

Effects of environmental variables on burial depth of two infaunal bivalves inhabiting a tidal flat in southern Chile

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The annual pattern of burial depth in natural populations of the infaunal bivalves *Tagelus dombeii* (Tellinacea) and *Venus antiqua* (Veneracea) is described in relation to annual food availability in both the water column and the sediment and abiotic factors (temperature and salinity) at Coihúin tidal flat, in southern Chile. A field experiment in which burial depth was measured *in situ* each month (over 14 months), with the aid of a fixed-length nylon thread attached to the shell. For *T. dombeii* the results showed a significant increase in burial depth with increasing bivalve size and syphon weight. *Tagelus dombeii* had a mean burial depth of 17.5 cm, which was three times more than in *V. antiqua* (5.30 cm). The burial depth dynamics for both species displayed a strong correlation with food availability in the water column. Approximately 60% of the variability in burial depth in *T. dombeii* and *V. antiqua* was explained by concentration of chlorophyll-*a* in the water column. Food concentration on the sediment surface did not effect burial depth, i.e. deposit feeding seems to be of minor significance in either species.

INTRODUCTION

Syphon length in bivalves has been directly related to burial capacity, and constitutes a good predictor for strategic response to various habitat characteristics. As bivalves must usually maintain direct contact with the water column, from which they obtain both oxygen and food, species with slender bodies and long syphons have the capacity to reach greater depths than animals with short syphons and more rounded body shapes. Infaunal bivalves present different patterns of burial depth and recently this parameter has been utilized for evaluating different strategies in the ecology of bivalves, on an intra-specific level (feeding mode) as well as in interactions with other species (e.g. predation, competition). Burial depth may be influenced by internal (ecophysiological) and environmental factors, such as season (Zwarts & Wanink, 1989), body condition (Zwarts, 1986), tidal movements (Roberts et al., 1989), water flow (Levinton, 1991), sediment transport (Levinton, 1991), predatory pressure (Zwarts & Wanink, 1989), and extreme temperature (Ratcliffe et al., 1981), and may also vary between locations (Zwarts & Wanink, 1989). Larger infaunal organisms tend to be buried deeper than smaller conspecifics. Zaklan & Ydenberg (1997) indicated that increased burial depth enhanced the survival of *Mya arenaria*, but reduced their feeding rate. In addition, larger individuals were able to feed more rapidly than small individuals at any depth, thus maximizing their fitness.

Members of the superfamily Tellinacea show the largest repertoire of feeding strategies, ranging from strictly suspension feeders to primarily deposit feeders. Some tellinaceans like the suspension feeding *Macoma balthica* and *Scrobicularia plana* can demonstrate facultative deposit

feeding, permitted by their functional morphology (Yonge, 1949; Gilbert, 1977; Zwarts & Wanink, 1989), but this depends on the interaction of both sediment organic content and seston concentration (Hummel, 1985; Olafsson, 1986).

The tellinacean *Tagelus dombeii* (Lamarck, 1818) (Tellinacea: Solecurtidae) inhabits coastal areas from tidal flat habitats to the subtidal zone. This species is considered a facultative deposit feeder due to the characteristics of its functional morphology: a great portion of mantle cavity is allocated to the palps (Villaroel & Stuardo, 1977), which are believed to sort and reject coarse sand grains (Hughes, 1969); the presence of large separate syphons; and a strong muscular foot. Further laboratory observations (Clasing et al., 1995), showed that the inhalant syphon of this species adopts a position typical of deposit feeding in the absence of a suspended food supply. In contrast, *Venus antiqua* King & Broderip, 1835 (Veneracea: Veneridae) is considered to be a strict suspension feeder, and does not extend its short and fused syphons above the sediment surface. Growth, gonadic maturity, gamete emission, and recruitment of this species in southern Chile occurs in the period of high food supply in the environment. This species reduces its metabolism during the rest of the year (Navarro et al., 1993; Clasing et al., 1994; Stead et al., 1997).

We hypothesized that burial depth for suspension feeding species should be closely coupled to pelagic primary production than would be the case for facultative deposit feeders. Using *V. antiqua* and *T. dombeii* as models, we tested this prediction. We compared the temporal variation of burial patterns of different size-classes of *V. antiqua* and *T. dombeii* coexisting in the same community, in relation to the annual cycle of sediment characteristics,

Table 1. Linear regression analysis to evaluate the significance between size and syphon weight, and body weight and syphon weight.

| Species | N | Syphon weight = a×size ^b | | | | Syphon weight = a+b×body weight | | | |
|------------------------|-----|-------------------------------------|-----------|----------|----------|---------------------------------|-----------|----------|----------|
| | | Slope | Intercept | <i>r</i> | <i>P</i> | Slope | Intercept | <i>r</i> | <i>P</i> |
| <i>Tagelus dombeii</i> | 100 | 0.0393 | 2.2401 | 0.6514 | <0.0001 | 19.3020 | 5.4218 | 0.7371 | <0.0001 |
| <i>Venus antiqua</i> | 100 | 0.0661 | 0.6017 | 0.6925 | <0.0001 | 11.351 | 2.5018 | 0.6481 | <0.0001 |

a, intercept; b, slope.

