Attachment L-21

Nashville Crayfish Survey Protocols

Appendix L-21

NASHVILLE CRAYFISH SURVEY PROTOCOLS

These protocols are currently being prepared and will be included in this MSHCP when available from the Service. These protocols will be based, in part, on the specifications provided in Nowicki et al. 2008, *Monitoring crayfish using a mark-recapture method: potentials, recommendations, and limitations* (attached).

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ORIGINAL PAPER

Monitoring crayfish using a mark-recapture method: potentials, recommendations, and limitations

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Abstract Crayfish are regarded as useful indicators of environmental quality and freshwater biodiversity. However, reliable methods for monitoring their populations are needed so that this potential can be fully utilised. We report and discuss methodological aspects of the white-clawed crayfish (*Austropotamobius pallipes* complex) survey conducted in Piedmont, Italy, with the use of mark-recapture. The results suggest that the method can serve as a convenient tool for estimating the size of crayfish populations and inferring their temporal trends. The two populations investigated appeared closed except for wintertime and July. Consequently, the Robust Design, which is regarded as the most reliable mark-recapture approach, can be easily applied. The minimum effective sampling plan for monitoring purposes should comprise one primary period per year, conducted in the summer–autumn season, and consisting of three capture sessions. If gaining insight into the ecology of the investigated species is the prime objective and sufficient resources are available, the optimal plan should include two primary periods (in spring and the summer–autumn season) of five capture sessions each. Capture sessions need to be separated by roughly 2-week intervals in order to avoid the strong, but short-term, negative effect of capturing crayfish on their recapture chances. As the model without heterogeneity in capture probabilities ensures better estimate precision we recommend that data collected for both sexes are analysed separately. Taking into consideration higher male catchabilities and sex ratio being invariably 1:1, it also seems beneficial to estimate only male numbers and double them to achieve total population sizes.

Keywords *Austropotamobius pallipes* complex · Jolly-Seber model · Model selection · Population size estimation · Relative abundance methods · Robust design · Sampling intensity · Survival patterns

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Introduction

Crayfish are a highly diverse and important invertebrate group, with many species playing a prominent role in freshwater ecosystems. They are keystone consumers (Nyström et al. 1996) feeding on algae, macrophytes, invertebrates, and detritus (e.g. Lodge et al. 1994; Whitledge and Rabeni 1997). In turn, they are preyed upon by various fish, birds, and mammals (Holdich and Lowery 1988; Reynolds 1998; Holdich 2003). In addition, their burrowing behaviour considerably modifies river banks (Dorn and Mittelbach 1999), creating microhabitats that constitute a refuge from drought and extreme winter conditions for many small organisms (Usio and Townsend 2004; Zhang et al. 2004; Pintor and Soluk 2006). For the above reasons crayfish have recently been regarded as potential useful indicators of freshwater biodiversity (Reynolds and Souty-Grosset 2003; Gherardi and Souty-Grosset 2006). Moreover, some crayfish, especially long-lived species of cool waters, are sensitive to pollution and thus may serve as useful bioindicators of water quality (Jay and Holdich 1981; Holdich and Reeve 1991; Reynolds et al. 2001).

Several freshwater crayfish species are currently endangered in various parts of the world and listed in the IUCN Red List (Baillie and Groombridge 1996; Souty-Grosset et al. 2006). Apart from their sensitivity to pollution, this is mainly caused by the competition with exotic crayfish introduced by man as well as disease and parasite transmission or even predation by them (Gherardi and Holdich 1999; Taugbøl and Skurdal 1999; Lodge et al. 2000; Gherardi 2006). The negative impact of these invasive exotics is not restricted to native crayfish species; in fact they have been reported to seriously reduce biomass and species richness of many other groups of fauna and flora too (Wilson et al. 2004; Rodríguez et al. 2005; Crawford et al. 2006; Rogowski and Stockwell 2006; Rosenthal et al. 2006; Willis and Magnuson 2006).

Consequently, monitoring both native and invasive crayfish species is not only essential for assessing the status of the former (in many cases being a legal obligation), but also important in much broader conservation programmes targeting whole communities or even the entire biodiversity of freshwater areas. The problem, however, lies in the lack of a well-established methodology for monitoring crayfish populations. The methods traditionally used for assessing crayfish abundance, such as manual searching, trapping, and night viewing, are not fully reliable (Rabeni et al. 1997; Peay 2003; Dorn et al. 2005; also see the Discussion section for further explanation).

One of the potential remedies could be the application of mark-recapture methods, which are particularly useful for studying population trends in small animals, and have been successfully harnessed in monitoring programmes for rodents, birds, reptiles, amphibians, and butterflies (Baillie 1995; Marunouchi et al. 2002; Flowerdew et al. 2004; Julliard et al. 2004; Moore et al. 2007; Nowicki et al. 2008). In crayfish, these methods have been used mainly for investigating dispersal (e.g. Robinson et al. 2000; Gherardi et al. 2000; Byron and Wilson 2001), whereas studies aimed at population parameters were short-termed and focused on population structure (Parkyn et al. 2002; Maguire et al. 2004; Jones and Coulson 2006) or spatial abundance patterns (Guan and Wiles 1996; Hicks 2003; Hockley et al. 2005) rather than on temporal trends.

The aim of the present study was to test the applicability of mark-recapture for monitoring crayfish populations. Our motivation was stimulated by the fact that crayfish may be expected to be rather easy to sample with mark-recapture, based on characteristics of their biology. The ease of sampling crayfish derives from their relatively high local densities (e.g. Guan and Wiles 1996; Hicks 2003; Jones et al. 2005), high site-fidelity (Bubb et al. 2002, 2006; Webb and Richardson 2004), and considerable longevity (Parkyn et al. 2002;

Holdich 2003), which together make it possible to achieve adequate recapture rates. We were also interested in assessing which mark-recapture models would fit the data best, thus ensuring unbiased and relatively precise population size estimates. Finally, our intention was to propose a simplified protocol for data collection and analysis in monitoring of freshwater crayfish populations.

