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# Sources of carbon and dietary habits of new Lessepsian entry *Brachidontes pharaonis* (Bivalvia, Mytilidae) in the western Mediterranean

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**Abstract** The sources of carbon and the dietary habits of *Brachidontes pharaonis* (Mollusca, Bivalvia), a new Lessepsian entry in the western Mediterranean, living in a cooling vat of a saltworks system in western Sicily (MED), were assessed by estimating throughout a season the relative abundance of a stable carbon isotope ($\delta^{13}C$) in particulate organic matter (POM), sedimentary organic matter (SOM), primary organic matter sources (seagrasses, sand microflora, macroalgae), *Brachidontes pharaonis* and its biodeposition material. In the saltworks the most enriched primary food source potentially fuelling the saltworks food web was *Cymodocea nodosa* (seasonal average $-7.9 \pm 0.6$‰), *Laurencia papillosa* and *Cystoseira* sp., which represented the predominant macroalgae (seasonal average $-19.0 \pm 1.0$‰) and sand microflora $\delta^{13}C$ ($-14.7 \pm 0.11$‰). POM annual mean $\delta^{13}C$ was $-17.4 \pm 0.9$‰, and that of SOM was $-17.0 \pm 2.3$‰. The seasonal mean isotopic value of *B. pharaonis* was $-14.7 \pm 0.7$‰; while its faeces was more depleted ($-17.7 \pm 2.4$‰), while the pseudofaeces ($-14.6 \pm 3.6$‰) was similar to somatic *B. pharaonis* in composition. Our study showed that *Brachidontes* assimilated mostly mixed sedimentary organic carbon re-arranged *via* a detritus route dominated mainly by macroalgae and sand microflora and that it was able to exploit almost all the predominant carbon sources available in its colonised environment both directly (sand microflora) and indirectly via the POM/SOM detritus route. These carbon sources incorporated most of the environmental variability relative to the isotopic composition of primary producers (about –11‰ throughout the year).

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## Introduction

Despite growing concern over the negative effects of biological invasions, we still know surprisingly little about what determines the distribution and abundance of invading species and the conditions under which they will successfully invade and establish themselves in new communities (Carlton et al. 1990; Cohen et al. 1995; Crooks 1996, 1998; Ruiz et al. 1997).

In the last few decades some Indo-Pacific species have colonised several Mediterranean marine ecosystems, entering from the Red Sea after the opening of the Suez Canal in 1869. These are known as Lessepsian migrants (Por 1971). Apart from a few well known invaders, such as *Portunus pelagicus* (L.), many bivalve molluscs, such as *Musculista senhousia* (Benson in Cantor), *Xenostrobus securis* (Lamark) and *Perna picta* (Von Born) have appeared along the Adriatic and Tyrrhenian coasts (western Mediterranean), influencing the functioning of ecosystems to a great extent.

Together with some other species, *Brachidontes pharaonis* (Fischer P., 1870; *Brachidontes variabilis* Krauss, 1848) (Bivalvia, Mytilidae) was never found in the Mediterranean before 1869 (Safriel et al. 1980) and its introduction and consequent diffusion may be due to human phoresys (e.g. ballast waters). It has now invaded some parts of western Mediterranean coasts (Di Geronimo 1971) and represents a potential resource and space competitor of its Mediterranean ecological equivalent, *Mytilaster minimus* (Safriel and Sasson-Frostig 1988).

The most westerly Mediterranean report of *Brachidontes pharaonis* is in the cooling vats of a saltworks system in western Sicily (Sarà et al. 2000), where it has largely colonised hard substrates. These environments are characterised by hypersalinity (>45‰), partial enclosure and carbon sources dominated by seagrass [Cymodocea nodosa (Ucria, Ascherson)] detritus.

Many physical, chemical and trophic factors may be responsible for the biology and distribution of invaders.

The occurrence of *B. pharaonis* in sheltered Mediterranean coastal environments greatly influenced by large quantities of available detrital organic matter (Sarà et al. 2000) has stirred interest in the role played by the nature of food availability (organic matter quantity and quality) in determining the limits of its distribution.

The overall independence of food acquisition, ingestion and absorption with respect to salinity and temperature has been documented in a Sicilian saltworks by Sarà et al. (2000). This finding corroborates the hypothesis that the main cause of *B. pharaonis* invasion in the western Mediterranean is its ability to exploit different trophic positions and substrates as a function of their availability. However, more knowledge about its trophic adaptability and feeding preferences is needed to infer the causes of its invasive ability. Like other bivalve molluscs, *B. pharaonis* is an active suspension feeder that filters and sorts available particles from the sea water (Sarà et al. 2000). The nature of the available particles (Seiderer and Newell 1985; Mann 1988; Langdon and Newell 1990) can be affected by the types of primary producers of organic matter and by distribution factors (i.e. physical constraints such as wind-wave-induced resuspension from sediments). Thus, quantification of the contribution of each organic source to the available food may be important to assess the dietary habits of suspension feeders. In coastal environments the high number of primary producers, the importance of the detrital pool, and physical constraints can complicate the identification of suspensivore food sources (Ostrom and Fry 1993). Nevertheless the analysis of stable carbon isotopic ratios ($\delta^{13}$C; ‰) represents a powerful tool for determining the contribution of different sources to organic matter and the source of carbon in an organism's diet where sources differ in their isotopic compositions (Fry and Sherr 1984).

Accordingly, the aim of this paper was to assess the dietary habits of the Lessepsian bivalve mollusc *Brachidontes pharaonis* by studying seasonal changes in the carbon isotopic composition of organic matter (OM) in: (1) primary producers as original and potential food sources for *B. pharaonis*; (2) particulate (POM) and sedimentary (SOM) organic matter as sinks and distribution vectors of potential and/or available food; and (3) *B. pharaonis* themselves.

## Materials and methods

### Study site

The study was carried out in the Stagnone di Marsala saltworks system (western Sicily 37°52′N, 12°28′E) between summer 1999 and spring 2000. *Brachidontes pharaonis* is naturally present in an enclosed cooling vat (60,000 $m^2$; 48,000 $m^3$; 80 cm average depth) of the saltworks and dominates the mediolittoral–upper infralittoral. A channel is occasionally opened to allow the inflow of water from the adjacent sound (Stagnone di Marsala). Consequently, the balance between evaporation and rainfall controls the hydrodynamics and the water level. The cooling vat is characterised by diel wind-induced cycles of resuspension–sedimentation–accumulation in the sediments (Sarà et al. 2000). Water temperature undergoes wide annual fluctuations (min. 9°C in December, max. 30°C in August), while salinity values are typical of a hypersaline environment (about 40‰ in winter and 53‰ in summer).

