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Kingiella chilenica (Bivalvia: Cyamiidae); population dynamics, rates of survival, embryo production and annual recruitment of a semelparous brooding clam

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Kingiella chilenica, a brooder mollusc, inhabiting soft bottoms of estuarine tidal flats of southern Chile, is well suited to study larval recruitment. It is a tiny semelparous clam with an annual cycle, and whose recruits must survive an inhospitable winter season prior to growing and reaching reproductive maturity in the following summer season. The population dynamics of this clam was studied through periodic sampling over two successive years to follow fluctuations in its' abundance. Obtained data on embryo production and recruit survival over both periods shows that population abundance varied widely between the two years of study. A high level on recruit survival through the winter of the first year resulted in high numbers of adults in the corresponding summer reproductive season. An inverse situation occurred in the second year, with lower recuit survival and, consequently, fewer reproducing adults. However, the lower abundance of adults in the second year was compensated by their having a higher survival rate over the reproductive season as compared with adults of the previous year. Independently of the abundance of the adults, the number of embryos incubated per female was very similar between both periods. Consequently, we suggest that the net contribution of juveniles produced by females per unit substrate was similar between the annual cycles studied. As predicted for a semelparous species (high reproductive effort), the maximization of the reproductive contribution was clearly reflected by a drop in adult somatic weight, particularly in incubating females. Previous data on abundance for this population suggested inter-annual differences of a high magnitude, with periods (e.g. 1986–1988) with abundances reaching 2–6× that presently reported. Probably, stable environmental conditions (e.g. 1986–1988) promote high abundance and survival of reproducers allowing a large contribution of recruits, which in turn show high degrees of survival through the adult phase. The years reported here (2003–2005), however, represent a period of population decline to lower, perhaps minimum, levels.

INTRODUCTION

Fluctuations in larval recruitment have important effects on changes in abundance and on the population dynamics of marine benthic invertebrates (Gaines & Roughgarden, 1985; Roughgarden et al., 1988; McGuinnes & Davis, 1989; Underwood & Fairweather, 1989; Sale, 1990). A classic paradigm underlying this assumption is that species whose larvae pass through a planktonic developmental phase experience greater fluctuations in abundance than those whose larvae avoid the planktonic phase by having direct development (Thorson, 1946, 1950). This assumption is poorly documented, however, as until now, no evidence has been presented showing that the mode of development affects the degree of fluctuation of benthic populations (Levin & Hugget, 1990; Levin & Bridges, 1995). Maybe species with direct development demonstrate indeed important population fluctuations as a consequence of variations in recruitment of their juveniles on a local scale. In these species, recruitment may be directly affected by both the numbers of embryos produced in the population at a given time and the local environmental factors affecting survival and development of those recruits over time. The consequences of these fluctuations may be critical for semelparous holobenthic invertebrates in which population's abundance may strongly depend on the production of embryos during a one-and-only reproductive event occurring in the life cycle of the species in question. Here, semelpary implies maximum reproductive effort (Aldridge, 1982; Giangrande et al., 1994) which can be reflected in an important loss of somatic mass as the reproductive season progresses, eventually leading to the death of the adults following the reproductive season.

Kingiella chilenica Soot-Ryen, 1957, is a tiny clam commonly found in estuarine tidal flats in southern Chile. It is a convenient species for the study of both the relations cited above, as well as its effects on the abundance and population stability in this clam over successive years. Preliminary studies (Gallardo, 1993) showed that this is a semelparous species, with an annual cycle characterized by direct development of embryos brooded within the branchial chamber of the female. The reproductive season was restricted to the summer and beginning of autumn (January through April). Recruits for the new generation, measuring about 0.5 mm in length, became established at the end of the reproductive period, followed by mortality of the post-reproductive adults. No data, however, was obtained on either the degree of population fluctuations over time, or in which way any inter-annual fluctuations were dependent on local embryo production or survival to adulthood of locally recruited individuals. Also, there was no information on the magnitude of the somatic effect of the reproductive output of the adults after their single reproductive event, although this appeared to contribute to their mortality.

The present study looks at the population stability of *K. chilenica* as reflected by its relative abundance during successive annual cycles on a tidal flat in southern Chile. Inter-annual variations in the abundance of pre-adult and adult individuals in the population were analysed, and how it accounted for the annual recruitment between successive years relative to the embryo production in the population. We estimated the level of this recruitment comparing it with the abundance of the pre-adult juvenile fraction that would give rise to the new reproductive generation at the end of each annual life cycle (Gallardo, 1993). The impact of the reproductive output on the somatic biomass of both reproductive and post-reproductive adults was estimated for each sex, as well as its possible relation with the mortality typically experienced by these adults at the end of the reproductive season.

