PREDATOR SIZE, PREY SIZE, AND THE SCALING OF VULNERABILITY: HATCHLING GASTROPODS VS. BARNACLES[1]

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Abstract. To examine the size-dependence of prey vulnerability, replicate groups of hatchling *Nucella emarginata* (= *Thais emarginata*) were held in cages in the laboratory with five size categories of barnacles (*Balanus glandula* and *Chthamalus dalli*). By measuring the diameters of both successful drill holes and unsuccessful drill attempts, and by using the close correspondence observed between shell length and drill hole diameter, a detailed picture emerged of the ability of hatchlings (1.1–5.3 mm shell length) to attack and consume barnacles of various sizes (1.0–6.0 mm opercular diameter). These data yielded some important general insights into the shape of the vulnerability function and the nature of the size race between predator and prey. They also revealed several interesting features about the size-dependence of this particular predator–prey interaction.

For three size classes of hatchlings (<3.5 mm), the vulnerability of barnacles (percent successful attacks) decreased roughly sigmoidally with increasing barnacle size. The sigmoidal shape of this vulnerability function seems likely to be a general feature of the size-dependence of prey vulnerability, because the size at which prey achieve an escape in size is unlikely to be discrete. Furthermore, the recognition that this vulnerability function is sigmoidal in shape suggests a theoretically sounder descriptor for the maximum size of prey vulnerability ("critical size" of Vermeij): the median vulnerable size (SV_{50}).

Another intriguing feature of these data was the relationship between barnacle SV_{50} and hatchling size. Regardless of whether length or body mass were compared, barnacle SV_{50} increased isometrically with hatchling size. In other words, for the size-ranges examined in this predator–prey system, neither prey nor predator appeared to achieve a disproportionate advantage from an increase in size. The relation between prey SV_{50} and predator size, on log-transformed axes, provides a convenient way of summarizing the size race.

This study also revealed a number of interesting features about the feeding biology of hatchling *N. emarginata*. Surprisingly, even the smallest hatchlings (1.45 ± 0.022 mm shell length) were able to consume at least a few of the largest barnacles offered (6.0 mm opercular diameter), hence no discrete upper size limit of prey was observed. Attacks on barnacles of this size, however, were successful <10% of the time. By a size of 5 mm shell length, hatchlings were able to consume nearly all sizes of barnacles with at least 50% success. These data also revealed rather nicely that the apparent preference of smaller barnacles by hatchlings when given a choice, was actually an artifact of differential attack success: although attacked with equal frequency, larger barnacles were less likely to be drilled successfully. The average growth rate of hatchlings declined significantly with increasing barnacle size due in large part to a decrease in attack success, but the variation within cages was large. The attack behavior of hatchlings depended upon both hatchling size and barnacle size. The frequency of attack at sutures between skeletal plates vs. through skeletal plates, and the frequency of attack in the opercular vs. the lateral region of barnacles, both increased with increasing hatchling size and decreased with increasing barnacle size. The increased frequencies of sutural and opercular attacks appeared to be adaptive because attacks by hatchlings at these locations were significantly more successful; however, other changes with size were not associated with differences in attack success.

Key words: *allometry;* Balanus glandula; *behavior; critical size; drilling; feeding; growth; juvenile; laboratory experiment;* Nucella emarginata.

INTRODUCTION

Among many invertebrate predator–prey systems, the relative sizes of predator and prey often determine whether an attack is successful or not (Paine 1976,

Vermeij 1978, 1987, Palmer 1979, 1985, Bertness and Cunningham 1981, Kitchell et al. 1981, Reimchen 1982, Boulding 1984). In these systems, size alone may be a very effective predator deterrent. Even where prey may ultimately achieve an escape in size (Paine 1976), they are still vulnerable when small. An unresolved question in these systems, then, is the degree to which

either the predator or the prey gains a disproportionate advantage from an increase in size, i.e., who wins in the size race? Stated more precisely, what is the relationship between prey size and prey vulnerability for a given sized predator, and how does this relationship change with increasing predator size?

To answer these questions for a particular predator–prey system, detailed information is required about the size-dependence of both success and failure of attacks. Unfortunately, few predator–prey systems allow such information to be obtained easily. How often, for example, can one tell whether an uneaten prey item was attacked but escaped, or whether it simply was never attacked (see Schoener 1979, Vermeij 1982a)? Rates of success and failure are worth examining because they provide insight into both the attributes of predators that make some more successful than others, as well as the attributes of prey that influence their vulnerability (Vermeij 1978, 1987, Palmer 1979, 1982a, 1985, Lively 1986). For example, certain size-dependent predator behaviors may or may not be adaptive. The adaptive significance, or lack thereof, must thus be inferred from the size-dependent patterns of success and failure. Furthermore, where evidence of both successful and unsuccessful attacks is left in the hard parts of prey, it may be used to deduce the relative success of predators and prey over evolutionary time (Vermeij 1982b, c, reviewed in Vermeij 1987, DeAngelis et al. 1985).

The interaction between drilling gastropods and their hard-shelled prey is unusual in that both success and failure of an attack can be recognized virtually without error: drill holes are either complete or they are not. Furthermore, because drill hole diameter correlates highly with predator size (Kitchell et al. 1981, Palmer 1988), one can infer with reasonable confidence the size of the predator in each encounter. As a consequence, data may be collected for a large number of individual predator–prey encounters without extended hours of direct observation. I report here an analysis of the outcome of 823 encounters between various sized hatchlings of a common rocky shore gastropod of the northeastern Pacific, *Nucella emarginata* (= *Thais emarginata*) (Deshayes 1839), and their most common prey, the barnacles *Balanus glandula* Darwin 1854 and *Chthamalus dalli* Pilsbry 1916.

METHODS

To obtain different size classes of barnacles, small stones covered predominantly with *Balanus glandula* or *Chthamalus dalli* of a given size were collected from a north-facing shore just south of Dixon Island (48°51′00″N, 125°07′12″W). Stones were selected as much as possible to have a uniform but sparse spacing of barnacles so that hatchlings would have access to all sides of the barnacles. To try to ensure that only a particular size range of barnacles were available, and to be able to assess the total number eaten over the

duration of the experiment, all dead barnacles or barnacles of inappropriate size were removed. To minimize scavenging, care was taken to remove barnacles damaged during this procedure as well as residual tissue left after barnacles were removed. The barnacle-covered stones were then placed in 1-L plastic freezer containers (10 × 12 × 14 cm) whose sides and tops had been cut out and replaced with 550 μm NITEX screen. These were immersed in continuously running seawater at the Bamfield Marine Station, Bamfield, British Columbia. A total of 10 cages were initiated: two replicates for each of five approximate size categories of barnacles: <2, 2–3, 3–4, 4–5, and >5 mm opercular diameter (for actual sizes, see Fig. 1 and Table 1). These sizes reflected the normal size range of *B. glandula* found in the field.

Hatchling *Nucella emarginata* were obtained from egg capsules laid in the laboratory by females collected along the shore to the south of Scott's Bay, Barkley Sound, Vancouver Island, Canada (48°49′56″N, 125°08′54″W). Starting ≈2½ mo after laying, the capsules were monitored weekly for signs of hatching, and when a number of hatchlings were available, the experiments were initiated. On 19 February 1987, six hatchlings were placed in each cage: shell lengths (apex to tip of siphonal canal) ranged from 1.1 to 1.6 mm in the first replicate and from 1.5 to 2.3 mm in the second replicate cage for each size category of barnacles. Because the size range of hatchlings available at the beginning of the experiment was larger than desired, smaller hatchlings were placed in one replicate and larger ones in the second to avoid the possibility that one or two large hatchlings per cage might induce an upward bias in the estimates of maximum size of prey vulnerability. This precaution turned out to be unnecessary because at the end of the experiment both the size of all hatchlings attempting an attack and the success of each attack could be determined from a close inspection of individual drill sites (see next paragraph). Approximately 2 wk later (6 March 1987), more smaller hatchlings became available and an additional six were added to all cages (1.1–1.9 mm shell length for all cages) to increase sample sizes. To monitor the rates of hatchling growth, shell lengths were measured at the middle (2 April 1987) and end of the experiment (8 May 1987). Seawater temperature in the laboratory ranged from 8.8° to 10.0°C during this time.

At the end of the experiment, stones were removed from the cages, rinsed in tap water and allowed to dry. For all cages except those two containing the smallest size class of barnacles, all the barnacles in each cage were inspected individually under a dissecting microscope for evidence of drilling. Because of the large number present, only a random sample of 150–200 barnacles was examined from the two cages holding the smallest barnacles. For each barnacle, the opercular diameter (from the inside edge of the rostral to the inside edge of the carinal plate) was measured to the

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nearest 0.1 mm using inside-measuring, vernier calipers or an ocular micrometer depending on barnacle size, and its fate, dead (presumably eaten) or alive, recorded. A red felt-tip pen was used to mark each barnacle after measurement to prevent duplicate measurements. Where any evidence of drilling was apparent, the location of attack was noted, the outer diameter of the drill hole was measured using an ocular micrometer to an accuracy of 0.031 mm, and each was noted as being either complete or incomplete. Drill hole diameters were measured by positioning barnacles under the microscope so as to view directly down the drill hole; where holes were not circular, the average diameter was estimated by eye. In the event of uncertainty about drill hole completion, a Pasteur pipette was used to place a drop of water inside the barnacle's skeleton; if water (or body fluids if the barnacle was not completely eaten) could be observed seeping out through the hole it was scored as being complete.

