

# Hair-trigger autotomy in porcelain crabs is a highly effective escape strategy

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The benefits of autotomy, the voluntary shedding of limbs, have been adequately demonstrated in vertebrates but are poorly studied in invertebrates. We provide strong experimental evidence for an antipredatory benefit to autotomy in two porcelain crabs (*Petrolisthes cinctipes* and *P. manimaculis*). Since the outcome of autotomy depends critically on the species of predator and prey involved, we first surveyed field populations of porcelain crabs to identify ecologically relevant predators to use in subsequent experiments. We then examined the escape tactics of the porcelain crabs in response to the four potential predators we identified, all larger predatory crabs. Cheliped autotomy was induced by three of the predator species (*Cancer antennarius*, *Hemigrapsus nudus*, *Pachygrapsus crassipes*); the fourth did not attack porcelain crabs. Autotomy occurred in response to 34% of all attacks, and in 67% of attacks in which the prey was held at some point by only the cheliped. Autotomy was a highly effective escape mechanism against these predators; 58 of 59 crabs that autotomized escaped, usually while the predator stopped pursuit to eat the shed cheliped. Reliance on autotomy as a primary mechanism for escaping predators may be particularly common in small crabs that cannot adequately defend themselves by other means and in suspension-feeding crabs that do not need their chelipeds for feeding. *Key words*: autotomy, crabs, Crustacea, escape strategy, predation. [*Behav Ecol* 13:481–486 (2002)]

Autotomy, the ability to voluntarily shed a limb or body part, typically at a predetermined breakage plane, has evolved many times among animals. Rodents, salamanders, lizards, geckos, and skinks shed their tails (Arnold, 1988); crabs drop their chelipeds (clawed anterior appendages) and other limbs (Juanes and Smith, 1995; McVean, 1982); spiders release their legs (Formanowicz, 1990), and brittle stars and sea stars cast off their arms (Lawrence, 1992; Mauzey et al., 1968). There is an extensive literature documenting numerous costs to limb loss (reviewed by Arnold, 1988; Juanes and Smith, 1995), particularly in lizards and in crabs. The animal must pay short-term costs (e.g., to foraging and defense) of doing without the limb and long-term costs (e.g., to growth and reproduction) of replacing it.

The repeated independent evolution and maintenance of autotomy suggest that there are strong selective advantages to this behavior that outweigh the costs. Two such benefits have been suggested, the ability to limit damage to wounded body parts and escape from predation (Arnold, 1988; McVean, 1982). Limiting damage is likely the ancestral function in each lineage and may be the main current benefit in some species. However, for animals that shed undamaged limbs, this explanation does not suffice, and it is generally presumed that such autotomy is a device for escaping predators. Most investigation into such an antipredatory benefit has focused on caudal autotomy in vertebrate taxa (e.g., salamanders, reviewed by Brodie, 1983; lizards, geckos, and skinks, reviewed by Arnold, 1988). About a dozen studies, ranging from anecdotal observations to small laboratory experiments, have found that autotomy can facilitate escape in these taxa.

The benefit to autotomy in invertebrates has received much less attention. Most previous studies in invertebrates have focused on assessing the costs of autotomy, particularly in crustaceans, typically by tracking the subsequent fitness of animals already missing limbs (Juanes and Smith, 1985; McVean, 1982). To understand the benefits of autotomy, however, it is necessary to directly observe predatory encounters between prey and the relevant predators. We chose porcelain crabs (*Petrolisthes* spp.) as ideal subjects for a rigorous investigation of the role of autotomy as an escape tactic. Their well-known “hair-trigger” autotomy response, shedding limbs at the slightest provocation, made it likely we would observe the behavior in controlled predation trials and also suggested to us that there might be a marked benefit to the behavior.

Our first goal was to locate likely predators of porcelain crabs in the field. The effectiveness of escape tactics varies among predators, so identification of natural predators is crucial to an understanding of autotomy. Second, we carried out controlled laboratory trials to determine whether various predatory species attacked porcelain crabs in such a way as to induce autotomy. To rigorously distinguish autotomy from forced removal of limbs, we developed and then applied a strict definition of what constituted autotomy. Third, having identified relevant predators that induce autotomy, we carried out trials with three predatory and two prey species to compare predation efficiency of the predators and to examine the effectiveness of autotomy as an escape mechanism for two species of porcelain crabs.

