Geologie en Mijnbouw **70**: 59–73, 1991.
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Growth rates and population dynamics in *Crassostrea cf. rarilamella* from the Lower Eocene Roda Formation (southern Pyrenees, Spain)

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Received 30 October 1990; accepted 16 November 1990

Key words: population dynamics, survivorship curve, growth curve, functional morphology, *Crassostrea*, Tremp-Graus Basin

Abstract

An oyster bed of *Crassostrea cf. rarilamella* was preserved in life position in muddy estuarine sediments of Lower Eocene age in the Roda Formation, southern Pyrenees, Spain. Its population structure was studied by counting and measuring annual growth increments in the hinge plate of the oyster. The population structure is normal and indicates a time averaged death assemblage. The life table and survivorship curve show that *C. cf. rarilamella* had a high juvenile mortality and constant adult mortality pattern. The mean yearly decrease of the adult population was very low, as is shown by the regression coefficient. Growth line analysis revealed slower and faster growth. The cumulative growth curve does not show a gradual decrease in inclination, which confirms the interpretation of the functional shell morphology (adaptation to a muddy substrate) of *C. cf. rarilamella. C. cf. rarilamella* shows characteristics of an equilibrium species or K-strategist, to be expected in this sedimentological setting.

Introduction

Oysters received considerable attention in paleontological literature (e.g. Stenzel 1971, Seilacher 1984, Chinzei 1986, Ohno 1989). They often are excellent indicators of the paleoenvironment and yield valuable ecological and sedimentological information. 350 autochthonous *Crassostrea cf. rarilamella* (MELLEVILLE), a boulder shaped reclining oyster (Seilacher 1984) from a horizon in the Roda Formation (Lower Eocene) of the southern Pyrenees, were collected with the object of attempting to ascertain growth and mortality patterns (population dynamics) and to obtain related paleoenvironmental information.

Geological and paleontological setting

The oyster population occurs in estuarine sediments of Lower Eocene age in the south-central Pyrenean Tremp-Graus Basin (Spain).

The outcrop is located approximately 1 km southeast of the village La Puebla de Roda (42° 18′ N. lat., 0° 32′ E, long) on the eastern side of the river Isábena (Fig. 1). It forms part of the Roda Formation which is characterized by several vertically stacked sandstone bodies, interbedded with silty marls and thin limestone beds and as a whole deposited on a shallow shelf on the lower delta plain (Nijman & Nio 1975, Nio 1976, Nio & Yang 1983, Yang & Nio

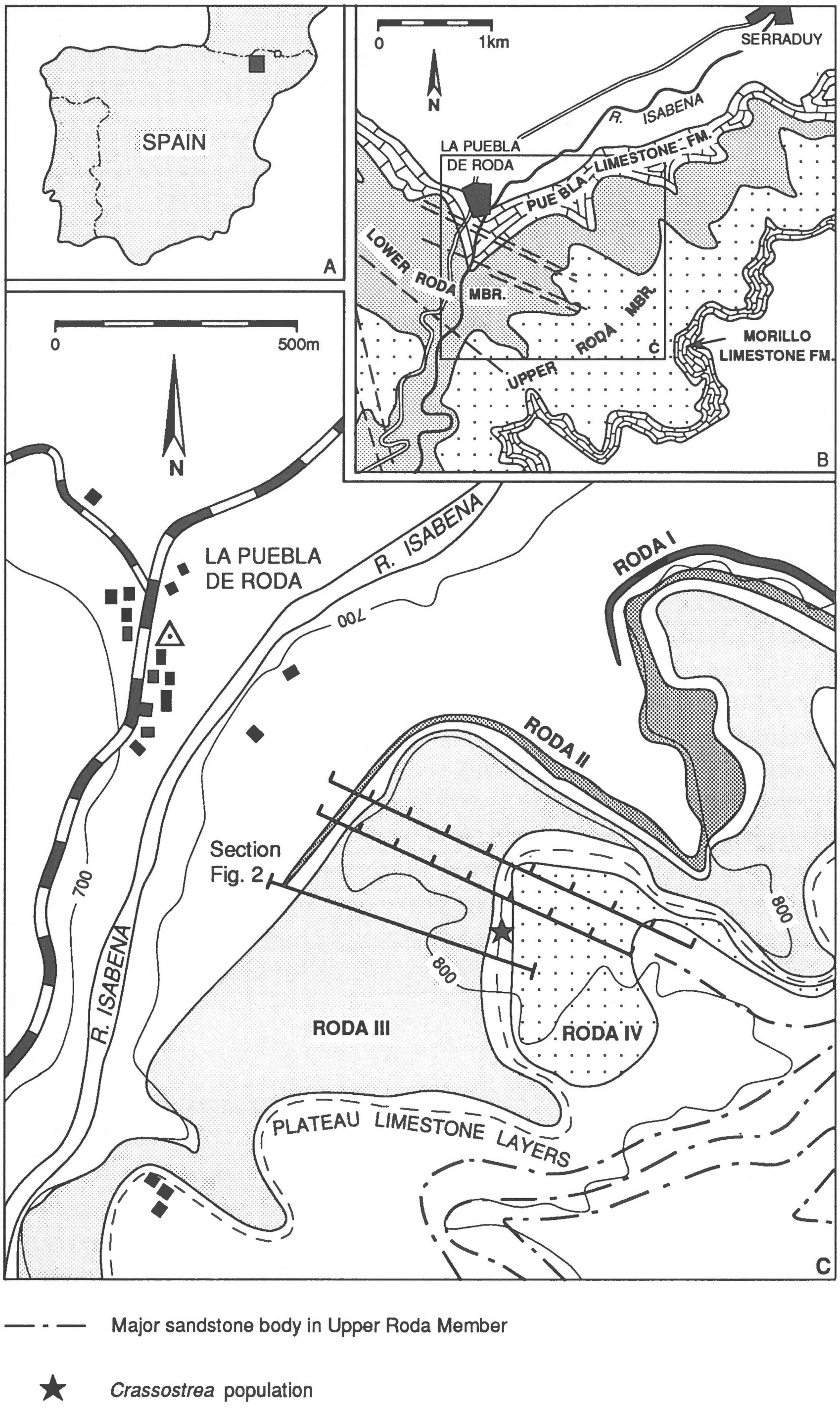

Fig. 1. Geological map of the Roda Formation. The locality of the oyster population is indicated (*); the inset shows the setting of the Tremp-Graus Basin within the southern Pyrenees.

