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Original Citation:

Structure and dynamics of an invasive population of the red swamp crayfish (*Procambarus clarkii*) in a Mediterranean wetland / M. SCALICI; F. GHERARDI. - In: HYDROBIOLOGIA. - ISSN 0018-8158. - STAMPA. - 583:(2007), pp. 309-319. [10.1007/s10750-007-0615-8]

Availability:

This version is available at: 2158/252674 since:

Published version:

DOI: 10.1007/s10750-007-0615-8

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Structure and dynamics of an invasive population of the red swamp crayfish (*Procambarus clarkii*) in a Mediterranean wetland

Massimiliano Scalici · Francesca Gherardi

Received: 11 October 2006 / Revised: 15 January 2007 / Accepted: 22 January 2007 / Published online: 9 March 2007
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Abstract This study analyzes the population structure and dynamics of an invasive population of *Procambarus clarkii* (Girard, 1852) in a Mediterranean wetland using the Bhattacharya's and Von Bertalanffy's analytical methods. The main purpose was to collect biological data necessary for the management of this nuisance species. A maximum of five age classes were identified for both sexes, three of which being composed of a few or zero individuals. Age classes were classified into two subgroups—spring (SpL) and summer (SuL) lines—on the basis of the different hatching periods. Individuals of SpL showed a faster growth rate and reached a larger body size than those belonging to SuL, probably because they were able to grow for a longer time. No between-sex differences were found in growth patterns except for the asymptotic length (L_{∞}), which was reached faster by the females. Other population properties were

analyzed, such as a high mortality rate, a maximum longevity of 4 years, and a low mean life-time (<12 months). Finally, a relatively small fraction of individuals seemed to survive after the first reproductive peak in spring. Consequently, the structure and dynamics of the study population seem to reveal its stability and spreading potential, as a confirmation of the invasiveness of *P. clarkii* in Mediterranean wetlands.

Keywords *Procambarus clarkii* · Red swamp crayfish · Growth patterns · Population dynamics · Wetlands · Italy

Introduction

From its native range – north eastern Mexico and south central USA (Hobbs, 1972), the red swamp crayfish, *Procambarus clarkii* (Girard, 1852), has been successfully introduced, mostly for aquaculture purposes, into several states of the continental USA and into other countries, including Hawaii, western Mexico, Costa Rica, Dominican Republic, Belize, Brazil, Ecuador, Venezuela, Japan, mainland China, Taiwan, the Philippines, Uganda, Kenya, Zambia, Republic of South Africa, and Europe (Huner, 2002). As a result of this massive translocation, today *P. clarkii* is the most cosmopolitan crayfish, being found in the wild in all continents except

Handling editor: P. Viaroli

M. Scalici (✉)
Dipartimento di Biologia, Università degli Studi
"Roma Tre", viale G. Marconi 446, Rome 00146,
Italy
e-mail: scalici@uniroma3.it

F. Gherardi
Dipartimento di Biologia Animale e Genetica "Leo
Pardi", Università degli Studi di Firenze, via Romana
17, Florence 50125, Italy
e-mail: francesca.gherardi@unifi.it

Australia and Antarctica (Huner, 1977; Huner & Avault, 1979).

A long list of studies (reviewed in Gherardi, 2006) has proved the invasive character of this crayfish, where for invasive we mean here a non-indigenous species “which becomes established in natural or semi-natural ecosystems or habitats, is an agent of change, and threatens native biological diversity” (IUCN, 2001). To synthesize, *P. clarkii* has been found to exhibit properties of an *r*-selected species, including early maturity at small body size (Paglianti & Gherardi, 2004), rapid growth rates (Paglianti & Gherardi, 2004), large number of offspring at a given parental size (L. Aquiloni, unpublished data), and relatively short life spans (Lindqvist & Huner, 1999). It is also characterized by a wide plasticity of life cycle (e.g. Gutiérrez-Yurrita et al., 1999) that allows the species to invade diversified environments. Its invasive potential is therefore high, being enhanced by its outstanding dispersal capability (e.g. Gherardi & Barbaresi, 2000). The species is also adapted to extreme environments, such as temporary streams (Gherardi et al., 2002a) and polluted habitats (Gherardi et al., 2000), and is capable to accumulate heavy metals (Gherardi et al., 2002b) and toxins (i.e. microcystin) in its organs and tissues (E. Tricarico et al., unpublished data). Its habit of burrowing (Barbaresi et al., 2004) aids the crayfish to withstand environmental extremes like dehydration, but it may also cause bank collapse and increased water turbidity with the consequent inhibition of primary production (Rodríguez et al., 2003) and structural damages to cultivated fields (Correia & Ferreira, 1995; Huner, 2002). The negative impact of this species on both macrophytes and macro-invertebrates has been experimentally proved (Acquistapace et al., 2006; F. Gherardi & P. Acquistapace, unpublished data). Finally, because of its aggressiveness and predatory ability, it poses threats to the native fauna (e.g. amphibians, Gherardi et al., 2001; Renai & Gherardi, 2004), including endangered indigenous crayfish, such as the white-clawed crayfish, *Austropotamobius pallipes* (Lereboullet, 1858).

