

J. Stewart · S. J. Kennelly

Growth of the scyllarid lobsters *Ibacus peronii* and *I. chacei*

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Abstract The growth rates of the morphologically similar scyllarid lobsters *Ibacus peronii* (Leach, 1815) and *I. chacei* (Brown and Holthuis, 1998) are described using data from a tag/recapture study and from tagged lobsters kept in captivity. Within particular size classes, we found no differences in moult increments between male and female *I. peronii* nor between male and female *I. chacei*. Small individuals of both species always had larger moult increments than larger individuals. For *I. peronii*, females moulted more frequently than males, and smaller size classes moulted more frequently than larger size classes. Female *I. peronii* therefore grew more quickly than males and reached their estimated size at sexual maturity (51 mm carapace length) after ~2 yr. Moulting of *I. peronii* was seasonal, with most lobsters (96.3%) moulting between October and January. We found no differences in growth rates of *I. peronii* at two locations along the east coast of Australia: Coffs Harbour in New South Wales (30°18'S; 153°08'E), and Lakes Entrance in Victoria (37°53'S; 148°00'E). For *I. chacei*, we found no differences in the frequency of moulting between males and females and, because we also found no differences in the moult increments between males and females, the growth rates of both sexes were the same.

Introduction

The growth rates of large marine decapods is one of the most difficult parameters of their life-histories to estimate (Aiken 1980). Increases in the lengths of such animals only occurs during times of moulting when the entire hard exoskeleton is shed (Phillips et al. 1980; Ruppert and Barnes 1994), resulting in discontinuous growth. Growth in decapods is usually described, therefore, in terms of two components which can vary according to the size and sex of the animal (Aiken 1980; Hartnoll 1982): (i) the size increment at each moult (moult increment); and (ii) the frequency of moulting (intermoult period).

Moult increments are directly measurable from tagged individuals that have moulted while at liberty and, for a particular species, tend to be similar for individuals of a given size, allowing one to estimate whether observed increments are from one or more moults (Conan and Gundersen 1979; Caddy 1987). However, moult frequency is a more difficult variable to measure because: (i) large crustaceans moult infrequently, and many tagged individuals are recaptured that have not moulted while at liberty; and (ii) data from tag/recaptures only provides information on the time at liberty between tagging and recapture – not on the time elapsed between tagging and moulting. Therefore, moult frequency must be approximated using the number of recaptured individuals that have moulted with increasing time at liberty. Several methods have been described for deriving such estimates, but none have been accepted as globally successful (see Munro 1983; Annala and Bycroft 1988; Restrepo and Hoenig 1988; Melville-Smith 1989; Chen and Kennelly 1999).

Although the growth of crustaceans is a discontinuous process, historically it has been described by mathematical functions that produce smooth growth curves. Despite its almost universal use, there are concerns that the von Bertalanffy growth function may be unsuitable for describing crustacean growth (Breen 1994) because

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J. Stewart (✉)
New South Wales Fisheries Research Institute,
P.O. Box 21, Cronulla,
New South Wales 2230, Australia

Fax: 0061 (0) 29527 8576
e-mail: stewartj@fisheries.nsw.gov.au

S. J. Kennelly
Centre for Research on Ecological Impacts of Coastal Cities,
Marine Ecology laboratories, A11,
University of Sydney, New South Wales 2006,
Australia

of its implicit assumption concerning continuous growth. Despite this, it is still useful to provide estimates of von Bertalanffy's growth coefficient K and asymptotic length L_∞ when describing growth, in order to compare them with those published for other species. A different approach – probabilistic stepwise growth simulation (PSGS: Chen and Kennelly 1999) describes the growth of a large decapod crustacean *Ranina ranina* using tag/recapture data. This technique uses relationships between the probabilities of moulting with size increments per moult to generate growth curves that mimic discontinuous growth patterns and take into account variations in raw data.

In any tagging study, it is important to have some estimate of the effect that tagging has on the animal (Hartnoll 1982), and this is most easily done in captivity. While any results from captive animals may be confounded by the effects of being in an artificial environment, observations on the effect of tagging on moulting and survival can be used to provide a measure of confidence in the results obtained from tagging animals in the field.

Balmain bugs *Ibacus peronii* (Leach, 1815) and smooth bugs *I. chacei* (Brown and Holthuis, 1998) are the two most important commercially exploited scyllarid lobsters off the coasts of New South Wales and Victoria, Australia (Kailola et al. 1993), with over 112 tonnes being landed in New South Wales during the 1996/1997 financial year, at an estimated landed value of over 1.1 million Australian dollars. Despite their economic importance, the biology of these lobsters has received little attention (but see Marinovic et al. 1994; Stewart et al. 1997; Stewart and Kennelly 1997, 1998; Brown and Holthuis 1998), and their growth rates remain unknown. However, a recent paper by Marinovic et al. (1994) on the larval development of *I. peronii* provides some useful data on moult increments and intermoult periods for small, post-larval individuals in captivity. This work is useful for estimating growth in animals up to 39 mm carapace length (CL), which are too small to tag using conventional tagging methods.

In this paper we describe the growth of *Ibacus peronii* and *I. chacei* using data from recaptured tagged individuals, and from *I. peronii* kept in captivity. Data from lobsters tagged and recaptured in the field are used to describe growth using two methods: (i) the programme GROTAG (Francis 1988), which provides estimates of the von Bertalanffy growth-function parameters; and (ii) the PSGS approach (Chen and Kennelly 1999), which describes growth in terms of the probabilities of moulting and moult increments. We also incorporate Marinovic et al.'s (1994) data on post-larval growth to provide the most likely growth curves for these species. Finally, *I. peronii* tagged and kept in captivity have been used to quantify the effects of tagging on moulting, survival and tag loss, and to make general observations on their behaviour during moulting.

Materials and methods

Field study

A large-scale, field-based tagging study was carried out between April 1993 and May 1994 to provide data on the growth of *Ibacus peronii* (Leach, 1815) and *I. chacei* (Brown and Holthuis, 1998) in the wild. Both species were tagged out of Coffs Harbour in New South Wales (30°18'S; 153°08'E), where their geographical distributions overlapped, but only *I. peronii* were tagged out of Lakes Entrance in Victoria (37°53'S; 148°00'E). Standard T-bar tags (made by Hallprint Pty Ltd) were inserted dorsally into the musculature at the interface between the carapace and abdomen, at a point halfway between the midline and the left-hand edge. The carapace length of all tagged individuals was measured as the distance between the rostral sinus and the posterior edge of the carapace (for complete details on the methodology used see Stewart and Kennelly 1998). All *Ibacus* spp. captured that appeared to be in good health and larger than ≈ 30 mm CL were sexed, measured and tagged. Individuals smaller than this size were not tagged because we assumed that they would not survive tagging. Recaptured lobsters provided precise data on their time at liberty and growth in CL. Data from recaptured individuals that had grown have been used to describe the relationships between growth increment per moult and size for each species, sex and location.

