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Reproductive cycle of *Zidona dufresnei* (Caenogastropoda: Volutidae) from the southwestern Atlantic Ocean

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Abstract Gonadal development of *Zidona dufresnei* (Donovan, 1823) (Caenogastropoda: Volutidae) was studied over a period of two consecutive years, through analysis of gonadal tissue. Individuals were sampled monthly at the Mar del Plata area, Argentina. Gonadosomatic index was estimated for males and oocyte size was used to estimate the stage of gonadal development in females. The reproductive season in this species in the sampled locality extended from October to March (austral spring–summer). During summer, a stage of advanced gonadal development and spawning predominated in the adult population. In autumn, gonads were generally under atresia; during wintertime (June–August), they underwent a period of recovery that lasted until the spring months, when gametes were released again. Synchronism between both sexes was evident. Marked periods of spawning were followed by resorption periods and then a growing phase; it was very clear that reproductive seasonality was linked to changes in bottom water temperature. These results suggest that *Z. dufresnei* gonads have a yearly cycle of gamete production, with two major activity peaks in September–October and January–February.

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Introduction

Zidona dufresnei (Fig. 1) inhabits the western coast of the southern Atlantic Ocean, at 35–60 m depth on sandy bottoms from the Río de Janeiro, Brazil (22°S), to Patagonian waters, San Matías Gulf, Argentina (42°S) (Kaiser 1977). Previous studies have described *Z. dufresnei* taxonomy (Clench and Turner 1964) and geographic distribution (Kaiser 1977), but there is very little literature on the reproduction of volutids in general. It is an abundant species on the continental shelf of Buenos Aires province (Argentina) and Uruguay. *Z. dufresnei* is a dioecious species with copulatory organs. The animals lay egg capsules, and each capsule contains from two to six embryos; the development is direct (Penchaszadeh and de Mahieu 1976). Adults of this species are commercially exploited, with yields that reach 1,300 metric tons of meat per year. The most important commercial Argentinean harbors for *Z. dufresnei* fisheries are Mar del Plata, yielding 90% of the catch, and Necochea, which yields the remaining 10% (e.g. SAGyP 1987). In Uruguay, main landings are at La Paloma Harbor. Considering the relatively high rates of exploitation, the Argentinean and Uruguayan populations of this species could be seriously endangered. Hence, studies on its biology and life cycle are important and necessary to maintain sustainable fishing policies. Because of the need to regulate the fishery of this species, studies on its reproductive biology are required.

D'Orbigny (1847), Clench and Turner (1964), Novelli and Novelli (1982), Penchaszadeh and de Mahieu (1976), Penchaszadeh et al. (1999) and Penchaszadeh and Miloslavich (2001) have described various aspects of the biology of South American volutids. We studied the reproductive cycle of *Z. dufresnei* using histology, and observing gonadal maturation at macroscopic (color, weight of gonads) and microscopic levels.

Materials and methods

Collection of *Zidona dufresnei*

Adults of both sexes were collected monthly by bottom trawling, from January 1999 to December 2000 in the Mar del Plata area, Argentina (38°20′S; 57°37′W), at 40–60 m depth. A total of 30–40 snails per month, ranging from 15.0 to 21.0 cm total shell length, which corresponds to sexually developed animals (Giménez and Penchaszadeh 2000).

Each snail was measured (shell length) with a vernier caliper at a precision of 1 mm, and weighed at a precision of 0.1 g (total soft fresh body weight without shell: BW). Gonads were removed and fixed in Bouin's solution for 18 h. A medial portion of the preserved gonads was dehydrated in alcohol, embedded in paraffin wax and sectioned at 6 μm. The sections were stained with hematoxylin-eosin (H/E). The diameter of all unbroken oocytes with conspicuous nucleoli were measured with a micrometer, including those found free in the follicular lumen and those still attached to the wall.

Gonad from each male, from a total number of 432, was dissected and weighed. Gonad weight (GW) and body weight (BW) were measured, and the gonadosomatic index (GSI) was calculated as follow: $GSI = (GW/BW) \times 100$.

