SEASONAL CHANGES IN BIOCHEMICAL COMPOSITION OF THE CLAM, *EURHOMALEA EXALBIDA* (BIVALVIA: VENERIDAE), FROM THE BEAGLE CHANNEL, ARGENTINA

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ABSTRACT Seasonal changes in biochemical composition (protein, glycogen, and lipid content) of different organs (FV, foot-visceral mass; M, adductor muscles; and GMS, gills-mantle-siphons) of the clam *Eurhomalea exalbida* from Ushuaia Bay (54°50'S, Beagle Channel, Tierra del Fuego) were examined to describe changes in relation to reproduction and growth. A maximum level of protein content was observed during winter in all tissues with other increase during the spawning event (November) in FV and in November and January in GMS. In the adductor muscle, the protein content shows low variability during the year, except in June. These results suggest that all these tissues are involved in the storage of proteins, which are thought to play a role in the gamete maturation. The percentage of glycogen content for FV, M, and GMS showed low values (0.03% to 4.7% AFDW) along the year, which suggests that this component did not have an important function as energetic reserve. Low values of lipid content for FV were found in November with increased levels in summer season. Thus, variations in lipid content can principally be related to gamete emission in November and gamete maturation in summer season. The high levels of lipid content in FV over the rest of the year, except in June, were correlated with the presence of mature gonads throughout the major part of the year. Therefore, our results suggest that in *E. exalbida,* (a) proteins are the most important component stored, and (b) the relative content of protein, lipid, and glycogen of the adult specimens vary seasonally in accordance with the reproductive cycle and the season of maximum shell growth; when the organism reaches reproductive maturity (summer), shell growth slows down because of reproductive investment.

KEY WORDS: Beagle Channel, biochemical composition, bivalve, clams, *Eurhomalea exalbida*

INTRODUCTION

Seasonal changes in biochemical composition (protein, glycogen, and lipid content) may be of great importance in relation to energy metabolism necessary to growth and reproduction (Jayabal & Kalyani 1986, Lodeiros et al. 2001, Navarro et al. 1989). In the tropical scallop *Lyropecten (Nodipecten) nodosus,* it was observed that when the organism reaches reproductive maturity, growth slows down as a result of the reproductive investment, and the biochemical composition may change according to the reproductive requirements (Lodeiros et al. 2001).

The relationship of the energy transfer between different tissues, their capacity of reserve amounts under food availability, and their positive relationship with the high temperature and gonadal maturation have been shown in different species of bivalve mollusks such as scallops (MacDonald & Thompson 1986, Robinson et al. 1981, Sundet & Vahl 1981, Villalaz 1994), mussels (Zandee et al. 1980), and clams (Robert et al. 1993, Urrutia et al. 2001). The scallops *Argopecten ventricosus* (Villalaz 1994), *Chlamys islandica* (Sundet & Vahl 1981), and *Placopecten magellanicus* (Robinson et al. 1981) stored glycogen and lipids in their adductor muscles and digestive gland, respectively, and used them up in gonadal maturation. The mussel *Mytilus edulis* (Zandee et al. 1980) stored glycogen in mantle and digestive gland during the period of food availability to be used in the gametogenic period. Alternatively, some bivalves (i.e., *Abra alba, Meretrix meretrix*) can obtain energy directly from food (Ansell 1974a, Jayabal & Kalyani 1986, Lucas 1996).

Biochemical component (lipids, proteins, or carbohydrates) fluctuations have been observed in bivalves and related to the reproductive cycle showing which components were the most important source of energy (Martínez 1991). Bivalves generally store

carbohydrates in large amounts during their growing season and use them over the rest of the year (Beukema 1997); although proteins may be an energy reserve in some bivalve species (Beninger & Lucas 1984, Brockington 2001, Galap et al. 1997). Lipid variation has principally been related to gamete development (Martínez 1991) with the highest levels of lipids during the period when gonads are ripe.

