THE NEW LESSEPSIAN ENTRY BRACHIDONTES PHAROANIS (FISCHER P., 1870) (BIVALVIA, MYTILIDAE) IN THE WESTERN MEDITERRANEAN: A PHYSIOLOGICAL ANALYSIS UNDER VARYING NATURAL CONDITIONS

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ABSTRACT  The feeding behavior of Brachidontes pharaoensis (Mollusca, Bivalvia), a new Lessepsian entry in the western Mediterranean, living in a cooling vat of a saltworks system in western Sicily, was assessed by estimating its physiological rates throughout a 6-month-long study (May 1997 to March 1998). Clearance, filtration, ingestion, and food absorption rates were estimated using the biodeposition method and the results correlated to variations in temperature, salinity, and quality and quantity of available food. Measured water concentrations were on average 81.5 ± 95.5 mg L⁻¹, its labile fraction (estimated as the sum of particulate lipids, carbohydrates and proteins) was on average 0.55 ± 0.07 µg L⁻¹, representing only 15% of the total organic. Phytoplankton biomass, as suspended chlorophyll a, was on average 0.88 ± 0.42 µg L⁻¹. Mean weight standardised rates of Brachidontes pharaoensis were clearance rate 1.04 ± 0.821 h⁻¹, filtration rate 40 ± 0.97 mg h⁻¹ of total suspended material, and egestion rate 0.42 (± 0.15 mg material h⁻¹). There was a mean selection efficiency of 0.47, 0.22 ingested organic matter varied between about 2 mg h⁻¹ and 270 mg h⁻¹, and food absorption efficiency ranged between 0.01 and 0.23. The Brachidontes feeding process seems to be regulated at the initial filtration stage, and most of the control determines the quantity of absorbed ration. Clearance rate is maintained independent of changes in water temperature and salinity but reflects fluctuations in quantity of available food. Varying the rate of predation on, digestion, regulated ingestion rate, although this mechanism is not efficient as a response to local environmental conditions. Absorption efficiencies may be sensitive to the balance of biochemical components. The physiological plasticity of B. pharaoensis is expressed in this study is believed to have played a major role in its ability to reach the western Mediterranean.

KEY WORDS: Lessepsian, Brachidontes pharaoensis, bivalve molluscs, feeding behaviour, shallow environment, Mediterranean sea

INTRODUCTION

The common Indo-Pacific mussel Brachidontes pharaoensis (Fischer P., 1870) = Brachidontes variabilis Krauss (1844) recently has appeared in the western Mediterranean, reaching the Sicilian coast through the Suez Canal (Safriel et al. 1980). This hyperhaline mussel is a Lessepsian "new entry" (Por 1971) which, with a few other species (e.g., Pinctada penguin (Linnæus 1758) and Cerithium stradoni (Philippi 1848)), has been able to cross the Red Sea Barrier (Safriel and Rütte 1977) and reach the temperature eastern Mediterranean.

B. pharaoensis was never found in the Mediterranean before the opening of the Suez Canal (1869), and its penetration and consequent diffusion has been rapid, due possibly to human agency. The species was first recorded in the Eastern Mediterranean 7 years after the opening of the Suez Canal (Fuchs 1878), and approximately 60 years passed before B. pharaoensis was recorded along the coasts of Lebanon (Safriel et al. 1980). B. pharaoensis has been able to cross the barrier of the Levantine Basin and has successfully colonized the western Mediterranean basin. It has now colonized several parts of western Mediterranean coastal (Di Giennimo 1971, Gianguzza et al. 1997) and is becoming a potential resource and space competitor (Safriel and Saxson-Frostig 1988) with its Mediterranean ecological equivalent Mytilaster miliarius (Poli). B. pharaoensis has been documented in cooling vats of a saltworks system in western Sicily (Gianguzza et al. 1997, Vittori et al. in press), where it has extensively colonized hard substrates.

Nevertheless, little is known about small Mytilus (Brachidontes or Mytilaster), which have a low importance for aquaculture (as inedible species) but which represent key species in the recycling of matter and energy in some aquatic ecosystems (Rüegg 1988, Duine 1996).

To our knowledge, there are no previous studies on trophic preferences, adaptability, and physiological plasticity in these bivalve species. Very few data exist on the Brachidontes genus (Stern and Achten 1978), except for some information on B. exustus (Rüegg 1988), and there are no data on the feeding activity and physiological features of Brachidontes pharaoensis. Moron et al. (1988) reported only that B. pharaoensis, like many other bivalve molluscs, is an active suspension feeder that filters and some particles (organism) from the seawater.

Analysis of physiological features considered among the best tools for investigating plasticity in mollusc bivalves (Sensu Bayne 1998), especially when experiments are carried out in situ with natural food concentrations. The main aims of the present article are thus to describe for the first time some features of the feeding behaviour of B. pharaoensis estimated using the biodeposition method (Iglesias et al. 1992 and following related literature) and to measure food consumption, rejection, ingestion, and absorption rates throughout an annual cycle in the field. Consequently, the physiological responses of this species are determined under a wide range of ambient conditions of temperature, salinity, and food supply.

Description of the Study Area

This study was carried out between May 1998 and March 1999 in a cooling vat (60,000 m²; 48,000 m³; 1 m average depth) of a saltworks system adjacent to the Stagione di Marsala shallow in western Sicily (37°52′ NORD: 12°28′ EAST). B. pharaoensis has extensively colonized the submerged hard substrates on the saltworks bottom. The soft substrates in the saltworks mainly been colonized by Conchicola miliaris, whereas the hard substrates are covered with a number of species of macroalgae such as Laurencia papillosa, Pavlova pavonica, and Arcelina amethystina.
MATERIALS AND METHODS

Experimental Design

On the day before the filtration experiments, specimens were collected randomly from both the saltworks. Individuals from a 30 ± 1.5-mm size class were selected, cleaned of epibionts and byssus, and then placed overnight in small plastic net-bags in the saltworks water to permit re-acclimatization after the manipulation. In the early morning of the following day, 14 organisms were carefully collected from the acclimatized groups and put into 14 small experimental rectangular chambers (20 × 5 × 5 cm; available volume about 500 mL) with a V-shaped bottom. After the valves of the mussels had opened and as soon as their filtration activity was stabilized, the experiments were started. Two chambers without mussels were used as controls. Filtration measurements were carried out in continuous flow, with water from the saltworks continuously pumped into a head-tank (about 50 L). The saltworks water was agitated well by a magnetic stirrer in the tank to avoid particle settling. The continuous flow was regulated at about 180 mL·h⁻¹ (±30 mL), and the flow was maintained by means of a peristaltic pump placed between the head-tank and the experimental chambers. At this flow rate, little or no sedimentation occurred. Any sedimentation of suspended particles was accounted for by the control chamber (no animals). After approximately 1 h of active filtration under continuous flow conditions, water samples were collected at the end of the experimental chambers. On completion of the filtration experiments, the organisms were kept in a further 2-3 h in their respective chambers. Separately, faeces and pseudofaeces were carefully collected. This material was filtered on pre-weighed and ashed GF/F filters, washed with ammonium formate to remove seawater salts, and processed, as described later, to determine the total mass and organic content of the biodeposits.

