PREDATOR–PREY INTERACTIONS BETWEEN *LEPSIELLA* (*BEDEVA*) *PAIVAE* (GASTROPODA: MURICIDAE) AND *KATELYSIA SCALARINA* (BIVALVIA: VENERIDAE) IN PRINCESS ROYAL HARBOUR, WESTERN AUSTRALIA

BRIAN MORTON

Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

ABSTRACT

On a sandy beach at Shoal Bay in Princess Royal Harbour, Albany, southwestern Western Australia, lives a small muricid gastropod that feeds virtually monotonically on the overwhelmingly dominant resident bivalve *Katelysia scalarina*. *Lepsiella paivae* lives buried in the sand and attacks its prey within it. Because of its small size ($<$13 mm shell height), bivalve prey is also small and this study demonstrates a preference for *K. scalarina* of 5 mm shell length, i.e. juveniles. Laboratory experiments also suggested a possible preference for attack of the right valve. *Lepsiella paivae* can and does, however, attack larger prey (up to 15 mm shell length), but cannot consume them completely. A second visit to Princess Royal Harbour in the Austral winter, when there was no juvenile *K. scalarina* present, showed *L. paivae* to be attacking at the sand surface, also by drilling, the small ($<$4 mm) gastropod *Hydrococcus brazieri* (Hydrococcidae). SEM studies of experimentally determined drill holes of *L. paivae* show them to be of variable form, some straight sided, others bevelled (like a naticid) and $<$500 µm in diameter. On this sheltered Southern Ocean beach, therefore, *L. paivae* has specialized to attack juvenile bivalves by burrowing after them. It can, however, attack other species opportunistically on the sand surface when seasonally favoured juvenile bivalve prey are not present.

INTRODUCTION

Worldwide, representatives of the caenogastropod Muricidae usually attack bivalves and other prey, which can include barnacles, limpets and tubeworms, by either drilling in a stereotypical manner (Hart & Palmer, 1987), marginal wedging or chipping, or apertural engulfment. According to habitat and prey availability, muricids play an important role in regulating the population dynamics of the species they consume and have thus been shown to be major structuring elements, especially of rocky shore communities (Navarette, 1996; Navarette & Menge, 1996). Taylor (1998) most recently reviewed the large literature on the gastropod predator–prey relationship.

Most experimental studies of the Muricidae have been undertaken on the temperate European *Nucella lapillus* (Dunkin & Hughes, 1984; Hughes & Dunkin, 1984a, b; Hughes & Drewett, 1985; Burrows & Hughes, 1989, 1991; Hughes & Burrows, 1990, 1991), the North American *Ocenebra lucida* (Palmer, 1988; Navarette, 1996; Navarette & Menge, 1996), *Morula marginalba* on the east coast of Australia (Moran, Fairweather & Underwood, 1984; Moran, 1985; Fairweather, 1988) and on the subtropical *Thais clavigera* and *Morula musiva* in Hong Kong (Tong, 1986; Liu, 1995; Taylor & Morton, 1996). In Western Australia, on a subtropical rocky shore on Rottnest Island, *Dicathais orbita* was shown to attack many components of the resident fauna, including the mussel *Septifer bilocularis* (Morton & Britton, 1993).

On Southern Ocean shores, there are a number of species of *Lepsiella* Iredale, 1912 (Wilson, 1994) that have been revised taxonomically most recently by Tan (2003) and although they are little studied it is clear that they are ecologically important in a variety of marine habitats. On a temperate southwestern

Australian rocky shore in Princess Royal Harbour, Albany, *Lepsiella flindersi* fed monotonically on *Xenostrobus pulex* by drilling at the posterior end (Morton, 1999). Within the protection of Princess Royal Harbour, there is a marsh where another mussel, *Xenostrobus inconstans*, is the prey of a second species of *Lepsiella*, *L. vinosa* (Morton, 2004). *Lepsiella vinosa* is unusual not only because of its high-zoned habitat, but also because in southeastern Australian mangroves it is reported to feed on littorines, e.g. *Littorina unifasciata*, and barnacles (McKillup, 1982; Bayliss, 1982), but on rocky shores in Victoria it feeds on barnacles, tubeworms and mussels, notably *Xenostrobus pulex* (Macpherson & Gabriel, 1962; Ward & Quinn, 1988). In the South Australian mangrove environment, *L. vinosa* exercises prey choice in that it preferentially attacks *Balanus amphitrite* when it is present in high densities. If this prey species is present in low densities, however, *L. vinosa* switches to *Elminius adelaidae* and consumes proportionately more of them because of their smaller size (Bayliss, 1982). In New Zealand, *Lepsiella scobina* more typically drills oysters (Gardner, 1978), but also attacks littorines in Australia (McKillup, 1981).

A few muricids live on subtidal and intertidal soft sediments. In the subtidal waters of Hong Kong, *Rapana bezoar* feeds at the sediment surface, attacking both bivalves and gastropods by engulfment (Morton, 1994). On Malaysian mudflats, *Thais carinifera* feeds by drilling on the shallow-burrowing ark *Anadara granosa* at the surface (Broome, 1981). On Indonesian mudflats, *Bedeva* (= *Lepsiella*) *blosvillei* also attacks *A. granosa* by drilling (Vermeij, 1980). In waters around Antarctica, the muricid *Trophon longstaffi* feeds, albeit only very occasionally, on the burrowing bivalves *Laternula elliptica* and *Yoldia eightsi*, and the brachiopod *Liothyrella uva* sometimes by valve wedging but also by drilling (Harper & Peck, 2003). On the shores of Princess Royal Harbour, Albany, Western Australia, occurs another small species of *Lepsiella* that has been identified as

Correspondence: e-mail: prof_bsmorton@hotmail.com

L. (*Bedeva*) *paivae* (Crosse, 1864) by Peterson & Black (1995). The species is unusual in that, unlike the other muricid inhabitants of soft habitats identified above, it burrows after its prey and is rarely seen on the surface. Although Peterson & Black (1995) showed that in aquaria *L. paivae* feeds on all size classes of the bivalve *Katelysia scalarina*, nothing is known of its natural prey. The principal aim of this study was, therefore, to examine the natural diet of *L. paivae* in Princess Royal Harbour by experimentally offering it individuals of the species of co-occurring gastropods and bivalves. Once the principal prey had been identified, a second aim was to experimentally determine if *L. paivae* exhibits the same prey preferences as have been demonstrated for other muricids and, third, to examine additional aspects of the species' behaviour.

