Changes in egg production of the western rock lobster (*Panulirus cygnus*) associated with appendage damage

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Abstract—Data collected during fishery-independent sampling programs were used to examine the impact of appendage damage (indicated by lost or regenerated legs and antennae) on the reproductive output of female western rock lobster (*Panulirus cygnus*). Most of the damaged females sampled had one (53%), two (27%), or three (13%) appendages that had been lost or that were regenerating. Appendage damage was associated with the reduced probability of a female developing ovigerous setae; and if setae were produced, with the reduced probability that females would produce more than one batch of eggs within a season. These effects were more pronounced as the number of damaged appendages increased. From data collected in 2002, it was estimated that the total number of eggs produced by mature females caught in the fishery was significantly reduced ($P<0.001$) by 3–9% when the impact of appendage damage was included.

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Western rock lobster (*Panulirus cygnus*) are found only off Western Australia, where they form the basis of an intensive commercial fishery (Phillips and Melville-Smith, 2005). One result of the high exploitation rates experienced by western rock lobster (Brown and Caputi, 1985, 1986), and other decapod species (Krouse, 1976; Smith and Howell, 1987), is the damage sustained by the catch that is returned to the water. Damage, whether caused by aggression between conspecifics trapped in pots, desiccation on board boats before processing, or rough handling during sorting, is generally a combination of dehydration, broken body parts, and the loss of entire appendages. Apart from the mortality of animals due to processing, both the growth rate and fecundity of the surviving animals can be significantly reduced (Davis, 1981; Brouwer et al., 2006). Damaged animals appear to reallocate energy stores towards regenerating damaged appendages and away from growth and reproduction (Norman and Jones, 1992; Juanes and Smith, 1995; Mariappan and Balasundaram, 2001).

In the western rock lobster fishery, sustainability of the resource has been achieved by management regulations that include limited entry to the commercial fishery, a closed fishing season from July to mid-November, and return to the water of all lobsters that are outside the maximum and minimum legal size limits or that are in a breeding condition (i.e., bearing ovigerous setae) (Caputi et al., 2000; de Lestang and Melville-Smith, 2006). Anecdotally, these regulations are believed to result in 55% of the *P. cygnus* catch being returned to the sea. This species is especially susceptible to autotomizing (dropping) limbs (Brown and Caputi, 1983, 1985): 40–80 tonnes of legs are estimated to be lost from the landed catch of *P. cygnus* each year (Davidson and Hosking, 2002).

We used data from a variety of existing and new sources to examine the effect of appendage loss and regeneration (both antennae and legs) on the reproductive biology of female *P. cygnus*. We believe this study to be the first comprehensive assessment of the impact that appendage damage has on the reproductive output of a decapod species. This study assesses the impact of appendage damage on the proportion of females developing ovigerous setae, the proportion of females that will produce one or more batches of eggs within a breeding season, and the number of eggs in a batch.

Materials and methods

Sampling regime

Data were collected during a fishery-independent breeding stock survey (hereafter referred to as "the survey"), which has been conducted annually at three localities (Lancelin, Dongara, and Abrolhos Islands) and intermittently at three others (Fremantle, Jurien, and Kalbarri) since 1992. The commercial fishery in Western Australia is divided into three management zones: the Abrolhos Islands (zone A), north coastal (zone B), and south coastal (zone C) (Fig. 1). In some cases data were pooled into these zones for analysis.

The surveys were undertaken over the course of ten days before the start of the commercial lobster fishing season on 15 November. This period is very close to the annual peak of the egg-bearing season, which is considered to occur in November of each year (Chubb, 1991). Because this survey was designed to be repeatable, the same fishing gear (batten pots with closed escape gaps), bait (a combination of north sea herring [*Clupea harengus*] and Australian salmon [*Arripis truttaceus*]), and locations (same GPS coordinates) were used. The results are therefore directly comparable between years. For more details on the survey sampling regime see Chubb (2000).

