The Banc d'Arguin, Mauritania, as nursery for shrimps

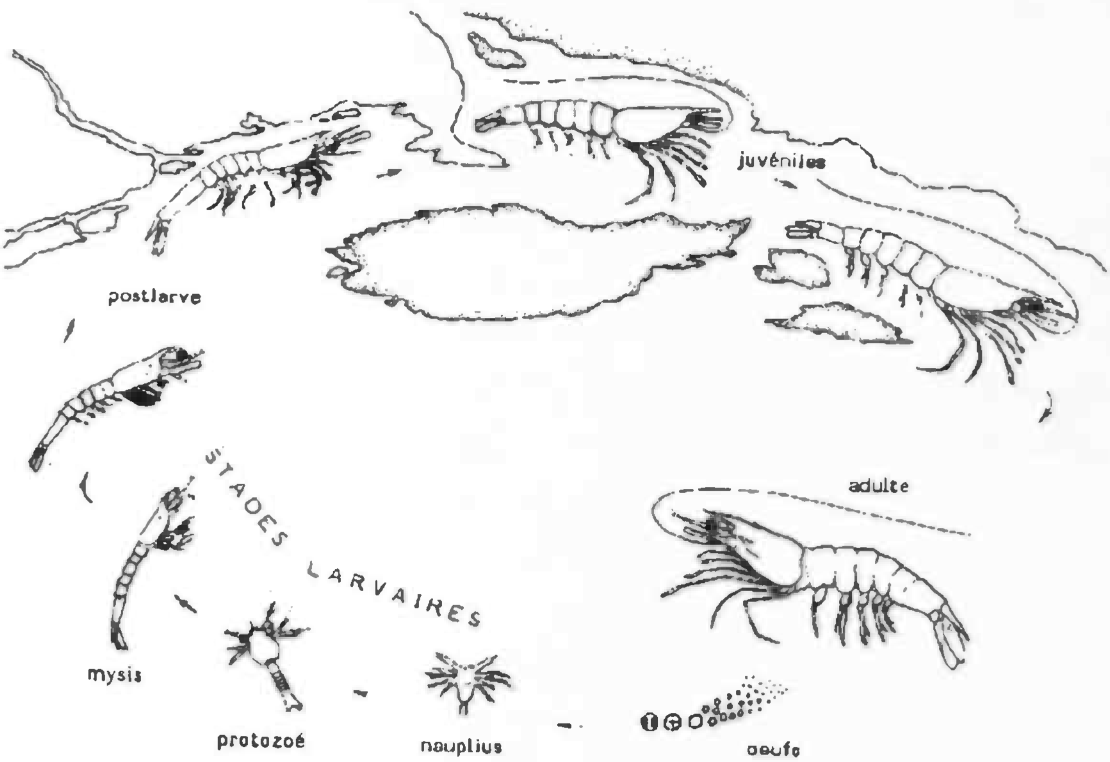

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Fig 1 Biological cycle of Penaeus shrimps[2]

[2] http://www.fao.org/docrep/x0169f/x0169f3j.htm

Summary

The Banc d'Arguin in Mauritania is an area characterised by shallow waters with extensive seagrass beds and tidal flats. This Mauritanian shelf acts as a source of exploitable stocks of shrimps for one of the most important fishery areas of the world. The relationship between these stocks and the nursery areas is important for the management of Mauritanian marine living resources. The aim of this study is to determine the role of the Banc d'Arguin tidal flats as a nursery area for shrimps. This has been investigated by sampling during high and low tide in the Baie d'Aouatif with a push-net (171 m^2 intertidal; ponds, seagrass beds and bare substrates) and a beamtrawl (5552 m^2 intertidal and 629 m^2 subtidal; Cymodocea nodosa and Zostera noltii) from January until March 2002.

In total eleven species (9349 specimens) of the infraorders Caridea and Penaeidea were found, of which the most abundant were Palaemon elegans (2978), Hippolyte longirostris (2598), H. inermis (2952 in subtidal) and Penaeus sp. (504; P. kerathurus & P. notialis). Penaeus sp. are commercially very important. Extrapolation of estimated Penaeus sp. densities to the total area of the Banc d'Arguin gives, if the specimens reach adulthood, a minimal harvest for the Mauritanian fishery of 772-1158 tonnes. These numbers are based on densities found from January till March.

Other species caught were Athanas nitescens (24), Leander tenuicornis (29), Palaemon adspersus (78), Pontophilus fasciatus (76), Sicyonia carinata (109) and Processa edulis subsp. crassipes (1). For some species tidal influences, habitatpreferences and population structure in the period studied could be indicated. High percentages of specimens with eggs (> 50 % for egg carrying size classes) were found for five species of caridean shrimps. Ten of eleven species caught were also found in juvenile form. The results of this study combined with other studies indicate that the Banc d'Arguin plays an important role as nursery for shrimps.

Résumé

Le Parc National du Banc d'Arguin (République Islamique de Mauritanie) est une région caractérisé par des eaux territoriales bas-fonds avec des herbiers extensives et des vasières. Ce récif Mauritanien fonctionne comme une source des provisions de crevettes exploitables pour une des régions de pêche la plus importante du monde. La relation entre ces provisions et les nurseries est importante pour l'arranger des ressources vivants de Mauritanie. Le but de cette étude est déterminer le rôle du Banc d'Arguin comme un nurserie pour crevettes. Ce rôle a été recherché par des enchantillons pris pendant marée haute et marée basse au Baie d'Aouatif avec un filet à main (171 m^2 vasières, herbiers et substrats dénudés) et un chalut (5552 m^2 vasières et 629 m^2 au-dessous de la superficie; *Cymodocea nodosa* & *Zostera noltii*) entre janvier et mars 2002.

Au total, onze espèces étaient trouvé (9349 spécimens) des infraordres Caridea et Penaeidea. Les espèces les plus abondantes étaient *Palaemon elegans* (2978), *Hippolyte longirostris* (2598), *H. inermis* (2952) et *Penaeus* sp. (504 *P. kerathurus* & *P. notialis*). Le groupe de *Penaeus* sp. est assez d'importance commerciale. Extrapolation de densités estimés de *Penaeus* sp. au total du Banc d'Arguin (si les spécimens deviennent adultes) donne une récolte minimale de 772-1158 tonnes pour la pêche Mauritanienne. Ces nombres sont fondés sûr les densités trouvées entre janvier et mars.

Les autres espèces qui nous avons trouvé au Baie d'Aouatif sont Athanas nitescens (24), Leander tenuicornis (29), Palaemon adspersus (78), Pontophilus fasciatus (76), Syconia carinata (109) et Processa edulis subsp. crassipes (1). Pour quelques de ces espèces on pouvait indiquer des influences de la mouvement de la marée, préférence d'habitat et structure de la population pendant la période d'étude. Percentages hauts pour espèces trouvées avec des œufs (>50 % pour des catégories de taille portant d'œufs) sont trouvé pour cinq espèces de crevettes de l'ordre de Caridea. Dix espèces étaient trouvées en forme juvénile aussi. Les résultats de cette étude combiné avec des autres études indiquent que le Banc d'Arguin joue un rôle très important comme un nurserie pour des crevettes.

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Introduction

Most shrimp species belong to the infraorders Penaeidea and Caridea shrimps (fig 2). Most of these species are predatory, many being omnivorous and often scavenging for food. They are preyed upon to a great extent by fish, wadingbirds (Wolff & Smit 1990, Howard & Lowe 1984, Mukherjee 1971) and to a lesser extent by other invertebrates. Active fisheries also account for large numbers of certain species (Hayward & Ryland 1990).

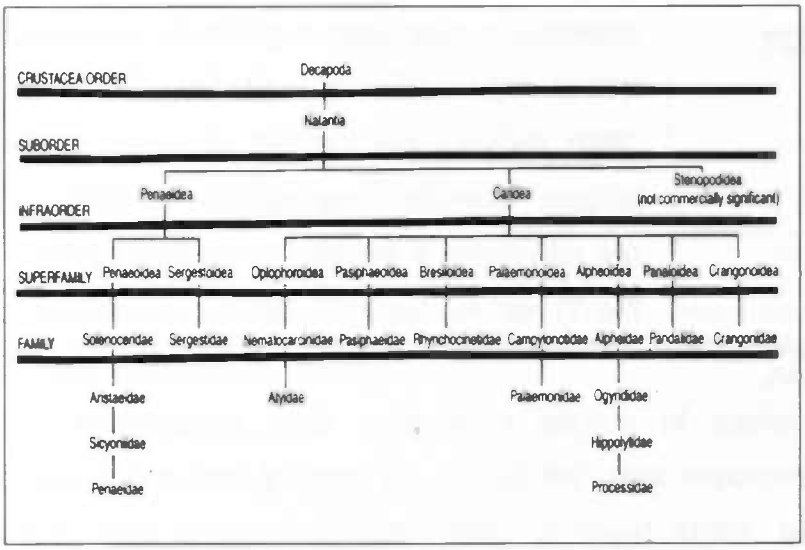


Fig 2 Biological phylogeny of shrimp families

Shallow parts of estuaries and coastal bays serve as important nursery areas for young stages of several epibenthic animals such as shrimps (Boddeke 1978, Berghahn 1983, Kuipers & Dapper 1984, Henderson & Holmes 1987). After hatching in offshore areas, postlarvae of these species (Penaeidea) invade shallow coastal areas if rich in food. This is especially true of tidal flats. Such sand and mud flats in the Wadden Sea, the Netherlands, are inhabited by huge numbers (up to thousands) of juvenile brown shrimp (Kuipers & Dapper 1984). Juveniles of this species grow rapidly on the flats for some months and subsequently leave the intertidal for deeper waters, at first during low tide and later on permanently (Janssen & Kuipers 1980). A study of the population dynamics of small tiger prawns (*Penaeus* spec.) in three seagrass communities in the western Gulf of Carpentaria, Australia, highlighted the importance of intertidal and shallow subtidal seagrasses to the settling postlarvae and early juvenile tiger prawns (Loneragan *et al.* 1994). Similar results have been found for inshore hatching *Palaemon* shrimp species (Caridea) in Dutch and French tidal areas (Berglund 1983).

The Banc d'Arguin National Park in Mauritania is a transition zone between the Sahara Desert and the Atlantic Ocean with large expanses of mudflats and particularly well developed tidal flats (fig 3). The shallow water vegetation comprises extensive seagrass beds and various seaweeds, covering a total area of between 600 to 800 km^2 (Monod 1977, PNBA 1987). The seagrasses present are *Zostera noltii*, *Cymodocea nodosa* and *Halodule wrightii* and they provide a favourable habitat for the reproduction and development of fish (Wolff & Smit 1990, Jager 1993).

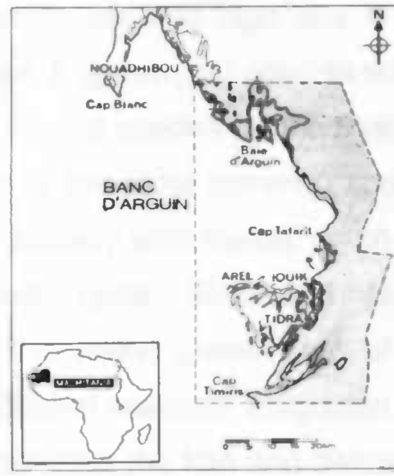


Fig 3 Map of the Banc d'Arguin, Mauritania

The Mauritanian shelf acts as a source of exploitable stocks of fish, cephalopods and shrimps for one of the most important fishery areas of the world. This is the continental shelf of West Africa, between the Straits of Gibraltar and Cape Verde (Duineveld *et al.* 1993).

The potential function of the Banc d'Arguin as a nursery for postlarvae and juvenile shrimps has, however, hardly been investigated. In a report by Campredon and Schrieken (1986) of a Dutch-Mauritanian project the presence of shrimp species and their importance in the foodweb of the Banc d'Arguin (fig 4) have been investigated, but the data were insufficient for far-reaching conclusions. They found especially shrimps that belonged to the species *Palaemon elegans* and some of the genus *Penaeus.* Shrimps of this genus live offshore as adults and reproduce in Mauritanian waters from May till August. The larvae are found in inshore waters; they migrate to tidal flats during nightly high tides. *P. elegans* is an estuarine species, which is able to produce several batches of eggs a year (Campredon & Schrieken 1986).

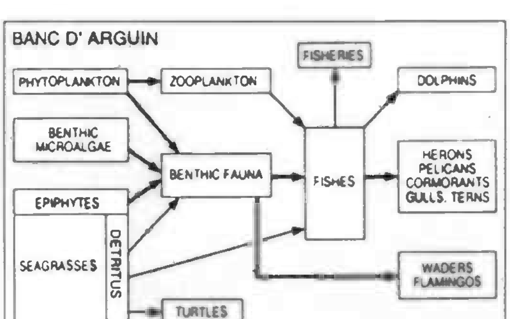


Fig 4 Foodweb of the Banc d'Arguin (Wolff & Smit 1990)

The aim of this study is to determine the role of the Banc d'Arguin tidal flats as a nursery area for juvenile shrimps. This will be done by identifying shrimp species present and estimating their abundance in the inter- and subtidal zone. Different substrates will be sampled during low and high tide to find possible habitat preferences and tidal influences. Egg carrying species will be counted to assess the reproductive state of all shrimp species on the tidal flat. Furthermore will length-frequency distributions of the most common species indicate the structure of their populations from January until March, which can be expressed in stages of the biological cycle. Repeated length measurements will result in an estimate of the mean growth rate of the population over a short period (3 months). Additional research (migration and stomach content) will possibly indicate a link between the tide and behaviour of the shrimps (shelter and foraging).

Study area & Methods

Site description

The Banc d'Arguin is situated on the Atlantic coast of Mauritania between about 19º20' and 20º30'. The area of tidal flats is estimated to cover 491 km^2, of which about 193 km^2, are covered by dense seagrass beds (mostly *Zostera noltii*) and about 219 km^2 consist of muddy flats with usually a less dense seagrass cover (fig 5). *Cymodocea nodosa* is largely restricted to places covered with water at all times. Such places are pools and small creeks at the flats, the larger tidal channels in between the flats and the sublittoral areas of the Banc d'Arguin (Wolff & Smit 1990). Depth generally does not exceed 4 meter, except in the eastern part where depths down to 16 meter occur (Jager 1993). Salinity values vary between 38 and 42 ‰, but can even reach more extreme values close to the shore. This is because no inflow of fresh water from the continent exists (Wolff & Smit 1990).

