

Modelling of common European cockle *Cerastoderma edule* fishing grounds aimed at sustainable management of traditional harvesting

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Abstract In the Bay of Saint-Brieuc, a 3,110-ha tidal bay in NW France, English Channel, the cockle *Cerastoderma edule* has been collected by traditional fishing methods for many decades without any evaluation or management of this resource taking place. Since 2001, the National Natural Reserve of the bay of Saint-Brieuc has carried out an evaluation of the stock and a mapping of the cockle fishing grounds each year. Analysis of the spatial structure of the population is approached by cartography through interpolation of the data using the kriging method. The recruitment zones are geographically quite well defined and located in areas limited to the mean-tide zone. The distribution of the population was affected by passive displacement of juvenile cockles. Evaluation using the matrix of individual numbers for each age group found the inter-annual mortality rates to be about 60%. Somatic production was estimated and expressed in ash-free dry weight. The average annual production ranged from 7.4 to 14.5 g/m². In the autumn of 2006, the minimum legal fishing size changed from 30 to 27 mm (corresponding to individuals aged about 2.5 years). The model developed shows that this change has led to a doubling of the fishable stock.

Keywords *Cerastoderma edule* · Cockle · Mortality · Production · Recruitment · Stock assessment · Tidal flat

Introduction

The cockle *Cerastoderma edule* is one of the most abundant mollusc species that occur on tidal flats in the bays and estuaries of Europe [1–3]. It is a commercially important species and a major prey of crustaceans [4, 5], fishes [6], and wading birds [7].

The cockle is collected by hand-raking on a large number of tidal flats on the coastline of France and other European countries [8]. In the Bay of Saint-Brieuc, the cockle has been collected by traditional fishing methods for many decades. This still represents a certain economic sector. There are currently 25 professional harvesters, as well as a large number of amateur fishers and tourists who also collect cockles.

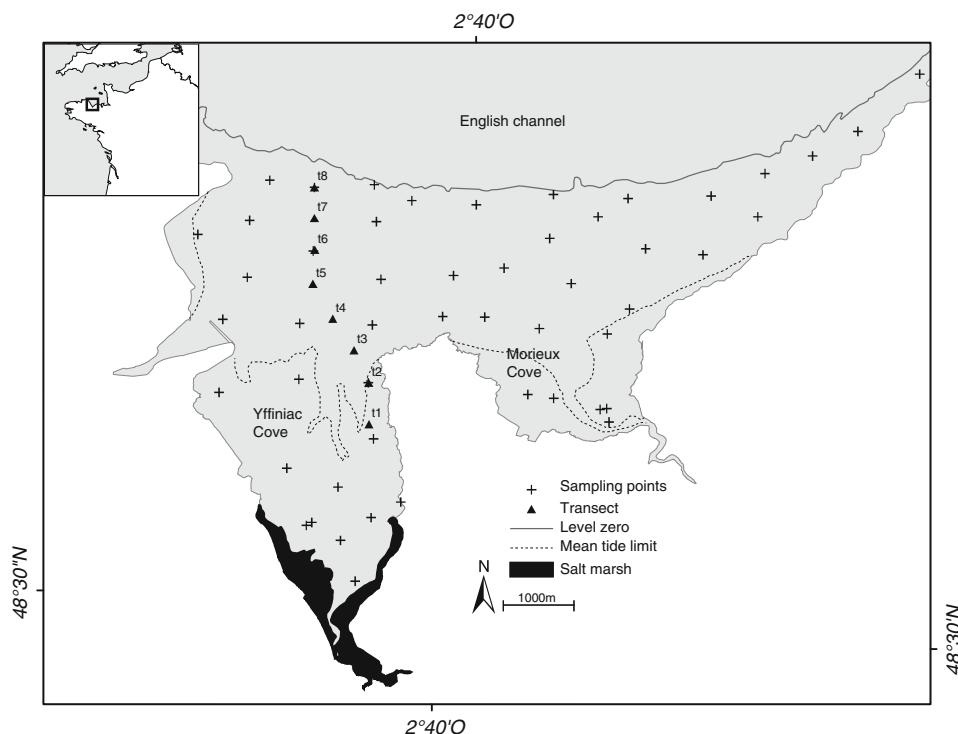
Statistics taken from European studies mentioned below show significant variations in density from year to year, depending on the success of spat-fall and on mortality [9], sometimes leading to a serious fall in stocks as in the Bay of the Sommes [10] or in the Wadden Sea, resulting in an increase in the mortality rate of bird species feeding on the cockles [2]. In the Bay of Saint-Brieuc, a large shrinkage of the cockle fishing grounds between 1988 and 2001 was observed according to the French Research Institute for Exploitation of the Sea (IFREMER, unpublished data). This has led to the implementation of an annual evaluation of the grounds within the Natural Reserve of the Bay of Saint-Brieuc.

The main aim of the managers of marine protected areas and of the Natura 2000 European network sites is to balance conservation with resource exploitation, to try to ensure that activities such as fishing, hunting, tourism and water sports do not impact on the conservation status and biodiversity of the designated sites [3, 11].

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Fig. 1 Map of the Bay of Saint-Brieuc. Presented with sampling stations to investigate abundance and shell length of *Cerastoderma edule* and transect to collect *C. edule* for age determination



When the concrete elements of the population dynamics are reported to the fishers and to the authorities who regulate the fishing activities, those with political interest in the areas and professional fishing organizations are more likely to accept the protection measures implemented [12, 13].

