RESEARCH ARTICLE

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Age, growth, and mortality of the prosobranch *Zidona dufresnei* (Donovan, 1823) in the Mar del Plata area, south-western Atlantic Ocean

Abstract The volutid snail *Zidona dufresnei* is a benthic top predator in the Mar del Plata (Argentina) shelf area where it was subjected to unregulated commercial exploitation for more than 20 years. So far there is no stock management, and hitherto even the most basic information on population dynamics of this species is missing. Annual formation of internal shell growth bands visible by x-ray was confirmed by the stable oxygen isotope record in the shell carbonate that reflects seasonal oscillations in water temperature. A Gompertz growth function ($SL_\infty = 208.84$ mm, $K = 0.211$ year^{-1}, $t_0 = 5.496$) fitted 142 pairs of size-at-age data (30 shells) best. Maximum individual production amounted to 26.8 g shell-free wet mass (SFWM) at 115 mm shell length. Based on a size-frequency distribution derived from commercial catches, annual mortality rate of *Z. dufresnei* was estimated to be 0.61 (± 0.21) year^{-1}.

Introduction

The snail *Zidona dufresnei* (Caenogastropoda, Volutidae) is endemic to the south-western Atlantic Ocean from Río de Janeiro, Brazil (22°S) to San Matías Gulf, Argentina (42°S), where it inhabits sandy bottoms

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between 35 and 60 m water depth (Kaiser 1977). Owing to its predatory lifestyle and large size, *Z. dufresnei* is likely to be a key species of these shallow water ecosystems. Since 1983, *Z. dufresnei* has supported a fishery throughout the Mar del Plata area (38°20′S, 57°37′W). Over the last 5 years, however, landings in Argentina fell from 1,300 to 500 metric tons per year. At present this fishery is not regulated and the development of management strategies is difficult, as most basic information on population dynamics of *Z. dufresnei* is missing, except for the reproductive cycle (Giménez and Penchaszadeh 2002) and size at first maturity (Giménez and Penchaszadeh 2003). Our study provides first estimates of individual growth, production, and mortality in this species.

Material and methods

Sampling

Specimens of *Zidona dufresnei* were collected during commercial bottom trawling off Mar del Plata, Buenos Aires, Argentina (38°20′S, 57°37′W) (Fig. 1) in 40–50 m water depth (annual temperature range 9–17°C, constant salinity of 35 psu, Guerrero et al. 1997) during the years 1999 and 2000. On 24 different cruises, 96 hauls were taken with bottom trawls of 4- to 6-m mouth opening and 42×42-mm mesh size in the cod end. In all, 1,051 individuals were collected randomly from the catches and taken to the laboratory.

Shell length (SL), that is, the distance between apex and aperture, and shell width (SW) were measured with a vernier caliper to the lower millimetre and shell-free wet mass (SFWM) was determined with ± 0.1 g precision. The relation between size and mass was established by linear regression of log(SFWM) versus log(SL).

Age and growth

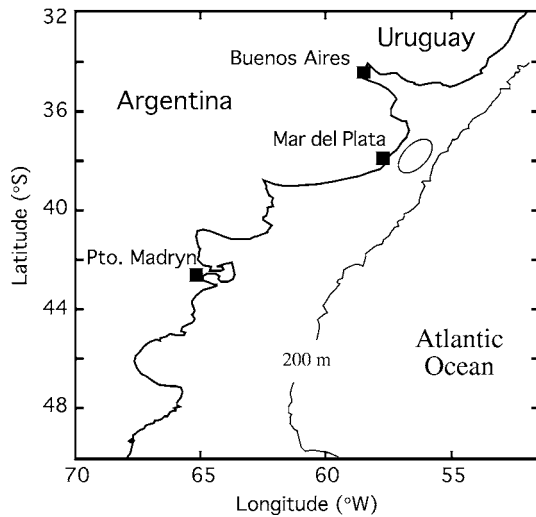Individual age was inferred from internal shell growth bands by a three-step process: (1) growth band identifi-

Fig. 2 Determination of the relation between age and shell size in *Zidona dufresnei*. Carbonate samples were positioned along the spiral growth trajectory of the shell edge (*solid line*). The shell length corresponding to a certain carbonate sample or to a certain internal shell growth mark, respectively, was defined as the distance between the apex and the growth trajectory at this position and was measured as indicated by the *stippled lines* SL_1 and SL_2

cation, (2) validation of annual growth band formation, and (3) quantitative size-at-age determination. Shells were cut sagitally from the apex to the anterior canal, that is, following the growth trajectory along the shell spiral. X-ray photographs of shells (Hewlett Packard Faxitron 43855 mammograph with fixed anode, using AGFA-Strukturix D4 FW film and the parameter settings: focal film distance 45 cm, voltage 40 kV, 60- to 70-s exposure time) revealed macroscopically visible bands of higher density perpendicular to the shell growth trajectory. These bands were interpreted as growth marks caused by a slowdown in the rate of shell formation.