1985, Jimenez 1987, Molenaar et al. 1988, Molenaar 1990, Molenaar & Martinius 1990).

The Tremp-Graus Basin is an intermontane foreland basin, situated in the southern part of the Pyrenean range. It was shaped during an episode of thin-skinned thrust sheet movement in the Paleocene (Williams 1985, Camara & Klimowitz 1985, Puigdefabregas & Souquet 1986). The basin has two major sedimentation zones, the Tremp-Graus Platform and the Ainsa Deep (Nijman & Nio 1975). The basin (with an east-west axis) was connected with the eastern part of the Atlantic Ocean. The Roda Formation is located at the northern margin of the Tremp-Graus Basin. The oyster fossils occur in a thin, 30–40 cm thick, yellow-brown (ochre) bioclastic wacke- to packestone, sandwiched between a series of thin limestone beds, mudstone intervals and a storm layer, and between two major sand bodies, showing large scale cross-bedding (estuary mouth facies zone; Fig. 2). The oyster bed has a present lateral extent of approximately 2 km. Its matrix is very fine grained and micritic with clay mostly concentrated along stylolites around large bioclasts. The medium sized quartz grains are reasonably well sorted and subangular; 95% is monocrystalline. Few other inorganic grains occur (K-feldspar crystals, muscovite laths and zircon). Traces of late dolomitization were observed in the matrix. Fine material accumulated from suspension, and the oysters are likely to have contributed by producing faecal pellets.

General paleontology, taphonomy and environmental setting

Taphonomic processes are likely to have considerably modified the associated fauna. Lawrence (1968) showed the differences between the original and the preserved oyster fauna associations by comparison of a recent and a fossil oyster community. Oyster beds are probably richer in all kinds of animal life than any other single portion of the soft sea bottom for they offer a hard substrate. A total fauna of about 300 species belongs to the studied modern oyster community. However, due to scavengers, decomposer organisms, bioturbation and chemical diagenetic processes the remains of only a few species were preserved in the Roda outcrop. The original shell structure of the oysters has been preserved, no diagenesis or recrystallization has occurred.

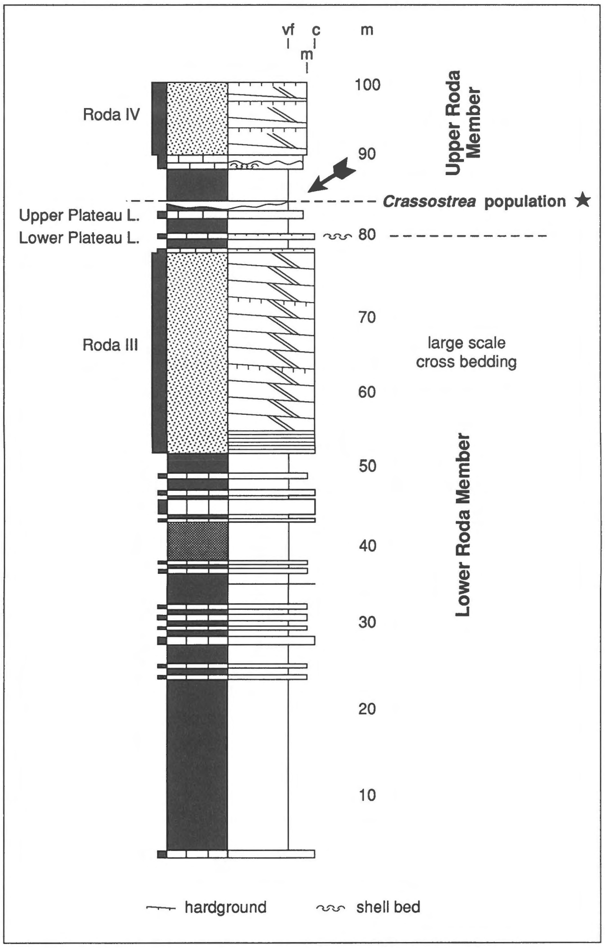

Fig. 2. Schematic section of a part of the Roda Formation showing the stratigraphic location of the oyster population (locality of section indicated in Fig. 1).

The matrix contains many *Nummulites N. globulus* (LEYMERIE), *N. subramondi* (DE LA HARPE) and *N. increscens* (SCHAUB); Jimenez 1987). Other bioclasts are *Discocyclina,* miliolinid and *Alveolina* ghosts, echinoid and encrusting bryozoan remains, and some sparitic shell remains. The diversity in the fossil assemblage is low and bioclasts form about 25% of the sediment volume. The miliolinids and *Alveolina* are abraded and reworked (Jimenez 1987). Neomorphs of *Nummu-*

lites are common; regularly dark brown, well but irregularly rounded homogenized peloids occur, probably secreted by the oysters. Occasional borings in the hinge plate or commissure of the oysters (small round cavities at the surface, connected by a tunneling system) were probably caused by boring sponges after death. *Goniaraea* corals, which settled on oyster shells, reflect a fully marine environment after death of the *Crassostrea* population.

Biostratigraphy based on *Nummulites* reveals an Upper Ilerdian age for the deposit (Jimenez 1987). *Nummulites* tolerates a certain terrigenous influx and lives at water depths between 10 and 80 m in temperatures around 20 degrees and normal salinity waters (Blondeau 1972). The foraminifera are characteristic of a shallow bay facies. A tidal current system from the SSW, as deduced from the basin configuration and a sedimentological analysis of the Lower Roda Member (Nio & Yang 1983, Yang & Nio 1985), introduced reworked miliolinids and *Alveolina* specimens (Jimenez 1987). During the Eocene, the Pyrenees were situated at lat. 30° N. The Paleocene-Eocene climate was on average warmer than it is today. A wider tropical belt must have hemmed the equator. The presence of coral reefs, numerous (sub-)tropical mollusc species (De Renzi 1971, Llompart 1977, Gaemers 1978, Martinius 1988), and the occurrence of large benthonic foraminifera (Gaemers 1978, Jimenez 1987), reflect these tropical conditions.