To obtain a regression of drill hole diameter on hatchling shell length, three size classes of hatchlings (mean ± SD: 2.23 ± 0.096 mm [N = 4, range = 2.1–2.3 mm], 4.04 ± 0.089 mm [N = 5, range = 3.9–4.1 mm] and 5.9 ± 0.115 mm [N = 4, range = 5.8–6.0 mm]) were taken at the end of the experiment and placed for 10 d (18 May–29 May 1987) in separate cages with small-to-intermediate sized barnacles (≈2–4 mm opercular diameter). At the end of the 10-d interval, the shell length of each hatchling was remeasured and the diameters of drill holes and drill attempts were measured as above. Because hatchlings gained from 0.5 to 1 mm in shell length over the 10-d interval (final shell lengths were 2.60 ± 0.245 mm, 4.45 ± 0.346 mm, and 6.98 ± 0.096 mm for the three cages, respectively), and because it was impossible to know which hatchling at which size had created a particular hole, drill hole diameters were regressed against the average of all initial and final shell lengths pooled within each cage.

Statistical analyses were conducted using the microcomputer routines in Statview 512+ (Version 1.0, Abacas Concepts, Berkeley, California) except for the multiway contingency table analyses, which were conducted with a mainframe version of BMDP4F (Dixon et al. 1983), and the inverse predictions from regression which were conducted with a spreadsheet constructed according to the calculations outlined in Sokal and Rohlf (1981:498).

RESULTS

Patterns of consumption and attack

Somewhat surprisingly, at least some barnacles were eaten in all cages regardless of size (Fig. 1). Most barnacles ≤2 mm opercular diameter were *Chthamalus dalli*, whereas those >2.5 mm were exclusively *Balanus glandula*. Unfortunately, in spite of the initial care setting up the experiment, some very small *C. dalli* escaped detection in cages that were supposed to contain only larger barnacles (e.g., cages 6 and 7, Fig. 1). For the two smallest size classes (cages 1–4), barnacles appeared to be eaten at random with respect to size (Fig. 1, Table 1). For the larger three size classes of barnacles, however, smaller barnacles were more likely to be consumed than larger ones (P < .05 in 5 of 6 cages, P = .061 for cage 8; Table 1). Because barnacles were unlikely to have grown while being held in the laboratory, these sizes represent those initially available in each cage.

The patterns of attack, however, differed from those based on barnacle fate. Except in cage 10 (Table 1), barnacles that had been attacked at least once, regardless of the success of the attack, did not differ in size from those not attacked at all. The size differences observed in most cages between live and dead barnacles at the end of the experiment thus appeared to result from differential attack success rather than from preferential attack of smaller barnacles.

Rates of hatchling feeding and growth

The rates at which *Nucella emarginata* hatchlings attacked and consumed barnacles depended on the size class of barnacles being attacked and upon the time interval over which the rates were measured (Table 2). The average rate of attack on intermediate-sized barnacles (cages 3–6) was 0.118 attacks·hatchling^{-1}·d^{-1}, which was nearly 50% higher than that observed for larger barnacles (0.083 for cages 7–10, N = 4). Both of these estimates, however, were considerably lower than those observed over a shorter time interval among hatchlings from the cages used to estimate drill hole diameters from hatchling shell lengths (0.317 attacks·hatchling^{-1}·d^{-1} for cages A–C, Table 2). Similarly, consumption rates by hatchlings were more than three times as high on intermediate- (cages 3–6) as on large-sized barnacles (cages 8–10; 0.059 vs. 0.017 barnacles·hatchling^{-1}·d^{-1}, respectively, Table 2).

Growth rates of individual hatchlings could not be monitored in these experiments because the hatchlings were too small to mark. Hence, to try to scale out differences in initial shell length among cages, growth rates (millimetres shell length per day) were calculated for each cage assuming all hatchlings in that cage were the same initial shell length (that of the observed average initial length for that cage). To complicate the analysis further, some small barnacles were present in two cages where only larger barnacles should have been available (cages 6 and 7, Fig. 1). In spite of these difficulties with the analysis, hatchling growth rate declined significantly with increasing average size of barnacle eaten (P = .046; Fig. 2a). Although statistically significant overall, considerable variation in growth was observed within each cage, and only a small fraction of the total variance was explained by barnacle size (r^2 = 0.040).

Except for the group of largest size, which grew nearly 0.1 mm/d (3 mm/mo), rates of growth in hatchlings
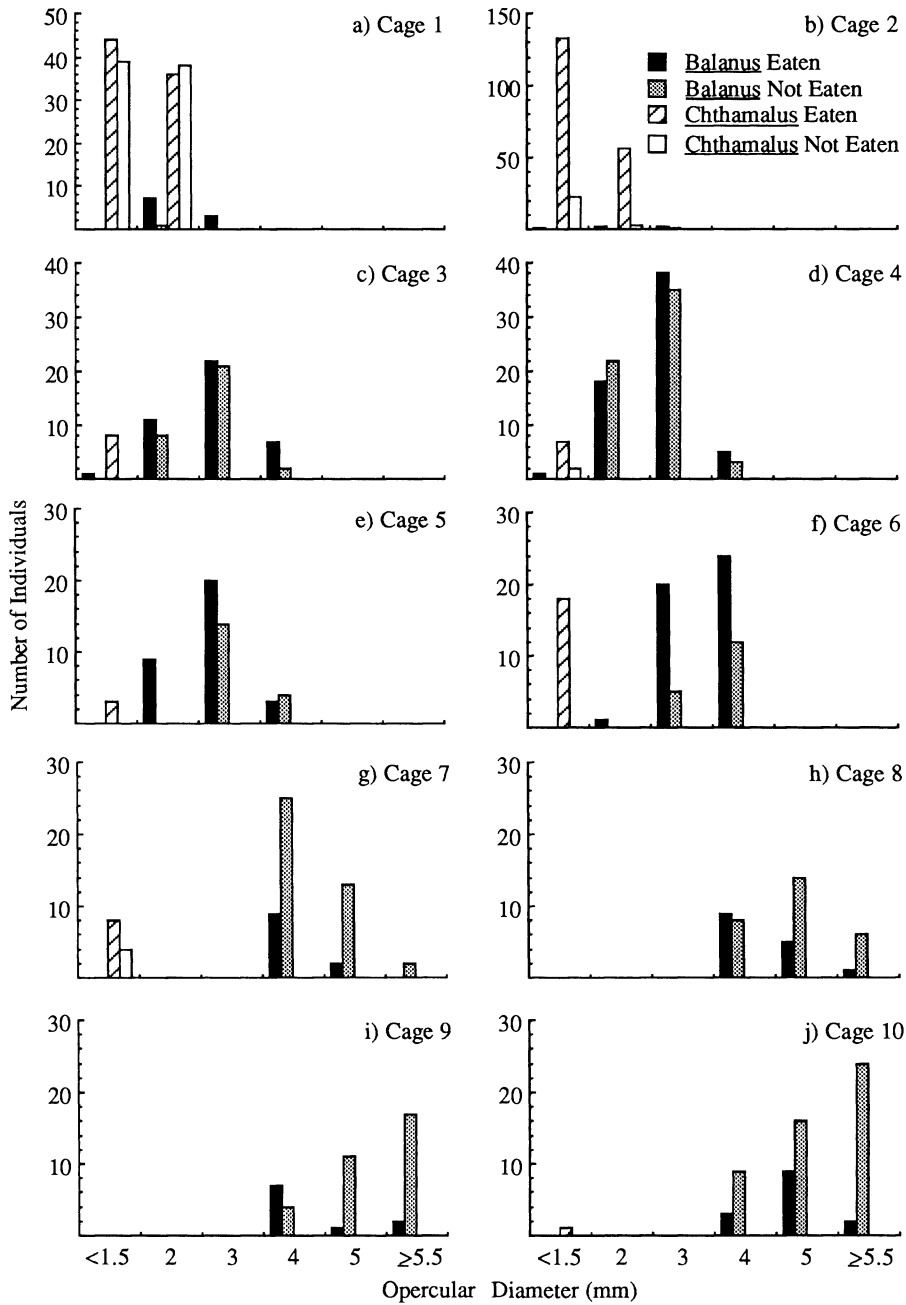
FIG. 1. Numbers of barnacles (*B. glandula* and *C. dalli*) eaten and not eaten as a function of barnacle size in each of the 10 experimental cages. Except for the largest and smallest size categories, opercular diameters on the abscissa are class marks for a size class ranging from 0.5 mm below to 0.49 mm above the class mark.

used to estimate hatchling length from drill hole diameter (Fig. 2b) were comparable to those in the main experiment (Fig. 2a). Hence, the use of a shorter time interval did not appear to influence the estimate of average rate of hatchling growth.

Estimating hatchling size from drill hole diameter

To determine the size-dependence of attack success, drill hole diameter was used to estimate the size of the

hatchling responsible for each individual attack. Two types of data were used to establish the relationship between drill hole diameter and hatchling shell length. In Group I two data points were obtained for each cage (a total of 20 points) by assuming that the smallest observed drill hole in that cage was made by the smallest hatchling at the beginning of the experiment and that the largest observed drill hole was made by the largest hatchling at the end of the experiment. In Group II three size classes of hatchlings were allowed

TABLE 1. Sizes of live and dead (presumably eaten) barnacles of each species available in each cage at the end of the experiment (see also Fig. 1). N = number of barnacles.