TAXONOMIC CONSIDERATIONS

The prey

Lamprell & Whitehead (1992) recognized three species of *Katelysia* in Australia: *K. scalarina* (Lamarck, 1818), *K. rhytiphora* (Lamy, 1937) and *K. peronii* (Lamarck, 1818). The same three species occur in Western Australia (Wells & Bryce, 2000) and, importantly for this study, Wells & Roberts (1980) and Wells & Threlfall (1980) showed that *K. scalarina* was overwhelmingly abundant in Princess Royal Harbour and a preliminary examination of the resident bivalves supported this view. Using monthly size-frequency distributions, Roberts (1984) was able to show that *K. scalarina* recruited a new cohort of juveniles into its population in Princess Royal Harbour between early July and late August 1979, that is, the Austral winter. During the course of this study too (July–August 2003), there were many juveniles in the Princess Royal population of *K. scalarina*.

The predator

There are five known potential predators in Princess Royal Harbour. These are the two buccinids, *Cominella eburnea* (Reeve, 1844) and *C. tasmanica* (Tenison Woods, 1876), the naticid *Polinices conicus* (Lamarck, 1822) (Wells, 1984) and two muricids, *Lepsiella vinosa* (Lamarck, 1822) and the species herein under study. The high-zoned *L. vinosa* is almost exclusively confined to the *Juncus* marsh that fringes much of the harbour (Morton, 2004), so that there is only one, burrowing muricid in Shoal Bay. It is generally believed that there are two species of *Bedeva* in Australia (Wilson, 1994), *B. paivae* (Crosse, 1864) and *B. hanleyi* (Angas, 1867). K. S. Tan (personal communication) considers that the Princess Royal Harbour species is *L.* (*B.*) *paivae*. I am therefore studying the same species that has also been reported upon from Princess Royal Harbour by Peterson & Black (1995).

MATERIAL AND METHODS

In July and August 2003, visits were made to Shoal Bay (Morton, 2004: Fig. 1), Princess Royal Harbour, Albany, Western Australia, and from where individuals of *Lepsiella paivae* and any potential prey were collected for experimental study. The shell heights and lengths of all the collected gastropods and bivalves were measured using Vernier calipers to the nearest 0.5 mm. A short return visit to Shoal Bay was made in February 2004.

Laboratory experiments

Collected individuals of *Lepsiella paivae* and all other living molluscan potential prey items were taken to a field laboratory and kept in aquaria containing aerated seawater that was changed every day.
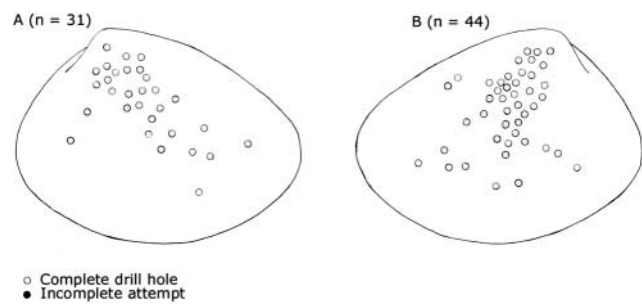

Figure 1. The distribution of drill holes in the left (**A**) and the right (**B**) shell valves of *Katelysia scalarina*, after being preyed upon by *Lepsiella paivae* during the laboratory experiments.

Over a period of 37 days from 14 July to 19 August 2003, inclusive, four experiments were conducted on *Lepsiella paivae* to test for prey preferences. In these experiments, individual predators of various, known, shell heights were placed in 250-ml pots containing ambient seawater. This was changed once every day at the time when the pots were drained to approximately mimic the tidal regime that *L. paivae* (and its prey) is naturally accustomed to in Shoal Bay (described by Morton, 2004). Moreover, in the experiments, consumed prey items were only removed at the time of water exchange to further standardize all methodologies, although visual checks of the predators were made at least every hour to obtain an estimate of total prey handling time, that is, times of arrival at and departure from the prey. All predators and prey were only ever tested once. Thereafter, predators were returned alive to Shoal Bay.

In a first experiment, 10 *Lepsiella paivae* individuals of 7.5–8.0 mm shell height were offered a variety of potential gastropod prey: *Clanculus dunkeri* (Koch, 1843) (Trochidae), *Hydrococcus brazieri* (Tenison Woods, 1876) (Hydrococcidae), *Batillariella estuarina* (Tate, 1893) (Potamididae) and *Zeacumantus diemenensis* (Quoy and Gaimard, 1834) (Potamididae), but not one was attacked. All the gastropods seemed to be too active for *L. paivae* although, as will be discussed, *H. brazieri* was identified as a prey item in the field during a visit to Shoal Bay in the Austral summer.

In a second experiment, 10 different *Lepsiella paivae* individuals of 7.5–8.0 mm shell height were each offered a choice of three *Katelysia scalarina* of 5, 10 and 15 mm shell lengths. The 10 *L. paivae* were allowed to feed on their first choice of prey, leaving them only the other two bivalves to feed on and eventually only the third. This experiment was continued for 37 days and tested whether the muricid had a sequence preference for bivalve prey of a particular size.

In a third experiment, 10 different *Lepsiella paivae* individuals of 7.5–8.0 mm shell height were each offered a choice of three individuals of *Katelysia scalarina* of 5, 10 and 15 mm shell lengths. Unlike the previous experiment, however, any consumed prey items were replaced by a same-sized conspecific. This experiment tested whether *L. paivae* had a consistent preference for prey of a particular size.

In a fourth experiment, 50 *Lepsiella paivae* were divided into five groups of 10 individuals with mean shell heights of 7.5, 8.5, 9.0, 10.5 and 11.5 mm. Each group was offered seven *Katelysia scalarina* individuals of 5, 7, 9, 11, 13, 15 and 20 mm shell length categories. Again, each set of the 10 *L. paviae* individuals experienced replacement of any consumed *K. scalarina* by a same-sized conspecific. This experiment further tested prey size preference of *L. paivae* but also attempted to ascertain whether larger predators attacked larger prey.