Eurhomalea exalbida (Dillwyn 1817) is a subtidal species with a wide geographic distribution all along the southern tip of South America, from the Chiloe Island (42°S) on the Pacific side (Dell 1964, Osorio et al. 1979, Soot-Ryen 1959) to the Beagle Channel (54°50'S), up to the Buenos Aires province (36°S) on the Atlantic side (Carcelles 1944, Carcelles 1950). *E. exalbida* is commercially exploited throughout the Pacific Coast of South America (Osorio et al. 1979). No records of commercial exploitation exist from the Atlantic side. The Beagle Channel population represents the extreme south of the species' distribution, withstanding large temperature variations (4–11°C), with marked seasonal variation in the biomass of phytoplankton (Hernando, pers. comm.). In the Ushuaia Bay (54°50'S, Beagle Channel), this clam shows a seasonal shell growth pattern (Lomovasky et al. 2002), with adult specimens growing in spring with shell growth slowing down in summer and juveniles growing in both seasons. The parameters of the von Bertalanffy growth function were estimated to be $height_\infty = 74$ mm, $k = 0.18$ y^{-1}, $t_0 = 0.15$ y, with a maximum age of 70 y reached (Lomovasky et al. 2002). This species was characterized by an important spawning event in November, followed by a quick recovering in summer with the presence of ripe gonads in the rest of the year (Morriconi et al. 2002). The monthly variations of the energetic content of different organ groups show a positive relationship between higher energy content and the presence of ripe gametes (Lomovasky et al. 2001).

Seasonal variations in growth and reproduction have been correlated with changes in the energy content of different organs (Jobling 1994, Lucas 1996), thereby reflecting the spatial and tem-

poral energy distribution within the organism. This distribution closely reflects the seasonality of the cost of reproduction and growth and the capacity to accumulate reserves within the organism (Martínez & Mettifogo 1998, Navarro & Torrijos 1995, Robinson et al. 1981, Zandee et al. 1980). Thus, the aim of the current work was to describe the biochemical seasonal changes in different tissues of the clam *E. exalbida* from Ushuaia Bay and the relationship between the observed variations with the gametogenic activity and the maximum shell growth season.

MATERIALS AND METHODS

Samples of *E. exalbida* were collected in Ushuaia Bay (54°50'S, Beagle Channel; Lomovasky et al. 2002) in a subtidal flat at a depth between 2 and 4 m at low tide. Seasonal sampling was conducted by scuba diving between June 1999 and March 2000. Twenty to 30 clams, of shell length $\geq$38 mm (size at first maturity; Morriconi et al. 2002), were sampled each time ($n = $ 120) and kept in aquarium for 24 h. Shell length (anterior-posterior axis, SL), measured to the nearest 0.01 mm and total weight (TW, ±0.1 g) were recorded for each individual. Monthly mean surface temperature was recorded. The minimum mean seawater temperature (4.6°C) was recorded in August and the maximum (8.5°C) was recorded in February (Fig. 1).

After removing the valves, the sex of each individual was determined using gonadal smears. The soft parts were separated into three groups: foot-visceral mass (gonad, digestive gland, and gastrointestinal tract; FV), adductor muscles (M), and gills-mantle-siphons (GMS). These divisions were made based on the presence or absence of gonads in the tissues and on their potential capacity to fulfill a storage function (Lomovasky et al. 2001). The soft parts were dried at 80°C to constant weight and stored at –20°C until processing for biochemical analysis. Ash content was determined by igniting a subsample of tissue in a muffle furnace at 450°C for 24 h.

Condition Index

The relationships between shell length and FV dry mass, M dry mass, and GMS dry mass are represented (Lomovasky et al. 2002) by:
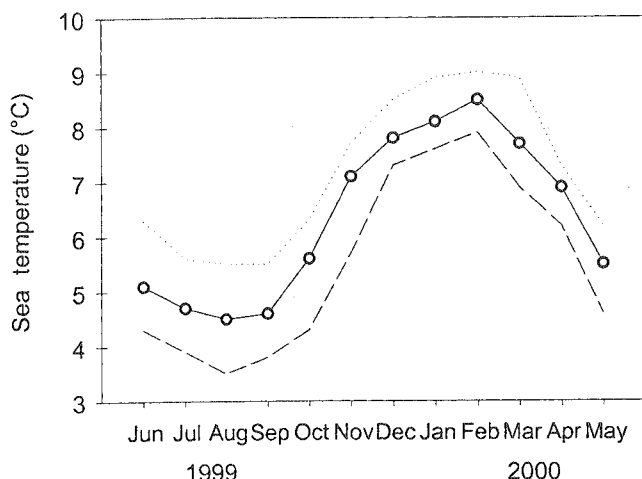

Figure 1. Monthly means of seawater temperature in Ushuaia Bay with maximum and minimum values between June 1999 and May 2000.