Stable oxygen isotope ratios ($\delta^{18}O$) were used to analyse whether these bands were formed annually, as described recently by Brey and Mackensen (1997), Lomovasky et al. (2002), and others. The ratio of the stable oxygen isotopes ^{16}O and ^{18}O in biogenic calcium carbonate structures is inversely proportional to temperature during shell deposition. This relation is nearly linear between 5 and 30°C, as demonstrated empirically by Epstein et al. (1951) and Epstein and Lowenstam (1953). Therefore, a mollusc shell from an environment with rather constant salinity and a distinct annual temperature cycle will show an oscillating pattern of $\delta^{18}O$ along the major growth axis (see examples in Krantz et al. 1987; Richardson 2001; Lomovasky et al. 2002). Five representative specimens (two males of 50 and 170 mm SL and three females of 80, 161, and 198 mm SL) of *Z. dufresnei* sampled in Spring 2001 were selected for isotope analysis. The soft parts were removed and the shell was cleaned with 5% NaCl. In *Z. dufresnei* the shell is completely covered by the snail's mantle; that is, only the central layer of the three-layered shell represents an unbiased archive of temperature history. Therefore the outermost shell layer was carefully removed using a fine corundum paper prior to carbonate sampling. Samples (approx 150 μg each) were taken from the central layer by a small dental drill at 1–15 mm distance along the spiral growth trajectory from apex to shell aperture. The corresponding SL, that is, the straight distance of sample to apex, was recorded (Fig. 2). The stable oxygen isotope composition was determined in the Stable Isotope Laboratory of the Alfred Wegener Institute with a Finnigan MAT251 mass spectrometer coupled to an automatic carbonate preparation device. The results were reported in δ-notation versus PDB (Vienna Pee Dee belemnite) standard calibrated via NIST 19 (National Institute of Standards and Technology isotopic reference material 19). The precision of measurements was better than ±0.08‰ for $\delta^{18}O$, based on repeated analysis of a laboratory working standard over a 1-year period. Counting $\delta^{18}O$ troughs/peaks (i.e. summers/winters) from apex towards aperture provided the age of each trough and the distance of the corresponding sample from the apex provided the corresponding shell length at this age. The annual formation of x-ray-visible growth bands is confirmed if the position of these bands coincides with the position of $\delta^{18}O$ peaks.

On confirmation of annual growth band formation, x-ray photographs of shells of 30 individuals (15 females and 15 males) were taken and age and corresponding SL of each growth band in every shell were recorded (Fig. 2). The iterative non-linear Newton algorithm was used to fit growth models to the resulting size-at-age data pairs. A Gompertz growth model was found to fit these data best:

$$SL_t = SL_\infty * e^{-e^{-K*(t-t_0)}} \tag{1}$$

Mortality

Total mortality rate Z according to the single negative mortality model

$$N_t = N_0 * e^{-Z*t} \tag{2}$$

was estimated by a size-converted catch curve (Pauly 1984a, 1984b)

$$\ln(N_i/\Delta t) = a + b * t_i \tag{3}$$

where N_i is number in size class i, Δt is the time required to grow through this size class, t_i is age at midsize of size class i, and $Z = -b$. This curve was based on the size-frequency distribution of the 1,051 individuals sampled and the Gompertz growth function.

Production

Individual annual somatic production P_i (SFWM) was calculated by the mass-specific growth rate method according to Crisp (1984) and Brey (2001) from the size-growth function and the size-body mass relation:

$$P_i = M_i * G_i \qquad (4)$$

where M_i is mean individual body mass at size i and G_i is the annual mass specific growth rate at size S_i as calculated by

$$G_i = b * K * \ln(SL_\infty / SL_i) \qquad (5)$$

Results

Size and mass

The 1,051 specimens collected ranged from 50 to 210 mm shell length (mean $SL = 159.8$, $SD = 17.63$) but with the majority of animals > 140 mm (Fig. 3). SFWM ranged from 28 to 350 g and was related to SL by

$$\log(\text{g SFWM})$$
$$= -1.482 + 1.733 * \log(\text{mm SL}) \quad N = 140, \ r^2 = 0.609$$