Materials and methods

Study species and sites

As a model for the analyses we chose the white-clawed crayfish (*Austropotamobius pallipes* complex). The white-clawed crayfish are native to western Europe with a wide historical distribution ranging from the Balkans and Italy in the south-east to Ireland in the north-west (Reynolds 1998; Holdich 2003; Souty-Grosset et al. 2006). However, over the last 150 years they experienced a dramatic decline, and are currently mostly confined to small and isolated relict populations (Holdich and Lowery 1988; Reynolds 1998). Consequently, the white-clawed crayfish are protected by national laws in the countries where they occur as well as listed in the Annexes II and V of the Habitats Directive (van Helddingen et al. 1996; Holdich 2003). The distinction between the two recently separated white-clawed crayfish species, *A. pallipes* and *A. italicus*, is possible only on basis of genetic data (Santucci et al. 1997; Grandjean et al. 2002; Fratini et al. 2005). As species identity, however, is of little relevance due to their similar life-history traits, we did not classify the species sampled as either of the two, but refer to it as the *A. pallipes* complex.

We investigated two local populations of the *A. pallipes* complex inhabiting the Rio dell'Osio and the Rio Pilatu streams in the hydrographical basin of the Malone river, located north of Turin in the foothills of the Italian Alps (Fig. 1). Rio dell'Osio (N 45°18′52″, E 7°33′31″, 530 m a.s.l.) has an average width of ca. 4 m and consists of rapid flow stretches with a depth of 20–30 cm, interspersed every 10–40 m with slow flow pools (max. dimensions: 9 × 7 m; avg. depth: 2 m). Rio Pilatu (N 45°17′26″, E 7°29′19″, 570 m a.s.l.) shows the same general characteristics, but it is only ca. 2.5 m wide and with smaller pools (max. dimensions: 3 × 2 m; avg. depth: 1.2 m). In both streams we sampled approximately 450 m long sections, where the habitat is apparently optimal for the white-clawed crayfish. Diverse banks with numerous tree roots, trunks and holes serve as potential refuges, while the surrounding lush vegetation provides shade and a large supply of organic material. More importantly for our purposes, crayfish populations within the sampled sections were effectively spatially isolated. Upstream, the sections are blocked by man-made cascades, while downstream the habitat becomes unsuitable for crayfish due to strong anthropogenic impact.

Field sampling

The mark-recapture surveys of the white-clawed crayfish populations in Rio dell'Osio and Rio Pilatu have been carried out since 2005 within the framework of the Action Plan for the species in the Piedmont region (Tirelli et al. in press). Our study is based on the data gathered so far, comprising years 2005–2006 and the first half of 2007. In 2005 the sampling was conducted from April to November with 13 two-day capture sessions held roughly every 2 weeks. In the following year, the capture sessions were made more

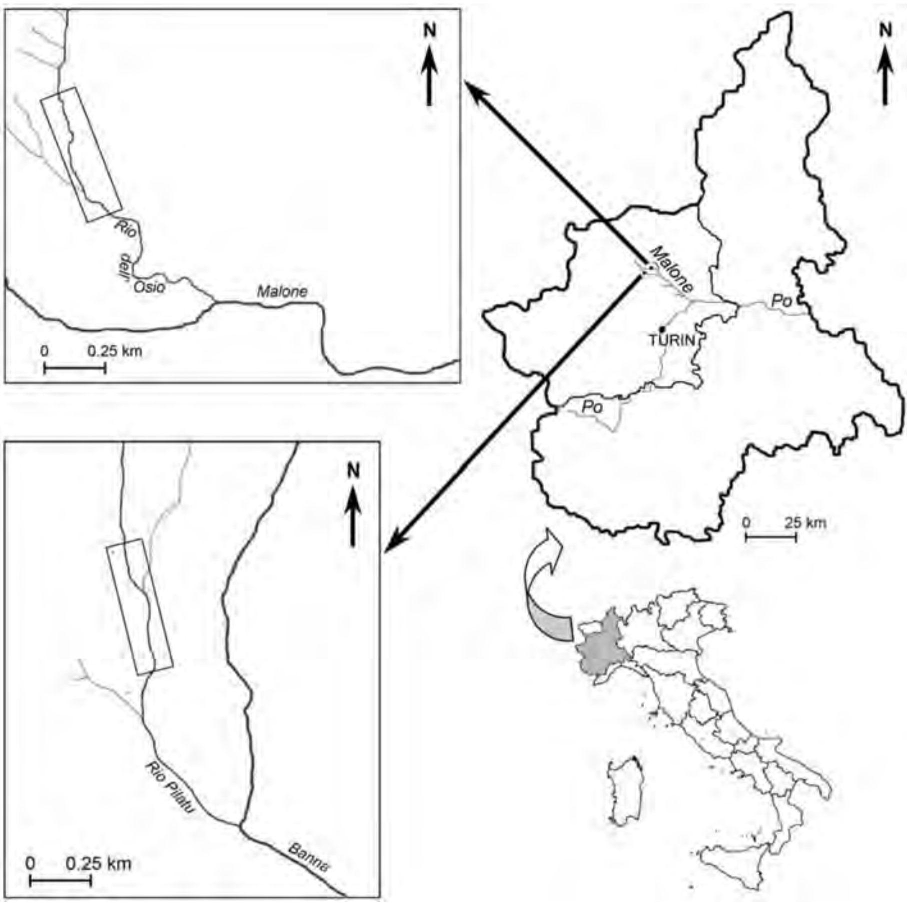


Fig. 1 Schematic map showing location of the two study sites in the Piedmont region, Northern Italy

intensive as the investigated sections of both streams (hereafter called sites) were subdivided into 5 units of approximately equal length (80–100 m). Each unit was sampled on a different day, and thus a single capture session lasted 5 days. There were six capture sessions conducted roughly once a month from May to October. Finally, in 2007 the sampling plan resembled that of 2006, but the intervals between capture sessions were shortened to two weeks, which made it possible to have three sessions in April and May.

