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Aquatic Botany 84 (2006) 93–100

Aquatic botany

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Circular pools in the seagrass beds of the Banc d'Arguin, Mauritania, and their possible origin

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Received 22 September 2003; received in revised form 13 July 2005; accepted 14 July 2005

Abstract

The tidal flats of the Banc d'Arguin, Mauritania, are covered by vast beds of *Zostera noltii*. At low tide these seagrass beds appear to be interspersed with partly vegetated, circular pools of 5–25 m diameter. Between February and May 2001 we described these pools and studied their possible origin. Several hypotheses regarding the origin have been developed. The first group of hypotheses assumes that the pools result from erosion activity. Since human disturbance of seagrass beds at the Banc d'Arguin is virtually non-existent, causes should be found in natural bed disturbances and/or tide or wave action. Therefore, small gaps, simulating holes dug by the crab *Callinectes marginatus*, were made to see if they would further erode by tidal currents or waves. The experiments showed no erosion. Neither we found support for other hypotheses assuming erosion to be the cause of circular pools. The alternative group of hypotheses stated that sedimentation on the flats would be responsible. We conclude that accretion of creek remnants is the most likely process behind the development of the pools; this conclusion is based on both mapping of the pattern of pools, the sediment profile in and around the pools and the distribution of seagrass biomass. Also the disturbance experiments showed bed accretion rather than bed erosion and support this hypothesis.

Keywords: Circular pools; Seagrass; *Zostera noltii*; *Cymodocea nodosa*; Banc d'Arguin; Mauritania

1. Introduction

A remarkable feature of the intertidal seagrass (*Zostera noltii* Hornemann) beds of the Banc d'Arguin, Mauritania (Fig. 1), is the presence of circular and semi-circular pools during low tide (Fig. 2). In most cases the bottom of these pools is covered, at least partly, by seagrasses. The only earlier reference to this phenomenon at the Banc d'Arguin is by Wolff and Smit (1990), who briefly stated: "Most tidal flats covered with seagrass beds are interspersed with 0.2–1.0 m deep semi-circular pools with a diameter of 5–25 m." We are not aware of any other study describing similar pools elsewhere.

This study first aims to describe these circular pools and their occurrence at the Banc d'Arguin. Second we attempt to explain their origin. In the following paragraphs we develop, partly based on the literature, a number of alternative hypotheses for the formation of such pools. Subsequently, we use our field data to critically evaluate these hypotheses.

The hypotheses fall in two categories, viz.: (a) the pools are the result of accretion processes on tidal flats or (b) the pools are the result of erosion processes, either leading directly to the formation of pools, or starting from small disturbances gradually enlarging until they result in circular pools.

The accretion category leads to the formulation of two main hypotheses.

(1) The circular pools result from large-scale movements of sediment such as sandwaves travelling slowly over the tidal flats (Patriquin, 1975; Marbá and Duarte, 1995; Bell et al., 1999), or terrestrial sand dunes blown into the tidal flat area (Wolff, unpublished observations).
(2) The circular pools are the result of modification through accretion of existing non-circular depressions in the seagrass beds.

The erosion category of hypotheses necessarily starts with processes creating gaps in closed seagrass vegetation. Around the world many natural as well as anthropogenic causes have been found for such gaps. Large-scale, severe damage may result from storms and flooding (Poiner et al., 1989), disease

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doi:10.1016/j.aquabot.2005.07.009

