

ORIGINAL ARTICLE

Autotomy in porcelain crabs is an effective escape mechanism from rockfish predation

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Anti-predatory behavior; crabs; natural selection; porcellanidae; rockfish; seabastes.

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Abstract

Porcelain crabs possess a 'hair-trigger' propensity to autotomize their chelipeds (claws), and laboratory studies have demonstrated that this ability is highly effective in avoiding predation from other crabs. However, porcelain crabs are also subject to predation from fishes, which use a very different means of capture. In this study, we investigated whether autotomy in porcelain crabs is also effective against predation by fishes. To do this, we examined stomach-contents data from four common species of kelp-forest rockfishes and determined the frequency of disassociated chelipeds (those with no associated bodies) in porcelain crabs and in brachyuran crabs, which do not readily autotomize their chelipeds. We found that disassociated chelipeds of porcelain crabs were six times as common as those of brachyuran crabs (35% of the remains of all porcelain crabs *versus* 6% of the remains of all brachyuran crabs). We interpret this difference to be evidence that, through autotomy, porcelain crabs escaped ingestion of their entire bodies, and thus certain mortality, at a higher rate than did brachyuran crabs. We conclude that autotomy constituted an effective escape strategy from rockfish predation. This evidence, in conjunction with previous studies, suggests that autotomy of chelipeds in porcelain crabs is an effective anti-predatory strategy against phylogenetically disparate predatory groups.

Introduction

Predation is arguably the strongest selective force imposed by heterospecifics on life history and behavioral evolution (e.g. Reznick & Endler 1982; Stearns 1992). Among the many anti-predatory mechanisms observed in animals is autotomy, the ability to voluntarily shed an appendage. Autotomy has evolved independently in a wide variety of animals (Wood & Wood 1932; McVean 1982; Wasson *et al.* 2002; Bely & Nyberg 2010). For example, some rodents, salamanders, and lizards autotomize their tails, and the thrashing tail often distracts the predator while the prey escapes (Arnold 1988; Maginnis 2006; Fleming *et al.* 2007; Bateman & Fleming 2009). Additionally, spiders and insects autotomize legs (Arnold 1988; Maginnis 2008), sea stars and brittle stars autotomize arms (Mauzey

et al. 1968; Lawrence 1992), and crabs autotomize chelipeds and other appendages (McVean 1982; Juanes & Smith 1995; Wasson *et al.* 2002; Wasson & Lyon 2005). Despite its apparent immediate advantages for survivorship, autotomy can have important negative consequences for the prey. The costs can include impaired locomotion, foraging, survivorship, and/or reproduction, in addition to the long-term energetic costs of replacing the autotomized appendage (Arnold 1988; Juanes & Smith 1995; Barriá & González 2008).

Porcelain crabs (Porcellanidae) readily autotomize their chelipeds (claws) and the value of this behavioral trait in escaping predation has been well demonstrated (Wasson *et al.* 2002; Wasson & Lyon 2005). In laboratory trials, porcelain crabs whose chelipeds were grasped by predatory brachyuran crabs often autotomized those chelipeds

and escaped (Wasson *et al.* 2002). This behavior was complex, in that porcelain crabs often did not autotomize when attacked by smaller predatory crabs, and instead used their chelipeds to fight off the predators, which also often resulted in escape (Wasson & Lyon 2005). However, porcelain crabs are also preyed upon by a variety of fishes (Randall 1967), including fish of the genus *Sebastes* (e.g. Larson 1972; Murie 1995; Kosman *et al.* 2007). Rockfishes are typically much larger than predatory crabs, and their mode of predation is different. As generalized acanthopterygian predators, rockfish (Hobson 2006) typically engulf or otherwise grasp porcelain crabs and swallow them whole, whereas the predatory crabs grasp parts of the porcelain crabs, subdue them, and consume them in pieces (Wasson *et al.* 2002). In this study we attempt to determine whether porcelain crabs use autotomy as a successful defense against predation by these crab-consuming fishes.

