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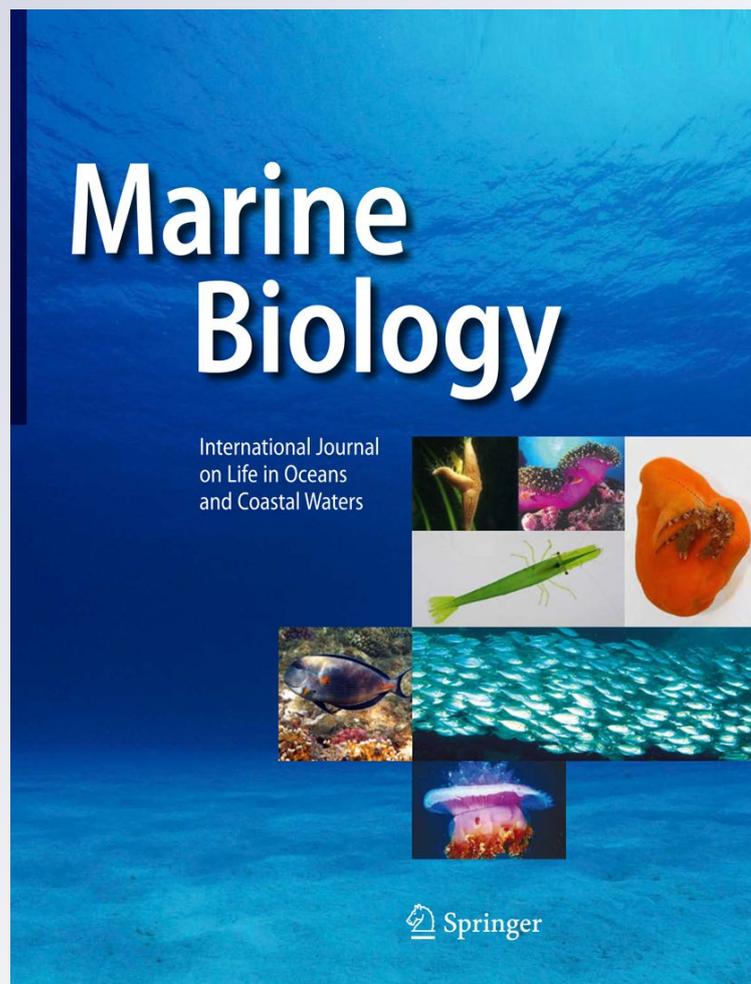
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# Effects of autotomy on long-term survival and growth of painted spiny lobster (*Panulirus versicolor*) on the Great Barrier Reef, Australia

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**Abstract** The effects of autotomy (shedding of appendages) on survival and growth rates of painted spiny lobster were investigated at Northwest Island (23° 18' S, 152° 43' E) during the period 2003–2006. Adult lobsters were captured, tagged, and classified as either uninjured ( $n = 68$ ), minimally injured ( $n = 39$ ) or moderately injured ( $n = 19$ ) depending on the number and type of appendages that were autotomized during capture and handling. Six to thirty-six months after release, 86 lobsters were recaptured (mean time at large = 305 days). Recapture rates of uninjured (64.7%), minimally injured (71.8%), and moderately injured lobsters (73.7%) were not significantly different. Similarly, mean annualized growth rates of uninjured, minimally injured, and moderately injured lobsters were not significantly different. This suggests that the energetic cost of a single episode of autotomy is either negligible or exists as a trade-off with some other life history trait, such as reduced reproductive performance. These results support the use of certain management tools (e.g., size limits) that prescribe release of non-legal lobsters, regardless of their injury status.

## Introduction

Autotomy, the shedding of an appendage at a specialized breakage point, is a common event in the life of many crustaceans, including spiny lobsters (Family Palinuridae).

