a week after onset of the experiment, whereas those collected in early winter began feeding only after 3 weeks (Fig. 4c). Three of the six snails tested in the summer experiment laid eggs in the aquarium. Although the whelks in the winter experiments demonstrated low feeding rates, they were not completely dormant and did move in the aquaria. During the January 1996 experiment, the whelks changed their location in the tank in 41.1 ± 8.2% of successive observations.

Discussion

Three major findings are highlighted in our investigation: (1) large whelks have a very narrow window of opportunity to forage in tide-limited highly disturbed shores; (2) even during the most favorable conditions for foraging the proportion of feeding individuals is < 40%; and (3) the reduced winter activity of whelks is most probably tuned by an endogenous clock. We suggest that these biological constraints strongly affect the distribution of large intertidal predators along the shore.

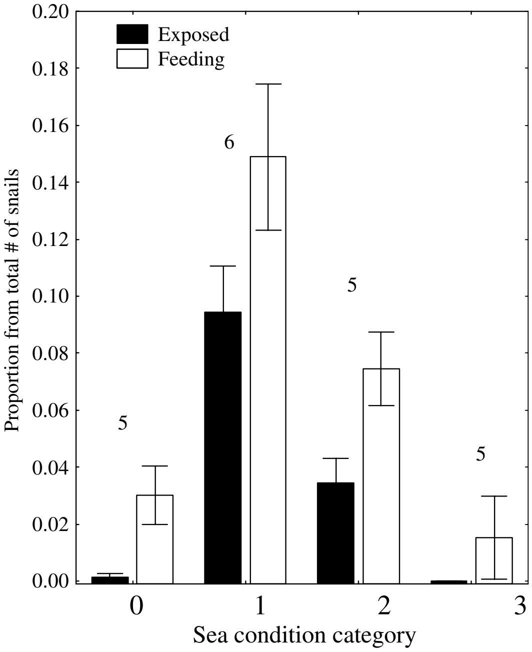

Fig. 2 *Stramonita haemastoma*. The proportion (+ SE) of individuals out of the total number of whelks in the 1×10-m fixed plot that was exposed on the rocks and engaged in feeding in different sea conditions. Categories: *0* hot and dry weather, calm sea, and rocks exposed to air; *1* wave height < 0.5 m; *2* wave height 0.5–1 m; and *3* wave height 1–1.5 m. The number of replicates (observation days) in each category is designated above the *bars*. The number of whelks in the plot ranged between 40 and 71

Along the Israeli coast, the combination of a very small tidal amplitude (maximum range < 0.5 m) and a straight shoreline facing the dominant winds exposes the intertidal zone to almost constant wave action. We found that in more than 85% of the time maximum wave heights along the shore are > 0.5 m, conditions that hinder foraging activity, as shown by the very low proportion (< 8%) of *Stramonita haemastoma* feeding on the rocks at such times. With high rates of wave exposure that alternate during spring and autumn with periods of harsh desiccation conditions, intertidal predatory whelks have thus a very small window of opportunity to forage, even where shelter is abundant. Because the whelk faces a risk of dislodgement it is forced to limit its activity to times of relatively calm sea conditions.

Risk of dislodgement by wave-generated currents most probably dictates the pattern of distribution and activity of *S. haemastoma*. It is most abundant in rocky sites where shelters such as holes and crevices are plentiful (Rilov et al. 2001) and even there it forages only during times of calm sea (this study). At other times it is found sheltered inside holes and crevices. In wave-swept shores, the Atlantic whelk *Nucella lapillus* (Menge 1978a, 1978b; Burrows and Hughes 1989) and its Pacific counterparts *N.* (*Thais*) *canaliculata* and *N.* (*T.*) *emarginata* (Denny et al. 1985) also respond by sheltering. The latter have been shown to forage only when the environment was "mechanically safe" (Denny et al. 1985). Fairweather (1988a) found that the whelks *Morula marginalba* and *T. orbita* in Australia quickly move away from areas without shelter even when prey is abundant. Correspondingly, predation of these whelks is greatly reduced in areas where shelter is scarce (Fairweather 1988b). These findings along with ours strengthen our earlier hypothesis (Rilov et al. 2001) that the distribution pattern of *S. haemastoma* in intertidal habitats along the Israeli Mediterranean shore is strongly influenced by shelter availability. It can explain why this whelk is extremely rare on platforms where