The aim of this paper is to show that relatively simple modelling tools allow maps of the fishing grounds to be created and also enable detailed evaluations of what these grounds produce to be carried out. By linking growth data to this model, a reasonably reliable system for predicting future production in the short term can be obtained. The mortality parameters, density and biomass for each year and age group can also be obtained using this model. Through the results supplied by this model the resource manager gains a better understanding of spatial and temporary variation of populations, and therefore is able to regulate and organise fishing activity more easily. The limits and the precautions of the models are also discussed.

Materials and methods

The site

The Bay of Saint-Brieuc ($48^{\circ}32'N$; $2^{\circ}40'W$) on the north coast of Brittany occupies a surface area of 800 km^2 up to an isobath of 30 m. The study area extends over 2,600 ha of sandy foreshore, of which 1,136 ha have been classed as a

natural reserve since 1998. The study area is divided mainly into two large coves (Morieux Cove and Yffiniac Cove) and represents an ecological entity (Fig. 1). The water temperature varies from 5°C in January to more than 20°C during the summer period (average = $15 \pm 4.67^\circ\text{C}$ SD, $n = 5,621$, water immersion temperature sensor with three measurements per day over 5 years). The average salinity is $34.9 \pm 0.04\text{‰}$ SD ($n = 42$, one measurement per week during the year 2002). The monthly average salinity varies from 34.7‰ in May to 35‰ in October. The variations in salinity are thus very weak during the year, even during periods of flooding. Salinity can, however, fall to 34‰.

The tidal range varies between 4 m at neap tide and nearly 13 m at spring tide (average tidal range 6.5 m). The tidal currents are alternating, moving to the southeast on an incoming tide and to the northwest on an outgoing tide. In spite of a significant tidal range, the speeds of the tidal currents are low, never exceeding 0.5 m/s. At the bottom of the bay, the residual currents are weak to non-existent and the water masses are rarely renewed by the tidal phenomenon [14].

The foreshore consists of sediment that has been classified at between 63 and 200 µm. The spread of the sediment in the Yffiniac Cove is distinguished by a granulometric gradient decreasing from the north to the south, with a transition of average sand from fine to large to sludgy silt in the sectors further inside the Yffiniac Cove. The Morieux Cove, which is shallower and more open, consists of sedimentary facies that are less fine than those

of Yffiniac Cove, and silt is only present in the section upstream from the Gouessant Estuary. The sediments of the Yffiniac Cove varied from fine sand at the bottom of the foreshore to average sand at the top of the beach [15]. With regard to the Morieux Cove, fine sediment was found at the top of the beach within the Gouessant Estuary.

Sampling design

Annual evaluation of the population

In 1987, IFREMER defined a sampling network of 51 stations covering the whole of the inter-tidal foreshore of the Yffiniac and Morieux Coves (Fig. 1). The distance between each station is about 1 km. Benthic fauna and sediment structural analyses were carried out for these stations in March 1988 and March 2001 [16]. This network of stations was used each year from 2001 to 2006 to evaluate the cockle grounds. This network of annually checked stations is supplemented each year by about 30 extra stations to better define the scope of the fishing grounds. Geographical position of all the sampling stations was obtained by GPS (to within about 3 m).

For each station, the cockles are harvested within a square of 0.25 m^2 , an area that is suitable for estimations of the abundance of the bivalves [17, 18]. The entire sediment sampled to a depth of 10 cm by hand is sieved using a 2 mm mesh. The choice of a surface of 0.25 m^2 is justified by the fact that most of the studies carried out on the benthos in the inter-tidal zone show that this surface is sufficiently large and is recognised as the best adapted surface area for estimating the abundance of bivalves [18]. This surface allows a suitable and satisfactory sample of the fauna to be taken whatever its distribution (aggregated distribution, regular or random), even for populations that are small in number [19–21].

The shell length (SL) of each cockle was measured to the nearest 0.1 mm using a vernier calliper. The evaluation of the entire fishing ground was carried out between the end of July and mid-August of each year. As the results of this evaluation are helpful to the statutory management of the fishing grounds, the chosen sampling period was in the summer to make it possible to respond to the request from the Sea Fisheries Committee, which meets annually in September.

Transect for evaluating individual ages

The growth of bivalve molluscs fluctuates in space and time essentially in response to abiotic factors [22–25]. Among the factors studied, the duration of emersion, hydro-dynamism, temperature, silting up, and the phenomenon of runoff were identified. In particular, de Montaudouin and

Bachelet [26] showed that the growth of cockles was linked to their positions on the foreshore. Cockles were sampled twice in 2006 at eight plots to read the growth line on the shell and to determine the growth curve. Using the half-tide level, eight stations were defined in Yffiniac Cove, about 500 m apart. These stations are spread over decreasing bathymetric levels on a southeast–northwest axis (Fig. 1). Sampling along this transect was performed alongside the annual fishing ground evaluation in 2006 only, in January (the winter low-growth period when the water temperature is at its lowest: $7 \pm 0.6^\circ\text{C}$) and a second time as a control at the start of August. The cockles were harvested within a sample surface of 1 m^2 at each of eight stations. The 1,323 cockles sampled were frozen to analyse the growth rings.

Reading the individual age

The growth of cockles is seasonal (spring and summer) [27, 28] and leads to growth lines on the shell (winter rings) which enable the age of the individual to be determined, as well as the differential growth of the populations to be studied [13, 29–32]. In areas subject to severe annual changes in temperature, such as in the English Channel, the seasonal growth is marked in the mineralised tissue. Fluctuation in the speed of growth led, in these examples, to an alternation of wide and narrow growth zones. Reading annual rings remains difficult, however, since variations in growth during the same year lead to the possible formation of extra stria [33, 34]. For each winter ring observed, the SL of the cockle was measured (antero-posterior axis; Fig. 2) using a vernier calliper, after checking the lines under a binocular microscope. To minimise the risk of error the measurements were carried out by two people separately. If there was a difference in opinion in determining the age, a third person was brought in to measure the sample. Only when two of the three measurements were equal was the sample included in the data. As errors of reading are more likely for cockles aged 5 years or more, only the age groups 0, 1, 2, 3 and 4+ were considered.