If a lobster's leg (pereiopod) is grasped or damaged by a predator, for example, the autotomizer muscle (in the basipodite and ischiopodite leg segments) contracts violently as a reflex. This bisects a preformed fracture plane in the exoskeleton and releases the leg, thereby affording the lobster a chance to escape from the predator. An antenna, on the other hand, must be pulled off, since there is a fracture plane but no autotomizer muscle (Phillips et al. 1980). Regeneration of an autotomized appendage begins with formation of a limb bud, which grows to 80–90% of the original limb length after a single molt (Phillips et al. 1980; Plaut and Fishelson 1991).

Despite the immediate survival benefits of autotomy, there may be long-term functional and energetic consequences. Parsons and Eggleston (2005) found a threefold difference in the mean survival rates of injured (missing one antenna and two legs) and uninjured Caribbean spiny lobster (*Panulirus argus*) that were tethered in the wild. They postulated that the lower survival rate of injured individuals was due to (1) enhanced prey detection by predators due to release of body fluids (e.g., blood), (2) impaired ability to escape from, or defend against, predators, and (3) loss of cooperative group defence due to the tendency of conspecifics to avoid injured individuals. It is also plausible that a reduced complement of walking legs impairs foraging efficiency, with the result that injured individuals are predisposed to starvation or forced to take greater risks to obtain food.

Another potential consequence of autotomy is reduced growth. In all crustaceans, growth rate is a function of both change in size at each molt (molt increment) and time period between molts (molt interval). Injured lobsters typically have smaller molt increments than uninjured lobsters (Chittleborough 1975; Davis 1981; Brown and Caputi 1985; Negrete-Soto et al. 2002; Brouwer et al.

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2006), presumably because of the energetic cost of replacing autotomized limbs. In contrast, the effects of autotomy on molt interval are variable and probably depend on a number of factors such as season and body condition (Juanes and Smith 1995). Autotomy can either shorten (Chittleborough 1975; Brouwer et al. 2006) or lengthen (Davis 1981; Hunt and Lyons 1986) molt interval, but a net decrease in growth rate is observed in both cases.

Much of the evidence regarding the effects of autotomy on spiny lobsters comes from studies that observed captive (tank-bound, caged or tethered) individuals over relatively short time periods (e.g. Chittleborough 1975; DiNardo et al. 2002; Parsons and Eggleston 2005; Brouwer et al. 2006). However, the degree to which previous results are representative of wider populations is not known because captive lobsters may behave, grow, and survive differently from wild lobsters due to differences in food supply, predation risk, et cetera (Cobb 1980; Alcock 1998). Furthermore, short-term studies may over- or underestimate the effects of autotomy because growth in lobsters is discontinuous, and any effect of autotomy may take considerable time to manifest (and detect). To address these shortcomings, it is important to compare the performance of injured and uninjured lobsters in the wild over long-term (multi-year) periods.

Given the prevalence of autotomy in spiny lobster populations (e.g., Negrete-Soto et al. 2002), the physiological costs involved, and the ecological importance of many palinurid species (Butler et al. 2006), autotomy has the potential to affect population dynamics and community processes (Juanes and Smith 1995). The effects of autotomy are also important considerations for effective fishery management as many harvest techniques (e.g., traps, noose, hand) inadvertently capture and sometimes injure under-size, berried (gravid) or otherwise non-legal lobsters that must be returned to the sea. Simulation modeling suggests that injuries incurred in this way can significantly reduce both population size and commercial catch of spiny lobsters (Parsons and Eggleston 2007). The same considerations must also be applied to mark-recapture studies, since any injuries incurred by individuals during the marking process may ultimately bias estimates of population parameters (Dubula et al. 2005).