and SL was related to shell width (SW) by

$$SL = 1.211 + 2.660 * SW \quad N = 1,051, \ r^2 = 0.947$$

Age and growth

In all five shells analysed for stable isotopes the $\delta^{18}O$ profile showed a distinct oscillatory pattern that reflects a cyclical environmental temperature regime (Fig. 4). According to Epstein and Lowenstam's (1953) paleo-temperature equation the observed difference in $\delta^{18}O$ of up to 1‰ corresponds to a temperature amplitude of about 4°C. As the annual cycle is the only temperature signal of this magnitude in Mar del Plata waters (Ramírez et al. 1973; Guerrero et al. 1997; Carreto et al. 1998), the $\delta^{18}O$ profile reflects the seasonal temperature pattern. The positions of x-ray visible bands coincide very well with the position of $\delta^{18}O$ peaks (Fig. 4); that is, one growth band is formed each austral winter. The 142 size-at-age data pairs derived from the 30 x-rayed specimens were fitted best by the Gompertz equation (Fig. 5):

$$SL_t = 208.84 \text{ mm} * e^{-e^{-0.2111*(t-5.496)}} \qquad N = 142, \ r^2 = 0.980$$

Individual production and population mortality

Individual somatic production P_i increases with size up to a maximum of 26.8 g SFWM year^{-1} at 115 mm shell width and decreases again towards larger sizes (Fig. 3). The size-converted catch curve (Fig. 6) indicates that animals younger than 12 years are strongly under-represented in our sample. Annual mortality rate of $Z.$ dufresnei amounted to 0.61 year^{-1} (95% confidence range ± 0.21).

Discussion

Sampling

Our size-frequency data (Fig. 3) are based on commercial catches with 42×42-mm mesh size in the cod end. Hence animals up to about 60 mm shell width (SW), that is, 160 mm SL ($= \pm 12$ years), may slip through the meshes. The size-converted catch curve (Fig. 6) indicates that sampling efficiency is distinctly $< 100\%$ below this size (age) limit; that is, the size-frequency distribution of Zidona dufresnei is heavily biased towards larger animals (Fig. 3). Therefore estimates of production and of pro-

