*J. Mar. Biol. Ass. U.K.* (2003), **83**, 1261–1265
Printed in the United Kingdom

# Spatial and temporal patterns in the moulting cycle of *Liocarcinus arcuatus* (Brachyura: Portunidae) in the Ría de Arousa, Spain

R. Muiño and E. González-Gurriarán

Departamento de Bioloxía Animal, Bioloxía Vexetal e Ecoloxía, Facultade de Ciencias,
Universidade da Coruña, Campus da Zapateira s/n, E-15071, A Coruña, Spain. E-mail: rmuino@udc.es

Moult cycle of *Liocarcinus arcuatus* in the Ría de Arousa (Galicia, north-west Spain) was analysed in relation to: (a) temporal changes; (b) spatial variability associated with both different environmental patterns (type of bottom, depth, etc.); (c) sex; and (d) body size. A total of 4275 females and 4103 males of *L. arcuatus* were caught in three different areas of the Ría de Arousa, selected as being representative of two types of habitat: a beach zone and two mussel raft culture zones (in the inner ría and in the outer area). Five moult stages were established on the basis of the degree of calcification in the exoskeleton. Only a small portion of the population (less than 15% in practically the whole year) were found monthly in one of the early postmoult stages (Stages A and B). Spatial and temporal variability of the moult cycle of *L. arcuatus* in the Ría de Arousa was found to be significant ($P<0.001$). There were no important spatial differences in the moult cycle of *L. arcuatus* females, by contrast, males showed a greater degree of spatial variability.

## INTRODUCTION

All processes which take place before and after the actual time of moulting are known as the premoult and postmoult stages, respectively and the period in between the two is called the intermoult stage. Most of the portunid species undergo numerous moults throughout their lives and do not exhibit, like most majids, the so-called pubertal moult. One of the reasons that these animals carry out these periodic, successive moults is to facilitate mating. To copulate, the majority of portunid females are bound by anatomical necessity to be in an early postmoult stage, while males must be in the intermoult stage (Hartnoll, 1969), and this requires a close spatial and temporal coordination between the male and female moulting cycles. It has been well documented that portunid species have a markedly seasonal moult cycle, which exhibits a greater or lesser degree of variability depending on several factors; as well as on the active selection of the habitat where moulting will take place (Shirley et al., 1990), related to aspects such as predation and mating.

This paper analyses the moult cycle of *Liocarcinus arcuatus* (Leach, 1814) in the Ría de Arousa (north-west Spain), in relation to: (a) temporal changes; (b) spatial variability associated with both different environmental patterns (type of bottom, depth, etc.); (c) sex; and (d) body size.

## MATERIALS AND METHODS

A total of 4275 females and 4103 males of *Liocarcinus arcuatus* were caught in three different areas of the Ría de Arousa, (north-west, Spain): a beach zone (P3) located in the mid-inner ría, with seasonal salinity variations, shallow (3–5 m) and sandy bottoms; and two mussel raft culture zones: B1 in the inner ría, with deep/shallow bottoms (between 10–20 m), strong fluctuations in salinity, and muddy bottoms, and B6, located in the outer area, with strong oceanic influence, stable salinity, deeper (between 20 and 30 m) and sandy–muddy bottoms.

Crabs were sampled monthly from July 1989 to June 1990, with the exception of December 1989 due to climatological conditions. Specimens were caught using a trawl gear with a variable number of 10 min-tows in each sampling station depending on the number of individuals caught per tow. After each tow, the specimens of *L. arcuatus* were selected, counted and sexed. Their carapace width (CW) was measured between the 5th pair of anterolateral spines and their moult stage was determined. Five moult stages were established on the basis of the degree of calcification in the exoskeleton which was measured by determining the resistance offered by different regions of the carapace (cheliped meros, subbrachial region, etc.) on applying pressure with the fingers:

*Stage A.* Intemediate postmoult. Specimens have moulted very recently and have an extremely soft exoskeleton (Stage A1 according to Drach & Tchernigovtzeff (1967)).

*Stage B.* Postmoult. The calcification of the exoskeleton begins; it has a paper-shell consistency. The chelae and pereiopod dactyls are harder than the rest of the carapace (Stages A2–B2).

*Stage C.* Advanced postmoult. The exoskeleton is only flexible in the pterygostomial region of the carapace (Stages C1 and C2).

