CSIRO PUBLISHING

Marine and Freshwater Research, 2013, **64**, 317–323
http://dx.doi.org/10.1071/MF12350

The mark–recapture method applied to population estimates of a freshwater crab on an alluvial plain

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Abstract. Mark–recapture methods are a useful population estimation tool, although with many assumptions that cannot always be satisfied for all types of organisms and environments. In the present study, three mark–recapture methods (Petersen, Schnabel and Schumacher–Eschmeyer) were applied in a preliminary trial to estimate the population size of the crab *Trichodactylus borellianus* and to gain information that would support the use of the methods in the field. The accuracy of these estimates was verified by analysing the percentage of bias, the width of the confidence intervals, and by a chi-square test. The assumptions of equal catchability and closed population were verified, along with assumptions related to the efficiency of marking. The adjusted methodology was applied in a short-term study of a pond on the Paraná floodplain. The results showed that the assumptions were satisfied for both the experimental and field studies. The Schnabel was the most accurate method evaluated in both studies. Although the Schumacher–Eschmeyer method also provided accurate results in the field study, it needed large samples to give reliable estimates. The applicability of these methods depends on the stage of the hydrological cycle. The choice of a short-term research design will ensure that the assumption of a closed population is valid for research of this type on an alluvial plain.

Additional keywords: Paraná River, Petersen, Schnabel, Schumacher–Eschmeyer, Trichodactylidae.

Received 1 August 2012, accepted 23 January 2013, published online 10 April 2013

Introduction

The mark–recapture method is a frequently used tool for estimating the population size of mobile organisms and has been applied since the 17th century (Graunt 1662). Over time, many authors improved the techniques and developed methods that were especially appropriate for use, in conjunction with different population and environmental characteristics (Bailey 1952; Jolly 1965; Seber 1965; Roff 1973; Burnham and Overton 1979; Yamamura *et al.* 1992, 2003; Wileyto *et al.* 1994; Bell *et al.* 2003; Crespin *et al.* 2008). Despite the improvements that have been made, the inherent characteristics of the population and its environment vary and require the use of specific approaches. Hence, the satisfaction of all assumptions of the available methods cannot always be expected (Roff 1973; Mares *et al.* 1981). The methods and their assumptions may not even be completely understood by users who apply the techniques on occasion (Minta and Mangel 1989).

Despite the many assumptions inherent in each estimator, all such estimators have at least the following five assumptions in common: animals do not lose their marks, marked and unmarked animals are correctly classified, the marks do not affect survivorship, the marks do not affect the behaviour of the animals and the captured animals represent a random sample from the population (Pollock *et al.* 1990; Krebs 1999). Among these estimators are the Petersen (P), Schnabel (S) and Schumacher–Eschmeyer (SE) methods. These methods have two principal assumptions, including a closed population and an equal capture probability for all individuals. The P method is simplest because it is based on a single marking and a single recapture. In contrast, the two other methods involve multiple episodes. A preliminary study can be very useful to help improve the efficiency of marks. Moreover, it is valuable to investigate the accuracy of the selected estimators relative to the characteristics of the data used for the estimates, before the initiation of the fieldwork.

In the present study, we applied mark–recapture techniques to estimate the population size of the freshwater crab *Trichodactylus borellianus* Nobili, 1986. This species belongs to the familiy Trichodactylidae and is very common in the alluvial plain of the Paraná system (Collins *et al.* 2007). The mark–recapture method has not previously been applied to estimate the size of a trichodactylid population. In conjunction with the use of this method, we considered the characteristics of the species and the habitat. *T. borellianus* is an abundant small crab that lives in the roots of macrophytes (primarily the floating *Eichhornia crassipes*), usually in lentic waters. Because ponds have distinct degrees of connection with lotic bodies, the degree to which floating aquatic vegetation drifts from one site to another will depend on the degree of connection and on the water level (Thomaz *et al.* 1997; Collins *et al.* 2007). Because of oscillations in the limnological parameters, the reduction of light penetration during the low-water period (Thomaz *et al.* 1997) and the effects of the dense aquatic vegetation present during the summer, the capture–resighting method cannot be applied. Therefore, an efficient mark is required. An obvious (but nevertheless important) characteristic of the crab is that it is an aquatic animal that grows through ecdysis. Therefore, the ideal type of mark should be waterproof and resist the moult process. However, moult-resistant tags are invasive, expensive and difficult to implant in this small crab. The present study did not examine the growth, migration or recruitment of this freshwater species (i.e. long-term research). Therefore, because of the passive dispersal of the crabs and the short duration of the marks, the methodology was designed for short-term application (days).