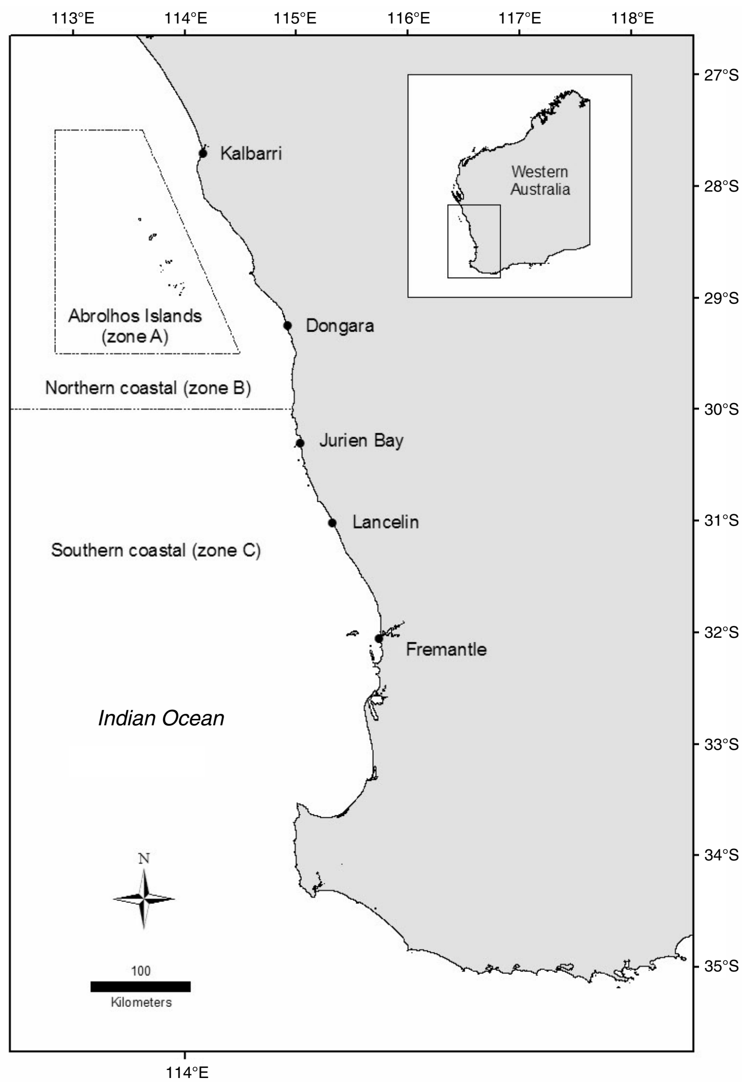


Figure 1

Management zones (zone A, Abrolhos Islands; zone B, northern coastal; zone C, southern coastal) in the western rock lobster (*Panulirus cygnus*) fishery, and six sites (five on the coast of Western Australia and one comprising the Abrolhos Islands) used for fishery-independent breeding stock surveys and commercial monitoring of the catch.

Measurements and records

During the surveys, the carapace length (CL) of each lobster was measured to the nearest 1 mm from midpoint between the preorbital spines down the mid-dorsal line to the posterior edge of its carapace. The presence of gonopores on the base of the fifth pair of pereiopods was used to identify males. For females, the presence of ovigerous setae attached to the endopodites, the visual appearance of the ovaries through the dorsothoracic musculature, the presence and developmental stage of external ova attached to the setae, and the presence of a spermatophoric mass attached to the fifth abdominal segment were recorded. These data have been used to predict whether a female would produce one or two batches of eggs in a spawning season (such females are known as "single breeders" and "double breeders, respectively)"—see Melville-Smith and de Lestang (2005) for a full description of this method).

Loss and regeneration of antennae and limbs were also recorded during the survey as either an old loss, new loss, or as a regenerated appendage and all three categories were grouped collectively and referred to as "appendage damage." Old loss was identified by dark melanization at the site of the lost appendage and new loss by exposed flesh without melanization. Although new leg losses were recorded, nearly all were considered to have resulted from capture and handling during the survey and therefore were excluded from our analysis of the impact of appendage damage on reproductive output. Regenerated limbs of *P. cygnus* were only easily identifiable in the first intermoult period after the limb was lost and were distinguished by being greenish in color and noticeably smaller or thinner than existing limbs. Because old and new losses have been recorded since 1992 and regenerated limbs have been recorded since 2001, we used only the data collected since the 2001 survey. The incidence of old losses, new losses, and regenerated appendages between zones, sex, and carapace size was compared by using ANOVA.

Effect of appendage damage on fecundity estimates

Because most of the lobsters sampled in zone A (the Abrolhos Islands) during the 2001–03 surveys were larger than the size at maturity (Melville-Smith and de Lestang, 2006), data derived from sampling in this location were used to examine whether the incidence of old appendage-losses and regenerated appendages affects the reproductive state of female *P. cygnus*.