Paleobotanical evidence includes the calcareous green algae (Gaemers 1978) and pollen flora found in the Ager and Castisent Formations including Taxodiaceae, Nyssaceae, *Sabal* and Myricaceae, all fresh water coastal swamp dwellers. Pollen and fruits of *Nypa* have also been found and proven to be autochthonous (Haseldonckx 1972, Van Buchem & de Boer 1986, Hoorn & Kluiving 1986). The Nypa palm is a tropical brackish water mangrove swamp dweller. The tree genus *Carapoxylon* (Meliaceae) from the Roda Formation, represented by wood fragments, is a typical representative of tropical rainforests (Van der Burgh 1990, pers. comm). As pollen grains of coastal swamp plants are more numerous than those of mangrove swamp plants, it is likely that the fresh water swamps occupied larger areas than the brackish swamps (Gaemers 1978).

Material and methods

The annual growth increments (calcium-carbonate-rich regions between successive growth stop lines) in the hinge plate of the left valve of 333 (out of 350 collected) oysters have been counted from the umbo forward. The specimens were collected on ten 4 square meter surfaces on (and where possible in), the outcrop, randomly distributed. The only criterium was that specimens should show a well preserved, complete umbo regardless of their size.

After cleaning, the annual growth increments were counted. Widths of external annual increments in the hinge plate of left valves with the umbo well preserved have been measured with a reflexmicroscope (three-dimensional measurement), originally designed for tooth measurements in micromammal paleontology, and computed by means of BASIC system software. First, the centre of the cross-lines of the ocular was placed precisely above an external annual line and its position was recorded in three dimensions with the first annual line as point zero. In the second step, the position of the following annual line was recorded twice; firstly to calculate the width of the just passed annual increment and secondly for first position determination in the next annual increment. This procedure was repeated along the entire measurable length of the hinge plate and resulted in accurate width measurements.

Functional morphology

Crassostrea cf. rarilamella is a large (length up to 30 cm, height to 20 cm) inequivalved oyster. It belongs to the so-called soft-bottom dwellers (Fig. 3a; Seilacher 1984). These are forms, derived from cemented ancestors, that have secondarily adapted a reclining mode of life on areas of marine soft bottoms (sands and muds). Passive stabilization

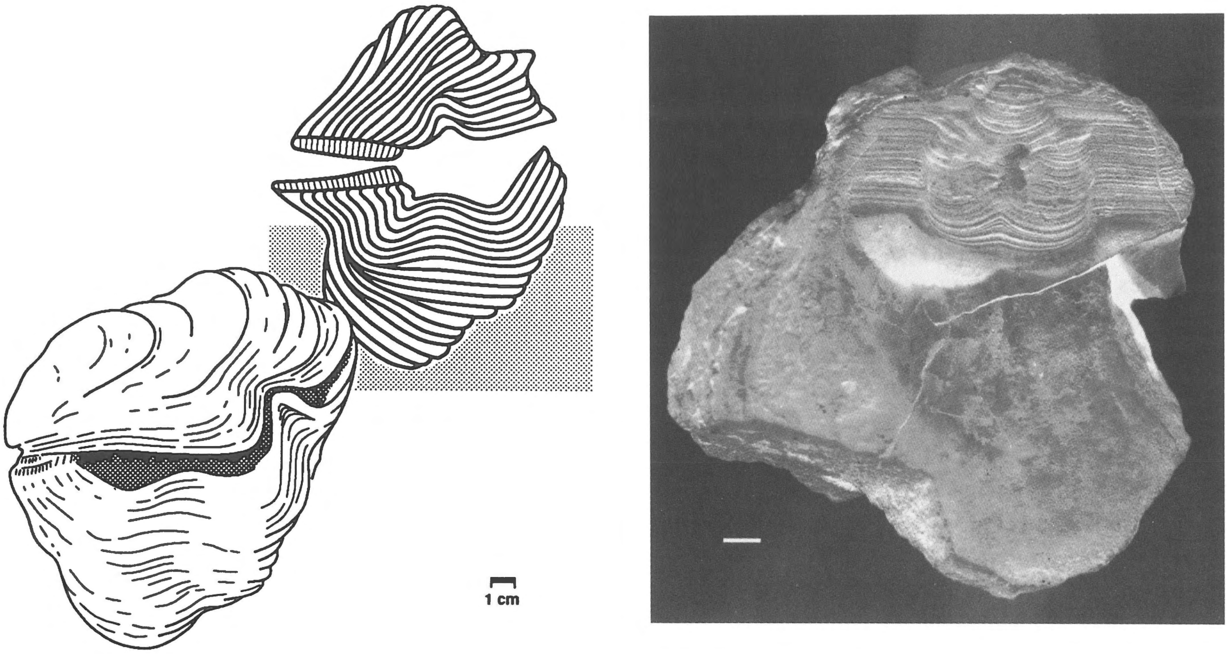

Fig. 3. A: Boulder form of *C. cf. rarilamella;* note raised commissure (from Seilacher 1984). B: Multiple resilifers in left valve of *C. cf. rarilamella.* Scale bar is 1 cm.

without cementation was achieved by developing a stable shape and/or a heavy and commonly oversized skeleton. Several strategies were developed. *C. cf. rarilamella* belongs to the boulder-shaped recliners, which show extreme thickening of both shells. The centre of gravity is not necessarily placed beneath the centre of the shell. Overal shell morphology is slightly variable, as in typical *Crassostrea.* The left valve has a well developed umbonal cavity (in the hinge plate), which may have a length of up to 5 cm. During the adult stage, no further growth of the soft body occurred but continuing shell secretion thickened the valves. Thus the space between both valves is only a small fraction of the total shell volume, and diminishes proportionally with oyster age. Continuing shell secretion also was a function of the calcium metabolism of the oysters and a protection against boring sponges and shell crushing predators as rays. Remains have been found of *Aetobatis* sp. in the Roda Formation (Martinius 1988).

Distribution and ecology

Crassostrea cf. rarilamella was a suspension feeding, sessile animal, inferred from recent oysters of the *Crassostrea* group. The opening between both shells was very small. The heavy upper valve had to be opened against the pull of gravity. Therefore, the ligament had to be tense and the shell opening had to be minimized. The commissure of the left valve is raised, which means that the upper (right) valve fitted within the lower (left) valve when closed (see also Seilacher 1984). The animal could seal itself from a temporarily unfavourable environment.

Self-cleansing of recent *Crassostrea* (Stenzel 1971) is achieved by generating a powerful stream through a sudden contraction of the adductor muscle and this expulses pseudofaeces. As a result, the mantle cavity is kept from fouling and the food-filtering gills are kept from clogging. In addition, the immediate surroundings of a living oyster are squirted free and cleaned of encroaching freshlydeposited silt, mud, faeces and pseudofaeces. This self-cleansing mechanism enables recent and fossil *Crassostrea* to live in brackish coastal waters, lagoons and estuaries. By producing faeces and pseudo-faeces, *Crassostrea* increased sedimentation of very fine and organic rich sediment in its neighbourhood and *Crassostrea* communities formed centres of mud deposition.