These experimental procedures allowed clearance rates to be calculated, by applying the following formula:

\[ CR = \frac{f}{t} \left( \frac{[Cl] - [Ci]}{[Cl]} \right) \]  

where \( CR = \) the clearance rate in liters h⁻¹

\( f = \) the flow rate of water through the chambers (1 h⁻¹)

\( [Cl] = \) the concentration of labile particulate organic matter (LPOM; mg L⁻¹) in the inflowing water (determined from the mean of the concentration of LPOM in the water in the tank and in the control chamber)

\( [Ci] = \) the concentration of LPOM (mg L⁻¹) in the out-flowing water from the experimental chamber.

The labile fraction of particulate organic matter (LPOM, mg L⁻¹) was calculated from the sum of particulate lipids, proteins and carbohydrates (Wildedows et al. 1979, Fichet 1991, Navarro et al. 1993, Sara et al. 1998).

In order to confirm the estimates obtained using this method, clearance rates were also estimated using the biodeposition method (Iglesias et al. 1992) as follows: \( CR = \frac{mg \text{ inorganic matter produced both as true faeces and pseudofaeces per hour}}{\text{mg inorganic matter per liter in saltworks water}} \). All clearance rates were corrected to a 1 g dry weight standard-sized individual using the weight exponent 0 (0.53) reported in Labarta et al. (1997). Results obtained using both methods described were compared and averaged. Production rates of pseudofaeces (namely rejection rates; RR, mg h⁻¹) were calculated both for inorganic (IRR, mg h⁻¹) and organic (ORR, mg h⁻¹) suspended matter. Also, production rates of true faeces (TR, mg h⁻¹) were calculated for both inorganic (IER, mg h⁻¹) and organic suspended matter (OER, mg h⁻¹). Assuming that absorption of inorganic material through the digestive system was negligible (Iglesias et al. 1992, Iglesias et al. 1998), the rate of inorganic material filtration (IFR, mg h⁻¹) was calculated by summing IRR and IER. Thus clearance rates (CR, L h⁻¹) were estimated as \( CR = \frac{IFR}{BSM} \) where BSM (mg L⁻¹) was total suspended inorganic matter (Iglesias et al. 1996, Wong and Cheung 1999). By multiplying clearance rates by the total suspended matter (TSM, mg L⁻¹) and by its own organic fraction (OM, mg L⁻¹) total (FRBSM, mg L⁻¹) and organic matter filtration rates (FRBSM, mg h⁻¹) were estimated. Ingestion rates of total (IRBSM, mg TSM h⁻¹) and organic matter (IRBSM, mg TSM h⁻¹) were extrapolated as follows: \( IRBSM = \frac{FRBSM}{BSM} - RR \) and IBSM = FRBSM - ORR, respectively. Absorption food rates (AR, mg h⁻¹) were extrapolated as follows: \( AR = \frac{IRBSM}{BSM} - OER \), while absorption efficiencies (AE) as \( AE = \frac{AR}{IRBSM} \). Preingestive selection efficiencies for the total filtered organic matter (SEBSM) were also estimated according to Navarro et al. (1992).

Chemical Analyses

In the laboratory, samples of water collected in the saltworks and from the experimental filtration chambers, faeces and pseudofaeces were filtered onto pre-washed, precombusted (450°C, 4 h) and pre-weighed Whatman GF/F filters to determine organic and inorganic matter contents.

All measurements of total organic content in the food (OM), faeces (FOM), and pseudofaeces (POM) were obtained using the difference on ignition method. Filters were weighed after desiccation (105°C, 24 h) using a Sartorius A200 balance (accuracy ± 1 mg) and the inorganic fractions of total matter were calculated as the weight of the material remaining after combustion at 450°C for 4 h. TSM, POM, and FOM were calculated from the differences between the weights obtained after desiccation and those obtained after combustion.

For the water samples, the particulate carbohydrate concentrations (P-CHO, mg L⁻¹), particulate proteins (P-PT, mg L⁻¹), and particulate lipids (P-LIP, mg L⁻¹) were determined using methods reported by Sara et al. (1998).

LPOM as defined above was also converted into carbon equivalents using 0.75, 0.40, and 0.49 mg C mg⁻¹ conversion factors for particulate lipids, carbohydrates, and proteins, respectively and used as an expression of the bioplastic fraction of particulate organic carbon (BPC) (Sara et al. 1998). Suspended chlorophyll-a (CHL-a) and photosynthesis (PHAE) concentrations were measured according to Lorenzen and Jeffrey (1980). Pigments were extracted with 90% acetone and photosynthesis determined after acidification with 0.1 N HCl.

The ISM/OM, LPOM/TSM, and LPOM/OM ratios (Wildedows et al. 1979, Navarro et al. 1993, Navarro and Thompson 1995, Sara et al. 1998) of the C-CHL/a/BPC ratio (the concentration of CHL-a converted into carbon units using 52 as the conversion factor, Nival et al. 1972) and the P-PT/P-CHO ratio (Navarro and Thompson 1995, Sara et al. 1998) were used as tools for gathering information about the nutritional value of the particulate organic matter. Temperature (T, °C) and salinity (SAL) were measured at each sampling of the saltworks water using a Hydrolab (Inc. Hauri...
ion, TX, USA) multiprobe. Salinity signals from the probe were tested monthly using AgNO₃ titration.

The relationships between physical, chemical, and trophic variables with physiological changes were assessed using regression and Spearman correlation (z) tools (Sokal and Rohlf 1981). Statistical package (Release 5.1: StatSoft, Inc.) was used to perform statistics.

