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Habitat use of shrimps in the intertidal and shallow subtidal seagrass beds of the tropical Banc d'Arguin, Mauritania

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Abstract

The Banc d'Arguin in Mauritania is an area characterised by shallow waters and tidal flats with extensive seagrass beds. The aim of this study was to determine the role of the Banc d'Arguin tidal flats as a habitat and a nursery for shrimps. Shrimps were sampled in the Baie d'Aouatif in the intertidal (ponds, *Zostera noltii* seagrass beds and bare sediment) with a push net during high and low tide, a beam trawl during high tide and in the subtidal (*Cymodocea nodosa* and *Zostera noltii* seagrass beds) with a beam trawl during low and high tide from January to March 2002. In total, eleven shrimp species (9349 individuals) were found, the most abundant of which were *Palaemon elegans*, *Hippolyte longirostris*, *H. inermis* (in subtidal) and *Peneaus* spp., whereas *Athanas nitescens*, *Leander tenuicornis*, *Palaemon adspersus*, *Pontophilus fasciatus*, *Sicyonia carinata* and *Processa edulis* subsp. *crassipes* were less abundant. At high tide in the intertidal all species were mainly found in sheltered areas (ponds and seagrass) rather than in unvegetated habitats. Mark-recapture experiments showed that shrimps migrate between intertidal ponds during high tide. Densities in the subtidal were similar during high and low tide, suggesting that there is no substantial tidal migration to and from the tidal flats for any of the species. Two subtidal shrimp species seemed to prefer *Cymodocea nodosa* beds. A large fraction of the individuals of five shrimp species carried eggs. Ten of the eleven species caught were also found as juveniles. The results of this study, and earlier studies, indicate that many shrimp species reproduce in or near the tidal-flat area of the Banc d'Arguin. Some shrimp species, notably *Penaeus kerathurus* and *P. notialis,* are likely to use the area as a nursery, migrating offshore as adults. This suggests that the Banc d'Arguin is an important resource for commercial fishery.

Keywords: Shrimps; Nursery; Migration; Seagrass; Tidal flats; Mauritania; Banc d'Arguin

1. Introduction

Shallow parts of estuaries and coastal bays serve as important nursery areas and adult habitats for many invertebrates and fish, including many species of shrimps (Kuipers and Dapper, 1984; Henderson and Holmes, 1987; Beck et al., 2001). Intertidal and shallow areas are assumed to be good habitats because they offer refuges from predation and a high food abundance. *Peneaus* spp. and *Crangon crangon* are examples of shrimp species that use intertidal nurseries. After hatching in offshore areas, postlarvae of *Penaeus* species invade shallow coastal areas which are rich in food, in particular tidal flats. Huge numbers (up to several tens m^{-2}) of juvenile brown shrimp *C. crangon* inhabit

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sand and mud flats in the Wadden Sea (Berghahn, 1983; Kuipers and Dapper, 1984; Beukema, 1992). Nearly all of these smallest shrimps in the Wadden Sea live permanently on the tidal flats, buried in the sediment during low tide. Shrimps smaller than 15 or 20 mm are hardly ever found in subtidal parts of the Wadden Sea. Larger shrimps (>25 mm) start living more or less permanently in subtidal areas, some of them initially migrating up and down the edges of the tidal channels with the tides (Janssen and Kuipers, 1980).

Seagrass beds have been suggested to be particularly important as nursery areas (Loneragan et al., 1994; Heck et al., 2003). Juveniles of tiger prawns such as *Penaeus esculentus* and *P. semisulcatus* are found only in seagrass communities and other littoral vegetation (Coles et al., 1993; Haywood et al., 1995). Similar results have been found for inshore hatching *Palaemon* shrimp species in Dutch and French tidal areas (Berglund, 1983). Crustaceans may use seagrasses as habitat because the physical structure reduces the likelihood of being detected and eaten by predators (Bell and Pollard, 1989; Heck and Crowder, 1991). Kenyon et al. (1995) showed that small juvenile tiger prawns suffer higher rates of predation in short, thin seagrass and unvegetated habitats and this leads to a decrease in abundance in these habitats. Two species of juvenile tiger prawns preferred seagrass above unvegetated areas when given the choice between seagrass and bare sediment. This indicates that the distribution of juvenile tiger prawns is mainly based on an active choice of habitat and this may be due to the greater predation rates in open areas (Kenyon et al., 1997).

The Banc d'Arguin in Mauritania, West Africa, is a transition zone between the Sahara Desert and the Atlantic Ocean and consists of large expanses of tidal flats (Fig. 1). The shallow water vegetation comprises extensive seagrass beds of *Zostera noltii*, *Cymodocea nodosa* and *Halodule wrightii* which provide a favourable habitat for feeding, reproduction and development of fish and invertebrates (Wolff and Smit, 1990; Jager, 1993). The continental shelf of West Africa, between the Strait of Gibraltar and Cape Verde, Senegal, acts as a source of exploitable stocks of fish, cephalopods and shrimps for one of the most important fishery areas of the world (Duineveld et al., 1993). Apart from being a target species, shrimps may also be an important food item of commercially important fish species (J.A. Vonk, unpubl. results). The potential function of the Banc d'Arguin as a habitat and nursery for postlarvae, juvenile and adult shrimps has, however, hardly been investigated. Preliminary results reported by Campredon and Schrieken (1986) showed that shrimps of the commercially important genus *Penaeus* were present, and that some individuals of *Palaemon elegans* were carrying eggs.

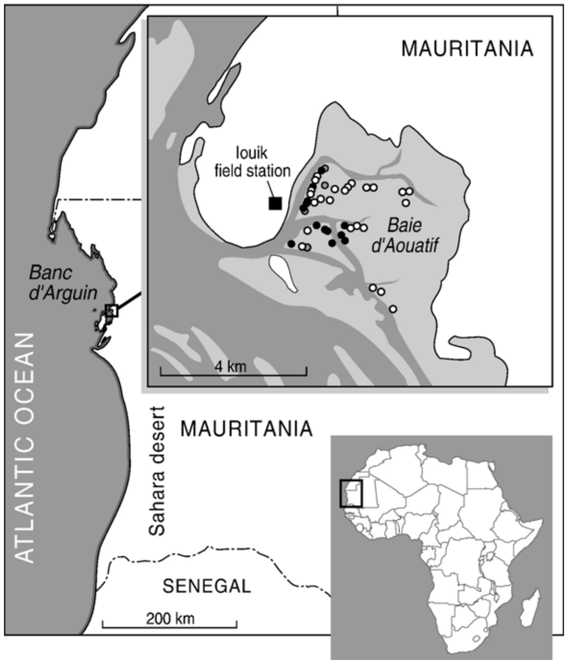

Fig. 1. The study area at the Banc d'Arguin, Mauritania. (a) Location of Mauritania in Africa. (b) Location of the Banc d'Arguin. (c) Intertidal sampling stations in the Baie d'Aouatif (n = 38 sampled with the push net and n = 10 sampled with the beam trawl) each containing a pond, seagrass and bare sediment. The stations sampled with the push net during the daytime only are white and the ones sampled during both day-and night-time are black. The stations sampled with the beam trawl during day-time are grey. Land is white, tidal flats light grey.

