Natural mortality of the cockle *Cerastoderma edule* (L.) from the Ria of Arousa (NW Spain) intertidal zone

Mortalidad natural del berberecho *Cerastoderma edule* (L.) en la zona intermareal de la ría de Arousa (NO de España)

José M. Parada¹ and J. Molares²

¹Centro Tecnolóxico do Mar. Apdo. 13. Vilanova de Arousa. 36.620. Pontevedra, Spain
²Centro de Investigacións Mariñas. Eduardo Cabello S/N. Vigo. 36208. Pontevedra, Spain
paradajm@gmail.com

**Resumen.**- El berberecho *Cerastoderma edule* (L.) se asienta preferentemente, en áreas estuáricas intermareales, enterrado bajo los primeros centímetros del sedimento. En este ambiente la densidad de sus poblaciones se ve afectada no sólo por diferentes interacciones biológicas, sino también por los fenómenos meteorológicos, sobre todo durante la bajamar. A lo largo de siete años se estudió la dinámica de poblaciones del berberecho y su pesquería en dos bancos intermareales de la ría de Arousa (NW de España). En este periodo se ha analizado la relación entre la mortalidad de juveniles y la densidad total de la población, la precipitación y la temperatura atmosférica. El modelo de regresión múltiple que incluye las cuatro variables estudiadas explica satisfactoriamente las mortalidades observadas entre los periodos comparados. Este modelo permite estimar la mortalidad natural a partir de variables relativamente fáciles de obtener, y constituye una herramienta de cálculo útil para reajustar las estimaciones del tamaño de los stocks en función de las condiciones meteorológicas registradas.

Palabras clave: Marisqueo, bivalvos, meteorología, densodependencia

**Abstract.**- The cockle *Cerastoderma edule* (L.) settles preferably in intertidal estuarine zones, buried under the uppermost centimetres of the sediment. Owing to this specific environment, the density of its populations is affected not only by biotic interactions, but also by meteorological phenomena, especially during low tide. A study was conducted over the course of seven years on the population dynamics and fishery of the cockle in two intertidal beds of the Ria of Arousa (NW Spain). The relationship between mortality and the population total density, precipitation and atmospheric temperature was analyzed during this period. The multiple regression model that includes the four variables under study provides a satisfactory explanation for the mortalities observed during the periods being compared. This model allows us to estimate the natural mortality by using variables that are relatively easy to obtain. It also proved to be a useful computational tool for readjusting the estimations of stock sizes in light of the meteorological conditions recorded.

Key words: Shellfish harvest, bivalves, meteorology, density-dependence

**Introduction**

In Galicia (NW Spain) shellfish is commercially harvested using traditional methods by some 13 000 shell-fishermen (CES 2001), with an annual production ranging from 6 000 to 9 000 t for the period 1997-2005. The cockle *Cerastoderma edule* (Linnaeus, 1758) accounted for 40% of the total production in tons with a mean value of about 13 million euros annually between 2001 and 2005 (data derived from the Plataforma Tecnolóxica da Pesca. Consellería de Pesca e Asuntos Marítimos. Xunta de Galicia (CPAM-XG)). Fishermen’s unions are responsible for the management of shellfish beds, the rights to which are granted by the Galician Government under Administrative Authorization. Each year, at the end of October, the unions must present an annual harvest plan to the Regional Government, also including a fishery strategy for the next year. The plan is based on the production and economic results of previous harvesting seasons, as well as on stock estimates made in September and October and the average mortality expected during the following year.

The occasional decline in the stock owing to massive mortalities gives rise to much controversy and a large number of complaints among the shell-fishermen’s unions. Therefore, a tool to discriminate between mortalities caused by «normal» conditions and those related to exceptional causes would be necessary. Moreover, decision-making in shellfish harvest management requires computational tools that will enable the readjustment of stock estimations obtained by annual population sampling depending on the environmental conditions recorded.