Species of *Crassostrea* require higher summer temperatures for successful propagation than *Ostrea,* but most species of both genera live within the tropical and subtropical climatic belts (Stenzel 1971).

Crassostrea seems to be the most euryhaline oyster genus. Some species are predominantly estuarine in distribution (Hudson & Palmer 1976). In the modern *C. virginica* (LINNAEUS) neither eggs nor functioning spermatozoa develop unless salinity exceeds 7.5 per mil. Larvae and young adults grow best at 17.5 per mil and tolerate 10 to 40 per mil (Stenzel 1971).

Thin-sections of the sediment show many faecal pellets. Arakawa et al. (1971) calculated that a raft (one raft carries on the average 420.000 oysters) of the economically important oyster *Crassostrea gigas* THUNBERG from the Hiroshima Bay (Japan) produces 20 metric tons of dry faeces and pseudofaeces. Of these, 20–30% may be settled onto the bottom as biodeposits within one culture cycle (from August to April). The rate of defecation largely increases during autumn, passes through a maximum in October, and gradually falls in winter. Daily studies indicate that larger quantities of faecal matter are produced at night than during daytime. As a result of this biodeposition, the physical and chemical characteristics of the bottom sediment are altered and often cause a high oyster mortality during summer when temperatures are high and waters are stratified. Therefore, fresh input of water by e.g. a tidal current is necessary (Arakawa et al. 1971).

The time-averaged population density of the oyster can be measured directly where the original relative positions of the individuals are preserved. Although many specimens were affected by weathering in the Spanish outcrops, they were still in the original life position. As one may walk on the actual bed in which the oysters occur, it was possible to determine the oyster density on the paleosurface. Six square metres were measured. Densities found are 9, 13, 11, 14, 13 and 12/m^2 (mean: 12; st. dev.: 1.8). This gives an idea of the accumulated oyster shells at a specific level (weathering surface) in the layer.

Only one example was found of two adult *C. cf. rarilamella* specimens still attached to one another. Most probably, young animals started their life attached to tiny shell fragments or other *Crassostrea* specimens. Almost all the specimens are found in life position; only 8% of them have been overturned. Several specimens exhibit divided resilifers in their left valve (Fig. 3b). The reason of this duplication or even triplication is not known.

Population structure

Introduction

Growth banding of annual origin has long been recognized in bivalves. It has usually been explained as caused by slowing down of growth during the winter months. Davenport (1938) recognized annual bands on fossil *Pecten* shells. Hall et al. (1974) distinguished annual fast-growing bands and slow-growing bands on the basis of the number of daily growth lines. Tevesz & Carter (1980) analyzed growth banding of a.o. annual origin in Unionacean bivalves. Ohno (1989) even determined paleotidal characteristics by micro-growth patterns of Late Pleistocene oysters.

An organism is both sensitive and responsive to its environment. A bivalve may preserve these variations within or on its shell as growth lines. Growth lines are defined as abrupt or repetitive changes in the character of an accreting tissue, which means the sudden transition from fast growth to slow growth. Although there is often a direct relationship between internal and external growth lines, either one can occur independently of the other (Hughes & Clausen 1980). External growth lines may reflect growth rate, direction of growth or environmental variations far better than internal growth lines. A growth increment is defined as the interval between two growth lines. The position of the annual line is usually defined as the end of the summer band. Yearly growth speed of molluscan populations is subject to seasonality, therefore, an annual growth increment often consists of a wide band and a narrow band. These variations differ from season to season and cause a fluctuating growth speed. In addition, each oyster has its own growth rhythm.

A life table, constructed with data on annual growth banding, gives the history of a hypothetical group of organisms or cohort (the group of individuals in a population that are all spawned at the same time). Growth and death rates are assumed to have been similar for successive cohorts. The life table group originates from a standard number of births (settlement of oyster larvae), often 1000, which is the so-called 'radix' of the life table (Reyment 1971).

The life table may be used for making hypothetical paleoecological models. The Lx column of a life table may be looked upon as a hypothetical population, classified by age. The hypothetical population is closed to newcomers and to loss by emigration and births are made equal to the number of deaths; hence, this produces a stationary population model. Since of *C. cf. rarilamella* only age at death is known, and since no data on reproduction are available, it is impossible to conclude whether population size varied.

A life table can only be constructed if the population size is stable, and if each individual cohort (for every year class) has the same life table. In order to ascertain this, one would have to determine the ages of the *living* animals and calculate the losses between age x and x + 1. From the life table of *C. cf. rarilamella* it may not be concluded whether the population was stable in number and age distribution. In the present study, such a stability has been assumed in order to be able to discuss and analyze the population structure.

The survivorship curve, constructed from data of the life table, is a graph which shows the number of survivors versus time since birth, or, in other words, the ages of most rapid loss in numbers among the survivors of the cohort. With time, individuals of the cohort gradually die off, leaving a certain number of survivors.

Several factors in the life history of a species influence the shape of the survivorship curve. These include the number and times of the year when recruitment occurs, the type of reproduction, growth rates, mortality rates, and the seasonality of growth interruptions due to unfavourable growing or reproductive conditions.

According to Deevey (1947) and Craig & Hallam (1963), oysters have a survivorship curve which shows a strong positive skewness due to catastrophic juvenile mortality. This is presumed to be characteristic of marine species with pelagic larvae. Almost invariably juvenile mortality for molluscs is high (Cummins et al. 1986); even more, oysters are the type example of a mollusc species with high juvenile mortality. Korringa (1941) gives an example of the high juvenile mortality of oysters. He calculated that out of one million larvae produced of cultivated *Ostrea edulis* only about 250 attach themselves and metamorphose, and of this newly settled spat 95% dies before the onset of the first winter. One of the reasons for this high larval mortality is seasonal or yearly influxes of fresh water. Oyster larvae can only float and spread in normal marine waters; they sink in brackish or fresh waters. Therefore, massive influxes of fresh water cause the death of most oyster larvae. This might have been an important causative death in the Roda paleoenvironment, which would implicate that the population lived at the edge of its distribution area. In general, juvenile mortality of oysters in environments comparable with the paleoenvironment of the Roda Formation (e.g. the Grevelingen and Oosterschelde tributaries in the Netherlands; Nio & Yang, 1983) is high (Dijkema, 1990, pers. comm.).