The aim of the present study was to determine the role of the Banc d'Arguin tidal flats and shallow subtidal areas as a habitat for juvenile and adult shrimps.

2. Study area and methods

2.1. Site description

The Banc d'Arguin is situated on the Atlantic coast of Mauritania between 19°20′ and 20°30′ N (Fig. 1). It comprises large areas of shallow water and ~500 km^2 of tidal flats. About ~193 km^2 of these flats are covered with dense seagrass beds (almost exclusively *Zostera noltii*) and another ~219 km^2 consist of muddy flats with a less dense seagrass cover. A remarkable feature of the intertidal seagrass beds of the Banc d'Arguin is the presence of circular ponds near the tidal channels with a diameter of 5–25 m and a depth up to 1 m (Wolff and Smit, 1990; Van der Laan and Wolff, in press). The seagrass *Cymodocea nodosa* is largely restricted to places that are covered with water at all times such as the ponds mentioned above, small creeks, larger tidal channels and sublittoral areas of the Banc d'Arguin (Wolff and Smit, 1990). Depth of the tidal channels generally does not exceed 4 m (Jager, 1993). Salinity values usually vary between 38 and 42 psu, but can reach higher values close to the shore (Wolff and Smit, 1990).

The research was carried out in the Baie d'Aouatif (Fig. 1), near the field research station of the Parc National du Banc d'Arguin at Iouik. All sampling was carried out from 22 January to 20 March 2002. In this period the average tidal amplitude amounted to 1.6 m (Wolff and Smit, 1990). Smit et al. (1989) found that water temperatures increased from 18–19 °C in mid February to about 21–22 °C in mid April 1986. The winds were mostly from northern directions and varied between 4 to 6 Beaufort (Wolff and Smit, 1990).

Within the Baie d'Aouatif we distinguished as major types of habitat (1) unvegetated (bare) intertidal flats, (2) intertidal seagrass beds covered by *Z. noltii*, and (3) subtidal seagrass beds with mainly *C. nodosa* but with some *Z. noltii* just below low-water mark. Within the intertidal seagrass beds two sub habitats occurred: (2a) seagrass beds more or less dry at low tide, and (2b) circular ponds containing water at low tide and partly or wholly covered on the bottom by the two species of seagrass. Soon after the start of our study we discovered the importance of these ponds for the occurrence of shrimps and decided to make them an integral part of our sampling scheme.

2.2. Intertidal day-and night-time densities

Many studies (e.g. Young, 1978; Turnbull and Watson, 1992; O'Brien, 1994) indicate that shrimps are more active at night than in the daytime around high tide and therefore more catchable, implying that night samples give better abundance estimates than day samples. As it was not possible to do all sampling at night, day-and night-time catches at high tide were compared for the most abundant shrimp species.

Thirteen intertidal sampling stations (each containing a pond, seagrass and bare sediment) were selected in the area of the Baie d'Aouatif (Fig. 1) and marked with a handheld GPS and poles. Since ponds were located mainly near the tidal channels, the distribution of the sampling stations over the tidal flats is not random. The sampling ponds were chosen at random from the available ponds, however. These stations were sampled once during the day and again during the night (at least half an hour after sunset) between 31 January and 5 March 2002. The stations, each containing three types of habitat, were sampled with a push net (mouth width 40 cm, mesh size 2×2 mm) during high tide at water depths between 0.5 and 1 m. A person walking on the tidal flats, and therefore between knee-and waist-deep in the water, pushed the net over the bottom at an approximate speed of 1 m s^{-1}; fishing speed was probably lower in deeper waters. The area fished was calculated from the number of pushes (standardised at a length of 1 m) with the net. The sampled area was adjusted to shrimp density and varied from 0.4 (one push) to 0.8 (two pushes) m^2. The ponds were sampled from the edges, which were covered with *Z. noltii* and/or *C. nodosa*.

All samples taken in this study were sorted to species and counted. Densities (n m^{-2}) were calculated and all calculated densities were ${}^{10}\log(x+0.01)$ transformed before the statistical analyses presented in this paper. If this or any other transformation did not result in normality, we used non-parametric tests.

Day-and night-time densities were compared within each type of habitat (pond, seagrass and bare sediment). If the densities were distributed normally (one-sample Kolmogorov-Smirnov test) and the variances between treatments were homogeneous (Levene's test of equality), a t-test with equal variances was performed. If the variances were inhomogeneous a t-test with unequal variances was used. In case of non-normality, a non-parametric Mann-Whitney U-test was carried out.

2.3. Intertidal densities

Shrimp densities were estimated in the intertidal in three types of habitat: pond, seagrass and bare sediment. To do so we selected from the available pond sites 38 stations at random, including the 13 stations used for the day-night comparison. These intertidal sampling stations each contained a pond, a seagrass bed and bare sediment. Since ponds were located mainly near the tidal channels, the distribution of the sampling stations over the tidal flats is not random. The sampling ponds were chosen at random from the available ponds, however. These types of habitat were sampled with a push net during the daytime at low tide (ponds) and again during high tide (all habitats) between 29 January and 7 March 2002 (Fig. 1). Sampling was carried out in the same way as for the day-night comparison. The presence of shrimps on the tidal flats on seagrass and bare sediment at low tide was examined by taking bottom samples (0.25 m^2, depth 10 cm) by excavating the sediment, because it was not possible to use the push net on dry tidal flats. These bottom samples were taken at 50 random points on the tidal flats, which were not necessarily located at the 38 stations used for the push net samples. The samples were sieved through a 1 mm mesh size.

Differences between low and high tide densities were tested with the non-parametric Mann-Whitney U-test. Differences in densities between the three types of habitat during high tide were tested with Kruskal-Wallis tests and the differences between pairs of habitats (ponds/seagrass, ponds/bare sediment, and seagrass/bare sediment) were tested with Mann-Whitney U-tests.