Data analysis

Estimates of the von Bertalanffy growth-function parameters k and L_∞ were obtained using the maximum-likelihood method and programme GROTAG (Francis 1988). GROTAG also provided estimates of the parameters g_a and g_b , which describe the mean annual growth of an animal at two different sizes, a and b . These sizes were chosen to span the range of lengths at tagging and, to allow direct comparisons to be made, were selected as 40 and 60 mm CL, respectively, for both species, sexes and locations in the present study. Another parameter used in the model describes errors due to measurement (s), which were estimated by comparing the sizes at tagging versus the sizes at recapture for those individuals that were recaptured without having moulted. The standard deviation of the measurement error, s , was calculated to be 0.14 and was fixed for all of the GROTAG growth models.

Recaptured tagged *Ibacus* spp. provided data on increments per moult and times at liberty. These data were used in a modified version of the PSGS growth model described for spanner crabs, *Ranina ranina* (Chen and Kennelly 1999). The PSGS approach firstly estimated the probability of a recaptured tagged individual having moulted, depending on its time at liberty. This was done separately for male and female *I. peronii* from Coffs Harbour and Lakes Entrance and for male and female *I. chacei*. Recaptured lobsters were grouped into days at liberty, using intervals of 50 d, and the proportion of lobsters that had moulted once was calculated for each 50 d grouping. The relationship between the proportion of lobsters that moulted with days at liberty tended to increase from 0 to 1, and was best described by the logistic equation

$$P_i = \frac{1}{(1 + e^{-m(D_i - D_{50})})} + e_i, \quad (1)$$

where P_i = proportion of lobsters that had moulted in the 50 d interval i , D_i = median number of days in that grouping, m = parameter describing the rate of P_i increasing from 0 to 1, D_{50} = number of days at liberty at which 50% of the lobsters had moulted, and e_i = error term. Because crustaceans tend to have longer intermoult periods as they increase in size and age (Mauchline 1977), the lobsters were grouped into different size-classes depending upon the spread of the data at each location. *I. peronii* from Lakes Entrance were grouped into < 55 and ≥ 55 mm CL at tagging and *I. peronii* from Coffs Harbour were grouped into < 60 and ≥ 60 mm CL at tagging. Insufficient *I. chacei* were recaptured to allow grouping into different size-classes. The

parameters m and D_{50} were estimated in a non-linear least-squares analysis, weighted by the sample size in each day class, using SAS. An analysis of the residual sum-of-squares (ARSS; Chen et al. 1992) was performed to examine significant differences between size-classes and sexes.

The PSGS approach next used tag/recapture data to examine the relationships between moult increment (log-transformed) and pre-moult carapace length for each species, sex and location. Significant differences in these relationships were tested using analysis of covariance and, if there was no difference between sexes, the data were pooled. The data were separated into the same size-classes as those for estimating moult probabilities (i.e. <60 or ≥60 mm CL for *Ibacus peronii* from Coffs Harbour and <55 or ≥55 mm CL for *I. peronii* from Lakes Entrance). The proportion of lobsters with moult increments of any given size (rounded to the nearest whole millimetre) was calculated, and was used to determine the probability of an individual having a moult increment of a particular size within a size-class.

The PSGS model generates stepwise growth curves by combining the probability of moulting with estimates of the probability of a particular increase in size at moulting. The following procedure was used to apply this approach to the tag/recapture data for each species, sex and location: (i) A start size L_1 was chosen as the smallest tagged lobster recaptured. (ii) The probability of a moult occurring during the first 50 d at liberty was calculated from the logistic functions (see above). (iii) A random number was chosen from a uniform distribution between 0 and 1 and, if less than the calculated probability of a moult during the first 50 d, then a moult was concluded to have occurred; if greater, then no moult was concluded to have occurred and the probability of a moult occurring after the next 50 d at liberty was calculated; this was repeated until a random number was drawn that represented a moulting event. (iv) Binomial sampling based on the probability of having a particular size increment when moulting was carried out to determine the new size L_2 ($L_2 = L_1 + \text{size increment}$). These steps were repeated until a pre-determined upper limit in size was reached (L_{max} , the largest tagged lobster recaptured for each species, sex and location).

By repeating this procedure 100 times, a distribution of stepwise growth curves was simulated to provide estimates of variation within the data sets.

Laboratory tagging study

Ibacus peronii were tagged and kept in aquaria at the New South Wales Fisheries Research Institute to assess the success of the tagging method, to estimate moult frequency, and to observe behaviour. Aquarium facilities consisted of four round 4000-litre tanks for experimental lobsters and two 1000-litre tanks for spare lobsters. Water was pumped continuously from the ocean, and

filtered through sand and into the tanks at ambient temperatures (range 13.5 to 25 °C). Each tank contained an undergravel filter covered with 5 cm of shell grit and 10 cm of clean sand.

Live *Ibacus peronii* were purchased from commercial fishers in Coffs Harbour and from the Sydney Fish Markets. These were transferred into the tanks and left to acclimatize for 3 wk before being used. Twenty *I. peronii* were then chosen at random to be placed in each experimental tank. Two of the 4000-litre tanks contained 20 tagged lobsters each, and two contained 20 untagged lobsters each. All *I. peronii* were sexed and measured before being placed in the tanks, and the tagged individuals were tagged with standard T-bar tags in a method identical to that used in the field.

Spare lobsters were kept in the two 1000-litre tanks and were used as replacements for individuals that died to maintain equal stocking densities in each experimental tank. Replacement lobsters were marked by cutting a wedge-shaped piece out of their telson. All individuals were fed a diet of chopped squid, fish, prawns and mussels, with identical quantities of food placed in each tank every day. Uneaten food, dead lobsters, moults and faecal material were removed each day. All dead lobsters and moults were sexed and measured.

