



The ecological consequences of limb damage and loss in decapod crustaceans: a review and prospectus

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Abstract

Autotomy, the reflex severance of an appendage, is considered an adaptation to avoid predators and limit wounds. While an autotomy response may provide immediate survival benefits, the loss of one or more appendages can result in long-term functional and energetic costs. In this paper, we present an overview of the incidence of limb damage and loss in decapod crustaceans; review the literature on the ecological consequences of such injury; and suggest areas for future research. A survey of limb damage and loss in field populations showed consistently high incidences of injury in 14 reviewed species. Typically, chelipeds were the limb type lost most often and injuries were distributed symmetrically. No consistent correlation existed between injury frequency and body size among species. In general, the frequency of injury was independent of sex and moult stage. Fishery practices were responsible for substantial limb loss in some commercial species. In terms of energetic costs, experiments demonstrated that limb injury could reduce growth increment and affect intermoult duration. Functionally, limb damage was capable of reducing foraging efficiency and mating success, and increasing vulnerability to intra- and interspecific attack. The magnitude of these effects depended on the type and number of limbs lost. Given the prevalence of injury in decapod crustacean populations, the costs involved, and the ecological importance of many crustacean species, nonlethal injury has the potential to affect population dynamics and community processes. Convincing evidence of autotomy's effects beyond the level of the individual, however, is, at present, lacking. Future work should redress this shortcoming. In addition, comparative studies are needed on decapod species from different habitats and with different lifestyles before generalizations can be made about the costs and benefits of autotomy.

Keywords: Autotomy; Decapod crustacean; Functional and energetic costs; Injury frequency; Limb damage; Limb loss; Regeneration; Survival benefits

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1. Introduction

Autotomy is a reflexive response to injury or its threat that results in the casting off of an appendage at a predetermined breakage plane (Wood & Wood, 1932; Hopkins, 1993). Tail autotomy by vertebrates (lepidosaurans, salamanders, and rodents) (Arnold, 1988) and limb autotomy in asteroids, ophiuroids (Mauzey et al., 1968; Lawrence, 1992) and spiders (Formanowicz, 1990) is usually a response to predator attack that facilitates escape but one that also carries ecological costs (Arnold, 1988; Lawrence & Larrain, 1994). Many decapod crustaceans are capable of autotomizing limbs; evidence of the response can be found in primitive fossil crabs from the Cretaceous (Wood & Wood, 1932). Frédéricq published a description of the crustacean autotomy mechanism in 1882, and since that time, most of the research has focused on the physiology and anatomy of limb loss and how it affects moulting and regeneration (see reviews by Wood & Wood, 1932; Bliss, 1960; Needham, 1965; Goss, 1969; McVean, 1975, 1982; Skinner, 1985; Hopkins, 1988). In contrast, relatively few studies have examined the ecological causes and effects of such trauma in decapod crustaceans.

The benefits of autotomy are thought to include predator avoidance and wound limitation (Bliss, 1960; McVean, 1982). The response likely serves as a final means of preventing subjugation by a predator after other avoidance measures have failed (crypsis, fleeing; Endler, 1986). For example, Lawton (1989) noted that autotomy in the anomuran *Porcellana platycheles* was effective in preventing capture by the brachyuran *Cancer pagurus*. Autotomy may be particularly important in aquatic environments, where waterborne chemical cues can alert predators (e.g. Zimmer-Faust, 1989) to a wounded animal's predicament. Injury, however, is not requisite to autotomy. Robinson et al. (1970) demonstrated that some species of tropical terrestrial crabs will grasp attacking predators with their cheliped(s) and actively autotomize the limb(s).

Benefits of autotomy will be partially offset if functional and energetic costs are incurred. These potential costs include reduced growth, lowered foraging efficiency and mating success, and increased vulnerability to intra- and interspecific attack (e.g. Kuris & Mager, 1975; Sekkelsten, 1988; Smith & Hines, 1991a; Davenport et al., 1992; Smith, 1992, 1995). The effects of limb loss on growth are potentially important because differences in relative body size have been shown to be critical to the outcome of various ecological interactions such as predator-prey encounters and intraspecific competition (O'Neill & Cobb, 1979; Hyatt, 1983; Garvey et al., 1994). Body size can also strongly determine the ability to attract mates (e.g. Salmon, 1983; Sekkelsten, 1988; Reid et al., 1994; van der Meeren, 1994) and the level of reproductive output (Hines, 1982). The degree to which individual performance is handicapped will vary with the type and number of missing or regenerating limbs (Smith & Hines 1991a, Smith 1992, 1995) and with the length of time the animal must function without its services. In turn, the extent to which populations are affected by autotomy will depend on the frequency and type of limb loss in the population and the cumulative effect these injuries have on survival and reproduction (Harris, 1989). Many decapod crustaceans are

important predators, grazers, and bioturbators in aquatic communities (e.g. Abrahamsson, 1966; Bertness, 1985; Coen, 1988; Hines et al. 1990). If injury is common in such species and costs are significant, autotomy could have profound direct and indirect effects in the community. Commercially, knowledge of the extent of injury in fishery populations (including injury due to the fishing process itself) and the effects of injury on growth and reproduction should be incorporated into population growth models to produce improved stock assessments. In this paper, we present an overview of the incidence of limb damage and loss in field populations; review the literature on the ecological effects of limb loss and damage; suggest important individual, population and community effects; and finally give a prospectus in which we outline specific areas where more work is needed.

2. Prevalence of limb loss in natural populations

Table I summarizes a literature survey of the incidence of injury in natural populations of decapod crustaceans. A total of 14 species in 27 studies are represented, of these, four were commercially important (*Cancer magister*, *Callinectes sapidus*, *Paralithodes camtschatica*, *Homarus americanus*). Injury was measured in a variety of ways (e.g. missing limbs only, missing and regenerating limbs, missing chelipeds only), but for all species, injury was consistently high. Various studies noted lower frequencies of regenerating than missing limbs, suggesting that animals may experience increased mortality following injury (McVean & Findlay, 1979; Shirley & Shirley, 1988). Such comparisons are difficult to interpret, however, because: (1) animals that have nearly regenerated a limb of normal length are easily missed (instances of reversal of cheliped asymmetry being an exception), and (2) the relative frequency of injured animals will increase in populations dominated by older individuals and in species with a terminal ecdysis.