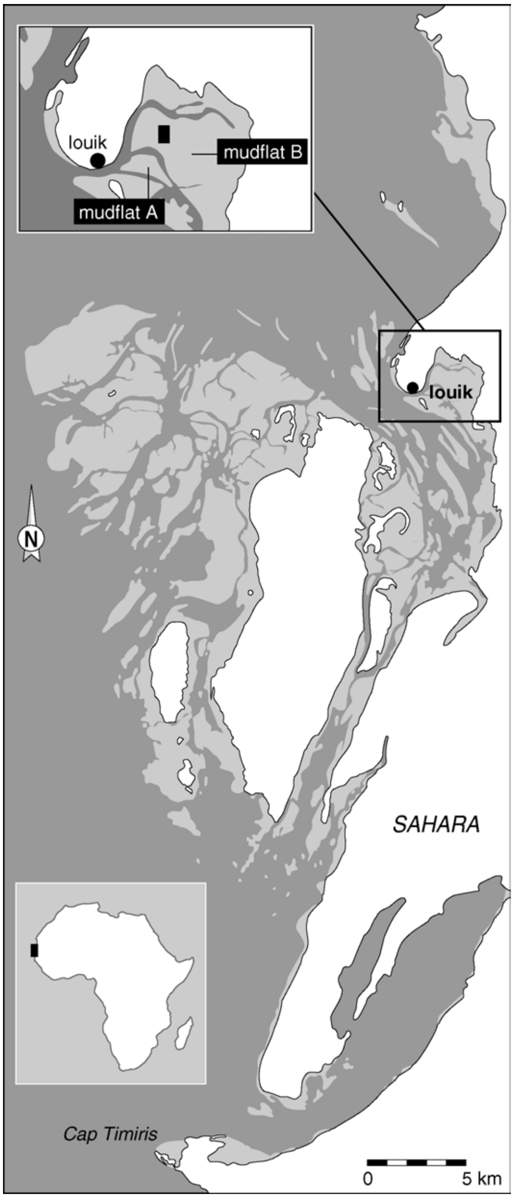

Fig. 1. The area of the Banc d'Arguin, Mauritania, showing the occurrence of tidal flats (light grey). The upper inset shows the Baie d'Aouatif with mudflats A and B; the black rectangle in the upper inset shows the position of the map in Fig. 4.

(Short, 1987), agricultural run off (Preen et al., 1995), industrial run off (Shepherd et al., 1989), oil spills (Jackson et al., 1989) and dredging (Pringle, 1989). It is, however, hard to imagine how such large-scale processes may result in the formation of pools of 5–25 m diameter in otherwise healthy seagrass beds. Hence, we do not consider these potential causes any further.

Small-scale damage to seagrass beds has been demonstrated to be caused by grazing birds, turtles (Thayer et al., 1984; Bjørndal, 1997; Williams, 1988a) or manatees (Preen, 1995), by demersal fish (Orth, 1975) and crustaceans (Suchanek, 1983), erosion by wind and wave action (Patriquin, 1975; Shepherd et al., 1989), as well as propeller (Zieman, 1976) and anchor (Williams, 1988a) damage from boats. Patchy deposition of mats of drifting macroalgae (Cowper, 1977; Holmquist, 1997) or drifting seagrass leaves (Hemminga and Nieuwenhuize, 1991) could result in die-off of the seagrass vegetation and subsequent erosion. Die-off also could result from strong insolation during low tide (Dr. J.E. Vermaat, personal communication). Another possibility is escape of natural gas from the sediment resulting in die-off of seagrasses and subsequent erosion (Prof. P.L. de Boer, personal communication). The relationship between seagrass cover on the one hand and wave exposure and current speed on the other hand (Fonseca and Bell, 1998; Frederiksen et al., 2004) points to the possibility that wind and wave action may cause small disturbances. Such small-scale damage could directly lead to pool formation, or be the starting point for erosion due to waves and currents leading gradually to pool formation.

Fig. 2. Photograph (courtesy Dr Jean Worms) of circular pools in a seagrass bed in the Baie d'Aouatif at the Banc d'Arguin, Mauritania.

Based on the literature, our general knowledge of the Banc d'Arguin environment and common sense we have considered the following hypotheses.

(3) The pools directly result from human activity (e.g. digging for shellfish, bomb craters).
(4) The pools directly result from the activity of large animals (e.g. whales, sharks; Hall et al., 1992).
(5) The pools are started as small disturbances of the seagrass vegetation and are gradually enlarged by erosion due to currents or waves. Causes of small disturbances could be (Hall et al., 1992) damage by waves or strong currents, escaping gas, strong insolation, deposited mats of drifting macroalgae or seagrass leaves, animals digging holes in the sediment, damage caused by feeding animals (e.g. manatees, birds, turtles, fish), and boats.

2. Area, materials and methods

2.1. Study sites

The Banc d'Arguin (Fig. 1) is situated on the west coast of Mauritania between the Sahara desert and the Atlantic Ocean. Due to a tidal range of 1.5–2 m it comprises vast areas of intertidal flats. The greater part of these usually very muddy flats is covered with seagrass (*Zostera noltii*) meadows.

Approximately 412 km^2 have been characterized as *Zostera* flats; of these 193 km^2 is densely covered and the remaining 219 km^2 is less densely covered (Altenburg et al., 1982; Wolff and Smit, 1990; Hemminga and Nieuwenhuize, 1991). A second seagrass species is *Cymodocea nodosa*, growing only at places always covered by water. A third species *Halodule wrightii* occurs less frequently. Wolff and Smit (1990) and Campredon (2000) present reviews of the ecological conditions at the Banc d'Arguin.