The first objective of the present study was to evaluate three widely used methods of population estimation (Petersen modified by Bailey (P), Schnabel (S) and Schumacher–Eschmeyer (SE)) in a preliminary experiment with mesocosms. This stage of the study served to verify the efficiency of the marks, the extent to which the assumptions of the methods were satisfied and the accuracy of the estimators in a species of freshwater crab, *Trichodactylus borellianus*. The second objective of the study was to apply the adjusted methodology on a small scale in the field, in a pond on the Paraná floodplain, to evaluate the population size of this crab during the drought period.

Materials and methods

Mesocosm experiment

Crabs were sampled in the field with a 1-mm mesh-size hand net and separated from the vegetation. All individuals collected were transferred to the laboratory and stored in 4 50-L aquaria provided with refuges for the crabs. The individuals were maintained in the aquaria until a sufficient number of crabs was captured. The individuals were then separated by sex and measured. Juveniles were not considered in the present preliminary study.

The experiment was performed during the summer in two circular pools (designated R1 and R2). The pools, 2.44 m in diameter, were filled with 1000 L of well water and provided with floating aquatic vegetation (primarily *E. crassipes*). To simulate actual field conditions and the normal movements of the crab among the roots of the vegetation, on the bottom and in the water column, the pools were stocked with organisms from the pleuston, benthos and zooplankton. The pleuston was collected from aquatic vegetation in a net with a 50-cm mouth opening and a mesh size of 200 μm. All of the macrophytes collected to stock the pools were first examined to avoid the addition of an unknown number of crabs and then placed into the pool with the associated fauna. To maintain a constant amount of vegetation, four nets with the above characteristics were used to stock each pool. The zooplankton was sampled and filtered from the field with a Schindler–Patalas trap. A total of 200 L of lake water was filtered and added to each pool. A total of 20 L of sand was placed at the bottom of each pool. Each pool received 300 mL of sediment containing the oligochaete *Limnodrilus udekemianus*, obtained from cultures at the Instituto Nacional de Limnología. The pools, without crabs, were then placed in the shade under a tree (*Enterolobium contortisiliquum*) for 1 week.

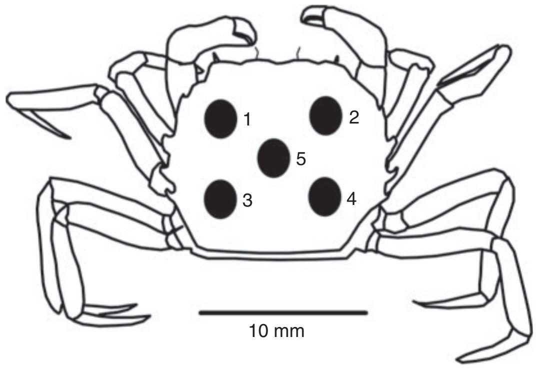

Fig. 1. Position of marks on the dorsal side of the carapace of *Trichodactylus borellianus*, as shown by the number next to each mark.

During the same week, 10 randomly selected adult crabs of both sexes were marked with a correction pen (Liquid Paper, Newell Rubbermaid, Ontario), 10 crabs were marked with a paint marker (Edding792A, edding Argentina S.A., Buenos Aires) and 10 were left without marks. The crabs were then separated into groups and placed in containers (one container per group) containing of 20 L of water and macrophytes. During a 5-day period, the crabs were observed twice to verify the behaviour occurring in the containers. After this period, individuals with and without marks were counted to establish the persistence of marks and to determine the rate of survival. After this preliminary investigation, 97 previously measured crabs (48 males and 49 females) were placed in each pool and left for 2 days to acclimatise and to attain a homogeneous distribution. The experiment was conducted over four consecutive days, with 3 days of recapture. Individuals were always sampled with a circular hand net with a 615-cm^2 net opening and a mesh size of 0.5 mm. The pools were divided with two imaginary lines into four sectors of equal size. These sectors were previously selected at random to establish the sequence of sampling on each day. The sampling sequence covered all sectors without repetition. Each sector was always sampled twice. On the first day (Day 0), animals were caught in each sector with the hand net, separated from the vegetation, dried with absorbent paper and marked on the dorsal side of the carapace. The marks were specific to the sampling day (Fig. 1). All samples were performed with replacement. After Day 0, the numbers of unmarked and recaptured individuals were recorded.