Table 2. Textural characteristics of total sediment and sand fraction proceeding from the tidal flat of Coihuin.

| Samples | September 1996 | | | | November 1996 | | | | April 1997 | | | October 1997 | | |
|-----------------------|----------------|-------|-------|-------|---------------|-------|-------|-------|------------|-------|-------|--------------|-------|-------|
| | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 1 | 2 | 3 |
| Total sediment | | | | | | | | | | | | | | |
| % gravel | 0.97 | 4.78 | 3.55 | 7.08 | 3.19 | 4.33 | 4.66 | 6.01 | 2.36 | 4.29 | 5.32 | 0.97 | 4.78 | 3.55 |
| % sand | 98.67 | 95.05 | 96.07 | 92.69 | 95.97 | 95.27 | 94.53 | 93.70 | 96.48 | 94.25 | 92.70 | 98.67 | 95.05 | 96.07 |
| % mud | 0.035 | 0.023 | 0.037 | 0.037 | 0.027 | 0.034 | 0.059 | 0.060 | 1.04 | 1.36 | 1.53 | 0.035 | 0.023 | 0.037 |
| % biogenic aggregates | 0.32 | 0.14 | 0.29 | 0.19 | 0.83 | 0.37 | 0.75 | 0.21 | 0.12 | 0.10 | 0.45 | 0.32 | 0.14 | 0.29 |
| % organic matter | 6.31 | 2.82 | 2.62 | 0.72 | 2.61 | 2.45 | 2.62 | 0.72 | 0.84 | 0.93 | 1.03 | 6.31 | 2.82 | 2.62 |
| Sand fraction | | | | | | | | | | | | | | |
| Mean size ϕ (x) | 1.00 | 0.55 | 0.78 | 0.52 | 0.94 | 0.55 | 0.99 | 0.71 | 0.84 | 0.56 | 0.85 | 1.00 | 0.55 | 0.78 |
| Sorting (SD) | 0.93 | 0.70 | 0.77 | 0.74 | 0.92 | 0.78 | 0.83 | 0.88 | 0.79 | 0.70 | 0.75 | 0.93 | 0.70 | 0.77 |
| Skewness (Sk) | 3.79 | 0.47 | 0.13 | 0.99 | 0.29 | 0.70 | 0.31 | 0.77 | 0.13 | 0.68 | 0.20 | 3.79 | 0.47 | 0.13 |
| Kurtosis (K) | 31.98 | 2.97 | 2.48 | 3.70 | 2.22 | 3.33 | 2.55 | 3.02 | 2.45 | 3.46 | 2.76 | 31.98 | 2.97 | 2.48 |

abiotic factors, and food concentrations. In addition, the possible duality of suspension- and deposit-feeding behaviour of *T. dombeii* was estimated using variations in its burial depth with respect to food availability.

MATERIALS AND METHODS

Field experiments

The burial depth experiments were carried out at the Coihuin tidal flat, Puerto Montt, southern Chile (41°29'S 72°54'W), between September 1996 and October 1997, using the species *Venus antiqua* (Veneracea, Veneridae) and *Tagelus dombeii* (Tellinacea, Solericutidae). The method described by Zwarts (1986) was used, in which a nylon thread with a numbered tag is attached to the shell. *Venus antiqua* and *T. dombeii* individuals of different sizes (N=200) were marked and allowed to bury within an experimental area. Burial depths were measured *in situ*, every month, using a ruler to the nearest 1 mm. Measurements were made during low tide (with overlying water), since intertidal deposit feeders only protrude their syphons far from the syphon hole at low tide, avoiding frequent intertidal flat predators (fish, crabs) which arrive during high tide (Hughes, 1969).

Morphometric and gravimetric variables

For each species, 100 individuals of all size-classes were collected during September 1997 (austral spring), from the

Coihuin tidal flat. The length of the bivalves was measured along the antero-posterior axis using vernier callipers (Fowler Silvac Ultra-Cal Mark III) to the nearest 0.01 mm. The inhalant syphon of each clam was cut off and dried to a constant weight at 60°C for 48 h (constant weight), and thereafter combusted for 3–5 h at 500°C to obtain the ash free dry weight (AFDW) by difference. The same methods were applied for the rest of the flesh for both bivalve species.

