

Population Biology of the Intertidal Snail *Chilina ovalis* Sowerby (Pulmonata) in the Queule River Estuary, South-Central Chile

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ABSTRACT: The temporal variability in abundance and population structure of the gastropod *Chilina ovalis* Sowerby was studied in the upper intertidal zone of Queule River estuary, south-central Chile (c. 40°S). Snails were collected monthly (September 1995–December 1997) from haphazardly-located quadrats (50 × 50 cm, n = 5 each time), and counted and measured (shell height) in the laboratory. Water and sediment samples were collected at the same time to study the snail's habitat characteristics. Overall mean abundance was 115 individuals m⁻² (SD = 55). Monthly abundance estimates indicated a clear decrease during 1997. This decrease appeared to be related to the annual recruitment success of the species and at least partially to water temperature and sedimentological variability. Overall size range of *C. ovalis* was 1.5–27.5 mm shell height. Growth varied seasonally with highest growth rates observed after recruitment (November–February). Slower growth continued throughout the austral winter months. Despite changes in abundance between 1996 and 1997, no differences were detected when population growth estimates were compared between years. A maximum longevity of approximately 4 yr was estimated from the growth curves of the cohorts, and a life cycle with more than one reproductive period is suggested.

Introduction

Studies relating population changes to habitat variability are central to understanding life history patterns within a species or group of species (Newell 1964). Soft-bottom epibenthic gastropods, particularly those associated with habitats with variable physical conditions such as estuarine intertidal flats (Meadows and Tait 1989), are interesting in the context of habitat-population relationships. Epibenthic gastropods present a wide reproductive and morphological diversity (Barnes 1990) and are closely related to sediment properties because of their active substrate selection and feeding (e.g., Forbes and Lopez 1990; Levinton et al. 1995). These species are also important because of their role as microorganism consumers (Bianchi and Levinton 1981), macroinfaunal predators (Edwards and Huebner 1977; Hunt et al. 1987), and sediment disturbers (Boyer 1980).

Epibenthic gastropods, such as those of the genera *Hydrobia*, *Littoridina*, and *Ilyanassa*, are typical organisms inhabiting soft-bottom intertidal sediments around the world (Cherril and James 1985; Hershler and Longley 1986; Davis et al. 1989; Barnes 1990; Altaba 1993; Ponder and Clark 1993). Some of the lesser known gastropod species, such as those of the South American endemic genus *Chilina*, are spread widely among limnetic and es-

tuarine intertidal habitats. The few published studies on this genus deal with morphology (Miquel 1983; Brown and Pullan 1987), geographical distribution (de Castellanos and Gaillard 1991; de Castellanos and Miquel 1991), life history (Miquel 1986; Bosnia et al. 1990), and recently their role as disturbers of shallow water sediments (Quijón and Jaramillo 1999).

These studies have helped to clarify systematic and geographical relationships within the genus (e.g., de Castellanos and Gaillard 1991). The information about their ecology is fragmentary and inconclusive when compared to tidal flat or salt-marsh species such as those of the genus *Hydrobia*. Habitat influences on life history of chilinid species have received little attention (Miquel 1986; Bosnia et al. 1990). Most of this research has focused on freshwater populations, with little attention directed toward estuarine populations. Because intertidal estuarine habitats are extremely variable habitats, both spatially and temporally (Meadows and Tait 1989), *Chilina* species inhabiting these areas offer a valuable source of information about the range of population variability within the genus.

The macrofauna of the upper intertidal zone of the tidal flats of south-central Chilean estuaries (c. 40°S) is dominated by the epibenthic snail *Chilina ovalis* Sowerby. Its specific habitat extends along mud or gravel-sand patches of sediment associated with stem fronds of the cattail *Scirpus americanus* Pers (Quijón and Jaramillo 1999). The seasonal abundance and size of this species might deter-