Field sampling

The field work was conducted during the summer in a pond on the Paraná alluvial plain. The pond was directly and permanently connected with the Ubajay stream (S 31°33′43.45″, W 60°30′58.73″) in Santa Fe province, central Argentina (Fig. 2). Environmental parameters (temperature, pH and conductivity) were measured with digital sensors every sampling day. The area of the sampling site was determined with a GPS (e Trex Vista®Cx, Garmin, USA) and used to calculate the estimated

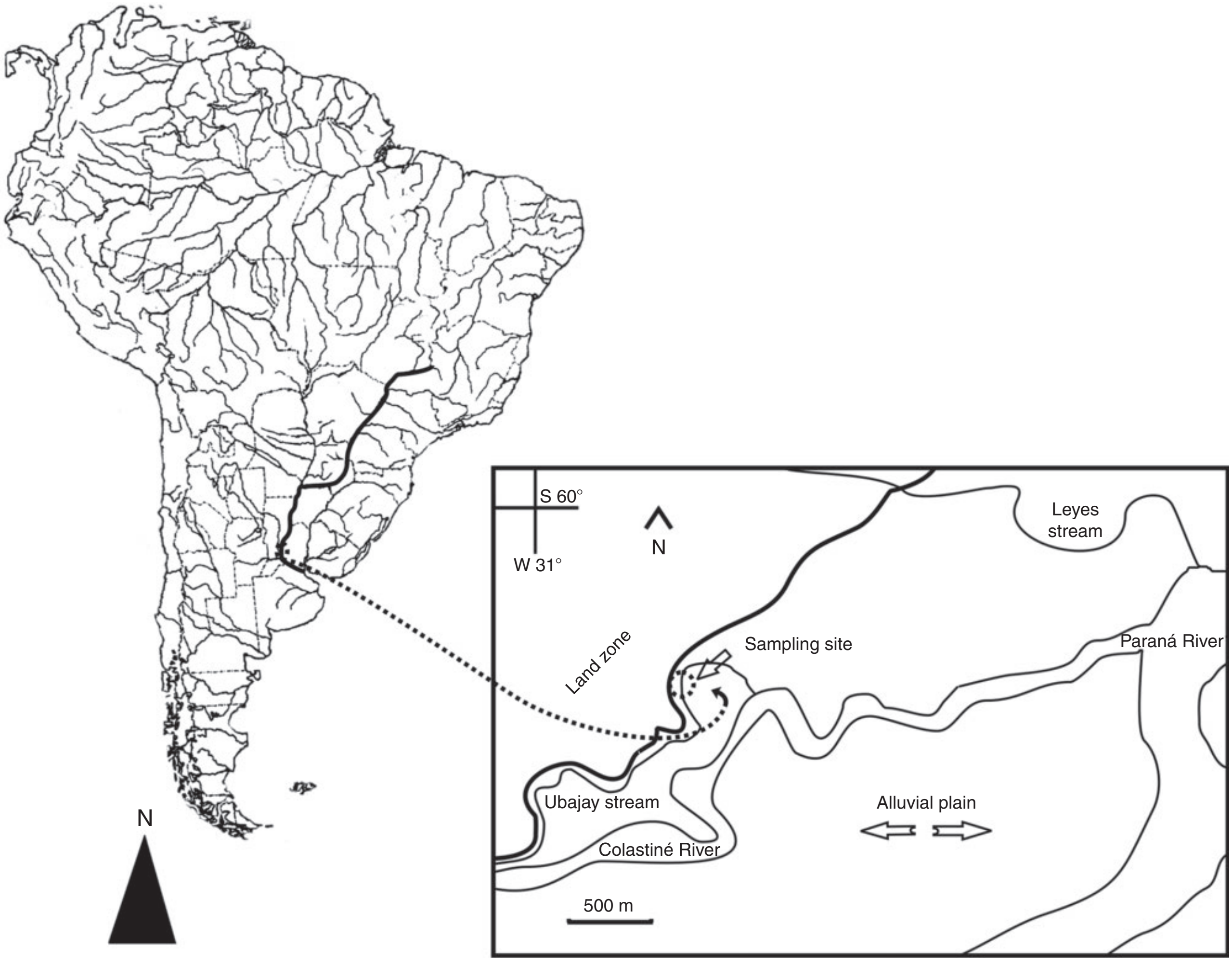

Fig. 2. Schematic map of the alluvial plain where the field study was performed.

