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Meat yield of *Bolinus brandaris* (Gastropoda: Muricidae): Comparative assessment of the influence of sex, size and reproductive status

Paulo Vasconcelos [1,2], Carlos M. Barroso [2], Miguel B. Gaspar [1,3]

[1] Instituto Português do Mar e da Atmosfera (IPMA, I.P.), Avenida 5 de Outubro s/n, 8700-305 Olhão, Portugal.
(PV) (Corresponding author) E-mail: paulo.vasconcelos@ipma.pt. ORCID iD: http://orcid.org/0000-0002-2119-2297
(MBG) E-mail: mbgaspar@ipma.pt. ORCID iD: http://orcid.org/0000-0001-9245-8518
[2] Centro de Estudos do Ambiente e do Mar (CESAM), Departamento de Biologia, Universidade de Aveiro, Campus de Santiago, 3810-193 Aveiro, Portugal.
(CMB) E-mail: cmiguez@ua.pt. ORCID iD: http://orcid.org/0000-0003-0493-3185
[3] Centro de Ciências do Mar (CCMAR), Universidade do Algarve, Campus de Gambelas, 8005-139 Faro, Portugal.

Summary: The present study assessed the influence of sex, size and reproductive status on the meat yield (soft tissues proportion) of the purple dye murex (*Bolinus brandaris*) from the Ria Formosa lagoon (southern Portugal). During one year of monthly sampling (October 2008 - September 2009), average meat yield of *B. brandaris* was 40.5±6.1% (range: 25.8-56.1% wet weight), with no significant differences between sexes. Relationships established between specimen size and soft parts weight indicated that both shell length and total weight are excellent indicators of meat yield. Significant differences in meat yield between size classes further reinforced the trend of increasing meat yield during ontogeny. Meat yield exhibited significant monthly variation and a similar temporal trend in both sexes, which were directly related to the reproductive status. Meat yield of *B. brandaris* was compared with that of other muricid species and the marked influence of the reproductive status on meat yield prompted a comparative assessment of the spawning season and peak of three sympatric muricids (*B. brandaris, Hexaplex trunculus* and *Stramonita haemastoma*). Overall, these findings have implications at diverse levels, including the management, regulation and inspection of this fishing/harvesting activity and the commercialization and consumption of this seafood product.

Keywords: purple dye murex; *Bolinus brandaris*; meat yield; sex; size; reproductive status; spawning season and peak.

Proporción de tejidos blandos de *Bolinus brandaris* (Gastropoda: Muricidae): Evaluación comparativa de la influencia del sexo, la talla y el estado reproductivo

Resumen: El presente estudio evaluó la influencia del sexo, la talla y el estado reproductivo en la proporción de tejidos blandos de la cañaílla (*Bolinus brandaris*) de la laguna Ria Formosa (sur de Portugal). Durante un año de muestreo mensual (octubre de 2008 - septiembre de 2009), la proporción global de *B. brandaris* fue de 40.5±6.1% (rango: 25.8- 56.1% peso húmedo), sin diferencias significativas entre sexos. Las relaciones establecidas entre la talla de los ejemplares y el peso de las partes blandas indicaron que tanto la longitud de la concha como el peso total son excelentes indicadores de la proporción de tejidos blandos. Las diferencias significativas entre clases de talla reforzaron aún más la tendencia creciente durante la ontogenia. La proporción de tejidos blandos mostró una variación mensual significativa y una tendencia temporal similar en ambos sexos, que estaban directamente relacionadas con el estado reproductivo. La proporción de tejidos blandos de *B. brandaris* se comparó con otras especies de murícidos y la marcada influencia del estado reproductivo impulsó una evaluación comparativa de la época y pico de desove de tres murícidos simpátricos (*B. brandaris, Hexaplex trunculus y Stramonita haemastoma*). En general, estos hallazgos tienen implicaciones a diversos niveles, incluyendo la gestión, regulación e inspección de esta actividad de pesca/marisqueo y la comercialización y consumo de este marisco.

Palabras clave: cañaílla; *Bolinus brandaris*; proporción de tejidos blandos; sexo; talla; estado reproductivo; época y pico de desove.

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INTRODUCTION

The purple dye murex, *Bolinus brandaris* (Linnaeus, 1758), is a common muricid species that is extensively dispersed throughout the Mediterranean Sea, whereas its distributional range along the adjacent Atlantic Ocean is restricted mainly to the coasts of Portugal and Morocco (Poppe and Goto 1991, Macedo et al. 1999, Houart 2001). Probably as a consequence of accidental introduction of juveniles, *B. brandaris* has extended its distributional range northwards, and has already been recorded in Galicia (northwestern Spain) (Bañón et al. 2008). This species usually occurs in shallow waters of the sub-littoral zone (Dalla Via and Tappeiner 1981), but can also be found at 100 m (Muzavor and Morenito 1999), 150 m (Houart 2001) or even 200 m depth (Macedo et al. 1999, Malaquias 2007), inhabiting sandy, sandy-muddy and muddy bottoms (Macedo et al. 1999, Muzavor and Morenito 1999, Malaquias 2007).

The purple dye murex was harvested during the Roman Empire using baited wicker baskets (Spanier and Karmon 1987) in order to extract the purple dye that was greatly prized in the ancient Mediterranean (e.g. Reese 1980, 2010, Oliver 2015). Today, *B. brandaris* is fished for human consumption using diverse types of artisanal fishing gears (Poppe and Goto 1991, Houart 2001), mainly in Portugal (Vasconcelos et al. 2008a) and Spain (Martín et al. 1995, Tirado et al. 2002, Mallol et al. 2004), where this species is an important gastronomic resource and is highly valued in local seafood markets (Ramón et al. 2005, Vasconcelos et al. 2008a), but also in France (Bartolome 1985), Italy (Ramón and Amor 2001, Cecalupo et al. 2006) and Greece (Katsanevakis et al. 2011), and occasionally in Turkey (Ramón and Flos 2001) and Tunisia (Elhasni et al. 2013).

Knowledge on meat yield (weight and proportion of the raw edible content) of seafood products is important, both as general information for the consumers and as specific data for the seafood processing and marketing industry. However, despite its importance and the existence of specialized literature on seafood worldwide (e.g. FAO 1989), information on the meat yield of shellfish and specifically of gastropod species is still relatively scarce and restricted to a few commercial species (either fishery-exploited or aquaculture-produced species) (see compilation by Vasconcelos et al. 2009). In Portugal, the purple dye murex is fished along the Algarve coast (southern Portugal), mainly in the Ria Formosa lagoon. It is a greatly appreciated seafood with high demand and commercial value in local seafood markets, reaching prices of around 20-25 € kg^{-1} for first sale (Vasconcelos et al. 2008a). In addition, the commercial value of *B. brandaris* has prompted a few studies to assess its potential as a candidate species for molluscan aquaculture in both Spain (Ramón and Flos 2001, Vela and Moreno 2004, Ramón et al. 2005) and Portugal (Vasconcelos et al. 2012a).

The present study reports the estimation of meat yield and analyses the influence of factors such as sex, size and reproductive status on the meat yield of *B. brandaris* from the Ria Formosa lagoon (southern Portugal). Besides improving the overall knowledge on the species biology, this kind of information is important to increase the awareness on the need to sustainably harvest *B. brandaris*, as well as to support a responsible commercialization and consumption of this locally important shellfish resource.