Cage	Status	Balanus glandula opercular diam. (mm)		Chthamalus dalli opercular diam. (mm)		Mann-Whitney U test (all barnacles; dead vs. alive)	Mann-Whitney U test (B. gl. only; no attack vs. attacked)
		Mean ± SE	N	Mean ± SE	N	P†	P†
1	dead	2.3 ± 0.12	10	1.5 ± 0.04	80 (212)‡	0.33	0.34
	alive	2.2 ⋯	1	1.5 ± 0.04	77 (197)‡		
	total	2.3 ± 0.11	11	1.5 ± 0.03	157 (409)‡		
2	dead	2.2 ± 0.24	5	1.3 ± 0.03	189 (425)‡	0.50	0.99
	alive	2.9 ⋯	1	1.2 ± 0.04	25 (115)‡		
	total	2.3 ± 0.23	6	1.3 ± 0.02	214 (540)‡		
3	dead	2.9 ± 0.09	41	0.7 ± 0.08	8	0.30	0.24
	alive	2.9 ± 0.10	31	⋯ ⋯	0		
	total	2.9 ± 0.07	72	0.7 ± 0.08	8		
4	dead	2.8 ± 0.06	62	0.7 ± 0.07	7	0.84	0.54
	alive	2.7 ± 0.06	60	1.2 ± 0.15	2		
	total	2.8 ± 0.04	122	0.8 ± 0.09	9		
5	dead	3.8 ± 0.11	32	0.6 ± 0.07	3	0.017*	0.86
	alive	4.1 ± 0.11	18	⋯ ⋯	0		
	total	3.9 ± 0.08	50	0.6 ± 0.07	3		
6	dead	3.5 ± 0.07	45	0.6 ± 0.04	18	0.008**	0.43
	alive	3.7 ± 0.09	17	⋯ ⋯	0		
	total	3.6 ± 0.05	62	0.6 ± 0.04	18		
7	dead	4.3 ± 0.10	11	0.6 ± 0.02	8	0.007**	0.28
	alive	4.5 ± 0.08	40	0.6 ± 0.07	4		
	total	4.5 ± 0.06	51	0.6 ± 0.03	12		
8	dead	4.5 ± 0.14	15	⋯ ⋯	0	0.061	0.10
	alive	4.9 ± 0.14	28	⋯ ⋯	0		
	total	4.8 ± 0.11	43	⋯ ⋯	0		
9	dead	4.8 ± 0.28	10	⋯ ⋯	0	0.009**	0.58
	alive	5.6 ± 0.16	32	⋯ ⋯	0		
	total	5.4 ± 0.15	42	⋯ ⋯	0		
10	dead	4.8 ± 0.16	14	1.0 ⋯	1	0.003**	0.003**
	alive	5.4 ± 0.11	49	⋯ ⋯	0		
	total	5.3 ± 0.10	63	1.0 ⋯	1		

† P = approximate probability from Mann-Whitney U test (Sokal and Rohlf 1981:434) comparing the sizes of all barnacles dead vs. alive, or sizes of barnacles with one or more attacks vs. no attacks (for *B. glandula* only). * $P < .05$, ** $P < .01$; "dead" includes some barnacles for which evidence of drilling was lacking because opercular plates were missing and drilling was not evident on lateral plates. Note, however, that all dead barnacles were removed from stones prior to the experiment (see Methods).

‡ Because of the large numbers in cages 1 and 2, only a subset of all *C. dalli* available were measured and inspected for evidence of drilling. Numbers in parentheses indicate the total number of barnacles, including those only scored as live or dead and not measured.

to feed for only a short time (11 d) and all drill hole diameters were plotted against the average hatchling shell length for that cage (see Methods).

Both groups of data were adequately described by a single regression of drill hole diameter on hatchling shell length (Fig. 3). Furthermore, even when all the data were pooled ($N = 60$), multiple regression analysis revealed that the size of the barnacle through which the hole had been made had no significant effect on drill hole diameter ($P = .24$; Table 3a). A simple regression that accounted for 93% of the variation (Table 3b) was thus used to obtain hatchling shell length in millimetres (X) from drill hole diameter in millimetres (Y) for all sizes of barnacles: $X = 13.210\ Y - 1.248$ (see Sokal and Rohlf 1981:496–498 for a discussion of in-

verse prediction). All subsequent analyses were conducted with hatchling shell lengths estimated from this regression.

Attack behavior and attack success

As in earlier studies (Palmer 1982a, Hart and Palmer 1987), the locations of attack were grouped by site (through skeletal plates vs. at the suture between plates) and by region (lateral vs. opercular plates) to facilitate analysis. For hatchlings of *N. emarginata*, both the frequency of attack at a given site (S) and in a given region (R) depended upon barnacle size (B) and hatchling shell length (L) (Fig. 4; SR, RB, SL, RL in Table 4a). When pooled across all sizes of hatchlings, the percent of sutural attacks (Fig. 5a) and the percent of

TABLE 2. Rates at which hatchling *Nucella emarginata* attacked and consumed barnacles.†

Cage	Total attacks	Total barnacles eaten‡	Total hatchlings	Total days	No. attacks· hatchling⁻¹·day⁻¹	No. barnacles eaten·hatch-ling⁻¹·day⁻¹
3	84	49	9	78	0.120	0.070
4	115	62	11	78	0.134	0.072
5	84	32	11	78	0.099	0.037
6	93	45	10	78	0.119	0.058
7	60	11	9	78	0.085	0.016
8	56	15	12	78	0.060	0.016
9	65	10	9	78	0.093	0.014
10	67	15	9	78	0.095	0.021
Average					0.101	0.038
A	16	···	4	11	0.364	···
B	16	···	5	11	0.291	···
C	13	···	4	11	0.296	···
Average					0.317	···

† Cage: 3–10 were main experimental cages (attack rates could not be computed for cages 1 and 2 because all barnacles in the cage were not scored for the presence or absence of attacks); A–C were cages in which different size classes of hatchlings were held to determine the drill hole diameter vs. hatchling shell length regression (mean hatchling shell lengths = 2.41, 4.25, and 6.44 mm, respectively). Total attacks: the total number of attacks observed per cage regardless of whether they were successful or not. Total days: total number of days for which hatchlings were caged with barnacles.

‡ *Balanus glandula* only from Table 1 (i.e., small *Chthamalus dalli* excluded).

opercular attacks (Fig. 5b) both declined with increasing barnacle size. Conversely, when pooled across all sizes of barnacles, both sutural (Fig. 5a) and opercular (Fig. 5b) attacks increased with increasing hatchling size. The influence of relative size of predator and prey
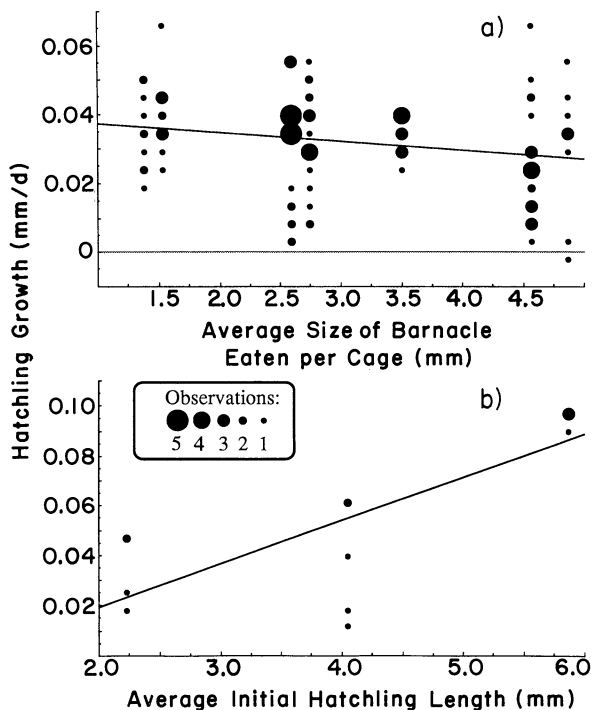

FIG. 2. Rate of growth of hatchling *Nucella emarginata* as a function of (a) average size of barnacle eaten per cage or (b) as a function of initial hatchling shell length. Regression equations for the lines displayed are: (a) $Y = -0.0025X + 0.040$, SE of slope = 0.00125, $r^2 = 0.040$, $P = .046$, $N = 101$; (b) $Y = 0.017X - 0.016$, SE of slope = 0.0043, $r^2 = 0.60$, $P = .002$, $N = 13$.

on attack behavior was also apparent in the pattern of attack on lateral plates. The frequency with which hatchlings attacked the upper half of lateral plates declined with increasing barnacle size but increased with increasing hatchling size (Fig. 5c, Table 4b).

The presence of a completed drill hole on a given barnacle (D) was independent of the number of times that particular barnacle had been attacked unsuccessfully (A; $P = .67$ and $P = .42$ for partial and marginal association of effect AD in Table 4c; see also Fig. 6). This suggests that individual barnacles within a cage were attacked at random, i.e., successful attacks did not occur more frequently on barnacles with a greater number of unsuccessful attacks. Note that the high incidence of multiple unsuccessful attacks is almost certainly an artifact of confining many snails in cages in the laboratory (see Discussion: Attack Behavior of Hatchling Snails).