Two people were involved in sampling that typically lasted for ca. 2–3 h per day on each site, though its intensity had to be lower on many occasions in spring 2006 due to rainy weather, and in spring 2007 due to high water conditions. Crayfish were either actively searched for and hand-netted in shallow water during daytime or caught using eight traps set in deeper places in evenings and examined the following mornings. The traps were 50 × 25 × 25 cm, and with pig or chicken liver used as bait. All individuals captured were sexed and measured. Subsequently those with a total length greater than 40 mm were considered adults and were individually marked. In this way, during the three years of the study we recorded altogether 1,709 captures of 747 males and 439 females in Rio dell'Osio, and 1,278 captures of 521 males and 434 females in Rio Pilatu.

Marking was done with the method described by Guan (1997), which uses a code system based on holes punched in different positions of telson and uropods. The trouble with Guan's method is that the duration of marks depends on their position. However, as we applied marks on the most durable positions (for details see Guan 1997) they should last for at least 2–3 moulting events, which corresponds to over 1 year in full-grown white-clawed crayfish (Lowery 1988), or even more as our findings suggest (see the Results section). Juveniles were released without marking for both ethical and practical reasons. The former are related to the fact that marking is known to reduce crayfish growth rate (Guan 1997). A strong practical argument against marking juveniles is little feasibility of their use in mark-recapture studies due to very low catchability (Rabeni et al. 1997; Gherardi et al. 2000; Dorn et al. 2005) as well as frequent moultings (up to six per year) leading to increased loss of marks.

Data analysis

The sampling plan, at least for the first 2 years of the study, was designed under the conservative assumption that the investigated crayfish populations would be open for most of the time. Nevertheless, in the first step of our analysis we evaluated the validity of this assumption. This was done through assessing the survival (ϕ) and recruitment (B) of individuals between capture sessions with the open population Jolly-Seber type models (Schwarz and Arnason 1996; Schwarz and Seber 1999). Strictly-speaking ϕ should be called residence as it is affected not only by mortality but also by emigration, yet we retain the term survival for the sake of consistency with the standard mark-recapture nomenclature. Recruitment in turn includes both births (in fact in our case it is maturation as we only investigated the adult fraction of crayfish populations) and immigration. Either survival significantly lower than 1 or recruitment significantly different from 0 would indicate population openness. The models were fitted using the program POPAN (Arnason and Schwarz 1999). The program provides the estimates of capture probabilities ($\hat{p}_i$) for consecutive capture sessions as well as estimates of survival ($\hat{\phi}_i$) and the 'probability of entrance' into a population ($\hat{b}_i$, which is a relative measure of recruitment $\hat{b} = \hat{B}_i/\sum \hat{B}_i$) for intervals between sessions. Both temporal variation (t) and inter-sexual differences (s) in parameters were of prime interest. Thus we only considered the estimates of the unconstrained model $p(s * t)\phi(s * t)b(s * t)$, which anyway performed very well as indicated by the Akaike's Information Criterion (Akaike 1973; Hurvich and Tsai 1989).

Since the analysis of survival and recruitment patterns revealed that the investigated populations remained effectively closed for long periods (see the Results section), we decided to apply the Robust Design model (Pollock 1982; Pollock et al. 1990). The Robust Design is a mixed model using two types of capture periods: each primary period consists of several secondary periods. Population is assumed to be closed within primary periods, but open between them. Data on captures and recaptures during each secondary period are used to estimate population sizes within primary periods, while the data pooled within each primary period are used to estimate survival and recruitment between the periods. We adopted five primary periods comprising spring seasons 2005, 2006, and 2007 with respectively 6, 3, and 3 capture sessions constituting secondary periods, as well as summer–autumn seasons 2005 and 2006 with respectively 7 and 3 secondary periods.

For comparative purposes the data were analysed separately for males and females as well as jointly for the entire adult population. The analysis was conducted with the software MARK 4.3 (White and Burnham 1999), including the program CAPTURE (Otis et al.