2.4. Intertidal densities of Palaemon spp.

Additional data on densities of *Palaemon* spp. with a carapace length larger than 10 mm in ponds, on seagrass and bare sediment in the intertidal were collected with a small beam trawl between 3 February and 14 March 2002. Ten intertidal sampling stations (each containing a pond, seagrass and bare sediment) were selected (see Section 2.3.) over the area of the Baie d'Aouatif (Fig. 1) and marked with a handheld GPS and poles. These stations were sampled during high tide when water depth allowed trawling (more than 1.5 m). The stations were sampled with a beam trawl with a mouth width of 192 cm and knotless nylon netting with a mesh size of 10 mm, hauled by a dinghy with a 15 hp outboard engine at a speed of approximately 0.70 m s^{-1}. The trawled area was calculated from the distance the net was hauled according to a metre-wheel. The sampled area varied from 18 to 100 m^2. The type of habitat sampled was checked by visual inspection.

Differences in densities between the three habitats were tested with a Kruskal-Wallis test and the significant differences between pairs of habitats (ponds/seagrass, ponds/bare sediment, and seagrass/bare sediment) were tested with Mann-Whitney U-tests.

2.5. Subtidal densities

Subtidal sampling stations (five on *C. nodosa* seagrass beds and five on *Z. noltii* seagrass beds) were distributed randomly along edges (>1.5 m deep during low tide) of the tidal channels of the Baie d'Aouatif and marked with a handheld GPS. The type of seagrass at the station was identified from the leaves and roots in the catch. These stations were sampled during both high (tidal flats were flooded) and low tide (tidal flats were dry) between 26 January and 17 March 2002. Any differences in shrimp densities between tidal states can indicate the existence of tidal migration to the tidal flats at high tide, while differences between the two habitats indicated the possible seagrass preferences of the species. Sampling was carried out with the beam trawl in the same way as in the intertidal as described in Section 2.4. The sampled area was adjusted to the seagrass volume in the sample and varied from 3 to 21 m^2 during low tide and 12 to 194 m^2 during high tide.

Densities of shrimps in the subtidal area on *C. nodosa* were compared to densities on *Z. noltii* during low and high tide. For the species with homogeneous variances (Levene's test of equality) among treatments, a two-factor ANOVA was performed, with tidal state (high and low tide) and habitat type (*C. nodosa* and *Z. noltii*) as factors. For the species with inhomogeneous variances two t-tests with unequal variances were performed. First differences in densities between low and high tide within each habitat were analysed and secondly differences in densities between the habitats within each tide-zone were compared.

2.6. Reproductive state

The fraction (%) of animals carrying eggs per length class of each species was calculated to give an indication of the reproductive activity of the species between January and March and an estimation of minimum size of reproducing (adult) animals. The carapace lengths (CL) of shrimps caught on the intertidal and subtidal stations between 26 January and 17 March 2002 were measured with electronic callipers to the nearest 0.1 mm. If the number of animals in the samples was over a 100 individuals, a subsample of minimally 20 individuals of each species was measured. From these samples, the number of individuals carrying eggs was noted. In total 2497 *Palaemon elegans*, 78 *P. adspersus*, 257 *Hippolyte inermis*, 572 *H. longirostris* and 20 individuals of *Athanas nitescens* were measured.

2.7. Population structure

Length-frequency distributions (mean densities per length class) for the most abundant shrimp species were calculated to examine the presence of age-classes during this study, which would give information on the use of nurseries. The CL of *P. elegans* and *H. longirostris* sampled with the push net at the intertidal stations (n = 38, only pond and seagrass) during high tide between 29 January and 7 March 2002 were already measured as described in Section 2.6., additionally this was done for *Peneaus* spp. In total 278 *P. elegans*, 267 *H. longirostris* and 31 individuals of *Peneaus* spp.

Table 1
Mean density (n m^{-2}) of shrimp species caught with the push net (171 m^2 sampled) and the beam trawl (6181 m^2 sampled)

Species	Push net intertidal	Trawl intertidal (>10 mm CL)	Trawl subtidal
Athanas nitescens	0.06	–	0.02
Hippolyte inermis	0.02	–	4.69
Hippolyte longirostris	9.20	–	1.63
Leander tenuicornis	0.00	–	0.05
Palaemon elegans	13.34	0.07	0.46
Palaemon adspersus	0.00	0.01	0.07
Penaeus spp.	0.76	0.05	0.14
Processa edulis subsp. *crassipes*	0.00	–	0.00
Pontophilus fasciatus	0.05	–	0.11
Sicyonia carinata	0.04	–	0.16
Total shrimp density (n m^{-2})	23.47	0.13	7.34

The beam trawl in the intertidal (5552 m^2) only presents individuals with carapace lengths >10 mm, smaller individuals in the sample were not analysed (–).

were measured for this analysis. The length-frequency distribution was calculated for the three species.

2.8. Intertidal migration

To determine whether shrimps on the tidal flats migrate at high tide, a mark-recapture experiment lasting 24 h was carried out. For this experiment a tidal flat area with four ponds close together was selected. In the central pond juvenile (CL 4–8 mm) and subadult (CL 8–12 mm) *P. elegans* were caught during low tide and immediately measured, marked with bright nail polish (large dot on the carapace) and put back into the same pond. At the following high tide (during the daytime, approximately 6 h after marking) shrimps were sampled with the push net (sampling size 0.8–1.6 m^2 per point) in all four ponds and on the seagrass in between them and the number of marked and unmarked shrimps was counted. At the next low tide during the daytime (approximately 24 h after marking) all ponds were sampled again. This experiment was carried out three times on different locations at the tidal flat starting on 2, 8, and 19 March 2003. In total 330 juvenile *P. elegans* (212, 51 and 67 per experiment) and 136 individuals of subadult *P. elegans* (50, 49 and 37 per experiment) were marked. The fractions of shrimps recaptured at each of the three locations (marked pond, seagrass and adjacent ponds) during high and low tide were calculated for each experiment.

3. Results

3.1. Species composition

In total 9349 individuals of eleven different shrimp species were caught on 6352 m^2. The mean densities per species (n m^{-2}) are listed in Table 1. Because *Penaeus kerathurus* and *Penaeus notialis* could not always be distinguished with certainty, they have been grouped as *Peneaus* spp. Overall *Palaemon elegans, Hippolyte longirostris* and *Peneaus* spp. were the most abundant species in the intertidal, whereas in the subtidal *Hippolyte inermis* was the most common species.