Indeed, after the introduction of *P. clarkii* in southern Europe, populations of *A. pallipes* were found to decrease in both number and distribution,

as the result of a combination of several interacting mechanisms, including competitive exclusion and differential susceptibility to predation in the increasing areas of syntopy (Gherardi & Cioni, 2004). These mechanisms add to the well-known dangers posed by *P. clarkii* as a vector of the fungus-like *Aphanomyces astaci* Schikora, 1922 (Diéguez-Urbeondo & Söderhäll, 1993), responsible for the several outbreaks of the so-called crayfish plague recorded in Europe since 1860 (Vogt, 1999).

It is widely acknowledged today (e.g. Gherardi, 2006) that preventing the introduction of this invasive species is “the only environmentally sound approach” (Gollasch & Leppäkoski, 1999). However, after the establishment of *P. clarkii*'s nuisance populations in no-native habitats attempts to eradicate them or, at the best, to mitigate their impact are often felt as a priority within any restoration project (Holdich et al., 1999). Sometimes, eradication at an early stage of invasion may be effective with little or superficial knowledge of the population biology of the invasive species (Simberloff, 2003). But once the opportunity for rapid eradication has been lost, biological details, including population structure and dynamics, seem to be useful in developing procedures for an effective maintenance management.

Based on these premises, the present study aims at understanding some still unknown aspects of the population dynamics of *P. clarkii* by applying the modal progression analysis. Specifically, we used the Bhattacharya's (1967) and Von Bertalanffy's (1938) analytical methods to analyze the status (i.e. structure, growing rate, longevity, and mortality of an established population) of a population of this species inhabiting an inland wetland in Central Italy.

Materials and methods

Study area

The study population inhabited the “Padule di Fucecchio” in Tuscany (43°48'0" N, 10°47'38" E; 13–16 m above sea level), the largest Italian wetland (1,800 ha), in part (230 ha) protected as a Nature Reserve. It consists of a net of channels

connected to the River Arno. Water depth varies among seasons, ranging between 0 and 3 m, and water regime changes from lotic during the rainy period (October–January) to lentic in summer. Water temperature ranges 15–28°C and pH 6–7.

Situated on the boundary between the Mediterranean and continental climates of the Italian peninsula, the Padule hosts plants adapted to cold (*Sphagnum* spp.) and to warm wet climates (e.g. the frogbit, *Hydrocharis morsus-ranae*, and the royal fern, *Osmunda regalis*). It offers refuge for species, now regarded as extremely rare: the southern bladderwort (*Utricularia australis*), the fringed water-lily (*Nymphoides peltata*), and the water floating fern (*Salvinia natans*). Other more abundant floral entities are: *Azzolla caroliniana*, *Carex elata*, *C. riparia*, *Phragmites australis*, *Lemma minor*, *L. gibba*, *Lythrum salicaria*, *Scirpetum maritimum*, and *Sparganium erectum*. It also forms a basic area for the migratory birds; over 190 species of birds can be seen during the year; at least 70 nest here, among which Ardeidae (night heron, little egret, squacco heron, and cattle egret).

Collection of data and analytical procedures

Five sampling sessions were conducted between May and June, 2004 (1: 26–28 May, 2: 3–4 June, 3: 8–11 June, 4: 16–17 June, and 5: 22–24 June) as a part of a more extensive study aimed at quantifying the ecological impact of *P. clarkii* in the Padule di Fucecchio (Gherardi & Lazzara, 2006; F. Gherardi & P. Acquistapace, unpublished data). Sampling was conducted in a 110 × 7 m reach of a channel (about 50–100 cm water height) by intensively capturing crayfish using 12 baited traps. The estimated density of the study population was 14 crayfish/m². Upon capture (for details see Gherardi & Lazzara, 2006), individual crayfish were sexed and their cephalothorax dorsal mid-line (CTL: from the tip of the rostrum to the carapace posterior portion) was measured. Crayfish were not released back into the point of capture but transported in the laboratory for their use in other studies.

