

High energetic cost of oviposition in an edible marine gastropod



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ABSTRACT

The edible neogastropod *Buccinanops cochlidium* from Patagonia, Argentina, reproduces by means of egg capsules attached by the female to its own shell. Gravid females lay an outstanding mean of 500,000 eggs that nurse around 800 embryos, which hatch as crawling juveniles (4 mm in shell length) after four months of intracapsular development. This reproductive investment could be expressed as the energy content (EC) estimated for the production of a complete egg mass (33.94 ± 12.85 KJ), representing a conservative estimation of the total EC needed for an adult female to spawn, which is in average $\sim 12\%$ of the total EC in gravid females. This high maternal investment allows a considerable offspring size, which confers them high survival chances. A translocation of energy stored in the foot during the oviposition season is shown in a relative decrease of $\sim 10\%$ in the foot EC in respect of the total EC (61.8% in non-gravid females vs. 51.3% in gravid females). Gravid females showed significantly higher body wet mass/shell length index and higher total EC than non-gravid females (266.0 ± 66.4 KJ vs. 184.3 ± 69.6 KJ), suggesting that a body condition threshold is required for females to reproduce. These values represent an energetic surplus of over 40% of the total EC per individual when compared to non-gravid females. Protecting gravid females from fisheries would ensure the sustainability of the resource and must be taken into account when establishing fisheries policies.

1. Introduction

Marine gastropod reproductive modalities vary from the production of many small eggs evacuated to the water column with a reduced success rate to the spawn of a reduced number of larger eggs/embryos that receive protection during their development to potentiate their chances of success (Pianka, 1970). Those species that present encapsulated embryonic development invest great amounts of energy in reproduction. This investment is mainly represented by eggs (including nurse eggs), intracapsular liquid (including nutritive substances), egg capsule production and oviposition (Perron, 1981; Kideys et al., 1993; Miloslavich, 1996) and, in some cases, maternal care of the egg capsules (Penchaszadeh, 1971; Brown, 1982; Chaparro et al., 1999; Averbuj and Penchaszadeh, 2010). Male contribution, including sperm formation and copulation, appears irrelevant in terms of energetic comparisons in most animal groups, in particular in marine gastropods (Riechert, 1988). The energetic cost of reproduction in the marine gastropod *Buccinum undatum*, studied by means of a calorimetric analysis of the gonad (Kideys et al., 1993), showed a seasonal variability in its

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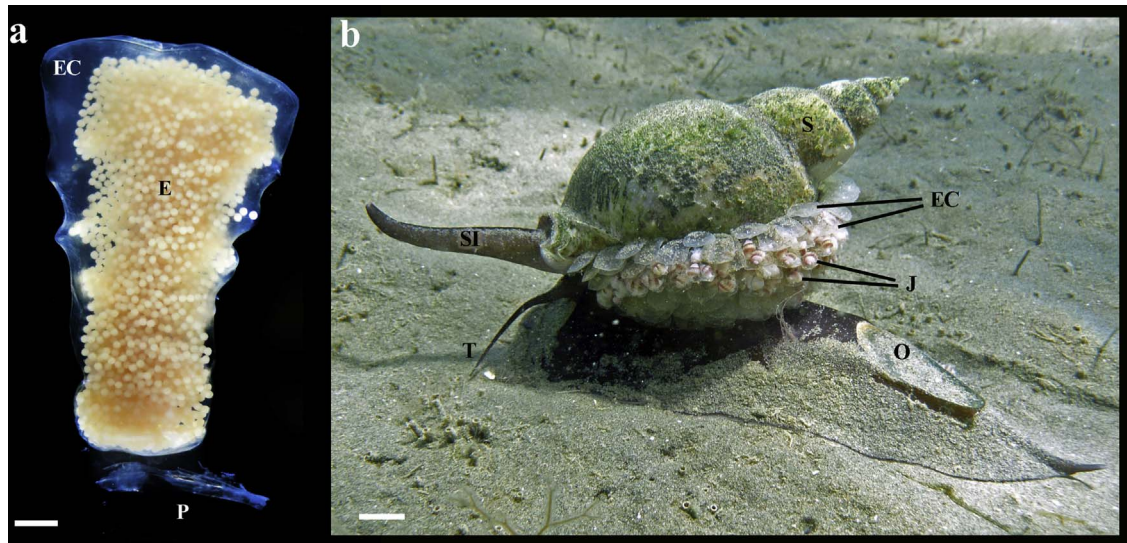