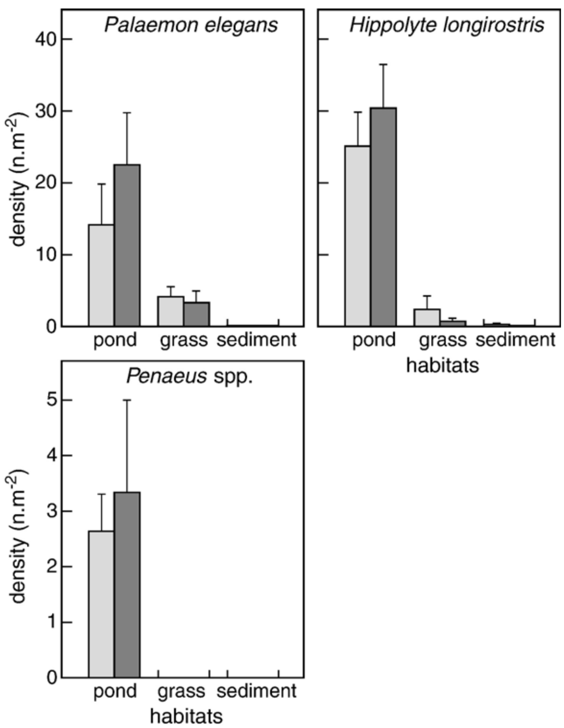

Fig. 2. Intertidal day-(light grey) and night-time (dark grey) densities (+SE) of *Palaemon elegans*, *Hippolyte longirostris* and *Peneaus* spp. Specimens were caught with a push net at 13 stations on three different types of habitat (pond, seagrass and bare sediment) during high tide (HT). Note the different scales on the density axes.

3.2. Intertidal day-and night-time densities

A comparison between densities caught on different habitats in the intertidal (high tide) during day-and night-time was made for *P. elegans*, *H. longirostris* and *Peneaus* spp. (Fig. 2). The mean densities of *P. elegans* in ponds at night seemed to be higher than those during the day, although this difference was not significant (p = 0.092; t-test unequal variances). *H. longirostris* and *Peneaus* spp. occurred, regardless of the time of the day, at similar densities in the ponds (p = 0.568, t-test with equal variances and p = 0.400, Mann-Whitney U-test, respectively).

Much lower densities of *P. elegans* and *H. longirostris* occurred on seagrass outside ponds and no differences between day-and night-time densities were found (p = 0.438, t-test equal variances and p = 0.168, Mann-Whitney U-test, respectively). *Peneaus* spp. was not found on seagrass at all in this sampling. Hardly any shrimps were caught on bare sediment neither during the day nor at night, so no statistical comparisons have been carried out.

3.3. Intertidal densities

The densities of the three most abundant species on the tidal flat are shown in Fig. 3. No shrimps were found in the bottom samples taken at low tide on seagrass and bare sediment, even though in total 12.5 m^2 was sieved. The mean density of *P. elegans* in the ponds at low tide was significantly higher than during high tide (p < 0.001; Mann-Whitney U-test). During high tide the mean densities of *P. elegans* in the three habitats differed significantly (p < 0.001; Kruskal-Wallis test). However, no significant different densities were found between ponds and seagrass (p = 0.824; Mann-Whitney U-test), whereas on bare sediment densities of *P. elegans* were significantly lower (p < 0.001; Mann-Whitney U-test). The mean density of *H. longirostris* in the ponds was not significantly different between high and low tide (p = 0.104; Mann-Whitney U-test). During high tide the mean densities of *H. longirostris* in the three types of habitat differed significantly (p < 0.001; Kruskal-Wallis test) with significantly higher densities in ponds than on seagrass (p = 0.025; Mann-Whitney U-test) and significantly lower densities on bare sediment (p = 0.025; Mann-Whitney U-test). The mean density of *Peneaus* spp. in the ponds at low tide did not differ significantly from that at high tide (p = 0.072; Mann-Whitney U-test). During high tide the mean densities of *Peneaus* spp. on the three habitats differed significantly (p < 0.001; Kruskal-Wallis test) with higher densities in the ponds than

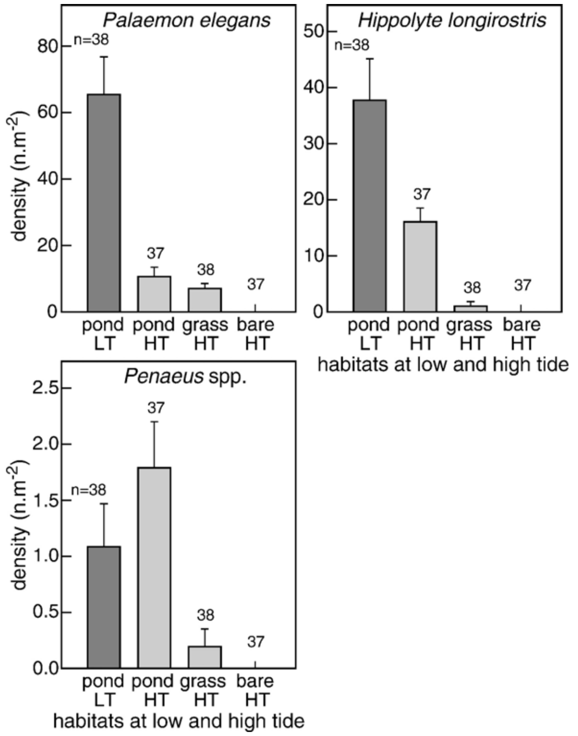

Fig. 3. Intertidal densities (+SE) of *Palaemon elegans*, *Hippolyte longirostris* and *Peneaus* spp. Specimens were caught with a push net in the ponds during low tide (LT) and in all habitats (pond, seagrass and sediment) during high tide (HT) at 37–38 stations. Note the different scales on the density-axes.

on the seagrass (p < 0.001; Mann-Whitney U-test) and bare sediment, which had similar densities (p = 0.553; Mann-Whitney U-test).

3.4. Subadult and adult intertidal densities of *Palaemon* spp.

The mean densities of *P. elegans* with carapace lengths (CL) exceeding 10 mm on the three habitats during high tide differed significantly (p < 0.001; Kruskal-Wallis test) (Fig. 4). The mean density in the ponds was significantly higher than on the seagrass (p < 0.001; Mann-Whitney U-test) and bare sediment, which had equal densities (p = 0.684; Mann-Whitney U-test). *Palaemon adspersus* with CL > 10 mm (Fig. 4) were less abundant than these larger size classes of *P. elegans*. A Kruskal-Wallis test indicated that the mean densities of *P. adspersus* on the three habitats during high tide were not significantly different (p = 0.368).