Body dimension data were used to generate polymodal frequency distribution histograms then analyzed using the Bhattacharya's method by a routine of the FiSAT (FAO-ICLARM Stock

Assessment Tools) computer program (Gayaniilo et al., 1996). This method can decompose size-frequency distributions into diverse normal components, every component being identified as an age class or cohort. This method is based on the assumption that the observed distribution in size classes results from the overlap of diverse normal distributions. The process converts normal distributions into lines that simplify the procedure, linearization being performed by computing the natural logarithms of frequencies. Intercepts and slopes of the regression lines were used to estimate the parameters of each normal distribution. Given a distribution in size classes, the Bhattacharya's method allows for the iterative computation of regressions lines until to the total decomposition of the overall size-frequency distribution. The program provides values for each Gaussian components, i.e. means, standard deviations, numbers of individuals per size class, regression lines (and the respective R²), and separation index values (S.I.) for each adjacent groups. In particular, S.I. denotes when two adjacent Gaussians can be separated, i.e. S.I. is ≥ 2 (Sparre & Venema, 1996). In a univoltine population, where S.I. values decrease below 2, the last class (composed of a few individuals) is included in the preceding component. At the end of the separation process, the program provides χ^2 -test values.

This modal-progression analysis has been extensively used for the assessment of marine and freshwater fish stocks, and less frequently for other taxa, such as reptiles (Salvidio & Delaguerre, 2003), mussels (Ardizzone et al., 1996), marine crustaceans (Orsi Relini & Relini, 1985; Leonardi & Ardizzone, 1994; Merella et al., 1998), and crayfish (Hogger, 1984; Zekhnini & Chaisemartin, 1991; Fidalgo et al., 2001; Chiesa et al., 2006).

Other aspects of the population dynamics were also analyzed. First, growth rate was assessed by applying the Von Bertalanffy's equation (according to Jamieson & Bourne, 1986):

$$L(t) = L_{\infty} * [1 - \exp(-k*(t - t_0))]$$

where L(t) is the CTL of the individuals at the time t; L_∞ is the mean CTL of the oldest individuals, i.e.

the “asymptotic length” (computed as $L_{\max}/0.95$, where L_{\max} is the maximum recorded length, according to Beverton, 1963; and Pauly, 1981); k is the rate at which L_{∞} is reached, i.e. the “curvature parameter”; t_0 is the “initial condition parameter” and determines when the specimens have a CTL equal to 0. From a biological viewpoint, a CTL equal to 0 is obviously meaningless, being however an important component of the curve (Sparre and Venema 1996).

The curvature parameter (k) was assessed from non-linear regression analyses and the growth performance index (ϕ') was obtained from k and L_{∞} by applying the equation:

$$\phi' = \log k + 2 \log L_{\infty}$$

Second, the mortality index (Z) was obtained from the Powell-Wetherall Plot equation (Powell, 1979; Wetherall, 1986) that computed the asymptotic length and the ratio between the mortality coefficient and the curvature parameter (Z/k) using length-frequency data imported in the FiSAT program. Z is the total mortality, i.e. the sum of natural mortality and the mortality due to fishing. In this study, Z is equal to the natural mortality as the *P. clarkii*'s population living in the study area is not subject to fishing.

Third, the decrease in the population size was assessed from a diagram of species survival obtained by plotting the overall number of individuals obtained after the Bhattacharya's method against time.

Finally, mean life-time ($t_{1/2}$) and longevity estimate (t_{\max}) were computed from the equations (Gayaniilo & Pauly, 1997):

$$t_{1/2} = \{ \sum [n(t) * t] \} / N$$

$$t_{\max} = (3/k) + t_0$$

where $n(t)$ is the number of individuals at the time t and N is the total number of individuals.

Statistical analyses

All the statistical analyses were made using the STATISTICA Statsoft software version 6.0.

Apart from the above-cited linear regression analysis, χ^2 tests were used to analyze frequencies. Data on body dimensions and age classes were first checked for normality and homogeneity of variance using the Kolmogorov-Smirnov test and, when necessary, were $\ln(x + 1)$ transformed to remove heteroscedasticity. They were then compared between sexes and among sessions using two-way ANOVAs. Where significant P -values (<0.05) were obtained by ANOVA, Tukey's post hoc tests were computed to identify which treatments differed from each other. Text and figures provide means \pm SD.