MATERIALS AND METHODS

Study area and sampling

Commercial samples (≈50 individuals per month) of purple dye murex (*B. brandaris*) were purchased from a local shellfish supplier during a one-year study period (October 2008 - September 2009). Individuals were caught in the Ria Formosa lagoon (Algarve coast, southern Portugal) (Fig. 1), using an artisanal fishing gear baited with cockles (*Cerastoderma edule*), locally known as “wallet-line” (Vasconcelos et al. 2008a), which is a non-size-selective fishing gear and thus collects individuals with broad size and weight ranges.

Because fishing operations and handling procedures frequently damage *B. brandaris* shells, in order to avoid biased measurements and weight discrepancies, specimens with damaged shells (e.g. injured shell aperture and/or broken siphonal canal) were discarded for the purpose of the present analyses. In the laboratory, a few colonizing algae and/or encrusting epibionts were removed from the shells with a hard brush; then the shells were drained to remove excessive water retained inside the mantle cavity (sealed by the operculum) and blotted dry onto absorbent paper.

Estimation of raw meat yield

Live *B. brandaris* were measured for shell length (SL) using a digital calliper (precision of 0.01 mm) and weighed for total weight (TW) on a top-loading digital balance (precision of 0.01 g). Subsequently, individuals were de-shelled in a bench vice in order to remove the soft parts of the organism (edible content=foot and visceral mass) together with the attached operculum (Fig. 2), which were also drained and blotted dry onto absorbent paper to eliminate extra-visceral water.

Because *B. brandaris* lacks external sexual dimorphism, individuals were sexed after breaking the shells, removing the soft parts of the organism and exposing

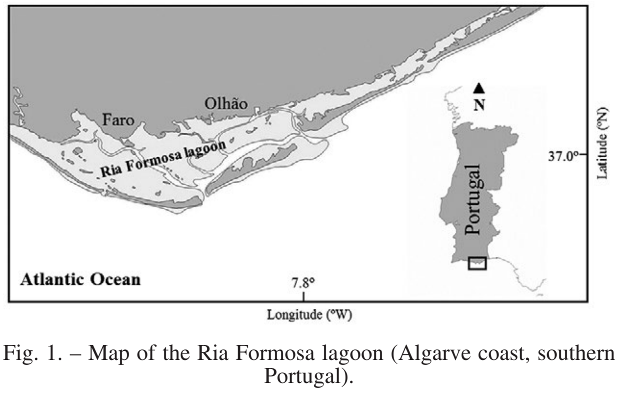

Fig. 1. – Map of the Ria Formosa lagoon (Algarve coast, southern Portugal).

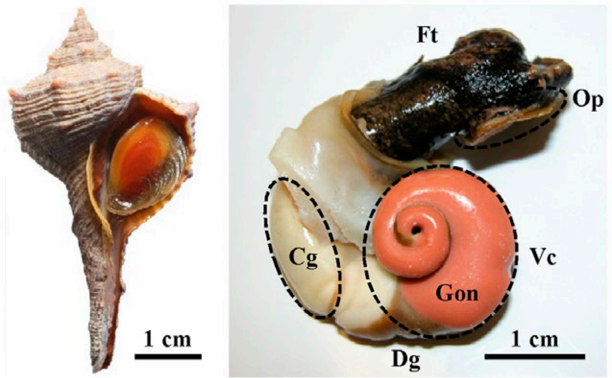

Fig. 2. – Purple dye murex (*Bolinus brandaris*): live specimen and soft parts of the organism (edible content) after shell breakage. Abbreviations: Cg, Capsule gland; Dg, Digestive gland; Ft, foot; Gon, gonad; Op, operculum; Vc, visceral coil (digestive gland and gonad complex).

the mantle cavity to observe the sexual organs in both sexes. Since *B. brandaris* is highly sensitive and severely affected by the imposex phenomenon in the Ria Formosa lagoon (Vasconcelos et al. 2010, 2011), which further complicates sexual identification, males were identified by the presence of penis and lack of capsule gland, while females were identified by the presence of vagina and capsule gland.

After removing the operculum, the whole meat (soft parts of the organism, i.e. foot and visceral mass) constitutes the edible portion of *B. brandaris* as it is consumed locally, so this assemblage of tissues was weighed for soft parts weight (SpW) on the top-loading digital balance (precision of 0.01 g). The raw meat yield (MY) was calculated as the proportion of the SpW relative to TW (MY=SpW/TW), with results expressed as mean±SD percentage of wet weight (i.e. g/100 g ww) (Vasconcelos et al. 2009).

Data treatment and statistical analysis

The relationships between specimen SL, TW and the respective SpW were assessed through regression analyses (least squares method), by fitting the power function to raw data ($Y=aX^b$) and assessing the degree of association between variables by the correlation coefficient (r). The relative growth between variables (isometry vs. allometry) was analysed through the allometry coefficient (regression slope - b) of the morphometric relationships. In relationships between the same type of variables (both ponderal, such as TW vs. SpW) isometry occurs for b=1, whereas in relationships between different types of variables (linear and ponderal, such as SL vs. TW and SL vs. SpW) isometry occurs for b=3, meaning that growth rates of both variables are identical throughout ontogeny (Huxley and Teissier 1936). Subsequently, a t-test (H_0: b=1 or 3; H_A: b≠1 or 3) (Sokal and Rohlf 1987) was applied to confirm whether the slopes (b) of those morphometric relationships were isometric (b=1 or 3) or included in the allometric ranges (negative allometry: b<1 or 3; positive allometry: b>1 or 3) (Huxley and Teissier 1936). Finally, in order to assess possible differences in relative growth between sexes, the slopes (b) of the morphometric relationships of males and females were compared using a specific *t*-test for this purpose (H_0: $b_M=b_F$; H_A: $b_M \neq b_F$) (Zar 1996).

The sex ratio (M:F) of the overall samples was compared with parity (1:1) using the chi-square test (χ^2 test). In order to assess the influence of specimen size on the respective MY, individuals of both sexes were grouped into five size classes (<60, 60-70, 70-80, 80-90 and ≥90 mm SL). In addition, individuals were further grouped into two broader size classes (<65 mm and ≥65 mm SL) defined according to the minimum landing size (MLS=65 mm SL) legally established for the catches of *B. brandaris* in the Ria Formosa lagoon (D.R. 1990, 2001). The influence of the reproductive status on MY was assessed using information previously obtained through histological techniques and the calculation of diverse reproductive condition indices of *B. brandaris* from the Ria Formosa lagoon during the same study period (October 2008 - September 2009). Based on the gonadal maturation stages detected in the histological sections of the gonads of *B. brandaris* (Vasconcelos et al. 2012b), the mean gonadal index [GI=(∑ individuals each stage × stage ranking)/total individuals each month] in both sexes was calculated (Seed 1976). For each stage of gonadal development, a numerical stage ranking was assigned as follows: I - resting=0; II - pre-active=3; III - active=4; IV - ripe=5; V - partially spent=2; VI - spent=1. Accordingly, the GI ranged from 0 (all individuals in the monthly sample in the resting phase) to 5 (all individuals in the monthly sample in the ripe stage). In addition, based on data gathered on the visceral coil weight (VcW), female capsule gland weight (CgW) and male penis length (PL), the following bio-physiological indices of *B. brandaris* were calculated and expressed in percentage (weight or length): gonadosomatic index (GSI=VcW/SpW) in both sexes (Vasconcelos et al. 2012b), the male penial index (PI=PL/SL) (Vasconcelos et al. 2011) and the female capsule gland index (CGI=CgW/SpW) (Vasconcelos et al. 2012b).