Sand-muddy bottoms were covered by the seagrass *Cymodocea nodosa*, and *Cystoseira* sp., *Chaetomorpha linum* (O.F. Müller) Kützing and *Laurencia papillosa* (C. Agardh) Greville were the predominant macroalgae. In the vat, phytoplankton density was quite low (Sarà et al. 1999, 2000; Pusceddu et al. 1999), with annual average chlorophyll-*a* concentrations of $0.9 \pm 0.4$ $\mu g$ $l^{-1}$ (range 0.5–1.7 $\mu g$ $l^{-1}$); the microphytobenthic biomass showed a higher annual average than that measured in the western Mediterranean ($3.9 \pm 2.1$ $\mu g$ $g^{-1}$, range 1.6–6.7 $\mu g$ $g^{-1}$; Sarà, unpublished data).

### Data collection

The study was carried out for 10 months from August 1999 to May 2000. Two sampling "times" were randomly chosen within each "season" (summer 1999; autumn 1999; winter 2000 and spring 2000) for a total of eight sampling times. We did not sample at different sites to consider potential spatial variability because of the small size of the saltworks basin (6 ha). At each sampling time particulate organic matter (POM), sedimentary organic matter (SOM), primary organic matter sources, mainly seagrasses, microphytobenthic algae [i.e. sand microflora, mostly represented by benthic diatoms (Vizzini 2001) and macroalgae] and *Brachidontes pharaonis* were collected from the saltworks. Samples of sea water, collected in 5-l Niskin bottles, were filtered through pre-combusted (450°C, 4 h) fibreglass filters (Whatman GF/F) for the isotopic analysis of the particulate organic matter (POM). The first centimetre of sediment was scraped from corers to investigate the isotopic composition of the sedimentary organic matter (SOM).

Macrophytes, including the predominant seagrass *Cymodocea nodosa* (in this study we reported isotopic mean values of both *C. nodosa* detritus and live plant, but we analysed and studied only the pattern of the detritus fraction) and macroalgae (*Chaetomorpha linum*, *Cystoseira* sp. and *Laurencia papillosa*) were collected seasonally by hand in the saltworks. Epiphytic material was removed from leaves and stems by gentle scraping.

Specimens of adult *Brachidontes pharaonis* (size-class 20–30 mm) were collected manually, cleaned of epiphytes and kept alive in filtered saltworks water for at least 24 h to allow gut evacuation. Ejection (faeces) and egestion (pseudofaeces) materials were collected separately using tweezers. All individuals were killed by freezing and the flesh dissected from the shell. After acidification (2 N HCl), all samples (POM, SOM, primary organic matter sources and *B. pharaonis* flesh, faeces and pseudofaeces) were dried at 60°C for several hours (from 24 to 72 h as a function of the substrate analysed) and ground with a mortar and pestle. The $CO_2$ produced by combustion of the tin capsule containing the sample in a Carlo Erba elemental analyser (mod. EA1110) was analysed in a mass spectrometer (Delta Plus, Finnigan MAT). The isotopic ratios were expressed in $\delta$ notation as parts-per-thousand deviations from standard reference material (Peedee belemnite limestone):

$$\delta^{13}C\left[\left(^{13}C/^{12}C_{sample}/^{13}C/^{12}C_{standard}\right) - 1\right] \times 10^3$$

The reproducibility of the $\delta^{13}$C determination was $\pm 0.2$‰.

### Statistical analysis

To test the hypothesis that seasonal changes in carbon isotopic composition of potential organic matter sources can affect the carbon isotopic composition of *Brachidontes pharaonis* through food-habit changes, a two-way ANOVA was performed for all response variables. Season (SEAS; 4 levels) was treated as a fixed factor and time (TIME; 2 levels) was treated as a random factor and nested in season. Two replicate samples were taken randomly at each time; each replicate represented the mean value ($\pm$ SE) of 5

individuals randomly chosen and 3 subsamples were taken for each of them. Thus, each replicate was obtained by pooling 15 subsamples. Owing to the small size of the saltworks, we decided not to examine spatial variability and accordingly we did not consider small-scale areas within the sites. For all the analyses, the heterogeneity of variance was tested using Cochran's C test prior to the analysis of variance and the Student–Newman–Keuls (SNK) test (Underwood 1997) allowed the appropriate means comparison.

To identify the most important carbon sources determining the isotopic composition of POM and SOM considered, the direct trophic substrates for suspension feeders (Dame 1996), we first applied seasonal-mixing equations (Phillips 2001; Phillips and Gregg 2001, 2003; Phillips and Koch 2002; Phillips, personal communication) with POM and SOM as targets in the model and source isotopic signals of primary producers and secondary products as main determinants. The contribution of main carbon sources to POM and SOM thus estimated, we again applied seasonal-mixing models, but in this case with the *Brachidontes* carbon isotopic signature as the target and POM and SOM and sand microflora as the main determinants.

## Results

### Seasonal variability in the main carbon sources

The seagrass *Cymodocea nodosa* was the species most enriched in $\delta^{13}C$ (–7.9 ± 0.1‰), while its detritus was slightly depleted (–8.4 ± 0.1‰). In Table 1, we report statistics only of *C. nodosa* detritus collected by hand in the study saltworks. *C. nodosa* detritus $\delta^{13}C$ was similar in summer and autumn (about –7.8 ± 0.2‰), significantly enriched (ANOVA, $P < 0.05$ and SNK test; Tables 2, 3) in winter (–7.5 ± 0.3‰) and more depleted in spring (–10.5 ± 0.2‰). *Cystoseira* sp. $\delta^{13}C$ (Table 1) ranged between the most depleted significant value of –18.4 ± 0.2‰ in spring and the most enriched significant value of −16.0 ± 0.2‰ in summer (mean throughout the study period was –17.4 ± 0.9‰) (ANOVA, $P < 0.05$ and SNK test; Tables 2, 3). *Chaetomorpha* reached a significantly higher enrichment (ANOVA, $P < 0.05$ and SNK test; Tables 2, 3) in autumn (–17.5 ± 0.1‰) and was significantly depleted in winter (–21.0 ± 0.4‰). Significant differences were not detected between summer and spring (ANOVA, $P > 0.05$, and SNK test; Tables 2, 3).