Fig. 1. *Buccinanops cochlidium* spawn. a-Egg capsule of *B. cochlidium* in early developmental stage. Note the abundance of eggs inside, b-Female of *B. cochlidium* carrying egg capsules in late developmental stage. Abbreviations: E: eggs, EC: egg capsule, F: foot, J: hatching juveniles, O: operculum, P: peduncle, S: shell, SI: siphon, T: tentacle. Scale Bars: (a) 1 mm, (b) 1 cm.

reproductive behaviour accompanied by a variation in the energy content, with differences between males and females. The energetic budget needed by the female to afford reproduction includes not only egg production, but also oviposition. Perron (1981) determined that egg capsule and ova production costs in marine gastropods of the genus *Conus* were approximately partitioned into 50–50%, although not considering capsule modelling and care. Meanwhile, Chaparro et al. (1999) determined that 90% of the reproductive cost in *Crepidula dilatata* corresponded to egg production, probably because modelling and care of the very thin capsule was reduced due to incubation. Marine gastropod females may invest a large amount of energy in egg capsule formation, which is explained by their protective role conferred to the offspring, resulting in higher survival rates (Perron, 1981).

Buccinanops cochlidium (Dillwyn, 1817) is a common gastropod that inhabits marine sandy bottoms from Argentine Patagonia (Averbuj and Penchaszadeh, 2010). It is the species of the genus *Buccinanops* that shows the largest spawn in terms of number of egg capsules, eggs and hatchlings per female (Penchaszadeh, 1973; Averbuj and Penchaszadeh, 2016), with an outstanding mean of 500,000 eggs per female, from which around 800 are embryos and the rest nurse eggs (Fig. 1). The hatchlings emerge as fully developed crawling juveniles after 4 months of maternal care (Averbuj and Penchaszadeh, 2010).

In northern Atlantic Patagonia, *B. cochlidium* shows reproductive seasonality: mating occurs from March to October, followed by oviposition, that begins in July and peaks in October (few females spawn until December); then, intracapsular development takes place and, finally, hatchlings emerge in February (Averbuj et al., 2010; Averbuj and Penchaszadeh, 2010).

In Argentina, artisanal fisheries of *B. cochlidium* are being developed in northern Patagonic gulfs and although no massive captures are reported, the product is commercialized into the local and Asian markets (Bigatti et al., 2015); however, no official capture records are available. Although the regulation of this resource is absent until present, it appears as a potential complement to artisanal bivalve fisheries in the region (FAO, 2002; Bigatti and Ciocco, 2008; Bigatti et al., 2015). In this respect, previous studies raised an alert about its fragility and risk of stock depletion if a massive fishery is established. This alert was related to *B. cochlidium* low embryonic dispersion, long reproductive periods with high extraembryonic nutrition (nurse eggs) investment and a feeding dependence of juveniles from adults in early life stages, that affects growth at initial sizes (Averbuj et al., 2010; Averbuj and Penchaszadeh, 2010; Averbuj et al., 2012; Averbuj and Penchaszadeh, 2016).

A complete understanding of the reproductive process is essential to the management of marine invertebrate fisheries (Barber and Blake, 2006). Studies on the reproductive biology of marine gastropods usually focus on reproductive modalities or seasonality patterns (Underwood, 1974; Giese and Pearse, 1977; McKillup and Butler, 1979). However, there are still no available studies on the energy content and cost of oviposition of any gastropod species from the Argentine Sea. The aim of this study is to estimate the energetic cost of reproduction in the edible gastropod *B. cochlidium* from San José Gulf, Argentina. This information will be useful to understand the utilization of energetic resources during reproduction that may influence fisheries management decisions.

