

Decadal demographic trends of a long-lived temperate encrusting sponge

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ABSTRACT: Demographic data play a central role in determining the overall dynamics of species and forecasting the effects of global change. We examined a decadal pattern of population dynamics and its underlying mechanisms in a population of the encrusting sponge *Crambe crambe*. A photographic series monitored yearly for 14 yr (1993 to 2007) was analyzed. A total of 133 genets and 157 ramets were individually identified and followed over 14 yr to record their fates: survivorship, partial mortality, recruitment via larvae, asexual events (fission and fusion), and growth. The number of genets varied little over time; their survival was high and differed significantly with size class (52, 82, and 100 % for size classes 0–250, 250–700, and >700 mm², respectively), while recruitment via larvae was very low. Overall, the population was characterized by the inputs and outputs of asexual ramets. Patterns of partial mortality were (1) significantly related to size and (2) did not differ significantly among years, and (3) no patch >500 mm² suffered any type of mortality. We give the first evidence that net growth over more than a decade was close to zero for the larger specimens, while the smallest specimens exhibited the highest growth rates, quadrupling in size over 14 yr. Low mortality combined with the slow growth of large specimens indicates that *C. crambe* may live for several decades. This study provides rigorous baseline information necessary to uncover general patterns in the demography of marine sessile species and better predict the long-term fate of populations.

KEY WORDS: *Crambe crambe* · Life history · Long-term studies · Modular animals · Population dynamics

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INTRODUCTION

The long-term survival of sessile species, including plants and marine sessile organisms, is determined by their vital rates, e.g. reproduction, recruitment, growth, and mortality (Hall & Hughes 1996). These processes can be difficult to estimate as they may vary significantly over space and time (Connell et al. 1997, Adondakis & Venable 2004, Miriti 2007). Populations of slow-growing, long-lived sessile species do not often undergo marked declines and even populations with little or no regeneration capacity are projected to survive for decades or even centuries (Stephenson 1994,

Linares et al. 2007, Miriti 2007). In particular, when rates of change are very slow or when crucial events occur rarely (e.g. severe disturbances or exceptional recruitment), detecting the effect of these on populations requires long-term records (Connell et al. 1997, Rees et al. 2001). Therefore, detailed long-term studies following the fate of species may be the only reliable way to uncover general patterns in the demography of sessile species and better predict the long-term fate of populations. In contrast to terrestrial plant systems, such data are scarce for marine benthic habitats and there is little empirical work on the population dynamics of long-lived marine sessile species.

Clonal benthic invertebrates are composed of repeated 'modules' (polyps or zooids), which are derived asexually by vegetative growth. Sponges are not clonal organisms from a morphological point of view because of the lack of identifiable modules. However, they are ecologically equivalent to clonal groups since they share with them the potential for indeterminate growth, both fusion and fission, and the capacity to recover from partial mortality (Jackson 1979, Hughes 1989, Pronzato & Manconi 1995). Generally, life history attributes of clonal animals (e.g. reproduction, competition, recovery, and survival) have been observed to be highly related to colony size (Hughes & Jackson 1985). In clonal species, the genet is considered to be the sum of all the genetically identical modules coming from the same zygote, whereas a ramet is a physiologically independent part of a genet (*sensu* Harper 1977). These features make the demographic analyses of clonal species difficult. However, accurate demography for both genets and ramets is necessary to understand the population dynamics and life history evolution of these species. Ramet demography gives a perspective on the long-term persistence of a population, whereas genet demography provides basic information about changes in the genetic population structure and evolutionary processes (Silander 1985, Tanner 2001). Moreover, patterns of ramets and genets may differ considerably within a given population (Eriksson 1993).

In this study, we present the first long-term demographic analysis of genets and ramets with high-temporal resolution on a long-lived sponge. Studies assessing population dynamics of sponges have shown long lifespans, slow growth, and low recruitment (Dayton 1979, Ayling 1983, Pansini & Pronzato 1990, Pronzato & Manconi 1995). The existence of large individuals also suggests longevity (Sarà 1970, Ayling 1983, Pansini & Pronzato 1990), estimated to reach several decades or even centuries (Dayton 1979, Leys & Lauzon 1998). As they persist for such long time periods, sponges are thought to greatly influence other benthic community members (Bergquist 1978, Wulff 2006). Therefore, a detailed understanding of the life cycle of such species and the long-term temporal variation in their vital rates is crucial, not only to comprehend the mechanisms underlying their dynamics, but also for the effective management and conservation of ecosystems.

We investigate the population dynamics of the sponge *Crambe crambe* over 14 yr on a north-facing sublittoral wall in the NW Mediterranean Sea. For this purpose, a photographic series of permanent plots monitored yearly (1993 to 2007) was analyzed. Different parameters of demographic processes (population structure, survivorship, recruitment, partial and whole

mortality, fission and fusion events, and growth) were recorded. The results of the present study offer the first detailed, long-term data providing new insights into the life history traits of this species. This work attempts to contribute to the general knowledge of marine communities characterized by long-lived species.

MATERIALS AND METHODS

Study species. *Crambe crambe* (Schmidt, 1862) is a Poecilosclerid red-orange encrusting sponge, which can reach surface areas of 0.5 m². It is one of the characteristic species of all the littoral communities in the western Mediterranean (Boury-Esnault 1971, Uriz et al. 1992, 1998), but is also present in the Aegean and Levantine seas in the eastern Mediterranean (Voultsiadou 2005), the Adriatic Sea (Schmidt 1862), and on the Atlantic coast of Portugal and the Canary Islands (Duran et al. 2004). This sponge inhabits both photophilic and sciaphilous habitats with a depth range from 1 to 60 m (Uriz et al. 1992). *C. crambe* is one of the most well-known sponges, through its biological and ecological characteristics (Turon et al. 1996, Becerro et al. 1997, Uriz et al. 1998).

