MALACOLOGIA, 1973, 14: 223-232

PROC. FOURTH EUROP. MALAC. CONGR.

THE USE OF ECOLOGICAL DATA IN THE ELUCIDATION OF SOME SHALLOW WATER EUROPEAN *CARDIUM* SPECIES

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INTRODUCTION

Throughout the last 2 centuries there has been much controversy concerning the validity of various *Cardium* species, in particular *C. glaucum* Bruguière, due to both the lack of ecological data and the widely accepted use of the morphological characters of shell material alone as a basis for their classification (Russell, 1969). The resulting confusion was highlighted recently by the description of a new species from Danish waters (*Cardium hauniense*), which had been identified as *C. exiguum* Gmelin for more than a century (Petersen & Russell, 1971a). The nomenclatural problems within this genus have already been dealt with by us at this Congress; however, it should be noted that the present nomenclature is based on the acceptance of *C. aculeatum* L. as the type species of the genus name *Cardium* (Lamarck, 1799).

It will be shown that by the combination of field observations, laboratory tolerance tests and field transplant experiments considerable insight may be gained into the taxonomic and ecological interrelationships of the species.

MATERIALS AND METHODS

Our studies involved *Cardium edule* L., *C. glaucum*, *C. exiguum* and *C. hauniense* Petersen & Russell (1971a), which were identified using the methods of Petersen (1958), Russell (1969) and Petersen & Russell (1971b).

Detailed accounts of the methods involved may be seen from Russell (1969) and thus only a brief summary will be given. The preferred habitat of each species was found by measuring parameters, such as salinity, temperature, exposure, exposure to air, tidal amplitude, etc., of the environments of many populations covering as wide a geographical range as possible. The tolerances of the species to those parameters which may be limiting their distributions were tested under controlled laboratory conditions, using samples from populations having similar environmental histories; populations consisting of 2 species were used frequently for direct comparisons thus avoiding non-genetic adaptations (Kinne, 1964). To test the conclusions reached from the laboratory tests, large numbers of cockles were transplanted to sites differing only in certain required respects and their survival recorded. If the transplanted cockles grew they provided a unique opportunity to check the validity of the use of certain shell features by taxonomists wishing to separate the species.

RESULTS

Field observations: From our field observations the preferred habitats of the 4 species (Table 1) show marked differences.

Laboratory tolerance tests: The type of information gained from tolerance tests can be seen from the following results:

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TABLE 1. The habitat preferences and habits of the species, based on field observations.

	C. edule	*C. glaucum*	*C. exiguum*	*C. hauniense*
Salinity range (°/oo)	15 - 35	4 - 100	20 - 35	8 - 12
Temperature range (°C.)	3 - 25	0 - 32	3 - 25	0 - 25
Exposure to air (as % time)	0 - 40	0 - 5	0 - 5	0
Habitat exposure	Estuarine	Lagoon	Estuarine/ Lagoon	Lagoon
Tidal amplitude (m.)	0.2 - 10	Zero - 5	Zero - 10	Zero - 0.1
Habit	Buried in substrate	Buried or on surface	Attached by byssus	Attached by byssus

TABLE 2. The salinity tolerances of the species based on samples from various habitats.

	Site	Habitat	Salinity (°/oo) Tolerances Lower LS_{50}	Upper LS_{50}
C. edule	Lille Strand	20	12.5	38.5
C. glaucum	"	20	14.5	39.5
C. exiguum	Portsmouth	30	24.0	39.0
C. hauniense	Dybso Fjord	11	9.0	13.0
C. glaucum	Orford	10	3.7	30.5
C. glaucum	Etang de l'Arnel	52	22.5	82.5

TABLE 3. The upper lethal temperatures of 2 species under conditions of different seawater availability.

Seawater availability (ml / day)	Upper lethal temperature (LT_{50} in ^{o}C.)	
	C. edule	*C. glaucum*
200	18.7	31.4
1,000	31.4	32.2

TABLE 4. The susceptibility of 2 *Cardium* species, originating from homogeneous and heterogeneous populations, to 'cockle-water.'

