ABSORPTION OF BIOCHEMICAL COMPONENTS AND FEEDING BEHAVIOR WITH NATURAL AND CARBOHYDRATE-RICH DIETS IN RUDITAPES DECUSSATUS AND VENERUPIS PULLASTRA CLAMS

M. ALBENTOSA1*, M. J. FERNÁNDEZ-REIRIZ2, U. LABARTA2, AND A. PÉREZ-CAMACHO1
1Instituto Español de Oceanografía, Centro Oceanográfico de A Coruña, Muelle de Animas, s/n, 15001 A Coruña, Spain and 2Consejo Superior de Investigaciones Marinas, Instituto de Investigaciones Marinas, Eduardo Caballo, 6, 36208 Vigo, Spain.

Abstract The feeding behavior and the efficiency of the absorption of biochemical components in the diet of specimens of two species of clams, Ruditapes decussatus and Venerupis pullastra fed on natural and carbohydrate-rich diets were studied. Both the natural diet, which consisted of the microalga Isochrysis aff. galbana, clone T-ISO and ashed sediment, and the carbohydrate-rich diet, which consisted of microalgae and corn starch as organic ingredients, and ashed sediment as the inorganic component, were assayed at a concentration of total particulate matter close to 1 mg TPM L⁻¹, and a concentration of particulate organic matter of approximately 0.6 mg POM L⁻¹, which are similar conditions to those found in the Galician Rias. The feeding behavior of both species for each diet is described with reference to the clearance and ingestion rates, whereas the absorption of the biochemical components of the two diets was determined by biochemical analysis of the diet and the resulting feces. Both ingestion and absorption rates were higher for V. pullastra when the clams were fed on a natural diet. Enriching the diet with carbohydrates led to a notable increase in the ingestion and absorption rates in both species, although this increase was greater in R. decussatus than in V. pullastra, and in consequence the energy absorbed from the carbohydrate-rich diet was greater in the case of R. decussatus. The energy absorbed by R. decussatus fed on this latter diet was three times greater than that absorbed on the natural diet, allowing it to maintain similar rates of protein absorption for both diets. However, in the case of V. pullastra, the amount of total energy absorbed that derived from proteins is 50% lower in the carbohydrate-rich diet than in the natural diet. The energy absorbed from carbohydrates in the carbohydrate-rich diet was greater for R. decussatus than for V. pullastra. The contribution of lipids to the total energy absorbed was found to be almost double in R. decussatus fed on the carbohydrate-rich diet, in comparison with the natural diet, although in V. pullastra this contribution was lower. Thus, the effect of diet on the feeding behavior of both species, i.e., the increase in the ingestion rate and the corresponding increase in the absorption rate, allows R. decussatus to compensate for the nutritional deficiencies of the carbohydrate-rich diet, whereas in the case of V. pullastra it does not appear to be sufficient for the clams to maintain the same protein absorption rate as on the natural diet. These results are discussed in relation to the possible existence of major differences in the metabolism of the two species of clams, differences which would be connected to the habitats in which they live.

Keywords: absorption, biochemical components, clams, diets, feeding behavior, Ruditapes

INTRODUCTION

Differences in the characteristics of the habitat occupied by a given species, particularly food availability and quality, give rise to functional adjustments in individual members of the species to allow them to maintain adequate levels of energy acquisition. These adjustments can take place at different levels, e.g., filtration activity, production of pseudofeces, ingestion rate, digestive capacity, transfer of food to the digestive gland, and enzyme production. The efficiency with which the food is absorbed after ingestion, i.e., absorption efficiency, is one of the most decisive parameters in establishing the amount of energy available to a specimen for growth and reproduction.

Although the absorption processes of bivalves, in terms of total organic matter, have been the subject of extensive study (Thompson & Bayne 1972, Widdows 1978, Griffiths & King 1979, Navarro & Winter 1982, Bayne & Newell 1983; Bayne et al. 1989, Beiras et al. 1993, Navarro & Thompson 1996, Pérez-Camacho et al. 1997, amongst others), there are few references in the bibliography on the efficiency with which each individual biochemical component in the diet is absorbed (Langdon 1989, Bayne et al. 1993; Kreeger & Langdon 1994, Ibarrola et al. 1996, 1998), it having been observed that the quality of the diet affects the efficiency with which its different components are absorbed, this being closely related to the digestive processes.