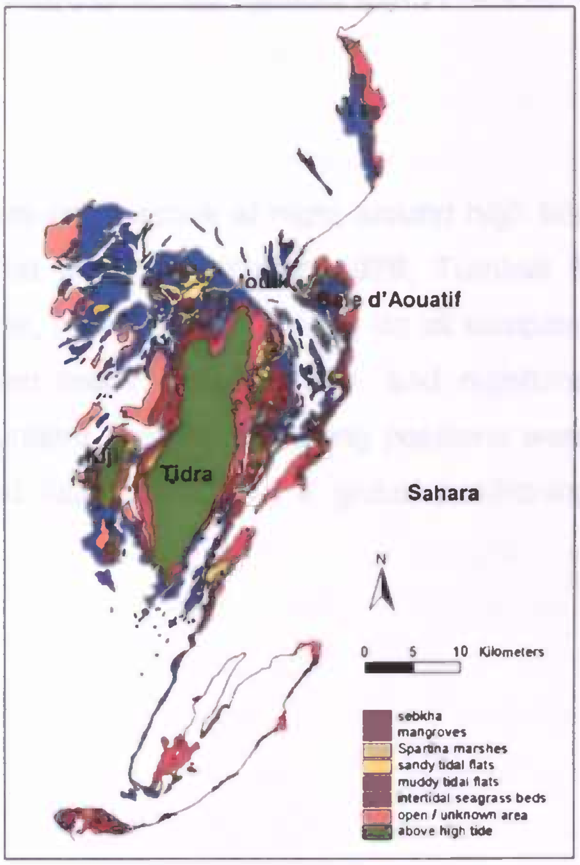


Fig 5 Mudflat and seagrass areas of the Banc d'Arguin (PNBA, unpublished)

The research site was located at the Baie d'Aouatif near the field research station of the Parc National du Banc d'Arguin (PNBA) at Iouik. The research was carried out from the 22nd of January till the 20th of March 2002. In this period the average tidal amplitude amounts to 1.61 meter (Wolff & Smit 1990). Smit *et al.* (1989) measured water temperatures that increased from 18-19ºC in mid February to about 21-22ºC in mid April 1986. The winds are mostly from northern directions and vary between 4 to 6 Beaufort (Wolff & Smit 1990).

Species composition

Most of the shrimp species present on the tidal flats have been identified with *The Marine Fauna of the British Isles and North-West Europe* (Hayward & Ryland 1990) and an identification key for shrimps of North Mauritania by Schrieken (unpublished). Some have been sent to Dr. C.H.J.M. Fransen (Naturalis, the Netherlands) for identification. A summary was made of the most important features of these species, containing pictures and descriptions of morphology and habitat.

Densities

Many studies indicate that shrimps are more active at night around high tide and therefore more catchable at that time (e.g. Young 1978, Turnbull & Watson 1992, O'Brien 1994). However, it was not possible to do all sampling at night, so a comparison has been made between day- and nighttime catches at high tide for the most abundant species. Sampling positions were distributed over the area (fig 6) and found back with a global positioning system (handheld GPS) and stacks.

Fig 6 Positions of sampling at Baie d'Aouatif, from January to March 2002. Blue marks were sampled at high and low tide (each point contains a pool, seagrass and bare substrate) during the day (N=25), yellow marks (N=13) were sampled at night as well.

Samples were taken in the intertidal with a push-net (mouth width 40 cm, mesh size 2 x 2 mm) at high tide, standing in the water hip-high, during the day and at least half an hour after sunset. One push with the net over the substrate (pools, seagrass and bare substrate) was standardised at a length of 1 meter (thus sample size 0.4 or 0.8 m^2). To see if the pools on the tidal flat could be compared at all, size-estimations were made during low tide and substrates within the pools were described (figure 7, appendix A-I). With this the total abundance of three species has been calculated per pool and it has been checked if these abundances are normally distributed over the tidal flat.
The density of shrimps during high tide in the intertidal (three substrates) was compared to the densities during low tide (fig 8). All samples during high tide were taken with the push-net in the same way as described before. During low tide, the edges of the pools were sampled with the push-net as well, where as samples of seagrass and bare substrates were obtained from the sieve experiments of an *Anadara senilis* study at the same time (H.J. Boer, pers.comm.). In this study samples (surface area 0.25 m^2, depth 10 cm) were taken at 50 random points on the tidal flats and sieved through a 1 mm mesh size.

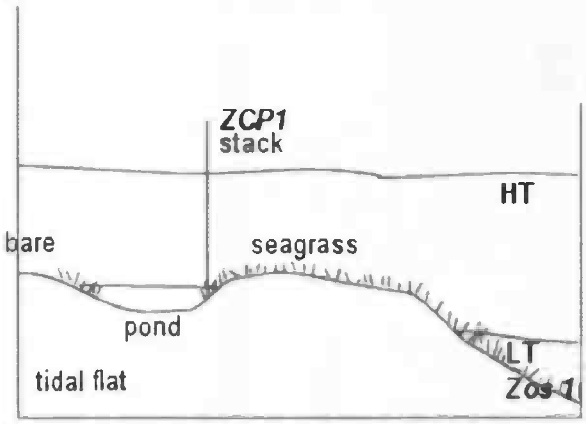


Fig 8 Transversal drawing of the contents of one marked (stack) point (ZCP 1, total N=38) in the intertidal (pond, seagrass & bare substrate) and one marked point (Zos 1, total N=10) in the subtidal (Zostera or Cymodocea) during high (HT) and low (LT) tide

Additional data about densities of some larger shrimp species (only specimens with a carapace length larger than 10 mm) in pools, on seagrass and bare substrate in the intertidal were achieved from a juvenile fish study (J.P.C. van Etten, pers.comm.) by trawling. In this study repeated (3x) sampling at 8 points (each containing a pool, seagrass and bare substrate) has been done with a beam trawl (mouth width 192 cm, knotless nylon netting with a mesh size of 10 mm) with a trawling speed of approximately 2.5 km per hour.

Densities of shrimps in the subtidal part on *Zostera* were compared to densities on *Cymodocea* during low and high tide. This division between *Zostera* and *Cymodocea* beds was based on visual leaf and root examination in the catch. Sampling has been done with the beamtrawl in the same way as described before, except for the repeatment.

Sampling methods

Comparisons between the two used catch methods (push-net and beamtrawl) have been made and they indicate that all length-classes of *Palaemon elegans* and *Hippolyte longirostris* are best caught by the push-net (fig 9).

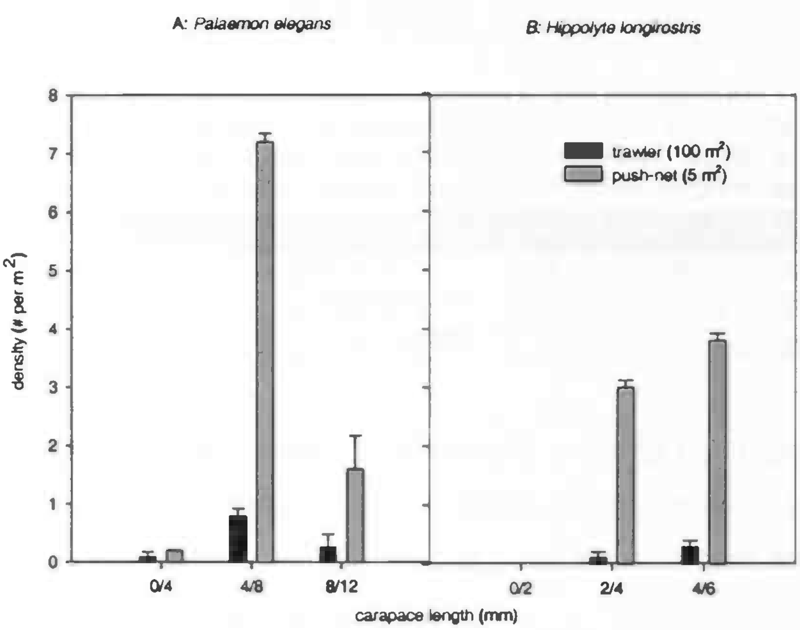


Fig 9 Comparison between catches (mean densities with standard errror) with the push-net and the beamtrawl for all length-classes of A: Palaemon elegans and B: Hippolyte longirostris

Therefore, the data from the beamtrawl, will give an underestimation of densities on the tidal flats. An advantage is the bigger sampling area covered, which provides more reliable data.

Analysing methods

All catches were sorted to species and counted. The number of shrimps of a certain species per square meter in the different habitats is an indication of habitat preferences of shrimps. Comparisons between high and low water densities show any tide influences. The carapace length (CL) of the shrimps has been measured with an electronic callipers. This has been compared to the total length and weight of some shrimp species. Results can be found in fig 10 & 11.

Fig 10 Comparison of carapace length (x) versus total length (y) with standard errors, all in mm, of nine species. Statistical values for each function (N, R^2 and P-value) are given as well.

SPECIES	FUNCTION	±SE	N	R^2	P-VALUE
Palaemon elegans	y=4.02+2.05x	1.74	150	0.82	< 0.0001
Palaemon adspersus	y=5.81+2.12x	2.55	37	0.90	< 0.0001
Penaeus sp.	y=-0.63+2.75x	1.65	58	0.98	< 0.0001
Hippolyte longirostris	y=4.94+1.72x	1.03	40	0.76	< 0.0001
Pontophilus fasciatus	y=2.99+2.11x	0.55	58	0.95	< 0.0001
Hippolyte inermis	y=3.96+2.55x	0.60	31	0.82	< 0.0001
Sicyonia carinata	y=0.99+2.54x	0.65	45	0.97	< 0.0001
Athanas nitescens	y=2.21+2.09x	0.52	17	0.90	< 0.0001
Leander tenuicornis	y=-1.89+2.53x	0.64	15	0.99	< 0.0001

Fig 11 Comparison of carapace length (x in mm) versus weight (y in mg) with standard errors, of nine species. Statistical values for each function (N, R^2 and P-value) are given as well.

SPECIES	FUNCTION	±SE	N	R^2	P-VALUE
Hippolyte longirostris	$y=7.3*10^{-2}x^{2.30}$	0.09	26	0.99	< 0.0001
Penaeus sp.	$y=9.2*10^{-3}x^{3.07}$	2.19	25	1.00	< 0.0001
Palaemon elegans	$y=3.8*10^{-2}x^{2.58}$	2.26	55	0.94	< 0.0001

Counting the number of individuals carrying eggs gives an indication for the reproductive state of the species from January until March. Calculated percentages per length class of each species give an estimation of minimum carapace lengths for carrying eggs.

The data obtained from the density-experiments can be used to make length-frequency distributions. These distributions show which length classes (stages of the biological cycle) are abundant and thus give insight in the structure of the shrimp populations during this study.

Repeated measurements (January, February and March) of carapace lengths in 8 pools with the push-net were used as a mean growth-rate for two shrimp species (*P. elegans* and *H. longirostris*).

Migration experiment

To determine whether shrimps migrate on the tidal flats or not, a migration experiment during 24 hours was carried out. For this a part of the tidal flat with 4 pools close together was chosen (fig 12). In the central one, shrimps (*P. elegans*) of two different size classes were caught at low tide and immediately marked with nailpolish and released. At the following high tide (during daytime) shrimps were caught with the push-net (sampling size 0.8-1.6 m^2 per point) in all pools and on the grass in between and marked ones were counted. At the next low tide (during daytime) all 4 pools were sampled again. Percentages of shrimps caught back were calculated. This experiment was repeated three times on different spots.

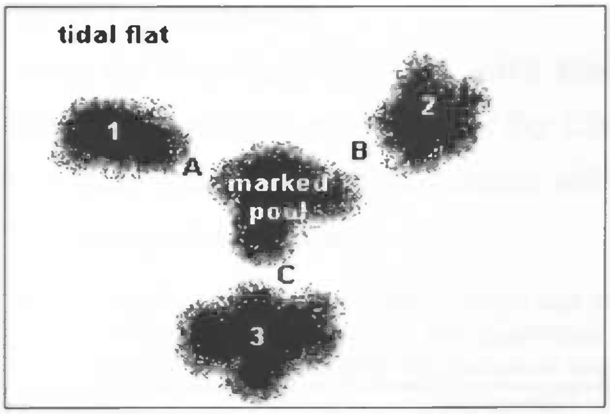


Fig 12 Experimental design of a migration experiment on the tidal flat. In the marked pool the shrimps were coloured with nailpolish and released, points 1,2 & 3 are neighbouring pools (max. distance 5 m) and points A,B & C are seagrass fields in between the pools

Stomach contents

To position the shrimps in the food web of the Banc d'Arguin and to find out if they migrate to forage at high tide, some *Penaeus sp.*, *P. elegans* and *H. longirostris* (total N=106) caught during low and high tide, were conserved in alcohol and brought back to the Netherlands. Here the stomach was cut out of the body and the contents were suspended in water. With a binocular (50x enlargement) the substances found were identified.

Statistics

It was not possible to use statistics for all the data, because of the high numbers of zero-abundance samples and large variances. All data were $^{10}\log(x+0.01)$ transformed before testing.

The comparison between night- and daytime catches has been done with the PAIRED T-TEST. To check normal distribution of the densities in the pools, the ONE-SAMPLE KOLMOGOROV-SMIRNOV test has been used. The different densities during low and high tide in the pools were tested with a T-TEST. The differences between the substrates at high tide have been tested with different ANOVA-tests. Sometimes if the variances between groups were not equal, an UNEQUAL-VARIANCE T-TEST has been done.

Results

Species composition

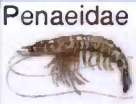
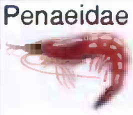
During the investigation in total 9349 specimens of eleven different species were caught on 6352 square meter (fig 13). Because *Penaeus kerathurus* and *P. notialis* could not be distinguished with certainty, they will be grouped to *Penaeus* sp. in this report.

Fig 13 Total numbers of specimens caught with the pushnet (171 m^2 area) and the beamtrawl (total 6181 m^2). The beamtrawl in the intertidal (5552 m^2) only accounts for specimens with carapace lengths larger than 10 mm.

SPECIES	PUSH-NET INTERTIDAL	TRAWL INTERTIDAL	TRAWL SUBTIDAL	TOTAL
Athanas nitescens	11	-	13	24
Hippolyte inermis	3	-	2949	2952
Hippolyte longirostris	1573	-	1025	2598
Leander tenuicornis	0	-	29	29
Palaemon elegans	2281	406	291	2978
Palaemon adspersus	0	31	47	78
Penaeus sp.	130	285	89	504
Processa edulis subsp. *crassipes*	0	-	1	1
Pontophilus fasciatus	8	-	68	76
Sicyonia carinata	7	-	102	109
TOTAL	4013	722	4614	9349

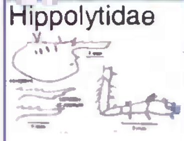
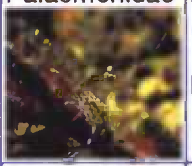
Overall *P. elegans, H. longirostris* and *Penaeus* sp. were most abundant in the intertidal, whereas in the subtidal *H. inermis* was the most common species. The morphology and habitat preferences of the ten species caught, are listed in figures 14 and 15.

