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Thorn fish *Terapon jarbua* (Forskål) predation on juvenile white shrimp *Penaeus indicus* H. Milne Edwards and brown shrimp *Metapenaeus monoceros* (Fabricius): the effect of turbidity, prey density, substrate type and pneumatophore density

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Abstract

A series of laboratory experiments was conducted at Inhaca Island Marine Biological Station, Mozambique, in order to assess the separate effects of turbidity, prey density, substrate type, pneumatophore density, and the combined effects of turbidity with the latter three, on rate of predation by the thorn fish *Terapon jarbua* (Forskål, 1775) on white shrimp *Penaeus indicus* and brown shrimp *Metapenaeus monoceros*.

Significant interactions between turbidity and the other three factors on shrimp predation for both prey species were detected. Regardless of prey density, increasing turbidity decreased predation on *P. indicus*, but not on *M. monoceros*, for which increasing densities reduced the protective effect of turbidity. Increasing prey density increased predation on *P. indicus* in clear water, and increased predation on *M. monoceros* in low and high, but not in intermediate turbidity or clear water. The presence of a substrate suitable for burying decreased predation on *M. monoceros* in clear water, solely sandy-shell substrate afforded protection to *P. indicus*, while in turbid water, no substrate offered significant protection and muddy substrate even increased prey vulnerability to fish probably as a result of increased preys' locomotor activity. Raising pneumatophores density seems to lower the protective

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value of turbidity for both species. In clear water, only low and high structure density provided a deterrent effect on predation on *P. indicus*; in turbid water, intermediate and higher structure density increased predation. Increasing structural complexity reduced predation on *M. monoceros* linearly in clear water; but in low turbid water it increased. In high turbid waters, the increase was only significant in intermediate pneumatophore density. High structural complexities impair the pursuing capacity of fish and thus decreased predation rates. The results indicate that the effective provision of shelter of different habitats depends not only on the various environmental parameters analysed, but also on the way they interact and on the behaviour of prey and predator as well.

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1. Introduction

Juvenile penaeid shrimps have been reported to have a marked preference for coastal wetlands, such as mangroves, and adjacent intertidal habitats, such as nursery areas (Staples et al., 1985; Robertson and Duke, 1987; De Freitas, 1986; Chong et al., 1990). Some of the reasons why juveniles select these different nursery areas are believed to be related to food availability (litter, detritus, primary productivity) and to high survival promoted by the abundance of protective bottom substrates and structural complexity (substrate type, turbidity, mangrove roots, submerged macrophytes, etc.) reducing or impeding their predation (Williams, 1958; Macnae, 1974; Minello and Zimmerman, 1983; Minello et al., 1989; Zimmerman and Zamora, 1984; Staples et al., 1985; De Freitas, 1986; Coles et al., 1987; Dall et al., 1990; Laprise and Blaber, 1992; Robertson and Blaber, 1992; Vance et al., 1996; Primavera, 1997; Rönnbäck et al., 1999).

Predation is a key mechanism in structuring and maintaining diversity and stability in aquatic communities as one of the effects on prey populations is intraspecific resource partitioning (Stein, 1977). Several studies have suggested that fish predation on juvenile penaeid shrimps may be one of the most important processes causing natural mortality and consequent recruitment variability, both of which contribute to the annual fluctuations observed in commercial catches (Minello and Zimmerman, 1983; Minello et al., 1989; Dall et al., 1990). Many species of fish have been identified as shrimp predators (see Minello and Zimmerman, 1983; Dall et al., 1990). Dall et al. (1990) identified at least 14 families of fish that predate on juvenile penaeid shrimps from bottom fish commonly found in the same areas as penaeids.

Penaeid shrimps respond to predation pressure (as a defence strategy) by means of a series of specific behaviours that include reducing visibility through burying in the soft substrate or using escape movements and vegetation structures to hide when attacked (see Main, 1987; Dall et al., 1990). Accordingly, some penaeid species remain buried in the substratum during the day to emerge at night (Minello et al., 1987; Dall et al., 1990; Vance, 1992; Primavera and Lebata, 1995), while others occupy highly turbid waters (Dall et al., 1990; Chong, 1995). Primavera and Lebata (1995) found that juvenile

Metapenaeus anchistus and *Metapenaeus* sp. burrow much more frequently than *Penaeus merguiensis*, and *Penaeus monodon* during the day and night, respectively. *Metapenaeus monoceros* also stays mostly buried during daylight (Joshi et al., 1979), whereas *Penaeus indicus* have been reported to bury very seldom, if ever, but commonly occur in turbid waters and close to mud banks (Hughes, 1966; De Freitas, 1986; Dall et al., 1990).

Despite the lack of comparative studies of shrimp predation in mangrove and nonmangrove areas, the importance of structural complexity in reducing predator efficiency is well established (Vance et al., 1990; Rönnbäck et al., 1999), although this shelter function is species-specific, depending on prey behaviour and predator strategies and efficiency (Minello and Zimmerman, 1983; Primavera and Lebata, 1995; Primavera, 1997). For instance, *Penaeus* species seem to depend more on structural complexity for shelter when compared to *Metapenaeus* species. The lack of confinement to vegetated habitats for *M. monoceros* might thus probably be explained by behavioural differences between the genus *Penaeus* and *Metapenaeus*. Accordingly, the protective value of a given habitat is dependent upon the specific behaviour of the predator and prey species (e.g. Minello and Zimmerman, 1983; Loneragan et al., 1998; Primavera, 1997).

Although visual defence against predators by penaeid shrimps is well documented, only a few studies have attempted to assess substrate type and structural complexity (resulting from prop roots, pneumatophores, seagrass, etc.) and turbidity (see Minello et al., 1987; Laprise and Blaber, 1992; Chong, 1995; Primavera, 1997; Primavera and Lebata, 1995) as refugia and how these factors interact with prey density in predator avoidance.

This study was conducted in Mozambique, where the export of penaeid shrimps is a significant source of foreign currency income contributing to ca. 21% of the current exports (INE, 1999). The experiments focused on the two major commercial penaeid species, the white shrimp *P. indicus* and the brown *M. monoceros*, which together comprise 85% of the country's shrimp harvest (Macia, 1990; Palha de Sousa, 1996), and their juvenile stages are found predominantly associated with mangroves and estuarine areas as well as adjacent intertidal flats and turbid waters (De Freitas, 1986; Hughes, 1966; Rönnbäck et al., 2002). The main objective was to quantify predation by thorn fish (*Terapon jarbua*—a voracious and common shrimp predator) on juvenile stages of these two penaeid species under the influence of different levels of turbidity, prey density, substrate type and pneumatophore density. These data will allow for comparison of the shelter efficiency provided to shrimps by the different levels of the environmental factors analysed, as well as the interactive effect of turbidity.

The experiments were designed to test the following hypotheses: (i) that predation on both prey species decreases with increasing turbidity and (ii) that it increases with increasing prey density; (iii) that the presence of a substrate suitable for burrowing decreases the vulnerability of burrowing shrimps to predation; (iv) that increases in the fine fraction of sediment affects significantly the burrowing efficiency and consequently predation rates on burrowing shrimps; (v) that increase in above ground structural complexity results in a decrease in mortality rate for both prey species; and (vi) that there are significant synergistic effects between turbidity and each of the other environmental parameters considered on predation rates.

2. Materials and methods

This study was performed between October and December 2000 at the Marine Biological Station at Inhaca Island (lat. 26°00'S; long. 33°00'E), Maputo province, Southern Mozambique.

2.1. Experimental design

Shrimp mortality rates from thorn fish *T. jarbua* predation were tested at four turbidity levels, three prey densities, three types of substrate and three pneumatophore densities, as well as in every combination of the three lower levels of turbidity and each level of the other factors, except the prey density factor, where 0.64 g l^{-1} turbidity was used as well. The factors were analysed for the respective responses of predation mechanisms studied separately. In all experiments there were four replicates, which were run simultaneously, and in each group of experiments the sequence of treatments applied was chosen randomly. This procedure avoids potential biases caused by the temperature and photoperiod modifications over time. Order of addition of thorn fish and shrimps to experimental tanks, as well as order of removal from tanks, was also changed in each trial to avoid bias.