Our study takes advantage of an earlier comparative stomach-contents analysis of four species of kelp-forest rockfishes (*Sebastes*) (Larson 1972). These rockfishes consume a variety of small crabs, including porcelain crabs [primarily *Pachycheles rudis* (Stimpson, 1859), but also *Petrolisthes* sp.], which are common inhabitants of temperate kelp forests and rocky reefs off California (Haig & Abbot 1980). Field and laboratory observations (R. J. Larson, personal observations, Van Syoc 1983) indicate that these species of fish typically lie in wait for prey, and capture them by suction or grabbing in a quick lunge. Accordingly, crabs in stomach contents almost always occurred as complete carcasses, usually with chelipeds attached. However, the data sheets for Larson's (1972) study also noted instances in which chelipeds with no

corresponding crab body occurred in stomachs. We took advantage of these observations to explore the possibility that autotomy of chelipeds by porcelain crabs was also an effective defense against a very different type of predator from the predatory crabs studied previously (Wasson *et al.* 2002; Wasson & Lyon 2005). Porcellanid crabs are taxonomically diverse and geographically widespread (Haig 1960; Stillman & Reeb 2001; and references therein), and autotomy seems to be a general characteristic of the group (Wasson *et al.* 2002). It is not possible to know the conditions under which autotomy first evolved in this group, but to be truly successful, this defense mechanism should be effective against a range of predators that may use different methods of subduing and capturing prey. This paper provides a first attempt to address the generality of the defense offered by cheliped autotomy in porcelain crabs.

Study Area

To determine whether autotomy of chelipeds plays any role in predation by rockfish upon porcelain crabs, we report the occurrence of either complete crab carcasses or disassociated chelipeds in the stomach contents of four species of rockfish (*Sebastes atrovirens* (Jordan & Gilbert 1880), *Sebastes carnatus* (Jordan & Gilbert 1880), *Sebastes chrysomelas* (Jordan & Gilbert 1881), and *Sebastes caurinus* (Richardson 1844; Fig. 1) from rocky reefs and kelp forests off Southern California. One hundred specimens of each species were collected by spear in 34 collections made between November of 1969 and April of 1972 at a number of locations near Santa Barbara and Santa Cruz Island, California (approximately

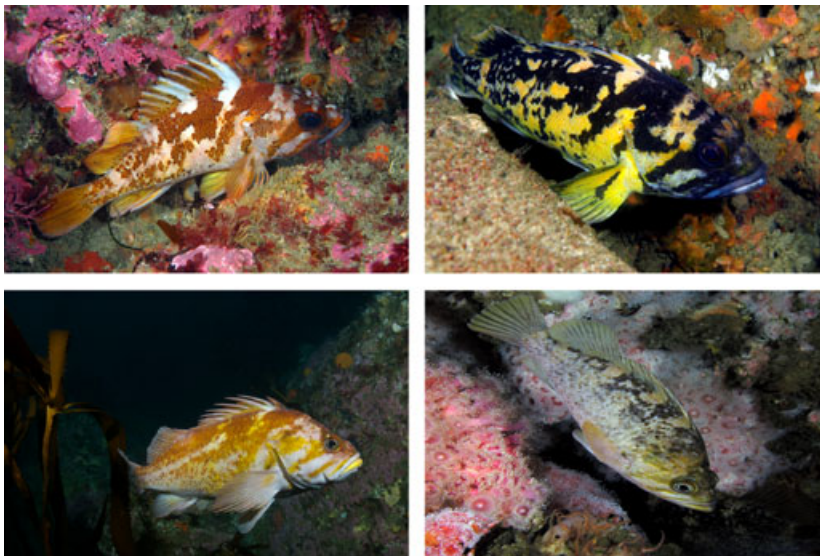


Fig. 1. The four species of nearshore rockfish included in this study (clockwise from top left): *Sebastes carnatus*, *Sebastes chrysomelas*, *Sebastes atrovirens*, and *Sebastes caurinus*. Photo credits: first three clockwise photos from top left by Kevin Lee, and bottom left by Clinton Bauder.