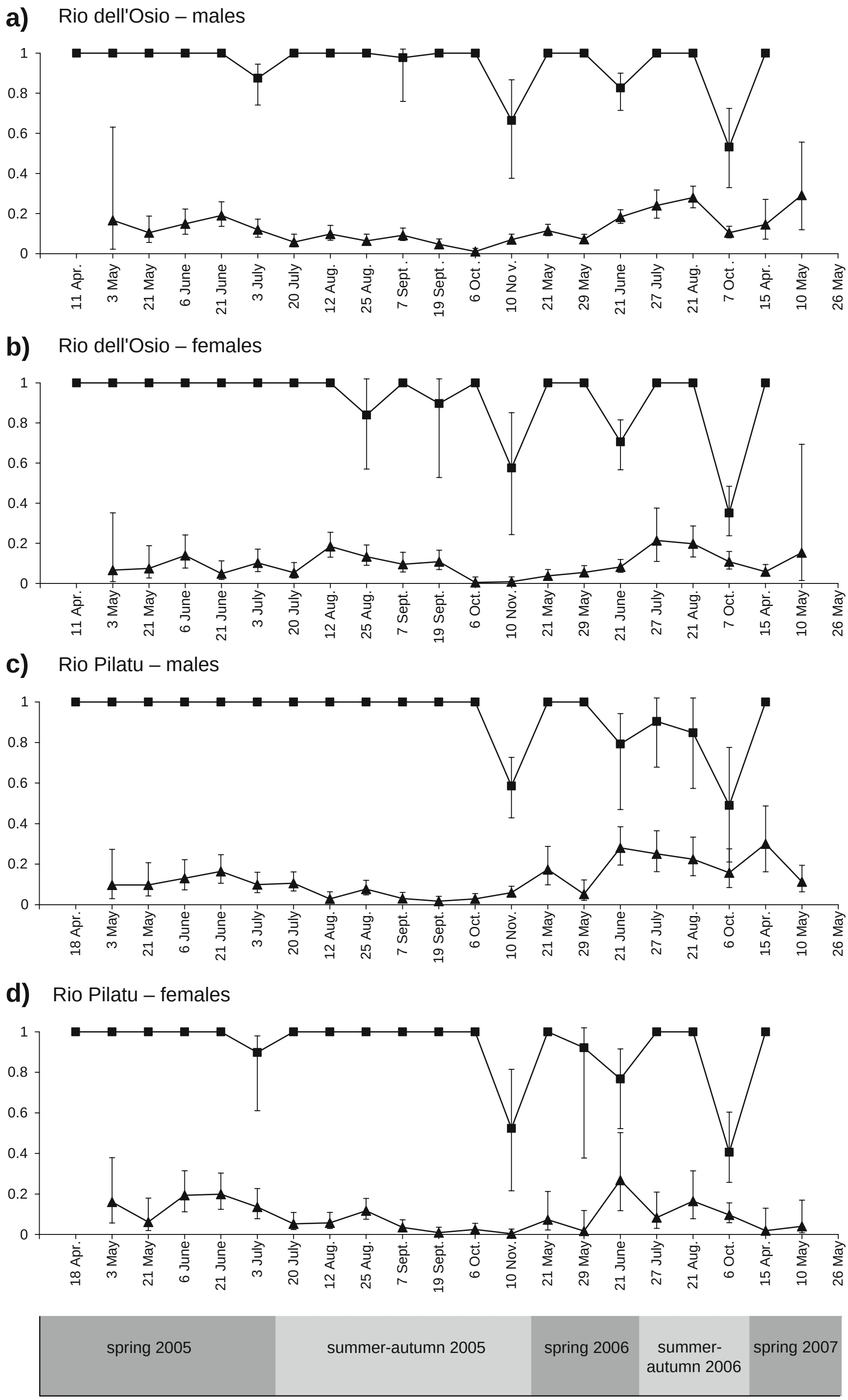
Fig. 2 Parameter estimates (squares = survival, triangles = capture probability; both with 95% confidence intervals) of the open population Jolly-Seber model applied to the crayfish populations investigated in 2005–2007. It should be noted that survival estimates presented for any given capture session actually refer to the interval between this session and the following one (e.g. the estimates given for 21 June 2006 represent the fractions of individuals surviving between 21 June and 27 July 2006). Estimates of probability of entrance into population are not included, but they were never significantly different from zero and generally of low precision. The bottom bar shows the resulting division of capture sessions into Robust Design primary periods

1978; Rexstad and Burnham 1991) incorporated as an independent module into MARK. The program CAPTURE was applied for selecting the most appropriate closed population models and the subsequent derivation of population size estimates for primary periods. The candidate models involved the null model assuming equal and constant capture probability for each individual (M_0) and models accounting for different types of violations to this assumption, such as time variation (M_t), heterogeneity (M_h), behaviour response (M_b), or their combinations (M_{bh}, M_{tb}, M_{th}, M_{tbh}) (Otis et al. 1978). As it was reasonable to expect that the nature of possible violations to equal catchability assumption was similar for both investigated populations and across seasons we opted to use the same closed model for all primary periods within a particular system (i.e. male/female fractions or entire adult population) as recommended by Williams et al. (2002). The selection of the most appropriate models followed the routine of the program CAPTURE in its first step. Subsequently, based on its outcome for the two primary periods of 2005, we calculated the weighted mean fit of different models with weights being numbers of individuals captured. The primary periods of 2006–2007 were not used in this analysis, because with only three secondary periods available the selection routine of the program CAPTURE would have had too little power (Otis et al. 1978; Menkens and Anderson 1988).

In addition, we investigated how representative the five sampling units were for the entire study sites in 2006–2007. For this purpose, population size estimates were also derived, using the Robust Design, from the data collected within sampling units. The division of sampling sessions into primary periods and the closed population models applied within them were identical as for the entire data sets. Obviously, with individuals moving between the sampling units spatial closure was not maintained and thus the population size estimates produced for the units should be expected to be positively biased (Kendall 1999). However, the biases were likely to be only slight, thanks to the aforementioned high site-fidelity of crayfish.

Results

Capture probability estimates yielded by the Jolly-Seber model were generally higher for males, although for both sexes their temporal variation was much more pronounced (Fig. 2). As expected capture probabilities grew substantially between 2005 and the two following years, corresponding to the increased sampling intensity, but even within the same season they were extremely variable. The recruitment between consecutive capture sessions according to the Jolly-Seber model was never significantly different from zero. In contrast, the analysis of survival revealed a fairly distinct and consistent pattern with significant losses of individuals occurring in July (though less clearly so in 2005) and over winter, but not in any other period (Fig. 2). Consequently, while applying the Robust Design, we divided capture sessions into the following five primary periods: April–early July 2005 (spring 2005); late July–November 2005 (summer–autumn 2005); May–June


a)
Rio dell'Osio – males
b)
Rio dell'Osio – females
c)
Rio Pilatu – males
d)
Rio Pilatu – females
1
0.8
0.6
0.4
0.2
0
11 Apr.
18 Apr.
3 May
21 May
6 June
21 June
3 July
20 July
12 Aug.
25 Aug.
7 Sept.
19 Sept.
6 Oct.
10 Nov.
21 May
29 May
21 June
27 July
21 Aug.
7 Oct.
6 Oct.
15 Apr.
10 May
26 May
spring 2005
summer-autumn 2005
spring 2006
summer-autumn 2006
spring 2007

2006 (spring 2006); late July–October 2006 (summer–autumn 2006); April–May 2007 (spring 2007).