2. Materials and methods

2.1. Sampling

Thirty two individuals [11 males, 10 non-gravid females and 11 gravid females (carrying egg capsules attached to their shells)] were collected by scuba diving on sandy bottoms at 5–15 m depth in Playa Villarino, San José Gulf (42°25'S, 64°31'W), Patagonia, Argentina, in October 2010. Samples were collected within a week period to avoid temporal variations. Gastropods were taken alive

to a conditioned aquarium at the *Experimental Aquarium Service (Servicio de Acuario Experimental CCT- CONICET CENPAT)* until processing them.

Gastropod shell length (SL) was measured from the apex to the top of the siphonal channel using a 0.1 mm precision calliper. The shell was detached and each individual was sexed by the presence or absence (female or male, respectively) of reproductive accessory glands (albumen and egg capsule gland) and vagina.

An estimation of the proportion of gravid females on the total number of females above the maturity size (Averbuj et al., 2010) during the spawning months (September–March) was achieved based on data from monthly samples carried out for two consecutive years (2005 and 2006; Averbuj, 2009).

2.2. Energy content

The soft bodies of the gastropods (N = 32; N males = 11, N non-gravid females = 11, N gravid females = 10) were dissected and separated into the following tissue groups: 1, gonad, 2, digestive gland, 3, rest of the body, 4, foot, 5, spawn in early developmental stage (only in gravid females). All samples were weighed to the nearest 0.1 g (total mass – TM, shell free wet mass – WM), and frozen separately at –20 °C. Frozen tissue groups were dried at 60 °C to constant mass (DM), weighed, and then finely ground using a mortar and pestle and homogenized. WM and DM were used to calculate moisture content (%).

Dry and ground samples were used to make pellets for calorimetric determinations with a Parr 2812 press. The energy content (EC) of each sample was obtained by burning 20–200 mg pellets in a Parr 1425 micro-bomb calorimeter. A PREC Dbh-600 digital top balance was used to determine sample weights prior to ignition. Periodical calibrations were carried out using benzoic acid. The values obtained were corrected for ash and acid content and expressed as KJ/g ash-free dry weight (AFDW) to obtain the energy density (ED). The energy content of gonads, digestive gland, rest of the body, foot, and spawn was calculated as:

$$EC = ED * DM$$

2.3. Statistics

As the assumptions for the parametric ANOVA (normality of data and homogeneity of variances) were not fulfilled, the non-parametric Kruskal-Wallis ANOVA was used to test the hypotheses on differences in: 1) shell length among males, gravid females and non-gravid females, 2) energy content among tissues (for males, gravid females and non-gravid females), 3) WM/SL index among males, gravid females and non-gravid females, 4) energy content (EC per gram and total EC) among males, gravid females and non-gravid females, and to test the null hypothesis of no differences among %EC in each tissue (for males, gravid females and non-gravid females). If significant interaction terms were detected, multiple comparisons (z) tests were used to determine differences among treatments.

3. Results

The mean shell length (SL) of sampled individuals was 85.6 ± 8.9 mm for non-gravid females (N-GF), 85.6 ± 6.6 mm for gravid females (GF), and 81.4 ± 5.6 mm for males (M). No significant differences in shell length were found among males, gravid females and non-gravid females ($P = 0.4841$, $df = 2$, $K = 1.4509$, $N = 32$). The mean wet mass (WM; sum of all tissues) was 38.3 ± 14.3 g, 48.4 ± 12.3 g and 34.7 ± 7.4 g, for non-gravid females, gravid females and males, respectively.

The mean WM/SL index was 0.44 ± 0.12 for non-gravid females, 0.58 ± 0.11 for gravid females and 0.42 ± 0.07 for males. The Kruskal-Wallis ANOVA detected significant differences in the WM/SL index among the studied groups (M, GF and N-GF) ($P = 0.004115$, $df = 2$, $K = 10.986$, $N = 32$), being significantly higher in gravid females (even after oviposition occurred and not considering the spawn weight) than in non-gravid females and males.