Patterns of limb loss were remarkably consistent within and among species and probably reflect both the limb function and the behavioral response of the animal to the injury-causing agent. In species where it was examined, single limb loss was the most common injury; chelipeds were the limb type lost most often (exceptions are *Cyrtograpsus angulatus*, *Paralithodes camtschatica*, and *Chionoecetes bairdi* where walking legs were most often autotomized); and injuries were typically distributed symmetrically (when exceptions occurred, injuries were all biased to the right side). These patterns would be expected if: (1) animals seek to minimize the number of limbs lost; (2) autotomy's effectiveness as an escape mechanism differs along the anterior-posterior axis; and (3) prey movement and predator attack are random in direction. In any encounter with a predator, decapod crustaceans should attempt to escape with the loss of, at most, a single limb. In fact, multiple limb loss is relatively rare, yet it occurs more frequently than would be predicted by chance. A number of authors (e.g. Needham, 1953; Easton, 1972; McVean, 1976; Shirley & Shirley, 1988) have suggested that prior limb loss

Table 1
Incidence of limb damage and loss in natural populations of decapod Crustaceans

| Species | Size (mm) ^a | Sex ratio ^b (or other sorting) | Sampling time | No. of animals examined ^c | % Injury | Methods used to measure injury ^d | Most injured limb ^e | Symmetry in limb loss ^f | Size correlation ^g | Sex bias ^h | Reference |
|----------------------------|------------------------|--|-------------------|--|------------------------|--|--------------------------------------|--|----------------------------------|--------------------------|-----------------------------|
| <i>Cancer magister</i> | 159-169 | 65:35 | May-Nov. '84-'85 | 878 | 25.0 | E | C | Y | 0 | 0 | Shirley & Shirley, 1988 |
| <i>Cancer magister</i> | 62-197 | 89:11 | Dec. '71-Feb. '73 | 3085 | 66.0 | B | C | Y | | | Durkin et al., 1984 |
| <i>Cancer magister</i> | | | Jan.-Sept. '47 | 3886 | 15.8 | M ^m | | | | | Cleaver, 1949 |
| <i>Cancer magister</i> | | (offshore) | Jan.-Sept. '48 | 5383 | 20.1 | | | | | | |
| <i>Cancer magister</i> | | (bays) | Nov. '47-Jan. '50 | 4092 | 23.1 | M | | | | | Waldron, 1958 |
| <i>Cancer magister</i> | | | Nov. '47-Jan. '50 | 2157 | 37.8 | | | | | | |
| <i>Cancer magister</i> | | | '70-'72 | | 17.0 | | | | | | Ames, pers. comm. in Durkin |
| <i>Cancer magister</i> | >100 | Females | May '86 | 181 | 12.0 (60) ⁱ | E | C | Y | | | Juanes & Hartwick, 1990 |
| | | Mated males | | 227 | 8.0 (9) | | | | | | |
| | | Unmated males | | 500 | 22.0 (60) | | | | | | |
| <i>Cancer pagurus</i> | | Females | Summer '72 | 938 | 4.8-9.9 | B | C | Y | 0 | | Bennett, 1973 |
| | | Males | | 1482 | 8.1-13.2 | | | | | | |
| <i>Callinectes sapidus</i> | 12:48:40 ⁱ | 67:33 | July-Nov. '86 | 1400 | 24.8 | B | C | Y | + | 0 | Smith, 1990b |
| | 20:26:54 | 81:19 | May-Nov. '87 | 622 | 18.8 | | | Y | + | 0 | |
| <i>Callinectes sapidus</i> | 21:38:41 ⁱ | 83:17 | May-Nov. '88 | 649 | 17.5 | B | C | N (r) | 0 | 0 | Smith & Hines, 1991b |
| | 32:18:50 | 76:24 | May-Nov. '89 | 692 | 17.8 | | | Y | - | 0 | |
| | 1:25:74 | 40:60 | Aug.-Sept. '89 | 679 | 19.1 | | | Y | + | 0 | |
| | 0:12:88 | 51:50 | Oct. '89 | 103 | 38.8 | | | Y | 0 | 0 | |
| | 16:9:75 | 26:74 | Oct. '89 | 224 | 33.0 | | | Y | 0 | 0 | |
| | 17:17:66 | 61:39 | May '89 | 204 | 31.9 | | | N (r) | - | M | |
| | 25:5:70 | 32:68 | May '89 | 201 | 34.3 | | | Y | 0 | 0 | |
| | 15:28:57 | 37:63 | May '89 | 260 | 26.5 | | | Y | 0 | 0 | |
| <i>Portunus pelagicus</i> | 60-148 | 37:63 | Jan.-Dec. '90 | 951 | 10.8 | B | C | Y | 0 | 0 | Shields, unpubl. data |
| <i>Carcinus maenas</i> | 20-34.9 | Males | June-Aug. '85 | 173 | 1.7 | C | | | + | | Sekkelsten, 1988 |
| | 35-44.9 | only | | 144 | 3.5 | | | | | | |
| | 45-54.9 | | | 150 | 10.0 | | | | | | |
| | 55-64.9 | | | 237 | 16.0 | | | | | | |
| | 65-79.9 | | | 134 | 17.9 | | | | | | |

| | | | | | | | | | | | |
|----------------------------------|-------------|------------------|------------------------|-------|-----------|---|-----|-------|------------------|----------------|--------------------------------|
| <i>Carcinus maenas</i> | 11-57 | Females | Summer '89 and '91-'93 | 1116 | 7.9 | C | | N (r) | 0/+ ⁿ | M | Abello et al., 1994 |
| | 10-75 | Males | | 2457 | 12.5 | | | | | | |
| <i>Carcinus maenas</i> | 5-80.1 | Females | Sept. '73 | 633 | 40.0-55.0 | B | C | | + | M ^k | McVean, 1976 |
| | | males | | 390 | 27.0-53.0 | | | | | | |
| <i>Carcinus maenas</i> | 8-88.1 | Females | Feb. '76-Jan. '77 | 1917 | 16.5 | B | C | | + | 0 | McVean & Findlay, 1979 |
| | | Males | | 1421 | 20.0 | | | | | | |
| <i>Cancer maenas</i> | 3-38.1 | | | 234 | 26.5 | B | C | N (r) | | | Needham, 1953 |
| <i>Porcellana platycheles</i> | | | | 115 | 28.8 | B | C | Y | | | |
| <i>Necora puber</i> | <40 | 49:51 | May '86-April '87 | 448 | 23.1 | M | C | Y | + | 0 | Norman & Jones, 1991 |
| | 40-80 | 60:40 | | 1079 | 28.5 | | | R | | | |
| <i>Cyrtograpsus angulatus</i> | <15 | 62:38-41:59 | Aug. '86-May '87 | 2243 | 50.0 | B | 3,4 | | i | F | Spivak & Politis, 1989 |
| | 15-24.9 | 62:38-41:59 | | | 60.0 | | | | | | |
| | 25-34.9 | 38:72-94:6 | | | 80.0 | | | | | | |
| | >35 | 38:72-94:6 | | | 70.0 | | | | | | |
| <i>Pachygrapsus crassipes</i> | | | | >1000 | 30.0 | B | | | | | Hiatt, 1948 |
| <i>Chionoecetes bairdi</i> | | Juvenile males | | 202 | 34.6 | B | WL | Y | ⊙ ⁱ | M | Edwards, 1972 |
| | | Adult males | | 196 | 43.0 | | | | | | |
| | | Juvenile females | | 67 | 34.0 | | | | | | |
| | | Adult females | | 90 | 23.3 | | | | | | |
| <i>Paralithodes camtschatica</i> | | Juvenile males | Sept.-Oct. '69 | 291 | 25.6 | B | PWL | Y | - | 0 | Edwards, 1972 |
| | | Adult males | | 372 | 14.7 | | | | | | |
| | | Juvenile females | | 228 | 29.3 | | | | | | |
| | | Adult females | | 487 | 16.6 | | | | | | |
| <i>Paralithodes camtschatica</i> | 8.5-30.2 CL | | May-June '61 | 371 | 57.0 | B | | | | | Kurata, 1963 |
| <i>Paralithodes camtschatica</i> | 106-191 CL | Males | April-June '62 | 33744 | 15.3 | B | PWL | N*(r) | - | 0 | Niwa & Kurata, 1964 |
| | 82-176 CL | Females | | 1783 | 19.5 | | | | | | |
| <i>Panulirus argus</i> | 15-101 CL | | FEB. '76-Dec. '77 | 7643 | 40.3 | I | | | | | Davis, 1981 |
| <i>Nephrops norvegicus</i> | | Females | Sept. '68 | 100 | 41.0 | D | C | | | | Chapman & Rice, 1971 |
| | | Males | | 100 | 62.0 | | | | | | |
| <i>Homarus americanus</i> | <63.5 CL | | Spring '71-'72 | 12344 | 3.0-18.0 | C | | | | | Scarrat, 1973 |
| | 63.5-80.9 | | | 4266 | 5.0-24.0 | | | | | | |
| | >81 | | | 411 | 0.0-11.5 | | | | | | |
| <i>Homarus americanus</i> | | | | 47320 | 5.0-12.0 | C | | | | | Wilder, pers. comm. in Scarrat |
| <i>Homarus americanus</i> | 36-101 CL | (research) | Jan.-Dec. '69-'74 | 6417 | 21.0 | C | | | - | | Krouse, 1976 |
| | 81->121 | (commercial) | 68-'74 | 20226 | 6.5 | | | | - | | |