A significant seasonality was found in the values for *Laurencia papillosa* (ANOVA, $P < 0.05$ and SNK test; Tables 2, 3), which reached the maximum in summer (–17.9 ± 0.2‰) and the minimum in autumn (–21.2 ± 0.2‰).

Sand microflora $\delta^{13}C$ values were similar throughout the study period, with a significant variation only in spring decreasing to −15.0 ± 0.2‰ with respect to the other seasons (ANOVA, $P < 0.05$ and SNK test; Tables 2, 3).

All macrophyte $\delta^{13}C$ means ranged between –16.7 ± 0.1‰ in spring and –15.1 ± 0.1‰ in summer. Unfortunately, analysis of variance could not be performed because of heteroscedasticity, even after transformation of the data (significant C value for Cochran's test; Table 2).

**Table 1** Statistics of carbon isotopic composition ($\delta^{13}C$‰) measured seasonally in the primary producers, particulate organic matter (POM) and sedimentary organic matter (SOM) and *Brachidontes pharaonis* and its biodeposits collected in the saltworks. *SUM* summer; *AUT* autumn; *WIN* winter; *SPR* spring; *YEAR* study year; *SE* standard error of the mean

| | Mean | ± SE | Min | Max |
|---|---|---|---|---|
| *Cymodocea nodosa* detritus | | | | |
| SUM | –7.7 | 0.1 | –7.8 | –7.5 |
| AUT | –7.9 | 0.2 | –8.0 | –7.7 |
| WIN | –7.5 | 0.3 | –7.8 | –7.1 |
| SPR | –10.5 | 0.2 | –10.7 | –10.3 |
| YEAR | –8.4 | 1.3 | –10.7 | –7.1 |
| *Laurencia papillosa* | | | | |
| SUM | –17.9 | 0.2 | –18.1 | –17.6 |
| AUT | –21.2 | 0.2 | –21.4 | –21.0 |
| WIN | –19.6 | 0.1 | –19.7 | –19.4 |
| SPR | –20.0 | 0.1 | –20.2 | –19.8 |
| YEAR | –19.7 | 1.2 | –21.4 | –17.6 |
| POM | | | | |
| SUM | –16.3 | 0.5 | –16.8 | –15.7 |
| AUT | –17.7 | 0.4 | –18.2 | –17.3 |
| WIN | –18.4 | 0.2 | –18.6 | –18.2 |
| SPR | –17.2 | 0.3 | –17.5 | –16.8 |
| YEAR | –17.4 | 0.9 | –18.6 | –15.7 |
| Pseudofaeces | | | | |
| SUM | –10.2 | 0.3 | –10.5 | –9.9 |
| AUT | –12.6 | 0.2 | –12.8 | –12.3 |
| WIN | –16.7 | 0.1 | –16.8 | –16.6 |
| SPR | –19.1 | 0.2 | –19.3 | –18.9 |
| YEAR | –14.6 | 3.6 | –19.3 | –9.9 |
| *Cystoseira* sp. | | | | |
| SUM | –16.0 | 0.2 | –16.2 | –15.7 |
| AUT | –17.7 | 0.2 | –17.9 | –17.5 |
| WIN | –17.6 | 0.3 | –17.8 | –17.2 |
| SPR | –18.4 | 0.2 | –18.6 | –18.2 |
| YEAR | –17.4 | 0.9 | –18.6 | –15.7 |
| Sand microflora | | | | |
| SUM | –14.7 | 0.2 | –14.9 | –14.5 |
| AUT | –14.7 | 0.3 | –15.0 | –14.3 |
| WIN | –14.7 | 0.2 | –14.9 | –14.5 |
| SPR | –15 | 0.2 | –15.3 | –14.9 |
| YEAR | –14.7 | 0.2 | –15.0 | –14.3 |
| SOM | | | | |
| SUM | –15.7 | 0.4 | –16.2 | –15.1 |
| AUT | –14.9 | 1.3 | –16.5 | –13.6 |
| WIN | –20.4 | 0.3 | –20.7 | –19.9 |
| SPR | –16.9 | 0.8 | –17.7 | –16.0 |
| YEAR | –17.0 | 2.3 | –20.7 | –13.6 |
| Total biodeposits | | | | |
| SUM | –12.8 | 0.3 | –13.1 | –12.5 |
| AUT | –14.1 | 0.2 | –14.3 | –13.9 |
| WIN | –18.5 | 0.2 | –18.8 | –18.4 |
| SPR | –19.6 | 0.1 | –19.6 | –19.5 |
| YEAR | –16.2 | 2.9 | –19.6 | –12.5 |
| *Chaetomorpha linum* | | | | |
| SUM | –19.4 | 0.1 | –19.5 | –19.3 |
| AUT | –17.5 | 0.1 | –17.7 | –17.4 |
| WIN | –21.0 | 0.4 | –21.4 | –20.5 |
| SPR | –19.5 | 0.1 | –19.7 | –19.3 |
| YEAR | –19.4 | 1.3 | –21.4 | –17.4 |
| Macrophyte | | | | |
| SUM | –15.1 | 0.1 | –15.2 | –15 |
| AUT | –15.8 | 0.1 | –15.9 | –15.7 |
| WIN | –16.1 | 0.2 | –16.3 | –15.9 |
| SPR | –16.7 | 0.1 | –16.8 | –16.6 |
| YEAR | –15.9 | 0.6 | –16.8 | –15 |
| Faeces | | | | |
| SUM | –15.4 | 0.5 | –16 | –14.9 |
| AUT | –15.5 | 0.2 | –15.8 | –15.4 |

**Table 1** (Contd.)

| | Mean | ±SE | Min | Max |
|---|---|---|---|---|
| WIN | –20.4 | 0.4 | –21 | –20 |
| SPR | –19.6 | 0.4 | –19.6 | –19.1 |
| YEAR | –17.7 | 2.4 | –21 | –14.9 |
| *Brachidontes pharaonis* | | | | |
| SUM | –14.4 | 0.5 | –15 | –13.9 |
| AUT | –14.3 | 0.4 | –14.8 | –13.9 |
| WIN | –15.5 | 0.4 | –15.5 | –14.6 |
| SPR | –14.7 | 1.2 | –16.2 | –13.7 |
| YEAR | –14.7 | 0.8 | –16.2 | –13.7 |

The particulate organic matter (POM) annual mean $\delta^{13}C$ value was $-17.4 \pm 0.9‰$. The most-enriched values were observed in summer ($-16.3 \pm 0.5‰$) and the most depleted in winter ($-18.4 \pm 0.2‰$). The latter season differed significantly from the other seasons (ANOVA, $P < 0.05$ and SNK test; Tables 2, 3), with a range of variation of about 2‰.