Moreover, the Kruskal-Wallis ANOVA detected significant differences in EC among tissues, i.e., the EC in gonad and digestive gland was higher than in foot and rest of the body. Non-gravid females ($P < 0.0001$, $H = 29.576$, $df = 3$, $N = 43$), gravid females ($P < 0.0001$, $H = 31.712$, $df = 3$, $N = 40$) and males ($P < 0.0001$, $H = 28.176$, $df = 3$, $N = 42$) showed the same pattern. The EC values per tissue for non-gravid females, gravid females and males are expressed in Table 1.

Complementarily, considering the individual as a whole, EC per gram ($P = 0.5622$, $df = 2$, $K = 1.1518$, $N = 32$) was not significantly different among the studied groups (M, GF and N-GF); however, when considering total EC, there were significant differences among these groups ($P = 0.02175$, $df = 2$, $K = 7.6559$, $N = 32$). Particularly, gravid females showed significantly higher total EC values than non-gravid females and males (Fig. 2).

The mean EC value for the whole spawn (in early developmental stage) was 33.94 ± 12.85 KJ, which represents 12.8% of the total EC of the gravid females. The EC in other tissues decreased approximately 10% (foot), 1% (gonad; it is remarkable that this value is half of the total EC in this tissue), and 1% (digestive gland), when comparing non-gravid and gravid females. There were no differences in EC for males, gravid females and non-gravid females in the digestive gland ($P = 0.2065$, $df = 2$, $K = 3.1554$, $N = 32$) and in the rest of the body ($P = 0.9159$, $df = 2$, $K = 0.17572$, $N = 32$). However, significant differences occurred in the gonad ($P = 0.01226$, $df = 2$, $K = 8.8033$, $N = 32$), explained by significantly lower values in males than in females (no differences between gravid and non-gravid females) and in the foot ($P = 0.0001822$, $df = 2$, $K = 17.221$, $N = 32$), explained by significantly lower values in gravid females than in non-gravid females and males.

Table 1

Energy content in *Buccinanops cochlidium* tissues of gravid females, non-gravid females and males. Values are presented as energy content (EC) per gram (KJ/g dry tissue), total EC per individual (KJ) and percentage of the whole individual EC (between brackets), when corresponding. Different letters (a, b) represent statistically significant differences ($p < 0.05$) among sampled tissues.

		Gonad	Digestive Gland	Rest of the body	Foot	Spawn	Total
Gravid Females N = 11	EC per gram (KJ/g)	24.26 ± 2.66 a	24.96 ± 1.40 a	19.30 ± 1.15 b	19.82 ± 0.91 b	18.97 ± 1.94 b	19.91 ± 0.50
	EC per ind. (KJ)	4.11 ± 4.13	22.38 ± 13.22	68.41 ± 11.23	137.17 ± 39.69	33.90 ± 12.90	266.0 ± 66.40
	% EC (KJ)	1.40%	7.95%	26.50%	51.31%	12.85%	100%
Females N = 10	EC per gram (KJ/g)	23.99 ± 2.31 a	24.07 ± 1.89 a	18.96 ± 1.22 b	19.63 ± 1.98 b	–	19.91 ± 1.37
	EC per ind. (KJ)	7.22 ± 13.34	20.0 ± 14.43	54.98 ± 19.09	131.6 ± 51.71	–	184.3 ± 69.90
	% EC (KJ)	2.49%	9.12%	26.63%	61.76%	–	100%
Males N = 11	EC per gram (KJ/g)	23.42 ± 3.27 a	25.18 ± 3.21 a	19.05 ± 1.07 b	19.88 ± 1.34 b	–	20.13 ± 0.76
	EC per ind. (KJ)	1.20 ± 0.18	20.82 ± 10.64	48.23 ± 13.66	120.71 ± 25.75	–	191.0 ± 42.10
	% EC (KJ)	0.67%	10.55%	25.24%	63.53%	–	100%