This study is based in the first place on fieldwork, including surveys of a large part of the tidal flat area of the Banc d'Arguin, by the second author in 1985, 1986, 1988, 2001 and 2002. Against that background the first author has made detailed field observations and executed field experiments to collect arguments pro and contra the different hypotheses in February–May 2001.

A large part of the tidal flat area of the entire Banc d'Arguin was surveyed in February–April 1986 and in September 1988 (Wolff et al., 1993; Michaelis and Wolff, 2001). More detailed fieldwork was carried out in the Baie d'Aouatif (Fig. 1) near the fishing village of Iouik (or Iwik; 19°53′ N, 16°17′ W) in 1985, 1986, 2001 and 2002 (Wolff et al., 1987; Schaffmeister et al., in press; Wolff and Montserrat, 2005). This bay was also the site of our detailed study on circular pools between February and May 2001. The area was revisited for follow-up observations in February–March 2002.

The Baie d'Aouatif is situated East of Iouik; it is sheltered against the prevailing northerly trade winds and resulting wave action by the Iouik peninsula. Ocean swell does not penetrate into the bay because it is situated behind vast areas of tidal flats and shallow water. The bay covers about 10 km^2 of which about 90% consist of tidal flats. About 70–80% of these tidal flats are covered by seagrass beds, the remainder of the flats is sandy. The bay is surrounded by sebkha, very saline soils without plant growth just above mean high-water mark, and by more or less flat desert areas. Large sand–dune complexes do not occur in the near vicinity. During sand storms a few mm of dust may settle on the seagrass beds, but we never observed that major quantities of sand were deposited on the beds (Wolff, unpublished observations).

2.2. Detailed description of pools

Two areas with pools have been investigated. We started to describe 66 pools on mudflat A (Fig. 1), but for logistic reasons we later switched to mudflat B where we described 30 pools and mapped their distribution. At low tide the water level in the pools was always equal to the level of the adjoining seagrass bed. In both areas the depth of the pools relative to the water level in the pools at low tide was measured with a rod of one meter. The diameter of the pools was determined with a measuring-tape. Pools with a depth less than 10 cm were not included in our study. On mudflat A we assessed the amount of cover by different plant species of the bottom of the pools; if a certain type of cover, e.g. *Zostera*, *Cymodocea*, or Bare-, exceeded fifty percent of the total bottom area, the pool was classified as belonging to that type. On mudflat B a more detailed assessment of all types of cover has been made, not only on the bottom, but also at the rim and in the immediate surrounding area, i.e. up to 2.5 m from the rim. Also the water levels of the pools with respect to each other and that in the nearby tidal creek running across mudflat B were visually estimated during low tide.

Sediment and seagrass biomass profiles have been determined for five pools. Along two perpendicular radial cross-sections soft sediment depths were determined with a rod with a length of 100 cm. The rod was pushed into the muddy sediment until a hard layer, presumably sand or shells, was hit. The seagrass material was obtained with a corer 10 cm in diameter. The corer was thrust into the sediment until a depth of 30 cm, if possible, to obtain all root material. The obtained material was sieved (2.5 mm sieve) at the sample site and stored in plastic bags. The samples were immediately processed in a field laboratory or stored for one night in a dark and cool place. The living seagrass was separated from other material and rinsed. The epiphytes were also removed from the leaves. Fresh weight was obtained and the samples were dried and stored in paper bags. Dry weight measurements were performed in a well equiped laboratory at Haren, the Netherlands, after which the samples were incinerated at 550 °C for 2 h to acquire ash-free dry weight.

2.3. Erosion experiments

To determine if, in case of disturbance, disturbed areas of the seagrass meadow would be enlarged by erosion, fifteen randomly chosen patches of about 40 cm × 30 cm were dug out to a depth of 13 cm. They differed both in distances from the low-waterline and in percentage of *Zostera* coverage. The size was based on the size of the holes dug by the swimming crab *Callinectes marginatus*. Also the kind of substrate was categorized, including the approximate thickness of the soft layer. The duration of the experiment was 45 days and included the equinoctial spring tide with relatively high current speeds. No storms occurred during this period. Higher wind speeds and occasional thunderstorms occur in summer (Wolff and Smit, 1990). The sites were revisited 1 year later in 2002; over the year high winds and thunderstorms will have occurred.