During the 24 h preceding the experiments, fish and shrimps were held in the tanks where the experiments would be carried out, separated by a dividing net (1-mm mesh size). Fish–shrimp exposure was initiated by removing the net and the animals were left to interact for 12 h, after which the fish were removed with a small dip net and the surviving shrimps counted in order to determine the number of shrimps predated. New animals (both fish and shrimps) were used on each trial.

2.2. Experimental animals

The fish were obtained from the wild, captured by hand trawling (8-mm mesh size) in Saco da Inhaca during the end of ebbing tides along the small draining channels and held in a flow-through glass aquarium $110 \times 50 \times 50$ cm set outdoors and were fed daily with live juvenile shrimps.

Shrimps were captured in the mangrove creeks fringed by *Rhizophora mucronata* by means of a small beach seine net (1-mm mesh size) during low tides, usually less than 24 h before acclimation period, except in a few cases, where the shrimps were captured 2 days before. Prior to the acclimation period, shrimps were held in a 60-l capacity circular flow-through tank and fed with prawn pellets.

2.3. Experimental procedure

The experiments were performed in eight circular plastic tanks 30-l capacity (50 cm in diameter of aperture; 0.14 m^2 bottom surface; 16 cm deep). Each set of four tanks was connected in a closed system of constant and permanent flow-through seawater maintained by means of two identical water pumps (10 W). This allowed us to run two levels of each factor simultaneously. From a mother-tank, the water was pumped into

each tank and a collector tube conducted it back, closing the circuit. The tanks were covered with removable light brown nets (1-mm mesh aperture), which allowed the penetration and use of natural light and photoperiod but prevented shrimps from jumping out of the tanks when chased by fish. No attempt was made to regulate the amount of light entering the troughs. All the experiments were undertaken during daylight (started between 0500 and 0600 h), as most of the shrimp and visual fish predator species have a diel activity pattern (e.g. Möller and Jones, 1975; Minello et al., 1987). At the beginning of the study, sunrise and sunset occurred at about 0520 and 1700 h, respectively, and at the end occurred at about 0400 and 1900 h, respectively.

In each tank, a dividing net (1-mm mesh aperture) kept fish and shrimps apart during acclimation so that the animals could exploit the new "environment" and get used to each other's presence. These nets divided the tanks in two halves, and were suspended by horizontal sticks and anchored to the tanks' bottoms by means of small leads, or glued with silicone as in the case of the structure density study. Predator and prey were stocked simultaneously at a ratio of 1 fish:6 shrimps, except for the study of prey density factor, where 12 and 18 penaeids per tank were used as well. Preliminary trials revealed that the maximum feeding capacity of fish was about seven *P. indicus* and about six *M. monoceros* juveniles for 12 h (daylight) and, consequently, this latter density was set as the reference density for all experiments.

The 24-h acclimation period enables both the fish and shrimps to recover from handling stress and to explore the structures in the tank. Fish starvation during acclimation and stocking of shrimps at higher densities (43 juveniles/m²) than those in the field $(5-15/m^2 \text{ among pneumatophores in Saco da Inhaca mangrove forest, according to Rönnbäck et al., 2002) ensured predation on shrimps during the experiments. At the end of the experiments, the fish were removed by means of a small dip net, the tanks were drained and the surviving shrimps counted. All shrimps missing from the tanks were considered predated. Preliminary trials revealed that we could consistently recover all shrimps from tanks that did not contain predators. Shrimps' non-predation mortality was observed in three clear water tanks. The dead shrimps were considered as not eaten, as the fish are known to eat dead shrimps as well as live ones in clear water conditions (author's observation).$

All fish and shrimps were measured to the nearest millimeter (total length) prior to each experimental set. We attempted to use fish and shrimps as similar as possible in size in each experiment and to keep the size range of fish and shrimps as narrow as possible to avoid problems with size-selective predation. Hence, only fish within the 7.0–7.9 cm and shrimps within the 2.5–3.5 cm (*P. indicus*) and 2.4–3.6 cm (*M. monoceros*) size range were used (total length). The sizes of fish and shrimps used were chosen such that the total length of prey was between 30% and 50% of that of the predator, for it is known that this is the preferred length of penaeid prey for fish (Minello et al., 1989; Dall et al., 1990; Minello and Zimmerman, 1991). Salinity, temperature and turbidity were monitored throughout the experiments in each tank, including the mother-tank. The variation of turbidity was never higher than 0.03 g 1^{-1} throughout the experiments. Table 1 summarizes the temperature and salinity means and ranges for each set of experiments.

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Table	1

Summary data on mean values and ranges of temperature and salinity in each set of experiments

Experiment	Temperature (°C)			Salinity (‰)		
	Min	Max	Mean	Min	Max	Mean
Turbidity						
P. indicus	19.2	24.3	22.4	32.2	35.5	33.4
M. monoceros	20.2	24.0	22.7	32.4	35.2	33.2
Prey density						
P. indicus	19.2	27.1	21.8	32.2	34.5	33.5
M. monoceros	21.4	24.8	22.7	32.0	35.0	33.4
Pneumatophore density						
P. indicus	21.6	26.2	24.1	30.7	34.4	32.8
M. monoceros	21.6	28.0	24.9	30.7	35.0	32.7
Substrate type						
P. indicus	21.6	27.7	24.4	32.2	34.8	33.5
M. monoceros	21.8	27.9	24.4	35.4	28.3	32.3

Min-minimum; Max-maximum.

2.4. Turbidity

Shrimps' predation rate in four different turbidity levels was investigated in order to determine to what degree turbidity provides protection. The turbidity levels tested were 0.00 (control), 0.16, 0.32 and 0.64 g l⁻¹. The initial density of shrimps considered was 6 per tank. Turbidity was produced by means of fine sediment collected in the mangrove area and sieved with a 250- μ m mesh sieve in order to retain any particle or organism that could interfere with the experiments. The sediment was carefully added to the running water until the intended turbidity level was achieved. A water pump (28 W) placed inside the mother-tank maintained the particle suspension, and associated turbidity level.

2.5. Prey density

In order to test the predation rate in different prey density conditions, experiments with 6, 12 and 18 shrimps per tank (43, 86 and 129 m⁻²) were run for each species. Three levels of turbidity were considered on the analysis of the synergistic effects of turbidity and prey density: 0.00, 0.16 and 0.32 g l⁻¹.

2.6. Substrate type

This experiment attempted to compare the importance of three substrate types in protecting the shrimps from the thorn fish. The manipulation yielded four very discrete microhabitats: no substrate (control), mud, sand and a sandy-shell mixture. Each tank contained a 5-cm layer of sediment (except the control tanks). Three levels of turbidity were also tested in a two-way design with the substrate types: 0.00, 0.16 and 0.32 g l^{-1} .

The three substrates chosen are representative of bottoms that are widely but not uniformly distributed over the island. The first substrate was taken from a sand bank, Banco Xidjane, off the southwestern coast of the island, and consisted of shell debris and gravel to coarse sand (shell-sand mixture 33.7% \oslash size of >2000 µm, 35.7% \oslash of 2000–1000 µm, 26.5% 1000–>500 µm, 3.3% 500–>250 µm). It was obtained with a shovel from the superficial layer of the bottom. The second was clean sand from the beach in front of the Marine Biology Station, which was sieved and washed (sand and fine sand 9% \oslash size of 500–>250 µm, 90.1% \oslash of 250–125 µm and 0.7% <125 µm \oslash). The third consisted of mud (100% very fine sand, silt and clay fraction \oslash <125 µm) from the area of *R. mucronata* in Saco da Inhaca mangrove. It was sieved, washed in salt water and left to rest for some days, until it was sufficiently compact to be used on the experiments. New substrates were used in each trial.