SOM $\delta^{13}C$ values ranged around $-15.3 \pm 1.0‰$, (ANOVA, $P > 0.05$; Table 2) in summer and autumn, whereas in winter and spring the values differed significantly ($-20.4 \pm 0.17‰$ and $-16.9 \pm 0.8‰$; ANOVA, $P < 0.05$; Table 2). The SOM range of variation was about 6.5‰. SOM and POM were positively correlated (linear regression $a = -14.9 \pm 1.47$; $b = 0.2 \pm 0.08$; $r = 0.61$, $P < 0.05$; $n = 16$).

## Seasonal contribution of the main carbon sources to POM and SOM

To identify the carbon sources which affect the isotopic composition of POM and SOM in each season, assuming that POM and SOM were the ultimate trophic substrata directly available to *Brachidontes pharaonis*, we performed a mixing-model analysis (Table 4). In the application of the mixing model we excluded a priori *Chaetomorpha linum* because it represented a non-dominant macroalga with respect the other two dominant taxa in the vat (*L. papillosa* and *Cystoseira* sp.). In addition, we have not considered the phytoplankton isotopic signal (even extrapolated from Mediterranean literature) because of the marked and well documented oligotrophy of the saltworks water. Two such secondary and less important signals should complicate the mixing scenario, and likely not provide correct information. Thus, mixing analysis performed on the summer matrix (Table 4) showed that POM and SOM, having a similar isotopic composition, seemed to be strongly constrained by isotopic signatures of macroalgae, *L. papillosa* (51.7% and 34.2%, respectively, in POM and SOM) and *Cystoseira* sp. (17.8% and 23.4%, respectively, in POM and SOM). *Brachidontes* faeces and sand microflora were secondary carbon sources, both with a contribution around 15%, while *C. nodosa* and *Brachidontes* pseudofaeces showed a contribution of less than 10%. In autumn, POM and SOM had very different isotopic values (about 3‰ difference). Mixing-model results showed *L. papillosa* as the main source of the POM (43.1%) with *Cystoseira* sp. (~21%), while *Brachidontes* biodeposition material (~38%) and sand microflora (20%) were the main contributions of the SOM. The POM winter value could be justified by the high incidence of *L. papillosa* (28.7%) and *Brachidontes* faeces (32%). In the SOM, faeces were the dominant source, with about 95%, while all other sources did not exceed 3–4%. In spring POM (–17.2‰) and SOM (–16.9‰) had very similar isotopic signatures. All considered sources contributed with a similar magnitude around 15%, both in POM and SOM, with only the values of sand microflora (~20%) being higher.

The annual analysis showed that POM and SOM seemed to be coupled through time (–17.4‰ and –17.0‰, respectively) and that, to obtain their averaged annual values (–17.2‰), we can consider all items except *Cymodocea* which contributed less than 5%. Macroalgae (*L. papillosa* and *Cystoseira* sp.) were the main sources (~33%), sand microflora, the second source (~10%) together with biodeposition materials from *Brachidontes* (~9%).

## $\delta^{13}C$ of *Brachidontes pharaonis* and its biodeposits

The isotopic composition of *B. pharaonis* (Table 1) collected in the study area ranged significantly (Tables 5, 6) between the most enriched value of $-14.3 \pm 0.4‰$ in autumn and the most depleted value of $-15.5 \pm 0.4‰$ in winter (annual mean value $-14.7 \pm 0.8‰$). The *B. pharaonis* isotopic composition was strongly and

**Table 2** Results of ANOVA carried out on primary producers, POM and SOM collected seasonally in the saltworks. *n.s.* no significant difference (at $P > 0.05$); *df* degrees of freedom; *MS* mean squares; *F* Fisher value; *P* probability level; *SEAS* season

| Source of variation | *df* | *C. nodosa* | | | *C. spinosa* | | | *C. linum* | | | *L. papillosa* | | | Sand microfl-ora | | | Macro-phytes | | | POM | | | SOM | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | MS | *F* | *P* | MS | *F* | *P* | MS | *F* | *P* | MS | *F* | *P* | MS | *F* | *P* | MS | *F* | *P* | MS | *F* | *P* | MS | *F* | *P* |
| SEAS | 3 | 8.2 | 438.3 | *** | 4.4 | 36.9 | ** | 8.0 | 750.5 | *** | 7.4 | 915.8 | *** | 0.1 | 13.0 | ** | – | – | – | 3.1 | 18.9 | ** | 23.1 | 34.0 | ** |
| Time (SEAS) | 4 | 0.0 | 0.4 | n.s. | 0.1 | 10.0 | ** | 0.0 | 0.2 | n.s. | 0.0 | 0.2 | n.s. | 0.0 | 0.1 | n.s. | – | – | – | 0.2 | 1.2 | n.s. | 0.7 | 1.0 | n.s. |
| Residual | 8 | 0.0 | | | 0.0 | | | 0.1 | | | 0.0 | | | 0.1 | | | – | – | – | 0.1 | | | 0.7 | | |
| Cochran's C | | | | n.s. | | | n.s. | | | n.s. | | | n.s. | | | n.s. | | | ** | | | n.s. | | n.s. |

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

**Table 3** Student-Newman-Keuls (SNK) test (see Table 2 for details) to compare appropriate means of primary producers and bulks

| Source | SNK test |
|---|---|
| *C. nodosa* | SUM = AUT; AUT < WIN; WIN > SPR |
| *C.spinosa* | SUM > AUT; AUT = WIN; WIN > SPR |
| *C. linum* | SUM > AUT; AUT < WIN; WIN < SPR |
| *L. papillosa* | SUM > AUT; AUT < WIN; WIN > SPR |
| Sand microflora | SUM = AUT; AUT = WIN; WIN > SPR |
| POM | SUM > AUT; AUT = WIN; WIN > SPR |
| SOM | SUM = AUT; AUT > WIN; WIN < SPR |

positively correlated with the isotopic composition of its faeces, which were more depleted (linear regression, $a = 9.1 \pm 8.53$; $b = 1.8 \pm 0.6$; $r = 0.71$; $P < 0.01$; $n = 16$). Pseudofaeces were, on average, more enriched than *B. pharaonis* somatic and faecal material: the most enriched values of $-10.2 \pm 0.3‰$ in summer decreased constantly reaching the most depleted value of $-19.1 \pm 0.2‰$ in spring (Tables 5, 6).