*C. edule* is characterized by marked interannual variability in both population density and biomass (Coosen *et al*. 1994, Beukema & Dekker 2006). Many
authors have linked these fluctuations to a broad range of factors, that may be autoecological, e.g. density, competition for space, adult-recruit interactions and the animal’s age; synecological, e.g. predation (Carcinus maenas (L.), Crangon crangon L., Pleuronectes platessa L., and Haematopus ostralegus L.); and environmental, e.g. rainfall, temperature, emersion time, etc. (Boyd 1971, Ansell et al. 1981, Ducrotoy et al. 1991, Meire 1993, Guillou & Tartu 1994, Honkoop & van der Meer 1998, Johnstone & Norris 2000, Strasser et al. 2001, Declaux et al. 2002, Philippart et al. 2003, Beukema & Dekker 2006). A detailed overview of the influence of various factors on successful recruitment, growth and mortality rate, can be found in Kristensen (1958) and Hancock & Urquhart (1965).

Most of the fishermen’s unions cannot afford to have the water temperature and salinity monitored. On the other hand, it is quite easy nowadays to access meteorological data, such as rainfall or atmospheric temperature, from meteorological stations situated near the shellfish beds. The small size of the siphons of C. edule obliges the animals to bury themselves very near the surface, causing them to be in close contact with the water layer immediately above the sediment (Ansell et al. 1981), which leaves them poorly sheltered from atmospheric conditions during low tide. In this way, available data such as atmospheric temperatures and rainfall could be used as indirect parameters to explain part of the natural mortality observed in shellfish beds. On the other hand, most of the fishermen’s unions engage a biologist whom they consult for advice on adaptive management and to estimate stock density. Density has been described by many authors –and not without controversy– as being one of the factors that could affect both the growth and mortality of cockles and other bivalves in relation to intraspecific competition and the incidence of predators (Montaudouin & Bachelet 1996).

The goal of this paper is to show the relationship found between the natural mortality observed in cockle stock and the data related to temperature, rainfall and density collected during the seven year period that a fishermen’s union was receiving expert advice. When an extraordinary mortality event occurs, the application of this relationship might be able to determine if this mortality is truly an extraordinary event, on the basis of temperature, rainfall and density, or if it is due to other factors that have not been studied here.

Material and methods

This study was conducted at two sites (Barraña and Mañóns) located in the inner Ría of Arousa, less than 2 km apart (Fig. 1). From these two beaches important shellfish beds with an area of 780750 and 249000 m², respectively, are harvested. The slope is similar in both beds (from 0.7 to 1.9%) and the tidal level ranges from 0 to 2.5 m over the maximum low tide. Following the procedure described by Buchanan (1984) for sediment with less than 5% silt and clay content, the sediment granulometry was primarily sandy, with a wide range of gravel (particles greater than 2 mm in diameter) from <1% to >40% in weight, also containing some silt and clay (<63 μm in diameter) that did not reach 3% in weight. Meteorological conditions are similar at both sites. Mean accumulated rainfall in autumn-winter is 1012 mm, average temperature 14.6ºC and the thermal amplitude 12.6ºC (Martínez Cortizas et al. 1999). In the autumn-winter period of 2000-2001, exceptionally heavy rainfalls were recorded (accumulated precipitation of 2862 mm). Following that winter, massive mortality of shellfish inhabiting both beaches occurred, and there was no harvest for one year. In addition to several clam species, mainly Tapes decussatus (L., 1758), T. philippinarum (Adams & Revé, 1850) and Venerupis senegalensis (Montagu, 1803), the cockle C. edule is the most important resource harvested from these beaches, with a maximum extraction of 461 t annually (CPAM-XG). These species are exploited by more than 300 shell-fishermen belonging to the Fishermen’s Union of Cabo de Cruz.

