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)

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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 período 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 períodos 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 13000 shell-fishermen (CES 2001), with an annual production ranging from 6000 to 9000 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. (Boyden 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
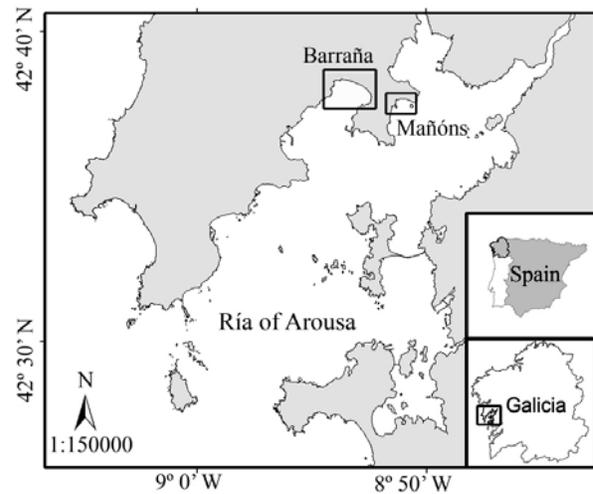
Figure 1

Situation of the beds studied in the intertidal zone of Barraña and Mañóns beaches, in the Ría of Arousa

Situación de los bancos estudiados en la zona intermareal de las playas de Barraña y Mañóns, en la ría de Arousa

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 ìm 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 14.6°C and the thermal amplitude 12.6°C (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* (Montagui, 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
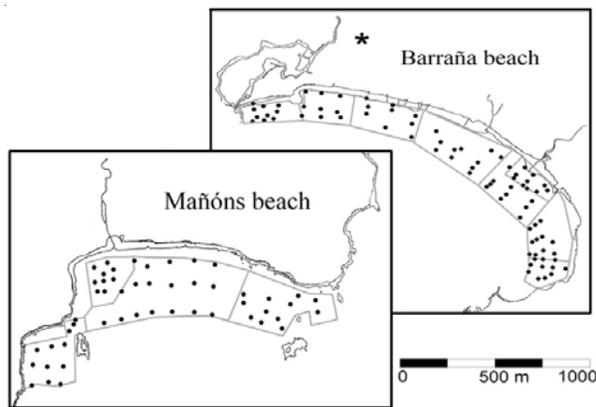
Figure 2

Sampling stations (points) and strata (polygons) at the beaches of Barraña and Mañóns. The asterisk (*) indicates the position of the weather station

Estaciones (puntos) y estratos (polígonos) de muestreo en las playas de Barraña y Mañóns. El asterisco (*) muestra la posición de la estación meteorológica

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:

$$z = 1 - (D_2 / D_1)$$

$$f = D_C / D_1$$

So, in this study m was calculated as:

$$m = 1 - ((D_2 + D_C) / D_1)$$

where D_1 is the mean density of the size groups present in the first sampling (Date 1 in Fig. 3), D_2 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
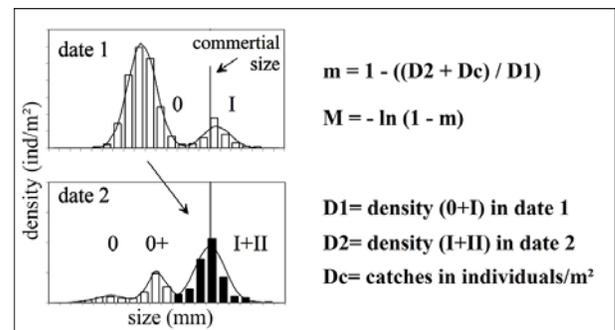
Figure 3

Procedure for calculating the finite natural mortality rate (m) and the instantaneous natural mortality rate (M) from data density size classes. Ind. m⁻², individuals per square meter

Procedimiento de cálculo de la tasa finita de mortalidad natural (m) y la tasa instantánea de mortalidad natural (M) a partir de datos de densidad de clases de talla. Ind. m², individuos por metro cuadrado
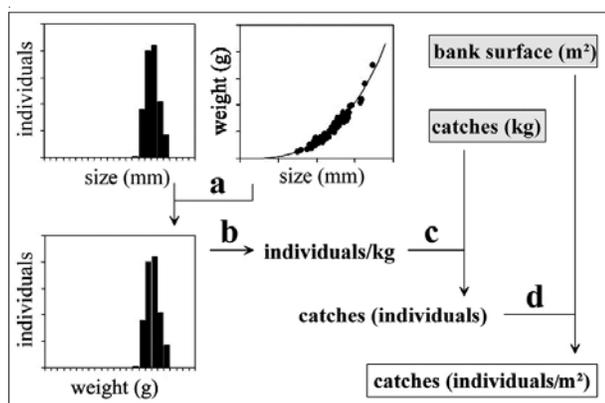
Figure 4