## Discussion

### Isotopic composition of primary organic matter sources

The primary producers of the saltworks were characterised by high and significant seasonal variability, with the macrophytes presenting more than 3‰ variability in their isotopic carbon ratios over the seasons. Similarly large ranges in $\delta^{13}C$ variation in primary producers have already been observed in other areas (Simenstad and Wissmar 1985; Riera and Richard 1997).

In the saltworks it was possible to identify the potential contribution to primary production of several macrophytes covering a wide range of carbon isotopic signatures (about –11.5‰). The most enriched detritus source potentially fuelling the saltworks food web was that coming from *Cymodocea nodosa*, which had carbon isotopic signatures (seasonal average $-8.4 \pm 1.3‰$) that fell well within the range observed for detritus of other seagrasses (McMillan et al. 1980; Hemminga and Mateo 1996).

The algae were more depleted in $^{13}C$ than *Cymodocea*, ranging from the enriched values of sand microflora (likely mostly diatoms; $-14.8 \pm 0.2‰$) to the depleted values of *Laurencia papillosa* ($-19.7 \pm 1.2‰$).

### Seasonal isotopic variability effect of primary producers on POM and SOM isotopic composition

As described above, the stable carbon isotopic ratios of all the primary producers in the saltworks varied seasonally, in accordance with the findings of several authors, who showed variability in macroalgae and other organisms (Cooper and McRoy 1988; Simenstad et al. 1993). Nevertheless, such an evident variability as that found in the saltworks macrophytes has very rarely been observed because seasonal changes in carbon isotopic ratios have been studied very little (sensu Rolff 2000) and in very few organisms. Most authors have limited their studies to validating spatial mono-temporal hypotheses (sensu Underwood 1997) dealing with differences between and within sites in only one period of the year (e.g. Dauby 1989; Jennings et al. 1997;

**Table 4** Mean contribution (% followed by seasonal range, %, in brackets) of each organic matter source collected in the study saltworks to POM and SOM calculated by a mixing model run according to Phillips and Gregg (2001, 2003) using an increment of 1% and a tolerance of 0.1 per mil. *CYM C. nodosa* detritus;*PSEUDO B. pharaonis* pseudofaeces; *SM* sand microflora; *FAE B. pharaonis* faeces; *CYS Cystoseira* sp.; *LAU L. papillosa*

| | CYM | PSEUDO | SM | FAE | CYS | LAU |
|---|---|---|---|---|---|---|
| POM | | | | | | |
| SUM | 2.8 (0–22) | 4.0 (0–16) | 10.3 (0–53) | 13.4 (0–68) | 17.8 (0–89) | 51.7 (11–85) |
| AUT | 4.9 (0–26) | 8.1 (0–41) | 10.9 (0–55) | 12.4 (0–63) | 20.6 (0–100) | 43.1 (0–75) |
| WIN | 3.5 (0–16) | 12.1 (0–56) | 8.1 (0–36) | 32.0 (0–84) | 15.6 (0–74) | 28.7 (0–90) |
| SPR | 12.6 (0–27) | 17.3 (0–81) | 19.3 (0–57) | 16.5 (0–77) | 18.3 (0–87) | 16.0 (0–74) |
| YEAR | 3.7 (0–20) | 9.1 (0–46) | 9.3 (0–47) | 8.1 (0–42) | 24.0 (0–100) | 45.8 (0–81) |
| SOM | | | | | | |
| SUM | 4.0 (0–22) | 5.7 (0–30) | 14.3 (0–72) | 18.4 (0–92) | 23.4 (0–97) | 34.2 (0–79) |
| AUT | 12.5 (0–46) | 18.0 (0–73) | 20.1 (0–97) | 19.7 (0–94) | 16.7 (0–73) | 13.0 (0–54) |
| WIN | 0.0 (0–0) | 0.4 (0–2) | 0.2 (0–1) | 95.3 (88–100) | 0.7 (0–3) | 3.4 (0–12) |
| SPR | 14.5 (0–29) | 16.4 (0–78) | 20.7 (0–62) | 15.7 (0–74) | 17.6 (0–84) | 15.1 (0–71) |
| YEAR | 4.5 (0–24) | 10.8 (0–55) | 11.4 (0–56) | 9.3 (0–49) | 24.0 (0–96) | 40.0 (0–77) |

**Table 5** Results of ANOVA carried out on *B. pharaonis* and its biodeposits collected seasonally in the study saltworks. *n.s.*no significant difference (at $P > 0.05$)

| Source of variation | *df* | *B. pharaonis* | | | Faeces | | | Pseudofaeces | | | Total biodeposits | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | MS | *F* | *P* | MS | *F* | *P* | MS | *F* | *P* | MS | *F* | *P* |
| SEAS | 3 | 1.2 | 20.4 | ** | 28.2 | 1,505.9 | *** | 64.0 | 3,794.9 | *** | 42.9 | 3,574.3 | *** |
| Time (SEAS) | 4 | 0.1 | 0.1 | n.s. | 0.0 | 0.2 | n.s. | 0.0 | 0.3 | n.s. | 0.0 | 0.3 | n.s. |
| Residual | 8 | 0.7 | | | 0.1 | | | 0.0 | | | 0.0 | | |
| Cochran's C | | | | n.s. | | | n.s. | | | n.s. | | | n.s. |

*$P \leq 0.05$; ** $P \leq 0.01$; ***$P \leq 0.001$

**Table 6** SNK test (see Table 5 for details) to compare appropriate means of *B. pharaonis* and its biodeposits

| Source | SNK test |
|---|---|
| *B. pharaonis* | SUM = AUT; AUT > WIN; WIN > SPR |
| Faeces | SUM > AUT; AUT < WIN; WIN < SPR |
| Pseudofaeces | SUM = AUT; AUT = WIN; WIN > SPR |
| Total biodeposits | SUM > AUT; AUT = WIN; WIN > SPR |

Hwey-Lian et al. 2000). The examination of variability at different temporal scales has very often been neglected. In contrast, in our saltworks we observed that the seasonal changes in primary producers and the other carbon sources were well able to affect the isotopic composition of organic matter (viz. POM–SOM) and, ultimately, through a cascade, the primary consumers. Our mixing-model outcomes seem to support this.