Food supply and physical variables

Water sampling was carried out monthly at high tide in the water column, directly above the experimental sites. Available food (seston, chlorophyll-*a*, and phaeopigments) in the water column was estimated using the techniques described by Strickland & Parsons (1972). Water samples (1–2 l) were pumped from a distance 10 cm above the sediment surface and immediately prefiltered (pore size 333 μ m) to eliminate large zooplankton and debris, before filtration through prewashed, precombusted Whatman GF C filters (pore size 0.45 μ m) and the extraction of pigments was subsequently carried out in 90% acetone. In order to determine the food supply in the substratum, superficial sediment samples were obtained (5 mm depth) by means of the technique described by Anderson & Black (1980). The pigments were quantified following the recommendations of Strickland & Parsons (1972), where known volumes of sediment chlorophyll-*a* and phaeopigments are extracted with 90% acetone.

Salinity and temperature in the water column were measured *in situ* using a WTW LF 320 conductivity meter.

Substrate characteristics

Sediment samples were randomly obtained in triplicate from the experimental area, using a corer (diameter 3.5 cm) to a depth of 3 cm. The textural characteristics of sediment were determined through the wet method described by Anderson et al. (1981). The proportion of silt was determined by the pipette method (Folk, 1980), and the proportion of biogenic aggregates was determined by sonication of sand fraction for 30 min (Anderson et al., 1981).

Statistical analyses

All data were tested for normality and homogeneity of variances prior to analysis. Linear regression analysis was used to evaluate the significance of the relationships between variables (i.e. body size and syphon—body weight); linearization was achieved by log-transformation, when necessary. To test for differences in the composition of the substrate (different components), and the weight of the inhalant syphon between species, a one-way analysis of variance (ANOVA) was used. An analysis of covariance (ANCOVA) was used for the evaluation of the relationship between depth burial and body size, with the species as covariate. Forward stepwise multiple regression was used to identify the environmental variables that accounted for the most variability in burial depth. For this analysis we utilized raw data, i.e. 2515 and 2262 burial depth measures for *V. antiqua* and *T. dombeii*, respectively. The environmental variables used were: salinity, temperature, water column phaeopigments and chlorophyll-*a*, sediment phaeopigments and chlorophyll-*a*, and total and organic seston. Correlations for the variables are included in the model. These analyses were conducted for each species. Variables were added to the model only if the *F* statistic for the factor was >1.0 . Thus, significant regression models potentially up to eight environmental factors. All statistical analyses were conducted using STATISTICA version 5.0 (Statsoft, Inc., Tulsa, Oklahoma, USA).

RESULTS

Sediment characteristics

The intertidal sediment of Coihúin was predominantly sandy (93.81%) (Table 2). The content of mud (particles $<63 \mu\text{m}$ diameter) was low in Coihúin, with an annual average of 1.83% ($\pm\text{SD}$). The same pattern was observed in organic matter content (0.68%), and in the biogenic aggregates, which represented an average of 0.58% (Table 2). The composition of the sediment was excluded from the multiple regression analysis as it did not vary significantly between seasons (one way ANOVA, $P>0.05$, for different sediment components), and so the variations in the burial depth of the species cannot be attributed to a change in sediment components. Graphical analysis only emphasizes a smooth increase in organic matter in September of 1996 and October of 1997, reaching an

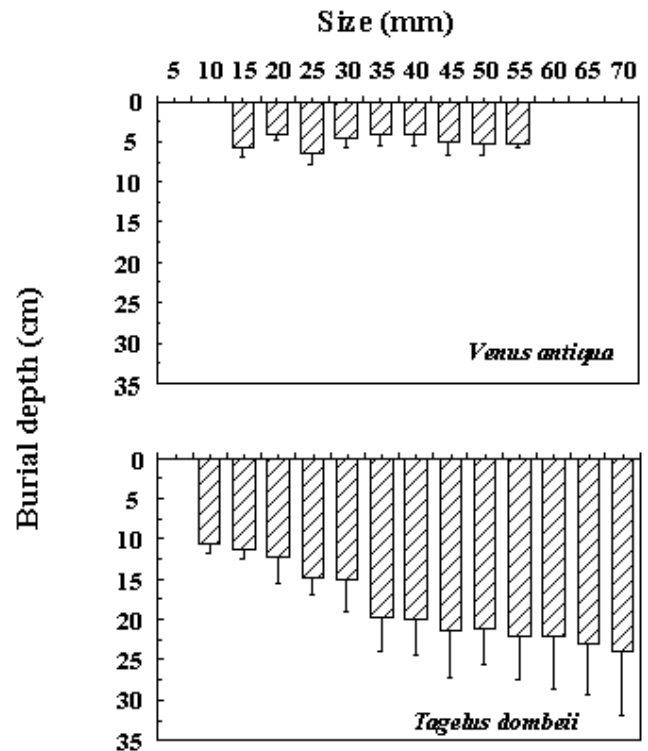


Figure 1. Relation between burial depth and clam size-class. Average values $\pm\text{SD}$.