MATERIALS AND METHODS

Study area

The object of the present study was a population of *Kingiella chilenica* located on an estuarine tidal flat of the Queule River (39°23′S 73°14′W), southern coast of Chile. This is the same population used earlier to study the life cycle and natural history of this species (Gallardo, 1993).

Sampling and processing

Estimation of population's pre-adult and adult components was carried out by monthly sampling of intertidal sediments from the tidal flat. Replicate surface sediment samples (upper 3 cm with a $0.25\,m^2$ frame) were taken within an intertidal vertical transect. Two collecting intertidal sites (named 'high' and 'low') ~18 and 6 m, respectively, from the mean lower low water edge of the flat were sampled for this purpose. Water surface temperature was recorded in the study area with each sampling. The sediment samples were fixed in 6% formalin-seawater for subsequent processing in the laboratory. In the laboratory each sample was sieved through a 1.2-mm mesh screen to recover pre-adult and adult clams following the previously described methodology (Gallardo, 1993). The specimens thus obtained were counted, measured (maximum diameter or shell length), and their sex determined using a stereo microscope with an ocular micrometer. Based on prior methodology and data (Gallardo, 1993), clams below the minimum reproductive size were considered 'pre-adults'. The cut-out size, indicated by the presence of gonadal material and/or the presence of incubated embryos, was about 3 mm in shell length. This same study also demonstrated that recruits that survived the winter grew and re-established the population level towards the end of spring (typically in December). At this time this new cohort begins to appear in the samplers we employed (mesh 1.2 mm) and whose abundance was used to estimate the survival rates in the new year-classes of recruits.

The relative production of embryos in the population throughout each reproductive season (January to March of each year) was compared interannually over a period of two years extending from 2003 to 2005. We considered on the one hand the relative abundance of females in the samples (mean monthly females in the transect) for each annual reproductive season, and on the other hand the mean number of embryos incubated per female for this same period. Estimation of the latter value was done by haphazardly selecting 50 females from all those collected per monthly transect (or all available females if the total of them was less than 50). Counts were made on the numbers of embryos incubated as a function of the size (shell length) for each of the females selected. In this way we obtained an indirect estimator of the number of embryos expected per transect sampled for each annual reproductive season.

Concurrently to the preceding, we measured the somatic biomass (soft parts) of both males and females throughout the reproductive and early postreproductive seasons. This was used to estimate the magnitude of the reproductive effort of this species among successive years, and to know if this effort was different between sexes in the population. The biomass value was calculated as the dry weight of the soft parts in relation to the length of the shell of each individual, using the same 50 females examined for embryo content, and 50 similarly selected males.

Linear regression ($P<0.01$) and analysis of covariance ($P<0.05$) (Zar, 1996), following log transformations of shell length, body mass, and number of embryos, were used to analyse the variation in the number of embryos related to the female size, and the variation of adult body mass throughout the reproductive season, respectively.

RESULTS

Population dynamics, inter-annual fluctuations in abundance of pre-adult and adult clams, and abiotic conditions

Figure 1 shows the total number of individuals recovered from the transect (upper and lower quadrat) for each month, and the size frequencies in 0.2 mm intervals. The population dynamics observed represented an annual life cycle supporting previous observations on this population. Adult (>3 mm) individuals were abundant during the summer, when they were actively reproductive, with numbers decreasing gradually towards autumn, and disappearing during the austral winter–spring season. New recruits (<3 mm) were captured in the samplers primarily towards the end of spring, reaching a peak in December (start of summer). Beginning in this month there were more recruits surviving through year one (December 2003) than the survivors of year two (December 2004). This was correlated with the relative abundance of reproducers observed between the reproductive seasons of these years, particularly during January and February (i.e. austral summer 2004 vs austral summer 2005). The higher abundance of reproducers in the summer of 2004 ended rapidly at the end of this