The positions of any drill holes (or attempts) on the prey items attacked in experiments 2–4 described above were mapped onto master diagrams of left- and right-shell valves. Subsequently, the

drill holes made by eight individuals of *Lepsiella paivae* in *Katelysia scalarina* shells were examined using scanning electron microscopy (SEM).

Statistical analyses

A Kruskal–Wallis test was used to determine if there were any differences in the numbers of days to the next meal if *Lepsiella paivae* fed first on the experimentally offered *Katelysia scalarina* of 5, 10 or 15 mm shell length in experiments 2–4 above. A *t*-test was employed to determine if there were any differences between predator shell height, prey shell length and feeding time when *L. paivae* consumed either completely or incompletely experimentally offered *K. scalarina*.

RESULTS

The shell heights of *Lepsiella paivae* collected from Shoal bay ranged from 6.0 to 13.0 mm, with a mean of 9.6 mm. In addition, the population comprised two peaks of individuals (not illustrated) at shell heights of 8.5 and 11.0 mm. The shell lengths of *Katelysia scalarina* from Shoal Bay ranged from 2.5 to 30.0 mm, with a mean of 24 mm. Since none of the other gastropods offered experimentally to *L. paivae* were attacked, their shell-height data are not given.

Prey-size preferences

Table 1A summarizes the results of the prey-size choice (Experiment 2) using *Katelysia scalarina* individuals of 5, 10 and 15 mm shell lengths with no replacement of consumed prey. Over the 37-day study period, five of the 15 mm, eight 10 mm and seven 5 mm *K. scalarina* were consumed. All individuals of *Lepsiella paivae* fed, but two only consumed one 5 mm and one 10 mm *K. scalarina*, respectively; the other eight individuals fed either two or three times.

With replacement of consumed prey by same-sized conspecifics in Experiment 3 (Table 1B), only one 15 mm *K. scalarina* was drilled in the first 10 days post-initiation. After day 11, two more 15 mm, seven 5 mm and seven 10 mm individuals were attacked before the experiment was terminated. Over the 37-day experiment, one *Lepsiella paivae* individual never fed,

four others fed only once, three fed twice, while two fed three and four times, respectively.

Table 1C shows the results of Experiment 4 in which 50 *Lepsiella paivae* held in groups of 10 (of different mean shell heights) were offered a choice of seven individuals of *Katelysia scalarina* of 5, 7, 9, 11, 13, 15 and 20 mm shell lengths with replacement of consumed bivalves by same-sized conspecifics. Over the 37-day experimental period, totals of 12 (5 mm), nine plus one attempt (7 mm), seven (9 mm), three (11 mm), two (13 mm), one (15 mm) and zero (20 mm) attacks upon the proferred *K. scalarina* were recorded. The 10 *L. paivae* individuals with mean shell heights of 7.5, 8.5, 9.0, 10.5 and 11.5 mm, consumed 4, 5, 7, 14 and 4 (plus one attempt) *K. scalarina*.

Table 2 summarizes the experimental data obtained in Experiments 2–4 using *Katelysia scalarina* as prey. With a shell height range of between 6.5 and 13.0 mm, it is clear that *Lepsiella paivae* is able to attack large prey bivalves of up to 15 mm shell length. Notwithstanding, *L. paviae* did generally prefer smaller *K. scalarina*, particularly 5 mm long juveniles.

Table 3 summarizes the data obtained in Experiment 4 using different-sized groups of *Lepsiella paivae* and *Katelysia scalarina*. Over the experimental period, the group of smallest predators only fed four times as did the largest (plus one attempt). The group of 10.5 mm mean shell height predators fed the most times (14). The size range of prey consumed was approximately the same although smaller *L. paivae* did not attack the largest (13, 15 and 20 mm) *K. scalarina*. Mean prey size did not seem to vary in direct proportion to predator size and ranged between 6.2 and 9.0 mm shell length.

Locations of the drill holes

Of the total of 75 experimentally induced drill holes made by *Lepsiella paivae* in the shells of *Katelysia scalarina* (Fig. 1), 31 were on the left valve and 43 on the right. There was also one attempt recorded from the right valve. The majority of holes were located on the mid-dorsal region of the shells.

Complete and incomplete drill holes

In the feeding experiments on *Katelysia scalarina* described above, *Lepsiella paivae* individuals did not always consume their prey

Table 1. A. Experiment 2. A summary of the numbers and shell lengths (in mm) of three categories of *Katelysia scalarina* (5, 10 and 15 mm) consumed by 10 *Lepsiella paivae* individuals with no replacement of prey by similar-sized conspecifics. **B**. Experiment 3. A summary of the numbers and shell lengths (in mm) of three categories of *Katelysia scalarina* (5, 10 and 15 mm) consumed by 10 *Lepsiella paivae* individuals with replacement of prey by similar-sized conspecifics. **C**. Experiment 4. A summary of the total numbers and shell lengths (in mm) of seven categories *Katelysia scalarina* (5, 7, 9, 11, 13, 15 and 20 mm) individuals eaten by 50 *Lepsiella paivae* in five groups of 10 individuals of different mean shell height categories with replacement of prey by similar-sized conspecifics.

Day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
A							15		10	5	10		10	10			5		5	15		10		10	5				10	15	15		5	10			
										5										15																	
																				5																	
B			15								5	10	5				5			10	10							15		5	5	10		5			
												10								10		5									15						
																				10																	
C						5	9						7	13			9	5		7	15	5/9	11	5			5	7	7			11	5/9	5	7(A)		5
													13	5			7				7			9				5			7/7	9			5		

Table 2. Summary of the total numbers and shell lengths of *Katelysia scalarina* consumed by *Lepsiella paivae* in the three experiments described in Table 1.

