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Cymbium spp. (Gastropoda: Mollusca) as bivalve predators at the tidal flats of the Banc d'Arguin, Mauritania

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Two species of the genus of large gastropods *Cymbium* were observed on the tidal flats of the Banc d'Arguin, Mauritania: *C. pepo* and *C. tritonis*. Average densities on a flat studied in detail were 0.0009 and 0.0014 individuals per m^2, respectively. Both species leave the tidal flats in April and are absent until at least September. Their density on the tidal flats was maximal on sandy sediments. Probably the distribution of their prey species determines the distribution of *Cymbium*. Prey species observed were the bivalves *Anadara senilis* (97%), and an occasional *Solen vagina* and *Venerupis* sp. The annual predation pressure of *Cymbium* on intertidal *Anadara* was estimated to be <1%.

INTRODUCTION

The large shells of the West African gastropod genus *Cymbium* Röding, 1798, have received considerable attention from shell collectors and taxonomists (e.g. Weaver & du Pont, 1970; Bruynseels, 1975; Poppe & Goto, 1992) but ecological studies so far have been rare. The information is restricted to a few details on life history and ecology in taxonomic works, records of species of *Cymbium* in ecological surveys of coastal waters and an occasional publication on the ecology of some species of *Cymbium* (Marche-Marchad, 1977; Marche-Marchad & Rosso, 1978).

All species of the genus *Cymbium* seem to be ovoviviparous (Poppe & Goto, 1992). After fertilization a small number of embryos develops in a pedal gland serving as an incubation pocket. Bratcher (1977; in Poppe & Goto (1992)) records a specimen of *C. marmoratum* containing six juveniles. Poppe & Goto (1992) also record specimens of *C. olla* carrying ten and 12 juveniles, respectively. The juveniles are expelled by the adult at a relatively large size; Poppe & Goto (1992) record a juvenile of *C. pepo* of 55 mm. All species seem to be predators on other Mollusca. They envelop their prey with their giant foot before consumption (Poppe & Goto, 1992).

Dutch ecologists were involved in fieldwork in Mauritania at the Banc d'Arguin tidal flats in 1980, 1985, 1986, 1988, 2001, 2002, and 2003. At all occasions at least some data were collected on *Cymbium* spp. and in 2001 the second author focused his attention on the ecology of *Cymbium*. In this paper we want to summarize our information on *Cymbium* spp. at the tidal flats of the Banc d'Arguin.

MATERIALS AND METHODS

Study area

The Banc d'Arguin (Figure 1) is situated on the west coast of Mauritania (about 20°N) and, due to its tidal range of about 2 m at spring tides, comprises vast areas of intertidal flats. The greater part of these usually very muddy flats is covered with sea grass (*Zostera noltii*) meadows. Based on Landsat-4 MSS data and ground truth (Altenburg et al., 1982; Wolff & Smit, 1990) approximately 412 km^2 are characterized as *Zostera* flats; of these 193 km^2 is densely covered and the remaining 219 km^2 is less densely covered. About 80 km^2 consist of sandy flats. Minor types of flats are dominated by the alga *Vaucheria* (3 km^2) or by dense concentrations of the bivalve *Anadara senilis* (10 km^2). Due to its location adjacent to the Sahara the climate at the Banc d'Arguin is tropical and very arid. The average monthly air temperatures range between 18 and 23°C. Water temperatures in a tidal channel increased

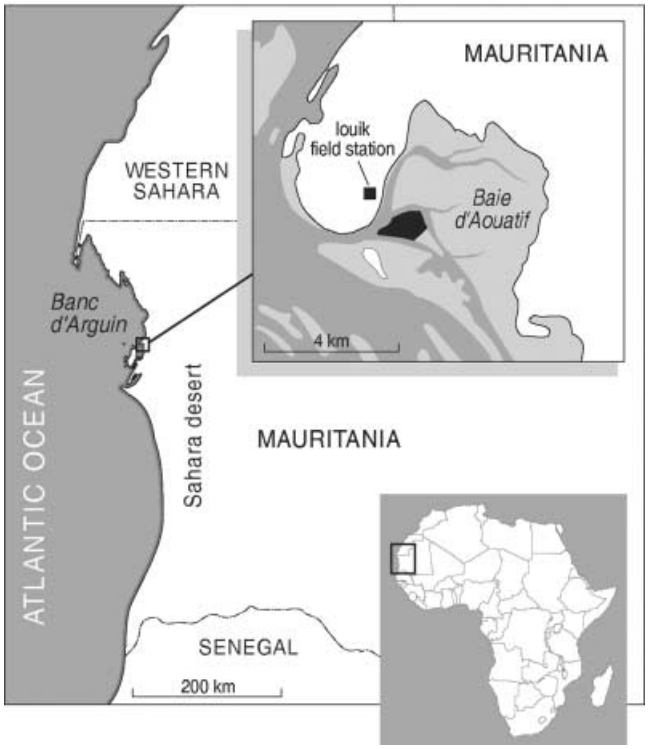

Figure 1. Map of the Banc d'Arguin tidal flat area. The black area represents the *Cymbium* study site in 2001.