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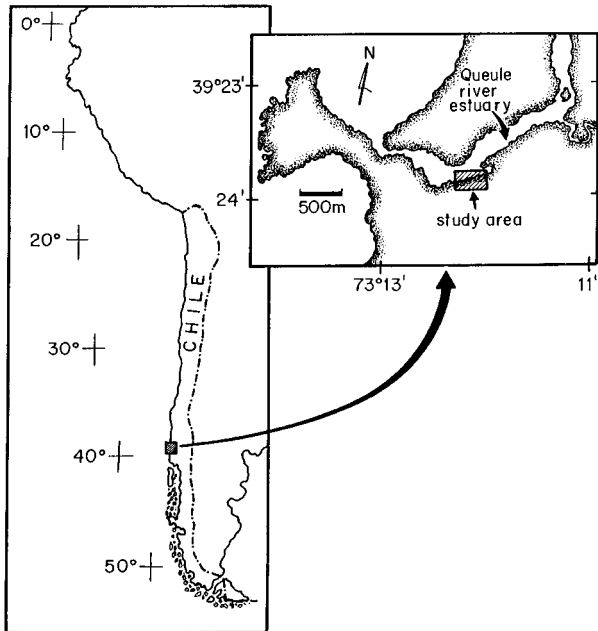


Fig. 1. Map of the study area at the middle reach of Queule River estuary, south central Chile.

mine its interactions with benthic diatoms (its primary food source) (Bosnia et al. 1990) and other components of the benthos. Abundance and body size changes have not been evaluated, particularly in the context of habitat characteristics and temporal variability. In this 2.5-yr study, we analyzed the fluctuations in abundance and population structure of *C. ovalis* in the Queule River estuary as functions of the temporal variability of its habitat characteristics. The primary aims of this study were to study the monthly variability in population abundance and size structure of *C. ovalis*, to analyze the interannual variability in these population characteristics and compare them with those of similar gastropods elsewhere, and to analyze the relationship between the fluctuation of population abundances and that of habitat characteristics.

Material and Methods

STUDY SITE

The study area was located in the middle reach of the Queule River estuary, south-central Chile (39°41'S, 73°13'W, Fig. 1). Sediment characteristics of the area, as well as hydrographic characteristics, have been described previously (Campos and Moreno 1985; Pino 1995). Sampling was conducted in the mostly mesohaline region of the estuary (Campos and Moreno 1985). In the muddy and gravel-sandy sediments of the upper intertidal zone, *C. ovalis* occurs with other gastropod species of the genus *Littoridina*, the grapsid crab *Hemigrapsus cren-*

ulatus, and macroinfaunal assemblages dominated by spionid (e.g., *Prionospio (Minuspio) patagonica* Augener) and nereid polychaetes (*Perinereis gualpensis* Jeldes) (Quijón and Jaramillo 1993).

WATER AND SEDIMENT SAMPLING

Monthly water samples ($n = 3$) were collected from a shallow area immediately adjacent to snail sampling sites at high and low tides during September 1995–December 1997. The samples were analyzed for temperature ($\pm 0.1^\circ\text{C}$), chlorophyll *a* (chl *a*) content, and suspended particulate matter (hereafter termed seston). The selection of these variables was based on their close relationships with the temporal variability patterns observed for other benthic species analyzed previously in Queule River estuary (see correlative studies by Quijón and Jaramillo 1993 and Quijón et al. 1996). Because it was impossible to obtain quantitative population estimates of the main food source for the snails (benthic diatoms), water column chl *a*, organic seston, and sediment organic matter (see below) are used here as indirect estimators of food availability. Chl *a* content of the overlying water (as a surrogate for phytoplankton biomass) was estimated by filtering water samples through GF/C (Millipore filters, 47 mm diam) and applying the spectrophotometric method of Strickland and Parsons (1972). The concentration of seston and its organic and inorganic components were measured by filtering water samples through pre-weighed GF/C filters (Millipore) and estimating the loss in weight after drying (80°C for 72 h) and subsequent ignition (550°C for 4 h).