$$log(mass) = a + b \times [log(SL)] \qquad (1)$$

Seasonal condition values were analyzed using the condition index:

$$CI = mass/shell\ length^b \qquad (2)$$

where b is the slope in (1), and were normalized using the relative condition index:

$$RCI = (CI - mean\ CI)/(SD\ of\ CI) \qquad (3)$$

To evaluate the null hypothesis of no difference between seasons in relative condition index in each of the organ groups (FV, M, and GMS), we performed an analysis of variance (ANOVA). The assumptions of normality and homogeneity of variances were tested, and the appropriate transformations were applied when necessary. Unplanned comparisons (modified Tukey test) were made when significant differences were found (Sokal & Rohlf 1995, Zar 1984).

Biochemical Composition

The biochemical composition of dry tissue subsamples from the three organ groups of approximately 20–30 individuals per season was analyzed. Proteins were determined after hydrolysis with NaOH 0.5 N and using BSA 1 mg/mL as standard following the method of Lowry et al. (1951). Glycogen of tissues was extracted by boiling with 30% (p/v) KOH and was determined as total carbohydrates using the method of the Anthrone reagent (Carroll et al. 1956, Seifter et al. 1949). Glycogen was quantified after precipitation with 99% (v/v) ethanol and using glucose standard solution containing 20 µg/mL. The difference between protein and glycogen content was considered as lipid content. The results were expressed as milligram (mg) biochemical component per gram (g) of tissue ash-free dry weight (AFDW).

Linear regressions were used to determine the possible relationship between the biochemical content (mg protein, glycogen, and lipid AFDW) of the three organ groups (FV, M, and GMS) and the size of the clams (SL) for each sex. As biochemical content (protein, glycogen, and lipid) per gram were found not to be related to the size of the organisms analyzed in this study, we performed an ANOVA to evaluate the null hypothesis of no difference between seasons in the biochemical content in each of the organ groups. The assumptions of normality and homogeneity of variances were tested, and the appropriate transformations were applied when necessary. A nonparametric test was used (Kruskal-Wallis) when required. Unplanned comparisons (modified Tukey test to parametric analysis or multiples contrast test to nonparametric analysis) were made when significant differences were found (Sokal & Rohlf 1995, Zar 1984).

RESULTS

Condition Index

Significant exponential size-mass relationships between FV, M, and GMS shell-free dry mass (SFDM) as dependent variables and shell length (SL) as the independent variable were found in females and males (Table 1).

The analysis of the relative condition index (Fig. 2A) for FV over time showed the highest values in January 2000 in both sexes whereas the lowest values occurred in June, September, and November for females and in September, November, and March for males (modified Tukey test, $P < 0.05$).

TABLE 1.

Size-mass relationships in *Eurhomalea exalbida* from Ushuaia Bay, Beagle Channel, as described by linear regression log Y (SFDM) = a + b × log X.

Y	X	Females				Males			
		a	b	r²	n	a	b	r²	n
FV	SL	−5.832	3.3199	0.64	109	−5.615	3.2104	0.45	97
M	SL	−5.1593	2.6909	0.63	109	−5.1156	2.661	0.48	97
GMS	SL	−4.9685	2.7252	0.73	109	−4.9496	2.7223	0.61	97

SL, shell length; FV, foot-visceral mass; M, adductor muscles; GMS, gills-mantle-siphons; SFDM, shell-free dry mass. All significant relationships ($P < 0.05$).

No significant changes in the relative condition index over time were found for either M or GMS in either sex (one-way ANOVA, $P > 0.05$, Figs. 2B and 2C).

Biochemical Composition

No significant dependence ($P > 0.05$) was observed for the relationships between the protein, glycogen, and lipid content and the size of the clams (SL) for each sex. Biochemical content (protein, glycogen, and lipid) per gram were found not to be related to the size of the organisms analyzed in this study.

Foot-Visceral Mass

The mean protein content (Fig. 3A) was significantly different between sexes (two-way ANOVA, $F_{\alpha=0.05,1,110} = 31.22$; $P < 0.001$). Significant higher values in June and November 1999 with minimum values in September 1999 and January 2000 (two-way ANOVA, $F_{\alpha=0.05,4,110} = 72.79$, $P < 0.001$; modified Tukey test, $P < 0.05$) in both sexes were observed. No significant differences were found in the protein content of FV attributable to date-sex interaction ($F_{\alpha=0.05,4,110} = 2.37$, $P > 0.05$).