Studies of the absorption efficiencies of specific elements of the diet, such as carbon or nitrogen, are to be found in greater number (Hawkins and Bayne 1985, Cranford 1995, Iglesias et al. 1996, Urrutia et al. 1996), and from these it is possible to predict efficiencies for proteins in relation to carbohydrates and lipids. Another approach to establishing the nature of the mechanisms by which different components of the diet are used is based on the oxygen consumption : nitrogen excretion (O:N) ratio, which is an indirect indicator of the relative use of protein (Kreeger & Langdon 1993).

As a result of the work of our group in recent years on the two species of clams included in the present study, Ruditapes decussatus and Venerupis pullastra, we have established the existence of major differences between these two species in terms of both nutritional requirements and physiological parameters, as a result of the different ecological niche they each occupy (Labarta et al. 1997). The purpose of the present work has been to study the absorption of the biochemical components of the diet and the feeding behavior of the two species of clam when fed on a natural diet and on a carbohydrate-rich diet.

MATERIAL AND METHODS

Acclimatization

Specimens of the clams, R. decussatus and V. pullastra, of approximately 40 mm in length were collected in the surrounding

*Corresponding author.
Tel.: +34-81-205362; Fax: +34-81-229077; e-mail: marina.albentosa@co.ieo.es
area and transferred to the Centro Oceanográfico de A Coruña, where they were acclimatized to laboratory conditions over a minimum of 7 days. Throughout the whole of the acclimatization process, clams were kept in an open-flow system with a flow rate of approximately 2 L ind⁻¹ h⁻¹ of seawater filtered to 1 μm and enriched with the microalgae *Isochrysis aff. galbana*, clone T-ISO. The organic weight of microalgal cells was calculated by filtration of a volume of the algal cultures through Whatman GF/C glass fibre filters that had previously been ashed and then rinsed with a 0.5-M ammonium formate solution. Filters were dried to constant weight at 100°C and ashed at 450°C in a muffle furnace. The concentrations of the microalgal cultures were determined using a Multisizer Coulter Counter. The daily food ration during the acclimatized period, approximately 3%, expressed as a percentage of organic matter in the diet in relation to total flesh dry weight, was supplied at a concentration of approximately 0.5 mg MO L⁻¹, these being similar conditions as those applying during the experimental period. Water temperature was maintained at 19 ± 1°C.

**Experimental Conditions**

Similar-sized specimens (n = 10) of each species were chosen from the stock of acclimatized clams and placed in individual vessels connected to an open-flow system by multichannel peristaltic pumps. Each vessel was fitted with an inlet-tube at the base and an outlet-tube near the surface, the latter being covered with a nylon mesh to prevent loss of feces. Each pump was also connected to two vessels containing no clams to obtain samples of the diet supplied. The flow-rate was 2 L ind⁻¹ h⁻¹ and the temperature was maintained at 19 ± 1°C in a controlled environment.

**Experimental Diets**

The natural diet was designed so as to reproduce the annual average values of total particulate matter (TPM; mg L⁻¹), hence particulate organic matter (POM; mg L⁻¹), and percent organic matter observed in the Galician Rias. The diet comprises two particulate components: *Isochrysis aff. galbana*, clone T-ISO, cells, and sediments from underneath the bottom that had been ashed and freeze-dried.

The carbohydrate-rich diet consisted of a mixture of microalgae and corn flour starch (commercial corn starch MAIZENA from Bestfoods España, S.A.) as its organic components and ashed sediment as the inorganic component. The stability of the diet over a 24-h period, in both quantitative and qualitative terms, was monitored from samples obtained from the outlet tubes of the clam-free control vessels. The daily ration of corn flour starch and sediment was resuspended in seawater, using an electrical stirrer and sieved at 60 μm before adding to the system. Size of the corn starch particles used ranged from 4 to 30 μm, being the mean particle size 15 μm.

Both diets (Table 1) were assayed at a concentration of total particulate matter of approximately 1 mg TPM L⁻¹, and a concentration of particulate organic matter of around 0.6 mg POM L⁻¹, these being similar to the conditions prevailing in the Galician Rias (Babarro et al. 2000). The concentration of organic matter in the carbohydrate-rich diet was increased to 0.77 mg POM L⁻¹, so that when expressed in units of energy (Table 1) this concentration would be equivalent to that assayed in the natural diet, given the lower energy content of corn flour starch in comparison with microalgae. Both experiments were conducted in summer, being the water temperature for both experiments around 19°C.