Data

Absolute age at death of the *C. cf. rarilamella* specimens was determined from the total number

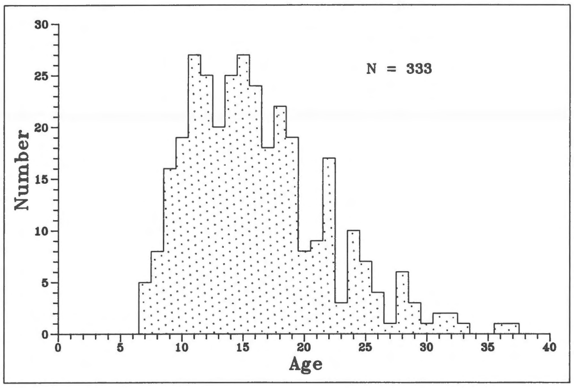

Fig. 4. Age-frequency histogram of *C. cf. rarilamella.* Absolute age at death of 333 specimens has been determined by counting the growth bands (calcium-carbonate-rich regions between successive organic-rich lines) in the hinge plate forward from the umbo. Only complete specimens were measured.

of growth increments of each specimen. The data are compiled in an age-frequency histogram (Fig. 4). Based on this histogram, a life-expectancy table has been constructed (Table 1).

As shown in Fig. 4, a maximum age of 38 years was found (with a mean age of 17 years). This is remarkably close to data supplied by Stenzel (1971) who records two examples of *Crassostrea* species in which the annual layers indicate ages of more than 43 and 47 years, and by Chinzei (1986) who postulated an age of several tens to a hundred years for *Konbostrea konbo* (CHINZEI), a species of the *Crassostrea* group. The median (Table 1) is given because the age-frequency histogram is asymmetrical. Under the microscope a small and a wide band within each annual increment were distinguished and both were measured. Six examples are given in Fig. 7. On the horizontal scale the number of measured bands and on the vertical axis the width of each individual band is given. Fig. 7 gives widths of macroscopically visible bands, separated by (supposed) growth stops.

Discussion and interpretation

The distribution of age classes (or cohorts) can be considered as normal since 95% of the individuals has an age at death which falls within the range of 5–28 years (2 × S); 72% falls within the 11–23 age range (1 × S; Reyment 1971). It provides the statistical base to carry out further research. Normal populations result from the gradual accumulation of shells over a period of time (Dodd & Stanton 1981), a community- (Cadée 1982) or time-averaged death assemblage.

However, it is obvious from Fig. 4 that the age distribution in the histogram is not normal but is positively skewed. This means that the population experienced a high juvenile mortality.

Each value of ‘ex’ in Table 1 summarizes the survival expectancy of individuals beyond age x. As for the other columns, it does not depend on the radix. One expects the value of ‘ex’ to decrease as the age x increases, because, in this case, juvenile oysters (spat as well as the first age classes) have not been found. The value ‘ex’ is only increasing during the beginning of the first year (of which no specimens have been found) when the oyster spat is not yet settled. This is supported by the calculated figures in Table 1. Thus, the life expectancy of these bivalves is gradually decreasing. Irregularities of the histogram are probably the result of small sample size and may be ignored. Thus, the age-frequency distribution can also be considered as unimodal. Unimodality is considered the standard size-frequency distribution in time-averaged death assemblages were taphonomy altered the distribution (Cummins et al. 1986); accumulation of dead shells in the range of 1 to 3 centuries took place in the bed. Size-frequency histograms, however, indicate preserved death in each size class; age-frequency histograms reflect age mortality rates (Craig & Hallam 1963). This does not contradict the in situ and even the in life position of the shells of the adult animals. Death of animals occurred over a long period of time; 100 to 300 cohorts may have been accumulated although not every year will necessarily produce a cohort.

Oyster spat and oysters of the first 5 year classes are not represented in Fig. 4. Reasons why shells of juvenile oysters were not found (except some very young oysters, 0.8–1.3 cm long, attached to adult oysters of which age could not be determined) are manifold.

Size-selective taphonomy is an important factor affecting the number of adults in death assemblag-

Table 1. Life table for the population of *C. cf. rarilamella*

Age x	age interval	f	F	dx	lx	qx	Lx	Tx	ex	px
0	0– 1	0	0	0	1000	0	1000	16814	16.81	1
1	1– 2	0	0	0	1000	0	1000	15814	15.81	1
2	2– 3	0	0	0	1000	0	1000	14814	14.81	1
3	3– 4	0	0	0	1000	0	1000	13814	13.81	1
4	4– 5	0	0	0	1000	0	1000	12814	12.81	1
5	5– 6	0	0	0	1000	0	1000	11814	11.81	1
6	6– 7	0	0	0	1000	0	1000	10814	10.81	1
7	7– 8	5	5	15	1000	0.015	993	9814	9.81	0.985
8	8– 9	8	13	24	985	0.124	973	8821	8.96	0.976
9	9–10	16	29	48	961	0.050	937	7848	8.17	0.950
10	10–11	19	48	57	913	0.062	885	6811	7.57	0.938
11	11–12	27	75	81	856	0.095	816	6026	7.04	0.905
12	12–13	25	100	75	775	0.097	738	5210	6.72	0.903
13	13–14	20	120	60	700	0.086	670	4472	5.94	0.883
14	14–15	25	145	75	640	0.117	603	3802	5.66	0.857
15	15–16	27	172	81	565	0.143	525	3199	5.52	0.851
16	16–17	24	196	72	484	0.149	448	2774	5.52	0.851
17	17–18	18	214	54	412	0.131	385	2226	5.40	0.869
18	18–19	22	236	66	358	0.184	325	1841	5.14	0.816
19	19–20	19	255	57	292	0.195	264	1516	5.19	0.805
20	20–21	8	263	24	235	0.102	223	1252	5.33	0.898
21	21–22	9	272	27	211	0.128	198	1029	4.88	0.872
22	22–23	17	289	51	184	0.277	159	831	4.52	0.723
23	23–24	3	292	9	133	0.068	129	672	5.05	0.932
24	24–25	10	302	30	124	0.242	109	543	4.38	0.690
25	25–26	7	309	21	94	0.223	84	434	4.62	0.777
26	26–27	4	313	12	73	0.164	67	350	4.79	0.836
27	27–28	1	314	3	61	0.049	60	283	4.64	0.951
28	28–29	6	320	18	58	0.310	49	223	3.84	0.690
29	29–30	3	323	9	40	0.225	36	174	4.35	0.775
30	30–31	1	324	3	31	0.097	30	138	4.45	0.903
31	31–32	2	326	6	28	0.214	25	108	3.86	0.786
32	32–33	2	328	6	22	0.273	19	83	3.77	0.812
33	33–34	1	329	3	16	0.188	15	64	4.00	0.812
34	34–35	1	330	3	13	0.231	14	49	3.77	0.769
35	35–36	0	330	0	10	0	10	35	3.50	1
36	36–37	0	330	0	10	0	10	25	2.50	1
37	37–38	1	331	3	10	0.300	9	15	1.50	0.700
38	38–39	1	332	3	7	0.429	6	6	0.86	0.571