Histological analyses of samples from each male gonad were performed using the same technique previously described. In all males studied, the testes could be easily distinguished from the adjacent hepatopancreas due to their color. The color of the gonad was recorded, and the relationships between color, GSI and light microscopy results were analyzed. To find a relationship between color and GSI, we pooled the data from gonads that had been surveyed over a period of 24 months. One-way analysis of variance (ANOVA) was used to investigate differences in the variation of testis color and the relationship between GSI and gonad color. Tukey's test was used as a suitable a posteriori test to determine whether there was significant variation among gonad colors (Sokal and Rohlf 1995).

All the histological photographs were taken through a Zeiss Axiostar microscope with a digital camera.

Results

The total number of captured animals analyzed (880) showed a 1:1 sex ratio for males to females. Males were clearly distinguishable from females by their conspicuous penis.

Fig. 1 *Zidona dufresnei*. Detail of a commercial yield

Females

Females were in the early active stage from January to March and in the growing phase from June to September (Table 1). Oogonia and previtellogenic oocytes started to propagate within the ovary (Fig. 2a). Previtellogenic oocyte sizes ranged from 10 to 20 μm. Snails collected during December, January and August were in the so-called active stage (Fig. 2b). A number of early vitellogenic oocytes were seen, ranging from 60 to 80 μm in diameter. During the ripe stage, oocytes grew >80 μm in diameter and there was an increase in the ratio of the cytoplasm, which contained a larger number of yolk granules (Fig. 2c). Post-spawning stage individuals were found during March, April, November and December, after the spawning period. The undischarged oocytes within the ovary underwent lysis, and the oocyte products seem to be reabsorbed, with the presence of yellow brownish "residual bodies" (Fig. 2d).

We observed different stages of gonadal development during the study period. During January 1999, ovaries contained oocytes of all sizes, from 10 to 130 μm (Table 1). In February, oocytes measured ranged from 10 and 70 μm, but none of the larger oocytes were intact, indicating they were left over from a previous reproductive season. From February on, residual mature oocytes that were not spawned began to degenerate.

April was characterized by gonadal resorption. After May, we observed both residual oocytes and small oocytes beginning to grow. In winter (June–August), oocytes underwent vitellogenesis and growth. During September, oocytes grew up to 150 μm in diameter (Table 1), and, in October, a new spawning period began and continued until November. In December, "residual bodies" were again present within the ovary. Periods of gonad resorption were identified in April, May and December 1999 and in May and November 2000 (Fig. 2d). The resorption process was characterized by the presence of yellow-brownish bodies within the ovarian follicles that represented degenerated or unspawned oocytes. This phenomenon was evident after the two reproductive periods.

Males

During the growing stage, testes with different stages of spermatogenesis were observed within the spermatogenic tubules (Fig. 3a). Individuals in the early active stage were present during all year around. Ripe gonads were found from August to March, and the spermatogenic lumen was full of sperm. A large number of spermatozoa were also observed within the spermatic duct before spawning (Fig. 3b, c). The spawning period occurred from January to March and from October to November. After the reproductive stage, the lumen of each spermatogenic tubule was empty of sperm and testis were in the resting stage (Fig. 3d).

Table 1 *Zidona dufresnei*. Monthly values of oocyte size and stages of oocyte development (x mean oocyte size; N number of females; n number of measured oocytes)

Months	Oocyte size (μm)	$x \pm$ SD (μm)	N	n	Stage of oocyte development
1999					
Jan	10–130	60.74 ± 5.57	10	170	Growing and ripe
Feb	10–70	61.03 ± 4.17	11	179	Growing and spawned
Mar	10–70	49.64 ± 11.86	9	152	Growing and spawned
Apr	10–50	40.09 ± 9.69	8	200	Growing, resorption
May	10–50	32.17 ± 9.4			Growing, resorption
			10	152	
Jun	10–50	50.83 ± 16.12	12	145	Growing
Jul	10–90	53.45 ± 12.32	10	156	Growing
Aug	10–90	66.75 ± 16.25	9	158	Growing
Sep	10–150	88.43 ± 12.45	11	185	Growing and ripe
Oct	10–70	47.81 ± 12.45	11	198	Growing and spawned
Nov	10–130	56.63 ± 16.35	10	185	Growing and ripe
Dec	30–110	82.73 ± 25.34	12	202	Growing, resorption
2000					
Jan	10–110	75.90 ± 26.45	11	164	Proliferation growth and ripe
Feb	10–130	46.87 ± 20.32	11	139	Proliferation growth and ripe
Mar	30–90	41.25 ± 1.76	10	125	Growing and Spawned
Apr	10–70	46.37 ± 10.35	11	172	Proliferation growth
May	10–70	49.27 ± 9.86	10	102	Proliferation growth and resorption
Jun	30–70	50.42 ± 8.68	9	96	Growing
Jul	20–80	52.5 ± 11.65	10	137	Growing
Aug	20–80	70.34 ± 15.42	11	189	Growing
Sep	60–140	65.57 ± 17.40	10	197	Growing and ripe
Oct	20–100	42.20 ± 6.07	10	235	Growing and spawned
Nov	20–140	58.13 ± 13.8	12	141	Growing, ripe and resorption
Dec	20–110	68.54 ± 25.20	9	186	Growing