Crambe crambe is a hermaphrodite and viviparous species, releasing lecithotrophic larvae from the end of July to the end of August (Uriz et al. 1998). Asexual processes (fission and fusion) have been regularly observed (Turon et al. 1998, Garrabou & Zabala 2001). Two previous studies where data was collected over 2 yr show that this sponge grows slowly (Turon et al. 1998, Garrabou & Zabala 2001).

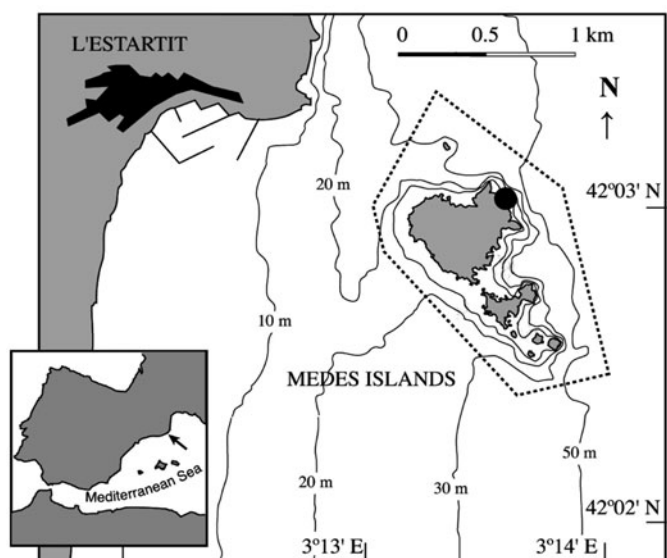


Fig 1. Map of the study site 'Pota de Llop' in the Medes Island Marine Protected Area (42° 3' N, 3° 13' E, NE Spain), NW Mediterranean Sea

Study area. A population of *Crambe crambe* was studied at one locality in the NW Mediterranean Sea: La Pota de Llop, in the Medes Island Marine Protected Area (42° 3' N, 3° 13' E, NE Spain) (Fig. 1). The study population is found on a north-facing sublittoral wall and is distributed in a shaded habitat, between 12 and 16 m depth. The study site is characterized by the co-dominance of perennial animals (mainly encrusting sponges, cnidarians, bryozoans and compound ascidians) and encrusting coralline algal species. The rock surface is partially covered by a canopy of seasonal fleshy algae and soft hydrozoans and bryozoans during the spring and summer months (for detailed information see Gili & Ros 1985, Garrabou et al. 2002).

Study design and photo sampling. Thirty-two permanent frames were monitored photographically over a 14 yr period (1993 to 2007) at intervals ranging from ~4 mo to annually. These frames were installed within a 60 m² sampling area with a depth range of 12 to 16 m. The photo frames were treated as statistical replicates in a repeated-measures design testing for differences among time. The pictures were taken with a Nikonos V camera (Nikon) equipped with UW 28 mm and close-up lenses from 1993 to 2005. From 2006 onward, a Nikon D70S digital SLR camera fitted with a Nikkor 20 mm DX lens (3000 × 2000 pixels resolution) in a Subal D70S housing was used. Lighting was achieved by 2 electronic strobes fitted with diffusers (Nikonos SB 105 and various Sea & Sea strobes). The permanent frames were marked with 2 plastic clips attached to the substrate (50 to 70 cm apart). The clips together with a PVC custom-built fixed the camera ensuring that photographs were obtained in the same position and focal distance (Garrabou & Zabala 2001). Each 35 mm frame recorded an area of 310 cm² and each digital frame recorded an area of 575 cm², respectively. We restricted our analyses to the 310 cm² initial area despite the larger area covered by the digital camera to ensure the same measurements over time. For the present study, we selected the photographs taken yearly in winter (when available), as this season showed the lowest vegetation coverage and the specimens of *Crambe crambe* were not hidden. A total of 480 photographs were analyzed and are available online (<http://doi.pangea.de>) (see Appendix 1, (available as an electronic supplement at www.int-res.com/articles/suppl/m375p113_app.pdf, for further details).

Demographic analysis. Demographic parameters were quantified using digital images, which, for the color slides, were obtained by scanning the originals (300 dpi, 1632 × 1080 pixels resolution). All specimens analyzed were individually labeled in Adobe Photoshop 7.0. We defined a specimen (= genet) as any physically separate patch of sponge growing independently of its neighbors. Before any measurement was

performed, we first observed each specimen and identified any fission and fusion events throughout the 14 yr study period. All patches originating from any asexual event were scored as different fragments (= ramets) of the same specimen. Therefore, a specimen could have 1 or more fragments depending on the number of fission and fusion events. Finally, after tracking the life history of each specimen and their ramets throughout the study period, they were labeled and further analyzed. A total of 133 genets and 157 ramets present at the start of the study (1993) were individually identified and followed throughout 14 yr to record their fates: survivorship, partial mortality, recruitment via larvae, asexual events (fission and fusion), and growth.

Population size distribution. The population structure of *Crambe crambe* was determined by quantifying ramet abundance and size-frequency distribution at the start (1993) and end (2007) of the study. These patches were assigned to 1 of 11 size classes (0–100, 100–200, 200–300, ... and >1000 mm²) in order to provide a detailed view of size distribution.

Partial and whole mortality. Population dynamics were quantified by recording whether the specimens present in 1993 were alive or dead in 2007, and if alive, their fate. We considered whole mortality to occur in the year when the entire specimen had completely disappeared from the analyzed plot. In addition to whole mortality of specimens, events of partial mortality (the death of a ramet) were recorded every year, including the area of the dead ramet. In order to observe the effects of size on survivorship, the specimens were grouped into 3 size classes: I (0–250 mm²), II (250–700 mm²), and III (>700 mm²). These size classes were selected to encompass the size range encountered in the study site and to increase the number of measurements per group.

Fusion and fission events. A fission event was considered to have occurred when a single specimen fragmented into physically separate patches; a fusion event occurred when separated patches joined together, appearing as a single specimen for 2 consecutive years. For example, if a specimen split into 3 fragments or 3 fragments fused, 2 fission or fusion events would be recorded.