The painted spiny lobster *Panulirus versicolor* inhabits coral reefs of the Indo-West Pacific Ocean (George 1974) and is a target of artisanal, recreational, and commercial fisheries throughout much of its range (Mutagyera 1978; Kuthalingam et al. 1980; MacDonald 1982; Pitcher 1993; Frisch 2008). It is reluctant to enter traps (the standard fishing gear for temperate palinurids), so fishers must use spears, hand nets, or their hands (Dalzell et al. 1996). By world standards, catches of *P. versicolor* are small, ranging from approximately 1,000 to 8,000 kg year<sup>-1</sup> per country

(Kuthalingam et al. 1980; MacDonald 1982; Kailola et al. 1993). Due to low local abundances, however, fishing pressure on *P. versicolor* may be very high in some places. Although the prevalence of autotomy is yet to be determined in any population of *P. versicolor*, there is potential for significant ecological and economic consequences as a result of fishing-related injuries to this species. The aim of this study, therefore, was to assess the effects of injury (autotomy) on survival and growth rates of *P. versicolor*. Importantly, this study employed a mark-recapture program to facilitate monitoring of injured and uninjured lobsters over long-term periods under natural conditions.

Despite the importance of *P. versicolor* as a fishery resource, there have been few previous studies of this species. One population of *P. versicolor* for which some ecological data are available is the population at Northwest Island in the Great Barrier Reef, Australia. At this location, adult (>88 mm carapace length;  $L_c$ ) lobsters have molt intervals of 131–284 days, molt increments of 2–3 mm  $L_c$ , and lifetime growth trajectories that are similar to those of other tropical Pacific palinurids (c.f. Ebert and Ford 1986; Skewes et al. 1997; Coutures and Chauvet 2002; Frisch 2007a) except that growth rate is not sex-specific (Frisch 2007a). Although *P. versicolor* has the capacity to move considerable distances during short periods of time, individuals at Northwest Island tend to inhabit the same, readily identifiable dens (shelters) for long-term periods (Frisch 2007b, 2008). This high level of site-fidelity renders *P. versicolor* an ideal species to study the long-term effects of autotomy on palinurid survival and growth.

## Materials and methods

### Study site

The study was conducted on the coral reef at Northwest Island (23° 18' S, 152° 43' E) in the southern section of the Great Barrier Reef, Australia (see Frisch 2007b for a map of the study area). This reef has a high diversity and coverage of scleractinian corals, and modest numbers of adult *Panulirus versicolor* can be found wherever suitable dens exist. For logistical reasons, the study site (i.e., search zone) was confined to an area of approximately 60 ha adjacent to the exposed reef crest. This area was shallow (1–3 m in depth) and relatively homogeneous, consisting of scattered coral “bombras” with interspersed sand patches (locally known as a “bommie” field). A campground on the island supports up to 150 people, and small catches of *P. versicolor* are regularly made by local fishers (Frisch 2008). However, the 60 ha study site experienced relatively light fishing pressure because it was located on the exposed side of the reef, away from the most popular

fishing areas. This ensured an adequate number of marked lobsters were available for recapture, and avoided the confounding effects of repetitive injuries caused by heavy fishing pressure.

#### Mark–recapture surveys

Lobsters were captured by hand (with the aid of SCUBA) and transferred to a shallow, water-filled box onboard a nearby support vessel.  $L_c$  was measured to the nearest 0.5 mm with a vernier caliper and lobsters were categorized as either uninjured, minimally injured (missing 1–2 legs) or moderately injured (missing  $\geq 3$  legs and [or] one or both antennae). Autotomy of an antenna was considered to be a more severe injury than autotomy of a leg because antennae are used as weapons against predators (Kanciruk 1980; Herrnkind et al. 2001) and are fewer in number than legs (2:10, respectively). Virtually all autotomy occurred as a result of capture and handling, since few lobsters (<5%) had missing appendages when first sighted in their den. Care was taken to ensure that lobsters were not injured other than via autotomy (e.g., broken leg or damaged exoskeleton). Captured lobsters were marked with internal elastomer implants (Northwest Marine Technology, Shaw Island, USA), and then photographed ventrally to facilitate individual identification when later recaptured (Frisch and Hobbs 2007). Previous studies indicate this marking and identification system is reliable (i.e., the frequency of misidentification is nil or negligible) and was not likely to affect survival or growth of spiny lobsters in the wild (Woods and James 2003; Frisch and Hobbs 2006). Onboard processing of lobsters took approximately 5 min, after which each lobster was manually returned to its den.