The closed model selection procedure within primary periods indicated that the model with temporal variation in capture probabilities (M_t) was the most appropriate for both sexes (Table 1), which concurs with the aforementioned results of the Jolly-Seber model. In the case of the data pooled together for both sexes, heterogeneity in capture probabilities, apparently reflecting inter-sexual differences, could also be detected, and the M_{th} model performed the best (Table 1). At the same time intra-sexual heterogeneity was rather unlikely since the M_h model performed poorly within any sex. Similarly, there was very little indication of behavioural response effect on capture probabilities. However, the above refers only to the effect between capture sessions, i.e. over periods of 2 weeks or more, and does not preclude a strong negative behavioural response within the few days following capture. We hardly ever (altogether less than 10 cases) managed to recapture an individual within the same session.

The results of the M_t and M_{th} models applied to the investigated crayfish populations within the five seasons of the survey are given in Table 2. Capture probabilities were highest summer–autumn 2006 when the sampling was intensive and conducted in optimal conditions, but considerably lower in the springs of 2006 and 2007 with occasional unfavourable conditions, and even lower in 2005 when the capture sessions were less intensive, despite their twice higher number. With the slight exception of Rio Pilatu in spring 2005, males had catchabilities approximately twice as high as females ($\hat{p} = 0.24 - 0.53$ vs. $0.11 - 0.39$). Consequently, the precision index of their seasonal number estimates was about twice as good (Table 2). Also noticeable was a generally better precision of population size estimates obtained through summing male and female numbers as compared with those derived from the pooled data, which reflected the advantage of using the M_t rather than the M_{th} model. Nevertheless, estimates yielded by both methods were highly concordant (Kendall's $\tau = 0.733$, $n = 10$, $P = 0.0032$). The Rio dell'Osio population appeared relatively stable, while the Rio Pilatu population less so ($CV = 0.19$ and 0.43 respectively; based on the summed male and female numbers). However, this pattern can be explained at least partly by worse precision of the estimates for the latter site. Through the course of the study adult crayfish numbers grew gradually from ca. 900 to 1,100 individuals in Rio dell'Osio and ca. 600–700 individuals in Rio Pilatu in 2005 to roughly 1,400 individuals per site in summer–autumn 2006, but in the following spring they dropped back to initial (or even a bit lower) levels (Table 2, Fig. 3). Estimated sex ratio was invariably very close to 1:1.

Approximately 90% of individuals survived from spring to summer–autumn season each year, whereas the survival over winter was only about 50% in Rio dell'Osio and 30–40% in Rio Pilatu (Fig. 3). The average adult survival rate over the entire survey period was 0.952 per month (SE = 0.012) in Rio dell'Osio and 0.939 per month (SE = 0.009) in Rio Pilatu, with absolutely no inter-sexual differences. These correspond to the average residence time of 20 months (95% CI: 12–33) and 16 months (95% CI: 12–22) respectively for both populations. Because of the possible problem of mark loss, these figures should actually be regarded as the lower limits of mark duration. In this respect it is also worth mentioning that in spring 2007 we recaptured a considerable number (15 in Rio dell'Osio and 9 in Rio Pilatu) of individuals that had been marked 2 years before.

With few exceptions season-to-season trends (defined as $\hat{r}_i = \hat{N}_{i+1}/\hat{N}_i$) recorded within the sampling units were highly consistent for each site and period, regardless of whether local abundance estimates were produced separately for both sexes and then summed (intra-class correlation coefficient $r_I = 0.801$, $P = 0.0010$) or derived from the pooled data

Table 1 Performance of different closed population models (see the Data analysis section for their description) within the first two primary periods of the Robust Design

System	Site	Season	Model							
			M_0	M_h	M_b	M_t	M_{bh}	M_{th}	M_{tb}	M_{tbh}
Males	Rio dell'Osio	Spring 2005	0.75	0.83	0.05	1	0	0.31	0.41	0.15
	Rio dell'Osio	Summer–autumn 2005	0.12	0	0.03	1	0.07	0.70	0.26	0.17
	Rio Pilatu	Spring 2005	0.80	0	0.17	0.90	0.13	0.28	0.44	1
	Rio Pilatu	Summer–autumn 2005	0.14	0	0.04	1	0.06	0.68	0.33	0.21
	Weighted mean		0.41	0.24	0.06	0.99	0.06	0.52	0.35	0.29
Females	Rio dell'Osio	Spring 2005	0.46	0.24	0	1	0.24	0.97	0.31	0.56
	Rio dell'Osio	Summer–autumn 2005	0.13	0	0.34	0.58	0.18	0.38	1	0.40
	Rio Pilatu	Spring 2005	0.11	0.90	0.15	1	0	0.28	0.43	0.79
	Rio Pilatu	Summer–autumn 2005	0.13	0	0.36	1	0.18	0.58	0.39	0.39
	Weighted mean		0.19	0.24	0.24	0.83	0.15	0.51	0.62	0.51
All adults	Rio dell'Osio	Spring 2005	0.86	1	0.30	0	0.37	0.74	0.53	0.99
	Rio dell'Osio	Summer–autumn 2005	0.18	0	0.56	0.54	0.14	1	0.83	0.58
	Rio Pilatu	Spring 2005	0.76	0.85	0.05	0.04	0	1	0.40	0.29
	Rio Pilatu	Summer–autumn 2005	0.14	0	0.35	0.63	0.17	0.72	1	0.40
	Weighted mean		0.45	0.40	0.36	0.33	0.18	0.88	0.71	0.59