Samples (2 L) were taken daily from the outlet-tubes of the clam-free vessels directly on to Whatman GF/C fibreglass filters that had previously been washed, ashed, and weighed. After filtration, these filters were rinsed with a 0.5 M ammonium formate solution. Samples were taken in triplicate over a 24-h period to determine both particulate matter, whether total (after oven-drying to constant weight at 100°C) or organic (after ashing in a muffle furnace to constant weight at 450°C) and biochemical components. The filters used for biochemical analysis were freeze-dried and stored at −30°C until the analyses were performed.

**Physiological Parameters**

The physiological rates were established from the total amount of feces produced over a specific period of time by means of the biodeposition method (Iglesias et al. 1998). The clams were maintained on the experimental diet for 24 h, after which they were cleansed of feces and the period of accumulation of total feces commenced, these being collected after 24 h. The total feces produced were collected on Whatman GF/C filters that had been treated as described above. A proportion of the feces were used to establish their inorganic content and thus determine ingestion rates and absorption efficiency. The remainder were collected on filters, which were freeze-dried, weighed to obtain the total ingestion rate, and then stored at −30°C until biochemical analyses were performed.

The sum of the weight of the feces distributed among the different filters (total egestion rate), together with their inorganic content (inorganic and organic egestion rate) and the inorganic content of the diet allows us to calculate the clearance rate, which when multiplied by the concentration of organic matter in the diet gives us the organic ingestion rate. Absorption efficiency was obtained from the organic content of the feces (ε) and the diet (f), according to the formula established by Conover (1966):

\[
AE = (\varepsilon - e)/(1 - e)f.
\]

**TABLE 1.**

<table>
<thead>
<tr>
<th>Diet</th>
<th>TPM (mg L⁻¹)</th>
<th>POM (mg L⁻¹)</th>
<th>Energy (J L⁻¹)</th>
<th>POM/TPM</th>
<th>Protein (mg L⁻¹)</th>
<th>Carbohydrate (%)</th>
<th>Lipids (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natural</td>
<td>0.77 ± 0.07</td>
<td>0.56 ± 0.07</td>
<td>14.1</td>
<td>0.73</td>
<td>40.5 ± 6.5</td>
<td>17.1 ± 2.5</td>
<td>42.4 ± 4.8</td>
</tr>
<tr>
<td>Carbohydrate-rich</td>
<td>0.95 ± 0.10</td>
<td>0.77 ± 0.06</td>
<td>15.1</td>
<td>0.82</td>
<td>7.0 ± 0.1</td>
<td>79.7 ± 0.2</td>
<td>13.3 ± 0.3</td>
</tr>
</tbody>
</table>

TPM, total particulate matter; POM, particulate organic matter. Average values ± standard deviations are shown (n = 6).
Clearance rates were standardized for both species for a specimen of 1 g flesh dry weight using the expression:

$$CR_s = (1/W_s)^bCR_s$$

where $CR_s$ is the standardized clearance rate, $W_s$ is the flesh dry weight of each specimen, and $CR_s$ is the observed clearance rate of the same specimen. The exponent applied, $b$, was 0.68, which relates clearance rate to the size of the specimen, expressed in terms of weight, for clams (Delgado 2002).

**Absorption of Biochemical Components**

The biochemical composition of the diet and the feces produced was ascertained by analyzing the contents of the filters of food and feces, according to the following methodology. Proteins were calculated using the method described by Lowry et al. (1951) after alkaline hydrolysis with NaOH 0.5N/30°C. Carbohydrates were quantified as glucose by the phenol-sulphur method (Strickland & Parsons 1968). Lipids were extracted according to a modified Bligh and Dyer (1959) method (Fernández-Reiriz et al. 1989). Total lipids were determined by the Marsh and Weinstein method (1966), with tripalmitine used as a standard. Based on the results of the biochemical analyses of the contents of the food and feces filters, ingestion rates for the different biochemical components were calculated from the product of the organic ingestion rate and the proportion of each biochemical component in the diet. The absorption efficiencies of the various components ($AE_{comp}$, $AE_p$, $AE_C$, and $AE_L$) were obtained by applying the following formula (Ibarrola et al. 1998):