Recruitment. We estimated larval recruitment annually by monitoring the appearance of new specimens that were clearly not created by fission within the established permanent frames. Larval recruits were not easily identified from photographic frames, and to avoid confusion with small and orange 'points' of a different nature, we scored new recruits via larvae if they reached a minimal size (~1 mm²) and survived >1 yr, giving a conservative estimation of *Crambe crambe* recruitment.

Growth rates. Growth of specimens was estimated as any change (gain or loss) in planar surface area from 1993 to 2007. Individual specimen areas as well as the summed areas of different ramets (resulting from fission and fusion processes) from the same specimen were recorded each year to give a single value per date. Growth measurements were performed only with the specimens that were alive during the entire study period. A total of 47 specimens were analyzed and classified at the beginning of the study into the 3 size classes: I (N = 20), II (N = 15), and III (N = 12). Annual growth rate was calculated as:

$$[A_i - A_{(i-1)}] / A_{i-1} \quad (1)$$

where A_i and $A_{(i-1)}$ are the area values at Year i and the previous Year ($i - 1$), respectively. The outlines of the monitored patches were traced and their surface values were calculated using the program CPCe 3.4 (Kohler & Gill 2006).

Statistics. The population structure of *Crambe crambe* at the beginning and end of the study was compared using the nonparametric Kolmogorov-Smirnov 2-sample test. Survival of the 133 specimens was analyzed using 'life tables' statistics (Fox 1993). Significant differences among size classes were estimated by 'Comparing Survival in Multiple Groups'. After that, comparisons between each pair of size classes were completed using the Gehan-Wilcoxon test. Chi-square contingency tables were used to compare frequency of partial and whole mortality as well as the frequency of fission and fusion events among years. This statistical test is unreliable with small expected values (<5), so 2×2 frequency tables were used to compare frequencies (partial and whole mortality, fission and fusion) among size classes. Thus, the 3 size classes were pooled into 2 size categories: small (size class I) and large (size classes II and III).

In order to calculate changes on growth over time, a permutation method was used to test for differences through time and size classes. This test, based on Manly (1991), consisted of a 2-stage data permutation: first, individuals were randomly reassigned to the 3 size classes, then readings for each specimen were randomly rearranged among observation times. This permutation test was considered an adequate analysis since growth data did not comply with the circularity and homogeneity of variance-covariance matrix assumptions. The sum of squares associated with each factor and their interactions were then calculated as in standard ANOVA analysis. This procedure was repeated 4999 times (plus the observed one) to obtain the frequency distribution of the sum of squares of each factor and its interactions. The val-

ues of the statistics for the observed data were compared in these distributions. An effect was judged significant when the observed sum of squares was exceeded by <5% of the corresponding values in the randomization series. If the permutation method denoted significant differences in growth, further analyses testing differences among size classes were performed. In these post hoc analyses, Bonferroni's correction was applied as different comparisons were calculated against the same distribution. Finally, a t -test for dependent variables was used to analyze differences in growth relative to size in 1993 and 2007, among the different size classes. Tests were computed using the program STATISTICA (version 6.0, StatSoft) and permutation tests were performed in a modified version of the Turbo Pascal program (Turon et al. 1998).

RESULTS

Population structure

Analyses of the permanent frames identified 133 genets and 157 ramets of *Crambe crambe* that could be tracked over 14 yr. Most ramets (75 and 80%) were <300 mm² and few (7 and 15%) were >700 mm² for both years 1993 and 2007, respectively. Additionally, 9 of the patches tracked were >1000 mm² in area in 2007. The frequency distribution of *C. crambe* did not vary considerably between 1993 and 2007 (Kolmogorov-Smirnov test, $p = 0.10$) (Fig. 2). Mean \pm SE patch

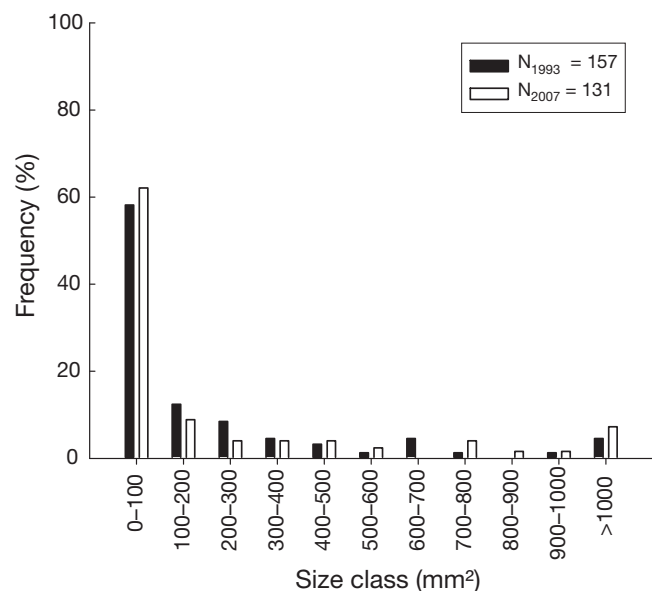


Fig. 2. *Crambe crambe*. Size-frequency distribution of ramets at the beginning (1993) and end (2007) of the study

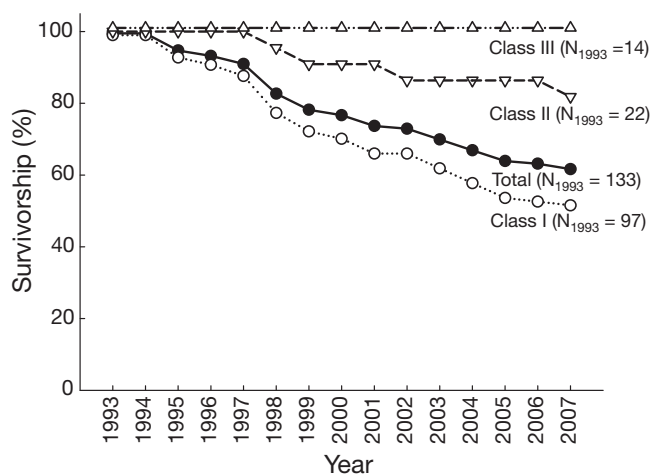


Fig. 3. *Crambe crambe*. Survivorship over 14 yr at Pota de Llop. Data are for the whole population (black dots) and for 3 size classes (open symbols) as a function of their size in 1993. Size classes: I (0–250 mm²), II (250–700 mm²), III (>700 mm²)

size ranged from 240 ± 479 mm² in 1993 to 328 ± 800 mm² in 2007.