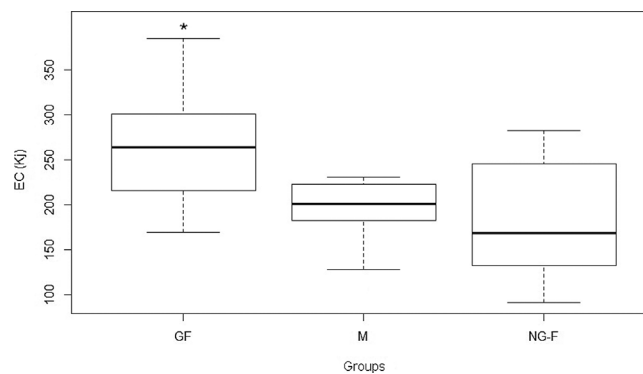


Fig. 2. Comparison among gravid females (GF), non-gravid females (N-GF) and males (M) on the energy content (EC) of the whole individual, in total KJ. Asterisk represents statistically significant differences ($p < 0.05$) in the total EC.

During the 2005–2006 oviposition season 49.5% of the sampled females were gravid ($n = 99$).

4. Discussion

Reproduction generally implies high energetic investment. In particular, in marine gastropods with encapsulated development (neogastropods), it involves the partitioning of energy between gonadal products (eggs and sperm) and extraembryonic structures such as egg capsules or extraembryonic nutritive resources (Perron, 1981). In the neogastropod *Buccinanops cochlidium*, a large energetic investment in reproduction occurs including copulation, gamete production (including ~ 0.5 million nurse eggs), oviposition, an extended 4-month maternal care period (Penchaszadeh, 1971; Averbuj and Penchaszadeh, 2016); also gravid females show a defence behaviour against predators, typical of nassarids (Brown, 1982; Averbuj, 2009).

Energy content (EC) values estimated to obtain a complete egg mass in *B. cochlidium* were in average 33,900 J. Chaparro et al. (2012) reported the energetic maternal investment in spawning for two species of the neogastropod genus *Crepidatella*, *C. dilatata* (direct development, feeding on nurse eggs) and *C. fecunda* (planktonic development). *C. fecunda* invested in average 2320 J in the spawn to achieve 46,000 larvae (~ 330 µm in length), while *C. dilatata* invested 223 J per spawn to obtain 255 offsprings (0.8–1.6 mm in length). This represents 10 times more energy invested per spawn in *C. fecunda* than in *C. dilatata*. However, *C. dilatata* invested 20 times more energy per offspring than *C. fecunda* (0.914 J vs. 0.05 J). *B. cochlidium* invested almost 50-fold more energy per offspring than the direct developer *C. dilatata* to obtain ~ 800 crawling juveniles of 4.0 mm in length, representing a maternal investment of 44.1 J per hatchling, which ingested in average 574 nurse eggs (Averbuj and Penchaszadeh, 2010). The enormous amount of eggs spawned by *B. cochlidium* (500,000 per spawn, although slightly smaller in diameter compared to those of *C. dilatata* and *C. fecunda*) appears as a high energetic investment that results in a considerable amount of crawling juveniles with a hatching size that should confer them high survival chances (Spight, 1976; Moran, 1999). However, this analysis should be taken carefully as comparisons among species with contrasting reproductive modalities and living habits (sessile vs mobile) are tough and may lead to misinterpretations. For example, other intracapsular feeding resources as intracapsular fluid (de Mahieu et al., 1974; Pechenik et al., 1984; Moran, 1999) or progressive disintegration of the internal capsular wall (Hendler and Franz, 1971; de Mahieu et al., 1974; Ojeda and Chaparro, 2004) were not considered in the cited studies, nor were other aspects as the different brooding periods (Chaparro et al., 2012).

In *B. cochlidium*, EC values estimated to produce a complete egg mass represent a conservative estimation of the total energetic cost for an adult female to spawn, which is in average ~ 12% of the total EC in the gravid female. This energy could be mainly

provided by the foot, since there was a relative decrease in the EC in this tissue from 61.8% in non-gravid females to 51.3% in gravid females. Another probable source of energy are the gonads, as the mean EC value for this tissue in gravid females (that already evacuated most of the egg production) was almost 2-fold the mean value in non-gravid females (Averbuj et al., 2010; Averbuj and Penchaszadeh, 2010).