The experiment was terminated 12 mo after commencement, and all *Ibacus peronii* were removed, sexed and measured. Data on moulting were obtained from 24 tagged individuals in the aquaria. Daily inspections provided data that were used to compare rates of moulting and mortality rates between tagged and untagged individuals using chi-square tests. Observations were made on moulting, tag shedding, and of the general behaviour of the lobsters. The effects of tagging on *I. chacei* were assumed to be similar to those on *I. peronii* because of their morphological similarities and overlapping distributions (Brown and Holthuis 1998).

Results

Field study

Of the 3892 *Ibacus peronii* and 716 *I. chacei* tagged and released during the study, 546 (14%) *I. peronii* and 91 (12.7%) *I. chacei* were recaptured by the end of 1996. Of these, 135 *I. peronii* and 37 *I. chacei* had moulted during their time at liberty, providing data on moult increments and moult frequencies.

The software programme GROTAG estimated parameters which described growth for male and female *Ibacus peronii* from Coffs Harbour and Lakes Entrance and for male and female *I. chacei* (Table 1). The

Table 1 *Ibacus* spp. Growth parameter estimates (means + SE) from GROTAG programme (Francis 1988). Standard errors estimated from simulated data ($n = 100$ simulations). Maximum sizes are in mm carapace length (CL) g_{40} , g_{60} mean increase (mm) in CL in 1 yr of 40 and 60 mm CL individuals, respectively; K growth coefficient; L_{∞} asymptotic length; M males; F females; N sample size

Parameter	<i>Ibacus peronii</i>				<i>Ibacus chacei</i>	
	Coffs Harbour		Lakes Entrance		M	F
	M	F	M	F		
Mean growth rate (mm yr ⁻¹)						
g_{40}	9.8 (0.07)	14.4 (0.18)	8.6 (0.83)	10.6 (2.1)	11.7 (0.24)	16.5 (0.11)
g_{60}	1.9 (0.01)	7.4 (0.08)	2.7 (0.23)	5.0 (0.2)	4.6 (0.09)	6.14 (0.04)
SD measurement error						
S	0.14	0.14	0.14	0.14	0.14	0.14
von Bertalanffy parameter						
K	0.504	0.431	0.346	0.323	0.440	0.730
L_{∞}	64.8	81.1	69.3	78.2	72.8	71.9
Max. size in study (mm CL)	78.3	86.3	70.3	83.3	67.2	69.4
N	41	36	30	21	9	26

parameters g_{40} and g_{60} (mean growth in 1 yr of 40 and 60 mm CL individuals, respectively) showed that males grew less in 1 yr than females of the same size for each species at each location. Estimated values of L_{∞} tended to be less than the maximum sizes recaptured during the study.

Growth curves generated using the estimated von Bertalanffy growth function parameters in Table 1 and a size of 12.2 mm CL at Age zero (from Marinovic et al.'s, 1994 study of juvenile *Ibacus peronii*) are presented in Fig. 1. These plots indicate that growth is relatively rapid during the first 4 to 5 yr for *I. peronii*, but slows dramatically thereafter. For *I. chacei*, growth during the first 3 to 4 yr is rapid, and then declines as the maximum size is reached. The curves showed that females grow

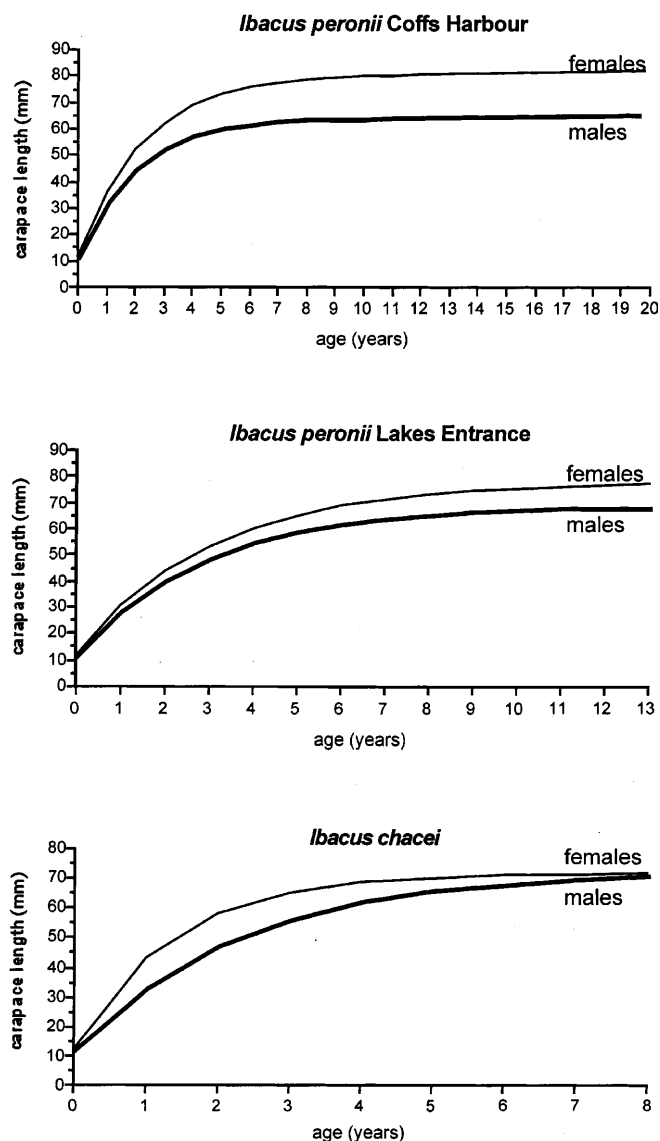


Fig. 1 *Ibacus peronii* and *I. chacei*. Growth curves constructed from von Bertalanffy growth-function parameters in Table 1. Size at Age zero set at 12.2 mm carapace length (from Marinovic et al. 1994) for all curves

Fig. 2 *Ibacus* spp. Relationships (with fitted logistic curves) between probability of moulting and days at liberty for different size-classes, sexes and locations for *I. peronii* and for all *I. chacei* (pooled across sexes and locations). Parameter estimates have standard errors in parentheses. (D_{50} number of days at liberty at which 50% of lobsters had moulted; m rate of increase from 0 to 1)

faster than males, particularly during the first few years, and reach larger sizes.