3.5. Subtidal densities

The densities of the species that were caught with the beam trawl at the edge of the tidal channel are

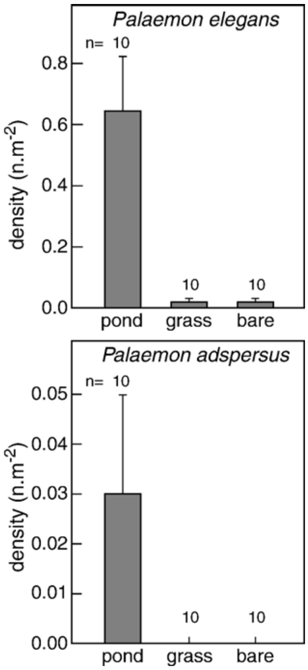

Fig. 4. Intertidal densities (+SE) of *Palaemon elegans* and *Palaemon adspersus* subadults with CL > 10 mm. Specimens were caught with a beam trawl in three different types of habitat (pond, seagrass and bare sediment) during high tide at ten stations. Note the different scales on the density axes.

presented in Fig. 5. *P. adspersus*, *Sicyonia carinata* and *Pontophilus fasciatus* densities showed inhomogeneous variances between treatments and therefore t-tests (unequal variances) were performed for these species. The densities of *P. elegans* were significantly influenced by the tidal state ($p = 0.030$; 2 factor ANOVA). Densities of *P. elegans* were very low at low tide compared to the densities at high tide in *Z. noltii* fields. *P. fasciatus* was significantly affected by the tidal state ($p = 0.018$; t-test unequal variances), and was more abundant on *C. nodosa* than on *Z. noltii* during low tide. Only two species showed significantly different densities between the two species of seagrass. The densities of both *H. inermis* ($p < 0.001$; 2 factor ANOVA) and *H. longirostris* ($p = 0.018$; 2 factor ANOVA) were significantly higher on *C. nodosa* than on *Z. noltii.* Densities of *S. carinata, P. adspersus*, *Peneaus* spp., *Athanas nitescens* and *Leander tenuicornis* were not significantly affected by the tidal state or type of seagrass. Although almost all shrimp densities on *Z. noltii* seemed to be low during low tide, there was no significant effect of the interaction between tidal state and seagrass type on the densities of any of the shrimp species.

3.6. Reproductive state

None of the individuals of *Peneaus* spp., *P. fasciatus*, *L. tenuicornis* and *S. carinata* carried eggs. The fraction of shrimps carrying eggs per length class of the five other species can be found in Fig. 6. For all

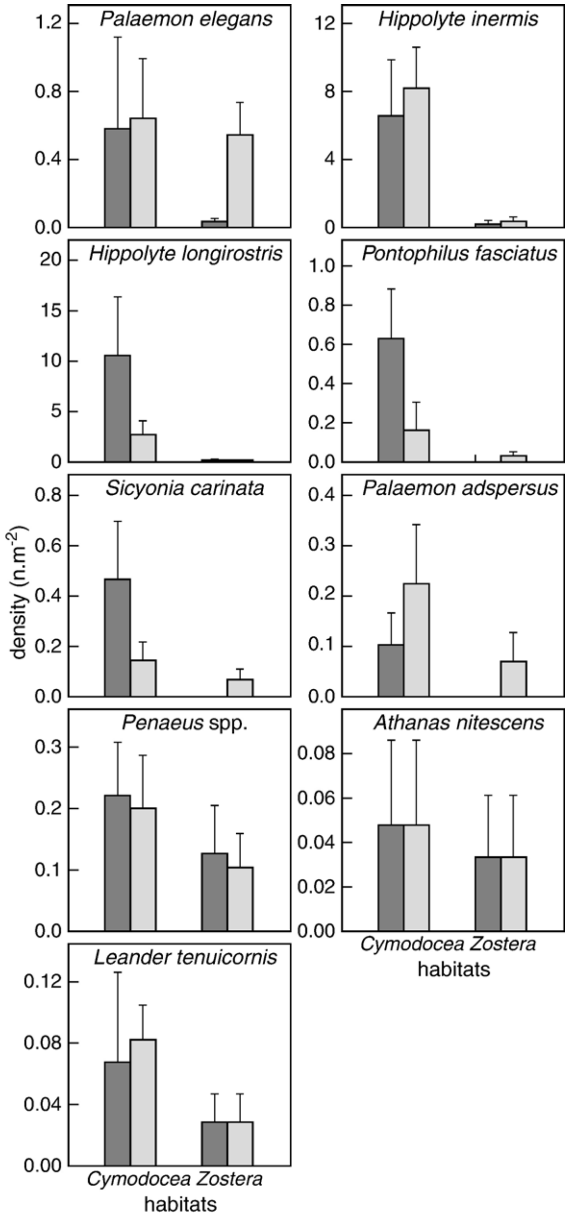

Fig. 5. Subtidal densities (+SE) of *Palaemon elegans*, *Hippolyte inermis*, *Hippolyte longirostris*, *Pontophilus fasciatus*, *Sicyonia carinata*, *Palaemon adspersus*, *Peneaus* spp., *Athanas nitescens* and *Leander tenuicornis*. Specimens were caught with a beam trawl on *C. nodosa* (*Cymodocea*) and *Z. noltii* (*Zostera*) fields (five locations each) during low (dark grey) and high tide (light grey). Note the different scales on the density axes.

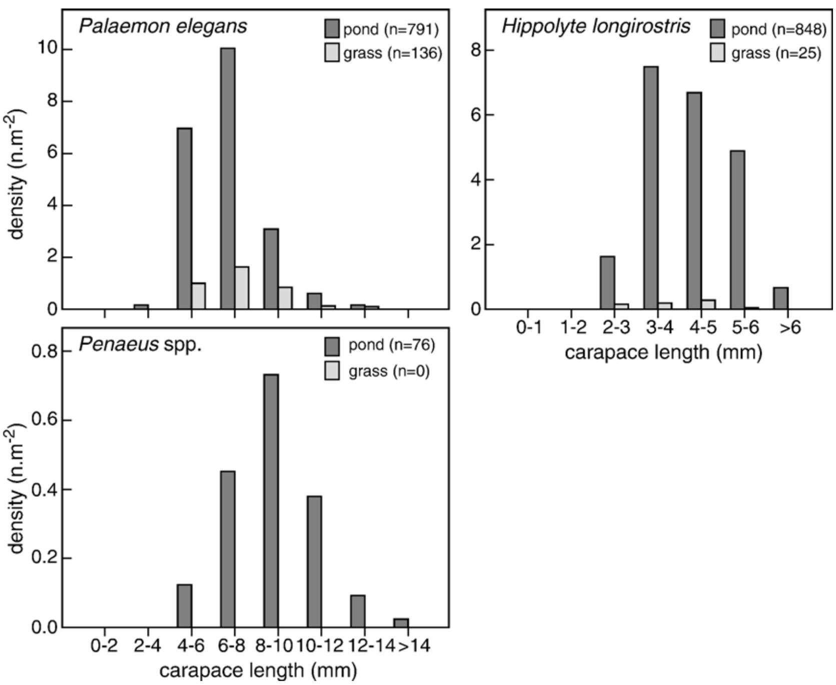

Fig. 6. Percentage of egg-carrying shrimps (+SE) of *Palaemon elegans*, *Palaemon adspersus*, *Hippolyte inermis*, *Hippolyte longirostris* and *Athanas nitescens* per length class (0–1 = 0.1–1.0 mm; 1–2 = 1.1–2.0 mm etc.). The number of shrimps in each length class is indicated above the bars. Shrimps were caught with a push net and beam trawl during the whole study period. Note the different scales on the length axes.