*Stage I.* Intermoult. The exoskeleton is rigid and hard all over (Stages C3–D1).

*Stage D.* Premoult. The new skeleton is completely formed under the old one. The carapace breaks easily along the epimeral line and is sometimes already broken on capture (Stages D2–D4).

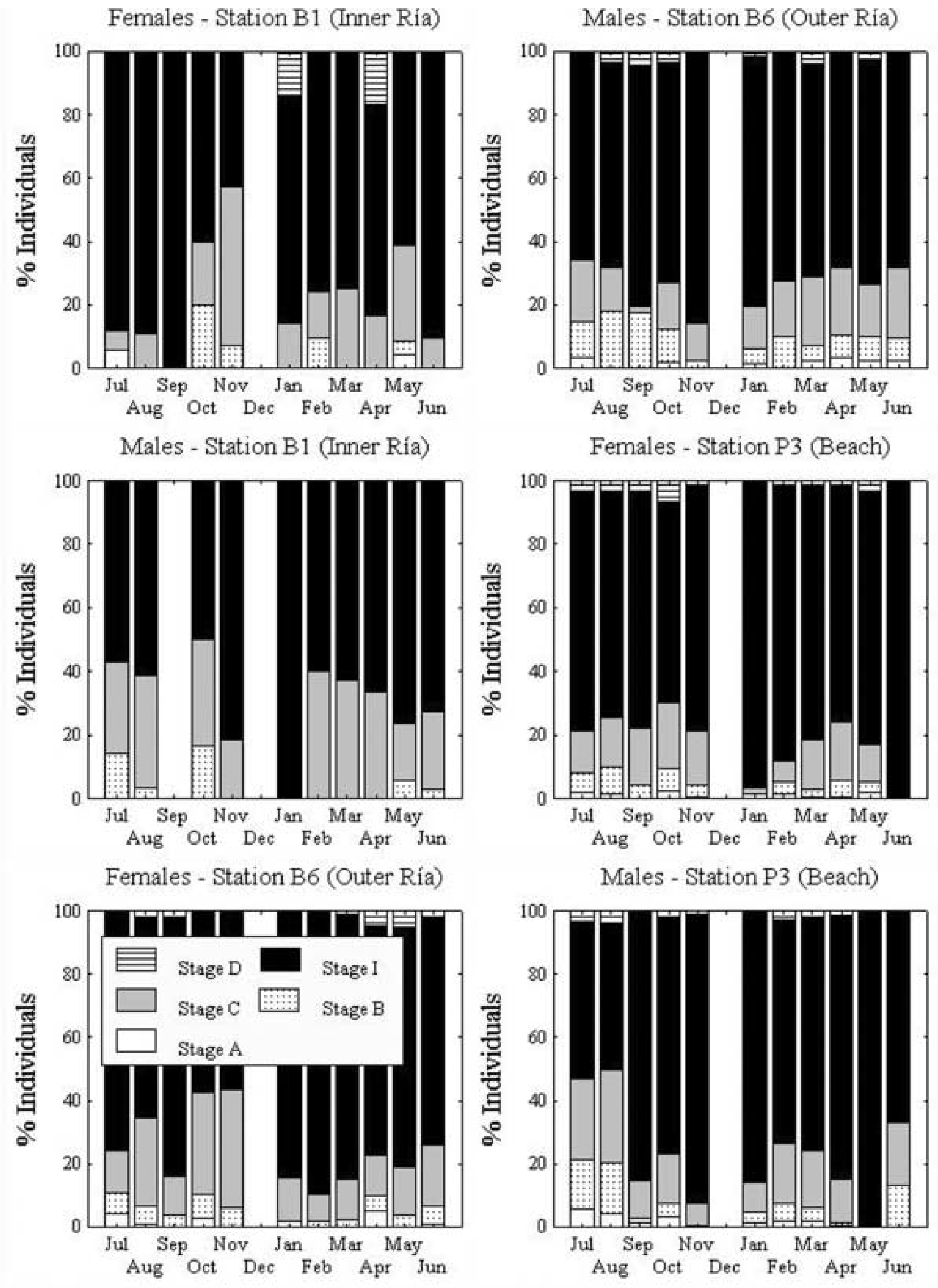


**Figure 1.** Monthly percentage of the different moult stages (A, early postmoult; B, postmoult; C, advanced postmoult; I, intermoult; D, premoult) for females (left) and males (right) in all of the stations sampled.