The study site was surveyed for ten consecutive days on six occasions: December 2003, June 2004, December 2004, June 2005, December 2005, and December 2006 (June and December occur during the austral winter and summer, respectively). Lobsters were captured during the first five surveys (December 2003–2005) and recaptured during the last five surveys (June 2004–December 2006). Thus, time-at-liberty (i.e., time spent in the wild) ranged from 0.5 to 3 years depending on when the lobster was captured and recaptured. All recaptured lobsters were remeasured for  $L_c$  and photographed. If a lobster was recaptured multiple times, time-at-liberty was regarded as the time between initial capture and final recapture, but only if the lobster avoided injury during all interim recapture events. Thus, the lobsters described here endured only a single episode of autotomy. Note that these lobsters are a subset of those described in previous studies of *P. versicolor* at Northwest Island (Frisch and Hobbs 2006, 2007; Frisch 2007a, b, 2008).

#### Statistical analyses

Length–frequency distributions of uninjured, minimally injured, and moderately injured lobsters were compared using a  $\chi^2$  homogeneity test (Zar 1999). If the average expected cell frequency was less than six, the critical value of  $\chi^2$  was “scaled” using the procedure of Lawal and Upton (1984). Given that hand collection is non-selective, the probability of recapturing a lobster was assumed to be directly proportional to its survival rate (and inversely proportional to its mortality rate). As such, the relative survival rates of uninjured, minimally injured, and moderately injured lobsters were inferred from the proportions of recaptured individuals. These proportions were compared using a  $\chi^2$  homogeneity test (Zar 1999).

Absolute growth (mm) was calculated as change in  $L_c$  during the inter-survey period, while growth rate ( $\text{mm year}^{-1}$ ) was calculated as change in  $L_c$  over the time at large. Because growth rate in *P. versicolor* is size-specific (Frisch 2007a), a Gulland and Holt (1965) plot and least-squares regression were used to compare growth rates of uninjured, minimally injured, and moderately injured lobsters. Specifically, the slopes and elevations of regression lines were compared using the *F*-test procedure described by Zar (1999). Note that data from male and female lobsters were pooled because growth rate of adult *P. versicolor* was not sex-specific (see Introduction).

Mean absolute growth of uninjured, minimally injured, and moderately injured lobsters was compared by one-way analysis of variance (ANOVA). Homoscedasticity of treatment groups was checked a priori using Levene’s test (Zar 1999). To standardize the time at liberty, only lobsters that were recaptured after 0.5 years (i.e., after approximately one molt interval: Frisch 2007a) were included in the analysis. Molting was inferred to have occurred in any lobster that grew during the inter-survey period. A  $\chi^2$  homogeneity test (Zar 1999) was used to compare the proportions of uninjured, minimally injured, and moderately injured lobsters that molted. All statistical analyses were performed using SPSS computer software (SPSS, Chicago, USA), and a significant difference was considered to exist if  $p < 0.05$ .

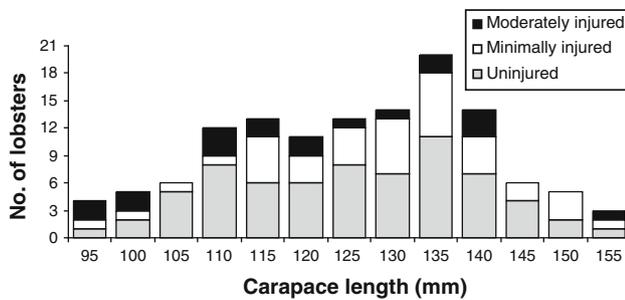
#### Results

A total of 126 adult lobsters (size range: 93–156 mm  $L_c$ ) were marked and released between December 2003 and December 2005. In total, 68 lobsters (54.0%) were uninjured, 39 lobsters (30.9%) were minimally injured, and 19 lobsters (15.1%) were moderately injured. Minimally injured lobsters were missing a mean of 1.2 legs while moderately injured lobsters were missing a mean of 2.6