Results

We collected a total of 5,443 individuals, more than 2,000 in the most abundant sampling session 3 ($\chi^2 = 9.71$, $df = 4$, $P < 0.05$; Fig. 1). Of the total sample, 2,834 were females and 2,609 were males, without any significant difference from the expected 1:1 sex ratio ($\chi^2 = 6.12$, $df = 4$, ns). The mean CTL was 29.4 ± 7.7 mm in females (min-max: 12.89–63.87 mm) and 29.36 ± 7.07 mm in males (min-max: 12.28–61.16 mm).

A between-sex comparison of log-transformed CTL data per sampling session did not show any significant difference ($F_{[4,5412]} = 0.44$, $P = 0.61$). On the contrary, CTL differed significantly among sampling sessions in both females ($F_{[4,2639]} = 737.2$, $P = 0.0004$) and males ($F_{[4,2546]} = 656.8$, $P = 0.0013$), the two sexes reaching larger mean sizes in the sampling

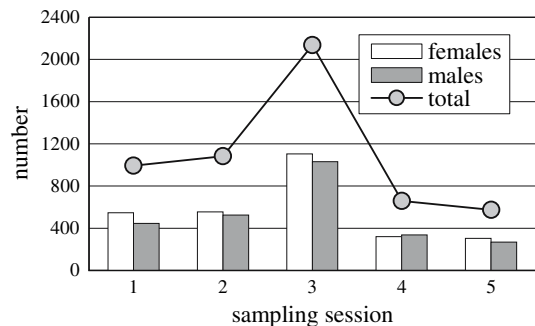


Fig. 1 Number of captured crayfish per sampling session. Sampling sessions correspond to 1: 26–28 May, 2: 3–4 June, 3: 8–11 June, 4: 16–17 June, and 5: 22–24 June

sessions 1, 2, and 3 ($1 = 2 = 3 > 4 = 5$, after Tukey's post hoc test: $P < 0.05$) (Fig. 2). The interaction between the two variables ("sex" and "sampling session") did not show significant differences ($F_{[4,5426]} = 1.73$, $P = 0.14$).

The application of the Bhattacharya's method, combined to information on the reproductive biology of the species in Central Italy (Gherardi et al., 1999a; Chiesa et al., 2006), allowed us to classify the crayfish collected in the five sampling sessions into 2–5 age classes (Table 1). In both sexes, two alternated groups of age classes were also distinguished, the first group denoted here with Arabian numbers and the second with Roman numbers (Fig. 3). These represented two seasonal lines resulting from two different hatching periods, the summer line (SuL) and the spring line (SpL), respectively. This seasonal distinction was based on the previous knowledge of the species' reproductive biology. In fact, we know that in Central Italy reproduction occurs in late spring and early autumn (Gherardi et al., 1999a; Chiesa et al., 2006), with peaks in May/June and August/September (Fig. 4). We found that all the outputs from the Bhattacharya's analysis were not significant (P always >0.05 after χ^2) and the

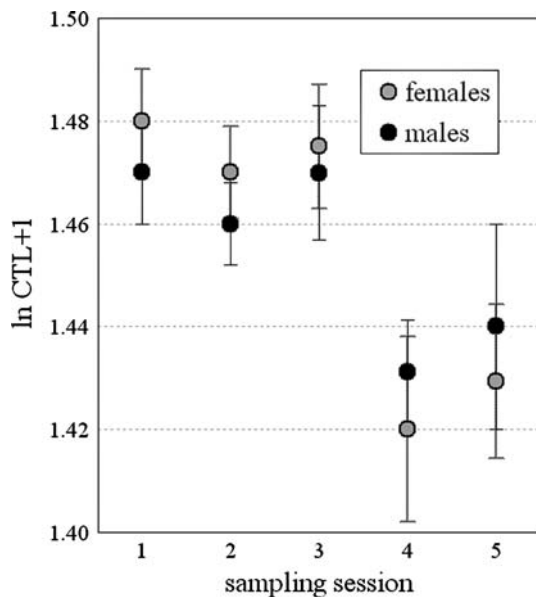


Fig. 2 Mean values (\pm SD) of the $\ln(n+1)$ -transformed data of body size (CTL = cephalothorax dorsal mid-line)

classes apparently belonging to the same year (i.e. I/I and 2/II) had a lower S.I. values than those adjacent but apparently belonging to different years (i.e. I/2 and II/3) (see Table 1).