Estimations of possible temporal, spatial, sex and size-related (CW) differences in the moult cycle were based mainly on crabs caught in Stage A (early postmoult) and Stage B (postmoult), since they were indicative of a recent moult. A joint analysis on the impact of the above-mentioned factors (month, station, sex and size) was also done by fitting log-linear models using maximum likelihood estimation to contingency tables made up of moult factors (Stages A, B, C, I and D), Station factors (B1 inner raft, B6 outer raft and P3 beach), sex (males or females), and size-class (size-classes of 2 mm CW) to determine the relationship between the different moult stages and the other factors.

## RESULTS

Nearly all the specimens of both sexes caught monthly in all of the stations sampled were in the intermoult Stage I (intermoult, >50%), Stage C (advanced postmoult) ranked second (20%), only a small portion of the population (less than 15% in practically the whole year) were found monthly in one of the early postmoult stages (Stages A and B), Stage D (premoult) was the one that occurred less frequently (<5%) (Figure 1).

Some variations, both spatial but mainly temporal, were observed in the percentage of crabs found in the different moult stages (Figure 1). Significant spatial



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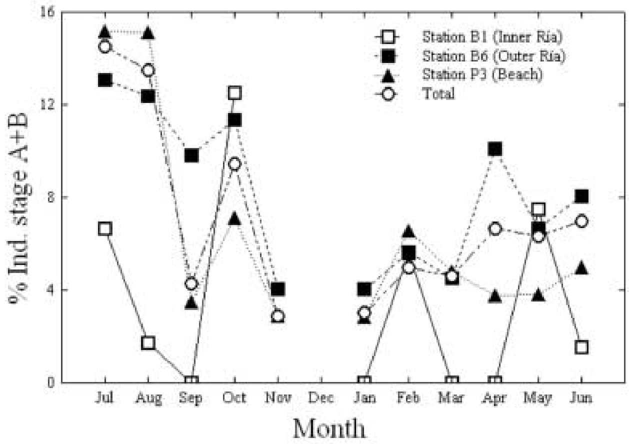


**Figure 2.** Evolution of the monthly percentage of crabs caught in moult cycle Stages A+B in all of the stations sampled and in the Ría de Arousa as a whole.

differences were found ($P<0.001$) in the percentages of animals in the different moult stages among the various habitats (Figure 1, Table 2). In the raft stations, Bl and B6, there were striking monthly variations in the percentage of crabs that had moulted recently with successive peaks, especially between January and June (Figure 2). The beach station tended to have a much more homogeneous moult cycle throughout the year (Figure 2). Also, the temporal variability was found to be significant ($P<0.001$) (Table 2), showing a clear seasonal pattern in each of the sampling stations. It was during the summer that the maximum percentages of Stages A and B were witnessed. These values dropped sharply in September in all the areas, recovering once again in October (Table 1, Figure 2). The lowest values in terms of the percentage of crabs in Stages A and B were found in the winter, increasing again during the spring until they reached the summer maximum. The overall pattern, however, would seem to indicate that in all three stations, the number of animals that have moulted tends to rise as we approach the summer months.

The low number of specimens caught at Station Bl (Table 1), may somehow disguise possible differences related to sex, size, etc. In B6, the maximum values of newly moulted males are in the summer and early autumn coinciding with the minimum levels in the percentage of newly moulted females, which had highly homogeneous values over the yearly cycle. In P3, the most important moulting periods for males occurred during the summer, and the winter. Newly moulted females appeared almost all year with very similar percentages all the months. So, there were no important spatial differences in the moult cycle of *Liocarcinus arcuatus* females, while the moult cycle of males showed a greater degree of spatial variability mainly between B6 and P3 (Figure 1).

To analyse the possible effect of size on the moult cycle the percentage of newly moulted crabs was recorded for a size-class of 2 mm in carapace width in each station over the course of the whole yearly cycle. In B6 and also in P3, we did not observe a greater percentage in the moulting frequency of smaller-sized individuals vs the larger specimens during the greater part of the year. It was basically the average sizes that presented the highest percentage of newly moulted animals. However, in P3 during the months when recruitment took place (unpublished data), the percentage of newly moulted animals rose in the smaller sizes, and was null or negligible in the other size-classes.