Modelling

All statistical analyses were performed with R software for Windows (<http://www.R-project.org>). The calculated means are shown with their standard deviations (mean \pm SD, standard deviation).

Evaluation of the length–mass relationship

The biomass produced from the cockle grounds in the Bay of Saint-Brieuc was estimated using the allometric

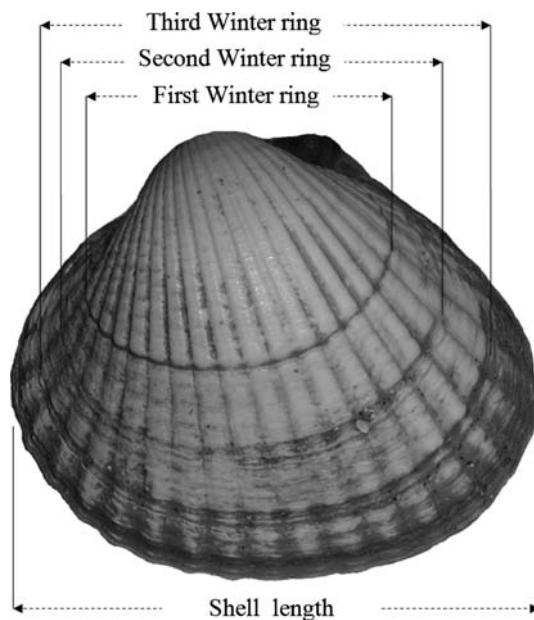


Fig. 2 The common cockle *Cerastoderma edule* collected from the Bay of Saint-Brieuc during January 2006, with the maximum shell length and three annual rings measured

body-size ratio. The SL to ash-free dry weight (AFDW) relationship was established using a sample of 64 cockles picked in August 2004 from the entire sampling area. The standard protocol according to Kamermans was used as follows: soft tissue was dried for 3–5 days at 60°C, weighed, heated at 560°C for 2 h and weighed again [25].

There is an allometric relationship which links the SL of the individual (measured in mm) and the mass of living material produced (mass of dry material without remains). This equation is expressed in the form:

$$W = a \times L^b,$$

where W is ash-free dry weight (g/m^2), L is SL of the individual (mm), and a and b are parameters of the equation established for the site, estimated by least-squares regression.

The estimation of the cockle biomass of each sample was carried out by totalling the individual biomasses using the length–mass relationship.

Modelling the growth

The growth stages of each individual can be determined using the annual growth lines. The modelling of the cockle growth can be adjusted to the model by von Bertalanffy [35], which is generally used to compare mollusc growth rates [33]. The parameters of the von Bertalanffy growth model were estimated by an iterative non-linear least-squares method [36].

The growth model for length L_t at time t is given by

$$L_t = L_\infty(1 - e^{-k(t-t_0)}),$$

where L_∞ is the asymptote of the curve (often referred to as the “maximum length”), k is the coefficient of initial growth and t_0 is the theoretical date of birth (zero length).

Evaluation of mortality

The inter-annual mortality rate can be understood using the global evaluation data for the site and its age structure. The mortality rate (Q) is the ratio of the number of individuals that have disappeared due to natural mortality and mortality through fishing during a time interval to the initial number: $Q = \frac{(N_{t_0} - N_{t_1})}{N_{t_0}}$.

Spatial structure of the population

The spatial structure of the site is approached by cartography through interpolation of the data [37]. Kriging is a geostatistical interpolation technique that considers both the distance and the degree of variation between known data points when estimating values in unknown areas [38]. A kriged estimate is a weighted linear combination of the known sample values around the point to be estimated.

When the study of the biological process is approached, highly structured methods of spatial organisation are encountered. Via kriging, a statistical method, the complexity of the spatial structures observed can be reported upon and recreated [39] by analysing the variability according to various spatial scales [40].

In comparison to other methods of interpolation, kriging is distinguished by its characteristics of non-biased estimating and estimating of an associated variance. This methodology, used for the first time in the Bay of Saint-Brieuc by IFREMER, means that the estimators of the parameters of the population such as density, surfaces and biomass can be obtained as well as cartographies.

The package Gstat [41] is an R package that provides basic functionality for univariable and multivariable geostatistical analysis, modelling, prediction and simulation including kriging [42]. This package was used in association with the package SP for visualising spatial data. This method of analysis has the advantage of being widely used in the spatial analysis of data, and there are numerous works available detailing the methodology, as well as numerous tutorials accompanying the software [43–46].

Spatialised modelling of the population dynamic

The length frequency distribution of the winter growth lines was normal and overlapped increasingly for older age groups. In the global evaluation of the grounds carried out each year, to try to differentiate the probability of cockles

belonging to one or other of the cohorts, the probability of each cockle belonging to a cohort according to the size (SL) was calculated using the normal curves of the different cohorts obtained by analysing the rings. The parameters of the cohorts making up the demographic structure established each year were optimised by maximum-likelihood estimation (MLE) [47]. The NLM algorithm was used (with R software), which is an efficient iterative procedure to compute the maximum likelihood [48]. Then, using the Bayesian method, each individual was placed in the most probable class [49]. From this probability calculation the geographical spread cards of the different age groups (0, 1, 2, 3, 4+) could be established by kriging.