The density of the cockle standing stock was estimated in both beaches annually in September or October, as part
of the preparatory work needed to devise the exploitation plan for the Fishermen’s Union of Cabo de Cruz. Extra sampling campaigns were carried out for other research at both sites, Mañóns (March and May 1998 and November 2003) and Barraña (March and May 2003). Stratified samplings were designed for each beach. The strata were defined by means of a similarity analysis based on granulometric data. However, the boundaries of each stratum were fitted according to the sectors into which the beds had been previously divided for the organization and strategy of the harvest. Seven strata with a total of 81 sampling stations were established at Barraña beach. At Mañóns beach 4 strata were identified, among which 51 sampling stations were distributed (Fig. 2). Sampling was conducted during low tide with a small shovel and a metallic square. In each sampling station a 30 x 50 cm (0.15 m²) sample was collected down to 15 cm depth and then rinsed in a 4 mm mesh sieve. The specimens collected were counted to estimate average density and their anterior-posterior axis was measured to obtain frequency histogram size. Mean density was calculated by following the indications of Elliot (1977) and Krebs (1998) for stratified sampling of populations with a negative binomial distribution. Based on the frequency histogram size, age groups were identified through both Bhattacharya and NORMSEP procedures, found in the FiSAT II software by FAO-ICLARM.

The general expression used to calculate the finite natural mortality rate (m) of exploited populations between two consecutive samplings was:

\[
m = z - f
\]

where \( z \) is the natural mortality and \( f \) is fisheries mortality (King 1995) according to the expressions:

\[
z = 1 - \left( \frac{D_2}{D_1} \right)
\]

\[
f = \frac{D_c}{D_1}
\]

So, in this study \( m \) was calculated as:

\[
m = 1 - \left( \frac{(D_2 + D_c)}{D_1} \right)
\]

where \( D_1 \) is the mean density of the size groups present in the first sampling (Date 1 in Fig. 3), \( D_c \) is the mean density of individuals belonging to the groups in the next sampling (Date 2 in Fig. 3) and \( D_c \) is the density of individuals harvested estimated from catch data recorded during the implementation of the exploitation plan.

The implementation of the harvest plan involves the opening and closure of different sectors of the shellfish beds and requires the recording of data on the bed of origin, quantities harvested and the size of the individuals caught. The size of the individuals was recorded every time the exploitation changed sectors. These data were recorded at the shellfish market, by randomly sampling the catches and measuring the antero-posterior axis from a known number of cockles. Along with a size-weight relationship for \( C. \) edule and the surface of each bed harvested, these data allowed us to estimate the catch in terms of density (individuals m⁻²) following the procedure shown in Fig. 4. A size-weight relationship for the cockles from each beach was estimated by means of a regression.
between the antero-posterior length and fresh weight at the beginning of the study. A comparison of slopes between regressions was made before joining the two data sets to obtain only one regression for the two beaches. Through the size-weight regression, the routine data from size frequency were transformed into a frequency of weights for a number of known individuals (Fig. 4a). This allowed us to determine how many cockles comprised one kg in each recorded catch (Fig. 4b) and, then, to convert kilograms caught into individuals (c). Knowing the surface of the bed where the cockles were harvested allows knowing catches in terms of individuals per square meter from catches in individuals (d).

The finite mortality rate was converted to a natural mortality instantaneous rate (M) by means of the algorithm

$$M = \frac{M}{d}$$

Mean daily rainfall and atmospheric temperature data were provided by the weather station of the National Meteorology Institute located at the westernmost end of Barraña Beach (Fig. 2).