Among molluscs, there is evidence that much of the energy is stored in the muscles (Pazos et al., 1996; Berthelin et al., 2000) and the digestive gland (Sastry and Blake, 1971; Berthelin et al., 2000), which is also implicated in energy transfer to other tissues. In the pectinid *Argopecten irradians*, the adductor muscle acts as a reserve of energy that is translocated prior to the reproductive season (Barber and Blake, 1981; Barber and Blake, 2006). The basic metabolic levels usually observed for mollusc biochemical components are high lipid and low carbohydrate levels in the gonad and the opposite situation in the muscular tissue, particularly in the foot (Najmudeen, 2007). Mobilization of biochemical components (lipids, proteins and carbohydrates) associated to the reproductive cycle was also reported in gastropods, in particular in abalones (Litaay and De Silva, 2003; Najmudeen, 2007). Gharsallah et al. (2010) showed that in the marine caenogastropod *Hexaplex trunculus* (direct development) the main energetic reservoir for reproductive activities was the gonad; on the contrary, the foot showed an unclear pattern of biochemical (proteins and glycogen) mobilization attributed by these authors to its involvement in growth and metabolism rather than in reproduction, in agreement with Najmudeen (2007). In this study, the results support the hypothesis of a translocation of energy from the foot during the reproductive season (which coincided with a decrease in the foot EC) and, to a lesser extent, from the gonads of gravid females.

In order to be able to reproduce, a marine gastropod as *B. cochlidium* needs not only to reach maturity in terms of anatomical development of reproductive organs, gametogenic development (Averbuj et al., 2010) and behavioural and shell development (Marquez and Averbuj, 2016), but also to reach a suitable body condition or, in other words, to be over an energy content threshold (Barber and Blake, 1981; Barber and Blake, 2006). In this study, the occurrence of such a condition is supported by a higher WM/SL index in gravid females (even when not considering the spawn) than in non-gravid females, which suggests a better physiological and somatic condition in the former ones before the reproductive event. The occurrence of a body condition threshold, required for the females to reproduce, is also supported by the results in this study, that showed that the total energy content (EC), considering the whole individual (including the spawn), was significantly higher in gravid females than in non-gravid females. This energetic surplus represented ~44% more of the total EC per individual, and is probably originated in the foot (Pazos et al., 1996; Berthelin et al., 2000), where EC decreases (relative to the total EC) in gravid females.

Considering the previously mentioned EC and WM/SL index results, together with the fact that the proportion of gravid females registered in this species is ca. 50% during the reproductive season (Averbuj, 2009), it is plausible that at least some of the non-gravid females were energetically not ready to reproduce, even when the gonads were ripe, their reproductive organs developed and the shell size/morphology relationship was adequate (Averbuj et al., 2010; Marquez and Averbuj, 2016). This could be related to the energy balance achieved throughout the year previous to the oviposition season, especially considering that the gravid females would have to afford a 4-month period of carrying the spawn attached to their own shells. Feeding activity was not observed in non-gravid females during this 4-month period (Averbuj, 2009; Averbuj et al., 2012); posteriorly, hatching juveniles fed on prey remains captured by the adults, thus facilitating food availability and survivorship (Averbuj et al., 2012). It should be noted that maternal investment is expected to vary according to female and mating males conditions. Females should invest more in offspring when their breeding attempt is likely to succeed (Collin and Ochoa, 2015).

Taking into account the EC relative loss of ~10% in the foot (edible portion) of gravid females, their consumption is not recommended during the oviposition season, although nutritional composition studies should be performed for this species. Protecting gravid females from fisheries also ensures the sustainability of the resource and must be taken into account when establishing fisheries policies. The management of the edible gastropod *Buccinanops cochlidium* before it turns into a massive artisanal fishery target will allow its conservation through time.