$$AE_{comp} = (comp_D - comp_F)/(1 - AE)$$

in which $comp_F$ ($P_F$, $C_F$, and $L_F$) and $comp_D$ ($P_D$, $C_D$, and $L_D$) are the contents of each component in the feces ($F$) and the diet ($D$), respectively. The absorption rates of the different biochemical components were obtained from the product of the ingestion rate of the biochemical component in question and its absorption efficiency. Component absorption rates were transformed to energetic units using the following energy equivalents: 18.0 KJ (g protein)$^{-1}$, 17.2 KJ (g carbohydrate)$^{-1}$, and 35.2 KJ (g lipid)$^{-1}$ (Beukema & de Bruin 1979).

**Statistical Analysis**

The differences observed in the different physiological parameters between the experimental diets used and between the two species studied in this experiment were submitted to statistical analysis of variance (ANOVA, $P < 0.05$; Zar 1984). Angular transformation (arc sin $\sqrt{(AE/100})$) was used to transform the results for absorption efficiency in order to guarantee standardisation of the data. The Bartlett test was used to check homogeneity of the variances. In the case of non-homogenous variances, logarithmic or reciprocal transformation was used to transform the data, after which their homogeneity was once again checked.

**RESULTS**

**Characteristics of the Diets**

Table 1 shows the characteristics of the diets used. The main components of the organic fraction in the natural diets were proteins and lipids, each accounting for approximately 40%, whereas the proportion of carbohydrates is much lower at 17.1%. In the carbohydrate-rich diet, however, the relative percentages of proteins and lipids are much lower, with values of 7.0 and 13.3%, respectively, the main component being carbohydrates, which account for 79.7%.

Both diets were assayed at concentrations similar to those observed in their natural environment (Navarro et al. 1991, Babarro et al. 2000). The ratio of the concentration of organic matter to total particulate matter was 0.75 for the natural diet and 0.82 for the carbohydrate-rich diet. Food concentrations, expressed as energy equivalents, were similar for both diets, being 14.1 and 15.1 J L$^{-1}$ for the natural and carbohydrate-rich diets, respectively.

**Physiological Parameters**

Average clearance rates ($CR_s$), organic ingestion rates ($IR_s$), organic absorption efficiencies ($AE_s$) and organic absorption rates ($AR_s$) together with their standard deviations for a specimen of 1 g flesh dry weight for each species of clam and for both diets are shown in Table 2. Organic ingestion rates of natural diet were significantly higher in *V. pullastra* than in *R. decussatus* ($P < 0.05$, ANOVA test). When clams were fed on the carbohydrate-rich diet organic ingestion rates were significantly higher than those registered for the natural diet. This increase in the ingestion rate was much more noticeable in *R. decussatus* than in *V. pullastra*, thus leading to higher rates in *R. decussatus*.

The absorption efficiencies of total organic material were similar for both species fed on the natural diet (ANOVA; $P > 0.05$), with a value of close to 70%. However, when the clams were fed on the carbohydrate-rich diet, absorption efficiencies decreases in both species at around 37%. Thus, the increase in the proportion of carbohydrates in the diet leads to an increase in the ingestion rate, and this in turn supposes a decrease in the efficiency with which the ingested food is absorbed. The relation between the ingestion rate and the absorption efficiency is given by a model that fits the equation $AE = a1^IR$, in which $a = 6.37$ ($\pm 0.575$) and $b = -0.404$ ($\pm 0.095$) ($r = -0.9493$, $R^2 = 0.9013$, $P = 0.007$).

The organic absorption rate ($AR_s$) behaves in a similar manner to the $IR_s$ in natural-diet fed clams: the $AR_s$ was significantly higher (ANOVA, $P < 0.05$) in *V. pullastra* than in *R. decussatus*.

When the carbohydrate diet was used, organic absorption rate was three times greater than that for the natural diet in the case of *R. decussatus*, but only 50% higher in comparison with the natural diet in the case of *V. pullastra*.

**Absorption of Biochemical Components**

The difference in biochemical composition between the two diets determines the ingestion rates of each biochemical components of the diet. In *V. pullastra*, although the total ingestion rate of the carbohydrate-rich diet is three times greater than that of the natural diet, the quantity of protein ingested in the former is only half that in the latter (Table 2). The value of lipids ingested is similar in both diets in this species, whereas the quantity of carbohydrates ingested is much greater in the carbohydrate-rich diet.