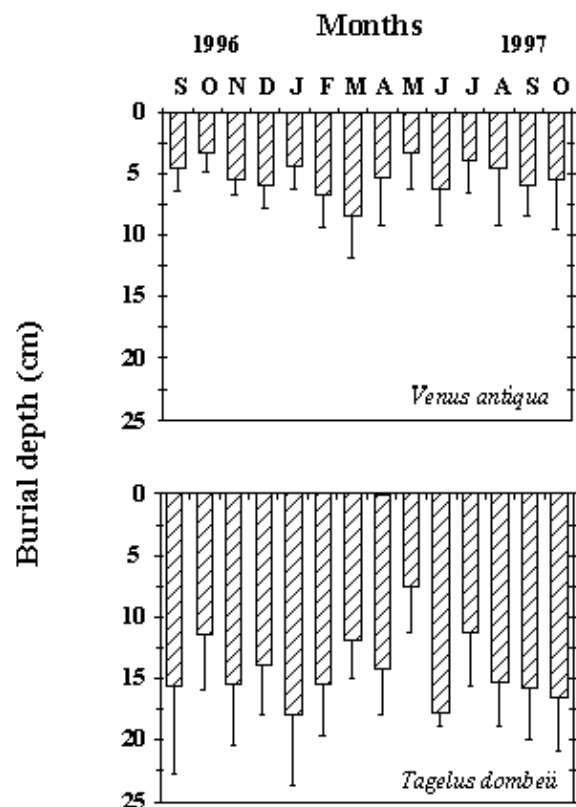


Figure 2. The mean burial depth (30–50 mm) of both bivalves throughout the study period in the Coihúin tidal flat. Average values $\pm\text{SD}$.

average of 3.30 and 3.91% of the composition of the sediment in all samples (Table 2). The sand mean size and particles sorting (0.83 y 0.84 phi, respectively) for the sediments of Coihúin coarse and moderate sized particles were selected (Folk, 1980).

Temperature and salinity

Water temperature followed a seasonal pattern at Coihúin, with the lowest values occurring during the winter months of 1997 (7°C), increasing towards the summer maximum in January (18.5°C) (Figure 3). Salinity values presented large fluctuations in concordance with a seasonal pattern: maximum in summer (32.5 psu, October 1997) and minimum in winter (24 psu, August

1997) (Figure 3) characterizing the area as typically euryhaline.

Food availability

In general, total seston displayed a seasonal pattern, increasing during autumn and winter months ($\sim 6 \text{ mg l}^{-1}$), and diminishing in the spring (3 mg l^{-1} in September) (Figure 4). The highest values were observed at the end of the spring of 1996 (16.7 mg l^{-1} in December) and in the winter of 1997 (10.5 mg l^{-1} in July) probably due to the effect of resuspension of bottom deposits due to harsh meteorological conditions during sampling. The organic fraction of seston presented a pattern similar to total seston, showing rises in autumn–winter (May and July),

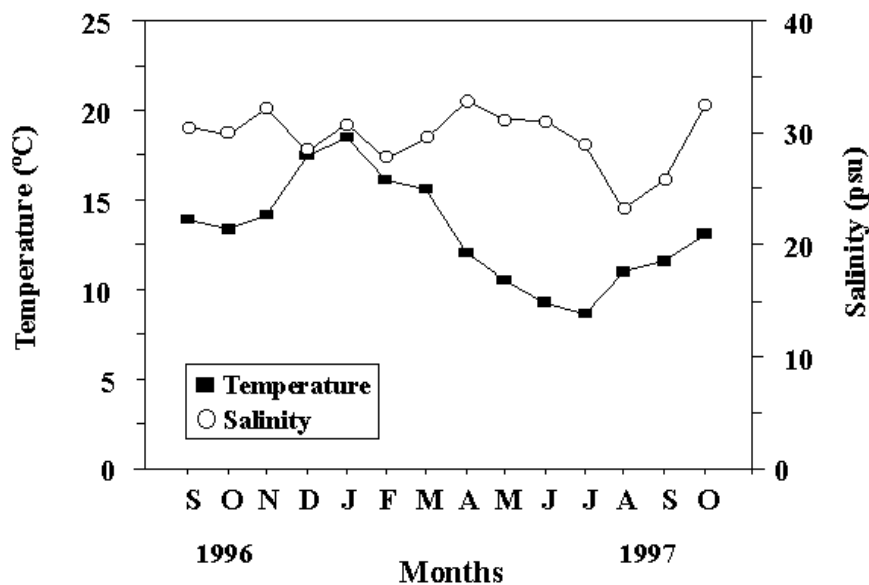


Figure 3. Seasonal fluctuation of salinity and temperature measured at the Coihúin tidal flat.