mean X = 16.71, standarddeviation S = 5.75, median = 15.78
age interval in standard time-spans x to x + 1

f = frequency of individuals occuring in age interval
F = cumulative frequency
dx = number dying in interval (x, x + 1) out of 1000 born
qx = proportion dying in interval (x, x + 1): mortality rate
lx = number living at age x out of 1000 born
Lx = number of time-spans lived in interval (x, x+ 1)
Tx = total number of time-spans lived beyond age x
ex = observed expectation of life at age x
px = proportion of survivors

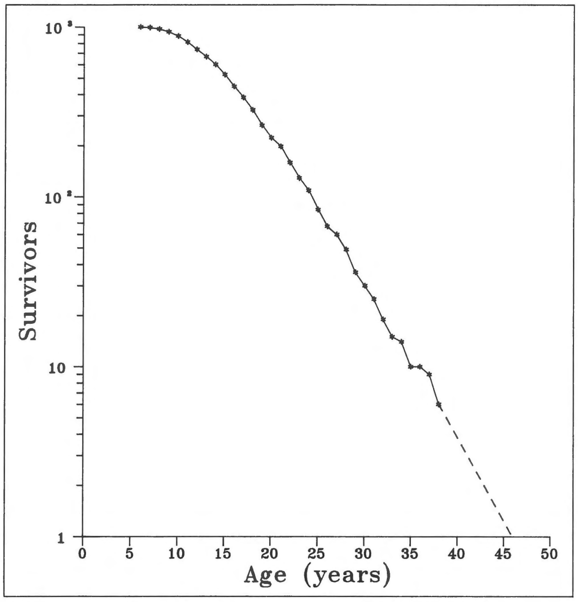

Fig. 5. Logarithmic survivorship curve of *C. cf. rarilamella.*

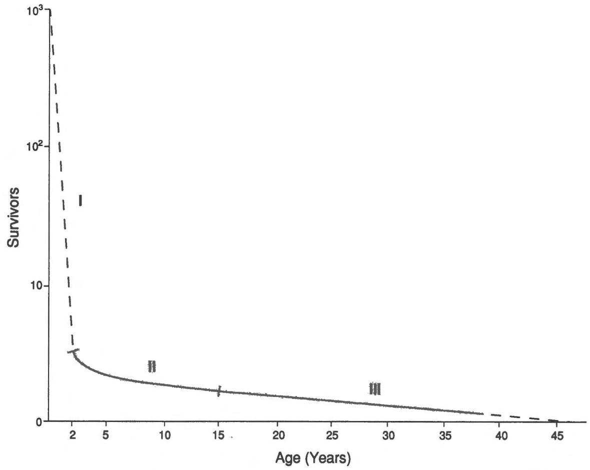

Fig. 6. Hypothetical complete logarithmic survivorship curve of *C. cf. rarilamella.*

es (Cummins et al. 1986). It can be explained for a large part by juvenile-specific taphonomy; adults were preserved better regardless of size (Cummins et al. 1986). Other reasons are: method of collection, mode of death, life and death position, size-selective predation by vagile carnivores (Stump 1975), postmortem transport away from the site of death of smaller individuals (e.g. during storms or spring tide), mechanical destruction, and size-selective diagenetic processes. The larval shell of *Crassostrea* is entirely composed of aragonite, whereas the adult shell is almost entirely calcitic (Stenzel 1971). The largest size classes became proportionally more important because more shells in the smallest size classes dissolved (see Cummins et al. 1986).

Another reason for the absence of small specimens might be that oyster spat and adults lived at spatially different life sites. Juvenile individuals could have migrated during their first or second year to their definite life site where the adults lived. Cadée (1968, 1982) gives examples of spatial separation of adults and juveniles for different groups of marine organisms which shows this phenomenon to be widespread and not only occurring in vagile animals. Adult individuals (age classes 4–40) could not migrate; they did not posses a foot and were to heavy. Therefore, they were fixed in one place (Seilacher 1984). Of course, some of the above mentioned factors could have cooperated.

The logarithmic survivorship curve (Fig. 5 and 6) can be divided into three parts: part I consisting of the missing first year classes, part II with specimens between 6 and 15 years, and part III with specimens older than 15 years.

Part II shows a low but increasing mortality rate. Juveniles between 5 and 15 years apparently had a rather high life expectancy; they were like impregnable forts for predators.

Part III shows a straight line; the proportion dying is the same for each year and is independent of age; in this interval young and old animals all had the same change of dying. Therefore, after the age of 15 years, mortality for *C. cf. rarilamella* was almost constant. This is in agreement with the histogram (Fig. 4) because positively skewed distributions normally indicate something approaching constant mortality (Craig & Hallam 1963).

As part I is not preserved, the survivorship curve shows only a part of the ideal standard curve of Deevey (1947), representing the post-larval life stages of the oyster. However, oysters are the type example of a mollusc species with high juvenile mortality (Deevey 1947) and therefore it is concluded that the complete survivorship curve of *C. cf. rarilamella* probably consisted of a stretch with high juvenile mortality during the first, and probably second, year (part I in Fig. 6), which was followed by a stretch showing a decrease in mortality, and approaching a low mortality level (part II of Fig. 6). In part III mortality reached a low, constant level.