## METHODS

### Field surveys for predators

To identify potential predators that co-occurred in the same habitat as porcelain crabs, we haphazardly overturned 222 medium-sized (approximately 20–50 cm in maximum diameter) rocks in mid-intertidal boulder fields at two sites near Trinidad, northern California (41°06' N, 124°08' W). We turned over 70 rocks at the south end of Baker Beach on 14 May

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1999, 100 rocks at the north end of Baker Beach on 17 May 1999, and 52 rocks at Indian Beach on 17 June 1999. The number of porcelain crabs (*Petrolisthes* spp.) per rock was rapidly estimated because the crabs fled in all directions immediately after the rock was overturned. We also searched under each rock for potential predators. Because predators were rarer, slower, and easier to identify, we obtained exact counts and identified them to species.

### Collection and maintenance of prey and predatory crabs

We periodically collected porcelain crabs under rocks in the mid-intertidal zone at Baker and Indian Beaches during low tides from April to August 1999. A total of 458 porcelain crabs were collected: 221 *Petrolisthes cinctipes*, 102 *P. eriomerus*, 118 *P. manimaculis*, and 17 that belonged to one of the two latter species but were missing both chelipeds, which are diagnostic for telling them apart. *P. manimaculis* was previously known only as far north as Bodega Bay (Jensen, 1995), so our work incidentally represents a northward range extension for this species. Only *P. cinctipes* and *P. manimaculis* individuals were used in predation trials. The average size (maximum carapace width) of these porcelain crabs was about 9 mm; crabs ranging from about 4–14 mm were used in trials.

Collected porcelain crabs were maintained in buckets of running seawater at Humboldt State University's Telonicher Marine Laboratory. The crabs were given rocks to use as cover and were fed with phytoplankton cultures approximately twice a week. We always used porcelain crabs that had been collected within the previous 2 weeks for predation trials. Porcelain crabs not used for trials, and those surviving trials, were released back to their original field sites about 2 weeks after collection (fieldwork occurred at roughly 2-week intervals because sites were only accessible on low [spring] tides).

Potential predators for use in experiments were obtained from Baker Beach, Indian Beach, and Shelter Cover on low tides from April to June 1999. We collected 17 purple shore crabs (*Hemigrapsus nudus*), 7 Pacific rock crabs (*Cancer antennarius*), 6 black-clawed crabs (*Lophopanopeus bellus*), and 3 striped shore crabs (*Pachygrapsus crassipes*). Each crab was measured (carapace width) and then labeled with a number painted on the carapace with nail polish.

Predators were maintained individually in otherwise empty 12-l buckets supplied with running seawater. Within a week of collection, they were offered porcelain crabs to determine whether they were appropriate predators. All except the black-clawed crabs were subsequently used in predation trials. The black-clawed crabs were released back to the field site where they had been collected about 2 weeks after collection; the other predators were released within days of the end of the study.

### Predation trials

We used staged encounters between potential predators and prey in buckets in order to clearly observe whether autotomy was induced and whether it was effective as an escape mechanism after capture. Such laboratory trials are useful for understanding the final stages of predator-prey interactions, but they do not shed light on early stages of encounters in the field; for instance, predator avoidance mechanisms by the prey, such as hiding in tight crevices, were not the subject of this study.

Preliminary trials were conducted in April and May 1999 to design effective protocols for later trials and data sheets for scoring behavioral interactions. Because different methods were being tested, we did not collect data from these trials in a consistent manner, and these data were not included in the

subsequent analysis, although the same trends were evident. Standardized trials were run from 19 June to 16 August 1999. The majority of trials were conducted with purple shore crabs, the most abundant predatory species co-occurring with porcelain crabs. During the 2-month duration of the experiment, each of the 17 purple shore crabs was used in about 9 trials, each of the 7 rock crabs was used in about 6 trials, and each of the 3 striped shore crabs was used in about 2 trials.