Fishable stock prediction for 1 year hence

First, the parameters of the growth curve were applied to each individual sampled in year n . For each individual the estimated size of the cockle for year $n + 1$ can be calculated. Then kriging was carried out on this data to obtain the total amount of cockles which will be legally large enough to be fished ($SL > 30$ mm). Lastly, the average inter-annual mortality rate was applied to these results in order to estimate the theoretical amount of cockles that can be expected for the year $n + 1$.

Results

Structure of the population

During the annual August population evaluation sampling, the size (SL) of the cockles measured varied between 2 and 42 mm. The different cohorts making up the population (Fig. 3) could not be clearly differentiated. Globally these bar charts are bimodal (except for the year 2001, which is trimodal, and for 2005, which is unimodal). For the years 2002 and 2005, the principal mode was about 22 mm, whereas for the years 2003 and 2004 the principal mode was about 10 mm. For 2001 and 2006, these two modes can be seen simultaneously.

From the viewpoint of the spatial distribution of the fishing grounds, the maximum densities were observed in the Bay of Saint-Brieuc at the mean-tide line (Fig. 4). The spatial distribution varied according to the SL of the individual. The size classes of the larger cockles were found at the weakest topographic elevation (bottom of the tidal zone). There was a correlation between the average SL (t_{mm}) of the cockles at each station and the topographic elevation of the stations (bathy_m): $t_{mm} = -2.31 \times \text{bathy}_m + 34.31$ ($r^2 = 0.62$, $n = 143$, $P < 0.05$).

However, these spatial structures were not static and changed over this short sampling period (6 years). During