species, in the largest size classes the fraction of egg-carrying shrimps exceeded 50%. The smallest adult *P. elegans* carrying eggs had a carapace length of 10.1–12.0 mm, while the smallest adults of *P. adspersus* carried eggs at a length of 12.1–16.0 mm. *H. inermis* and *H. longirostris* started carrying eggs at 2.1–3.0 mm and 3.1–4.0 mm CL, respectively. All size classes of *A. nitescens* that were caught carried eggs; the smallest individuals caught had a CL length of 3.1–4.0 mm.

3.7. Population structure

The length-frequency distributions of the three most abundant species on the tidal flat are shown in Fig. 7. No shrimps were caught on bare sediment. The most abundant size class of *P. elegans* had carapace lengths between 2.1 and 6.0 mm. The most abundant size class of *H. longirostris* had carapace lengths between 1.1 and 2.0 mm, but lengths from 2.1 to 5.0 mm were also well represented. *Peneaus* spp. were mostly found in the ponds and only present in very small densities on seagrass, so the latter densities are not depicted in the graph. The most abundant carapace lengths were between 1.1 and 8.0 mm. No age-classes could be distinguished for any of the three species.

3.8. Intertidal migration

In total 330 juvenile *P. elegans* (CL 4.1–8.0 mm) were marked. During the next high tide 0.0–2.0% were recaptured in the pond where they were originally marked (Table 2a), whereas 0.0–4.5% were caught on the seagrass between the ponds, but not in neighbouring ponds (0.0%). During the following low tide higher numbers of marked shrimps were caught than at high tide. Most juvenile shrimps were found back in the pond where they were marked (0.0–8.5%), but some were caught in neighbouring ponds (0.0–3.0%). Subadult *P. elegans* (CL 8.1–12.0 mm) were less abundant and a smaller number (136) was marked (Table 2b). Marked subadult shrimps were recaptured in the pond where they were originally marked during high tide (0.0–2.0%) and during low tide (0.0–2.7%). No marked subadult shrimps were caught elsewhere.

4. Discussion and conclusions

4.1. Sampling methods

Hiddink et al. (2002) calculated the efficiency of a 4 × 4 mm mesh push net (considering only escape through meshes), based on shrimp length as recorded

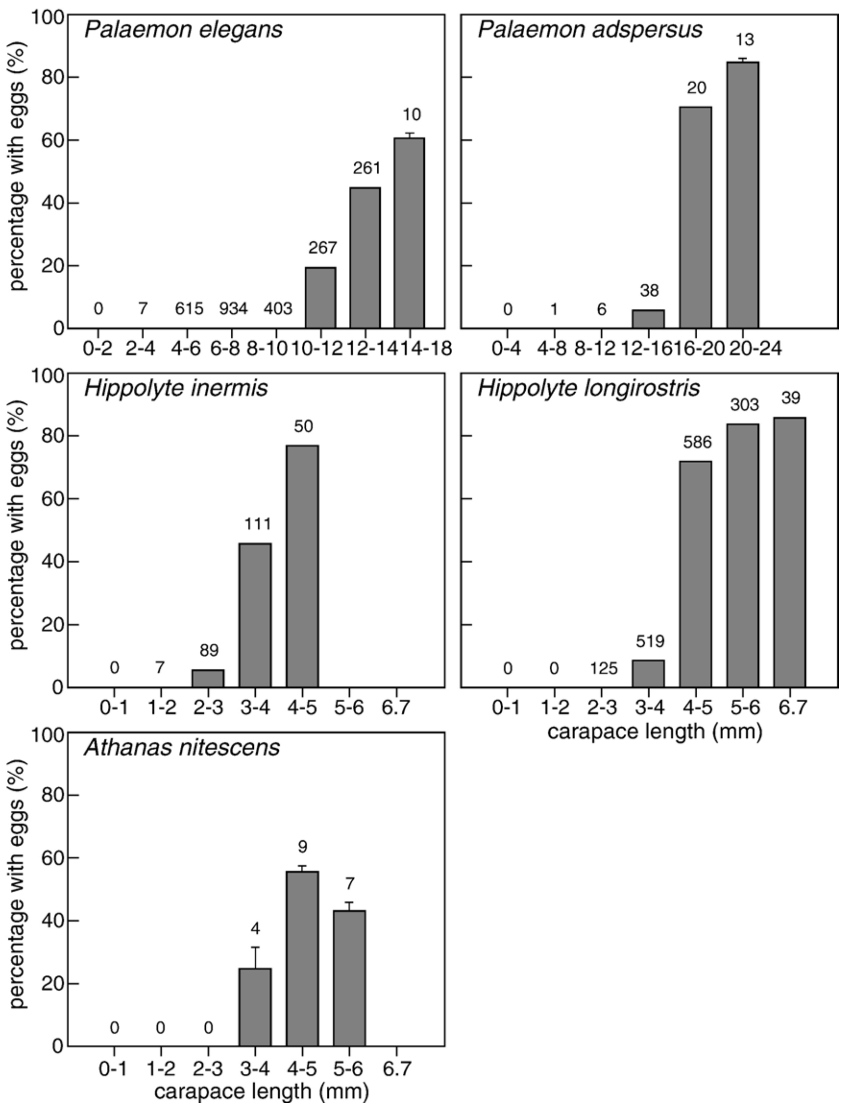

Fig. 7. Length-frequency distribution (mean densities per length class: 0–2 = 0.1–2.0 mm; 2–4 = 2.1–4.0 mm etc.) of *Palaemon elegans*, *Hippolyte longirostris* and *Peneaus* spp. Specimens were caught with a push net in two habitats (pond and seagrass) at 38 locations during high tide. Note the different scales on both axes.

in the field. They found a catch-efficiency of 55% for *Crangon crangon*. In the present study the catch-efficiency of small shrimps was probably higher, because a 2 × 2 mm mesh was used. Further, densities of larger shrimps were probably underestimated because shrimps could escape in front of the net. Densities were probably strongly underestimated with the beam trawl, because of the high disturbance by the boat's outboard engine and trawl in shallow waters (Jager, 1993) and the large mesh size (10 × 10 mm) of the net (see also Table 1). At high tide when the water is deeper, the net efficiencies will be lower, because the shrimps are more active at high tide than at low tide and can also escape over the net (Loneragan et al., 1995).