Shell length (mm)	Experiment 2 (No replacement)	Experiment 3 (With replacement)	Experiment 4 (With replacement)
5	7	7	11
7	–	–	10
9	–	–	7
10	8	7	–
11	–	–	3
13	–	–	2
15	5	3	1

completely (Fig. 2; Table 4). In all the experiments except no. 4 there was no significant difference ($P = 0.413$) in the shell heights of the *L. paivae* used. There were, however, significant differences ($P < 0.001$) in the shell lengths of the completely and incompletely drilled *K. scalarina* and the times spent feeding, again either completely or incompletely, by *L. paivae*. Thus, generally, smaller prey items were consumed completely at a mean shell length of 6.8 mm (SD = 2.3 mm), whereas larger prey, with a mean shell length of 11.8 mm (SD = 2.7 mm), were not. Moreover, small prey was attacked, drilled and consumed completely quickly (mean = 46.3 min, SD = 28.1 min), whereas larger prey was incompletely consumed over a much longer time period (mean = 92.3 min, SD = 35.2 min), i.e. a difference of 46.0 min.

Feeding intervals

Further analysis of Experiments 2 and 3, using predators of the same shell heights (Table 1A, B) give an indication of feeding intervals when prey items of a particular size were consumed first (Table 5). In the two experiments there were 17 repeat attacks by identified predators. Most repeats were after a 5-mm shell length *Katelysia scalarina* had been consumed. The number of days for a repeat attack after the first (or second) was 5.6 (range = 1–19, SD = 5.5 days), 9.0 (range = 5–11, SD = 2.8 days) and 14.2 (range = 9–17, SD = 3.8 days) days for initial prey shell lengths of 5, 10 and 15 mm, respectively. These data were all significantly different from each other at $P = 0.036$.

SEM photomicrographs of Lepsiella paviae drill holes

The drill holes made by eight individuals of *Lepsiella paivae* in the shells of *Katelysia scalarina* in the experiments described above

Table 3. Summary of the ranges and mean numbers of *Katelysia scalarina* of 5, 7, 9, 11, 13, 15 and 20 mm shell length consumed in Experiment 4 by the five size categories of *Lepsiella paivae*.

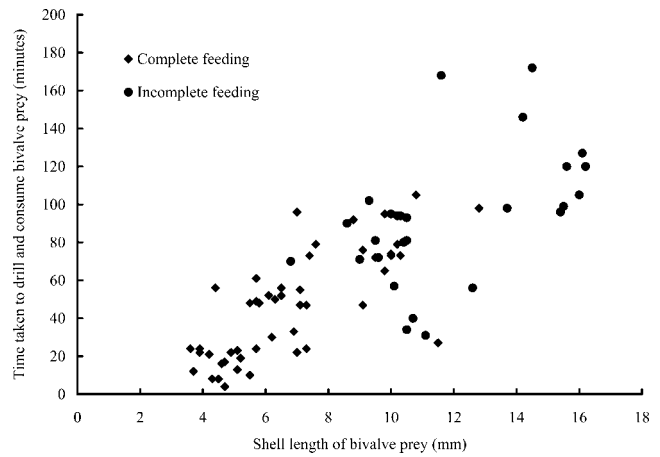| *Lepsiella paivae* mean shell height (mm)	Number of attacks	Range of shell length *Katelysia scalarina* attacked (mm)	Mean shell length of *Katelysia scalarina* attacked (mm)
7.5	4	5–11	8.0
8.5	5	5–9	6.2
9.0	7	5–13	9.0
10.5	14	5–13	7.4
11.5	4 (plus 1 attempt)	5–13	7.4

Figure 2. The times taken for experimentally held individuals of *Lepsiella paivae* to feed on *Katelysia scalarina* individuals of different shell lengths. Individual prey items that were either completely or incompletely consumed are identified.

were examined using SEM. Eight such holes are illustrated in Figure 3. Of the eight, five were approximately straight sided (A, C, E, F and H) whereas three were more typical of a naticid (B, D and G) and were slightly bevelled. Figure 3D and H (arrows) illustrate two drill holes that show differential etching of the prey's concentric commarginal lamellae.

The single incomplete drill hole made in a shell of *Katelysia scalarina* by a *Lepsiella paivae* individual of 7-mm shell height (Experiment 4) is illustrated in Figure 4. Marks made by the radula are shown by arrows in Figure 4A, where the chemically etched floor of the drill hole can be seen. The radula-abraded periostracum is seen in greater detail in Figure 4B.

DISCUSSION

In Shoal Bay, Albany, *Lepsiella paivae* occupies the whole of the eulittoral and feeds virtually monotonically on small individuals (5 mm) of the bivalve *Katelysia scalarina* by drilling and, occasionally, also by drilling the body whorl of small (∼4 mm) *Hydrococcus brazieri*. No attacks were evident upon this gastropod in the Austral winter (July) when *K. scalarina* recruitment occurs (Roberts, 1984), but they were in the summer (February) when no bivalve juveniles were present (Roberts, 1994; personal observations).

Ward & Quinn (1988) showed that on rocky shores in Victoria *Lepsiella vinosa* drilled the mussel *Xenostrobus pulex* prey

Table 4. The mean shell heights of *Lepsiella paivae*, mean shell lengths of *Katelysia scalarina* and mean feeding times (all with standard deviations) taken for the predator to either completely or incompletely consume prey items.

Shell height/length of predator/prey	Prey completely/ incompletely consumed	*n*	Mean	SD	Significance
Predator shell height (mm)	Complete	48	11.90	13.63	$P = 0.413$
	Incomplete	27	9.72	0.91	
Prey shell length (mm)	Complete	48	6.85	2.33	$P \leq 0.001$
	Incomplete	27	11.80	2.72	
Feeding time (min)	Complete	48	46.27	28.12	$P \leq 0.001$
	Incomplete	27	92.30	35.24	

t-tests identify the significance level of each pair of datasets.

Table 5. Summary of the mean numbers of days (plus ranges) *Lepsiella paivae* fed again after consuming a *Katelysia scalarina* of a particular shell length.

Prey shell length (mm)	Number of feeding events	Mean number of days to next meal	SD	Range of days to next meal
5	9	5.6	5.5	1–19
10	4	9.0	2.8	5–11
15	4	14.2	3.8	9–17

Data obtained from Table 1.

over the 4–15 mm size range but most (>70%) fed preferentially on individuals of intermediate, 7–11 mm, shell lengths. A prey-size preference has been reported previously for other muricid species, e.g. *Nucella lapillus* and *Ocenebra lurida*, which first consume larger mussel prey items as they provide more reward in terms of relative handling time (Hughes, 1980; Palmer, 1983; Dunkin & Hughes, 1984; Hughes & Dunkin, 1984a, b; Hughes & Drewett, 1985).