Growth rates per sex and seasonal line were obtained using the same asymptotic length (L_{∞}) value for both SpL and SuL, and $L(0) = 4.1 \pm 0.4$ mm ($n = 25$) (Fig. 5). Table 2 reports the Von Bertalanffy's parameters (k , L_{∞} , and t_0) and its derivatives per sex and seasonal line, i.e. \emptyset' index, mortality rate (Z), mean lifetime, and longevity (t_{\max}), while survival diagrams are shown in Fig. 6.

Our results are synthesized in Fig. 7, showing the growth pattern of the study population, distinguished for seasonal line, obtained by simulating captures for five consecutive years under the assumption that the population structure remains constant through the year.

Discussion

This study benefited of a large size of the analyzed sample (more than 5,000 crayfish) that was mostly composed of sexually mature crayfish, i.e. individuals with CTL longer than 27.7 mm if female and 20.7 mm if male (Huner, 2002), with a balanced sex ratio (for other data on *P. clarkii*'s sex ratio see: Oluoch, 1990; Anastácio & Marques, 1995; Costa et al., 1996; Gutiérrez-Yurrita et al., 1996; Frutiger et al., 1999; Gherardi et al., 1999b; Pérez-Bote et al., 2000; Fidalgo et al., 2001).

To define age classes in the study population we applied the Bhattacharya's method on size frequencies. This is instrumental in compensating for the obvious absence of more reliable data from skeletal structures, such as scales, vertebrae, and otoliths used, e.g. for teleosts. Doing so, a maximum of five age classes were identified for both sexes in the study population. However, three of these classes (i.e. 2, II, and 3) were composed of a few or zero individuals, whereas the younger age classes were more abundantly represented as the expression of a fast growing population. As revealed by previous studies, *P. clarkii*'s age classes vary in their number across the populations analyzed: Lozano-Guerra &

Table 1 Results of the length-frequency analysis after the application of the Bhatthacharya's method. The periods of the different sampling sessions (SS) are indicated in Fig. 1.

S.I. indicates separation index values; R^2 is the statistical output of the FiSAT computer program

SS	class	females						males					
		mean	SD	n	%	S.I.	R^2	mean	SD	n	%	S.I.	R^2
1	1	24.62	3.97	292	47.9	–	0.947	24.39	3.94	249	53.5	–	0.951
	I	35.75	2.95	221	36.2	3.22	0.811	34.01	3.46	146	31.4	2.6	0.814
	2	46.99	2.45	45	7.4	4.16	0.774	44.01	4.29	39	8.4	3.58	0.839
II	1	54.59	2.11	45	7.4	3.33	0.701	50.58	1.48	18	3.9	2.28	0.714
	3	59.64	2.36	7	1.1	2.26	0.645	55.42	1.69	13	2.8	3.05	0.684
	I	24.02	3.55	335	62.4	–	0.991	24.7	3.96	310	52.5	–	0.931
I	I	33.43	3.37	164	30.5	2.72	0.759	35.78	2.38	246	41.6	3.5	0.803
	2	47.65	3.21	17	3.2	4.32	0.822	45.8	1.85	23	3.9	4.74	0.645
	II	52.77	1.48	18	3.4	2.42	0.615	51.82	1.13	12	2.0	3.04	0.584
2	3	59	1.15	3	0.6	4.74	0.512	–	–	–	–	–	–
	1	26.03	4.07	784	64.2	–	0.845	26.81	4.55	791	67.0	–	0.943
	I	36.2	2.66	385	31.5	3.02	0.712	35.72	2.53	280	23.7	2.52	0.797
2	2	47.46	2.68	45	3.7	4.22	0.707	43.36	2.33	81	6.9	3.74	0.845
	II	53.7	1.59	7	0.6	2.92	0.585	50.6	2.79	20	1.7	2.83	0.612
	3	–	–	–	–	–	–	55	2.65	8	0.7	2.62	0.557
II	1	24.62	5.12	260	67.5	–	0.872	24.81	3.76	262	72.2	–	0.899
	I	34.1	3.46	125	32.5	2.21	0.699	35.73	3.06	97	26.7	3.2	0.745
	2	–	–	–	–	–	–	45	2.69	4	1.1	3.9	0.613
3	1	26.71	3.75	247	75.1	–	0.913	25.12	3.15	172	57.0	–	0.908
	I	35.17	1.88	80	24.3	3.01	0.816	33.35	2.59	128	42.4	2.87	0.742
	2	43	1.74	2	0.6	4.33	0.649	43	2.24	2	0.7	4	0.703

Escamilla-Niño (1995) and Chiesa et al. (2006) distinguished three age classes, while, according to Huner (2002) and Frutiger et al. (1999), *P. clarkii* may live up to 4 and 5 years, respectively.