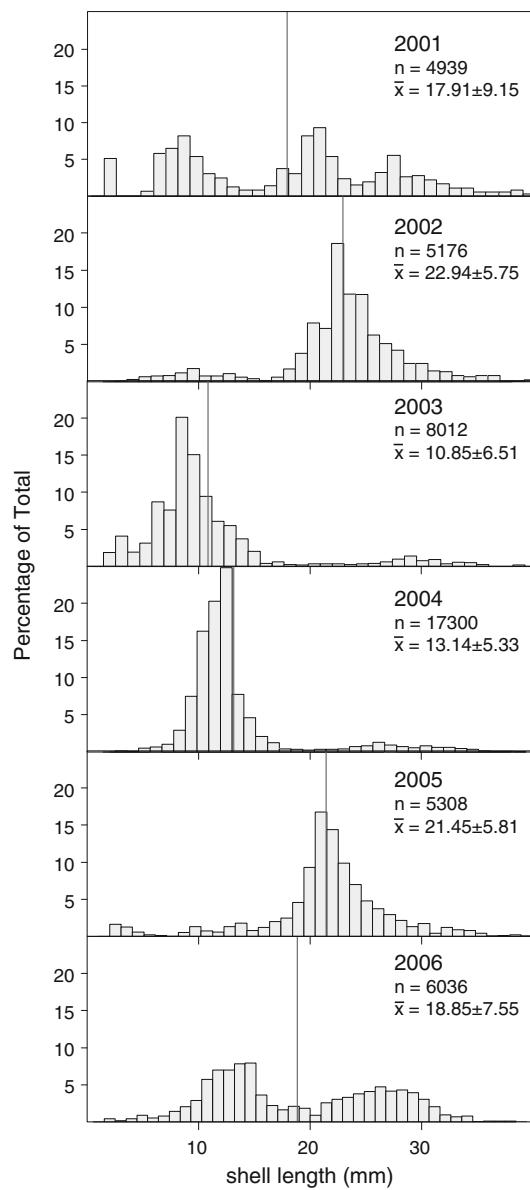


Fig. 3 Size-frequency bar charts between 2001 and 2006

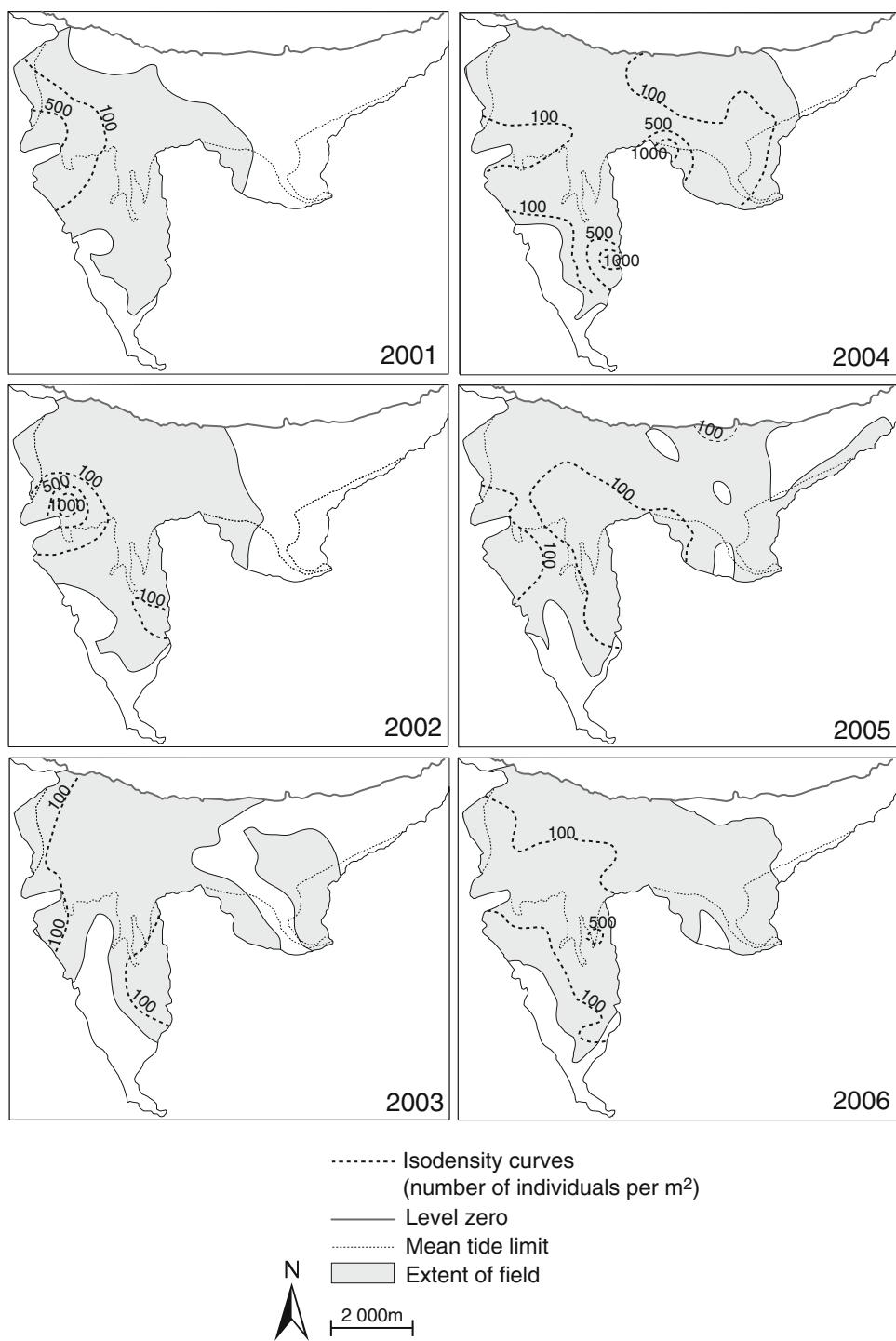
this period of time a change in the spatial extent of the fishing grounds was observed with a progressive movement toward the Morieux Cove to the east of the bay as well as a fluctuation in the abundance of cockles just after settlement of the young cockles. In fact there was a correlation for age group 0 between the covered surface and abundance (Spearman's rank correlation $r_S = 0.88$, $n = 6$ years, $P < 0.05$).

Evaluation of production

Allometric ratio

The allometric ratio obtained between SL and mass is:

Fig. 4 Maps showing the extent of the cockle fishing grounds between 2001 and 2006



$$W = 4 \times 10^{-6} \times L^{3.35}$$

(correlation $r^2 = 0.92$, $n = 64$, $P < 0.01$).

Evaluation of the biomass

Using the allometric ratio and the kriging table, the biomass could be estimated in AFDW (g/m^2), as well as the total

production of the cockle fishing grounds. This average production varied according to the year from 7.4 to 14.5 g/m^2 (Table 1) with the observed maximums varying between 43 and 301.6 g/m^2 .

For the whole of the fishing ground in the Bay of Saint-Brieuc, the biomass produced varied between 2001 and 2006 from 118 to 317 tMS (metric tons).

Table 1 Evaluation of the parameters of the biomass produced by the cockle field in the bay of Saint-Brieuc, evaluated by kriging

Year	Area of the field (ha)	Total biomass (tMS)	Average biomass (g/m^2)		SD	Maximum biomass observed (g/m^2)
			For the total modelling zone (3,110 ha)	For the actual area of the field		
2006	2,328	231.2	8.74	9.93	8.7	100.76
2005	2,345	316.8	9.61	13.51	11.2	62.58
2004	1,915	191.8	6.07	10.02	8.4	55.7
2003	1,596	118.3	3.7	7.41	6.6	50.83
2002	1,135	164.8	5.16	14.52	20.6	301.58
2001	1,525	132.5	4.15	8.69	7.5	43.52

Table 2 Sizes (in mm) of the winter rings measured on the cockles from eight transect stations in decreasing order of bathymetric level

Station no.	Ring from first winter			Ring from second winter			Ring from third winter			Ring from fourth winter			Ring from fifth winter		
	n	Av. size	SD	n	Av. size	SD	n	Av. size	SD	n	Av. size	SD	n	Av. size	SD
1	263	13.60	4.17	166	20.37	2.62	5	24.52	2.75						
2	96	15.22	3.39	76	21.67	2.08	4	27.35	2.46						
3	136	16.14	2.65	91	23.58	2.31	3	25.20	1.71	1	28.30	2.40			
4	119	17.12	3.61	97	25.58	2.35	5	28.48	3.50						
5	163	18.89	3.89	163	26.14	3.08	54	28.77	2.15	12	30.75	2.19			
6	107	17.74	4.29	107	26.11	3.39	32	29.68	2.99	3	35.90				
7	63	20.39	2.97	62	29.93	3.19	10	32.95	2.89	1	34.00		1	36.2	
8	62	17.61	3.88	62	26.25	3.74	41	31.07	2.79	20	33.86	2.52	5	36.43	1.6
$\Sigma/\bar{x}/\text{SD}$	1009	16.48	4.29	824	24.51	3.98	154	29.59	3.1	37	32.87	2.97	6	36.37	1.31

For the 0-year-old cockles measured in January, SL represents the first winter ring

Determination of the structure of the age group by analysing the rings

In 2006, samples for the growth ring analysis were obtained using the eight stations positioned regularly (transect, Fig. 1) between the average mean-tide level and the bottom of the tidal zone. Of the 1,323 cockles harvested, the age and growth of 1,256 individuals were determined (therefore 5% of the individuals were eliminated). In total 2,031 growth rings were measured (Table 2).