The batch fecundity (number of eggs in one batch) of 50 female *P. cygnus* with early-stage eggs that ranged in carapace length (CL) from 67.1 to 96.2 mm was determined. Twenty-three females had either one or two damaged appendages and 27 had no damaged appendages; females with early-stage eggs and more than two damaged appendages were seldom caught and therefore were not assessed. The endopodites with eggs were removed from the lobsters and dried in an oven for 24 hours. The eggs were then separated from the setae and weighed to the nearest 0.0001 g. Three subsamples of each brood (each of ~0.05 g) were taken and weighed. The number of eggs in each subsample was counted to determine the mean number of eggs per gram of dry egg weight, and the mean of these values was used to estimate the total number of eggs in the brood. The mean fecundity per spawning season was compared for females with and without appendage damage after standardizing for carapace length with ANCOVA.

The total number of eggs produced by all mature female *P. cygnus* caught during the 2002 survey in each of the three commercial fishing zones was estimated by using an equation that incorporates the number of broods of eggs produced each spawning season and the effects of appendage damage on the likelihood of spawning once or twice.

$$(TF = NB \times F \times PO_{DA}),$$

where TF = the total fecundity (number of eggs produced) by mature females;
NB = the probability of a female producing one or two broods each spawning season, on the basis of their CL;
F = s the relationship of fecundity to carapace length; and
PO = the probability that females with damaged appendages DA will produce eggs.

$$P_1 = \left(1/1 + \exp\left(-\ln(19) \times (CL - SB_{50})/(SB_{95} - SB_{50})\right)\right),$$

$$P_2 = \left(1/1 + \exp\left(-\ln(19) \times (CL - DB_{50})/(DB_{95} - DB_{50})\right)\right),$$

where SB_{50} and SB_{95} = the CLs at which 50 and 95%, respectively, of the population at each location produced one brood of eggs (P_1); and

DB_{50} and DB_{95} = the CLs at which 50 and 95%, respectively, of the population at each location produced two broods of eggs (P_2) per spawning season (de Lestang and Melville-Smith, 2006).

Results

Frequency of appendage damage in 2001—05 surveys

The percentage of western rock lobster with damaged appendages in the 2001–05 survey catches decreased as the number of damaged appendages increased (Fig. 2, A–C). For example, in zone A, about 82% of all female and male *P. cygnus* in the catches had no appendage damage, whereas about 9%, 4%, and 2% of both sexes had one, two, and three damaged appendages, respectively. Only 1% of the catch of each sex had four damaged appendages and less than 0.5% of all lobsters had more than five damaged appendages.

Table 1

Percentage of all female and male western rock lobster (*Panulirus cygnus*) with old damage, or regenerated appendages, in the three management zones of the fishery. Data are from the 2001–05 fishery-independent breeding stock survey.

	Fishing zone		
Sex	Zone A	Zone B	Zone C
Female	17.8%	12.4%	20.9%
Male	18.9%	8.7%	17.2%