Table 1 (continued)

| Species | Size (mm) ^a | Sex ratio ^b (or other sorting) | Sampling time | No. of animals examined ^c | % Injury | Methods used to measure injury ^d | Most injured limb ^e | Symmetry in limb loss ^f | Size correlation ^g | Sex bias ^h | Reference |
|---------------------------|------------------------|--|--------------------|--|-----------|--|--------------------------------------|--|----------------------------------|--------------------------|-------------------------------|
| <i>Homarus americanus</i> | 21–120 CL | Females | May–Oct. '74–'75 | 22513 | 4.6–27.6 | C | | | | | Briggs & Mushacke, 1979 |
| | 17–126 | Males | and Jan.–April '76 | 6096 | 5.9–22.8 | | | | | | |
| <i>Homarus americanus</i> | 19–155 CL | Females | June–Oct. '76–'77 | 1523 | 0.0–30.2 | C | | | | | Briggs & Mushacke, 1980 |
| | 36–165 | Males | | 1325 | 0.0–40.0 | | | | | | |
| <i>Homarus americanus</i> | 30–85 CL | Females | May '84–Sept. '84 | 7097 | 9.0–61.0 | C | | | – | F | Moriyasu et al., unpubl. data |
| | 30–85 | Males | | | 3.0–44.0 | | | | | | |
| <i>Homarus americanus</i> | 30–170 CL | 40:60 | May–Nov. '81–'93 | ≈324000 | 10.0–21.0 | B | | | | | Estrella & Armstrong, 1994 |

^a All measurements are for carapace width (except, where noted, for carapace length, CL) and are in mm.

^b Sex ratio is shown as M:F.

^c When only one number appears it represents total for study.

^d M = missing limbs; R = regenerating limbs; B = both missing and regenerating limbs; D = damaged limbs (i.e. worn or broken dactyls); E = missing, regenerating and damaged limbs; C = missing and regenerating chelae; I = missing limbs and antennae and bodily damage.

^e C = chelipeds; R = random; 3,4 = 3 and 4th walking legs; PWL = posterior walking legs; WL = walking legs.

^f Y = yes; N = No; r = biased toward right side; N* = not symmetrical for chelae but symmetrical for walking legs.

^g + = injury positively correlated with size; – = injury negatively correlated with size; 0 = no size correlation; i = maximum injury at intermediate sizes.

^h M = male bias; F = female bias; 0 = no bias.

ⁱ Size ratio: (S:M:L, S = <61; M = 61–110; L = >110).

^j Numbers in parentheses refer to proportion of animals with worn claws.

^k Sex bias was only present in animals from subtidal habitats. Intertidal animals showed no sex bias in the proportion of injured animals.

^l A negative correlation in females and a positive correlation in males.

^m Note that for columns d, g–k the information in the first line is valid for all components of the study unless otherwise noted. Blank spaces in the first line of these columns means that this aspect was not investigated in the study.

ⁿ No correlation in green crab phenotype and a positive correlation in red crab phenotype.

increases an animal's vulnerability to subsequent injury. An alternative explanation is that multiple limbs are lost in a single attack event (Smith, 1990a). The latter interpretation is supported by observations that multiple limb loss is most often associated with sequential limb loss (i.e. losses tend to occur on the same side and in adjacent limbs) (Spivak & Politis, 1989; Norman & Jones, 1991). Most brachyurans respond to threats with outstretched claws (Schöne, 1968; Robinson et al., 1970; Jachowski, 1974). While this behavior makes anterior limbs particularly vulnerable to injury, the chances of surviving an anticipated attack are relatively high. In contrast, surprise attack from the rear may often prove fatal; consequently, damage to posterior limbs will be observed infrequently in populations. The predominance of symmetrical injury is not surprising. Although asymmetrical limb loss might be expected in crabs that move predominantly in one direction (Needham, 1953), in most populations, directionality of movement is probably random (e.g. *Callinectes sapidus*, Smith, 1995). Furthermore, predators would not be expected to attack one side preferentially.

The correlation between injury frequency and body size is not consistent among species and can vary within a species over temporal and geographic scales (Smith & Hines, 1991b). Three species generally experienced increased frequency of injury as body size increased (*Callinectes sapidus*, *Carcinus maenas* and *Necora puber*); two species showed no size correlation (*Cancer pagurus* and *Portunus pelagicus*); one species had maximum levels of injury at intermediate sizes (*Cyrtograpsus angulatus*); and three species showed a negative correlation (*Paralithodes camtschatica*, *Chionoecetes bairdi* and *Homarus americanus*). A positive correlation between injury and body size may result from decreased predator efficiency as prey size increases (Smith 1990a) and an accumulation of damage in older animals due to longer intermoult periods, reduced regeneration potential (Hamilton et al., 1976; Spivak & Politis, 1989; Smith & Hines, 1991b) and attainment of terminal moult (Sekkelsten, 1988). The incidence of injury can also be a function of moult stage (Juanes & Hartwick, 1990) and season (Shirley & Shirley, 1988). Limb loss is generally independent of sex, although exceptions, which may be habitat-specific, occur. For example, McVean (1976) noted that there was no difference between the sexes in the incidence of autotomy in *Carcinus maenas* found in the intertidal zone. However in sublittoral habitats, males showed significantly greater incidences of autotomy than females.