According to the Wentworth grade classification (Krumbein and Sloss, 1963), the fraction passing the 0.125-mm sieve contains very fine sand, silt and clay. The combined weight of this fraction, expressed as a percentage of the total weight, was used for regression with shrimp mortality. In the text, this fraction is referred to as "fine fraction of sediment".

2.7. Pneumatophore density

Relative predation rates by the thorn fish were studied in four pneumatophore density treatments: 0 (control), 15, 30 and 45 per tank. Pneumatophores 16.1 ± 0.2 cm long collected from the fringing *Avicennia marina* mangrove were attached to the tanks' bottoms with silicone, in an approximately homogenized distribution. The distribution, density and size of pneumatophores of *A. marina* in the field are highly variable $(80-180/m^2)$ and all densities used varied from lower, equal to or higher than those found naturally in the Saco da Inhaca mangroves. In these experiments, the dividing nets were also attached to the tanks' bottoms by means of silicone, and after the experiment, the fish and remaining shrimps were recovered by draining the tanks with a filtering net, as it was not possible to use a dip net.

Three turbidity levels were also tested in a two-way design with the pneumatophore density: 0.00, 0.16 and 0.32 g l^{-1} .

2.8. Statistical analysis

In the experiments concerning solely the turbidity, the data were analysed using the mean numbers of shrimps eaten in a tank over the experimental period as the observation in a one and two-way analysis of variance (ANOVA), where the main factors of turbidity and prey species were considered. For each of the remaining factors analysed (prey density, substrate type and pneumatophore density), the main effect of turbidity and the respective environmental factor were considered in a two-way ANOVA on shrimps' mortality rates. If a significant ($p \le 0.05$) F value resulted from the ANOVAs, an HSD Tukey's multiple comparison test was used to determine which means differed significantly. Examination of residual plots and univariate tests (Cochran C, Hartley F_{max} and Bartlett chi-square) revealed whether the assumption of homogeneity of variance was satisfied.

Differences in mortality rates were also tested in a multiple regression-based approach. Accordingly, in order to assess the relative importance of each parameter as a factor which might influence predation rates, both turbidity level and each of the other factors analysed were included in a backward stepwise multiple regression of the form:

$$M = \alpha + \beta_1 T + \beta_2 X + \beta_3 T^2 + \beta_4 X^2 + \beta_5 T X$$

where *M* is mortality, *T* is turbidity (g l^{-1}) and *X* is the other physical factor, depending on which experiment was being analysed. The terms T^2 and X^2 represent the quadratic effects and *TX* the intersection effect. Those components of the model that were not significant were eliminated from the equation one at a time, and were included only if significant at the 5% level and if that accounted for more than 5% of the total variation. In order to facilitate the perception of relationships, mortality response surfaces to turbidity and each of the others parameters were constructed using the quadratic smoothing procedure, which fits a second-order polynomial function to the data.

3. Results

Upon contact with the thorn fish, both shrimp species showed evasion by locomotion. Each attack elicited an escape response that consisted in a rapid flexing of the abdomen causing a jump through the water.

3.1. Turbidity

Shrimp mortality from thorn fish predation was affected by turbidity (Table 2) and turbidity–prey species interaction (Table 3). In general, predation decreased with increasing turbidity. However, that decrease was not similar for both species (Fig. 1). In 0.00, 0.16 and 0.64 g l⁻¹, predation rates were similar for both species, but in 0.32 g l⁻¹ conditions, less *P. indicus* juveniles were eaten than *M. monoceros*. However, the Tuckey HSD test did not detect a significant difference at the 5% level (p = 0.0593), probably due to the fact that *M. monoceros*^{*} mortality rate was 0.0% in one replica, and 66.7% in the remaining three replicas. This difference between experiments was the largest of the series and was probably responsible for the non-significance of the test.

3.2. P. indicus

A significant negative linear regression was detected between the mortality rate (number of shrimps predated per tank) and turbidity (g l⁻¹) ($F_{(1,14)}$ = 34.184; p = 0.0000), for which

Table 2 ANOVA tests of *P. indicus* and *M. monoceros* predation in different turbidity conditions (df=degree of freedom, MS=mean squares, $F=F_{max}$ Hartley)

Species	df effect	MS effect	F	p level
P. indicus	3	23.75	33.53	< 0.0001
M. monoceros	3	17.56	14.29	0.0003

Tal	ble	3

Two-way ANOVA on differences in mean number of shrimps eaten in each set of experiments

Experiment			Source	df effect	MS effect	F	p level
	Turbidity		Sp	1	2.53	2.61	0.1191
			Т	3	38.03	39.26	< 0.0001
			$Sp \times T$	3	3.28	3.39	0.0345
Penaeus indicus	Prey density	п	Т	3	87.69	161.9	< 0.0001
			D	2	6.9	12.73	0.0001
			$\mathbf{T} imes \mathbf{D}$	6	0.92	1.71	0.1481
		%	Т	3	8536.25	107.28	< 0.0001
			D	2	1143.1	14.37	< 0.0001
			$\mathbf{T} imes \mathbf{D}$	6	728.58	9.16	< 0.0001
	Substrate type		Т	2	33.77	54.64	< 0.0001
			S	3	24.13	39.04	< 0.0001
			$T \times S$	6	7.63	12.35	< 0.0001
	Pneumatophore		Т	2	21.02	40.36	< 0.0001
	density		Р	3	11.08	21.27	< 0.0001
			$\mathbf{T} \times \mathbf{P}$	6	4.41	8.47	< 0.0001
Metapenaeus	Prey density	п	Т	3	21.52	26.49	< 0.0001
monoceros			D	2	15.08	18.56	< 0.0001
			$\mathbf{T} imes \mathbf{D}$	6	4.42	5.44	0.0004
		%	Т	3	3141.28	70.98	< 0.0001
			D	2	2182.78	49.32	< 0.0001
			$\mathbf{T} imes \mathbf{D}$	6	1485.82	33.57	< 0.0001
	Substrate type		Т	2	5.15	8.93	0.0007
			S	3	23.24	40.32	< 0.0001
			$\mathbf{T} \times \mathbf{S}$	6	6.53	11.34	< 0.0001
	Pneumatophore		Т	2	7.77	7.77	0.0016
	density		S	3	22.25	22.25	< 0.0001
	-		$T \times S$	6	6.6	6.6	0.0001

Sp corresponds to shrimp species, T is turbidity, D is the initial density of shrimps, *n* corresponds to the results of the ANOVA on number of shrimps eaten and % corresponds to the ANOVA on percentage of shrimps eaten, S is the substrate type (analysed as percentage of fine fraction) and P is the pneumatophore density (df=degrees of freedom, MS=mean squares, $F=F_{max}$ Hartley test).

the regression coefficient (*r*) is 0.89 (slope = -7.95, intercept = 4.35). Accordingly, significantly more *P. indicus* juveniles were eaten in clear water (91.7%) than in 0.16 (37.5%), 0.32 (12.5%) and 0.64 g l⁻¹ (0%) turbidity conditions (p = 0.0022, p = 0.0001 and p = 0.0001, respectively). Predation rates were also higher in 0.16 than in 0.64 g l⁻¹ conditions, though the differences were not significant at the 5% level (p = 0.0593). The number of shrimps eaten in 0.32 g l⁻¹ turbidity was not statistically different from the one detected for 0.16 and 0.64 g l⁻¹ conditions (p = 0.4109 and p = 0.9556, respectively), though the predation rate tended to decrease with increasing turbidity from 0.16 up to 0.64 g l⁻¹ (see Fig. 1).

3.3. M. monoceros

Predation rates on *M. monoceros* juveniles also tended to decrease with increasing turbidity. In fact, more shrimps were eaten in clear water (91.7%) than in 0.16 (25.0%),



Fig. 1. Shrimp mortality (mean \pm S.E.) from thorn fish predation at different prey density (6, 12 and 18/tank) and turbidity conditions. Above: number of shrimps eaten; below: percentage of shrimps eaten.