Analyses of variance (ANOVA) were employed to compare specimen SL and TW between sexes and to assess the influence of sex, size class and reproductive status of the individuals on the respective MY. Whenever ANOVA assumptions (normality of data and homogeneity of variances) were not fulfilled, the non-parametric Kruskal-Wallis test (ANOVA on ranks) was performed. Each time significant differences among groups were detected by the ANOVA or Kruskal-Wallis test, pairwise multiple comparisons were made using Tukey or Dunn post-hoc tests, respectively. ANOVA's were performed following Zar (1996) and using the software package SigmaStat© (version 3.5). In all statistical analyses, significance level was considered for p<0.05.

RESULTS

A total of 563 individuals of *B. brandaris*, with broad ranges in both SL (48.6-107.7 mm) and TW (4.6-79.7 g), were subjected to analyses for estimating MY (Table 1). In the overall samples, females (n=308)

Table 1. – Descriptive statistics of the samples and meat yield of the purple dye murex (*Bolinus brandaris*) from the Ria Formosa lagoon. M, males; F, females; N, number of individuals; SL, shell length; TW, total weight; MY (%), meat yield. Data presented as mean±SD and range (minimum – maximum).

Sexes	N	SL (mm)	TW (g)	MY (%)
both	563	73.3±8.2 (48.6-107.7)	20.6±7.8 (4.6-79.7)	40.5±6.1 (25.8-56.1)
M	255	72.7±7.4 (51.6-96.7)	20.0±6.2 (5.0-46.8)	40.7±6.2 (25.8-55.3)
F	308	73.8±8.7 (48.6-107.7)	21.1±8.8 (4.6-79.7)	40.4±6.0 (27.2-56.1)

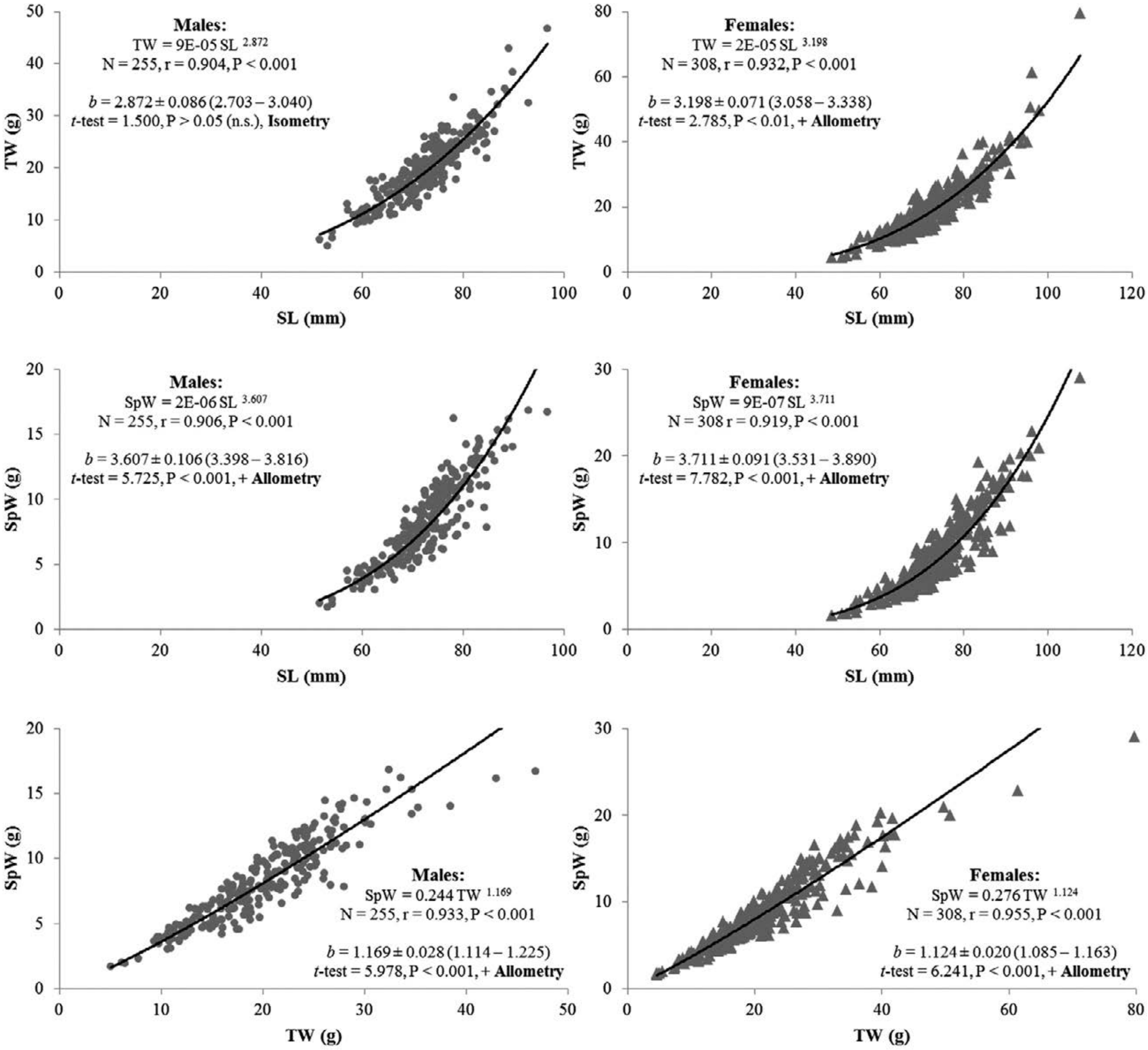

Fig. 3. – Relationships established between shell length (SL), total weight (TW) and soft parts weight (SpW) of *Bolinus brandaris*.

were significantly more abundant than males (n=255) (chi-square test: χ^2=4.803, p<0.05), corresponding to a female-biased sex ratio of 1 M:1.2 F. Male and female *B. brandaris* showed similar mean shell length (males 72.7±7.4 mm SL; females 73.8±8.7 mm SL) and mean total weight (males 20.0±6.2 g TW; females 21.1±8.8 g TW), without statistically significant differences between sexes in either shell length (H=1.039, p>0.05) or total weight (H=0.326, p>0.05) (Table 1). Overall, average MY of *B. brandaris* was 40.5±6.1%, ranging from a minimum of 25.8% to a maximum of 56.1%. There were no statistically significant differences (H=0.667, p>0.05) in the average MY obtained from males (40.7±6.2%; range=25.8-55.3%) and from females (40.4±6.0%; range=27.2-56.1%) (Table 1).

The relationships established between specimen SL, TW and SpW in males and females of *B. brandaris* are presented in Figure 3. In both sexes, all relationships were highly significant (p<0.001) and invariably displayed high correlation coefficients (r=0.904 to 0.955), slightly higher in females (r=0.919 to 0.955) than in males (r=0.904 to 0.933) (Fig. 3). Overall, these relationships indicated that specimen size (in both SL and TW) is an excellent indicator of SpW, and consequently of raw MY. Regarding the relative growth between variables (isometry vs. allometry), only the relationship SL vs. TW in males showed isometric growth (b=2.872±0.086; range=2.703-3.040), while all remaining relationships showed positive allometries (b=1.124 to 3.711) that revealed that throughout ontogeny the SpW increased at a proportionally faster rate than SL and TW (Fig. 3). Regarding the comparison of relative growth between males and females, the relationship TW vs. SpW displayed similar growth between sexes ($b_M=b_F$: t-test=1.514, $p>0.05$), whereas statistically significant differences between males and females were detected in the relationships SL *vs.* TW ($b_M<b_F$: t-test=8.704, $p<0.001$) and SL vs. SpW ($b_M<b_F$: t-test=2.660, $p<0.01$), with females showing proportionally faster grow rates than males in both TW and SpW during ontogeny (Fig. 3).