Another type of limb damage, chelae tooth wear, is prevalent in the two species where it has been documented (*Menippe mercenaria*, Bender, 1971; *Cancer magister*, Juanes & Hartwick, 1990). Chelae tooth wear results from feeding activity (as opposed to inter- or intraspecific aggression) and can range from slight to extreme wear where half or more of the tooth volumes have disappeared (Juanes, 1992).

Humans can be responsible for substantial limb loss in some commercially fished species, either through intentional harvesting of claws (e.g. *Menippe mercenaria*, Savage & Sullivan, 1978) or as a result of incidental damage associated with fishing gear (e.g. trawls, Reilly, 1983) or culling of undesirable individuals (Bennett, 1973; Kennelly et al., 1990). For example, Krouse (1976)

showed a direct relationship between fishing intensity of lobsters (*Homarus americanus*) and the incidence of culls (i.e. individuals missing or regenerating chelae). Similarly, Scarratt (1973) has suggested that claw loss in commercially caught lobster may be due not only to the handling and moving of fishing gear but also to the local (Prince Edward Island, Canada) practice of harvesting Irish moss by rakes. Sublegally sized spanner crabs (*Ranina ranina*) can lose on average 3–4 dactyli and 7 limbs while being disentangled from the commercial tangle-nets (Kennelly et al., 1990). The potential for extensive injury as a consequence of fishing (both directly and indirectly) suggests that fishing seasons should be timed with life history events so as to avoid fishing during those times when animals are particularly susceptible to injury. For example, Shirley & Shirley (1988) found that appendage injuries increased 157% from July to August, a period of simultaneous moulting, mating and fishing.

3. Ecological consequences of limb damage

Consistently high levels of injury in natural populations of decapod crustaceans suggest important fitness benefits to the autotomy response, but also raise the question of potential costs of limb damage and loss. Functional costs are likely, otherwise, animals would not invest the energy necessary to regenerate the missing structure (Goss, 1969). While these costs may be ameliorated in crustaceans because of limb redundancy (Reichman, 1984), loss of more specialized limbs (e.g. dimorphic chelipeds, swimming legs) should still impose significant handicap. Below we review the consequences of limb damage on feeding, growth, regeneration, reproduction, competitive ability, predator avoidance, and survival. Much of this work was performed by manipulating levels of damage and loss in laboratory situations although a few studies also performed experiments in field situations. Studies have typically focused on the effects of damage to chelipeds (versus walking or swimming legs), because of their functional importance and their relatively large biomass.

3.1. Feeding

Chelipeds are used by decapod crustaceans to capture, manipulate, and subdue prey (e.g. Vermeij, 1982; ap Rheinallt & Hughes, 1985; Lawton, 1989). Their damage or loss could have profound effects on foraging efficiency, yet few studies have tested for foraging costs. Juanes & Hartwick (1990) demonstrated that Dungeness crabs, *Cancer magister*, with damaged (broken dactylus or propodus) or worn chelae were unable to feed successfully on a hard-shelled bivalve, *Protothaca staminea*. Crabs with worn chelae teeth had significantly longer handling times than uninjured individuals feeding on similarly-sized prey. Blue

crabs, *Callinectes sapidus*, missing both chelipeds had significantly lower feeding rates and ate smaller sized soft-shell clams (*Mya arenaria*) than intact crabs or crabs missing one cheliped (Smith & Hines, 1991a). The absence of one cheliped, however, did not significantly affect blue crab feeding rate or size selectivity on this lightly armored bivalve. Compensatory use of walking legs in the absence of chelipeds has been observed in *Callinectes sapidus* (Smith & Hines, 1991a), stone crabs, *Menippe mercenaria* (Savage & Sullivan, 1978) and lined shore crabs, *Pachygrapsus crassipes* (Hiatt, 1948).

Reduced feeding efficiency may persist throughout the regenerative process. Elner (1980) showed that shore crabs, *Carcinus maenas*, with smaller-than-average (i.e. presumably regenerating) chelae had a lower energy intake rate than “normal” crabs because they chose smaller sized mussels. Brock & Smith (unpubl. data) recorded significantly lower maximum crushing forces in regenerating claws than contralateral normal claws of *Cancer productus* even after two instars had passed since autotomy. In addition, when adjusted for propodus length, maximum crushing forces delivered by the regenerating and opposite “normal” claws of injured crabs were significantly less than those produced by normal claws of intact crabs. This overall weakening of chelipeds in injured crabs might be expected if exercise influences claw size and crushing force (Smith & Palmer, 1994) and crabs were selecting smaller prey.

In heterochelous species, loss of a major cheliped could permanently impact foraging success if dimorphism is not re-established. Reversal of handedness is an often noted consequence of autotomy in certain species of heterochelous decapods (Przibram 1931; Hamilton et al., 1976; Cheung, 1976; Vermeij, 1977; Barnwell, 1982; Abello et al., 1990; Norman & Jones, 1991). Following loss of the major cheliped, the existing minor claw transforms into a major claw and the autotomized limb is replaced by a minor claw. The reversal process generally takes two to three moults to complete and intermediate stages resemble homochelous animals with two minor chelae (Przibram, 1931; Lewis, 1969; Hamilton et al., 1976; Savage & Sullivan, 1978; Abby-Kalio & Warner, 1989; Norman & Jones, 1991). If chelotomy of a major claw occurs in older individuals (even older juveniles), claw dimorphism may never be recovered (Smith, 1990b). Smaller claw sizes and the absence of specialized crushing dentition in homochelous individuals could reduce foraging efficiency. Even if claw reversal is accomplished, regenerated major claws may be less effective as foraging instruments. Govind & Blundon (1985) showed that left crushers of blue crabs were weaker and had a smaller mechanical advantage than similarly-sized right crushers. Furthermore, if right-handedness is, in fact, an adaptation to maximize peeling efficiency of dextrally coiled marine gastropods (Ng & Tan, 1985), left-handed crabs would be at a disadvantage when trying to cut spirally into the shell.

Lastly, injury to chelipeds may lead to a shift to alternative prey. For example, chelotomized stone crabs alter their diet to consume soft invertebrates, detritus, algae and grasses (Bender, 1971) and injured blue manna crabs (*Portunus pelagicus*) switched to a herbivorous diet from the more typical carnivorous diet

(Edgar, 1990). These changes in diet (either to different prey species or smaller sizes of the same species) could have direct effects on growth and regeneration.

3.2. Growth and regeneration

In decapod crustaceans, growth and limb regeneration are intimately linked to the moulting cycle. Several reviews (e.g. Bliss, 1960; Skinner, 1985) have summarized an extensive literature on the physiological effects of limb loss on growth, regeneration and moulting frequency; in this section, we will discuss the ecological ramifications.