Attack success depended upon a variety of factors including both attack site and attack region. As reported previously for larger *N. emarginata* (Palmer 1982a), the attack success of hatchlings (F) depended upon attack site (S): attacks at sutures were more likely to be successful than those through the barnacle's skeletal plates (Fig. 7; FS in Table 4d). This dependence of attack success on attack site also depended upon barnacle size (FSB in Table 4d). The increased frequency of attack success at sutures was most apparent for hatchlings attacking larger barnacles (Fig. 7b). Intriguingly, attack success (F) also depended upon attack region (R; Fig. 8, FR in Table 4e). On smaller barnacles (1.5–3.5 mm opercular diameter), opercular attacks were notably more successful than lateral attacks for all but the smallest hatchlings (1.66 mm, Fig. 8a). The pattern of success was similar on larger barnacles (≥3.5 mm, Fig. 8b), but sample sizes were too small to place
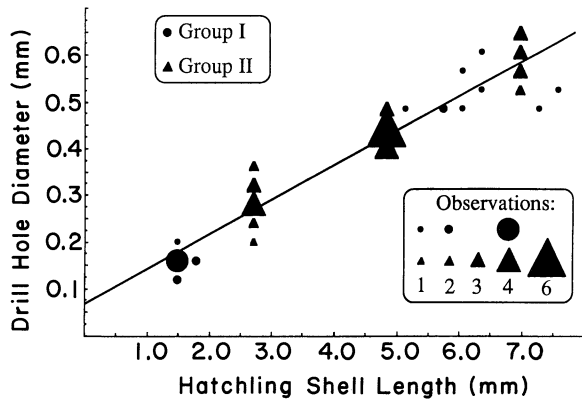
FIG. 3. Diameter of drill hole made by hatchling *Nucella emarginata* as a function of hatchling shell length. See Table 3 for regression equation and statistical analysis, and Results: Estimating Hatchling Size From Drill Hole Diameter for a description of groups I and II.

much confidence in the results. Overall, the dependence of attack success on attack region (FR) did not appear to be influenced by either hatchling or barnacle size (FRL and FRB were not significant, Table 4e).

Not surprisingly, and as elaborated in the next section, attack success depended heavily upon both hatchling shell length (FL) and barnacle size (FB, Table 4d). Attack success increased with increasing hatchling size, and it was higher overall on smaller vs. larger barnacles (<3.5 mm vs. ≥3.5 mm opercular diameter, respectively; Fig. 7). In addition, the dependence of attack

TABLE 3. Results of multiple and simple linear regression analysis of drill hole diameter (mm) as a function of *Nucella emarginata* shell length (mm) and *Balanus glandula* opercular diameter (mm).†

a) Multiple regression coefficients

Parameter	Coefficient	SE	P
Barnacle opercular diam.	−0.0046	0.00386	0.24
Hatchling shell length	0.0765	0.00279	<0.001***
Intercept	0.1046		
r^2	0.93		

b) Simple regression coefficients

Parameter	Coefficient	SE	P
Hatchling shell length	0.0757	0.00271	<0.001***
Intercept	0.0945	0.00519	<0.001***
r^2	0.93		

*** $P < .001$.

† The analysis included both (a) maximum and minimum drill hole diameters paired with the maximum final and minimum initial hatchling sizes from each of the 10 barnacle-size treatment cages, and (b) the data obtained from hatchlings grouped by size into separate cages (see Fig. 3). SE = standard error, P = exact probability, $N = 60$.

success on hatchling shell length was significantly more apparent on larger barnacles (Fig. 7; FLB, Table 4d).

Size and attack success: the vulnerability function

The large number of successful and unsuccessful drilling attacks observed ($N = 823$) permitted a detailed
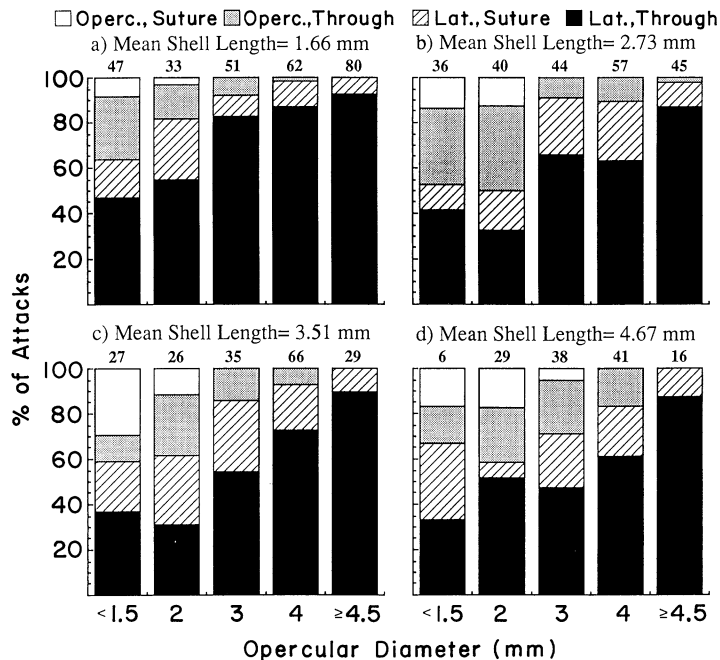

FIG. 4. Percent of attacks by hatchling *Nucella emarginata* at four locations on barnacles as a function of barnacle size and hatchling size. Numbers above each bar indicate sample size. Opercular diameter class marks as in Fig. 1. Statistical analysis shown in Table 4a.
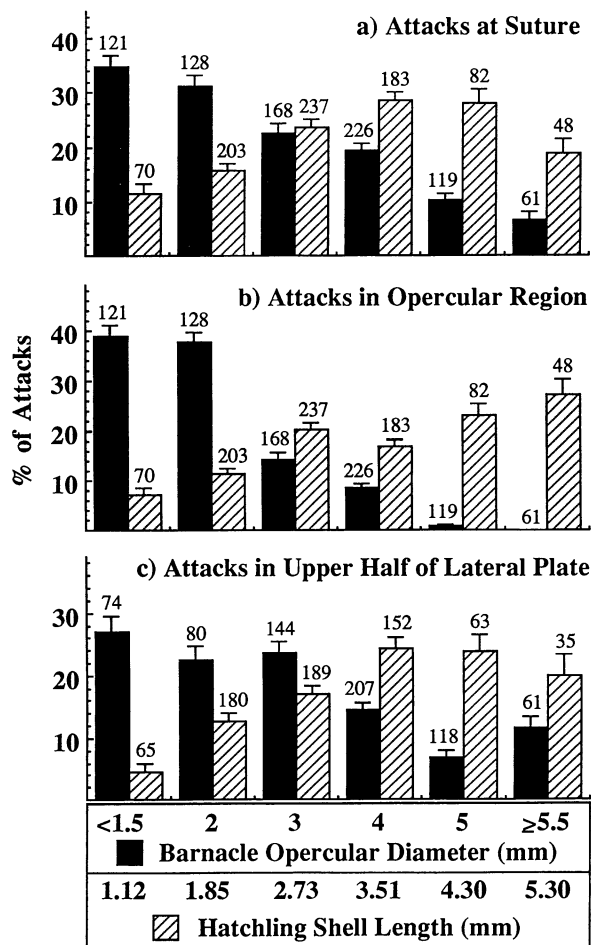
FIG. 5. Percent of attacks ($\bar{X}$ + SE) by hatchling *Nucella emarginata* at different locations on the skeleton of barnacles as a function of barnacle size and hatchling size: (a) attacks at sutures vs. attacks not at sutures of skeletal plates (data for opercular and lateral region pooled), (b) attacks in opercular vs. lateral region (data for attacks at sutures and plate margins pooled), (c) attacks in upper vs. lower half of lateral plates (data for lateral region only; attacks at sutures and plate margins pooled). Number above each bar indicates the size of the sample for which the percent was computed. Attacks as a function of barnacle opercular diameter (■) were pooled across all sizes of hatchlings. Attacks as a function of hatchling shell length (▨) were pooled across all sizes of barnacles. Opercular diameter class marks as in Fig. 1, hatchling shell lengths are class marks. Statistical analyses shown in Table 4a and 4b.

view of the variation in attack success as a function of both hatchling and barnacle size (Fig. 9). To obtain these data, barnacles from all cages exhibiting any evidence of drilling were divided into six size classes based on opercular diameter (e.g., see Fig. 1). For each size class of barnacles, completed drill holes and unsuccessful attempts were divided into five size classes based on their diameter (which was converted to hatchling shell length). Then, for each hatchling size class, the percent of all attacks that were successful was computed. For a given hatchling size class, if <10 attacks

were present for a given barnacle size class, adjacent size classes of barnacles were pooled.

For three of the five size classes of hatchlings examined, attack success declined roughly sigmoidally with increasing barnacle size (Fig. 9). Too few data were available to describe this relation fully for the largest hatchling size class. An intriguing feature of these curves was the observation that both of the smallest size classes of hatchlings (1.45 and 2.30 mm shell length) were able to consume at least some of the largest barnacles offered (>5.5 mm opercular diameter), however <10% of the attacks on these large barnacles were successful.

These vulnerability curves (Fig. 9) were also used to estimate the size of barnacle at which hatchlings were successful 50% of the time (SV_{50} = median vulnerable barnacle size). The increase in SV_{50} with increasing hatchling size was not noticeably allometric regardless of whether sizes were expressed as length (Fig. 10a) or body dry mass (Fig. 10b) or whether SV_{50} was obtained from a linear interpolation between the size categories immediately above and below 50% attack success or from inverse prediction using probit-transformed percent success (see Discussion for more detail regarding these analyses). A unit increase in hatchling size did result in less than a unit increase in SV_{50} (coefficients of allometry ranged from 0.79 to 0.86), however in no instance did these coefficients differ significantly from 1.0 ($P > .10$ for linear interpolation and $P > .20$ for interpolation based on probits). The rather large error bars associated with the estimates of SV_{50} (Fig. 10a) caution against a detailed interpretation of these slopes.

DISCUSSION

Peters (1983) and Schmidt-Nielsen (1984) review, respectively, the manner in which many ecological and physiological phenomena scale with body size. Although exceptions exist, the average size of prey species eaten appears to increase isometrically with increasing predator size across a broad range of vertebrate predators (Peters 1983:108–112). An aspect of predator–prey relationships that does not appear to have been addressed from a formal scaling perspective, however, is the manner in which prey vulnerability scales with predator size *within* species pairs. In other words, where a single prey species has the potential to achieve an escape in size (Paine 1976) from a particular predator species, what is the relationship between maximum size of prey vulnerability and predator size? This relationship, when examined on log-transformed axes (see below, Scaling of Vulnerability), will reveal (a) whether vulnerability increases isometrically or allometrically with predator size and (b) whether the predator or prey achieves a disproportionate advantage from an increase in size.