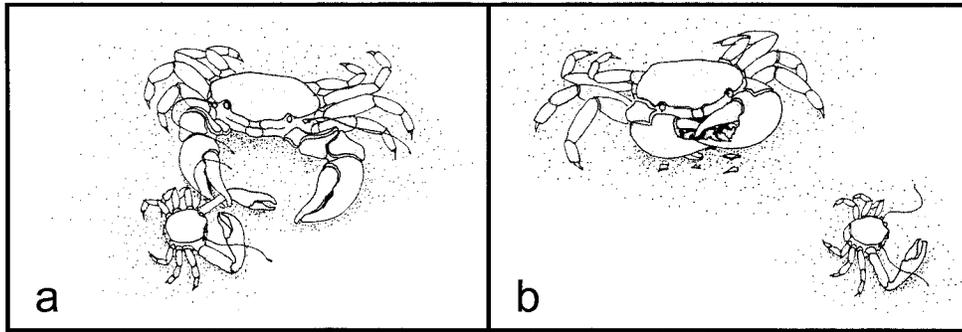
Each trial began with the addition of a single porcelain crab to the opposite end of the bucket from a labeled predator. During our pilot studies, it became clear that human observers frightened the crabs, preventing normal hunting behavior by the predators. We therefore recorded the encounters with a video camera positioned on a tripod directly above the bucket and let trials run for 2 h. Prey that were alive at the end of this period were removed and placed in the holding tank for release.

Video analysis was also essential for objectively scoring the outcome of trials; we used time-stamped video recordings of the trials to score various sequential behaviors and the time they occurred. The first behavior to be recorded was an attack, which we defined as the predator grabbing or attempting to grab the prey. We next determined whether the predator managed to obtain a secure hold on the prey. This was a somewhat subjective assessment consisting of our impression of whether the predator seemed to be in control of the prey (this typically occurred after a period of struggling during which the prey was not firmly grasped). After scoring a secure hold, we determined whether the prey escaped (was able to completely free itself from the predator and move away), and if so, by what means. The two most common escape mechanisms were autotomy and behavior we categorized as struggling/pinching. For crabs that escaped, we continued watching the sequence to follow subsequent attacks, captures, and escapes. For crabs that autotomized, we noted whether the predator ate the cheliped before resuming pursuit. Predatory behavior was compared for the different predator species by calculating for individual predators the attack rate (the proportion of trials in which the prey was attacked) and escape rate (the proportion of captured prey that escaped a secure hold).

The traditional definition of autotomy involves voluntary discarding of a body part. However, we found it impossible to objectively distinguish voluntary from involuntary (forced) limb loss. Therefore, we used a more workable definition of autotomy as "loss of a cheliped when the prey was held only by that cheliped" (see Figure 1). By using slow-motion video analysis, it was straightforward to score whether the predator ever held the prey only by the cheliped and whether cheliped loss occurred during this period. Our preliminary trials revealed that there was a nearly perfect correspondence between cheliped loss that we subjectively scored as voluntary and our objective measure of autotomy. Cheliped loss while the prey was grasped by both the body and the cheliped almost always looked involuntary, with the predator forcefully plucking off the offensive pinching appendages. On the other hand, cheliped loss while held only by the cheliped never looked forced. Indeed, it seems unlikely that a predator would have enough leverage to pull off a cheliped without having grasp on the body of the prey. Therefore our easily scored, working definition probably was an accurate assessment of autotomy.

### Statistical comparisons

We used Kruskal-Wallis tests to determine whether there were differences among the predator species in aspects of predation. Where significant differences were found, we used



**Figure 1**  
 (a) A purple shore crab captures a porcelain crab by firmly grasping its cheliped. (b) The porcelain crab has autotomized and is escaping while the shore crab eats the shed cheliped.

Mann-Whitney *U* test comparisons, with sequential Bonferroni-adjusted alpha levels (Rice, 1989) as post-hoc comparisons to determine which species in particular differed. For comparisons addressing attributes of the predator, we used mean values for the individual predators as the independent data points to avoid pseudoreplication. Analysis revealed that predator identity did not influence the autotomy decisions of the prey. Therefore, when investigating decisions of or consequences to prey, individual prey were used as the independent data points.

**RESULTS**

**Field determination of likely predators on porcelain crabs**

Porcelain crabs were extremely abundant under the 222 rocks we turned over in the mid-intertidal zone at two sites near Trinidad, northern California. In this survey, we found 1146 porcelain crabs (*Petrolisthes* spp.), with an average of about five per rock (Table 1). The most common potential predators under these rocks were five other crab species (Table 1), of which the purple shore crab (*H. nudus*) was by far the most abundant; 12% of the 158 rocks with *Petrolisthes* were also shared with at least one *H. nudus*. However, there was a significant negative correlation between numbers of porcelain crabs and purple shore crabs under rocks (Spearman rank correlation,  $r_s = -.24$ ,  $N = 222$ ,  $p = .0005$ ). The other crab species were too rare for any correlation to be determined.

