Life History and Population Structure of the Exploited Mangrove Crab *Ucides cordatus cordatus* (Linnaeus, 1763) (Decapoda: Brachyura) in the Caeté Estuary, North Brazil

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SUMMARY

The semiterrestrial crab *U. cordatus* is one of the most heavily exploited resources of Brazilian mangrove forests. The growing interest in protecting and managing *U. cordatus* populations increases the need for research on socioeconomical and biological aspects. In the present study, reproduction, growth, population structure and size of commercially landed crabs were investigated in the mangrove fringed estuary of the river Caeté, situated at the North Brazilian coast about 200 km east-north-east of Belém. The Caeté peninsula is primarily covered by dense *Rhizophora mangle* dominated forest stands which are only inundated during spring tides. Since 15 years access to the forest and exploitation of *U. cordatus* is facilitated by a tarred road crossing the peninsula. Today, the species constitutes the main income source for 50% of the rural households, which was demonstrated by parallel running socioeconomical investigations. The results of the here presented study will contribute to the evaluation of the need for protecting and managing the *U. cordatus* population of the Caeté estuary and are of direct significance for local environmental institutions who consider to implant temporal and spatial capture restrictions.

Reproduction of *U. cordatus* was seasonal and followed a strict lunar rhythm. Each study year (1997-1999) four to five andança events (times of mate searching) took place within four days after new moons between December and April with a peak occurring in either January or February. Shortly after andança activities females extruded eggs and incubated them until they spawned within four days around the following new moon. Zoea larval release was precisely timed. Females spawned in the flooded mangrove forest around slack spring high tides. Peak spawning activity always occurred one day before new moon. Larvae were rapidly washed out of the forest into estuarine channels where initial zoea densities of up to 230000 larvae per m^3 were recorded. Ebbing water masses exported the zoeae from tidal channels to coastal waters. Later stage zoeae were absent in estuarine water courses which indicates that larvae remained offshore throughout their three to four weeks of development until the postlarval stage (megalopa). Estuarine re-invasion of *U. cordatus* megalopae was recorded for the first time. Up to 128 individuals per m^3 were found within distinct recruitment phases for a maximum of eight days before until four days after new moons.

U. cordatus grows according to the indeterminate pattern. Moulting continues after sexual maturity and occurred over the whole size range of the specimens (0.13 - 8.25 cm carapace width) studied in the laboratory and in a 100 m^2 field enclosure. Relative growth increment and moulting frequency decreased distinctly with size. First instar crabs had a carapace width of 0.12 to 0.17 cm and attained a size between 0.87 and 1.15 cm after six months. Within this time span crabs had moulted at least eight to ten times and mean biweekly growth increment was 23%. In males and females between 2.0 and 4.0 cm carapace width mean size increment per moult was 13% and 14%, respectively, and decreased to 5% (males) and 2% (females) in crabs with a carapace width ☛ 5.0 cm. Specimens with a size of approximately 4.5 cm only moulted once per year during the dry season. The results indicate that *U. cordatus* is a long living brachyuran species with a maximum life-span of more than ten years. The onset of sexual maturity is relatively early when compared to the life span, the smallest female with eggs had a size of 3.1 cm which corresponds to an estimated age of 2.1 to 3.0 years. Males are approximately 7.1 to 8.7 years old when they reach commercial size with 6.5 cm carapace width.

Population structure was studied at three *R. mangle* forest sites with differing distance to the road and thus differential fishing pressure. At all three sites large crabs predominated, whereas smaller ones were more abundant in peripheral habitats, such as near the embankment of the road and in large forest gaps. This heterogeneous size distribution is probably caused by intraspecific competition with larger crabs displacing smaller ones into suboptimal habitats. Mean crab abundance and biomass in the *R. mangle* habitat was 1.7 individuals and 142 g per m², respectively. Sex ratio was skewed towards males (between 53% and 62%) although crab collectors almost exclusively harvest this sex. Market sized specimens (carapace width ☛ 6.5 cm) constituted 40% of the total male catch. An indication for the impact of fishery was obtained by the lower proportion of market-sized males at the near and thus more frequently exploited site (29%), when compared to the number of large males at the distant location (53%). Accordingly, mean size of males landed by professional crab collectors from near sites was generally lower than for distant sites. Overall mean landing size was 7.3 cm.

The size and sex selectivity of crab fishery yields a high potential for sustainability and the present study indicates that the population in the Caeté estuary has neither been growth nor recruitment overfished. Whether recruitment is at all a function of the local breeding stock is not yet clear as the exported zoea larvae are possibly drifted away over long distance, whereas the Caeté population may depend upon megalopae originating from other regions. It is remarkable that despite long lasting fishery and the slow growth of *U. cordatus* large males are still so abundant. This points to a high buffer capacity of the system which may result from numerous refugia, such as areas with dense stilt roots, which are unsuited to crab capture. Blanket coverage exploitation is thus prevented and the mosaic refugia may act as source for replenishment of fishable patches. However, the reduced number of males in the uppermost size classes in frequently exploited areas indicates, that the buffer capacity at these sites is becoming depleted. This may in future result in a distinct drop in the yield, particularly if fishing pressure increases.

RESUMO

O caranguejo semi-terrestre *U. cordatus* é um dos recursos mais explorados dos bosques de manguezal brasileiros. O crescente interesse na proteção e manejo das populações de *U. cordatus* intensifica a necessidade de pesquisar os aspectos biológicos e sócio-econômicos. No presente estudo, a reprodução, o crescimento, a estrutura de população e o tamanho de comercialização dos caranguejos foram pesquisados na faixa de manguezal do estuário do rio Caeté, situado no norte da costa brasileira, a aproximadamente 200 km este-norte-este de Belém. A península do Caeté está recoberta, em primeira linha, por um denso bosque onde predominâ a *Rhizophora mangle*, e que é inundado somente durante as sizígias. Há 15 anos, o acesso a esse bosque e a exploração de *U. cordatus* vêm sendo facilitados por uma estrada de asfalto que cruza a península. Atualmente, essa espécie de caranguejo constitue a principal fonte de recursos econômicos para 50% dos orçamentos rurais, fato demonstrado por pesquisas paralelas na área de sócio-economia. Os resultados do presente estudo contribuirão para a avaliação das necessidades de proteção e manejo da população de *U. cordatus* do estuário do Caeté, sendo ainda diretamente relevantes às instituições locais responsáveis pelo meio-ambiente, que planejam a implantação de restrições de coleta espaciais e sazonais.

A reprodução de *U. cordatus* foi sazonal, seguindo um ritmo estritamente lunar. Em cada ano de pesquisa (1997 - 1999), de quatro à cinco andanças (atividades de parceiro) ocorreram durante os quatro dias após a lua nova entre dezembro e abril, com um pico em janeiro ou fevereiro. Logo após a andança, as fêmeas emitiram ovos e os encubaram até a sua desova, que aconteceu durante os quatro dias próximos à lua nova seguinte. A emissão de larvas zoea ocorreu precisamente sincronizada. As fêmeas desovaram nos manguezais inundados, em torno das marés paradas antes das marés vazantes. Os picos de desova sempre ocorreram um dia antes da lua nova. As larvas foram rapidamente transportadas aos canais estuarinos fora do bosque, onde foram registradas densidades zoea iniciais de 230000 larvas por m^3. Massas de água de maré vazante exportaram as zoea dos canais de maré para as águas costeiras. Registrou-se ausência de estádios de zoeae posteriores, nas águas estuarianas, o que indica que as larvas permaneceram fora da costa, durante as suas três ou quatro semanas de desenvolvimento, até o estágio pós-larval (megalopa). A re-invasão estuarina de megalopas de *U. cordatus* foi registrada aqui pela primeira vez. Cerca de 128 indivíduos por m^3 foram encontradas em fases distintas de recrutamento de no máximo oito dias antes e até quatro dias após a lua nova.

O crescimento de U. *cordatus* segue um padrão indeterminado. A muda de carapaça continua depois da maturidade sexual e foi observada em quase todo os exemplares (com medida de carapaça entre 0.13 cm e 8.24 cm de largura) estudados em laboratório e em um cercado de campo de $100m^2$. Aumentos relativos de crescimento e freqüência de muda, diminuem distintamente com o tamanho. Os primeiros caranguejos apresentaram uma largura de carapaça de 0.12 a 0.17 cm e atingiram um tamanho entre 0.87 e 1.15cm após 6 meses. Durante esse período de tempo, os caranguejos mudaram pelo menos oito ou dez vezes e tiveram um aumento quinzenal no crescimento de 23%. Em machos e fêmeas entre

2.0 e 4.0 cm de largura, o aumento por muda foi de 13% á 14% respectivamente, diminuindo para 5% (machos) e 2% (fêmeas) em caranguejos com uma largura de carapaça ☛ 5.0 cm. Animais com um tamanho aproximado de 4.5 cm tiveram só uma muda anual, durante a estação seca. Os resultados indicam que U. *cordatus* é uma espécie de brachyura longevo, com um período máximo de vida de mais de dez anos. O alcance da maturidade sexual ocorre relativamente cedo, comparado com o tempo de vida. As menores fêmeas com ovos apresentaram um tamanho de 3.1 cm, o que corresponde a uma idade estimada entre 2.1 e 3.0 anos. Os machos tiveram idade aproximada entre 7.1 e 8.7 anos, ao alcançar o tamanho comercial de largura de carapaça de 6.5 cm.

A estrutura de população foi estudada em locais nos bosques de *R. mangle* de distâncias differentes em relação à estrada e portanto, com pressão de pesca variada**.** Nos três lugares houve predominância de caranguejos grandes, enquanto que os menores foram mais abundantes nos habitats periféricos, como o das proximidades da beira da estrada e nos grandes clareiras do bosque. Essa distribuição heterogênea de tamanho, é provavelmente causada pela competição intra-específica com caranguejos maiores deslocando os menores para habitats piores. A abundância e biomassa médias dos caranguejos no habitat bosque de *R. mangle,* foi respectivamente, de 1.7 indivíduos e 142 g por m^2. A relação entre os sexos foi de predominância de machos (entre 53% e 62%), apesar de que os tiradores de caranguejos capturam quase exclusivamente exemplares desse sexo. Exemplares de tamanho comercial (largura de carapaça de ☛ 6.5 cm), constituíram 40% do total de machos tirados nos locais de estudo, no bosque de *R. mangle*. Obteve-se uma indicação sobre o impacto da captura com a comparação entre a mais baixa proporção de machos de tamanho comercial nas proximidades dos locais de estudo mais acessíveis (29%), e o alto número de machos grandes em locais distantes (53%). Correspondentemente, o tamanho de machos capturados para fins comerciais, nos locais mais próximos, foi geralmente menor do que nos locais distantes. O tamanho médio de caranguejos comercializáveis capturados foi 7.3 cm.

As seletividade sexual e de tamanho na pesca de caranguejo, incluem um alto potencial de sustentabilidade . O presente estudo mostra que a população do estuário do Caeté não sofre sobrepesca de crescimento ou de recrutamento. Não está claro ainda, se o recrutamento é uma função da população local, porque as zoeas exportadas talvez sejam tranportadas à longas distâncias, sendo possível que a população do Caeté dependa de megalopas originárias de outras regi✳es. É notável que a despeito da grande duração pesqueira e do crescimento vagaroso do U. *cordatus,* machos grandes ainda são encontrados em abundância. Isso indica para uma alta capacidade de amortessimento do sistema, possivelmente resultante dos numerosos refúgios, como as áreas de densas raízes, inadequadas para captura de caranguejo. Desse modo, a exploração de cobertura total é evitada e o mosaico de refúgios pode atuar como fonte de reposição de locais favoravéis à pesca. Entretanto, o número reduzido de machos de classes de tamanho maiores nas áreas frequentemente exploradas, indica que a capacidade de amortessimento desses locais, está se esgotando. No futuro, isso poderá resultar em uma notável baixa na produção, especialmente se a pressão de pesca aumentar.

1 GENERAL INTRODUCTION

1.1 Frame and objective of the study

About 60-75% of tropical and subtropical coasts are fringed with mangrove forests with a world-wide extension of approximately 181000 km² (Spalding et al. 1997). In the inner tropics, mangrove trees exceed 40 m in height and form dense closed canopy-forests, with an unique association of plants, animals and microorganisms adapted to the life in the changing environment of the intertidal zone (Kjerfve et al. 1997). Mangroves are highly productive ecosystems and support a rich trophic net including small mammals, birds, fish, crustaceans and numerous invertebrates (Golley et al. 1962, Lugo and Snedaker 1974, Odum and Heald 1975, Hatcher 1989, Robertson et al. 1992, Twilley et al 1996). In terms of species number and biomass, brachyuran crabs are a very prominent element of the forest macrofauna and play an important role in nutrient cycling and energy flow (Golley et al. 1962, Jones 1984, Robertson 1986, Macintosh 1988, Robertson and Daniel 1989, Smith III et al. 1991, Koch 1999). Due to their high productivity, mangroves bear a large economical potential and are subject to strong exploitation.

A recent revision upon the status and management of Brazilian mangroves - which fringe the coastline along a length of 6800 km (Kjerfve and Lacerda 1993, Spalding et al. 1997) - has emphasised the significance of crustacean fishery as the major financial income for rural populations in coastal regions (Kjerfve and Lacerda 1993). The semiterrestrial ocypodid crab *Ucides cordatus cordatus* is one of the most heavily harvested resources, due to its large size of more than 9 cm carapace width, high abundance and nutritional value (Nascimento 1993). Concern about decreasing crab numbers in strongly exploited areas has promoted a growing interest in protecting and managing *U. cordatus cordatus* (Nascimento et al. 1982, Santarosa-Freire 1998, Glaser 1999).

The here presented study focuses on an exploited population of *U. cordatus cordatus* in the mangrove estuary of the river Caeté, which is located in northern Brazil about 200 km east of Belém (Fig. 3). The overall objective is to generate knowledge on the biology of *U. cordatus cordatus* in this area, which, in conjunction with socioeconomical studies, may serve as a bases for local management and protection plans, currently under discussion by national government organisations. The study is an integral part of the multidisciplinary research project MADAM [1] (**Ma**ngrove **D**ynamics **A**nd **M**anagement) which aims to provide in-depth knowledge of diverse natural processes as well as relevant institutional, cultural, and economical dynamics for achieving sustainable exploitation of the Caeté estuary (Berger et al. 1999). The estuary includes a 250 km² large peninsula of which about 110 km² is covered with mangrove forest. A paved road connecting the city of Bragança with the seaward side of the peninsula facilitates commercial exploitation of the area (Fig. 4). Beside the extraction of numerous fish species, shrimps and mangrove wood (Glaser and Grasso 1999, Costa et al. 1999, Filgueiras and Isaac 1999), socioeconomic research has emphasised the central role of *U. cordatus cordatus* in sustaining more than 50% of the rural households in the area (Glaser 1999).

U. cordatus cordatus, distributed along the subtropical and tropical Atlantic coast of America (Fig. 2), is a true mangrove crab as it does not occur outside this habitat (Türkay 1970). It constructs and lives in burrows that extend to a sediment depth of 0.6 to 1.6 m (Nascimento 1993, Rademaker 1998). The crab feeds upon leaf litter (Fig. 1) which it collects and stores in the burrows (Rademaker 1998, Wessels 1999), and it is likely to play an important role in the mangrove ecosystem by fuelling the detritus based food web (Ostrensky et al. 1995, Koch 1999). Adult specimens have few natural predators of low abundance such as crab racoons, capucin monkeys and crab hawks (Koch 1999, own observations). The most important predation pressure is undoubtedly exerted by man for human consumption. A prominent feature in the life history of *U. cordatus cordatus* is its seasonality. Reproduction is confined to the rainy season, whereas moulting in adult crabs occurs primarily during the dry season (Alcântara-Filho 1978, Geraldes and Claventi 1983, Nascimento 1993, Santarosa-Freire 1998 pers. comm.). As in most other brachyurans the life cycle of *U. cordatus cordatus* involves pelagic larvae and their development has been investigated in the laboratory (Rodriguez and Hebling 1989). A recent field study has focussed upon the abundance and dispersal of larvae (Santarosa-Freire 1998), but until today no data are available upon post-larval supply and recruitment. Beside the lack of knowledge in this important aspect of the life cycle of *U. cordatus cordatus,* information upon its growth is very limited. The few available size increment data suggest that *U. cordatus cordatus* is very slow growing (Geraldes and de Claventi 1983, Ostrensky et al. 1995), but the results are questionable as they were obtained from crabs kept under artificial

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[1] The bilateral research project MADAM (http://www.zmt.uni-bremen.de), initiated in 1996, is co-ordinated by the University of Pará (UFPa) in Brazil and by the Centre for Tropical Marine Ecology (ZMT) in Germany. Funding is provided by the German "Ministry for Education, Science, Research and Technology" (BMBF) (code 03F0154A) and the Brazilian "Conselho Nacional de Desenvolvimento Científico e Tecnológico" (CNPq). It is a fully recognised LOICZ project (Land-Ocean Interactions in the Coastal Zone), a subproject of the International Geosphere-Biosphere Program (IGBP).

laboratory conditions. However, for resource evaluation and management a profound knowledge upon growth of the species under concern is a crucial prerequisite.

Fig. 1: Small specimen of *U. cordatus cordatus* at its burrow entrance with a newly collected mangrove leaf.

In order to extend the currently available knowledge upon the biology of *U. cordatus cordatus* and to determine the present state of the population in the Caeté estuary, the following aspects were investigated:

- timing and intensity of reproductive activities such as mate searching, breeding, spawning
- larval dispersal, development and recruitment (occurrence of the post-larval stage)
- growth in a wide range of different sized specimens under laboratory and field conditions
- size-frequency distribution of the population, sex ratio, abundance and biomass
- size of commercially landed crabs

The research was conducted between January 1997 and October 1999. Applied methods include monitoring of mate searching activities and abundance of ovigerous females at various locations of the Caeté peninsula, biweekly to monthly larvae sampling with a plankton net and additional post-larval sampling with a passive plankton collector, determination of growth of tagged specimens kept under quasi-natural conditions in a large field enclosure and of small juveniles in the laboratory, bimonthly crab sampling at three locations over 13 months and weekly monitoring of the size of landed crabs during 17 months.

The results are separately presented and discussed in the three chapters "Reproduction", "Growth", "Populations structure and commercial exploitation". A synthesis is given in "Conclusions and perspectives" which special emphasis on the significance of the findings for management purposes.

1.2 Short note on the systematic position and distribution of the genus *Ucides*

The ocypodid genus *Ucides* (Rathbun 1897) has provisionally been included into the subfamily Heloecinae, but due to differences in morphology its position within the Ocypodidae is still uncertain (Türkay 1983). The genus comprises two subspecies which are distributed along the coastline of tropical and subtropical America (Fig. 2): *U. cordatus cordatus* - the here studied Atlantic form and *U. cordatus occidentalis*, the Pacific form. The most reliable character for distinguishing between the two is the varying degree of chelae thornation (Türkay 1970). Transitional forms occur in north Peru and Columbia. However, the differentiation into subspecies still needs to be ascertained as so far only few specimens were considered for character analyses (Türkay pers. comm.). In the following of the here presented study on *Ucides cordatus cordatus*, for simplicity the term *U. cordatus* will be used instead of the complete name.

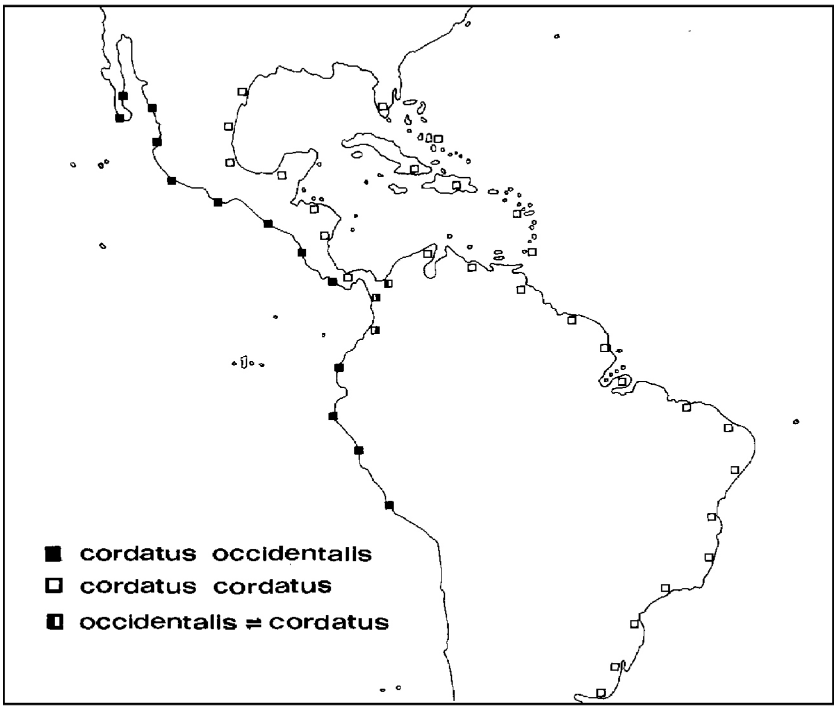


Fig. 2: Distribution map of *U. cordatus cordatus* and *U. cordatus occidentalis*, Türkay 1970.

2 ENVIRONMENTAL SETTING

The research area is located in the mangrove fringed estuary of the river Caeté at the North Brazilian coast 200 km east-north-east of Belém, the capital of the federal state Pará (Fig.3). The Caeté river has a length of 100 km and drains 3000 km² of hinterland and an additional 100 km² of coastal wetland including salt swamps and mangrove forests

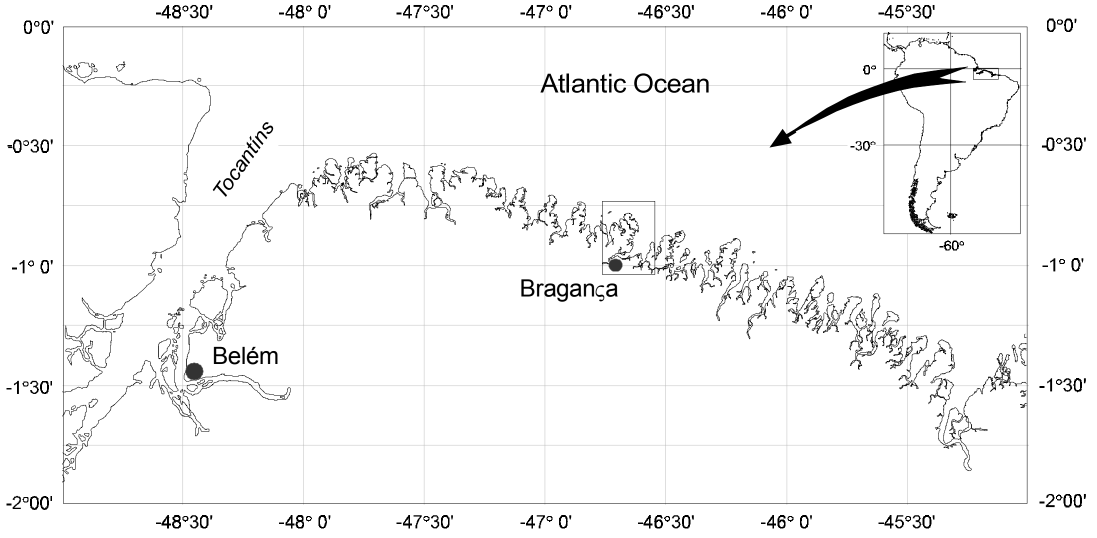


Fig. 3: North Brazilian coastline east of the mouth of the Tocantíns river. Small square near Bragança highlights the study area.