population abundance. The lake border was covered with floating and emergent macrophytes, primarily *E. crassipes*. Because low water occurred during summer (2.5 m at Puerto Santa Fe), the floating aquatic vegetation was stagnant during the study period, and no vegetation entered or left the pond. For this reason, the population was considered closed during the brief duration of the study. Specimens of *T. borellianus* were sampled from the vegetation with a hand net with a 1230-cm^2 mouth opening and a mesh size of 1 mm. Four samples were collected randomly from the vegetation. Using the same methodology as described above, crabs were marked and captured over six consecutive days. The cephalothorax width (CW), sex, number of unmarked crabs and number of recaptured individuals were recorded each day. To prevent confusion from newly hatched animals, crabs less than 3 mm in CW were not marked. Individuals between 3 and 6 mm were considered juveniles, on the basis of the development of the pleopods and their sexual maturity (V. Williner, pers. comm.).

Data analysis

The values of the three estimators and their 95% confidence limits were calculated for both the mesocosm study and the field work. All formulae and confidence limits, as well as the foundations of each method, were obtained from Krebs (1999). For the simplest method (P), calculations were made using two data points: first day of mark (Day 0) and of one day of recapture (Day 1, Day 2 or Day 3). Hence, estimates were made for each day of recapture. For the multiple methods (S and SE), the estimates were calculated accumulatively for the period between the second and last days of recapture. This means that the estimate for Day 2 had three data points (Day 0, Day 1, Day 2), the estimate for Day 3 had four data points (Day 0, Day 1, Day 2, Day 3) and so on. A chi-square test was performed for the mesocosm experiment to evaluate the differences between the real and calculated population sizes (Zar 1996).

To evaluate the assumptions of equal catchability and closed population, we plotted a through-the-origin regression of the accumulated number of marked individuals (M) against the proportion of marked individuals (R/C) (number of recaptures/number of caught) at each sampling day. This plot should be linear if the assumptions underlying the method are satisfied (Krebs 1999). The through-the-origin regression was plotted and analysed with R (version 2.15.1) (R Development Core

Team 2011). To evaluate the assumption of equal catchability for the field study, we used a Chapman test (Krebs 1999).

To verify the accuracy of the results obtained from the mesocosms, we analysed the percentage of bias and the confidence limits for the estimators. The percentage of bias (%Bias) was calculated with the formula %Bias = (Nc − Nr)/Nr × 100, where Nc is the calculated population size and Nr is the true population size (Manly 1970). The confidence limits calculated for each method were based on the specifications in Krebs (1999) and serve as an accuracy measure (Roff 1973).

Results

Mesocosms

Despite the similar behaviour of marked and unmarked animals, the crabs tagged with the paint mark did not lose their marks after 5 days, whereas 60% of those tagged with the correction pen lost their marks, either partially or totally. No individuals moulted during the experimental period. Because of the greater persistence of the paint marker and the lack of any observable effect on the behaviour and survival of the crabs, we selected the paint to mark the animals.

The size ranges of the crabs used in this experiment were as follows: males, 8.7 ± 1.6 mm and females, 10.0 ± 1.7 mm (R1); males, 10.0 ± 10.1 mm and females, 9.8 ± 1.4 mm (R2). The regression analysis of R/C *v.* M yielded significant results (R1: $P = 0.0042$, $R^2 = 0.9386$; R2: $P = 0.0158$, $R^2 = 0.8543$). These results indicated that the assumptions underlying the method were satisfied (Fig. 3*a*, *b*).

The confidence limits followed the binomial, Poisson and normal distributions for the P, S and SE methods, respectively. The results varied greatly for each method. However, the chi-square test identified two groups of estimates that did not differ from the true population size, namely, the P estimates for R2 ($\chi^2 = 5.69$, $P = 0.11992$) and the S estimates for R1 ($\chi^2 = 3.58$, $P = 0.16547$). Despite the similar number of individuals captured for the first time in R1 and R2, the total number of crabs captured was greater in R2 than in R1. Nevertheless, the total number caught in both pools was too small for the SE method to be used reliably. Although some estimates of this method were close to the real population size, the lower confidence limits were negative and the upper limits did not include the estimate within the confidence interval (e.g. for R1, the SE method gave a population size of 113, with a lower limit of −21 and upper of 15). Hence, the population sizes calculated by this method were not included in the results because of their low reliability.