The variation in MY as a function of the size of *B. brandaris*, with individuals of both sexes grouped into five SL size classes, is presented in Figure 4. Both males and females displayed highly significant differences in MY between size classes (males H=53.801, $p<0.001$; females H=56.595, $p<0.001$), clearly reflected in an evident trend of growing MY with increasing SL (Fig. 4). Similarly, the comparison of MY obtained from individuals below and above the MLS established for *B. brandaris* (MLS=65 mm SL) also showed highly significant differences in the MY obtained from individuals of both sexes below and above the MLS (males F=56.675, $p<0.001$; females H=27.004, $p<0.001$), reflecting much lower MYs in individuals below the MLS (males=34.4±4.7%; females=35.6±4.5%) than in individuals above the MLS (males=41.8±5.8%; females=41.0±5.9%) (Fig. 4). In both cases, i.e. with individuals grouped into five size SL classes and distributed below and above the MLS, there were no statistically significant differences (F or H, $p>0.05$) in MY between sexes within the same size class.

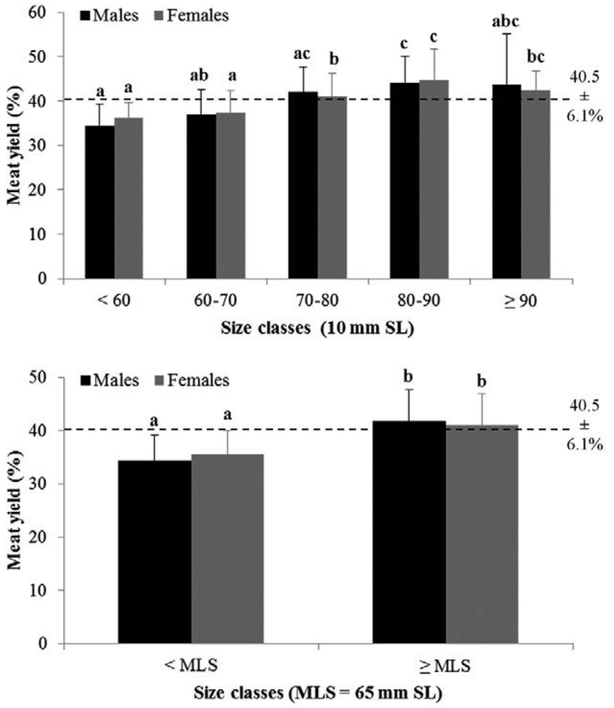

Fig. 4. – Average MY according to specimen size (individuals grouped into 10 mm SL classes) and as a function of the MLS=65 mm SL established for *Bolinus brandaris*. Interrupted lines denote average MY (mean±SD). In each sex, different superscript letters denote statistically significant differences ($p<0.05$) in MY between size classes.

The monthly variation in the MY obtained from *B. brandaris* is presented in Figure 5. The MY of both males and females displayed highly significant monthly oscillation throughout the one-year study period (males F=37.583, $p<0.001$; females F=33.827, $p<0.001$), with both sexes reaching minimum yields in January (males 33.5±4.8%; females 34.2±3.7%) and maximum yields in June (males 49.4±2.6%; females 50.2±3.6%) (Fig. 5). Although the MY in both sexes exhibited a fairly similar and synchronous temporal trend, namely a marked decrease between December and January, followed by a clear increase from January to February, and another simultaneous sharp decrease between June and July, still some statistically significant differences in MY between sexes were detected in the monthly samples of October (females>males F=4.132, $p<0.05$), February (males>females F=6.860, $p<0.05$), March (females>males H=4.987, $p<0.05$) and September (males>females F=6.527, $p<0.05$) (Fig. 5).

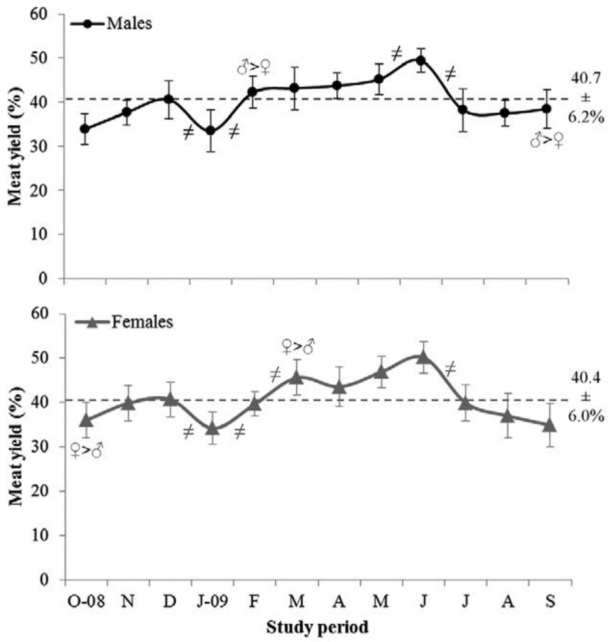

Fig. 5. – Monthly variation in the average MY of *Bolinus brandaris* males and females during the study period (October 2008 - September 2009). Interrupted lines denote average MY (mean±SD). In each sex, symbols denote statistically significant differences ($p<0.05$) in MY between consecutive months (≠) or between sexes in each month (♂>♀ or ♀>♂).

The influence of diverse indicators of the reproductive status on the MY of *B. brandaris* is depicted in Figure 6. The monthly variation in MY in both sexes slightly reflected the fluctuation in the mean GI during late spring - early summer. Indeed, sharp declines in male GI in May-August (from a maximum of 5.0 to a minimum of 1.1) and in female GI in June-August