A similar experiment with *Cymodocea* growing in the pools was performed during the same period as the *Zostera* bed erosion experiment. Ten patches were completely cleared of *Cymodocea*. The patches were approximately 0.18 m^2. The time needed to refill the gap could give an estimation of the time needed to overgrow an entire pool.

2.4. Field observations on disturbance

During our entire study period in 2001 we have looked for newly created natural and anthropogenic disturbances of the seagrass beds almost daily. We have intensified these observations during the equinoctial spring tide with high current speeds. Observations were made to see if gaps were created and if small experimental gaps had grown. At the same time we monitored the presence of deposited mats of drifting macroalgae and seagrass leaves.

Finally we collected information on disturbances created by animals, in particular turtles, fish, and crabs, as well as by humans. This was done by investigating disturbed sites carefully for animal traces, and by recording, if possible, the presence of supposedly disturbing animals and humans.

3. Results

3.1. Description of the pools

Circular and semi-circular pools occur all over the Banc d'Arguin. Unfortunately, during our tidal flat surveys of 1986 and 1988 we were not yet aware of the peculiarity of this phenomenon and we did not systematically record the occurrence of pools. From memory, however, we recall that circular pools were common. We have also identified (semi) circular pools on oblique aerial photographs made from a small plane at different places at the Banc d'Arguin in 1986. Finally, Campredon (2000) presents some aerial pictures from different parts of the Banc d'Arguin on which (semi-)circular pools may be recognized.

The pools we measured varied between 2 and 9 m diameter, and 11–53 cm depth at low tide (Fig. 3A and B). Some pools were almost perfectly circular (Figs. 2 and 3A), others more or less oval (Figs. 3A and 4). Length and width of the pools were significantly correlated (Fig. 3A). The water in the pool at low tide was always level with the adjoining seagrass bed. The bottom of the pools is more or less flat. Smaller pools appear to have smaller depths (Fig. 3B).

The seagrass coverage on the bottom of the pools changes character with increasing depth. The results from 66 pools at mudflat A show that the type of bottom coverage is related to the mean depth of the pools (Fig. 5A). Bare pools and *Zostera* pools were significantly deeper (t-test; $p < 0.001$; $n = 66$) than *Cymodocea* pools. Also on mudflat B *Cymodocea* prevails in the shallow pools (ranging from 10 to 30 cm depth). *Zostera* is the major species when the pools are deeper (30 cm and more; Fig. 5B). The distribution of the two species is significantly different (Friedman test: $p < 0.0001$; $n = 31$). A large part of the bottom of the pools can be bare, however (Fig. 5A and B).

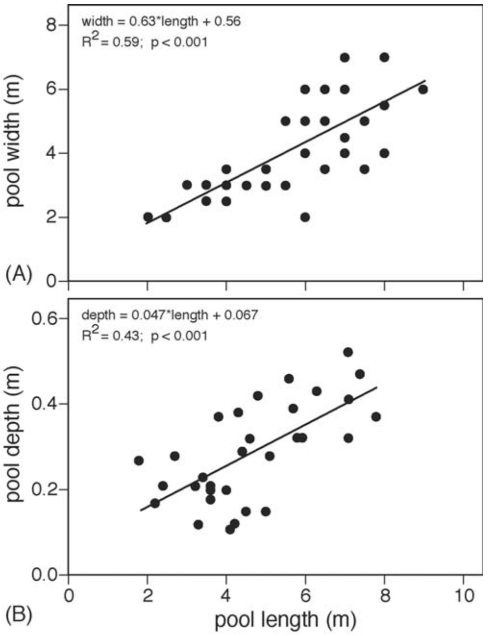

Fig. 3. (A) Length (m) and width (m) of pools. (B) Length (m) and depth (m) of pools. Data courtesy of Britta Schaffmeister.

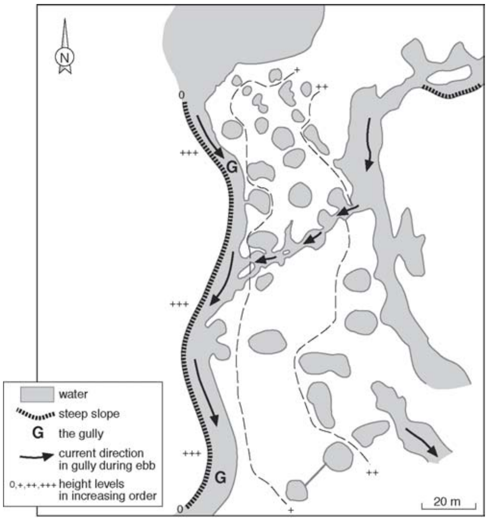

Fig. 4. Map of part of mudflat B. Shown are tidal creeks and pools as occurring at mean low tide. + denotes the water level approximately 1 h after low tide, ++ after about 2 h, and +++ after about 3 h (MSL). All pools shown are among the 30 pools measured on mudflat B (Fig. 5B).