Different regression analyses were performed under the hypothesis that high density, amount of rainfall, low temperatures and/or high temperatures recorded between sampling campaigns might be related to the natural mortality observed in the cockle stock. The dependent variable was daily natural mortality and the independent variables were: the population density recorded at the first of each pair of samplings on the basis of which mortality was calculated; the accumulated rainfall (in mm) during that time period; and the highest and lowest atmospheric temperature taken from the averages of the daily temperatures recorded in the same period. The number of sampling pairs obtained to calculate the mortality was 11. The dataset used in this study included the samplings of stock assessments carried out from 1997 to 2004, except those from the autumn-winter of 2000-2001. The mass mortality of cockles after that winter was followed by a late recruitment, whose resulting cohort could not be included in its entirety in the sampling. Before carrying out the regression analysis, all the variables were log-transformed so that they could be fitted to a normal distribution. After the values were transformed, the relationship between each independent variable and the daily natural mortality instantaneous rate was examined. Both the linear and logistic model were tried to fit the natural mortality instantaneous daily rate to the four independent variables used. The logistic model was applied with the assistance of the Origin program (version 7). The expression of the logistic curve used was:

$$y = A_2 + \left(\frac{(A_1-A_2)}{1+(x-x_0)^P}\right)$$

where $y$ is the logarithm of the daily natural mortality instantaneous rate and $x$ is the logarithm of the corresponding variable. In this equation $A_1$ and $A_2$ represent the minimum and maximum values at which $y$ becomes asymptotic; $x_0$ is the value of $x$ at which $y$ acquires a value equal to half of the amplitude of the curve, i.e., the point midway between $A_1$ and $A_2$ and, lastly, $P$ is a power.

Finally, a multiple linear regression analysis was conducted with the assistance of the MINITAB program. The variance inflation factor (VIF) was calculated as a measurement of collinearity between the independent variables.
variables. According to Graybill & Iyer (1994), VIF is a scaled version of the multiple correlation coefficient between variable j and the rest of the independent variables, expressed as:

$$VIF_j = 1 / (1 - R^2_j)$$

where $R^2_j$ is the multiple correlation coefficient. A value greater than 10 is an indication of potential multicollinearity problems.

For the selection of the best variables to be included in the multiple regression model, the all-subset procedure was used following Graybill & Iyer (1994). According to these authors, $r^2$, $r^2_{adj}$, Mallow’s criterion (Cp) and the root mean squared error ($s$) were the criteria adopted to select the best subset model.

**Results**

No significant differences were found between the size-weight regressions for cockles from the two sites; therefore just one regression was enough to represent the size-weight relationship for both beds (Table 1).

The range of values corresponding to the daily natural mortality instantaneous rate fluctuated between 0.00194 and 0.00778. These values, along with those of the independent variables between each pair of sampling dates, are shown in Table 2.

The linear model only fitted the relation of total density (TD) and high temperature (HT) with natural mortality ($M_d$). These variables explained 42.3% and 31.3% of the variation in the natural mortality observed (Table 3). By contrast, with the logistic model, the relationship between the natural mortality rate and each of the variables had a significant correlation coefficient ($P<0.05$) in all cases.

**Table 1**

<table>
<thead>
<tr>
<th>Site</th>
<th>$a$</th>
<th>$b$</th>
<th>$r^2_{adj}$</th>
<th>SE</th>
<th>n</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mañón</td>
<td>-3.4961</td>
<td>3.0222</td>
<td>0.9895</td>
<td>0.051</td>
<td>423</td>
<td></td>
</tr>
<tr>
<td>Barraña</td>
<td>-3.2756</td>
<td>2.8994</td>
<td>0.9679</td>
<td>0.0427</td>
<td>215</td>
<td>0.0665</td>
</tr>
<tr>
<td>Mañón+Barraña</td>
<td>-3.4931</td>
<td>3.0335</td>
<td>0.9842</td>
<td>0.0548</td>
<td>638</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

**Table 2**

Pairs of compared samplings and values of variables obtained over the study period in the two beaches. ID, identifier; Md, daily natural instantaneous mortality rate; TD, total initial density of the population in individual per square meter (ind. m$^{-2}$); R, accumulated rainfall between sampling dates (mm); LT and HT, lowest and highest mean daily atmospheric temperatures recorded between sampling dates (°C). Dates indicate month and year of each pair of compared samplings