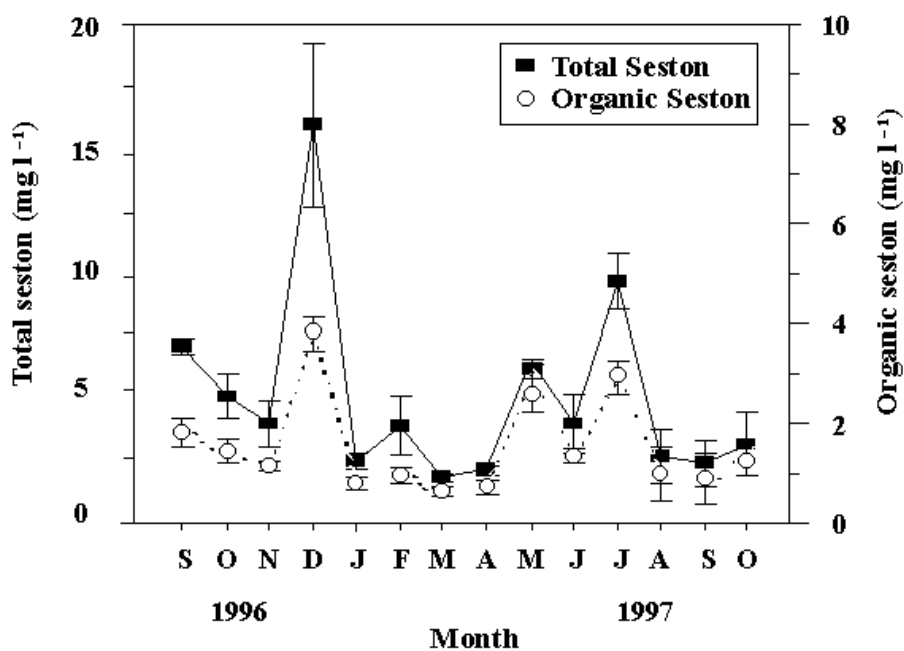


Figure 4. Average (\pm SD) concentrations of organic and total seston during sampling period in the Coihúin tidal flat.

where this fraction almost equalled total seston (Figure 4). The rest of the study period was characterized by a low total and organic seston concentration with values below 6 and 3 mg l^{-1} respectively (Figure 4).

Fluctuations in chlorophyll-*a* concentrations in Coihuín presented an unusual pattern for the area, as it reached maximum and minimum concentrations during autumn and winter months (May 1997, $17.5 \mu\text{g l}^{-1}$; April 1997 $0.5 \mu\text{g l}^{-1}$) (Figure 5). During late spring of 1996 and summer of 1997 (September to January) chlorophyll-*a* concentrations reached a peak of $4 \mu\text{g l}^{-1}$, after which concentrations decreased (Figure 5). Concentrations of phaeopigments were stable, with low values in spring and summer ($0.3 \mu\text{g l}^{-1}$ mean) and some non-significant high values during winter ($2 \mu\text{g l}^{-1}$ in July) (Figure 5). Pigment concentrations in the sediment show an increase in both pigments from early spring (September) 1996 and towards the summer, reaching maximum chlorophyll-*a* and phaeopigment values of 7.53 and $3.96 \mu\text{g g}^{-1}$,

respectively (Figure 6). A comparison of Figures 5 & 6 reveals a lag of approximately one month in pigment content of the sediment relative to pigments contained in the water column. In 1997 an increase of chlorophyll-*a* was observed towards the end of autumn (with a maximum in May of $5.47 \mu\text{g g}^{-1}$), and another maximum was observed in the spring ($4.15 \mu\text{g g}^{-1}$ in September) (Figure 6), this pattern is consistent with the pigment concentrations of the water column (see Figure 5).

Animal size–syphon weight relationship and burial depth

The length of individuals ranged between 5 and 55 mm in *Venus antiqua* and from 5 and 70 mm in specimens of *Tagelus dombeii*. There was a significant correlation between syphon weight and individual length for both species (Table 1). Inhalant syphons were significantly heavier in equally sized *T. dombeii* compared to *V. antiqua* (one way ANOVA, $F_{1,195}=4.182$; $P<0.05$).