Interestingly, our study showed that such a large significant seasonal variability (between producers and within each producer's seasonal range) was mirrored in POM and SOM isotopic composition. Conversely, the wide range of POM and SOM variation shows the heterogeneity of such a storage compartment and as a principal consequence POM varied significantly on a seasonal basis in a range of 3‰. SOM covered a much wider isotopic range than POM of about 7‰.

By contrast, data from the most-nearshore marine habitats indicated that the isotopic composition of POM and SOM are generally fairly constant (around 1–2‰) throughout the seasons, unless direct run-off of terrestrial organic matter (freshwater inputs) alters the isotopic signatures of the bulk organic matter (Odum and Heald 1975; Chong et al. 2001). For example, in Malaysian coastal marine waters, seston signatures were around –21‰ while SOM varied very little (about 1‰; Chong et al. 2001). In the Mediterranean, Gulf of Gaeta seston varied over a small range (1.5‰; Mazzola and Sarà 2001) and in the Stagnone di Marsala lagoon (close to the saltworks) POM and SOM isotopic composition was constant throughout the study period (Sarà et al. 1999; Mazzola et al. 2001). In addition, evidence that our saltworks was a particularly highly variable environment was substantiated by the POM and SOM pattern, coupled throughout most of the year. This may be due to the coupling between sediments and water column that results from both the shallowness and the constant wind influence producing highly mixed conditions (Sarà et al. 1999). In shallow environments, there are many mechanisms for removing organic matter trapped in the sediments, of which wind-wave-induced resuspension from sediments seems to be the primary one (Smaal and Haas 1997; Sarà et al. 1999). Thus, in our saltworks, different kinds of organic matter accumulate in the sediments, depending on their biological cycles. Through resuspension, acting as an "over-exposure mechanism" allowing SOM to re-enter the water column and increasing the likelihood that consumers in the water column exploit sedimentary particles, different sources of carbon can become available to suspension feeders. Evidence that the $\delta^{13}C$ signatures of POM (–17.4 ± 0.9‰ in the saltworks) were more enriched than those found in other seagrass systems (Dauby 1989; Mazzola et al. 1999) fits the above dynamics well and suggests: (1) a marked input of sedimentary organic matter to the bulk suspended particulate organic matter (see also in the Results section the significant linear regression between POM and SOM) determining POM enrichment; (2) a scant contribution of phytoplankton (in MED usually –21‰ / 22‰), in accordance with the well documented oligotrophy of Mediterranean waters (Margalef 1985) and the usual trophodynamics of seagrass systems (Moncreiff and Sullivan 2001); and (3) an important role played by macroalgae and sand microflora (viz. mostly diatoms) as the main determinants of POM and SOM isotopic signatures throughout the year (Moncreiff and Sullivan 2001).

Not only the macroalgae and sand microflora, but also the isotopic signature of *Brachidontes* biodeposits (i.e. faeces and pseudofaeces) seem to be constantly present throughout the year as the main carbon regulator of POM and SOM. *Brachidontes* faecal material $\delta^{13}C$ value, which is more depleted than that of pseudofaeces, was strongly and positively correlated to sedimentary organic matter (linear regression, $a = -3.6 \pm 1.8$; $b = 0.8 \pm 0.2$; $r = 0.82$; $P < 0.001$; $n = 16$) and when detected, its contribution to SOM was never lower than 15%. Bacterial rearranging (via decomposition) may increase the availability of faeces, which could then represent an optimal food source for suspension feeders throughout the year (Fabiano et al. 1994).

In contrast, the pseudofaeces $\delta^{13}C$ value was correlated significantly with *Cymodocea* detritus ($a = 15.9 \pm 4.3$; $b = 3.7 \pm 0.5$; $r = 0.90$; $P < 0.0001$; $n = 16$) and contributed less than 10% to organic matter. If, on one hand, our mixing outcomes lead us to exclude the direct contribution of *Cymodocea*-derived detritus to POM and SOM, on the other, this carbon source could contribute to high trophic levels re-entering via *Brachidontes* pseudofaecal production. In this way, *Cymodocea* carbon which contributed secondarily to bulk organic matter (not more than 4%), being largely composed of organic molecules that are recalcitrant to decomposition and with low direct availability to secondary consumers (Mann 1988), should re-enter the trophic web by way of pseudofaecal capsules. In fact, the mucopolysaccharides contained in the pseudofaecal capsules produced in abundance by mussels and which represent a rich organic matter source (Dame 1996) should assume the role of rendering ("a labilisation mechanism") highly refractory material more labile and thus more available to consumers. Support for this hypothesis would confirm the role of pseudofaecal production in suspension-feeding bivalves as an overflow mechanism (Bayne 1976) that allows the transfer of organic matter from the water column environment to the benthos.