Survivorship

After 14 yr, 62% of the total population of *Crambe crambe* was still alive (82 out of 133 specimens survived) (Fig. 3). The lowest survivorship value (52%) was recorded for specimens in size class I and differed significantly from the other 2 size classes (Gehan-Wilcoxon test, $p < 0.001$ for both comparisons between each pair of size classes). Survivorship between size classes II and III was statistically indistinguishable over the study period ($p > 0.05$). No specimen (14) of the larger size class (>700 mm²) died during the study period (Fig. 3).

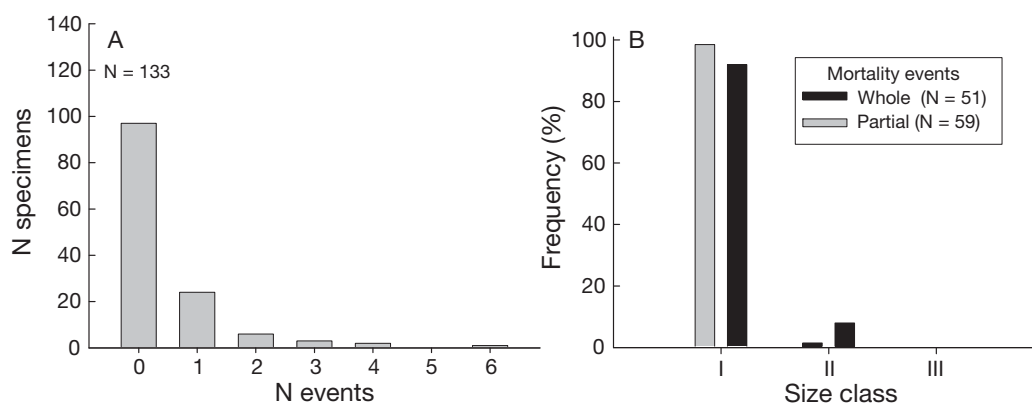


Fig. 4. *Crambe crambe*. (A) Total number of partial mortality events suffered by each specimen on the whole population under study. (B) Effect of size on partial and whole mortality. Size classes are defined in Fig. 2

Partial and whole mortality

During the study period, 59 partial mortality events were recorded for 36 specimens with >60% of them only suffering 1 event (Fig. 4A). The highest partial mortality value (6) was recorded for a specimen of size class III in 1993 (723 mm²) but the dead fragments were of small sizes (mean: 26.36 ± 9.3 mm²) (Fig. 4B). Patterns of partial and whole mortality were significantly related to size (2×2 frequency tables, $\chi^2 = 35.6$, $df = 1$, $p < 0.0001$ for partial and $\chi^2 = 29.7$, $df = 1$, $p < 0.0001$ for whole mortality). Small patches suffered both partial (mean area: 33.1 ± 6.7 mm²) and whole mortality (mean area: 76.1 ± 14.6 mm²) (Fig. 3B). Interestingly, no patch >500 mm² suffered any type of mortality over 14 yr. Overall, partial and whole mortality were low (annual mean: 3.9 ± 0.75 and 4 ± 0.76 , respectively) and did not differ significantly among years (Appendix 2, available at www.int-res.com/articles/suppl/m375p113_app.pdf) ($\chi^2 = 22.9$, $df = 13$, $p > 0.05$ for partial and $\chi^2 = 27.3$, $df = 13$, $p > 0.05$ for whole mortality).

Fission and fusion

Table 1 shows the descriptive statistics of the asexual events recorded over 14 yr. A total of 53 monitored specimens underwent 118 fissions, while 25 specimens suffered 46 fusions (Table 1, Fig. 5). Approximately 60% of specimens were involved in only 1 event (Fig. 5). The maximum number of fission or fusion events observed for a single specimen during the 14 yr was 7 fissions and 5 fusions, which occurred in specimens from the second and third size classes, respectively (Table 1, Fig. 5). Mean annual values for these asexual events were 8.4 ± 0.9 for fission and 3.3 ± 0.5 for fusion (Table 1). There was not a trend in asexual

Table 1. *Crambe crambe*. (A) Fission and (B) fusion events for each size class (includes data calculated yearly and for all years combined). The mean annual probability of fission and fusion were determined by dividing the yearly number of specimens suffering the event by the total yearly population size. Patches were classified based on the 3 size classes before the asexual event. Numbers in parentheses are minimum and maximum values