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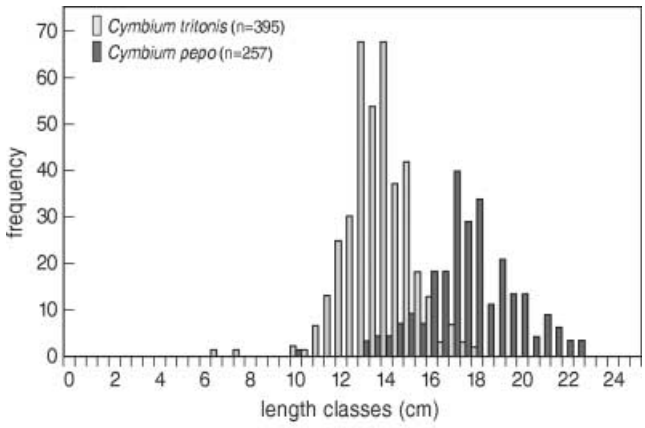

Figure 2. Frequency distribution of shell-length classes of *Cymbium tritonis* and *C. pepo*.

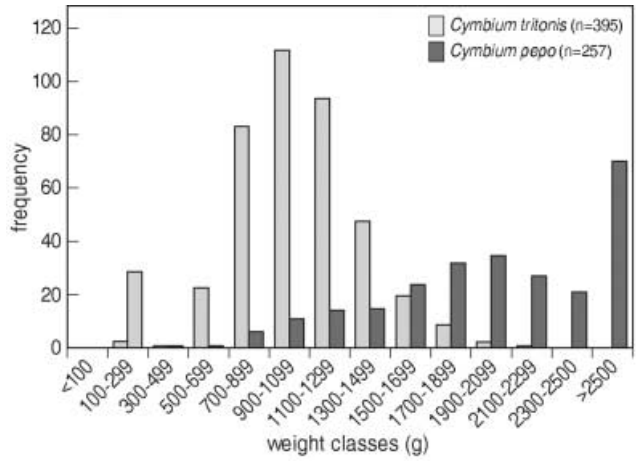

Figure 3. Frequency distribution of wet-weight classes of *Cymbium tritonis* and *C. pepo*. The large number of *C. pepo* heavier than 2500 g is caused by our inability to weigh animals heavier than this value.

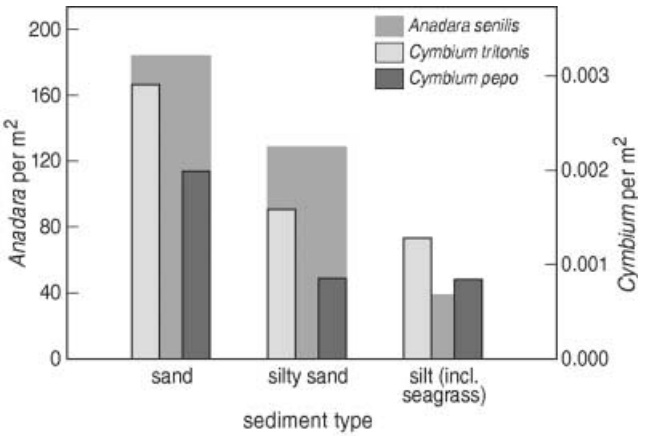

Figure 4. Numerical abundances of *Anadara senilis*, *Cymbium tritonis* and *C. pepo* on different types of sediment.