Fig 14 Morphology and habitat of Penaeidea shrimps, caught in Mauritanian waters (identification key of Schrieken, unpublished and own observation)

FAMILY	SPECIES	COLOUR	LENGTH MAX. (mm)	ROSTRUM	HABITAT
Penaeidae 	*Penaeus kerathurus* (Forskål 1775)	purple, green or brown transversal bands on abdomen	230	1 ventral tooth, no dorso-lateral groove	shallow water, down to 40 m on sandy bottoms
Penaeidae 	*Penaeus notialis* Perez Farfante 1967	equally beige	190	2-3 ventral teeth, 6th abdominal segment with dorso-lateral groove	mud or sandy patches among rocks, adults strictly marine dwelling down to 50-100 m
Sicyoniidae[2] 	*Sicyonia carinata* (Brünnich 1768)	from olive greenish to reddish/ brownish; hard body	80	6-7 dorsal teeth of which 3 postorbital, 1 ventral tooth, the tip of the rostrum ends in 2-3 teeth.	shallow water, down to 35 m on sand between seagrass beds

[2] http://www.fao.org/docrep/x0169f/x0169f4r.htm

Fig 15 Morphology and habitat of Caridea shrimps, caught in Mauritanian waters (Hayward & Ryland 1990 and own observation)

FAMILY	SPECIES	COLOUR	LENGTH MAX (mm)	ROSTRUM	HABITAT
Alpheidae 	*Athanas nitescens* (Leach 1814)	variable, may be green, blue or red-brown often with a white dorsal stripe	20	Straight and unarmed	lower shore to about 60 m
Hippolytidae 	*Hippolyte inermis* Leach 1815	usually green, ocasionally crimson or brown specimens	42	Longer than carapace, usually without dorsal tooth at base in adults	subtidal to about 50 m on seagrass beds
Hippolytidae 	*Hippolyte longirostris* (Czerniavsky)	variable, greenish brown to almost transparent with flecks of red-brown	20	Almost as long as carapace in adults, less in juveniles; posterior dorsal border of rostrum with 2-4 teeth	intertidal and lower shore
Palaemonidae 	*Leander tenuicornis* (Say 1818)	brown, mostly with two big blue/white rounds at both sides of abdomen	45	Straight or very slightly upcurved, 8-10 dorsal teeth of which 2 postorbital and a 3rd directly above the edge, 5-6 ventral teeth	*Sargassum* in open water and bentic vegetation at lower shore
Palaemonidae 	*Palaemon adspersus* Rathke 1837	uniform yellowish grey or transparent, pigment spots on lower half of the rostrum	80	Straight, 5-6 dorsal teeth of which 1 postorbital and a 2nd directly above the edge, 3 ventral teeth	shallow sublittoral to about 10 m amongst seagrass and algae
Palaemonidae 	*Palaemon elegans* Rathke 1837	transparent, thorax and pleon usually bearing dark yellow-brown and blue bands	63	Straight or very slightly upcurved, 7-9 dorsal teeth of which 3 postorbital, 3 ventral teeth	intertidal
Processidae 	*Processa edulis* subsp. *crassipes* Nouvel & Holthuis	whitish, with pale green hue	44	Slightly downturned, little shorter than eye, ventral tooth at tip longer than dorsal	lower shore to about 20 m on seagrass beds
Crangonidae 	*Pontophilus fasciatus* (Risso 1816)	whitish, with usually dark brown band on pleon segment 4 and 6	19	Broadly truncate at apex, one spine on median line of carapace	lower shore and shallow sublittoral to about 50 m

Intertidal day- and nighttime densities

A comparison between densities caught during day- and nighttime on different substrates in the intertidal (high tide) has been made for *P. elegans*, *H. longirostris* and *Penaeus* sp. (fig 16).

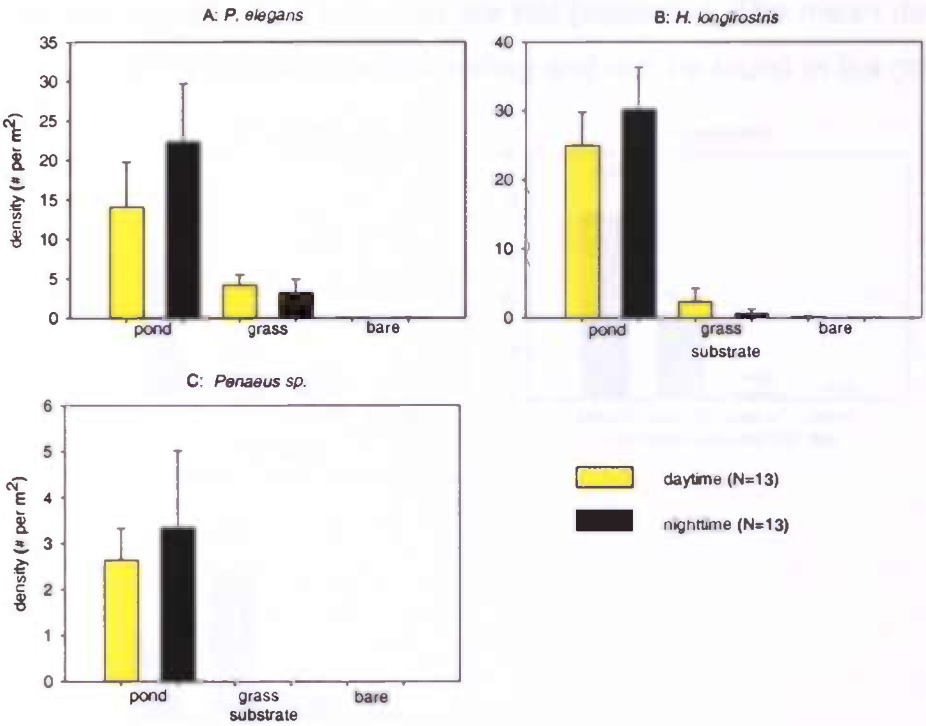


Fig 16 Comparisons between mean day- and nighttime densities on 13 waypoints (push-net)with standard error on different substrates (pond, seagrass and bare) in the intertidal during high tide

For all three species it seems like a larger number of individuals is caught at night in the pools, but this is only significant for *P. elegans* (mean density: night 22.3 ± SE 7.4 versus day 16.0 ± SE 5.7) (p=0.042; *paired t-test*). *H. longirostris* shows mean pool-densities around 25 to 30 individuals per square meter and *Penaeus* sp. around 3 specimens per square meter regardlessly of the time of day. Much lower densities of *P. elegans, H. longirostris* and *Penaeus* sp. occur on seagrass (around 0.4, 0.3 and 0.0 respectively per m^2) and bare substrates (around 0.0 specimens) and no differences between day- and nighttime densities have been found.

Furthermore the densities of *P. elegans* and *H. longirostris* are normally distributed over the pools on the tidal flats, which means that comparisons between densities in the pools during low and high tide can be made. This is not the case for *Penaeus* sp. (p<0.001; *One-Sample Kolmogorov- Smirnov test*).

Intertidal densities

The densities of the three most abundant species on the tidal flat are shown in fig 17 (original data in fig 18, appendix B-II/VIII). At low tide no shrimps were caught with the sieve on seagrass and bare substrate (in total 12.50 square meter was sieved), so these data are not presented. The mean density in the pools during low tide is more interesting and can be found in the graphs.

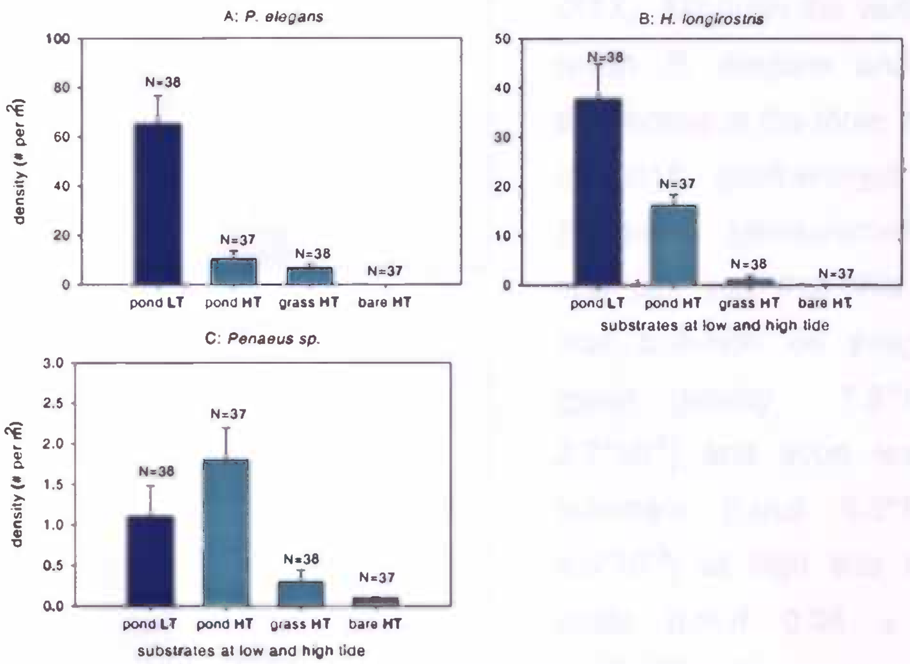


Fig 17 Mean densities with standard error in the intertidal, during low tide (LT) in the pools and during high tide (HT) on all substrates (pool, seagrass and bare) for A: P. elegans, B: H. longirostris and C: Penaeus sp.

The mean density in the pools at low tide (65.24 ± SE 11.36) is higher than at high tide (10.46 ± SE 2.97) for *P. elegans* ($p<0.001$; *t-test*). During high tide there are equal mean densities in pools and on the seagrass, where as on bare substrate no *P. elegans* individuals were caught ($p<0.001$; *one way Anova*).

For *H. longirostris* the mean density in the pools is not different during high and low tide (between 16 and 38 individuals per m^2). During high tide the mean density is highest in the pools ($p<0.001$; *one way Anova*). The mean density on seagrass (1.07 ± SE 0.66) is higher than on bare substrate (0.13 ± SE 0.03)($p=0.02$; *unequal variance t-test*).

The mean densities of *Penaeus* sp. in the pools are equal at low and high tide (around 1 or 2 specimens per m^2). At high tide the mean density in the pools is highest ($p<0.001$; *unequal variance t-test*). Seagrass and bare substrate show equal mean densities (between 0.10 and 0.33 per m^2).

Postjuvenile and adult shrimp densities

To obtain the abundances of larger postjuvenile and adult specimens of *P. elegans* and *P. adspersus*, specimens with carapace lengths exceeding 10 mm were taken from the repeated trawls for juvenile fish during high tide. Results can be found in fig 19 (original data in fig 20, appendix B-IX&X). Although the variances differ within *P. elegans* and there are differences in the three repeatments ($p=0.015$; *contrasts-within-subjects, Repeated Measurements Anova*), one can see that this species is less common on seagrass (total mean density $7.8 \cdot 10^{-2} \pm$ SE $2.7 \cdot 10^{-2}$) and even less on bare substrate (t.m.d $6.5 \cdot 10^{-3} \pm$ SE $4.5 \cdot 10^{-3}$) at high tide than in the pools (t.m.d $0.38 \pm$ SE 0.11) ($p=0.029$; *effects-between-subjects, R.M. Anova*). The same phenomenon, but with much smaller densities (e.g. pools; t.m.d. $2.0 \cdot 10^{-2} \pm$ SE $1.9 \cdot 10^{-2}$) is seen for *P. adspersus* ($p=0.018$; *e-b-s, R.M. Anova*). Here the variances are equal, but there are also differences between the measurements ($p=0.045$; *c-w-s, R.M. Anova*).

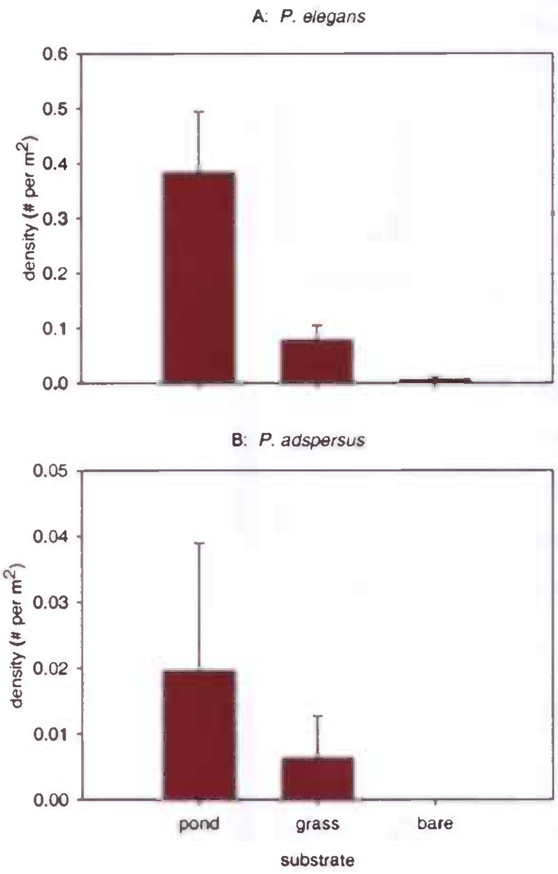


Fig 19 Mean densities with standard error of A: P. elegans and B: P. adspersus (CL >10 mm) on three different substrates (pond, seagrass and bare) at high tide in repeated (3x) trawl catches

Subtidal densities

The densities of the species present at the edge of the gully are presented in fig 21 (original data in fig 22, appendix B-XI&XII).

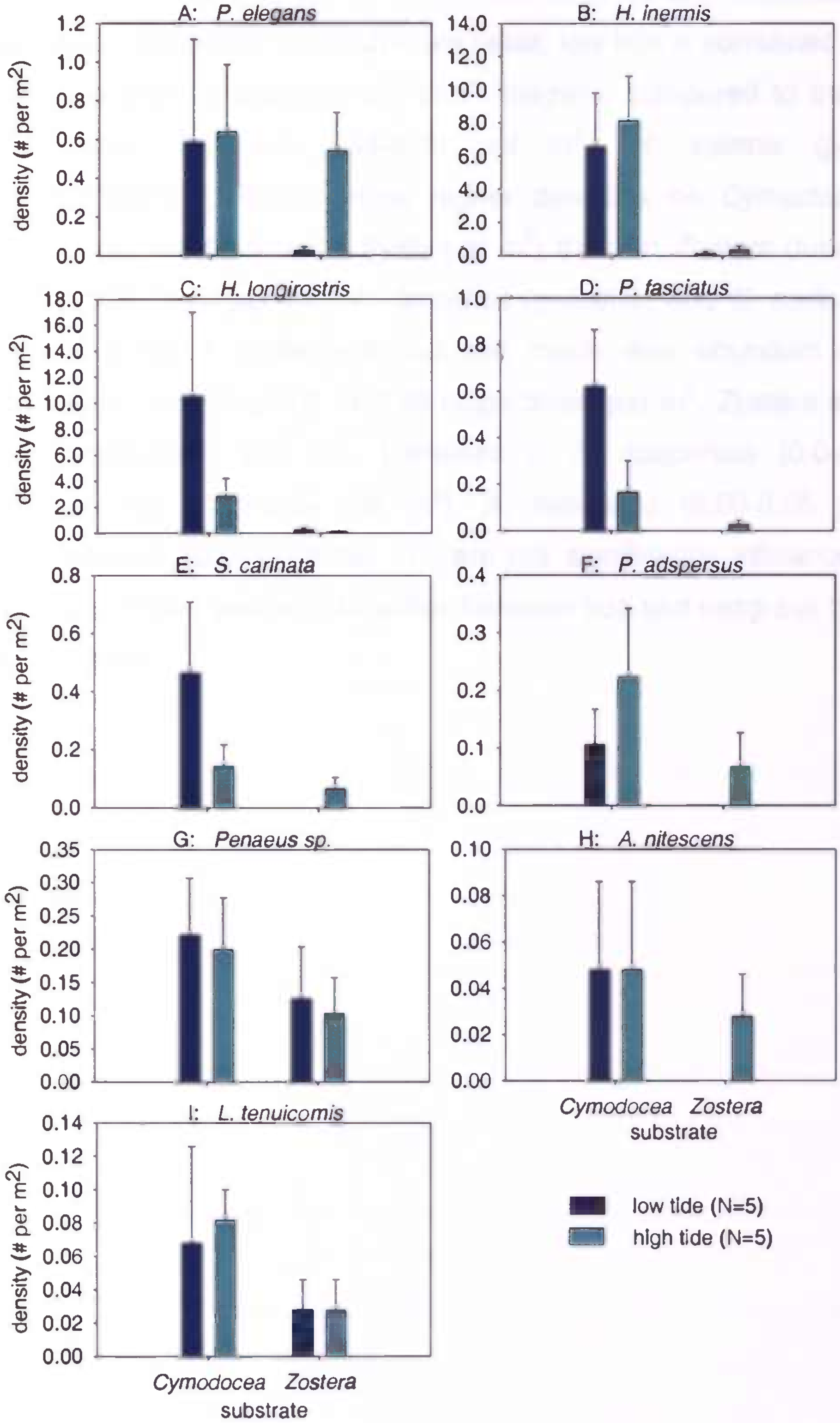


Fig 21 Mean densities with standard error in the subtidal on Cymodocea and Zostera fields during low and high tide for A: P. elegans, B: H. inermis, C: H. longirostris, D: P. fasciatus, E: S. carinata, F: P. adspersus, G: Penaeus sp., H: A. nitescens and I: L. tenuicornis

Although *P. adspersus*, *S. carinata* and *P. fasciatus* show unequal variances ($p=0.003$, 0.000 and 0.031 respectively; *Levene's Test of Equality*), a 2 factor (tide and substrate) Anova has been conducted on the data. It appears that *P. elegans* is the only species of which densities are influenced by the tide ($p=0.030$). Especially in the *Zostera* fields, low tide is correlated with very low densities (around 0.03 per m^2) of *P. elegans*, compared to the high tide in both fields (between 0.54-0.64 per m^2). *H. inermis* ($p<0.001$) and *H. longirostris* ($p=0.018$) show higher densities on *Cymodocea* (between 6.6-8.2 and 2.8-10.5 respectively per m^2) than on *Zostera* (around 0.30 and 0.18 respectively per m^2). *P. fasciatus* ($p=0.006$) and *S. carinata* ($p=0.041$) show the same preference, but are much less abundant (*Cymodocea*; between 0.18-0.62 and 0.14-0.46 respectively per m^2, *Zostera* max. 0.03 and 0.07 respectively per m^2). Densities of *P. adspersus* (0.0-0.2 per m^2), *Penaeus* sp. (0.12-0.24 per m^2), *A. nitescens* (0.00-0.05 per m^2) and *L. tenuicornis* (0.02-0.08 per m^2) are not significantly influenced by tide or substrate. There was no interaction between tide and seagrass type for any of the shrimps.