	Size I	Size II	Size III	All sizes
(A) Fission				
Mean \pm SE no. fissions specimen ⁻¹ yr ⁻¹	0.11 \pm 0.02 (0–3)	0.17 \pm 0.04 (0–4)	0.25 \pm 0.04 (0–3)	0.16 \pm 0.02 (0–4)
Mean \pm SE annual fissions specimen ⁻¹	1.15 \pm 0.08 (1–3)	1.41 \pm 0.16 (1–4)	1.27 \pm 0.09 (1–3)	1.27 \pm 0.06 (1–4)
Mean \pm SE no. fissions yr ⁻¹	2.7 \pm 0.7 (0–7)	2.7 \pm 0.7 (0–9)	3.0 \pm 0.5 (1–7)	8.4 \pm 0.9 (4–18)
Mean \pm SE no. fissions specimen ⁻¹ in 14 yr	1.5 \pm 0.2 (1–4)	2.4 \pm 0.4 (1–6)	3.5 \pm 0.6 (1–7)	2.2 \pm 0.2 (1–7)
Mean \pm SE size before fission (mm ²)	113.8 \pm 12.5 (5–246)	445.9 \pm 26.7 (255.5–700)	2591.4 \pm 688.9 (700–9904.3)	–
Mean \pm SE size after fission (mm ²)	40.9 \pm 8.4 (0.5–263.5)	168.8 \pm 30.1 (1.62–566.1)	1224.8 \pm 555.8 (9.9–10419.8)	–
Total no. specimens suffered fission in 14 yr	25	16	12	53
No. fragments formed by fission	38	38	42	118
% of 1993 population	25.8	72.7	85.7	39.9
Mean \pm SE annual probability of fission	0.04 \pm 0.01 (0.00–0.12)	0.14 \pm 0.03 (0.00–0.41)	0.21 \pm 0.03 (0.07–0.50)	0.08 \pm 0.008 (0.03–0.14)
(B) Fusion				
Mean \pm SE no. fusions specimen ⁻¹ yr ⁻¹	0.12 \pm 0.03 (0–2)	0.15 \pm 0.05 (0–3)	0.13 \pm 0.04 (0–2)	0.13 \pm 0.02 (0–3)
Mean \pm SE annual fusions specimen ⁻¹	1.06 \pm 0.06 (1–2)	1.25 \pm 0.18 (1–3)	1.18 \pm 0.12 (1–2)	1.15 \pm 0.07 (1–3)
Mean \pm SE no. fusions yr ⁻¹	1.3 \pm 0.2 (0–3)	1.1 \pm 0.4 (0–4)	0.9 \pm 0.3 (0–3)	3.29 \pm 0.52 (1–7)
Mean \pm SE no. fusions specimen ⁻¹ in 14 yr	1.6 \pm 0.2 (1–3)	2.1 \pm 0.6 (1–5)	1.9 \pm 0.6 (1–5)	1.84 \pm 0.33 (1–5)
Mean \pm SE size before fusion (mm ²)	71.4 \pm 9.1 (0.7–227.7)	474.5 \pm 37.4 (266.9–749.4)	4282.8 \pm 1829.2 (1492.5–10419.8)	–
Mean \pm SE size after fusion (mm ²)	870.4 \pm 367.5 (6.1–10405.5)	735.2 \pm 82.1 (394.2–1394.4)	4408.1 \pm 1775.4 (1449.4–10405.5)	–
Total no. specimens suffered fusion in 14 yr	11	7	7	25
No. fragments fused	18	15	13	46
% of 1993 population	11.3	31.8	50	18.80
Mean \pm SE annual probability of fusion	0.02 \pm 0.005 (0.00–0.06)	0.05 \pm 0.02 (0.00–0.21)	0.07 \pm 0.02 (0.00–0.21)	0.03 \pm 0.005 (0.01–0.08)

events among years ($\chi^2 = 21.8$, $df = 13$, $p > 0.05$ for fission and $\chi^2 = 16.9$, $df = 13$, $p > 0.05$ for fusion) (Fig. 5). Overall, the mean annual probability of fission (0.04 ± 0.01) and fusion (0.02 ± 0.03) was also relatively low. However, the relationship between size and the annual probability fission was significant (2×2 frequency tables, $\chi^2 = 29.2$, $df = 1$, $p < 0.0001$) (Table 1). This reflects specimens of the largest size class being almost 4 times more likely to undergo fission than the smallest specimens. Size of fragments before and after fission and fusion is presented in Table 1.

Recruitment

A total of 14 recruits were observed in a surface of ~ 1 m² during each year over the study period. Larval recruitment was low, oscillating between 0 (1995, 2001, 2003, 2004, and 2007) and 3 (2006). The mean value of larval recruitment was 0.9 ± 0.26 recruits yr⁻¹. Survivorship among the recruits was almost 86% and 1 recruit survived >10 yr and was still alive in 2007. The mean value of size in the first year of observation was 5.4 ± 1.6 mm².

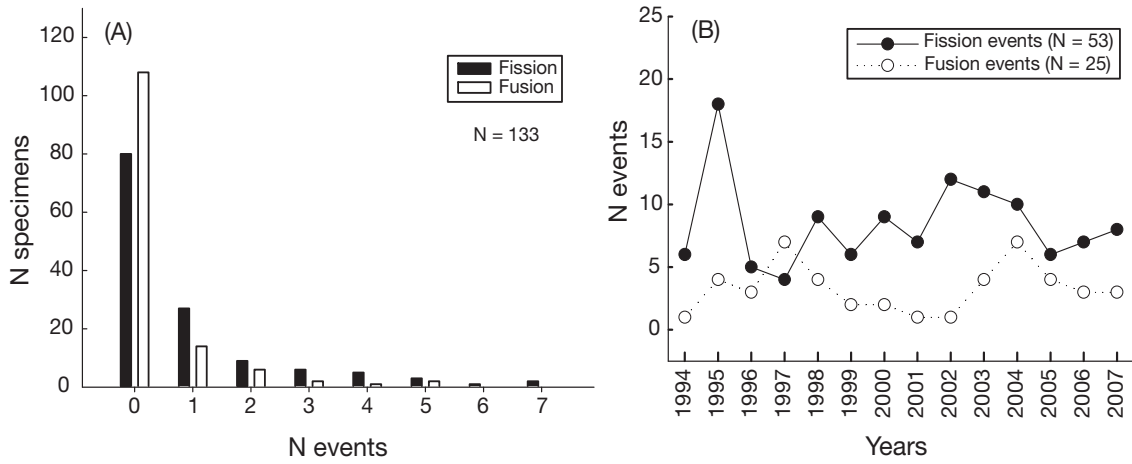


Fig. 5. *Crambe crambe*. (A) Total number of fission and fusion events suffered by each specimen. (B) Events suffered annually by the monitored specimens