Many studies (e.g., Young, 1978; Turnbull and Watson, 1992; O'Brien, 1994) indicate that penaeid shrimps are more active at night around high tide and therefore more catchable at that time. The comparison between day-and night-time catches made in the present study (Fig. 2), indicated no significant differences in catchability for *Palaemon elegans*, *Hippolyte longirostris* and *Peneaus* spp., and therefore it can be assumed that the daytime catches give a representative estimate of shrimp abundance.

Table 2
Mark-recapture experiment of (a) juveniles (CL 4.1–8.0 mm) and (b) subadults (CL 8.1–12.0 mm) of *Palaemon elegans*

Exp.	N	*HT*			*LT*	
		Marked pond %	Grass %	Adjacent ponds %	Marked pond %	Adjacent ponds %
(a) Juveniles						
1	212	0.0	0.9	0.0	8.5	1.4
2	51	2.0	0.0	0.0	0.0	0.0
3	67	1.5	4.5	0.0	4.5	3.0
(b) Subadults						
1	50	0.0	0.0	0.0	0.0	0.0
2	49	2.0	0.0	0.0	0.0	0.0
3	37	0.0	0.0	0.0	2.7	0.0

For each separate experiment (Exp. 1–3), the number (N) of marked *Palaemon elegans* and the percentages recaptured are noted. The shrimps were sampled during high tide (*HT*) in the marked pond, the adjacent ponds (4) and the seagrass between the ponds. During low tide (*LT*) this has been done in the marked pond and the adjacent ponds only.

4.2. Species composition

In total eleven different shrimp species were caught during this study. *P. elegans, H. longirostris* and *Penaeus* spp. were the most abundant intertidal species, and *H. inermis* was the most common subtidal species. Most of these species seem to inhabit either intertidal or subtidal areas. Only *H. longirostris* was found abundantly in both intertidal and subtidal areas.

Earlier studies in the Banc d'Arguin tidal flat area found eight (Hazevoet, 1985) and ten (Campredon and Schrieken, 1986) shrimp species. As in the current study, *P. elegans* was the most abundant species in these two studies. The small shrimps *H. inermis*, *A. nitescens*, and *Processa edulis* subsp. *crassipes* were not found in earlier studies, which may be due to the smaller mesh size used for the push net in the present study. Probably for the same reason, abundances of small shrimps we found were generally higher than in earlier studies. Campredon and Schrieken (1986) caught the species *Gennadas* spec. and *Latreutes fucorum*, which were not found in this present study. In general, the differences in the catches between the three studies are probably caused by the time of year in which the studies were carried out and the gear and mesh size used.

4.3. Habitat use and tidal migration

In general, all species in the intertidal were mainly found in sheltered areas (ponds and seagrass) rather than in unvegetated habitats, which may be an active habitat choice or predation related. Even during high tide *H. longirostris* and *Peneaus* spp., and to a lesser extent *P. elegans*, seem to prefer to stay in the ponds.

No shrimps were found in the bottom samples from dry seagrass and bare sediment at low tide in the intertidal. Apparently, the shrimps spend low tide in the ponds or the subtidal rather than buried in dry flats. This result confirms observations by Wolff et al. (1993) who surveyed the benthic fauna of the tidal flats of the Banc d'Arguin and found no shrimps in the intertidal sediment samples obtained at low tide. *P. elegans* was highly abundant in the intertidal ponds during low tide, whereas during high tide similar densities occurred in the ponds and on the seagrass. No *P. elegans* were caught on bare sediment. This distribution, and the results of the mark-recapture experiment, indicate that they migrate out of the ponds during high tide, but apparently the animals remain in the shelter of seagrass. The reason is probably that seagrass provides shelter from light, water motion and predation, and has a higher food availability and number of microhabitats. Additionally, it could be that small juvenile shrimps suffer higher rates of predation in short, thin seagrass and unvegetated habitats, and this would lead to decreased abundance in these habitats (Kenyon et al., 1995). The subadult *P. elegans* (CL > 10 mm) caught with the beam trawl showed a higher density in the ponds during high tide, but the absolute density was low (around 0.6 ind m^{-2}). Subadult *P. adspersus* were even less abundant and showed no density differences between different habitats. Juvenile *P. elegans* forage on organisms such as benthic diatoms and foraminiferans (own obs.). They probably do this during high tide. During low tide they hide in the ponds, where seagrass densities are high (Van der Laan and Wolff, in press). This would be advantageous, because wading birds that are significant predators of shrimp in seagrass beds (e.g., Howard and Lowe, 1984; Zwarts et al., 1990) forage in shallow waters. Larger shrimps probably have to forage over a much greater distance to find more diverse food items (live animal matter) which comprise their diet (Vance, 1992). This could explain why no migration events of subadult individuals between nearby ponds have been detected: they swam out of the experimental area. *H. longirostris* was also abundant in the intertidal. No difference could be found between densities in ponds at high and low tide, suggesting that they do not migrate out on to the tidal flats at high tide. This may, however, be due to a lack of statistical power caused by high variability between the ponds. Nevertheless, at high tide, some individuals migrated out of the ponds and were found on the seagrass, e.g. *P. elegans*. On the bare sediment no *H. longirostris* were caught. The mean density of *Peneaus* spp. in the ponds was similar during low and high tide (around 1–2 ind m^{-2}). At high tide, densities were highest in ponds and lowest on seagrass. As for the other species, no *Peneaus* spp. were caught on bare sediment.

Shrimp densities were generally lower in the subtidal than in the intertidal, although this difference may partly be explained by the different gears used. In subtidal *C. nodosa* fields, *H. inermis* and *H. longirostris* were most abundant. Even though *H. inermis* is small and likely to be caught more efficiently with the push net than with the beam trawl, subtidal densities were much higher than intertidal densities, showing a very strong selection for subtidal habitats. In the subtidal, densities of *P. elegans* and *Pontophilus fasciatus* were much lower in the *Zostera* fields during low than at high tide. *P. fasciatus, S. carinata*, *P. adspersus*, *Peneaus* spp., *A. nitescens* and *L. tenuicornis* were caught in the subtidal in small numbers only and their densities were not affected by the tidal state or habitat. Because for none of the species the high tide densities were lower than low tide densities (and in some cases high tide densities in the subtidal were even higher than low tide densities), it seems unlikely that for any of the species there is any substantial tidal migration to the tidal flats at flood tide. Janssen and Kuipers (1980) found that *C. crangon* juveniles stay on the tidal flats during this life stage and leave the intertidal for deeper waters during later life stages, first during low tide and later permanently. The same results have been found for plaice (Kuipers, 1977) and shore crabs (Klein Breteler, 1976). In the Wadden Sea, these migrations are probably related to avoiding subtidal predators but also to higher food supplies in the intertidal (Kuipers and Dapper, 1984). As shrimps living in subtidal seagrass beds can find refuge from predation and an abundance of food among the seagrass, tidal migration may not be necessary in the Banc d'Arguin.