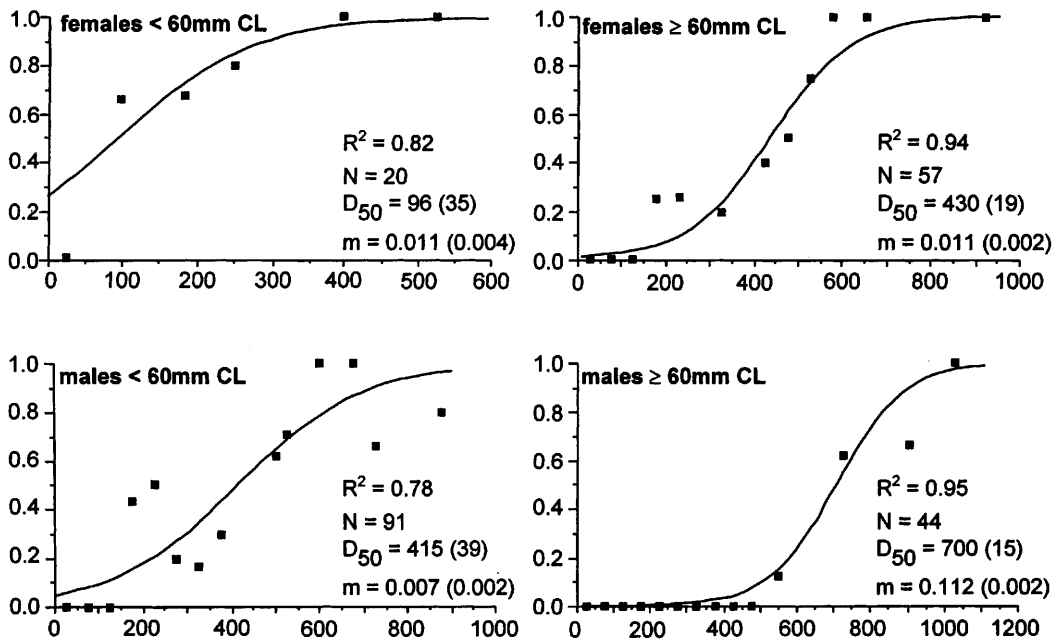
The relationships between the probability of an individual having moulted and its time at liberty, determined using the PSGS approach, are shown in Fig. 2. The residual sums-of-squares from the analyses of these data revealed that these relationships were significantly different for each size-class and sex for *Ibacus peronii*. Because the relationships were not different for male and female *I. chacei* ($F_{2,12} = 1.68$), these data were pooled. Estimated values of D_{50} always increased with increasing size-classes, indicating that intermolt period increases with size. Estimates of D_{50} were always much greater for males than females in any size class, indicating that males moulted less frequently than females for both species at each location.

All relationships between log moult-increment and pre-moult CL displayed negative slopes (Fig. 3), indicating that large individuals had smaller moult increments than small individuals. Analyses of covariance revealed no significant differences between the slopes or y -intercepts of these regressions for male and female *Ibacus peronii* from Coffs Harbour ($p = 0.65$ and 0.18), male and female *I. peronii* from Lakes Entrance ($p = 0.81$ and 0.87), nor male and female *I. chacei* ($p = 0.25$ and 0.29). The data were therefore pooled across sexes. There were no differences in either slope or y -intercepts in these relationships for *I. peronii* from Coffs Harbour and *I. chacei* ($p = 1.22$ and 0.47), but the slopes and y -intercepts were significantly different for *I. peronii* from Coffs Harbour and Lakes Entrance ($p = 0.003$ and 0.005 , respectively).

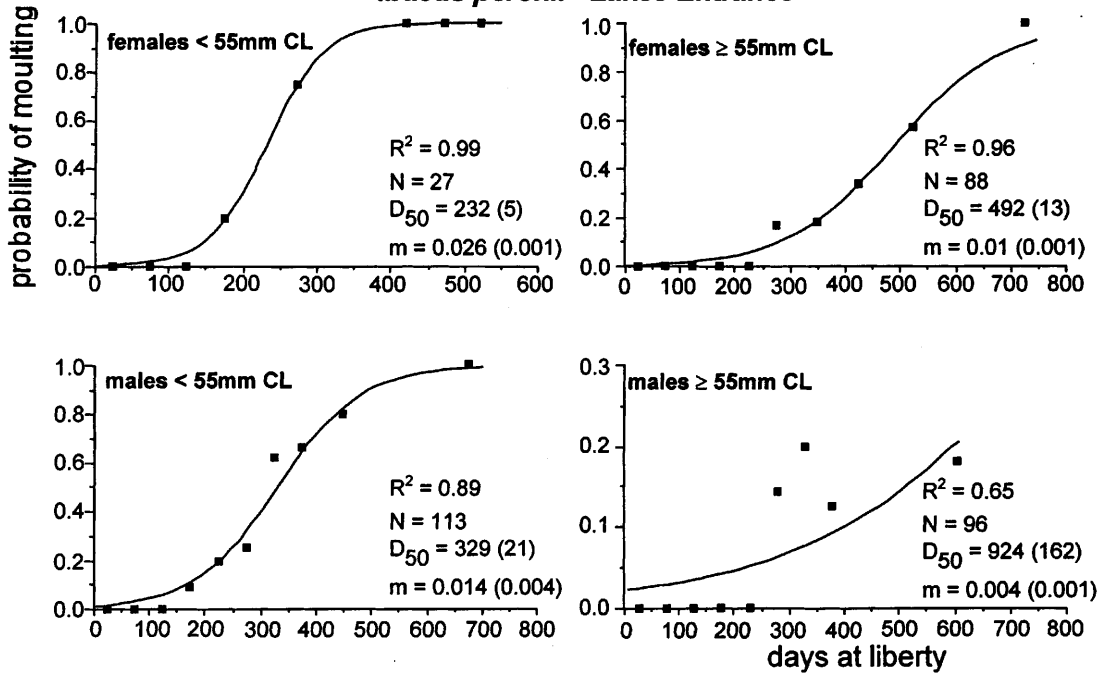
The proportions of lobsters with moult increments for each size-grouping, species and location are shown in Fig. 4. *Ibacus peronii* from Lakes Entrance tended to have larger increments than those from Coffs Harbour, which may have been caused as a result of the smaller individuals tagged at Lakes Entrance. Whilst the smaller size-classes of *I. peronii* from Coffs Harbour and Lakes Entrance had some very small moult increments, they tended to have larger moult increments than the larger size-classes (see also Fig. 3).