<table>
<thead>
<tr>
<th>ID</th>
<th>Beach</th>
<th>Initial date</th>
<th>Final date</th>
<th>$M_d$ (ind. m$^{-2}$)</th>
<th>TD (ind. m$^{-2}$)</th>
<th>R (mm)</th>
<th>LT (°C)</th>
<th>HT (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Mañón</td>
<td>10/1997</td>
<td>3/1998</td>
<td>0.00194</td>
<td>207</td>
<td>1238</td>
<td>5.75</td>
<td>16</td>
</tr>
<tr>
<td>3</td>
<td>Mañón</td>
<td>10/1998</td>
<td>10/1999</td>
<td>0.00778</td>
<td>1570</td>
<td>1633</td>
<td>6.00</td>
<td>26</td>
</tr>
<tr>
<td>4</td>
<td>Mañón</td>
<td>10/1999</td>
<td>10/2000</td>
<td>0.00592</td>
<td>493</td>
<td>1754</td>
<td>5.75</td>
<td>27</td>
</tr>
<tr>
<td>5</td>
<td>Mañón</td>
<td>9/2003</td>
<td>11/2003</td>
<td>0.00518</td>
<td>212</td>
<td>308</td>
<td>9.50</td>
<td>25</td>
</tr>
<tr>
<td>6</td>
<td>Barraña</td>
<td>10/1998</td>
<td>10/1999</td>
<td>0.00574</td>
<td>690</td>
<td>1656</td>
<td>6.00</td>
<td>26</td>
</tr>
<tr>
<td>7</td>
<td>Barraña</td>
<td>10/1999</td>
<td>10/2000</td>
<td>0.00646</td>
<td>780</td>
<td>1756</td>
<td>5.75</td>
<td>27</td>
</tr>
<tr>
<td>8</td>
<td>Barraña</td>
<td>10/2001</td>
<td>9/2002</td>
<td>0.00417</td>
<td>204</td>
<td>1245</td>
<td>2.50</td>
<td>23</td>
</tr>
<tr>
<td>9</td>
<td>Barraña</td>
<td>9/2002</td>
<td>3/2003</td>
<td>0.00712</td>
<td>544</td>
<td>1479</td>
<td>2.00</td>
<td>20</td>
</tr>
<tr>
<td>10</td>
<td>Barraña</td>
<td>3/2003</td>
<td>5/2003</td>
<td>0.00474</td>
<td>132</td>
<td>220</td>
<td>9.75</td>
<td>21</td>
</tr>
<tr>
<td>11</td>
<td>Barraña</td>
<td>10/2003</td>
<td>9/2004</td>
<td>0.00387</td>
<td>478</td>
<td>1647</td>
<td>5.75</td>
<td>27</td>
</tr>
</tbody>
</table>
Table 3

Values obtained for both linear and logistic models of the individual relationship between the log-transformed daily natural instantaneous mortality rates (Log(Md)) and the different independent variables (TD, total density; R, rainfall; LT, lowest mean atmospheric temperature; HT, highest mean atmospheric temperature); y, independent variable; x, dependent variable; a, constant of the linear model; b, slope; n, number of pairs of data; SS, sum of squares; r²adj, adjusted r-square; r, coefficient of correlation; P, probabilistic significance of the model; n.s., no significant probability; A1, A2, x0 and P, constants of the logistic model