A joint analysis of the effects of the different factors on the moult cycle of *L. arcuatus*, was conducted by fitting log-linear models to contingency tables whereby the different moult stages are analysed in terms of the sampling station, month, sex and size-class (Table 2). All of the interactions of the first magnitude analysed are significant ($P<0.001$), as are most of the interactions of the second magnitude. All significant interactions ($P<0.01$), including the month variable, have the highest values of statistic $\chi^2$ (Table 2).

**Table 1.** *Total number of individuals caught and monthly percentage of animals in Stages A+B of the moult cycle in all of the stations sampled and in the Ría de Arousa as a whole.*

| | Station Bl | | | | Station B6 | | | | Station P3 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Females | | Males | | Females | | Males | | Females | | Males | |
| | Number | % | Number | % | Number | % | Number | % | Number | % | Number | % |
| July | 17 | 5.88 | 28 | 14.29 | 74 | 10.82 | 117 | 14.53 | 376 | 8.25 | 290 | 21.38 |
| August | 27 | 0.00 | 31 | 3.23 | 92 | 6.52 | 94 | 18.09 | 287 | 10.10 | 262 | 20.61 |
| September | 2 | 0.00 | 0 | 0.00 | 56 | 3.57 | 46 | 17.39 | 303 | 4.29 | 414 | 2.90 |
| October | 10 | 20.00 | 6 | 16.67 | 105 | 10.48 | 97 | 12.37 | 339 | 9.44 | 333 | 7.80 |
| November | 14 | 7.14 | 11 | 0.00 | 32 | 6.25 | 42 | 2.38 | 316 | 4.43 | 207 | 0.48 |
| December | — | | — | | — | | — | | — | | — | |
| January | 7 | 0.00 | 2 | 0.00 | 57 | 1.75 | 67 | 5.97 | 393 | 1.27 | 307 | 4.88 |
| February | 21 | 9.52 | 15 | 0.00 | 49 | 2.04 | 40 | 10.00 | 161 | 4.97 | 234 | 7.70 |
| March | 8 | 0.00 | 8 | 0.00 | 204 | 2.45 | 153 | 7.19 | 247 | 2.83 | 338 | 6.21 |
| April | 6 | 0.00 | 6 | 0.00 | 193 | 9.84 | 263 | 10.64 | 281 | 5.70 | 226 | 1.32 |
| May | 23 | 8.70 | 17 | 5.88 | 240 | 3.75 | 211 | 9.95 | 58 | 5.17 | 21 | 0.00 |
| June | 32 | 0.00 | 33 | 3.03 | 221 | 6.78 | 190 | 9.47 | 25 | 0.00 | 15 | 13.33 |
| Total | 167 | 4.79 | 157 | 5.03 | 1323 | 5.97 | 1320 | 10.83 | 2786 | 5.65 | 2647 | 7.71 |



https://doi.org/10.1017/S0025315403008610 Published online by Cambridge University Press

**Table 2.** *Results of the fit of a log-linear model to the contingency table of the number of specimens caught in each moult stage (A, early postmoult; B, postmoult; C, advanced postmoult; I, intermoult; D, premoult) in terms of sampling station, month, sex and size-class. Fits having statistical significance (*P*<0.05) appear in bold print.*

| Effect | df | $\chi^2$ | (*P*) |
|---|---|---|---|
| Moult×station | 4 | **22.96** | (**<0.001**) |
| Moult×sex | 2 | **48.17** | (**<0.001**) |
| Moult×size | 22 | **78.21** | (**<0.001**) |
| Moult×month | 20 | **264.44** | (**<0.001**) |
| Moult×station×sex | 4 | 8.36 | (0.079) |
| Moult×station×size | 44 | 29.52 | (0.954) |
| Moult×station×month | 40 | **83.91** | (**<0.001**) |
| Moult×sex×size | 22 | **69.42** | (**<0.001**) |
| Moult×sex×month | 20 | **189.05** | (**<0.001**) |
| Moult×size×month | 220 | **272.65** | (**<0.009**) |

Moreover, the magnitude of the variability found between the moulting cycle of males and females of *L. arcuatus*, depends both on size ($P<0.001$) as well as on the month ($P<0.001$), and not on the habitat ($P>0.01$) (Table 2).