Procedure for estimating catches in terms of density (ind. m⁻²). (a) The size-weight relationship makes it possible to convert size frequency data into a weight histogram. (b) The weight histogram provides information about how many cockles are in a kg, so that it is possible 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)

Procedimiento de estimación de las capturas en términos de densidad (ind. m⁻²). (a) La relación talla-peso permite convertir los datos de frecuencia de tallas en un histograma de pesos. (b) El histograma de pesos contiene información sobre cuántos berberechos hay en un kg, de esta forma es posible convertir las capturas en kg a capturas en individuos (c). Conociendo la superficie del banco en el que se capturaron los berberechos se puede conocer las capturas en términos de individuos por metro cuadrado a partir de las capturas en individuos (d)

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 catches in kg to catches in number of individuals (Fig. 4c). The last step was to estimate the catch in terms of individuals per square metre (D_C), by dividing it by the area of the bed harvested (Fig. 4d).

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

$$M = -Ln\,(1\text{-}m)$$

The natural mortality instantaneous rate was fitted to a daily rate (M_d) depending on the number of days (d) that

had passed between each pair of compared samplings according to algorithm

$$M_d = M\,/\,d$$

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:

$$y = A_2 + ((A_1\text{-}A_2)\,/\,(1 + (x\text{-}x_0)^P))$$

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. 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 multi-collinearity 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

Size-weight regression of *C. edule*. Analysis of the difference between the slope of regressions from each bed. Regression analysis for the two beds together. a, constant; b, slope, r^2_{adj}, adjusted r-square; SE, standard error; SE(b-b), standard error for the difference between slopes of regressions compared; *P*, probabilistic significance of differences between slopes; n.s., no significant probability

Regresión talla-peso de *C. edule*. Análisis de pendiente entre las regresiones de cada banco y regresión para los dos bancos juntos. a, constante; b, pendiente; r^2_{adj}, coeficiente de determinación ajustado; SE, error estándar; SE(b-b), error estándar de la diferencia de pendientes de las regresiones comparadas; *P*, significación probabilística de las diferencias entre pendientes; n.s., probabilidad no significativa

site	a	b	r^2_{adj}	SE	n	SE(b-b)	P
Mañóns	-3.4961	3.0222	0.9895	0.051	423		
Barraña	-3.2756	2.8994	0.9679	0.0427	215	0.0665	n.s.
Mañóns+Barraña	-3.4931	3.0335	0.9842	0.0548	638		

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 (ºC). Dates indicate month and year of each pair of compared samplings

Pares de muestreos comparados y valores de las variables obtenidos durante el periodo de estudio. ID, identificativo; Md, tasa instantánea de mortalidad natural diaria; TD, densidad total inicial de la población en individuos por metro cuadrado (ind. m²); R, precipitaciones acumuladas en el período de tiempo entre muestreos (mm); LT y HT, temperatura atmosférica media diaria más baja y más alta registradas entre muestreos (ºC). Las fechas indican el mes y el año de cada par de muestreos comparados

ID	Beach	Initial date	Final date	M_d	TD (ind. m⁻²)	R (mm)	LT (ºC)	HT (ºC)
1	Mañóns	10/1997	3/1998	0.00194	207	1238	5.75	16
2	Mañóns	3/1998	5/1998	0.00221	153	485	9.50	22
3	Mañóns	10/1998	10/1999	0.00778	1570	1633	6.00	26
4	Mañóns	10/1999	10/2000	0.00592	493	1754	5.75	27
5	Mañóns	9/2003	11/2003	0.00518	212	308	9.50	25
6	Barraña	10/1998	10/1999	0.00574	690	1656	6.00	26
7	Barraña	10/1999	10/2000	0.00646	780	1756	5.75	27
8	Barraña	10/2001	9/2002	0.00417	204	1245	2.50	23
9	Barraña	9/2002	3/2003	0.00712	544	1479	2.00	20
10	Barraña	3/2003	5/2003	0.00474	132	220	9.75	21
11	Barraña	10/2003	9/2004	0.00387	478	1647	5.75	27