<table>
<thead>
<tr>
<th>Log(Md)</th>
<th>y</th>
<th>x</th>
<th>a</th>
<th>b</th>
<th>n</th>
<th>SS</th>
<th>r²adj</th>
<th>r</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log(TD)</td>
<td>-3.3576</td>
<td>0.3977</td>
<td>11</td>
<td>0.1991</td>
<td>0.4230</td>
<td>0.6933</td>
<td>&lt;0.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Log(R)</td>
<td>-2.8108</td>
<td>0.1586</td>
<td>11</td>
<td>0.3557</td>
<td>-0.0310</td>
<td>0.2687</td>
<td>n.s.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Log(LT)</td>
<td>-2.1270</td>
<td>-0.2927</td>
<td>11</td>
<td>0.3347</td>
<td>0.0297</td>
<td>0.3560</td>
<td>n.s.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Log(HT)</td>
<td>-4.7007</td>
<td>1.7327</td>
<td>11</td>
<td>0.2370</td>
<td>0.3131</td>
<td>0.6179</td>
<td>&lt;0.05</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The initial density of the total population (TD) explained 27.8% of the variation in daily natural mortality. In the comparison between each pair of samplings (R), the accumulated rainfall explained 10.5% of the variation in the natural daily mortality estimated between them. The lowest mean daily atmospheric temperature (LT) explained 19.8% and the highest mean daily temperatures (HT) accounted for 9.8% of the variation. Parameter x0 of the logistic functions corresponds to the threshold starting at which mortality undergoes a rapid increase, exceeding the mean value recorded for the dataset used. This parameter was 2.5539, 3.1512, 0.7376 and 1.3809 for log (TD), log (R), log (LT) and log (HT) respectively (Table 3). Hence, by back logarithmic transformation, we would expect mortality higher than the mean when the initial density (TD) is greater than 469 ind. m⁻², the accumulated rainfall between samplings (R) is over 416 mm and mean daily temperatures below 5.5ºC (LT) or above 24ºC (HT) are recorded.

The values obtained for VIF, which were always less than 10, allowed us to rule out the existence of multicollinearity between the independent variables (Table 4). Table 5 shows the results of the all-subset procedure. The most promising multiple regression model was the one taking the four independent variables into account, followed by the one omitting the highest daily mean temperature (HT) and using the three remaining variables. The multiple linear regression model with the set of four independent variables (model 1) explained 78.5% of the variation in the daily natural mortality instantaneous rate between sampling dates. In this model, all of the variables made a significant contribution with the exception of the highest mean daily temperature (Table 6). The second multiple linear regression model (model 2) which only included the three variables that contributed significantly (total initial density, accumulated rainfall and the lowest mean daily temperature between samplings), explained 70.1% of the variation in the mortality rate (Table 7).

The relationship between observed and expected natural mortality in model 2 had a slope close to 1 and an adjusted r-square (r²adj) of 0.7215 (Table 8, Fig. 5).
Table 4

Multicollinearity analysis. Independent variables log transformed: total density, Log(TD); rainfall, Log(R); lowest mean atmospheric temperature, Log(LT); highest mean atmospheric temperature, Log(HT); $r^2$, coefficient of determination between each variable and the other three; VIF, Variance inflation factor

<table>
<thead>
<tr>
<th></th>
<th>Log(TD)</th>
<th>Log(R)</th>
<th>Log(LT)</th>
<th>Log(HT)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r^2$</td>
<td>0.6927</td>
<td>0.7227</td>
<td>0.4784</td>
<td>0.3711</td>
</tr>
<tr>
<td>VIF</td>
<td>3.2541</td>
<td>3.6065</td>
<td>1.9172</td>
<td>1.5901</td>
</tr>
</tbody>
</table>

Table 5

All subsets regression. The letter X indicates the combination of independent variables included in each analysis. The combinations not shown resulted in regressions that were not significant. Asterisks (*) indicate the combinations of variables that generated the best multiple regression models taking into account the coefficient of determination ($r^2$), the adjusted $r$-square ($r^2_{adj}$), Mallow’s criterion (Cp) and the root mean squared error (s). Total density, Log(TD); rainfall, Log(R); lowest mean atmospheric temperature, Log(LT); highest mean atmospheric temperature, Log(HT)