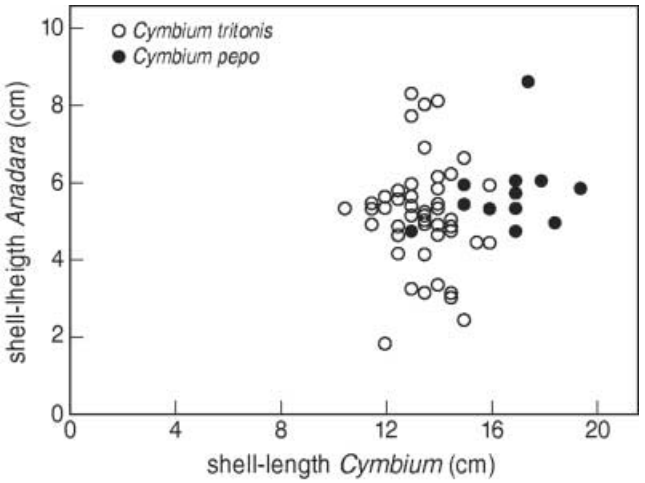

Figure 5. Relationship between shell-lengths of *Cymbium tritonis* and *C. pepo* and shell height of their main prey *Anadara senilis*.

from 18–19°C in mid February to about 21–22° C in mid April 1986; further data are lacking. The winds are mostly from northern directions (trade winds) and vary between 4 to 6 Beaufort; they are strongest in summer. Salinity varies between 38 and 42 psu, but can reach values of more than 50 psu in sheltered creeks close to the shore (Wolff & Smit, 1990).

The Banc d'Arguin is a nearly pristine area. A national park established in 1976 covers about 10,000 km^2 of coastal desert, tidal flats and shallow water. Within the boundaries of this national park about 1500 humans live, whose sole occupation is fishing. They target only fish species and do so from sailing vessels without engines. Other fishermen are not allowed to enter the national park. Pollution is virtually absent because of the very low population density, the absence of any industries or agriculture, and the absence of any river discharge (Campredon, 2000).

The 1980 and 1985 projects at the Banc d'Arguin aimed at ornithological research, in particular at shorebirds. In addition attention was paid to the food of shorebirds and the benthic fauna of the tidal flats. During the 1986 project the ornithological studies were complemented by benthic research, among which was a survey of the entire tidal flat area (Wolff et al., 1987, 1993; Wijnsma et al., 1999). This survey used 82 randomly distributed sampling stations. Although *Cymbium* was never found in the core samples taken, its occurrence at or near the sampling stations was noted. The 1988 project (Michaelis & Wolff, 2001) repeated part of the 1986 spring survey in autumn with the same methods; *Cymbium* was not observed.

Our fieldwork in 2001, which was focused on *Cymbium*, was carried out in the Baie d'Aouatif (Figure 1) near Iwik (between 19°51′56″ and 19°52′32″N and between 16°16′39″ and 16°17′38″W) between February and May 2001. Our observations were made on one particular tidal flat of about 0.6 km^2; at this flat we collected by hand all *Cymbium* we could discover in an area of about 0.28 km^2 at low tide. We not only gathered the gastropods at the dry parts of the flats, but also in shallow creeks running across the flat up to a depth of about 0.5 m. Figure 2 suggests that it is unlikely that we missed many small specimens; this also follows from the relatively large size

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at which juveniles are born (Poppe & Goto, 1992). For each animal encountered we recorded on what type of sediment it occurred (sand, silty sand, silt, or silty sea grass bed). It was also recorded if the animals were found single or mating. If the animal was found with its foot enveloping a prey, species and size of the prey were recorded. For each specimen encountered we recorded shell colour, colour of the foot, length from the tip of the protoconch to end of the siphonal canal, and wet weight, including the shell and any water present within the animal and its mantle cavity. Unfortunately, we were unable to weigh some animals that were heavier than 2500 g due to the maximum limit of our field scale. We also attempted to measure the speed and distance that animals moved across the tidal flats. To this end we numbered the animals on their shell with coloured nail-polish. We intended to determine the position of the animals on the tidal flat daily, but in practice we were unable to recover most of the animals as many of them appeared to move over quite large distances.

Densities of the large bivalve *Anadara senilis* on the same flat (Figure 1) were determined by counting the animals *in situ* in 0.25 m quadrats following the methods explained by Wolff et al. (1987). This method overlooks the 0 year-class; from the size distribution of the animals found we concluded that most individuals were between 4 and 15 years old.

RESULTS AND DISCUSSION

Identification

In 2001 it became clear that the population of *Cymbium* in the Baie d'Aouatif consisted of two different morphological types. We found consistent differences in shell morphology, shell colour, colour of the foot, size, weight and mating behaviour.

One type has a large globose shell with a large protoconch covered by a heavy callus. The protoconch is not entirely surrounded by a low shoulder ridge. The columella usually has four plaits. The inside of the shell is always orange-rose. The foot has a uniform colour without any spots of a different colour. The colour of the foot ranges from orange to flesh-coloured to greyish with either blue or flesh-coloured shades. Based on these characteristics and according to Weaver & duPont (1970), Bruynseels (1975), and Poppe & Goto (1992) this type was identified as the well-known *Cymbium pepo* (Lightfoot, 1786). According to the same authors this species does occur all along the Mauritanian coast.