Reproductive state

The reproductive state was indicated by the percentage of egg carrying individuals per species. *Penaeus* sp. and *S. carinata* both belong to the infra-order Penaeidea and spawn in offshore waters. No specimens of *P. fasciatus* and *L. tenuicornis* have been found with eggs. The calculated percentages per length class of the other species can be found in figure 23.

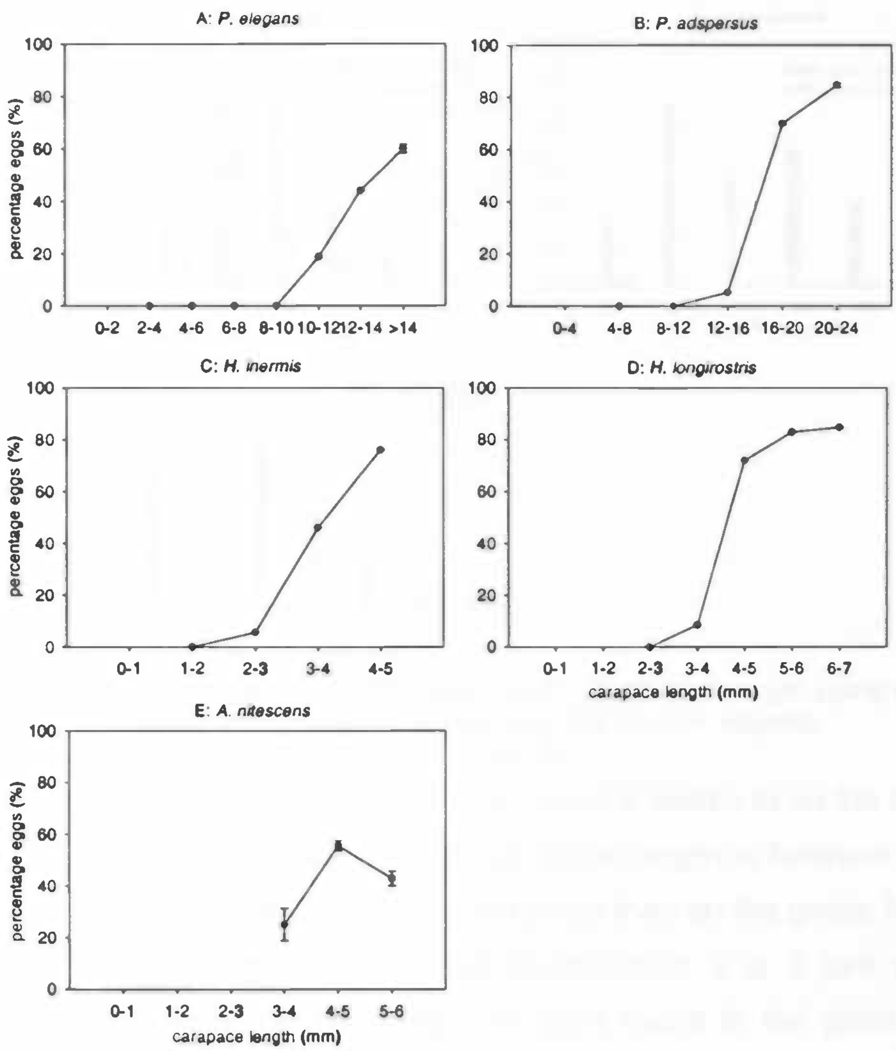


Fig 23 Percentage of egg carrying shrimps per length class with standard error for A: P. elegans, B: P. adspersus, C: H. inermis, D: H. longirostris and E: A. nitescens

For all species the percentage of the largest size classes carrying eggs exceeds 50 % and the standard errors are very small. *P. elegans* starts bearing eggs at a carapace length of 10-12 mm. *P. adspersus* starts at a length of 12-16 mm, where as *H. inermis* and *H. longirostris* stay much smaller and start carrying eggs at 2-3 mm and 3-4 mm CL, respectively. *A. nitescens* bears eggs at a length of 3-4 mm CL, but no minimal egg carrying length can be estimated, because no smaller specimens have been caught.

Population structure

The length-frequency distributions of the three most abundant species on the tidal flat (intertidal) are shown in figure 24. The data obtained with the push-net during high tide are divided into carapace length classes and for each class the mean density in the pools and the seagrass is shown. On bare substrate no specimens were caught, so these data are not presented.

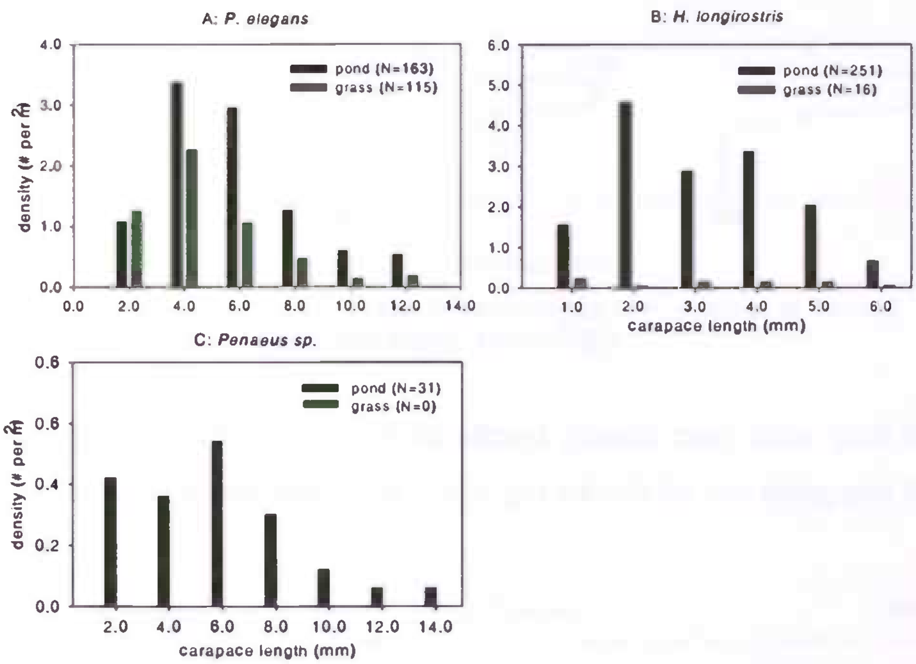


Fig 24 Length-frequency distribution (mean densities per length class) in the ponds and on seagrass during high tide for A: P. elegans, B: H. longirostris and C: Penaeus sp.

The length-frequency distribution of *P. elegans* seems to be the same in pools as in the grass. The most common carapace length is between 4 and 8 mm. *H. longirostris* is more abundant in the pools than on the grass. Most common is the 2 mm carapace length, but lengths from 3 to 5 mm are also well represented. *Penaeus* sp. have only been found in the pools. The most abundant carapace lengths are between 2 and 8 mm.

Growth

Repeated measurements at the end of January, February and March 2002 have resulted in an estimation of the growth rates of *P. elegans* (figure 25) and *H. longirostris* (figure 26).

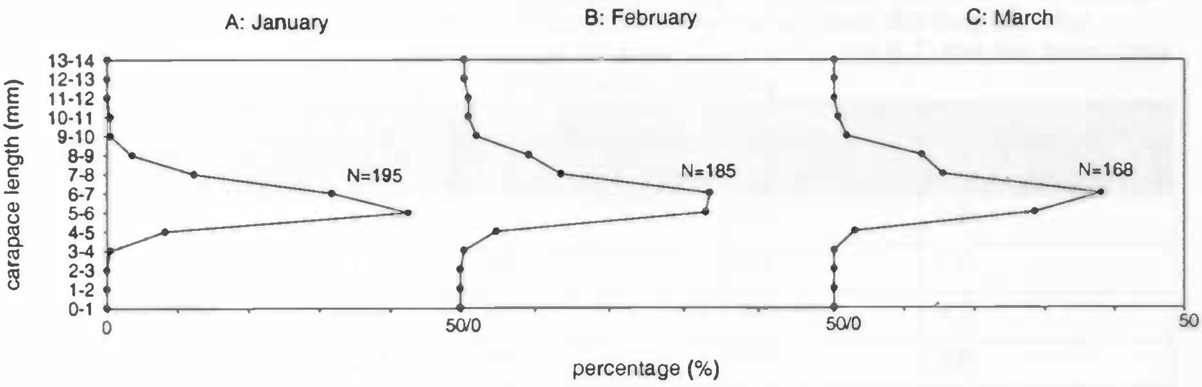


Fig 25 Length-frequency distribution in percentages of P. elegans at the end of A: January, B: February and C: March 2002

The carapace length of *P. elegans* shows growth over time ($p<0.001$; *R.M. Anova*). This can be estimated at 1 mm per month for the carapace lengths of 4 to 6 mm.

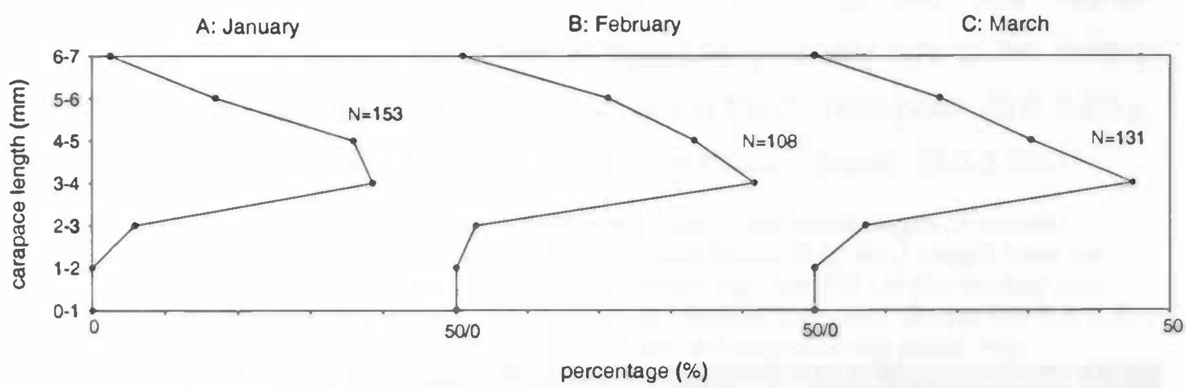


Fig 26 Length-frequency distribution in percentages of H. longirostris at the end of A: January, B: February and C: March 2002

H. longirostris does not show any growth ($p=0.176$; *R.M. Anova*) during these three months. According to the curves it seems like carapace lengths between 3 and 4 mm are becoming more abundant over time.

Both growth rates are not significantly influenced by the substrate the species live on.

Migration

The results from the migration experiment, repeated at different locations are summarised in figure 27 and 28.

Fig 27 For each seperate migration experiment (1a-3), the percentages of marked juvenile P. elegans (carapace length 4-8 mm) caught back are noted. The shrimps were caught back during high tide (HT) in the marked pool, the neighbouring pools and the seagrass between the pools. During low tide (LT) this has been done in the marked pool and the neighbouring pools only.

EXP.	MARKED POOL HT	GRASS HT	NEIGHBOURING POOLS HT	MARKED POOL LT	NEIGHBOURING POOLS LT
1a	-	-	-	5.3	0.8
1b	0.0	1.0	0.0	5.8	1.0
2	2.0	0.0	2.0	0.0	0.0
3	1.8	5.4	0.0	5.4	3.6

In total 319 juvenile *P. elegans* (carapace length 4-8 mm) were marked. Some were caught back in the same pool as they were marked in (marked pool) during the next high tide (0.0-2.0%). They also migrated out of the pool and were found on the seagrass between the pools (0.0-5.4%) and in neighbouring pools (0.0-2.0%). During the following low tide higher percentages were caught back than at high tide, probably due to the limited distribution area (pools). Most shrimps stayed in the marked pool (0.0-5.8%), but some migrated during high tide to the neighbouring pools (0.0-3.6%).

Fig 28 For each seperate migration experiment (1a-3), the percentages of marked post juvenile and adult P. elegans (carapace length 8-12 mm) caught back are noted. The shrimps were caught back during high tide (HT) in the marked pool, the neighbouring pools and the seagrass between the pools. During low tide (LT) this has been done in the marked pool and the neighbouring pools only.

EXP.	MARKED POOL HT	GRASS HT	NEIGHBOURING POOLS HT	MARKED POOL LT	NEIGHBOURING POOLS LT
1a				0.0	0.0
1b	0.0	0.0	0.0	0.0	0.0
2	2.0	0.0	0.0	0.0	0.0
3	0.0	0.0	0.0	3.0	0.0

The post juvenile and adult *P. elegans* (carapace length 8-12 mm) were less abundant and a smaller amount (132) was marked. Shrimps were only caught back in the marked pool during high tide (0.0-2.0%) and during low tide (0.0-3.0%). No migration events were detected for this larger size class.

Stomach content

P. elegans, *H. longirostris* and *Penaeus sp.* were caught during low and high tide. Stomach contents were analysed and are summarised in figures 29, 30 and 31 (appendix B-XIII&XIV).

P. elegans, caught during high tide, had mostly empty stomachs, some had consumed sand and three specimens contained diatoms and Foraminifera. During low tide much more individuals with mostly Foraminifera and some diatoms in their stomach were found.

Half of the *H. longirostris* stomachs contained undefined foodparticles, the other half was empty. No differences in stomach contents between low and high tide could be seen.