In our survey, we encountered no other likely predators on porcelain crabs among the invertebrates seen under rocks; the various sea stars, anemones, and snails we found are not likely to attack rapidly enough to capture highly mobile prey such as porcelain crabs. Among vertebrates, we saw six monkey-faced eels (*Cebidichthys violaceus*) under these rocks; these fish may be potential predators on porcelain crabs but were rare and difficult to capture and thus were not collected for use in predation trials. Larger fish feeding in the area at high tide or shorebirds feeding at low tide may be significant predators. However, we observed none of these other vertebrate predators during the survey, and they were not included in our study.

**Experimental tests of four crab species as predators**

Predation experiments revealed that three of the four potential predators we collected will capture and eat porcelain crabs when given the opportunity. Purple shore crabs (*H. nudus*), striped shore crabs (*P. crassipes*), and Pacific rock crabs (*C. antennarius*) all ate the first porcelain crab they encountered in the laboratory, usually within minutes and in all cases within 24 h of enclosure with it. In subsequent trials with each of these species, a large proportion of porcelain crabs were attacked (Table 2), and there was no difference among these three species in the attack rates of individual predators (Figure 2; Kruskal-Wallis test:  $H = 0.003$ ,  $df = 2$ ,  $p = .99$ ). In contrast, none of the six black-clawed crabs (*L. bellus*) captured the porcelain crabs offered them in lab trials even after 4 days of enclosure with them. We therefore did not consider *L. bellus* a predator on porcelain crabs.

Although all three species attacked porcelain crabs, they were not equally effective as predators. The species differed in the rate at which prey escaped from individual predators following a secure hold (Figure 2; Kruskal Wallis test:  $H = 12.85$ ,  $df = 2$ ,  $p = .0016$ ). Turning to the perspective of individual prey (Table 2), all six crabs captured by *Pachygrapsus* escaped after being caught, whereas 69% (77/111) escaped from *Hemigrapsus* and only 29% (9/31) escaped from *Cancer*.

The differences in escape rates among predators mirror differences in mean predator body size: 25 mm for *Pachygrapsus* (the least effective predator), 36 mm for *Hemigrapsus*, and 57 mm for *Cancer* (the most effective predator). In addition, *Cancer* appeared to be a qualitatively superior predator, striking more rapidly and thereafter maintaining a firmer grip by using more appendages to clasp the prey tightly under the body.

**Frequency of autotomy in response to crab predation**

Both porcelain crab species used in our trials autotomized their chelipeds readily in response to crab predation, and autotomy occurred in response to attack by all three larger crab species (Table 2). Autotomy was a frequent event in the predation trials, occurring in 34% (59/173) of trials in which the

**Table 1**

**Abundance of porcelain crabs and their potential predators under 222 rocks at 2 sites near Trinidad, California, in May and June 1999 (crab species are listed in order of decreasing abundance)**

	<i>Petrolisthes</i> spp.	<i>Hemigrapsus</i> <i>nudus</i>	<i>Lophopanopeus</i> <i>bellus</i>	<i>Cancer</i> <i>antennarius</i>	<i>Pachygrapsus</i> <i>crassipes</i>	<i>Hemigrapsus</i> <i>oregonensis</i>
Total number found	1146	112	33	13	9	5
Average per rock	5.16	0.51	0.15	0.06	0.04	0.02
SD	6.78	1.41	0.50	0.31	0.41	0.17
Maximum per rock	40	7	3	2	5	1

**Table 2**  
Summary of the outcomes of predation trials with three species of predators and two species of prey

Predator	Prey species	No. of trials	Attacks	Secure holds	Autotomy with escape	Autotomy without escape	Escape by other means	No escape
<i>Pachygrapsus</i>	M	8	6	6	4	0	2	0
	C	24	18	16	2	0	1	13
<i>Hemigrapsus</i>	M	15	15	15	6	0	0	9
	C	66	62	54	19	1	13	21
Totals	C	79	72	57	27	0	18	12
	M	192	173	148	58	1	34	55

Prey species denoted by C = *Petrolisthes cinctipes*, M = *P. manimaculis*. The "no. of trials" column indicates the total number of trials carried out with each predator-prey combination; subsequent columns indicate the number of these trials that resulted in each different outcome. Each trial that resulted in a secure hold had one of the four possible outcomes listed in the rightmost four columns.

predator attacked the porcelain crabs. The porcelain crabs did not always have the opportunity to autotomize because in some trials they were continuously grasped tightly by the whole body, never just by the cheliped. Autotomy occurred in 67% (59/88) of cases where crabs were held by only the cheliped. Thus, among animals that had the opportunity to employ it, the frequency of autotomy was very high.