0.32 (50.0%) and 0.64 g l⁻¹ (12.5%) conditions (p=0.0003, p=0.0270 and p=0.0001, respectively). The number of shrimps predated increased slightly from 1.50 ± 0.29 to 3.00 ± 1.00 (mean \pm S.E.) as turbidity increased from 0.16 to 0.32 g l⁻¹ (see Fig. 1), but results of the Tuckey HSD test were not significant for this comparison (p=0.4109). As the turbidity increased from 0.32 to 0.64 g l⁻¹, the number of shrimps eaten decreased from 3.00 ± 1.00 to 0.75 ± 0.25 (mean \pm S.E.), but again, the differences were not statistically significant at the 5% level (p=0.0593).

3.4. Prey density

3.4.1. P. indicus

Although according to the ANOVA and multiple regression on number of shrimps eaten the predation rates were only affected by turbidity and prey density, the analysis of proportional data also detected a significant turbidity-prey density interaction (Tables 3 and 4).

In the experiments with clear water, the number of shrimps eaten increased with increasing prey density (Fig. 1). However, significant differences at the 5% level were only found between the experiments with 6 and 12 shrimps per tank (p=0.0207), but not between 12 and 18 shrimps per tank (p=0.0678).

In the three remaining levels of turbidity, the number of shrimps predated was not significantly affected by increasing prey density. However, it was possible to observe that in 0.32 and 0.64 g l^{-1} conditions, it seemed to increase slightly with increasing prey

Table 4

Multiple backward correlation summary for the correlation model $z = \alpha + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1^2 + \beta_4 X_1 X_2 + \beta_5 X_2^2$ fit to the data of mortality rates

Experimen	t	Penaeus indicus	Metapenaeus monoceros
Density	Ν	$z = 5.18 - 26.75t + 0.11d + 28.19t^{2}$ $R_{2}^{2} = 0.88 F_{C2} = 112.85 n \le 0.0000$	z = 5.08 - 10.12t + 0.45xtd $R^{2} = 0.59 F_{0.45} = 34.217 n \le 0.0000$
	Р	$z = 103.33 - 345.49t - 3.40d + 265.72t^2 + 7.30td$	z = 96.09 - 137.21t - 3.81d + 7.03td
Substrate type		$\begin{aligned} R_{\rm A}^{-} = 0.86, \ F_{(4,43)} = 71.382, \ p < 0.0000 \\ z = 5.25 - 11.79t - 0.04s + 0.13ts \end{aligned}$	$R_{\rm A}^{-}=0.58, F_{(3,43)}=22.644, p < 0.0000$ z=1.98-0.02t
Pneumatonhore		$R_{\rm A}^2 = 0.56, F_{(3,44)} = 20.691, p < 0.0000$ z = 4.70 - 13.52t - 0.04n + 0.30tn	$R_{\rm A}^2 = 0.19, F_{(1,46)} = 12.243, p < 0.0011$ $z = 4.79 - 9.05t - 0.22tn - 0.001n^2$
density		$R_{\rm A}^2 = 0.46, F_{(3,44)} = 14.595, p < 0.000$	$R_{\rm A}^2 = 0.23, F_{(3,44)} = 75.6670, p < 0.002$

N corresponds to the results of correlation on number of shrimps eaten, P corresponds to the correlation on percentage of shrimps eaten, *t* is the turbidity level, *d* is the density of prey, *s* is the fine fraction of the sediment (as percent weight) and *p* is the pneumatophore density. The adjusted multiple correlation coefficient (R_A^2) was used as a measure of the explained variation.

density. The analysis of proportional data revealed that there was a decrease of percentage of shrimps eaten in 0.16 g l⁻¹ conditions as prey density increased from 6 (37.5%) to 12 (14.6%) and to 18 (15.3%) per tank (p=0.0353 and p=0.0462, respectively). In 0.32 and 0.64 g l⁻¹ conditions, however, no differences were detected between percentages of shrimps eaten in different prey density conditions.

In the experiments with 12 shrimps per tank, predation rates decreased with increasing turbidity from 0.00 (60.4%) to 0.16 g l⁻¹ (14.6%) (p=0.0001), but remained constant as the turbidity increased further (10.4% shrimps eaten in 0.32 g l⁻¹ and 8.3% in 0.64 g l⁻¹ turbidity conditions). Similarly, in experiments with 18 shrimps per tank, the predation rates were higher in clear water (41.7%) when compared to 0.16 (15.3%) (p=0.0084), 0.32 (11.1%) (p=0.0014) and 0.64 g l⁻¹ (8.3%) (p=0.0004) conditions, and between 0.16, 0.32 and 0.64 g l⁻¹ turbidity conditions, no significant differences were detected (p>0.05).

The results of the multiple regression analyses are presented in Table 4, together with the adjusted multiple regression coefficients (R_A^2), *F* ratios and probability levels. The regression models show the variation of prey mortality (in number and percentage of shrimps eaten) in relation to turbidity, prey density and their interaction. To illustrate the relative effects of these two variables on shrimp predation, response surface was obtained, representing a smoothed image of the data following the quadratic smooth procedure (Fig. 2).

3.4.2. M. monoceros

The number and percentage of *M. monoceros* juveniles predated were affected by turbidity, prey density and their interaction (Tables 3 and 4). In clear water experiments, the mean number of juvenile shrimps eaten was maximum and corresponded to the maximum feeding capacity of thorn fish. Consequently, it was similar in the different prey densities analysed (5.50 ± 0.29) (Fig. 1). In low (0.16 g l^{-1}) turbidity condition, the number of shrimps eaten was significantly higher in tanks with 12 (5.25 ± 0.48) and 18 (4.75 ± 0.25) than in tanks with 6 shrimps (1.50 ± 0.29) (p=0.0002 and p=0.0007, respectively), and there were no significant differences between mortality rates in tanks with 12 and 18 shrimps. In intermediate (0.32 g l^{-1}) and high (0.64 g^{-1}) turbidity conditions, the number



Fig. 2. Contour plots of mortality response to turbidity and prey density, representing a smoothed image of the number (above) and percentage (below) of the eaten shrimps data following the quadratic smoothing procedure.

of shrimps eaten increased proportionally with increasing prey density. In 0.32 g l⁻¹ conditions, the number of shrimps predated was significantly higher in tanks with 18 $(4.00 \pm 0.41 - 22.2\%)$ shrimps $(p_1 = p_2 = 0.0001)$ when compared to tanks with 12 $(3.50 \pm 0.50 - 29.2\%)$ and 6 $(3.00 \pm 1.00 - 50.0\%)$. Similarly, in 0.64 g l⁻¹ conditions, the mean number of shrimps predated increased from 6 (0.75 ± 0.25) to 12 (2.00 ± 0.41) and to 18 (4.00 ± 0.41) , but the only significant difference was detected between the 6 and 18 shrimps per tank experiments (p=0.0007).

In the analyses of proportional data, an outlier was removed from the original data regarding 0.32 g l⁻¹ experiments with 6 shrimps per tank in order to satisfy the normality and homoscedasticity assumptions. This lead to the detection of significant differences between predation rates in 0.32 and 0.16 g l⁻¹ and also between 0.32 and 0.64 g l⁻¹ in tanks with 6 shrimps by the HSD Tukey test, which were not evident in the analyses regarding solely the turbidity. Accordingly, in experiments with 6 shrimps per tank, mortality rates in 0.00 g l⁻¹ conditions (91.6%) were higher compared to 0.16 (25.0%) (p=0.0001), 0.32 (50.0%) (p=0.0012) and 0.64 g l⁻¹ (12.5%) (p=0.0001) conditions, and were also higher in 0.32 than in 0.16 and 0.64 g l⁻¹ conditions (p_1 = p_2 =0.0001).

In intermediate prey density conditions (12 per tank), predation rate only decreased in higher turbidity conditions, and even then the number of shrimps eaten was relatively high (3.50 ± 0.50 in 0.32 and 2.00 ± 0.41 shrimps eaten in 0.64 g l⁻¹ conditions). Mortality rate was higher in clear water (45.8%) and 0.16 g l⁻¹ (43.8%) than in 0.64 g l⁻¹ turbidity

(16.7%) (p=0.0003 and p=0.0007, respectively). In higher prey density conditions (18 per tank), predation rates were not affected by turbidity. Table 4 shows the results of the multiple regression analyses and Fig. 2 illustrates the response surfaces of mortality to variations in turbidity and prey density.