On an exposed rocky shore on Rottnest Island, Western Australia, however, the large muricid *Dicathais orbita* showed few preferences either in terms of prey species or their size, actually attacking smaller individuals (Morton & Britton, 1991), even though it is capable of successfully killing quite large animals, e.g. the turbinid *Ninella torquata* surprisingly by drilling at the thick operculum (Taylor & Glover, 1999). This is because the waves at the study location are so strong that *D. orbita* has no time (at low tide) to select the most energy-rewarding largest individuals but feeds opportunistically (Morton & Britton, 1991). *Morula marginalba* in southeastern Australia and *Nucella lapillus* in northern Europe experience the same constraints (Fairweather, 1988; Burrows & Hughes, 1989) as *D. orbita*. Hughes & Burrows (1990, 1991), however, showed that *Nucella lapillus* attacks a broader range of prey sizes in the field
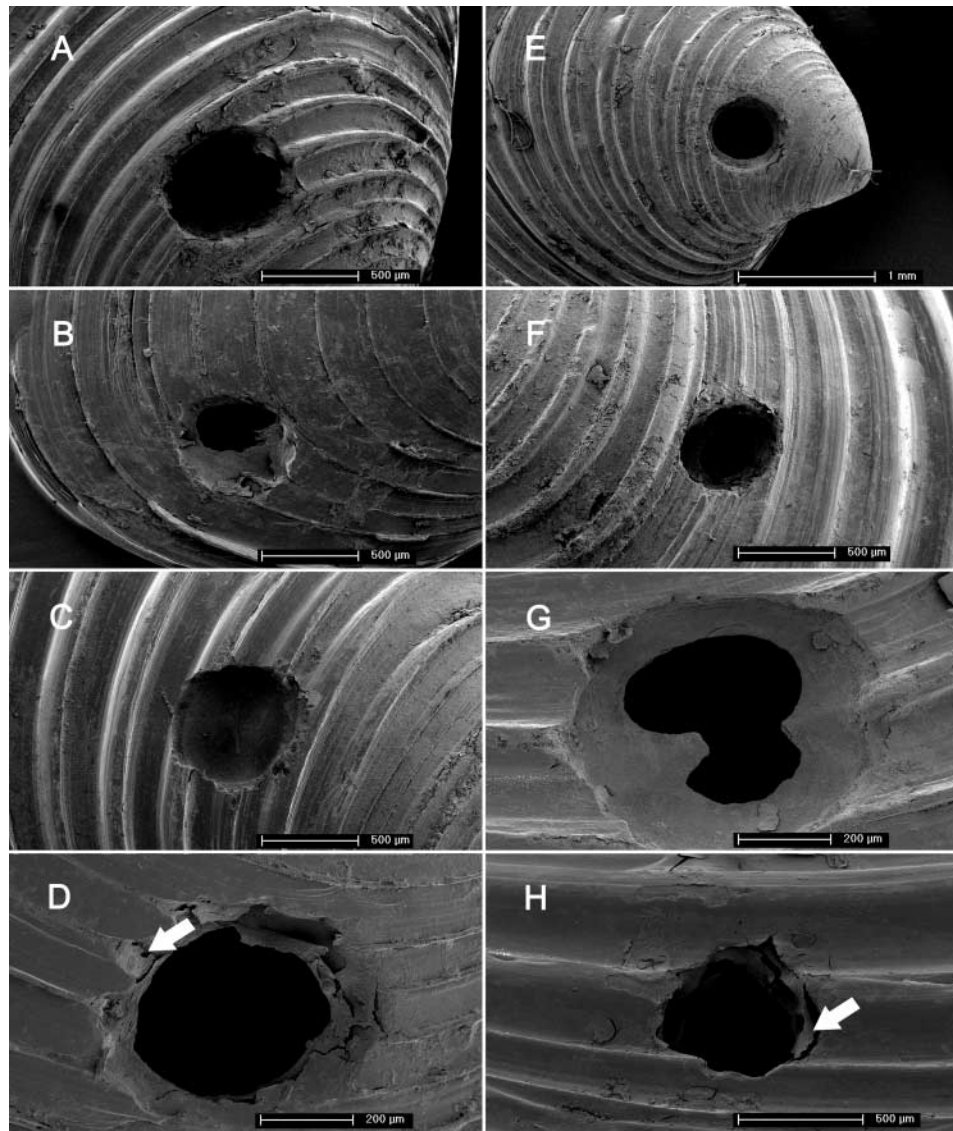

Figure 3. Eight SEM photographs of the drill holes made by experimentally-held *Lepsiella paivae* in the shells of *Katelysia scalarina*. Note that some resemble straight-sided muricid drill holes (**A**, **C**, **E**, **F** and **H**), and others naticid drill holes (**B**, **D** and **G**). D and H show the differential etching (arrows) of the commarginal lamellae of the prey shell.
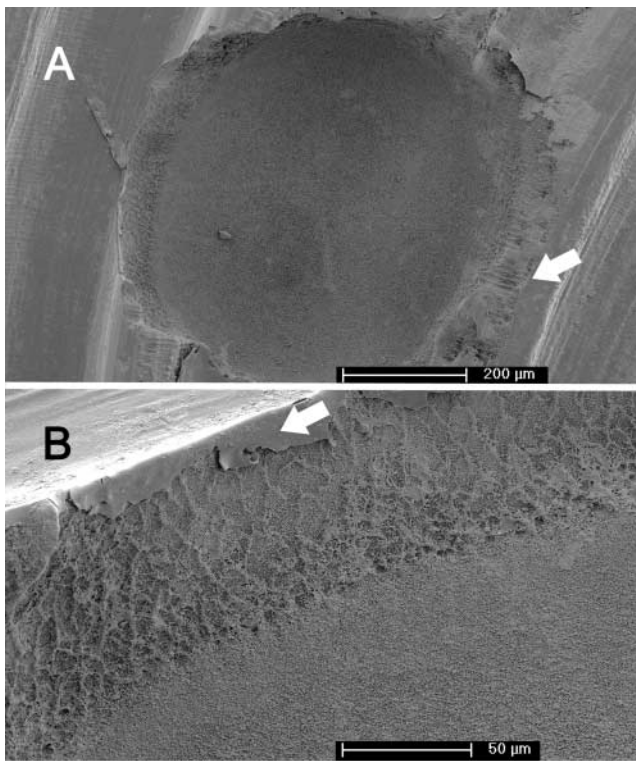
375

Figure 4. SEM photographs of the drill holes made by experimentally held *Lepsiella paivae* in the shells of *Katelysia scalarina*. **A**. An incomplete drill hole showing the chemically etched base with (arrowed) radula abrasions marginally. **B**. The same drill hole but with the periostracum (arrow) identified.

than in the laboratory, resulting in a change of titles to account for such behaviour from 'optimal foraging' (Hughes, 1980) to 'energy maximization' (Hughes & Burrows, 1990) to 'constrained optimization' (Hughes & Burrows, 1991).