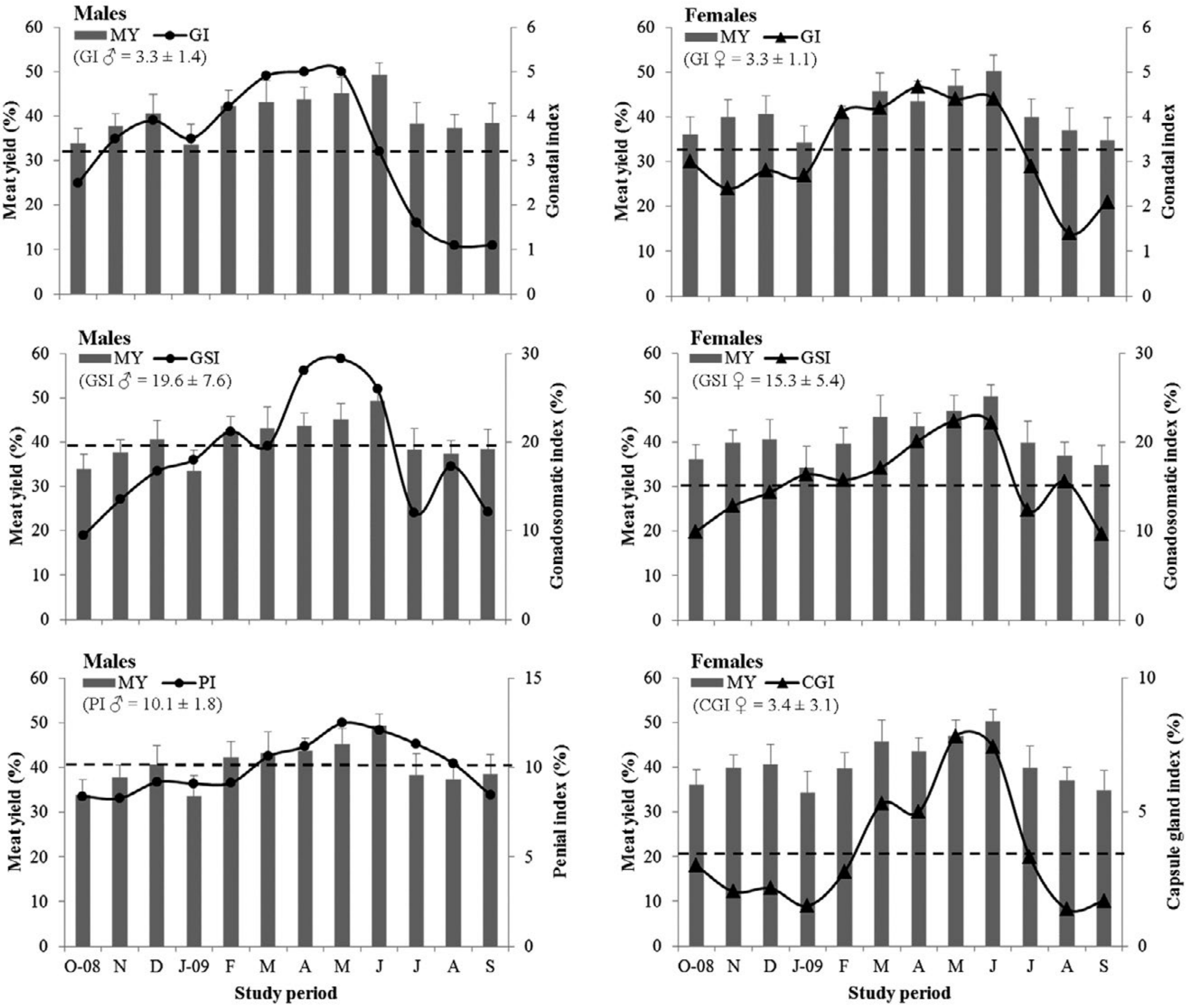

Fig. 6. – Influence of diverse indicators of the reproductive status of *Bolinus brandaris* males and females on the respective MY during the study period (October 2008 - September 2009). Interrupted lines denote average gonadal index, gonadosomatic index, penial index and capsule gland index (mean±SD).

(from 4.4 to a minimum of 1.4), reflecting the decrease in the proportion of ripe gonads and the subsequent increase in the proportion of partially spent and spent gonads, coincided with significant reductions in the MY of both males (from 45.1% in May to 37.4% in August) and females (from 50.2% in June to 37.0% in August) (Fig. 6). Similarly, the gonadosomatic index (GSI), indicative of gonadal maturation and inherent variation in gonad weight in both sexes, displayed abrupt decreases during the above period (males May-July; females June-July), reflecting gonad emptying during gamete release and female spawning. These decreases in both male GSI (from 29.4% in May to 12.2% in July) and female GSI (from 22.2% in June to 12.4% in July) were accompanied by marked reductions in MY in both males (from 45.1% in May to 38.2% in July) and females (from 50.2% in June to 39.9% in July) (Fig. 6). The sex-specific indices (male PI and female CGI) also exhibited the same general temporal trend of the previous bio-physiological indices. The PI, indicative of the copulative activity and consequent male gamete release, decreased continuously between the peak of copulation in May (12.5%) and September (8.5%), encompassing the period of marked reduction in male MY (from 49.4% in June to 37.4% in August). The CGI also displayed a sharp decrease between a maximum in May (7.8%) and a minimum in August (1.4%), indicating the deposition of egg capsules (oothecae) during the spawning season and consequent emptying of the capsule gland, which further contributed to the reduction in female MY recorded from June (maximum of 50.2%) to August (37.0%) (Fig. 6).

DISCUSSION

The average MY obtained from the purple dye murex (sexes combined) from the Ria Formosa lagoon was 40.5±6.1%, ranging between 25.8 and 56.1% during the study period. As stated above, information on the MY of gastropod species is still relatively scarce, and to the author's best knowledge in the available literature there is only one other study reporting the

Table 2. – Comparison of the meat yield of *Bolinus brandaris* from the Ria Formosa lagoon and other species within the family Muricidae, including some edible and/or commercially valuable muricids. Notes: Meat yield data presented as mean±SD and range (minimum – maximum); *, edible species; **, commercially valuable species; [a], data converted from percentage shell weight to total weight; [b], data expressed as percentage of soft-body total weight; [c], variable depending on collecting site and date; N, number of individuals; SL, shell length range (mm); TW, total weight range (g); ♂+♀, sexes combined.

Species	Common name	Location	Meat yield (%)	Observations	Reference
Bolinus brandaris (Linnaeus, 1758)	purple dye murex**	Ria Formosa (Portugal), Atlantic Ocean	40.5±6.1 (25.8-56.1)	N=563; SL=48.6-107.7; TW=4.6-79.7; ♂+♀	present study
		Bay of Piran (Slovenia), Adriatic Sea	42.5[a]	N=5	Dalla Via and Tappeiner (1981)
Chicoreus ramosus (Linnaeus, 1758)	branched murex**	Mandapan - Gulf of Mannar (India), Indian Ocean	≈50[b]	–	Raghunathan et al. (1992)
Hexaplex trunculus (Linnaeus, 1758)	banded murex**	Bay of Piran (Slovenia), Adriatic Sea	33.6[a]	N=20	Dalla Via and Tappeiner (1981)
		Kalithea Bay - Rhodes (Greece), Mediterranean Sea	34.2 (28.5-39.3)[a]	N=7; SL=39.0-8.0; TW=7.1-18.1	Alyakrinskaya (2005)
		Pathos Town (Cyprus), Mediterranean Sea	33.3 (31.6-37.6)[a]	N=5; SL=41.0-49.0; TW=8.3-14.3	Alyakrinskaya (2005)
		Ria Formosa (Portugal), Atlantic Ocean	37.9±4.6 (22.5-59.7)	N=1418; SL=40.2-82.8; TW=5.3-58.2; ♂+♀	Vasconcelos et al. (2009)
Pinaxia coronata A. Adams, 1853	rock shell**	Cross River Estuary (Nigeria), Atlantic Ocean	16.3 (11.9-19.5)	N≈500; SL=11.0-46.8	Udoh and Abiaobo (2014)
Rapana venosa (Valenciennes, 1846)	veined whelk	Novorossiysk Bay - Krasnodar (Russia), Black Sea	30.1 to 34.1[c] (22.1-46.8)[a]	N=59; SL=43.0-80.0; TW=15.4-71.3	Alyakrinskaya (2005)
Stramonita haemastoma (Linnaeus, 1767)	red-mouthed rock shell*	Magaluff Cape - Majorca (Spain), Mediterranean Sea	34.1 (22.1-53.3)[a]	N=3; SL=42.0-56.0; TW=11.3-27.7	Alyakrinskaya (2005)
		Las Galletas Bay - Tenerife (Spain), Atlantic Ocean	22.8 (16.4-26.9)[a]	N=6; SL=35.0-43.0; TW=5.0-10.1	Alyakrinskaya (2005)