The second type has a shell morphology similar to that of the first one but its appearance is more slender. Seen from the ventral side the area of the shell aperture compared with the whole area is clearly smaller. The inside of the shell is ivory white or light yellow. The foot is ivory white and has a uniform pattern of orange, green, and blue spots of about 1–2 mm diameter. Among the 16 different species of *Cymbium* distinguished by Weaver & duPont (1970), Bruynseels (1975) and Poppe & Goto (1992), only two resemble our second type: *C. marocanus* and *C. tritonis*.

Cymbium marocanus is recognized only by Weaver & duPont (1970). Bruynseels (1975) considers it to be a junior synonym of *C. cucumis* and Poppe & Goto (1992) simply write that this species is 'not valid'. Weaver & duPont's (1970) picture of the shell bears resemblance to our material. The inside of the shell, however, in their picture looks orange. They describe the live animal as 'gaudily coloured, with a cream base spotted and splashed with varying shades of blue, green, rose and orange'. This agrees well with our animals.

Cymbium tritonis is considered a junior synonym of *C. pepo* by Weaver & duPont (1970). Bruynseels (1975) and Poppe & Goto (1992), however, consider it to be a valid species. It has a flat, somewhat elevated protoconch not covered by a callus. The inside of the shell is cream-white (Poppe & Goto, 1992) or orange (Bruynseels, 1975). A dead animal was pure white with a pattern of blue, green and orange spots on the foot. The species occurs from Morocco to Mauritania. Marche-Marchad (1977) gives a colour photograph of *Cymbium tritonis tritonis* observed at Nouadhibou, Mauritania, which exactly matches our animals.

So, in conclusion, our second type is identical to *C. tritonis* (Broderip, 1830) as conceived by Poppe & Goto (1992), but also to *C. marocanus* (Pallary, 1930) as described by Weaver & duPont (1970). For the time being we will call our second species *C. tritonis*. Our conclusions are in agreement with the revision of the genus in progress by Bail (1999).

Now, *C. pepo* and *C. tritonis* as distinguished in our study area might be no more than the two sexes of a single species. This is unlikely. We investigated 652 specimens among which 88 specimens apparently were copulating. We never observed that *C. pepo* paired with *C. tritonis*; an outcome unlikely to have been caused by chance (χ^2-test for goodness-of-fit; $P \ll 0.001$).

Piersma & Molenbeek (1982) recorded four species of *Cymbium* from the Banc d'Arguin, among other places from the Baie d'Aoutif area near Iwik, viz. *C. cymbium*, *C. marmoratum*, *C. pepo*, and *C. glans*. The first one was found living on the tidal flats, the first three were (also) found recently dead, and the fourth one was considered to be a fossil. The same authors record that *C. cymbium* is used as bait by the fishermen. Wolff et al. (1993) followed the former authors and record *C. cymbium* as a common species at the Banc d'Arguin tidal flats. This must be wrong. It is likely that all earlier records of living *Cymbium* at the Banc d'Arguin by Piersma & Molenbeek (1982) and Wolff et al. (1993) in fact pertain to *C. pepo* and *C. tritonis*.

Size and weight

Figure 2 gives the shell length distribution of the two species. The population of *C. pepo* is significantly (independent t-test; $P < 0.0001$) larger than that of *C. tritonis*. This is reflected in the weight of the two species (Figure 3) showing that *C. pepo* is nearly twice as heavy as *C. tritonis*. The wet weight (g)–length (cm) relationship of the two species is described by $\text{weight} = 5.27 \times \text{length}^{1.9956}$ for *C. tritonis* ($N = 395$; $R^2 = 0.62$; $P < 0.0001$) and $\text{weight} = 5.48 \times \text{length}^{2.041}$ for *C. pepo* ($N = 187$; $R^2 = 0.43$; $P < 0.0001$). In the calculation for *C. pepo* animals heavier than 2500 g have been omitted.

Distribution over time

Cymbium species do not occur on the tidal flats throughout the year. Unfortunately, our research projects

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Table 1. *Number and species of prey taken by* Cymbium tritonis *(N=395) and* C. pepo *(N=257).*

Predator/Prey	*Anadara senilis*	*Solen vagina*	*Venerupis* sp.
Cymbium tritonis	50	1	1
Cymbium pepo	12	0	0

in the various years were mainly carried out in winter and spring. The species were observed in fair numbers on the flats in January, February, March and April. At the end of April 2001 it was clear that the density of both species at the tidal flats had strongly diminished. No *Cymbium* were found on the tidal flats in May 1986 and 2001 and in September 1988. T. Piersma (personal communication) observed the same species in the same area in December 2003. Apparently, *Cymbium* spends only part of the year on the tidal flats. It seems to withdraw to the tidal channels during the hot and windy summer period.