Generally, larger predators attack larger prey individuals (Moran, 1985; Palmer, 1988). It has been shown here, however, that *Lepsiella paivae* of virtually all sizes attack *K. scalarina* individuals of up to 15 mm shell height (never 20 mm) with equal success, but generally prefer smaller individuals. Populations of *Nucella lapillus* show field variations in behaviour with respect to the species and size of its prey (Burrows & Hughes, 1991).

Lepsiella paivae is unusual in that it attacks and consumes its prey within the sand, although it is behaviourally flexible enough to attack *Hydrococcus brazieri* on the surface (personal observations). Interestingly, the drill holes made by *L. paivae* in the shells of *Katelysia scalarina* were sometimes straight-sided or bevelled (like a naticid) and Harper & Peck (2003: Fig. 2A–D) have shown the same for *Trophon longstaffi* from Antarctica. Carriker (1981) first pointed out that although naticid drill holes are consistently bevelled, those of muricids are considerably more varied in vertical section. Such observations raise important questions about the routine use of these characters, particularly in the fossil record (Taylor, 1981, 1998; Taylor, Cleevely & Morris, 1983), to differentiate between naticid and muricid attacks in studies of predated bivalve assemblages.

Further interest in *Lepsiella paivae*, however, arises from the fact that it can and does attack relatively large prey items, which it does not consume completely. This is energetically wasteful since, as this study shows, it takes a long time to penetrate such prey items to obtain the reward of a meal. Optimal foraging theory, first developed in the 1960s by Emlen (1966)

for predatory gastropods and Hughes & Elner (1979) for the shore crab *Carcinus maenas*, proposed that a predator would attack prey the size of which would optimize the energy spent on penetrating its defences in return for maximizing the gain obtained. Since this pioneer concept was propounded and reviewed by Hughes (1980) it has undergone modification, as described above. This study shows, however, that experimentally held *L. paivae* would attack *K. scalarina* individuals of 15 mm shell length (but not 20 mm), but which were not consumed totally, even in the presence of small conspecifics. This study further shows that it took longer times to penetrate the shell defences of larger prey items to obtain the same rewards it could have obtained by attacking a conspecific half its size. In the small intertidal nassariid *Nassarius festivus*, the energy obtained from a single meal to satiation of carrion was sufficient to provide energy for about 20 days of expenditure (Cheung, 1994). In the laboratory experiments reported here, *L. paivae*, which is of a similar shell height to *N. festivus*, fed again after 5.6, 9.0 and 14.2 days following consumption of *K. scalarina* individuals of 5, 10 and 15 mm shell lengths, respectively. Such figures are not that different from those obtained for *N. festivus*, bearing in mind that this species does not have to drill its carrion food. For example, for its preferred *K. scalarina* prey of approximately 5 mm shell length, *L. paivae* would have to eat, for 20 days survival, around four individuals, or one individual of such a shell length plus one individual of 15 mm as was recorded in the feeding trials reported here (see Table 4). The long quiescent periods between meals exhibited by *L. paivae* suggest that the time spent drilling and ingesting prey is not limiting energy intake and possibly that factors other than simple maximization of energetic returns might influence prey choice. Such factors might include exposure to predation risk, the ability to sustain a prolonged attack or the inability to ingest all the flesh from a single prey (this study). The last of these would reduce significantly the profitability of larger prey by reducing the energy gain for a prolonged drilling time (this study).

Ansell (1982) showed for the naticid *Polinices alderi* that during non-reproductive phases, approximately 40%, and during reproductive phases approximately 50%, of consumed energy was accounted for by the sum of respiration, somatic growth and egg-capsule production. For the same naticid, oxygen consumption increases with temperature (Mace, 1981) and burrowing by the nassariid *Bullia digitalis* accounts for a further surprisingly low value of 6%, in contrast to the 20% efficiency generally assumed for surface locomotion (Brown, 1979). Extrapolating such observations to the general situation of *Lepsiella paivae*, this species has a low energy expenditure in the Austral winter when temperatures are low and it burrows to attack small, thin-shelled bivalves allowing it to reproduce at this time (Roberts, 1984; this study). In the Austral summer, however, when temperatures and thus respiration rates are higher and with no small *K. scalarina* available to feed on, *L. paivae* is forced to hunt at the surface on the active *Hydrococcus brazieri*, further increasing energy expenditure. Probably, therefore, both reproduction and somatic growth are minimal and at this time *L. paivae* must have problems of survival. The life cycle of *L. paivae* in Shoal Bay can therefore best be described as opportunistic, which is also suggested by its small size (<13 mm shell height). Further evidence that *L. paivae* is opportunistic comes from the experimental results obtained that it can attack but incompletely consume larger individuals of *K. scalarina*. Since, moreover, *L. paivae* rarely attacked *K. scalarina* of more than 15 mm and never 20 mm shell length, the foraging behaviour identified is more appropriately described as 'constrained' (by prey size). *Lepsiella paivae* is thus best defined as a 'constrained opportunist' that has evolved an unusual naticid-like life style of burrowing for its prey, but like all predators it lives in an economic environment as much as an ecological one.

ACKNOWLEDGEMENTS

REFERENCES

ANSELL, A.D. 1982. Experimental studies of a benthic predator prey relationship: 2. Energetics of growth and reproduction, and food-conversion efficiencies, in long-term cultures of the gastropod drill *Polinices alderi* feeding on the bivalve *Tellina tenuis*. *Journal of Experimental Marine Biology and Ecology*, **61**: 1–30.