	Tidal Amplitude (m)	Survival time (days)		Susceptibility
		Membrane Filtered 'Cockle-water'	Membrane Filtered 'Seawater'	$\frac{\text{Control}}{\text{Test}} \times 100$
C. glaucum	0	85.0 +	93.8 +	110
C. glaucum	0.2	47.8	97.8	204
C. edule	0.2	53.8	114.4	213
C. edule	4	58.8	87.0	148

Salinity. Table 2 shows the results of 3 comparative experiments. The salinities in which 50% of the sample died (LS_{50}) were read off from salinity/response curves constructed from the survivals of the cockles in various salinities after a given time. In contrast to *Cardium edule* and *C. glaucum*, between which no inherent difference in salinity tolerance can be seen, *C. exiguum* and *C. hauniense* exhibit markedly different salinity tolerances. The significance of the latter result can be seen from a comparison with the overlapping tolerances of 2 populations of *C. glaucum* despite the fact that their environmental salinities differed to a greater extent.

Temperature. Field observations suggested that *Cardium edule* was absent from areas liable to summer water temperatures in excess of 25°C. Temperature tolerance tests demonstrated this clearly (Table 3). However, in another test, in which more water was made available to the cockles, the upper LT_{50} was markedly higher. Thus temperature was significant only in conjunction with seawater availability.

Stagnation. From the field observations it appeared that *Cardium edule*, in contrast to *C. glaucum*, required a tidal amplitude in excess of 0.2 m, suggesting that the former required the removal from its vicinity of a toxic metabolite. To test this theory the survivals of samples of *C. edule* and *C. glaucum* from homogeneous and heterogeneous

TABLE 5. The survival and shell features of *Cardium edule* and *C. glaucum* after transplantation to different environments.

	Widewater lagoon		Chichester harbour	
	C. edule	*C. glaucum*	*C. edule*	*C. glaucum*
survival (%)	0	70	87	96
posterior shell margin	crenulate	straight	crenulate	almost straight
internal ribbing	present	present	absent	absent
Periostracum thickness	thin	thick	thin	thick
Mean shell height (as % increase)	16.7	36.6	48.2	48.7

TABLE 6. The geographical distribution of the species. (+ = present; - = absent)

	C. edule	*C. glaucum*	*C. exiguum*	*C. hauniense*
Eastern Baltic	-	+	-	-
Central Baltic	-	+	-	+
Western Baltic	+	+	-	+
Kattegat	+	+	+	-
North Sea	+	+	+	-
Channel	+	+	+	-
North eastern Atlantic	+	+	+	-
Mediterranean	-	+	+	-
Black Sea	-	+	+	-

populations in seawater, in which *C. edule* had been living for a given time (cockle-water), were checked. The results (Table 4) demonstrated an inherent difference between the species; samples of *C. glaucum* from stagnant (i.e., non-tidal) lagoon conditions are less susceptible to cockle-water than those from tidal waters, whereas