We classified the observed age classes into two subgroups, i.e. the spring (SpL) and the summer (SuL) lines. These may correspond to two mating phases, as also found by Cano & Ocete in Spain (1997), so that we classified SpL and SuL on the basis of the hatching period, i.e. spring and summer, respectively. This implies a shift of about three months between them.

The distinction we made into two seasonal lines seems to be confirmed by the analysis of S.I. values. In fact, to separate two adjacent age classes, S.I. should be ≥ 2 and should decrease as the analysis proceeds. On the contrary, this condition was not met in the cases of those classes that apparently belonged to the same year but to a different seasonal line.

Two growth functions were described for each seasonal line where SpL showed a faster growth rate than SuL (as shown from the curvature

parameters and growth performance indices), probably because the crayfish that hatched in spring have a longer favorable time (the summer) available to grow. Indeed, individuals of the SuL age classes show significantly smaller body sizes than SpL ones.

When compared with other studies on other populations of the same species, we obtained different values for some of the Von Bertalanffy's growth parameters. Specifically, the asymptotic length computed in this study was higher than the one obtained by Anastácio & Marques (1995), Fidalgo et al., (2001), and Chiesa et al., (2006), whereas the curvature parameter (close to 0.7 in both sexes) did not seem to differ, notwithstanding the different method (ELEFAN) adopted by some of the previous studies (e.g. Anastácio & Marques 1995). Conversely, the growth rate of 0.23 obtained by Fidalgo et al. (2001) seems to be low for an *r*-selected species such as *P. clarkii*, whereas the growth rate of 1 obtained by Dörr et al. (2006) in Lake Trasimeno is particularly high, notwithstanding the different ecological