The highest GSI values in 1999 (Fig. 4c) were observed in January (1.90), September (1.65) and December (2.05). A decrease in GSI was recorded from January 1999 to April 1999 (1.15) and in October 1999 (1.21), and a gradual decrease was also evident in the summer, from December 1999 to March 2000 (1.35). In September 2000, the highest GSI values were recorded (2.1), followed by a decrease in November 2000 (1.35). The lowest gonad indexes corresponded to April 1999 and March 2000 (1.23). This series of events marked an annual cycle.

In January 1999, there was a maximum gonad index, spawning began and lasted until May. This was a period of male gamete release, without massive new production of sperm. From May on, the gonad began to grow again and the GSI increased. Growth was maintained until September. In September, a period of gamete release began again until October (GSI = 1.2), although of lesser intensity than that of December 1999–May 2000. In December, gonads began to recover, and the maximum GSI reached 2. Immediately afterwards, males entered into a period of maximum reproductive activity in summer (December–March), repeating the annual cycle. From March on, gonads began to grow again and the GSI increased until September 2000 (2.15), with the highest values for that year; however, after September, the GSI decreased until November 2000 (1.3). From September to November 2000 there was again a period of copulation.

In males, there was considerable variation in gonad color and also in the relationship between GSI and gonad color (pale yellow, brownish orange and dark brown). Table 2 shows GSIs (means ± SD) for each gonad color (ANOVA, $P < 0.001$).

Annual cycle of reproductive activity

The period of oocyte growth and maturation, from January to June 1999, corresponded to an increase in seawater temperature (Fig. 4a, d). In Fig. 4d, we can observe that temperature increased from its minimum in winter (9–10°C) to its maximum in summer–early autumn (17–18°C). Afterwards, a gradual decrease in water temperature reconstituted the cycle. Oocytes > 80 μm were spawned from January to March 1999 and from January to April 2000. Moreover, another reproductive activity peak occurred from September to October 1999, while from September to October 2000 there was a period of spawning that was followed again by a new oocyte proliferation.

Histological sections of specimens collected after the periods of maximum spawning indicate that approximately 10–30% of the oocytes with nuclei and visible nucleoli showed degradation. The largest numbers of degrading oocytes were observed in April 1999 and in April and May 2000, after the end of the summer spawning season (Fig. 4a). Residual oocyte material was