Fig. 3 Size-frequency distribution of Z. dufresnei ($N = 1,051$) in commercial catches from the Mar del Plata area in the years 1999 and 2000, using class intervals of 5 mm. *Dots* Superimposed curve of individual production P_i (grams shell-free wet mass year^{-1}) versus size in Z. dufresnei
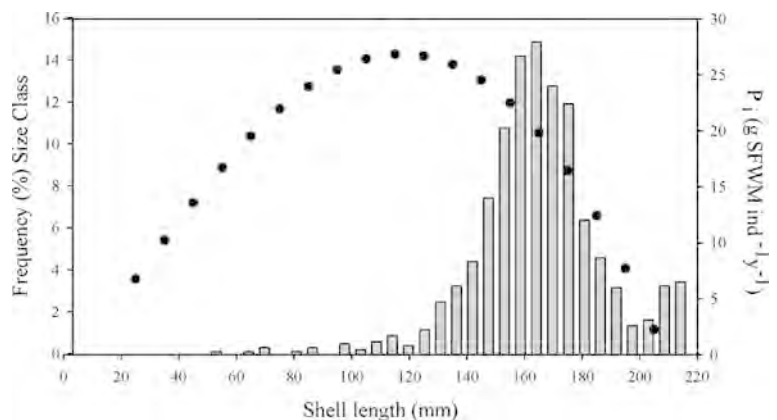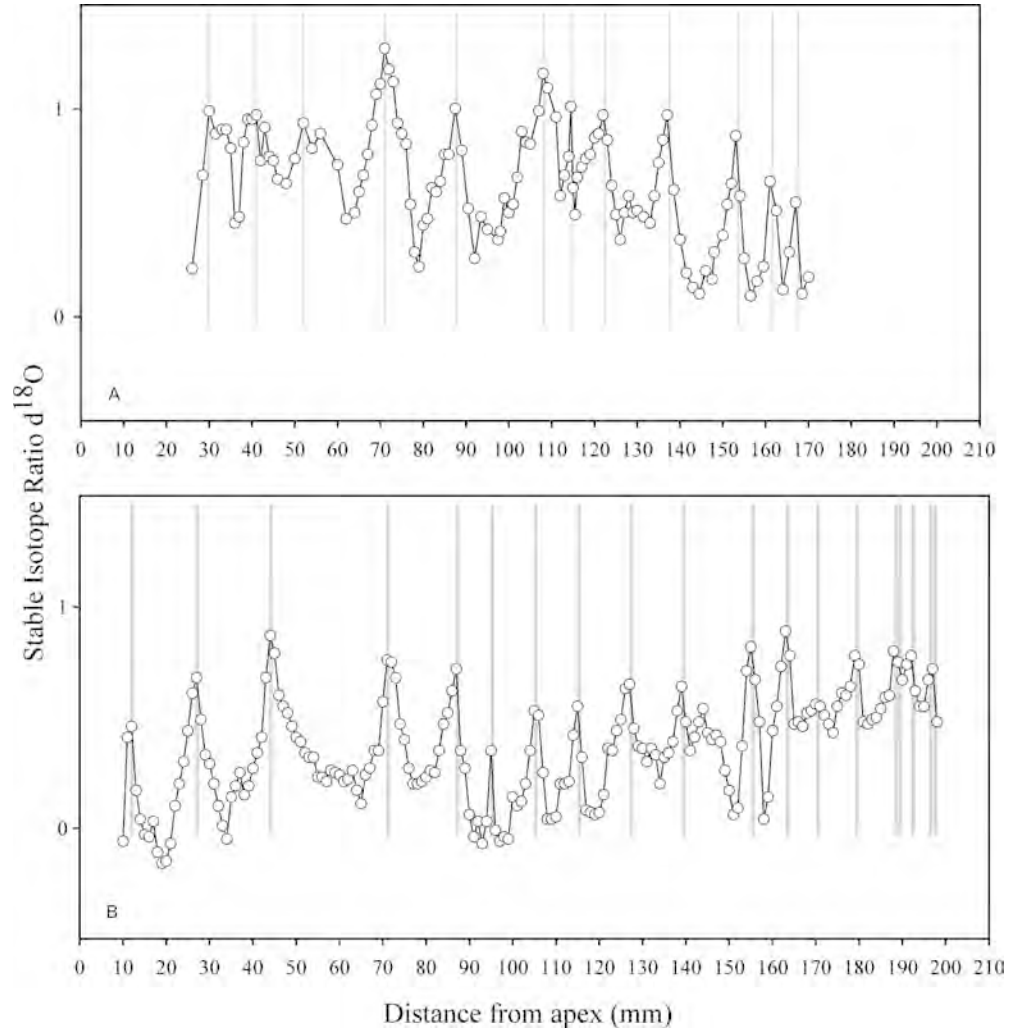
Fig. 4A, B $\delta^{18}O$ profile along a transect from apex to shell edge in two individuals of *Z. dufresnei*. **A** 170 mm SL, 13 years old; **B** 198 mm SL, 17 years old. *Peaks* correspond to temperature minima (winter), *troughs* to temperature maxima (summer). *Grey bars* indicate position of x-ray-visible growth bands

duction-to-biomass ratio based on this distribution clearly underestimate population values and are hence not provided here.
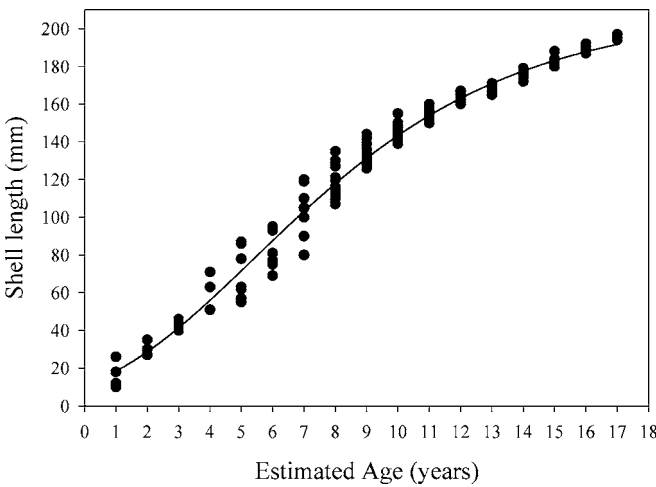

Fig. 5 Gompertz growth curve fitted to 142 size-at-age data pairs obtained from 30 x-ray-photographed shells of *Z. dufresnei*: $SL_{\infty} = 208.84$ mm $* e^{-e^{-0.2111*(t-5.496)}}$; $N = 142$, $r^2 = 0.980$
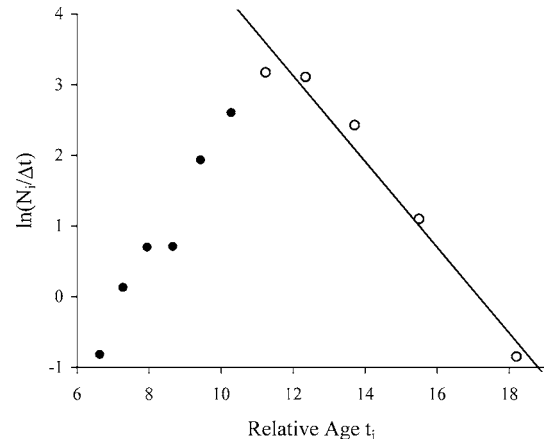