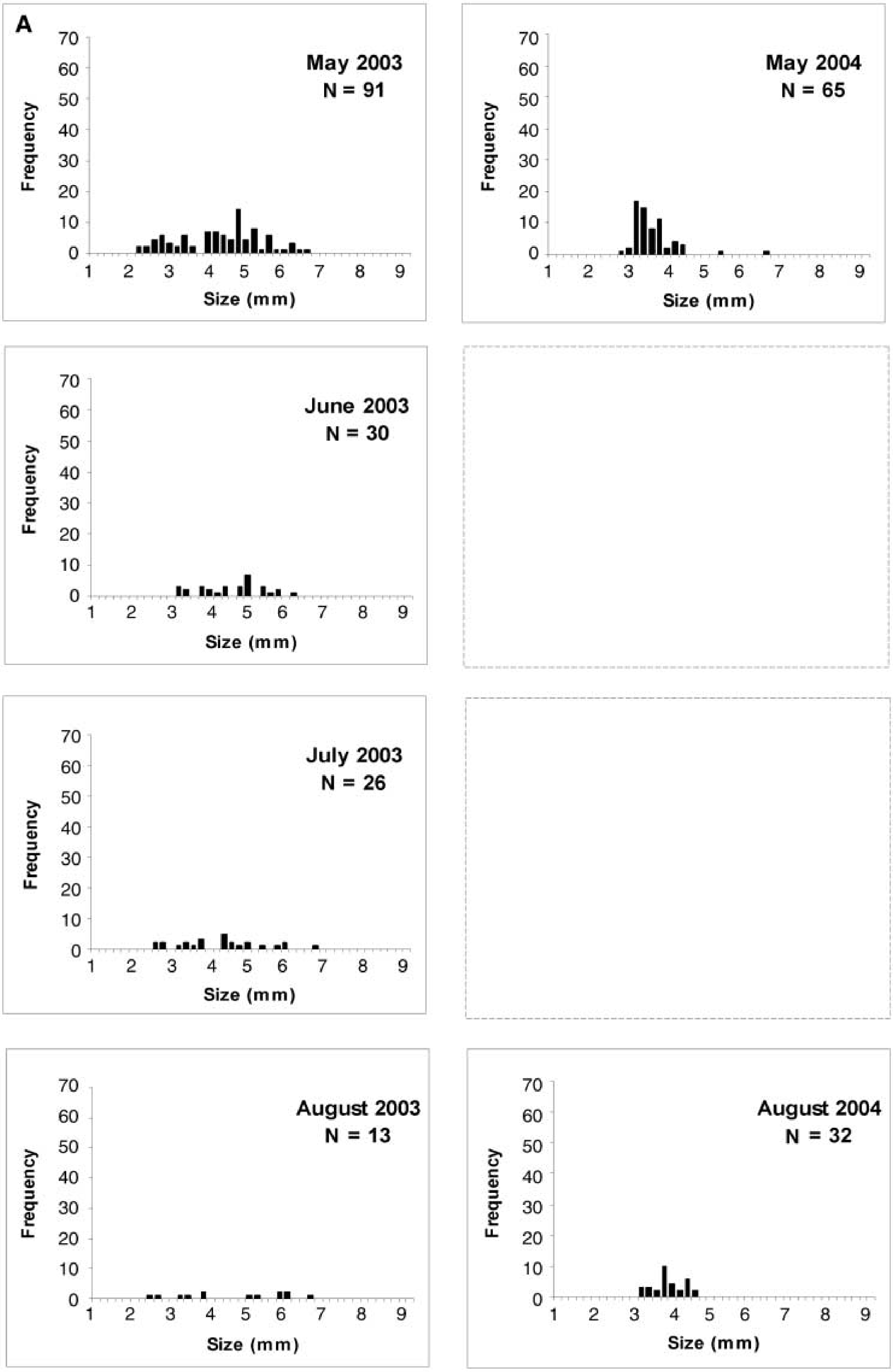

Figure 1. Monthly abundance and size–frequency distribution of the Queule River marsh population. (A) Late autumn and winter seasons (empty boxes indicate months without samples).