Monthly surface sediment samples (0–0.5 cm depth, $n = 4$) were collected using PVC cores (2.0 cm diam) for analysis of textural characteristics and organic content. Textural analyses determined percentages of gravel (in this study particles $> 2,000 \mu\text{m}$), sand (63–2,000 μm), biogenic aggregates (i.e., animal feces and tubes), and mud ($< 63 \mu\text{m}$) (Anderson et al. 1981). The organic matter content in the sediment was determined as described for seston. Stem densities of *S. americanus* located along and around the snail sampling sites (middle reach of the estuary) were also estimated. Previous observations suggested a strong effect of stem density in determining spatial patterns and, eventually, temporal patterns of *C. ovalis*. Stem densities were estimated monthly by counting the number of stems inside 50×50 cm haphazardly distributed quadrats ($n = 4$ per sampling event).

ABUNDANCE AND POPULATION STRUCTURE OF *CHILINA OVALIS*

The abundance of *C. ovalis* was estimated from monthly samplings during the period September

1995–December 1997. Gastropods were collected each month from five 50 × 50 cm quadrats placed haphazardly at the upper intertidal zone among patches of *S. americanus* stems (Fig. 1). Snails were counted and measured (maximum shell height ± 0.1 mm) at the laboratory. Correlation analysis was conducted on abundance of *C. ovalis* versus time (measured in mo) and abundance versus each of the habitat variables measured in the water (temperature, chl *a*, total and organic seston) and in the substrate (percentages of gravel, sand, aggregates, mud and organic matter, stem density).

The abundance and shell height of individuals collected during 1996 and 1997 (10 sample sets for each year) were used to estimate the size structure of the population. The appropriate size intervals (1 mm) for growth analyses were based on the criteria outlined by Sparre (1989). Battacharya's method (Gayanilo et al. 1996) was used to identify modes in the size-class distribution data. The program decomposes polymodal size-frequency data into normal curves (each representing one cohort) which, added together, represent the best fit to the observed data. As in other studies examining growth parameters of *Chilina* species (Bosnia et al. 1990) and mollusc and crustaceans in general (e.g., Rosenberg et al. 1986), it was assumed that internal growth (soft tissues) is well represented by shell growth. The ELEFAN Program (Electronic Length Frequency Analysis; developed by the International Center for Living Aquatic Resources Management, Manila, Philippines), was applied, assuming that body growth follows the von Bertalanffy growth equation (VBGE) (von Bertalanffy 1938; Gayanilo et al. 1996). We used a seasonally oscillating version of the VBGE model as described by Hoenig and Hanumara (1982):

$$L_t = L_\infty(1 - e^{[-K(t-t_0) + (KC/2\pi)\sin 2\pi(t-t_s) - (KC/2\pi)\sin 2\pi(t_0-t_s)])}$$

Where L_t = shell length (i.e., shell height in *C. ovalis*) at age t , L_∞ = maximum asymptotic length (shell height), K = growth curvature parameter, t_0 = computed age at length zero, C = parameter reflecting the intensity of seasonal growth oscillation, and t_s = time at start of a sinusoid growth oscillation with respect to $t = 0$.

The winter point (WP) was defined as the time (expressed as a decimal fraction of the year) when growth is slowest (Pauly and Gaschütz 1979). The ELEFAN program fits the growth curve that passes through a maximum number of peaks in the size frequency distribution (Pauly et al. 1984). An index of goodness of fit, called R_n , was determined from Gayanilo et al. (1989). In order to compare growth rates from 1996 and 1997 data, the standard growth index ϕ' , a measure of overall growth

performance (Pauly and Munro 1984; Vakily 1990), was used. The index is defined as:

$$\phi' = 2 \log_{10}(L_\infty) + \log_{10}K$$

Chilina ovalis lacks a larval stage and eggs are developed inside zig-zag ovoposition gels produced and attached to hard surfaces or stable soft-sediments (Miquel 1984). Snails hatching from ovopositions and colonizing the substrate, had a shell height of approximately 1 mm and will be considered hereafter as recruits. Recruitment patterns were generated from the estimated growth parameters, by backward projection of length frequency data onto the time axis. This type of back calculation usually allows the identification of the number of seasonal pulses of recruitment that have been generated by the population represented in the length frequency data (Pauly et al. 1984; Gayanilo et al. 1989). The recruitment patterns were identified using a maximum likelihood approach with the program "NORMSEP-Hasselblad" to fit a Gaussian distribution (Gayanilo et al. 1996).