There are significant differences (ANOVA with Tukey's post hoc tests; $p < 0.001$; $n = 18$) in seagrass biomasses within the pools as shown in Fig. 5C. There is a general trend that the highest seagrass biomasses can be found at the rim of the pool. There is only little biomass in the deepest parts of the pools, while the seagrass at the rim grows vigourously (Fig. 5C). The leaves on the bottom are also shorter and mostly covered by sediment or epiphytes whereas the leaves on the rim are relatively clean.

The depth of the hard sediment layer with respect to the water level in the pool at low tide differs between 25 and 65 cm. The hard sediment layer occurs at comparable depths inside and outside the pools (Fig. 5D; ANOVA with Tukey's post hoc tests: $p = 0.45$; $n = 18$).

Most of the pools in the mapped area of mudflat B (Fig. 4) are situated on one side of the tidal creek. The slope on this side is also less steep than the opposing bank. The pools are situated in the lower regions of the mudflat. During neap low tides most of the pools do not emerge.

3.2. Potential natural and human-caused seagrass bed disturbances

Neither in our large-scale surveys nor in our detailed investigation we found indications that waves or currents were responsible for the formation of gaps in an otherwise closed seagrass cover. We paid special attention to the situation around equinoctial spring tide with high current velocities, but also in that case we found no signs of damage. Winds during our study period did not surpass an estimated 6–7 Beaufort.

We never observed mats of deposited drifting macroalgae on the seagrass beds of the Banc d'Arguin. In comparison to seagrasses macroalgae are uncommon at the Banc d'Arguin tidal flats (Wolff, unpublished observations). Deposited leaves of seagrasses sometimes were observed but never longer than a single low-water period.

No live turtles were observed during our investigation in February–May 2001, therefore, the population density in Baie d'Aouatif in the period of our detailed study will have been close to zero. In September 1988, however, green turtles (*Chelonia mydas*) were common, as were observations of drifting *Z. noltii* leaves, which might have resulted from turtle grazing. The distribution of the turtle observations in 1988 suggested that they were mainly feeding on subtidal *Cymodocea*, however. In that period we found no traces on the tidal flats, which could be related to turtle grazing.

In the seagrass beds, also within the circular pools, a swimming crab (*Callinectes marginatus*) digs holes with a diameter of approximately 30 cm. Crab burrows were fairly abundant with about 300/ha. In areas with little or no seagrass the foraging marks of small rays or other demersal fish showed a similar density. We found no indications that such disturbances of the seagrass cover were enlarged by tidal currents or wave action.

The very small local population of fishermen employs wooden sailing vessels. They only catch fish, and no other types of seafood. Their only interference with the tidal flats is placing nets. Usually, however, they fish in the subtidal areas. Anchoring is nearly always done below the low-water line. During our study period in February–May 2001 only one fishing vessel moved around in the Baie d'Aouatif during 5–6 days. We did not observe any damage to the seagrass beds resulting from this activity.

The only vessels with propellors are used by, respectively, illegal foreign fishermen, the wardens of the National Park and scientists. We have no observations that foreign fishermen or the wardens were active above tidal flats; we never observed traces of propellers, which could be ascribed to these people. A few times, however, we did observe minor propellor damage due to outboard engines used by small research vessels. In all cases these traces had disappeared completely a year later.

3.3. Erosion experiments

Measurements of the fifteen patches cleared of *Zostera* showed no increase in dimensions during a period of 45 days. The length and width remained the same and the seagrass boundaries remained sharp, i.e. no new shoots started growing in the dug out patches. The depth, however, changed because along the sides the patches had become shallower. In the centre of the patches the depth had remained the same. One year later, the patches had completely recovered. This was the same for the ten patches cleared of *Cymodocea*.

4. Discussion

4.1. Pools as a direct result of animal or human activity (hypotheses 3 and 4)

In the introduction we developed several hypotheses about the development of the circular pools. Some hypotheses can be rejected right away. The pools most probably do not result from human activities (hypothesis 3). The area is part of the National Park Banc d'Arguin established in 1976. The only activity allowed within the park is fishing by the sparse local population. These people do not dig or otherwise damage the tidal flats, neither before nor after the creation of the national park (Campredon, 2000). This is confirmed by our observations.