119°40'–58' W, 34°22'–26' N, and 119°30'–48' W, 33°57'–34°5' N, respectively).

Study Species

The four species of rockfish used in this study are closely related, forming a monophyletic clade (Hyde & Vetter 2007), and are morphologically similar (Fig. 1). They do not possess specialized or highly differentiated oral or pharyngeal dentition. Our laboratory and field observations indicate that they typically ambush and swallow prey whole. They consume the same general array of prey but differ in the proportions of different types of prey consumed (Larson 1972; see also Hobson & Chess 1976; Van Dykhuisen 1983; Hallacher & Roberts 1985; Murie 1995).

Methods

Fish were collected by SCUBA divers roughly as they were encountered, except that sampling was limited to post-juveniles (greater than about 100 mm standard length). Within hours of a collection, specimens' abdomens were incised, and specimens were fixed in 10% formalin. Later, specimens were rinsed in fresh water and stored in 45% ethanol. Stomach contents were later examined, and prey identified to the lowest possible taxon. In the original data sheets, crabs were typically noted by species, number present, and the estimated percentage of the entire stomach contents volume constituted by members of a species, and sometimes as well-digested masses that were difficult to identify beyond general categories. No particular note was ever made of crab bodies without chelipeds present,

and chelipeds were typically attached to bodies or, less often, were separate but could be matched with bodies (R. J. Larson, personal communication). However, the data sheets did specifically note those cases in which chelipeds were found alone, not matched with any other remains. For this study, we reviewed the original data sheets, and recorded the number of clearly identifiable complete carcasses (the typical notation of crabs present with no other comment) and of chelipeds found unassociated with other remains for three brachyuran genera (*Cancer*, *Lophopanopeus*, and *Paraxanthias*; Fig. 2) and two porcellanid genera (primarily *Pachycheles*, but also one instance of *Petrolisthes*; Fig. 2). These species of brachyuran crabs have relatively large chelipeds (in comparison with majid crabs, for example), although not as large in proportion to body size as those of porcelain crabs. Individual *Cancer* crabs averaged about 1 ml 'standardized' volume (standardized for fish size), *Lophopanopeus* crabs averaged about 0.6 ml, *Paraxanthias* averaged almost 2 ml, and porcelain crabs averaged 3.7 ml (Larson 1972).

We considered the occurrence of either an entire crab carcass or a disassociated cheliped to be the result of a 'successful' attack, a strike in which the fish captured some food, as opposed to the unknowable number of strikes in which the entire crab escaped. We interpret the occurrence of a disassociated cheliped to be evidence of a strike in which the fish obtained only the cheliped but the crab itself escaped. It seems most likely that the presence of a disassociated cheliped would be the result of either autotomy (in which the crab voluntarily shed its cheliped upon being grasped by the fish) or forced removal (in which the fish grasped the cheliped but the



Fig. 2. Representative species of porcelain and brachyuran crabs (clockwise from top left): *Petrolisthes manimaculis*, *Pachycheles rudis*, *Lophopanopeus bellus*, and *Cancer productus*. Photo credits (clockwise from top left): Dr. Jonathan Stillman (San Francisco State University), Dr. Jim Nestler (Rosario Beach Marine Laboratory), Dr. Thomas M. Niesen (San Francisco State University), and Dr. Jim Nestler (Rosario Beach Marine Laboratory).