To analyze the outcome of the size race between a particular species of predator and prey, a formal descriptor of maximum size of vulnerability is required.

TABLE 4. Results from log-linear analyses of multiway contingency tables of the patterns of barnacle attack by hatchling *Nucella emarginata*.†

a) Dependence of attack site (S) and attack region (R), on barnacle size (B) and hatchling shell length (L; data in Figs. 4, 5a, 5b).§

Statistical signifi- cance of effect	Effect‡	
	Partial association	Marginal association
$P < .05$	SRL	
$P < .01$	SB	SB
$P < .001$	S, R, B, L, SL, RB, RL, BL	SL, RB, RL, BL
Best model:	SB, RB, SL, RL, BL	
Comments:	BL interaction not of interest in this analysis; note absence of SR and all third-order effects from best model.	

b) Dependence of height of attack on lateral plate (H), on barnacle size (B) and hatchling shell length (L; data in Fig. 5c).§

Statistical signifi- cance of effect	Effect‡	
	Partial association	Marginal association
$P < .05$		
$P < .01$	HL, BL	HL, BL
$P < .001$	H, B, L, HB	HB
Best model:	HB, HL, BL	
Comments:	BL interaction not of interest in this analysis; note absence of HBL from best model.	

c) Association of number of unsuccessful drill attempts per barnacle (A) with number of successful drill holes per barnacle (D) and cage (C; data in Fig. 6).‖

Statistical signifi- cance of effect	Effect‡	
	Partial association	Marginal association
$P < .05$		
$P < .01$		
$P < .001$	C, A, S, AC, CD	AC, CD
Best model:	AC, CD	
Comments:	Note absence of AD and all higher order effects from best model.	

d) Association of drill hole fate (F) with attack site (S), hatchling shell length (L), and barnacle size (B; data in Fig. 7).¶

Statistical signifi- cance of effect	Effect‡	
	Partial association	Marginal association
$P < .05$	FS, SL, FSB, FLB	FSB
$P < .01$	SB	SL, FLB
$P < .001$	F, S, L, B, FL, FB	FS, FL, FB, SB
Best model:	FSB, FLB	
Comments:	Note significant FS and FSB, and no significant FSL.	

TABLE 4. Continued.

e) Association of drill hole fate (F) with attack region (R), hatchling shell length (L), and barnacle size (B; see Fig. 8).¶

Statistical signifi- cance of effect	Effect‡	
	Partial association	Marginal association
$P < .05$		LB, FLB
$P < .01$	FR, RL	
$P < .001$	R, L, B, FL, FB, RB, FLB	FR, FL, FB, RL, RB
Best model:	RL, FR, RB, FLB	
Comments:	Note significant FR interaction and no significant FRL or FRB.	

† Analyses conducted with BMDP program 4F (Dixon 1983: see pp. 178–81 of that work for an explanation of partial and marginal effects and pp. 183–89 for determination of the "best model"). In the cases where partial and marginal chi-square values were not consistent, the "best model" for the above examples was the same whether it was arrived at by deleting effects from a fully saturated model (best fit = that model from which deletion of any additional effects resulted in a statistically significant decrease in the overall goodness of fit) or by adding higher order effects to main effects (best fit = that model for which no additional effects contributed to a statistically significant increase in the overall goodness of fit).

‡ Details of effects symbolized: A = number of unsuccessful drill attempts per barnacle (three categories: 0, 1, >1); B = barnacle opercular diameter (five size classes [<1.5, 1.5–2.49, 2.5–3.49, 3.5–4.49, >4.5 mm], however only two size classes in Table 4d and 4e [1.5–3.5 mm, ≥3.5 mm; i.e., very small barnacles were excluded from these analyses]); C = cage (five categories: pooled cages 1 and 2, 3 and 4, 5 and 6, 7 and 8, 9 and 10); D = number of successful drill holes per barnacle (two categories: 0, ≥1; multiple successful holes were too infrequent to examine as a separate category); F = fate of drill hole (two categories: successful, unsuccessful); H = height of drill hole above base of lateral plate (two categories: lower half, upper half); L = shell length of hatchling (four categories: mean = 1.66, 2.73, 3.51, and 4.67 mm); R = "region" of attack on barnacle (two categories: lateral, opercular); S = "site" of attack on barnacle (two categories: at suture between plates, through skeletal plate).

§ All drill attempts were included in these analyses regardless of whether they were successful or not and regardless of the number of attempts per barnacle. Barnacles from all cages were pooled because the purpose of these analyses was solely to examine the influence of hatchling size and barnacle size on location of attack.

‖ For this analysis, barnacles were grouped by cage because the purpose was (a) to determine whether the number of unsuccessful drill attempts per barnacle by hatchlings in replicate cages of comparable barnacle size was related to whether barnacles had been drilled successfully (i.e., was the effect AD statistically significant?), and (b) to determine if any such relationship depended upon barnacle size (ADC as determined by the cages in which the barnacles were held). Only data from cages 3 to 10 were included.

¶ Barnacles from all cages pooled and grouped into two size classes (see B in footnote ‡ above). For the analysis in Table 4d, only attacks in the lateral region were included; for that in Table 4e attacks at both sites (at sutures and through plates) were included.

Vermeij (1976) suggested the term critical size. This term unfortunately conveys the impression of a step function, and because of its ambiguity different authors have applied it in different ways (see below, The Vulnerability Function). A moment's reflection upon the
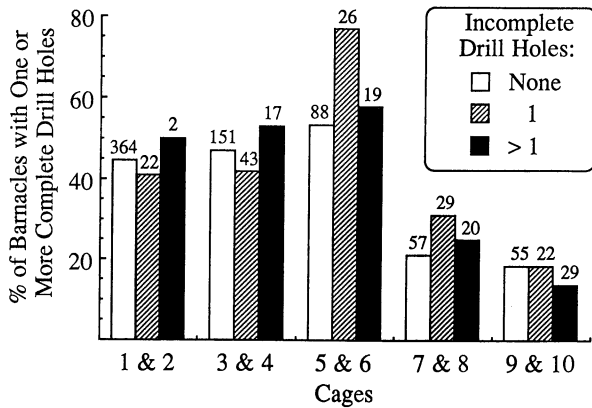
FIG. 6. Percent of barnacles with at least one complete drill hole vs. number of unsuccessful drill attempts for each of five size categories of barnacles. Numbers above each bar indicate sample sizes. For actual barnacle sizes see Fig. 1 and Table 1. Statistical analysis shown in Table 4c.

intraspecific variability of both feeding and defensive structures will disclose how ill-suited the notion of a step function is to describe the maximum size of prey vulnerability. For a given size of a given predator, a size range of a single species of prey should exist within which vulnerability declines according to some function from 100 to 0% with increasing prey size. As with many such functions (e.g., dose-response, dosage-mortality), one must choose an arbitrary reference point along the function for comparative purposes. Below, I suggest the median size of vulnerability (SV_{50}) as a
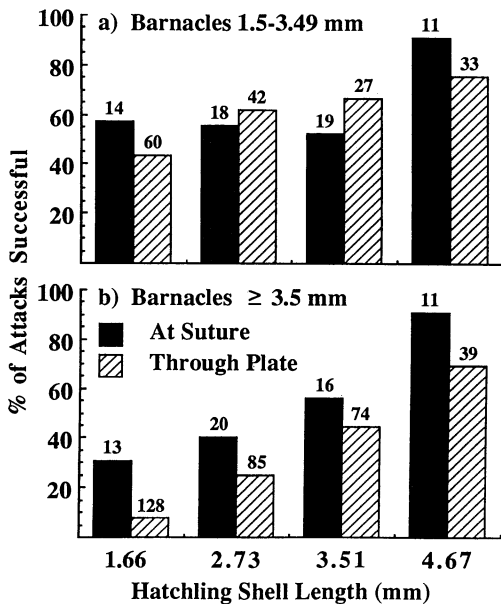

FIG. 7. Percent of attacks by hatchling *Nucella emarginata* that were successful at two different sites of attack (sutural, nonsutural) as a function of hatchling and barnacle size (barnacles were pooled from all cages; attacks in the lateral region only). Numbers above each bar indicate sample sizes. Statistical analysis shown in Table 4d.
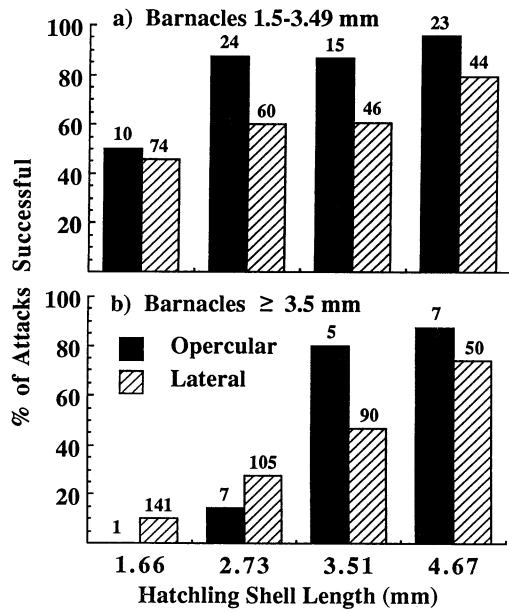

FIG. 8. Percent of attacks by hatchling *Nucella emarginata* that were successful at two different attack regions (opercular, lateral) as a function of hatchling and barnacle size (barnacles were pooled from all cages; attacks at both sites pooled). Numbers above each bar indicate sample sizes. Statistical analysis shown in Table 4e.

more rigorously defined point of reference for the maximum size of vulnerability and illustrate how it may be applied to the particular predator–prey system examined here.