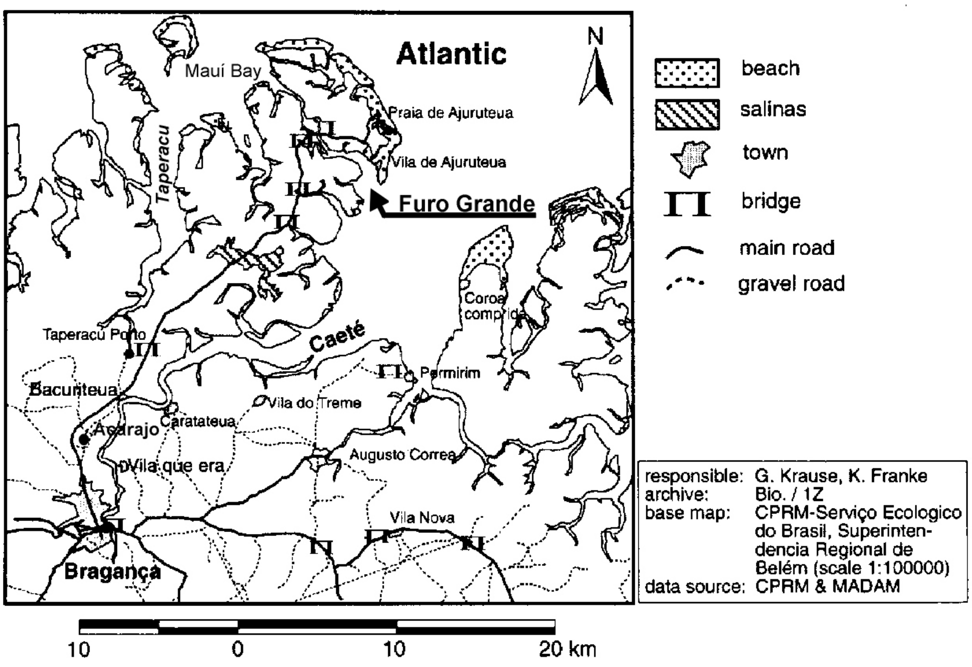


Fig. 4: Research area.

(Schwendenmann 1998). Its estuary is part of an extensive mangrove belt stretching along the Brazilian coastline along a length of 6800 km (Kjerfve and Lacerda 1993). The nearest town is Bragança, 30 km upstream of the Caeté Bay (Fig. 4). About 78000 people inhabit the city and the hinterland which has a very low degree of industrial development (Lara and Dittmar 1999). Between Bragança and the village Bacuriteua agriculture and cattle farming is abundant, but for the majority of the rural households in neighbouring villages resources extracted from the adjacent Caeté estuary are the major income source (Glaser 1999).

The climate in the Bragantine region is characterised by a marked seasonality with most rainfall occurring between January and June (Fig. 5 and 6). Mean annual precipitation and air temperature, measured from 1973-1997 at Tracuateua 50 km south-west of Bragança, are 2500 mm and 25.9°C, respectively (INMET 1992) (Fig. 5). Corresponding to the seasonal precipitation pattern salinity in estuarine watercourses fluctuates strongly (Fig. 6).

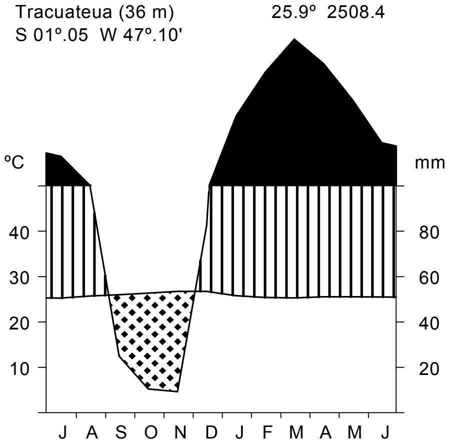


Fig. 5: "Klimadiagramm" after Walter and Lieth (1967), Tracuateua 1973-1997 (INMET 1992, Mehlig in prep.).
Dotted pattern: Arid period; Hatched pattern: Humid period. Black field: more than 100mm precipitation in scale 1:10. Numbers in upper right corner: Annual temperature mean and annual sum of precipitation.

The Caeté estuary is influenced by a semidiurnal macro-tidal regime with tidal amplitudes of more than 5 m. Most parts of the elevated mangrove forest are only inundated during spring tides. In estuarine watercourses current velocities can reach 2 m/s around new and full moons (Schwendenmann 1998), which consequently leads to a high erosion rate and sediment transport. The estuary can be described as well-mixed due to its shallow water depth and high tidal amplitude (Dittmar 1999).

The Caeté peninsula, which lies between the river Taperacú and Caeté, is the main research area of the MADAM project (Fig. 4). It has an extension of about 220 km² of which about 110 km² are covered by well-developed mangrove forests. Isolated sandy elevations that occur inside the forests are interpreted as dune remainders of a former coastline (Souza Filho 1995). A paved road connects the city of Bragança with the fishing village Ajuruteua and the beach at the seaward side of the peninsula (Fig. 4). Most forest stands are dominated by *Rhizophora mangle* (Rhizophoraceae) with interspersed trees of *Avicennia germinans* (Avicennicaceae). *A. germinans* also forms pure stands, for example south of the Salinas da Rocha in the central part of the peninsula (Fig. 4). The third mangrove tree species that occurs in the area is *Laguncularia racemosa* (Combretaceae) which grows mostly at disturbed sites such as near the road or at banks of the numerous tidal creeks that intersect the peninsula. The intertidal epifauna is dominated by brachyuran crabs including species of the families Ocypodidae, Grapsidae, Xanthidae, Portunidae, Gecarcinidae, Diogenidae and Porcellanidae (Koch 1999). Koch (1999) has shown that *U. cordatus* accounts for 84% of the epibenthic biomass in the forest.

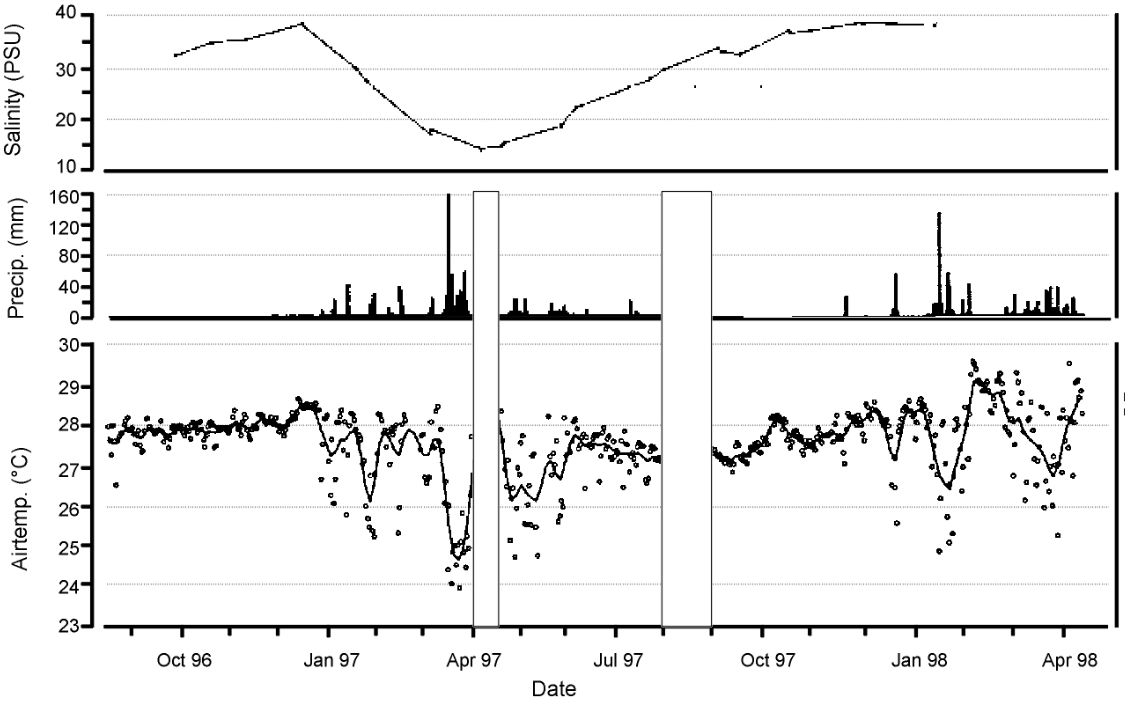


Fig. 6: Average daily air temperature, precipitation and salinity measured at Furo do Meio, Caeté estuary (MADAM, Koch 1999).
Missing data are indicated by vertical bars. Until 03/97 the meteorological station was located at Furo Grande, 7 km north of Furo do Meio.

In the course of the here presented study, *U. cordatus* was sampled at numerous sites from the central to the northern part of the peninsula, primarily in *R. mangle* dominated forest stands. Capture locations are demonstrated in maps in the subsequent chapters. The tidal channel Furo Grande at the northern end of the peninsula was chosen for sampling of *U. cordatus* larvae (Fig. 4). Furo Grande has a length of about 12 km and connects Mauí and Caeté Bay. The bay mouths have a width of 1 to 1.5 km. The channel has a large catchment area with many side creeks. At low tide numerous sandbanks emerge, that are totally inundated during high tides. In deeper parts of Furo Grande water depth at spring high tides reaches a maximum of 7.8 m. During the three study years considerable movement of sandbanks and erosion at the banks of the channel were observed.

3 REPRODUCTION

3.1 Introduction

Reproductive biology is a crucial factor for understanding the population dynamics of a given species and the persistence of populations generally depends upon successful recruitment of juveniles into the adult habitat. Knowledge upon reproduction and recruitment is also integral for the development of management strategies which aim to optimise sustainable exploitation of commercially harvested species.

Breeding of *U. cordatus* is restricted to the rainy season and associated with a phenomenon called „andança“ which occurs around full and new moon. During these times crabs show an unusual high activity outside their burrows and continue to move around in the mangrove forest despite disturbance by man (Alves 1975, Alcântara-Filho 1978, Nascimento 1993, Santarosa-Freire 1998). The high activity outside the burrows is referred to mate searching and copulation. Due to the improved catchability of the crabs, andança events are times of particularly high crab extraction. In Pará as well as in other states of Brazil (e.g. Paraná; Santarosa-Freire 1998) the implementation of temporal capture restrictions during the reproductive season is currently under consideration (see chapter 6).

As in most other brachyurans, the life cycle of *U. cordatus* involves pelagic larvae. Their development has been studied in the laboratory (Rodriguez and Hebling 1989) and encompasses 5 to 6 zoea stages until megalopa – the transitional stage between the planktonic larvae and benthic adult. The abundance and dispersal of *U. cordatus* larvae in estuarine channels has only recently been investigated in an mangrove estuary in Paraná, South Brazil (Santarosa-Freire 1998). Here, newly spawned larvae were exclusively present around new and full moons. Despite an estimated density of 75 females per 100 m^2 and ca. 200000 eggs per crab, only few first zoeae were encountered in the inner estuary of the ca. 800 ha covering mangrove area. The low number of zoeae has led Santarosa-Freire to assume, that a large percentage of larvae had died shortly after their release due to low salinity of the water course. Beside the first larval stage, neither later zoea stages, megalopae nor first instar crabs were encountered. Up to date, development time of *U. cordatus* larvae in the field and occurrence of recruitment back into the mangrove forest environment is unknown.

The aim of the present study is to delineate course and length of the reproductive season of *U. cordatus* in the Caeté estuary, and to determine timing and periodicity of andança events and spawning cycles. Larval output of breeding cycles within and between the three study years is compared in order to gain information upon possible fluctuations. Furthermore, the dispersal mode of the larvae is of particular interest. Two strategies are generally distinguished for estuarine brachyurans with pelagic larval phase: During their development zoeae are either retained inside the parent estuary (e.g. Sandifer 1975, Cronin 1982, Morgan 1987a) or are flushed away to continental shelf or oceanic waters (e.g. Smyth 1980, Christy and Stancyk 1982, Epifanio et al. 1989, McConaugha 1988, Querioga 1996). Once outside the estuary, the larvae may be transported long distances away from the parent habitat, hence dispersing over a wide geographic area (Palmer and Strahtmann 1981, Botsford et al. 1989, Underwood and Fairweather 1989, Anger et al.1994). In such larvae exporting species, population persistence depends on re-immigration mechanisms and it generally is the megalopal stage that re-invades the estuarine environment. It is often assumed, that these re-invaders are genetically less homogenous than the megalopal population of species whose larvae are retained within the parental estuary (Hines 1986, Roughgarden and Iwasa 1986, Harrison and Quinn 1989). Hence, the two principal alternative dispersal and recruitment strategies may have different implications for the management and protection of populations and an important first step is to delineate the mode of dispersal of the species under concern. The current study therefore aims to determine whether *U. cordatus* larvae are retained within or exported from the Caeté estuary during their development. Recruitment of *U. cordatus*, defined as presence of megalopae in the estuary, will be described for the first time.

3.2 Methods

3.2.1 Determination of breeding cycles and abundance of ovigerous females

The occurrence of andança events was recorded from January 1997 until April 1999. Professional crab collectors provided monthly information on when and at which days they had observed andança activities. According to the number of crabs observed outside their burrows, the overall intensity of an monthly andança event was classified as low, medium or high.

For determining when females ovulate (extrusion of the egg-mass after internal fertilisation) and for how long eggs are being incubated until spawning, 20 non-ovigerous females were captured during andança activities on the 11th of January 1997. It was suspected that some of them might have already had copulated and stored spermatophores in receptacula seminis. These females were kept in tanks (50x50x80 cm) in a shaded area under ambient air temperature in an outside laboratory. Each tank held 5 females and one part was filled with approximately 25 cm of mud, whereas the other remained free of sediment. The tanks were filled with mangrove creek water to a height of approximately 8 cm so that females could immerse themselves. Water and food (mangrove leaves) were changed every second day, the light regime was 12 hours light and 12 hours darkness. Whether ovulation or larval release had occurred was checked daily. A subsample of approximately 40 eggs was taken from each egg-carrying female every second day and examined under a Zeiss microscope. Only crabs with healthy egg-masses were kept until spawning.

The abundance of ovigerous females over different reproductive cycles was investigated in 1997 and 1998 when crabs were sampled after preceding andança activities in January, February and March ("post-andança sampling program"). Monthly sampling was commenced 4 or 5 days after new moon. Per reproductive cycle up to 9 locations each covering an area of approximately 500 m² were sampled within a time span of three days. For practical purposes most locations were situated in the mangrove forest near the road (see Fig. 9 and 10, 3.3.1). Only *Rhizophora mangle* dominated forest stands with soft mud were selected in order to enhance catching efficiency (5.4.2). Per site at least 100 crabs were generally captured and immediately sexed and measured with a calliper rule to the nearest millimetre. The number of sampled females was a function of the prevalent sex ratio at a given site and ranged between 16 and 69% of the total catch. The abdomen of the females was checked for presence of eggs.

While each site was sampled once in 1997, 6 sites were sampled repetitively from January to March 1998. This approach was chosen because the 1997 data had revealed large differences in the proportion of ovigerous females for the various sampling sites within respective breeding cycles. As it is possible that females do not ovulate continuously over consecutive reproductive cycles, the observed within-month differences might have reflected site specific temporal variations in breeding activity. For example a site where only few ovigerous females were encountered in one month might have held many egg carrying females in another month. In order to test this assumption a repetitive sampling strategy with marked crabs was required. At each of the 6 sampling sites in 1998, a capture-recapture experiment was conducted by tagging all measured crabs with month-specific marks including separate keys for females with and without eggs during the first two post-andança sampling occasions. The crabs were marked by sawing an approximately 1 mm deep scratch into the merus of both claws. Preliminary experiments had shown that these marks remained well recognisable for at least 7 weeks. Recaptured females would thus provide information on the ovulation frequency over consecutive months.

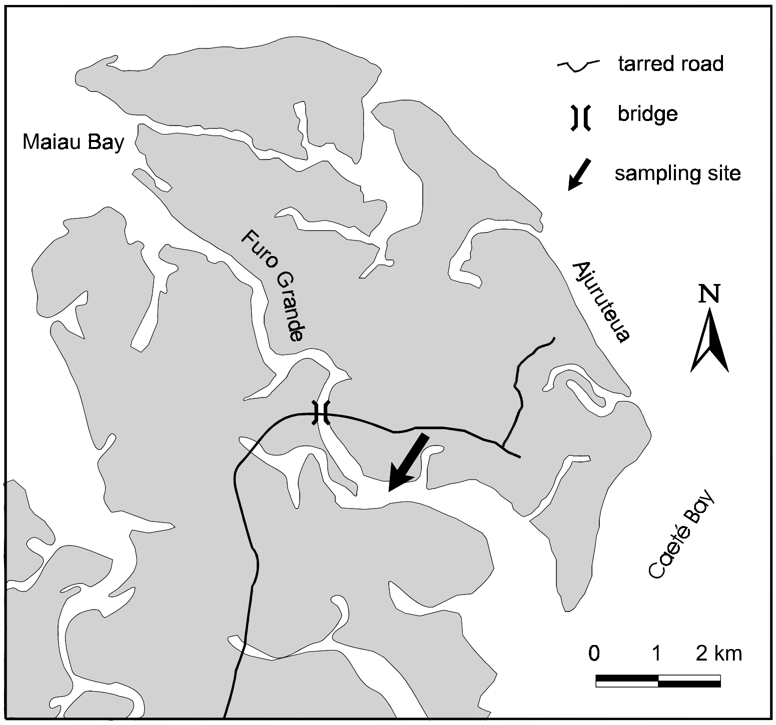
3.2.2 Plankton sampling

3.2.2.1 Net-sampling

Sampling in the mangrove forest Qualitative sampling in the flooded mangrove forest was conducted in the evening of the 6th and morning of the 7th of January 1997 as well as in the evening of the 24th of April 1998. Three samples were taken at each date and sampling was commenced during flood tide when the water height in the forest had reached approximately 30 cm. The second sample was collected at slack high tide and the last approximately 20 minutes later. Half of the opening of the plankton net (40 cm diameter, 1m length, 250 µm meshsize, Hydrobios Kiel) was dipped into the water and towed by slowly walking 10 to 15 m on the forest floor or – at high tide – on a boardwalk in an area with few *R. mangle* prop roots.

Sampling in the tidal channel Furo Grande Quantitative estuarine plankton sampling was performed at Furo Grande (Fig. 7) from January 1997 to April 1999 (Table 1 and 2). Samples were taken on board of small boats with 45 HP or 15 HP outboard motors. The employed net had a mesh size of 300 µm, diameter was 40 cm and length 2 m (Hydrobios, Kiel). Towing speed was 0.9 to 1.8 kn. The water column was filtered from 10 to 50 cm below surface. At times of particular high current speeds (up to 2 m per second) quantitative sampling could not be conducted as the net was clogged by stirred detritus. In addition to the upper water column, in 1997 sampling was performed in a depth of 1m to 1.4 m over ground. Except for samples taken around slack tides a quantitative analysis of depth samples was hampered as the net was frequently clogged with detritus. Therefore, depth samples were not further analysed. Filtered water volume was determined by the use of a calibrated mechanical flowmeter (General Oceanics, 2030R), samples were immediately conserved in 4% buffered formaline. Parallel to net-sampling water temperature (WTW OXI 196) and salinity (WTW LF 197) was measured at a depth of approximately 15 cm below surface. At each sampling occasion times of slack high and slack low tide were recorded.

Sampling schedule Plankton sampling was primarily conducted during the rainy season when *U. cordatus* reproduces (3.1). For establishing a sampling schedule which allows a quantitative comparison of larval densities in different months, precise knowledge upon dates and times of larval release is required. As no such information existed for *U. cordatus* in the Caeté estuary at the beginning of the field study, the first two dates for sampling the tidal channel were selected following the results from a study in South Brazil (Santarosa-



Base map: CPRM / MADAM (G.Krause, K. Franke)

Fig. 7: Location of the plankton sampling site in the tidal channel Furo Grande

Freire 1998). Santarosa-Freire had captured freshly hatched zoea larvae one and two days after both full and new moon. However, during preliminary full and new moon sampling conducted at Furo Grande on the 24th/25th of January and 8th/9th of February 1997 (Table 1) no larvae were encountered. Instead, the samples taken before new moon in the flooded mangrove forest in February 1997 (see above) contained comparably large numbers of first zoeae. This finding pointed out that qualitative plankton sampling had to be advanced to days before new moon. In order to precisely delineate the larval release pattern within a monthly spawning cycle, in March and April 1997 as well as in February 1998 new moon sampling was conducted over 6 consecutive days (Table 1) with samples being taken within at least the first 3.5 hours after high tide. In all three months peak spawning events with highest densities of newly released larvae were recorded one night before new moon (see Fig. 13, 3.3.2.2). Consequently, during all subsequent study months zoea densities were determined and compared for this particular time (Table 1).

Once per monthly spawning cycle sampling was conducted over a time span of either ca.15 hours (April, May and June 1997, January until April 1998, March and April 1999) or 27 hours (March 1997, May and June 1998). During dry season sampling (July to October 1998) and in January 1999 sampling was restricted to 3.5 hours after the evening high tide. Sampling was always commenced during the flood in the late afternoon or at slack high tide in the evening. The plankton net was generally towed at least every two hours. In order to maximise the chance of matching peak larval densities, the sampling interval was reduced at times of larval release which was indicated by abrupt increases in zoea densities. Such variations in larval abundance could be directly observed in the net bucket due to the high numbers and predominance of *U. cordatus* zoeae in samples taken during or shortly after spawning times. Sampling was occasionally interrupted for longer time spans, which is particularly true for 1997, due to ongoing technical problems with the outboard motors.

Beside the monthly new moon sampling after spawning events, daily plankton samples were taken between last and first quarter moons in March and April 1999 (Table 1). This schedule was chosen for monitoring megalopal abundance over consecutive days and samples were taken 60 to 45 minutes before nocturnal low tides.

Table 1: Surface net-samples taken around new moons at Furo Grande from February 1997 to April 1999 and between last and first quarter moon in 1999 (*).

Date	Days before (-), at (o) and after (+) new moon	Number of samples taken	Number of samples selected for analysis
08/09.02.97	+1/+2	14	6
06-10.03.97	-3/-2/-1/0/+1	39	35
04-09.04.97	-3/-2/-1/0/+1/+2	33	30
05/06.05.97	-1/0	8	8
04/05.06.97	-1/0	9	9
03/04.07.97	-1	4	4
27/28.01.98	-1/0	10	10
23-28.02.98	-3/-2/-1/0/+1/+2	35	35
27/28.03.98	-1/0	12	12
25/26.04.98	-1/0	13	13
23/24.05.98	-2/-1	17	17
22/23.06.98	-2/-1	20	20
22.07.98	-1	5	4
21.08.98	-1	3	3
19.09.98	-1	3	3
19.10.98	-1	3	3
16.01.99	-1	4	4
10-24.03.99	-7 to +7 *	12	12
16/17.03.99	-1/0	18	18
09-22.04.99	-7 to +6 *	11	11
15/16.04.99	-1/0	18	18
Total		291	275

Quantitative plankton sampling was also conducted at full moon from January until June 1997 and in April 1998 (Table 2). However, according to the timing of andança and breeding activities it became clear that females did not release zoeae at times other than new moon (3.3.1). As in addition megalopal settlement was also confined to other lunar phases

Table 2: Full moon surface net-samples taken at Furo Grande from January 1997 to April 1998.

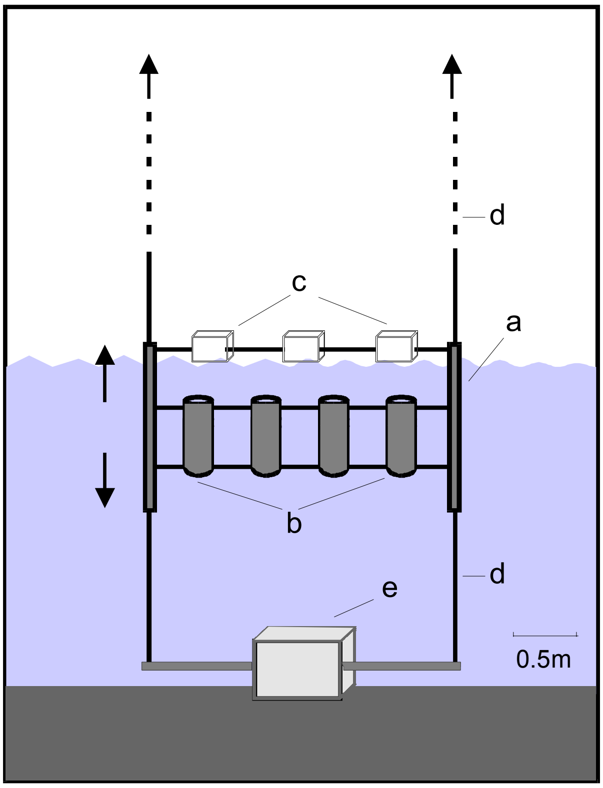
Date	Days before (-), at (o) and after (-) full moon	Number of samples taken	Number of samples selected for analysis
24/25.01.97	+1/+2	23	5
22/23.02.97	0/+1	11	5
22/23.03.97	-2/-1	13	7
21/22.04.97	-1/0	13	5
22/23.05.97	0/+1	6	3
19/20.06.97	-1/0	6	3
11/12.04.98	-1/0	10	6
Total		82	34

(3.3.2.4) full moon sampling was consequently ceased. Nevertheless, 40% of the full moon samples that had been taken were analysed.