MY of *B. brandaris* (42.5%) from the Adriatic Sea (Dalla Via and Tappeiner 1981). The comparison of the MY obtained from *B. brandaris* with that of other species of the family Muricidae, including some edible and/or commercially valuable muricids, is compiled in Table 2. It is worth stating that such comparisons in some muricids (e.g. *B. brandaris, H. trunculus* and *S. haemastoma*) should be cautiously interpreted because their edible content varies depending on the country where these species are used for human consumption. For instance, whereas in the northeastern Atlantic and northern Mediterranean the whole meat (foot and visceral mass) is ingested, in the southern Mediterranean only the foot is consumed. In general, the average MY of the purple dye murex from the Ria Formosa lagoon (40.5%) is higher than that obtained from other sympatric muricid species, namely *H. trunculus*, with values of 33.3% in Cyprus (Alyakrinskaya 2005), 33.6% in Slovenia (Dalla Via and Tappeiner 1981), 34.2% in Greece (Alyakrinskaya 2005) and 37.9% in Portugal (Vasconcelos et al. 2009), and *S. haemastoma* with values ranging from 22.8% in Tenerife (Alyakrinskaya 2005) to 34.1% in Majorca (Alyakrinskaya 2005) (Table 2). This higher MY of *B. brandaris* compared with *H. trunculus* and *S. haemastoma* is due to marked differences in their shells in terms of thickness, strength and ornamentation, and consequently, in their shell relative weight (e.g. Dalla Via and Tappeiner 1981, Alyakrinskaya 2005, Vasconcelos et al. 2016). For instance, the contribution of shell weight to TW in *H. trunculus* is almost 10% higher than that in *B. brandaris* (Dalla Via and Tappeiner 1981), whereas in *S. haemastoma* the contribution is over 10% higher than that in *H. trunculus* (Alyakrinskaya 2005).

The relationships established between *B. brandaris* size and the respective SpW revealed that both SL and TW are excellent indicators of SpW, and therefore of the raw MY that can be obtained from the purple dye murex. This information is most useful both for the seafood processing industry and for consumers, because the relationships SL vs. SpW and TW vs. SpW allow us to predict the edible content of *B. brandaris* as a function of the individual size (either in SL or TW), and thus estimate the MY that can be obtained from a batch of purple dye murexes with a certain size or weight range. Concerning relative growth, both males and females displayed positive allometries in the relationships SL vs. SpW and TW vs. SpW, revealing that during growth the edible content increased at a proportionally faster rate than SL and TW (i.e. the largest and heaviest individuals provide proportionally higher MYs), which in practice means that *B. brandaris* allocates more energy resources to somatic growth than to shell secretion throughout ontogeny. Inter-specific comparisons of the type of growth (isometry *vs.* allometry) are rather complicated due to high variability in shell morphology and structure between species and their variation during growth. Still, in *B. brandaris* the allometry coefficients of the relationships SL vs. SpW (males, b=3.607; females, b=3.711) and TW vs. SpW (males, b=1.169; females, b=1.124) are higher than those reported for other muricid species, such as *Chicoreus ramosus* (SL vs. meat weight, b=2.805) (Thapnu and Tantichodok 1991), *Pinaxia coronata* (SL vs. fresh tissue weight, b=2.801) (Udoh and Abiaobo 2014) and *H. trunculus* (SL *vs.* meat weight, b=3.557; TW vs. meat weight, b=1.118) (Vasconcelos et al. 2009). Concerning the comparison of relative growth between sexes, in the relationships SL vs. TW (males, b=2.872;

Table 3. – Comparative assessment of the spawning season and peak, including spawning events in the field and in the laboratory, of three sympatric muricid species, the purple dye murex (*Bolinus brandaris*), the banded murex (*Hexaplex trunculus*) and the red-mouthed rock shell (*Stramonita haemastoma*), throughout their geographic distributional range. $^{\text{Atl}}$, Atlantic Ocean; $^{\text{Med}}$, Mediterranean Sea; $^{\text{Adr}}$, Adriatic Sea; $^{\text{Aeg}}$, Aegean Sea; n.a., data not available; N, number of individuals; SL, shell length range (mm); SLwS, shell length without siphonal canal (mm); FO, field observations; LO, laboratory observations; GH, gonadal histology; GM, gonadal macroscopic examination; CI, condition indices.

Species	Location	Study period	Spawning period		Spawning events		Observations	Reference
			Season	Peak	Field	Laboratory		
Bolinus brandaris (Linnaeus, 1758)	Gulf of Naples, Italy $^{\text{Med}}$	n.a.	May-Jun				n.a.	Lo Bianco (1888)
	Dor, Haifa, Palmahim, Tel-Aviv and Tel-Barukh, Israel $^{\text{Med}}$	Jul 1945 – Jun 1977			May-Jul		FO (spawns cast ashore + dredged spawns)	Barash and Zenziper (1980)
	Golfe du Lion, France $^{\text{Med}}$	n.a.	Spring				n.a.	Bartolome (1985)
	Sant Carles de la Ràpita, Catalonia, Spain $^{\text{Med}}$	Nov 1992 – Oct 1993	Jun-Jul		Aug		FO (dredged spawns)	Martín et al. (1995)
	Andalucía, Spain $^{\text{Atl, Med}}$	n.a.	May-Jun				n.a.	Anon. (2001)
	Catalonia, Spain $^{\text{Med}}$	May-Dec 2000			May-Jun		FO (collected spawns)	Ramón and Flos (2001)
	Sant Carles de la Ràpita, Catalonia, Spain $^{\text{Med}}$	Feb 1999 – Mar 2000	Apr; Jun-Jul	Jun-Jul			GH + GM; N=240; SLwS≈26-52	Ramón and Amor (2002)
	Marbella, Andalucía, Spain $^{\text{Med}}$	Jun 1999-May 2000	May-Jul				GH + CI; N=2364; SL≈30-60	Tirado et al. (2002)
	Gulf of Roses, Catalonia, Spain $^{\text{Med}}$	Mar-Apr 2001	May-Jul				FO (dredged spawns)	Mallol et al. (2004)
	Algarve coast, Portugal $^{\text{Atl}}$	n.a.	May-Jun				n.a.	Malaquias (2007)
	Ria Formosa lagoon, Portugal $^{\text{Atl}}$	Jul 2005-Jun 2006			Jun		FO (observed spawns)	Vasconcelos et al. (2008a)
	Ria Formosa lagoon, Portugal $^{\text{Atl}}$	Oct 2008-Sep 2009	May-Jul	Jun-Jul			CI; N=573; SL=51.6-97.9	Vasconcelos et al. (2011)
	Bizerte lagoon and small Gulf of Tunis, Tunisia $^{\text{Med}}$	Mar 2007-Feb 2008	Mar/Apr-May; Jun-Aug				GM + CI; N=2131; SLwS=17.0-50.0	Abidli et al. (2012)
	Ria Formosa lagoon, Portugal $^{\text{Atl}}$	Oct 2008-Sep 2009	May-Jul	Jun-Jul			GH + CI; N=567; SL=48.6-107.7	Vasconcelos et al. (2012b)
	Gulf of Gabès, Tunisia $^{\text{Med}}$	Jan-Dec 2007	Apr-Jul	May-Jun			GH + GM + CI; N=1929; SL=31.0-95.1	Elhasni et al. (2013)
Hexaplex trunculus (Linnaeus, 1758)	Gulf of Naples, Italy $^{\text{Med}}$	n.a.	May-Jun				n.a.	Lo Bianco (1888)
	Banyuls-sur-Mer and Endoume, France $^{\text{Med}}$	Apr-Jul 1932				mid-Jun – late-Jun	LO (spawns in aquaria)	Fischer and Raffy (1933)
	Lago di Faro, Sicily, Italy $^{\text{Med}}$	n.a.				May-Jun	LO (spawns in aquaria); SL=50.0-100.0	Dulzetto (1946)
	Messina, Sicily, Italy $^{\text{Med}}$	Jul 1949				Jul	LO (spawns in aquaria)	Dulzetto (1950)
	Istria coast, Croatia $^{\text{Adr}}$	Jan-Feb 1974				Jan-Feb	LO (spawns in aquaria)	Wondrak (1974)
	Banyuls-sur-Mer, France $^{\text{Med}}$	n.a.				May-Jun	LO (spawns in aquaria)	Bandel (1975)
	Dor, Herzliyya, Nahal Poleg, Tel-Aviv, Tel-Barukh, Israel $^{\text{Med}}$ and Cyprus $^{\text{Med}}$	Jun 1965-Oct 1977	year-round	May-Jul			FO (spawns cast ashore)	Barash and Zenziper (1980)
	Akko Bay, Israel $^{\text{Med}}$	May 1979-Sep 1980			May		FO (diving surveys)	Spanier (1981)
	Lago di Faro, Sicily, Italy $^{\text{Med}}$	Jan-Dec 1983	Jun-Jul				GH	Albanese et al. (1983)
	Israel $^{\text{Med}}$	n.a.			mid-Mar-Jun	mid-Mar-Jun	FO + LO (spawns in aquaria)	Spanier and Karmon (1987)
	Baie de Calvi, Corsica, France $^{\text{Med}}$	Oct 1982-Sep 1984	Jul				GH; N=109	Martoja and Bouquegneau (1988)
	Italy $^{\text{Adr}}$ + Ionian and Tyrrhenian coasts $^{\text{Med}}$	n.a.				May-Jun	LO (spawns in aquaria)	Terlizzi et al. (1999)