Finally, because of their small size and cryptic behavior, little is known about the natural history of postlarval gastropods (Jablonski and Lutz 1983). In addition to providing some intriguing insights into the size relations of predators and prey that seem relevant to a variety of predator/prey interactions, the results of the present study revealed a great deal about the feeding biology of hatchling thaidine gastropods.

Rates of hatchling feeding and growth

Estimates of the rates at which hatchlings attacked barnacles, whether attacks were successful or not, varied by nearly fourfold (Table 2). Rates of attack on larger barnacles were lower over the duration of the experiment than on smaller barnacles, however rates of attack over a much shorter time interval were more than twice as high as the highest rate observed over the longer interval (11 vs. 78 d; cages A–C, Table 2). It is difficult to say which of these estimates is a more accurate descriptor of the maximal attack rate. The estimates made over a shorter time interval are probably more reliable because hatchlings would have been less likely to wander off the stones during this time, and fewer extrinsic factors would have influenced attack rate. In addition, when filter feeders are held in the laboratory for extended periods of time, their met-
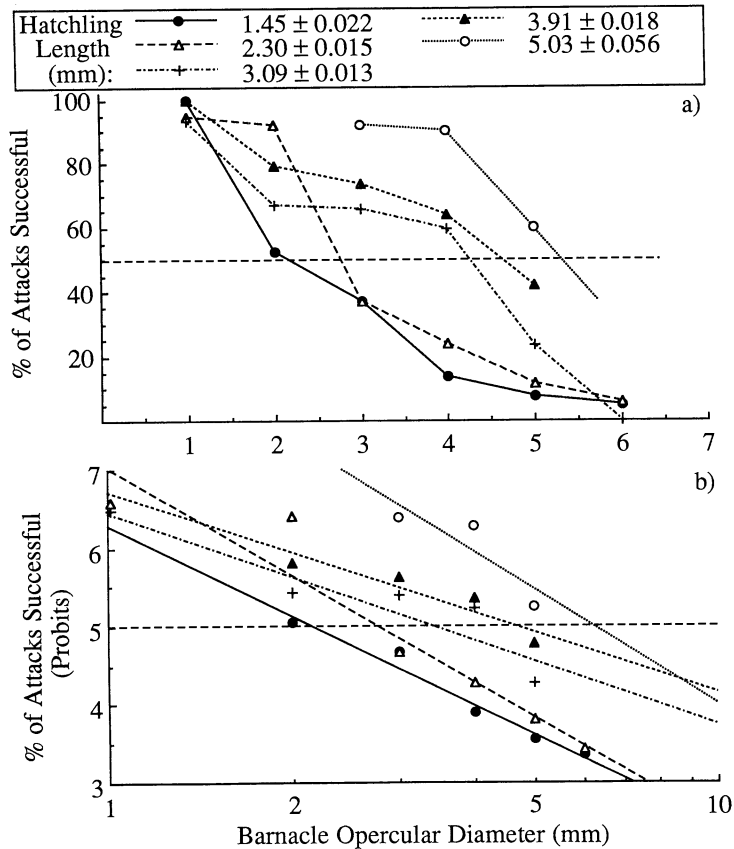
FIG. 9. Percent of attacks by hatchling *Nucella emarginata* that were successful, as a function of barnacle size, for each of five size categories of hatchlings (mean ± SE): (a) raw percentages, (b) probit-transformed percentages from Table IX of Fisher and Yates (1943) with least squares regression lines. Total sample sizes for each hatchling size category were: 181, 194, 236, 136, and 76 for the smallest-to-largest size categories, respectively.

abolic rates drop (Bayne and Thompson 1970), which may make them appear less desirable to predators (Blake 1960). The above estimates of attack rates, however, are probably close to the maximum possible rates because hatchlings were held continuously immersed in the laboratory. Attack rates in the field would most likely be much lower.

When compared to data from a previous study, the rate of barnacle consumption increased nearly 10-fold for a 10-fold increase in shell length. On similar sized barnacles (≈ 3 mm opercular diameter), the rate at which hatchling *Nucella emarginata* (1.5 mm) consumed barnacles in the laboratory (0.071 barnacles·snail^{-1}·d^{-1}; cages 3 and 4; Table 2) was ≈ 10 times lower than that of mid-sized juveniles (13.3 mm) feeding on *B. glandula* in field enclosures (0.68 barnacles·snail^{-1}·d^{-1}; Palmer 1980). The rate of feeding by these hatchlings was also from 5 to 10 times lower than that reported for other drilling gastropods feeding on barnacles (12-mm *Morula marginalba* consumed 2.1 mm *Tesseropora rosea* in cage enclosures at a rate of 0.24 barnacles· snail^{-1}·d^{-1} [Moran 1985], and 25–30 mm *Nucella lapillus* consumed 2.0–3.9 mm *Semibalanus balanoides*

at a rate of 0.76 barnacles·snail^{-1}·d^{-1} in laboratory aquaria [Hughes and Dunkin 1984]). As for rates of attack, however, the rates of barnacle consumption by hatchling *N. emarginata* reported above are almost certainly close to the maximum possible rate of feeding because the hatchlings were held continuously immersed in the laboratory.

Although the rate of hatchling growth generally declined on larger barnacles (Fig. 2), the variation in rates of growth among individuals within cages was large and exceeded by several fold the variation in average growth rate among cages. One possible explanation for this high within-cage variance in rate of growth involves chance differences in initial attack success. The average size at hatching of the *N. emarginata* used in these experiments was 1.54 ± 0.240 mm (mean ± SD, $N = 120$, range = 1.1–2.3 mm), which compares favorably to that reported previously for other populations (1.2–1.7 mm; Spight 1976). Hatchlings of this size experienced a rate of failure exceeding 50% when attacking intermediate-to-large sized barnacles (>2.5 mm opercular diameter, Fig. 9). In addition, although attacks at sutures between lateral plates were more like-
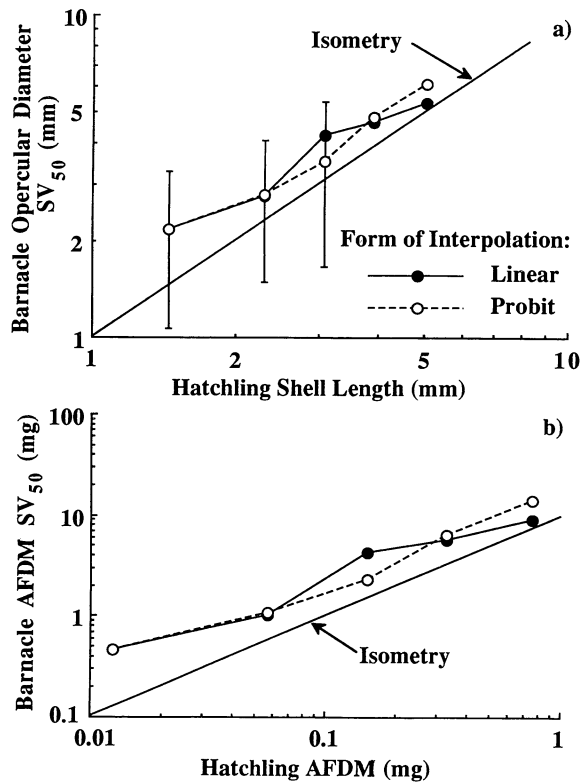
FIG. 10. Change in median vulnerable size of barnacle (SV_{50}) with increasing size of hatchling *Nucella emarginata*: (a) size measured in linear units, (b) size measured as ash-free dry mass (AFDM). AFDM for hatchlings from regression 13 in Table 1 of Palmer (1982b). AFDM of barnacles from the following regression: log(AFDM) = 3.285 log(opercular diam.) − 1.439. Each point in (a) corresponds to the intersection of a curve with the 50% line in Fig. 9 ("linear" from Fig. 9a, "probit" from Fig. 9b). SE's for hatchling shell lengths were all less than the diameter of the symbols. SE's for the probit interpolation were obtained via inverse prediction and were undefined for the largest two size categories of hatchlings (see Discussion). Coefficients of allometry ($X \pm$ SE) were: 0.79 ± 0.091 and 0.86 ± 0.087 in (a), and 0.79 ± 0.091 and 0.86 ± 0.086 in (b) for linear and probit interpolation, respectively. Coefficients were computed using reduced major axis regression (see LaBarbera 1989:104).

ly to be successful (Fig. 7), hatchlings <2 mm in length appeared to attack at sutures no more than would be expected due to chance (Fig. 5a; see below, Scaling and Attack Behavior). Because the initial rate of growth of an individual hatchling will depend upon how many of its first attacks are successful, and because the success of a given attack probably varies at random, the net effect will be to create differences in the rate of growth among hatchlings. Furthermore, the increase in size which a hatchling experiences after its first successful attack will increase its overall probability of success in subsequent attacks. In this manner, chance differences in attack success early on will be amplified the longer hatchlings are allowed to grow. The increase in the within-cage coefficient of variation in shell length over time (Fig. 11) is consistent with this suggestion. Genetic

differences, however, could also have been responsible for the high within-cage variance in rates of growth. Although all hatchlings were obtained from a few adult females collected from a single site, I cannot rule out this possibility.

The growth rates of hatchlings over a shorter period of time (11d) were consistent with those from the main experiment, except for the largest sized group of hatchlings, which grew more rapidly (Fig. 2b). If the largest hatchlings continued at this rate of growth, they would reach reproductive maturity in 5–6 mo. Here again, because hatchlings were held continuously immersed with abundant food in the laboratory, these rates are probably close to the maximum possible rate of growth.