Limb loss can affect crustacean growth, and potentially fitness, by reducing size increase at the moult, altering the timing of ecdysis, and impairing foraging efficiency (see above). Limb loss is known to reduce moult increment (e.g. percent increase in carapace width at the moult) in various decapod species (Hiatt, 1948; Hughes & Matthiessen, 1962; Bennet, 1973; Kuris & Mager, 1975; Savage & Sullivan, 1978; Davis, 1981; Hopkins, 1982; Ary et al., 1987; Smith, 1990b; Cheng & Chang, 1993; Moriyasu et al., unpubl. data). Because chelipeds comprise a substantial portion of the total body weight in many decapods (e.g. 20% in *Carcinus maenas* and *Liocarcinus holsatus*; Lee & Seed, 1992; 50% in *Menippe mercenaria*, Simonson & Steele, 1981), their replacement should divert the greatest amount of energy from growth relative to other limb types. It is somewhat surprising, then, that the loss of one cheliped had no effect on size increase at the next moult in *Hemigrapsus oregonensis* (Kuris & Mager, 1975), *Cancer pagurus* (Bennett, 1973) or *Callinectes sapidus* (Smith, 1990b). A likely explanation is that although significant biomass is lost following chelotomy, individuals reduce their total energetic burden by replacing limb mass incrementally over several moults. Because the majority of injured crabs in Bennett's (1973) and Smith's (1990b) study populations were missing a single cheliped, both authors concluded that autotomy had little overall effect on crab population growth. Foraging costs in these laboratory experiments, however, were negligible (crabs were given abundant, easily consumed food); such may not be the case in the wild. Using mark-recapture techniques in the field, Davis (1981) recorded significant reductions in growth in spiny lobster, *Panulirus argus*, as a result of injury (usually 1–2 antennae and 1–2 legs). He estimated an additional 33 wk for injured juveniles to reach legal harvestable size compared to uninjured juveniles.

Reductions in growth increments become evident as more limbs are lost (Bennett, 1973; Chittleborough, 1975; Kuris & Mager, 1975; Hopkins, 1982; Smith, 1990b, but see Davis, 1981). Skinner (1985) termed this phenomenon "regenerative load", where the size increase at the moult will be devalued by the extent of regeneration required. She proposed that the maximum amount of tissue a crab could regenerate during a single moult cycle was equivalent to 12–15% of the metabolically active weight of the premoult animal. Thus, lobster moult increments are reduced 30–40% in autotomized animals that regenerated limbs, but

are only reduced 5–10% in autotomized animals that do not regenerate limbs (Cheng & Chang, 1993). Ecological costs of smaller body size are well known for many organisms (Werner & Gilliam, 1984). If smaller animals are forced to reduce activity levels to avoid predators (Smith, 1995), abandon shelter to larger conspecifics (O'Neill & Cobb, 1979,) or eat less valuable prey (Bender, 1971), the cumulative effects of the initial injury on growth could be profound.

Functional costs associated with limb autotomy can be ameliorated if limbs are regenerated quickly. The rate of replacement depends on the moulting frequency and the limb length regenerated at each ecdysis. Autotomy can either shorten or prolong the instar period (Hiatt, 1948; Cleaver, 1949; Skinner & Graham, 1970; Stoffel & Hubschman, 1974; Kuris & Mager, 1975; Fingerman & Fingerman, 1976; Davis, 1981; Hopkins, 1982; Skinner, 1985; Spivak, 1990; Cheng & Chang, 1993) depending on the timing of the injury with respect to the moult cycle (Bliss, 1960; Savage & Sullivan, 1978; Skinner, 1985; Spivak & Politis, 1989) and number and types of limbs lost (Skinner & Graham, 1970; Fingerman & Fingerman, 1976). Such variation in moulting times may be detrimental if, as Reaka (1976) has suggested, moult synchronization is a strategy to avoid cannibalism. Weis (1976, 1977) showed that conspecific presence can retard or stop limb regeneration in fiddler crabs and suggested that these responses may be a mechanism to reduce vulnerability to conspecifics. In contrast, Moriyasu et al. (unpubl. data) found that in an estuarine lobster population, two distinct moulting peaks are obvious. In the first season (May–June) both normal and injured lobsters moulted; in the second season (August–September), mostly claw-missing individuals (81–83%) moulted. This second season may result from delays in moulting caused by breakage late in the previous intermoult period.

The ability and length of time required to regenerate a missing limb to normal size can vary dramatically between life-history stages and species. In general, regeneration potential and success decreases with size (age) of the individual and stops when the animal reaches terminal anecdysis (Hartnoll, 1965; Cheung, 1973; Miller & Watson, 1976; Brock & Smith, unpubl. data). For example, small blue crabs are able to regenerate almost 90% of the normal limb length in the first post-autotomy moult and nearly 100% of the length regenerated after the second moult (Smith, 1990b). Because small blue crabs moult every 3 to 4 wk, complete regeneration can occur in a single season. Mature female blue crabs, in contrast, are in terminal anecdysis and can no longer replace missing limbs. King crabs (*Paralithodes carinisthaica*) recover substantially less limb length at each moult and regeneration of a normal length limb can take 4–7 instars. While this process can be accomplished within a year in juveniles, it is estimated to take four to 7 yr in young adults (Niwa & Kurata, 1964; Edwards, 1972). A variety of other species that have been examined have regeneration rates intermediate to these extremes (Emmel, 1907; Hiatt, 1948; MacGinitie & MacGinitie, 1949; Skinner & Graham, 1972; Bennett, 1973; Miller & Watson, 1976; Savage & Sullivan, 1978; Brock & Smith, unpubl. data).

Limb types that are critical to overall fitness might be expected to regenerate

more quickly than less important appendages, and, in some species, regenerative allocation varies with limb type and sex. For example, Kurata (1963) showed that for *Paralithodes camtschatica*, the recovery rate at the first post-regenerational moult was greater in chelipeds than in the other walking legs. Similarly, Hopkins (1985) found that multiple autotomy affected growth and regeneration differently in *Uca pugilator* depending on whether the large male cheliped was left intact or autotomized. Mohrherr (1987), working on fiddler crabs (*U. lactea* and *U. chlorophthalmus*), found that the rate of regeneration was sex-biased. In males, accelerated regeneration would result if either of the chelipeds was autotomized; whereas, in females, both chelipeds had to be autotomized for a similar effect to occur. He suggested that for males, loss of a minor cheliped would severely impair feeding, while loss of a major cheliped would strongly handicap mating success. Finally, cheliped reversal following loss of the major claw may be an adaptation for recovering a full-size crushing appendage in the least amount of time possible (Przibram, 1931).

Regeneration of parts of limbs (e.g. a dactylus of a cheliped) has not been explored, but presumably these can rapidly return to normal size in the next moult (Edwards, 1972). Typically, damage to the dactyl or propodus tips does not stimulate autotomy of the entire limb. This lack of response may be adaptive, particularly if the potential for such breakage during foraging is high. Although foraging costs exist (Juanes & Hartwick, 1990), the missing tips can be replaced much more rapidly than entire limbs. Various reports of abnormal appendages (Butler, 1956; Shelton et al., 1981; Carvacho, 1988; Juanes & Hartwick, 1990) however, suggest that partial limb loss (or perhaps limb loss without autotomy) may lead to permanent damage. Moreover, Hopkins (1993) has shown that regeneration of limbs in crustaceans is most efficient when it follows autotomy.