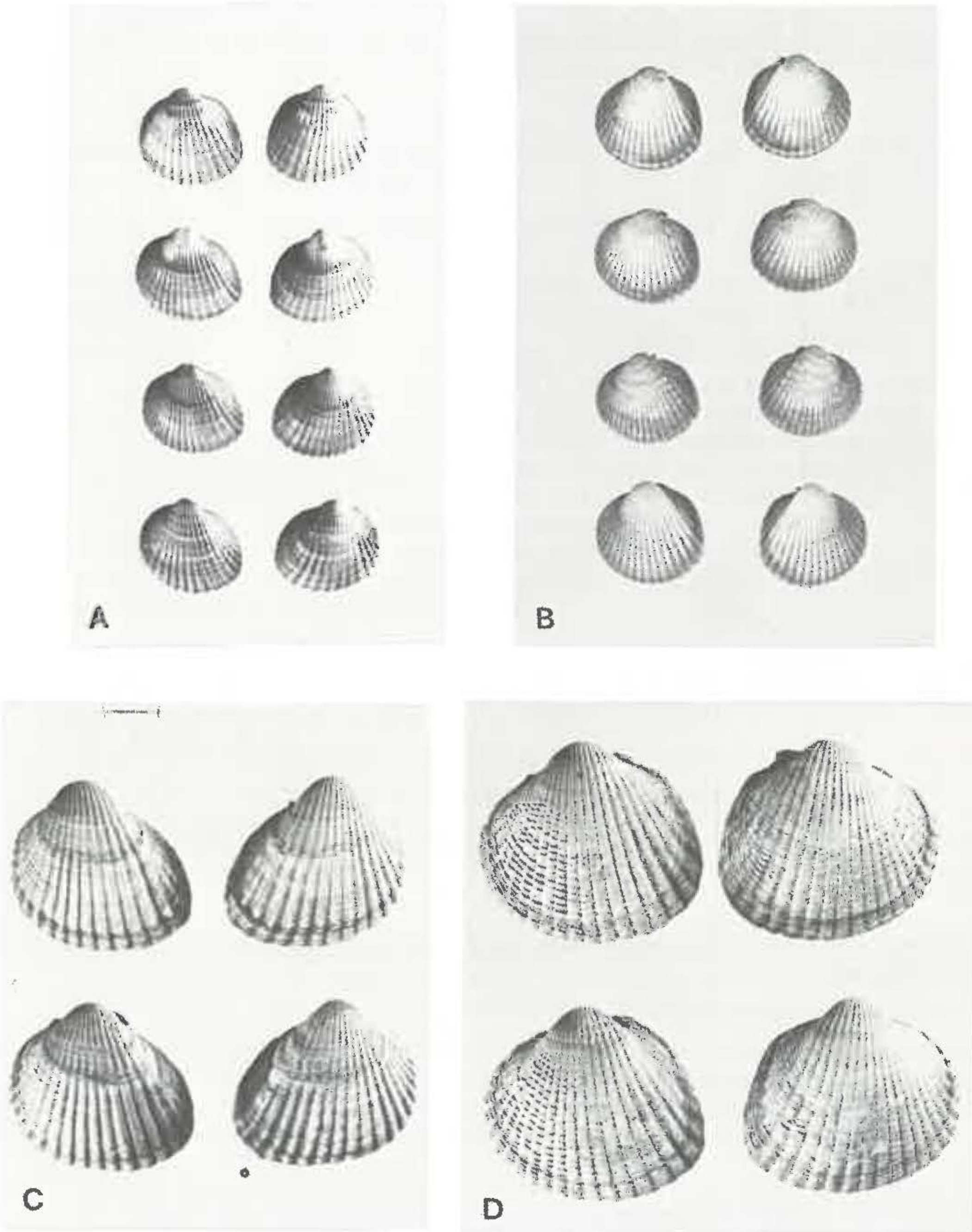

PLATE 1

A, *Cardium glaucum,* before; B, *Cardium edule,* before; C, *Cardium glaucum,* 18 months after transplanting to Langstone Harbour; D, *Cardium edule,* 18 months after transplanting to Langstone harbour. Scale = cm.

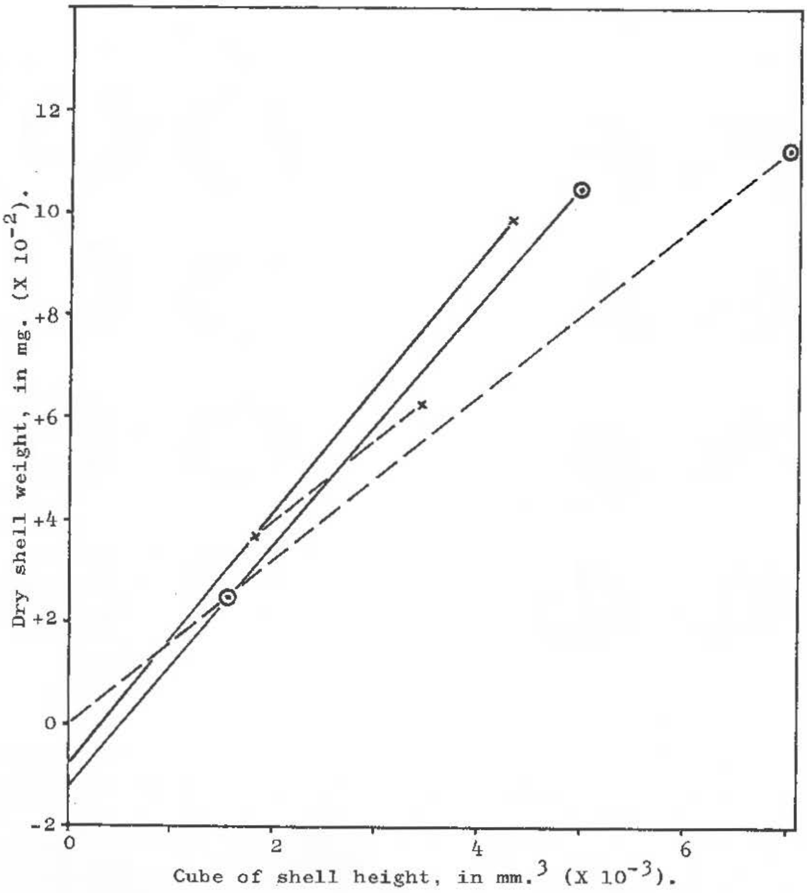

FIG. 1. Mean dry shell weight against the cube of mean shell height for transplanted *Cardium edule* (X) and *C. glaucum* (O), at Ellenore (——), a tidal mud flat, and Widewater (- - -), a nontidal lagoon.

samples of *C. edule* from less tidal waters are *more* susceptible than those from fully tidal estuaries.