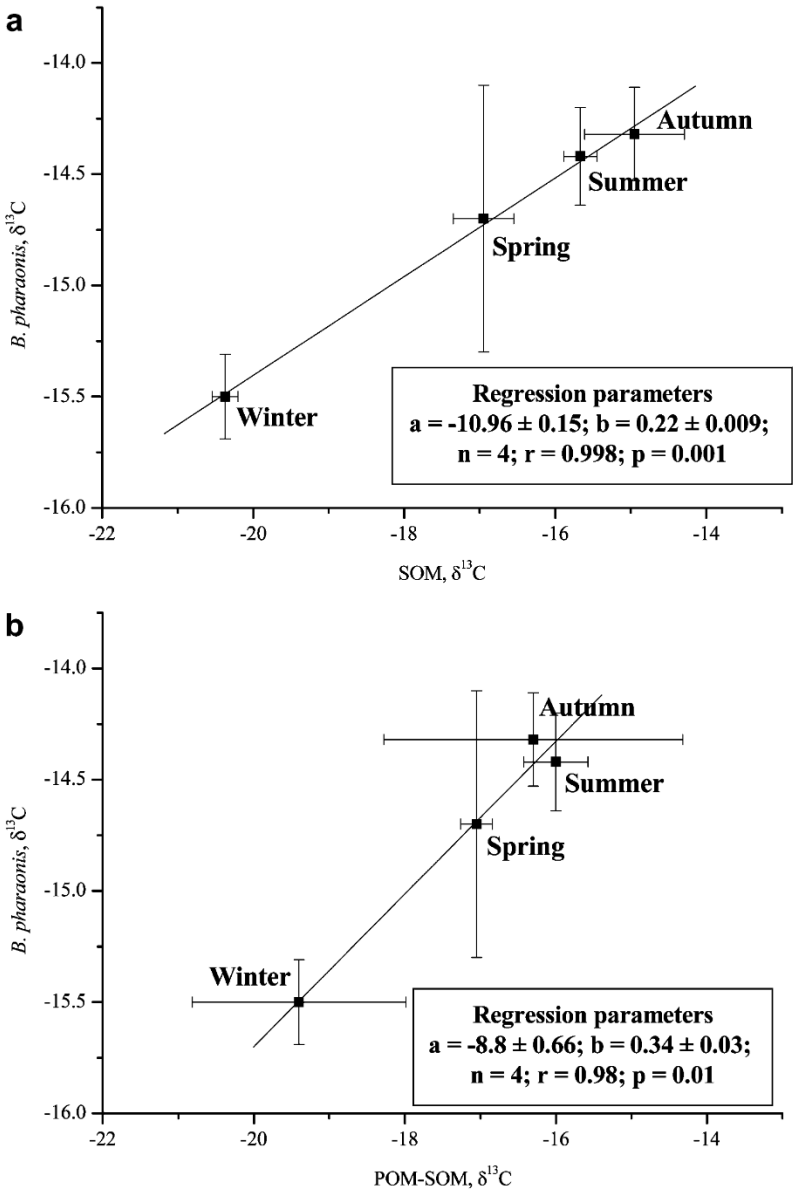


**Fig. 1** Seasonal relationship between **a** sedimentary organic matter (SOM) and *B. pharaonis* $\delta^{13}C$ values, and **b** POM and SOM (averaged) and *B. pharaonis* $\delta^{13}C$ values. Regression parameters are given in the graph

Food sources for *B. pharaonis*

In accordance with the above scenario, we can deduce that *Brachidontes pharaonis* in the study area and throughout the study period experienced highly variable feeding conditions with many carbon sources, including its biodeposition products, representing potential available trophic substrata.

It seems fairly evident that, as a result of the more abundant carbon sources within each season, the SOM isotopic signal represented the basal source directly determining the isotopic composition of *Brachidontes* assimilated organic matter. Accordingly, in Fig. 1a, we show the relationship between SOM and *Brachidontes* $\delta^{13}C$ and in Fig. 1b, the same relationship obtained with averaged POM and SOM isotopic values. The result was a very marked and significant dependence of *Brachidontes* $\delta^{13}C$ values on SOM and slightly less on mixed POM and SOM. By contrast, the POM values alone did not produce a significant relationship. This could provide further confirmation that wind-driven hydrodynamism coupled with both the shallowness of the basin and the marked oligotrophy of the waters may produce highly mixed water which makes mainly sedimentary re-arranged particles available. In most seagrass systems the carbon isotopic composition of secondary consumers, including suspension feeders, very rarely matches that of dominant seagrass or phytoplankton (Dauby 1989; Dauby et al. 1995; Loneragan et al. 1997; Moncreiff and Sullivan 2001). In fact it often mirrors the carbon isotopic composition of mixed sedimentary phytodetritus (including sand microflora and leaf epiphytes). In contrast, it has been observed that a number of other suspension feeders such as mussels, oysters and cockles living along Mediterranean, Atlantic and Pacific coasts very rarely assimilate sedimentary

**Table 7** The seasonal fractionaction scheme of *B. pharaonis* extrapolated from a mixing model (Phillips 2001; Phillips and Gregg 2003) using POM and SOM and sand microflora isotopic signals as main carbon sources. We adjusted, according to Phillips and Gregg (2001; and personal communication), the food source C isotopic ratios by a hypothetical non-fractionation, a trophic fractionation of 0.5%, and of 1‰ before applying the mixing model.*SM* sand microflora $\delta^{13}C$; *B.p. Brachidontes pharaonis* somatic $\delta^{13}C$; *FR* fractionation; *%* percentage contribution of each source to the diet of *B. pharaonis*

| | POM | | SOM | | SM | | Mean sources | *B. p.* | FR |
|---|---|---|---|---|---|---|---|---|---|
| | $\delta^{13}C$ | % | $\delta^{13}C$ | % | $\delta^{13}C$ | % | $\delta^{13}C$ | $\delta^{13}C$ | |
| Hypothetical non-fractionation | | | | | | | | | |
| SUM | –16.3 | – | –15.7 | – | –14.7 | – | –15.6 | –14.0 | 1.6 |
| AUT | –17.7 | – | –14.9 | – | –14.7 | – | –15.8 | –14.3 | 1.5 |
| WIN | –18.4 | 11.0 (0–24) | –20.4 | 7.0 (0–15) | –14.7 | 82.0 (76–87) | –17.8 | –15.5 | 2.3 |
| SPR | –17.2 | – | –16.9 | – | –15.0 | – | –16.4 | –14.7 | 1.7 |
| YEAR | –17.4 | 1.0 (0–3) | –17.0 | 2.0 (0–4) | –14.7 | 97.0 (96–100) | –16.4 | –14.7 | 1.7 |
| Trophic fractionation of 0.5% | | | | | | | | | |
| SUM | –15.8 | – | –15.2 | – | –14.2 | – | –15.1 | –14 | 1.1 |
| AUT | –17.2 | 2.0 (0–6) | –14.4 | 36.0 (0–100) | –14.2 | 62.0 (0–99) | –15.3 | –14.3 | 1.0 |
| WIN | –17.9 | 18.0 (0–37) | –19.9 | 11.0 (0–24) | –14.2 | 71.0 (63–78) | –17.3 | –15.5 | 1.8 |
| SPR | –16.7 | 5.0 (0–13) | –16.4 | 6.0 (0–15) | –14.5 | 89.0 (85–95) | –15.9 | –14.7 | 1.2 |
| YEAR | –16.9 | 9.0 (0–22) | –16.5 | 11.0 (0–26) | –14.2 | 80.0 (74–85) | –15.9 | –14.7 | 1.2 |
| Trophic fractionation of 1‰ | | | | | | | | | |
| SUM | –15.3 | 10.0 (0–25) | –14.7 | 16.0 (0–40) | –13.7 | 74.0 (60–87) | –14.6 | –14.0 | 0.6 |
| AUT | –16.7 | 17.0 (11–23) | –13.9 | 43.0 (0–89) | –13.7 | 40.0 (0–83) | –14.8 | –14.3 | 0.5 |
| WIN | –17.4 | 24.0 (0–51) | –19.4 | 16.0 (0–33) | –13.7 | 60.0 (49–70) | –16.8 | –15.5 | 1.3 |
| SPR | –16.2 | 16.0 (0–36) | –15.9 | 19.0 (0–42) | –14.0 | 65.0 (58–72) | –15.4 | –14.7 | 0.7 |
| YEAR | –16.4 | 19.0 (0–40) | –16.0 | 21.0 (0–47) | –13.7 | 60.0 (53–66) | –15.4 | –14.7 | 0.7 |