Penaeus sp. had mostly empty stomachs during high tide; some had consumed sand, undefined foodparticles and a couple of diatoms. Compared to high tide, a higher percentage of full stomachs were found during low tide, but the food consumed was not different.

Discussion & Conclusions

Sampling methods

Few estimates of absolute efficiency have been made for the nets that are used to catch fish and crustaceans in inshore marine and estuarine nursery habitats (Allen *et al.* 1992). In this study no net efficiencies were calculated. As mentioned in the methods, a comparison has been made between the push-net and the beamtrawl used (figure 9 in study area & methods). This indicates a much higher catch efficiency of the push-net for all carapace lengths. Densities estimated with the beamtrawl will therefore be underestimated, as well because of the high disturbance by a boat and a trawl in shallow waters of about 2 m deep (Jager 1993). The densities assessed by the push-net will show higher variability, because of the smaller area sampled. Disturbance by human impact (walking through the water) will probably have an impact as well. Furthermore do both methods catch animals that are on, or disturbed from, the substrate and that could not avoid the net. At high tide when the water is deeper (1.6 to 1.9 m), the net efficiencies will be lower, because the shrimps are more active at high tide then at low tide and can also escape above the net (Loneragan *et al.* 1995). It is obvious that the sampling of juvenile shrimps is complicated by the extreme variability in catch rates of trawl gear in time and space. Two approaches to overcome variability in time can be considered. One is to standardise sampling by using gear (e.g. jet nets to flush shrimps from the sandy substrate or drop traps that capture all enclosed shrimps) that is not susceptible to changes in catchability of the prawns over short periods of time. The second approach uses sampling gear that is affected by short-term changes in the availability and catchability of shrimps but standardises sampling by limiting it to the period of highest catch rate each day (Vance & Staples 1992). These approaches were not used in this study so the variability in the catches is rather high.

A lot of studies indicate that shrimps are more active at night around high tide and therefore more catchable at that time (e.g. Young 1978, Turnbull & Watson 1992, O'Brien 1994). The comparison between day- and nighttime catches made in this study, gives the same result for *P. elegans* in the pools ($p=0.042$), but not on other substrates. Differences in catchability for *H. longirostris* and *Penaeus* sp. are not found. This can be explained by the

short period of the experiment and therefore a variable combination of conditions, which can influence catchability as well (e.g. spring or neaptide and sampling at different stages of high tide).
Comparisons between densities in the pools during low and high tide can be made, because *P. elegans* and *H. longirostris* densities are normally distributed over the pools on the tidal flat. This is not the case for *Penaeus* sp. ($p<0.001$), because of the overall low densities (between 0 and 9 specimens per square meter) caught of this species.

Species composition

In total 9349 specimens of eleven different shrimp species were caught with the push-net (171 m^2) and beamtrawl (6181 m^2) on the tidal flats, which were mainly *P. elegans* (2978), *H. longirostris* (2598) and *Penaeus* sp. (504; *P. kerathurus* and *P. notialis*). In the subtidal *H. inermis* (2952) was most caught. All identified species belong to the infraorders Penaeidea and Caridea.
In December 1984, Hazevoet (1985) used a two meter beamtrawl (mesh width 0.5 cm) in the same area, east of Iouik peninsula. He caught eight shrimp species. They were mainly *P. elegans*, 773 of a total 850 caught shrimps, and a few *P. notialis.* Campredon and Schrieken (1986) made twenty hauls with the same beam trawl used in this experiment and on the same place, between December 1984 & December 1985 and five additional ones in March 1986. They found ten different shrimp species of which *Gennadas* spec. and *Latreutes fucorum* were not found in this present study. Most shrimps belonged to the species *P. elegans* (7455 of a total 9244 caught shrimps). They found increasing numbers of *P. adspersus*, *P. elegans* and *P. kerathurus* during summer. Differences found between these three researches are probably caused by the different times of year in which these studies were carried out and the extra catch method (push-net) used in this study. Especially the larger densities of smaller shrimp species and the new identified species for the area (*H. inermis*, *A. nitescens*, and *Processa edulis* subsp. *crassipes*) found in this study can be influenced by the mesh-size used and/or the smaller samples taken, which allows a more careful and precise identification and quantification of all organisms (also the small ones) caught in the net.

Densities

In the intertidal at low tide no shrimps were caught with the sieve on grass and bare substrate, apparently the shrimps stay in the pools rather than on dry flats. *P. elegans* was most abundant in the pools (65 specimens per m^2) during low tide, where as during high tide equal densities (around 10 specimens per m^2) occur in the pools and the grass. No shrimps were caught on bare substrate. This indicates a migration out of the pools during high tide, but still in the shelter of seagrass, because it provides shelter to light intensity, water motion and predation, by increasing microhabitats and food availability[3]. Additional it could be that small juvenile shrimps suffer higher rates of predation in short, thin seagrass and unvegetated habitats, and that this would lead to a decrease in abundance in these habitats (Kenyon *et al.* 1995). The larger postjuvenile and adult *P. elegans* and *P. adspersus* (CL>10 mm) caught with the beamtrawl show a preference for the pool during high tide, but the mean densities are not very high (around 0.4 and 0.02 specimens per m^2 respectively).

Densities of *H. longirostris* in the pools vary between 16 and 38 individuals per m^2. No difference between high and low tide could be found, probably due to high variability between the pools. During high tide some individuals migrate out of the pools (1 per m^2), but stay on the seagrass as well. Around one or two *Penaeus* sp. per square meter are found in the pools. During high tide very low densities occur on seagrass and bare substrate.

In the subtidal *H. inermis* (6.6-8.2 specimens per m^2) and *H. longirostris* (2.8-10.5 individuals per m^2) are most abundant on *Cymodocea*. *P. fasciatus* and *S. carinata* show the same preference, but are much less present (less than one individual per m^2). *P. elegans* is the only species of which densities are influenced by the tide. Especially in the *Zostera* fields, almost no specimens were caught during low tide, which does not sound very logical considering the smaller area containing water. An explanation could be the very strong wind during sampling, which brought large quantities of *Zostera* to the surface and probably a lot of *P. elegans* as well. During high tide the mean density was around 0.60 per m^2 in both fields. *P. adspersus*, *Penaeus* sp., *A. nitescens* and *L. tenuicornis* were caught in very small numbers and the

[3] http://www.szn.it/actrep92/aqua_206.htm

densities found show no influences from tide or substrate at all. There was no interaction between tide and seagrass type for any of the shrimps.

Reproductive state

Penaeus sp. and *S. carinata* belong to the infra-order Penaeidea and spawn in offshore waters. Consequently only juveniles of these species have been found in Mauritanian waters. In the infra-order Caridea the females carry eggs in inshore waters, but *P. fasciatus* and *L. tenuicornis* were apparently not in their reproductive period, because no specimens with eggs have been found.

For all the 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 species all individuals change sex, in others a variable percentage of the population are primary females or males (Bauer & VanHoy 1996). Bearing eggs starts at a carapace length of 10-12 mm for *P. elegans* and 12-16 mm for *P. adspersus*. *H. inermis* and *H. longirostris* stay much smaller and start carrying eggs at 2-3 mm and 3-4 mm respectively. *A. nitescens* carries eggs at a length of 3-4 mm, but no minimal length can be estimated because no smaller length classes were caught.

Altogether it can be stated that there are reproductive specimens present in Mauritanian waters, which probably spawn here as well.

Population structure & Behaviour

The length-frequency distribution of *P. elegans* seems to be the same in pools as on the seagrass. The most common carapace length is between 4 and 8 mm, meaning that they are juveniles. The growth rate of these juveniles can be estimated at 1 mm per month, which is probably an underestimation, because the data are not corrected for new recruitment. The growth rate is independent of the substrate the shrimp is caught on. This can be explained by the migration of the juveniles from one pool to another during high tide. Juvenile *P. elegans* forage on organisms like bentic diatoms and Foraminifera. They do this probably during high tide. During low tide they hide with a full stomach in the pools, were seagrass densities are highest (own observation). This would be advantageous because wadingbirds that are significant predators of shrimp in seagrass beds in other areas (e.g. Howard &

Lowe 1984) fish 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 that no migration events of postjuvenile and adult specimens between nearby pools have been detected, because they swam out of the experimental area.

H. longirostris is more abundant in the pools than on the seagrass. Juveniles are most abundant, but postjuveniles and adults are also well represented. No growth has been detected during this study, though it seems like adult carapace lengths became more abundant in time. This is probably caused by continuous recruitment. No feeding behaviour could be detected.

Juveniles of *Penaeus* sp. have only been found in the pools and because of the low densities, no growthrate has been measured. According to other experiments the growthrate of the carapace will be around 1 mm per week for juvenile penaeids (Minello *et al.* 1989, Haywood & Staples 1993, O'Brien 1994). During low tide most of *Penaeus* sp. stomachs were full with undefined food and some diatoms. This indicates a similar behaviour as juvenile *P. elegans*, especially because wading birds are also significant predators of penaeid prawns in estuaries (Mukherjee 1971).

Nursery

In the area were the research was conducted, the Baie d'Aouatif, high percentages of adults with eggs were found for five different species of caridean shrimps. Ten of eleven species caught of both infraorders (Caridea and Penaeidea) were also found in juvenile form. The most abundant species are *P. elegans, H. longirostris, H. inermis* and *Penaeus* sp. (both *P. kerathurus* & *P. notialis)*, of which the latter one is commercially very important. During low tide the shrimps stay in the tidal pools with dense seagrass cover. Some migrate out of the pools on the seagrass beds during high tide, probably for foraging. Concluding it can be said that the tidal flats of the Baie d'Aouatif have a role in the reproduction of the shrimp species caught. But this area is only about 20 square km.

The total area of tidal flats in the Banc d'Arguin is estimated to cover 491 km^2, of which about 193 km^2, are covered by dense seagrass beds (mostly *Zostera noltii*) and about 219 km^2 consist of muddy flats with usually a less dense seagrass cover (Wolff & Smitt 1990). So the same kind of habitat, shallow seagrass beds, can be found in the rest of the Parc National as well. Personal observations on the tidal flats near the islands Nair and Niroumi gave the same impression of the species composition as in the Baie d'Aouatif.

If the mean density of *Penaeus* sp. on seagrass beds and in pools (1.0 ± SE 0.2 individuals per m^2 during high tide) in the studied area is extrapolated to all tidal flats with dense seagrass cover of the entire Banc d'Arguin (193 km^2), the total abundance of *Penaeus* sp. in Mauritanian waters is 193,000,000 ± 38,600,000 juvenile specimens. Probably this will be an underestimation of the total population, because the tidal flats with less dense seagrass cover are not encountered for. If one takes the minimal authorised catch weight (5 gram in Senegal) of an individual and does not compensate the numbers for possible mortality; the total harvest for the Mauritanian fishery would be between 772 and 1158 tonnes. This because *P. kerathurus* and *P. notialis* migrate to open waters at the age of about one year and reproduce there, probably from May till August (Campredon & Schrieken, 1986). If one looks at the production of the fishery of Senegal in one year (e.g. 9,603 tonnes in 1997[4]) the contribution of the Mauritanian nursery based on the densities during this study (January till March) would account for 8.0 to 12.1 %. This will be an underestimation again because shrimps can grow heavier than 5 grams and thus contribute more to the total production. It has to be stressed that comparisons between different years are not completely reliable because populations are renewed every year (lifecycle of 20-24 months) and their densities are dependent on hydro-climatic conditions which determine the good arrival of the larvae[4] and which can differ each year.

Furthermore the tidal flats of the Banc d'Arguin are relatively isolated from other major tidal flat areas. The nearest areas are found about 500 km to the north and are relatively small. To the south the nearest area is about 400 km further at the mouth of the Senegal River, but only few tidal flats occur in that region. Further south in Senegal, the Gambia and especially in Guinea-Bissau much larger tidal flats occur (Wolff & Smit 1990).

Altogether it can be stated that the Banc d'Arguin plays an important role as nursery for shrimps. This conclusion is congruent with several other studies about shallow parts of estuaries and coastal bays serving as important

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[4] http://www.refer.sn/oeps/thiof/thiof_av3.htm

nursery areas for young stages of shrimps (Boddeke 1978, Berghahn 1983, Kuipers & Dapper 1984, Henderson & Holmes 1987). This importance has also been highlighted in the population dynamics of *Penaeus* spec. and *Palaemon* shrimps in intertidal and shallow subtidal seagrasses (Loneragan *et al.* 1994, Berglund 1983). Duineveld *et al.* (1993) already stated that the Mauritanian shelf acts as a source of expoitable stocks of shrimps for one of the most important fishery areas of the world. Together with the research of Campredon and Schrieken (1986) this study makes clear that several species reproduce in Mauritanian waters and migrate in adult form to the stocks in open water.

Further research

It is necessary to conduct more research on the juveniles present in the Banc d'Arguin to get a broader picture about how this nursery functions. Especially because shrimp catches during the following year are predictable to a certain extent from the numbers of subadult juvenile shrimp leaving the shallow nurseries. The estimation of this output requires regular surveys in the nursery (Kuipers & Dapper 1994). So first thing to do is to get a survey of juvenile and reproducing species present throughout the year and to recognise their reproductive periods. When these periods are known one can start quantifying settlement. A good way of doing that is to work with portable artificial seagrass units (ASU) to quantify settlement of postlarvae temporally (e.g. daily or tidally) or spatially (e.g. distinct areas affected by different current regimes). The strength of settlement can be used to evaluate the productivity of nursery habitat for fishery populations (Kenyon *et al.* 1999). Furthermore it is important to get more inside into their life history (e.g. distribution, migration, predation rate and age), maybe by tagging individuals or by aquaria-experiments.

The most important aspect of the recruitment issue from a fisheries perspective is identifying the spawning area from which the nursery habitats draw their maturing larval populations. This is what Rothlisberg *et al.* (1996) referred to as the advection envelope. Effective spawning distribution can identify different stocks of commercial prawns. If there are different stocks in the fishery area, management to reduce the impacts of fishing on spawning penaeid prawns could be closing selected inshore areas within the main fishing grounds, rather than seasonal closures (Condie *et al.* 1999).