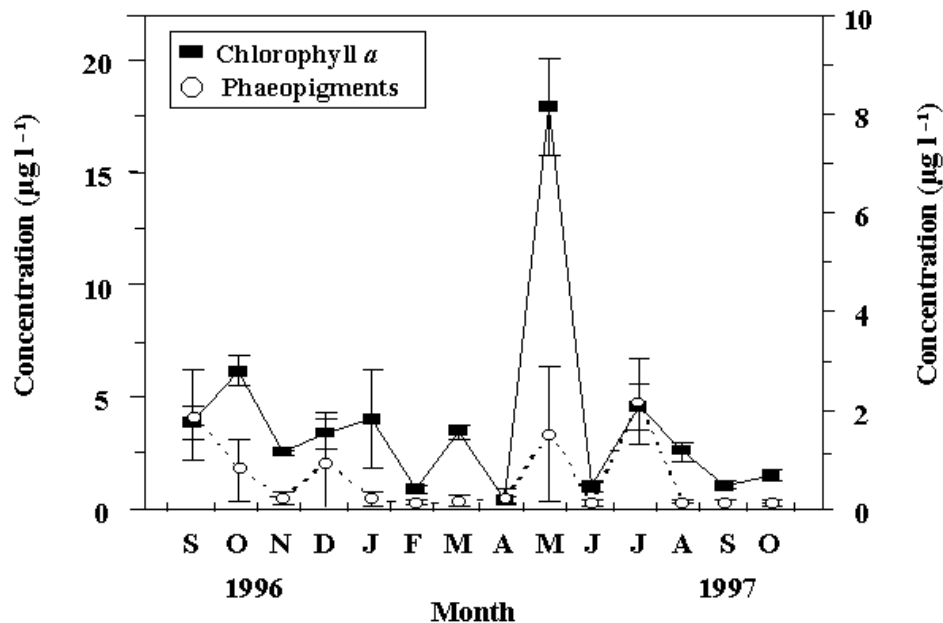


Figure 5. Water concentrations of chlorophyll-*a* and phaeopigment measured at the tidal flat of Coihuín. Values are averages (\pm SD).

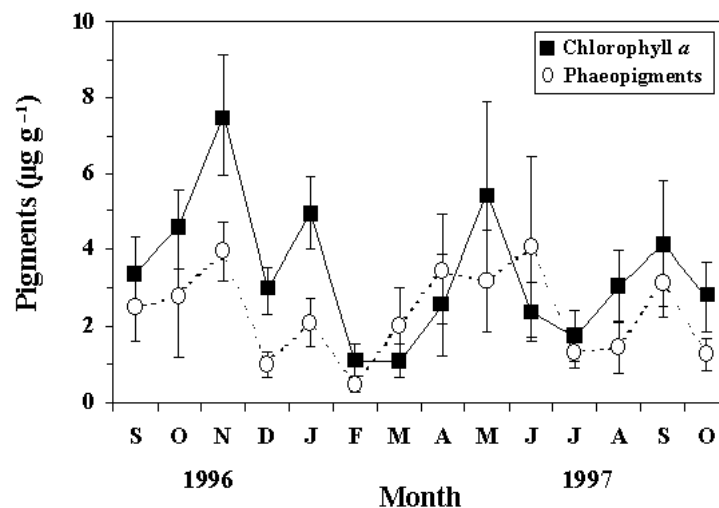


Figure 6. Pigment concentration in sediment during study period in the Coihuín tidal flat. Values are averages (\pm SD).

Table 3. Results of forward stepwise linear regressions using environmental variables as independent variables.

| Variables | Beta | SE | R ² | F | P | Variables included |
|-----------------------------|--------|--------|----------------|---------|--------|--------------------|
| <i>Tagelus dombeii</i> | | | | | | |
| Water chlorophyll- <i>a</i> | -0.710 | 0.1349 | 0.6093 | 18.7155 | 0.0014 | 1 |
| Water phaeopigments | -0.500 | 0.1476 | 0.7158 | 4.1239 | 0.0697 | 2 |
| Temperature | 0.382 | 0.1508 | 0.8266 | 6.3911 | 0.0299 | 3 |
| <i>Venus antiqua</i> | | | | | | |
| Water chlorophyll- <i>a</i> | -0.559 | 0.1852 | 0.3449 | 6.3187 | 0.0287 | |
| Water phaeopigments | -0.529 | 0.1852 | 0.6235 | 8.1410 | 0.0157 | |

Beta, standardized regression coefficient (for each variable); SE, standard error of Beta; R², multiple correlation coefficient (for all variables included in the model).

The results of these experiments clearly show a significant increase in burial depth with an increase in shell length for *T. dombeii* individuals, but this trend was not observed in *V. antiqua* individuals (one way ANCOVA, $F_{1,2115}=78.086$; $P<0.05$). In addition in some small size classes *V. antiqua* are able to bury more deeply than larger individuals (Figure 1). Therefore, monthly depth measurements were restricted to individuals in the 30–50 mm size range in both species. *Tagelus dombeii* had a mean burial depth of 17.5 cm which was three times more than *Venus antiqua* (5.30 cm).