An average growth curve could be estimated for all the eight stations adjusted to von Bertalanffy's model. The model parameters are: $L_\infty = 34.36$, $k = 0.64$ ($r^2 = 0.97$, $n = 2031$, $P < 0.001$). The value t_0 is not modelled and is set at 0.

The growth and immersion time may be correlated. The slopes of the growth curves obtained from the eight stations situated in descending order of bathymetric level can be compared by using von Bertalanffy's model, setting the parameters t_0 and L_∞ to the same values for all the stations. The parameter k corresponding to the initial slope of the curve increases as the topographic level decreases ($k = -0.0355 \times \text{bathy}_m + 0.706$; $r^2 = 0.65$, $n = 8$, $P < 0.05$) or

the immersion time increases ($k = 0.682 \times \text{length}_{\text{immersion}} + 0.3156$; $r^2 = 0.68$, $n = 8$, $P < 0.05$) (Table 3). The doubling of the immersion time (between stations 1 and 5, Table 3) explains about 30% of the increase in growth for the rings of the first winter, 20% for the rings of the second winter, and 10% for the rings of the third winter (Table 2).

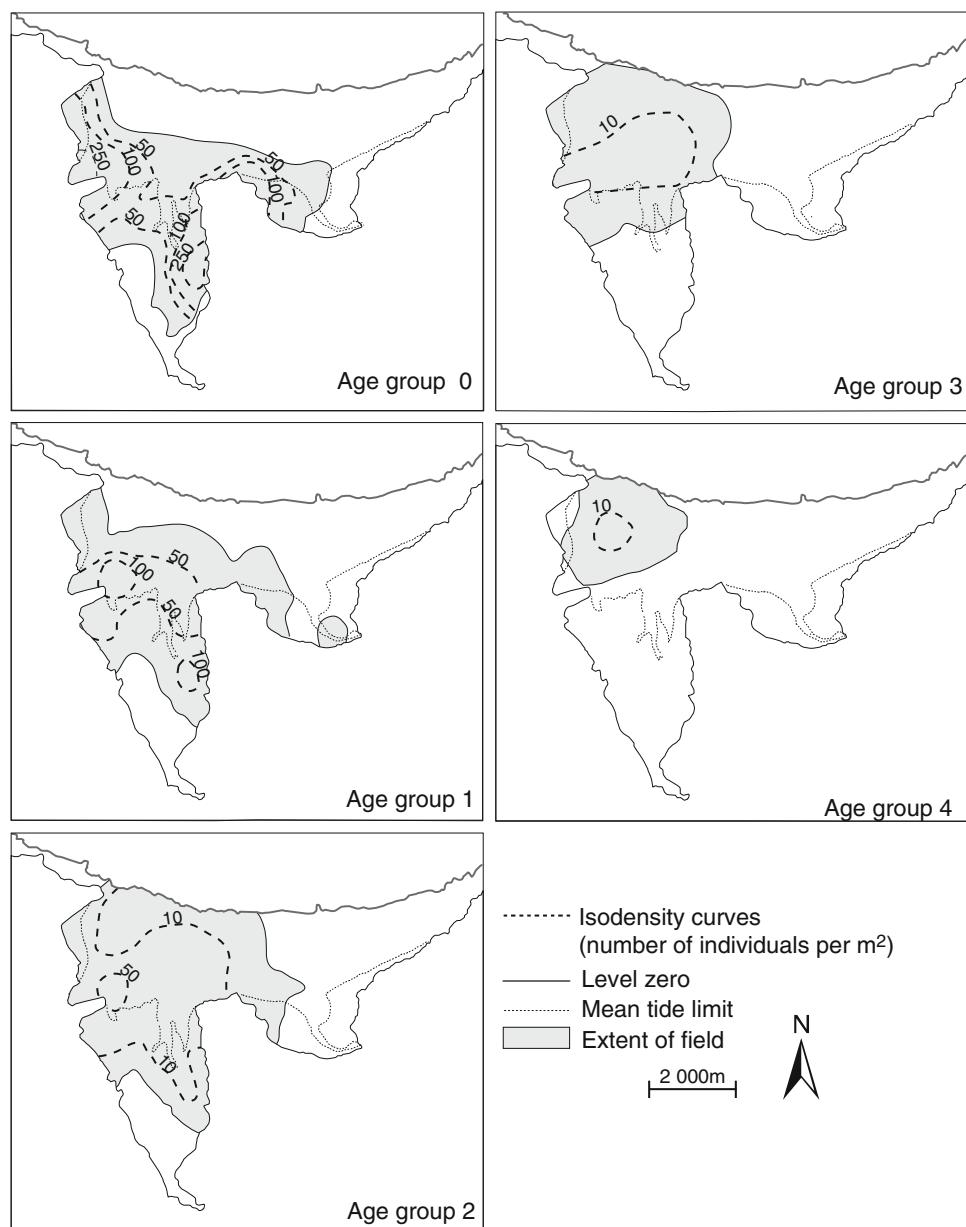
Table 3 Value of parameter k (coefficient of initial growth) defined by von Bertalanffy's model according to the bathymetric level and the immersion periods of the eight transect stations (the parameters $t_0 = 0$ and $L_\infty = 38.84$ mm are identical for all the stations)

Station no.	n	Bathymetric level (in m)	Immersion period (h/day)	k Parameter	SD
1	375	7.97	03:44	0.40	0.006
2	133	7.16	04:49	0.44	0.008
3	157	5.53	06:40	0.50	0.007
4	161	5.39	06:49	0.55	0.009
5	206	3.90	08:44	0.58	0.008
6	99	3.28	09:53	0.57	0.010
7	63	2.52	10:56	0.73	0.015
8	62	1.32	11:57	0.57	0.011

Spatialised modelling of the population dynamic

The juveniles larger than 2 mm (group 0) were distributed over a surface area of about 1,300 ha ($1,302 \pm 591$ ha), with zones of heavy concentration near each side of Yffiniac Cove, at the mean-tide level (Fig. 5). The zones where the concentrations of young cockles were greater than 100 individuals per square metre were, with the exception of 2004, less than 400 ha. In 2004, a year of massive recruitment, a settlement zone extended over the whole of the Yffiniac and Morieux Coves in the mean-tide zone covering an area of 1,891 ha, of which 1,127 ha had a concentration greater than 100 individuals per square metre.