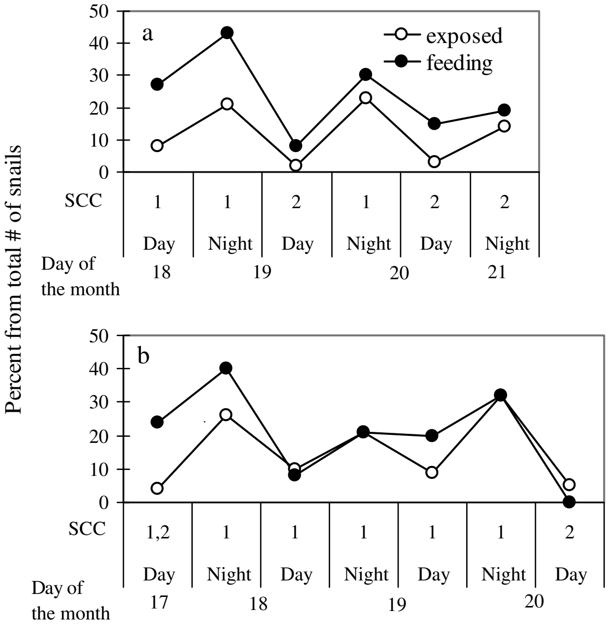

Fig. 3 *S. haemastoma.* Percentage of whelks exposed on the rocks/mussel beds and observed feeding during the day (0900–1000 hours) and at night (midnight–0200 hours) on three consecutive days in October 1996 (**a**) and September 1997 (**b**) in a fixed plot on the incisioned-rock habitat in Akhziv. *SCC* sea condition category. Number of whelks in the plot varied between 37 and 64

prey is plentiful but shelters are scarce. In another study (Rilov et al. 2004a) we found that *Hexaplex trunculus*, another eastern Mediterranean whelk similar in size to *S. haemastoma* but with a greater shell height and projected area to foot area, is completely excluded from exposed intertidal sites, most probably because of a morphology and behavior less adapted to strong waves. We suggest that this is probably the rule for other large whelks in other wave-exposed regions globally.

Desiccation appears as another factor that considerably limits foraging of whelks in the eastern Mediterranean. It occurs under calm sea conditions mainly in spring and autumn when the air temperature is high (> 20°C). Under prolonged desiccation (a few days), the whelks' density decreases substantially. They move away from exposed rocks either toward the subtidal zone or into wetted holes and crevices. However, the frequent wave action substantially reduces events of desiccation in the lower midlittoral zone. This situation is different from the bi-weekly cycle driven by the tide cycle as was shown for the small *Morula marginalba* in Australia (Moran 1985).

The low activity of *S. haemastoma* in the intertidal, even where it is abundant, is reflected in the abundance of its prey. At our study site, the cover of the whelks' favorite prey, the invasive mussel *Brachidontes pharaonis* (Rilov et al. 2002), is more than 85% (Rilov et al. 2004b) and mussel hallows around whelk holes and crevices shelters are very restricted (G. Rilov, personal observations). This suggests that the predator has limited control of the distribution and abundance of its prey.