Glycogen content was comparatively lower than the other components and varied between 0.2% to 4.6% in both sexes (Fig. 3B). No significant differences were found in the glycogen content between sexes (one-way ANOVA, $F_{\alpha=0.05,1,118} = 0.11$, $P > 0.05$). There were significant differences in glycogen content over time (Kruskal-Wallis; $H = 48.77$, $P < 0.001$) with the lowest values in June and November and the maximum value in January (multiples contrast test, $P < 0.05$).

Significant higher values in the FV lipid content in September 1999 and January 2000 in both sexes (for females: Kruskal-Wallis, $H = 37.31$, $P < 0.001$; for males: Kruskal-Wallis, $H = 39.60$, $P < 0.001$) were observed (Fig. 3C).

Adductor Muscles

Proteins were the major biochemical component of the adductor muscle (Fig. 4A). The average protein content showed significant differences between sexes (one-way ANOVA, $F_{\alpha=0.05,1,118} = 5.29$, $P < 0.05$), with slightly higher values in June 1999 in both sexes (females: Kruskal-Wallis, $H = 10.39$, $P = 0.034$; males: one-way ANOVA, $F_{\alpha=0.05,4,54} = 33.80$, $P < 0.001$; modified Tukey test, $P < 0.05$).

The mean glycogen content of M over time for females ($n = 61$) and males ($n = 59$) were significantly different (one-way ANOVA, $F_{\alpha=0.05,1,118} = 4.26$, $P < 0.05$). The differences among
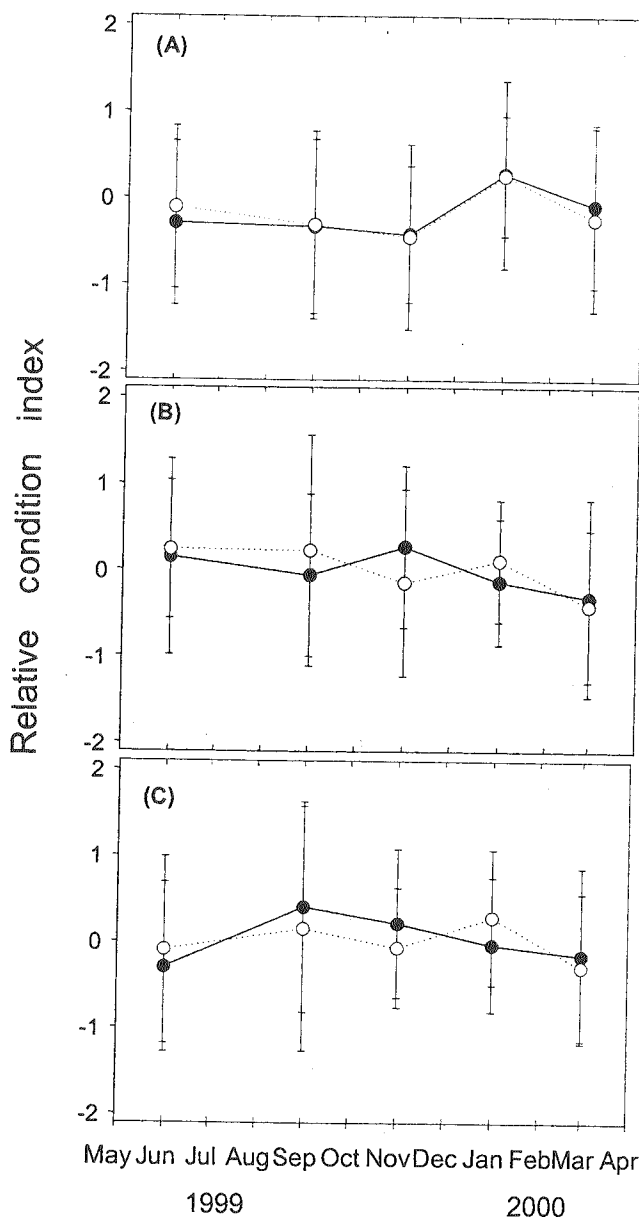

Figure 2. Relative condition index over time in *E. exalbida* from Ushuaia Bay: (A) foot-visceral mass, (B) adductor muscle, (C) gills-mantle-siphons. (●) females, (○) males.

the months were highly significant in both females (one-way ANOVA, $F_{\alpha=0.05,4,56} = 11.67$, $P < 0.001$) and males (Kruskal-Wallis, $H = 32.32$, $P < 0.001$). It was shown in the unplanned comparisons (modified Tukey test) that the glycogen content for females was significantly lower in June and September 1999 ($P < 0.05$) and higher in January and March 2000. Higher significant values in glycogen content among males occurred in November 1999 and January 2000 ($P < 0.05$) than in the rest of the year (Fig. 4B).