3.3. Reproduction

Limb loss could be detrimental both to individual fitness and to population growth if it significantly impaired reproductive success and was common in the population. Limb loss might decrease an individual's ability to attract mates, lower competitive performance, physically hinder copulation, or reduce fecundity (Smith, 1992), yet few studies have addressed these possible costs. In many decapod crustaceans, chelae size is critically important to mating success (Stein, 1976; Salmon, 1983; Christy, 1987; Snedden, 1990; Garvey & Stein, 1993; Claxton et al., 1994), therefore their loss would be predicted to be especially costly. Among field-collected *Carcinus maenas*, mating males have larger-than-average chelae compared to the entire male population (Lee & Seed, 1992), and limb damage has a negative effect on male pairing success (Sekkelsten, 1988; Abello et al., 1994). Sekkelsten (1988) noted that medium-sized damaged males were able to carry a female in precopula to the same extent as normal males but tended to lose their mates before copulation. Abello et al. (1994) found that the proportion of male crabs with missing chelae found in mating pairs, both in precopula

(15.9%) and copula (12.9%), was much lower than that found in the adult unpaired (24.8%) population. I.P. Smith (1990) noted that injured *Necora puber* crabs were less active than uninjured individuals and were never found in sexual activity (pre-copulatory, copulatory or post-copulatory pairing). Similarly, few (5/176) mature male tanner crabs, *Chionoecetes bairdi*, with regenerated claws were found grasping mature females (Stevens et al., 1993).

In one of the few experimental studies to date, Smith (1992) showed that guarding male blue crabs missing one or both chelipeds were at a significant disadvantage in trying to prevent displacement by similarly sized intact males. In contrast, intact males in precopula were able to ward off both injured and intact intruders. This mating handicap was not evident in *Callinectes sapidus* males in the field (Smith, 1992). There, paired and unpaired males did not differ in the frequency of limb injury. These differences between experimental and field results may have reflected: (1) greater opportunity for handicapped guarding males to escape in the field; (2) a low incidence of autotomy in the study population; or (3) confounding effects of male body size during competition. If body size is the chief determinant of male mating success in this species (Smith, 1992; unpubl. data), then limb loss will only be important in competitive bouts where the size difference between opponents is small. In a similar experiment using shore crabs, Abello et al. (1994) found that chela loss was a handicap for a male crab when either competing for or defending a paired pre-molt female. The authors estimated this handicap to be equivalent to a reduction in size of 7–8 mm carapace width relative to the size of the competitor. However, in contrast to blue crabs, field-collected shore crabs exhibit a mating handicap due to limb loss (see above; Sekkelsten, 1988; Abello et al., 1994).

The effect of autotomy on female reproductive performance has received remarkably little attention, given the potential for damage to the female during courtship and trade-offs that might exist between fecundity and regeneration. In staged competitions in pools, prepubertal female blue crabs suffered significantly higher limb loss than males, most probably as a result of combat between the guarding and intruding males (Smith, 1992). In the field, paired prepubertal females showed a tendency toward higher frequency of limb loss than did unpaired prepubertal females. Pre-copulatory interactions may also be responsible for limb damage in five species of the genus *Trapezia* (Huber, 1985). When single males and females were presented to each other, injuries were relatively low (6% of trials). Injuries were more frequent in male (two females and one male) and female (two males and one female) mate choice experiments and reflected the higher levels of aggression in these trials. Interestingly, more injuries occurred to the sex being chosen than to the “choosing sex” (i.e. to females in the male-choice trials and to males in the female-choice trials). Reproductive trade-offs between fecundity and regeneration are well known in lizards and salamanders (e.g. Smyth, 1974; Maiorana, 1977; Dial & Fitzpatrick, 1981), but few data exist for crustaceans. Norman & Jones (1993) showed that field-collected female velvet swimming crabs (*Necora puber*) with missing limbs had smaller brood sizes than

uninjured females. Although the mechanism is unknown, the authors suggested that energy available for reproduction was shunted to growth and repair.

3.4. Intraspecific aggression and competitive ability

Limb loss also has the potential to alter the outcome of competition for resources. Reduced ability to obtain or defend shelter could result in mortality if predation intensity were high, or lower reproductive fitness if mating opportunities were lost. Among stomatopods (which are similar to decapods in general body plan), loss of one or both raptorial appendages severely limited fighting ability, so that injured animals were less able to defend cavities or evict intact intruders (Berzins & Caldwell, 1983). Similarly, cheliped loss reduced competitive ability for refuge in alpheid shrimp (Conover & Miller, 1978), lobsters (O'Neill & Cobb, 1979), and hermit crabs (Neil, 1985). Blue crab males missing one or both chelipeds were hampered in their ability to guard females from intact intruders and were unable to displace intact males (Smith, 1992). It should be noted that these agonistic interactions are not likely to be a major source of limb loss. In crustaceans, most intraspecific competitive interactions are highly ritualized and do not result in autotomy (e.g. Hiatt, 1948; Jachowski, 1974; Sinclair, 1977; Hyatt & Salmon, 1978).

3.5. Predator avoidance

If the primary function of autotomy is to prevent subjugation of crustacean prey by a predator, then prior limb loss should increase prey vulnerability in subsequent attacks by impairing defensive capacity or escape ability (Bildstein et al., 1989; Davenport et al., 1992; Smith, 1995). The net effect of these handicaps on survival will vary with the extent and type of injury, escape mode, and the behavioral response to such injury. Chelipeds are important defensive weapons (e.g. Robinson et al., 1970; Stein, 1977; Lawton, 1989), and crabs missing claws are more vulnerable to vertebrate and invertebrate predators than are intact crabs. For example, predatory diamondback terrapins (*Malaclemys terrapin*) showed strong preference for shore crabs without chelipeds (Davenport et al., 1992), and ibises (*Eudocimus albus*) selectively ingested female and declawed male crabs more often than intact male sand fiddler crabs (*U. pugilator*) (Bildstein et al., 1989). Using large (10 m²) field enclosures, Smith (1995) showed that cheliped loss increased juvenile blue crab vulnerability to cannibalistic adults, but only when escape was restricted by a tether. Untethered, injured animals experienced significantly less mortality, illustrating the importance of escape in this species. Surprisingly, severely injured juveniles (missing both chelipeds, one walking and one swimming leg) suffered relatively little mortality, suggesting that injury may also alter activity patterns so as to decrease vulnerability. While reduced activity could improve chances of surviving until limbs regenerate, such behavior might also decrease feeding rates or mating success (Sih, 1982, 1992). Limbs other than chelipeds may also be critical for predator avoidance. For example, loss of a single

swimming leg or asymmetrical limb loss can reduce escape speed (Spirito, 1972; Smith, 1995).