One hundred simulations of the PSGS model were run for male and female *Ibacus peronii* from Coffs Harbour and Lakes Entrance and for all *I. chacei*. These simulations revealed variations in the spread of the raw data as scatterplots of size at relative age (Fig. 5). Variation in the scatterplots is similar for each model, and indicates significant variability in growth, such that male and female *I. peronii* from Coffs Harbour may reach their L_{\max} any time between 7 and 18 yr, and 5

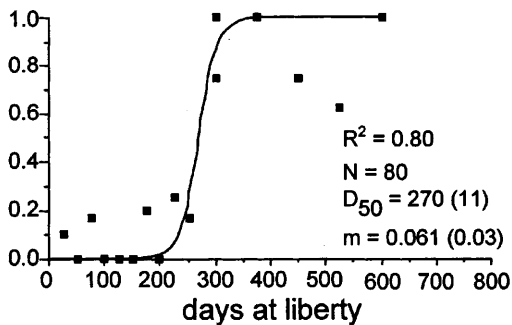
***Ibacus peronii* - Coffs Harbour**



***Ibacus peronii* - Lakes Entrance**



***Ibacus chacei* - sexes combined**



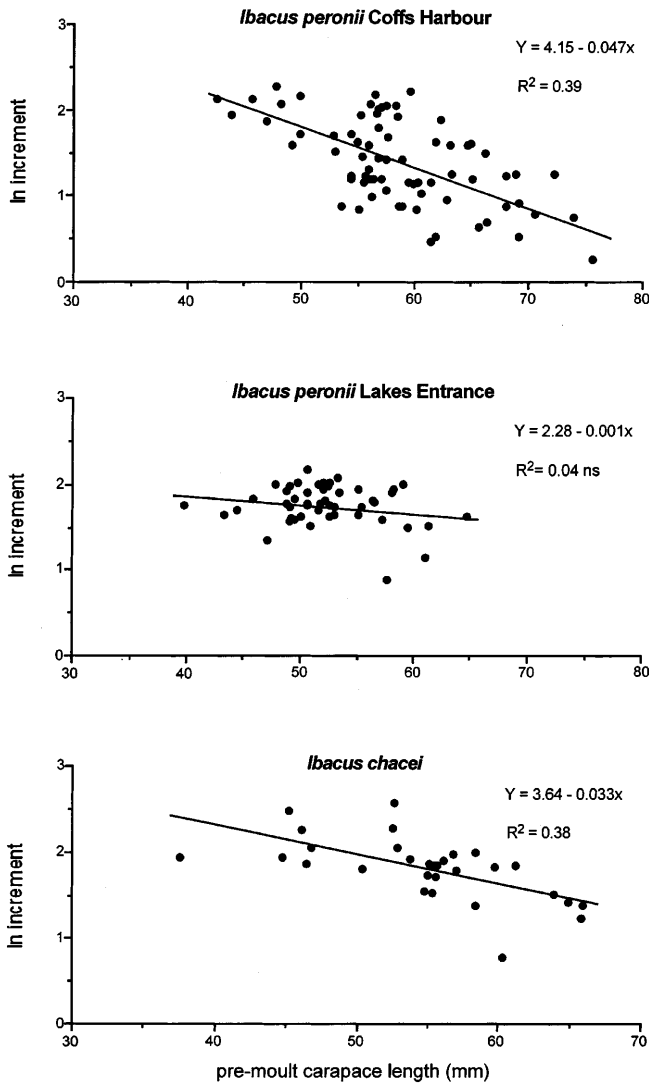


Fig. 3 *Ibacus* spp. Relationships between log moult-increment and pre-moult carapace length for *I. peronii* from Coffs Harbour and Lakes Entrance and for all *I. chacei*. Sexes combined for each species and location (*ns* non-significant regression)

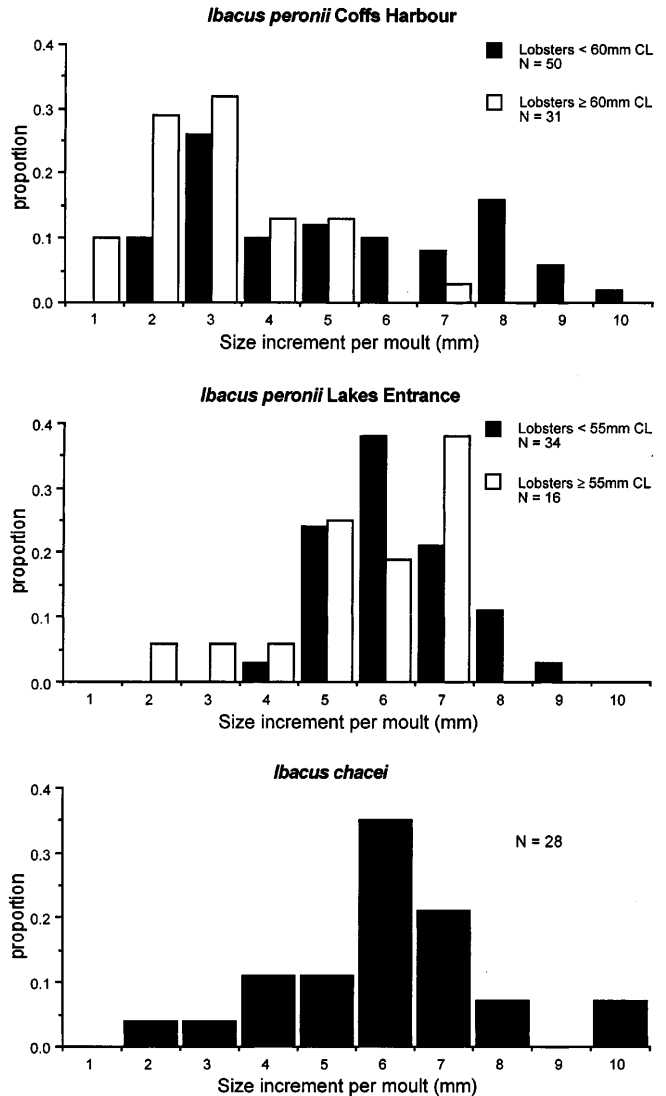


Fig. 4 *Ibacus* spp. Proportions of size increments per moult for different size-classes of *I. peronii* from Coffs Harbour and Lakes Entrance, and for all *I. chacei*. All sexes combined

and 11 yr after L_1 , respectively. Male and female *I. peronii* from Lakes Entrance may reach their L_{max} anytime between approximately 4 and 7 yr and 5 and 11 yr after L_1 , respectively. *I. chacei* may reach their L_{max} between 4 and 7 yr after their L_1 .