Between age 15 and 34 the hypothetical model (as discussed above) seems to be: $lx = ap$, which would mean that $\ln(x) = \ln(a) + x\ln(p)$ with $a = 1000$. Computation of the regression coefficient (with lx on the vertical and x on the horizontal axis) gave a value of -0.0836 (with 95 percent confidence; two-sided student t-test). The regression coefficient is a measure for the mean yearly decrease of a population. It is thus concluded that the mean yearly decrease for the *Crassostrea* population after the first ten years was very low. The oysters could expect a high maximum age. The number and times of the year recruitment occurs has only very indirect influence on the survivorship curve, because the oyster lived in (sub-)tropical regions and year classes are being examined. Peaks in a living population caused by annual recruitment will not appear in the dead population in the absence of an annual growth or mortality variation (Sørensen 1984).

The growth curve patterns (Fig. 7) show that growth was indeed not a constant factor. Considerable variations in the widths of the individual bands occur within one annual growth increment. In a study on the variability in the formation and detection of growth increments in bivalve shells, Hughes & Clausen (1980) found that different specimens collected from the same biotope did not show any one-to-one increment relationship, although increment width trends may be present.

The increment width variations in *C. cf. rarilamella* are caused by seasonal variations and internal rhythms of the oysters; regular yearly variations in e.g. nutrient or oxygen supply, and temperatures cause variations in growth speed. Peaks reflect faster growth, depressions reflect slower growth. Occasional extreme variability in the width of the bands or breaks in growth pattern might have been caused by variations in growth for morphological or structural reasons. This could happen at the phase in which increase of the soft body more or less stopped but the shell continued to be thickened.

Figure 7 can be changed into a cumulative growth curve by summing the widths of the individual bands. This gives the length of the hinge plate which is plotted on the vertical axis. On the horizontal axis, the corresponding ages are given. The relation between the length of the hinge plate and the age of an oyster is nonlinear and is often sigmoidal in form (Cerrato 1980). Growth curves in general are habitat- and species-specific; no general model has been recognized that may account for all the different types of growth curves. Size-age relationships depend on many local environmental factors. Figure 8 shows a plot in which the growth curves of 6 specimens are given. They were chosen arbitrarily and only because their measured growth pattern curve was long enough. Curves of oyster 7 and 21 deviate from those of oysters 4, 6, 12 and 19. The last show a more or less similar curve, although their inclinations differ. No growth curve will precisely match another because every specimen has experienced slightly different environmental conditions; even more so in a time-averaged death assemblage. The curves do not show a gradual decrease in inclination at higher age, as is usually the case for bivalves. This is due to the fact that the shell of *C. cf. rarilamella* continued to grow and thicken during the adult stage, even when the soft body stopped growing. Thus, their functional morphology (life position and adaption to a muddy substrate; Seilacher 1984) is expressed in their cumulative growth curve.

r- and K-strategy

An organism adapted to a stable, predictable environment has less need for rapid dispersal, growth, or reproductive capabilities. In stable habitats, population abundances are close to the carrying capacity of the environment. To maintain itself in such an environment, the organism is dependant primarily on its ability to compete for resources. Natural selection favours increased specialization at the expense of a high reproductive capacity. An organism adapted to a stable environment will

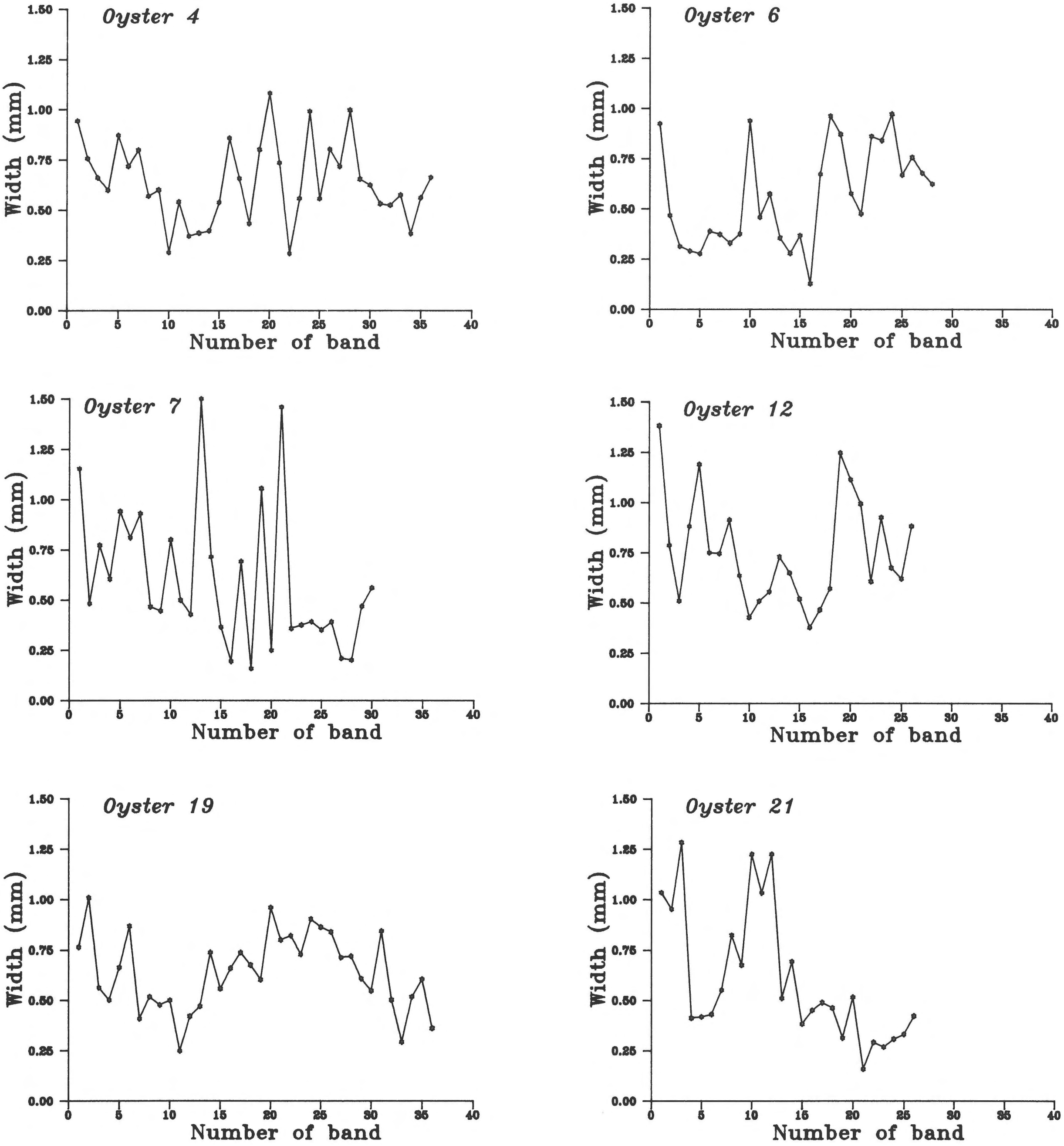

Fig. 7. Graphs of growth pattern of *C. cf. rarilamella* (oysters no. 4, 6, 7, 12, 19 and 21). Distances between macroscopically visible growth lines have been measured (see text for explanation).