Prey vulnerability vs. predator preference

The contrasting results obtained when comparing the size-dependence of barnacle survival to that of likelihood of attack (Table 1) reveal how differential attack success can confound the inference of predator preferences from patterns of prey mortality. Consider a simple case where all prey are equally likely to be detected and captured once detected. If, once captured, all prey are also equally likely to be consumed, then patterns of prey mortality will correlate well with predator preference. Alternatively, if some prey items are more likely to survive an attack than others, patterns of prey mortality will reflect some (unknown) combination of prey vulnerability and predator preference; the two are inseparable. Only if one has information on all attacks, whether successful or not, can one assess whether the predator is actively attacking prey in a nonrandom fashion, because each attack reflects a decision by the predator that the prey item is desirable.

For hatchling, *N. emarginata,* the size-dependence of barnacle mortality was not a product of predator preferences. In the six cages containing larger barnacles (cages 5–10), smaller barnacles in these cages were significantly (or nearly so) more likely to have been consumed than larger ones (Fig. 1, Table 1). For only one of these cages, however, was there any evidence that smaller barnacles were also more likely to have been
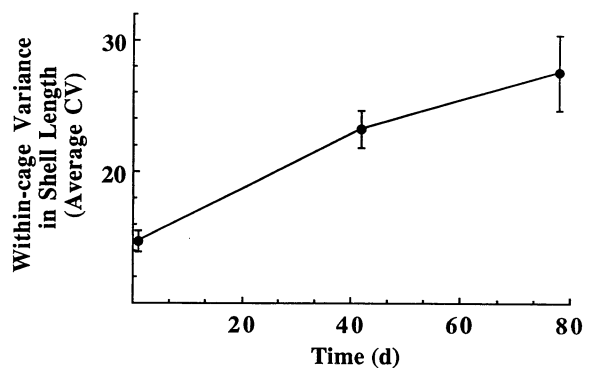

FIG. 11. Change of within-cage coefficient of variation in hatchling shell length (mean ± SE; $N = 10$) as a function of time.

attacked by hatchling *N. emarginata* (Table 1). Hence in all but one cage, barnacles were attacked at random with respect to size, but because attacks on smaller barnacles were more likely to be successful, mortality was higher among smaller barnacles. The evidence that hatchling snails can distinguish among different sizes of barnacles, when the barnacles are considerably larger than they are, is thus weak at best. This apparent inability of hatchlings to distinguish sizes of larger barnacles is perhaps not surprising because the body mass of a barnacle of 5 mm opercular diameter is ≈1000 times larger than that of a hatchling of 2 mm shell length (see Fig. 10). To test this hypothesis, however, a broader size range of barnacles than that available in the above experiments would have to be offered to hatchlings.

Attack behavior of hatchling snails

Hart and Palmer (1987) reported two ontogenetic trends in the behavior of thaidine gastropods attacking barnacles: (1) an increased tendency to attack at the margins of skeletal plates, and (2) an increased tendency to attack in the opercular region. Both of these ontogenetic trends were also apparent for hatchling *N. emarginata* (Figs. 4 and 5a, b). Hence, even though much smaller snails were examined here (1–6 mm shell length) than in the previous study (8 mm, 11 mm and >15 mm), the ontogenetic patterns were the same.

Because of the large number of both successful and unsuccessful attacks recorded per cage, the data could also be used to answer a rather intriguing question about the perception of barnacle desirability by hatchling snails: were some individual barnacles perceived to be more desirable than others? If so, barnacles that were finally drilled successfully should have been attacked more frequently, i.e., more attempts should have been made on a desirable barnacle until it was finally penetrated. The logic behind this argument is as follows. The vast majority of the barnacles in the cages analyzed in this manner (cages 3–10) were >3 mm opercular diameter (Fig. 1). Most hatchlings remained <2.5 mm for at least half of the experiment (data not presented). For these small hatchlings, the success rate of attacks on barnacles ≥3 mm did not exceed 35% (Fig. 9a), and the drilling times were probably long (3–10 d; see Table 2). Assuming a hatchling continued to drill until it could drill no further each time it attacked a barnacle unsuccessfully, and assuming that hatchlings were capable of detecting desirability differences among barnacles, a more desirable barnacle should have accumulated more unsuccessful attacks on average, both from the same hatchling making multiple attempts as well as from additional hatchlings being attracted to it, before it was finally drilled successfully and consumed. The data suggest that no such desirability differences existed among barnacles. Regardless of size, barnacles with two or more unsuccessful drill attempts were no more likely to have been drilled successfully

than barnacles with no other drill attempts (compare solid vs. open bars, Fig. 6). In other words, the presence of a successful attack on a barnacle was statistically independent of the number of unsuccessful attempts on that barnacle.

The high frequency of multiple unsuccessful attacks per barnacle (Fig. 6), as well as the not infrequent occurrence of more than one completed drill hole per barnacle, were almost certainly artifacts of the experimental conditions. Except in cages containing the smallest barnacles (cages 1 and 2), 10 hatchlings were caged for 78 d with generally <100 barnacles per cage (Table 1). Coupled with the long handling times for barnacles of this size (probably 3–10 d), multiple incomplete as well as complete drill holes by hatchlings would be almost unavoidable under these conditions.

Attack behavior, attack success, and adaptive value

As observed for larger *Nucella* attacking *Semibalanus cariosus* (Palmer 1982a), hatchling *N. emarginata* were more successful when attacking at the sutures between rather than through the skeletal plates of *B. glandula* (Fig. 7, Table 4d). Hence, even for hatchlings, the advantage to sutural attacks seems clear. Sutural attacks, however, were most consistently successful only for larger barnacles (compare Fig. 7a vs. 7b).

This apparent decreased importance of sutural attacks for hatchlings attacking smaller barnacles suggests an adaptive explanation for the overall ontogenetic shift towards increased sutural attacks with increased snail size (Hart and Palmer 1987). Because the success of a given attack is most likely a function of the thickness of barnacle skeleton at the point of attack, the lack of consistent differences in success between attacks at the suture and those through the skeletal plates of small barnacles (<3.5 mm opercular diameter, Fig. 7a) suggests that plate thickness does not vary as much over the surface of a small compared to a large barnacle. As a consequence, if larger snails feed preferentially upon larger barnacles, they should experience a greater selective pressure to attack at sutures because of the decreased drilling time. Similarly, for smaller snails feeding on smaller barnacles, selection for sutural attacks should be much weaker.

An important implication of past studies was confirmed by the above data for hatchling *N. emarginata*: opercular attacks were significantly more successful than lateral attacks (Fig. 8, Table 4e). All four species of *Nucella* from the northeastern Pacific attack *B. glandula* more frequently in the opercular region with increasing snail size (Hart and Palmer 1987), yet we had no clear evidence for any adaptive value to this behavior. The increased attack success in the opercular region, like the increased attack success at plate margins, suggests very strongly that the preference for opercular attacks is adaptive.
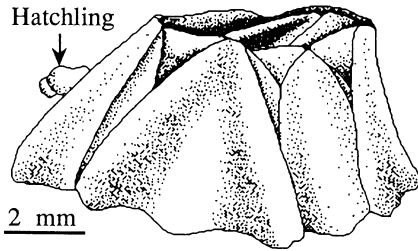
Hatchling

FIG. 12. A 1.5-mm hatchling *Nucella emarginata* on the rostral plate of a 5.0 mm opercular diameter *Balanus glandula*.

2 mm

Scaling and attack behavior

Although adaptive explanations are possible for some of the ontogenetic patterns in attack behavior, a closer examination suggests that, because of the very small size of a hatchling compared to a barnacle (Fig. 12), one of the ontogenetic trends observed may have been due to size differences alone. Larger hatchlings attacked barnacles more frequently in the upper half of the lateral plates compared to the lower half (Fig. 5c). In addition, this tendency to attack in the upper half of lateral plates declined with increasing barnacle size (Fig. 5b, c). However, a multiway contingency table analysis identical to that in Table 4d, except that height of attack (upper 0.5 or lower 0.5) was substituted for site of attack and only attacks on lateral plates were considered, revealed no significant difference in the percent of *successful* attacks in the upper vs. the lower half of lateral plates (FH: partial $P = .139$, marginal $P = .402$; higher order interactions with FH were also not significant [FHB and FHL], $P > .22$). The simplest explanation for this tendency is that, as hatchlings increase in size, they are more likely to crawl higher up on a barnacle before beginning to drill, hence no particular advantage to attacks in the upper half of lateral plates need be invoked. Direct observations of hatchling behavior, however, would be required to confirm this. The tendency for larger hatchlings to crawl higher up on barnacles before beginning to drill may be adaptive for other reasons, but it appears to have nothing to do with increased attack success higher on the lateral plates.

This interpretation implies that some of the increased tendency towards opercular attacks with increased hatchling size (Fig. 5b) may result solely from the increased tendency of larger hatchlings to crawl higher up on a barnacle. The decline in opercular attacks with increasing barnacle size also suggests that the sheer size of the barnacle relative to the hatchling may influence the height to which a hatchling will crawl. Although opercular attacks are clearly more successful than attacks at lateral plates (Fig. 8, Table 4e), small hatchlings may be more vulnerable to dislodgement or predation, and thus may not climb as high before attacking.

The declines in the frequency of sutural attacks with

increasing barnacle size and with decreasing hatchling size (Fig. 5a) are also unlikely to be adaptive because attacks at sutures were consistently more successful on larger barnacles (Fig. 7b). Hatchlings may simply be less able to detect sutures on larger barnacles because of the relatively small surface of the barnacle they can sense at any one time. This interpretation is also supported by the observation that the frequencies of attack at sutures on the largest two barnacle size classes were very close to that expected by change, $\approx 15\%$ based on the percent of surface composed of sutures (Palmer 1982a).