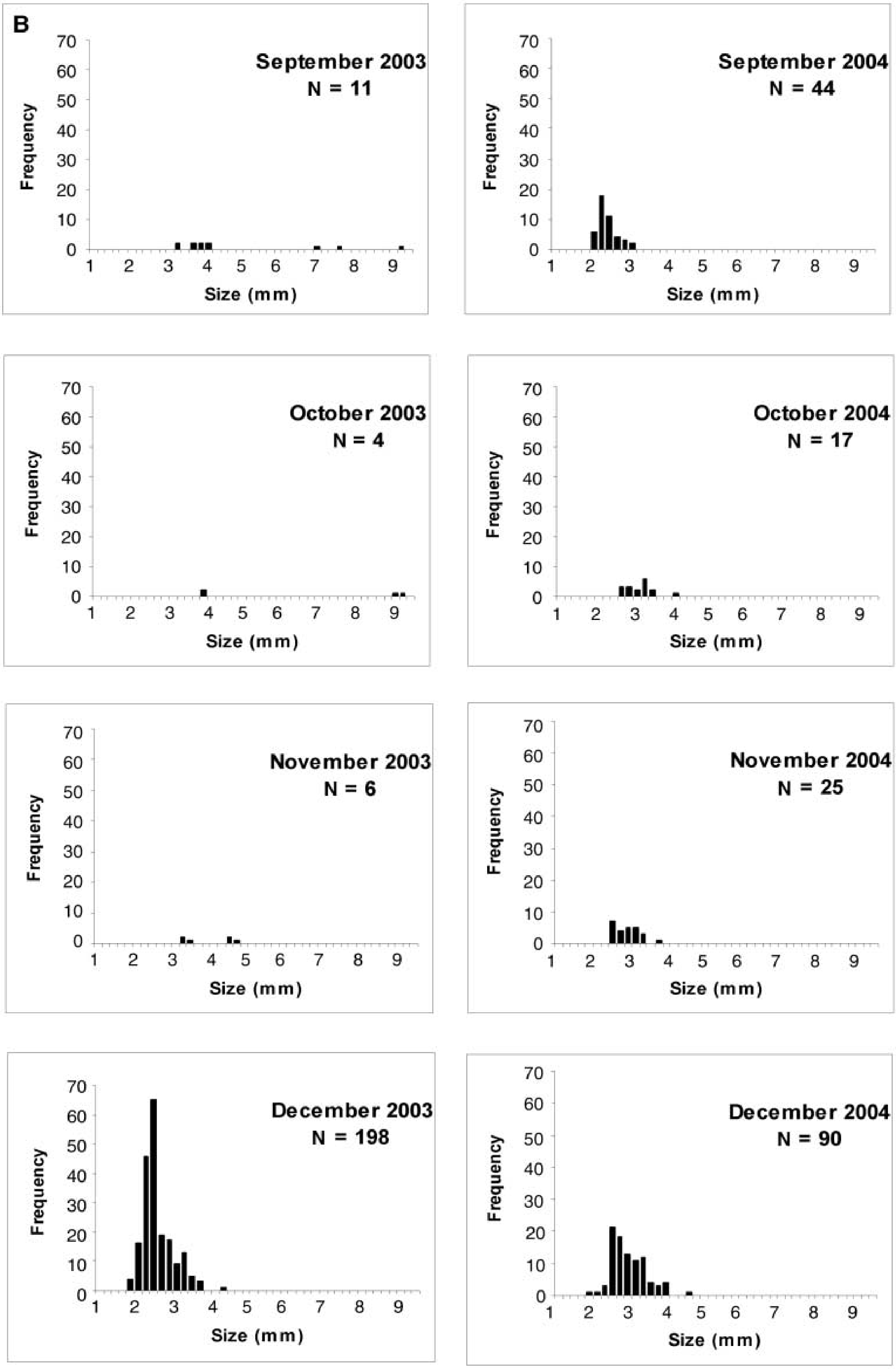

Figure 1. Monthly abundance and size–frequency distribution of the Queule River marsh population. (B) Spring seasons.