3.5. Substrate type

3.5.1. P. indicus

According to the ANOVA results, there was a significant effect of turbidity, substrate type and their interaction on predation rates (Table 3). In muddy substrate conditions, the water turbidity had no effect on predation rates as these were statistically similar on the various turbidities analysed (Fig. 3). The sandy sediment, however, had no effect on predation protection for *P. indicus* as it did not increase nor decrease the predation relatively to control conditions in the entire analysed turbidity spectrum. In this manner, and as happened in control tanks, in sandy substrate conditions, more shrimps were eaten in 0.00 (87.5%) when compared to 0.16 (20.8%) and 0.32 g 1^{-1} turbidity conditions (16.7%) ($p_1 = p_2 = 0.0001$)—the predation curves in the experiments without sediment and with sandy sediment are identical. In sandy-shell substrate predation rates were higher in 0.0 and 0.32 g 1^{-1} (91.7% in both cases) conditions than in 0.16 g 1^{-1} (54.2%) ($p_1 = p_2 = 0.0120$).

In clear water conditions, only sandy-shell substrate provided a significant protection to *P. indicus* juveniles, as significantly fewer shrimps were eaten in this substrate (29.2%) when compared to control (87.5%), muddy (91.7%) and sandy substrate (91.7%) (p=0.0001 for all comparisons). Predation rates in the three latter conditions (control, muddy and sandy substrates) were statistically similar. In 0.16 g l⁻¹ turbidity conditions, greater predation rates were observed in the presence of muddy sediment (91.7%) when compared to control (20.8%) (p=0.0001), sandy substrate conditions (37.5%) (p=0.0002) and sandy-shell (4.2%) (p=0.0001), and in control when compared to sandy substrate conditions (p=0.0385). In 0.32 g l⁻¹ conditions, predation was higher in tanks with muddy sediment (54.2%) than in tanks with no sediment (21.5%) (p=0.0036) and with



Fig. 3. Shrimp mortality (mean \pm S.E.) from thorn fish predation at different turbidity and substrate type conditions.

sandy-shell sediment (16.7%) (p=0.0121), but not than in sandy substrate conditions (33.3%) (p = 0.5281).

Table 4 shows the results of a multiple regression analysis, according to which turbidity and fine fraction of sediment have a significant effect on P. indicus mortality from thorn fish predation. Note that in this analysis, the data of predation rates in control tanks were not considered. Fig. 4 illustrates the response surfaces of mortality rate as a function of these variables (for easier identification on this relationship, percentage of fine fraction is arcsine-transformed).

3.5.2. M. monoceros

There was a significant effect of turbidity, substrate type and their interactions on M. monoceros juveniles' predation rates (Table 3). In clear water conditions, more shrimps were eaten in tanks with no sediment (91.6%) than in tanks with any type of sediment (0.0% in mud, 20.8% in sand and 4.2% in sandy-shell conditions) (p=0.0001 for each comparison) (Fig. 3). In 0.16 g 1^{-1} turbidity conditions, predation rate was lower in muddy substrate (0.0%) when compared to sandy (50.0%), sandy-shell (37.5%) and control experiments (41.7%) (p = 0.0002, p = 0.0082 and p = 0.0023, respectively), but in 0.32 g l⁻¹ conditions, the presence or type of substrate had no significant effect on predation rates.

In muddy and sandy sediment conditions, predation rates were not affected by turbidity. In sandy-shell sediment conditions, however, these were higher in 0.16 g l^{-1} (37.5%) compared to 0.00 in 0.32 conditions (0.0% in both cases) ($p_1 = p_2 = 0.0082$).



Fig. 4. Predation on shrimps (%) as a function of turbidity and substrate type (expressed as arcsine-transformed percentage of fine fraction-ffs) based upon the quadratic smoothing procedure fitted to the mortality data. According to the multiple backward regression, the following equations are the quadratic polynomials that best describe the response surfaces:

- *P. indicus:* $M = 54.53 108.5lt + 10.20(\sin(\sqrt{ffs}))^{-1} (R_A^2 = 0.59, F_{(2,33)} = 25.76, p < 0.0000);$ *M. monoceros:* $M = 24.96 2.57((\sin(\sqrt{ffs}))^{-1})^2 + 0.12t(\sin(\sqrt{ffs}))^{-1} (R_A^2 = 0.66, F_{(2,33)} = 30.405,$ *p* < 0.0000).

Table 4 shows the results of a multiple regression analysis, according to which there is a significant effect of substrate type and turbidity–substrate type interaction on shrimp mortality. Fig. 4 illustrates these results.

3.6. Pneumatophore density

In all experiments, fish were able to swim easily between the pneumatophores but the pursuing activity in higher pneumatophore density conditions was more difficult.

3.6.1. P. indicus

Shrimp mortality from thorn fish predation was affected by turbidity, pneumatophore density and their interaction (Tables 3 and 4). More shrimps were captured in the absence of pneumatophores and in the presence of 30 pneumatophores (91.7% for both cases) than in tanks with 15 (45.8%) ($p_1 = p_2 = 0.0003$) or 45 pneumatophores (41.7%) ($p_1 = p_2 = 0.0001$) (Fig. 5).

In low turbidity conditions (0.16 g 1^{-1}), fish captured *P. indicus* juveniles more effectively in tanks with 30 (58.3%) than in tanks with 15 pneumatophores (20.8%) (p=0.0045), and in all the remaining comparisons no differences were detected. In 0.32 g 1^{-1} conditions, greater predation was observed in intermediate and high pneumatophore density conditions (50.0% and 45.8% mortality, respectively), compared to control (12.5%) (p=0.0045 and p=0.0170, respectively). More shrimps were also eaten in conditions of 30 than in conditions of 15 pneumatophores per tank (16.7%) (p=0.0170).

In the experiments with 15 pneumatophores per tank, the mortality rate decreased with increasing turbidity, though no differences were detected at the 5% level (p = 0.0580 for the comparison between predation in 0.32 and 0.00 g 1⁻¹). In 30 pneumatophores per tank conditions, predation rates were higher in clear water (91.7%) compared to turbid waters (58.3% in 0.16 g 1⁻¹ and 50.0% in 0.32 g 1⁻¹) (p = 0.0170 and p = 0.0012, respectively). Turbidity had no detectable effect on predation rates in 45 pneumatophores per tank conditions. Fig. 6 illustrates the mortality response surfaces to turbidity and pneumatophore density.



Fig. 5. Shrimp mortality (mean \pm S.E.) from thorn fish predation in different turbidity and pneumatophore density conditions.



Fig. 6. Predation rates as a function of turbidity and pneumatophore density based upon the quadratic smoothing procedure fitted to the mortality data.

3.6.2. M. monoceros

Shrimp mortality from fish predation varied according to turbidity, pneumatophore density and their interaction (Tables 3 and 4). Fig. 6 illustrates the response surfaces of mortality to variations on turbidity and pneumatophore density.

In clear water conditions, the vulnerability of *M. monoceros* shrimps to predation decreased with increasing habitat complexity (Fig. 5). However, the only significant difference found by the ANOVA was between predation rates in tanks with 45 and tanks without pneumatophores (p = 0.0010). A significant negative relation of regression between predation rates and pneumatophore density was detected ($F_{(1,14)} = 12.06$; p = 0.0037), for which the regression coefficient (r) is 0.68 (slope = -0.06, intercept = 5.18).