RESULTS

Physical Conditions and Seston Characteristics in the Saltworks

The food composition available to suspension feeders in the study area as a function of different experimental periods is summarized in Table 1. The average temperature was 18.6 ± 7.4°C, ranging between the minimum measured in December (9.5°C) and the maximum in August (30°C). The saltwater waters were consistently hyperhaline, showing SAL ranging between 40 and 53 (average 47 ± 4.3). Average seston concentrations throughout the experimental periods were 81.5 ± 95.5 mg L⁻¹, ranging between an average minimum condition of 1.2 ± 2.7 mg L⁻¹ (average of December, January, and June values) and an average maximum condition of 153 ± 86.7 mg L⁻¹ (average of March, August, and October values). In the low TSM range, the inorganic fraction greatly exceeded the organic fraction (78% TSM vs 22% OSM), while the seston was completely inverted in the high TSM range, where the organic fraction was more abundant than the inorganic one (97% OSM vs. 3% TSM).

### Table 1

Mean values of chemical, physical, and trophic variables measured during experimental periods.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Jun</th>
<th>Mar</th>
<th>Jun</th>
<th>Aug</th>
<th>Oct</th>
<th>Dec</th>
</tr>
</thead>
<tbody>
<tr>
<td>T °C</td>
<td>12.5</td>
<td>15.1</td>
<td>25.0</td>
<td>30.0</td>
<td>20.0</td>
<td>9.5</td>
</tr>
<tr>
<td>SAL</td>
<td>58.0</td>
<td>45.0</td>
<td>48.4</td>
<td>53.0</td>
<td>39.6</td>
<td>40.0</td>
</tr>
<tr>
<td>CHL-a, µg L⁻¹</td>
<td>0.7</td>
<td>1.7</td>
<td>1.0</td>
<td>0.6</td>
<td>0.8</td>
<td>0.5</td>
</tr>
<tr>
<td>PHADO, µg L⁻¹</td>
<td>0.3</td>
<td>0.9</td>
<td>0.4</td>
<td>0.2</td>
<td>0.3</td>
<td>0.8</td>
</tr>
<tr>
<td>TSM, mg L⁻¹</td>
<td>10.0</td>
<td>66.6</td>
<td>13.0</td>
<td>24.0</td>
<td>33.2</td>
<td>7.6</td>
</tr>
<tr>
<td>OSM, mg L⁻¹</td>
<td>3.0</td>
<td>63.8</td>
<td>2.7</td>
<td>23.0</td>
<td>14.9</td>
<td>3.3</td>
</tr>
<tr>
<td>ISM, mg L⁻¹</td>
<td>7.0</td>
<td>7.0</td>
<td>10.3</td>
<td>4.8</td>
<td>6.5</td>
<td>6.4</td>
</tr>
<tr>
<td>ISM/OSM, fraction</td>
<td>2.4</td>
<td>0.6</td>
<td>3.8</td>
<td>6.0</td>
<td>0.9</td>
<td>5.9</td>
</tr>
<tr>
<td>OSM/ISM, fraction</td>
<td>0.1</td>
<td>1.0</td>
<td>0.2</td>
<td>1.0</td>
<td>1.0</td>
<td>0.3</td>
</tr>
<tr>
<td>LIP, mg L⁻¹</td>
<td>0.1</td>
<td>0.1</td>
<td>0.1</td>
<td>0.1</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>PRT, mg L⁻¹</td>
<td>0.3</td>
<td>0.3</td>
<td>0.3</td>
<td>0.2</td>
<td>0.4</td>
<td>0.2</td>
</tr>
<tr>
<td>CHO, mg L⁻¹</td>
<td>0.2</td>
<td>0.1</td>
<td>0.2</td>
<td>0.2</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>PHA/CHO fraction</td>
<td>1.3</td>
<td>2.6</td>
<td>1.4</td>
<td>1.0</td>
<td>1.9</td>
<td>0.6</td>
</tr>
<tr>
<td>LIPOM, mg L⁻¹</td>
<td>0.6</td>
<td>0.5</td>
<td>0.5</td>
<td>0.6</td>
<td>0.6</td>
<td>0.6</td>
</tr>
<tr>
<td>BPC, mg C L⁻¹</td>
<td>0.3</td>
<td>0.2</td>
<td>0.2</td>
<td>0.3</td>
<td>0.3</td>
<td>0.2</td>
</tr>
<tr>
<td>C-CHL/a/BPC, %</td>
<td>10.2</td>
<td>33.2</td>
<td>16.1</td>
<td>9.8</td>
<td>10.6</td>
<td>7.3</td>
</tr>
<tr>
<td>LIPOM/TSM, %</td>
<td>5.5</td>
<td>7.7</td>
<td>4.0</td>
<td>0.2</td>
<td>0.4</td>
<td>8.3</td>
</tr>
</tbody>
</table>

Phytoplankton biomass was quite low, with mean CHL-a concentrations of 0.88 ± 0.4 µg L⁻¹ with a maximum measured in March (1.7 µg L⁻¹) and a minimum in December (0.5 µg L⁻¹). Phytoplankton represented on average 32% of total chlorophyll. Chlorophylls were almost twofold higher in the high TSM range compared to the low range (1.1 vs. 0.6 µg L⁻¹).

Mean labile fraction concentration (LIPOM) of suspended organic matter was 0.55 ± 0.07 µg L⁻¹ and throughout the experimental periods represented about 15% of OSM and only 3.2% of TSM. Two conditions to be identified: at low TSM values LIPOM represented 29% of OSM, while at high TSM values LIPOM represented only 0.45%. Particulate lipids were about 0.07 ± 0.01 mg L⁻¹, representing 13% of LIPOM, particulate proteins were 0.27 ± 0.05 mg L⁻¹, representing approximately 49% of LIPOM, while carbohydrates were 0.21 ± 0.08 mg L⁻¹, representing about 37% of LIPOM. There were no evident differences in lipid concentrations between conditions of low and high TSM concentrations, while proteins were higher (54% LIPOM) at high TSM values compared to low TSM values and, vice versa, carbohydrates were higher in the low TSM range (43%). In the low TSM range, proteins and carbohydrates showed approximately the same concentrations in LIPOM producing a P/R/P/C ratio ratio of about 1, while proteins exceeded carbohydrates twofold in the high TSM range (P/R/P/C ratio ratio about 2). The unicellular autotrophic fraction represented about 15% of the labile fraction, ranging from 11% in the low TSM range to 18% of LIPOM in the high TSM range.