All of these patterns emphasize how important scaling considerations are when attempting to infer the adaptive value of particular predatory behaviors. To infer that some size-dependent pattern in feeding behavior is adaptive, a net advantage to that behavior must be demonstrated. The declines, with increasing barnacle size, in the frequency of attacks (a) at sutures, (b) in the opercular region, and (c) in the upper half of lateral plates (Fig. 5a–c) are clearly not advantageous as far as feeding is concerned because attack success is either significantly higher at these locations (Figs. 7 and 8), or not significantly different. These patterns seem more likely to be a product of other size-dependent factors, such as the ability of a very small snail to detect features like a suture in a barnacle's skeleton that is nearly as large as the hatchling itself (Fig. 12), and such as the absolute height to which a hatchling will crawl up a barnacle before beginning an attack.

Some of the behaviors that changed with hatchling size may possibly have been a result of learning, although the present data cannot distinguish between learning and a genetically programmed change in behavior with size. Dunkin and Hughes (1984), for example, demonstrated very nicely that prior experience with barnacles influenced the frequency with which *Nucella lapillus* prised vs. drilled barnacles. Hence, with experience, dogwhelks appeared to learn to use the more rapid attack method of prising more frequently. Hart and Palmer (1987), on the other hand, found that juvenile *N. emarginata* grown on mussels exhibited nearly the same size-dependent change in drill-site selection on barnacles as those grown entirely on barnacles, and hence they concluded that the observed ontogenetic changes were genetically programmed rather than learned. Whether elements of predator behavior are learned or genetically programmed thus appears to depend upon the behavior being considered.

The vulnerability function

Size not only influences predator behavior (Hughes 1980, Dunkin and Hughes 1984), but it also influences prey vulnerability (Vermeij 1987). The relative vulnerability of different prey species or forms of prey are often assessed by comparing their "critical size" (Vermeij 1976), where critical size is usually interpreted as that size above which a given type of prey cannot be

consumed by an individual predator of a given size. A larger critical size thus indicates prey that are more vulnerable (i.e., that are vulnerable to a larger size). Stated in this way, the term critical size conveys the image of a step function where all prey below a particular size are vulnerable and all above that size are invulnerable, although this function has not been described formally. However, given that both the feeding structures and feeding experience of the predator, as well as the antipredatory armor of the prey, may vary among individuals of the same body size, this transition from vulnerable to invulnerable is unlikely to be discrete (e.g., see Lawton and Hughes 1985: Fig. 1a; Wainwright 1987: Fig. 4).

Because of this lack of discreteness, the critical sizes of prey species or prey forms have been computed in different ways. Vermeij (1976; footnote to his Table 1) defined critical size as the average size of the largest prey item eaten and the next larger one offered (Method I). This procedure is necessary where smaller prey were available, yet not eaten, and where one cannot be certain that these smaller prey were actually attacked by the predator, i.e., one cannot distinguish prey that survived an attack from those not attacked at all. Elsewhere I have computed critical size as the average size of the largest prey eaten and the smallest prey known to have been attacked (Method II). This method can only be applied where all prey items that have been attacked are known, as would be the case where, for example, prey items are offered individually to a predator and their fate recorded (Palmer 1979) or where unsuccessful attacks leave identifiable traces on the prey (Palmer 1985). It differs from Method I in that the smallest prey surviving an attack may be smaller than the largest one eaten because the dimension used to describe size (e.g., shell length of a gastropod) is not the dimension that determines vulnerability of the prey directly (e.g., shell thickness or shell sculpture). Finally, Bertness and Cunningham (1981) and Boulding (1984) computed critical size by progressively offering prey items larger than the last one eaten to a given predator until none were subsequently consumed within a given length of time; here the critical size was taken as the size of the largest prey item eaten (Method III).

The attack of barnacles by hatchling *N. emarginata* (Fig. 9a) reveals more clearly the relationship between size and vulnerability and suggests a more appropriate method for computing a descriptor of vulnerability, i.e., the size of prey at which 50% are vulnerable (SV_{50}). The curves in Fig. 9a are analogous to dosage-mortality curves used to establish, for example, the median lethal dose (LD_{50}) of a toxic substance. The appropriate analysis of such curves involves transforming percent success to a probit scale (Sokal and Rohlf 1981: 544–546), which linearizes cumulative percent data (Fig. 9b), and then using linear regression to estimate SV_{50} via inverse prediction (Sokal and Rohlf 1981:496–498). In this manner, one may also obtain a standard error or 95%

confidence interval for the estimate of SV_{50} (Fig. 10a). Furthermore, Wainwright (1987) has found that both SV_{50} and critical size estimated by Method III scale similarly with predator size.

Unfortunately, the ability to estimate SV_{50} with much confidence depends rather heavily upon sample size. Minimally three but ideally four or more prey size classes would be required among which attack success should range between 16 and 84% (Goulden 1952:400). Even with the present data, however, sample sizes were too small and the scatter about the probit regressions too large to permit standard errors to be estimated using inverse prediction for the largest two size categories of hatchlings (Fig. 10a).

Given that SV_{50} can only be estimated with confidence for relatively large sample sizes, why should it be considered a more useful descriptor of the maximum size of vulnerability than the critical size of Vermeij (1976)? First, it is a less ambiguous term, which explicitly recognizes that the decline in vulnerability with increasing prey size is continuous rather than discrete. Second, even where sample sizes are too small to calculate SV_{50} properly, if one recognizes (a) that the vulnerability function (Fig. 9a) should generally be similar in shape to a dosage-mortality curve, and (b) that from a theoretical perspective the most useful reference point to estimate on this curve is the median size of vulnerability, then the best procedure for estimating SV_{50} can be determined for a data set of any size. For example, where a large number of prey have been offered to a predator within the size range between the largest prey item eaten and smallest attacked but not eaten, the inverse prediction of SV_{50} may provide a more accurate descriptor for comparing vulnerabilities than critical size using either Methods I or II. Alternatively, where too few prey have been offered within this vulnerable size range to permit inverse prediction, the prey in this range could be divided into two equal-sized groups and SV_{50} could be interpolated between these two estimates of percent success. This also would yield a better descriptor than critical size using Methods I or II above. The above discussion should make it apparent that Method III will always underestimate both critical size and SV_{50}, although the degree of underestimation will depend upon how closely spaced the sizes of offered prey are. Furthermore, I should emphasize that, where differences between the size of the largest prey item eaten and the smallest item not eaten are small relative to the differences in SV_{50} among the prey species or prey forms being compared, any of the four methods described above should be adequate to reveal the pattern qualitatively. Estimates of SV_{50}, however, will always be more accurate quantitatively.

Scaling of vulnerability: Who gains more from an increase in size?

Because estimates of SV_{50} were obtained for several

size categories of predator, one may estimate the degree to which either the predator or the prey gains disproportionately from an increase in size. For hatchling snails attacking barnacles, the size race appears to be isometric (Fig. 10a, b). Regardless of whether SV_{50} was computed by interpolating linearly between the size categories immediately above and below 50% success or by using probits, and regardless of whether lengths (Fig. 10a) or body masses (Fig. 10b) were compared, the coefficients of allometry were similar. The coefficients were all <1 (0.79–0.86), suggesting perhaps that barnacles gain a greater advantage from a given increase in size than do hatchling *N. emarginata,* however, none was significantly different from 1.0 ($P > .10$ in all four cases; Fig. 10).

This approach to the scaling of vulnerability has two attractive features that seem relevant to a variety of predator–prey systems. First, by using log-transformed axes as in other studies of scaling (Peters 1983, Schmidt-Nielsen 1984), one may describe very conveniently the proportional increase in SV_{50} with increasing predator size (i.e., a static description of the size race) so long as the size of predator and prey are both measured in units having the same dimensionality (e.g., size measured as length for both or size measured as mass for both). If this proportionality (= coefficient of vulnerability) is equal to one, then prey vulnerability increases at the same rate as predator size. If it is <1, then prey are proportionally less vulnerable to larger predators (i.e., the median size of vulnerability is proportionally less), whereas if it is >1 the converse is true. A second appealing aspect of this approach is that the coefficients of vulnerability for various predator–prey relationships may be compared even where the sizes of predators and prey are measured in very different units. For example, opercular diameters of barnacles, shell lengths of snails, test diameters of sea urchins, and carapace widths of crabs are all commonly used measures of "size," but they are not directly comparable. If, however, barnacle vulnerability to snails increased with a coefficient of vulnerability <1, and sea urchin vulnerability to crabs also increased with a coefficient <1, this would indicate that in both predator–prey systems prey became proportionally less vulnerable to their predators with increased size.

Some intriguing predictions arise when vulnerability is considered from a scaling perspective. For example, for species where a trade-off exists between rate of growth and development of antipredatory armor, as is the case for gastropods (Palmer 1981), vulnerability should scale with a coefficient <1. This would suggest that juveniles are proportionally more vulnerable than adults and would reflect the price juveniles pay in order to maintain higher rates of growth. Similarly, where the proportion of life spent as an adult is large relative to that spent as a juvenile, adults should be proportionally less vulnerable than juveniles (i.e., vulnerability should also scale with a coefficient <1).

One aspect of this approach to the size race should be clarified. Coefficients of vulnerability only provide a static description of the relation between prey vulnerability and predator size. The population dynamic consequences (e.g., selection on rates of growth, or for development of antipredatory traits) will depend on a number of other attributes of predators including rates of growth, densities, and size distributions, among other things. In other words, the coefficient of vulnerability only describes how the probability of death once captured depends on both predator and prey size; it does not contain any information about the probability of capture.

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