In 0.16 g l⁻¹ conditions, the predation rates increased with increasing pneumatophore density from 0 to 15 and to 30 per tank (25.0–58.3–87.5%), though the only significant difference found was between tanks without and tanks with 30 pneumatophores (p=0.0004). However, as the density of pneumatophores increased from 30 to 45 per tank, the predation induced mortality decreased significantly (87.5–8.3%; p=0.0001). Predation rates in 45 pneumatophores (p=0.0071), and were not statistically different from those in experiments with no pneumatophores (p=0.9530). In 0.32 g l⁻¹ conditions, the predation rates decreased as structure density increased up to 15 per tank (50–16.7%), though the difference was not significant at the 5% level (p=0.2179). As pneumatophore density increased from 15 to 30 per tank, predation rates also increased (16.7–70.8%) (p=0.0027), and then decreased again as pneumatophore density increased up to 45 per tank (70.8–25.0%) (p=0.0183).

In the presence of 15 pneumatophores per tank, the predation rates remained constant as the turbidity increased from 0.00 to 0.16 g l⁻¹ (54.2–58.3%) and decreased as it increased from 0.16 to 0.32 g l⁻¹ (16.7%) (p=0.0449). In 30 and 45 pneumatophores per tank conditions, the turbidity had no effect on predation rates.

4. Discussion

4.1. Turbidity

Turbidity provides predatory protection to *P. indicus* and *M. monoceros* juveniles as it decreases predation rates by thorn fish, but its effect on predator–prey relationships depends upon the behaviour of the prey. In fact, the visual reactive distance of the predator is reduced in turbid water (as reported by Moore and Moore, 1976) and thus prey detection capacity decreases confirming the strict reliance on visual capacities of this predator in prey detection.

The reduced predator efficiency on capturing P. indicus and M. monoceros in turbid waters agrees with Minello et al.'s (1987) findings for the pinfish predation on Penaeus aztecus. However, the prev response to predation by thorn fish showed different pattern between the two prey species. P. indicus exhibit an approximately linear negative response to predation as far as turbidity increases while predation rate on M. monoceros decreases with increasing turbidity up to 0.16 g 1^{-1} . An increase in predation rate as water turbidity reached 0.32 g l^{-1} was observed, which can be related to a specific effect of turbidity on M. monoceros juveniles behaviour. In fact, it seems to be a result of a significant increase in locomotor activity of shrimps due to the decrease in light intensity. A similar predation response was found by Minello et al. (1987), where high turbidity increased predation rates of the southern flounder *Paralichthys lethostigma*, an ambush predator, on brown shrimp *P*. *aztecus*. As happens with these species, many benthic invertebrates are negatively phototactic and their locomotor activity decreases with increasing turbidity (e.g. Wickham and Minckler, 1975; Minello et al., 1987; Brewer et al., 1989). Hence, at 0.32 g l^{-1} turbidity, the fish were not capable to see the prey perfectly, but because shrimps were more active than in lower turbidity conditions, the encounter rates and consequently the predation rates increased. The synchronization of the circadian activity rhythms of many shrimp species is actually known to be controlled mainly by light intensity (e.g. Hughes, 1968; Möller and Jones, 1975), but other environmental parameters can also influence it (e.g. Fuss and Ogren, 1966; Wickham and Minckler, 1958; Wickham, 1967; Williams and Naylor, 1967). In this manner, the adaptiveness of the visual sense of fish as a mechanism of prey detection is apparently lowered. However, some species of fish that use visual cues are able to detect, pursuit and capture prey at very low light intensity, and according to Minello and Zimmerman (1983), reduced light intensity does not always restrict predation by visual feeders during the night. On the other hand, shrimps do not avoid solely visual predators.

It also seems that there is a turbidity threshold above which the thorn fish actually changes its foraging tactics due to a decline on its visual acuity becoming in very turbid water conditions an ambush type predator. This type of behavioural shift by the predator is relatively common (see Stoner, 1979, 1982; Anderson, 1984) and often lead to a real threshold response of predation rate to turbidity (Nelson and Bonsdorff, 1990). Accordingly, as the turbidity level increased from 0.32 to 0.64 g 1^{-1} , the predation rates on *M. monoceros* juveniles are lowered as a consequence of a decrease of the fish's reactive distance. By affecting prey and predator interactions, turbidity shows to plays an important role on regulating distribution and mortality of *P. indicus* and *M. monoceros* at Saco da Inhaca.

4.2. Prey density

As with most fish (see Minello et al., 1989; Bailey and Houde, 1989), predation rate of thorn fish on shrimps increases with increasing prey density. This functional response is known to be one of the two basic components of predation (Holling, 1959a,b), and in the present study, it seems to vary according to turbidity level for both prey species, indicating that a clear turbidity–prey density interaction on predation rate is present. These changes in functional response probably lead to important modifications in the shape of the mortality curve of prey in natural conditions. Tidal variations in the mangroves and adjacent intertidal areas may affect water turbidity and cyclically modifies shrimps' density.

Although it was not possible to clearly detect the exact shape of the prey density– predation rate function, in clear water conditions, predation seems to increase with increasing prey density until a plateau corresponding to fish' maximum feeding capacity, or satiation, is attained (linear or type I response) (Holling, 1959a,b). To this value corresponds the number of shrimp juveniles needed to feed one thorn fish for 12 h. Accordingly, around seven *P. indicus* or five/six *M. monoceros* juveniles are needed to feed one of these fish for that period of time. The higher mortality rate of *P. indicus* in higher density conditions can be explained by the higher probability that a fish might encounter the prey. Predation on *M. monoceros* juveniles in low and high turbidity conditions also increased probably as a result of higher encounter rates between prey and predator. In contrast, in high turbidity conditions, the increase is much smoother due to the more gradual increase of encounter rates between predator and prey (as the visual capacity of predator is no longer good as previously referred) and a behavioural shift has already taken place in which the predator changed from active chasing to ambush.

A minimum shrimp density is required before *T. jarbua* starts feeding on juvenile shrimps in higher turbidity conditions. For *P. indicus* juveniles prey that minimum is probably between 6 and 12 shrimps per tank (43 and $86/m^2$), as no shrimp was eaten in 6 shrimps per tank conditions, and for *M. monoceros* juveniles that minimum is below 6 shrimps per tank.

In intermediate turbidity conditions, predation on *M. monoceros* juveniles was not affected by prey density because the shrimps' locomotor activity was higher than in lower turbidity conditions and, hence, encounter rates between prey and predator increased. However, this effect was reduced as prey density increased, because in higher prey density conditions, changes in prey activity should only have negligible effect on encounter rates with predators. Consequently, predation rates were constant along the analysed turbidity spectrum.

M. monoceros juveniles are probably more visible to fish than *P. indicus* as they are dark pigmented, and *P. indicus*, in addition to being a very transparent species, is a faster swimmer (author's observation). Thus, in higher turbidity conditions, predation rates on *P. indicus* juveniles were often lower than those of *M. monoceros*. Previous studies with other species have actually shown that the increased visibility associated with pigmentation can be more important than either size or density in prey detection and selection by fish (e.g. Zaret and Kerfoot, 1975; Kislalioglu and Gibson, 1976; Kneib, 1987). Results also seem to indicate that the increase in locomotor activity of *M. monoceros* juveniles with increasing turbidity (decreasing light intensity) is much steeper than that of *P. indicus*, as even in higher turbidity conditions the number of *M. monoceros* juveniles eaten was elevated.

In turbid waters, the number of *P. indicus* eaten is not affected by increasing prey density, at least from 6 to 18 per tank $(43-128/m^2)$. As only four levels of turbidity and three levels of prey density were analysed, it was not possible to assert which functional response corresponds exactly to each turbidity condition analysed. Hence, additional experiments with higher levels of replication and the analysis of more levels of prey density are needed. These findings could also indicate that predation in turbid areas (mangrove areas) only acts as a fine-tuner of abundance when shrimp densities exceed a given threshold (as suggested by Strong, 1984), from which it does serve a useful purpose in holding prey population sizes low, but quickly loses its impact on the prey population when these grow rapidly.