Sampling in the Caeté bay and offshore Presence of *U. cordatus* larvae outside the inner estuary was studied at new moon on the 26th of April 1998. Plankton was sampled until a maximum distance of approximately 20 km offshore of Ajuruteua beach (Fig. 20, 3.3.3). Surface samples were taken on board of a rented fisher boat. The aim was to confirm that newly spawned zoea larvae of *U. cordatus* are exported from the inner estuary to coastal waters – as indicated by the inner-estuarine sampling - and to investigate megalopal presence.

3.2.2.2 Passive collector-sampling

Daily abundance of megalopae was investigated by deploying a passive plankton collector. This technique has been successfully applied for other estuarine brachyurans and exploits the high thigmokinesis of megalopae which cling to the artificial substrate (Lipicus et al. 1990, Van Montfrans et al. 1990, Boylan and Wenner 1993, Metcalf et al.1995, Shanks 1998). For the present study, a collector was constructed which could be permanently installed at the bridge crossing Furo Grande (Fig. 8). The settlement substrate consisted of air-conditioner filter-wool wrapped around 4 plastic cylinders, that floated ca. 20 cm beneath the water surface. Filters were changed daily at diurnal slack high tides between 12th March and 1rst July 1998. The filter material was immediately soaked in fresh water for 45 minutes and thoroughly rinsed. The sample was concentrated in a 500µm sieve and fixed in 4% formaline. Altogether 103 daily samples were taken and analysed, data are missing for 9 dates when the collector was trapped by drifting wooden logs and could not be retrieved.



Construction details:

The collector consists of an vertically movable iron frame (**a**) carrying 4 plastic cylinders (**b**) (40 cm length, Ø 19 cm). The cylinder walls wear 40 holes to allow water to pass through. Each cylinder was encoated with commercial air-conditioner filter material (0.6 mm thick) as artificial settlement substrate. Three foam buoys (**c**) maintained the movable iron frame in a position such that the upper edge of the cylinders floated about 20 cm beneath the water surface. The collector construction was held by two steel cables (Ø 0.7 cm) (**d**) attached to the railing of the bridge at one end. The other end was fastened to a massive iron tube held by a 120 kg concrete block (**e**) positioned on the bottom of the tidal channel. Due to strong tidal currents the concrete block had to be fixed with 4 wooden stakes that were rammed approx. 1m into the sediment.

Fig. 8: Schematic of the megalopae collector

3.2.2.3 Processing of samples

Net-samples containing high zoea numbers were divided with a Folsom Plankton Splitter and 50 to 25% of the material was further subsampled with a volumetric procedure according to Russel and Colman (1931). Three subsamples were counted (0.2% to 4%). Samples with low zoea numbers (< 10 per m^3) remained unsplitted and 6 volumetric subsamples were analysed. Megalopae generally occurred in much lower densities than zoea-larvae. Therefore, in most cases 15 to 20% of the entire net-sample was sorted for megalopae. Collector-samples were dyed with Bengal Rose and *U. cordatus* megalopae of the entire or half sample counted. Zoeae were not quantified, but their presence recorded.

Larvae were identified under a Zeiss microscope using laboratory-reared reference specimens and the description of Rodriguez and Hebling (1989). Counting was conducted under a Zeiss binocular microscope.

3.2.3 Larvae rearing in the laboratory

To obtain reference material for identification and information on development time from first zoea until megalopa, rearing trials were conducted in the laboratory. Ovigerous females were captured in the field three to two days before new moon and held in the laboratory in 60x40x20 cm plastic boxes. The boxes were filled with ambient estuarine water to a depth of approximately 6 cm, and females could avoid immersion by sitting on elevated tiles. Larvae were separated within 15 min after spawning and approximately 500 individuals were held in moderately aerated 5 l glass beakers filled with estuarine water. Water temperature was 27 to 29 °C and the light regime 12 hrs light : 12 hrs dark. Water was changed daily. Overall mortality of the larvae was high (see below), but 18 larvae could be reared until megalopa.

Rearing was tested under various salinity and food conditions. During the first 3 to 4 days after hatching, survival of the zoeae was always high (ca. 99%), irrespective of salinity (ranging from 8 to 25 ‰ in different trials) and food type (see below), whereas generally on day 5 mortality increased sharply. No larvae moulted to zoea III when they were held in filtered estuarine water (1 µm) with *Branchionus plicatilis* or nauplii of *Artemia salina* offered as artificial food source. Contrarily, the latter has been successfully fed to *U. cordatus* larvae by Rodriguez and Hebling (1989). When natural salinity of the estuarine water were below 15 ‰ larvae became heavily infected by endo- and exoparasites and did not survive past zoea II stage. The same was true when the salinity was increased by adding sea salt. Rearing to megalopa only succeeded in unfiltered estuarine water with natural salinity above 15 ‰. Additional food was provided by screening 10 l of estuarine water (taken at incoming tide) at 200 µm and concentrating it over 50 µm mesh.

3.3 Results

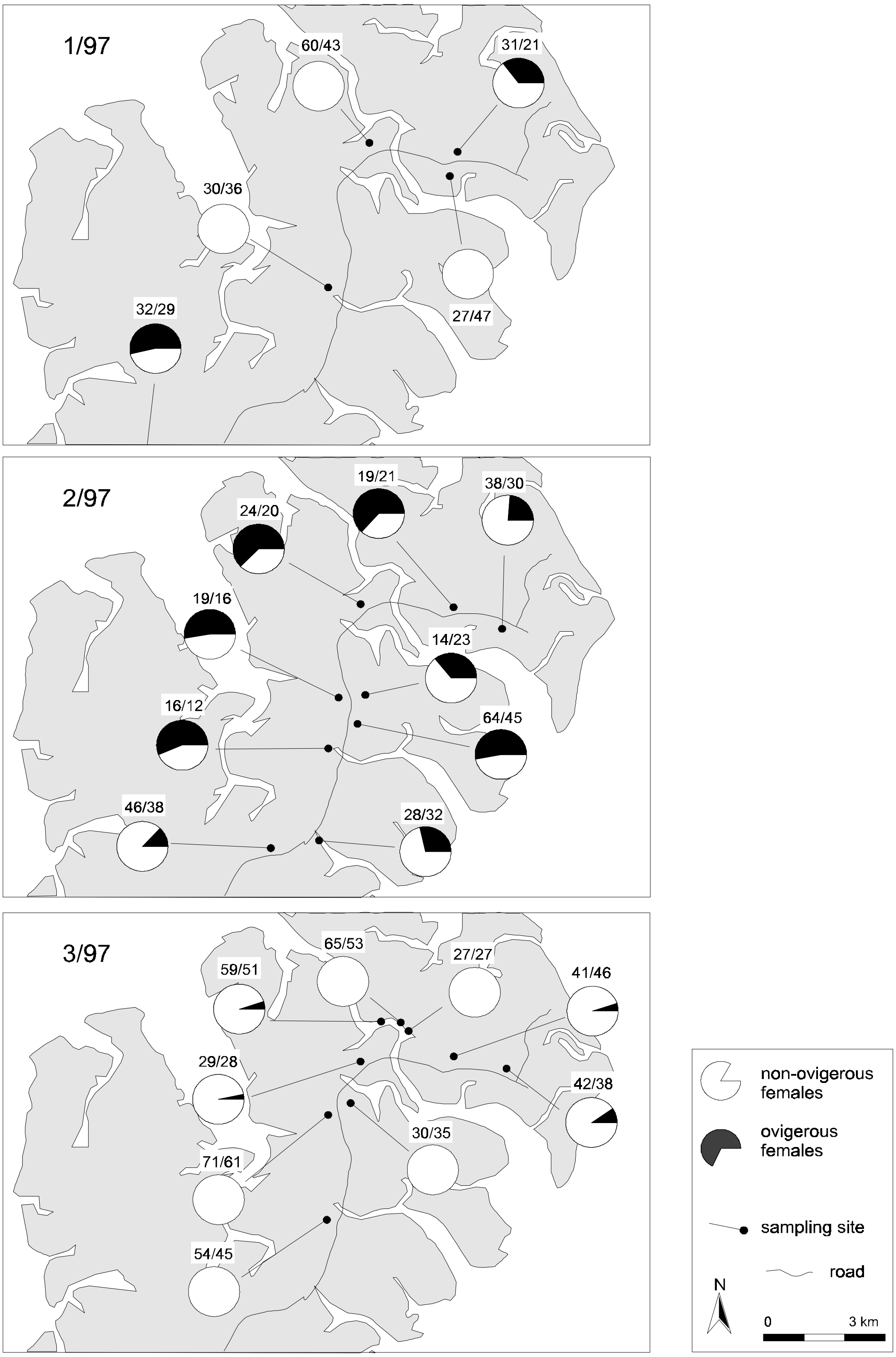
3.3.1 Breeding cycle, abundance and size-frequency distribution of ovigerous females

Four to five breeding cycles between December and April were recorded per rainy season, whereas from May until November respective activities were never reported. Each andança began one or two days after new moon and lasted two to four days (Table 3). Half of the non-ovigerous females that were captured during andança activities at the 11th of January 1997 ovulated in the laboratory within the following two days, revealing that the eggs had been fertilised with stored spermatophores shortly after the preceding andança. Females incubated their eggs between 24 and 27 days and spawned at the following new moon (3.3.2.2).

Table 3: Occurrence and intensity of andança events during the rainy season 1997, 1998 and 1999 and proportion of subsequently sampled ovigerous females.
n values indicate total female catch. Shaded fields: no data available. * low, ** medium, *** high intensity; scaling refers to relative within-year observations. The duration of andança in December 1997 and 1998 is not exactly known.

Date of New moon	Date of andança	Intensity of andança	Percent ovigerous females
09.01.97	11.01-13.01.97	**	13.3 (n = 180)
07.02.97	08.02-10.02.97	***	40.3 (n = 268)
09.03.97	10.03-12.03.97	*	2.9 (n = 417)
07.04.97	09.04-10.04.97	*	
29.12.97	ca. 30.12.98	*	
28.01.98	29.01-31.01.98	***	38.7 (n = 354)
26.02.98	28.02-02.03.98	*	6.9 (n = 407)
28.03.98	30.03-31.03.98	*	7.3 (n = 372)
18.12.98	ca. 19.12.98	*	
17.01.99	18.01-20.01.99	*	
16.02.99	17.02-20.02.99	***	
17.03.99	19.03-20.03.99	*	
16.04.99	18.04-19.04.99	*	

Monthly andança intensity and abundance of subsequently captured ovigerous females varied throughout the reproductive season. Highest within-season andança activities were recorded in February 1997 and 1999 and in January 1998 (Table 3). After these annual peak andanças approximately 40% of all females captured at the different sampling locations carried eggs (data pooled for all sites). After low and mid-intensity andança values for ovigerous females ranged between 3% and 13%, respectively (Table 3). However,



Base map after CPRM & MADAM (G.Krause, K.Franke)

Fig. 9: Frequency of ovigerous versus non-ovigerous females in %.

Captured at different sampling locations after the first three andança events in 1997. Numbers indicate total female catch and % females of total crab catch (both sexes).

Base map after CPRM & MADAM (G.Krause, K.Franke)

Fig. 10: Frequency of ovigerous versus non-ovigerous females in %.
Captured at different sampling locations after the first three andança events in 1998. Numbers indicate total female catch and % females of total crab catch (both sexes).

within each month a large spatial variability for both andança activities and proportions of subsequently sampled ovigerous females was frequently observed at different forest locations. For example in January 1997 values for egg-carrying females ranged between 0 and 68% (Fig. 9) and after the peak andança in January 1998 between 17 to 70% (Fig. 10).

Capture-recapture experiment For the capture-recapture experiment conducted during the post-andança sampling program in 1998, 1712 crabs (44% females, 56% males) were tagged. Only 6 males and 3 females were re-encountered during sampling of the same sites in subsequent months and information upon repetitive ovulation events in females could not be obtained.

Size-frequency distribution of ovigerous females The size of females captured with eggs ranged between 3.1 cm and 7.2 cm carapace width. The frequency data for ovigerous females (data source: post-andança sampling 97/98: n = 336; transect-sampling 98: n = 223, see 5.2.1) of different size classes from 3 cm carapace width onwards show a significant heterogeneous distribution (Chi Square = 81.8; P < 0.0001). In the classes from 3.0 to 4.5

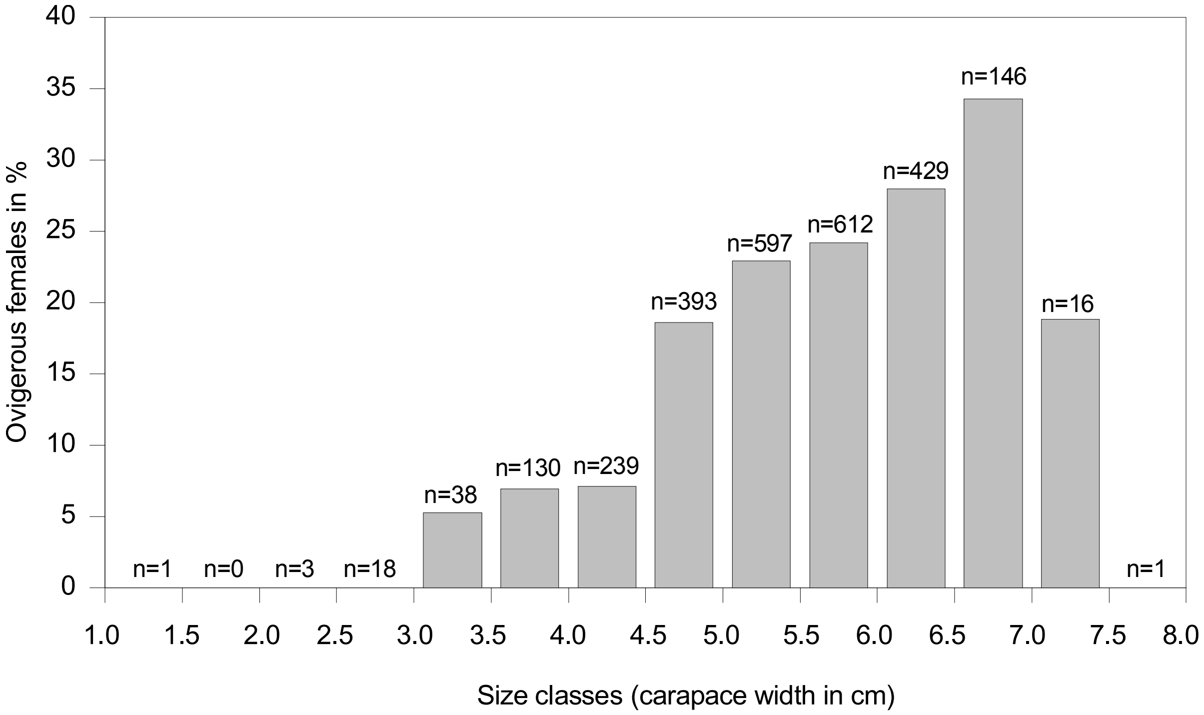


Fig. 11: Size-frequency distribution of ovigerous females captured in 1997 and 1998.
n values indicate total female catch including non-ovigerous individuals.

cm carapace width, less than 10% of the captured females were ovigerous, whereas for 4.5 to 5 cm large females a distinct increase to 18.6% can be observed. (Fig. 11). Numbers of egg-carrying females continuously rise in following size-classes and the maximum occurs at 6.5 to 7.0 cm carapace width (34.7%). Off the few captured females with 7.0 cm carapace width or larger still 20% were ovigerous.

3.3.2 Larvae findings in the estuary

3.3.2.1 Water temperature and salinity

Water temperature during sampling times at Furo Grande showed only little variation. Pooled over all measurements the average value was 29.01 ± 0.7 °C (n = 167), with a minimum and maximum of 27.8 and 30.7 °C, respectively. Salinity fluctuated considerably between months (Fig. 12). Values below 10 ‰ were recorded in the rainy season in April 1997 and March 1998. The highest salinity during plankton sampling occurred in the dry season in October 1998 (33.4‰) (Fig.12).

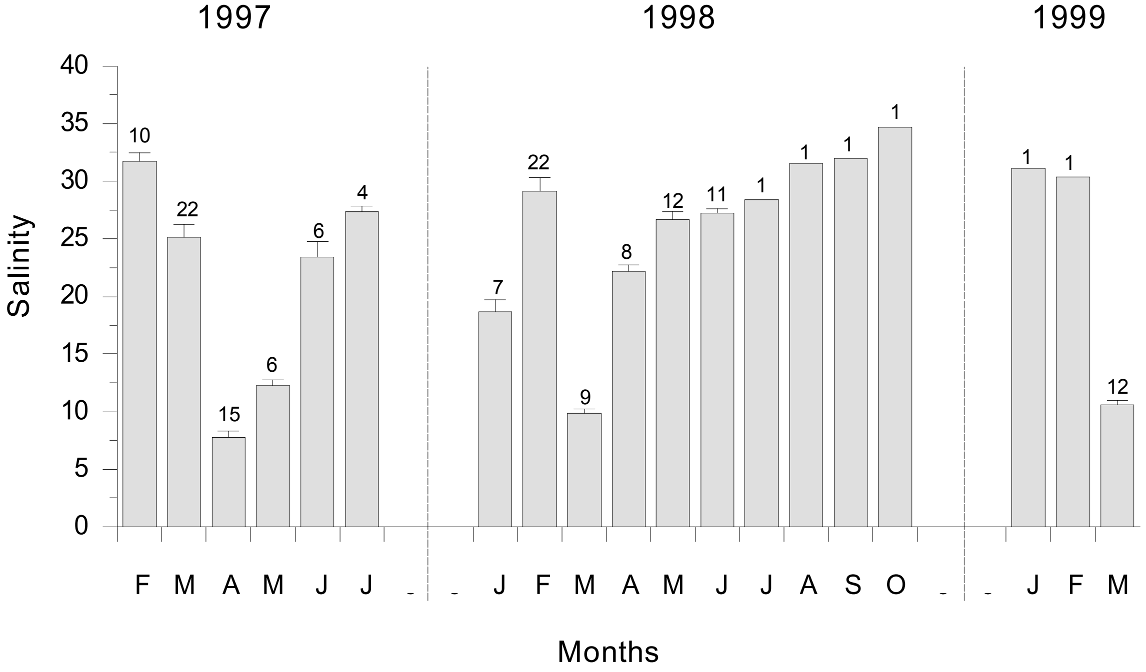


Fig. 12: Salinity measured during new moon plankton sampling occasions at Furo Grande. Average values and standard deviation are given, except for single measurements in July 1998-October 1998 and January/February 1999. Numbers above bars indicate sample size.

3.3.2.2 Seasonal and lunar abundance of zoea larvae

The presence of *U. cordatus* larvae was seasonally restricted. Zoea larvae were encountered from January until June, whereas plankton samples taken during the dry season between July and October 1998 did not contain any larvae. Of the 6 *U. cordatus* zoeal stages described by Rodriguez and Hebling (1982), only newly hatched first zoeae (stage I) were found in the tidal channel Furo Grande. They were regularly encountered in net- and collector samples taken around the date of new moon, whereas they were absent at other lunar phases.

The rhythm of new moon larval release was investigated by sampling over 6 consecutive days in March and April 1997 as well as in February 1998. In all three months larval peaks occurred from the second day before until new moon or one day thereafter (Fig. 13). These monthly spawning cycles revealed a characteristic pattern in which maximum larval densities always appeared one day before new moon (Fig. 13). The second highest monthly larval peak with 4 to 7 times lower values was observed either two days before (March and April 1997) or at the day of the moon (February 1998). One day after new moon larval output was close to zero or zero. No *U. cordatus* larvae were encountered at Furo Grande a day later.

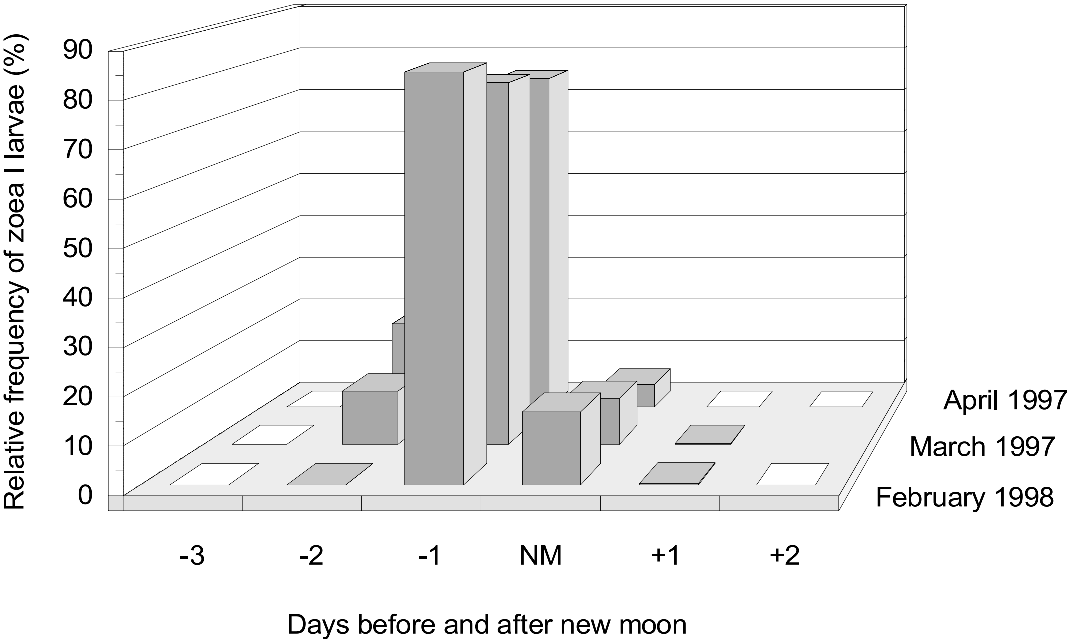


Fig. 13: Relative frequency of zoea I larvae at different spawning days around new moon in March and April 1997 and February 1998.
Percent values relate to total peak larval densities per month (sum of observed peak densities of the monthly three to four nocturnal spawning events). White fields: Absence of larvae.

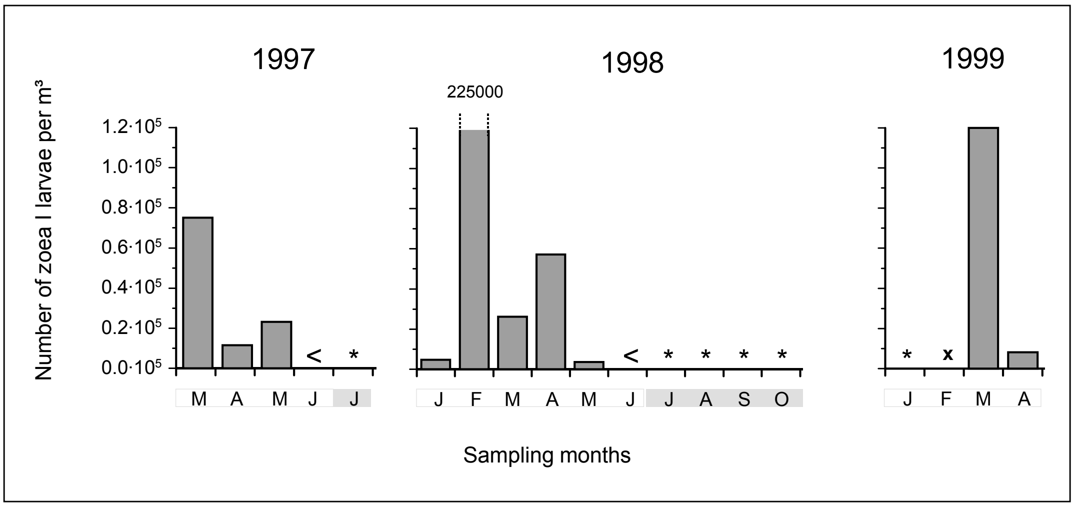


Fig. 14: Maximum first zoeae densities after peak spawning events from March to July 1997, January to November 1998 and January to April 1999.
Sampling was conducted one day before new moon. White fields: rainy season; dark fields: dry season; x: missing sample ; <: larvae present but less than 250 indiv./m³ ; *: no larvae present.

Within each annual study period, a distinct maximum in larval release was observed, with peak zoeae densities at least threefold higher than at other sampling months (Fig. 14). In 1998 this peak occurred in February when up to 225350 larvae per m³ were recorded. In 1997 and 1999 maximum larval output with peak densities of approximately 75100 and 141000 larvae per m³ was observed in March, but in these two years sampling did not comprise the entire spawning season. In all years a drastic drop in zoeal output with 7 to 12 times lower values occurred four weeks after the observed peaks (Fig. 14). A renewed rise in larvae densities was recorded in May 1997 (ca. 23120 indiv./m³) and April 1998 (ca. 57100 indiv./m³) which was again followed by a distinct drop a month later. In June, the last spawning event, peak larval densities were as low as approximately 229 indiv./m³ in 1997 and approximately 8 indiv./m³ in 1998.