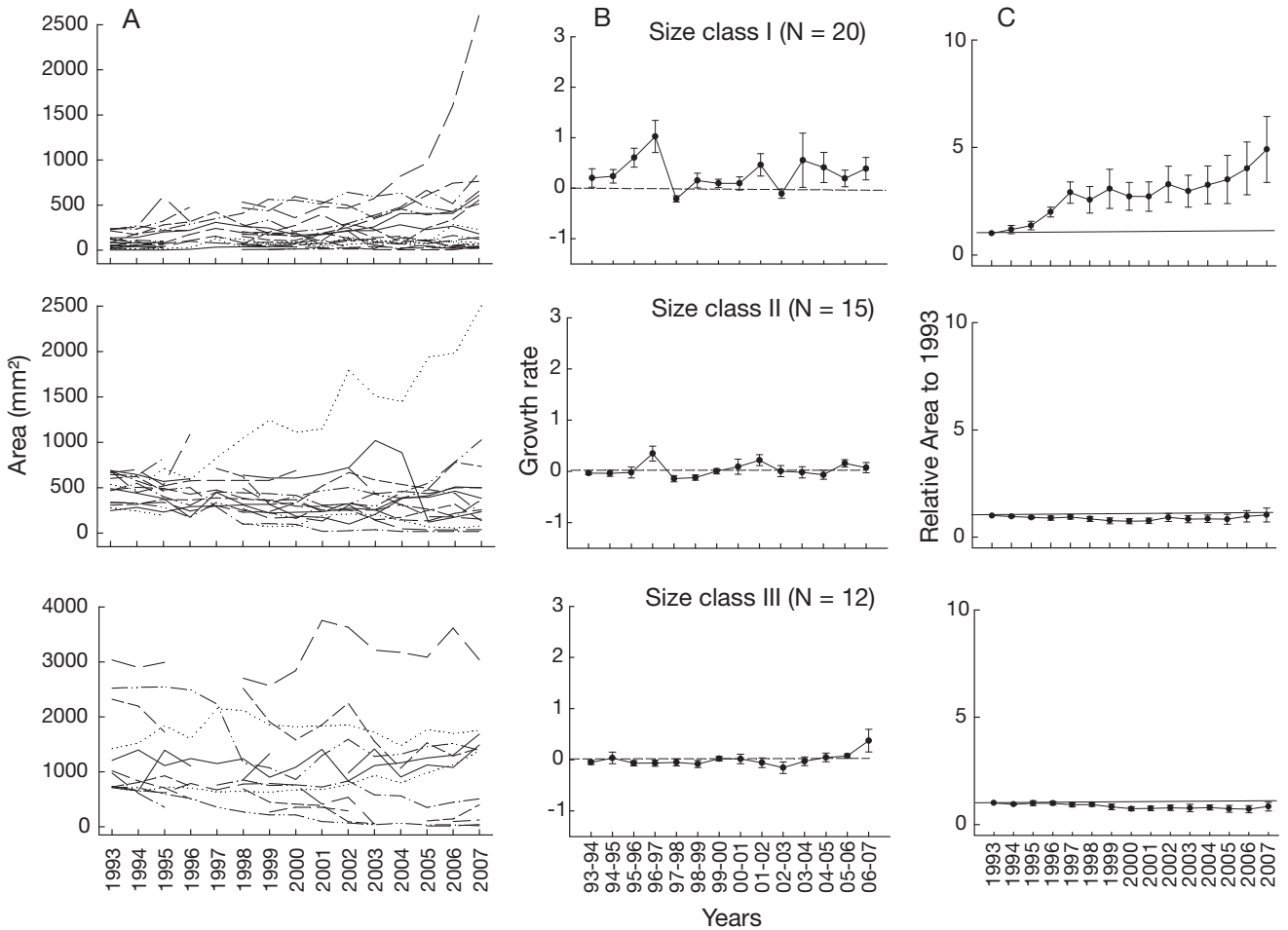


Fig. 6. *Crambe crambe*. (A) Changes in surface area, (B) yearly growth rate (mean \pm SE) and (C) relative area to 1993 of monitored specimens for 3 size classes from 1993 to 2007. Tendency of mean area (\pm SE) of monitored specimens relative to their size in 1993

Growth

Annual changes in the surface area of 47 specimens monitored from 1993 to 2007 are presented in Fig. 6A (see also Appendix 3, at www.int-res.com/articles/suppl/m375p113_app.pdf). The data on surface area represents net growth measurements for each sampling period over 14 yr. Overall, we observed low and asynchronous growth in all specimens across the 3 size classes.

Small specimens (size class I) displayed moderate growth and a slight increase over time (mean values: $98 \pm 17 \text{ mm}^2$ in 1993 and $383 \pm 132 \text{ mm}^2$ in 2007), whereas larger specimens (size classes II and III) did not show any remarkable growth over the study period (Fig. 6A). Interestingly, out of the 20 small specimens, 1 showed remarkably fast growth, yielding a total increase of $\sim 600 \text{ mm}^2$ in planar area over the 14 yr. Annual growth rates were also higher and more variable in size class I (total mean growth rate: $0.29 \pm 0.19 \text{ mm}^2$) than in classes II and III (total mean growth rate: 0.03 ± 0.09 and $0.01 \pm 0.08 \text{ mm}^2$, respectively) (Fig. 6B). The 2 latter classes show growth rates very close to zero, with neither growth nor loss of surface area.

No changes in (1) surface area, (2) annual growth rate, and (3) relative area of the initial size of *Crambe crambe* specimens were significantly different over the 14 yr (for all permutation tests, $p > 0.05$). However, they were strongly related to size class ($p < 0.0001$) and each of the 3 size classes differed significantly from the others ($p < 0.0001$; paired comparisons after Bonferroni's correction). The interaction term (time \times size class) was not significant for the 3 growth parameters. These results were not expected for the smallest size class as the faster growth of these specimens resulted in a net size increase of ~ 4 -fold between 2007 and 1993 (Fig. 6C). Therefore, we tested change in area relative to initial size among the 3 size classes at the beginning (1993) and end (2007) of the study. The net area increase was significantly different for size class I (t -test = -2.4627 ; $p < 0.01$). This result may indicate that growth within size class I was not statistically conspicuous through time, but significant when comparing the initial (1993) and final (2007) survey periods.