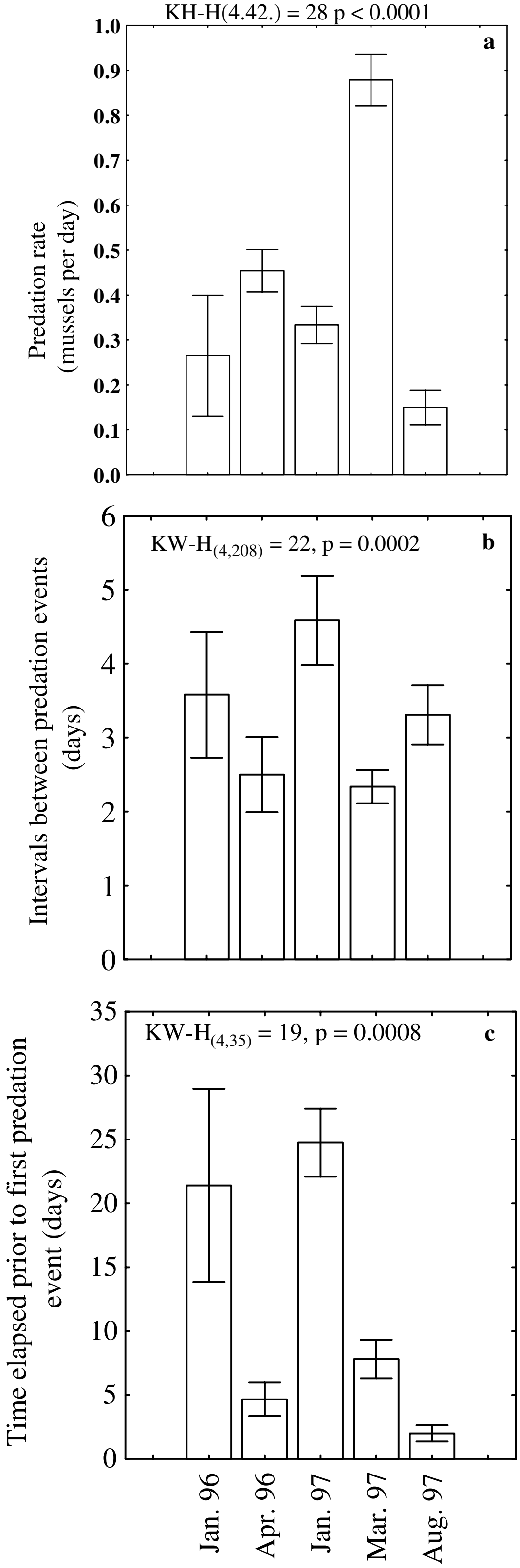

Fig. 4 *S. haemastoma.* Predation of the whelk on the mussel *Brachidontes pharaonis* in different seasons under similar water temperatures, 24–27°C. **a** Predation rates (only period from the first feeding event is considered). **b** Intervals between predation events. **c** Time elapsed prior to the first predation event. Kruskal–Wallis results are given. *Error bars* are standard errors

The relatively large benthic forager, *S. haemastoma*, due to environmental constraint, must sustain itself by feeding during a narrow temporal window of opportunity. However, when the conditions in its habitat seem favorable for feeding, for example, when the rocks are gently washed by waves, fewer than 50% of the snails seize the opportunity to engage in feeding. We found that under favorable sea conditions the highest proportion of *S. haemastoma* forage at night (30–40%). It was about twice as high as that observed feeding during the day. In contrast, more than 80% of the small Australian whelk *M. marginalba* were found foraging on exposed rocks at the best time of the tidal cycle (Moran 1985). One possible explanation for the reduced proportion of foraging whelks along the Israeli coast is that greater intervals between feeding events are needed for digestion of a relatively large prey (Hughes and Burrows 1994). These authors suggested that whelks feeding on larger prey in wave-exposed habitats seek shelter after feeding to minimize metabolic costs and to reduce the risk of mortality when digesting. In the present study we found that during the highest activity period of *S. haemastoma* (spring), when feeding on the mussel *Brachidontes pharaonis,* the mean interval between predation events lasted more than 2 days in the laboratory. In an earlier study we found that in the subtidal zone, where *S. haemastoma* mostly feeds on smaller prey such as barnacles, a greater percentage of the population (about 70%) was engaged in feeding (Rilov et al. 2002). Another explanation for the lower proportion of whelks feeding at all times may again be related to the size of the whelk. It is proposed that smaller taxa such as *Morula* may be able to find more sheltered spots near their prey than larger taxa such as *Stramonita* and *Nucella* when these taxa have lower availability of sheltering spots. Thus, the larger taxa take less risk.

Reduced foraging activity of *S. haemastoma* during winter cannot be explained merely by low water temperature, because artificially increasing the temperature failed to increase feeding rates. It appears that the whelks' activity is endogenously controlled by a seasonal biological clock. Biological clocks have been shown in other intertidal invertebrates, such as fiddler crabs, but were mainly related to daily or monthly rhythms associated with tidal changes or lunar cycles (Palmer 1995). Whelks in the early winter (January) commenced feeding at elevated temperatures only after several weeks while those in late winter to early spring (March–April) commenced feeding within days, demonstrating their "internal readiness" to feed as soon as temperatures increased. It is possible that whelks naturally reduce their foraging activity during winter due to a higher frequency of storms during that time of year as indicated by the maximum-wave-height data. Because seasonal internal clocks have not, to the best of our knowledge, been described for marine invertebrates, this aspect merits further study.

Low feeding activity of *S. haemastoma* in summer may be attributed to breeding that takes place during this period (Rilov 1999; this study). Belisle and Stickle (1978) suggested that *S. haemastoma* stores energy for the winter and reproduction periods, and that spawning activity might be intermittent with feeding. Another possible explanation for the low feeding rate of *S. haemastoma* during the summer may be a torpor response to heat, as was reported for *S. haemastoma* at 30 and 35°C (Stickle 1985).

In summary, our findings support earlier work (Menge 1978a, Menge and Sutherland 1987) and we conclude that large, slow predators in extremely environmentally constrained situations are either scarce (where shelters are rare) or, where shelter is available and whelks are abundant, unlikely to play a key role in shaping the structure of their community.

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