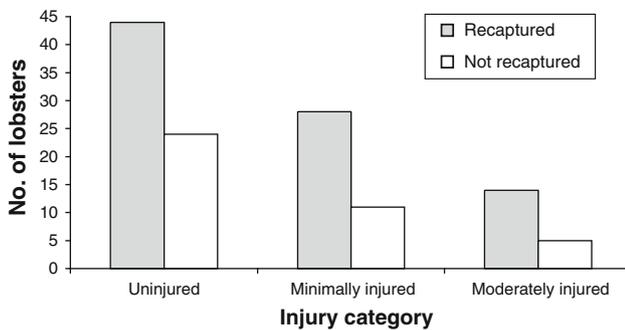
legs and 1.1 antennae. Uninjured, minimally injured, and moderately injured lobsters were homogeneously distributed across size classes ( $\chi^2$  test;  $\chi^2_{24} = 19.34$ ,  $p > 0.05$ ; Fig. 1).

A total of 86 lobsters (68%) were recaptured after 0.5–3 years (mean time at large = 305 days). This included two individuals that had previously lost both antennae, and another individual that had previously lost seven legs. All three of these (moderately injured) lobsters were recaptured after 0.5–1 years and all had regenerated their missing appendages (as did all other injured lobsters). Recapture rates of uninjured (64.7%;  $n = 44$ ), minimally injured (71.8%;  $n = 28$ ), and moderately injured lobsters (73.7%;  $n = 14$ ) were not significantly different ( $\chi^2$  test;  $\chi^2_2 = 0.87$ ,  $p > 0.90$ ; Fig. 2). Thus, injury (autotomy) did not affect survival rate of *Panulirus versicolor*.

Annualized growth rates ( $\text{mm year}^{-1}$ ) of uninjured, minimally injured, and moderately injured lobsters decreased with increasing  $L_c$  (Fig. 3). A significant linear regression model was computed for all three treatment groups (Table 1). Regression models were found to have



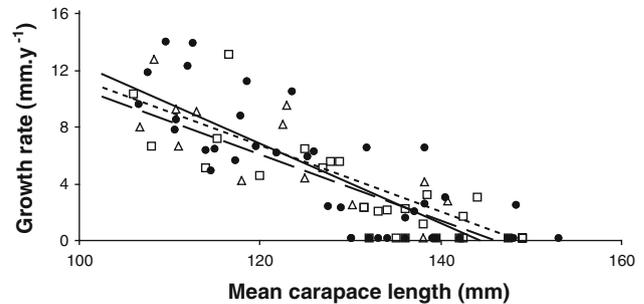
**Fig. 1** Length–frequency distributions for uninjured, minimally injured, and moderately injured *Panulirus versicolor* at Northwest Island. Differences between groups were not significantly different ( $p > 0.05$ ). See [Materials and methods](#) section for definitions of injury categories. The x-axis labels are size–class midpoints



**Fig. 2** Recapture frequencies for uninjured, minimally injured, and moderately injured *Panulirus versicolor* at liberty for 0.5–3 years. Differences between groups were not significantly different ( $p > 0.9$ ). See [Materials and methods](#) section for definitions of injury categories

slopes and elevations that were not significantly different among treatment groups (comparison of slopes:  $F$  test;  $F_{(2,76)} = 0.12$ ,  $p > 0.5$ ; comparison of elevations:  $F$  test;  $F_{(2,78)} = 3.18$ ,  $p > 0.05$ ). Thus, injury (autotomy) did not affect growth rate of *P. versicolor*.