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References

- Averbuj, A., Penchaszadeh, P.E., 2010. Reproductive seasonality, oviposition and development of the nassariid whelk *Buccinanops cochlidium* (Dillwyn, 1817) in Patagonia, Argentina. *J. Molluscan Stud.* 76, 25–32.
- Averbuj, A., Penchaszadeh, P.E., 2016. Reproductive biology in the South Western Atlantic genus *Buccinanops* (Nassariidae): the case of *Buccinanops paytensis*. *Molluscan Res.* 35, 75–83.
- Averbuj, A., Bigatti, G., Penchaszadeh, P.E., 2010. Gametogenic cycle and size at first maturity of the Patagonic edible snail *Buccinanops cochlidium* from Argentina. *Mar. Biol.* 157, 2229–2240.
- Averbuj, A., Palomo, G., Brogger, M.I., Penchaszadeh, P.E., 2012. Diet and feeding of the nassariid *Buccinanops cochlidium* from northern Patagonia Argentina. *Aquat. Biol.* 17, 261–268.
- Averbuj, A., 2009. Iología Reproductiva, Crecimiento Y Dieta Del Caracol Ciego *Buccinanops Cochlidium* (Gastropoda: Nassariidae) En Golfo San José, Argentina. Tesis Doctoral de la Universidad de Buenos Aires, U.B.A. Buenos Aires, pp. 186.