Field transplant experiments

By careful site selection it is possible to test the validity of both the conclusions reached from the laboratory tests and the use of various features in the identification of the species. Considering the results of a transplant of samples of young *Cardium edule* and *C. glaucum* to 2 sites having approximately the same salinities and temperatures but different tidal amplitudes (Table 5), it can be seen that both the survival of the cockles and certain shell features are dependent more on the different environments than on the species themselves (Pl. 1). Further information may be gained from a more quantitative approach; for example, from a graph of mean shell weight against the cube of shell height (Fig. 1) it can be seen that the slopes of the lines (i.e., the rates of increase of shell weight with shell height or shell thickness) of the 2 species are parallel at each site. Thus shell thickness is dependant to a marked extent on the environment and, consequently, associated features, like internal ribbing are of no value in the identification of *C. edule* and *C. glaucum*.

Geographical distribution

Having predicted which environmental parameters are limiting the habitat occupation of the species, their geographical distributions can be proposed (Table 6). The absence of a species from any large area, for example the Mediterranean, is impossible to prove but all the evidence to date agrees well with their suggested distributions (Russell, 1971). It is of interest that the range of each pair of closely related species almost covers the entire European coast.

INTERSPECIFIC RELATIONSHIPS

A close relationship between *Cardium edule* and *C. glaucum* is shown by the following features:

Hybridisation

In the laboratory, hybrid larvae which are viable at least to metamorphosis have been reared from gametes originating from homogeneous populations (Kingston, verbal commun.). However, in nature apparent hybrids (i.e., cockles with shell characters intermediate between the species) represent only 2 or 3% of some heterogeneous populations. Boyden (1971) accounted for this by demonstrating a displacement of spawning times in a mixed population, *Cardium glaucum* following some weeks after *C. edule*. Kingston (verbal commun.) has shown that this displacement only occurs in mixed populations and Russell (in prep.) has shown that it occurs when a mixed population is created by transplantation.

Character displacement

In heterogeneous populations some morphological features of the shell in *Cardium glaucum* appear to exhibit the phenomenon of character displacement (Brown & Wilson, 1956); for example:

(a) Despite the larger variation of the mean rib number in *Cardium glaucum* (20.8-27.2) compared with that in *C. edule* (22.5-25.6) from homogeneous populations, data from mixed populations show that the mean rib number in *C. glaucum* is always significantly less than that in *C. edule* (Table 7). The mean rib numbers of each species from partly mixed and partly unispecific populations (Table 8) show that it is the mean rib number in *C. glaucum* which is displaced and not that in *C. edule*.

(b) Some techniques for separating the species do not always hold good for the identification of individuals within unispecific populations, for example the ligament length/shell width ratio (Petersen, 1958). A shift in the plots representing *Cardium glaucum* towards those of *C. edule* occurs when data based only on unispecific populations are compared with data based only on mixed populations (Russell, 1969).

A close relationship between *Cardium exiguum* and *C. hauniense* is seen from their similar habits linked with the ability of the adult cockles to produce byssus; a feature not so far observed for any other *Cardium* species. No living mixed population has as yet been found, but it is proposed to investigate the possibility of hybridisation in the laboratory.

CONCLUSION AND DISCUSSION

From the field observations we conclude that each of the 4 *Cardium* species tends to occupy a different habitat, although each is capable of coexisting with at least 1 of the others; *C. glaucum*, the species tolerating the widest range of habitat, can coexist with all of the other species under various environmental conditions. It has been

TABLE 7. Mean rib number in *Cardium edule* and *C. glaucum* from mixed populations.