#### Effectiveness of autotomy as an antipredatory mechanism

Autotomy proved to be a highly successful antipredatory mechanism in our trials (Table 2); of 59 crabs that autotomized, 58 (98%) were able to escape the predator's grasp immediately after autotomy. In 50/59 trials, the predator completely stopped the pursuit and instead ate the shed cheliped following autotomy (Figure 1). In the eight cases where the

shed cheliped was not immediately consumed, the predator nevertheless tightly grasped the cheliped in its own claw, which probably reduced its efficiency to reattack the prey.

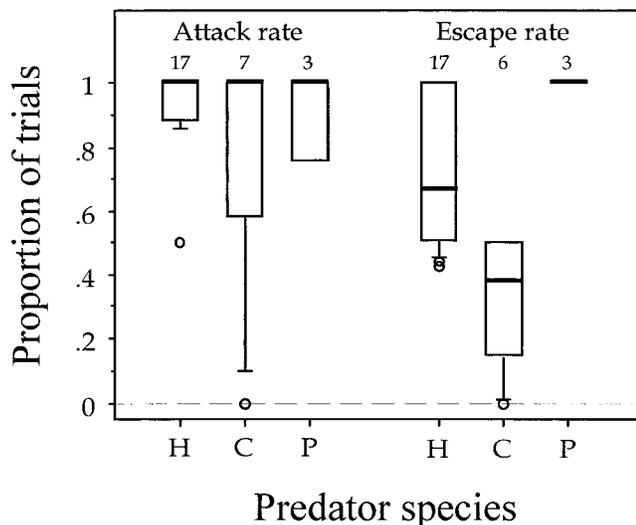
Autotomy was the only effective defense against *Cancer* predation; 8/9 crabs that escaped did so by autotomy, and the one crab that escaped without autotomy was let go for no apparent reason, not as a result of an alternative strategy. Autotomy was also effective against *Hemigrapsus* and *Pachygrapsus*, but porcelain crabs also escaped from these predators by using their claws to fight back. Overall, autotomy was the most frequent escape mechanism used against all three of the predators and by both of the prey species (Table 2).

## DISCUSSION

### Benefits of autotomy

We have demonstrated a strong antipredatory benefit to autotomy in crustaceans. Almost every porcelain crab that autotomized was able to escape the grasp of the predator, which typically halted the pursuit and instead consumed the shed cheliped. In contrast, the majority of crabs that did not autotomize never escaped. This certainly suggests that there is a strong selective advantage to autotomy. The generality of an antipredatory benefit is strengthened by our large sample sizes, by its demonstration in two different prey species (*P. cinctipes* and *P. manimaculis*), and by its effectiveness against three different predatory species.

The benefit to autotomy in invertebrates has received little previous attention. A benefit has been shown for spiders (Formanowicz, 1990; Klawinski and Formanowicz, 1994). Two studies suggest a benefit for crustaceans but did not quantify the benefit. In the first study, Robinson et al. (1970) twice observed a tame otter stop pursuit of a freshwater crab (*Potamocarcinus richmondi*) after a pinching cheliped was autotomized while still attached to the predator. However, it was not clear whether the crabs had already been securely captured when they autotomized. The benefit of such attack autotomy may therefore either be escape after capture, as with our porcelain crabs, or may be cessation of attack before capture. In the second study, Lawton (1989) examined the consequences of autotomy to the foraging success of a predator, the European edible crab (*Cancer pagurus*), that preyed on various other crab species. Lawton found that that cheliped autotomy was the most common cause of failure of the predator to capture large *Porcellana platycheles* but did not report the proportion of autotomies that resulted in escape. In contrast, autotomy by two other prey species was not effective against this predator. In an unspecified proportion of trials, *Pilumnus hirtellus* autotomized without escape. *Galathea*



**Figure 2**  
Variation within and among three predatory crab species in the proportion of trials in which individual predators attacked the prey (left) and the proportion of secure holds that were followed by escape by the prey (right). Box plots show the distribution of values for individual predators within each species: thick bar indicates median, box indicates 25th and 75th percentiles, thin bar indicates 10th and 90th percentiles, and points indicate values beyond 10th and 90th percentiles. Letters below box plot indicate predator identity: H = *Hemigrapsus nudus*, C = *Cancer antennarius*, P = *Pachygrapsus crassipes*. Number of predators in each sample indicated above plots.