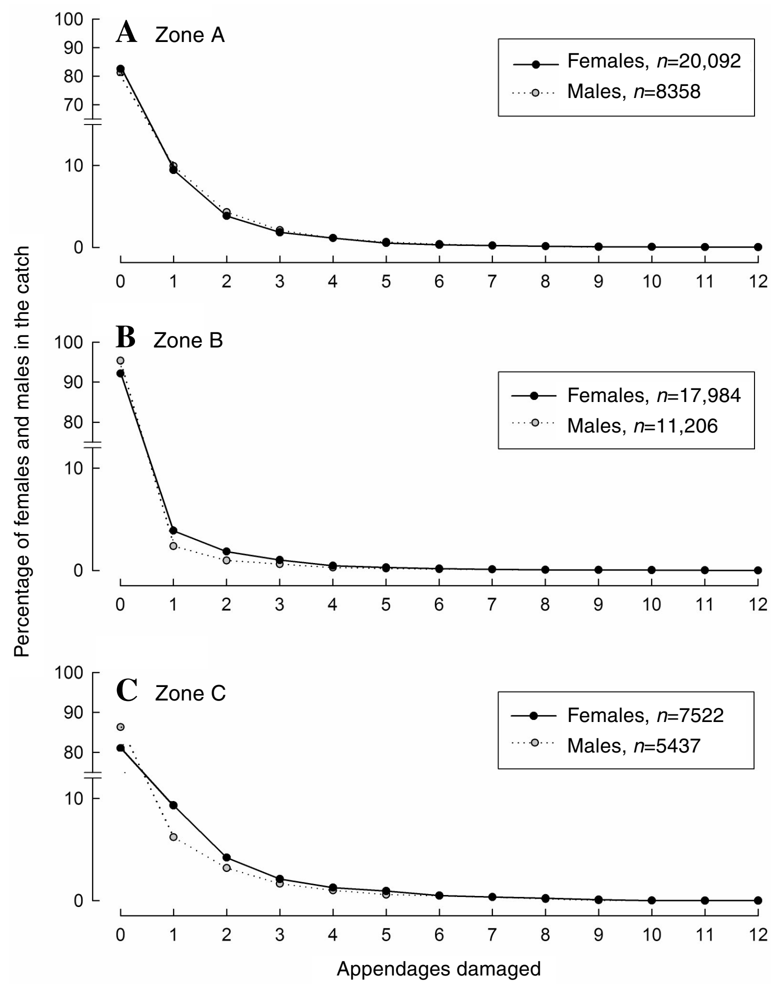
The incidence of appendage damage was significantly different between zones ($P<0.001$) and both zones A and C had higher incidences than zone B (Table 1) . In addition, within zones B and C, significantly ($P<0.001$) more females than males were caught with appendage damage. There was no significant difference ($P=0.14$) in the incidence of appendage damage for females and males caught at the Abrolhos Islands.

Relationship between appendage damage and carapace length

The incidence of new appendage loss differed significantly ($P<0.001$) between the two sexes in the various size classes (Fig. 3A). New appendage loss in females remained at about 17% in all the size classes, whereas in males this loss decreased from 15% to 8% in the first four size classes, then increased substantially to 28% and 20% in the larger size classes (110–119 and 120–129 mm CL, respectively).

The incidence of old appendage loss also differed significantly ($P<0.001$) between sexes in different size classes (Fig. 3B). Old appendage damage was slightly more common as females increased in size, i.e., from 7% to 11% between the 60–69 and 100–109 mm CL size classes. This increase also occurred for males but to a much greater extent, i.e., from 4% to 23% between the 60–69 and 100–109 mm CL size classes. The incidence of old appendage damage in males then declined slightly over the two largest size classes (110–119 and 120–129 mm CL) 22 and 16%, respectively (Fig. 3B).

Regenerated appendages in the catches of lobster differed significantly ($P<0.001$) between sex and size classes (Fig. 3C). Regenerated appendages were more commonly recorded for females than for males, but regenerated appendages for each sex remained relatively



constant at about 4% and 3%, respectively, in all size classes below 120 mm CL. Above this size class, the incidence of regenerated appendages increased markedly in females (10%) and declined to zero for males (Fig. 3C).