<table>
<thead>
<tr>
<th>Log(TD)</th>
<th>Log(R)</th>
<th>Log(LT)</th>
<th>Log(HT)</th>
<th>$r^2$</th>
<th>$r^2_{adj}$</th>
<th>Cp</th>
<th>s</th>
</tr>
</thead>
<tbody>
<tr>
<td>X</td>
<td>0.481</td>
<td>0.423</td>
<td>17.1</td>
<td>0.14872</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>X</td>
<td>0.382</td>
<td>0.313</td>
<td>21.7</td>
<td>0.16227</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>X</td>
<td>0.622</td>
<td>0.527</td>
<td>12.6</td>
<td>0.13459</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>X</td>
<td>0.564</td>
<td>0.455</td>
<td>15.3</td>
<td>0.14456</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>X</td>
<td>0.791</td>
<td>0.701</td>
<td>6.7</td>
<td>0.10704</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>X</td>
<td>0.660</td>
<td>0.514</td>
<td>12.8</td>
<td>0.13650</td>
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<td></td>
</tr>
<tr>
<td>X</td>
<td>0.871</td>
<td>0.785</td>
<td>5.0</td>
<td>0.09083</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 6

Multiple linear regression analysis. Model 1. Dependent variable: logarithm of the daily natural mortality instantaneous rate. Independent variables: logarithms of total density (TD), rainfall (R), and atmospheric temperature (LT, the lowest mean temperature; HT, the highest mean temperature between samplings). SE, standard error; t, statistic; SS, sum of squares; MS, mean squares; F, statistic

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>SE</th>
<th>T</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-3.0563</td>
<td>0.6846</td>
<td>-4.4646</td>
<td>0.0043</td>
</tr>
<tr>
<td>Log(TD)</td>
<td>0.5083</td>
<td>0.1518</td>
<td>3.7439</td>
<td>0.0096</td>
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<td>Log(R)</td>
<td>-0.5782</td>
<td>0.1645</td>
<td>-3.5155</td>
<td>0.0126</td>
</tr>
<tr>
<td>Log(LT)</td>
<td>-0.5229</td>
<td>0.1670</td>
<td>-3.1313</td>
<td>0.0203</td>
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<tr>
<td>Log(HT)</td>
<td>1.0007</td>
<td>0.5188</td>
<td>1.9286</td>
<td>0.1020</td>
</tr>
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</table>

Variance analysis

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<th>SS</th>
<th>MS</th>
<th>F</th>
<th>Probability</th>
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<td>Regression</td>
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<td>0.2338</td>
<td>0.0835</td>
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<td>Residuals</td>
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<td>0.0495</td>
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<tr>
<td>Total</td>
<td>10</td>
<td>0.3833</td>
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</table>

n = 11 $r^2_{adj} = 0.7847$
Discussion

The results obtained here show that mortality increases with initial population density, following a sigmoidal function. This type of function would imply that mortality is density-dependent and increases when density is higher than 500-600 ind. m⁻². Once the larval attachment and recruitment stages have been completed, the intraspecific competition related to density concerns two general areas: competition for food and competition for space (Margalef 1982). Some authors rule out the possibility that competition for food may affect the cockle’s mortality rates in densities of less than 1000 ind. m⁻² (Kreger 1940, fide Kristensen 1958, Beukema & Dekker 2006, Guillou & Tartu 1994). This threshold is higher than the one found here, but the difference may be attributed to spatial and temporal differences, or to the influence of the other variables taken into account in our work. The influence of density on competition for space was reported by Richardson et al. (1985). Collisions between individuals in close proximity cause the animals to emerge at the sediment surface, which makes them more susceptible to being entrained by hydrodynamic effects and also more
vulnerable to predators. The maximum density used by these authors in their trials was 535 ind. m⁻², which is near the density threshold of our results.

Among the cockle’s main predators in intertidal beds is the oystercatcher (Haematopus ostralegus L.), of bird species and the green crab (Carcinus maenas L.) among invertebrates. For the same type of sediment, in the case of both birds and crustaceans, the frequency with which the bivalves are captured increases with prey density (Johnstone & Norris 2000, Boulding & Hay 1984, Sponaugle & Lawton 1990). Both Eggleston et al. (1992) and Seitz et al. (2001) have demonstrated that the mortality of Mya arenaria L. and Macoma balthica L., owing to the blue crab, Callinectes sapidus (Rathbun), is density-dependent and, moreover, responds to sigmoidal-type curves similar to the one presented in this paper.