Values in the table represent relative fit of the models according to the model selection routine of the program CAPTURE, with 1s indicating the best-fitting models, and 0s being the worst ones. Weights used in the calculations of weighted mean fit of the models for each system (i.e. males, females, or entire adult fraction) were the numbers of captured crayfish as presented in Table 2

Table 2 Crayfish population characteristics within primary periods of the Robust Design

Site	Season	Males (M_t)				Females (M_t)				Sex ratio	Males (M_t) + females (M_t)				All adults (M_{th})			
		n	$\hat{N}$	$\hat{p}$	PI	n	$\hat{N}$	$\hat{p}$	PI		n	$\hat{N}$	$\hat{p}$	PI	n	$\hat{N}$	$\hat{p}$	PI
Rio dell'Osio	Spring 2005	110	432 (283–712)	0.25	0.24	46	429 (152–1,430)	0.11	0.65	50:50	156	861 (473–1,724)	0.18	0.35	156	1,085 (614–2,045)	0.14	0.32
	Summer–autumn 2005	132	419 (291–649)	0.32	0.21	99	491 (279–954)	0.20	0.33	46:54	231	910 (633–1,378)	0.25	0.20	231	1,007 (706–1,500)	0.23	0.20
	Spring 2006	184	571 (418–824)	0.32	0.18	50	400 (147–1,320)	0.13	0.64	59:41	234	971 (596–1,735)	0.24	0.28	234	1,134 (592–2,497)	0.21	0.40
	Summer–autumn 2006	385	725 (629–859)	0.53	0.08	239	616 (484–821)	0.39	0.14	54:46	624	1,341 (1166–1,572)	0.47	0.08	624	1,448 (1,179–1,846)	0.43	0.12
	Spring 2007	164	508 (350–803)	0.32	0.22	66	510 (212–1,417)	0.13	0.54	50:50	230	1,018 (617–1,836)	0.23	0.29	230	952 (479–2,330)	0.24	0.45
Rio Pilatu	Spring 2005	55	309 (144–779)	0.18	0.47	56	322 (150–813)	0.17	0.47	49:51	111	631 (353–1,230)	0.18	0.34	111	706 (378–1,440)	0.16	0.36
	Summer–autumn 2005	76	311 (181–607)	0.24	0.33	50	339 (145–931)	0.15	0.53	48:52	126	650 (375–1,227)	0.19	0.32	126	728 (417–1,374)	0.17	0.32
	Spring 2006	131	534 (323–977)	0.25	0.30	74	380 (174–1,015)	0.19	0.50	58:42	205	914 (569–1,585)	0.22	0.27	205	867 (501–1,690)	0.24	0.33
	Summer–autumn 2006	291	663 (541–843)	0.44	0.11	258	770 (589–1,051)	0.34	0.15	46:54	549	1,433 (1,200–1,749)	0.38	0.10	549	1,733 (1,318–2,374)	0.32	0.15
	Spring 2007	107	293 (199–485)	0.37	0.24	39	250 (97–814)	0.16	0.63	54:46	146	543 (322–1,040)	0.27	0.32	146	450 (246–1,078)	0.32	0.42

Parameters presented comprise the number of captured individuals (n), estimated population size ($\hat{N}$, with 95% confidence intervals in parentheses), capture probability $\left(\hat{p} = n/\hat{N}\right)$, precision index defined as standard error of population size scaled to its estimate $\left(PI = SE(\hat{N})/\hat{N}\right)$, and sex ratio based on estimated population sizes (males:females). Estimates for males and females were obtained with the M_t model (Chao 1989), while those for the entire adult fraction with the M_{th} model (Chao et al. 1992)

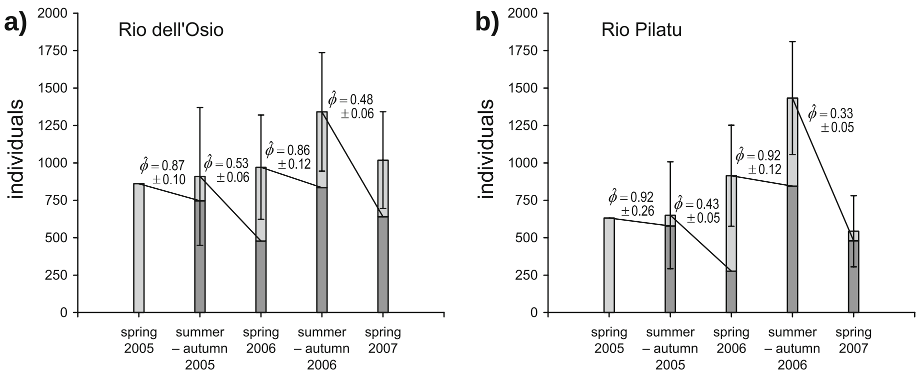


Fig. 3 Population dynamics of the investigated crayfish populations as revealed by the Robust Design. Except for the first season, when all the individuals were new to the survey, population size estimates were partitioned into recruitments of new individuals (light bars; shown with 95% confidence intervals), and fractions surviving from previous seasons (dark bars). Survival estimates (ϕ, presented with SE) refer to the entire adult fraction, while population sizes were estimated separately for males and females and then added up, since there was no difference in survival, but clear difference in capture probabilities between both sexes

($r_I = 0.760$, $P = 0.0026$). They were significantly affected by period, but not by site nor by interaction between site and period (MANOVA: period effect $F_{1,16} = 26.81$, $P < 0.0001$; site effect $F_{1,16} = 0.01$, $P = 0.9298$; interaction $F_{1,16} = 0.23$, $P = 0.6368$; the trends analysed were based on the summed male and female numbers, but the pattern was the same in the case of pooled data). This implies synchrony of population trends between the two sites. Most importantly, trends recorded within the sampling units reflected well those estimated for the entire study sites (Fig. 4). The sums of crayfish numbers estimated for the units exceeded the population size estimates for the entire sites only marginally, if at all, which suggests that there is no major effect of violations to the assumption of population closure within seasons resulting from possible crayfish movements between the units. The above prediction is confirmed by the low mobility that we recorded. During the whole survey only 20.3% of individuals recaptured in Rio dell'Osio and 21.7% in Rio Pilatu moved between the units, and among them less than half did so within a single season.