Annual pattern of burial depth and relationship with environmental variables

A seasonal pattern was observed in both species in the Coihuín locality, with a greater burying depth towards the austral summer months (Figure 2). In autumn and winter months, both species showed minimum burial depths (3.01 and 7.50 cm in May for *V. antiqua* and *T. dombeii*, respectively) (Figure 2).

In both bivalves, burial depth and food availability (phaeopigments, chlorophyll-*a*) were significantly correlated (Table 3). When relating water temperature to burial depth, the latter increased towards the summer months for both species, reaching a maximum of 24 cm (February 1997) for *T. dombeii* and 9.5 cm (April 1997) for *V. antiqua*. However, temperature was only a significant variable in the model ($F>1$) for *T. dombeii*. According to the forward stepwise regression procedure, the subset of environmental variables which best predicts the burial depth in *V. antiqua* includes chlorophyll-*a* and phaeopigments in the water column (Table 3). Therefore, the Beta coefficient (standardized regression coefficient) for both variables is negative, but the highest food availability in the water column *V. antiqua* had a lower burial depth. The environmental variables included in the model for *T. dombeii* were food availability (chlorophyll-*a* and phaeopigments) and temperature (Table 3). In *T. dombeii* the 60% ($r^2=0.60$) of original variability in burial depth is explained by chlorophyll-*a* in the water column (Table 3).

DISCUSSION

Burial depth, shell size and syphon weight

Burial depth in *Tagelus dombeii* increased with both increasing shell length and dry weight of the inhalant

syphon, although with variations (see Figure 1). Our results are in general accordance with the burial depth of other bivalves from temperate zones (see Zwarts & Wanink, 1989). The difference between species is obviously due to morphological differences in the syphons of those *T. dombeii* being separated, longer and protrusible, as compared to the syphons of *Venus antiqua* which are fused and short. As expected, the relationship between shell length and burial depth was positive for the *T. dombeii* population from Coihuín (Figure 1), however the absence of a relationship for the *V. antiqua* population may represent, among other reasons, the effect of low predation risk. Burial depth in *T. dombeii* is more variable, as they are able to use part of their long syphon to graze the surface, but *V. antiqua* being a suspension feeder, must remain near the surface. These results are in agreement with Lin & Hines (1994) who propose that burial depth in deposit-feeding individuals is more variable than in suspension-feeders.

Venus antiqua invest ~2.3% of their body weight in syphon mass (see Table 1), while *T. dombeii* invest 6.2%. Our results show that syphon weight is a good predictor of burial depth, although in a facultative deposit feeder burial depth is more complex, since a part of their syphon is extended to graze the surrounding surface. However, *T. dombeii* at Coihuín does not rely on deposit feeding, as they are able to filter large quantities of food from the overlying water while their syphon is just at the surface (M.A.L., personal observation). This behaviour has also been observed in the bivalves *Macoma balthica* (L.) and *Scrobicularia plana* (da Costa) in the Dutch Wadden Sea (Hummel, 1985; Zwarts & Wanink, 1989).

Environmental factors and seasonal pattern of burying depth

Food availability (phaeopigments, chlorophyll-*a*) explains the majority of the annual patterns of burial depth of *Venus antiqua* and *Tagelus dombeii*. Lin & Hines (1994) reported that *Macoma balthica*, under laboratory conditions, achieved shallower burial depths with decreasing food concentrations in the water column. These results are in agreement with results found for both species studied on the Coihuín tidal flat, since individuals ascended in the sediment when the chlorophyll-*a* concentration in the water column reached the minimum (April 1997, $0.5 \mu\text{g l}^{-1}$). The ascent of *T. dombeii* under conditions of low food availability corresponds to the typical behaviour of species with dual feeding modes (Hummel, 1985;

Beukema & Cadée, 1991). When food availability in the water column is high, deposit-feeding species descend because their long syphons permit filtration of suspended food particles and a deeper position helps to prevent the risk of predation (Hines et al., 1990; Lin & Hines, 1994). When the chlorophyll-*a* concentration in the water column is the highest (May 1997, $17.5 \mu\text{g l}^{-1}$), the individuals of both species on the Coihúin tidal flat remained near the surface, suggesting a similar feeding behaviour. Preliminary results on clearance rates suggest that *T. dombeii* has a behaviour typical of suspension feeder, with clearance rates ranging between 1.1 and 2.8 l h^{-1} (J.M.N., unpublished data). These values fall in the range reported for equally-sized suspension feeding species, e.g. *Mytilus edulis* (Bayne & Widdows, 1978; Thompson, 1984), *Mytilus chilensis* (Navarro & Winter, 1982), *Cerastoderma edule* (Newell & Bayne, 1980; Navarro et al., 1991; Navarro & Widdows, 1997). Observations of syphon behaviour in the laboratory showed that *T. dombeii* does not extend its syphons over the sediment when offered a diet with abundant organic material deposited on the top layer of the sediment (J.M.N., unpublished data). This observation agrees with our results, which showed no relation between food availability in the sediment and burial depth. On the other hand, burial depth in *V. antiqua*, a typical suspension feeder, is affected mainly by food availability. High clearance rates have been reported for individuals of *V. antiqua*, showing a great capacity for filtering food particles from the water column (Clasing et al., 1998).