## DISCUSSION

The moult cycle of *Liocarcinus arcuatus* in the Ría de Arousa have a clear temporal pattern, with a summer maximum in the percentage of crabs in the post-ecdysis stage, coinciding with the temporal pattern observed in other portunid species and geographic regions. However, the moult cycle of *L. arcuatus* in the Adriatic Sea (Stevcic, 1987) does not agree with the moult cycle of *L. arcuatus* in the Ría de Arousa. Marked geographic variations have been observed in the temporal patterns of the moult cycle among populations of the same species. Populations located farther to the north in the distribution range tended to moult during the summer months, while the southernmost populations moulted mainly in winter (Conan, 1985), linked to the different environmental conditions (temperature, photoperiod, salinity, food, etc.). So, the population of *L. arcuatus* in the Ría de Arousa may be considered as more northerly than the one in the Adriatic Sea, which could be the reason for the temporal differences.

In the Ría de Arousa, the spatial variability in the moult cycle of *L. arcuatus* is not especially pronounced, although there are a certain degree of segregation between sexes in terms of habitat (males showed a more distinguishable spatial pattern). A differential use of the habitat as related to the moult processes had already been mentioned (Shirley et al., 1990). Maximum percentages of ovigerous females are related to periods during which no courting, mating, etc. activities take place, and then males are able to moult. In these periods, spatial differences in the size–frequency distribution of the males of the Ría de Arousa were noticeable. In the raft stations we observed a shift in moulting to the average sizes of the range, while the beach station continued to have large-sized individuals with a slower growth rate (unpublished data). The increase in the moulting activity in the raft areas during spring may be attributed to the fact that average-sized males move from the beach zones to the raft zones to moult. The bottoms of the raft areas have large amounts of debris from mussel culture (ropes, crates, etc.), which offer a wide range of refuge possibilities for animals in the post-moult stages, as well as offering a greater abundance of numerous species that make up the diet *of L. arcuatus* (Freire et al., 1990). The possibility of *L. arcuatus* carrying out local migrations had been reported earlier (Stevcic, 1987; Freire et al., 1991) and it is a common occurrence in many portunid species.

Sex-related spatial differences may be due to the anatomical requirement of the females of most portunid species, to be in the early postmoult stage when mating occurs, while males must be in the intermoult stage (Hartnoll, 1969). The temporal differences observed in the Ría de Arousa between the moult cycle of both sexes are aimed at preventing the most important moult periods in both from coinciding in time. In most portunid species, females have a moult cycle characterized by sharp maximum and minimum values in the percentages of postmoult crabs, whereas males maintain more constant values throughout the year In contrast, *L. arcuatus* showed similar monthly values in the percentage of females in the A and B stages over the course of the yearly cycle in the Ría de Arousa, and it was the percentages of postmoult males that exhibited a higher between-month variability. Changes in the catchability of males and females, related to different behavioural manifestations in the postmoult stage or to the use of different habitats by males and females to carry out ecdysis may be able to explain these differences in the moulting cycle of *L. arcuatus* as compared to other brachyuran species.

Moreover, the moult cycle and the reproductive cycle are clearly synchronized. Therefore the maximum percentages of specimens of *L. arcuatus* in the postmoult stage coincide with a minimal proportion of ovigerous females in the population (unpublished data). Reproduction and moulting are two processes that require a substantial amount of energy to be expended by females, more so than in other activities, which means the two processes are separated in time, so that they never occur simultaneously (Aiken & Waddy, 1980).

Other studies on decapods have referred to size-related differences in the moulting cycle, and they have found that smaller-sized individuals moult less frequently than the larger sizes. (Reilly & Saila, 1978). In *L. arcuatus*, however, these differences were not clearly seen, and it was the average sizes that generally increased in moult frequency in the months that exhibited an overall rise in the percentage of moulting crabs. Only in the beach zones and in the months when recruitment took place was there evidence of a slight increase in the number of animals in the early postmoult stage among the small-sized specimens. This occurrence was not observed in the raft areas. Therefore, the beach zones, may be a more typical moulting area, possibly related to the substrate characteristics that offer greater protection against predators

This research was funded by the Consellería de Pesca, Marisqueo e Acuicultura of the Xunta de Galicia through FEUGA. C.P. Teed assisted in the preparation of the final English version of the manuscript.



https://doi.org/10.1017/S0025315403008610 Published online by Cambridge University Press

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*Submitted 12 December 2002. Accepted 10 November 2003.*