### Clearance, Filtration, and Ingestion Rates

The physiological variables estimated in B. pharaonis throughout an annual period are summarized in Table 2. Measurements of clearance rate performed using the trace-substance method were compared with values obtained with the biodetection method. The agreement between the two kinds of estimates is demonstrated by the following equation: CRₜₘₑₐₓ = 0.06 ± 0.01 + CRₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑₑ euler
TABLE 2.

Averaged physiological (n = 84) values estimated in Brachidontes pharaonis throughout an annual period in the Stagnone saltworks.

<table>
<thead>
<tr>
<th>CR&lt;sub&gt;TM&lt;/sub&gt;</th>
<th>FR&lt;sub&gt;TM&lt;/sub&gt;</th>
<th>FR&lt;sub&gt;OM&lt;/sub&gt;</th>
<th>IR</th>
<th>OIR</th>
<th>RR</th>
<th>SE&lt;sub&gt;OM&lt;/sub&gt;</th>
<th>TR&lt;sub&gt;OM&lt;/sub&gt;</th>
<th>IR&lt;sub&gt;OM&lt;/sub&gt;</th>
<th>OER</th>
<th>AR</th>
<th>AE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan</td>
<td>2.07</td>
<td>20.57</td>
<td>6.19</td>
<td>0.36</td>
<td>0.09</td>
<td>0.45</td>
<td>(0.31)</td>
<td>20.02</td>
<td>6.01</td>
<td>0.15</td>
<td>5.86</td>
</tr>
<tr>
<td>Mar</td>
<td>1.09</td>
<td>21.47</td>
<td>6.30</td>
<td>0.11</td>
<td>0.67</td>
<td>0.70</td>
<td>(0.11)</td>
<td>71.76</td>
<td>69.83</td>
<td>0.46</td>
<td>68.37</td>
</tr>
<tr>
<td>Jun</td>
<td>0.81</td>
<td>30.17</td>
<td>2.16</td>
<td>0.68</td>
<td>0.11</td>
<td>0.79</td>
<td>(0.33)</td>
<td>9.57</td>
<td>9.57</td>
<td>0.43</td>
<td>1.26</td>
</tr>
<tr>
<td>Aug</td>
<td>1.15</td>
<td>276.16</td>
<td>27.68</td>
<td>0.28</td>
<td>0.22</td>
<td>0.50</td>
<td>(0.50)</td>
<td>257.67</td>
<td>270.46</td>
<td>0.10</td>
<td>270.36</td>
</tr>
<tr>
<td>Oct</td>
<td>1.73</td>
<td>252.76</td>
<td>25.21</td>
<td>0.44</td>
<td>0.15</td>
<td>0.39</td>
<td>(0.74)</td>
<td>262.17</td>
<td>251.60</td>
<td>11.63</td>
<td>240.03</td>
</tr>
<tr>
<td>Dec</td>
<td>3.02</td>
<td>23.03</td>
<td>3.86</td>
<td>0.38</td>
<td>0.01</td>
<td>0.46</td>
<td>(0.89)</td>
<td>22.57</td>
<td>23.35</td>
<td>3.60</td>
<td>0.26</td>
</tr>
<tr>
<td>Mean</td>
<td>1.64</td>
<td>110.89</td>
<td>100.68</td>
<td>0.37</td>
<td>0.21</td>
<td>0.60</td>
<td>(0.49)</td>
<td>110.20</td>
<td>100.48</td>
<td>2.73</td>
<td>97.75</td>
</tr>
<tr>
<td>± SE</td>
<td>0.82</td>
<td>124.77</td>
<td>127.07</td>
<td>0.19</td>
<td>0.24</td>
<td>0.16</td>
<td>(0.30)</td>
<td>124.80</td>
<td>127.04</td>
<td>4.56</td>
<td>124.97</td>
</tr>
</tbody>
</table>

Annual means and standard errors for means are also reported.

Abbreviations: CR<sub>TM</sub>, L g<sup>-1</sup> h<sup>-1</sup> - weight standardised clearance rate; FR<sub>TM</sub>, mg TSM h<sup>-1</sup> - total suspended matter filtration rates; FR<sub>OM</sub>, mg h<sup>-1</sup> - organic matter filtration rates; RR, mg h<sup>-1</sup> - inorganic content of pseudofaeces; OIR, mg h<sup>-1</sup> - organic content of pseudofaeces; RR, mg h<sup>-1</sup> - rejection rates; SE<sub>OM</sub> = total filtered organic matter selection efficiencies; IR, mg h<sup>-1</sup> - ingestion rate of total suspended matter; IR<sub>OM</sub>, mg h<sup>-1</sup> - ingestion rate of total suspended organic matter; OER, mg h<sup>-1</sup> - organic content of true faeces; AR, mg h<sup>-1</sup> - food absorption rates; AE, fraction - absorption efficiencies).

FR<sub>TM</sub> produced a significant relationship with TSM, which are plotted in Figure 2a and described in Eq. 2 (Table 4). Accordingly, FR<sub>TM</sub> increases as a function of TSM up to about 100 mg TSM L<sup>-1</sup>, after which FR<sub>TM</sub> reaches a plateau. Filtration rate was also a decreasing function (Fig. 2b) of labile organic content of suspended material (LPOM/TSM ratio; Table 4; Eq. 3).

Rejection rate was on average 0.60 ± 0.16 mg ingested material h<sup>-1</sup>. The proportion of inorganic ingested material was on average 65% throughout the study period. Rejection rate (Fig. 3) reached minimum values in December and January (approx. 0.4 mg h<sup>-1</sup>), when TSM concentrations were lower (averages 8.8 ± 1.6 mg L<sup>-1</sup>) and ISM/OSM ratios were on average 3.5. RR reached its maximum values in June and March when TSM was below 100 mg L<sup>-1</sup>, after which RR decreased sharply.

Selection efficiency (SE<sub>OM</sub>) ranged between 0.1 (March) and 0.90 (December) (average 0.50 ± 0.22). SE<sub>OM</sub> did not show a significant relationship with ISM, while the relationship with LPOM was described by Eq. 4 (Table 3).