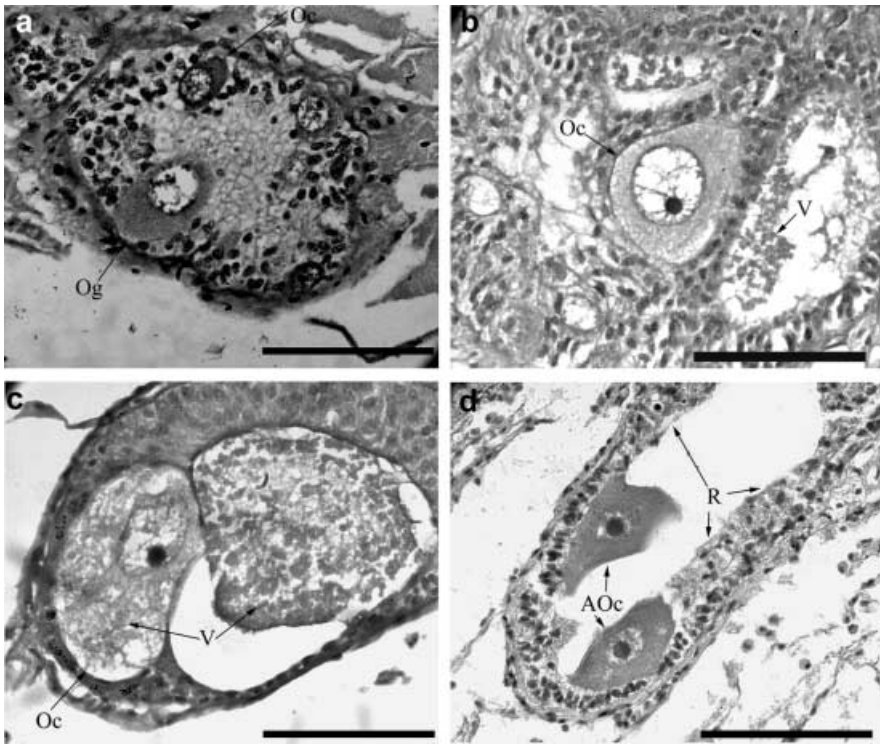

Fig. 2a–d *Zidona dufresnei*. Light micrographs showing histological sections of ovaries from adult females. **a** Early growing phase. Growing oogonia (*Og*) and previtellogenic oocytes are present along the follicle wall. **b** Active stage. Early vitellogenic oocytes (*Oc*) have increased in size, yolk (*V*) is present in the cytoplasm. **c** Ripe stage. Vitellogenic oocytes ready to release. **d** Post-spawning stage. Atresic oocytes (*AOc*). Some yellow brownish material was observed within the follicle as residual bodies (*R*). *Scale bars* = 100 μm

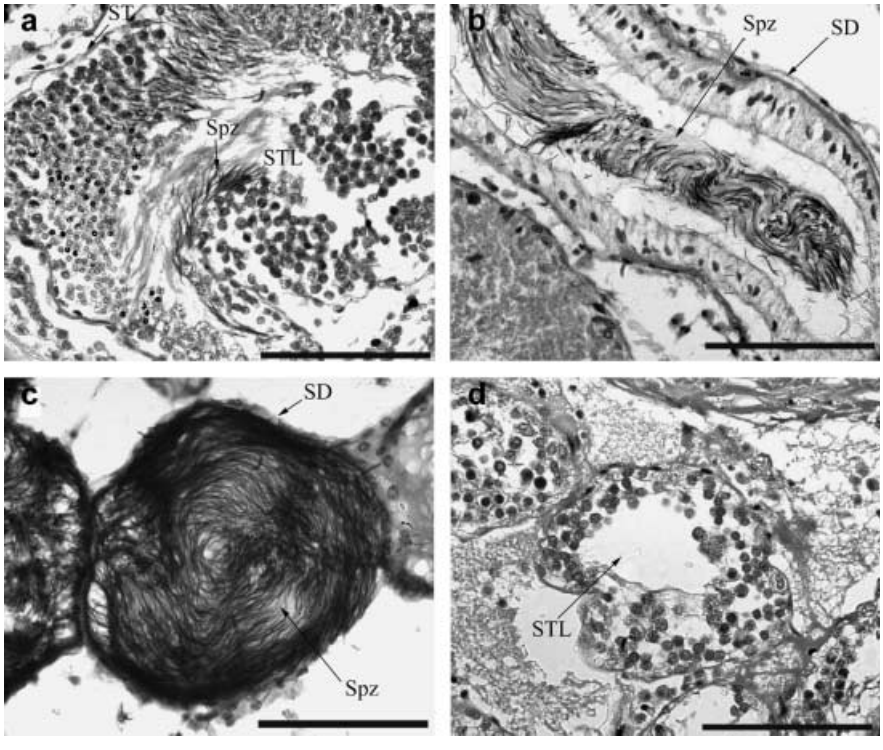

Fig. 3a–d *Zidona dufresnei*. Light micrographs showing histological sections of testes from males. **a** Growing stage (pale yellow). Testis with different stages of spermatogenesis within the spermatic tubule (*ST*), including some spermatozoa (*Spz*) in the spermatogenic tubule lumen (*STL*). **b** Ripe testis, sampled in October (dark brown gonad). The lumen of the spermatic duct (*SD*) is completely filled with spermatozoa. **c** Section of a spermatic duct filled with mature spermatozoa. **d** Testis after the reproductive period. Lumen of spermatogenic tubule without spermatozoa. *Scale bars* = 100 μm

observed in April–May 1999, December 1999, May 2000 and November 2000 (Fig. 4b).