Processes affecting population size

All processes seen to affect the population size of *Crambe crambe* over 14 yr are summarized in Table 2. *C. crambe* is a long-lived sponge; 60% of specimens of

Table 2. *Crambe crambe*. Summary of events affecting the population size over the entire study period. Note the differentiation between genets (considering the entire specimen) and ramets (all the fragments)

Factor affecting population size	Change	Result	
		Genets	Ramets
Original number of genets and ramets (1993)	–	133	157
Number of genets that died	–51	82	106
Original ramets that died	–5	–	101
Daughter ramets formed by division	+118	–	219
Daughter ramets formed by division that died	–54	–	165
N ramets lost by fusion	–46	–	119
Number of larval recruits	+14	96	133
Number of recruits that died	–2	94	131
N genets and ramets (2007)	–	94	131

unknown age identified in 1993 were still alive 14 yr later, and 85% of those newly recruited (mean age 6.3 yr) were still alive at the end of the study. Fission was a moderately important mechanism, depending on size class, occurring in $\sim 40\%$ of the population (Table 1). However, 45% of these additional fragments were lost in partial mortality. Interestingly, most of partial mortality (91%) affected small patches generated by fission. In contrast, fusion did not have a high impact on patch losses. At the end of the study in 2007, the net result was a 38% decrease in genet number and a 17% and decrease in ramet number, relative to 1993.

DISCUSSION

Relatively few demographic studies of long-lived, marine clonal sessile invertebrates consider sufficiently long time intervals to provide an accurate estimate of their demography (exceptions include Dayton 1979, Connell et al. 1997, Garrabou & Harmelin 2002, Edmunds & Elahi 2007). In our study population of *Crambe crambe* few dynamics were observed over 14 yr (Table 2). The number of genets varied little over time (annual mean change: 3.6 ± 0.76 genets), their survival was high and recruitment via larvae was very low (mean: 0.9 ± 0.26 recruits yr^{-1}). We did not detect mortality of large specimens despite their comparatively small size in relation to those encountered in the field and previously reported (Uriz et al. 1995, Turon et al. 1998). Overall, this population is mainly characterized by the inputs (fission) and outputs (fusion and partial mortality) of asexual ramets. Over 14 yr, the loss of ramets was approximately equal to the production of ramets by fission, so the number of patches remained relatively constant. Finally, we confirm that *C. crambe* grows slowly and exhibits long lifespans, which may encompass several decades. Based on a genetic study,

Calderón et al. (2007) highlighted the importance of long-term demographic data to understand processes acting in the clonality and genetic structure of this species. To our knowledge, the present study is the first to provide solid long-term demographic data for this species, with observations spanning more than a decade. Our results may permit extrapolation, elucidating the general variation of this sponge's life history patterns at larger scales.

There were no apparent changes in population patterns of the abundance and size distribution after 14 yr of study. Most patches belonged to small size classes (<200 mm²), with the largest size classes comprising a small percentage of the population in both 1993 and 2007 (Fig. 2). This pattern of relative constancy may result from the generally low dynamics of this species, where low mortality is accompanied by low growth and/or infrequent or unsuccessful recruitment events. This lack of recruitment is not due to the failure of larvae production, as specimens with a size range of 1 to 1000 mm² include larvae (Uriz et al. 1995), but rather the low survival of juveniles (Uriz et al. 1998, De Caralt et al. 2007). During the 14 yr study period, only 10% (14/132) of newly recruited sponges resulted from sexually produced larvae and survived successfully. However, we acknowledge that in non-manipulated photographic frames, patches smaller than ~1 mm² are difficult to detect. Other factors also play a role in larval recruitment and juvenile survivorship: low larval recruitment and survival are frequently reported for sponges due to predation, competition for substrate, and physical perturbations (Battershill & Bergquist 1990, Wulff 1991, Uriz et al. 1998). Mariani et al. (2005) identified filamentous and fast-growing algae proliferation as the main factor in recruit mortality for the bryozoan *Schizobrachiella sanguinea*. Overall, our findings are consistent with the overall paucity of sexual recruits in marine clonal organisms (Bak et al. 1981, Hughes & Jackson 1985, Garrabou & Harmelin 2002).

Survivorship was found to be relatively high and dependent on size (Fig. 3), with all the largest specimens surviving over the entire study period. In *Crambe crambe*, as in other sponges and benthic clonal animals, lower mortality of large individuals may result from the size-refuge effect, i.e. beyond a certain size, mortality decreases considerably (Connell 1973, Jackson 1979, Sebens 1982). The available photographs did not give direct evidence of the cause of mortality (damage by passing a sea urchin, sedimentation, etc.). Turon et al. (1998) suggested overgrowth by fast-growing algae to be the dominant factor of mortality in *C. crambe*. However, they reported survivorship values of only 60% over a 2 yr study of a population of larger individuals (mean size: 6886 mm²) dwelling in a shaded habitat but shallower than the one studied

here. We attribute the higher survivorship observed in this study (annual mean: ~80 ± 3.5%) to habitat differences, as a variety of abiotic (e.g. hydrodynamics, food supply, irradiance, water temperature) and biotic factors (e.g. competition for space) may affect the observed dynamics of each population. Specifically, we hypothesize that space competition pressure may enhance survivorship and thus the persistence of this species in the population discussed here. As has been amply demonstrated, sponges must compete for space with other sponges and with many sessile organisms (Sarà 1970, Jackson & Buss 1975, Aerts 2000, Wulff 2006). The study site is highly diversified and mainly dominated by perennial animals and algae species, which completely cover the space (Ros et al. 1984, Garrabou et al. 2002). *C. crambe* possesses highly active metabolites (e.g. Jares-Erijman et al. 1991) and the production of chemical and physical defences increases in a space-saturated community (in dimly lit conditions) dominated by slow-growing animal species (Uriz et al. 1995, Becerro et al. 1997). In addition, Garrabou et al. (2002) found in the same study site a decrease in community turnover related with depth (5 to 20 m), where species with the lowest growth rates were dwelling below 11 m. Under this scenario, it seems likely that space competition pressure and the investment in production of allelochemicals and physical defences may explain the higher survivorship over longer time observed in the present study.