Results

WATER COLUMN AND SEDIMENTS

Most of the values for temperature (9.5–20.0°C), chl *a* (0.1–29.2 $\mu\text{g l}^{-1}$), suspended particulate matter (4.0–50.2 mg l^{-1}), and particulate organic matter (1.0–11.0 mg l^{-1}) increased during late spring and summer (October–February), and decreased during the winter (June–August) (Fig. 2). Differences between high and low tide conditions (both in amount and direction) were detected for all these variables, except for temperature. During spring–summer of 1995 and 1996, most of the highest values of chl *a* and seston were detected during low tide conditions. In 1997, most of these highest values were detected during high tide. Apart from the seasonal variability, no interannual changes in monthly averages were evident for any of the water column variables analyzed (Fig. 2).

Sediments occupied by *C. ovalis* were comprised mostly of sand particles (58.0% overall, monthly average range: 18.7–82.5%). Gravel (5.9%, range: 0.8–10.3%), biogenic aggregates (7.9%, range: 3.4–20.3%), and mud (28.2%, range: 6.6–56.4%) were less abundant (Fig. 3). Percent of organic matter in the sediment averaged 10.1% (range: 3.1–32.1%) and, as with grain size, did not show a clear seasonal trend. Only two variables showed a clear (and inverse) pattern of temporal variability to one another during the whole period ($p < 0.05$): the sand content decreased nearly proportionally to the increase in mud percentage (Fig. 3). The density of *S. americanus* varied between 144 and 400 stems m^{-2} , with an overall average of 280

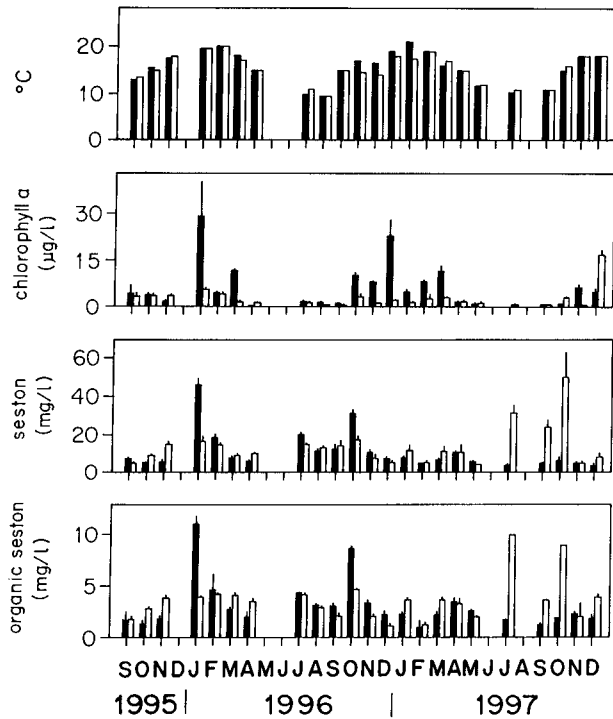


Fig. 2. Mean (SD) monthly water column characteristics at the study area. Black bars = high tide, white bars = low tide. $n = 3$; no samples were collected during December 1995, May and June 1996, and June and August 1997.

stems m^{-2} , although no clear seasonal trend was observed (Fig. 3).

ABUNDANCE AND POPULATION STRUCTURE OF *CHILINA OVALIS*

Monthly mean abundance of *C. ovalis* varied between 0 (June 1997) and 228 ind m^{-2} (March 1996), with an overall mean of 115 ind m^{-2} (SD: 55 ind m^{-2}) for the study period (Fig. 4). Despite a wide monthly variability in snail densities, *C. ovalis* showed a consistent decrease in abundance throughout the study period ($r = -0.71$, $p < 0.01$) (Table 1). Four environmental variables were correlated with the temporal change in abundance: water temperature (+), sand (+), mud (-), and organic matter content (-) (Table 1).