Given that the molt interval for adult *P. versicolor* ranges from 131 to 284 days (Frisch 2007a), lobsters at liberty for 0.5 years would have molted (on average) one time, such that absolute growth would be indicative of a single molt increment. After 0.5 years at liberty, mean absolute growth ( $\sim$ mean molt increment) was generally greater for moderately injured lobsters ( $x \pm \text{SE} = 3.71 \pm 0.83$  mm,  $n = 26$ ) than for uninjured ( $1.81 \pm 0.44$  mm,  $n = 11$ ) and minimally injured lobsters ( $1.64 \pm 58$  mm,  $n = 7$ ; Fig. 4). However, the differences were not statistically significant (one-way ANOVA;  $F_{(2,41)} = 2.4$ ,  $p = 0.10$ ). After 0.5 years at liberty, molting was more prevalent among moderately injured lobsters (85.7%) than among uninjured (50.0%) or minimally injured lobsters (54.5%). However, the differences were not statistically significant ( $\chi^2$  test;  $\chi^2_2 = 2.89$ ,  $p > 0.10$ ; Fig. 5).

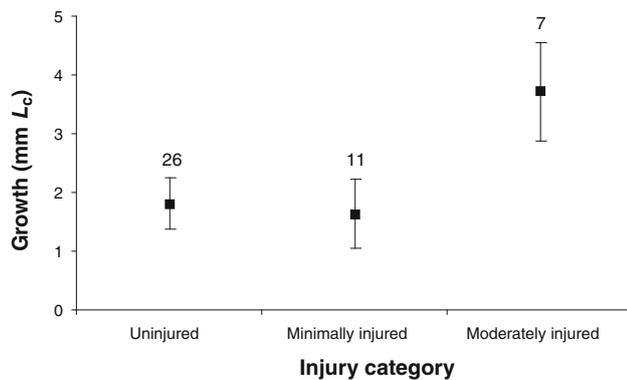


**Fig. 3** Gulland–Holt plot illustrating size-specific growth rates for uninjured (filled circles), minimally injured (open squares), and moderately injured (open triangles) *Panulirus versicolor* at liberty for 0.5–3 years. Regression parameters for uninjured (solid line), minimally injured (large dashed line), and moderately injured (small dashed line) *Panulirus versicolor* are presented in Table 1. See [Materials and methods](#) section for definitions of injury categories

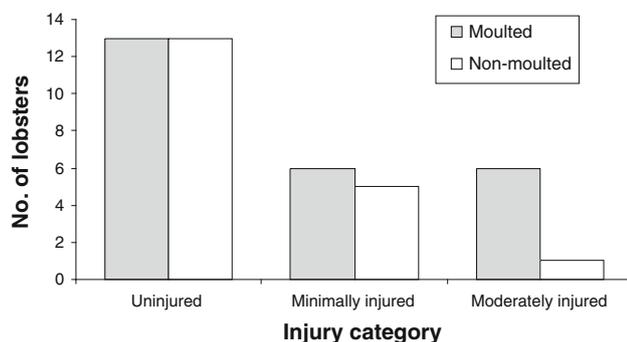
**Table 1** Regression parameters for uninjured, minimally injured, and moderately injured *Panulirus versicolor* at Northwest Island. See [Materials and methods](#) section for definitions of injury categories

Category	$n$	Regression equation <sup>a</sup>	$r^2$	$F$	$df$	$p$
Uninjured	44	$G = -0.28L_c + 40.21$	0.65	71.9	1.42	<0.001
Minimally injured	28	$G = -0.22L_c + 32.62$	0.60	38.2	1.26	<0.001
Moderately injured	14	$G = -0.23L_c + 34.60$	0.62	18.1	1.12	0.001

<sup>a</sup>  $G$  is growth rate in  $\text{mm year}^{-1}$  and  $L_c$  is carapace length in mm



**Fig. 4** Mean growth ( $\pm$  SE) for uninjured, minimally injured, and moderately injured *Panulirus versicolor* recaptured after 0.5 years at liberty (i.e., after approximately one molt interval). Differences between groups were not significantly different ( $p = 0.10$ ). Sample sizes are shown above each group. See [Materials and methods](#) section for definitions of injury categories