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; r^2_{adj}, 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

Valores obtenidos para los modelos lineales y logísticos de relación individual entre las transformaciones logarítmicas de la tasa instantánea de mortalidad natural diaria (Log(Md)) y las diferentes variables independientes (TD, densidad total; R, precipitaciones; LT, temperatura atmosférica media más baja; HT, temperatura atmosférica media más alta); y, variable independiente; x, variable dependiente, a constante del modelo lineal; b, pendiente; n, número de pares de datos; SS, suma de cuadrados; r^2_{adj}, coeficiente de determinación ajustado; r, coeficiente de correlación; *P*, significación probabilística del modelo n.s.; probabilidad no significativa; A_1, A_2, x_0 y P, constantes del modelo logístico

Lineal models								
y	x	a	b	n	SS	r^2_{adj}	r	*P*
$Log(M_d)$	$Log(TD)$	-3.3576	0.3977	11	0.1991	0.4230	0.6933	< 0.05
$Log(M_d)$	$Log(R)$	-2.8108	0.1586	11	0.3557	-0.0310	0.2687	n.s.
$Log(M_d)$	$Log(LT)$	-2.1270	-0.2927	11	0.3347	0.0297	0.3560	n.s.
$Log(M_d)$	$Log(HT)$	-4.7007	1.7327	11	0.2370	0.3131	0.6179	< 0.05

Logistic models									
y	x	A_1	A_2	x_0	*P*	n	SS	r^2_{adj}	r	*P*
$Log(M_d)$	$Log(TD)$	-2.7062	-2.1089	2.5539	13.0000	11	0.3175	0.2783	0.7034	< 0.05
$Log(M_d)$	$Log(R)$	-2.4724	-2.1700	3.1512	138.0316	11	0.3001	0.1051	0.6112	< 0.05
$Log(M_d)$	$Log(LT)$	-2.2529	-2.4234	0.7376	168.2806	11	0.3147	0.1979	0.6622	< 0.05
$Log(M_d)$	$Log(HT)$	-2.6961	-1.9172	1.3809	14.6817	11	0.3108	0.0979	0.6071	< 0.05

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 x_0 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 5.5°C (LT) or above 24°C (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 ($r^2_{adj.}$) 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); r², coefficient of determination between each variable and the other three; VIF, Variance inflation factor

Análisis de multicolinearidad. Variables independientes logarítmicamente transformadas: densidad total, Log(TD); precipitación, Log(R); temperatura atmosférica media más baja, Log(LT); temperatura atmosférica media más alta, Log(HT); r², coeficiente de determinación entre cada variable y las otras tres; VIF, factor de inflación de la varianza

	Log(TD)	Log(R)	Log(LT)	Log(HT)
r²	0.6927	0.7227	0.4784	0.3711
VIF	3.2541	3.6065	1.9172	1.5901

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 (r²), the adjusted r-square (r²$_{adj}$), 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)

Todos los subgrupos de regresión. Las X señalan la combinación de variables independientes incluidas en cada análisis. Las combinaciones no mostradas dieron como resultado regresiones no significativas. Los asteriscos (*) señalan las combinaciones de variables que producen los mejores modelos de regresión múltiple teniendo en cuenta el coeficiente de determinación (r²), el coeficiente de determinación ajustado (r²$_{adj}$), el criterio de Mallow (Cp) y la raíz cuadrada de la media del cuadrado de los errores (s). Densidad total, Log(TD); precipitación, Log(R); temperatura atmosférica media más baja, Log(LT); temperatura atmosférica media más alta, Log(HT)

Log (TD)	Log (R)	Log (LT)	Log (HT)	r²	r²$_{adj}$	Cp	s
X				0.481	0.423	17.1	0.14872
			X	0.382	0.313	21.7	0.16227
X	X			0.622	0.527	12.6	0.13459
X			X	0.564	0.455	15.3	0.14456
X	X	X		0.791	0.701	6.7	0.10704 *
X	X		X	0.660	0.514	12.8	0.13650
X	X	X	X	0.871	0.785	5.0	0.09083 *

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

Análisis de regresión lineal múltiple. Modelo 1. Variable dependiente: logaritmo de la tasa instantánea de mortalidad natural diaria. Variables independientes: logaritmos de la densidad total (TD), de las precipitaciones (R), y de la temperatura atmosférica (LT, temperatura media más baja; HT, temperatura media más alta entre muestreos). SE, error estándar; t, estadístico; SS, suma de cuadrados; MS, media de cuadrados; F, estadístico