- Barber, B.J., Blake, N.J., 1981. Energy storage and utilization in relation to gametogenesis in *Argopecten irradians concentricus* (say). *J. Exp. Mar. Biol. Ecol.* 52, 121–134.
- Barber, B.J., Blake, N.J., 2006. Reproductive physiology. *Dev. Aquacult. Fish. Sci.* 35, 357–416.
- Berthelin, C., Kellner, K., Mathieu, M., 2000. Storage metabolism in the Pacific oyster (*Crassostrea gigas*) in relation to summer mortalities and reproductive cycle (West Coast of France). *Comp. Biochem. Physiol. B: Biochem. Mol. Biol.* 125, 359–369.
- Bigatti, G., Ciocco, N.F., 2008. Volutid snails as an alternative resource for artisanal fisheries in Northern Patagonic gulfs: availability and first suggestions for diving catches. *J. Shellfish Res.* 27, 417–421.
- Bigatti, G., Cumplido, M., Averbuj, A., 2015. Gasterópodos de interés comercial en la Provincia del Chubut. In: LAPEMAR (Ed.), Technical Report. LAPEMAR-CENPAT-CONICET, Puerto Madryn, pp. 39.
- Brown, A.C., 1982. The biology of sandy beach whelks of the genus *Bullia* (Nassariidae). *Oceanograph. Mar. Biol. Ann. Rev.* 20, 309–361.
- Chaparro, O.R., Oyarzun, R.F., Vergara, A.M., Thompson, R.J., 1999. Energy investment in nurse eggs and egg capsules in *Crepidula dilatata* Lamarck (Gastropoda, Calyptraeidae) and its influence on the hatching size of the juvenile. *J. Exp. Mar. Biol. Ecol.* 232, 261–274.
- Chaparro, O.R., Lincoqueo, L., Schmidt, A., Veliz, D., Pechenik, J., 2012. Comparing biochemical changes and energetic costs in gastropods with different developmental modes: *Crepidatella dilatata* and *C. fecunda*. *Mar. Biol.* 159, 45–56.
- Collin, R., Ochoa, I., 2015. Access to multiple mates increases fecundity but does not affect per-offspring maternal investment in a marine gastropod. *Invertebrate Biol.* 134, 271–281.
- de Mahieu, G., Penchaszadeh, P.E., Casal, A.B., 1974. Algunos aspectos de las variaciones de proteínas y aminoácidos libres totales del líquido intracapsular en relación al desarrollo embrionario en *Adelomelon brasiliense* (Lamarck, 1811) (Gastropoda, Prosobranchia, Volutidae). *Cahiers de Biol. Mar.* 15, 215–227.
- Dillwyn, L.W., 1817. In: Arch, J.A. (Ed.), A Descriptive Catalogue of Recent Shells Arranged According to the Linnaean Method, with Particular Attention to the Synonymy, pp. 1122 (London).
- FAO, 2002. International workshop on factors contributing to unsustainability and overexploitation in fisheries. In: FAO (Ed.), Fisheries Report N(672). FAO, Thailand, pp. 173.
- Gharsallah, I.H., Vasconcelos, P., Zamouri-Langar, N., Missaoui, H., 2010. Reproductive cycle and biochemical composition of *Hexaplex trunculus* (Gastropoda: muricidae) from Bizerte lagoon, northern Tunisia. *Aquat. Biol.* 10, 155–166.
- Giese, A.C., Pearse, J.S., 1977. Reproduction of Marine Invertebrates. Academic Press, New York, San Francisco, London.
- Hendler, G., Franz, D.R., 1971. Population dynamics and life history of *Crepidula convexa* say (Gastropoda: prosobranchia) in Delaware bay. *Biol. Bull.* 141, 514–526.
- Kideys, A.E., Nash, R., Hartnoll, R., 1993. Reproductive cycle and energetic cost of reproduction of the neogastropod *Buccinum undatum* in the Irish sea. *J. Marine Biol. Assoc. U. K.* 73, 391–403.
- Litaay, M., De Silva, S.S., 2003. Spawning season, fecundity and proximate composition of the gonads of wild-caught blacklip abalone (*Haliotis rubra*) from Port Fairy waters, south eastern Australia. *Aquat. Living Res.* 16, 353–361.
- Marquez, F., Averbuj, A., 2016. Sexual dimorphism in the shell of a nassariid gastropod. A 3d geometric morphometrics approach. *J. Mar. Biol. Assoc. U. K.* 97, 249–255.
- McKillup, S.C., Butler, A.J., 1979. Modification of egg production and packaging in response to food availability by *Nassarius pauperatus*. *Oecologia* 43, 221–231.
- Miloslavich, P., 1996. Biochemical composition of prosobranch egg capsules. *J. Molluscan Stud.* 62, 133–135.
- Moran, A.L., 1999. Size and performance of juvenile marine invertebrates potential contrasts between intertidal and subtidal benthic habitats. *Am. Zool.* 39, 304–312.
- Najmudeen, T., 2007. Variation in biochemical composition during gonad maturation of the tropical abalone *Haliotis varia* Linnaeus 1758 (Vetigastropoda: haliotidae). *Mar. Biol. Res.* 3, 454–461.
- Ojeda, J.A., Chaparro, O.R., 2004. Morphological, gravimetric, and biochemical changes in *Crepidula fecunda* (Gastropoda: calyptraeidae) egg capsule walls during embryonic development. *Mar. Biol.* 144, 263–269.
- Pazos, A.J., Ruíz, C., García-Martin, O., Abad, M., Sánchez, J., 1996. Seasonal variations of the lipid content and fatty acid composition of *Crassostrea gigas* cultured in E1 Grove Galicia NW Spain. *Comp. Biochem. Physiol. B: Biochem. Mol. Biol.* 114, 171–179.
- Pechenik, J., Chang, S., Lord, A., 1984. Encapsulated development of the marine prosobranch gastropod *Nucella lapillus*. *Mar. Biol.* 78, 223–229.
- Penchaszadeh, P.E., 1971. Aspectos de la embriogénesis de algunos gasterópodos del género *Buccinanops* d'Orbigny, 1841 (Gastropoda, Prosobranchiata, Buccinidae). *Physis* 30, 475–482.
- Penchaszadeh, P.E., 1973. Nuevas observaciones sobre la reproducción de *Buccinanops gradatum* (Deshayes, 1844) (Gastropoda: Prosobranchiata, Dorsaninae). *Physis Sección A* 32, 15–18.
- Perron, F.E., 1981. The partitioning of reproductive energy between ova and protective capsules in marine gastropods of the genus *Conus*. *Am. Nat.* 118, 110–118.
- Pianka, E.R., 1970. On r-and K-selection. *Am. Nat.* 104, 592–597.
- Riechert, S.E., 1988. The energetic costs of fighting. *Am. Zool.* 28, 877–884.
- Sastry, A.N., Blake, N.J., 1971. Regulation of gonad development in the bay scallop, *Aequipecten irradians* Lamarck. *Biol. Bull.* 140, 274–283.
- Spight, T.M., 1976. Ecology of hatching size for marine snails. *Oecologia* 24, 283–294.
- Underwood, A.J., 1974. On models for reproductive strategy in marine benthic invertebrates. *Am. Nat.* 108, 874–878.