**Fig. 5** Molt status for uninjured, minimally injured, and moderately injured *Panulirus versicolor* recaptured after 0.5 years at liberty (i.e., after approximately one molt interval). Differences between groups were not significantly different ( $p > 0.10$ ). See [Materials and methods](#) section for definitions of injury categories

## Discussion

Despite the importance of spiny lobsters to benthic ecology and global fisheries (Phillips and Kittaka 2000; Butler et al. 2006), relatively little is known about the effects of sublethal injury on this group. This study investigated the effects of injury (autotomy) on survival and growth of *Panulirus versicolor*, a popular fishery species throughout its range. Unlike most other studies, however, this study monitored the experimental lobsters in the wild over long-term periods (0.5–3 years). This methodology is important given the discontinuous growth trajectories of spiny lobsters and the degree to which captive conditions can influence behavior, growth, and survival (Cobb 1980; Alcock 1998). In particular, captive lobsters may not have access to sufficient quality and (or) quantity of food, thereby aggravating any potential effects of autotomy. Thus, it is important to bear in mind that the effects of

autotomy may be substantially different in wild versus captive lobsters.

The most remarkable result of this study is that injured lobsters were recaptured in the same proportion as uninjured lobsters, which indicates that a single episode of injury (autotomy) does not affect long-term survival rate. Some lobsters survived for at least 1–3 years after losing up to seven (out of ten) pereopods (legs) or both antennae. It is apparent, therefore, that a reduced complement of appendages does not increase vulnerability of *P. versicolor* to either predation or starvation. This is surprising given that (1) pereopods and antennae are used, *inter alia*, to gather food and defend against predators, respectively (Phillips et al. 1980; Herrnkind et al. 2001), and (2) autotomy increases mortality rate in other palinurids (Brown and Caputi 1983; Barshaw et al. 2003; Parsons and Eggleston 2005; Brouwer et al. 2006). Perhaps the loss of anti-predatory and trophic functions associated with autotomy was ameliorated by specific behavior and habitat characteristics. In particular, it is hypothesized that strong fidelity to shallow water (Frisch 2007b) reduced exposure of *P. versicolor* to large predators (e.g., sharks and teleosts) and that an abundance of high quality coral dens (Frisch 2008) enhanced foraging capacity by enabling individuals to move among dens in search of food. In other locations, the functional cost of autotomy may be amplified because palinurids often have limited access to shelter (Herrnkind et al. 1997; Sharp et al. 1997; Briones–Fourzan and Lozano–Alvarez 2001) and regularly forage or migrate across exposed habitats (Kanciruk 1980; Herrnkind et al. 2001).

Another unusual finding of this study is that a single episode of autotomy does not affect long-term growth rate of *P. versicolor*. Previous studies report almost unanimously that appendage loss reduces growth rate of other palinurids (Davis 1981; Brown and Caputi 1985; Hunt and Lyons 1986; Negrete–Soto et al. 2002; Brouwer et al. 2006; but see Plaut and Fishelson 1991). The conflicting results are unlikely to be a product of differences in magnitude of injury, since the number of missing appendages per lobster was comparable among studies (c.f. Brouwer et al. 2006; this study). There were, however, likely to be differences in frequency and type of injury. When observed in situ prior to capture, less than 5% of *P. versicolor* were injured, indicating that fishing pressure at the study site was relatively light and that appendage loss was probably rare or occasional. In contrast, the lobster populations observed in other studies were heavily fished and individuals were subject to frequent injury, including injury other than autotomy (Davis 1981; Brown and Caputi 1985; Hunt and Lyons 1986). Together, these results suggest that palinurids carry enough energy reserves to recover from a single episode of appendage loss, but these reserves become depleted (and growth slows) when appendage loss is

repetitive. It is also possible that appendage loss impairs foraging efficiency (and reduces growth) only when lobsters are exposed to heavy fishing pressure (i.e., repetitive injury). Any such impairment could occur via repetitive functional incapacitation (e.g., loss of feeding appendages) or via behavioral modification (e.g., emigration from preferred habitat) (Parsons and Eggleston 2006).