force of movements during the strike caused the cheliped to separate from the body of the crab). We compared the relative incidence of disassociated chelipeds from porcellanid and brachyuran crabs, because the brachyuran crabs also have relatively large chelipeds (Garth & Abbot 1980), but do not readily autotomize (Wasson *et al.* 2002). In particular, we compared the ratio of chelipeds found alone with no associated carcass, with the total number of remains (disassociated chelipeds plus full carcasses) between porcelain and brachyuran crabs, as this is the measure of the percentage of strikes by rockfish that resulted in ingestion of only the cheliped out of all 'successful' strikes. A higher percentage of disassociated chelipeds in porcelain crabs would indicate the following: (i) it would indicate that autotomy likely occurred in porcelain crabs (that is, that the disassociated chelipeds are not simply the result of forced removal by the fish, which would occur with similar likelihood in porcellanid and brachyuran crabs in the absence of autotomy), and (ii) it would indicate that 'successful' predatory attacks on porcelain crabs did not lead as often to the immediate death of the crab (only ingestion of the cheliped) as in brachyuran crabs, so that autotomy reduced the rate of immediate mortality due to rockfish predation in porcelain crabs.

The disassociated chelipeds in the stomachs were all easily identifiable as such and none was noted as being highly digested. Additionally, the decalcified remains of crab exoskeletons in the anterior intestine, often with chelipeds attached, could sometimes be identified. Therefore, disassociated chelipeds were not the result of evacuation of the rest of the body while the cheliped remained in the stomach. We do not distinguish among brachyuran taxa in our results. Most of the disassociated chelipeds from this group were identified as 'Cancer-like' because the chelipeds, particularly of *Cancer* and *Lophopanopeus*, were difficult to distinguish. However, in general, *Cancer* was the most abundant genus, followed by *Lophopanopeus* and then *Paraxanthias* (Larson 1972).

We made several comparisons of the frequencies of whole carcasses versus disassociated chelipeds. Our primary hypothesis was that if autotomy allowed porcelain crabs to escape total consumption, the frequency of disassociated chelipeds should be higher in porcellanid crabs than in brachyuran crabs. We tested this by comparing the relative frequencies of disassociated chelipeds to whole carcasses in porcelain crabs to those of brachyuran crabs in the diets of all species of rockfish combined. We further compared these frequencies in *S. carnatus* and *S. chrysomelas* (the species which consumed the most crabs) separately, to evaluate whether this was consistent for both of the main crab-consuming species. We used additional comparisons to determine whether any differences in the manner of feeding among the species of

rockfish influenced the occurrence of disassociated chelipeds. To determine whether differences in the manner of feeding, if any, among the species of rockfish influenced the rate of presumed forced removal of chelipeds, we compared the frequencies of whole carcasses and disassociated chelipeds of brachyuran crabs alone between the four species and between *S. carnatus* and *S. chrysomelas* separately. Finally, to determine whether differences in the manner of feeding, if any, influenced the occurrence of disassociated chelipeds in the two species that were most likely to eat crabs (and which had a sufficient sample size for comparisons to be made), we compared the frequencies of whole carcasses and disassociated chelipeds of porcellanid crabs alone between *S. carnatus* and *S. chrysomelas*. Statistical comparisons employed log-likelihood tests of independence (G tests with Williamson's correction; Sokal & Rohlf 1995).

Results

Disassociated chelipeds represented over one-third of the total remains of porcelain crabs in the diets of the four species of rockfish, a significantly higher frequency than with brachyuran crabs. A total of 34 complete carcasses or disassociated chelipeds of porcellanid crabs occurred in the stomachs of the four fishes, of which 12 (35.7%) were disassociated chelipeds (Table 1). Of the 245 instances of brachyuran crabs or chelipeds recorded in the stomachs of the fishes, 14 (5.7%) were disassociated chelipeds. The frequencies of whole carcasses and disassociated chelipeds differed significantly between the brachyuran and porcelain crabs in the stomachs of all four species of fish combined ($G_{adj} = 10.16$, $df = 1$, $P < 0.005$). This difference was consistent in the two main crab-eating fishes, *S. carnatus* and *S. chrysomelas*. The frequency of disassociated chelipeds differed signifi-

Table 1. Number of individual prey that occurred as complete carcasses or as disassociated chelipeds in the stomach contents of four species of *Sebastes* rockfishes. In all, 100 specimens of each species of rockfish were examined.