Fig. 6 Size-converted catch curve based on the size-frequency sample (Fig. 2) and the growth function (Fig. 4) of *Z. dufresnei*. *Open circles* Data included in regression; *solid circles* data excluded from regression. $\ln(N_i/\Delta t) = 10.41 - 0.607*t_i$; $N = 142$, $r^2 = 0.983$, 95% confidence range of slope is ± 0.207

Age, growth, and sexual maturity

Potential lifespan of *Z. dufresnei* in the Mar del Plata region is >17 years, as the largest individuals recorded so far had a shell length of 198 mm. This is in the upper range of lifespans recorded for large gastropods such as *Buccinum undatum* Linnaeus (12 years; Gendron 1992), *Gazameda gunnii* (Reeve) (6–7 years; Carrick 1980), or *Strombus gigas* Linnaeus and *Strombus costatus* Gmelin (7 and 5 years, respectively; Wefer and Killingley 1980). *Z. dufresnei* starts to mature sexually at approximately 120–130 mm shell length, and 50% of all individuals are mature at about 150–160 mm (Giménez and Penchaszadeh 2003). According to our growth model (Fig. 5), maturation starts at an age of about 8–9 years and coincides with the end of the "quasi-linear" growth phase. This seems to be rather late compared to other large gastropods from boreal regions such as *B. undatum* (6–7 years; Gendron 1992), *G. gunnii* (2.5–3 years; Carrick 1980), or *Haliotis rubra* (6–7 years; Prince et al. 1988).

The question of why lifespan is so long and first maturity is so late in *Z. dufresnei* is still unanswered. As this is the first member of the Volutidae studied in such detail there exist no comparable data from within this family. The very peculiar egg capsules of the South American Volutidae (Penchaszadeh and de Mahieu 1976) may give some hints: they are fairly big, up to 50 mm in basal diameter and 35 mm high, generally attached to a substrate, and contain extra food for the embryos as albumine in the intracapsular fluid; no nurse eggs are present. *Z. dufresnei* has somewhat smaller egg capsules of about 20 mm in basal diameter, but egg capsule size and complexity may imply certain anatomical capabilities and capacities for egg production that could be met only beyond a certain size and age.

Fishery and its potential impact on the benthic system

Little is known of structure and functioning of the Mar del Plata shallow water ecosystem and of the role *Z. dufresnei* plays in this system. Major prey species of *Z. dufresnei* are the abundant bivalves *Mytilus edulis platensis* and *Aequipecten tehuelchus*. Large Volutidae, however, are voracious predators on almost all bivalves and gastropods available to them (e.g. Ponder 1970; Weaver and du Pont 1970; Taylor 1981, Morton 1986). Hence, *Z. dufresnei* is very likely to be linked trophically to many species and to be among the benthic top predators in the food web of the Mar del Plata shallow water system. The major competitors of *Z. dufresnei* are not yet identified, but other volutid species such as *Adelomelon beckii* or starfish are likely candidates.

So far, no studies on gear efficiency and size selectivity exist for gastropod fisheries in the south-western Atlantic Ocean. Our data indicate, however, that the gears applied in the Mar del Plata area endanger the reproductive capacity of the stock: gear efficiency approaches 100% at about 10–11 years of age (Fig. 6). About 50% of all individuals are mature at this age (Giménez and Penchaszadeh 2003); that is, only a very small part of the reproductive population is not under exploitation pressure. Both the sharp fall in landings over the last 5 years (2,300 to 1,000 tons in Argentinean and Uruguay fishery) as well as the decrease in maximum size (>190 mm SL in 1999–2000, <190 mm SL in 2001, personal observation) point towards continuous overexploitation of the Mar del Plata stock of *Z. dufresnei*. The continuation of the current exploitation level may cause the marginalization of *Z. dufresnei* in the system and, in the worst case, a permanent shift to a new stable trophic situation where competitors of *Z. dufresnei* take over its niche. Hence there is urgent need to establish regulative measures such as minimum size at landing and protected areas (e.g. Pauly et al. 2002) to maintain this valuable resource and to avoid potentially irrevocable changes of the ecosystem.

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