The estimates varied among days and showed the greatest positive bias in R2 for the S method. The P method produced the greatest underestimates (Table 1). According to the results of the chi-square test, the P and S methods produced estimates closest to the true values for R2 on Day 1 and for R1 on Day 2, respectively, with less than 5% bias (Table 2). However, a wider confidence interval was calculated for the P method (Table 1). Therefore, the S method was the most accurate in this case.

Field work

The environmental parameters remained stable throughout the sampling period (pH: 7.7 ± 0.6; conductivity: 0.2 ± 0.1 ppm; temperature: 23.4 ± 2.2°C). The area of the sampling site was ~359 m². In total, 271 (63 females, 66 males and 142 juveniles) crabs were captured and marked during the six consecutive sampling days. Of these crabs, only three had a soft carapace (1.1% of the total). Among the females, 30% carried eggs or newly hatched individuals. The size ranges of the crabs captured in the field study were 11.06 ± 2.6 mm for females, 9.67 ± 2.1 mm for males and 4.24 ± 0.65 mm for juveniles.

The regression analysis of R/C *v.* M yielded significant results ($P = 0.00013$; $R^2 = 0.948$), indicating that the assumptions

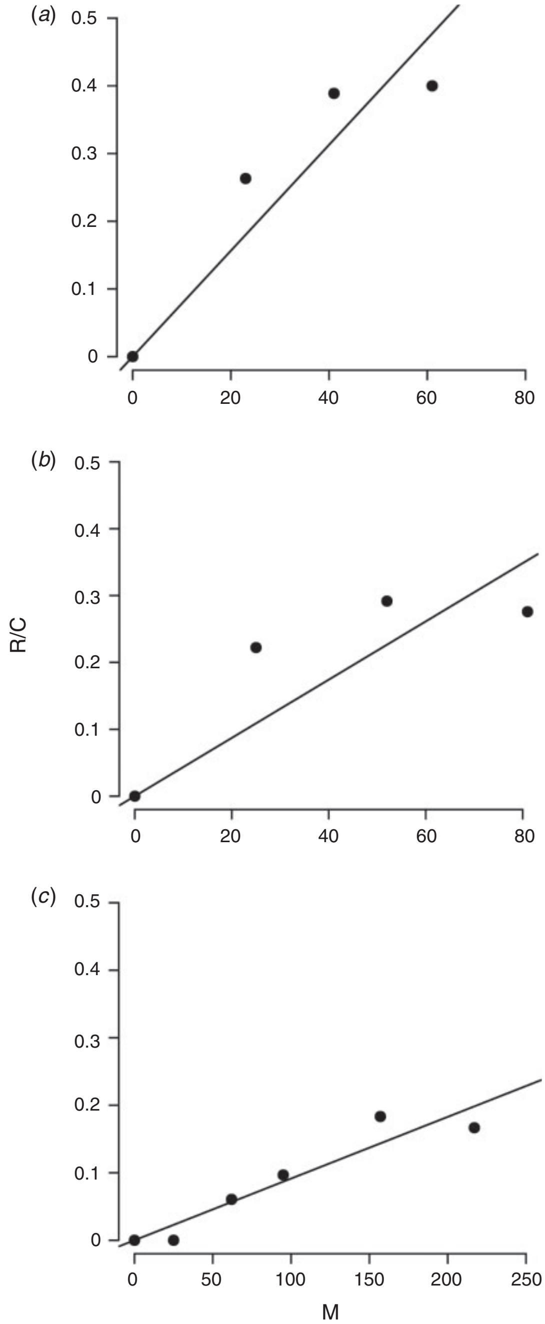

Fig. 3. Accumulated number of marked individuals (M) plotted against the proportion of marked individuals in each sample (R/C) for (*a*) R1, (*b*) R2 and (*c*) the field study.