	Andalucía, Spain $^{Atl, Med}$	n.a.	May-Jun				n.a.	Anon. (2001)
	Marbella, Spain ^{Med}	Jun 1999-May 2000	Apr-Jul				GH + CI; N=2222; SL=37-90 mm	Tirado et al. (2002)
	Bizerte lagoon, Tunisia ^{Med}	Jul 2002-Jul 2003	Jan-May; Aug-Sep	Apr-Jul			CI; N=2880	Lahbib et al. (2004)
	Bizerte channel, Tunisia ^{Med}	Jul 2002-Jul 2003	Feb-May; Jul-Oct				CI; N=2880	Lahbib et al. (2004)
	Ria Formosa lagoon, Portugal ^{Atl}	Apr-Oct 2004				late-Apr-early-Jun	LO (spawns in aquaria); SL=55.1-75.2	Vasconcelos et al. (2004)
	Ria Formosa lagoon, Portugal ^{Atl}	n.a.			Feb-Jun		FO (fishermen interviews)	Vasconcelos et al. (2004)
	Bizerte lagoon, Tunisia ^{Med}	n.a.				Mar	LO (spawns in aquaria)	Abidli et al. (2006)
	Bizerte lagoon, Tunisia ^{Med}	n.a.				Apr-Jul	LO (spawns in aquaria)	Lahbib et al. (2006)
	Bizerte lagoon, Tunisia ^{Med}	Jan-Jul 2003				Feb-Jul	LO (spawns in aquaria); N=100-150; SL=40-60	Trigui El-Menif et al. (2006)
	Bizerte channel, Tunisia ^{Med}	Jan-Jul 2003				Mar-Jul	LO (spawns in aquaria); N=100-150; SL=40-60	Trigui El-Menif et al. (2006)
	Algarve coast, Portugal ^{Atl}	n.a.	May-Jun				n.a.	Malaquias (2007)
	Ria Formosa lagoon, Portugal ^{Atl}	Mar 2003-Feb 2004	Mar-Jun	May-Jun			GH; N=1183; SL=40.2-82.8	Vasconcelos et al. (2008b)
	Ria Formosa lagoon, Portugal ^{Atl}	Mar 2003-Feb 2004	Apr-Jun	May-Jun			CI; N=903; SL=40.2-79.8	Vasconcelos et al. (2008c)
	North lake of Tunis, Tunisia ^{Med}	Feb-Jul 2006				early-Mar	LO (spawns in aquaria); N=600; SL=40-70	Abidli et al. (2009)
	Menzel Jemil, Bizerte lagoon, Tunisia ^{Med}	May 2004-May 2005	Jan-Feb				CI; N=720	Lahbib et al. (2009)
	Bizerte channel, Bizerte lagoon, Tunisia ^{Med}	May 2004-May 2005	Apr-May				CI; N=720	Lahbib et al. (2009)
	Menzel Jemil and Bizerte channel, Bizerte lagoon, Tunisia ^{Med}	Jan-May 2005				mid- to late-Apr	LO (spawns in aquaria); N=400	Lahbib et al. (2009)
	Gulf of Gabès, Tunisia ^{Med}	Jun 2007-May 2008	Apr-May				GM + CI; N=1870; SL=20.8-80.0	Elhasni et al. (2010)
	Bizerte lagoon, Tunisia ^{Med}	Oct 2004-Dec 2005	Mar-May	Mar-Apr			GM + CI; N=1478; SL ≥ 50	Gharsallah et al. (2010)
	Bizerte lagoon, Tunisia ^{Med}	Oct 2004-Dec 2005; May 2005 -Apr 2006	Mar-May	Apr-May			FO (fishing surveys) + FO (interviews of shellfish farmers)	Gharsallah et al. (2010)
	Menzel Jemil, Bizerte lagoon, Tunisia ^{Med}	Jan 2005-Dec 2007				late-Apr – mid-May	LO (spawns in aquaria); N=100; SL=35.2-57.4	Lahbib et al. (2010)
	Boughrara lagoon, Tunisia ^{Med}	Jun 2007-May 2008	Feb-Mar				GM + CI; N=343; SL=40-60	Lahbib et al. (2011a)
	Boughrara lagoon, Tunisia ^{Med}	Jun 2007-May 2008			late-Feb-Mar		FO (observed spawns)	Lahbib et al. (2011a)
	Urla, Izmir, Turkey ^{Aeg}	n.a.				May	LO (spawns in aquaria); N=39; SL=57.0-67.3	Güler and Lök (2014)
Stramonita haemastoma (Linnaeus, 1767)	Tel-Aviv, Israel ^{Med}	Aug 1957-Jun 1971			Jun-Aug		FO (collected spawns)	Barash and Zenziper (1980)
	Zarzouna, Bizerte lagoon, Tunisia ^{Med}	Mar-Aug 2007				late-May – mid-Jun	LO (spawns in aquaria); N=90; SL=40-80	Lahbib et al. (2011b)
	Zarzouna, Bizerte lagoon, Tunisia ^{Med}	Mar-Aug 2007			late-Apr – early-Aug		FO (observed spawns)	Lahbib et al. (2011b)
	Artificial channel, Bizerte lagoon, Tunisia ^{Med}	Jun 2009-May 2010	Jun-Jul; Sep-Oct				GM+CI; N=1035; SL=20.0-80.0	El Ayari et al. (2015)

females, b=3.198) and SL vs. SpW (males, b=3.607; females, b=3.711), females exhibited significantly higher allometry coefficients than males, indicating faster grow rates in both TW and SpW throughout ontogeny, which are probably due to particular features of the female reproductive system, namely a female-specific accessory sexual organ, the capsule gland that reaches a considerable size and weight during the spawning season (please see further details below about the influence of the reproductive status on the MY of *B. brandaris*).