In males, minimum GSI corresponded to maximum bottom water temperature. Gamete release began in January 1999 and continued until April 1999, when temperature increased. Release of sperm declined with the drop in temperature in April 1999. Winter (April–August) was a recovery period. The abrupt decrease in the male index between September 1999 and October 1999 coincided with the release of oocytes > 80 μm by

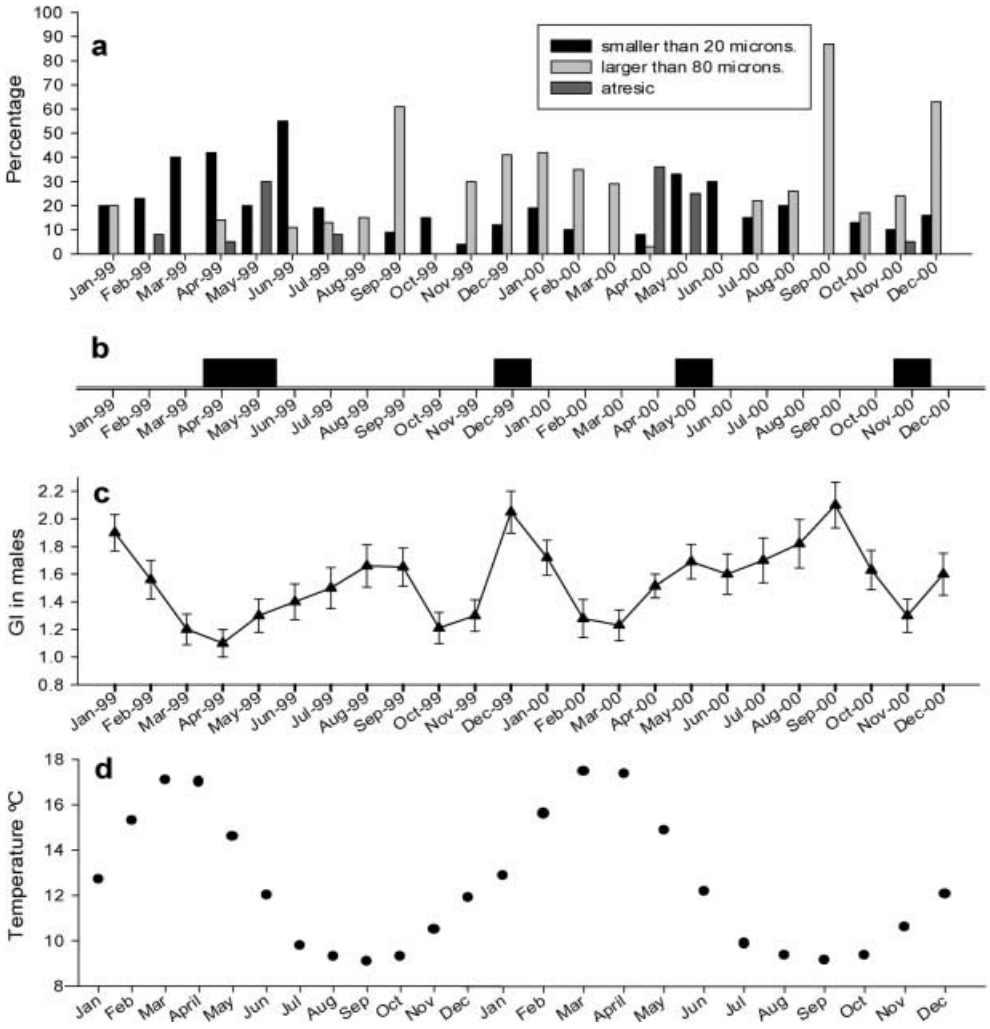

Fig. 4a–d *Zidona dufresnei*. Reproductive cycle from January 1999 to December 2000. **a** Percentage of oocytes < 20 μm (in diameter), percentage of oocytes > 80 μm and percentage of atresic oocytes. **b** Periods of oocyte resorption. **c** Gonadosomatic index in males. Bottom water temperature at 50 m depth in the study area [40 year sporadically recorded data from Carreto et al. (1998), Ramírez et al. (1973) and Guerrero et al. (1999)]

females and with the beginning of a rise in temperature. Male gonads began recovering, reaching their maximum GSI in December 1999. Sustained gamete release occurred until March 2000. Although with some minor variation, the cycle was repeated annually.