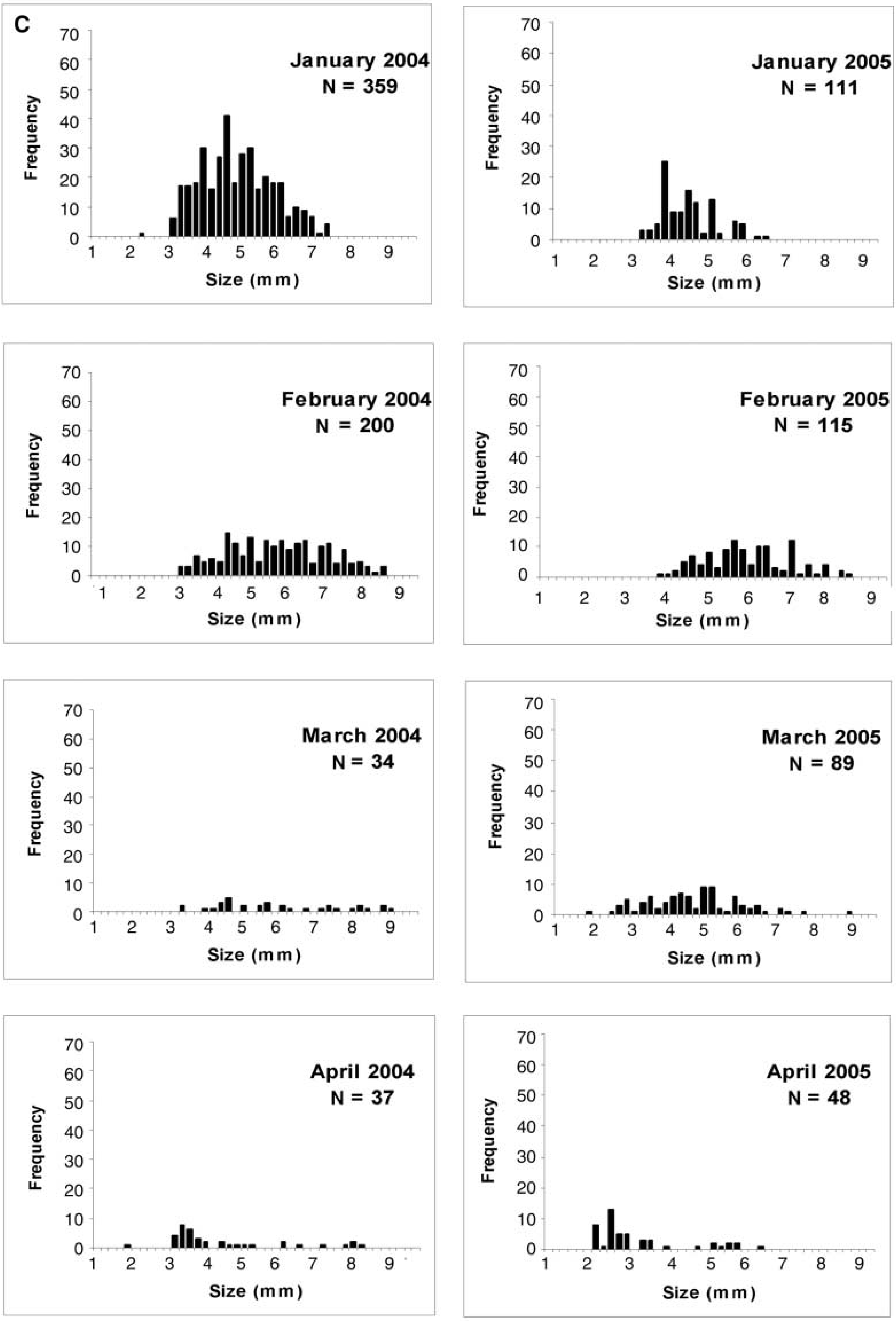

Figure 1. Monthly abundance and size–frequency distribution of the Queule River marsh population. (C) Summer and early autumn seasons.

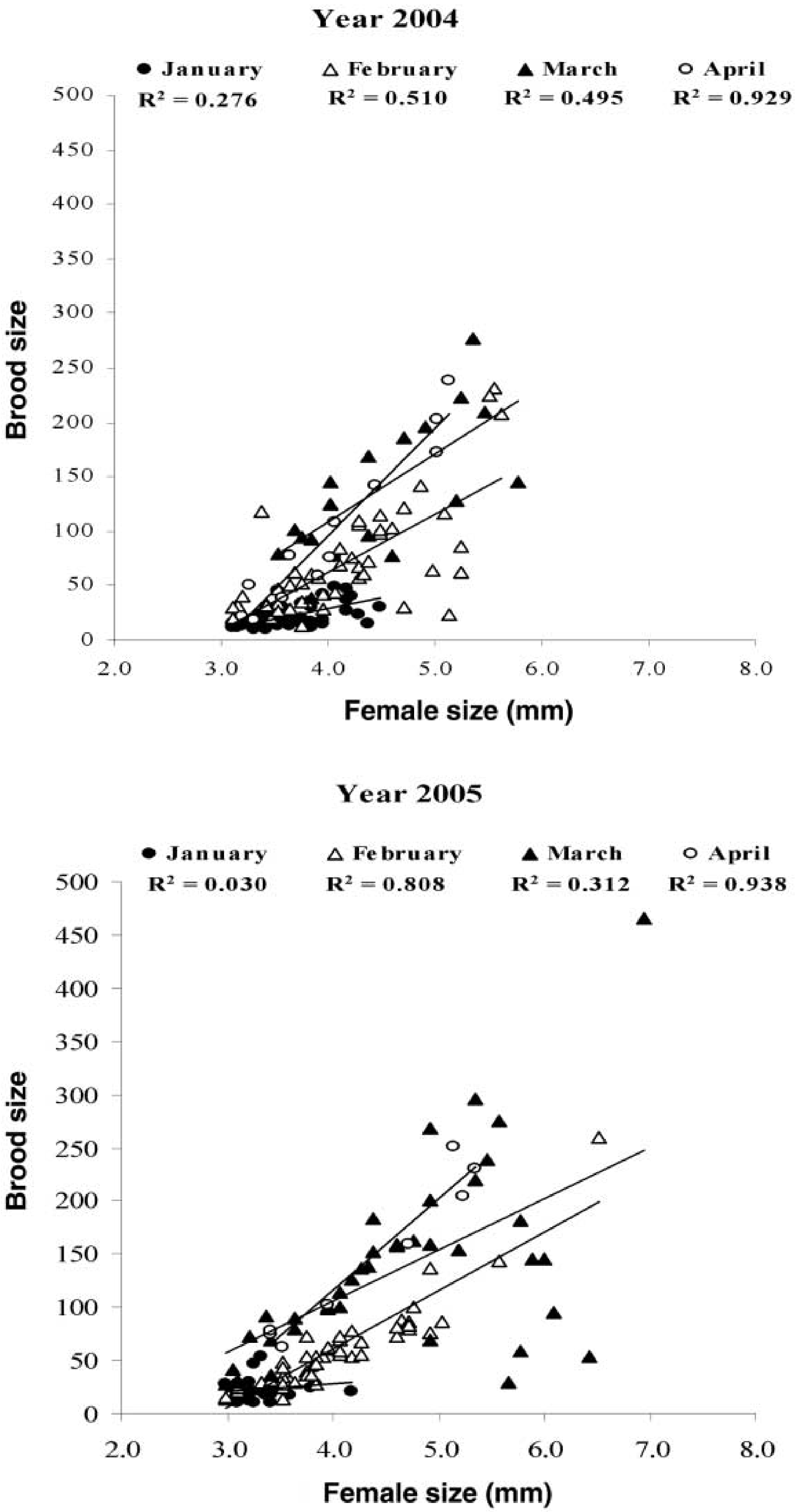

Figure 2. Brood size related to female size (shell length) during the breeding seasons of 2004 and 2005.