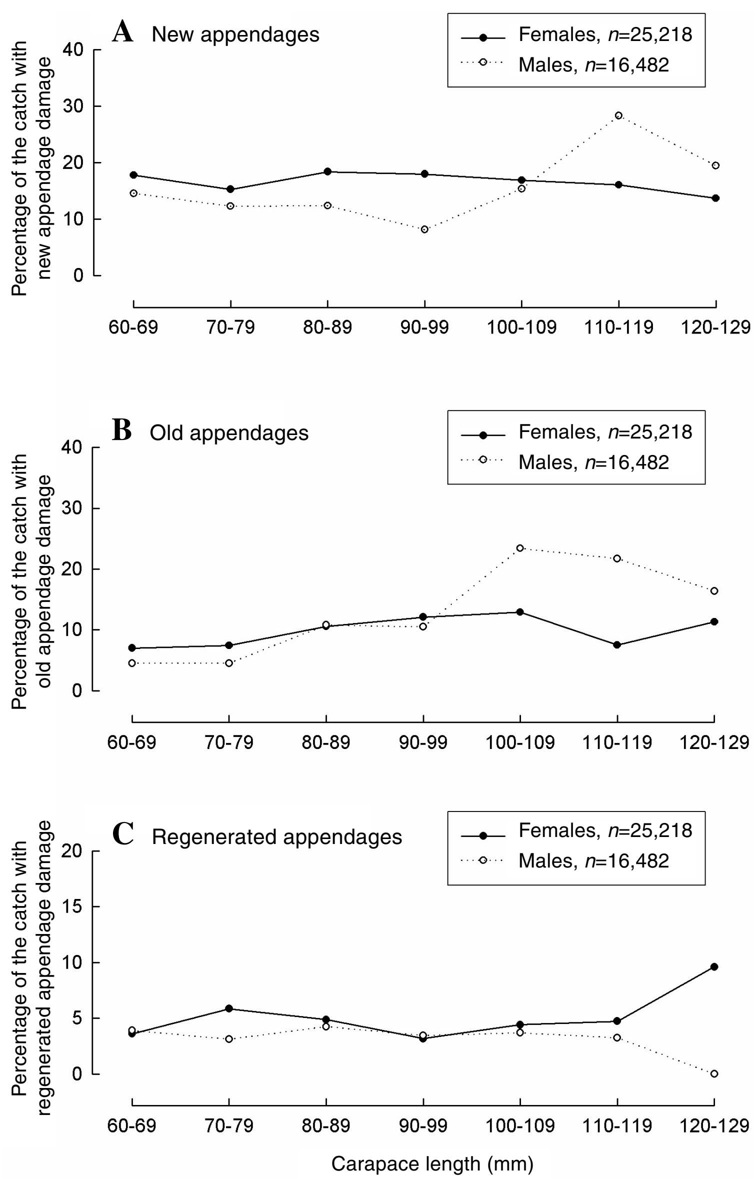
The influence of appendage damage on egg production

The proportions of female *P. cygnus* (CL>65 mm) from the Abrolhos Islands that were classified as having ovigerous setae, as being single breeders, and as being double breeders, all declined with increasing appendage damage (Fig. 4, A–C). A consistent trend existed between the various reproductive states and the magnitude of their appendage damage. For females at the Abrolhos Islands above the size at maturity, the likelihood of developing ovigerous setae declined with the number of appendages damaged: 98% likelihood (one appendage damaged), 95% (two), 80% (five), and 58% (six). This likelihood continued to decline until it reached zero for all females with either 11 or 12 damaged appendages (Fig. 4A).

For ovigerous females with damaged appendages, the likelihood of producing either one or two batches of eggs each spawning season declined more rapidly than the likelihood of developing ovigerous setae. Females with one damaged appendage were 20% and 19% less likely to produce one or two batches of eggs, respectively, whereas those with five damaged appendages were around 85% and 65% less likely to produce one or two batches of eggs, respectively. Females with more than seven damaged appendages did not produce eggs (Fig. 4, B and C). Equations describing the relationships between appendage damage and the likelihood of spawning once for single breeders and twice for double breeders were not significantly ($P=0.42$) different from each other and were thus combined to produce a single equation to describe the likelihood of producing one or two broods of eggs:

$$PO_{DA} = \exp[-0.31 \times \ln(DA+1) + 0.742] - 1.$$

The above relationship between appendage damage and the likelihood of lobsters developing ovigerous setae, or the likelihood of lobsters producing one or two broods of eggs at the Abrolhos Islands, was very similar in the other two coastal management zones.



The influence of appendage damage on fecundity

The mean fecundity per spawning season of female *P. cygnus* with a standardized CL of 77.0 mm did not differ significantly ($P>0.05$) between females with and without damaged appendages (i.e., 249,885 ±7873 eggs and 234,164 ±7094 eggs, respectively). Furthermore, regressions between fecundity (F) and carapace length (CL) of female *P. cygnus* with and without damaged appendages (Fig. 5) did not differ from each other ($P>0.05$) and were both very similar to the relation of carapace length to fecundity recorded for this species by Chubb (1991).

The effect of damaged appendages on the number of eggs produced per spawning season by female *P. cygnus* at the Abrolhos Islands was greater for large than for small females (Fig. 6). For example, two damaged appendages reduced the fecundity of a 70-mm-CL lobster by about 114,000 eggs, whereas the fecundity of a 120-mm-CL lobster was reduced by about 1,000,000 eggs (Fig. 6).