Table 1. Calculated population size (*N*) of *Trichodactylus borellianus* in the mesocosm experiment, based on the three estimators, with the lower and upper 95% confidence limits

Estimates were made from Day 1 to Day 3 for the Petersen (P) method and from Day 2 to Day 3 for the Schnabel (S) method. R1 = Pool 1, R2 = Pool 2

Pool	Method	Day	Lower	*N*	Upper
R1	P	Day 1	30	55	100
		Day 2	34	77	136
		Day 3	31	54	105
	S	Day 1	–	–	–
		Day 2	56	92	155
		Day 3	78	115	175
	P	Day 1	66	100	386
		Day 2	42	78	133
		Day 3	53	83	193
R2	S	Day 1	–	–	–
		Day 2	86	137	250
		Day 3	131	194	309

Table 2. Percentage of bias of the population estimates of *Trichodactylus borellianus* calculated by each method

P = Petersen method, S = Schnabel method

Method	R1			R2		
	Day 1	Day 2	Day 3	Day 1	Day 2	Day 3
P	−44	−21	−45	3	−19	−14
S	–	−5	18	–	45	100
	–	17	40	–	64	141

Table 3. Calculated population size (*N*) of *Trichodactylus borellianus* in the field study, based on the three estimators, with the lower and upper 95% confidence limits

Estimates were made from Day 2 to Day 5. P = Petersen method, S = Schnabel method, SE = Schumacher–Eschmeyer method

Method	Day	Lower	*N*	Upper
P	Day 2	111	283	627
	Day 3	114	225	436
	Day 4	76	127	241
	Day 5	77	138	252
S	Day 2	444	990	2225
	Day 3	557	985	2068
	Day 4	610	914	1501
	Day 5	736	1034	1496
SE	Day 2	–	–	–
	Day 3	563	1022	5602
	Day 4	639	904	1546
	Day 5	873	1082	1422

underlying the method were satisfied (Fig. 3*c*). A Chapman test had a *P*-value of 0.1052. On the basis of this result, the null hypothesis of equal catchability could not be rejected. Therefore, all individuals had the same probability of capture.

The confidence limits for the estimators followed the same distributions as obtained in the experimental work. Only Days 2 and 3 followed the Poisson distribution for the P method. The population estimates varied for each method (Table 3). Relatively low and relatively high estimates were furnished by the P and SE methods, respectively. The SE method again enabled no reliable population estimate to be calculated for Day 2. However, from Day 3, the total catches increased and estimates after this day were reliable, remaining within the confidence intervals. On the basis of the mesocosm results, it is probable that the S method calculated the most accurate estimate of population size. The narrowest confidence interval for this method was found on Day 5. On the basis of this result, the estimated population density in the study area was 2.9 crabs m^{-2}. However, the confidence interval on Day 5 for the SE method was also narrow and was very similar to that obtained for the S method on the same day, and estimated density at 3.1 crabs m^{-2}.

Discussion

The present study developed an approach to the use of mark–recapture methods for a closed population of crabs inhabiting the macrophytes of a river with a floodplain. Many previous studies of decapods involved marine species (Drummond-Davis *et al.* 1982; Beyers 1994; Bell *et al.* 2003; Corgos *et al.* 2007; Vay *et al.* 2007) or freshwater crustaceans of small streams or lakes without abundant aquatic vegetation (Rabeni *et al.* 1997; Bueno *et al.* 2007; Pilotto *et al.* 2008). Seasonal changes in the hydrological cycle, macrophyte community and physico-chemical factors (e.g. transparency and suspended solids) characteristic of the alluvial plain (Thomaz *et al.* 1997) make the application of the mark–recapture method in these systems a task that requires planning. If we want to ensure a closed population at the study site, for example, the low-water stage is the best period. In contrast, the type of mark should be selected according to the time scale of the research.

In the present work, the marks remained fixed and clearly visible throughout the study. Moreover, the marks were easy to apply to both adult and juvenile animals. Many other types of marks have been used in other decapod species, including micro-wire tags (de Graaf 2007; Vay *et al.* 2007), cauterisation (Bueno *et al.* 2007), epoxy-resin-based paint (Bell *et al.* 2003), visible implant elastomer tags (Pilotto *et al.* 2008), T-bar anchor tags (Williams 1986; Corgos *et al.* 2007) and even a staining method (Drolet and Barbeau 2006). Depending on the aim of the study, short-term or long-term analyses will be preferred. The type of tag selected will depend on the factors of permanence time, handling time and cost. In the present study, the paint marker satisfied the assumptions cited in the Introduction. The cost of the paint marker was very low, and the method was perfectly applicable to a short-term recapture interval. In a field study conducted over a few days during the low-water period, processes of population dynamics, such as recruitment and migration, can be considered negligible in the closed population. However, future investigations could extend the daily samplings to flooded areas just outside the working area to ensure the absence of migration. Nets can also be used to isolate the pond.