BAYLISS, D.E. 1982. Switching by *Lepsiella vinosa* (Gastropoda) in South Australian mangroves. *Oecologia*, **54**: 212–226.

BROOME, M.J. 1981. Size-selection, consumption rates and growth of the gastropods *Natica maculosa* (Lamarck) and *Thais carinifera* (Lamarck) preying on the bivalve, *Anadara granosa* (L.). *Journal of Experimental Marine Biology and Ecology*, **56**: 213–233.

BROWN, A.C. 1979. The energy cost and efficiency of burrowing in the sandy-beach whelk *Bullia digitalis* (Dillwyn) (Nassariidae*). Journal of Experimental Marine Biology and Ecology*, **40**: 149–154.

BURROWS, M.T. & HUGHES, R.N. 1989. Natural foraging of the dogwhelk, *Nucella lapillus* (Linnaeus); the weather and whether to feed. *Journal of Molluscan Studies*, **55**: 285–295.

BURROWS, M.T. & HUGHES, R.N. 1991. Variation in foraging behaviour among individuals and populations of dogwhelks, *Nucella lapillus*: natural constraints on energy intake. *Journal of Animal Ecology*, **60**: 497–514.

CARRIKER, M.R. 1981. Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. *Malacologia*, **20**: 403–422.

CHEUNG, S.G. 1994. Feeding behaviour and activity of the scavenging gastropod *Nassarius festivus*. In: *Proceedings of the third international workshop on the malacofauna of Hong Kong and southern China, Hong Kong 1992* (B. Morton, ed.), 327–338. Hong Kong University Press, Hong Kong.

DUNKIN, S. DE B. & HUGHES, R.N. 1984. Behavioural components of prey-selection by dogwhelks, *Nucella lapillus* (L.), feeding on barnacles, *Semibalanus balanoides* (L.), in the laboratory. *Journal of Experimental Marine Biology and Ecology*, **79**: 91–103.

EMLEN, J.M.(1966). *Time, energy and risk in two species of carnivorous gastropods*. PhD thesis, University of Washington, Seattle.

FAIRWEATHER, P.G. 1988. Movements of intertidal whelks (*Morula marginalba* and *Thais orbita*) in relation to availability of prey and shelter. *Marine Biology*, **100**: 63–68.

GARDNER, N.W. 1978. *Lepsiella scobina* (Q. & G.) – our oyster borer. *Poirieria*, **9**: 86–88.

HARPER, E.M. & PECK, L. 2003. Predatory behaviour and metabolic costs in the Antarctic muricid gastropod *Trophon longstaffi*. *Polar Biology*, **26**: 208–217.

HART, M.W. & PALMER, A.R. 1987. Stereotypy, ontogeny, and heritability of drill site selection in thaidid gastropods. *Journal of Experimental Marine Biology and Ecology*, **107**: 101–120.

HUGHES, R.N. 1980. Optimal foraging theory in the marine context. *Oceanography and Marine Biology: an Annual Review*, **18**: 423–481.

HUGHES, R.N. & BURROWS, M.T. 1990. Energy maximisation in the natural foraging behaviour of the dogwhelk *Nucella lapillus*. In: *Trophic relationships in the marine environment* (M. Barnes & R.N. Gibson, eds), 517–527. Aberdeen University Press, Aberdeen.

HUGHES, R.N. & BURROWS, M.T. 1991. Diet selection by dogwhelks in the field: an example of constrained optimization. *Animal Behaviour*, **42**: 47–55.

HUGHES, R.N. & DREWETT, D. 1985. A comparison of the foraging behaviours of dogwhelks, *Nucella lapillus* (L.), feeding on barnacles and mussels on the shore. *Journal of Molluscan Studies*, **51**: 73–77.

HUGHES, R.N. & DUNKIN, S. DE B. 1984a. Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.), feeding on mussels, *Mytilus edulis* (L.), in the laboratory. *Journal of Experimental Marine Biology and Ecology*, **77**: 45–68.

HUGHES, R.N. & DUNKIN, S. DE B. 1984b. Effect of dietary history on selection of prey and foraging behaviour among patches of prey by the dogwhelk, *Nucella lapillus* (L.). *Journal of Experimental Marine Biology and Ecology*, **79**: 159–172.

HUGHES, R.N. & ELNER, R.W. 1979. Tactics of a predator, *Carcinus maenas*, and morphological responses of the prey, *Nucella lapillus*. *Journal of Animal Ecology*, **48**: 65–78.

LAMPRELL, K. & WHITEHEAD, T. 1992. *Bivalves of Australia*. Crawford House Press, Australia.

LIU, J.H. 1995. Field experiments of predation by the muricid gastropods *Thais clavigera* and *Morula musiva* on the intertidal barnacle *Tetraclita squamosa* at Cape d'Aguilar, Hong Kong. *Asian Marine Biology*, **12**: 11–17.

MACE, A.M. 1981. Experimental study of ecophysiology of a gastropod borer, *Polinices alderi*: 2. Respiration and nitrogenous excretion. *Tethys*, **10**: 73–82.

MACPHERSON, J.H. & GABRIEL, C.J. 1962. *Marine molluscs of Victoria*. Melbourne University Press & National Museum of Victoria, Melbourne.

McKILLUP, S.C. 1981. Avoidance of the predatory whelk *Lepsiella scobina albomarginata* by *Littorina cincta* and *Littorina unifasciata*. *Veliger*, **24**: 161–171.

McKILLUP, S.C. 1982. The selective advantage of avoidance of the predatory whelk *Lepsiella vinosa* (Lamarck) by *Littorina unifasciata*. *Journal of Experimental Marine Biology and Ecology*, **63**: 59–66.

MORAN, M.J. 1985. Effects of prey density, prey size and predator size on rates of feeding by an intertidal predatory size on rates of feeding by an intertidal predatory gastropod *Morula marginalba* Blainville (Muricidae), on several prey species. *Journal of Experimental Marine Biology and Ecology*, **90**: 97–105.