Nevertheless, there are notable differences when comparing burial depth in *V. antiqua* with a population of the same species on the intertidal plain at Yaldad (Chiloé Island, southern Chile) (M.A.L., unpublished data). The individuals at Yaldad bury deeper and remain at a constant depth throughout the year (average of 8 cm). The grain size of the sediment at Coihúin tidal flat is twice that of Yaldad (Jaramillo et al., 1998), allowing easier movement and burial for both small and large individuals. Similarly, the presence of more fine sand and mud at the Yaldad tidal flat makes burial dynamics more difficult, as the sediment is more compact. This inter-population comparison emphasizes that substrate characteristics are of great importance in explaining and predicting the depth of internment for the studied species.

Burying deep in the sediment is one of the few defensive mechanisms against predators for a thin shelled bivalve like *T. dombeii* (Haddon et al., 1987; Lin & Hines, 1994). We observed many broken shells of *T. dombeii* on the tidal flat, presumably this mortality is caused by predation of flatfish, skates, and crabs which inhabit the area (M.A.L., personal observation). Also, during low tide there are a great number of bird predators (e.g. the oystercatcher, *Haematopus palliatus* Temminck 1820; shorebirds, *Numerius phaeopus* (Linné) 1758, *Limosa haemastica* (Linné) 1758; and at least three species of gulls) which feed on benthic bivalves, especially *T. dombeii* (von Meyer, personal communication). These observations explain, in part, why *T. dombeii* make such deep burrows as their average burial depth of 18 cm practically eliminates predation risk. However the small size-class (<30 mm) are exposed to a higher predation risk which is reflected in increased rates

of natural mortality (see Jaramillo et al., 1998). The strategy of *T. dombeii* to avoid predation could be quick growth, which effectively occurs (Clasing et al., 1998), with an exponential increase in syphon biomass, making a greater burial depth possible. This kind of strategy has been reported in other thin-shelled bivalves from temperate zones (Zwarts & Wanink, 1989). *Venus antiqua* are able to stay near the surface because they have heavy, coarse shells, making predation by invertebrates and vertebrates less likely since handling time increases with shell calcification (making them a less profitable food). We assume that predation rates are different among our study species, however, we cannot provide data to substantiate this assumption.

Levinton (1991) suggested that hydrodynamic conditions are a major determinant of feeding behaviour and burial depth. On the tidal flat at Coihúin water movement probably affects burial depth, since water flow is continuous and variable within a narrow time scale (between tides). However, we report on an annual pattern of burial depth in natural populations, which is governed by factors working on broad temporal scales, such as, food availability and temperature. Therefore, according to previous studies and our results we conclude that a complete understanding of burial depth dynamics in infaunal bivalves should consider many factors which act simultaneously on many spatial and temporal scales.

Feeding mode of Tagelus dombeii

Our experiment indicates that burial depth in *T. dombeii* is directly affected by food availability in the water column. If *T. dombeii* behaved like a deposit feeder, it would decrease its burial depth to syphon food off the surface during low productivity months (e.g. austral winter 1997). This does not occur, and the annual pattern of burial depth in *T. dombeii* is very similar to that of *V. antiqua*, varying only in depth. These results suggest that *T. dombeii* from Coihúin does not alternate between feeding modes (deposit vs suspender feeder), preferring the behaviour of a typical suspension feeding bivalve. However, the low organic content in the sediment at Coihúin, with high coarse sand percentages supports the idea that *T. dombeii* in Coihúin should behave like a suspension feeder. Olafsson (1986) reported that *M. balthica* individuals from sandy sediments behaved like suspension feeders while individuals from localities rich in organic content behaved like deposit feeders. Individuals of *T. dombeii* from populations at Coihúin (with low organic matter and mud, see Table 1) displayed a suspension feeding mode; probably adapted to local conditions. However populations of *T. dombeii* in localities with high organic matter and fine sediment probably show a duality in feeding mode. We do not have data to verify this hypothesis, although further investigations could test this possibility.

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