3.3.2.3 Tidal and diel pattern of zoeal abundance

The qualitative new moon plankton sampling conducted in the flooded mangrove forest during morning and evening spring high tides revealed location and timing of larval release. Females spawned in the mangrove forest instead of migrating to tidal creeks. Whereas samples taken at the beginning of the flooding did not contain any *U. cordatus* zoeae, high numbers of newly released larvae were encountered at slack high tide and in off-running water masses.

At Furo Grande, where quantitative net-samples were taken, a characteristic pattern in tidal and diel zoeal abundance was found. In Fig. 15 and 16 the temporal distribution of larvae after preceding spawning events is illustrated for sampling occasions with peak larval densities exceeding 200 indiv./m³. First larvae were generally encountered after the evening

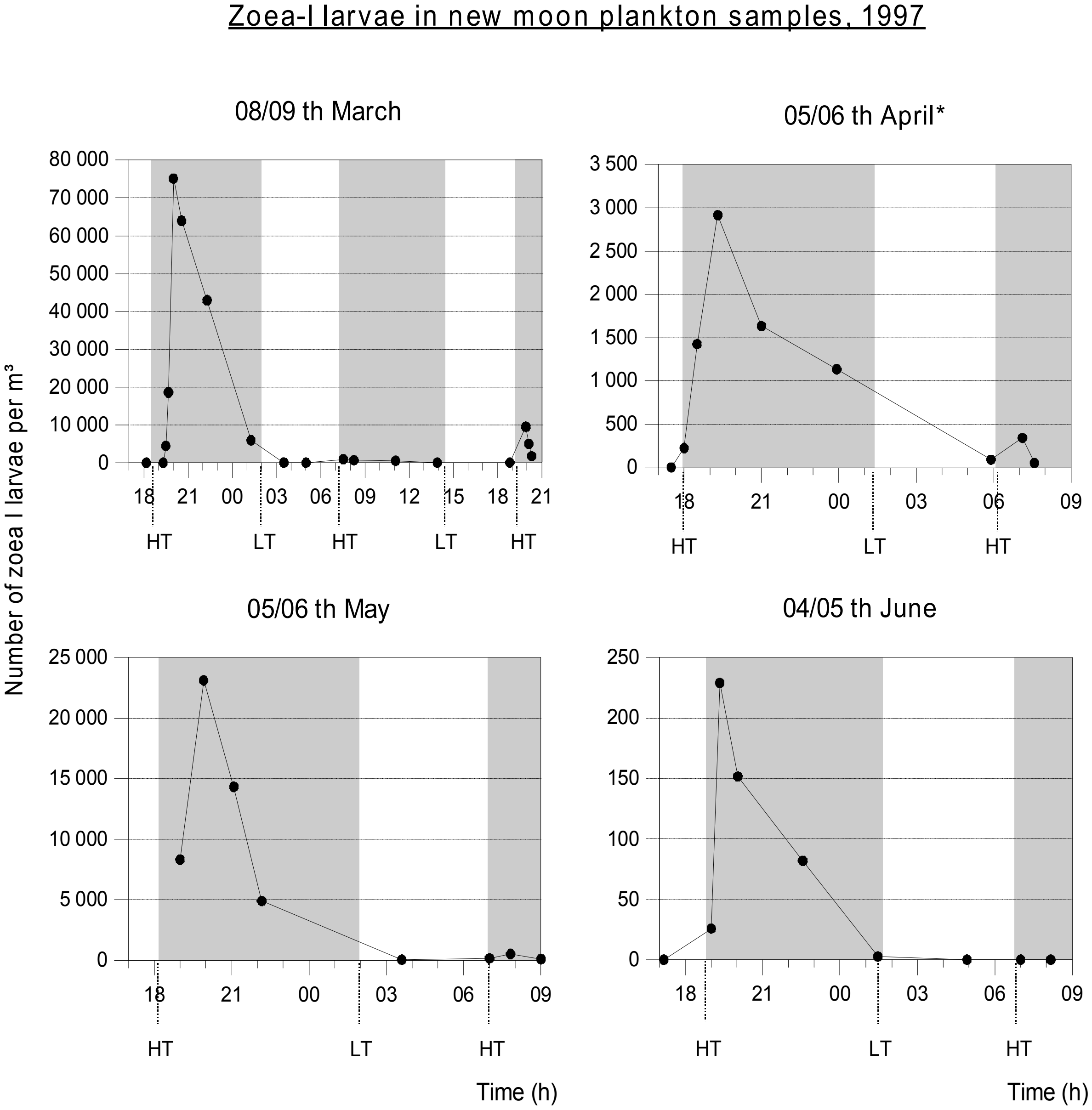


Fig. 15: Fluctuation in numbers of first zoeae after the larval release one or two (*) days before new moon from March until June 1997.
Shaded areas: ebb tide; white areas: flood tide; HT: high tide; LT: low tide.

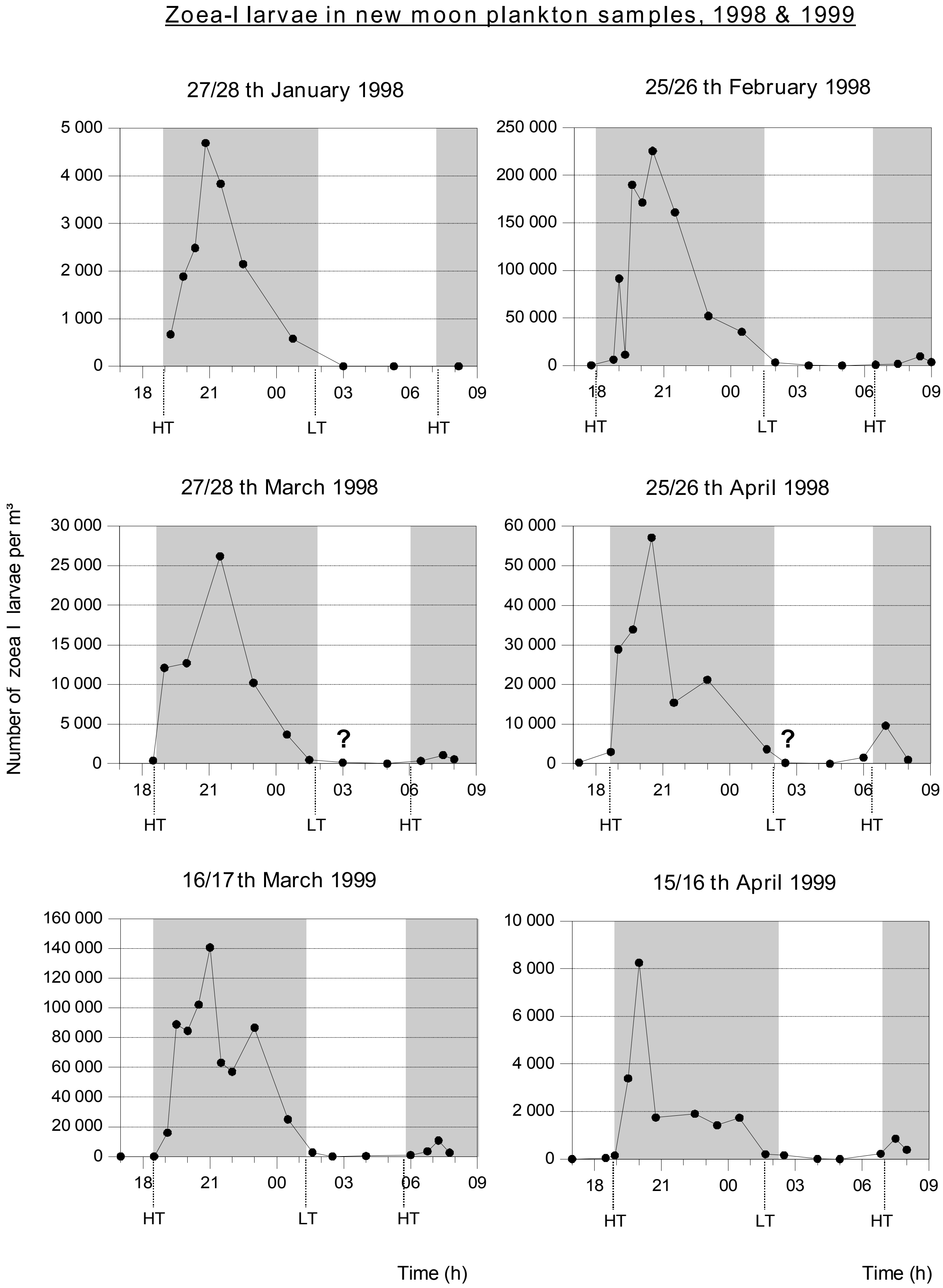


Fig. 16: Fluctuation in numbers of first zoeae after the larval release one day before new moon from January until April 1998 and March/April 1999.
Shaded areas: ebb tide; white areas: flood tide; HT: high tide; LT: low tide; ?: inaccurate measure due to clogged net.

slack high tide, whereas on some occasions they were already present shortly before the onset of the tidal change. Densities then rapidly increased and maximum values were always recorded within the first half of the ebb phase (Fig. 15 and 16). Thereafter larval abundance quickly dropped to low values towards the end of the ebb tide. During the consecutive flood phase densities remained low. After slack high tide in the morning numbers generally increased again. Morning peak densities were always distinctly lower than those of the preceding evening.

Differences in the overall course of the density curves become apparent when the spawning nights are compared on a finer temporal scale. The occurrence of peak densities varied between 30 minutes and 3 hours after high tide, and in February and April 1998 as well as in March 1999 more than one discrete peak in *U. cordatus* larval density was observed throughout the nocturnal ebb tide (Fig. 16).

3.3.2.4 Development time, seasonal and daily abundance of megalopae

Laboratory hatched first zoea developed to megalopa within 25 to 33 days (mean = 30.4 ± 2.3; n = 18). At Furo Grande megalopae were encountered in all three study years. Settlement phases were investigated in 1998, when a passive collector was installed. Between 11th March and 1rst of July - when the occurrence of megalopae was continuously monitored - four distinct settlement phases were determined, with peak numbers occurring around new moon (Fig. 17). At full moon megalopae were not encountered. In April 1998 they appeared from 8 days before until 4 days after new moon, which was the most prolonged settlement event, while the shortest (4 days) took place in June (Fig. 17). Numbers of megalopae were highest in March and April and distinctly lower in May and June.

The abundance of megalopae over subsequent days was also investigated in March and April 1999. Between last and first quarter moon daily plankton samples were taken shortly before nocturnal low tides, when the chance of encountering megalopae was high (3.3.2.5). Whereas in March megalopae were only encountered once (0.28 individuals per m^3 in the sample taken on the third day after new moon), in April 1999 they were observed from off the first sampling day at last quarter moon until two days after new moon. 88% of all megalopae occurred in the samples of the 15th and 16th with a maximum of 17.2 indiv./m^3 appearing on the 15th (Fig. 18).

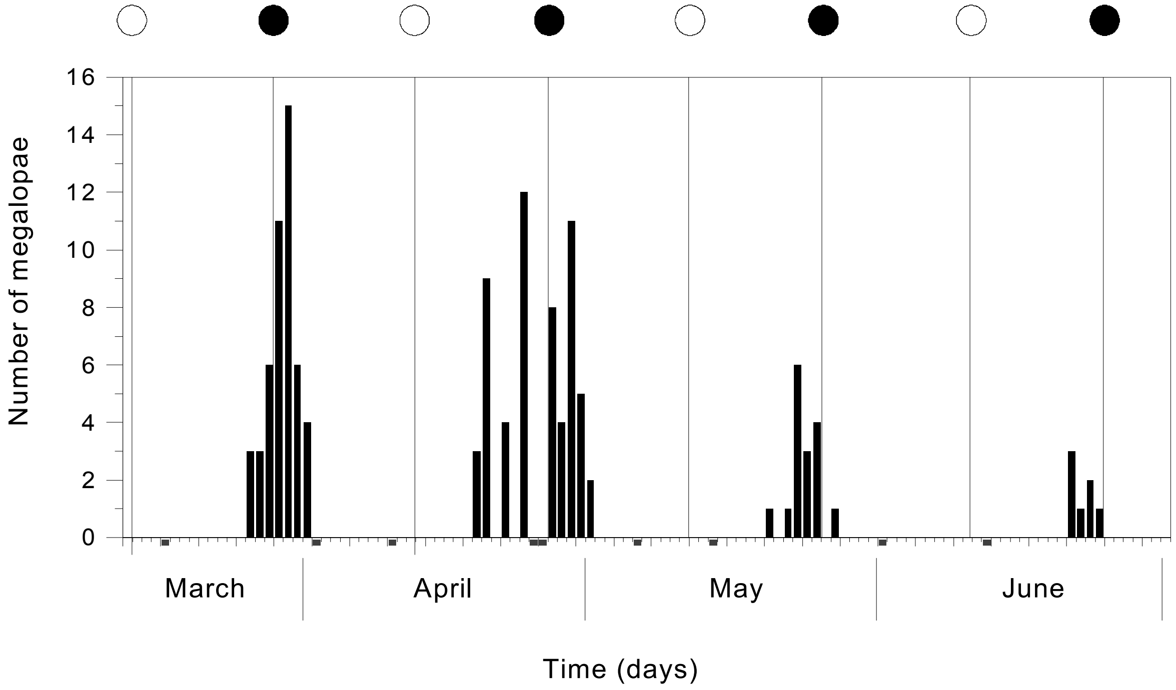


Fig. 17: Daily abundance of megalopae on artificial settlement substrate between 11 March and 1 July 1998.
Missing samples are indicated by dark fields between ticks of the x-axis. Black circle: New moon; White circle: Full moon

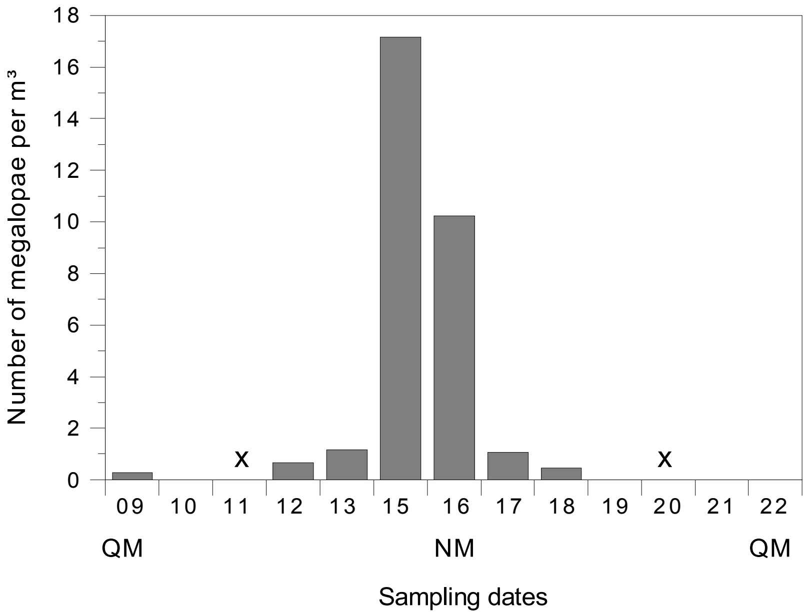


Fig. 18: Abundance of megalopae in net-samples from 9 to 22 April, 1999.
Samples were taken daily 60 to 45 minutes before nocturnal low tides.
QM: Quarter moon; NM: New moon; x: missing sample.

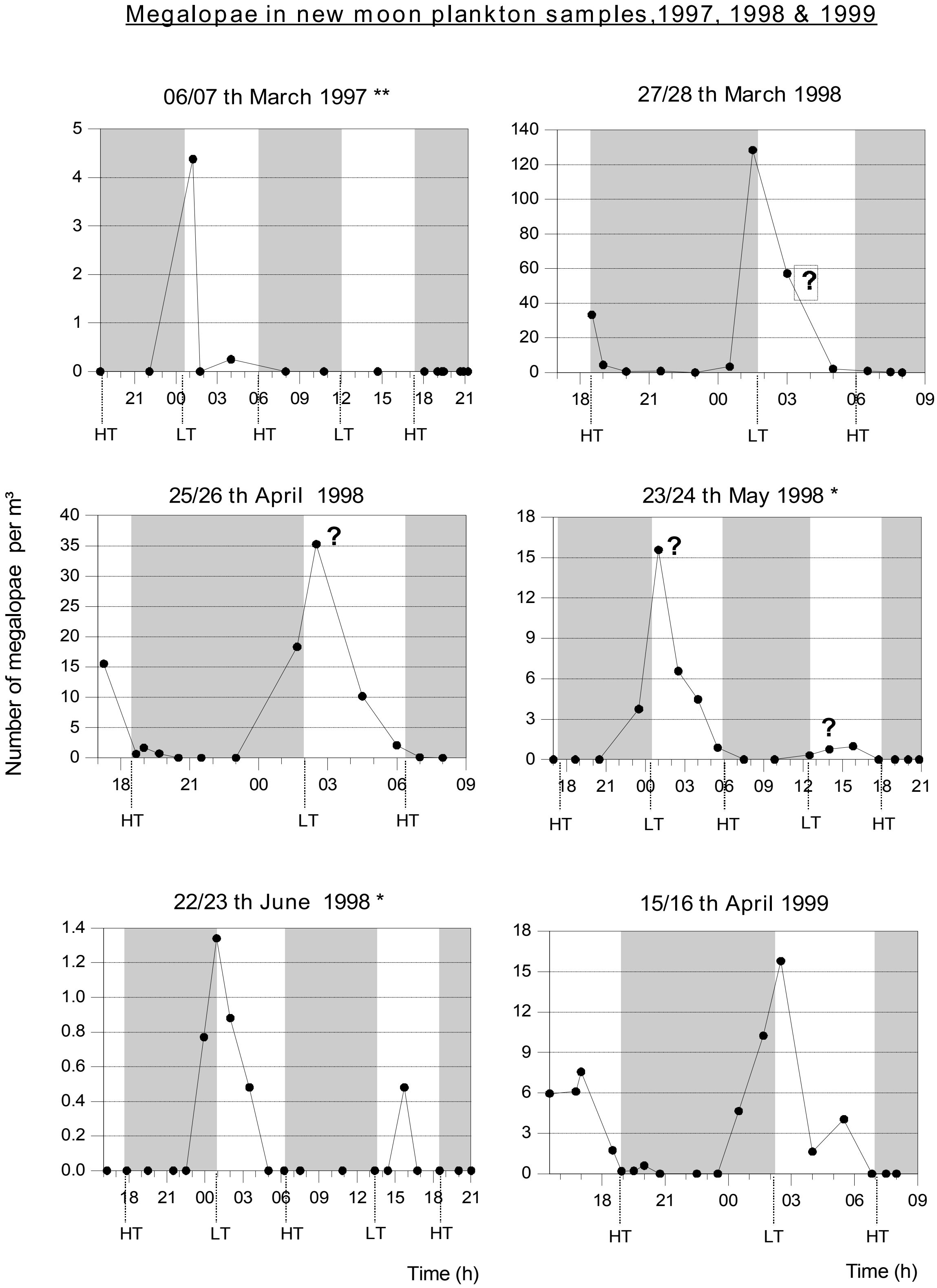


Fig. 19: Fluctuation in numbers of megalopae during new moon sampling occasions in March 1997, March to June 1998 and April 1999.

Sampling was started three (***), two (**) or one day (*) before new moon. Shaded areas: Ebb tide; white areas: Flood tide; HT: High tide; LT: Low tide; ?: unprecise value due to clogged net.

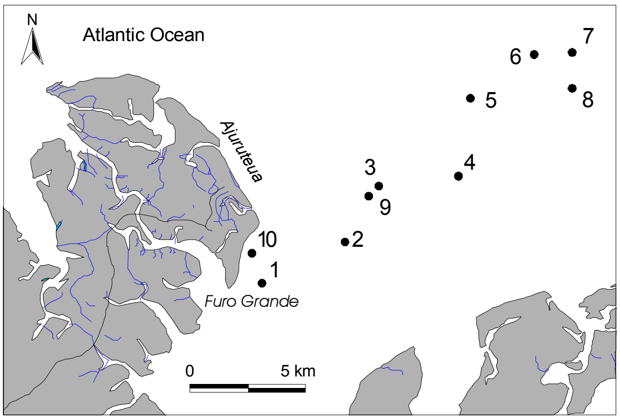
Beside the collector- and last to first quarter moon sampling in 1998 and 1999, the abundance of megalopae was investigated during the regular monthly plankton sampling program (3.2.2.1). As for the collector, no megalopae were encountered around full moons. In 1997 they were found in March, April and June. Of the altogether 74 new moon samples analysed for these three months, only 10 (14%) contained megalopae and observed monthly maximum densities were 4.36, 0.79 and 0.11, respectively. In 1998 megalopae were also recorded between March and June and were contained in 53% of all net-samples taken (n = 62). Maximum densities ranged between 128.33 indiv./m³ in March and 1.34 indiv./m³ in June (Fig. 19). In March 1999 no megalopae were found at the day of new moon sampling, but they were frequently encountered during the 18 hrs sampling in April (67% of 18 samples) and a maximum density of 15.78 indiv./m³ was recorded (Fig. 19).

3.3.2.5 Tidal pattern of megalopal abundance

The distribution of megalopae over subsequent tides showed a characteristic pattern. In Fig. 19 megalopal densities are presented for new moon sampling occasions with peak numbers exceeding 1.0 indiv./m³. First megalopae were generally encountered when sampling was commenced at flood tides in the afternoon. Values then distinctly dropped at the onset of ebb tide, when densities were low during all sampling dates. Towards the end of the nocturnal ebb phase a sharp increase in numbers always occurred and maximum densities were either observed at slack low tide or within the first hour of the subsequent flood tide. During the latter the quantification of megalopal numbers was occasionally hampered as the plankton net clogged with detritus at times of high water current velocities. During the remaining flood tide densities dropped until reaching values close to zero or zero shortly before the morning high tide and remained low throughout the subsequent ebb phase (Fig. 19, March 1997, May and June 1998). Only during the afternoon flood tide a distinct renewed rise in megalopal numbers occurred.

3.3.3 Larvae findings in offshore waters

Subsequent to the estuarine new moon plankton sampling during the night of the 25th/26th of April 1998 (Fig. 16), surface sampling was continued in offshore waters during the daytime of the 26th. Subsequent to the morning larval release recorded at Furo Grande one hour earlier (compare Fig. 16), the first sample (1) was taken at the mouth of the Rio Caeté Bay



Base map after CPRM & MADAM (G.Krause, K.Franke)

Site	Time	Tide	ZI / m^3	Meg./ m^3
1	9:12	LT	2843.62	0
2	9:40	LT	86.21	0.18
3	10:10	LT	610.93	0
4	10:51	LT	216.43	0
5	11:31	LT	136.72	0
6	12:25	HT	13.36	0
7	13:40	HT	0.79	1.04
8	14:11	HT	46.13	1.5
9	15:12	HT	8.65	0
10	16:00	HT	0	0.69

Fig. 20: Larvae findings at offshore sampling sites

at 9:00 during ebb tide and approximately 2800 first *U. cordatus* larvae were encountered per m^3. Zoea-I were also contained in all ebb- and floodtide samples that were taken further offshore until a distance of approximately 20 km off Ajuruteua beach. Densities ranged between 600 and less than one larvae per m^3 (Fig. 20). The last sample which was taken close to shore during flood tide at 16:00 did not contain any *U. cordatus* zoeae. In none of the samples *U. cordatus* zoeal stages other than the first were encountered.

Beside first zoeae, megalopae of *U. cordatus* were also present, and were primarily contained in the samples taken during flood tide at a distance of approximately 15 to 20 km offshore. In the sample taken close to shore in the Bay of Rio Caeté at 16:00 they were also encountered. Numbers ranged between 0.18 and 1.5 per m^3 (Fig. 20).

3.4 Discussion

3.4.1 Timing of reproduction and its implication for the dispersal of zoea larvae

Reproduction of *U. cordatus* in the Caeté Estuary is restricted to the rainy season, which was also reported from other regions of Brazil (Alves 1975, Alcântara-Filho 1978, Castro 1986, Nascimento 1993, Santarosa-Freire 1998) and is characteristic for many other terrestrial or semiterrestrial crab species (Henning 1975, Hicks 1985, Adiyodi 1988, Wolcott 1988, Diele 1993). During the three study years reproduction followed a strict lunar rhythm with both andança (mate searching) and spawning activities exclusively occurring around new moon [2]. In southern Brazil reproduction of *U. cordatus* is semilunar with major andança and spawning activities occurring at full moons (Santarosa-Freire 1998). In the mangrove estuary of the here presented study andança events were confined to a maximum duration of four days after new moon, and females fertilised, ovulated (extrusion of fertilised egg mass) and incubated their eggs highly synchronised. This again resulted in synchronous spawning events which occurred within a maximum of four days around the following new moon. Hence, a breeding cycle from mate searching, egg-fertilisation, embryogenesis to spawning of zoeae-larvae comprises approximately one lunar month.