Growth rates of the identified cohorts were similar (Table 2), with major net growth occurring immediately after recruitment followed by a reduction during the winter (June–August) (Fig. 5). Growth increased again in spring and summer but never achieved rates as high as those observed for recently recruited snails. The curves and parameters derived from the growth model (Fig. 5 and Table 2) were very similar for both years. The values of maximum asymptotic length (L_{∞}) for both years were similar and close to the observed max-

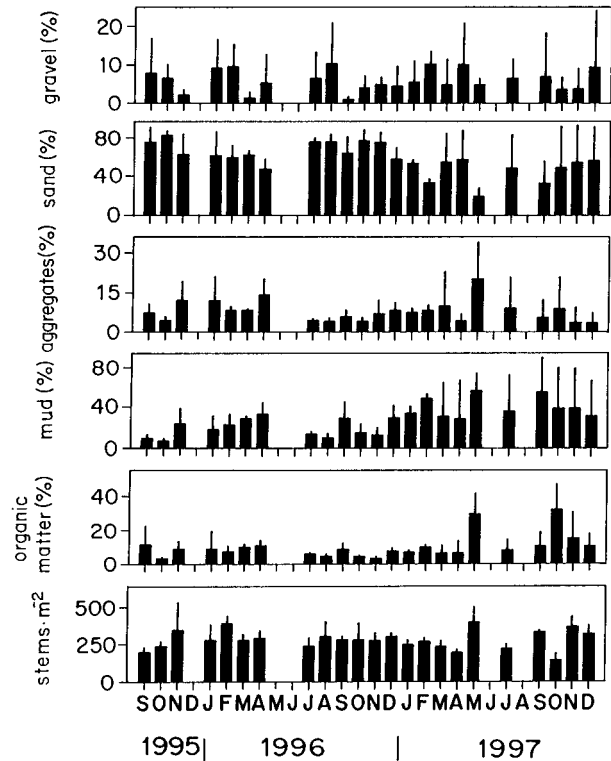


Fig. 3. Mean (SD) monthly sedimentary characteristics and density of stems of *Scirpus americanus*. $n = 4$; no samples were collected during December 1995, May and June 1996, and June and August 1997.

imum shell height (27.5 mm). Values for the growth curvature parameter (K , 0.61 and 0.64 in 1996 and 1997, respectively), and the intensity of the seasonal growth oscillation (C , close to 0.5), indicated a discrete seasonality of growth during 1996 and 1997. Estimates of winter point ($WP = 0.54$ and 0.55 in 1996 and 1997, respectively) indicated that the growth was lowest during June–July. Estimates of the standard growth parameter were also similar between years ($\phi' = 2.69$ and 2.75 in 1996 and 1997, respectively) (Table 2).

The smallest sizes of *C. ovalis* were measured during the summer of both years (February–March) and during the spring of 1997 (October–

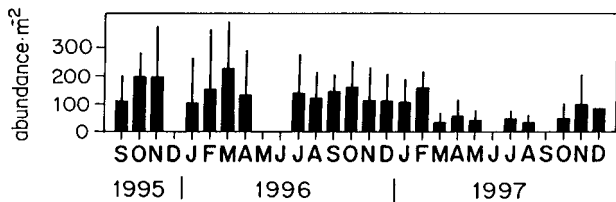


Fig. 4. Mean (SD) monthly abundances of *Chilina ovalis*. $n = 5$; no samples were collected during December 1995, May and June 1996, and June and August 1997.

TABLE 1. Correlation analyses of the abundance of *Chilina ovalis* and environmental variables in water column and sediments. Correlation between abundance and time (measured as number of months) is also presented. Statistical significance of the correlation coefficients is indicated by asterisks (* = $p < 0.05$; ** = $p < 0.01$).

Water Column	r	Sediments	r
Temperature (°C)	0.41*	Gravel (%)	-0.13
Chlorophyll <i>a</i> ($\mu\text{g l}^{-1}$)	0.16	Sand (%)	0.57**
Total seston (mg l^{-1})	-0.11	Aggregates (%)	-0.23
Organic seston (mg l^{-1})	-0.08	Mud (%)	-0.56**
		Organic matter (%)	-0.45*
Time (mo)	-0.71**	Stem density (no. m^{-1})	0.19

November) (Fig. 5). Predicted recruitment (Fig. 6) shows that most of the total annual recruitment was concentrated around October 1996 (23.0% of total) and October 1997 (23.4%).