In the case of *R. decussatus*, however, the protein ingestion rate is the same for both diets whereas lipid ingestion doubles with the carbohydrate-rich diet, in which the quantity of carbohydrates ingested increases considerably.

Although total organic absorption efficiency is the same for both species when fed on the same diet, the efficiency with which proteins are absorbed by *V. pullastra* on the carbohydrate-rich diet is less than that of *R. decussatus*, and this, together with the smaller amount of proteins ingested by *V. pullastra*, as described above.
### TABLE 2.

<table>
<thead>
<tr>
<th>Diet</th>
<th>CR</th>
<th>(\text{IR}_{\text{O}})</th>
<th>(\text{IR}_{\text{P}})</th>
<th>(\text{IR}_{\text{C}})</th>
<th>(\text{IR}_{\text{T}})</th>
<th>(\text{AR}_{\text{O}})</th>
<th>(\text{AR}_{\text{P}})</th>
<th>(\text{AR}_{\text{C}})</th>
<th>(\text{AR}_{\text{T}})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natural</td>
<td>0.30 ± 0.10b</td>
<td>169.1 ± 57.3b</td>
<td>68.5 ± 23.2b</td>
<td>28.8 ± 9.8b</td>
<td>71.7 ± 24.3b</td>
<td>67.0 ± 5.7b</td>
<td>78.5 ± 1.7b</td>
<td>67.2 ± 3.8b</td>
<td>56.0 ± 3.0b</td>
</tr>
<tr>
<td>Carbohydrate-rich</td>
<td>1.28 ± 0.38b</td>
<td>991 ± 311.5b</td>
<td>69.4 ± 21.8b</td>
<td>789.9 ± 248.3b</td>
<td>131.8 ± 44.1b</td>
<td>37.6 ± 10.8b</td>
<td>77.1 ± 5.5b</td>
<td>30.9 ± 2.6b</td>
<td>56.9 ± 14.3b</td>
</tr>
<tr>
<td>Natural</td>
<td>0.46 ± 0.12b</td>
<td>253.9 ± 71.9b</td>
<td>102.9 ± 29.1b</td>
<td>4.3 ± 12.3b</td>
<td>107.7 ± 30.5b</td>
<td>71.2 ± 6.4b</td>
<td>82.1 ± 2.9b</td>
<td>68.7 ± 5.5b</td>
<td>61.7 ± 3.8b</td>
</tr>
<tr>
<td>Carbohydrate-rich</td>
<td>0.95 ± 0.24b</td>
<td>731.3 ± 196.2b</td>
<td>51.2 ± 13.7b</td>
<td>582.9 ± 156.4b</td>
<td>97.3 ± 26.1b</td>
<td>36.8 ± 8.0b</td>
<td>68.9 ± 4.7b</td>
<td>30.6 ± 2.2b</td>
<td>56.9 ± 10.8b</td>
</tr>
</tbody>
</table>

The table above shows the absorption rates of biochemical components in *Ruditapes decussatus* and *Venerupis pullastra* clams fed on different diets. The data are expressed as percentage absorption rates, and the values are given with standard deviations in parentheses. The effect of feeding on carbohydrate-rich diets is compared to feeding on natural diets to illustrate the increase in absorption efficiency.

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**CR**, standardized clearance rates, expressed in L h⁻¹ for a specimen of 1 g flesh dry weight; **IR**, ingestion rates expressed in μg h⁻¹ of total organic matter (**IR_{O}**), proteins (**IR_{P}**), carbohydrates (**IR_{C}**), and lipids (**IR_{T}**); **AR**, absorption efficiencies expressed as a percentage. **AR_{O}**, absorption rates, expressed in μg of biochemical component h⁻¹. 