MORAN, M.J., FAIRWEATHER, P.G. & UNDERWOOD, A.J. 1984. Growth and mortality of the predatory intertidal whelk *Morula marginalba* Blainville (Muricidae): the effects of different species of prey. *Journal of Experimental Marine Biology and Ecology*, **75**: 1–17.

MORTON, B. 1994. Prey preference and method of attack by *Rapana bezoar* (Gastropoda: Muricidae) from Hong Kong. In: *Proceedings of the third international workshop on the malacofauna of Hong Kong and southern China, Hong Kong 1992* (B. Morton, ed.), 309–325. Hong Kong University Press, Hong Kong.

MORTON, B. 1999. Competitive grazers and the predatory whelk *Lepsiella flindersi* (Gastropoda: Muricidae) structure a mussel bed (*Xenostrobus pulex*) on a southwest Australian shore. *Journal of Molluscan Studies*, **65**: 435–452.

MORTON, B. 2004. Predator–prey interactions between *Lepsiella vinosa* (Gastropoda: Muricidae) and *Xenostrobus inconstans* (Bivalvia: Mytilidae) in a southwest Australian marsh. *Journal of Molluscan Studies*, **70**: 237–245.

MORTON, B. & BRITTON, J. C. 1991. Resource partitioning strategies of two sympatric scavenging snails on a sandy beach in Western Australia. In: *Proceedings of the third international marine biological workshop: the marine flora and fauna of Albany, Western Australia 1988* (F.E. Wells, D.I. Walker, H. Kirkmam & R. Lethbridge, eds), 579–595. Western Australian Museum, Perth, Western Australia.

MORTON, B. & BRITTON, J.C. 1993. The ecology, diet and foraging strategy of *Thais orbita* (Gastropoda: Muricidae) on a rocky shore of Rottnest Island, Western Australia. In: *Proceedings of the fifth international marine biological workshop: the marine flora of Rottnest Island, Western Australia 1991* (F.E. Wells, D.I. Walker, H. Kirkman &

R. Lethbridge, eds), 539–563. Western Australian Museum, Perth, Western Australia.

NAVARETTE, S.A. 1996. Variable predation: effects of whelks on a mid-tidal successional community. *Ecological Monographs*, **66**: 301–321.

NAVARETTE, S.A. & MENGE, B.A. 1996. Keystone predation and interaction strength: interactive effects of predators on their main prey. *Ecological Monographs*, **66**: 409–429.

PALMER, A.R. 1983. Growth rate as a measure of food value in thaidid gastropods: assumption and implications for prey morphology and distribution. *Journal of Experimental Marine Biology and Ecology*, **73**: 95–124.

PALMER, A.R. 1988. Feeding biology of *Ocenebra lurida* (Prosobranchia: Muricacea): diet, predator-prey size relations, and attack behaviour. *Veliger*, **31**: 193–203.

PETERSON, C.H. & BLACK, R. 1995. Drilling by buccinid gastropods of the genus *Cominella* in Australia. *Veliger*, **38**: 37–42.

ROBERTS, D. 1984. The genus *Katelysia* (Bivalvia: Veneridae) in southern Australia. *Journal of the Malacological Society of Australia*, **6**: 191–204.

TAN, K.S. 2003. Phylogenetic analysis and taxonomy of some southern Australia and New Zealand Muricidae (Mollusca: Neogastropoda). *Journal of Natural History*, **37**: 911–1028.

TAYLOR, J.D. 1981. The evolution of predators in the Late Cretaceous and their ecological significance. In: *The evolving biosphere* (P.L. Forey, ed.), 229–240. British Museum (Natural History), London.

TAYLOR, J.D. 1998. Understanding biodiversity: adaptive radiations of predatory marine gastropods. In: *The marine biology of Hong Kong and the South China Sea III. Proceedings of the third international conference on the marine biology of the South China Sea, Hong Kong 1996* (B. Morton, ed.), 187–206. Hong Kong University Press, Hong Kong.

TAYLOR, J.D. & GLOVER, A. 1999. Penetrating the defences: opercular drilling by *Dicathais orbita* (Mollusca: Gastropoda: Muricidae) on the turbinid gastropod *Ninella torquata*. In: *Proceedings of the ninth international marine biological workshop: the marine flora and fauna of Rottnest Island, Western Australia 1996* (D.I. Walker & F.E. Wells, eds), 177–198. Western Australian Museum, Perth, Western Australia.

TAYLOR, J.D. & MORTON, B. 1996. The diets of predatory gastropods in the Cape d'Aguilar Marine Reserve, Hong Kong. *Asian Marine Biology*, **13**: 141–166.

TAYLOR, J.D., CLEEVELY, R.J. & MORRIS, N.J. 1983. Predatory gastropods and their activities in the Blackdown Greensand (Albian) of England. *Palaeontology*, **26**: 521–533.

TONG, L.K.Y. 1986. The feeding ecology of *Thais clavigera* and *Morula musiva* (Gastropoda: Muricidae) in Hong Kong. *Asian Marine Biology*, **3**: 163–178.

VERMEIJ, G.J. 1980. Drilling predation in a population of the edible bivalve *Anadara granosa* (Arcidae). *Nautilus*, **94**: 123–125.

WARD, S. & QUINN, G.P. 1988. Preliminary investigations of the ecology of the intertidal predatory gastropod *Lepsiella vinosa* (Lamarck) (Gastropoda, Muricidae). *Journal of Molluscan Studies*, **54**: 109–117.

WELLS, F.E. 1984. *A guide to the common molluscs of south-western Australian estuaries*. Western Australian Museum, Perth, Western Australia.

WELLS, F.E. & BRYCE, C.W. 2000. *Seashells of Western Australia*. Western Australian Museum, Perth, Western Australia.

WELLS, F.E. & ROBERTS, D. 1980. Molluscan assemblages on an intertidal sandflat in Princess Royal Harbour, Western Australia. *Australian Journal of Marine and Freshwater Ressearch*, **31**: 499–507.

WELLS, F.E. & THRELFALL, T.J. 1980. A comparison of the molluscan communities on intertidal sand flats in Oyster Harbour and Peel Inlet, Western Australia. *Journal of Molluscan Studies*, **46**: 300–311.

WILSON, B.R. 1994. *Australian marine shells*, Vol. 2. Odyssey Publishing, Kallaroo, Western Australia.