Significant differences in the lipid content (Fig. 4C) were found between sexes (Kruskal-Wallis, $H = 5.35$, $P < 0.05$), and over time for females (Kruskal-Wallis, $H = 11.27$, $P < 0.05$) and males (Kruskal-Wallis, $H = 33.49$, $P < 0.001$). Lipid content varied significantly among males during June 1999 and was significantly less ($P < 0.05$) than in the rest of the year. For females, the
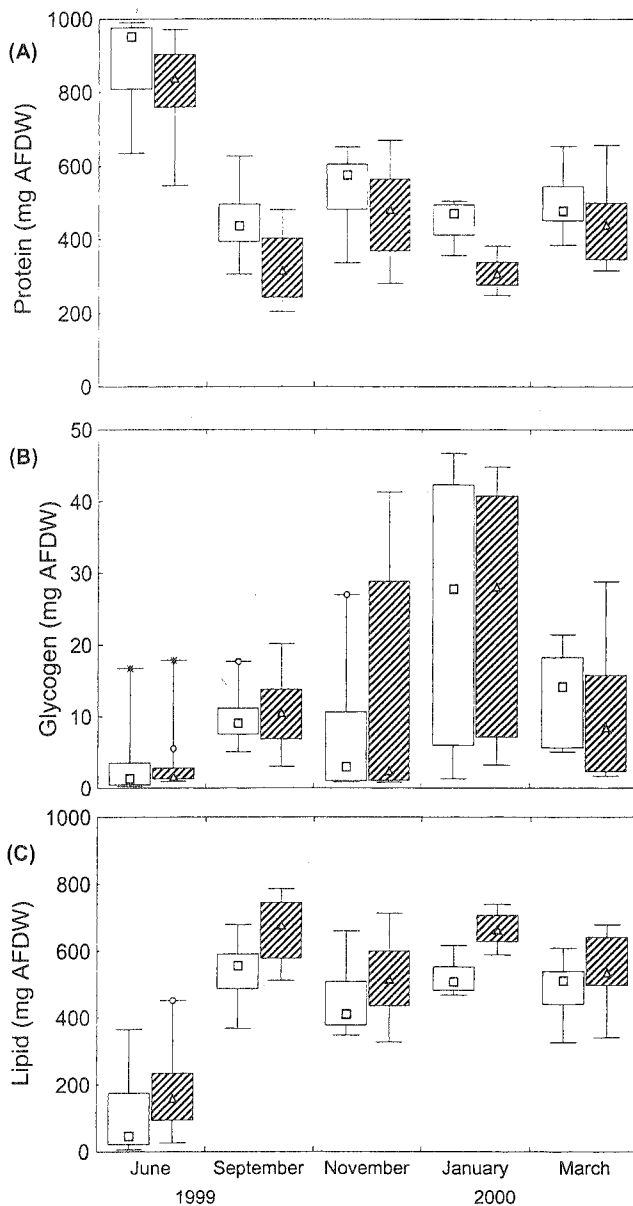
Figure 3. Seasonal variation in the biochemical components for foot-visceral mass (FV) in *E. exalbida* from Ushuaia Bay: (A) protein, (B) glycogen, and (C) lipid. Here and thereafter box plots are constructed with limits of boxes being the 75th and 25th percentile, lines represent maximum and minimum values, points inside boxes are medians, circles are outliers. White boxes: females; hatched boxes: males.

difference found was between the lesser value in June 1999 and the higher value in November 1999 ($P < 0.05$).

Gills-Mantle-Siphons

Protein content (Fig. 5A) was significantly the highest of the year in June and November 1999 and January 2000 in females (Kruskal-Wallis, H = 42.59, $P < 0.001$) and males (one-way ANOVA, $F_{\alpha = 0.05, 4, 54}$ = 9.37, $P < 0.001$). The average protein content was significantly different between sexes (one-way ANOVA, $F_{\alpha = 0.05, 1, 118}$ = 12.53, $P < 0.001$).