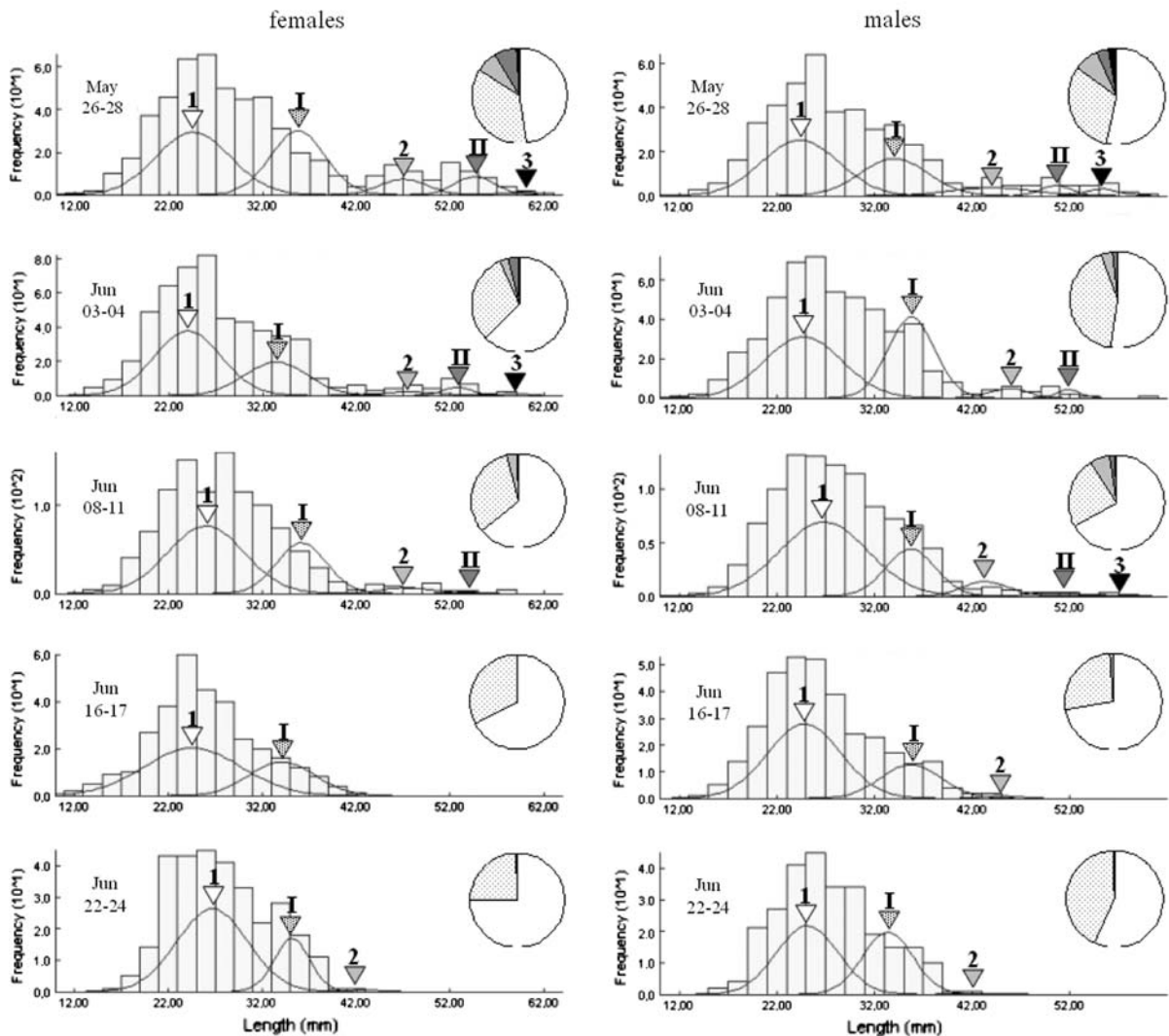


Fig. 3 Gaussian components per age class obtained after the application of the Bhattacharya's method for each sampling session in females and males. Pies show the frequency distribution of individuals per age class

conditions encountered by the species in that study area.

No appreciable between-sex differences were found in growth patterns except for the asymptotic length, males approaching the L_{∞} more slowly than females. This result is difficult to explain. Indeed, females should be subject to a strong selective pressure to quickly reach a large size, because clutch size (i.e. fecundity) significantly increases with body size (and larger females are also preferred by reproductive males;

L. Aquiloni & F. Gherardi, unpublished data). But a quick acquisition of a large size might be also favored in males; in fact, their likelihood to win intrasexual contests for the access of females is size-dependent (L. Aquiloni & F. Gherardi, unpublished data).

An additional property that we found in the study population is its elevated mortality rate. The maximum longevity we computed was 4 years, as also suggested by other authors (Huner, 2002). The mean life-time did not

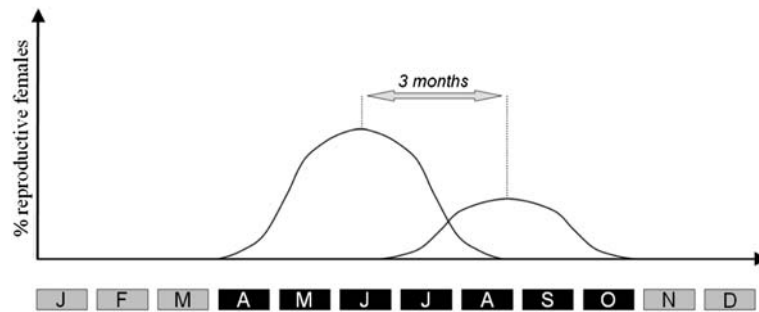


Fig. 4 Timing of reproduction in *P. clarkii*'s populations in Central Italy (after Gherardi et al., 1999a and Chiesa et al., 2006)