The assumptions of equal catchability and random sampling are more difficult to satisfy. Although certain algorithms can be used to verify that these assumptions are valid (see Krebs 1999), these algorithms are applied only after data collection. For this reason, the preliminary mesocosm study was very useful for verifying the assumption of equal catchability and for selecting the most accurate method of population estimation. Moreover, the analysis of the experimental results identified estimators whose accuracy was low and whose percentage of bias was high. The subsequent application of mark–recapture methodology in the field can then avoid estimators having less precision. According to Chao (1987), 'Schnabel'-type estimators could give negatively biased results because of the heterogeneity of the capture probabilities. However, this type of method produced overestimates in the present study.

Effectively, the regression analyses indicated that the assumptions (closed population and equal catchability) were satisfied in all cases. For this reason, it appears that the biased results are due to a cause other than unequal catchability. Non-random samples are a possible reason for the biased results. The manual capture technique may have intrinsically biased the sample and the crabs were not sampled randomly from the population (Minta and Mangel 1989). These questions are difficult to resolve because other types of sampling techniques, such as the use of traps, are also known to be a source of bias (Yamamura *et al.* 2003). The use of capture–resighting methods can allow the assumptions to be satisfied (Minta and Mangel 1989); however, it is impossible to apply this approach in an environment with turbid water and dense aquatic vegetation, such as in the present study. A preliminary analysis of different methods of capture and of the use of traps, such as that conducted for the crayfish *Paranephrops planifrons* (Rabeni *et al.* 1997), can provide valuable information about the most useful technique and can aid the selection of estimators whose bias is low.

Improved results will be obtained if all of the assumptions of the selected method are satisfied. However, the accuracy desired can differ according to the aim of the investigation (Roff 1973; Krebs 1999). In the present study, the preliminary experiment served to identify the most accurate method and helped improve the results of the field work. If preliminary studies are not possible, the confidence limits indicate the reliability of the estimates and must include the real population (Roff 1973). The results of the field study showed that the confidence intervals became narrower over time for the multiple methods. The SE estimator produced an estimate without a reliable confidence interval on Day 2 of the field study and in all days of the mesocosm study. The normal approximation confidence interval used by the SE estimator is essentially a 'large sample' method according to Krebs (1999). However, in agreement with the same author, the normal approximation must be used regardless of the number of recaptures. Thus, unreliable confidence intervals obtained in the present study may have been a consequence of the limited sampling period, with low numbers of recaptured crabs. Therefore, methods involving multiple capture events require an appropriate balance between the number of recaptures and the amount of sampling effort. For the simplest method (P), the present study showed that the results could differ substantially depending on the number of individuals captured and recaptured each day. Multiple mark and recapture designs are preferable to designs involving only single events. In the present study, the S method furnished the most accurate estimates in both mesocosms and field investigations. Notwithstanding, the SE method also gave accurate estimates in the field study; however, it requires a minimum number of recaptures to give reliable confidence intervals.

Although the true population size in the field remains unknown, the approach furnished by each estimator allowed us to infer that the population size was approximately equal to the values obtained for Day 5 by the multiple methods (Table 3). The estimated density calculated by the S method is greater than that previously determined by Renzulli and Collins (2001) for the same crab on the Pilcomayo River. However, note that the current study presents the first mark–recapture estimates ever obtained for *T. borellianus*. The population density of the crab at the present study site will certainly be different at a different time of the year, i.e. when high water causes the population to drift so that it is mixed with other populations inhabiting the alluvial plain. In any case, these estimates provide valuable information about the population status of this crab, e.g. following a prolonged drought. In fact, during the last extraordinary drought in 2009 due to a La Niña phenomenon, the populations of this crab decreased markedly in the aquatic vegetation of the ponds of the Middle Paraná River (pers. obs.). The estimates obtained in the present study showed that these crab populations have since been re-established. The methodology demonstrated in the study contributes to future short-term population estimates of the crabs of alluvial plains.

Acknowledgement

We thank Agencia (PICT 2007 N°01360) for the research support.

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