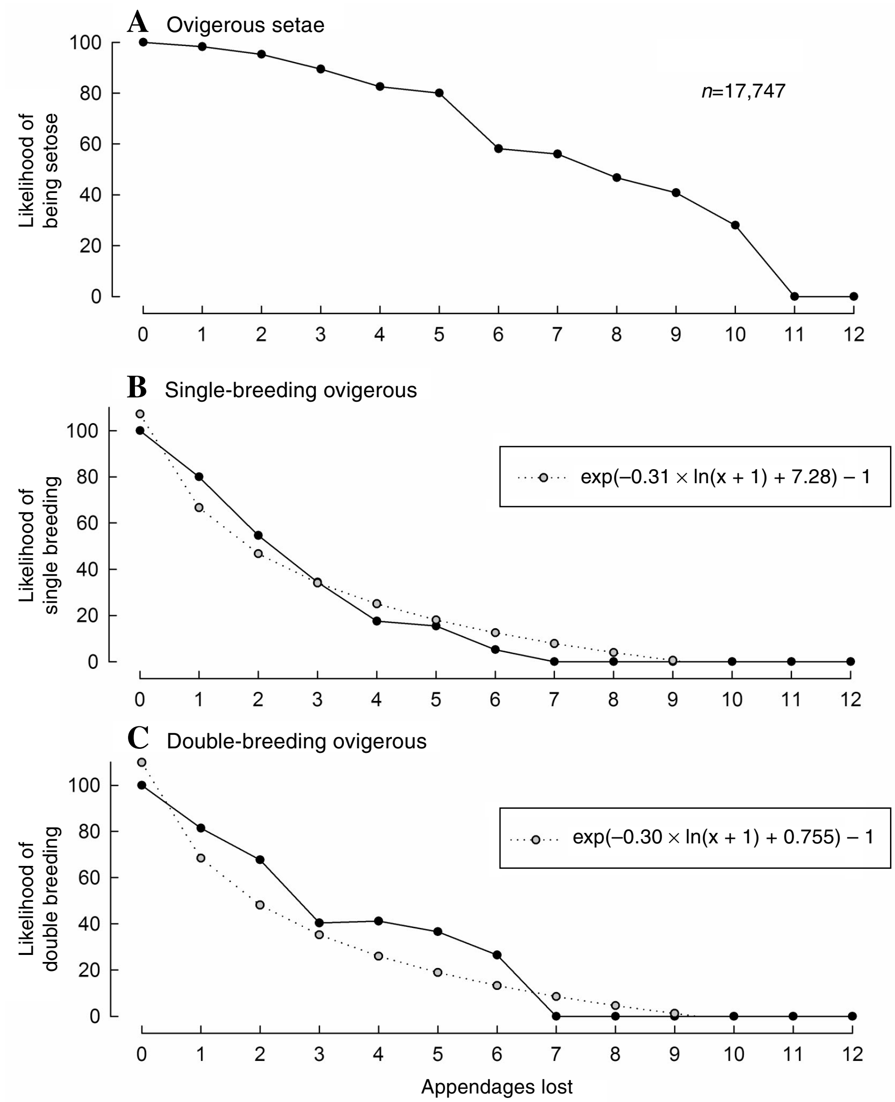
The total number of eggs produced in the 2002 survey was estimated for each of the three management zones separately for females with and without appendage damage. The inclusion of appendage damage significantly (all $P<0.001$, paired t-test) reduced egg production estimates by 8.5%, 3%, and 9% in zones A, B, and C, respectively.

Discussion

The incidence of appendage damage

The proportions of lobsters with damaged appendages varied markedly between sexes, sizes, and locations sampled. However, the timing and frequency within a year that molting takes place for the sexes, and for different-size animals, plays only a relatively minor role in influencing these differences. Female western rock lobsters generally molt twice a year: February–March and again in May. A significant proportion of large breeding females occasionally skip the February–March molt, but all take part in the May molt (de Lestang and Melville-Smith, 2006).

New appendage damage occurred around the time of capture and could mostly be attributed to the survey sam-