Effects of crowding or gregariousness of these species in nature are not well known, though individuals are found in close proximity to each other when swimming freely, resting on the surface, or when burrowed in the ground (personal observations). In aquaria, the most prominent anti-predator behaviour observed in P. indicus juveniles was the formation of both aggregations and schools. Formation of aggregation was also observed for M. monoceros juveniles, but not schools. School and aggregation formation are actually known to be very important anti-predator processes (e.g. Cushing and Harden Jones, 1968; Pitcher, 1973; Taylor, 1976; Sullivan and Atchinson, 1978; Turchin and Kareiva, 1989), as by grouping together, prey can reduce the risk of being eaten. In clear water conditions, the fish were able to pursue and capture shrimps very intensively and, hence, the number of shrimps eaten increased with increasing prey density, though the school effect was still present. In low turbidity conditions, on the other hand, the fish detection capacity was lower than in clear water and, consequently, the protection effect of schools was increased. In this manner, the number of shrimps eaten was almost constant along the prey density spectrum analysed. These results seem to indicate that the functional response is dependent on prey density and that it therefore contributes to population regulation (see Oaten and Murdoch, 1975). In intermediate and high turbidity conditions, predation rates varied proportionally to prey density, suggesting that the schooling behaviour was not present. The same result was found for M. monoceros juveniles in low and high turbidity, confirming that this species does not school. Demographic factors are thus important variables determining predator-prey interactions.

The constancy of *P. indicus* mortality rate with increasing turbidity from 0.16 to 0.64 g l^{-1} in experiments with intermediate and higher prey density suggests that as the turbidity increases there is a compensation of the decrease in predator's visual reactive distance with the increase in shrimps' locomotor activity. Consequently, the probability that a fish might encounter the shrimps remains constant, and turbidity has no apparent effect on predation. With 6 shrimps per tank, for instance, the mortality decreased with increasing turbidity along the entire turbidity spectrum analysed because prey density was low and even though the activity level of shrimps increased with increasing turbidity, encounter rates could not increase significantly in order to maintain the plateau level.

4.3. Substrate type

Substrate type influences predation on shrimp juveniles, and hence these should prefer substrates that offer maximum protection. Actually, several authors have identified correlations between sediment characteristics and shrimp abundance for several species (e.g. Williams, 1958; Möller and Jones, 1975; Branford, 1981a,b).

Because *P. indicus* juveniles do not bury in the laboratory (Hughes, 1966; personal observations), only sandy-shell substrate provided a deterrent effect on predation in clear water conditions. This was probably a result of the cryptic coloration, which combined with immobilization permitted blending in of the shrimps with their background, avoiding detection by visual predators (see Clements and Livingston, 1984; Russo, 1987). In fact, during preliminary trials, the animals were observed to remain immobile during the majority of the time, except when the predator approximated. Several studies have shown that movement of prey appears to elicit predator strikes and to evoke feeding behaviour in a variety of visual predators (e.g. Zaret and Kerfoot, 1975; Stein and Magnuson, 1976; Main, 1987). These results are not in accordance with *P. indicus* juvenile's distribution in nature, as according to Hughes (1966), Branford (1981a) and De Freitas (1986), they seem to prefer very muddy areas within mangrove swamps, both in the primary channels or the smaller creeks of the upper reaches. According to Rönnbäck et al. (2002) (author's unpublished data) at Inhaca Island, *P. indicus* in the mangrove forest does not show any preference to muddy substrate.

However, it is important to note that this species buries in natural conditions, though not completely (Hughes, 1966; author's observation). The presence of a light yellow sandy substrate had no effect on *P. indicus* vulnerability to predation, probably because this species does not bury and the substrate colour did not allow shrimps to blend with the background. The presence of sandy-shell substrate, however, decreased shrimps' vulnerability to thorn fish predation, probably as a result of a significant camouflage provided to the semi-transparent body, which made prey detection by fish more difficult. In this manner, the presence of this type of substrate may only affect predation by modifying the shrimps' activity levels. However, higher turbidity conditions already provided predation protection. In Maputo Bay, *P. indicus* is mostly captured in areas of turbid waters (commercial fisheries fleet) close to Maputo River estuary.

Whether shrimps bury, rest, perch or swim was found previously to depend on species, size, presence or absence of vegetation or other structures and time of the day, among other parameters (e.g. Möller and Jones, 1975; Minello et al., 1987). *M. monoceros* juveniles avoid detection by visual fish predators by burrowing during daylight (personal observations) and thus decreasing their apparent availability to visual feeding predators (see Minello and Zimmerman, 1984). This anti-predation behaviour has previously been observed in several penaeid species (see Ruello, 1973; Möller and Jones, 1975; Minello and Zimmerman, 1983; Minello et al., 1987; Dall et al., 1990). Möller and Jones (1975), working with *Penaeus semisulcatus*, suggested that burrowing is triggered by increasing light intensity, while emergence from the substratum at dusk is mainly governed by endogenous control.

The thorn fish were not able to detect or remove buried shrimps from the substratum and only attacked shrimps lying on the bottom or swimming in the water column, confirming again the Whitfield and Blaber's (1978) assessment that this species is a strictly visual feeder. However, some fish species that also rely on chemosensory abilities can locate and capture buried shrimps by moving the sand with their snout and pelvic fins.

M. monoceros juveniles can burrow completely both in muddy and sandy substrate, but in sandy-shell substrate, the burying is not complete as part of the dorsal area, eyes and

rostrum remain visible above the surface. The ability of brown shrimp to bury is thus affected by the substrate characteristics just as happens with several other burrowing penaeids (e.g. *Penaeus setiferus*, *P. aztecus* and *Penaeus dourarum*: Williams, 1958; *Penaeus japonicus*: Egusa and Yamamoto, 1961). In clear water, the presence of any substrate type provided deterrent effect on predation. Accordingly, the selection by juvenile *M. monoceros* of a substratum suitable for burrowing reduces significantly the predation success of fish that rely especially in visual cues for prey detection, and a soft substratum types were significantly different from those found in control experiments. These findings agree with the distribution of juveniles and sub-adults in Maputo Bay and Saco da Inhaca, where *M. monoceros* is more widespread than other species and can be found in a diverse number of habitats, from areas with submerged macrophytes to the deeper reaches of the mangrove swamps (Hughes, 1966; De Freitas, 1986; author's unpublished data).

In low turbidity conditions, the presence of substratum did not especially protect *M. monoceros* juveniles, confirming that in the absence of sediment the shrimps are not very active due to the high light intensity and that the fish' visual detection capacity is lowered due to the turbidity effect. As turbidity increased further, the *M. monoceros*' vulnerability to predation was minimum in the presence of muddy sediment, probably as a result of the shrimps' cryptic coloration that permits blending in with the dark background and avoid detection. Hence, in muddy substrate conditions, predation rates were not affected by increasing turbidity. In high turbidity conditions, the locomotor activity of shrimps was already high due to the low light intensity and, consequently, predation rates were higher in tanks with no sediment and with sandy-shell sediment when compared to low turbidity conditions. Actually, Macnae and Kalk (1962) and Joshi et al. (1979) have demonstrated that this species favours a muddy substratum, though that result was not confirmed by De Freitas (1986) work, in which it is shown that this species can be found in a wide variety of substrates.

In the presence of muddy and sandy sediment, turbidity had no effect on thorn fish's predation success, but in sandy-shell sediment, where the *M. monoceros*' burrowing is not complete, the effect of turbid water on predation rate was apparently increased by a reduction in shrimps' burrowing. In fact, burrowing by *M. monoceros* juveniles was reduced in turbid water, as happens with *P. aztecus* (Minello et al., 1987) and other penaeids. In this way, substrate type, as light intensity, also regulates the locomotor activity rhythms of shrimps. Actually, several studies have shown that the activity rhythms of many penaeid species are modified in the absence of substrate (e.g. *Metapenaeus bennettae, Metapenaeus macleayi* and *Penaeus plebejus*: Racek, 1959; *P. dourarum*: Fuss and Ogren, 1966; *Crangon crangon*: Hagerman, 1970; *P. semi-sulcatus* and *P. monodon*: Möller and Jones, 1975). These activity rhythms that depend upon the presence and type of substrate and upon the negative phototaxy are probably an efficient protection against visual predation, and the interaction between turbidity and substrate type on predation rates can thus influence distribution and abundance patterns of prey.