therefore be a specialist (equilibrium species or K-strategist; Cerrato 1980; Table 2). Several characteristics of the environment and the *Crassostrea* population are in agreement with K-selection; the fairly constant and predictable subtropical climate, the constant mortality and population size, the large body size, and the long length of life all indicate that *Crassostrea* was a K-strategist. However, some r-strategy influences can be found in e.g. the environmental setting (the inner part of an estuary) where channel shifting could occur and salinity might have fluctuated due to changes in freshwater influx. Organisms can be characterized by the relative importance of r- (rate of increase) and K- (saturation density) selection, the ends of a continuum, in their life cycles. *C. cf. rarilamella* was (much) more subject to K-selection. *C. cf. rarilamella* thus shows a survivorship curve of Type I (Deevey 1947) with high juvenile mortality and K-selection. This is an unusual combination because high juvenile mortality is most commonly linked with r-selection (Deevey 1947; Craig & Hallam 1963; Cummins et al. 1986).

External factors, like climate, sediment influx or salinity fluctuations, and invasions of durophage fishes such as rays might influence population size. Storms are known to have occured, as deduced from reactivation surfaces in the giant cross-bedded sets of the estuary mouth facies zone (Nio & Yang 1983) and from large irregular deviations of the bundle sequence, present in the third sand body of the Lower Roda Member. Maximum tidal range deviations for the presumed storm events were estimated to be more than 1 m; they are expressed in random variations as well as in long-period variations of the bundle thickness (Yang & Nio 1985). A tempestite cycle might have influenced the *Crassostrea* population drastically by causing irregular recruitment and death. Death, caused by these storms, would occur through all age classes (= cohorts) and is not limited to e.g. oyster spat. Therefore, this will not be visible as fluctuations in 'qx' (Table 1). Smaller, more frequent storms might have been a more disturbing factor, causing a temporary decrease in offspring. However, these storms are of limited significance for r- and K-strategy.

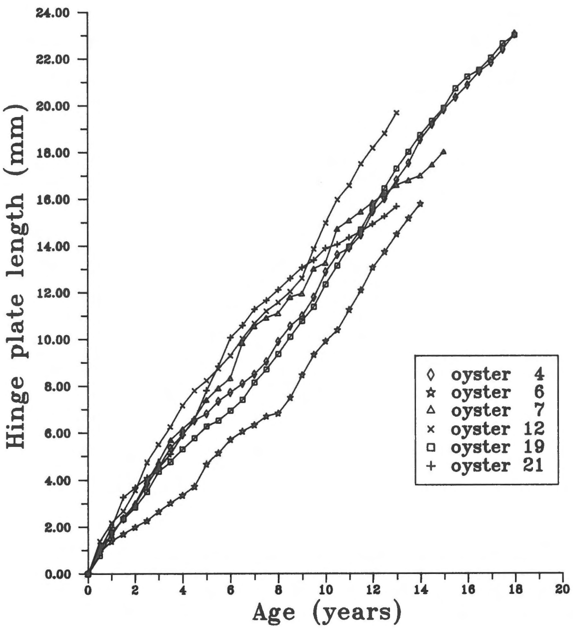

Fig. 8. Cumulative growth curves of oysters 4, 6, 7, 12, 19 and 21.

Conclusions

The oyster bed is intercalated between two ebb tidal delta depositional lobes within a prograding system in water with a normal marine salinity. The

Table 2. Characteristics of r- and K-strategy (modified after Dodd & Stanton 1981)

	r-Selection	K-Selection
Climate	Variable	Fairly constant
Mortality	Often catastrophic	Density dependant
Survivorship (Deevey 1947)	Often type I	Usually types II and III
Population size	Variable in time	Fairly constant in time; equilibrium
Selection favours:	1. Rapid development	1. Slower development
	2. Early reproduction	2. Delayed reproduction
	3. Small body size	3. Larger body size
Length of life	Short, usually less than 1 year	Longer, usually more than 1 year
Leads to:	Productivity	Efficiency

mud deposits in between the two lobes offered a suitable substrate and environmental conditions sufficiently quiet for *Crassostrea cf. rarilamella* to live for a long period. The paleo-environment is interpreted as a quiet shallow bay.

C. cf. rarilamella reached a proven maximum age of 38 years; extrapolation of the survivorship curve gives a possible maximum age of 46 years. The mean age was 17 years. The regression coefficient shows that yearly mortality in the population was low and constant after reaching 5 years.

The survivorship curve is part of the standard Type I curve of Deevey (1947) with high juvenile mortality. It shows a constant mortality for animals older than 15 years. Several characteristics of the animal (high maximum age, constant mortality, heavy thick shell, adaptations to mud sedimentation) indicate that *C. cf. rarilamella* was a K-strategist. This leads to the conclusion that *C. cf. rarilamella* shows the unusual combination of K-strategy and high juvenile mortality.

Adaptations to a muddy substrate (ongoing shell growth to cope with mud deposition) are confirmed by the cumulative growth curve which does not show a gradual decrease in inclination.

Growth pattern studies mostly confine themselves to determine rhythmic trends in growth (related to the earth-moon rotation). Such studies give insight in e.g. the number of days per year, characteristics of the tidal regime or periods of slower and faster growth during a year. This study has focused on population dynamics, using a time unit of one year.

Acknowledgements

I wish to thank G.J. Boekschoten, R.E. Goldring, G.C. Cadée, P.L. de Boer and R. Dijkema for critical comments and discussions on the first drafts of this paper. I am grateful to G. de Jong for the helpful discussions on the possibilities and impossibilities of analysis of the population dynamics of this fossil oyster, to J. van der Burgh for the determination of some wood fragments, and to M. van den Bosch for determination of some ray teeth. I thank M.C. Jimenez for the pleasant and highly stimulating cooperation in the field.

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