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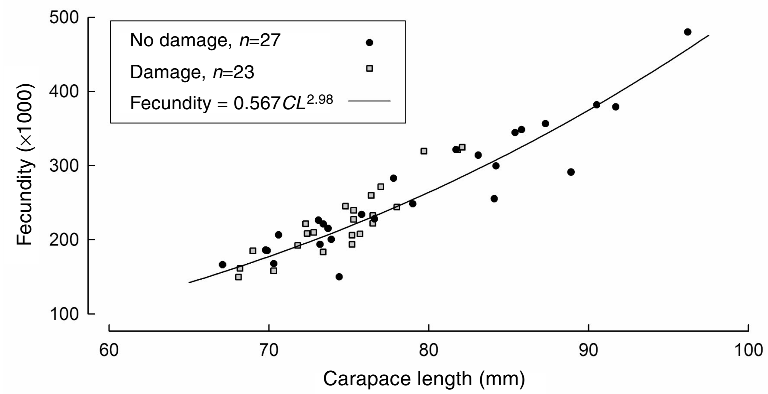
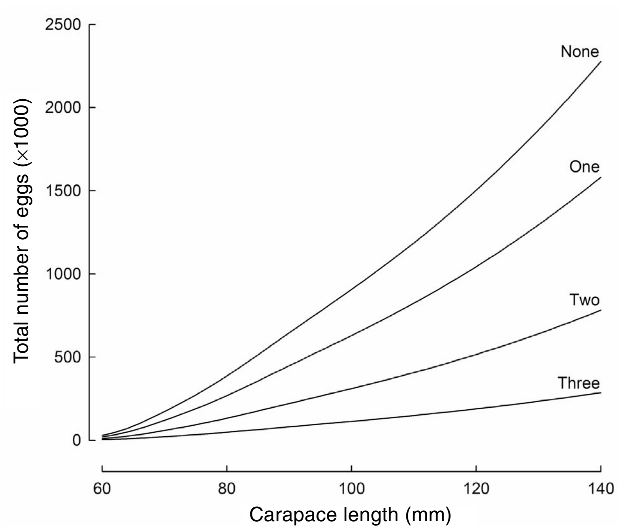
pling methods, either to capture in the pots or handling on deck. The slightly higher proportions of females than males recorded with new damage are possibly the result of the longer handling time needed to make additional observations, such as recording the presence or absence of eggs and spermatophores and visually assessing the condition of the ovary. In contrast to new appendage damage, the events that resulted in old damage and regenerated appendages occurred before the survey and, in the latter case (regenerated appendages), before the lobster's last molt, i.e., about May (de Lestang and Melville-Smith, 2006). It is therefore likely that much of this damage is inflicted during the commercial fishing season, possibly as a result of capture and handling. It is thus not surprising that the lobsters showing the greatest incidence of regenerated appendages are females above the maximum legal size (115 mm CL in zone C and 105 mm CL in zones A and B); many of these animals were likely handled and returned to the water many times during a season. Predators may be an additional cause of appendage damage. The fact that the incidence of old appendage damage increased in



both sexes with size may indicate that larger individuals are more likely to survive the attack of a predator, although perhaps with the loss of appendages.

The effect of appendage damage on reproductive output

Appendage damage can lead to an associated reduction in the reproductive output of female *P. cygnus* directly, namely as reduced proportions of females that develop ovigerous setae, and as a reduction in the proportions of



ovigerous females that will produce one or two batches of eggs within a season. Reproductive output is also affected indirectly when females with appendage damage do not molt into breeding condition (with ovigerous setae); a female above the legal minimum size without ovigerous setae can be legally retained by commercial and recreational fishermen and thus her contribution to the broodstock is removed.

The significant reduction in reproductive output of female *P. cygnus* with appendage damage is not surprising, because regeneration places large demands on energy reserves, often in the form of a reallocation of resources that were originally destined for reproduction and growth (Démeusy, 1965; Norman and Jones, 1992; Juanes and Smith, 1995). Moreover, if appendage damage is extensive, the process of regenerating multiple appendages may result in a long-term reallocation and an overall increase in energy demand (McVean, 1982).

Most *P. cygnus* caught during the survey were intact when examined; less than 15% of the entire catch had damaged appendages. This 15% was probably due, in part, to management measures based on previous work on the effects of appendage damage (Brown and Caputi, 1985, 1986) to initiate changes aimed at reducing limb loss. Methods for limiting appendage damage even further are being developed, i.e., cold stunning (Davidson and Hoskin, 2002). However, even with the best intentions, some appendage damage through handling is unavoidable.

This study has highlighted that management measures aimed at protecting the western rock lobster broodstock inevitably result in the animals being handled more than once (or multiple times) in the course of the fishing season, and the damage to appendages caused by handling produces a significant, and previously unrecognized, effect on the overall egg production of this resource. These effects need to be taken into account when considering the benefits of these management measures in this and other crustacean fisheries.

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