During the monthly new moon larval release peak spawning activity always took place one day before new moon. Zoea larvae were expelled around slack high tides with maximum larval output occurring after the evening high tide. Synchronous spawning at spring high tides has also been described for numerous other estuarine brachyurans (see overview in De Coursey 1983, Forward Jr. 1987). The consequence of this precisely timed spawning is a rapid seaward transport of the newly released larvae due to favourable export conditions (Christy and Stancyk 1982, Christy 1982, Cronin 1982, De Vries et al. 1994, Zeng and Naylor 1996). This was also demonstrated in the current study. In the total of 309 analysed plankton samples taken within the Caeté estuary and up to 20 km off the coast only freshly hatched zoea-I larvae and megalopae of *U. cordatus* were encountered. In the tidal channel Furo Grande larval release was reflected by an abrupt increase in zoeal densities which occurred between 30 minutes and 2.5 hrs after high tide. Early abundance peaks were most likely related to major spawning activities occurring close to the plankton sampling site, whereas larvae that had been released at distant upstream locations pass the plankton

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[2] The author was recently informed that in contrast to 1997-1999, this year andança events occurred at both new and full moon in January and February (23.02.2000, pers. comm. R. Saraiva, I. Nordhaus).

sampling site at a later time. Likewise, occasionally recorded multiple peaks in larval abundance probably reflected the spatial heterogeneity in reproductive activities that had been observed for different forest locations during the post-andança crab sampling program (see below). As shown by the successive plankton sampling at Furo Grande during spawning nights, ebb tide currents washed the initially high zoeae numbers rapidly away from the inner estuary to coastal. The absence of later stage *U. cordatus* zoeae in plankton samples taken at Furo Grande around full and quarter moons indicates that during their further development zoeae remain outside the estuary. This result coincides with the study conducted in south Brazil (Santarosa-Freire 1998).

What is the adaptive significance of reproductive rhythms with exclusive spring high tide spawning and subsequent larval export such as observed in *U. cordatus*? Whereas first zoeae of *U. cordatus* appear to be relatively euryhalin (3.2.3), survival of later zoea stages is greatly reduced at salinity below 16 ‰ (Rodriguez 1982, cited after Santarosa-Freire 1998). Thus, osmotic stress due to highly varying and often low salinity of the estuarine environment during the rainy season may be a driving force for the evolution of an rapid export mechanism based on synchronous spawning at spring high (Anger et al.1994). In March 1998 salinity as low as 10 ‰ and 6 ‰ were observed at Furo Grande and approximately 15 km offshore, respectively, which suggests that larval development must take place in considerable distance (possibly > than 50 km) to shore. From numerous crab species with larval export strategy later stage larvae have been found to accumulate at 40 km to more than 100 km offshore (Smyth 1980, McConaugha 1988, Epifanio et al. 1989, Querioga 1996). An alternative strategy to zoeae export is the retention of larvae within the estuary, as in *Rhitropanopeus harisii*, which requires a high tolerance towards osmotic stress. Larvae remain near the parent habitat by endogenously controlled vertical migrations between inflowing and outflowing water masses (Cronin 1982).

The hypothesis of osmotic stress avoidance as a promoting factor for larval export cannot account for the observation that *U. cordatus* larvae are primarily released at dusk high tides. Preferential nocturnal larval release at spring high tides has also been reported from numerous other intertidal crabs (Forward 1987, Morgan 1990) and predation pressure has been suggested as another or a further promoter for the larval export strategy (Morgan 1987b, Morgan 1990). Planktivorous fish larvae and juveniles concentrate in estuaries (Robertson and Duke 1987, Robertson et al. 1988, Sasekumar et al. 1992, Baltz et al. 1993, Barletta-Bergan 1999) and can have considerable impact on plankton communities (Thayer et al. 1974, Bengtson 1984). Hence, export of larvae to coastal waters where the risk of fish predation is lower than in the inner estuary (Morgan 1987b, Morgan 1990) could be of selective advantage. As planktivory is greatest during day time (Morgan 1990), larval release at dusk or night minimises the risk of encountering predators until zoeae have dispersed downstream. Further support for the hypothesis of fish predation exerting adaptive pressure on estuarine brachyurans comes from the finding, that decapod zoeae of species with estuarine larval retention show better behavioural or morphological antipredatory adaptations than those that are exported to coastal waters (Morgan 1987b, Morgan 1990). Morgan demonstrated that long carapace spination is an effective mean for reducing the vulnerability to fish predation. Zoea larvae of *U. cordatus* are only short-spined and therefore probably relatively susceptible to predation (Santarosa-Freire 1998).

In summary, preferential spawning at nocturnal spring high tides such as in *U. cordatus* ensures the rapid transport of larvae away from the estuary which presumably reduces both physiological stress (von Hagen 1970, Saigusa 1981) and predator related mortality (Christy 1982, Christy and Stancyk 1982, Morgan 1987a, 1990, Morgan and Christy 1995). Most intertidal crab species release their larvae on maximum amplitude high spring tides (e.g. Saigusa and Hidaka 1978, Saigusa 1981, De Coursey 1983, Forward 1987, Morgan and Christy 1994) which, as in the Caeté estuary, usually occur just after full and new moon. Interestingly, the spawning rhythm of *U. cordatus* showed a clear peak a day before new moon when the tidal amplitude had not yet reached its maximum. As tidal currents are most pronounced in inlets from the ocean such as estuaries and bays and decline towards the open oceans (Nicholson 1959), it can be speculated that this spawning rhythm is advantageous for long distance export. Tidal currents one or two days before new moon obviously suffice to rapidly flush the larvae away from the estuary to coastal waters and maximum amplitude tides a few days later could promote a further export from near to distant offshore localities. However, the distance over which larvae of *U. cordatus* are exported off coast still remains to be determined.

Export incorporates the risk of larval loss through drift to unsuitable environments, as the potential for dispersal over a wide area is generally assumed to be high (Palmer and Strahtmann 1981, Botsford et al. 1989). On the other hand, long distance dispersal by coastal and oceanic currents in itself may also be an additional advantageous trait of the export versus retention strategy (Anger et al. 1994) due to the increased chance for colonising empty spaces (Underwood and Fairweather 1989). Along a coastline, dispersal of the pelagic larvae can result in the interconnection of discontinuous adult populations to a metapopulation. Each subpopulation contributes its larvae into the common larval pool and since recruits can come from distant places, local populations may be semi- or even entirely open (Hines 1986, Roughgarden and Iwasa 1986, Harrison and Quinn 1989). As for other exploited populations under concern (e.g. *Cancer magister*, McConnaughey et al. 1992; *Callinectes sapidus*, Olmi and Orth 1995), a possible dependence of *U. cordatus* in the Caeté estuary on larval input from other coastal regions would have important implications for management and protection plans (see chapter 6). It is also possible, that oceanographic features as eddies withhold water masses (and larvae) in the region and thereby allow the population to be self-sustaining (Caddy 1989). Obviously, the determination of offshore larval dispersal as a function of season and region is an important factor in understanding the dynamics of a population (Botsford et al. 1994) and transport and re-invasion of *U. cordatus* larvae will be further investigated during the second phase of the MADAM project.

3.4.2 Within- and between-year differences in breeding activities and larval output

For the determination of reproductive activities three methods were simultaneously applied. Intensity of andança was qualitatively classified after the amount of involved crabs. Subsequent post-andança sampling indicated the proportional numbers of egg-carrying females, and by sampling the plankton during spawning times densities of newly released larvae were investigated. The complementary results obtained by the use of different methods indicate high reproductive intensities during the first- and low intensities during the second half of the rainy season. The latter remain hidden when reproduction is solely estimated by andança activities. In May (1998) and June (1997 and 1998) very low densities of newly spawned zoea larvae were still encountered in the tidal channel Furo Grande, although no preceding andança events had been observed. Thus, the most reliable method for determining the length of the breeding season proved to be plankton sampling.

In the Caeté estuary each rainy season was characterised by a distinct peak in reproduction when highest andança activities were recorded. This peak was followed by subsequent high numbers of ovigerous females and high larval densities at new moon one month later. For example during the peak spawning month in February 1998 up to 225350 zoeae/m^3 were recorded, whereas in January and March no more than 4690 and 26186 larvae per m^3 were found. This highly uneven distribution of reproductive activity over the course of the rainy season indicates, that most females only spawn once per year. Larval release outside the peak month may have been caused by a minority of "unsynchronised" females or by multiple spawners. Evidence that some females may release larvae more than once per breeding season is given by the smaller secondary peak which was observed in April 1998 (57100 indiv./m^3) and thus two months after the maximum larval output had occurred in that year. A large decline in numbers of spawned larvae at the new moon in-between these two months suggests, that females do not ovulate over two consecutive months. A similar pattern was also observed in 1997 when a small renewed rise in larval densities was recorded again two months after the high larval output in March.

Direct information on the number of egg clutches that females produce throughout the reproductive season and the proportion of multiple spawners could unfortunately not be determined, as the recapture rate of tagged crabs during the post-andança sampling in 1998 was very low (< 1%). It is possible that the latter was caused by "escape" of the tagged crabs to more distant areas as a result of the disturbance they had faced during previous handling. On the other hand, a month later the same sampling areas were repopulated by unmarked crabs which points to a relatively high mobility of *U. cordatus* (see 5.3.1.1), irrespective of handling effects.

Throughout the post-andança sampling, larger within-month variations in the relative abundance of ovigerous females were recorded for the different sampling locations. Biotic or abiotic factors that have accounted for these small-scale variations in timing of reproduction are unknown.

Reproductive activity during the three study years showed considerable inter-annual differences. Reproductive peaks occurred in different months of the rainy season: In 1997 and 1999 highest andança activities were observed after new moon in February and in 1998 after new moon in January. In contrast to the rainy season in 1997 and 1999, new moon in 1998 fell into the last week of the month, and this may possibly have accounted for the observed advanced peak andança in January. If this hypothesis is true, in 2001 – when new moon as in 1998 falls into the last week of the month – the peak andança event will again occur in January, whereas for 2000 and 2002 the same timing as in 1997 and 1999 is expected (peak in February). This prediction will be tested during the second phase of the MADAM project in which reproduction of the *U. cordatus* population in the Caeté estuary will be monitored until 2002 [3].

As it is generally assumed that precise timing of reproduction is critical for the survival of the young (McConaugha et al. 1983, Adiyodi 1988, Morgan and Christy 1994) it has to be questioned in what regard the advanced peak andança in January and subsequent early larval release in February 1998 could be advantageous. The present study indicates, that megalopae re-invade the estuarine environment approximately three to four weeks after hatching and moulted to first crab instar within 10 days after they had been captured. Thus, if peak spawning in 1998 had only occurred at new moon at the end of March instead of in February, subsequent high numbers of first crabs would have appeared at the end of April

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[3] The prediction for the current year seems to be correct: According to recently received information major andança activities occurred in February and not in January (pers. comm. 23.02.2000 R.Saraiva, I. Nordhaus). However, mate searching was now semi-lunar which stresses the need for continuous monitoring of reproductive timing if determining factors are to be understood.

and in the beginning of May which is relatively late in the rainy season. In May, precipitation rates are generally distinctly lower and temperatures correspondingly higher than during the preceding months of the rainy season and these conditions are possibly disadvantageous for the young when they settle in the mangrove forest. Most land crabs are rather poorly adapted to desiccation stress (Wolcott 1988) which should be especially true for the first crab stages due to their larger body-surface area. Therefore, by advancing peak reproductive activity in years with new moon occurring late in the month, first crabs would still encounter presumably favourable climatic conditions. However, after the peak spawning in February 1998 larvae were still released at new moon until June. Thus, if survival of the young crabs is higher during typical rainy season conditions, the question arises why zoea larvae, even though in significantly lower numbers, are spawned until the beginning of the dry season. Obviously, at the present stage of knowledge no satisfactory conclusion concerning the adaptive significance of advanced peak spawning can be drawn. Studies on the survival rates of zoeae, megalopae and first crabs stages under varying conditions are required to gain further insight into environmental constraints.

Inter-annual differences in reproduction also become apparent when larval output is quantitatively compared. In 1998 larval densities were generally higher than in the corresponding reproductive cycles sampled in 1997 and 1999. This is particularly true for the larval output recorded after preceding peak andanças where larval densities in 1998 were threefold higher than in 1997, whereas in 1999 values were intermediate. It has to be noted that despite these large differences in numbers of spawned larvae, approximately same proportions of ovigerous females were captured after the preceding peak andança in 1997 and 1998. It is presumed that insufficient spatial sampling of the female population may have been responsible for this dissimilarity. Plankton sampling during spawning times clearly provides more reliable data as the outflowing water masses pass through a very large catchment area before being sampled. However, it remains open, why the post-andança female sampling reflected low and high reproductive activities within years, whereas interannual fluctuations remain hidden.

What factors could account for the observed differences in annual larval output? A correlation between varying reproductive output and climatic factors – as for example precipitation – was not observed. Both 1997 ("low larval output") and 1998 ("high larval output") were – possibly due to El Ni☆o – relatively dry years, whereas 1999 ("intermediate larval output") was characterised by higher precipitation. As reproduction affords considerable energetic costs it can be suggested that annual differences in reproductive activities may be caused by variations in food quality or quantity and thus nutrient uptake. In the case of *U. cordatus* this would implicate variations in nutrimental composition and amount of litter fall of mangrove leafs. For the latter, throughout 1996 until 1999 no significant differences have been observed that could explain the annual variations in reproduction of *U. cordatus* (Mehlig, in prep.). Similar long-term studies on the nutritional content of mangrove leafs have not been conducted and whether this factor could have accounted for the variation in annual larval output remains open.

In an exploited population, variations in reproductive output may also be related to the impact of fishery. However, it seems most unlikely that this is the case for the *U. cordatus* population of the Caeté peninsula. Females are only occasionally captured and males are probably mature and able to participate in reproduction well before they reach commercial size (4.3.3) (Alves 1975, Nascimento 1993). Therefore, the reproductive potential of the population is considered to be relatively unaffected by the present state of exploitation.

Larval output of the *U. cordatus* population in the Caeté estuary appears high when compared to the only other study so far available. Whereas at Furo Grande peak numbers of up to 225350 first zoeae per m^3 were recorded, a maximum of only ca. 6700 indiv./m^3 was observed at sampling sites with large catchment areas in the Bay of Paranaguá in southern Brazil (Paraná State) (Santarosa-Freire 1998). However, a detailed comparison of these two studies is not possible due to different sampling designs. The here presented investigation has shown how important it is to delineate the larval release rhythm over subsequent days within monthly spawning cycles, as zoea output strongly fluctuates in a characteristic pattern. Furthermore, in order to match peak larval numbers, sampling has to be conducted in short time intervals during the first hours after larval release. If these prerequisites are not given, a comparison of larval output within and between seasons as well as for different regions remains difficult.

3.4.3 Size-frequency distribution of ovigerous females

The smallest female found with eggs had a carapace width of 3.1 cm (2.5 cm carapace length) which is distinctly below the size of onset of maturity recorded from other locations. Nascimento (1993) reports that in Sergipe females mature at a size of 3.4 cm carapace length, which corresponds to ca. 4.4 cm carapace width. With 3.0 cm carapace length (ca 3.9 cm width) males matured at a similar size as females. Alves (1975) analysed gonads of *U. cordatus* in Ceará. She recorded a carapace length of 3.5 cm (ca. 4.6 cm carapace width) in females and 3.7 cm (ca. 4.8 cm width) in males at size of sexual maturity. Whether the observed differences for sexual maturity between the population in the Caeté estuary and other regions relate to true regional differences or sampling bias (due to smaller sample size in other studies) is unclear.

According to growth increment experiments (chapter 4) a female body size of 3.1 cm carapace width corresponds to an age of approximately 2.1 to 3.0 years, whereas the largest egg-carrying female with a carapace width of 7.2 cm is more than 10 years old. It is remarkable that the highest proportion of ovigerous females was recorded in the size class of 6.5-7.0 cm and thus for relatively old crabs. Alcântara-Filho (1978) found the majority of ovigerous females within an approximately centimetre smaller size class (ca 5.5 to 5.9 cm carapace width, converted from carapace length data). The peak in abundance for larger ovigerous females in the current study cannot be related to sized biased sampling. Although small females (< 4 cm) are generally more difficult to catch, it seems unlikely that capture efficiency for ovigerous females versus non-ovigerous females within a given size class is different for large and small crabs. Furthermore, females with a carapace width of 5.5-6.0 cm were most frequently captured but distinctly less carried eggs than those a size class above. Hence, the results point to an overall higher reproductive activity of large females. This is also true in regard to egg-numbers, which increase with body size (64000 at sexual maturation and 195000 at ca. 6.3 cm carapace width) as was shown by Alves (1975). Thus, in reproductive terms large females are specifically valuable should be considered for the planning of size specific capture limitations. In the Caeté estuary *U. cordatus* females are relatively unaffected by fishery. Due to their larger chelae, male crabs are preferably captured by professional crab collectors for livestock sale on local markets and industrial meat extraction (5.1.2). Females are primarily harvested by unprofessional people during andança times, who collect both sexes for private consumption, again with preference for larger males. However, since 1997 female collection for all size classes is prohibited by law.

3.4.4 Timing of estuarine re-invasion by megalopae

Settlement phases and duration of larval development The present study is the first to show the occurrence of *U. cordatus* megalopae in the field. Monitoring of daily abundance on artificial settlement substrate over a time series of 3.5 months revealed, that megalopae re-invade the inner estuary in distinct monthly settlement phases around new moon. The observed timing and periodicity of re-invasion is a function of the highly synchronised larval release by the females in conjunction with the duration of subsequent larval development.

Information on development time from first zoea to megalopa stage was derived from 18 laboratory reared specimens that had survived despite the overall high mortality caused by sub-optimal rearing conditions. Hence, it can be argued that the data are little reliable and that the observed development time of 25 to 33 days may be significantly shorter under optimal environmental conditions. However, the time when zoeae moulted to megalopae in the laboratory coincided well with the distinct monthly settlement periods of megalopae recorded in the field. As on the other hand it is unlikely that larvae in the field developed at a rate twice as slow as those reared under inappropriate laboratory conditions (3.2.3), it is concluded that they had been released during spawning events of the previous month and not the one 8 weeks earlier. The possibility of the latter had originally been taken into account due to the laboratory studies of Rodriguez (1982, cited after Santarosa-Freire 1998), who recorded a highly variable development time of 43 to 69 days from first *U. cordatus* zoeae until megalopa. Simultaneous field investigations on megalopal occurrence were not undertaken.

As a result of the complementary field monitoring and laboratory rearing of *U. cordatus* megalopae conducted in the current study, the length of a reproductive cycle from andança over spawning to subsequent megalopal appearance is now known to comprise approximately 7 to 9 weeks in the Caeté estuary.

Occurrence and periodicity of megalopal settlement phases were successfully determined with the collector, but the information on relative post-larval abundance has to be critically regarded. A large discrepancy becomes visible, when the collector data are compared with the megalopal abundance determined by plankton sampling. Highest numbers of megalopae with up to 128 individuals per m³ were observed in the plankton sample taken shortly before nocturnal slack low tide on 27/28th of March 1998. A month later the respective plankton sample of the 25/26th of April only contained approximately 18 megalopae per m³. These large differences in monthly post-larval abundance were not adequately reflected by the respective collector samples where almost same numbers had settled on the artificial substrate (11 megalopae on the 27/28th of March, 8 megalopae on the 25/26th of April). It has to be considered that the collector was retrieved around diurnal slack high tides, which possibly explains the overall low number of megalopae clinging to the substrate. It is thinkable that many megalopae leave the collector during times of low current velocities to forage in the water column and possibly sink to the bottom at slack high tide (see below). However, this hypothesis could not be tested as it was impossible to retrieve the collector at high current velocities. On the other hand, low and high numbers in settled megalopae throughout respective settlement phases do suggest some correlation between daily abundance and settlement rate at the time of collector retrieval.

Whereas specific sampling dates for adequate zoea I sampling could be determined according to the observed spawning pattern with peak larval release one night before new moon, it proved to be difficult to sample megalopae in a way which allows a comparison of abundance in different months. Unlike first zoea larvae, the precise day of monthly peak megalopal abundance can hardly be predicted as it may depend on a variety of environmental factors (e.g. distance over which larvae were transported, possible variations in development time). Thus, in 1998 when plankton sampling was confined to the regular new moon sampling program it cannot be excluded that peak megalopal densities occurred at days other than the sampling date. In March and April 1999 this problem was addressed by taking plankton samples before nocturnal low tides over a time span of 13 days around new moon. In this way, monthly peaks of megalopal abundance can be accurately determined.

Abundance of megalopae over tidal cycles Throughout the new moon plankton sampling occasions megalopae were primarily found in the samples taken during the second half of the low tide phase and during flood tide. The latter corresponds to the typical pattern of megalopal re-invasion in zoea larvae exporting species, where - beside wind-driven surface water transport - flood tide currents carry post-larvae from coastal waters back to estuaries (e.g. Epifanio et al. 1984, Brookins and Epifanio 1985, Olmi 1994, Tankersly and Forward Jr. 1994). The finding of high numbers of *U. cordatus* megalopae towards the end of the ebb phase with a peak occurring at slack low tide calls for special attention. The sudden increase in abundance at times with slow or no current can clearly not be related to a sudden import of larvae from coastal waters. These larvae must have already been inside the estuary since at least the preceding flood tide and obviously have managed to avoid a renewed export from the tidal channel to coastal waters during times of strong ebb tide currents. Downstream transport could be prevented by dropping out of the water column to the bottom substrate prior to or during ebb tide, as was suggested for megalopae of *Callinectes sapidus* (Epifanio et al. 1984, Olmi 1994). This is also assumed for *U. cordatus* megalopae. In the laboratory they showed a high thigmokinesis and regularly clung to small pieces of dead wood when these were added to the rearing container. When mud was offered they build tiny burrows into which they retreated. On the muddy bottom of Furo Grande with abundant wooden logs such behaviour would allow the prevention of downstream transport during strong ebb tide currents. When current velocities cease, the potential for export is reduced and megalopae can forage in the water column without being washed away over larger distances. With subsequent flood currents they may be transported into estuarine localities further upstream. The above described scenario rises the question, why megalopae are not encountered in high abundance during slack water at high tide. On the one hand, if megalopae distribute homogeneously throughout the water column, this can be due to a "dilution-effect" resulting from the approximately 5 m higher water level at slack high tide when compared to slack low tide. On the other hand it is possible that megalopae have already descended to the bottom at slack high tide. An indication for how fast megalopae can drop out of the water column is given by the investigations of Sulkin and Van Heukelem (1982) on *Callinectes sapidus*, where passive sinking occurred at a mean rate of 1.8 cm per second. However, the database of the current study does not yet allow a full understanding of the mechanisms underlying estuarine re-invasion by *U. cordatus* megalopae. Basing upon the now available knowledge on the periodicity of megalopal settlement phases, further studies concentrating upon the temporal and spatial distribution of post-larvae within the water column can be designed to delineate the pattern of transport from coastal to estuarine waters and upstream transport within estuaries.

4 GROWTH

4.1 Introduction

The growth rate of a species is an important aspect of its biology and life history. In crustaceans growth is a function of size increment at each moult and moulting frequency, two factors that can vary with size and sex (Hartnoll 1982). For a determination of the relationship between age and size it is therefore necessary to study a wide range of specimens of both sexes. In commercially exploited species such as *U. cordatus* knowledge upon the growth rate is essential for resource evaluation and management because of the influence growth has on the way a stock responds to fishery (Fletcher et al. 1990). Despite its economical importance, information upon growth of *U. cordatus* is very limited. Geraldes and de Claventi (1983) who studied five later juveniles in the laboratory over few moults observed very small growth increments and assumed that *U. cordatus* needs 10 years to reach commercial size. Correspondingly, in their laboratory investigation upon the culture potential of male crabs, Ostrensky et al. (1995) extrapolated that *U. cordatus* would require 6 to 11 years to reach market size. Unfortunately, none of the above studies indicated what size "market-sized" specimens in their study areas are. In Bragança mean market size of males was shown to be 7.3 cm carapace width (5.3.2). Local consumers as well as crab collectors believe that these specimens are not older than two or three years as otherwise - according to them - fishery would have already depleted the crab population in the Caeté area. On the other hand crab collectors contradict themselves by reporting that moulting crabs do not increase much in size and they say that larger specimens only moult once per year during the dry season. This statement is confirmed by Nascimento (1993) who indicates that moulting is annual in crabs > 3cm carapace width and is confined to the dry season. Seasonal moulting in *U. cordatus* has also been described by many other authors (see Nascimento 1993 for review).