If prey vulnerability varies with prey size, then the relative costs and benefits of autotomy will change as the animal grows. For example, small *Callinectes sapidus* juveniles (<61 mm carapace width) tethered in the open field suffered similar, high levels of mortality and injury regardless of the type (chelipeds, walking or swimming legs) or number (0, 1, 2, or 4) of missing limbs (Smith 1990a, 1995). In contrast, larger juveniles (61–110 mm CW) experienced lower mortality rates, and their survival depended on the number of prior limbs lost. Severely injured larger juveniles had significantly higher mortality than similarly sized intact crabs or those missing one or two limbs. Adult intermoult blue crabs (>110 mm CW) were nearly invulnerable to attack in the Rhode River, Maryland. For small crabs, then, benefits of autotomy (increased survivorship) were relatively high, while costs of prior limb loss (increased vulnerability) were low. For crabs nearing a size refuge from predation, minor limb loss was still useful and carried no penalty, but severe limb loss imposed a high cost. A similar size-dependent pattern was observed in green crabs, *Carcinus maenas*, exposed to diamondback terrapins (Davenport et al., 1992). Small crabs (10–25 mm CW) were highly vulnerable to attack in aquaria (>80% eaten, <20% cropped); medium crabs (30–50 mm CW) were less vulnerable (<20% eaten, >60% cropped); and large crabs (52–75 mm CW) were relatively invulnerable to attack (0% eaten, 10% cropped).

3.6. Survival

Ultimately, we would like to know whether autotomy affects survival in crustaceans, but it is difficult to assess mortality in the field or reliably extrapolate estimates from laboratory experiments. Various authors have noted high mortality of autotomized individuals (e.g. Simonson, 1985). Figiel & Miller (1995) showed that, in the laboratory, chelotomized crayfish have significantly lower survival than intact animals and that these survival rates were density-dependent. Cleaver (1949) using data obtained from tag recoveries from the Dungeness crab fishery estimated that animals missing one claw suffered 20–30% higher mortality than normal crabs, and crabs with one claw and one walking leg missing experienced 40–50% greater mortality than normal crabs. The stone crab fishery in South Florida is unique in that only claws are harvested and declawed animals are returned to the water to regenerate new claws (Lindberg & Marshall, 1984). In one experiment, though, stone crabs suffered high mortality after claw removal; 47% of crabs experiencing double chelotomy died, whereas 28% with single claws removed died, usually within 24 h of declawing (Davis et al., 1978). The high mortalities experienced by damaged individuals of this species may be due, in part, to the disproportionately large size of stone crab claws, but also to whether claws are broken along the natural fracture plane (Simonson & Hochberg, 1986). Laboratory experiments have shown that the width of the wound following claw removal correlates significantly with survival (Davis et al., 1978). Based on this relationship and commercial catches, the authors estimated mortality rates from

23–51% following claw removal. These results, combined with the low regeneration frequencies in field populations (Savage et al., 1973) and the fact that claws are not likely to regenerate back to normal size before animals reach their terminal moult (Cheung, 1973), suggest that declawing is of limited value as a sustainable fishery management technique (but see Sullivan, 1979).

Survival can be affected by partial breakage as well as limb loss. The spanner crab, *Ranina ranina*, the only brachyuran reported to be incapable of autotomy, showed very high mortality (60–100%) after losing one or more limbs and moderate mortality (50%) in animals losing one or more dactyli (Onizuka, 1972; Kennely et al., 1990). Limb damage or loss may also increase the susceptibility to disease. For example, Moriyasu et al. (unpubl. data) have reported that claw loss in lobsters leads to increased disease. In their work on lobsters, they noted that 15 animals missing claws were infested with an unidentified ciliate species and died within 10 weeks in captivity.

3.7. Population and community effects

Most experiments on autotomy have focused on the consequences (primarily costs rather than benefits) of the response to the individual. Predicting what effects autotomy might have on the population and community has largely been a matter of extrapolation and supposition. Theoretical models suggest that nonlethal injury could result in population stabilization if (1) injury rates were density-dependent, and (2) injury significantly reduced survival or reproduction (Harris, 1989). This regulatory effect requires close coupling between predator and prey abundances; such coupling is most likely to occur if predator and prey are conspecifics. Figiel & Miller (1995) have shown that limb damage is related to density of conspecifics in crayfish and that mortality is density-dependent among injured animals. Similarly, unsuccessful predation by conspecifics is thought to be the primary source of injury to blue crabs in the Rhode River, Maryland, and the frequency of limb loss there correlated positively with annual blue crab abundances between 1986 and 1989 (Smith & Hines, 1991b). The critical question in terms of population effects, however, is whether *common* forms of injury meet the second of Harris's (1989) criteria; i.e. do these injuries significantly depress survival or reproduction? Based on the most complete data set available for a single species, Smith (1995) concluded that the costs of single cheliped loss (the most common injury) to blue crab growth (Smith, 1990b), foraging (Smith & Hines, 1991a), mating success (Smith, 1992), and predator avoidance (Smith, 1990a; 1995), were sufficiently small as to not affect the population. It is possible, however, that minor costs could become major ones during years of higher conspecific abundance, lower prey densities, or other unfavorable conditions. Undoubtedly, the severity of autotomy's effect on fitness will be species-specific. Many of the studies reviewed here suggest that limb loss can affect survival and reproduction, but comparative work is needed. Discerning the effects of injury on community processes will be particularly challenging. One of the most promising

areas for study will be to examine direct and indirect effects of reduced foraging efficiency on prey populations.

4. Prospectus

Unsuccessful predation is sufficiently common in the animal kingdom (Vermeij, 1982) that nonlethal injury is likely in the lifetime of any animal. Most ecological experiments, however, ignore wounded or injured individuals (Juanes, 1992). Given the prevalence of injury in decapod crustacean populations, the potential costs involved, and the ecological importance of many species in the community, it is surprising how little attention has been focused on the ecological ramifications of injury. In part, this is because the issue is complex, the incidence and effects of autotomy will be influenced by myriad factors, including phylogenetic history, foraging and locomotory modes, habitat type, nature of injury-causing agent, predator and prey densities, repair rates, size structure of population, and sex ratio. As a rule, more comparative work is needed on decapod species from different habitats (e.g. terrestrial vs. marine) and with different lifestyles (e.g. mobile vs. sedentary) before we can generalize about the costs and benefits of autotomy. Below, we present several areas we feel are in need of study.

4.1. Causal agents

Autotomy is presumed to be a defense against predators (Robinson et al., 1970), but this function has rarely been observed or tested experimentally. Such information is important if we are to explain patterns of limb loss in individuals and understand the general efficacy of the response in predator-prey encounters. Despite artifacts associated with tethers and enclosures (Peterson & Black, 1994), their use, in conjunction with a time-lapse underwater video system, may be the best way to identify sources of injury in mobile species in subtidal systems. Subtidal species that maintain territories, and certain intertidal, semi-terrestrial, and terrestrial species, however, might be monitored for injurious events without resorting to unnatural restraining devices. Once principal injury-causing agents have been identified, video systems may be used to study the kinematics of attack and avoidance in detail. It is important to realize that the degree of restraint utilized in such experiments will influence interpretations of the utility and cost of autotomy. For example, small enclosures (or short tethers) will increase encounter rates between predator and prey and decrease avenues for prey escape. These experiments, in effect, simulate the final stages of a predation sequence (Eadler, 1985), one in which the prey is attempting to avoid imminent capture and in which autotomy is most likely to be employed. In such cases, autotomy will appear to have large survival benefits and prior loss will have high costs. In contrast, if experiments are conducted in large enclosures and prey are free to move, prey may utilize avoidance mechanisms other than autotomy (e.g. swimming, burrow-

ing). Under these circumstances, prior limb loss may seem to impose little cost (Smith, 1995).