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Contents appendices

Appendix A: Sampling points

Waypoint	NB	NBm	WL	WLm	pond %	grass %	bare %	opp pond (m^2)	rim substrate	rim area (m^2)	Middle substrate	Middle area (m^2)
ZCP1	19	53,083	16	17,333	50	40	10	9.4	Zostera	4.4	Cymodocea	5.0
ZP2	19	52,713	16	17,063	10	50	40	6.9	*Zostera*	3.8	short *Zostera*	3.1
ZCP3	19	52,480	16	17,016	30	65	5	11.8	*Zostera*	8.2	Cymodocea	3.6
ZP4	19	53,115	16	17,322	5	15	80	3.9	*Zostera*	2.8	bare	1.1
ZP5	19	52,665	16	16,889	5	10	85	17.9	*Zostera*	6.3	bare	11.6
ZP6	19	52,782	16	16,811	25	40	35	18.8	*Zostera*	12.6	bare&*Zostera*	6.3
ZP7	19	52,769	16	16,722	30	50	20	3.9	*Zostera*	2.8	bare	1.1
CZA8	19	52,747	16	17,365	50	30	20	25.1	*Cymodocea*	17.0	bare	8.2
ZCP9	19	53,010	16	17,384	30	50	20	8.2	*Zostera*	4.1	bare	4.2
ZP10	19	53,574	16	17,117	40	40	20	38.5	*Zostera*	6.6	bare	31.9
ZP11	19	53,330	16	17,239	80	10	10	22.0	*Zostera*	13.8	bare	8.2
ZP12	19	52,591	16	17,512	25	55	20	3.9	*Zostera*	2.8	bare&*Zostera*	1.1
ZP13	19	52,501	16	17,410	20	65	15	9.4	*Zostera*	7.0	Zostera	2.4
ZP14	19	53,360	16	16,684	30	65	5	29.5	*Zostera*	7.9	bare	21.6
ZCP15	19	53,316	16	16,726	40	5	55	13.7	*Zostera*	4.0	bare	9.7
ZCP16	19	53,283	16	16,760	50	30	20	23.6	*Zostera*	6.9	Cymodocea	16.7
ZCP17	19	52,788	16	16,562	5	20	75	10.6	*Zostera*	2.4	bare	8.2
ZCP18	19	52,814	16	16,647	10	10	80	42.4	*Zostera*	7.1	Cymodocea	35.3
Bppoel	19	52,500	16	17,414	20	65	15	3.1	*Zostera*	2.5	bare	0.6
ZP19	19	52,598	16	16,850	5	65	30	34.6	*Zostera*	29.7	bare	4.9
ZCP20	19	52,806	16	17,152	30	35	35	45.0	*Zostera*	6.3	Cymodocea	38.7
ZP21	19	53,462	16	17,192	20	10	70	30.6	*Zostera*	2.0	bare	28.7
ZP22	19	53,491	16	17,171	15	45	40	8.2	*Zostera*	3.1	bare	5.2
ZP23	19	53,420	16	17,214	5	40	55	9.4	*Zostera*	5.0	bare	4.4
ZP24	19	53,289	16	17,261	15	80	5	9.4	*Zostera*	1.1	bare	8.3
ZCP25	19	53,252	16	17,271	15	25	60	33.0	*Zostera*	6.1	Cymodocea	26.9
ZCP26	19	53,305	16	16,431	15	50	35	28.3	*Zostera*	7.5	bare	20.7
ZP27	19	53,307	16	16,370	15	30	55	28.3	*Zostera*	7.5	bare	20.7
ZP28	19	53,256	16	15,791	10	85	5	7.1	*Zostera*	1.9	dead seagrass	5.2
ZP29	19	53,238	16	15,878	10	85	5	25.5	*Zostera*	12.6	bare	12.9

Fig 7 Position sample points push-net with the percentages of surrounding substrate and the total surface area of the pond, devided into the areas of the rim and the middle with the according substrates.

ZCP30	19	53,074	16	15,855	40	20	40	10.6	*Zostera*	2.4	Cymodocea	8.2
ZP31	19	53,108	16	17,248	15	40	45	20.6	*Zostera*	6.9	dead/short *Zostera*	13.7
ZP32	19	53,151	16	17,149	40	30	30	21.6	*Zostera*	6.6	bare&short *Zostera*	15.0
ZCP33	19	53,134	16	16,989	20	80	0	44.0	*Zostera*	38.9	Cymodocea	5.1
ZCP34	19	53,293	16	16,920	15	50	35	24.7	*Zostera*	5.4	*Cymodocea*	19.3
ZP35	19	51,802	16	16,478	40	30	30	7.9	*Zostera*	3.1	bare	4.8
ZP36	19	51,758	16	16,375	45	35	20	11.0	*Zostera*	5.3	dead seagrass&*Zostera*	5.7
ZP37	19	51,418	16	16,334	15	75	10	13.0	*Zostera*	6.7	dead seagrass&bare	6.3

Appendix B: Results

Fig 18 Push-net data (average carapace length in mm, standard deviation and mean densities in # per m^2) of P. elegans, H. longirostris and penaeus sp. caught *in the intertidal on 38 different waypoints each containing a pool, seagrass and bare substrate. The species are caught at low and high tide during daytime (daylight=1) and at some points during nighttime (daylight=0) as well*

						P. elegans			*H. longirostris*			*Penaeus sp.*		
date	tide	daylight	waypoint	habitat	substrate	av.car1	stdev1	dens1	av.car2	stdev2	dens2	av.car3	stdev3	dens3
01/29/02	HT	1	Bppond	bare		0.00		0.0			0.0	4.64		0.6
01/29/02	HT	1	Bppond	grass	*Zostera*	4.65	0.28	1.7			0.0			0.0
01/29/02	HT	1	Bppond	pond	*Zostera*	7.06	0.48	2.0	3.73	0.81	11.0	6.13	1.80	2.0
01/29/02	LT	1	Bppond	pond	*Zostera*	4.86	0.60	98.8	3.86	0.73	110.0			0.0
02/12/02	HT	1	CZA8	bare				0.0			0.0			0.0
02/12/02	HT	1	CZA8	grass	*Zostera*	7.41	0.59	7.5	4.44		2.5			0.0
02/12/02	HT	1	CZA8	pond	*Cymodocea*	9.48	1.35	5.0	4.35	0.42	15.0			0.0
02/10/02	LT	1	CZA8	pond	*Cymodocea*	6.19	0.62	70.0	3.95	1.15	27.5			0.0
01/31/02	HT	1	ZCP1	bare				0.0			0.0			0.0
02/02/02	HT	0	ZCP1	bare				0.0			0.0			0.0
01/31/02	HT	1	ZCP1	grass	*Zostera*			0.0			0.0			0.0
02/02/02	HT	0	ZCP1	grass	*Zostera*			0.0			0.0			0.0
01/31/02	HT	1	ZCP1	pond	*Cymodocea*			0.0	4.30		2.5			0.0
02/02/02	HT	0	ZCP1	pond	*Cymodocea*	7.99	1.22	15.0	5.29	1.42	12.5	11.69	0.00	5.0
01/31/02	LT	1	ZCP1	pond	*Cymodocea*	7.00	0.86	30.0	3.89	0.59	12.5			0.0
01/31/02	LT	0	ZCP1	pond	*Cymodocea*	6.33	0.54	27.5	4.07	0.82	17.5			0.0
02/04/02	HT	1	ZCP10	bare				0.0			0.0			0.0
02/04/02	HT	0	ZCP10	bare				0.0			0.0			0.0
02/04/02	HT	1	ZCP10	grass	*Zostera*	9.46	2.34	7.5			0.0			0.0
02/04/02	HT	0	ZCP10	grass	*Zostera*			0.0			0.0			0.0
02/04/02	HT	1	ZCP10	pond	*Zostera*	6.86	1.31	7.5	4.24	0.94	12.5			0.0
02/04/02	HT	0	ZCP10	pond	*Zostera*	6.42	1.02	17.5	4.51	0.59	22.5			0.0
02/04/02	LT	1	ZCP10	pond	*Zostera*	5.79	0.81	8.8	4.34	0.89	18.8			0.0
02/11/02	LT	0	ZCP10	pond	*Zostera*	4.67		2.5	4.33	0.90	50.0			0.0
02/08/02	HT	1	ZCP15	bare				0.0			0.0			0.0
02/08/02	HT	1	ZCP15	grass	*Zostera*	6.47	0.26	7.5			0.0			0.0
02/20/02	HT	1	ZCP15	pond	*Zostera*	7.49		2.5	4.48	1.16	5.0			0.0
02/20/02	LT	1	ZCP15	pond	*Zostera*	7.17	1.26	6.3			0.0			0.0

02/08/02	HT	1	ZCP16	bare				0.0			0.0			0.0
02/08/02	HT	1	ZCP16	grass	*Zostera*	11.28	2.89	10.0			0.0			0.0
02/20/02	HT	1	ZCP16	pond	*Zostera*			0.0	5.04		2.5			0.0
02/20/02	LT	1	ZCP16	pond	*Zostera*	7.82	2.12	27.5	5.67	0.76	5.0			0.0

						P. elegans			H. longirostris			Penaeus sp.		
date	tide	daylight	waypoint	habitat	substrate	av.car1	stdev1	dens1	av.car2	stdev2	dens2	av.car3	stdev3	dens3
02/10/02	HT	1	ZCP17	bare				0.0			0.0			0.0
02/10/02	HT	1	ZCP17	grass	*Zostera*			0.0			0.0			0.0
02/24/02	HT	1	ZCP17	pond	*Zostera*	7.91	1.36	30.0	5.24	0.46	5.0			0.0
02/23/02	LT	1	ZCP17	pond	*Zostera*			0.0	4.70		2.5	10.66		2.5
02/10/02	HT	1	ZCP18	bare				0.0			0.0			0.0
02/10/02	HT	1	ZCP18	grass	*Zostera*	7.49	1.60	7.5			0.0			0.0
02/10/02	HT	1	ZCP18	pond	*Cymodocea*			0.0	4.29	1.21	10.0			0.0
02/08/02	LT	1	ZCP18	pond	*Cymodocea*	7.74		2.5	5.27	0.19	5.0			0.0
02/12/02	HT	1	ZCP20	bare				0.0			0.0			0.0
03/05/02	HT	0	ZCP20	bare				0.0			0.0			0.0
02/12/02	HT	1	ZCP20	grass	*Zostera*			0.0			0.0			0.0
03/05/02	HT	0	ZCP20	grass	*Zostera*			0.0			0.0			0.0
02/25/02	HT	1	ZCP20	pond	*Zostera*	7.28	1.10	55.0	4.04	1.03	27.5	10.02		2.5
03/05/02	HT	0	ZCP20	pond	*Zostera*	6.65	0.85	25.0	3.66	0.59	17.5			0.0
02/24/02	LT	1	ZCP20	pond	*Zostera*	5.46	0.56	5.0	4.42	1.11	15.0			0.0
02/27/02	LT	0	ZCP20	pond	*Zostera*	5.88	0.39	15.0	4.28	0.65	35.0			0.0
02/18/02	HT	1	ZCP25	bare				0.0			0.0			0.0
02/18/02	HT	1	ZCP25	grass	*Zostera*	5.80	1.35	7.5			0.0			0.0
02/18/02	HT	1	ZCP25	pond	*Zostera*	7.76	1.09	7.5			0.0	7.40		2.5
02/17/02	LT	1	ZCP25	pond	*Zostera*	6.58	1.41	55.0	4.77	1.54	7.5			0.0
02/20/02	HT	1	ZCP26	bare				0.0			0.0			0.0
02/20/02	HT	1	ZCP26	grass	*Zostera*	7.02		1.3			0.0			0.0
02/20/02	HT	1	ZCP26	pond	*Zostera*	6.61	1.00	7.5	4.36	0.84	15.0			0.0
02/18/02	LT	1	ZCP26	pond	*Zostera*			0.0	5.39		2.5			0.0
02/01/02	HT	1	ZCP3	bare				0.0			0.0			0.0
02/02/02	HT	0	ZCP3	bare				0.0			0.0			0.0
02/01/02	HT	1	ZCP3	grass	*Zostera*	6.52	0.63	7.5			0.0			0.0
02/02/02	HT	0	ZCP3	grass	*Zostera*	8.72		2.5			0.0			0.0
02/24/02	HT	1	ZCP3	pond	*Zostera*			0.0	3.92	1.23	10.0			0.0

Fig 18 continued

02/01/02	LT	0	ZCP3	pond	*Zostera*	6.55	1.44	40.0	3.91	0.85	10.0			0.0
02/23/02	LT	1	ZCP3	pond	*Zostera*	6.53	0.69	65.0	4.08	1.00	12.5	9.55	2.67	5.0

Fig 18 continued

						P. elegans			H. longirostris			Penaeus		
date	tide	daylight	waypoint	habitat	substrate	av.car1	stdev1	dens1	av.car2	stdev2	dens2	av.car3	stdev3	dens3
02/20/02	HT	1	ZCP30	bare				0.0			0.0			0.0
02/20/02	HT	1	ZCP30	grass	*Zostera*	9.06	1.42	17.5			0.0	19.42		2.5
02/20/02	HT	1	ZCP30	pond	*Zostera*	8.50		2.5	4.06	0.93	7.5	6.44	1.45	7.5
02/20/02	LT	1	ZCP30	pond	*Zostera*			0.0	4.44	1.13	7.5			0.0
03/06/02	HT	1	ZCP33	grass	*Zostera*	6.17	0.99	40.0			0.0			0.0
03/06/02	HT	1	ZCP33	pond	*Zostera*			0.0	4.29	1.30	15.0	11.80		2.5
03/05/02	LT	1	ZCP33	pond	*Zostera*	7.60	1.23	57.5	5.06	1.43	12.5	10.07		2.5
03/06/02	HT	1	ZCP34	bare				0.0			0.0			0.0
03/06/02	HT	1	ZCP34	grass	*Zostera*	7.05	0.79	12.5			0.0			0.0
03/06/02	HT	1	ZCP34	pond	*Zostera*	6.69	0.40	7.5	5.44	0.13	5.0			0.0
03/05/02	LT	1	ZCP34	pond	*Zostera*	5.57	0.62	125.0	4.44	1.72	12.5			0.0
02/04/02	HT	1	ZCP9	bare				0.0			0.0			0.0
02/04/02	HT	0	ZCP9	bare				0.0			0.0			0.0
02/04/02	HT	1	ZCP9	grass	*Zostera*	7.65	0.86	5.0			0.0			0.0
02/04/02	HT	0	ZCP9	grass	*Zostera*	6.69	1.52	3.8			0.0			0.0
02/04/02	HT	1	ZCP9	pond	*Cymodocea*			0.0	4.56	0.75	7.5	9.69	1.66	3.8
02/04/02	HT	0	ZCP9	pond	*Cymodocea*	7.17	1.46	102.5	4.33	0.81	15.0			0.0
02/04/02	LT	1	ZCP9	pond	*Cymodocea*	6.15	0.95	167.5	4.70	1.21	17.5			0.0
02/11/02	LT	0	ZCP9	pond	*Cymodocea*	6.22	0.92	70.0	3.60	0.31	7.5	8.83		2.5
02/04/02	HT	1	ZP11	bare				0.0			0.0			0.0
02/04/02	HT	0	ZP11	bare				0.0			0.0			0.0
02/04/02	HT	1	ZP11	grass	*Zostera*	6.23		1.3			0.0			0.0
02/04/02	HT	0	ZP11	grass	*Zostera*	8.69	1.70	5.0	3.98	0.15	7.5			0.0
02/04/02	HT	1	ZP11	pond	*Zostera*	5.65		2.5	4.58	1.04	15.0	6.53		2.5
02/04/02	HT	0	ZP11	pond	*Zostera*	6.44	2.13	25.0	4.73	0.86	20.0	8.16	1.28	15.0
02/04/02	LT	1	ZP11	pond	*Zostera*	5.73	0.77	127.5	4.08	1.03	50.0	8.61	1.39	5.0
02/11/02	LT	0	ZP11	pond	*Zostera*	5.55	0.80	35.0	3.59	0.77	27.5	9.29	1.69	12.5
02/06/02	HT	1	ZP12	bare				0.0			0.0			0.0
02/06/02	HT	0	ZP12	bare				0.0			0.0			0.0

02/06/02	HT	1	ZP12	grass	*Zostera*	5.37	0.10	5.0			0.0			0.0
02/06/02	HT	0	ZP12	grass	*Zostera*	6.63	1.48	22.5			**0.0**			**0.0**