No differences (one-way ANOVA, $F_{\alpha = 0.05, 1, 118}$ = 0.11, $P > 0.05$) were observed between the mean values in glycogen
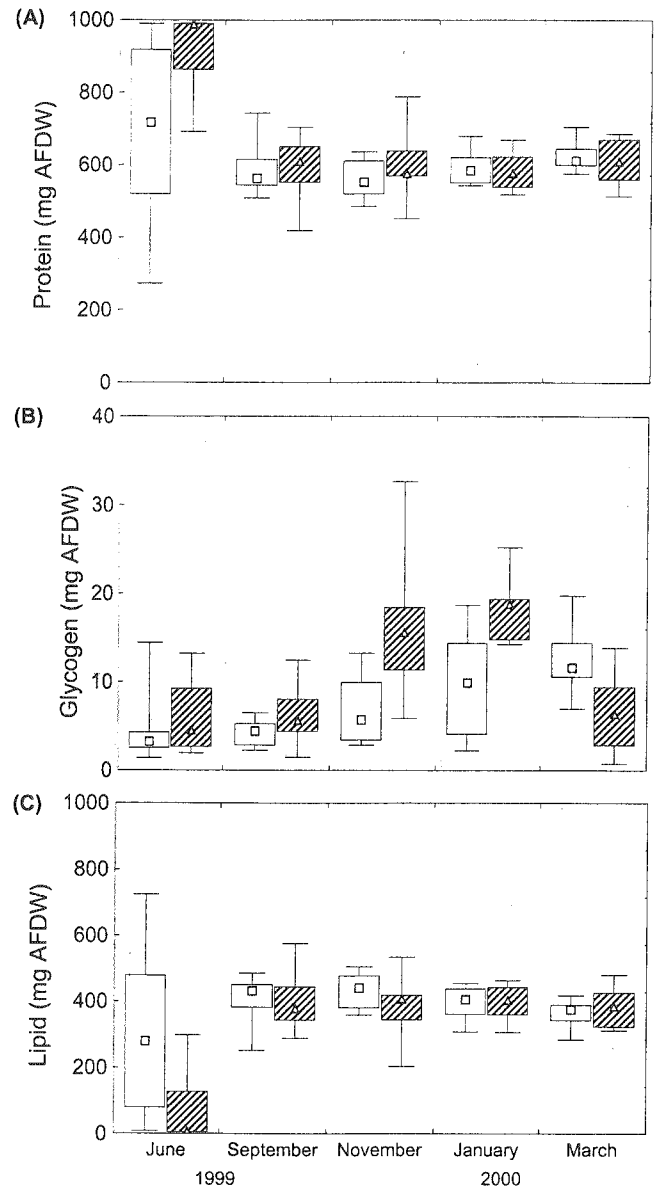

Figure 4. Seasonal variation in the biochemical components for adductor muscle (M) in *E. exalbida* from Ushuaia Bay: (A) protein, (B) glycogen, and (C) lipid. White boxes: females; hatched boxes: males.

content of females and males (Fig. 5B). There were significant differences in glycogen content over time (Kruskal-Wallis, H = 44.73, $P < 0.001$) with the lowest values in June 1999 and the maximum value in January 2000 (multiples contrast test: $P < 0.05$).

Significant differences in lipid content between sexes (Kruskal-Wallis, H = 11.13, $P < 0.001$) and over time in females (Kruskal-Wallis, H = 42.55, $P < 0.001$) and males (Kruskal-Wallis, H = 26.21, $P < 0.001$) were observed (Fig. 5C). Lipids were significantly highest in September 1999 and March 2000 in both sexes (multiples contrast test, $P < 0.05$).