We also reject hypothesis 4 on whales or large fish creating the pools. Large whales have never been observed in the tidal flat area; bottlenose dolphins (*Tursiops truncatus*) and Cameroon river dolphins (*Sousa teuszi*) do occur but generally keep to the tidal channels (Wolff and Smit, 1990; Campredon, 2000). Large sharks, rays and skates used to be common at the Banc d'Arguin but recently have largely disappeared due to overfishing. In the 1980s, however, we still observed hammerhead sharks (*Sphyrna* spp.) and guitar rays (*Rhinobatos* spp.) visiting the flats at high tide. We found no signs that hammerheads had interacted with the bottom, but guitar rays did. They caused feeding pits with a diameter of 20–40 cm (Wolff, unpublished observations). This type of disturbances will be discussed below.

4.2. Pools as a result of small disturbances enlarged by erosion processes (hypothesis 5)

Hypothesis 5 concerns small disturbances or destruction of the seagrass beds, which subsequently is the starting point for an erosion process. Below we discuss the presence of small disturbances, the results of our erosion experiments, and some observations on the circular pools themselves.

We never observed disturbances inside seagrass beds apparently caused by waves or currents. On the other hand, such disturbances might be very rare events, which we simply may have missed. We also did not find any indications that natural gas escaped from the tidal flats causing die-off of seagrasses.

We also never observed seagrass die-off because of deposition of drifting macroalgae or seagrass leaves. Hemminga and Nieuwenhuize (1991), however, recorded large quantities of seagrass leaves deposited around the high-water mark at the beach West of Iouik. This appeared to be a local phenomenon at a lee shore; they did not observe similar concentrations at the tidal flats. We conclude that seagrass die-off on the flats due to deposition of macroalgae or seagrass leaves is an unlikely cause of disturbance of seagrass beds at the Banc d'Arguin. We have no indications that seagrass die-off due to strong insolation plays a role; moreover, most circular pools occur in the lower part of the tidal zone, whereas *Z. noltii* still grows at much higher levels.

Manatees (*Trichechus senegalensis*) have never been observed at the Banc d'Arguin (Campredon, 2000), but green turtles (*Chelonia mydas*) are relatively abundant during part of the year. Perhaps several thousands of turtles occur on the entire Banc d'Arguin (Fretey, 2001; Wolff, unpublished observations). We made no observations, however, suggesting that turtles caused disturbances to intertidal seagrass beds. Grazing waterfowl are absent (Wolff and Smit, 1990). Guitar rays (*Rhinobatos* spp.) were found to make feeding pits in the tidal flats; other, less common species of rays probably do the same.

As appears from the Results section human-induced disturbances of the seagrass beds can be excluded, also because of the very low population density (about 1500 people in a national park of 10,000 km^2) and the practice of fishing from sailing boats (Campredon, 2000).

So the only causes of seagrass disturbances seem to be the holes dug by the crab *Callinectes marginatus*, the pits dug by foraging demersal fish, and possibly damage by grazing turtles. These disturbances are all small, and to develop into a pool of several meters diameter and up to 60 cm depth, waves or currents have to be invoked as an erosive force enlarging the small disturbances.

However, our erosion experiments showed no signs of erosion enlarging small disturbances; the cleared patches of both *Zostera* and *Cymodocea* remained approximately same size during 45 days. Even after high current velocities, e.g. after equinoctial spring tide, the patches had not increased in size nor were parts of the seagrass beds elsewhere on the tidal flats washed away. The created gaps had become completely overgrown 1 year later. This indicates that the seagrass beds we studied are not subject to severe erosion; instead, the system seems to be able to recover from small disturbances, such as *Callinectes* burrows. This is in line with observations at the Banc d'Arguin by Vuignier and Pergent (unpublished report) who followed six 0.5 m^2 quadrats from which they had removed all seagrass in November 1987. All quadrats had been recolonized completely within 6 months. Our observations are supported by the conclusions of Marbá and Duarte (1998) on horizontal rhizome elongation rates: 10–127 cm year^{-1} for *Z. noltii* and 7–204 cm year^{-1} for *C. nodosa*.