	brachyuran crabs <i>Cancer</i> , <i>Lophopanopeus</i> , and <i>Paraxanthias</i>		porcellanid crabs <i>Pachycheles</i> and <i>Petrolisthes</i>	
	complete	cheliped only	complete	cheliped only
<i>S. atrovirens</i>	8	1	0	0
<i>S. carnatus</i>	69	2	10	4
<i>S. chrysomelas</i>	116	8	11	7
<i>S. caurinus</i>	38	3	1	1
Total	231	14	22	12

cantly between brachyuran and porcellanid crabs in each of these species (*S. carnatus*: $G_{\text{adj}} = 7.152$, $df = 1$, $P < 0.01$; *S. chrysomelas*: $G_{\text{adj}} = 11.379$, $df = 1$, $P < 0.001$).

The disassociated porcelain crab chelipeds occurred at a consistent rate in the two main crab-eating species, *S. carnatus* and *S. chrysomelas* (29% and 39% of all porcellanid remains, respectively; Table 1). The relative frequency of whole carcasses and disassociated chelipeds in porcellanid crabs alone did not differ significantly between these species ($G_{\text{adj}} = 0.355$, $df = 1$, $P > 0.5$). This indicates that the high occurrence of disassociated chelipeds was not limited to one species of fish. The occurrence of porcelain crabs was too low in the other species for statistical comparisons.

Finally, the occurrence of disassociated chelipeds in brachyuran crabs was consistently low among the four species, and between the two main crab-eating species of fish (*S. atrovirens*: 11%, *S. carnatus*: 3%, *S. chrysomelas*: 7%, and *S. caurinus*: 7%; Table 1). The relative frequencies of whole carcasses and disassociated chelipeds in brachyuran crabs alone did not differ significantly across the four species of rockfish ($G_{\text{adj}} = 1.77$, $df = 3$, $P > 0.5$) or between *S. carnatus* and *S. chrysomelas* ($G_{\text{adj}} = 1.269$, $df = 1$, $P > 0.1$). This indicates that any differences in the methods of foraging among the species did not affect what we presume to be the rate of forced removal of chelipeds.

Discussion

Anti-predatory strategies are often effective against a range of predators, such as chemical and visual defenses, armor, speed, and schooling/herding behavior. However, not all defenses are effective against all types of predators. For example, visual defenses would be ineffective against non-visual predators, and schooling behavior in fishes is ineffective against some types of predators (e.g. Benoit-Bird & Au 2009). Further, differing induced defenses against different types of predators (e.g. Freeman 2007) are often cases in which a single defense is not useful against all types of predators. Similarly, caudal tail autotomy in lizards is more effective against some methods of attack than others (Bateman & Fleming 2009). However, for porcelain crabs, it has been unclear whether autotomy is only effective against predation by predatory crabs (Wasson *et al.* 2002; Wasson & Lyon 2005) and not effective against other groups, such as fishes, with an entirely different mode of attack.

Wasson *et al.* (2002) suggested that large benefits and small costs likely account for the exceptionally high incidence of autotomy in porcelain crabs. However, their studies applied to only one type of predator. The rockfishes we studied, especially *S. chrysomelas* and

S. carnatus, are effective predators of crabs (Table 1), and pose the threat of a different style of predation on porcelain crabs. However, although the rockfishes were capable of consuming whole porcelain crabs, autotomy apparently allowed porcelain crabs to escape in about one-third of the strikes in which the fish was able to grasp and consume at least part of the crab (Table 1).