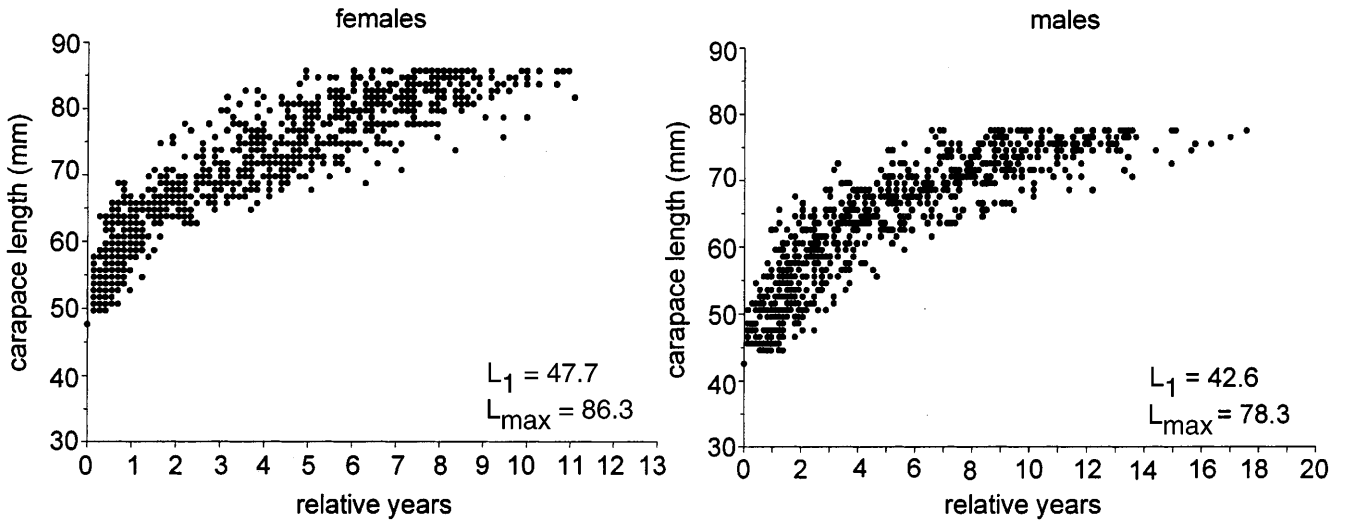
While estimates of the von Bertalanffy growth-function parameters provided reasonable descriptions of growth in *Ibacus peronii* and *I. chacei* (Table 1; Fig. 1), we considered that the results from the PSGS approach may be more appropriate for describing the growth of *Ibacus* spp. for several reasons presented in the “Discussion”. To derive the most realistic growth curves for these lobsters, we therefore combined results from the PSGS approach with Marinovic et al.’s (1994) data on the growth of very small *I. peronii* in captivity. Marinovic et al. described growth of juvenile *I. peronii* during their first year as:

$$CL = 10.2 + 0.18 \times \text{no. days} - 0.000254 \times (\text{no. days}^2), \quad (2)$$

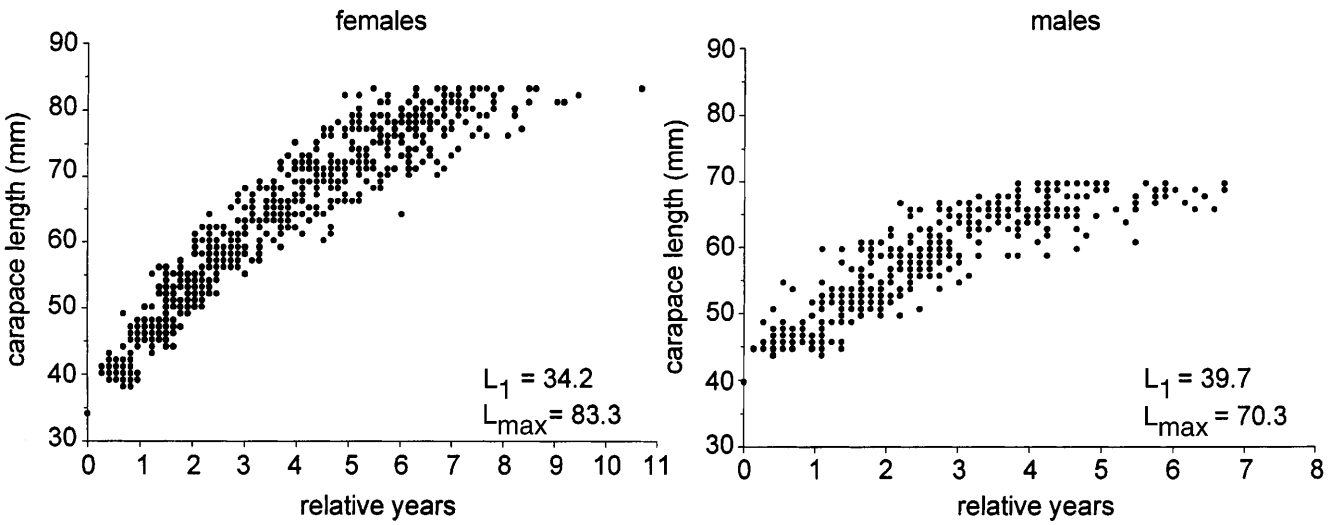
and this function was used to describe growth prior to our observed L_1 for each species, sex and location. The stepwise curves after each L_1 were drawn using the mean size after each 50 d grouping with 100 simulations of the PSGS model. These growth curves (Fig. 6) indicate that growth between male and female *I. peronii* at each location is sufficiently different to warrant separate curves for each sex. Two assumptions in deriving these curves

Fig. 5 *Ibacus* spp. Scatterplots of relative ages generated from 100 simulation runs using PSGS (probabilistic stepwise growth simulation) approach. Start size (L_1) and maximum observed size (L_{max}) are given for each sex, species and location

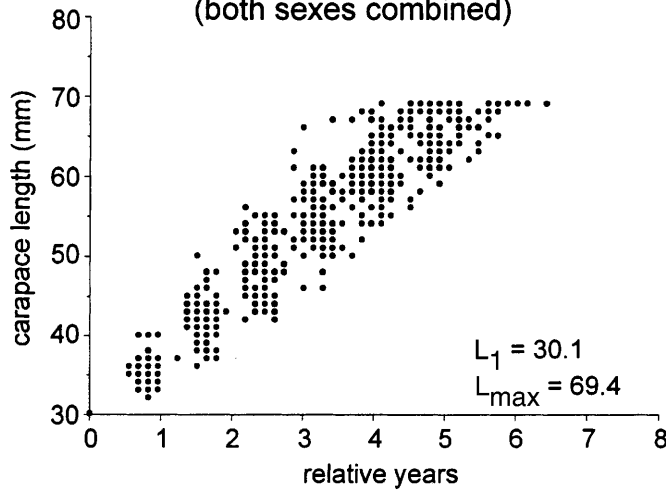
Ibacus peronii - Coffs Harbour



Ibacus peronii - Lakes Entrance



Ibacus chacei
(both sexes combined)