The presently available information upon growth in *U. cordatus* does not yet allow to determine the relationship between age and size as only few individuals within a very small range of size have been investigated (Geraldes and de Calventi 1983, Ostrensky et al.1995). The low growth increments that were determined in the laboratory may not adequately reflect growth of free-living specimens. However, determining growth in the field is complicated by the fact that exterior marks for identifying crabs are lost with the old exoskeleton.

The aim of the here presented study was to determine growth increments in males and females for a wide range of different sized specimens in order to develop growth curves and size at age estimates. Crabs measuring between 0.15 and 8.2 cm carapace width were included into the study. Growth in later juveniles and adult crabs was investigated for specimens kept under quasi-natural conditions in a field enclosure. Due to the difficulty in recovering crabs of small size, early juvenile growth until an age of six months was determined in the laboratory.

4.2 Methods

4.2.1 Laboratory studies on early juvenile growth

Field-captured megalopae were individually reared to crab in plastic containers with 100 ml unfiltered ambient estuarine water and small clumps of sediment. Whether moulting to crab stage had occurred was checked daily. One day after the moult, when the new integument had sufficiently hardened, the width of the carapace was measured under a Zeiss stereo microscope. A convenient method for measuring the highly agile small crabs was to set them in the centre of a water-drop whose cohesion kept them in position. Sex could not be determined for living specimens due to the small body size. After measurement of the initial size, crabs were held individually in 500 ml plastic containers. One half of the container was filled with sediment, the other half with ambient estuarine water. Shredded particles of *R. mangle* leaves were placed on the sediment surface. The rearing containers were held under ambient light and temperature conditions in a shaded outdoor laboratory. Water was replaced every second day and approximately every second week the sediment was changed and growth increment of the crabs measured. In order to reduce handling induced mortality, care was taken that crabs were not separated from the sediment (by sieving) when they were soft-shelled. A day before handling, burrow entrances were covered with a thin sediment layer. When crabs had not removed this layer until a day later, sieving was postponed until the sediment surface showed marks of crab activity. Animals were transposed to a 10 l bucket containing larger quantities of sediment and water after they had reached a carapace width of about 3 mm. Crabs were reared up to an age of approximately six months.

4.2.2 Field studies on later juvenile and adult growth

In order to measure growth increment of crabs in the field, plugged moulting burrows of larger specimens were excavated (n = 125) and searched for newly moulted crabs and their exuvia. If at all, only small fragments of the old exoskeleton were found, but in five cases the former carapace width could be reconstructed.

Due to the low success of the above approach, in 1997, 1998 and 1999 a capture-recapture experiment under quasi-natural field conditions was conducted in which growth for crabs with a carapace width > 2.0 cm was investigated. Tagged animals (see below) and controls were held in 100 m² enclosures in the mangrove forest. Prior to the capture-recapture experiment, all former inhabitants were removed from the enclosed area. The enclosures were then stocked at about natural densities with both male and female crabs. Only crabs of specific size classes were selected, thus creating artificial cohorts.

For the experiment it was important to inhibit escape of the experimental crabs on the one hand and immigration of foreign crabs into the enclosure on the other. As *U. cordatus* builds its burrows to a depth of up to 1.8 m and also is a capable climber, the enclosure walls were erected until 1.5m above ground and as deep as possible (1.0 – 1.2 m) below ground. For the growth studies in 1997 and 1998 an enclosure consisting of wooden logs was constructed, but subsequent crab emigration and immigration rates indicated, that neighbouring wooden logs did not seal sufficiently well below ground. Therefore, in 1999 another enclosure consisting of tightly interlocking plastic laths was built (Fig. 21), which considerably reduced crab migrations. In order to allow tidal water flow, numerous holes (1.0 and 1.5 cm diameter) were drilled into the walls both beneath and above the sediment surface. The enclosure was subdivided into a 75 m² compartment for larger crabs and two 12.5 m² parts, where smaller crabs were held.

Fig. 21: Field enclosure for capture-recapture growth study.

As a complete prevention of crab migrations to and out of the enclosures was unachievable, the experimental cohort crabs were additionally tagged which allowed to distinguish them from immigrants. Two methods were applied. During the first two years of the study animals were heatbranded on the anterolateral part of the cephalothorax (1997) or on the carpus of the chelipeds (1998). The contact heat destroys the chromatophores located in the epidermal/dermal layer of the carapace and leaves a white field. Branding was performed with a soldering iron for approximately 5 seconds. This technique was very successful for crabs between 2.0 and 3.5 cm carapace width, whereas many larger crabs did not carry the mark after they had moulted. Contrarily, in the coconut crab *Birgus latro* (Fletcher et al. 1989 and 1990) heatbranding was successful over a wide range of size classes.

In 1999 small crabs were continued to be heatbranded, whereas animals from off a carapace width of 5.0 cm were now individually marked by implanting passive integrated transponder (PIT) tags into the ventral basis of the merus of the third pereiopod. The leg was not shed during or after injection of the tag and the wound healed within two weeks (as observed in 25 test animals housed in the laboratory until 6 weeks after marking). The PIT tag (Trovan ID 100, AEG / Telefunken) consists of a glass-encapsulated cylinder measuring 2.2 mm in diameter and 11 mm in length and is injected with a pre-sterilised needle using a Trovan hand injector. The tag has an operating frequency of 128 kHz and provides an unique 12-digit code when energised by a 128 kHz external power source provided by the Trovan LID 500 hand-held reader exciter (maximum reading distance 16 cm). PIT tags have also been successfully applied for monitoring growth in other crustaceans (*Macrobrachium rosenbergii* and *Cancer magister*, Prentice 1990; *Paralithodes camtschaticus*, Donaldson et al. 1992, Pengilly and Watson 1994).

The time schedule for the capture-recapture experiments was as follows: Between April and end of May the pre-emptied enclosure was stocked with new crabs. Animals were tagged and released within two days after their first collection from elsewhere forest locations. In 1997 and 1998 time at free ranged between four and five months as recapture was conducted in September. In 1998 re-collected small crabs (up to 4.5 cm carapace width) were again released and recaptured in December. In 1999 smaller crabs were collected in August, whereas larger crabs were recaptured in the end of October. Carapace width of both released and recaptured crabs and thus increase in size was measured with a calliper rule to the nearest 0.1 mm. Each year, a new set of cohort crabs was used in order to exclude possible long-term effects of captivity on growth.

4.2.3 Age at size estimates

The von Bertalanffy growth function (von Bertalanffy 1934; Ricker 1975) was used for describing the growth of the crabs:

$$L_t = L_0 (1 - e^{-K(t - to)})$$

where L_t is length at time t, t_0 is the age at zero length, L_0 is the maximum asymptotic length and K is the curving parameter for the growth function. t_0 was set to -0.08 as development from spawning to juvenile moult encompasses approximately 1 month (3.3.2.4). The remaining parameters were calculated from individual growth increment data using the Munro-Plot (Munro 1982):

$$K_{(t_{i+1} - ti)} = \ln (L_0 - L_i) - \ln (L_0 - L_{i+1})$$

where L_i and L_{i+1} are the lengths at time t_i and t_{i+1} and K and L_0 are as described above. The optimum parameter combinations were obtained by varying L_0 until the coefficient of variation for the K value was minimised. The analyses was undertaken using the computer package FiSAT (Gayanilo et al. 1994). Calculations were made separately for the two sexes.

For comparision of growth of the studied *U. cordatus* population with that of other populations or crab species, the growth performance of males and females was calculated by Munros Ø´ (Pauly and Munro 1984; Sparre and Venema. 1989):

$$Ø' = \ln K + 2 \ln L_0$$

where K and L_0 are parameters derived from the von Bertalanffy growth equation.

4.3 Results

4.3.1 Early juvenile growth

Moult and behaviour Megalopae (Fig. 22) built small burrows in the sediment clump into which they retreated when not foraging in the water column of the rearing container. Within 3 to 8 days after their collection they moulted to crab (n = 209) (Fig. 22). Shedding the old integument took between 6 and 10 minutes (n = 17). Mortality during moulting to first crab instar and within 24 hours thereafter was 7.5% (n = 160) and decreased to 0.7% during the following 24 hours. Within the first two weeks after the juvenile moult, crabs built the entrances of their burrows in the sediment layer at or just above the water surface. From off the third week, burrow entrances were constructed in more elevated areas. Crabs were only little active above ground during the first four months of life and did not consume the shredded leaf particles offered on the sediment surface. Instead, they fed upon infauna as for example polychaets, which was directly observed when crabs were separated from the sediment by sieving. From off an age of four months they began to consume some leaf material.

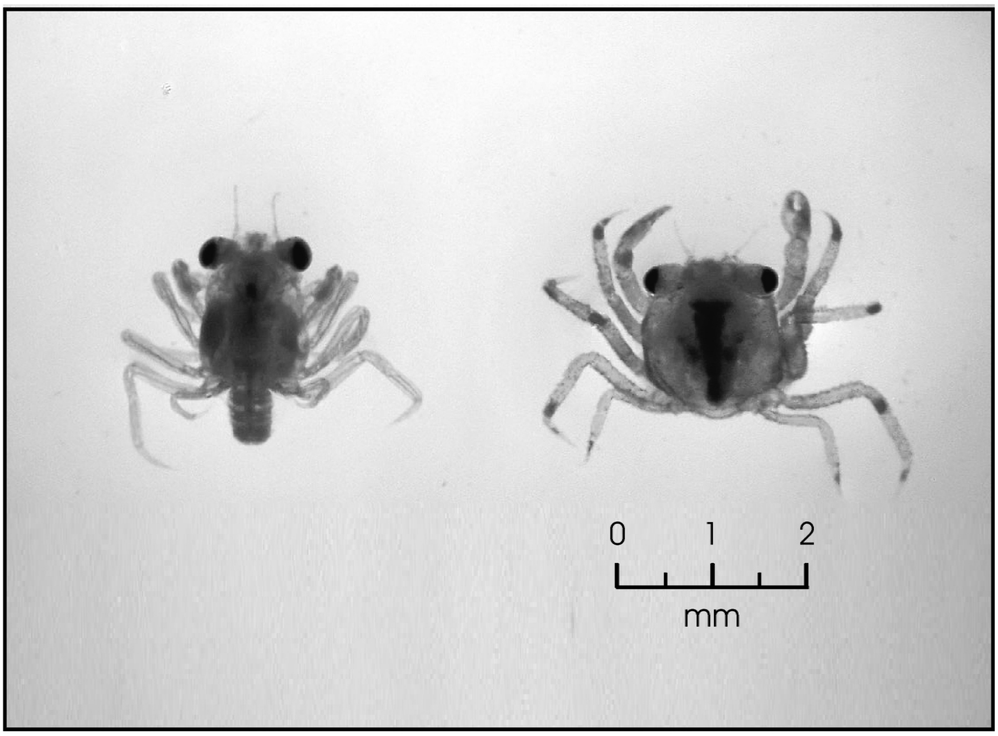


Fig. 22: Megalopa and first instar crab of *U. cordatus*.

Size at age, moulting frequency and growth increment Carapace width at first instar was measured for 223 crabs. Mean crab size was 1.51 mm ± 0.095 and maximum and minimum carapace width 1.20 mm and 1.71 mm, respectively. Crabs of this size were never encountered in the field. Despite extensive search in various habitats only one early juvenile specimen with a carapace width of 2.56 mm was captured.

Fig. 23 demonstrates individual growth series of seven crabs reared in the laboratory in 1998 from first instar (day of juvenile moulting defined as age 0) to an age of ca. 16 to 28 weeks. Crabs moulted during each approximately biweekly measurement interval until they were 5.5 to 6 weeks old. Thereafter moulting frequency decreased as indicated by occasional size constancy at subsequent measurements. At 10 to 11 weeks crabs had reached a carapace width of 3.7 to 4.6 mm. The variation in size increased with age and approximately six months old animals (28 weeks) ranged between 7.8 to 11.5mm carapace width (n = 4) (Fig. 23).

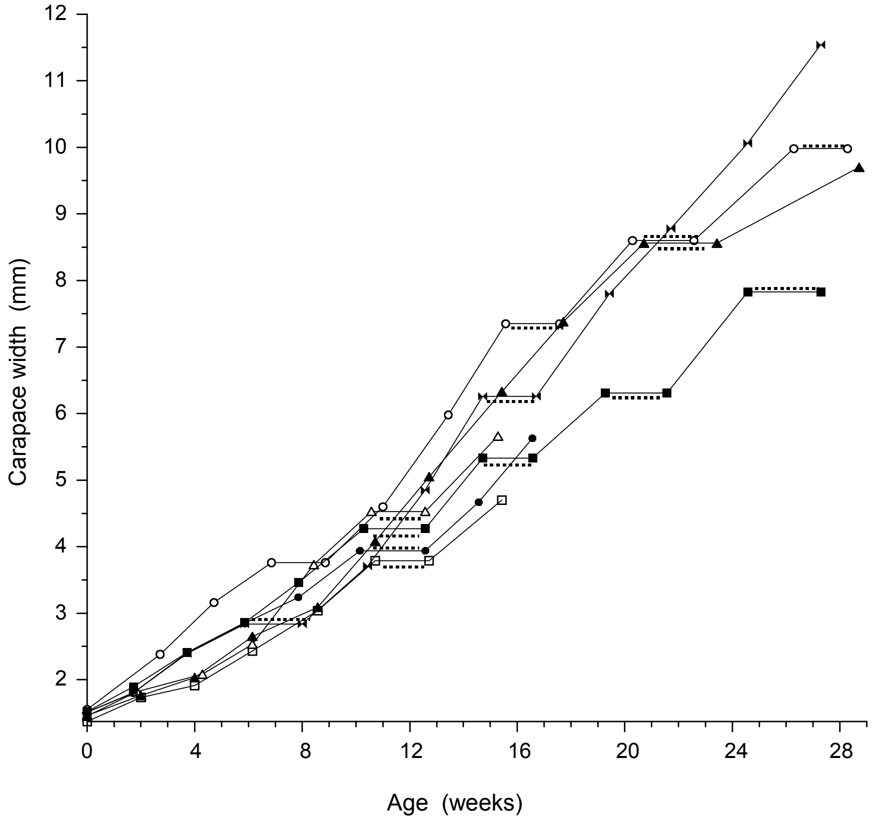


Fig. 23: Growth series of early juveniles (n = 7) reared in the laboratory in 1998 from first instar stage (day of juvenile moult = age 0) up to an age of approximately 16 to 28 weeks. Broken lines highlight zero growth between two measurements.

Growth increment between subsequent measurements is plotted in Fig. 24. Relative maximum and minimum size increments were 47.4% and 10.4% with a mean of 22.57 ± 6.75%. Percent growth increment decreased significantly with increasing size (r = 0.376, P<0.01), while absolute growth per sampling interval enhanced with size (r = 0.841, P<0.0001) (Fig. 24).

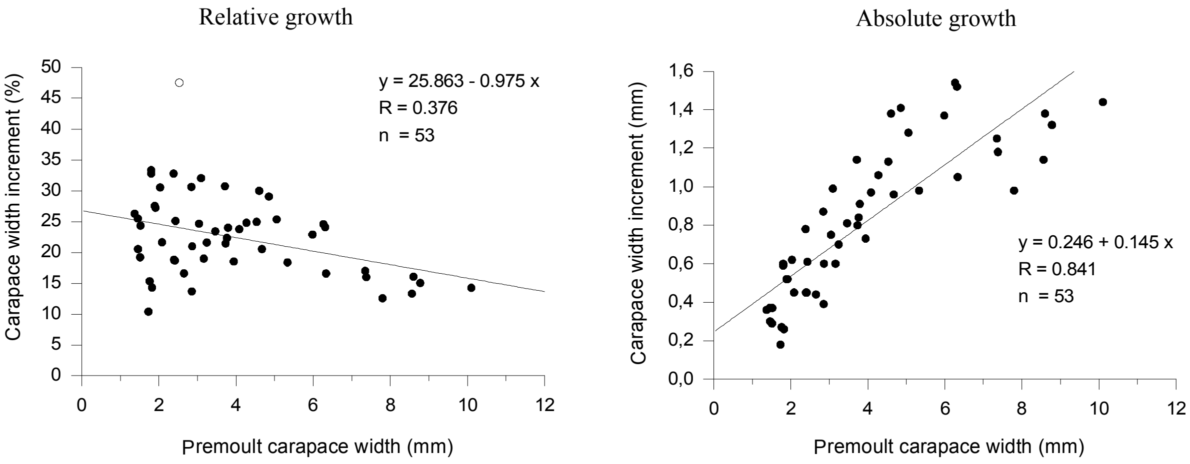


Fig. 24: Relative and absolute growth increment in laboratory reared early juveniles (n = 7, 1998) during approximately biweekly measurement intervals.
Unfilled marker: data point excluded for regression analyses.

In 1999 size increment between first instar and an age of 56 to 57 days was measured for eight crabs with biweekly sediment change. Despite same treatment their growth increment was significantly higher (t-Test: p<0.01 for both relative and absolute increment) than for crabs of similar age reared in 1998 (Table 4).

In order to investigate whether the frequency of sediment change influences the growth of young crabs, in 1999 a subset of crabs was reared with monthly instead of biweekly sediment change (Table 4). Growth increment in the latter group was significantly lower than for the group with monthly treatment (t-Test: p<0.01 for relative and p<0.05 for absolute increment).

Table 4: Relative and absolute growth increment since first instar size for 56 to 60 days old crabs reared in the laboratory in 1998 and 1999 (Mean values and standard deviation).
Brackets indicate (1) biweekly and (2) monthly sediment change.

Year	sample size	Age (days)	Increment in %	Increment in mm
1998 (1)	8	58.13 ± 2.59	120.88 ± 21.88	1.79 ± 0.33
1999 (1)	8	56.63 ± 0.52	155.12 ± 16.23	2.39 ± 0.31
1999 (2)	4	56.50 ± 0.57	121.45 ± 13.34	1.90 ± 0.20

4.3.2 Later juvenile and adult growth

Growth increment The three capture-recapture experiments conducted in field enclosures from 1997 to 1999 provide altogether 88 growth increment data for females (2.05 cm to 6.95 cm carapace width) and 101 for males (2.05 to 8.24 cm carapace width). During the time at free intervals (4.2.2) one male (7.0 cm carapace width) and three females (5.5, 6.5 and 6.6 cm carapace width) had moulted without attaining a larger size. The highest size increase with 32.7% (male) and 28.13% (female) was observed in small crabs with a premoult carapace width of 2.1 and 3.2 cm, respectively (Fig. 25). Average percent increment between 2.0 and 3.9 cm carapace width was 12.9 ± 6.6% in males and 13.7 ± 6.0% in females. Relative growth declined significantly with size (males: r = 0.648; P<0.0001; females: r = 0.746; P<0.0001) (Fig. 25) and from off 5.0 cm carapace width males only grew an average of 5.0 ± 2.1% and females 2.3 ± 1.5%. Absolute growth increment also decreased significantly with size (males: r = 0.339; P<0.001; females: r = 0.647; P<0.0001) with values ranging between 0.95 and 0.04 cm in males and 0.90 and 0.01 cm in females (Fig. 26). Size increment data from new and old exoskeletons of five excavated free-living crabs (two females, three males) fitted well into the growth pattern observed for crabs of corresponding size held in the enclosures (Fig. 25 and 26).

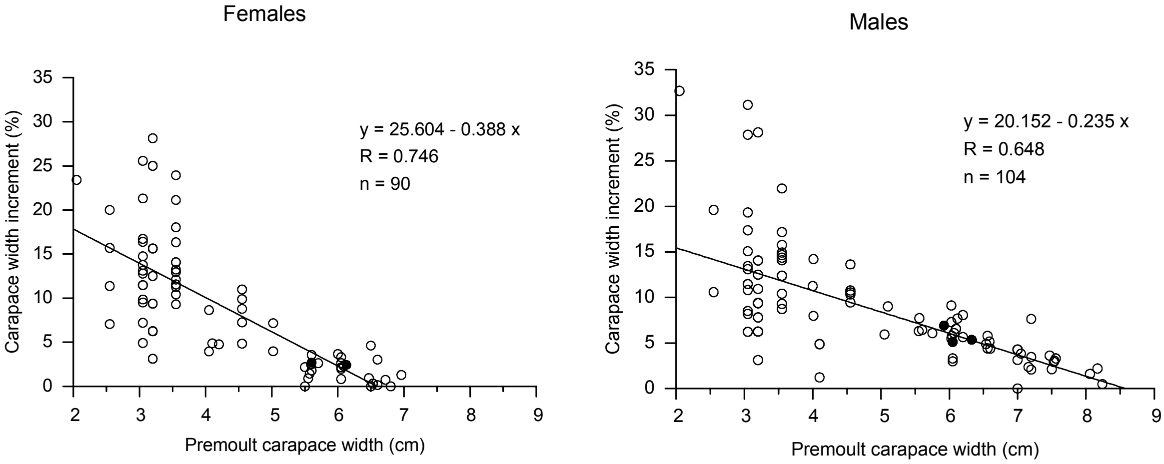


Fig. 25: Relative growth increment during time at free of crabs kept in field enclosures. Filled marker indicate growth increment of excavated free-living specimens.

Moulting frequencies and age at size estimations For the von Bertalanffy growth calculations the enclosure results were combined with the age at size data for early juveniles reared with biweekly renewed sediment. The description of growth requires information upon size increment and upon moulting frequencies. According to crab collectors working in the Caeté estuary and own observations, larger crabs with approximately 4.5 cm carapace

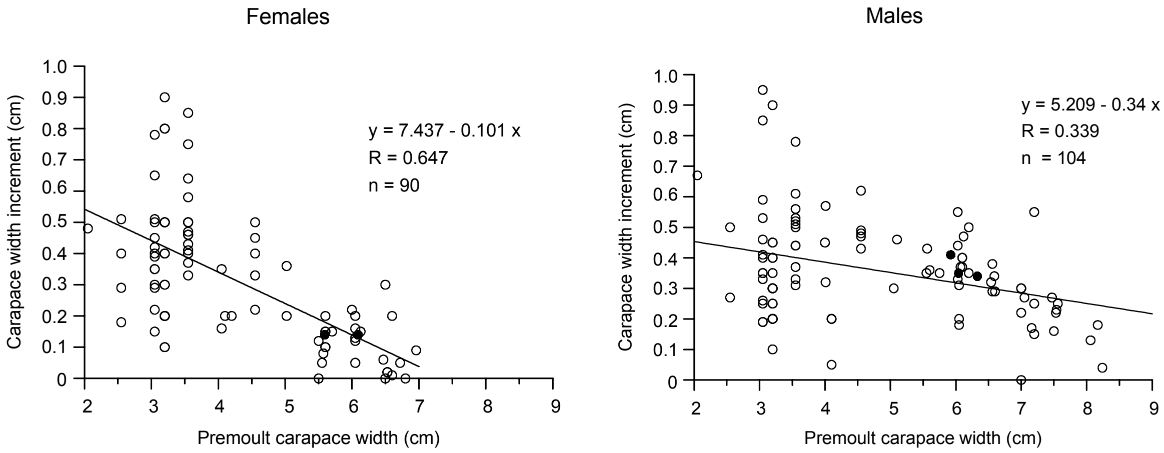


Fig. 26: Absolute growth increment during time at free of crabs kept in field enclosures.
Filled marker indicate growth increment of excavated free-living specimens.

onwards moult solely between June and December, and *U. cordatus* of this size is known to moult only once per year (Nascimento 1993). Multiple recaptures of crabs kept in the enclosures demonstrated that smaller animals (2.0 to 4.4 cm carapace width) may moult twice per year and a third moult cannot be excluded. Due to these uncertainties the von Bertalanffy growth function was calculated for two cases with following moulting frequency assumptions (Table 5):

- Case 1: carapace width 2.0 - 4.4 cm: two moults per year
  carapace width ≥ 4.5 cm: one moult per year

- Case 2: carapace width 2.0 - 3.9 cm: three moults per year
  carapace width 4.0 - 4.4 cm: two moults per year
  carapace width ≥ 4.5 cm: one moult per year

Calculated growth parameters, growth performance and resulting size at age estimates for the two cases of moulting frequency assumptions are given in Table 5. The underlying growth increment data were obtained from a wide range of size classes which ensures a good coverage of most of the calculated growth curve with true measurements (Fig. 27 and 28). The coefficient of variation of K, a measure for the goodness of fit of the curve, was low with values between 3.3 and 4.2% in males and 5.5 and 6.6% in females. The calculated K-values of females are higher, but they reach a smaller asymptotic size (L_0) than males. Variation in growth performance between sexes was small (< 10%).The calculated age at size estimates vary accordingly to the underlying moulting frequency assumptions.