DISCUSSION

The relative content of protein, lipid, and glycogen of the three organ groups for the adult specimens of *E. exalbida* from the
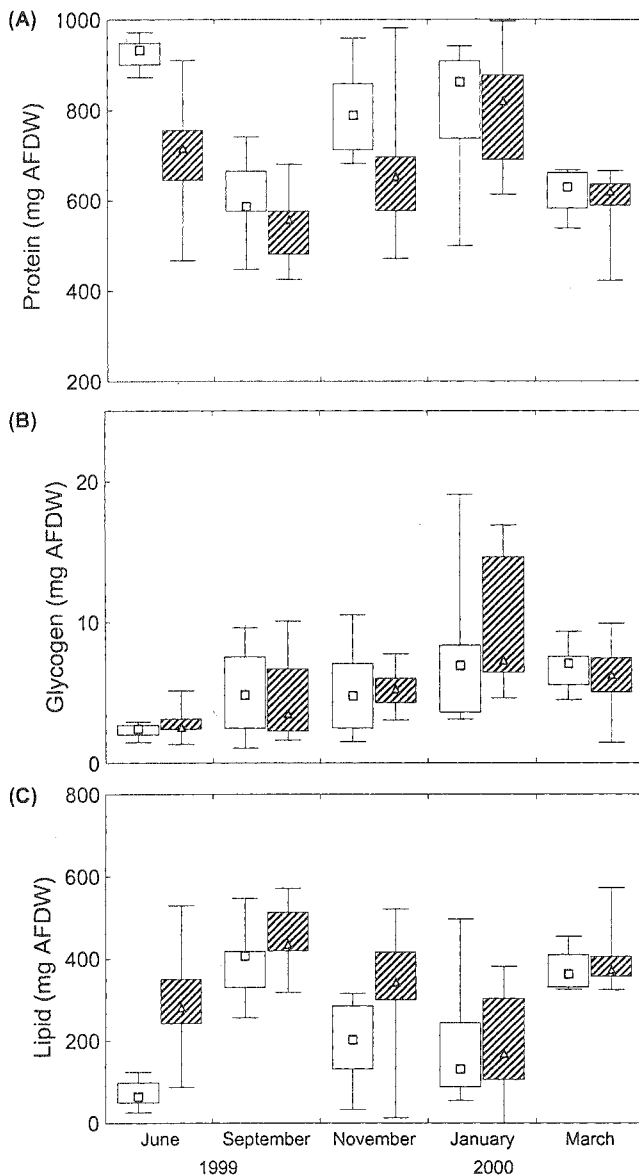
Figure 5. Seasonal variation in the biochemical components for gills-mantle-siphons (GMS) in *E. exalbida* from Ushuaia Bay: (A) protein, (B) glycogen, and (C) lipid. White boxes: females; hatched boxes: males.

Beagle Channel vary seasonally. These changes are principally related to the reproductive cycle and the season of maximum shell growth. Similar characteristics have been observed in other bivalves such as *Anomalocardia squamosa* (Morton 1978), *Donax trunculus* (Ramón et al. 1995), *Euvola (Pecten) ziczac* (Lodeiros & Himmelman 2000), *Lyropecten (Nodipecten) nodosus* (Lodeiros et al. 2001), *Macoma balthica* (Ankar 1980), *Mercenaria mercenaria* (Peterson & Fegley 1986), *Placopecten magellanicus* (MacDonald & Thompson 1986) and *Venus verrucosa* (Arneri et al. 1998).

The seasonal variations of the relative condition index for FV of *E. exalbida* were correlated with the gametogenic cycle (Morriconi et al. 2002) and the monthly relative condition index (Lomovasky et al. 2001) previously observed for this species. The lower RCI value was found in November in coincidence with a higher percentage of partially spawned stage (58.33% for males

and low mean number of mature oocytes for female; Morriconi et al. 2002), and the higher RCI value in January was coincident with the gamete maturation. For M and GMS, no significant changes in mass were observed among the year.

The seasonal biochemical analysis of the FV group showed low values of lipid content in November with an increased level in summer season. We suggest that the energetic variations in FV observed previously (kJ/g AFDW, Lomovasky et al. 2001) could principally be related to the lipid content variations produced by gamete emission in November and gamete maturation in summer season (Morriconi et al. 2002). Similar characteristics were found in *Glycymeris glycymeris* from South Brittany, France (Galap et al. 1997), *Macoma balthica* (Beukema & De Bruin 1977), and *Mytilus edulis* from Dutch Wadden Sea (Pieters et al. 1980, Zandee et al. 1980). The reproductive cycle of *E. exalbida* (Morriconi et al. 2002) showed the presence of mature gonads (60–100%) throughout the major part of the year in both sexes, corresponding with the high levels of lipid content in FV over the year, which has been observed in this study.

Glycogen is the major carbohydrate stored in bivalves (Beukema 1997). However, small amounts of free sugars are always present as well (Whyte & Englar 1982). The glycogen content for FV, M, and GMS found in *E. exalbida* was comparatively lower than the other components (0.03% to 4.7% AFDW), in contrast with other studies in bivalves where high values occurred (31.9% to 48.4%; Giese 1966, Paez-Osuna et al. 1993). Nevertheless, scarce glycogen stored in another burrowing bivalve, *Ensis siliqua*, has been observed (Martinez et al. 1997).