Table 1. *Frequency of adults (males and females) per sample area, proportion of brooding females, and number of embryos brooded.*

		Males		Females		Brooding females		Brooding females size (mm)			Number of brooded embryos per female		
Year	Month	No.	%	No.	%	No.	%	Range	Mean	SD	Range	Mean	SD
2004	January	88	49.7	89	50.3	59	66	3.1–4.5	3.65	0.35	10–76	23	13
	February	81	42.8	108	57.2	89	82	3.1–5.2	4.14	0.68	10–231	70	51
	March	19	52.7	17	47.3	17	100	3.6–5.8	4.51	0.71	10–277	140	62
	April	4	25	12	75	12	100	3.2–5.1	4.05	0.71	10–238	100	73
2005	January	26	44	33	66	25	75.7	3.0–4.2	3.35	0.29	11–53	23	11
	February	46	42.9	61	57.1	56	91.8	3.0–6.5	4.04	0.70	13–260	57	44
	March	40	51.2	38	48.8	37	97.3	3.0–7.0	4.65	1.04	30–465	137	90
	April	10	55.5	8	44.5	8	100	3.4–5.4	4.35	0.85	63–251	146	76

season (March–April), whereas in the same period in 2005 the reproducers had a much higher and sustained survival during late summer and the beginning of fall.

As expected, the water temperature in the study area varied during samplings, following a typical seasonal pattern. Although data was unavailable for the winter of 2004, the general information for the study period suggests that this year was notably warmer than 2003. During late winter and spring of 2004 the mean temperature was 22.3° and 24.8°C respectively, while in 2003 these values were only 11.4° and 17.7°C for the same periods. The following summers (January–March 2004 and 2005) also differed in average temperature, registering 20.7°C and 22.9°C respectively. The temperatures observed in 2003 were most similar to the data recorded for this area over recent decades, with the winter minima near 10°C and the summer maxima near 20°C (Quijón & Jaramillo, 1993; personal unpublished data).

Embryo production over successive reproductive seasons

The number of embryos incubated per female showed a positive correlation with the female's size (Figure 2). The production of embryos per brood followed a regular, stable pattern between the years of this study, and did not appear to be associated with females's abundance in each annual period. Females of a given size appeared to incubate a similar number of embryos between different annual generations (e.g. summer 2004/summer 2005). The number of embryos incubated per female increased gradually throughout the reproductive season, reaching its maximum in March, when the number varied according to the size of the female, from about 50 embryos in small individuals to over 400 in the largest females (~7 mm in length).

At the start of reproduction, the abundance of incubating females per area sampled (Table 1) was greater in 2004 (177 individuals) than in 2005 (126 individuals). However, the lower abundance of females during 2005 was followed by a greater survival during the second half of the reproductive season (March–April), when the highest embryo production per female is achieved. In spite of the fact that the embryos contribution to the population during the reproductive season was similar between the two years of the study (11,167 vs 10,060; Table 2), the number of surviving recruits, and the resulting adults, was quite different between these years.

Reproductive output at the expense of somatic mass

The effects of the reproductive output of both males and females on the relative body weight during, and at the culmination of reproduction was also analysed. Figure 3 shows the regressions between size and body mass between males and females during the reproductive season of 2004 and 2005. In general, the body mass of

Table 2. *Estimated contribution of embryos (released as juveniles) per sample area during each reproductive season (2004 versus 2005).*

	Reproductive season—Year 2004			Reproductive season—Year 2005		
Month	Total brooding females per sample	Number of brooded embryos (average) per female	Estimated contribution of embryos per sample area	Total brooding females per sample	Number of brooded embryos (average) per female	Estimated contribution of embryos per sample area
January	59	23	1357	25	23	575
February	89	70	6230	56	58	3248
March	17	140	2380	37	137	5069
April	12	100	1200	8	146	1168
Total contribution of embryos		11 167			10 060	