Fig. 5 Maps showing the spread by age group established by kriging (average 2001–2006)



For 1-year-old cockles (group 1), the field of the equivalent zone was found ($1,305 \pm 500$ ha) situated over the whole of the mean tide zone. For age group 2, and especially for group 3, a progressive movement of the field towards the lower levels of the tidal zone was observed with a decrease in the surfaces colonised. However, the analysis of the annual lines showed the presence of the cockles belonging to groups 4 and 5 only in the stations at the bottom bathymetric level (Table 2).

Modelling the strength of the age group

The number of cockles in each age group (0, 1, 2, 3 and 4+) was assessed each year using kriging. This matrix of

Table 4 Breakdown of the numbers (in bold) of cockles ($\times 10^6$) modelled from 2001 to 2006 by kriging, according to age group

cohort born in :	2001	2002	2003	2004	2005	2006	Age group	average strength	\pm sd	Mortality rate	accumulated Mortality
	1156	393	1279	3972	380	968	0	1358	1219		
2000	57%	47%	41%	67%	51%					60%	60%
	300	500	210	758	1320	185	1	546	398		
1999	11%	80%	38%	69%	63%					58%	83%
	147	267	101	130	236	484	2	228	129		
1998	52%	81%	50%	30%	31%					59%	93%
	130	71	50	50	91	164	3	93	42		
1997	90%	89%	20%	22%	83%					68%	95%
	65	13	8	40	39	16	4	30	20		
Year of obs. : 2001	2002	2003	2004	2005	2006						

The inter-annual mortality rates evaluation by cohort is shown in italics

numbers for each age group (Table 4) allows the inter-annual mortality rates to be evaluated.

Group 0 ($SL > 2$ mm) represented on average $52 \pm 25\%$ of the total population. The numbers in this age group fluctuated greatly from one year to the next ($1,358 \times 10^6 \pm 1,219 \times 10^6$). Starting with age group 1 and going onto the others, the inter-annual variation rate decreased progressively (Fig. 5). The average numbers of the age groups 0, 1, 2, etc. observed between 2001 and 2006 were adjusted to an exponential negative curve: $n_{age} = 3,605.7e^{-0.94age}$ ($r^2 = 0.99$, $P < 0.001$).

The stock of cockles exploitable by fishing (≥ 30 mm SL) represents about 7.3% ($\pm 2.66\%$) of the total cockle stock present in the Bay of Saint-Brieuc.

Evaluation of the inter-annual mortality parameters

Using the matrix of the numbers in the different age groups according to the observation years (Table 3), the inter-annual mortality rates was estimated for the different cohorts observed.

Overall, the inter-class mortality rate was relatively constant among the different age groups (about 60%). The rate increased slowly (although not significantly) between age groups 3 and 4 to reach 68%. The cumulative mortality

rate reached 90% during the third year of life (i.e., after the second winter).

Short-term fishable stock prediction (+1year)

Table 5 compares, from the data for the previous year ($n - 1$), the estimation of the quantity of cockles > 30 mm SL and the actual (n) quantity measured. The error is at most from 20% to 22% and corresponds to the years of high mortality. The error is due to the assumption that mortality remains unchanged (Table 4: average mortality rate, 61%) from year to year and due to approximations of the model.

Discussion

The cockle ground was characterised by strong geographic heterogeneity of the densities and biomasses. We have highlighted the existence of spatial segregation of the various cohorts. In contrast to what was observed in the Bay of the Somme [10] (France) or in Scotland [50], this spatial structuring was quite stable in the Bay of Saint-Brieuc over the 5-year tracking period. The recruitment (settlement) zones were geographically quite well defined and located in

Table 5 Fishable stock prediction

Number of cockles ($\times 10^6$) modelled from 2002 to 2007 from the data for the preceding year ($n - 1$) compared with the numbers obtained (year n)	Year	Fishable stock prediction	Fishable stock Obtained numbers ($\times 10^6$)	Differences (%)
		Estimated number of individuals (> 30 mm SL) from data for the preceding year ($\times 10^6$)		
2002	129		115	-12
2003	124		101	-22
2004	169		188	+10
2005	105		132	+20
2006	138		132	-4
2007	316		310	-2

the areas limited (except during the exceptional recruitment phases) to the mean-tide zone. The higher densities of older cockles (groups aged 4+) tended to be found towards the low-water mark. This spatial segregation of the generations highlighted in numerous sites for *Macoma balthica* [51, 52] and *C. edule* [13, 31] was probably due to a migration phenomenon, in the view of Hiddink and Wolff [52].

The model parameters of growth ($L_{\infty} = 34.36$, $k = 0.64$) were quite close to those obtained by Ramon [33] during growth tracking in experimentation cages in the Wadden Sea ($L_{\infty} = 34.24$, $k = 0.754$). The analysis of the winter annual lines has been criticized by several authors due to the existence of supernumerary marks [33, 53, 54]. By observing the winter growth lines under a stereomicroscope and by having two observers analyse the cockles, the risk of false analysis was minimised. From all the cockles analysed, only 5% of the tests were rejected. It is likely that the individuals rejected had atypical or chaotic growth. Nevertheless this technique allowed the components (averages, type differences) of each cohort to be obtained, and by adjusting these parameters to the SL frequency bar charts, a breakdown by cohort of the demographic structure of the fishing grounds was obtained.