						P. elegans			H. longirostris			Penaeus sp.		
date	tide	daylight	waypoint	habitat	substrate	av.car1	stdev1	dens1	av.car2	stdev2	dens2	av.car3	stdev3	dens3
02/06/02	HT	1	ZP12	pond	*Zostera*			0.0	4.71	1.0	50.0	7.46		2.5
02/06/02	HT	0	ZP12	pond	*Zostera*			0.0	4.21	0.77	30.0	9.06	0.65	5.0
02/05/02	LT	1	ZP12	pond	*Zostera*	6.10	0.93	102.5	4.14	0.83	62.5	7.76	1.04	5.0
02/11/02	LT	0	ZP12	pond	*Zostera*	6.93	2.71	17.5	4.46	0.75	42.5	8.84	1.13	12.5
02/06/02	HT	1	ZP13	bare				0.0			0.0			0.0
02/06/02	HT	0	ZP13	bare				0.0			0.0			0.0
02/06/02	HT	1	ZP13	grass	*Zostera*	6.15		2.5			0.0			0.0
02/06/02	HT	0	ZP13	grass	*Zostera*	5.87	0.86	5.0			0.0			0.0
02/06/02	HT	1	ZP13	pond	*Zostera*			0.0	4.33	0.9	25.0	7.55	2.6	5.0
02/06/02	HT	0	ZP13	pond	*Zostera*	9.78	4.65	5.0	4.21	0.78	85.0			0.0
02/05/02	LT	1	ZP13	pond	*Zostera*	5.84	1.04	357.5	4.28	0.80	107.5			0.0
02/11/02	LT	0	ZP13	pond	*Zostera*	5.00	0.81	95.0	4.22	0.85	75.0	9.64	1.43	12.5
02/07/02	HT	1	ZP14	bare				0.0			0.0			0.0
02/07/02	HT	1	ZP14	grass	*Zostera*			0.0			0.0	14.61	1.36	5.0
02/07/02	HT	1	ZP14	pond	*Zostera*			0.0	5.04	0.68	17.5			0.0
02/07/02	LT	1	ZP14	pond	*Zostera*	7.55	1.37	17.5	4.18	1.46	10.0			0.0
02/11/02	HT	1	ZP19	bare				0.0	3.05		1.3			0.0
03/05/02	HT	0	ZP19	bare				0.0			0.0			0.0
02/11/02	HT	1	ZP19	grass	*Zostera*			0.0	3.86	0.87	25.0			0.0
03/05/02	HT	0	ZP19	grass	*Zostera*			0.0			0.0			0.0
02/11/02	HT	1	ZP19	pond	*Zostera*	8.66	2.18	17.5	4.45	0.74	42.5	8.81	1.21	7.5
03/05/02	HT	0	ZP19	pond	*Zostera*	7.25	1.09	15.0	4.14	1.03	52.5	10.20	2.66	17.5
02/10/02	LT	1	ZP19	pond	*Zostera*	6.93	0.96	90.0	4.01	0.95	65.0	8.44	1.07	10.0
02/27/02	LT	0	ZP19	pond	*Zostera*	8.81	1.74	135.0	4.59	0.82	80.0	9.98	0.74	5.0
02/01/02	HT	1	ZP2	bare				0.0			0.0			0.0
02/02/02	HT	0	ZP2	bare				0.0			0.0			0.0
02/01/02	HT	1	ZP2	grass	*Zostera*	6.68	1.10	15.0	4.09		2.5			0.0
02/02/02	HT	0	ZP2	grass	*Zostera*	9.47		2.5			0.0			0.0
02/01/02	HT	1	ZP2	pond	*Zostera*			0.0	4.07	0.62	20.0	8.25	3.73	5.0

Fig 18 continued

02/02/02	HT	0	ZP2	pond	*Zostera*	6.01	0.57	15.0	4.41	0.76	52.5			0.0
02/01/02	LT	1	ZP2	pond	*Zostera*	5.58	0.57	137.5	3.88	0.78	50.0	7.41		2.5

Fig 18 continued

						P. elegans			*H. longirostris*			*Penaeus sp.*		
date	tide	daylight	waypoint	habitat	substrate	av.car1	stdev1	dens1	av.car2	stdev2	dens2	av.car3	stdev3	dens3
02/01/02	LT	0	ZP2	pond	*Zostera*	5.57	0.57	7.5	3.73	0.74	45.0			0.0
02/15/02	HT	1	ZP21	bare				0.0			0.0			0.0
02/15/02	HT	1	ZP21	grass	*Zostera*	5.78	0.60	7.5			0.0			0.0
02/15/02	HT	1	ZP21	pond	*Zostera*	6.24	0.60	15.0	3.61	0.50	10.0			0.0
02/15/02	LT	1	ZP21	pond	*Zostera*	5.94	0.33	5.0	4.60	0.08	5.0			0.0
02/15/02	HT	1	ZP22	bare				0.0			0.0			0.0
02/15/02	HT	1	ZP22	grass	*Zostera*			0.0			0.0			0.0
02/15/02	HT	1	ZP22	pond	*Zostera*	9.37	0.00	5.0	3.91	0.91	15.0			0.0
02/15/02	LT	1	ZP22	pond	*Zostera*	6.78	0.47	5.0	4.30	1.13	17.5			0.0
02/17/02	HT	1	ZP23	bare				0.0			0.0			0.0
02/17/02	HT	1	ZP23	grass	*Zostera*	5.41		2.5			0.0			0.0
02/17/02	HT	1	ZP23	pond	*Zostera*	9.19	2.12	5.0	4.13	1.16	11.3	11.49		1.3
02/17/02	LT	1	ZP23	pond	*Zostera*	8.25	1.12	27.5	4.31	1.06	20.0			0.0
02/18/02	HT	1	ZP24	bare				0.0			0.0			0.0
02/18/02	HT	1	ZP24	grass	*Zostera*	6.66	1.20	17.5			0.0			0.0
02/18/02	HT	1	ZP24	pond	*Zostera*			0.0	3.98	0.78	12.5	11.89	2.27	7.5
02/17/02	LT	1	ZP24	pond	*Zostera*	5.90	0.75	115.0	4.19	0.91	77.5	8.43	0.82	7.5
02/18/02	HT	1	ZP27	bare				0.0			0.0			0.0
02/18/02	HT	1	ZP27	grass	*Zostera*			0.0			0.0			0.0
02/18/02	HT	1	ZP27	pond	*Zostera*	8.25	0.07	5.0	4.53	1.35	20.0	10.66	2.81	5.0
02/18/02	LT	1	ZP27	pond	*Zostera*	6.77	1.26	50.0	4.86	1.17	10.0			0.0
02/20/02	HT	1	ZP28	bare				0.0			0.0			0.0
02/20/02	HT	1	ZP28	grass	*Zostera*			0.0			0.0			0.0
02/20/02	HT	1	ZP28	pond	*Zostera*	10.75	0.91	3.8			0.0			0.0
02/20/02	LT	1	ZP28	pond	*Zostera*	6.65	0.64	22.5	4.57	0.47	5.0			0.0
02/20/02	HT	1	ZP29	bare				0.0			0.0			0.0
02/20/02	HT	1	ZP29	grass	*Zostera*			0.0			0.0			0.0
02/20/02	HT	1	ZP29	pond	*Zostera*			0.0	4.82	1.47	15.0			0.0
02/20/02	LT	1	ZP29	pond	*Zostera*	6.61	1.16	185.0	4.60	1.05	47.5			0.0

03/06/02	HT	1	ZP31	bare				0.0			0.0			0.0
03/06/02	HT	1	ZP31	grass	*Zostera*	6.37	0.30	7.5			0.0			0.0

Fig 18 continued

						P. elegans			H. longirostris			Penaeus sp.		
date	tide	daylight	waypoint	habitat	substrate	av.car1	stdev1	dens1	av.car2	stdev2	dens2	av.car3	stdev3	dens3
03/06/02	HT	1	ZP31	pond	*Zostera*	8.27	1.31	10.0	5.71		1.3			0.0
03/05/02	LT	1	ZP31	pond	*Zostera*	6.82	0.77	70.0	3.98		2.5			0.0
03/06/02	HT	1	ZP32	bare				0.0			0.0			0.0
03/06/02	HT	1	ZP32	grass	*Zostera*	7.85	1.39	35.0	5.83		2.5			0.0
03/06/02	HT	1	ZP32	pond	*Zostera*	8.50	1.95	10.0	4.45	1.93	5.0			0.0
03/05/02	LT	1	ZP32	pond	*Zostera*	7.35	1.09	77.5	4.53	0.96	17.5			0.0
03/07/02	HT	1	ZP35	bare				0.0			0.0			0.0
03/07/02	HT	1	ZP35	grass	*Zostera*	9.84	2.89	7.5			0.0			0.0
03/07/02	HT	1	ZP35	pond	*Zostera*			0.0	5.40	0.66	12.5			0.0
03/07/02	LT	1	ZP35	pond	*Zostera*	6.34	0.56	115.0	4.39	1.05	75.0			0.0
03/07/02	HT	1	ZP36	bare				0.0			0.0			0.0
03/07/02	HT	1	ZP36	grass	*Zostera*	6.96	1.33	7.5			0.0			0.0
03/07/02	HT	1	ZP36	pond	*Zostera*			0.0	4.50	1.28	12.5			0.0
03/07/02	LT	1	ZP36	pond	*Zostera*	7.00	0.68	55.0	4.69	1.19	42.5			0.0
03/07/02	HT	1	ZP37	bare				0.0			0.0			0.0
03/07/02	HT	1	ZP37	grass	*Zostera*	8.79	1.67	8.8			0.0			0.0
03/07/02	HT	1	ZP37	pond	*Zostera*			0.0	4.14	1.06	27.5			0.0
03/07/02	LT	1	ZP37	pond	*Zostera*	6.73	0.85	162.5	4.04	1.09	35.0			0.0
02/02/02	HT	1	ZP4	bare				0.0			0.0			0.0
02/02/02	HT	0	ZP4	bare				0.0			0.0			0.0
02/02/02	HT	1	ZP4	grass	*Zostera*			0.0			0.0			0.0
02/02/02	HT	0	ZP4	grass	*Zostera*			0.0			0.0			0.0
02/02/02	HT	1	ZP4	pond	*Zostera*	7.39	1.65	27.5	4.75	1.01	17.5	9.51	0.33	5.0
02/02/02	HT	0	ZP4	pond	*Zostera*	6.42	0.83	42.5	4.16	0.62	27.5			0.0
02/02/02	LT	1	ZP4	pond	*Zostera*	6.30	0.69	87.5	3.94	0.64	135.0			0.0
02/11/02	LT	0	ZP4	pond	*Zostera*	6.51	0.86	107.5	4.23	0.70	25.0			0.0
02/11/02	HT	1	ZP5	bare				0.0			0.0			0.0
03/05/02	HT	0	ZP5	bare				0.0			0.0			0.0
02/11/02	HT	1	ZP5	grass	*Zostera*			0.0	3.44		1.3			0.0

03/05/02	HT	0	ZP5	grass	*Zostera*			0.0			0.0			0.0
02/11/02	HT	1	ZP5	pond	*Zostera*	7.78	2.27	15.0	3.84	0.86	35.0			0.0

						P. elegans			H. longirostris			Penaeus sp.		
date	tide	daylight	waypoint	habitat	substrate	av.car1	stdev1	dens1	av.car2	stdev2	dens2	av.car3	stdev3	dens3
03/05/02	HT	0	ZP5	pond	*Zostera*	8.69	1.04	10.0	4.84	0.27	17.5			0.0
02/10/02	LT	1	ZP5	pond	*Zostera*			0.0	4.45	0.97	27.5			0.0
02/27/02	LT	0	ZP5	pond	*Zostera*	8.19	0.68	17.5	4.22	1.00	67.5	11.76		2.5
02/10/02	HT	1	ZP6	bare				0.0			0.0			0.0
03/05/02	HT	0	ZP6	bare				0.0			0.0			0.0
02/10/02	HT	1	ZP6	grass	*Zostera*	7.29	1.07	10.0	4.72		1.3			0.0
03/05/02	HT	0	ZP6	grass	*Zostera*			0.0			0.0			0.0
02/10/02	HT	1	ZP6	pond	*Zostera*	8.29	1.78	57.5	3.86	0.69	60.0			0.0
03/05/02	HT	0	ZP6	pond	*Zostera*	7.21	1.20	17.5	3.81	0.58	37.5			0.0
02/08/02	LT	1	ZP6	pond	*Zostera*	8.32	0.80	7.5	3.96	0.82	135.0			0.0
02/27/02	LT	0	ZP6	pond	*Zostera*	6.58	0.95	92.5	4.14	0.90	115.0			0.0
02/10/02	HT	1	ZP7	bare				0.0			0.0			0.0
02/10/02	HT	1	ZP7	grass	*Zostera*	9.27		2.5	2.86		2.5			0.0
02/10/02	HT	1	ZP7	pond	*Zostera*			0.0	3.59	0.68	15.0	10.52		2.5
02/08/02	LT	1	ZP7	pond	*Zostera*	7.39	1.31	30.0	4.13	1.06	177.5			0.0

Fig 18 continued

Fig 20 Beamtrawl data (average carapace length in mm, standarddeviation and mean densities in # per m^2) of P. elegans and P. adspersus repeatedly caught in the intertidal at different waypoints (juvenile fish research, J.P.C. van Etten pers.comm.).

					P. elegans			*P. adspersus*		
datum	tide	waypoint	habitat	substrate	av.car1	stdev1	dens1	av.car2	stdev2	dens2
01/26/00	HT	86	grass	Zostera	11.55		0.0			0.0
02/12/02	HT	Agrass	grass	*Zostera*			0.0			0.0
02/26/02	HT	Agrass	grass	*Zostera*			0.0			0.0
02/26/02	HT	Agrass2	grass	*Zostera*	11.90	1.02	0.5			0.0
03/01/02	HT	Agrass2	grass	*Zostera*			0.0			0.0
02/12/02	HT	Apond	pond	*Zostera*	12.18	1.39	0.4			0.0
02/23/02	HT	Apond	pond	*Zostera*	11.91	1.01	1.0			0.0
02/26/02	HT	Apond2	pond	*Zostera*	12.65	0.99	0.5	11.97		0.0
03/01/02	HT	Apond2	pond	*Zostera*	12.40	0.98	3.1			0.0
02/12/02	HT	Azand	bare				0.0			0.0
02/23/02	HT	Azand	bare		11.75	1.32	0.1			0.0
02/26/02	HT	Azand2	bare				0.0			0.0
03/01/02	HT	Azand2	bare		11.16	1.48	0.0			0.0
02/11/02	HT	bare	bare				0.0			0.0
02/28/02	HT	bare	bare				0.0			0.0
03/04/02	HT	bare	bare				0.0			0.0
03/12/02	HT	bare	bare		10.77		0.0			0.0
03/15/02	HT	bare	bare				0.0			0.0
02/11/02	HT	Bgrass	grass	*Zostera*			0.0			0.0
02/24/02	HT	Bgrass	grass	*Zostera*			0.0			0.0
02/28/02	HT	Bgrass	grass	*Zostera*	12.43		0.0			0.0
03/10/02	HT	Bgrass2	grass	*Zostera*			0.0			0.0
03/13/02	HT	Bgrass2	grass	*Zostera*	11.02	1.45	0.1			0.0
03/18/02	HT	Bgrass2	grass	*Zostera*			0.0			0.0
01/28/00	HT	Bpgrass	grass	*Zostera*			0.0			0.0
02/03/02	HT	Bpgrass	grass	*Zostera*			0.0			0.0
02/03/02	HT	Bpgrass	grass	*Zostera*	12.37		0.0			0.0
02/13/02	HT	Bpgrass	grass	*Zostera*			0.0			0.0
02/15/02	HT	Bpgrass2	grass	*Zostera*			0.0			0.0
02/25/02	HT	Bpgrass2	grass	*Zostera*	11.82		0.0			0.0
03/03/02	HT	Bpgrass2	grass	*Zostera*	12.11	1.25	0.2			0.0
02/11/02	HT	Bpond	pond	*Zostera*	12.31	1.04	0.2			0.0
02/24/02	HT	Bpond	pond	*Zostera*	12.67	0.69	0.2			0.0
02/28/02	HT	Bpond	pond	*Zostera*	11.81	1.14	0.9			0.0
03/10/02	HT	Bpond2	pond	*Zostera*			0.0			0.0
03/13/02	HT	Bpond2	pond	*Zostera*	11.71	0.97	0.4			0.0
03/18/02	HT	Bpond2	pond	*Zostera*	11.52	1.38	0.3			0.0
01/28/00	HT	Bppond	pond	*Zostera*	11.23		0.0			0.0
02/03/02	HT	Bppond	pond	*Zostera*	14.64	0.08	0.1			0.0
02/13/02	HT	Bppond	pond	*Zostera*	13.27		0.0			0.0
02/15/02	HT	Bppond2	pond	*Zostera*			0.0			0.0
02/25/02	HT	Bppond2	pond	*Zostera*	11.91	0.65	0.2			0.0
03/03/02	HT	Bppond2	pond	*Zostera*			0.0			0.0
01/28/00	HT	Bpz	bare				0.0			0.0