*squamifera* autotomized in “most” of 30 trials, but only escaped in three of them (Lawton, 1989). Clearly, autotomy does not universally have an antipredatory benefit for all crab species against all predators.

### Identification of relevant predators that induce autotomy

Autotomy entails behavioral interactions between the predator and prey. Thus, for laboratory studies of autotomy to be relevant to elucidating the selective benefits of autotomy, it is critical to use predators that actually prey on the species being assessed. We identified three crab species (*C. antennarius*, *H. nudus*, *P. crassipes*) that not only readily attack porcelain crabs (*Petrolisthes* spp.), but regularly induce autotomy as a defense against their attacks. Although we were unable to directly confirm that these predators normally prey on porcelain crabs, several factors suggest that one or more of these species play a role in selecting for the maintenance of autotomy in the two porcelain crab species studied. These three larger crab species are the only potential predators that commonly co-occur with the prey species. All three showed high attack rates in the lab and captured a large proportion of the prey in the trials. Moreover, all prey that were killed were consumed by the predators; the relationship between these three species and porcelain crabs was clearly predatory, not competitive or territorial. The negative correlation we detected between purple shore crab (*H. nudus*) and porcelain crab abundance under rocks in the field may be due to the former eating the latter, or the latter avoiding the former. Moreover, the predators we brought to the laboratory gave us the impression of familiarity with porcelain crab prey by the rapidity with which they attacked the first one they were offered and by grabbing them in ways that minimized the chance of getting pinched. Indeed, this specific method of attack, grabbing the prey by a limb rather than the body, appears to be a prerequisite for successful autotomy by porcelain crabs, as it is in other taxa as well (e.g., legs rather than the body must be grasped to induce autotomy in spiders, Formanowicz, 1990).

### Distinguishing autotomy from other causes of limb loss

During the course of our study, it became clear that it was not always straightforward to distinguish autotomy, the voluntary shedding of limbs, from involuntary loss of limbs due to predator removal. We therefore used an explicit, objective definition of autotomy (cheliped autotomy = loss of cheliped while prey was held by only the cheliped) to prevent this ambiguity and to make our findings useful for comparative analyses. This issue is rarely discussed in the literature, possibly because most studies have focused on vertebrates where the nature of predation makes this ambiguity less relevant. While predators may rip off crabs' dangerous claws, presumably predators on vertebrates rarely intentionally remove tails, so all instances of tail loss during a predatory encounter are likely due to autotomy.

However, for invertebrates, and particularly for crustaceans, where there is a large literature on limb loss, it may be worthwhile to clarify the distinction between involuntary and voluntary limb loss (autotomy), both for field censuses and for laboratory experiments such as ours. Several studies have identified predators responsible for limb loss in crabs, but this is a broader category than autotomy and clearly includes forced prying off of limbs, which are severed at a predetermined breakpoint (autospasy *sensu* Wood and Wood, 1932). For instance, ibises have been observed (Bildstein et al., 1989) grasping sand fiddler crabs (*Uca pugilator*) by the base of a cheliped and shaking them vigorously until the cheliped is detached, and terrapins have been recorded (Davenport et

al., 1992) biting off the legs of European green crabs (*Carcinus maenas*). Smith (1995) found that some limb loss had occurred after small blue crabs (*Callinectes sapidus*) were enclosed with bigger ones, but whether the limbs were ripped off by the cannibalistic predator or self-amputated by the prey as an escape strategy was not clear. The distinction between autotomy and forced removal may not be critical for studies of the effects of limb loss on growth and reproduction, but it is critical to understand the autotomy decisions made by individuals in prey populations.