Discussion

Correlation analysis indicated a significant relationship between population abundance of *C. ovalis* and four environmental factors: water temperature and contents of sand, mud, and organic matter in the sediment. Although these variables are useful to explain the variability in abundance, some caution must be exercised when inferring causal relationships. Temperature has been shown to affect almost every aspect of invertebrate life history (see reviews by Spight 1976 and Giangrande et al. 1994). In general, high temperatures measured during spring-summer months coincided with the increase in number of recently recruited snails, and the relationship between water temperature and seasonality of the macroinfauna has been emphasized in previous studies dealing with benthic communities in the same area (e.g., Jaramillo et al. 1985). The role of sediments in explaining temporal population changes appear to be more indirect (e.g., Jaramillo et al. 1985; Bertrán 1989; Quijón and Jaramillo 1993; Quijón et al. 1996). The relationship between population abundance and sand, mud, or the grain size of the sediment may result from factors closely related to grain size, such as food availability, hydrodynamic characteristics, and disturbance frequency (Forbes and Lopez 1990; Bick and Zettler 1994; Kube et al. 1996).

TABLE 2. Growth characteristics of *Chilina ovalis* estimated by the von Bertalanffy growth equation for 1996 and 1997. Maximum asymptotic shell length (L_{∞}), growth curvature parameter (K), intensity of seasonal growth oscillation (C), winter point (WP), index of goodness of fit (Rn), and standard growth index (ϕ').

Year	Growth Parameters					
	L_{∞} (mm)	K (yr^{-1})	C	WP	Rn	ϕ'
1996	28.22	0.61	0.47	0.54	0.125	2.69
1997	29.72	0.64	0.45	0.55	0.122	2.75

Food availability has been used to explain population or community changes in spatial comparisons (e.g., Morrisey 1990), long-term monitoring (e.g., Davoult et al. 1993), or short-term studies on opportunistic macroinfaunal species (e.g., Marsh and Tenore 1990). The spionid *Streblospio benedicti* showed a strong association of growth and reproduction rates with food availability (estimations based on N and P) over a time period of weeks to months (Marsh and Tenore 1990). Habitat sedimentary change, like the increase in fine sediments observed in this study during a period of 2.5 yr, likely influences food availability for Queule River estuary residents. However, the expected response time for *C. ovalis* is considerably slower than

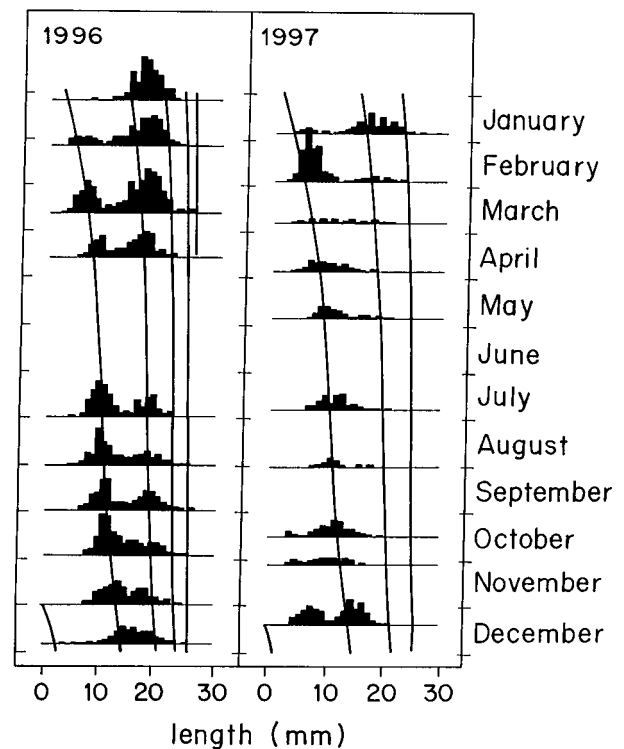


Fig. 5. Monthly variability in the size frequency distribution of *Chilina ovalis* throughout the study period. Lines superimposed on the histograms link successive growing cohorts as extrapolated by the model (see Material and Methods).