The relative contribution of sexual and asexual reproduction to the recruitment of new individuals into populations may vary considerably (Ayling 1980, Jackson & Coates 1986, Karlson 2002). Both sexual and asexual inputs were relatively low over the 14 yr, and the great majority (>89%) were formed vegetatively (Fig. 5, Table 1). Therefore, the population of *Crambe crambe* relied more on fission than sexual recruitment. The importance of asexual inputs is corroborated by genetic studies of population structure in this species (Calderón et al. 2007). However, it is important to note that <40% and 20% of the population underwent fission and fusion, respectively, with a minor annual contribution to the studied population (mean probability of fission ~0.1 and of fusion ~0.03 annually) (Table 1). Our results agree with previous research (Turon et al. 1998, Garrabou & Zabala 2001) demonstrating that fission in *C. crambe* is a comparatively moderate phenomenon compared with other sponges, which greatly relied on asexual mechanisms (values ranged from 97 to 72%) (Wulff 1991, Teixidó et al. 2006, Blanquer 2007). Interestingly, fission may be related to partial mortality, as ~50% of partial mortality of fragments occurred after a fission event and it was usual to observe fragments of ~200 mm² undergoing a size regression during the years prior to their death (~ 2 to 4 yr) (Fig. 4).

The decadal time-span and large number of individuals encompassed in the present study distinguish it from previous works analyzing population patterns of sponges. One of the most striking findings was the overall very slow growth pattern of *Crambe crambe* and the relatively high inter-individual variability of growth rate in the smallest specimens (Fig. 6A). This high variability has been noted in previous studies of clonal animal populations (Ayling 1983, Pansini & Pronzato 1990, Wulff 1991, Turon & Becerro 1992, Tanaka 2002). Small specimens exhibited the highest growth rates (net size increasing ~4 times in 14 yr) (Fig. 5C), which reinforces the size-refuge hypothesis as acting to reduce mortality. A similar relationship between growth pattern and size has been found in sponges (Dayton 1979, Pansini & Pronzato 1990, Garrabou & Zabala 2001) and some other clonal organisms (Bak et al. 1981, Hughes & Jackson 1985, Garrabou & Harmelin 2002).

Crambe crambe exhibits a seasonal pattern in life-history traits: e.g. maximum growth rates during summer and autumn, maximum investment in chemical defences in late autumn, and reproduction during summer (Uriz et al. 1995, Becerro et al. 1997, Turon et al. 1998, Garrabou & Zabala 2001). Although studies over 2 yr reported seasonal growth and shrinkage patterns (Turon et al. 1998, Garrabou & Zabala 2001), we show for the first time that net growth over more than a decade is close to zero for larger specimens. Moreover, this species exhibits a resting or dormant stage in late summer and autumn (Turon et al. 1999), when the site studied here is completely saturated by organisms, with strong competition with other animals and algae. This may indicate that although *C. crambe* exhibits seasonal growth and shrinkage peaks during an annual cycle, the result in the long term is a near lack of net growth.

Our 14 yr study gives the first evidence of the long lifespan of *Crambe crambe*. Based on the growth rates ($0.29 \text{ mm}^2 \text{ yr}^{-1}$) and the size of the largest specimens found in this study ($\sim 3000 \text{ mm}^2$), we suggest that their age could represent several decades. Bearing in mind the relatively small sizes of sponges analyzed in this study compared to the maximum reported size (e.g. 0.5 m^2), this estimation stresses the longevity of *C. crambe* and the role that may be played by episodic events. Age estimations from a 10 yr study of Antarctic hexactinellid sponges suggested similarly long lifespans (several hundred years for specimens 80 cm in height) (Dayton 1979). However, new hexactinellid recruits with heights >30 cm have recently been found on artificial panels (P. K. Dayton pers. comm.), suggesting that faster growth is possible. Another extreme example of this phenomenon is the prominent, long-lived, columnar saguaro cactus *Carnegiea gigantea*,

which reproduces and grows episodically when a series of climatic and microhabitat conditions meet (Drezner 2006). Episodic favorable conditions may also induce successful recruitment and periods of fast growth in *C. crambe*. This prediction of 'windows of opportunity' has also been suggested for other long-lived marine species with slow growth rates (Garrabou & Harmelin 2002, Teixidó et al. 2006, Linares et al. 2007). Additionally, many long-lived marine sessile species recruit episodically and so their populations fluctuate on decadal or longer scales (Hughes & Cancino 1985, Garrabou & Harmelin 2002, Coma et al. 2004). The slow pace of these processes relative to the human lifespan can create errors in our perception of a population's history and our predictions for its future, as such projections are often based only on recent trends. In the summers of 1999 and 2003, mass mortality events of macroscopic sessile invertebrates dwelling in sublittoral habitats occurred in the NW Mediterranean Sea over several hundred kilometers (Cerrano et al. 2000, Perez et al. 2000). In these summers, sponges (among them *C. crambe*) and cnidarian populations suffered mortality outbreaks during high seawater temperature anomalies (Cerrano et al. 2000, Perez et al. 2000, 2004). These mortality events involving slow-growing invertebrates reinforce and lend urgency to the need for long-term data sets and field observations at different spatial scales to foresee widespread population responses of long-lived sessile species under threat from climate change.

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