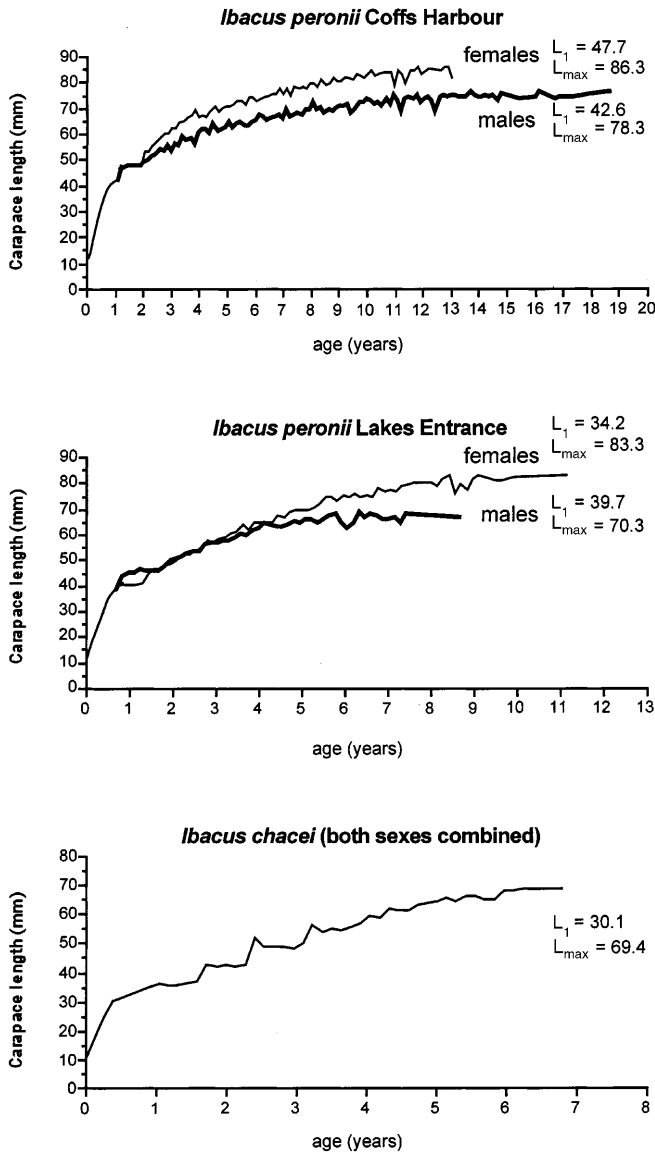


Fig. 6 *Ibacus* spp. Growth curves constructed from mean carapace sizes for each 50 d interval from 100 simulations of PSGS model. Growth data before L_1 from Marinovic et al. (1994)

were: (i) that growth before each L_1 is similar for males and females; and (ii) the growth of *I. chacei* of < 30.1 mm CL can be approximated by that for *I. peronii*.

Laboratory tagging study

The timing of moulting of tagged and untagged *Ibacus peronii* in captivity was similar, with most moults occurring between October and January (Fig. 7A). There was no significant difference between the number of surviving tagged *I. peronii* that moulted (81%) and the number of surviving untagged *I. peronii* that moulted (85%; chi-squared test, $p > 0.9$). The timing of moulting of male and female *I. peronii* (tagged and untagged combined) is shown in Fig. 7B and suggests that, on

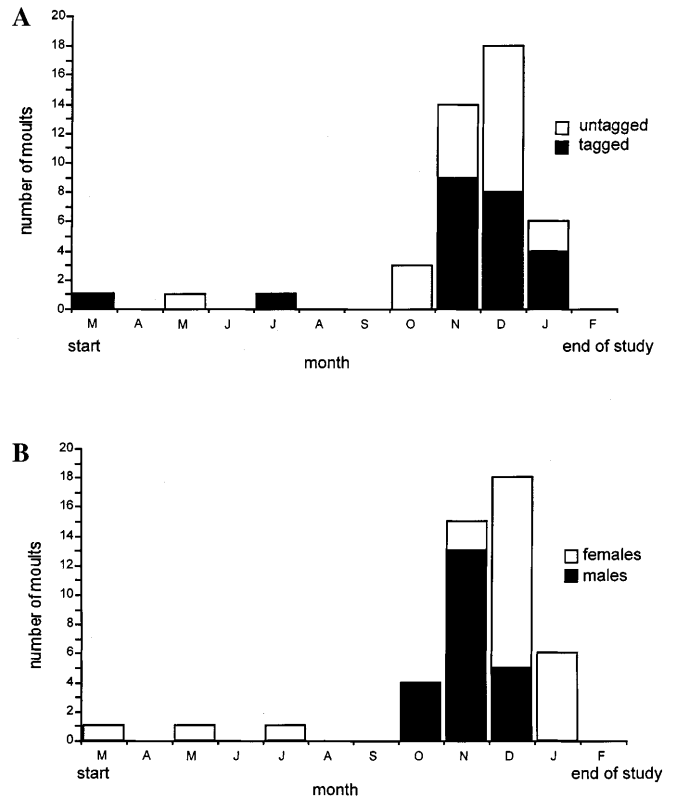


Fig. 7 *Ibacus peronii*. Moulting frequency of captive lobsters. Tagged and untagged; **B** males and females (tagged and untagged combined)

average, males moulted slightly earlier than females. Tags were shed from six *I. peronii* (out of a total of 40 tagged lobsters) and was associated with moulting in 5 of the 6 cases. There were no significant differences between the number of tagged *I. peronii* that died (32.5%) and the number of untagged *I. peronii* that died (35%) during the 12 mo in captivity (chi-squared test, $p > 0.75$).

Moulting always occurred at night for the captive lobsters, and the discarded exoskeleton was never eaten. Moulting was observed for two *Ibacus peronii* in glass tanks, and was similar to that described for the sand lobster *Thenus orientalis* by Rahman and Subramoniam (1989): moulting occurred above the substratum, with the lobster emerging from the old exoskeleton through a dorsal split between the carapace and the first abdominal segment.