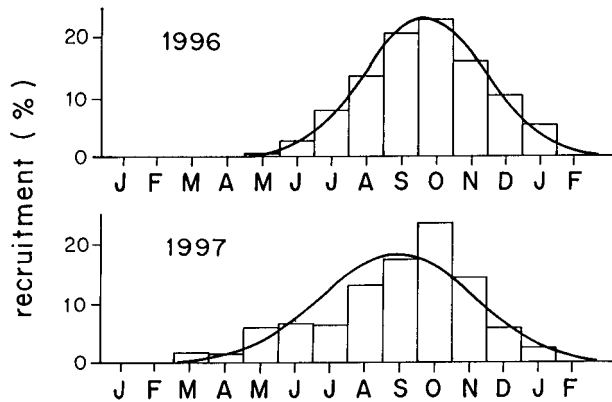


Fig. 6. Recruitment pattern of *Chilina ovalis* obtained from the ELEFAN program. Values on the y-axis correspond to monthly recruit percentages calculated from the total annual recruitment.

that expected for *S. benedicti* given their different life span and survival strategies.

The increase in mud and organic matter content may also result in accumulation of potentially toxic compounds (e.g., volatile sulfides). It may affect *C. ovalis* and more directly, the diatom assemblage associated with these sediments (Watling 1991). In a bottom increasingly affected by reducing conditions, coarser sediments are more permeable and present a higher porewater exchange (Pilditch et al. 1997). That may explain at least partially, the positive relationship between *C. ovalis* abundance and sand content. The effects of biological disturbance and stem density on these sediments are less likely to reduce the snail abundance directly or indirectly by affecting the sand:mud ratio.

The density of *S. americanus* seems to be important in determining the spatial distribution of *C. ovalis* (Quijón personal observation). Stems offer refuge against predators, improve deposition and accumulation of fine sediments (Yang 1998), and offer a substrate for ovoposition attachment (Miquel 1984). In a temporal scale, it is evident that changes in stem density were not related to changes in sediment grain size (Fig. 3) or *C. ovalis* abundance (positively but not significantly correlated; Table 1).

The temporal variability of the food source for *C. ovalis* (benthic diatoms) was not adequately tracked by the chl *a* content in the water (more properly a phytoplankton estimator), the organic seston, or even the sedimentary organic matter. The refractory component included in sedimentary organic matter (Johnson 1974; Mayer 1989) remains as the main explanation to understand why this parameter was not positively correlated to the abundance variability (Table 1).

The interannual variability of *C. ovalis* appears

to be related to recruitment success. The cohort derived from the 1996 recruitment event was clearly less well represented in 1997 than the 1995 cohort was in 1996. Differences in the recruitment intensity between 1995 and 1996 could explain the different representation of small size classes (below ~15 mm) during 1996 and 1997 (Fig. 5). Tallmark (1980) reported interannual changes in abundance of *Nassarius reticulatus* on the Swedish west coast, and also attributed these differences to variable recruitment success. Beukema et al. (1988) offered a similar explanation for their results when analyzing the bivalves *Donax vittatus* (Da Costa) and *Macoma balthica* (L.) and the polychaete *Nephtys hombergi* Savigny, in a wide latitudinal survey of the North Sea. It is not known presently whether interannual differences in recruitment are associated with temporal changes in sediment as those described above (some species recruit on sandy rather than on muddy sediments) (Olafsson et al. 1994), or with other factors operating at different temporal scales. According to the recruitment model, there was one annual pulse and that occurred in spring (September–October) of both years (Fig. 6). Interannual differences in the timing of recruitment were not as evident as in studies of species elsewhere (e.g., the crab *Carcinus maenas* (L.) in the Dutch Wadden Sea; Beukema 1991). In *C. maenas*, timing differences have been explained by changes in temperature ranges (very cold winters) over periods of 10 or more years. According to data from the Queule River estuary (Jaramillo unpublished data), such interannual changes in physical conditions are less likely to occur and affect residents as *C. ovalis*.