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*Note:* The standard error in the values is given in parentheses. The data represent the mean of three replicates. The differences in absorption rates between the two species are statistically significant (ANOVA, p < 0.05). The index of comparison between the two species was calculated on the basis of the quotient *V. pullastra*/R. decussatus for each of the physiological rates, and this is shown in brackets.
with the natural diet, although quantitatively much greater in the case of *R. decussatus*. If we bear in mind that the food concentration, expressed as total particulate matter, is only 1.4 times higher in the carbohydrate-rich diet than in the natural diet, these quantitative differences would not account for the increase in ingestion observed. Furthermore, when expressed in terms of energy, the food content of both diets was similar (Table 1). Navarro et al. (2000) describe a feeding behavior similar to the one observed in our study, in *Argopecten purpuratus*. These authors describe an increase in ingestion of up to 6 times, just as is the case with *R. decussatus* in our study, when the microalgal diet is supplemented with carbohydrates obtained from potato starch. They also note a similar behavior when the diet is supplemented with lipids, but this time the ingestion rate increases by a factor of 8 in comparison with that obtained on a pure microalgal diet. They suggest the existence of chemical receptors on the gills or labial palps that are capable of detecting specific nutritional components of the diet and which would stimulate an increase in the clearance rate and hence the ingestion rate. The corn flour starch used in the present study consists of particles of a much greater density than the microalgal cells, or if expressed in terms of unit volume, the organic content of corn flour starch particles are some 4 times greater than that of microalgal cells (unpublished data). If we consider that bivalves are continuous filter-feeders, i.e., their digestive system is continuously occupied by food, then we can assume that the digestive capacity of both species, expressed in terms of the amount of organic matter that can be contained inside the digestive tract, must be much greater when the clams are fed on a carbohydrate-rich diet than when fed on a natural diet, because of the above-mentioned difference in particle density between the two diets. Given the great similarity of food concentration at which both diets were assayed (0.6–0.8 mg POM L\(^{-1}\)), the total occupation for an equal volume of the digestive system would be obtained by the existence of higher clearance rates for the carbohydrate-rich diet, which would account for the differences found between the ingestion rates for the two diets.

Total organic matter absorption efficiency is reduced by half in both species when they are fed on a carbohydrate-rich diet, owing to the considerable increase in the ingestion rate. The relation between food ingestion rate and absorption efficiency has been much studied in bivalves (Foster-Smith 1975, Navarro & Winter 1982, Bayne & Newell 1983, Beiras et al. 1993, Albentosa et al. 1996, Ibarrola et al. 1998) with a similar behavior being described in all instances, i.e., a decrease in absorption efficiency as the ingestion rate increases, principally because of the reduced transit time through the digestive tract and hence the reduced length of time during which food is exposed to the digestive enzymes. Navarro et al. (2000) also describe a decrease in absorption efficiency when the microalgal diet is supplemented with either carbohydrates or lipids, although to a lesser extent than that observed in the present study.

Total organic matter absorption efficiency within each diet was the same for both species, so the differences observed between species in absorption rates (Vp/Rd = 1.59 for the natural diet and Vp/Rd = 0.72 for the carbohydrate-rich diet) reflect the differences observed in the ingestion rate. Although there is a considerable decrease in the efficiency with which ingested food is absorbed when the clams are fed on a carbohydrate-rich diet, the total organic matter absorption rates are higher, even more so in the case of *R. decussatus* (Vp/Rd = 0.72). The absorption of total organic matter was three times higher in the carbohydrate-rich diet than in

**DISCUSSION**

**Physiological Parameters**

The most important difference observed between the feeding physiology of the two species of clam when fed on a natural diet are caused by the ingestion rates. According to the results of our study, organic ingestion rates in *V. pullastrea* are 50% higher in *R. decussatus* (Table 2; Vp/Rd = 1.50), which when taken together with the slightly higher food absorption efficiency in *V. pullastrea* gives a total organic absorption rate for this species that is almost 60% higher than that of *R. decussatus* (Vp/Rd = 1.59). This difference in energy absorbed is in consonance with the findings of other authors (Pérez–Camacho 1980, Beiras et al. 1993, Albentosa et al. 1996, Laing et al. 1987, Laing & Child 1996), who in their studies note that both growth and food consumption rates in *R. decussatus* are lower than those observed in other venerids such as *V. pullastrea* or *Ruditapes philippinarum*.