Origin of Sample	Mean rib number (no. counted) *C. edule*	*C. glaucum*	Significantly different at P less than
R. Roach estuary	22.24 (62)	20.58 (62)	0.001
R. Crouch estuary	23.44 (35)	21.79 (65)	0.001
Pughavn	24.04 (57)	23.28 (48)	0.05
Ørø	24.62 (50)	23.04 (50)	0.001
Vellerup	24.10 (70)	22.60 (162)	0.001
Nykobing	23.75 (20)	22.04 (46)	0.001
Lynaes	23.75 (30)	23.12 (36)	0.05
Jaegerspris	24.25 (46)	22.91 (30)	0.001

shown previously (Petersen & Russell, 1971b and Russell, 1972) that on both morphological and ecological grounds *Cardium edule* and *C. glaucum*, and *Cardium exiguum* and *C. hauniense*, may be considered as 2 pairs of very closely related species or siblings.

From the laboratory tolerance tests we conclude that the allopatric distributions of *Cardium exiguum* and *C. hauniense* are maintained by the marked difference in their salinity tolerances. The allopatric[3] part of the distribution of *C. glaucum* (i.e., the Mediterranean basin and the majority of the Baltic) is preserved by the inability of *C. edule* to tolerate a low tidal amplitude, especially at high temperatures, and not its relative stenohalinity as suggested most recently by Muus (1967).

Over the sympatric[3] part of their distributions ecological isolation is almost complete; *Cardium glaucum*, being unable to occupy the typical estuarine environment of *C. edule*, possibly due to the inability of their larvae to withstand even moderate exposure (Kingston, verbal commun.) is limited to lagoon habitats. However, in habitats like the shallow semitidal Danish fjords where neither stagnation nor summer water temperatures are excessive the species can be found together. Under such

[3]Note that our usage of the term sympatric follows that of Kohn & Orians (1962) rather than that of its originator (Mayr, 1942).

TABLE 8. Mean rib number in *Cardium edule* and *C. glaucum* in unispecific and mixed populations at Pughavn and Vellerup.

Locality	Population Composition	Mean rib number (no. counted)		Significantly different at P less than
Pughavn	Only *C. edule*	23.68	(63)	no sig. difference
	Both *C. edule*	24.04	(57)	
	and *C. glaucum*	23.28	(48)	0.05
Vellerup	Both *C. edule*	24.11	(70)	0.001
	and *C. glaucum*	22.60	(162)	
	Only *C. glaucum*	23.56	(50)	0.001

conditions hybridisation is reduced to a minimum by the displacement of the spawning time in *C. glaucum* (Boyden, 1971). Also under these conditions *C. glaucum* exhibits character displacement, emphasising the morphological differences between the species.

Kohn & Orians (1962) pointed out that morphological character displacement may lead to the members of those populations sympatric with a closely related species being described as a distinct species. They cited the case of *Agelaius bicolor* Audubon, which was in fact *A. phoeniceus* from those areas where its distribution overlapped that of a sibling, *A. tricolor*, but nevertheless survived in the literature for over 50 years (Mailliard, 1910). Despite the fact that the character displacement in *Cardium glaucum* is nothing like so obvious as the plumage displacement in the male *A. phoeniceus*, similar invalid species, based on samples of *Cardium glaucum* taken from areas where this species is sympatric with *C. edule*, have been erected (Russell, 1972); for example, Reeve (1845) distinguished *C. lamarcki* from *C. belticum* Beck and it was not until more than a century had passed that they were finally amalgamated by Petersen (1958). It should be noted that until quite recently taxonomic studies of these cockles were based on shells in museum collections rather than on freshly collected material and thus the large morphological variation in *C. glaucum* served to confuse rather than elucidate the problem of its taxonomic status. However, it is of interest that the partly sympatric siblings were resolved before the allopatric siblings *C. exiguum* and *C. hauniense*, exemplifying the fact that character displacement results in sympatric siblings differing more from each other than closely related allopatric species (Brown & Wilson, 1956).

The suggestion by Purchon (1939) that transplant experiments would prove useful in the resolution of the taxonomic position of the 'varieties of *Cardium edule*' was indeed valid. However, it should be remembered that their use is limited to the study of siblings whose adults, at least, can coexist in the same habitat; thus with allopatric species the testing of their survivals in a number of different habitats may be an unrewarding prerequisite.

Finally we suggest that this ecological approach, which has clarified the taxonomic position of these 4 *Cardium* species and accounted for their distributions, might well be applicable to other closely related species in this and other genera of marine bivalves.

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