As shown by the seasonal growth oscillation (C) and the winter point (WP) parameters, growth followed a typical seasonal pattern, being lower during the winter and higher after the recruitment period (i.e., spring–summer). As has been described for *Ilyanassa obsoleta* (Cranford 1987) and some hydrobiids (Drake and Arias 1995), highest growth rates coincided with highest activity and feeding (Quijón personal observation). This pattern is most likely related to the organism's responses to warmer temperature than to higher food availability. *C. ovalis* does not undergo the hibernation period or diapause observed in many snails of the northern hemisphere, such as *Polinices duplicatus* (Say) and *Ilyanassa obsoleta* (Edwards and Huebner 1977; Curtis and Hurd 1983). *P. duplicatus* ceases feeding and growth for periods as long as 4 mo when ambient temperatures drop significantly, as occurs in tidal flats of northeastern U.S. that are subject to winter freezing (Edwards and Huebner 1977). Such harsh conditions do not occur at the Queule River estuary. In response to the

lowest temperatures observed in estuaries of the area (Jaramillo et al. 1985; Bertrán 1989), *C. ovalis* remains partially buried in the substrate displaying the same behavior reported for congeners living in subtidal soft-bottoms (Bosnia et al. 1990).

The growth curvature parameter (K) and the maximum asymptotic length (L_{∞}), suggest a longevity between 3.5 and 4 yr (Gayano et al. 1989) for *C. ovalis*. This longevity is high in relation to snails such as *Lymnaea peregra* (Müller) (1.4–1.5 yr, Gaten 1986) and several hydrobiids (1.4 yr, Drake and Arias 1995), but it is low when compared with snails of similar size such as *P. duplicatus* (5 yr, Edwards and Huebner 1977), *I. obsoleta* (7 yr, Curtis and Hurd 1983), and *Nassarius reticulatus* (L.) (15 yr, Tallmark 1980). A longevity > 2 yr in *C. ovalis* suggests the existence of more than one reproductive period in its life cycle (Giangrande et al. 1994). This repeated reproduction (iteroparity) contrasts with the semelparity (one reproductive period in the life span) reported by Miquel (1986) for the freshwater congeneric *Chilina fluminea fluminea*. Iteroparity is not surprising as chilinid and even basommatophoran snails have been described as groups with high flexibility of life history and reproductive strategies (Calow 1978; Russel-Hunter 1978). Caquet (1993) compared three basommatophoran species, *Lymnaea palustris* (Müller), *Physa fontinalis* Linnaeus, and *Anisus rotundatus* (Poiret), and identified iteroparity in the first species and semelparity in the other two. Based on his review of published works on these species, Caquet (1993) suggested that food and physical constraints can result in different reproductive strategies even at the population level. Warwick (1984) analyzed the reproduction and growth in long-lived bivalves and polychaete species and concluded that species with longevity > 3 yr often forego reproduction during their first year in order to allocate most of their energy to post-recruitment growth. Although our data do not allow us to separate reproduction and recruitment originating from different cohorts, a similar strategy of energy allocation in *C. ovalis* is clearly possible.

Alternative hypotheses to explain population variability in *C. ovalis* include predation on adults or eggs and parasitism. It has been shown that epibenthic predation affects macroinfauna community structure at the Queule River estuary (e.g., Venegas 1992), as well as in other estuarine and limnetic areas around the world (e.g., McCollum et al. 1998). Chilinid snails have been suggested as a major prey item of benthic-feeding fishes (e.g., the silverside *Patagonina hatcheri*) and birds (e.g., the red-gartered coot *Fulica armillata*) (Ferriz 1987; Bosnia et al. 1990). Predation on egg masses by small invertebrates such as leeches, as found by Mi-

quel (1984) for a *C. fluminea fluminea* population, could also account for variability in snail abundance. A last factor that could regulate population abundance of *C. ovalis* at any stage of the life cycle is disease. As in species of the genera *Littoridina* (de Ostrowski 1993) and *Ilyanassa* (Curtis 1995), different species of trematodes affect growth, gonadal development, and feeding rates of *Chilina* species (Brown and Pullan 1987; Bosnia et al. 1990). The importance of these factors to *C. ovalis* population density, as compared to food availability, sediment granulometry and temporal physical variability remains to be tested.

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