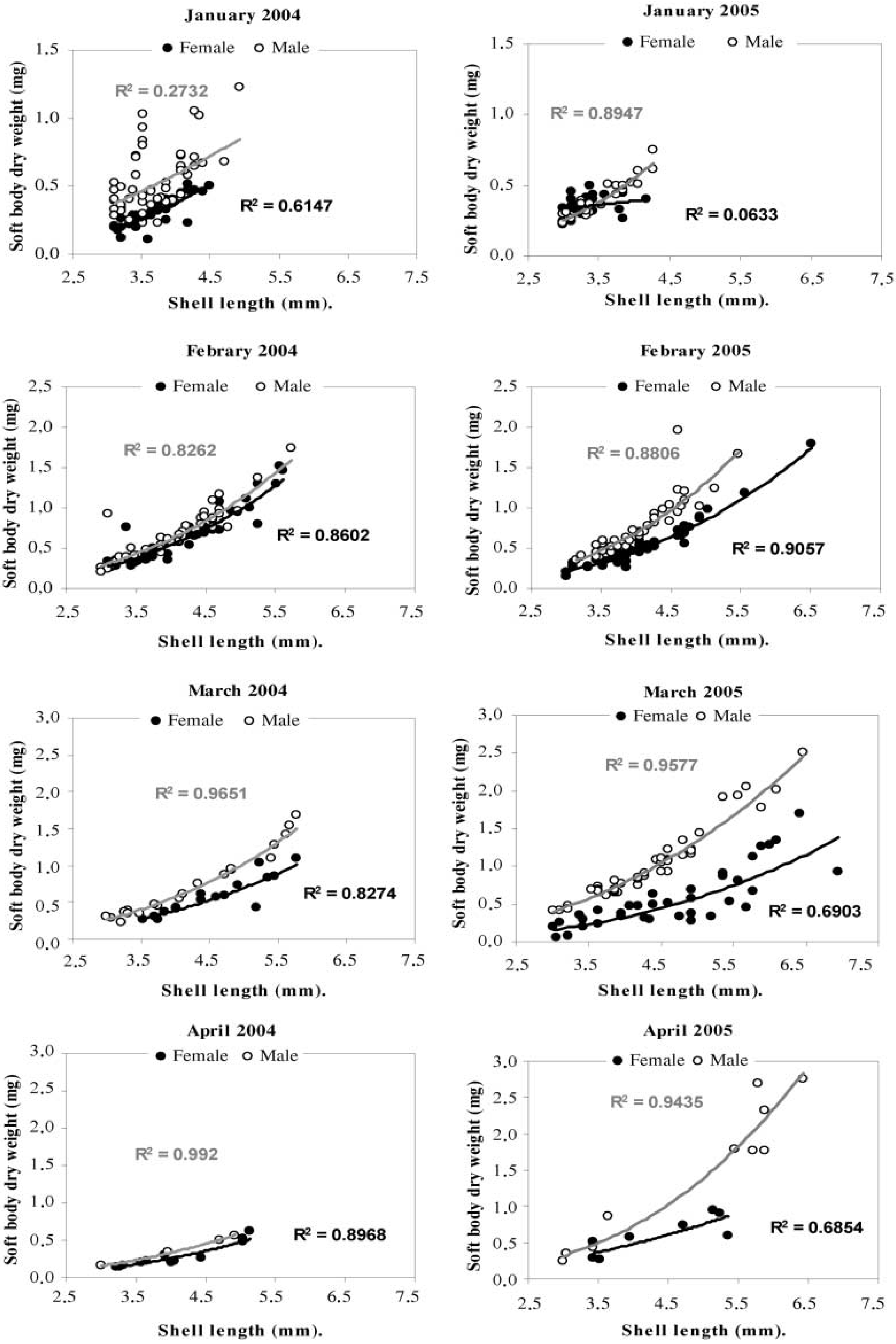

Figure 3. Body dry weight related to shell length between brooding females and males.

the females decreased faster than that of the males, becoming more evident as females reached the end of their reproductive activity at the end of summer/beginning of autumn.

DISCUSSION

Although *Kingiella chilenica* is not subjected to the randomness in recruitment common in species with an extended planktonic larval phase, it demonstrates well the important variation that can occur in population abundance of a benthic invertebrate. Contrary to what is expected from the classic paradigm (Thorson, 1950), this species shows important inter-annual fluctuations in recruits' survival. Local conditions directly or indirectly affect their survival rate through winter and early spring in the tidal flat, until they reach the pre-adult condition in late spring (November–December). Since this is an annual semelparous species with direct development (Gallardo, 1993), the immediate future of the population in each succeeding year depends on the success of the juveniles produced during the preceding reproductive season. High densities of pre-reproductive recruits result in high densities of reproductive individuals in the following summer season. However, the survival of the adult generation should also be considered. For example, although adult densities were very low in the summer of 2005, the high rate of their survival during this period allowed an estimated contribution of embryos to the population almost as high as that of the preceding year, when the reproductive season began with a greater abundance of adults. These, however, experienced a low survival rate during the second half of the summer.