### A low threshold for autotomy in porcelain crabs

In our study, two-thirds of porcelain crabs that were held by a cheliped autotomized. Porcelain crabs thus seem unusually prone to autotomize. Indeed, they are well-known for their propensity to drop their chelipeds at the slightest provocation (Jensen, 1995; McVean, 1982; Wood and Wood, 1932). It is difficult to collect porcelain crabs in the field without a significant portion autotomizing, even when attempting to touch them gently and to avoid the claws. In contrast, all other crabs commonly encountered in the intertidal zone in this region can be handled quite vigorously without autotomy occurring. What accounts for the hair-trigger autotomy response of porcelain crabs?

For autotomy to be selectively advantageous, the benefits must outweigh the costs. Moreover, lower threshold stimuli for triggering autotomy should evolve in species for which the benefits are particularly high or the costs particularly low. We suggest that both high benefits and low costs may account for the ease with which porcelain crabs shed their chelipeds. The benefit of autotomy, increased probability of escape from a predator, will be particularly high for prey that has a low probability of escape by other means. Porcelain crabs are small and may be less well able to defend themselves by fighting back than larger crab species. Indeed, even within the porcelain crab species we studied, larger individuals were better at fighting back and thus less likely to autotomize (Wasson et al., unpublished data). It would be interesting to examine the frequency of autotomy versus escape by other mechanisms for a variety of crab species of different sizes to determine whether the benefit appears greater, and the threshold lower, in smaller species.

There are many potential costs to autotomy, including the short-term costs of doing without the lost appendage (reduced ability to ward off further attacks, diminished attractiveness to the opposite sex, lower foraging ability, etc.) and the long-term costs to growth and reproduction of expending energy to replace it. There is an extensive literature (reviewed by Juanes and Smith, 1995) reporting that many such costs are indeed incurred by various crab species. One of these costs, reduced foraging ability, may be relatively lower in porcelain crabs because they do not need chelipeds for their primary feeding mode, suspension feeding using mouthparts. Again, comparative analyses could test the prediction that the threshold for autotomy is generally lower in suspension feeders than in otherwise comparable foragers that depend on their chelipeds for feeding. Elucidation of the selection pressures on autotomy thresholds in different species is a fruitful area for future research.

### Large chelipeds: the key to successful autotomy?

Autotomy, like any other defensive strategy, can be fully understood only by considering the behavior of both the predator and the prey and the interaction between them. Successful autotomy depends not only on the abilities of the prey but also on the perception and responses of the predator. For

porcelain crabs, escape by autotomy depends critically on the predator (1) grabbing the cheliped without firmly grasping the body and (2) abandoning pursuit after release of the cheliped. The remarkably large chelipeds of these porcelain crabs (more than double the body length) may increase the likelihood of both of the two requisite predatory behaviors.

The large chelipeds of porcelain crabs may serve as targets that divert a predator's attention away from the body. A similar function has been ascribed to the brightly patterned tails of some delicate, poorly defended lizards that rely on autotomy for escape (Vitt and Congdon, 1978). Besides making it more likely that the prey is grabbed in such a way that autotomy can occur, the possession of huge chelipeds may also improve the chance of escape after autotomy. Optimal foraging decisions are expected to be based on the nutritive value of the food items, all else being equal (Stephens and Krebs, 1986), so the likelihood that a predator will abandon pursuit after autotomy may increase with the size of the cheliped. In a detailed analysis of foraging profitability, Lawton (1989) concluded there was no energetic basis for *Cancer* crabs to concentrate on the autotomized chelipeds of their porcelain crab prey. However, his calculations were based on profitability after the prey item was already captured and did not take into account the time required to recapture a successful autotomist, nor the probability that the attempted recapture would be unsuccessful. Moreover, acquiring the cheliped may involve a lower risk of injury to the predator than obtaining the whole body. With these two additional costs factored in, the optimal foraging strategy for some predators on porcelain crabs might be to accept autotomized chelipeds or even to target chelipeds for attack and acquisition. Indeed, we found that the majority of predators abandoned pursuit and ate the large shed cheliped after autotomy.

The possibility that prey cheliped size affects predator tactics raises the intriguing prospect of predator-mediated natural selection on prey cheliped size. Indeed, the large size of porcelain crab chelipeds may have been selected for by interactions with their predators. In any case, the behaviors we documented in this study have no doubt been shaped by complex interplay between the foraging strategies of predators that induce autotomy and eat autotomized limbs and the defensive strategies of their autotomizing prey.

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