The first case gives 19% (males) and 23% (females) higher age estimates than the second case (Table 5).

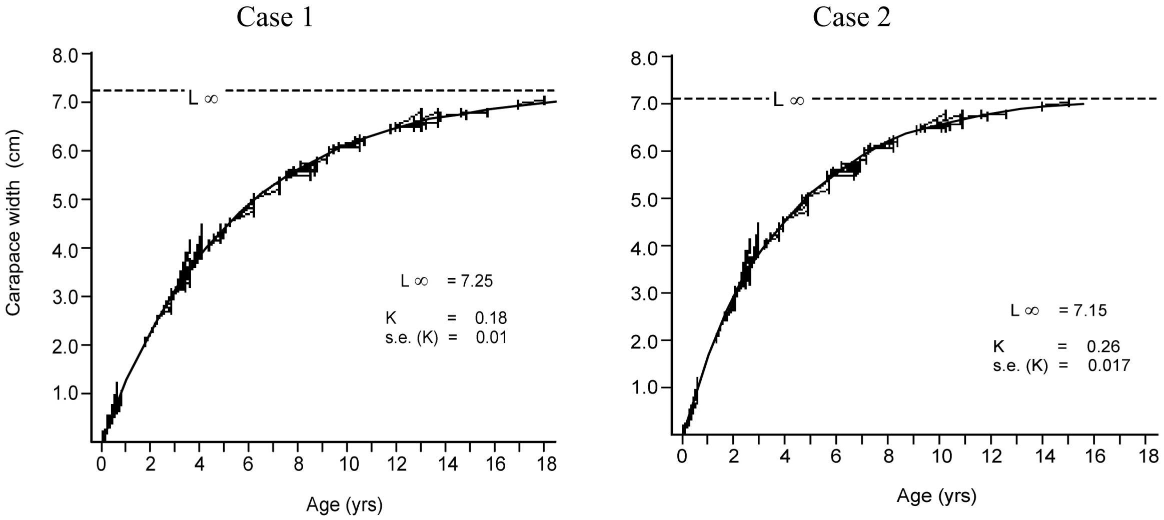


Fig. 27: Female growth curves for moulting frequency assumption case 1 and case 2. (see text for explanation).

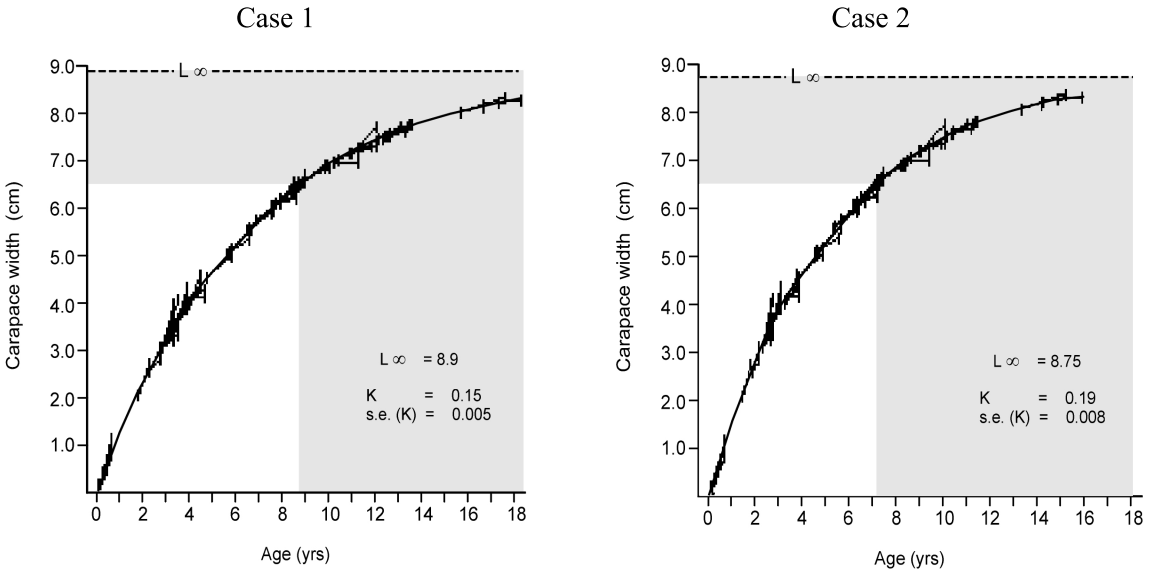


Fig. 28: Male growth curves for moulting frequency assumption case 1 and case 2 . (see text for explanation). Shaded field indicates range of market-sized specimens.

Table 5: Age at size estimates for males and females.
Calculations were conducted for two cases of moulting frequency assumptions (see text for explanation). L_0 (cm) and K (± standard error): Parameters of the von Bertalanffy growth function, Ø´ : Growth performance index.

	♂	♂	♀	♀
	Case 1	Case 2	Case 1	Case 2
	$L_0 = 8.9$	$L_0 = 8.75$	$L_0 = 7.25$	$L_0 = 7.15$
	K = 0.15	K = 0.19	K = 0.18	K = 0.26
	s.e = 0.005	s.e. = 0.008	s.e. = 0.01	s.e. = 0.017
	Ø′= 2.48	Ø′= 2.68	Ø′= 2.25	Ø′= 2.59
carapace width (cm)	age (yrs)	age (yrs)	age (yrs)	age (yrs)
3.0	2.7	2.2	3.0	2.1
3.5	3.3	2.7	3.7	2.6
4.0	4.0	3.2	4.5	3.2
4.5	4.7	3.8	5.4	3.8
5.0	5.5	4.5	6.5	4.6
5.5	6.4	5.2	7.9	5.7
6.0	7.5	6.1	9.8	7.0
6.5	8.7	7.1	12.6	9.2
7.0	10.3	8.5	18.7	14.9
7.5	12.4	10.2		

4.4 Discussion

4.4.1 Early juvenile growth

Growth in small crabs until an age of six months after the juvenile moult was determined for specimens held in the laboratory. Mean relative size increment within subsequent measurements was 23%. Throughout the six study months relative growth increment decreased with size as is also known from other crustaceans (Haefner and van Engel 1975, Donaldson et al. 1981, Hartnoll 1982,1983, Vinuesa et al. 1989, Fletcher et al. 1990). The same was true for the frequency of moulting. A relatively large number of eight to ten moults at a minimum occurred within the first six months of life. It is possible that true moulting frequency was even higher as more than one moult per approximately biweekly measurement interval may have caused the observed size increment. Only few data for early juvenile growth in other brachyurans are available for comparison. In the marine crabs *Cancer polyodon* (Wolff and Soto 1992) and *Lithodes santolla* (southern king crab) moulting frequencies are distinctly lower. *C. polyodon* moults no more than four times during the first six months of life and in *L. santolla* six to seven moults occur within the first year of life (Vinuesa et al. 1989)

Large variations in size of young *U. cordatus* of same age were observed, despite equal sediment renewal and similar initial carapace width: in 1998 a 1.51 mm first instar crab had reached a size of 11.53 mm after approximately six months, whereas a former 1.52 mm crab grew to only 7.83 mm within the same time span. Differences in growth also existed between years. It is rather unlikely that different quantities of infaunal food accounted for the observed size differences. Crabs were provided with equal amounts of well mixed sediment taken from the same location. Different sex (although unknown for the reared specimens) as a cause for the differential size increment is a further possibility, but studies on other crustaceans have shown that males and females have similar growth rates before the onset of maturity (Ehrhardt and Restrepo 1989, Methot 1989, Wolff and Soto, 1992). Possibly, genetic differences are responsible for the observed variations.

When growth is determined in the laboratory, the difficulties involved with rearing experiments have to be considered when interpreting size at age data. For example regular handling stress or sub-optimal food quantity and quality may negatively effect growth rate. The latter was indicated by reduced growth of a subsample of crabs that was reared without sediment change for more than 50 days, whereas animals of same age whose sediment had been renewed biweekly had grown larger. As conditions in the laboratory are different and most likely sub-optimal to those a crab encounters in the field, growth data obtained from reared specimens should be regarded as minimum values. As such they are particularly important when alternative field sampling – as in *U. cordatus* - is hampered by the small size and cryptic behaviour of the young (see below). Future laboratory studies should involve larger sample sizes under varying food types and quantities in order to better delineate the growth potential of young crabs. An additional attempt of determining juvenile growth was initiated in April 1999, when approximately 100 crabs between 1.3 and 1.5 mm carapace width were released into a 12.5 m² compartment of the field enclosure (4.2.2). It is hoped that a sufficient portion survives until crabs have grown to a size at which they can easily be captured (see below).

The difficulty in finding young of the year crabs in the field may be the reason, why former investigations have not paid attention to size classes below 1 cm. Despite extensive search within the present study, only one 2.5 mm large individual was encountered in the mangrove forest. Small size alone cannot account for the fact, that youngest crabs are rarely found in the field as small juveniles of other species (e.g. *Uca* spec) can easily be spotted on the sediment surface. However, the here conducted laboratory study on behaviour and growth of young *U. cordatus* crabs has demonstrated their cryptic lifestyle with little activity above ground, explaining the difficulty in encountering them in the field. The natural habitat of first crab stages is most likely the sediment substrate in the mangrove forest and not in tidal creeks, as with the exception of the first two weeks after the juvenile moult, burrow entrances were constructed well above the water table.

What is the cause for the observed low above ground activity of early juveniles and in how far is this behaviour advantageous? In contrast to larger juveniles and adult crabs who consume leaf litter accumulated on the sediment surface, first crab stages were observed to feed upon infauna, a resource of comparably higher nutritional value which allows faster growth during the early life phase. The infaunal food resource renders above surface activities unnecessary, whereby the risk of encountering potential predators such as carnivorous crabs, e.g. *Goniopsis cruentata*, or wading birds is greatly reduced. Furthermore, high air temperatures can be avoided. Juveniles are less tolerant of environmental extremes than adults (Wolcott and Wolcott 1988) and their comparably larger body surface area should render them more susceptible to desiccation stress. Hence, the humid under ground habitat seems to bear many advantages for juvenile crabs during their first months of life. Future research will address upon the question when the change in habitat use occurs and what factor constellations trigger this major switch in life strategy.

4.4.2 Later juvenile and adult growth and age at size estimates

The capture-recapture experiment with tagged crabs kept in enclosures provides the first data on growth of *U. cordatus* in the field. For later juveniles and adult crabs this approach was preferred to the artificial environment of laboratory studies which may suppress growth (see below). Under the quasi-natural field conditions animals fed upon leaf litter provided by *R. mangle* trees growing inside and around the enclosure. Normal tidal inundation was assured and crabs could burrow to unlimited depth. Growth does not seem to have been negatively influenced by tagging and captivity as pre- and postmoult size of excavated free-living specimens indicated similar size increment as observed for the crabs kept in the enclosure.

Very limited information upon growth in *U. cordatus* is available from the literature. Size increment of crabs measuring between 1.7 and 2.5 cm carapace width was investigated by Geraldes and Claventi (1983), who kept the animals in substrate free aquaria. After the first moult in captivity an average increment of 0.5 mm or 2.8% was observed which decreased to even lower values after the second moult (1.4%). Another laboratory study was conducted by Ostrensky et al. (1995), who measured size increment in males of approximately 4.0 to 5.0 cm carapace width. Crabs were kept in sediment filled tanks and were fed with mangrove leaves. With 2.5%, the average increase per moult was 50% lower than observed for males from 5.0 to 8.2 cm carapace width in the here presented study, although growth increment generally decreases with size (Hartnoll 1982, 1983). The lower values found in the former investigation probably relate to the fact, that crab density in the tanks was manifold higher than in the field. As a consequence energy expenditures for territorial behaviour may have been increased.

Despite the comparably higher growth increment determined in the field, the results still indicate that *U. cordatus* is a rather slow growing and long-living species. Its maximal life span of more than ten years is manifold higher than the one of other brachyuran species inhabiting the mangrove forests of the Caeté estuary, e.g. fiddler crabs (Koch 1999). However, whereas these are small deposit-feeding species (see below), the leaf litter consuming *U. cordatus* reaches a large body size. Its growth seems to be quite well described by the von Bertalanffy function, which yielded L_0-values closely agreeing to maximum crab sizes found in the field (9.1 cm carapace width in males, 7.3 cm in females). Between sexes growth performance differed less than 10% as the higher K-values in females were compensated by higher L_0-values in males. When applying age at size estimates (see below), it has to be considered that age near L_0 may be overestimated, as specimens reaching this large size may not be older but may simply have grown faster than other conspecifics (Sparre and Venema 1989). Faster growth can be due to genetical differences as greater fitness may result in higher food uptake, or simply to better food supply at a given location (Hartnoll 1982, Wenner et al. 1985). The age of a crab of particular size may on the other hand also be underestimated. For example, a specimen suffering from limb loss needs to allocate energy into regeneration, which may reduce overall growth increment at this stage (Fielder 1964, Hopkins 1985, Hartnoll 1988). However, despite possible intraspecific variations in growth rate and the resulting over and under-estimation of individual age, size at age calculations basing upon growth increment and moulting frequency data of a large set of specimens are a necessary and valuable tool for extrapolating the overall growth of a species.

In contrast to crustaceans with determinate growth who usually do not mature until they have reached full size and cease moulting thereafter (see Hartnoll 1983 and 1985), *U. cordatus* continues to grow after the puberty moult and follows the indeterminate growth pattern. *U. cordatus* attains sexual maturity at a relatively early age when considering its maximum life span. The smallest observed ovigerous females had a carapace width of 3.1 cm (3.3.1), which corresponds to an approximate age of 2.1 to 3.0 years, depending upon the underlying moulting frequency assumption (4.3.2). However, individual variations in growth rate (see above) can alter the size and age at onset of maturity and it also has to be considered that females, although mature, may not always extrude eggs (Wenner et al. 1985) (3.4.3). Assuming that male *U. cordatus* mature at a similar size as females (Alves 1975, Nascimento 1993), they have an age of ca. 2.2 to 2.7 years when they start to reproduce. Size and age at onset of maturity comparable to that of *U. cordatus* was described for the large terrestrial land crab *Gecarcinus lateralis* (Hicks et al. 1984, cited after Wolcott 1988). In this species age could be determined by following a cohort for three years after an event of highly synchronous recruitment. Females differentiated when approximately 2.5 to 3.0 years old which corresponds to 2.6 to 2.8 cm carapace width.

Early sexual maturity implies the ability to reproduce, even if mortality occurs before full size is reached. However, as growth and reproduction require limited energy resources and are thus competing processes, the allocation of energy into one process reduces the amount available for the other (Hartnoll 1985). Therefore, in species with indeterminate pattern such as *U. cordatus*, growth to full size can be slower than in species who delay reproduction until maximum size has been attained (Hartnoll 1985). In *U. cordatus* smaller specimens moult several times per year, whereas larger crabs (latest at a carapace width of approximately 4.5 cm) moult only once a year during the dry season. Annual moulting is also assumed for the large gecarcinid land crab *Cardisoma guanhumi* (Felicano 1962 cited after Wolcott 1988, Taissoun 1974) and the low moulting frequency is possibly related to the poor quality food consumed by these large land crabs (see below).

For an evaluation of the impact of fishery and an estimation of future yields, the age of commercially exploited males is of particular interest. According to this study, at 6.5 cm carapace width they are ca. 7.1 to 8.7 years old, and the more frequently harvested specimens with 7.0 to 7.5 cm carapace width (5.3.2) have an approximate age between 8.5 and 10.3, and 10.2 and 12.4 years, respectively. Many large marine crabs grow distinctly faster than *U. cordatus*. For example in the commercially exploited brachyurans *Chionecetes bairdi* (Donaldson et al. 1981) and *Cancer polyodon* (Wolff and Soto 1992), males with a carapace width of 6.5 cm have an age of only 3.9 and 1.2 years, respectively. However, other large land crabs seem to grow at a similar slow rate as *U. cordatus*. For example *C. guanhumi* is assumed to be 13 years old at a size of 9.8 cm carapace width (Henning 1975). In contrast to many marine brachyurans, large land crabs primarily feed upon plant material which generally contains less nitrogen than animal food. (Wolcott and Wolcott 1992, Mattson 1980). For *C. guanhumi* and *G. lateralis* it was demonstrated, that growth can be enhanced by protein supplementation (Wolcott and Wolcott 1984, 1987). *U. cordatus* also seems to be nitrogen limited as crabs fed with additional proteins grew twice as much as those supplied with pure mangrove leave diet (Ostrensky et al 1995). The relatively low metabolism and growth rate of many herbivorous versus detrivorous and carnivorous mangrove crabs (Koch 1999) and their large body size (selection for increased gut capacity) is likely to be an adaptive response to limited nitrogen (Wolcott and Wolcott 1987, 1992). Due to their size, many large land crabs are commercially important species, yet their slow growth rate suggests a high vulnerability to overfishing.

5 POPULATION STRUCTURE AND COMMERCIAL EXPLOITATION

5.1 Introduction

5.1.1 Frame of the study

As in many other coastal regions of Brazil (Ogawa et al. 1973, Nascimento et al. 1982, Castro 1986, Nordi 1994, Blanckensteyn and Cunha Filho 1997) *U. cordatus* is the most heavily exploited resource of the mangrove forest in the Caeté estuary. It constitutes the main income source for more than 50% of the rural households (Glaser 1999). When the MADAM project was initiated in 1996, no quantitative information was available upon the structure of the *U. cordatus* population in the Caeté estuary, the spatial dimension of fishery and size of commercially landed crabs. Obviously - beside important life history parameters such as reproduction (chapter 3) and growth (chapter 4) - knowledge upon these aspects are fundamental for a comprehensive resource evaluation of a given area. The latter will be approached during the second phase of MADAM, after the landed yield has been precisely quantified and larval export and recruitment patterns – which may have profound implications for fishery management – have been investigated in further detail (3.4.1).

The aim of the here presented study was to provide information upon the size and sex composition of the *U. cordatus* population and crab abundance as well as biomass. Special attention was given to the question whether the population shows signs of growth or recruitment overfishing. Since the construction of the tarred road crossing the Caeté peninsula 15 years ago, the number of traditional crab collectors (see below) working in the area reportedly augmented due to improved access to the mangrove forest, when compared to many other neighbouring peninsulas. As a consequence approximately eight to ten years ago traditional crab exploitation – formerly concentrating upon easy accessible areas near the road – expanded to more remote areas. Today the entire mangrove forest of the Caeté estuary is exploited for crabs, with even most distant regions being reached by boats. For determining how fishery influences the population structure of *U. cordatus*, crabs were sampled at three different sites along a gradient of accessibility from the road. A comparative study of a completely undisturbed control population was not possible due to the large spatial scale of crab exploitation in the Caeté estuary. Crab sampling was primarily conducted near the tidal channel Furo Grande in *R. mangle* dominated forest stands, the predominating vegetation type of the Caeté peninsula. Beside the analyses of population structure, commercial crab fishery in the catchment area of Furo Grande was investigated in regard to size of specimens landed from different capture localities by traditional crab collectors (see below).

5.1.2 Commercial crab capture and production systems

In the following a brief introduction concerning capture techniques and production systems is given, which is a prerequisite for an understanding of the present state of crab fishery in the Caeté estuary. This topic is addressed in detail by Glaser (1999).

Two producing systems – modern and traditional crab collection (sensu Glaser) can be distinguished in the Caeté estuary. Traditional crab collectors are independent workers who produce for local and regional livestock markets. They capture crabs by either pulling them out their burrows by hand (Fig. 29 a), or – when burrows are too deep – with a hook tied to a 1.5 m long stick ("gancho") (Fig. 29 b). Whenever possible capture is conducted by hand as crabs are easily injured when the hook is used. Traditional crab collectors travel by canoes to capture areas along the shores of tidal channels (Fig. 29 c). Immediately after their capture crabs are tied to so called cambadas which are strings of 14 living specimens that are sold on the markets (Fig. 29 d). Market demand exerts a strong influence upon the size and condition of landed crabs as consumers prefer fresh and large crabs. As a consequence cambadas with large specimens yield higher prices than those with comparably smaller crabs.

In contrast to traditional crab collectors, modern crab collectors are quasi-employees of persons owning motorised boats. Their yield is directed to the local crab meat industry and sold on regional and national markets (Glaser 1999). They work in groups of up to 30 persons per boat and per man daily yield is at a minimum twofold higher than the one of traditional collectors (Blandtt and Glaser 1999). This is not only due to timesaving motorised transport, but also a result of the different product destination and therewith working style. In contrast to the cambada producing traditional collectors, modern collectors sell baskets with chelae and legs (Glaser 1999). As crabs are killed immediately after capture, modern collectors need to pay less attention that crabs are not injured and use the hook more frequently than traditional collectors. Furthermore, time consuming tying of cambadas in the mangrove forest is unnecessary. Legs and chelae are separated from the carapace during the return boat journey and the latter discarded in the estuary. Compared to livestock consumers, the meat processing industry exerts less control upon the leg and chelae yield of modern collectors, which is sold in baskets of standardised volume.

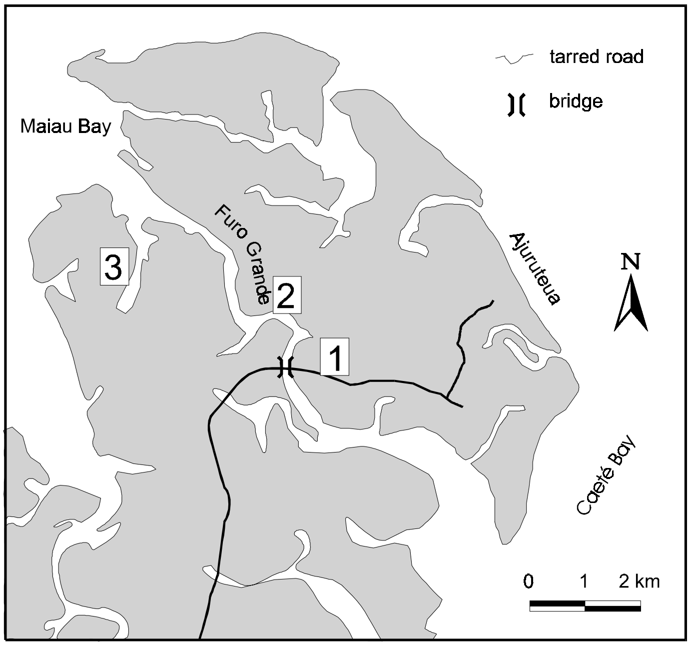
Working areas of modern and traditional crab collectors were originally spatially separated. Whereas traditional workers live near Bragança and enter the Caeté peninsula via the road (see above), modern collectors are villagers from Treme and Caratateua (Fig. 4, chapter 2) and initially exploited the mangrove forests in the vicinity of their villages and at the southern end of the Caeté peninsula. However, recently they also began to work in northern areas of the peninsula, that were formerly only exploited by traditional crab collectors. At Furo Grande – an important working area of traditional crab collectors - this situation occurred during the rainy season in 1998. A conflict between the two production groups arose which ended in a deplacement of modern workers by traditional crab collectors (5.4.2). However, with their motorised boats modern collectors are capable of exploiting areas outside the Caeté estuary and are known to travel as far as the neighbouring state Maranh�o (Blandtt and Glaser 1999).

Fig. 29: a) Crab capture by hand and b) with hooked stick (gancho). c) Traditional crab collectors landing their yield and d) crab seeling units (cambadas) at the market of Bragança.

5.2 Methods

5.2.1 Field sampling

Crab capture Crabs were sampled in a bimonthly interval between August 1997 and 1998 in dense *R. mangle* forests, which form the most characteristic vegetation type of the peninsula. Three locations with differing degree of accessibility were comparably investigated (see 5.1.1). One site is situated near the road about 1 km north of the Furo Grande bridge (Fig. 30). The other two sites, which are located approximately 1 km and 5 km upstream from the bridge, can only be reached by boat. According to traditional crab collectors who exploit the area around Furo Grande since many years, the distant site is subject to lower fishing pressure than the easy accessible site near the road.