Discussion

Applicability of mark-recapture in comparison with other crayfish monitoring methods

A detailed review of methods for monitoring freshwater crayfish abundance has been provided by Peay (2003). Electrofishing, despite its efficiency (Rabeni et al. 1997), is highly destructive not only to crayfish investigated, but also to the whole community of co-occurring water organisms. Consequently, it should not be considered for application in monitoring programmes, especially those motivated by conservation purposes. Searching over fixed areas, typically quadrats, has a clear advantage of yielding absolute density estimates. On the other hand, this method is very labour-intensive and thus sampling plots have to be small. This alone does not preclude its use in fairly large-scale studies (e.g. DiStefano et al. 2003). However, it is doubtful whether the estimates obtained for sampling

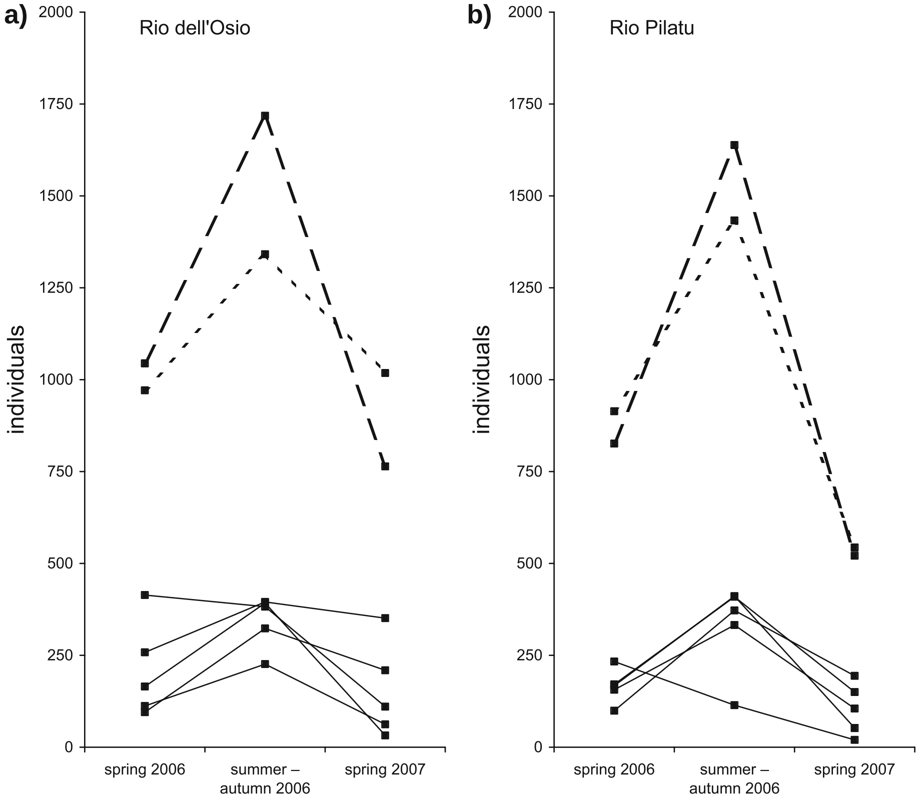


Fig. 4 Changes in crayfish abundance in 2006–2007 according to (i) individual numbers estimated for the five units of each study site (solid lines), (ii) the sums of numbers estimated within units (broken lines), and (iii) population sizes estimated for the entire study sites (dotted lines). In all cases the results presented are the sums of estimates obtained separately for males and females with the M_h model; the estimates obtained for the entire adult fraction with the M_{th} model indicated almost identical patterns

plots can be extrapolated to larger areas, especially that applying the method requires particular hydrological conditions.

Other methods reviewed by Peay (2003), i.e. searching for individuals in their refuges, night viewing, and trapping with baited or unbaited traps, are relatively labour-effective and non-destructive to crayfish populations. Nevertheless, one should remember that they are all relative abundance methods, which do not provide information about actual population size, and their results can serve at best as relative indices of abundance (e.g. Westman et al. 2002). Such indices may be useful for monitoring population trends only as long as the proportion of population sampled on each occasion remains constant. This last assumption is unlikely to be met, because the efficiencies of all the aforementioned methods are highly influenced by various environmental factors (Abrahamsson 1983; Skurdal et al. 1990; Acosta and Perry 2000; Maguire et al. 2002; Peay 2003). In the present study the proportion of individuals captured within each session was highly variable not only between season, which is not surprising because of differences in sampling intensity, but also within seasons, when this intensity was uniform. Hence, the proportion of population sampled may be expected to vary greatly even in the case of a standardised sampling protocol, such as the one proposed by Peay (2003).

We postulate that the mark-recapture approach offers a useful alternative. In its case variation in the proportion of population sampled is no longer a hindrance, because differences in catchability are estimated from the data and accounted for in the derivation of population size estimates. The applicability of mark-recapture depends on ensuring that the assumptions of theoretical models are met. For crayfish this seems relatively easy as compared to many other animals. The above statement is, of course, only true for their adult fraction, but surveys restricted to adults, which define effective population size, are sufficient for monitoring purposes, especially in invertebrates.