Although SE<sub>OM</sub> was not measured directly as a function of each food substrate (Urrutia et al. 1996), we tentatively fitted SE<sub>OM</sub> versus the different dietary features: CHL<sub>a</sub>, carbohydrates, and the P-PRT-P-CHO ratio in the labile particulate organic matter produced significant linear relationships with SE<sub>OM</sub>, which are plotted in Figure 4 and described by Eq. 5-7 (Table 3).

According to the above relationships, SE<sub>OM</sub> decreased as CHL<sub>a</sub> and P-PRT-P-CHO increased, but increased as a function of P-CHO.

TABLE 4.

Spearman correlation analysis relating standardized clearance rates and physical and dietary measured variables throughout the experimental period.

<table>
<thead>
<tr>
<th>CR vs.</th>
<th>Rs</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>SAL</td>
<td>-0.24</td>
<td>0.34</td>
</tr>
<tr>
<td>OSM</td>
<td>0.34</td>
<td>0.01 (**)</td>
</tr>
<tr>
<td>ISM</td>
<td>0.16</td>
<td>0.14 (**)</td>
</tr>
<tr>
<td>TSM</td>
<td>0.05</td>
<td>0.06 (**)</td>
</tr>
</tbody>
</table>
| ISM/OSM | 0.44 | 0.00 (***+)
| CHL<sub>a</sub> | -0.38 | 0.00 (***) |
| PHAEO | 0.31 | 0.00 (***) |
| LIP | 0.43 | 0.00 (***) |
| PRT | -0.25 | 0.02 (**) |
| CHO | 0.50 | 0.00 (****) |
| P-PRT-P-CHO | 0.50 | 0.00 (****) |
| LPOM | 0.59 | 0.00 (****) |
| LPOM/TSM | 0.49 | 0.00 (****) |
| CHL/CHO | 0.58 | 0.00 (****) |
| LPOM/OSM | 0.34 | 0.00 (****) |

<table>
<thead>
<tr>
<th>n = 84:</th>
<th>Rs = 0.05;</th>
<th>P = 0.05;</th>
<th>Rs = 0.05;</th>
<th>P = 0.05;</th>
<th>Rs = 0.05;</th>
<th>P = 0.05;</th>
<th>Rs = 0.05;</th>
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<tr>
<td>n = 84:</td>
<td>Rs = 0.05;</td>
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<td>Rs = 0.05;</td>
<td>P = 0.05;</td>
</tr>
</tbody>
</table>

Abbreviations: SAL, water salinity; CHL<sub>a</sub>, suspended chlorophyll a; PHAEO, suspended phaeopigments; TSM, total suspended matter; ISM, total suspended inorganic matter; OSM, total suspended organic matter; LPOM, labile particulate organic matter as the sum of LPOM, PRT and CHO; BPC, biomass fraction of particulate organic carbon calculated by converting LPOM into carbon equivalents; see text for LIP, PRT and CHO conversion factors; C-CHL<sub>a</sub>, carbon suspended chlorophyll a. See text for explanation of ratios.
A physiological analysis of the *Brachidontes pharaonis* 971

![Graph](image)

Figure 1. Relationship between a) temperature (T, °C); b) labile particulate organic matter concentrations (L-POM, mg L⁻¹); c) protein by (do you mean ‘over’ i.e., divided by?) carbohydrate ratio (fraction) and clearance rate (I, h⁻¹) as measured throughout the study period.

Total ingestion by the mussels was estimated by subtracting total rejection from total filtered suspended material (IR = FR - RR, Wong and Cheung 1999). The average ingestion rate during the experimental periods was 10.3 ± 124 mg TSM h⁻¹, with a maximum in August (276 mg TSM h⁻¹), and a minimum in June (10 mg TSM h⁻¹). The relationship between rates of seston ingestion (as IR_TSM) and TSM is described by Eq. 8 (Table 3).

![Graph](image)

Figure 2. Changes in filtration rates (FR_TSM, mg h⁻¹) as a function of a) total suspended material (TSM, mg L⁻¹) and b) labile particulate organic matter concentrations by total suspended material ratio (L-POM/TSM, fraction).

Ingested organic matter (IR_L-POM, mg h⁻¹) varied between about 2 mg OSM h⁻¹ (June) and 270 mg OSM h⁻¹ (August). Ingested organic matter presented the same kind of relationships observed between IR_TSM and TSM.

Absorption efficiency ranged between 0.1 (December) and 0.99 (March and August). AE increased as a function of ingested organic material (IR_L-POM; Fig. 5), showing a plateau after approximately 7 mg ingested OSM and as a function of nitrogen content in the available food (P-PRT: Eq. 9; Table 3). Also, AE showed a negative correlation with particulate carbohydrates, described by Eq. 10 (Table 3). Absorbed organic material was at a minimum in December (0.18 mg OSM h⁻¹) and June (1.6 mg OSM h⁻¹), and a maximum in August and October (270 and 240 mg OSM h⁻¹), respectively. Absorption rate was a positive linear function of the amount of seston organics (OSM) and of filtered organic matter (FR_L-POM; Eq. 11-12; Table 3).

The rate of absorbed organic matter seemed to reach a maximum at 0.2 mg P-CHO h⁻¹, after which a large decrease was observed when P-CHO reached higher concentration values. AR

![Graph](image)

Figure 3. Changes in rejection rates (RR, mg h⁻¹) as a function of total suspended material (TSM, mg L⁻¹).
Figure 4. Changes in selection efficiency (SE) as a function of: (a) chlorophyll-a (μg L⁻¹); (b) particulate carbohydrate (mg L⁻¹); (c) particulate protein by carbohydrate ratio (fraction); and (d) labile particulate organic matter concentrations (LPOC, mg L⁻¹).

seemed to assume a different relationship to particulate proteins (Eq. 13; Table 3).

**DISCUSSION**

The physiological process of *B. pharaonis* measured *in situ* using the biodeposition method provided a series of complex relationships. Although *B. pharaonis* represents one of the most common species along Red Sea, Pacific, and Indian coasts (Moron 1988), its physiological processes and feeding behavior have never been measured, either in the laboratory or in ambient conditions. Consequently, the general physiological responses of *B. pharaonis* are compared here with those of other species which have been investigated more closely.

The complexity of feeding behavior in *B. pharaonis* appears to be correlated with their complex and varying environmental conditions. Bivalve molluscs are a "species mirror" that describe well the conditions of their colonised environments. *B. pharaonis* is possibly a good example of a descriptor species because, like the other bivalves, it possesses compensatory mechanisms to regulate its behaviour in response to fluctuations in environmental and trophic factors.