In estuarine intertidal zones, rainfall is directly related to salinity (Cloern & Nichols 1985) and it is closely linked to the survival of the cockle (Kristensen 1958). The fact that there is a logistic relationship similar to the one found here is in agreement with the euryhaline nature of the cockle. This curve suggests that the mortality rate remains low within a wide range of rainfall values and that it does not rise gradually with increasing precipitation, but rather undergoes a sharp increase once a certain threshold has been crossed. The situation of the cockle beds in estuarine areas and inner ria zones, as well as their position in the surface layer of the intertidal sediment, cause them to be exposed to the strong variations in salinity originating from rainfall and changes in river flow volumes (Cloern & Nichols 1985). Despite the wide salinity range tolerated by the cockle (Kinne 1971a), massive mortality associated with heavy rainfall events is a common occurrence (Kristensen 1958).

Extreme atmospheric temperature is considered to be the cause of the alterations found in a number of factors - filtration capacity (Smaal et al. 1997, Newell & Bayne 1980), burrowing capacity (Desclaux et al. 2002), evolution of the body mass (Honkoop & Beukema 1997), effect of predators (Beukema & Dekker 2006), etc., which would act on the biology of the cockle and affect its mortality. In this paper we consider low atmospheric temperature to be an indicator of the relatively severe winter conditions for the latitudes where the study was conducted. The correlation found between the minimum atmospheric temperature of the daily averages and mortality would suggest that there is a threshold situated at around 5 to 6°C, below which the mortality rate increases substantially. On several occasions during the course of our study, coinciding with freezing conditions at low tide, temperatures of -1°C were recorded simultaneously with values of 4°C, at a depth of 1 cm in the sand -the depth at which cockle juveniles were buried-and 7°C in the seawater 1 m from the shore. These atmospheric temperatures are greater than those recorded at higher latitudes, associated with major episodes of mortality (Strasser & Günther 2001, Kristensen 1958, Hancock & Urquhart 1965). Three possible explanations may be considered to account for the difference between the critical temperature threshold suggested in this study and the one reported by authors for the northern coast of Europe. I) Kinne (1971b) reports that the minimum temperature tolerance range is lower in regions located at higher latitudes than in milder climates. II) For these temperature values, perhaps the effect of temperature on mortality -in conjunction with other factors- is not due so much to its absolute value, as to irregular thermal events or sudden changes in temperature (Kinne 1971b, Ducrotay et al. 1991). III) In addition to massive mortalities from freezing caused by extremely low temperatures, Honkoop & Beukema (1997) report that cockles lose more body mass at moderately low water temperatures (6.1°C) than at low water temperatures (1.5°C), and that if the animals have less body mass at the onset of spawning, this will lead to a lower survival rate, among other things.

As regards the highest mean temperatures, there are no references to high temperature tolerance in situ. According to Ansell et al. (1981), the upper water temperature tolerance in the laboratory is 29°C for 96 h or 35°C for 4 h and, Kristensen (1958) reports a tolerance of 31°C for 24 h. On the one hand, these values are far from the threshold of 24°C for the atmospheric temperature found in our work. On the other hand, Newell & Bayne (1980) and Ansell et al. (1981), attribute more importance to the sudden change in temperature, than to the absolute value of the upper temperature tolerance in the different physiological functions of the cockle.

The results of the multiple regression model showed that combining the readily available variables used here offers a satisfactory explanation for part of the decrease in cockle density. The model’s simplicity makes it a useful tool that will enable managers to update stock density estimations according to climate-related conditions or to quantify their influence on the natural mortality of cockles in beds. Nevertheless, it must be remembered that the data included in this study refer to a cockle population settled in intertidal beds. Hence, the application of the model must be restricted exclusively to habitats with characteristics that are similar to those in the study areas.

Acknowledgments

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