The populations of the white-clawed crayfish that we investigated were closed except for wintertime and the month of July. Openness in the former period apparently reflects high mortality during winter due to starvation, predation, and mating stress. The lack of closure in July is more difficult to explain, but it is probably associated with increased predation risk at moulting and (in females) release of juveniles as well as considerable mobility in this period (Gledhill et al. 1993; Reynolds 1998; Maguire et al. 2002). Obviously, the timing of periods of population openness (in particular the summer one) is likely to differ between regions (Reynolds 1998; Holdich 2003), and possibly even more so between species. Nevertheless, we strongly believe that a similar temporal pattern with long periods of population closure occurs in other freshwater crayfish of the temperate zone as well. Consequently, the Robust Design, which is regarded as the most reliable among mark-recapture models as it allows for unequal capture probability (Lancia et al. 1994; Williams et al. 2002), appears quite suitable for investigating freshwater crayfish populations. This model is in fact much more suitable for crayfish than for several other species groups, such as e.g. butterflies or fish, where it has already been tried successfully (Nowicki et al. 2005; Pollock et al. 2007).

Recommendations for optimal sampling plan

Under the Robust Design requirements the optimal survey plan for European freshwater crayfish should comprise two primary sampling periods per year: in spring and in summer–autumn season. The precise timing of these periods should be adjusted to the specific situation, but the months that turned out to be the most appropriate for the white-clawed crayfish populations in the present study, i.e. April–June and August–October respectively, may be used as preliminary settings if no a priori knowledge of the investigated system is available. In the case of logistic and/or financial constraints, a useful option may be to restrict the sampling to one primary period per year, especially if a survey is conducted for monitoring purposes rather than in order to gain an insight into the ecology of the investigated species. Our findings indicate that it would be more reasonable to omit spring sampling in such a situation, because of higher capture probabilities and slightly better chances for favourable weather conditions in the summer-autumn season.

Each primary period should optimally consist of five capture sessions (i.e. secondary periods) separated by two-week intervals. Shorter breaks are not recommended due to the fact that crayfish are very likely to strongly avoid being recaptured within a few days after the initial capture (Robinson et al. 2000; this study). Conducting five capture sessions separated by 2-week intervals within a 3-month period implies a rather densely-packed schedule and may be logistically difficult if several sites are going to be surveyed. Furthermore, bad weather or water conditions may occasionally make it impossible to perform some of the planned sessions. Fortunately, our results from the summer–autumn season of 2006 prove that even only three sessions may be sufficient for achieving precise estimates of crayfish population size provided that capture probabilities are high enough. The main disadvantage of having less than five capture sessions within a primary period is that the most appropriate closed population model cannot be reliably selected (Otis et al. 1978), but this problem is not insurmountable. Firstly, as highlighted by Skalski and Robson (1992) although inappropriate models lead to biased population size estimates, the biases should be consistent as long as the same model is used all the time. This results in unbiased estimates of population trends, which are typically the prime aim of monitoring programmes. Secondly, our findings concerning the closed model selection were fairly straightforward and repeatable, providing clear guidelines for dealing with crayfish populations in this respect. Therefore, unless there is significant evidence that some other model fits the data considerably better we recommend that (i) the model with time variation in capture probabilities (M_t) be applied for male and female fractions analysed separately, whereas (ii) the model with time variation and heterogeneity in capture probabilities (M_{th}) is used in the case of entire adult population analysed jointly. The former option is preferable because of higher precision of the M_t model.

Moreover, as both our survey and many other studies into crayfish population structure conducted for a wide array of species indicated a perfectly balanced sex ratio (Guan and Wiles 1996; Gherardi et al. 2000; Parkyn et al. 2002; Maguire et al. 2002, 2004; Scalici and Gibertini 2005) estimating only male numbers and extrapolating them to total population sizes by multiplying by two is worth considering. Such an approach should not only increase estimate precision, but also reduce the amount of work through refraining from marking females. Sexual dimorphism in crayfish is evident enough (Holdich and Lowery 1988) so that females can be identified and released immediately after capture, which in addition should save them and their offsprings some stress.

Practical constraints in the use of mark-recapture

Practical issues are very important to consider since it is the high labour-intensity of mark-recapture methods that is the usual argument against their use in the monitoring of many species groups. The peculiarity of crayfish monitoring is that virtually all other methods of abundance assessment involve capturing individuals as well (Peay 2003). Hence the effort required for applying mark-recapture, even though substantial, is only slightly higher than for relative abundance methods. According to our experience, two people should be easily able to conduct a simple capture session on a ca. 500-m long stream section within 2 days, and three people could potentially do it in a day. This translates into the annual field effort of 9–12 person-days in the case of the minimal sampling plan (a single primary period with three capture sessions), and 30–40 person-days for the optimal one (two primary periods of five sessions each). Optimistically, it seems that this substantial effort does not have to be reproduced over a large number of sites. Between- and within-site synchrony of crayfish population dynamics suggests that trends recorded at single sites, or even fragments of sites, are likely to be representative for broader areas. Nevertheless, testing the above hypothesis in a large-scale research is highly desirable.

Apart from labour-intensity a major obstacle to a wider use of mark-recapture is the difficulty in marking crayfish (cf. Westman and Savolainen 2002). With traditional marking techniques marks disappear after several moulting events (Guan 1997), although the outcome of the present study proves that the problem is less acute than expected. We discovered that marks on adults last for about a year and a half on average. With such a mark duration their loss should not affect population size estimates obtained with the Robust Design model, but only the parameters describing the turnover of individuals between seasons, leading to the underestimation of survival and the overestimation of recruitment (Arnason and Mills 1981). In other words, even though mark loss makes the investigation of the underlying demographic processes difficult, at least it does not obstruct the assessment of population trends, which meets the needs of most monitoring programmes. In addition, recent developments in marking techniques achieved in marine crayfish (e.g. Frisch and Hobbs 2006) give hope for cheap and long-lasting marks available to be applied in the near future.

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