The western Mediterranean saltworks environments, like other similar environments (Pusceddu et al. 1999, Sara et al. 1999), are characterized by shallowness and partial enclosure, which determine much of the variability in their physical, chemical, and trophic features. A good example is given by water temperature. The temperature of the Mediterranean never falls below 12–14 °C (except in the Adriatic) and above all never exceeds about 26.5 °C (Margalef 1985). Mediterranean benthic communities therefore experience a moderate temperature range throughout the year. In contrast, the Sicilian saltworks temperature ranges widely, between 9–10 °C in winter and 28–30 °C in summer—a range that is rarely found in other Mediterranean coastal areas (Margalef 1983). These wide variations can be correlated with atmospheric temperature changes and various meteorological phenomena which, in small enclosed shallow basins such as our study area, can strongly influence the usual physical and chemical dynamics (Sara et al. 1999). Throughout the year, *B. pharaonis* experienced physical conditions that were often close to the survival limits for Mediterranean bivalve molluscs (Sara et al. 1998). However, it has been documented that *B. pharaonis* is a typical intertidal and hyperhaline species (Por 1971), which can live in very different and quite extreme conditions (Stern and Achituv 1978; Moron 1988).

The average clearance rate (1.64 ± 0.82 L h⁻¹) measured in adults of *B. pharaonis* falls into the general range measured for many epifaunal bivalve molluscs (Widdows et al. 1978, Rosgaard 1988, Navarro et al. 1991, Navarro et al. 1992, Umida et al. 1996, Wong and Cheung 1999) and was quite similar to that mea-
sured in other experimental conditions for adults of *B. caudata* (range 1.2–1.7 L h⁻¹; Riisgård 1988).

The first response of *B. pharaonis* to temperature changes seems to be to regulate its clearance rate. The documented response of bivalves to temperature changes is a general reduction in clearance rates at low and high temperatures (Bayne 1976, Jorgensen 1990, Hawkins and Bayne 1992). This has been observed in many bivalve molluscs (Schulte 1975, Aldridge et al. 1995, Hawkins et al. 1998). However, as a general trend, our *Brachidontes* data did not fit with this documented response as its clearance rate showed higher values (2.54 ± 0.67 L h⁻¹; average of December and January values) at the lowest temperatures (10 and 12 °C) and lower CR values with an increase in temperature (up to 25 °C). It is difficult to explain the peak in clearance rate measured in January and December only as a function of temperature. It may be a species-specific response to thermal stress or changes in the endogenous reproductive phases. No literature data regarding similar behaviour in bivalve molluscs exist, and the presence of this species at low temperatures observed in winter in the study area has not been demonstrated previously. That this species may be better adapted at high than low temperatures (Stem and Ackroyd 1978) could be explained by the fact that *B. pharaonis* is stratificationally well equipped for bodies of water in which salinity is high and the temperature variable (Stem and Ackroyd 1978). Further research is needed to resolve the relationship between temperature, CR, and the role of the endogenous reproductive cycles in *B. pharaonis*.

The hypolimnetic environment did not seem to produce any effect on clearance, as demonstrated by its independence of salinity. Nevertheless, it has been reported (Bayne 1976, Widlowski 1985) that in some conditions salinity can be a regulating factor for clearance rates in several bivalve molluscs, often producing a decrease in clearance rate or, in my case, a certain dependency. However, literature findings refer to acclimatization in typical coastal or estuarine bivalve molluscs, which are generally adapted to sea salinity and are thus less comparable with *Brachidontes*, which are generally well adapted to high salinity (Por 1972, Morton 1988).

The clearance rate of western Mediterranean *B. pharaonis* does not appear to be fundamentally affected by physical factor (i.e., water temperature and salinity) but more likely by fluctuations in the feeding environment. The food supply in the saltwater environment investigated seemed to be limited by resuspension from sediment. The main effect of sediment resuspension is usually an increase in the organic fraction of the suspended bulk (i.e., silt material) (Peggey et al. 1992, Siri et al. 1999, Wong and Cheung 1999). Instead, in the particular conditions of the basin studied (i.e., shallow and enclosed), wind-driven resuspension events in (March, August, and October) led to a marked increase in sedimentary organic matter, producing an unusually high dominance of organic fraction over inorganic (ISM/OSM ratio < 0.1). Although similar results have been observed rarely in coastal environments around the world, the presence of a large amount of rich organic sedimentary detritus composed of seaweed wrack particles and filter feeder biodeposition products may justify organic contents with values that were higher than those for pure phytoplankton cultures.

The nature of the relationships between food acquisition processes in bivalve molluscs and the quantity and quality features of available food has been widely and well documented in the current literature (Widlowski et al. 1979, Iglesias et al. 1992, Bayne et al. 1993, Navarro et al. 1993, Narvarro and Thompson 1995, Hawkins et al. 1996, Iglesias et al. 1996, Urrutia et al. 1996, Navarro and Widlowski 1997, Hawkins et al. 1998, Iglesias et al. 1998, Wong and Cheung 1999). Most of the above cited articles have shown a general decline in clearance rate with an increase in the quality and quantity of available suspended food (Winter 1978, Bayne 1989, 1993). The present results are consistent with the findings in the literature. Indeed, our data show a general negative dependence of CR on total suspended matter and in particular on its total organic fraction (OSM) (Table 4). Furthermore, the food acquisition process in *Brachidontes* was also dependent on food quality, as highlighted by the relationships between CR and the dietary parameters (Table 4). This relationship has often been tested in laboratory experiments using phytoplankton-based diets. Such experiments have clearly highlighted that most bivalves reduce their clearance rate as a function of an increase in phytoplankton biomass (Winter 1978, Bayne et al. 1989). When the nutritional value of the phytoplankton diet was reduced using inorganic particles to simulate an artificial dilution effect (Iglesias et al. 1992, Bayne et al. 1993), the immediate physiological response was an enhancement of clearance rates. Similar findings have always led researchers to conclude that bivalves respond to food quality. However, these observations cannot be taken as general findings applicable to ambient conditions (Baez et al. 1981, Widlowski and Kristiansen 1997) and the necessity to gather information directly from the field has often been highlighted (Bayne et al. 1989, Widlowski and Kristiansen 1997).