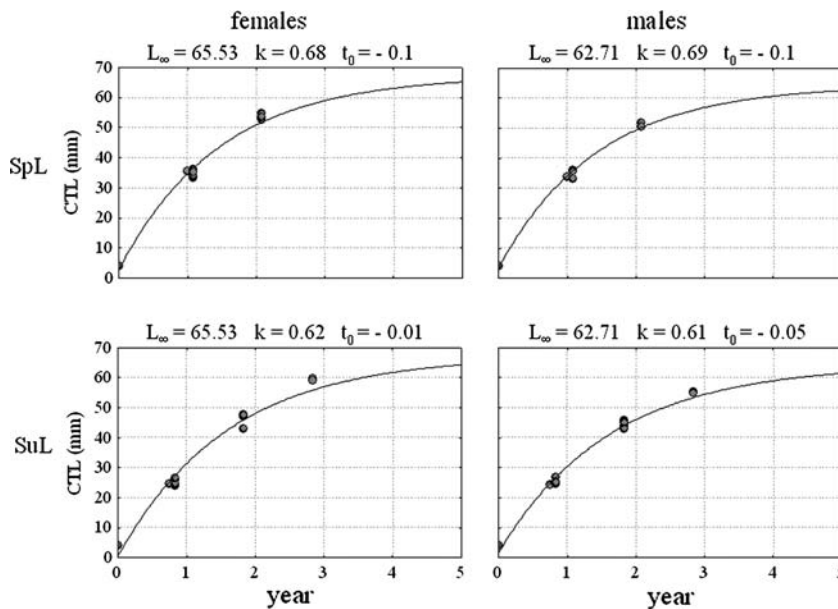


Fig. 5 Growth functions distinguished per sex and seasonal line (SpL = spring line, SuL = summer line)

Table 2 Growth performance index (ϕ'), longevity (t_{\max}), mean life-time ($t_{1/2}$), and total mortality rate (Z) of *P. clarkii*'s individuals distinguished per sex and seasonal line (SpL = spring line, SuL = summer line)

		ϕ'	t_{\max} (year)	$t_{1/2}$ (year)	Z
females	SpL	3.47	4.31	10.5	4.71
	SuL	3.43	4.83	10.9	5.16
males	SpL	3.43	4.25	10.6	2.99
	SuL	3.38	4.87	11.2	3.38

overreach 12 months, which is a lower time than the limit of 18 months proposed by Huner (2002). Finally, a relatively small fraction of individuals seemed to survive after the first reproductive peak in spring.

To conclude, in all their details the structure and dynamics of the study population of *P. clarkii* seem to reveal stability and spreading potential (e.g. Odum, 1983), both characteristics that confirm the invasiveness of this species.

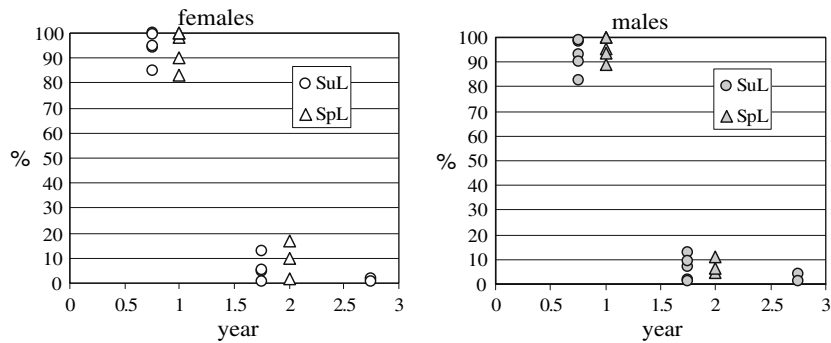


Fig. 6 Frequency (in percentage) of females and males in the two seasonal lines. For abbreviations see Fig. 4

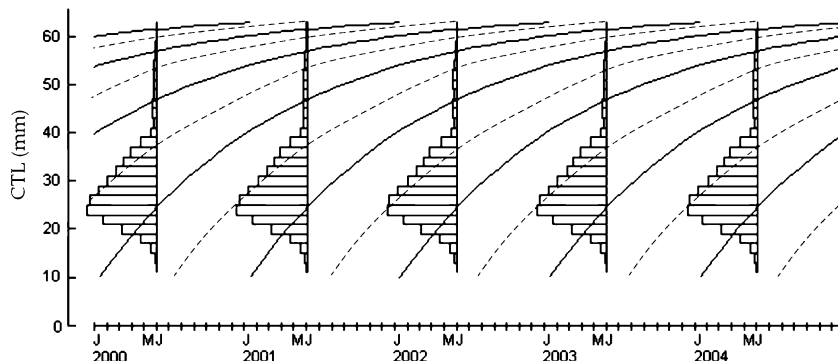


Fig. 7 Simulation of growth patterns in the study population (SpL = dotted line; SuL = continuous line)

Acknowledgements This study was made possible by a grant from “Provincia di Pistoia” to F.G. We thank Patrizia Acquistapace and Andrea Cacchiani for their precious help in the field work and the friends of the “Centro di Ricerca, Documentazione e Promozione del Padule di Fucecchio” for their constant support and encouragement.

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