Variable	Coefficient	SE	T	Probability
Constant	-3.0563	0.6846	-4.4646	0.0043
Log (TD)	0.5683	0.1518	3.7439	0.0096
Log (R)	-0.5782	0.1645	-3.5155	0.0126
Log (LT)	-0.5229	0.1670	-3.1313	0.0203
Log (HT)	1.0007	0.5188	1.9286	0.1020

Variance analysis					
Source	g.l.	SS	MS	*F*	Probability
Regression	4	0.3338	0.0835	10.1130	0.0078
Residuals	6	0.0495	0.0083		
Total	10	0.3833			
n = 11 r²$_{adj}$ = 0.7847					

Table 7

Multiple linear regression analysis. Model 2. Dependent variable: logarithm of the daily natural mortality instantaneous rate. Independent variables: logarithms of total initial density (TD), rainfall (R), and the lowest mean atmospheric temperature between samplings (LT). SE, standard error; t, statistic; SS, sum of squares; MS, mean squares; F, statistic

Análisis de regresión lineal múltiple. Modelo 2. Variable dependiente: logaritmo de la tasa instantánea de mortalidad natural. Variables independientes: logaritmos de la densidad total inicial (TD), de las precipitaciones (R), y de la temperatura atmosférica media más baja entre muestreos (LT). SE, error estándar; t, estadístico; SS, suma de cuadrados; MS, media de cuadrados; F, estadístico

Variable		Coefficient	SE	t	Probability
Constant		-2.0284	0.5064	-4.0055	0.0052
Log (DT)		0.7200	0.1530	4.7057	0.0022
Log (R)		-0.6108	0.1928	-3.1681	0.0158
Log (LT)		-0.4581	0.1928	-2.3765	0.0491
Variance analysis					
Source	g.l.	SS	MS	*F*	Probability
Regression	3	0.3031	0.1011	8.8194	0.0089
Residuals	7	0.0802	0.0115		
n = 11	r^2_{adj} = 0.7011				

Table 8

Relationship between the row data of both observed (M_{obs}) and expected natural mortality calculated from the second multiple regression model. SS, sum of squares; MS, mean squares; SE, standard error, t, statistic t; F, statistic F

Relación entre los datos sin transformar de la mortalidad natural observada (M_{obs}) y la estimada resultante del segundo modelo de regresión múltiple. SS, suma de cuadrados; MS, media de cuadrados; SE, error estándar; t, estadístico t; F, estadístico F

Variable		Coefficient	EE	t	Probability
Constant		-0.0128	0.1048	-0.1224	0.9052
$M_{obs.}$		1.0219	0.1970	5.1878	0.0005
Variance analysis					
Source	g.l.	SS	MS	*F*	Probability
Regression	1	0.3654	0.3653	26.9109	0.0006
Residuals	9	0.1222	0.0136		
n = 11	$r^2_{adj.}$ = 0.7215				
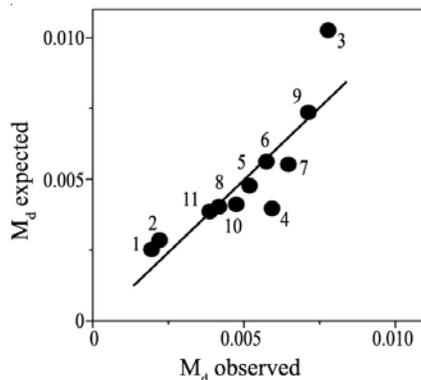
Figure 5

Relationship between the observed and expected daily rate of natural instantaneous mortality on the basis of the total initial density, accumulated rainfall and the lowest mean daily temperatures recorded between the samplings. The numbers correspond to the identifier in Table 2

Relación entre la tasa diaria instantánea de mortalidad natural observada y la estimada a partir de la densidad total inicial, precipitaciones acumuladas y las temperaturas medias diarias más bajas registradas entre los muestreos comparados. Los números se corresponden con el identificador de la Tabla 2

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 6ºC, 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 4ºC, at a depth of 1 cm in the sand -the depth at which cockle juveniles were buried- and 7ºC 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, Ducrotoy *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 (6.1ºC) than at low water temperatures (1.5ºC), 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 29ºC for 96 h or 35ºC for 4 h and, Kristensen (1958) reports a tolerance of 31ºC 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.

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