The CRs obtained in this study were negatively correlated with particulate proteins, suspended chlorophyll-a and consequently with the P/PROT/CHL and C-CHL/2BPC ratios in the particulate, suggesting that *B. pharaonis* reduces its clearance activity as a direct response to an increase in the labile fraction of the available food. In contrast, the positive correlation between CR and particulate carbohydrates and lipids could indicate that in the presence of these classes of compounds *B. pharaonis* increases its rate of clearance to enhance its food uptake. This picture would fit well with the particular feeding environment of *B. pharaonis*, in which the main vegetal component is *Cyanobacteria nodosa* detritus, which is, by definition (Mann 1988, Velimirov 1991) highly refractory and thus less available to benthic filter feeders (Mann 1988, Velička 1988). Although this kind of relationship has been hypothesized widely (Bayne 1976, Widlowski et al. 1979, Bayne et al. 1993, Dame 1996), it has not been documented clearly.

A diluted effect produced by inorganic material on bivalve clearance rate (see reviews by Hawkins and Bayne 1992 and Dame 1996) has been well verified on many occasions. Consequently, clearance rate increases in correspondence with increments in ISM. However, CRs of saltwaters *B. pharaonis* were “statistically independent” of ISM concentrations. Clearance reached its maximum in December and January while under high ISM/OSM ratios but at the lowest temperatures (10 and 12 °C). Such high values cannot be explained by the influence of temperature on CRs but may be explained by the dilution concept widely proposed in the literature (Widlowski et al. 1979). However, in order to explain the absence of a well-defined statistical relationship between CRs and inorganic material concentration, we could also hypothesize that in other experimental periods characterized by a large quantity of suspended organic (>60 mg OSM L⁻¹), part of the inorganic material was not sufficient to reduce the food value. Consequently, *B. pharaonis* did not need to offset the inorganic material dilution effect by increasing its clearance rate (Dame 1996).
*B. pharaonis* specimens were able to filter a wide range of total suspended matter (0–280 mg TSM h⁻¹), showing a great capacity to respond to wide changes in food supply. Although our measurements were performed over a wide TSM range, *B. pharaonis* filtering activity was related to seston concentration, like most suspension feeders investigated. The mass of filtered seston increased exponentially up to a certain TSM threshold, after which it reached a plateau followed by a possible decline (Dume 1996).

Similar behaviour has been widely observed in situ experiments carried out with a seston concentration of up to 100 mg L⁻¹ in *Perna viridis* (Hawkins et al. 1998), *Mytilus edulis* (Navarro and Winter 1982), *Crasostrea belcheri* (Hawkins et al., 1998), *Cerastoderma edule*, *Mytilus edulis*, and *C. riggs* (Hawkins et al. 1998). Our data would indicate that filtration depends also on the available food quantity (LPOP/TSM, Fig. 2b). When there was a high concentration of LPOP in the saltworks the filtration rate levelled off, whereas when the available organic matter was low the total mass filtered increased. Therefore it is hypothesised that when available food increases *B. pharaonis* levels off its filtration activity because it fulfills its energy requirements with sufficient organic-rich particles.

Our data demonstrate that *B. pharaonis* may not control ingestion rates by varying the rate of pseudofaeces production, and such a mechanism seems to be quite inefficient compared to other bivalve molluscs. Indeed, the average rejection rate by *B. pharaonis* (RR = 0.68 ± 0.16 mg h⁻¹) was lower than those documented for *Mytilus edulis* (1.2 mg h⁻¹), *Bayne et al. 1993), *Perna viridis* (0.2–5 mg h⁻¹), *Wong and Cheung 1999), *Cerastoderma edule* (2.9 mg h⁻¹), *Iglesias et al. 1992) and several tropical bivalves (Hawkins et al. 1998). In most bivalves the control of ingestion level by pseudofaeces production has already been observed (Forster-Smith 1975, Cranford and Gordon 1992, Iglesias et al. 1992, Bayne et al. 1993, Urrutia et al. 1996, Arfín and Bendell-Young 1997, Hawkins et al. 1998, Wong and Cheung 1999) and is considered to be an overhast mechanism. Pseudofaeces production together with the modulation of clearance rate (Winter 1978) can maintain bivalve ingestion rates constant (Iglesias et al. 1992) in order to reduce the “detrimental effect” of food dilution by organic material. The material rejected by the saltworks *B. pharaonis* was mainly represented by inorganic material (65%). However, only about 2.2% of filtered seston (7% and 23% of inorganic and organic material, respectively) was rejected as pseudofaeces, indicating that the feeding conditions of the saltworks did not induce a high level of rejection. As confirmation of this, the rejection rates are lower than those reported by Iglesias et al. (1992) for *C. edule*, which rejected material representing approximately 31% of filtered materials (approximately 87% and 13% inorganic and organic material respectively).

However, assuming that ingestion rates were extremely high as a specific response to very high seston organic availability (seston organic content >90%), it would seem that in *B. pharaonis*, there was a lack of ingestion regulation, which, under these trophic conditions would render digestive processes impossible. Without considering physiological compensatory mechanism that have yet to be found in a colonizer mollusc such as *B. pharaonis*, the ingestion rate measured in the saltworks conditions would imply mean gut passage times of about 30–60 min. Such time lengths would generally be incompatible with the breakdown and absorption of food in the mussel gut. We envisage that such discrepancies may be explained by the slight overestimation of ingestion rates due to the use of experimental methodologies (i.e., bioleposition method; Iglesias et al. 1998), which rarely have been tested in similar environments (with huge concentrations of particulate organic), coupled in the great capacity of *B. pharaonis* to adapt to very unusual variability in environmental conditions. On the other hand, the presence of active populations of *B. pharaonis* has also been documented in Mediterranean ultra-oligotrophic sea waters (ICH-UL < 1 µg L⁻¹; safety 37; Di Cerino 1971), and such a finding agrees with the huge physiological plasticity of this species.