The marked inter-annual fluctuations affecting this population are evident when we compare the present results with those obtained in 1986–1988 for the same population (Gallardo, 1993). Data for three reproductive periods showed unusually high population abundances, with 2–6 × more recruits and adults than those of the present study, for the same area of sampled substrate. We can assume that these changes are cyclical on a large scale. They may stabilize at high abundance as observed in 1986–1988, changing then over time to lower abundance as observed in the present study. However, stabilization at different levels of abundance probably has no major effects on the continuity of the population over time. Based on these results, we suggest that this population is currently experiencing a period of low relative abundance.

As expected for a semelparous species, the high reproductive effort (RE) of *K. chilenica* happens at the expense of somatic tissue. This dependence implies that any increase in the RE is done at the expense of survival and reduction in somatic investment (Williams, 1966; Gadgil & Bossert, 1970; Tuomi et al., 1983). Although both sexes show a decrease in soma, this is greater for females, probably due to their greater energy expense to produce and incubate the embryos. This condition may also explain the mass mortality undergone by *K. chilenica* adults following reproduction. Giangrande et al. (1994) summarize the role of demographic forces in the selection of semelparous life history strategies, and their predictions seem to agree with the characteristics shown here by *K. chilenica*. According to these authors, individuals of a semelparous species direct all their energy reserves into reproduction and then die. Also, when the survival between different reproductive seasons is low, or requires much energy, selection favours annual life cycles rather than perennial ones. Thus semelpary is a strategy rarely observed in organisms living more than two years.

Knowledge accumulated on this type of life cycle and the natural history of this species allows us to postulate that the observed population fluctuations are regulated by local events, although these may remain undefined. Biotic as well as physical interactions may be involved in the survival of both adults and recruits which are able to reach the adult reproductive stage in the following year class. We must assume that we deal with factors whose impact on survival of each new annual cohort may fluctuate widely over different inter annual generations. Among the physical factors, climate (particularly rain and temperature) may affect this population inasmuch as they undergo important inter annual variations in this region of the Chilean coast. Abiotic conditions reported for the study site indicate a marked decline in temperature between autumn and winter, with fluctuations of 7–10°C, and spring averages up to 20–21°C. Salinity reaches 25–29 ppm during summer, declining abruptly in autumn–winter to 1–7 ppm (Quijón & Jaramillo, 1993) due to local rains. Temperature measurements taken during sampling partially fit the normal pattern for 2003. They also point to high temperatures in 2005 which could have been responsible for the high adult mortalities suggested by our data on abundance for that year. It should also be noted that migratory birds exercise an important predation pressure on this clam, particularly on the larger, reproducing individuals during their summer visits to this tidal flat (E. Jaramillo, unpublished data). An important portion of the female clams, which incubate larger numbers of embryos, may also be lost during these visits. However, such type of pressure based on external factors and dependent on the abundance and permanence of the birds on the flat, which also will fluctuate inter annually, should not be constant over time.

Abundance fluctuations of reproducing clams has a direct effect on the number of recruits entering the population. Nevertheless, the number of embryos per female is a stable parameter over time (maximum reproductive effort per female) as shown if we compare the present study data with observations made almost two decades ago (1986–1988). This factor is correlated with the size of the female but does not seem to be associated with their abundance. Therefore can not be considered a parameter that accounts for the inter annual fluctuations of the embryos' contribution to the population observed by us. Such fluctuations would depend more on the abundance of incubating females, their persistence through the reproductive season, and their size structure. The last being the most affected by the above described size-selective predation.

In general, it should be noted that the life cycle and life history patterns of *K. chilenica* shows similarities with the model proposed by Warwick (1984) for other small invertebrates with annual cycles and inhabiting tidal flats. This model analyses the degree of stability characteristic of the habitat colonized by these species. It may shed light on the characteristics of the habitat of *K. chilenica*' population, thus helping to understand the pressures exerted on some key attributes of its life history. Warwick (1984) states that in tidal flats with broad environmental fluctuations, semelparous species do not survive for more than one year being affected by the fact that certain stages of their life cycle occur during an unfavourable season, thus making imperative the inter annual survival of recruits or juveniles, and producing large population fluctuations. One example of such life cycle is that of the polychaete *Ampharete acutifrons*. After spawning in the autumn, adults inevitably die. The descendants hibernate as vulnerable juveniles, whose survival varies over time, resulting in major population fluctuations in the following spring and summer even under the most favourable growth conditions (Price & Warwick, 1980). The parallelism between this type of life history and that of *Kingiella chilenica* in the Rio Queule tidal flat is evident. If this interpretative model is correct, unpredictable factors which differentially affect survival of hibernating juveniles and/or pre adult and adult stages would be an important source of population fluctuations for this tiny semelparous clam.

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