Distribution over the tidal flats

Cymbium is widely distributed over the tidal flats of the Banc d'Arguin. It was always observed in very low densities, but we have neither information on the specific identity nor on the exact densities. The average density on the tidal flat we investigated in 2001 was 0.0009 individuals m^{-2} for *C. pepo* and 0.0014 individuals m^{-2} for *C. tritonis*. The density of the two species over the different types of sediment is shown in Figure 4 together with the distribution of their main prey *Anadara senilis* (see below). The two species of *Cymbium* showed a similar distribution with regard to sediment (χ^2-test; $P>0.10$). They apparently occurred more on sandy sediments. The distribution of their prey was different (χ^2-test; $0.05>P>0.025$), but Figure 4, nevertheless, suggests that to some extent the distribution of *Cymbium* is governed by the distribution of *Anadara*.

Prey choice

Table 1 lists the prey species encountered. Clearly, *Anadara senilis*, which is by far the most abundant bivalve species, was the principal prey. However, *C. tritonis* appeared to be much better in finding other species than we did in our sampling. We never found *Solen* or *Venerupis* in our benthic samples (this study; Wolff et al., 1993; Michaelis & Wolff, 2001); apparently the density of these species was too low to be encountered. Perhaps this observation points to a preference of *C. tritonis* for thinner-shelled species than *A. senilis*. Figure 5 relates the shell length of the two species of *Cymbium* to the shell height (see Wolff et al. (1987) for definition) of *Anadara*. There was no significant relationship; larger *Cymbium* did not take larger prey.

How important are Cymbium *spp. as predators of* Anadara senilis?

The population of *Anadara senilis* at the Banc d'Arguin is virtually unexploited. Hence, it offers an excellent case to estimate natural mortality. Four species of predators have been identified at the Banc d'Arguin as predators of adult *Anadara*: the oystercatcher (*Haematopus ostralegus*) (Altenburg et al., 1982; Swennen, 1990), the two species of *Cymbium* (this study), and the pufferfish *Ephippion guttiferum* (J.A. Vonk, personal communication).

Wolff et al. (1987) estimated the natural mortality of the population of *Anadara senilis* in our study area the Baie d'Aouatif at 10% per year, of which oystercatchers would be responsible for 8% (Swennen, 1990). At our study site in 2001 the density of *A. senilis* was about 100 individuals m^{-2}. The density of the two species of *Cymbium* together was 0.0023 individuals m^{-2}. We observed that among 652 individuals collected, 62 specimens or nearly 10% were feeding on *A. senilis*. If we assume that this reflects the total uptake during the previous high-tide period, the uptake per m^2 per tide would amount to 0.0002 individuals of *A. senilis*. Assuming that annually *Cymbium* feeds for half a year on the tidal flats, their uptake per m^2 would amount to 0.08 *Anadara* m^{-2} or an annual mortality rate of about 0.08%. Therefore, we conclude that *Cymbium* does not play a major role as a predator of *Anadara*, even when we underestimated the uptake per tide by an order of magnitude. However, this conclusion only applies to our study area. Elsewhere at the Banc d'Arguin *Anadara* is less numerous (Wolff et al., 1987), whereas we do not have information on the densities of *Cymbium* on other tidal flats.

Given the low predation rate of *Cymbium* on *Anadara*, we wonder what factor might limit the numbers of *Cymbium* on the Banc d'Arguin tidal flats. One possibility is that population limitation takes place during summer when the animals retreat to the tidal channels. However, we have neither information on the conditions on the bottom of the tidal channels nor on the behaviour of *Cymbium* in this environment. A second possible explanation assumes that *Cymbium* are long-living animals. Figure 2 might be interpreted as showing a large population of old animals and a few recruiting young ones. Anyhow, Poppe & Goto (1992) show that the number of young produced by an adult *Cymbium* is extremely small; they record six to 12 juveniles per adult. We have no information on the age of *Cymbium* at the Banc d'Arguin, but we recall the observations of Wolff et al. (1987) on the age structure of another large mollusc of this area: the bivalve *Anadara senilis*. In 1986 the majority of the population of this species was between 15 and 25 years old. If a similar age structure also holds for *Cymbium*, it could be possible that population regulation takes place in exceptional years only. Finally, as a third possible explanation, we cannot exclude that we underestimated the *Cymbium* predation rates by more than an order of magnitude.

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