Mean absolute growth after approximately one molt interval (a proxy for molt increment) was not affected by injury, although it did tend to be greater in moderately injured lobsters than in minimally injured and uninjured lobsters (Fig. 4). This result is unexpected because injury reduces molt increment in other palinurids (Chittleborough 1975; Davis 1981; Brown and Caputi 1985; Negrete-Soto et al. 2002; Brouwer et al. 2006). The unusual trend is perhaps an artifact of sampling error (due to the small sample size of moderately injured lobsters) or an indication that moderate injury induces precocious molting. If the latter is true, most moderately injured lobsters would have molted multiple times within 0.5 years, thus giving a false impression that injury increases molt increment. In any case, caution is urged when interpreting these data.

The literature presents mixed results regarding the effects of injury on molt interval in palinurids. In particular, it has been demonstrated that injury can either induce (Chittleborough 1975; Brouwer et al. 2006) or delay molting (Davis 1981; Hunt and Lyons 1986), depending on a number of environmental and physiological factors (Juanes and Smith 1995). After 0.5 years, the prevalence of molting (an indicator of molt interval) was independent of injury in *P. versicolor*, although it did tend to be higher in moderately injured lobsters than in minimally injured and uninjured lobsters (Fig. 5). Although a type II statistical error cannot be dismissed (due to small sample size of moderately injured lobsters), it is apparent that molt interval in *P. versicolor* is not radically influenced by autotomy.

As noted above, the effects of autotomy on molt increment (Fig. 4) and molt interval (Fig. 5) were difficult to evaluate because of the small sample size, which precipitated from the requirement to standardize time at liberty (only those lobsters recaptured after 0.5 years could be analyzed). However, it must be remembered that the assessments of molt increment and molt interval were of secondary importance to this study; the primary objective was to assess the effects of autotomy on long-term survival and growth of *P. versicolor*. Importantly, the datasets relating to the primary objective (Figs. 2 and 3) were not bound by the requirement to standardize time at liberty and were not compromised by small sample sizes. Thus, the main conclusion of this study (i.e., autotomy has no significant effect on long-term survival

and growth of *P. versicolor*) is presented with an adequate level of confidence. The data in Figs. 4 and 5 are included here solely to illustrate that the effects of autotomy on molt increment and molt interval in *P. versicolor* are potentially unusual, and thus warrant further research.

Although a single episode of autotomy appears relatively benign to *P. versicolor*, it is important to recognize that loss of appendages may have other ecological consequences for this species. Firstly, energy and materials normally allocated to reproductive activities (e.g., gamete development) may instead be used to regenerate lost appendages. Secondly, some appendages have specialized communicative and reproductive functions that may be lost through autotomy. For example, the unique fifth pereopods of female palinurids are chelate, and are used to liberate sperm from spermatophores and to groom oviposited eggs (Aiken and Waddy 1980). Loss of a certain type or number of appendage(s), therefore, may hinder or even halt reproduction. Given the importance of reproductive performance to population dynamics and fishery yields, it is surprising that the effects of autotomy on reproduction have never been explored in any palinurid.

In summary, this study reveals that a single episode of injury (autotomy) does not significantly affect long-term survival and growth rates of *P. versicolor* on the Great Barrier Reef. In addition, a single episode of autotomy appears to have no major effect on molt increment and molt interval in this species. These results suggest that the energetic cost of autotomy is either negligible or exists as a trade-off with some other life-history trait, such as reduced reproductive performance. It is also apparent that *P. versicolor* is remarkably resilient to occasional capture and handling, even if moderate levels of autotomy are involved. This supports (1) the use of certain management tools (e.g., size limits) that prescribe release of non-legal lobsters, regardless of their injury status, and (2) the inclusion of minimally injured lobsters in mark-recapture studies of growth or survival. Lastly, due to the potential for cumulative effects of repetitive injuries, caution is warranted with regard to extrapolating the results of this study to heavily fished lobster populations.

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