The rate of recovery of such disturbances is most likely determined by their scale. Small disturbances of seagrass communities on intertidal flats all over the world have been found to recover quickly. The period of recovery of gaps ranged from approximately 7 months for *Halophila decipiens* for small disturbances (Williams, 1988b), to about 2 years for multi-species seagrass meadows and 0.25 m^2 artificial disturbances (Rollon et al., 1998) to several years for *Thalassia testudinum* (Zieman, 1976; Williams, 1988b). After severe disturbances removing the whole population, it took over 3 years to recover (Dethier, 1984; Bell et al., 1999; Olesen et al., 2004). Nutrients and light availability (Williams, 1988b) were identified as the main factors promoting the rate and pattern of recovery following loss.

The difference in seagrass growth between the bottom and the rim of the (semi-)circular pools, also does not indicate (rapid) erosion. Healthy shoots of *Zostera* grow especially along the rim all around the pools; this is rather a sign of sedimentation than erosion. These observations support our conclusion that erosion is unlikely to play a role in the creation of the pools.

So, in conclusion, small disturbances do occur in seagrass beds at the Banc d'Arguin, but observations on small experimental disturbances do not show enlargement to the size of the (semi-)circular pools described. Finally, also the absence of signs of erosion in the pools suggests that they are not subject to erosion.

4.3. Large-scale movements of sediment (hypothesis 1)

The first hypothesis stated suggested that pools could result from large-scale movements of sediment such as sandwaves travelling slowly over the tidal flats, or terrestrial dunes blown into the tidal flat area. Studies by Fonseca et al. (1982, 1983), Fonseca and Bell (1998), Marbá and Duarte (1998) and Frederiksen et al. (2004) indeed show interaction between the morphology of the seagrass beds and currents. This hypothesis cannot easily be rejected, mainly because the time scale of these processes is much longer than that of our research activities.

We do observe, however, that the topography of the tidal landscape is rather stable. The 2001 situation in the Baie d'Aouatif did hardly differ from that inferred from a LANDSAT picture obtained in 1984 (Wolff and Smit, 1990). We also observe that the water in the tidal channels of the Banc d'Arguin is usually very clear, suggesting that little sediment movement is taking place. Finally, there are no large, moving dune complexes close to the Baie d'Aouatif; this is different, however, for other parts of the Banc d'Arguin.

4.4. Modification of existing non-circular depressions in seagrass beds (hypothesis 2)

At site B the pools are mainly found on one side of the tidal creek, whereas on the other side the bank is steep. This and the topographical pattern of the pools (Fig. 4) could suggest a slow movement of the creek over the tidal flat, similar to river movements on land, leaving ox-bows in its trail by cutting off its bends and partial accretion of old distributaries. This hypothesis is in accordance with our measurements of the depth of hard sediment. We interpret the hard sediment layer underneath the seagrass bed outside the pools as the former creek bottom; this layer is found at approximately the same depth inside and outside the pools (Fig. 5D). It is no bedrock, also because the Banc d'Arguin sediments are geologically young (Vernet, 1993).

The occurrence of healthy vegetations of *Zostera* and *Cymodocea* on the bottom of more than half of the pools is another indication that pools are accreting rather than eroding. The active growth of *Zostera* along the rim of the pools further strenghtens the hypothesis that the pools are the result of a sedimentation process. The lush growth of *Zostera* in very shallow water along the rim of the pools may reinforce itself. Agawin and Duarte (2002) showed in their study that seagrass canopies are able to trap up to four times more suspended