Disassociated chelipeds from porcelain crabs occurred significantly more often than brachyuran chelipeds in the four fish species combined, and in both *S. carnatus* and *S. chrysomelas*, the main crab-eating species. Furthermore, no significant difference was observed between *S. carnatus* and *S. chrysomelas* in the frequency of disassociated chelipeds of porcellanid crabs, and no significant difference in the frequency of disassociated brachyuran chelipeds was found among the four species or between *S. chrysomelas* and *S. carnatus* when compared separately. These comparisons among species of fish predators indicate that other than the greater predilection for crabs in *S. carnatus* and *S. chrysomelas*, the predator-prey interactions between these fishes and crabs, insofar as they affect the consumption of chelipeds, were similar, and that the higher frequency of disassociated chelipeds in porcelain crabs than in brachyuran crabs was not a species-specific phenomenon. We interpret these results to mean that the high frequency of disassociated porcellanid chelipeds in the stomachs of these fishes was related to the ability of porcelain crabs to autotomize their chelipeds. We think it most likely that the comparison between porcelain crabs and brachyuran crabs means that the higher frequency of porcellanid chelipeds was not the result of forcible removal (which should have occurred at about the same frequency as in the brachyuran crabs) but the result of autotomy. However, it is also possible that the structure of the joint between the cheliped and the body in porcellanid crabs made forcible removal of chelipeds easier in porcelain crabs. In either case, each occurrence of disassociated chelipeds represents an instance in which a successful strike by a fish predator did not result in the immediate mortality of the crab.

Our personal observations of rockfish feeding in the laboratory and field suggest that the main defenses of crabs against rockfish predation are hiding (under rocks and algae), flight to cover, crypsis, and large size. Crabs in the size range consumed by the rockfishes might fend off a rockfish attack with its chelipeds (with chelipeds spread, the body of the crab in effect becomes larger; in Fig. 2, the *Lophopanopeus* specimen demonstrates this posture), but the crabs cannot fight (that is, attempt to injure) the much larger predator using their chelipeds. Autotomy, then, provides a partial defense against an effective predator, with little opportunity for the tradeoff

between fighting and autotomy observed against other crab predators (Wasson & Lyon 2005). Further analysis of the interactions between fish and porcelain crabs may be useful. For example, Van Syoc (1983) found that handling times for dead crabs (the time required to position food in the mouth before swallowing) increased in an almost exponential fashion with the size of crab in one species of rockfish. This handling may offer an opportunity for autotomy to occur. We predict, based on Van Syoc's results, that autotomy is more likely to lead to successful escape in larger porcelain crabs, which require longer handling time.

While autotomy appears to have been successful in reducing immediate mortality due to predator strikes in porcelain crabs, brachyuran crabs do not commonly employ autotomy. Porcelain crabs are filter feeders (Wicksten 1973; Haig & Abbot 1980; Jensen 1995), so autotomy of chelipeds may not have as negative an effect on foraging as in brachyuran and other crabs (Wasson *et al.* 2002). In addition, it would be valuable to observe the actual interactions between fish predators and porcelain crabs. Especially in relation to the porcelain crabs, the large chelipeds relative to their body size may increase the chance that a fish grasps mainly the cheliped when feeding, and in conjunction with autotomy and/or weakness in the joint with the body, helps increase the likelihood that porcelain crabs escape immediate predation.

Conclusions

We present evidence that porcelain crabs escape immediate mortality from rockfish predation more often than brachyuran crabs because the fish captures the cheliped but not the rest of the crab. We attribute this largely to autotomy, or autotomy-related anatomical features of the porcelain crabs (perhaps a weak cheliped-body joint, and the large size of the chelipeds). Brachyuran crabs do not utilize autotomy as often as porcelain crabs, possibly because they require their chelipeds for foraging, unlike porcelain crabs, which are filter feeders. This is the first demonstration of an anti-predatory benefit of the behavior for porcelain crabs from a vertebrate predator, and shows that anti-predatory autotomy in porcelain crabs is not limited to crab predators (Wasson *et al.* 2002; Wasson & Lyon 2005). This study also indicates that while prey must contend with varied selective pressures from multiple predators, autotomy may be effective against phylogenetically and ecologically disparate predators. Lastly, we suggest that more extensive comparisons of the effectiveness of anti-predatory strategies across widely dissimilar predators should be instructive for a more complete understanding of the factors that shape behavioral and life-history evolution.

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