Under our study conditions, *B. pharaonis* was able to perform sorting of filtered material with an efficiency (SEm = 0.5) similar to that reported for other bivalves (Kurome et al. 1981, Iglesias et al. 1992, Hawkins et al. 1996, Navarro and Widdows 1997, Hawkins et al. 1998, Wong and Cheung 1999). Although our experiments were not designed to test specifically the selection ability of the pallial organs in *B. pharaonis*, it appears that this species is able to sort between refractory and labile food (see Fig. 3). The general picture of selection efficiency in bivalves is that they have an ability to discriminate organic from inorganic material but generally are refractory from labile organelles. Nevertheless, the general tendency of *B. pharaonis* is to increase SEm when P-CHO in the available food increases (see Fig. 4b and 4c), producing a dilution of the particular protein nutritional value with CHL-a not exceeding 1 µg L⁻¹. In contrast, when inorganic material did not exceed 4 mg L⁻¹ selection efficiency decreased. The ability of the pallial organs to sort particles of different organic content and to respond to food quality has already been demonstrated in other bivalves. Thus we believe our results may be explained by (1) a species-specific response (Ward and MacDonald 1996, Wong and Cheung 1999) reflecting the huge plasticity of *B. pharaonis* and its ability to colonize a wide variety of tropical, sub-tropical, and temperature environments; and (2) a particular strategy activated at a local level by *B. pharaonis* in order to minimise the huge variability in the feeding environment.

Absorption efficiency in *Brachidontes* is a complex process that needs further investigation through specifically designed experiments. It has been documented that most bivalve absorption efficiency values are generally low, ranging from 0.4 to 0.6. In the present study, the average AE value of *B. pharaonis* (0.79) was comparable to those reported for other tropical bivalves (Hawkins et al. 1998) but higher than those for *Mytilus edulis* and cockles (Bayne et al. 1989, 1993, Navarro and Widdows 1997, Wong and Cheung 1999). Also, AE depended positively on ingested organic matter (IRorg), reaching higher values when IRorg exceeded 6–10 mg h⁻¹ and remaining fairly constant above this level.

This type of dependence agrees with that observed in *Perna viridis* and other tropical bivalves (Hawkins et al. 1998, Wong and Cheung 1999), but it differs from those obtained in *Mytilus edulis* (Bayne et al. 1989) and *C. edule* (Iglesias et al. 1992, Urrutia et al. 1996). Moreover, AEs of *Brachidontes* were apparently dependent on the quantity and quality of ingested matter. Significant positive relationships were observed between AEs and particular proteins, while particular carbohydrates showed a negative correlation. Indeed, it seemed that absorption efficiency reached higher values when proteins exceeded approximately 0.23 mg L⁻¹, while they decreased when carbohydrates increased. This suggests that *B. pharaonis* may preferentially absorb proteins with respect to carbohydrates and lipids. This hypothesis, however, is contradicted by the findings of Bayne et al. (1993), who described higher efficiencies for carbohydrates than for proteins and lipids. However, it agrees with the results of Hawkins et al. (1985), who recorded the same rank order of absorption efficiencies for biochemical components of the diet.
This B. pharaonis rank order of absorption efficiencies agrees with our unpublished data on suspended bacteria in the saltworks (Sarī, La Rosa and Mazzola, unpublished data). We found concentrations of attached-bacteria fraction in the saltworks water particulate of up to 10^4 (two orders higher than 10^4 vs. 10^1) than those found in Mediterranean fish farming impacted coastal waters and sediments (Mazzola et al., La Rosa et al., in press). This would clearly justify the preferential absorption of proteins by B. pharaonis. In addition, the marked dominance of the attached-bacteria fraction in the particulate also indicates that B. pharaonis may be able to actively exploit nitrogen from bacteria, as suggested by Langdon and Newell (1990), justifying estimated absorption efficiencies which are six high and so rarely documented in the current literature.

Our findings agree well with the good sorting ability observed in B. pharaonis. The hypothesized ability to sort labile mainly organic compounds originating from bacteria? from refractory material at the level of the pallial organs may allow B. pharaonis to maintain constant ingestion rates by channeling more labile (i.e., more digestible) material into the gut. Absorption rate followed the same trend and both the quantity and quality of ingested organic matter was affected. The correlation of absorption rate with filtration activity demonstrates that B. pharaonis control of feeding begins with food acquisition processes. Similar findings have been documented in many bivalves, above all in those environments that are highly variable in food supply (Iglesias et al., 1992, Bayne et al., 1993, Navarro and Widjow, 1997, Wong and Cheung, 1999).

CONCLUSIONS

The mechanisms controlling food acquisition processes in B. pharaonis appear to reflect the particular feeding environment in which it lives. The complex feeding process of B. pharaonis is regulated by the first stages of feeding (treatment and filtration), and most of the control reflects the quantity of food absorbed. In this paper, we have clarified the following points:

1. Clearance rate does not appear to be fundamentally regulated by physical factors (i.e., water temperature and salinity), but may reflect fluctuations in the feeding environment and, more closely, the quantity and quality of food available.

2. This finding is consistent with the idea of a trophic regulation of feeding processes in bivalves (Bayne, 1998). However, it contradicts Jørgensen's idea that food uptake in bivalves is an autonomous process which is not regulated at the organism level according to nutritional needs (Jørgensen 1990, Clausen and Riesgård 1990). Further investigation is needed to resolve and fully understand this apparent discrepancy.

3. B. pharaonis may control ingestion rate by varying the rate of pseudofaeces production, although our data demonstrate that this may not be a very efficient response under the prevailing environmental conditions. However, it is able to perform sorting of filtered material. These mechanisms may be used by this species to maintain the ingestion rate constant, as this rate may be affected by the "dilution effect" of both organic material and refractory matter in the available food.

4. Absorption efficiencies may be sensitive to the balance of biochemical components in the diet (on average composed of 50% P/RT, 38% P/CHO and 12% P/LIP). Accordingly, we can infer that B. pharaonis absorbed organic matter with different efficiencies for proteins, carbohydrates and lipids.

In conclusion, although these findings are currently being investigated further in a set of specifically designed experiments, in the meantime we can say that the Mediterranean B. pharaonis seems to be a "complex machine" that operates as a function of a complex synergy of trophic, chemical and physical factors. Such a fact may be the key to understanding the huge plasticity of this organism, which is able to colonize a great variety of habitats at different latitudes around the world.

ACKNOWLEDGMENTS

We thank Dr. John Widjow (Plymouth, UK) for his suggestions, which were invaluable for improving the experimental design, and for his precious comments on reading an early version of the manuscript. This work was funded by the Ministero Politiche Agricole (MIPA, Italy) and the Ministero dell' Università Ricerca Scientifica e Tecnologica (MURST, Italy). All literature cited in this article can be freely consulted by the scientific community through the corresponding author.

LITERATURE CITED


Vitoux, R., P. Gigantea, M.S. Colombo & S. Riggio in press. The cyanobacterial characterization of Brachiariidae. (Bivalvia)