So, overall we could not find a tidal migration on and off the flats as discussed before, but there are strong indications of tidal migration on the flat between the ponds. During low tide the shrimps stay in the tidal ponds with dense seagrass cover. Some migrate out of the ponds and can be found on the seagrass beds during high tide, probably for foraging.

4.4. Reproduction and nursery use

Adult *Peneaus* spp. live and spawn in offshore waters (Campredon and Schrieken, 1986). Bast et al. (1984) indeed found large quantities of adult *Penaeus notialis* and *Penaeus kerathurus* in the Atlantic Ocean off the Banc d'Arguin at depths of 20–50 m. In our study, only juveniles of these species were found. *P. fasciatus*, *L. tenuicornis* and S. *carinata* were apparently not in their reproductive period or also spawn offshore, because no individuals with eggs were found. According to Campredon and Schrieken (1986) *P. adspersus* spawns in offshore waters, and afterwards adults and larvae migrate shoreward. This is not congruent with the results of the present study, where *P. adspersus* carrying eggs have been found in inshore waters. For the five species carrying eggs, the percentage of larger size classes carrying eggs exceeds 50%. This suggests sexual reversal from males to females with increasing age and size of the individual. In some shrimp species all individuals change sex, in others a variable percentage of the population are primary females or males (Bauer and VanHoy, 1996). Ten of eleven shrimp species were found as juveniles and therefore the area of our study might be an important nursery area. Juveniles of *P. elegans, H. longirostris*, *H. inermis* and *Peneaus* spp. were most abundant. If, however, a nursery area is defined as 'a habitat for juveniles in which the contribution per unit area to the production of individuals that recruit to the adult population is greater, on average, than production from other habitats in which juveniles occur' (Beck et al., 2001), we cannot yet conclude that the Banc d'Arguin seagrass beds are a nursery area for shrimps. We still have to demonstrate that the Banc d'Arguin seagrass beds allow a higher recruitment to the adult shrimp populations than do other habitats. However, for *Penaeus* spp. we have several observations that point in this direction: (1) the presence of adults offshore, (2) the absence of adults and the presence of juveniles inshore, (3) the higher abundance of shrimps in seagrass beds compared to bare tidal flats, and (4) the nursery role of many beds of seagrasses and other macrophytes worldwide (Beck et al., 2001; Heck et al., 2003).

4.5. Population structure

Most *P. elegans* in the intertidal were juveniles with CLs between 2.0 and 6.0 mm. For *H. longirostris*, juveniles were most abundant, although adults (CL ≥ 3 mm) were also abundant. Relatively low densities of juveniles of *Peneaus* spp. were found. For none of the species, age-classes could be recognised in the length-frequency distributions.

4.6. General conclusions

Our study was limited both in time and in space. We effectively covered only two months (February-March) of one year (2002). We have only limited information on the efficiency of our nets. Our study area covered only about 2% of the entire tidal-flat area of the Banc d'Arguin. Finally, our choice of sampling stations was based on the presence of ponds. These ponds are not randomly distributed over the tidal flats (see Section 2.3.), so our sampling stations are not randomly distributed over the flats either. However, from all pond sites we selected our stations at random. We assume that this selection procedure will not, or hardly, affect our conclusions with regard to day-night rhythm, distribution over habitat types, reproductive state, population structure, and tidal migration. Our density estimates apply only to the types of habitats sampled, however; these may be collectively characterised as the lower half of the tidal flats and the shallow edges of the tidal channels.

Taking the above restrictions into account, we nevertheless will attempt to arrive at a general conclusion about the possible importance of the Banc d'Arguin tidal flats as a nursery for shrimps.

About 85% of the area of tidal flats in the Banc d'Arguin is covered by seagrass beds (mostly *Zostera noltii*) and most of the remaining area is unvegetated sandy flats (Wolff and Smit, 1990). Also the circular ponds investigated in our study occur all over the Banc d'Arguin (Van der Laan and Wolff, in press). Therefore, the habitats in the studied area seem to be representative of habitats in the rest of the Parc National. Personal observations on the tidal flats near the islands of Nair and Niroumi gave the same impression of the shrimp and seagrass species composition as in the Baie d'Aouatif. If the mean density of *Peneaus* spp. on seagrass beds and in ponds (1.0 + SE 0.2 ind m^{-2} during high tide) in the studied area is representative of all tidal flats with seagrass cover of the entire Banc d'Arguin (412 km^2), the total abundance of *Peneaus* spp. might be in the order of 400 million juveniles. However, our sampling stations were not spread randomly over the tidal flats of the Baie d'Aouatif due to the non-random distribution of ponds. Moreover, the Baie d'Aouatif itself might not be representative of the entire tidal-flat area of the Banc d'Arguin because of its relatively land-locked position. Nevertheless, our order-of-magnitude calculation suggests that the Banc d'Arguin could be an important resource for commercial fishery, as Duineveld et al. (1993) already argued.

Confirming the study of Campredon and Schrieken (1986), the present study makes clear that among the eleven species found several reproduce in the coastal waters of Mauritania and some of them probably use the area as a nursery and migrate as adults to the stocks in open water. Therefore, the Banc d'Arguin might play an important role as a nursery for penaeid shrimps. This conclusion is congruent with several other studies that show that shallow parts of estuaries, coastal bays and intertidal as well as shallow subtidal seagrasses are important as a nursery areas for young stages of shrimps (Berglund, 1983; Kuipers and Dapper, 1984; Henderson and Holmes, 1987; Loneragan et al., 1994, but compare Heck et al., 2003).

For all shrimp species, the ponds on the tidal flats appeared to be disproportionally important. Densities of shrimps were very high at low tide and, for most species, at high tide still much higher than those of the surrounding areas. In fact, the use of tidal-flat seagrass areas by shrimps at high tide probably depends on the presence of source ponds, which may serve as a home base for shrimps at both low and high tide, although the mark-recapture experiment showed that the shrimps do not necessarily return to the same pond.

Because the present study surveyed only a small part of the Banc d'Arguin during two months, we do not have information on the temporal variation in the distribution and reproductive behaviour of the species. Further studies may elucidate whether the high summer temperatures in the area have any effect on the use of the tidal flats by the shrimps, and whether the four carideid species of which no adults with eggs were found reproduce in other seasons.

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