Identification of principle injury-causing agents and their size- and density-dependent attack efficiencies are necessary if injury frequencies are to be used as an index of predation pressure (e.g. Ballinger, 1979; Aronson, 1987; McCallum et al., 1989). A number of authors (Schoener, 1979; Jaksic & Fuentes, 1980; Wilson, 1991) have indicated that injury frequency may be a poor predictor of predation intensity, and that additional data on injury rates, predator efficiency, and prey survivorship are needed. Injury frequency may prove most useful as a measure of predation intensity in simple predator-prey systems in which densities correlate directly with injury and indirectly with survival (e.g. if the principal predators are conspecifics; Morin, 1985; Petranka, 1989; Van Buskirk & Smith, 1991).

4.2. Behavioural decisions

Behavioural decisions of an animal can be strongly influenced by its perceived risk of danger (see review, Lima & Dill, 1990). If prior limb loss increases an animal's perception of its risk, then autotomy could indirectly impact foraging time and efficiency, habitat use, and mating behaviour. To understand fully the impact of autotomy on fitness, then, experiments must compare behaviours of injured and intact crustaceans in the presence and absence of predators. We also have little knowledge of the decision-making process that determines when prey should or should not autotomize a limb (e.g. Easton, 1972; Weis, 1977). Does this vary with the threat imposed by the predator (e.g. is autotomy used more readily for more dangerous predators) or alternatively as the level of prey vulnerability varies (e.g. size, injury, or moult status)?

4.3. Life-history variation

Arnold (1988) has argued that the value of autotomy depends on its cost:benefit ratio and will be selectively advantageous only when benefits exceed costs. If the main benefit is escape from certain death then almost any cost can be borne provided the animal survives to reproduce. Nevertheless, if vulnerability to predation is a function of body size or ontogenetic shifts in habitat or resource use, the cost:benefit ratio is likely to change during the animal's lifetime. Does the response diminish or disappear with age or vary with changes in habitat and resources or must an autotomy response always be maintained for use near vulnerable moulting events? Are animals with terminal moults more reluctant to shed limbs than those that continue to moult throughout life?

4.4. Functional costs

More comparative studies on functional costs in decapod crustacean species are needed. Future work should attempt to determine: (1) whether individual costs exist, (2) how long costs persist, and (3) whether these costs are sufficiently great

as to affect processes at the population and community levels. Undoubtedly, the costs (and benefits) of autotomy will vary with important external factors (e.g. food availability, predator density, shelter). Whenever possible, studies should manipulate one or more of these variables to determine the conditions in which autotomy will be most useful or costly.

Foraging costs: Juanes & Hartwick (1990) suggested that dactyl breakage and claw tooth wear were direct consequences of feeding on hard-shelled molluscan prey. Durophagous crabs are able to crush large clams by repeatedly loading them and eventually causing low-cycle fatigue (Boulding & LaBarbera, 1986). Similar fatigue damage, however, may occur in crab claws and ultimately lead to claw breakage. This risk of damage may be partially responsible for the observed trend of preference for small-sized molluscan prey by decapod crustaceans (Juanes, 1992). Does foraging behaviour lead to limb loss, partial claw breakage or wear in other species? How does limb loss or the threat of limb damage affect prey choice? Prey diet in crustaceans often changes during ontogeny (e.g. Stevens et al., 1982; Edgar, 1990); is limb loss more costly to foraging efficiency at certain of these life stages? Importantly, does reduction in foraging efficiency affect growth, or are injured animals able to switch to alternative prey until regeneration is completed? Finally, are foraging costs sufficiently great and injuries common enough to affect prey population dynamics?

Mating: Autotomy could have its greatest impact on individual fitness and population dynamics if reproductive effort is compromised, yet this topic of research remains largely unexplored. Brachyuran crabs exhibit a diversity of mating associations ranging from female- or resource-centered competition to ones based purely on encounter rate (Christy, 1987). The cost of autotomy might be expected to increase as the intensity of sexual selection increases, but perhaps to different degrees depending on the type of association. For example, cheliped loss in a territorial burrower (e.g. *Uca*) may have much higher reproductive costs than in a mobile species that intercepts wandering females (e.g. *Hemigrapsus*). Does prior limb loss affect male competition for females or male/female choice? Is limb loss a key factor to mating success or are other characteristics (e.g. body size, burrow quality) more critical? What, if any, energetic trade-offs exist between fecundity and regeneration? Comparative studies testing for trade-offs between closely related species with and without terminal moults might prove illuminating. By extrapolating the type and frequency of injury in a population to lost fecundity and mating opportunities, we can obtain estimates of its potential impact on population growth.

4.5. Temporal and geographic variation

Data on patterns of autotomy (e.g. limb type and number, size and sex biases) in study populations are essential if experiments designed to examine costs are to be ecologically relevant. In addition, records of temporal and geographic variation in injury frequency are necessary to determine how selective forces might vary over such scales. For example, are there specific areas where damage occurs or

where damaged animals aggregate? Results of several studies suggest that small estuaries may be places where damaged animals come to moult, perhaps attracted by lower predation risk (Shirley et al., 1990) or higher temperatures/lower salinities (which can facilitate moulting and regeneration, deFur et al., 1988). Does autotomy accurately reflect predation pressure over time or space (e.g. intertidal or latitudinal gradients)? Can injury frequencies be correlated with dominant predator densities? If cannibalism is a primary source of nonlethal (and lethal) injury in many crab populations, then the potential for density-dependent regulation exists (Harris, 1989). Good estimates of survivorship are needed. Mark-recapture techniques will be most effective in more sedentary species or in commercially important species.

4.6. Modelling

Models are needed to examine the effects of autotomy on individual behaviour and population dynamics and to generate testable hypotheses. For example, future work should explore an animal's decision to autotomize a limb using a dynamic programming approach, one which considers the current physiological state of the animal (Mangel & Clark, 1988). These models can also help elucidate the decision to accelerate or delay the next moult depending on the physiology, age, predation risk, and reproductive status of the animal. To allow a better understanding of population dynamics, models should incorporate size-dependent injury frequency and repair rates and costs of injury to survival, growth, and reproduction. Such models would be particularly useful for commercially-important species where limb loss can have considerable impacts on recruitment to the fishery (e.g. Davis, 1981).

4.7. Conclusion

The phenomenon of autotomy in decapod crustaceans provides an outstanding experimental system for studying physiological, behavioural and ecological trade-offs. Experimental removal of different types and numbers of limbs can be used to modify an animal's physical status and, presumably, decision-making processes. Assessment of injury patterns within and between species may provide evidence of how selective factors influence an animal's behaviour and life history. If costs of limb loss are significant and the frequency of injury high in a population, then nonlethal injury could have profound effects on the population and community.

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