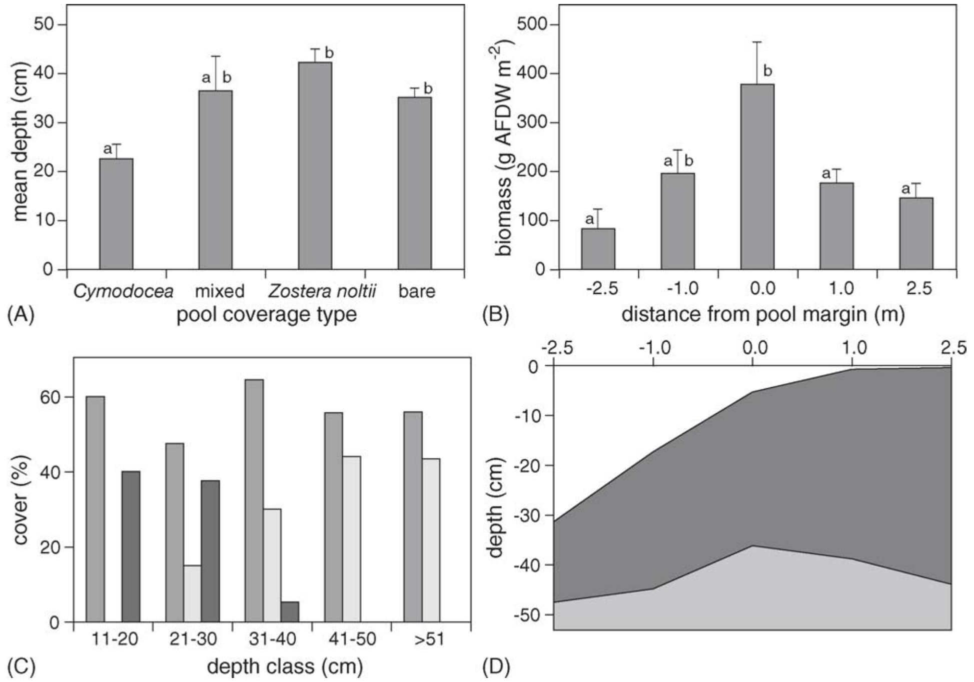

Fig. 5. Characteristics of pools. (A) Type of bottom coverage versus maximum depth for 66 pools on mudflat A with error bars. Pools are designated as a certain type when that type of vegetation covers more than 50% of the bottom. Pools designated 'Mixed' have no prevailing type. Different letters denote significant ($p < 0.05$) differences. (B) Average radial profile of 18 transects through 5 different pools: *Zostera noltii* biomass (g ash-free dry weight m^{-2}). Different letters denote significant ($p < 0.05$) differences. (C) Percentage bottom coverage vs. maximum depth for 30 pools on mudflat B. White columns = % bare; grey columns = % *Zostera noltii*; black columns = % *Cymodocea nodosa*. (D) Average radial profile of 18 transects through 5 different pools: depth (cm) of the soft bottom layer and the hard bottom layer underneath. White area = water; black area = soft muddy sediment; grey area = hard sandy sediment or shell bottom. Negative values on the horizontal axis denote distance from the rim into the pool, positive values distance from the pool into the surrounding seagrass bed.

particles than unvegetated bottoms. Although Mellors et al. (2002) concluded that seagrass beds in tropical Australia hardly trap sediments, we argue that sediment trapping should be substantial on the Banc d'Arguin. Almost all seagrass beds in this area are found on thick layers of very muddy sediment (see also Van Lent et al., 1991); this sediment probably arrives at least partly on the tidal flats with the frequently occuring dust and sand storms (Wolff, unpublished observations). Hootsmans et al. (1993) indeed found substantial trapping of sediment by periphyton on *Zostera* in the Baie d'Aouatif.

We thus suggest that the (semi-)circular pools are probably remnants of former tidal creeks that have silted up inhomogeneously because of localised *Zostera* expansion.

4.5. Final remarks

The clearing experiment with *Cymodocea* in pools showed no regrowth within 45 days. The time factor is obviously the main reason. The time needed to grow new shoots was probably longer than the duration of our experiment. Rasheed (1999) had to monitor cleared 0.25 m^2 patches of *Zostera capricorni* for 2 years to observe recovery. It took *Halophila decipiens* 6–8 months to recover from small disturbances (Williams, 1988b). This suggests that the dynamics of pools can be slow. We observed that pools studied in 2001 still were present, apparently unchanged, 1 year later in 2002. Incidental measurements of accretion rates made at the bottom of our pools in 2001, showed no measurable accretion. From this scanty evidence we are led to believe that the (semi-)circular pools may exist for many years, maybe even decades.

Although we now seem to be able to explain the process of pool creation as an interplay between the dynamics of the creeks on the tidal flats, accretion processes, and overgrowth by *Zostera* and *Cymodocea*, it is still not clear what causes many of the pools to be round and why silting up of these pools is such a slow process. The round shape is likely to be caused by processes at the rim of the pools. One may think of light erosion by wavelets during low tide or grazing of *Zostera* growing at the rim. Parts of the rim protruding into the pool might be more vulnerable to such processes than other parts of the rim.

Acknowledgements

We would like to thank the Director and staff of the Parc National du Banc d'Arguin for allowing us to work at Iouik and for their technical support and hospitability. For our financial support we would like to thank the Marco Polo Fund, the Schure Beijerinck Popping Fund and the Groninger Universiteits Fund. The following persons receive our thanks for not only their professional support, but also their companionship: all personnel at Iouik station, Jean and Elisabeth Worms, and Anne de Vries. Prof. P.L. de Boer we thank for his geomorphological advice. Dr J. Vermaat and two anonymous referees are thanked for constructive criticism of our manuscript.

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