So, fish predation on the burying shrimps can be affected by turbidity, substrate type, as well as by prey and predator species and their interactions.

4.4. Pneumatophore density

The use of mangrove structures (pneumatophores) by juvenile penaeid shrimps as refuge from predation was documented for the first time by Primavera (1997). Results of the present study indicate that, as assessed in her work, the presence of pneumatophores does provide shrimp a significant amount of protection from fish predators. However, the quality of refuge provided by pneumatophores in a certain microhabitat seems to depend upon its complexity, the prey species and its density.

In clear water conditions, increased structural complexity reduced the consumption of *M. monoceros* juveniles linearly, a result that is well documented by other experimental predator-prey studies (e.g. Crowder and Cooper, 1982; Coull and Wells, 1983; Anderson, 1984; Nelson and Bonsdorff, 1990). However, this result still lacks support from the field studies since at Saco da Inhaca M. monoceros appears in higher densities at the intertidal flats than within mangrove areas (Rönnbäck et al., 2002). A thorn fish can see much further in low structure conditions, and in high structural complexity, it probably goes through lengthy periods of search during which no shrimp prey is visible. Hence, the structures of the environment have an important role in reducing visual contact with prey and prey vulnerability is lower in these conditions simply because random visual encounters between predator and prey are reduced. On the other hand, as pneumatophore density increases, predator activity declines due to a decrease in behaviour associated with visual contact with prey. In fact, at low structural complexities, the thorn fish were observed to be active searchers whereas at high densities they became ambush predators, because in these conditions the pursuit of prey by the predator seems to be inhibited. Thus, the thorn fish also modifies its foraging tactics with changes in structural complexity, besides turbidity. These behavioural shifts were observed both in clear and turbid water and are probably a result of differential energy costs of the different foraging tactics in differentially structured habitats.

According to Anderson (1984), largemouth bass *Micropterus salmoides* in an environment with moderate density of vegetation had higher prey encounter rates than largemouth bass in a highly structured environment, and that the optimal behaviour in high structure was more complex than the best foraging mode in low structure. Some authors have also shown that the diet breadths of fish predators increase with increasing structural complexity (Vince et al., 1976; Anderson, 1984). In nature, structure should then mitigate the effect of predation on fish's preferred prey species, possibly resulting in changes in the overall composition of the prey community (e.g. Crowder and Cooper, 1982; Anderson, 1984).

In low turbidity conditions, increasing pneumatophore density up to 30 per tank seems to provide predators with increasing levels of cover, enabling them to catch more M. *monoceros* juveniles, as the locomotor activity of shrimps is already high due to the turbidity conditions and so they probably "feel safe" to search for food and/or a suitable substrate to burrow. In higher turbidity conditions, predation rates initially decreased with increasing pneumatophore density up to 15 per tank because in these conditions the prey detection and pursuing activity was more difficult. As the structural complexity increased up to 30 pneumatophores per tank, the predation rates increased significantly, suggesting that in those conditions the shrimps' locomotor activity increased significantly and,

consequently, predation rates also increased. Besides, the foraging behaviour of fish has also changed to ambush, allowing them to capture more prey. In turbid waters, as happened in clear water, there was a break in capture rates at higher pneumatophore density as a result of the lowered reactive distance of thorn fish and the consequent behavioural shift.

In low structural complexity conditions, the predation rates were not affected by increasing turbidity up to 0.16 g l^{-1} , suggesting that the shrimps' locomotor activity increases with increasing turbidity, as it is known that the reactive distance of fish decreased. In intermediate and higher structural complexity the turbidity level had no significant effect on predation rates, suggesting that the locomotor activity of shrimps is highly increased with increasing structural complexity, and consequently as it increases, the locomotor activity increase caused by the increasing turbidity becomes negligible.

Unlike M. monoceros, P. indicus vulnerability to predation in clear water conditions was not a linear function of increasing habitat complexity. Actually, the results indicate that small juvenile white shrimps would suffer higher rates of predation in conditions of null and 30 pneumatophores density than in conditions of low and high densities, which is apparently related to changes in prey and predator behaviour. Low structural complexity provides shrimps with cover, allowing the predation rates to decrease, but intermediate structure density probably provides predators with cover enabling them to catch more prey. According to Anderson (1984), fish learn as juveniles to forage on a certain group of prey species, or to apply different strategies in different structural complexity conditions, and thus the observed predation response to habitat complexity can be explained by modifications of thorn fish predator behaviour. As the survival in intermediate density was not significantly different from that on control tanks, shrimps selecting areas with intermediate pneumatophore density may not survive at greater rates than those found in areas without any type of structures. Thus, it may be expected that predators would be attracted to those intermediate structured areas, which provide them with cover, as long as the structure density is insufficient to reduce foraging efficiency to less than it would be in other habitats.

In high turbidity water (0.32 g l^{-1}) , the cover provided to fish in intermediate and higher levels of structural complexity seems to be highly significant. Thus, because *P. indicus* juveniles are not able to detect the predator that furthermore is immobile due to the behavioural shift, their locomotor activity increases, resulting in an increase in predation rates. However, it is not known if *P. indicus* schooling behaviour changes with structural complexity variation.

Since *P. indicus* juveniles do not burrow completely, in natural conditions the need for adequate cover is great, especially since many mangrove as well as seagrass predators consume primarily epifaunal species (Nelson, 1979; Stoner, 1979; Coen et al., 1981). In fact, according to Rönnbäck et al. (2002), this species exhibits a stronger preference for mangrove forest than *M. monoceros*. The pneumatophores provide three dimensions within which *P. indicus* juveniles may hide and space themselves. These shrimps were observed to attach their bodies parallel to the pneumatophores when they perceived the stalking behaviour of thorn fish and to remain immobile, avoiding detection. This strategy would protect *P. indicus* juveniles from many "active chase" predators that require a visual cue for prey detection. However, prey species that are protected from one search and

attack strategy (e.g. active chase or pursuit) may be extremely vulnerable to other mode of prey capture (e.g. stalking or ambush) (e.g. Neill and Cullen, 1974; Primavera, 1997) and, consequently, that anti-predator behaviour is not successful against all fish predation strategies.

In low and intermediate structural complexities, the *P. indicus* mortality rates' decrease with increasing turbidity is much smoother than in no pneumatophores conditions, as a result of an increase in shrimps' locomotor activity due to increasing turbidity combined with the cover provided to predator. These two factors seem to have an additive effect in increasing prey activity and in decreasing predators' prey visual detection and capture capacity, so that in higher structure density the turbidity effect was not detected. Thus, the effective provision of shelter of different habitats is highly variable and depends not only upon structure, density, but also on the behaviour of predator and prey as well (e.g. Minello and Zimmerman, 1983; Main, 1987; Primavera, 1997) and the way these factors interact.

5. Conclusions

Turbidity provides protection from thorn fish *T. jarbua* predation for both species of shrimps studied.

The borrowing behaviour of shrimps influences the predation rate of Thorn fish. Accordingly, the presence of a suitable substrate for burying decreases vulnerability to predation of *M. monoceros*, a borrowing shrimp, but not of the non-burying *P. indicus*.

The presence of pneumatophores does provide shrimp a significant amount of protection from fish predation. Thus the density and distribution of juvenile shrimps in the field can be partly explained on basis of predation pressure (Crowder and Cooper, 1982).

Our results confirms previous findings that comparing areas with regard to their protective capacity for juvenile shrimp are complicated as stated by Minello et al. (1987), due to the highly significant interactions among habitats structures, predators and prey species (different levels of each factor alter others). This study provides some information for the assessment of the ecological value of mangroves and adjacent intertidal substrate as well as estuaries as suitable shelter for juvenile penaeid shrimps (Minello et al., 1987; Primavera, 1997).

Validation of these conclusions is the subject of conjectures since the laboratory conditions are artificial and therefore making difficult extrapolations to natural environment.

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