Discussion

The tagging experiments on captive *Ibacus peronii* suggest that tagging *Ibacus* spp. has little effect on their growth rates or survival. It was not possible to quantify the effect of tagging on moult increments in this study, but other studies have shown that moult increments of crustaceans are mostly affected by nutrition and temperature, not by tagging (Aiken 1980; Melville-

Smith et al. 1997). In the present study, the large numbers of recaptured tagged individuals from the field (14% of *Ibacus peronii* and 12.7% of *I. chacei*) is further evidence that survival after tagging was probably quite high.

Ibacus peronii held in captivity moulted between October and January (Fig. 7), and this was supported in the field by the tag/recapture study in which 96.3% of lobsters (130 of 135) which had moulted were at liberty during these months. Therefore, for the majority of *I. peronii*, moulting seems to be a seasonal event but may not occur every year – several males were at liberty for more than 3 yr without moulting.

A possible bias that may have affected the results in this study involves tag-shedding during moulting (5 of the 6 tag-shedding events observed in the laboratory occurred during moulting). If tag-shedding in the field also occurs during moulting, then the observed numbers of lobsters recaptured which had moulted may be underestimates of the true proportions. However, unless the rate of tag-shedding in the field is much greater than that observed in captivity (i.e. 5 tag shedding events out of 23 moults), such bias is likely to be insignificant (see also Restrepo and Hoenig 1988).

The results from this study showed that for *Ibacus peronii*, females grew faster and reached larger maximum sizes than males (Fig. 6). However, this was not the case for *I. chacei* off the coast of New South Wales, for which there was no difference in growth between the sexes (Fig. 6). Growth of *I. peronii* was similar at both Coffs Harbour and Lakes Entrance, with females reaching their estimated size at sexual maturity 51 mm CL; see Stewart et al. 1997) at ~2 yr, after which growth slowed dramatically (Fig. 6).

As mentioned in the “Introduction”, growth in length of lobsters comprises two components: (i) the increment occurring at each moult; and (ii) the frequency of moulting.

Data from our tag/recapture study showed that, like other lobsters, (Mauchline 1977; Aiken 1980), larger individuals had smaller growth increments per moult than smaller individuals (Figs. 3, 4). However, there were no differences in increments per moult between males and females of either species, implying that the observed differences in growth between the sexes were due to differences in the frequency of moulting. There were significant differences in the slopes and y -intercepts of the relationships between log-moult increment and pre-moult carapace length for *Ibacus peronii* from Coffs Harbour and Lakes Entrance (Fig. 3), indicating that smaller individuals had larger increments per moult at Coffs Harbour than at Lakes Entrance, but that larger individuals had smaller increments at Coffs Harbour than at Lakes Entrance. However, this result may simply be an artefact of the smaller number of large individuals tagged and recaptured at Lakes Entrance.

The second component of lobster growth, moult-frequency, was estimated using the PSGS method of Chen and Kennelly (1999), which revealed no differences

in the probability of moulting between male and female *Ibacus chacei*. Because there were also no differences in increments per moult between sexes, growth was the same between sexes. In contrast, estimates of the proportion of lobsters having moulted within 50 d intervals at liberty for *I. peronii* were different between size-classes and sexes, with smaller lobsters always moulting more frequently than larger individuals and females always moulting more frequently than males of the same size-class. These results show that small individuals grow faster than large ones (having greater increments per moult and moulting more frequently), and females grow larger and faster than males (having equal increments per moult but moulting more frequently).

Growth curves derived from GROTAG's von Bertalanffy parameters and those derived using the PSGS approach were similar over the ranges of sizes modelled (Figs. 1, 6). However, estimates of von Bertalanffy's L_{∞} tended to be smaller than the maximum sizes recaptured during this study (Table 1) and, because L_{∞} s calculated from tagging data sets have been shown to approximate maximum lengths and not asymptotic mean lengths (Francis 1992), the von Bertalanffy growth function may not be a good descriptor of growth for the entire size range of *Ibacus* spp. Another reason for this conclusion is that estimates of growth prior to the smallest tagged individual, L_1 , for each species, sex and location differed markedly between the von Bertalanffy growth curves and what we considered to be the most realistic curves when incorporating Marinovic et al.'s (1994) data on small *I. peronii* (shown in Fig. 6). Whilst using Marinovic et al.'s data is far better than back-extrapolating growth curves below the minimum sizes tagged, it requires the assumption that the growth of their lobsters in captivity were representative of the growth of small individuals in the field, at different locations, of each sex and also of small *I. chacei*. If this is the case, we consider the growth patterns described in Fig. 6 to be the best descriptors of growth available for these species, and the spread of the data in Fig. 5 from 100 simulations of the PSGS approach provides an indication of variance around these patterns.

Whilst we have substantial confidence in our estimates of growth for *Ibacus peronii*, it is important to note that our description of growth for *I. chacei* is likely to be only representative of this species in New South Wales – it is probably not accurate for *I. chacei*'s entire population. There are two reasons for this: (i) there were no differences in growth rates between sexes for *I. chacei*, yet substantial differences between the growth rates of male and female *I. peronii*; (ii) the observed maximum size of 69.4 mm CL for *I. chacei* in this study is much smaller than its maximum recorded size of 80 mm CL (Kailola et al. 1993). These results can be explained by the fact that our tagging study concerned an essentially immature population towards the southern end of this species' distribution (see Stewart et al. 1997). Because growth rates are affected by factors such as reproductive maturity and water temperature (Aiken 1980), it is likely

that the growth of *I. chacei* will be different further northwards, where water temperatures are warmer and where they are known to become sexually mature.

By analysing the tag/recapture data for *Ibacus peronii* and *I. chacei* in two ways, the present paper has allowed us to compare the relative merits of using the conventional von Bertalanffy growth-function to describe growth with the PSGS approach. The former method, which assumes continuous growth, did not provide a good description of growth for the entire size range of *Ibacus* spp. However, the latter approach provided good descriptions of growth in terms of increments per moult and moult frequencies, allowing the discontinuous nature of crustacean growth to be more realistically modelled. We conclude that studies of the growth of large decapods such as lobsters (and, indeed, all animals that exhibit discontinuous growth like crustaceans) should use growth models that mimic discontinuous growth and incorporate variations in the raw data.

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