The allometric ratio obtained between SL and mass ($W = 4 \times 10^{-6} \times L^{3.35}$) was practically identical to those obtained in the Bay of the Sommes [55] or in Marennes Oléron [40] (France) and in Ireland [56].

Average biomass per square metre of tidal flat in August varied from 7.4 g in 2003 to 14.5 g AFDW in 2002, implying a total cockle stock on all tidal flats of 118 to 317 tMS, respectively. This production data varies but is comparable to and average for those found in Europe (reviewed by Beukema and Dekker) [2]. The dry weight was used in this model only to estimate the biomass. A sampling in August can lead to an overestimation in annual production due to the stress period and sexual inactivity. According to Beukema and Dekker [2], “biannual sampling might be optimal, with samples taken around the annual times of minimal and maximal biomass, i.e. in March and in August, respectively”.

The tracking of the cockle population dynamic over several years in the Bay of Saint-Brieuc made it possible to estimate that the average inter-annual mortality rate is globally constant during the lifetime of a cockle at between about 60–70% of the numbers present in the previous year. It should be noted that the mortality rate evaluated for the first year is an underestimate since it does not take into account the autumnal recruitment (as the stock evaluations were carried out in the summer) or the mortality of the cockles of <2 mm SL. Nevertheless numerous authors have shown that the survival rate of the secondary recruitment is much weaker than that of the spring recruitment [10].

Compared with the average from 2001 to 2006, the mortality rate increased in 2004 by about 30%. It can be assumed that there is a density-dependent relationship in the mortality rate of the juveniles. As Hancock [57], Coosen et al. [9] and Beukema and Dekker [2] have shown, there is a high level of inter-annual variability in the recruitment of cockles (factor of 10), and a high or very high recruitment level is followed the next year by a weak to very weak recruitment. Andre and Rosenberg showed a negative relationship between adult *C. edule* density and newly settled larvae [24].

The mortality rate calculated here is said to be total since it encapsulates all the natural or anthropogenic mortality causes. Several authors are interested in predation on the juveniles. In particular Reise shows clearly that the pressure of predation is concentrated on the smallest individuals in the population and decreases progressively during growth [58]. The examples of predation by flounder (*Platichthys flesus*) [6] and by the green crab (*Carcinus maenas*) [4, 59, 60] on the cockle juveniles can be cited. Predation by wading birds and in particular the Eurasian oystercatcher affects individuals of about 20 mm, or individuals about 1.5 years old [56].

The impact of fishing (professional or amateur) affects the size classes >30 mm SL corresponding to individuals aged about 3+ years. The stock of cockles exploitable by fishing (>30 mm SL) represents about 7% of the total cockle stock present in the Bay of Saint-Brieuc. The demographic structure of fishing grounds subject to high levels of fishing contains less than 5% of individuals of 30 mm SL. In all the sites studied in Europe where there are high levels of predation by fishing, a demographic structure of the reduced population beyond the marketable size is observed, whatever the growth rate of the individuals in these populations [53, 57, 61]. The hypothesis can be given that the mortality rate of this age group can be partially or totally attributed to fishing. In the autumn of 2006, the legal fishing size in France changed from 30 to 27 mm (corresponding to individuals aged about 2.5 years), which could have consequences on the demographic structure of these fishing grounds. The estimated proportion of fishable cockles on the fishing grounds changed from $7.3 \pm 2.6\%$ to $15.3 \pm 5.9\%$ (average over the 5 years). Reducing the legal fishing size by 3 mm allowed the quantity of fishable cockles to be doubled. In the end, this change of catch size should have an effect on the modelled value L_{∞} , as Hancock highlighted, independently of the growth rate of individuals in the population [57]. This individual growth depends on the bathymetric level, which itself is directly and linearly correlated with the immersion period. In the Bay of Arcachon (France), de Montaudouin and Bachelet showed that growth of cockles was linked to their positions on the foreshore [26]. This

immersion period also influences the early growth stages of the cockles (Table 3, k parameter).

The main interest of the model is to localise and to quantify the fishable stocks every year and also to offer predictive information. Indeed, considering the number of individuals in each cohort, the growth rate and the mortality, the prediction of the fishable stocks (>30 mm SL) in one year is relatively reliable, except in years where there is a high level of mortality. This prediction can allow fishing activity to be organised and regulated over 2 years by the marine authorities.

Ecological modelling of marine benthic species is a relatively recent discipline. However, since we are now aware of their importance in coastal ecosystems, research that is functional and quantitative (and no longer just descriptive) has been developed [62]. In the Bay of Saint-Brieuc, little research has been carried out up to now. However, the Bay has been classed as a national natural reserve for reasons of conserving its biodiversity, particularly in ornithology. Knowledge of the role of the benthos is an essential element in achieving the aims of conserving wintering birds and sustaining a commercial fishery.

The modelling of the fishing grounds developed in the Bay of Saint-Brieuc using the kriging methods allows a precise response to be given to the request from the institutional organisations regulating fishing. These modelling tools are quite accessible nowadays and can quite easily be routinely implemented. In addition to the statistics software, kriging can be carried out on the geo-referenced data with the help of SIG Geographic Information System software (ArcGIS Spatial Analyst, MapInfo, and so on).

These modelling tools are perfectly adapted to the requests of the co-management schemes of fishers and conservationists.

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