Fig 20 continued

					P. elegans			*P. adspersus*		
Datum	tide	waypoint	habitat	Substrate	av.car1	stdev1	dens1	av.car2	stdev2	dens2
01/29/00	HT	Bpz	bare				0.0			0.0
02/03/02	HT	Bpzand	bare		13.28		0.0			0.0
02/13/02	HT	Bpzand	bare				0.0			0.0
02/15/02	HT	Bpzand2	bare				0.0			0.0
03/03/02	HT	Bpzand2	bare				0.0			0.0
02/11/02	HT	Bzand	bare				0.0			0.0
02/24/02	HT	Bzand	bare		10.26		0.0			0.0
02/28/02	HT	Bzand	bare		12.96	0.47	0.0			0.0
03/10/02	HT	Bzand2	bare				0.0			0.0
03/13/02	HT	Bzand2	bare				0.0			0.0
03/18/02	HT	Bzand2	bare				0.0			0.0
03/18/02	HT	geul	subtidal	*Cymodocea*			0.0	11.68		0.0
02/03/02	HT	geul	subtidal	*Zostera*			0.0			0.0
02/11/02	HT	grass	grass	*Zostera*	11.84	0.93	0.1			0.0
02/28/02	HT	grass	grass	*Zostera*			0.0			0.0
03/04/02	HT	grass	grass	*Zostera*	12.23	0.64	0.1			0.0
03/12/02	HT	grass	grass	*Zostera*	11.92	0.84	0.1			0.0
03/15/02	HT	grass	grass	*Zostera*	12.70	0.94	0.2			0.0
02/18/02	HT	grass2	grass	*Zostera*	12.86	2.50	0.0			0.0
02/27/02	HT	grass2	grass	*Zostera*			0.0			0.0
02/11/02	HT	pond	pond	*Zostera*	11.99	0.78	0.4			0.0
02/28/02	HT	pond	pond	*Zostera*	12.34	1.12	0.2			0.0
03/04/02	HT	pond	pond	*Zostera*	12.85	1.10	0.1			0.0
03/12/02	HT	pond	pond	*Zostera*	12.08	0.95	0.4			0.0
03/15/02	HT	pond	pond	*Zostera*	11.73	1.39	0.3			0.0
01/27/00	HT	pond1	bare				0.0			0.0
01/27/00	HT	pond1	grass	*Zostera*	12.49	0.52	0.0			0.0
02/01/02	HT	pond1	pond	*Zostera*			0.0			0.0
02/18/02	HT	pond2	geul	*Cymodocea*			0.0			0.0
03/07/02	HT	pond2	geul	*Cymodocea*			0.0	21.77		0.0
02/18/02	HT	pond2	pond	*Zostera*	12.12		0.0			0.0
02/27/02	HT	pond2	pond	*Zostera*			0.0			0.0
02/18/02	HT	zand2	bare				0.0			0.0
02/27/02	HT	zand2	bare				0.0			0.0
03/11/02	HT	Zgrass	grass	*Zostera*	11.85	0.85	0.6			0.0
03/14/02	HT	Zgrass	grass	*Zostera*	11.87	0.79	0.1			0.0
03/17/02	HT	Zgrass	grass	*Zostera*	11.64	0.73	0.2			0.0
03/11/02	HT	Zgrass2	grass	*Zostera*			0.0			0.0
03/14/02	HT	Zgrass2	grass	*Zostera*			0.0			0.0
03/17/02	HT	Zgrass2	grass	*Zostera*	12.23	0.70	0.3	18.12		0.2
03/11/02	HT	Zpond	pond	*Zostera*			0.0			0.0
03/14/02	HT	Zpond	pond	*Zostera*	11.84	1.15	0.2			0.0
03/17/02	HT	Zpond	pond	*Zostera*	12.32	0.52	0.3			0.0
03/11/02	HT	Zpond2	pond	*Cymodocea*	12.34	0.79	0.4			0.0
03/14/02	HT	Zpond2	pond	*Cymodocea*	12.85	0.98	1.1	15.42	3.72	0.3
03/17/02	HT	Zpond2	pond	*Cymodocea*	12.42	1.26	0.8	15.79	3.18	0.5
03/11/02	HT	Zzand	bare				0.0			0.0
03/14/02	HT	Zzand	bare		11.99	0.40	0.1			0.0
03/17/02	HT	Zzand	bare		12.18	1.40	0.0			0.0
03/11/02	HT	Zzand2	bare				0.0			0.0
03/14/02	HT	Zzand2	bare				0.0			0.0
03/17/02	HT	Zzand2	bare		11.81		0.0			0.0

			P. elegans			*P. adspersus*			*Penaeus sp.*			*H. longirostris*			*S. carinata*		
date	tide	substrate	av.car1	stdev1	dens1	av.car2	stdev2	dens2	av.car4	stdev4	dens4	av.car5	stdev5	dens5	av.car6	stdev6	dens6
01/29/02	HT	*Cymodo*	8.96	1.66	0.8	18.39		0.0	16.26	8.46	0.2	3.96	0.63	0.0			0.0
02/07/02	HT	*Cymodocea*	6.91	2.00	0.1	16.14	3.99	0.1	19.88	4.58	0.1	4.65	0.54	1.1	7.57	2.28	0.2
02/27/02	HT	*Cymodocea*			0.0			0.0	20.30	7.06	0.5	4.32	0.41	7.9	5.94	2.86	0.4
03/13/02	HT	*Cymodocea*	9.07	2.01	1.9	15.07	4.03	0.6	7.79	0.56	0.1	4.23	0.46	3.0			0.0
03/13/02	HT	*Cymodocea*	9.44	2.03	0.4	15.54	3.22	0.4	22.21	7.19	0.1	4.21	0.80	2.2	6.53	1.12	0.1
02/28/02	LT	*Cymodocea*	8.52	0.90	2.7	13.44		0.3	17.28		0.3	4.09	0.01	0.7			0.0
02/28/02	LT	*Cymodoce*			0.0			0.0	17.54	5.55	0.5	3.89	0.54	34.0	5.82	0.21	0.7
03/01/02	LT	*Cymodocea*	7.05		0.2	14.75		0.2			0.0			0.0			0.0
03/17/02	LT	*Cymodocea*			0.0			0.0	16.94	2.40	0.1	4.33	0.49	14.8	6.45	1.27	0.3
03/17/02	LT	*Cymodocea*			0.0			0.0	20.22	8.97	0.2	3.91	0.64	3.2	6.02	1.14	1.3
01/26/02	HT	*Zostera*	8.23	1.97	0.6	16.22	4.37	0.0	13.49	3.61	0.1	5.00	0.78	0.1	7.83	2.59	0.2
02/26/02	HT	*Zostera*	8.16	1.33	0.9			0.0			0.0			0.0			0.0
02/26/02	HT	*Zostera*	8.34	1.70	1.0			0.0	8.61		0.1			0.0			0.0
03/15/02	HT	*Zostera*	8.01	1.32	0.2			0.0	10.35		0.0	4.95	0.74	0.2			0.0
03/15/02	HT	*Zostera*			0.0	12.39	0.60	0.3	14.62	7.56	0.3	4.31	0.52	0.3	7.50		0.1
02/28/02	LT	*Zostera*			0.0			0.0	22.96	6.07	0.4	3.97	0.86	0.9			0.0
03/01/02	LT	*Zostera*			0.0			0.0	26.62		0.2	3.31		0.2			0.0
03/01/02	LT	*Zostera*	12.30		0.1			0.0			0.0			0.0			0.0
03/17/02	LT	*Zostera*			0.0			0.0			0.0	4.52		0.2			0.0
03/17/02	LT	*Zostera*			0.0			0.0			0.0			0.0			0.0

deviation and mean densities in # per m^2) of species caught in the subtidal on Zostera (N=10) and Cymodocea (N=10) during high and low tide

IX

te	tide	substrate	*H. inermis* av.car7	stdev7	dens7	*P. fasciatus* av.car8	stdev8	dens8	*A. nitescens* av.car9	stdev9	dens9	*L. tenuicornis* av.car10	stdev10	dens10
29/02	HT	*Cymodocea*	3.58	0.58	0.2	5.66		0.0			0.0			0.0
02/07/02	HT	*Cymodocea*	3.23	0.92	13.1	5.77	1.36	0.1	4.67		0.0	7.82	2.32	0.1
02/27/02	HT	*Cymodocea*	3.38	0.46	14.8	5.21	1.20	0.7	4.35	1.10	0.2	9.99	1.07	0.1
03/13/02	HT	*Cymodocea*	3.26	0.70	7.4	5.11		0.0			0.0	9.29	0.97	0.1
03/13/02	HT	*Cymodocea*	3.57	0.55	5.3	3.14		0.0			0.0	13.27	1.88	0.1
02/28/02	LT	*Cymodocea*	3.51	0.61	1.4	3.98		0.3			0.0			0.0
02/28/02	LT	*Cymodocea*	2.86	0.45	16.2	5.16	1.26	1.4	4.48		0.2	8.88	0.04	0.3
03/01/02	LT	*Cymodocea*	3.75	0.15	0.7			0.0			0.0			0.0
03/17/02	LT	*Cymodocea*	3.15	0.66	12.4	4.97	0.95	0.9	4.77		0.0			0.0
03/17/02	LT	*Cymodocea*	2.86	0.47	2.2	5.28	1.05	0.5	4.57		0.0	9.77		0.0
01/26/02	HT	*Zostera*	3.44	0.95	0.8	5.71	1.10	0.0			0.0			0.0
02/26/02	HT	*Zostera*			0.0			0.0			0.0			0.0
02/26/02	HT	*Zostera*			0.0			0.0			0.0			0.0
03/15/02	HT	*Zostera*			0.0			0.0			0.0			0.0
03/15/02	HT	*Zostera*	3.51	1.02	1.0	4.71		0.1	5.32		0.1	12.82		0.1
02/28/02	LT	*Zostera*	2.75	0.54	0.6			0.0			0.0	8.80		0.1
03/01/02	LT	*Zostera*			0.0			0.0			0.0			0.0
03/01/02	LT	*Zostera*	2.87		0.1			0.0			0.0			0.0
03/17/02	LT	*Zostera*			0.0			0.0			0.0			0.0
03/17/02	LT	*Zostera*			0.0			0.0			0.0			0.0

Fig 22 continued

Fig 29 Carapace lengths in mm and stomach

TIDE	CARAPACE LENGTH (MM)	STOMACH CONTENT
HT	8.1	-
HT	9.5	-
HT	9.5	-
HT	9.5	sand, diatoms, ondef.
HT	9.6	-
HT	9.7	sand, ondef. (red)
HT	9.8	-
HT	9.8	-
HT	10.0	ondef. (rood)
HT	10.7	-
HT	10.8	-
HT	11.0	sand
HT	11.2	-
HT	11.5	sand, 1 diatom
HT	11.5	ondef.
HT	12.0	-
HT	12.6	-
HT	12.7	-
HT	12.8	sand
HT	12.9	-
HT	14.1	sand, 2 foraminifera, ondef.
HT	15.0	-
LT	4.4	1 foraminifera, ondef.
LT	4.5	-
LT	4.6	sand
LT	4.8	-
LT	4.8	-
LT	5.6	-
LT	5.6	sand, 1 foraminifera
LT	5.7	-
LT	5.7	sand, 1 foraminifera, ondef.
LT	5.7	-
LT	5.8	-
LT	5.8	sand, ondef.
LT	5.8	-
LT	5.8	-
LT	6.0	ondef. (brown/red)
LT	6.5	-
LT	6.7	5 foraminifera, ondef.
LT	7.2	-
LT	7.4	sand, pink bivalve, ondef.
LT	7.4	-
LT	7.5	-
LT	7.5	sand, 1 foraminifera, ondef.
LT	7.5	sand, 3 foraminifera, ondef.
LT	7.6	-
LT	7.8	-
LT	7.9	Sand, ondef.
LT	8.0	-
LT	8.0	Sand, 1 foraminifera, ondef. (brown)
LT	8.2	Sand, 1 diatom, 2 foraminifera, ondef.
LT	8.2	Sand, ondef.
LT	8.3	Sand, 3 foraminifera, ondef.
LT	8.4	Sand, 3 foraminifera, ondef.
LT	8.7	Sand, 3 foraminifera, ondef.

Fig 30 Carapace lengths in mm and stomach contents of H. longirostris during high (HT) and low (LT) tide

TIDE	CARAPACE LENGTH (MM)	STOMACH CONTENT
HT	1.9	ondef. (brown)
HT	2.1	-
HT	2.2	-
HT	2.2	-
HT	2.3	ondef.
HT	2.5	-
HT	2.8	ondef. (brown, red and green)
HT	2.8	-
HT	3.0	sand, ondef. (brown)
HT	3.0	ondef. (brown)
HT	3.4	ondef. (brown and white)
HT	3.4	sand
HT	3.5	sand, ondef.
HT	5.2	ondef.
HT	6.0	-
LT	2.1	-
LT	3.6	-
LT	3.9	sand, ondef. (brown)
LT	4.0	-
LT	4.0	-
LT	4.1	ondef. (brown)
LT	4.2	sand, ondef.
LT	4.3	-
LT	5.0	ondef. (green)
LT	5.1	sand, ondef.
LT	5.3	-

Fig 31 Carapace lengths in mm and stomach contents of Penaeus sp. during high (HT) and low (LT) tide

TIDE	CARAPACE LENGTH (MM)	STOMACH CONTENT
HT	7.5	-
HT	11.0	diatoms, ondef.
HT	12.1	sand, ondef.
HT	12.7	-
HT	12.8	sand
HT	13.0	-
HT	13.1	ondef
HT	13.2	-
HT	13.5	-
HT	13.5	sand, diatoms, ondef.
HT	14.5	-
HT	14.7	-
HT	14.8	-
HT	15.4	-
HT	15.7	-
HT	16.5	-
HT	19.5	-
HT	23.6	-
LT	4.6	-
LT	5.0	sand
LT	6.8	ondef
LT	7.5	sand
LT	9.0	ondef
LT	10.3	sand, 2 diatoms, ondef.
LT	10.9	1 diatom, ondef.