organic matter, feeding preferentially on suspended matter that is markedly constrained by fresh planktonic organic matter (Dauby 1989; Riera and Richard 1997; Jennings et al. 1997; Moncreiff and Sullivan 2001).

To determine which carbon sources ultimately control the isotopic composition of the food assimilated by *Brachidontes* we ran a mixing model according to Phillips and Gregg (2001, 2003). Accordingly we proposed the isotopic value of *Brachidontes* as the target in our mixing model, while potential carbon sources were the seasonal isotopic signals of POM and SOM and of the sand microflora isotopic signal considered alone (Table 7). Although sand microflora signals were already included in all seasons within POM and SOM, we preferred to consider them and their seasonal isotopic signals separately as a third potential source in the model. It has in fact been well documented that sand microflora include both living and non-living (i.e. detritus) forms, and are the only carbon source apart from bacteria (Langdon and Newell 1990; Dame 1996) that are directly digestible and assimilable by suspension feeders.

We use a mixing model to partition dietary sources for *B. pharaonis* and, according to Phillips (2001) and Phillips and Gregg (2001, 2003), we had to take into account the degree of "trophic fractionation" between the consumer's tissues and the food sources. In view of the lack of information coming from captive feeding trials (Phillips and Gregg 2001; Phillips, personal communication), in which only one type of food is provided, we proposed in Table 7 the outcome of a mixing model run with raw data, supposing a "trophic fractionation" of 0.5‰; and supposing a "trophic fractionation" of 1‰. According to such a scheme we substantially adjusted the food source C isotopic ratios by the amount of trophic fractionation before applying the mixing model. Outcomes shown in Table 7 suggest that sand microflora played a major role in the diet of our bivalve, varying from 60 to 80%, and then SOM which represented about 21% in the diet. However, considering no fractionation and 0.5‰ degree of trophic fractionation, it seems that mixing models should not provide correct fractionation information. Overall, the assimilated organic matter varied seasonally and this agrees with the fractionation pattern reported in the literature, which indicates that the carbon isotope ratio of an animal reflects that of the organic source plus a slight enrichment of about 0.5–1.5‰ (Michener and Schell 1994). Accordingly, the 1% fractionation showed (Table 7) an annual average of about 0.7‰, ranging between 0.5‰ in autumn and 1.3‰ in winter. The main conclusion drawn from this scenario is that *Brachidontes* assimilated mostly mixed sedimentary organic carbon re-arranged via a detritus route dominated mainly by macroalgae (*Laurencia papillosa* and *Cystoseira* sp.) and then by sand microflora. Thus, throughout the study period *B. pharaonis* was able to exploit almost all the dominant carbon sources available in its colonised environment both directly (sand microflora) and indirectly via POM/SOM detritus route in which macroalgae represented a dominant fraction. These carbon sources incorporated most of the environmental variability relative to the isotopic composition of primary producers (about –11‰ throughout the year).

The most enriched, represented by *Cymodocea nodosa*, should play a minor role in the diet of *B. pharaonis*, a finding that fits with the general outcome of the mixing model. Accordingly, considering its secondary role, it seems possible to partially exclude this source as the

main determinant of POM and SOM carbon isotopic composition and thus, in turn, of *B. pharaonis* assimilation. In particular, this supports a scenario in which the wrack particles that make up *Cymodocea* fine detritus should be less directly available to secondary consumers (Mann 1988). Consequently, the significant relationship between isotopic composition of the predominant seagrass and *B. pharaonis* pseudofaeces would support the idea of pseudofaecal production as an overflow mechanism able to reduce the effect of food dilution not only due to high concentration of inorganic material but also to that of refractory organic compounds (Sarà et al. 2000).

To conclude, *Brachidontes pharaonis* is a Lessepsian coloniser patchily distributed in the Mediterranean, substantially linked to a few types of environments. Its presence or absence seems to be correlated with the availability of particular high-variability habitats whose environmental features enable *Brachidontes* to reach its maximum fitness according to its adaptive capacity. Filter-feeder molluscs, such as mussels, oysters and cockles, are considered generalists, i.e. any phenotype whose fitness in a patch precisely equals its fitness in the other (Rosenweig 1981). From this viewpoint, we can deduce that these organisms can colonise many environments quite easily, reaching a similar degree of fitness in all colonised environments. From current literature (Coma et al. 2001) we can assert that, for example, filter-feeder organisms, such as those belonging to the genus *Mytilus* (the most abundant mussel in many worldwide coastal environments), present an opportunistic behaviour (i.e. the use of resources in the proportions in which they exist; Rosenweig 1981). The opportunistic–generalist dual concept (Hughes 1980; Coma et al. 2001) does not seem to be able to explain the patchy distribution of our *Brachidontes* whose behaviour seems better characterised by a picky-specialist food habit (Rosenweig 1981). In fact, our finding supports the view that *Brachidontes* was able to select (Sarà et al. 2000) food resources in proportions different from those it encounters, discharging the most abundant but less labile organic source, like the seagrass *Cymodocea nodosa* detritus. On the other hand, its absence in habitats well exploited by other mussels suggests that *Brachidontes* is not able to reach fitness similar to that known in its habitat. However, if its presence/absence can be considered a first indirect index of the fitness reached, further studies between different populations are needed to test their specialist food behaviour.

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