Under conditions of food scarcity, it has been suggested that glycogen from muscular tissues acts as the primary energy reservoir for the formation of gametes in bivalves, such as *Glycymeris glycymeris* (Galap et al. 1997). A reduction of this reserve in storage organs is also commonly correlated with an increase in gonadal lipids (Fernandez-Reiriz et al. 1996, Mann 1979). In the adductor muscle of *E. exalbida*, glycogen content increased during the spawning event (November, in males) and the gamete maturation (summer, males and females) and decreased in the rest of the year, suggesting that glycogen is used in these months but in a very low proportion (<3.3%). Thus, these changes had not been detected in a direct calorimetric analysis (Lomovasky et al. 2001). Therefore, the adductor muscle in *E. exalbida* does not have glycogen storage functions for energy reserves in contrast with previous reports for several bivalves such as scallops (Ansell 1974b, Martínez 1991, Robinson et al. 1981, Sundet & Vahl 1981, Villalaz 1994), mussels (Bayne et al. 1983, Lowe et al. 1982), and oysters (Fernandez Castro & Vido de Mattio 1987).

In FV, the glycogen content was higher in September and January, and a similar tendency for lipid content was observed. The positive correlation between the proportions of carbohydrates and lipids seems to be the rule rather than the exceptions (Beukema 1997). As described above for M, the glycogen content for FV and GMS showed the lowest values along the year, suggesting that this component did not have an important function as substrate for energy reserves in this species.

Alternatively, proteins may be an energy reserve in adult bivalves, particularly during gametogenesis (Beninger & Lucas 1984, Galap et al. 1997). In *E. exalbida*, a higher level of protein content was observed in winter in all tissues, with other increase during the spawning event (November) in FV and in November and January in GMS. In the adductor muscle, with the exception of June, the protein content was approximately constant during the

rest of the year. These results suggest that all these tissues could be involved in the storage of proteins in winter and which are thought to play a role in the gamete maturation. A higher level of protein content in winter has also been observed in digestive gland and gonad of *Spondylus leucacanthus* from the Gulf of California (Rodríguez-Astudillo et al. 2002). It seems therefore that in *E. exalbida*, proteins may be the more important component stored.

The energetically convenient degradation of glycogen has been studied in several species, such as *Mytilus edulis* (De Zwaan & Eertman 1996). *Scapharca inaequivalvis*, and *Venus gallina* (Brooks et al. 1991), related to the type of metabolic pathway used during environmental anaerobiosis when the metabolic rate is strongly suppressed compared with the aerobic resting rate (De Zwaan & Eertman 1996). *E. exalbida* is a subtidal, Sub-Antarctic species whose cold-waters habitat provides it with oxygen. Emersion and anoxia-adapted physiology (De Zwaan & Eertman 1996) may not be related to these species. The protein seems to be its only alternative resource of energy under conditions of food scarcity. However, it cannot be certain without further studies and proper investigation about the possible advantage of using protein as an energy reserve and the mechanisms of regulation (e.g., antifreezing proteins).

A relationship between the greater availability of phytoplankton (Hernando, pers. comm.), sea temperature, and gamete maturation with a slowed down shell growth has been suggested for this species (Lomovasky et al. 2001, Lomovasky et al. 2002, Morriconi

et al. 2002). Thus, food availability may be an important source of the nutrients required for the gonadal ripening process. Seasonal variation in temperature and the availability of food appear to be closely related to the energy available for growth and reproduction in other bivalve species (Beukema & De Bruin 1977, Griffiths & King 1979, Newell & Branch 1980, Jayabal & Kalyani 1986, MacDonald & Thompson 1986. Mann 1979, Navarro et al. 1989, Smaal et al. 1997, Sukhotin 1992, Zandee et al. 1980). In *E. exalbida* from Ushuaia Bay, shell growth in spring (Lomovasky et al. 2002) occurred during spawning (Morriconi et al. 2002). In summer, the shell growth slowed down, and gamete maturation was found whereby energy was allocated to reproduction rather than to growth. In contrast, juvenile organisms grew up such as in spring and in summer (Lomovasky et al. 2002). The differences detected between juvenile and adult organisms could be related to the energy partition between growth and reproduction.

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