When the clams are fed on a carbohydrate-rich diet, important differences can also be observed in the feeding behavior of the two species, although of an opposite nature to those described for the natural diet. In these circumstances, the ingestion rate for *R. decussatus* when fed on a carbohydrate-rich diet is higher than that observed for *V. pullastrea*, giving us in this case an index of Vp/Rd = 0.74. An increase in ingestion is observed in both species when fed on the carbohydrate-rich diet, this increase being of the order of 6 and 3 times greater in *R. decussatus* and *V. pullastrea*, respectively. It is therefore true to say that the effect of the diet is the same in both species, i.e., an increase in ingestion when compared
the natural diet for *R. decussatus*, whereas in the case of *V. pullastra* this increase was only 1.5 times greater.

**Absorption of Biochemical Components**

There are few references in the literature to the process of absorption of the various biochemical components of the diet in bivalves (Kreeger & Langdon 1994, Ibarrola et al. 1996, 1998), particularly when the biochemical composition of the diet differs as much as it does in the present study. Ibarrola et al. (1998), in studies of specimens of *Cerastoderma edule* fed on diets consisting of microalgae and sediment in varying proportions (some of which are comparable with the natural diet assayed in our study), show that the most efficiently absorbed biochemical component in high quality diets (i.e., diets with the highest proportion of organic matter) are carbohydrates, whereas in low quality diets lipids are the most efficiently absorbed component. The authors attribute this high rate of carbohydrate absorption in high quality diets to an increase in the activity of certain carbohydrates to be found in the digestive gland. Protein absorption efficiency, however, remains unaffected by the quality of the diet. In our study, on the other hand, the biochemical component that is most efficiently absorbed by both species is protein, regardless of diet. This discrepancy may be due to interspecies differences between enzyme production in the digestive systems of cockles and clams, or also to the different biochemical composition of the microalgae used in the two studies. The high protein content (63.9%) of the microalgal portion of the diets assayed by Ibarrola et al. (1998) when compared to the protein content of the two diets used in the present study (40.5% for the natural diet and 7.0% for the carbohydrate-rich diet) may well account for the differences in protein absorption efficiency registered between the two studies.

The effect of diet on the feeding behavior of the two species in our study, i.e., the increase in ingestion and the resulting increase in absorption, allows *R. decussatus* to compensate for the nutritional deficiencies of the carbohydrate-rich diet, whereas *V. pullastra* seems unable to compensate fully for these deficiencies because it does not maintain the same level of protein absorption as observed in the natural diet. This latter level of absorption can be taken to be sufficient for this species, because it is a reflection of the conditions found in its natural habitat. If we consider that protein absorption is of fundamental importance for all organisms, because proteins are the source of necessary essential amino acids in the biosynthetic routes in the metabolism, this leads us to suppose that *V. pullastra* has a lesser capacity to respond to diets with a high carbohydrate content than does *R. decussatus*, which may be an indication of the existence of different metabolic routes in the two species.

Studies that have been performed by our research group (reviewed by Labarta et al. 1997) in connection with feeding behavior, the biochemical composition of body tissues, and the nutritional requirements of the two species of venerid studied in the present work suggest that lipid demand is higher in *V. pullastra* than in *R. decussatus*, whereas carbohydrate demand is higher in the latter than in the former, provided that there is sufficient protein in the diet. This may be related to the mechanism by which each species adapts to its specific habitat: *R. decussatus*, which characteristically inhabits the inter-tidal zone and is subject to periods of emersion as a result of the tidal cycle, would possess an anaerobic metabolism in which carbohydrates are a more appropriate source of energy than lipids. *V. pullastra*, on the other hand, a species that is permanently submerged because of its subtidal habitat, would not have these same nutritional requirements, which are more appropriate to an anaerobic metabolism, and would instead find lipids to be a more relevant source of energy, since they are the appropriate fuel for the aerobic routes of the metabolism. In our experiment both species were exposed to a completely unbalanced diet that contained a very high proportion of carbohydrates at the expense of protein and lipids. Both species responded in a similar manner, in qualitative terms, showing a considerable increase in ingestion which allowed them to counter the low protein content (proteins being an essential component of the diet) of the unbalanced diet. In quantitative terms, however, there are major differences between the two species: *R. decussatus* is able to maintain protein absorption levels, and even manages to double the quantity of lipids absorbed, whereas *V. pullastra* is unable to keep protein absorption at the same level, registering a 60% decrease, and is barely able to maintain lipid absorption. These results would appear to reinforce the previously mentioned hypothesis regarding metabolic differences between the two species.

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**LITERATURE CITED**