Discussion

Several different methodologies have been used to study reproductive cycles in mollusks. The monthly variation of the GI has frequently been used in species with gonads that are easy to separate from the rest of the soma, because it is a good indicator of gonadal changes throughout the year (Grant and Tyler 1983).

In male *Zidona dufresnei*, it is easy to separate the testes from the rest of the soma, because testes are so evident, e.g. the color pattern is different, but it is not as easy in females. Thus, in the present study, only the GSI for males was used to complement the histological analysis.

The dynamics of the gametogenic stages in individuals of some snail species are known. There is often a resting state, in which gametogenic activity is minimal. Temperate species, in particular, show a resting phase in winter, when gametogenic activity is suspended (Giese and Pearse 1977). In the case of *Z. dufresnei*, there is a period of reduced reproductive activity, but not a suspension of gametogenic activity. In some species, however, there are differences in gametogenesis between sexes. According to Martel et al. (1986b), some marine

Table 2 Results of one-way ANOVA for gonadosomatic index

Color	Mean	Sample size	Group	SD
Pale yellow	1.1142	81	0.3499	
Brownish orange	1.6665	102	0.3115	
Dark brown	1.9459	87	0.3787	
Total	1.5909	270	0.3458	

Source	*df*	SS	MS	*F*	*P*
Between	2	29.949	14.9774	125.27	0.0005
Within	267	31.9229	0.11956		
Total	269	61.8778			

gastropod species have a completely inverse timing in the development of the testis and ovary, as in *Buccinum undatum*. We do not find separated periods of spermatogenesis and oogenesis in *Z. dufresnei*.

The histological examination showed that spermatogenesis in *B. undatum* began at the same time as copulation, and thus both may be stimulated by the slight increase in temperatures (Martel et al. 1986b). In *Z. dufresnei* spermatogenesis is evident throughout the year, but sperm release could be stimulated by an increase in temperature, coincidentally with the presence of ripe females in the population.

Temperature is often mentioned as a very important factor in gonadal development in caenogastropods (Giese 1959; Kinne 1963; Fretter and Graham 1964; Giese and Pearse 1974; Martel et al. 1986b). This also appeared to be the case for *Z. dufresnei* from the studied population. Temperate species often have extended spawning periods, although the basic pattern is seasonal. Most seasonal temperate species spawn during the summer, but some spawn in the winter months (Giese and Pearse 1977). *Z. dufresnei*, a temperate species, does spawn in austral spring and summer. The reproductive season in this species in the sampled locality extended from October to March (austral spring–summer). During summer, a stage of advanced gonadal development and spawning predominated in the adult population. In autumn, gonads were generally under atresia; during wintertime, they underwent a period of recovery that lasted until spring, when gametes were released again. In males, the GSI and, in females, the proportion of vitellogenic oocytes showed sharp decreases between October to March, indicating gamete release. This agrees with other studies of neogastropods. In *B. undatum* spawning occurs between late May and July in the northern Gulf of St. Lawrence (Martel et al. 1986a,b), in Europe from April to August in the White Sea (Kusnetsov 1963) and from February to September in Kristineberg (Aurivillus 1898). In other studies, however, *B. undatum* has been shown to lay eggs in Europe in fall and winter months (Cunningham 1899; Sykes 1905; Havinga 1922; Lebour 1937; Moore 1937; Kristensen 1959; Hancock 1960, 1967; Fretter and Graham 1962; Bruce et al. 1963; Kideys et al. 1993)

A similar phenomenon was observed betweentwo species of the genus *Neptunea*; *N. despecta* laid eggs during late spring and early summer in the Archipel de Mingan (Martel et al. 1986b), in contrast with the winter reproduction of *N. antiqua* in Europe (Pearce and Thorson 1967).

In most caenogastropods, gametogenic activity throughout the reproductive cycle is synchronous in a population and can be divided into distinct maturation stages (Giese and Pearse 1977). *Z. dufresnei* shows a very synchronous reproductive cycle among members of the population. Thus, as a clear reproductive season is recognized, fisheries management polices involving *Z. dufresnei* resources should take this important information into account in the future.

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