The trend of increasing MY during the ontogeny of *B. brandaris* was further highlighted by grouping the individuals of both sexes into SL size classes. Indeed, highly significant differences in MY between size classes in both males and females constitute additional evidence of growing MY with increasing SL, i.e. smaller individuals yield significantly less edible content than larger individuals. Accordingly, individuals below the MLS legally stipulated for *B. brandaris* (<65 mm SL) provided significantly lower MYs (males=34.4%; females=35.6%) than individuals that achieved the minimum landing size (≥65 mm SL) (males=41.8%; females=41.0%), further reinforcing the importance of compliance with the species MLS by fishermen/harvesters, seafood traders and shellfish consumers. In fact, since commercially undersized specimens yield significantly lower edible content than individuals above the MLS, this should also help discourage their commercialization and consumption, in order to avoid unconsciously paying for shells at the price of meat, considering the high commercial value of the purple dye murex (which fetches prices around 20-25 € kg^{-1} for first sale) (Vasconcelos et al. 2008a). Moreover, the existence of commercially undersized *B. brandaris* available in local shellfish suppliers and seafood markets justifies the need to improve regulation measures and reinforce inspection activities focusing on this artisanal fishery.

The MY of *B. brandaris* exhibited significant monthly variations and an analogous and synchronous temporal trend in both males and females during the study period, which were undoubtedly related to their reproductive status, as evidenced by the monthly oscillation in diverse bio-physiological indices calculated for both sexes. In fact, the most noteworthy monthly variation in the MY of both males and females was a significant decrease recorded from June to July, which was accompanied by a simultaneous reduction in most indices of reproductive condition, namely the mean GI and the GSI in both sexes, the male PI, and the female CGI. Chronologically, such sharp decreases in these indices correspond to the following sequential phases in the reproductive cycle of *B. brandaris*: peak of male copulative activity in May (PI); maturation peak in May (males) and June (females) followed by sharp decreases in both GI and GSI, which denote decreasing proportions of ripe gonads and consequent replacement by increasing proportions of partially spent and spent gonads (GI) as a consequence of gamete release (GSI) in both sexes; and female spawning peak between June and July (CGI). Overall, the sharp decreases in these bio-physiological indices reflect significant reductions in the size and weight of male and female gonads and in the female capsule gland, which are inevitably translated immediately into a substantial decrease in SpW and consequently a significant decline in the raw MY of the purple dye murex between June and July. Indeed, during the period of reproductive maturation, both male and female *B. brandaris* develop large gonads and females fill the capsule gland responsible for the formation of the egg capsules (oothecae) that encapsulate the developing eggs and embryos, an accessory sexual organ that also reaches considerable size during the spawning season (e.g. Amor et al. 2007, Vasconcelos et al. 2012b, Elhasni et al. 2013), and whose deflation and emptying after gamete release and spawning is noticeably reproduced as an abrupt decrease in the raw MY of the purple dye murex.

In certain fishing resources, the optimum harvesting season should coincide with the period of highest MY (e.g. Udoh and Abiaobo 2014), which allows the weight of the catches/landings and the respective commercial value and resulting profits to be maximized. In the present case, besides the general concerns related to the sustainability of the fishing/harvesting activity and the appropriate management of this fishing resource, data on the MY of the purple dye murex confirmed the importance and interest of accomplishing the MLS=65 mm SL legally stipulated for the catches of *B. brandaris* in the Ria Formosa lagoon (D.R. 1990, 2001), primarily by fishermen/harvesters, but also by seafood traders and shellfish consumers. In addition, the present data also confirmed the influence of the reproductive status on the edible content of the purple dye murex, with the highest MYs being recorded in the period of reproductive maturation (i.e. prior to the gamete release and the spawning peak). In this particular, it should be taken into account that the fishing/harvesting activity targeting *B. brandaris* is subjected to a closed season (1 May - 30 June) (D.R. 2010), which was deliberately implemented during the spawning season in order to protect the female broodstock and collective spawns (Vasconcelos et al. 2012b). For this reason, although the highest MYs of *B. brandaris* coincide with the closed season of the fishing/harvesting activity, this temporary prohibition of the catches should be rigorously fulfilled by fishermen/harvesters in order to ensure a balanced and sustainable long-term exploitation of this locally important fishing resource of the Ria Formosa lagoon.

Finally, the marked influence of the reproductive status on the MY detected in the present study prompted a comparative assessment of the spawning season and peak, including spawning events observed in the field and in the laboratory, of three sympatric muricid species (*B. brandaris, H. trunculus* and *S. haemastoma*) throughout their geographic distributional range (Table 3). This multi-species comparative approach compiles most relevant baseline information consulted in virtually all literature available on this subject, providing supporting data from a long-time period (1888-2015) and thus allowing analysis of long-term trends. In addition, this dataset comprises information gathered at locations covering a wide geographical area (Atlantic Ocean, Mediterranean, Adriatic, Tyrrhenian, Ionian and Aegean Seas) and including ecologically diverse habitats (e.g. coastal areas vs. coastal lagoons). Overall, 55 data records on studies of the spawning season and peak of those three muricid species, obtained through biological sampling and analyses, field and laboratory observations, were collected from 41 bibliographic sources published by 27 different authors (Table 3).

According to the information available in the literature, these gastropod species display slight variation in the timing of reproduction throughout their distributional range, namely in the spawning season and peak, most probably associated with the colder seawater temperatures in the Atlantic Ocean compared with the Mediterranean Basin. As a consequence, Mediterranean populations of these species show a lengthy spawning season, generally ranging from spring to summer (sometimes even with an unusual longer duration), as well as more than one spawning period during the year (Table 3). Gonadal ripening and spawning are apparently triggered by the progressive rise in seawater temperatures from late spring to early summer. This reproductive dynamics induces a significant increase in the volume and weight of the gonads and accessory reproductive organs, subsequently reflected in the species MY, as is clearly demonstrated in the present study.

Indeed, gastropod reproductive dynamics, including the seasonality of gonadal ripening and spawning, are regulated by environmental cues that allow reproduction to occur at the most favourable time (Wayne 2001, Harding et al. 2008, Hotchkiss et al. 2008), with seawater temperature and food availability controlling the timing of spawning and being responsible for interannual variations in the reproductive cycle (Sternberg et al. 2010). Accordingly, as for the sympatric *B. brandaris, H. trunculus* and *S. haemastoma*, similar reproductive patterns (i.e. spawning season coinciding with rising seawater temperatures) have been reported for several other muricid species worldwide, such as *Hexaplex nigritus* (Cudney-Bueno et al. 2008), *Rapana venosa* (Saglam and Duzgunes 2007, Harding et al. 2008, Saglam et al. 2009), *Reishia clavigera* (Tong 1988, Lee 1999), *Tenguella musiva* (Tong 1988) and *Trophon geversianus* (Cumplido et al. 2010).

In conclusion, the present study showed that MY of the purple dye murex increases during ontogeny, as revealed by the relationships established between specimen size and SpW and by significant differences in MY between size classes. In addition, MY exhibited significant monthly variation directly related to reproductive status, as evidenced by the calculation of bio-physiological indices. Overall, these findings have implications at diverse levels, including the management, regulation and inspection of the artisanal fishing/harvesting activity and the commercialization and consumption of this valuable seafood product. In addition to *B. brandaris*, the same applies to other muricid species exploited for human consumption, including *H. trunculus* and *S. haemastoma*.

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