Base map: CPRM / MADAM (G.Krause, K. Franke)

Fig. 30: Location of crab sampling sites at Furo Grande
1: near-road site; 2: near-upstream site; 3: distant-upstream site

Per site and month between six and eight 25 m² quadrats with a distance of 50 metres in between were sampled along a transect running perpendicular to a larger tidal watercourse. If quantitative crab capture was impossible due to environmental parameters (e.g. sandy / dry sediment, dense roots, creek), an alternative quadrat was selected at the nearest right or left hand side of the transect. Each month sampling was conducted along a new transect 70 metres aside the former one.

Quadrats were marked by ropes and all inhabited burrows (recognisable by faeces, tracks and sediment excavation) inside the delimited area were sampled. Those that were located exactly on the boarder line were only counted from two of the four sides. A professional crab collector tried to capture every crab, which was not always possible due to blocking roots or dead wood, but a sufficient portion (50-80%) was generally achieved. Total number of inhabited burrows was noted so that catch could be corrected for sampling efficiency. Transect sampling was always conducted around new and full moons. During these days high tides inundate the mangrove forest and crab capture at subsequent low tide is facilitated by the softened sediment.

Crabs were transported to Furo Grande bridge where they were sexed, measured with a calliper rule to the nearest millimetre and weighed to the nearest 0.1 gram. Presence of eggs was noted (see chapter 3.3.1 for results) and moult status checked by coloration and smoothness of the carapace.

As only few small crabs were encountered in the dense *R. mangle* forest habitat, in May 1998 additional specimens were captured near the embankment of the paved road and in a large forest gap. In these so called peripheral habitats small specimens had been observed to occur in high numbers. As crab density was considerably higher than in the forest habitat, quadrat size was reduced to 6.25 m². Per site five replicate quadrats were sampled.

Environmental parameters Canopy coverage and rooting of sediment surface was estimated in percentage of each 25 and 6.25 m² sampling area. Rooting by *A. germinans* pneumatophores and *R. mangle* stilt roots was separately determined. Silt/clay content of the sediment in each quadrat was determined by taking a sample with an open ended plastic syringe (50 ml) to a depth of 10cm. The analyses was conducted according to Holme and McIntyre (1984). After drying the sample to constant weight at 100°C, the sediment was diluted with hot water and passed through a 63µm sieve. The residue was then dried, weighed and the content of silt and clay calculated from the weight difference.

5.2.2 Size monitoring of commercial landings

In the catchment area of Furo Grande where investigations were conducted, approximately 35 traditionally working crab collectors regularly capture crabs in the mangrove forest fringing the 12 km long tidal channel. From Furo Grande bridge they travel by canoe to the various capture locations. Crabs are landed at the bridge and transported to Bragança by bus for sale.

Weekly on Friday or Saturday three to four cambadas (5.1.2) per site landed from at least three different localities along the tidal channel were selected at random. The carapace width of the crabs was measured to the nearest mm with a calliper rule and the name of the capture locality noted. Data collection started in February 1998 and measurements until end of July 1999 are presented.

For data analysis, capture locations were grouped into the categories "near" (within 2.5 km) and "distant" (> 2.5 km) from bridge (Appendix 6). Near sites can be reached faster and require less energy expenditure for canoeing than distant sites. Grouping of the data was conducted for testing the hypothesis that distant sites yield larger crabs due to lower fishing pressure (frequency) in the past or present.

5.2.3 Statistical analyses

Differences in the size frequency distribution of the investigated crab populations were tested with a chi^2-test. Analyses of variance was applied to test for differences between environmental parameters at the sampling areas, and for differences between abundance and biomass of crabs. Analyses of variance was also used for the detection of differences in mean carapace width of commercially landed crabs from near and distant sites and during the rainy season 1998, dry season 1998 and rainy season 1999. Sample sizes varied as at days of data collection crabs from different sites were not landed in same frequency. For statistical treatment data were balanced by random selection of one sampling date per site ($n = 42$ crabs) and season ($n = 3$). Prior to analyses of variance, heterogeneity of variance was tested with Hartley´s F-max test. Despite data transformation variances were often heterogeneous, but according to Underwood (1997, pp. 192-194) analyses of variance is robust when experiments, such as were conducted, include large and balanced sample sizes. Post hoc analyses was performed with Tukey´s HSD-test.

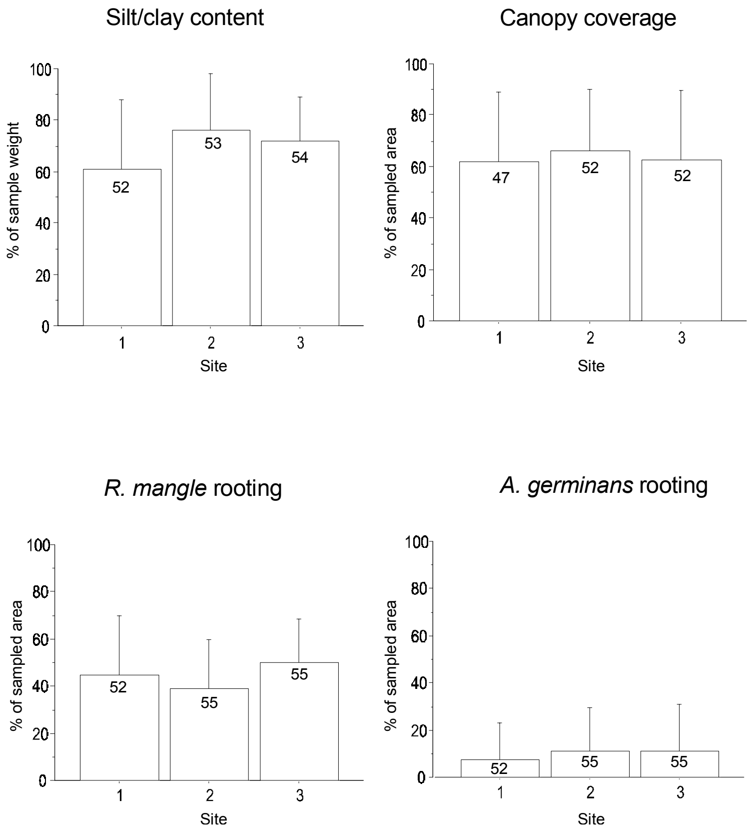
5.3 Results

5.3.1 Population structure

5.3.1.1 *Rhizophora mangle* forest habitat

Environmental parameters Canopy coverage and rooting of the sediment surface were similar at the three study sites (both p>0.05, Fig. 31, Appendix 1). Silt/clay content at the near road site was lower than at the near upstream site (p<0.01) and at the distant upstream site (p<0.05). Near and distant upstream sites had similar values (p>0.05).

Size-frequency distribution Altogether 4549 crabs were captured at the three study sites between August 1997 and 1998. The smallest and largest captured female had a carapace width of 1.4 and 7.3 cm, respectively. Males grow larger and minimum and maximum size was 1.7 and 8.75 cm. In Appendix 2 a-c size-frequency distributions are plotted per sampling month, site and sex. With few exceptions distributions are unimodal. Progressions


Silt/clay content

Canopy coverage

R. mangle rooting

A. germinans rooting

Fig. 31: Environmental parameters (mean and standard deviation) measured in *R. mangle* forests at the near road site (1), near upstream site (2) and distant upstream site (3). Numbers in bars indicate sampled 25 m² quadrats.

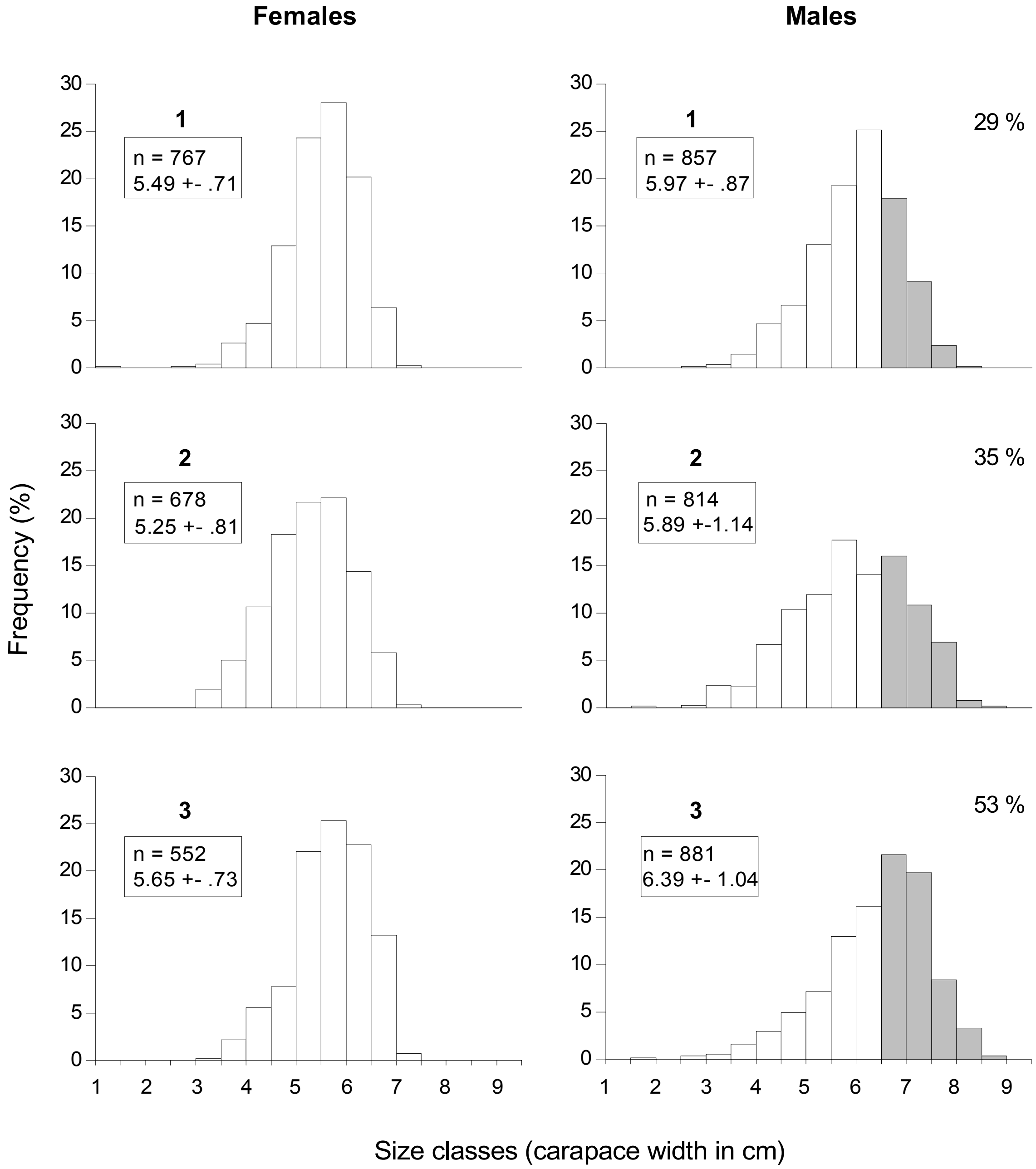


Fig. 32: Size frequency distribution of crabs sampled in three *R. mangle* dominated forest stands pooled over seven sampling occasions (08.97 – 08.98).

1: near-road site; 2: near-upstream site; 3: distant-upstream site. Dark bars indicate classes with market-sized males (≥ 6.5 cm carapace width). In square fields mean carapace width and standard deviation is given. Percent values in left corner of graphs indicate portion of market sized males.

of frequency per size class over time which would indicate growth of age groups are not recognisable. Combined over all sampling months size-frequency distributions are negatively skewed, regardless of site and sex with few crabs smaller than 4.0 cm carapace width (3.6% of total catch, n = 4549) (Fig. 32). Peak female abundance occurred in the size class 5.5-6.0 cm. In males the size class with highest numbers varies between sites and ranged between 5.5-6.0 and 6.5-7.0 for the pooled data (Fig. 32). Crabs of the three study site differ significantly in their size-frequency distribution (Appendix 3a, males: $chi^2 = 224.851$, $p<0.0001$; Appendix 3b, females: $chi^2 = 111.76$, $p<0.0001$; data pooled over all months).

Both sexes show a similar site-specific pattern. The distant-upstream location (site 3) has the greatest proportion of larger crabs, the near-upstream site (no. 2) the greatest proportion of small ones and site 1 (near-road location) lies between these two with the largest proportion of crabs in middle size classes (Fig. 32, Appendix 3). As a result of theses differences in both sexes mean carapace width of the catch was smallest at site 2 and greatest at site 3 (Fig. 32). The portion of market-sized males (≥ 6.5cm) was between 29 to 53% of total male catch per site and highest values were observed at the distant-upstream location (Fig. 32).

When considering possible fishery impact upon the size structure of the male population, the three uppermost size classes are of particular interest as within the range of market-sized males, they contain the specimens that are preferably captured (5.3.2). Females, who are rejected by traditional crab collectors (5.3.2) serve as a control group. For better visualisation, the proportions within the highest three size classes in each sex are separately plotted in Fig. 33. An interesting pattern emerges in which the proportion of both large females and males is increasing from the near-road site (no. 1) to the near-upstream site (no. 2) and distant-upstream site (no. 3), but in males this progression is distinctly more pronounced than in females. Furthermore, males falling into the uppermost size class (8.5-9.0) where only encountered at site 2 and 3, whereas females of respective class (7.0-7.5) were captured at all three sites. Another point that is noteworthy becomes apparent, when capture frequencies of the largest crabs are compared over the course of the seven sampling months (Appendix 2a-c, Table 6). In both sexes crabs of the uppermost size class were only sporadically captured and the number of months when they were encountered was lowest at site 1 and highest at site 3. Crabs falling into the second highest size class were captured at all sites and at all sampling occasions in females, whereas in males the number of months varied distinctly between sites (Appendix 2a-c, Table 6). At the near-road site (no. 1) they were only captured in October 1997, whereas they were present in all seven months at the distant-upstream site (no. 3). The near-upstream site (no. 2) was intermediary.

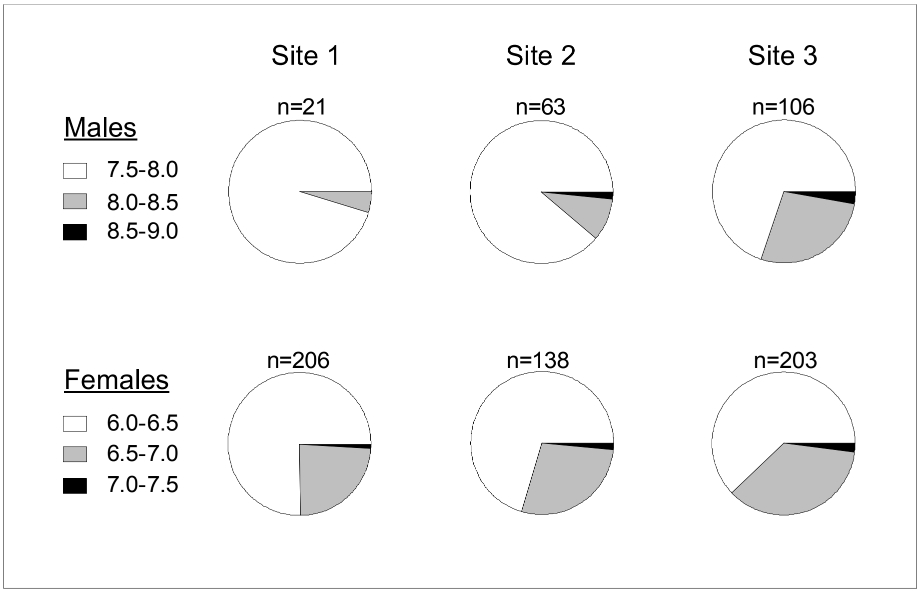


Fig. 33: Proportion of crabs in uppermost size classes captured between August 1997 and 1998 (data pooled over seven sampling occasions).
1: near-road site, 2: near-upstream site; 3: distant-upstream site.

Table 6: Number of months with females and males present in the respective highest and second highest size class (cm carapace width) of the seven sampling months.
A: highest size class; B: second highest size class. Site 1: near-road location, site 2: near-upstream location; site 3: distant-upstream location.

	Females		Males	
	A	B	A	B
site	7.0 < 7.5	6.5 < 7.0	8.5 < 9.0	8.0 < 8.5
1	1	7	0	1
2	2	7	1	5
3	4	7	2	7

Sex ratio At all three study sites male-female proportions of the total catch deviated significantly from the hypothesised 1:1 ratio (Fisher 1930) (Table 7). Males predominated with increasing proportions from the near-road site (no. 1) to the near-upstream site (no. 2) to the distant upstream site (no. 3).

When sex ratio is regarded as a function of size a controversial pattern emerges (Fig. 34 a). In larger crabs (≥ 6.0 cm carapace width) males always predominated and as expected by the differential maximum size in females and males, proportions of the latter reach 100% in the uppermost classes (Fig. 34 a). However, in smaller crabs (≤ 6.0 cm) females were more prominent with proportions of up to 63% in the 5.0 to 5.5 cm size class. Sex ratio as a function of time is plotted in Fig. 34 b. Only in December 1997 and June 1998 mean sex ratio of the three study sites was predominated by females.

Table 7: Number of males and females and sex-ratio for total catch obtained in three *R. mangle* forest stands.
Data pooled over seven sampling occasions. (1) Chi^2 test of goodness of fit testing the null hypothesis of equal proportions between sexes. * $p < 0.05$; *** $p < 0.001$

Site	Males	Females	% Males	Sex ratio	Chi^{2} (1)
1	857	767	53	1.1 : 1	4.88 *
2	814	678	55	1.2 : 1	12.22 ***
3	881	552	62	1.6 : 1	75.08 ***

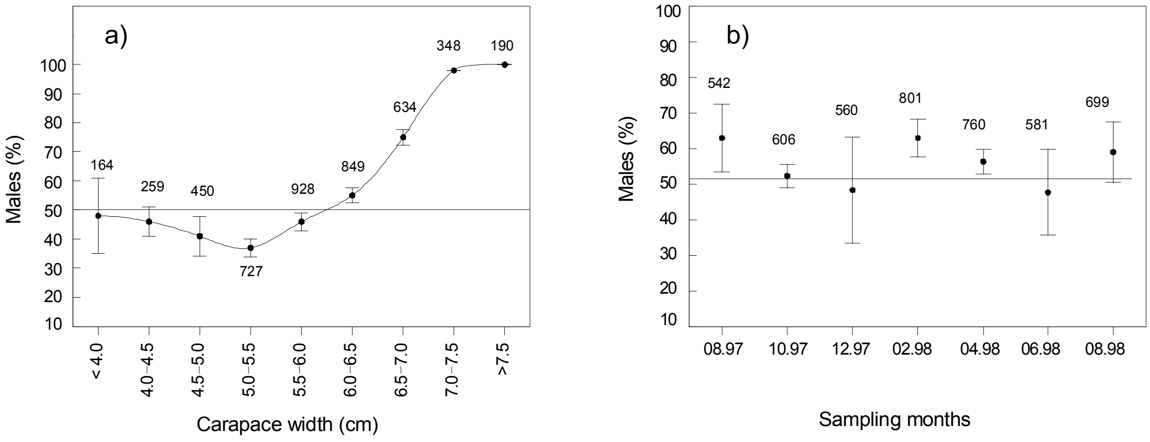


Fig. 34: Sex ratio analyses. a: Sex ratio as a function of size, classes of the lower and upper limit of the size range were combined until a minimum of 20 crabs per site was available for analyses. b: Sex ratio as a function of time.
Mean male proportion and standard deviation (bars) per size class or sampling month were calculated by combining the catch of the three study sites. Numbers indicate the total amount of captured crabs.

Abundance and biomass Combined over all sampling dates and sites mean total crab abundance and biomass was 1.65 indiv./m² and 142.03 g/m², respectively (Table 8). Values splitted per site and sex are demonstrated in Fig. 35 a-b and Table 8. Total crab abundance differed significantly between sites ($p<0.05$; Appendix 4). At the near-road site (no. 1) crabs were more abundant than at the near-upstream site (no. 2) and distant-upstream site (no. 3), with the latter two having approximately same numbers of specimens per square metre. Female abundance also differed significantly ($p<0.0001$) with highest and lowest values at site 1 and 3, respectively. Whereas no statistical differences were detected for total male abundance at the three study sites ($p>0.05$, Appendix 4), the abundance of market-sized males showed significant differences ($p<0.05$, Appendix 4) with highest values at the distant-upstream location. According to the larger portion of heavy weighing market-sized males at the distant location, total biomass was similar to site 1 ($p>0.05$), despite lower overall crab density. Site 2 had significantly lower total crab biomass than the other two sites ($p<0.05$, Appendix 4) resulting from the overall smaller size of captured crabs (Fig. 35 b, Fig. 32). Fresh weight corresponding to crab size is demonstrated in Fig. 36.

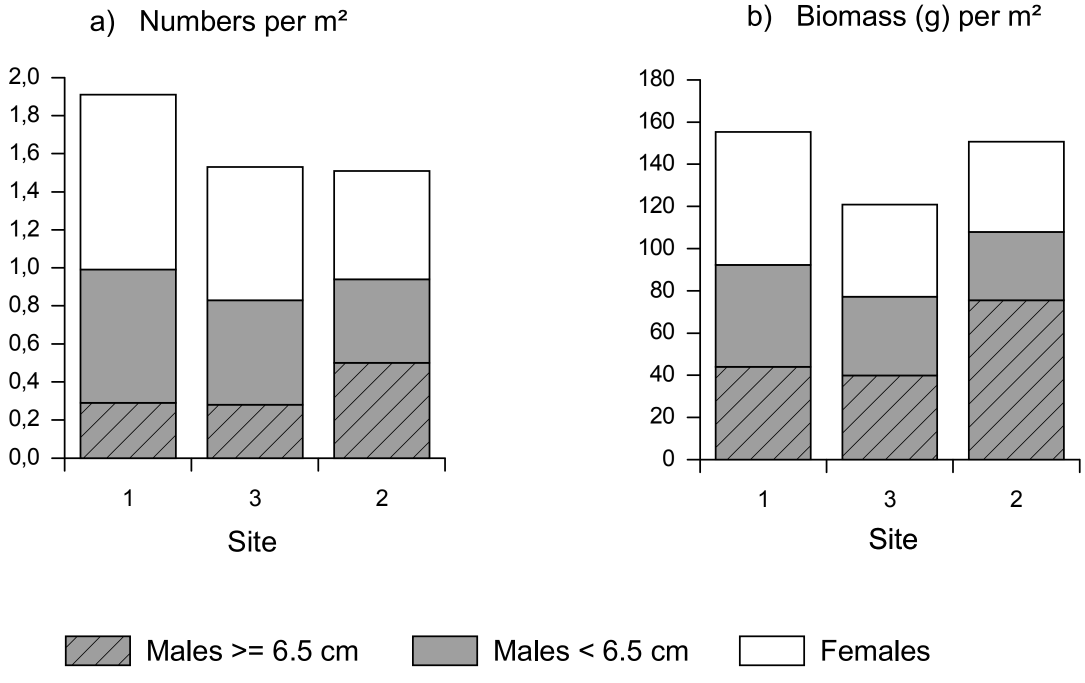


Fig. 35: Abundance (a) and biomass (b) per m² for females, total males and market-sized males (≥ 6.5 cm carapace width) at three *R. mangle* dominated forest stands.
Data combined over all sampling dates.

Table 8: Mean values and standard deviation for abundance and biomass (g) per m² for combined catch, females, total males and market-sized males (≥ 6.5 cm carapace width) at three *R. mangle* dominated forest stands.
A: Abundance; B: Biomass. * $p<0.05$; ** $p<0.01$; *** $p<0.001$ (Statistical test: Appendix 4).

	Total (n=162)		site 1 (n=52)		site 2 (n=55)		site 23 (n=55)		
	mean	stdev	mean	stdev	mean	stdev	mean	stdev	p level
A total	1.65	0.49	1.91	0.56	1.53	0.49	1.51	0.44	*
A females	0.73	0.32	0.92	0.37	0.70	0.21	0.57	0.26	***
A males	0.92	0.39	0.99	0.46	0.83	0.25	0.94	0.41	ns.
A males ≥6.5	0.36	0.28	0.29	0.25	0.28	0.18	0.50	0.33	**
B total	142.03	51.29	155.24	56.15	120.83	39.11	150.72	51.33	*
B females	49.49	22.84	62.88	25.27	43.56	16.13	42.76	20.92	**
B males	92.54	48.58	92.36	53.38	77.28	30.77	107.96	54.02	ns.
B males ≥6.5	53.35	45.81	44.06	45.77	39.92	26.68	75.56	52.88	**

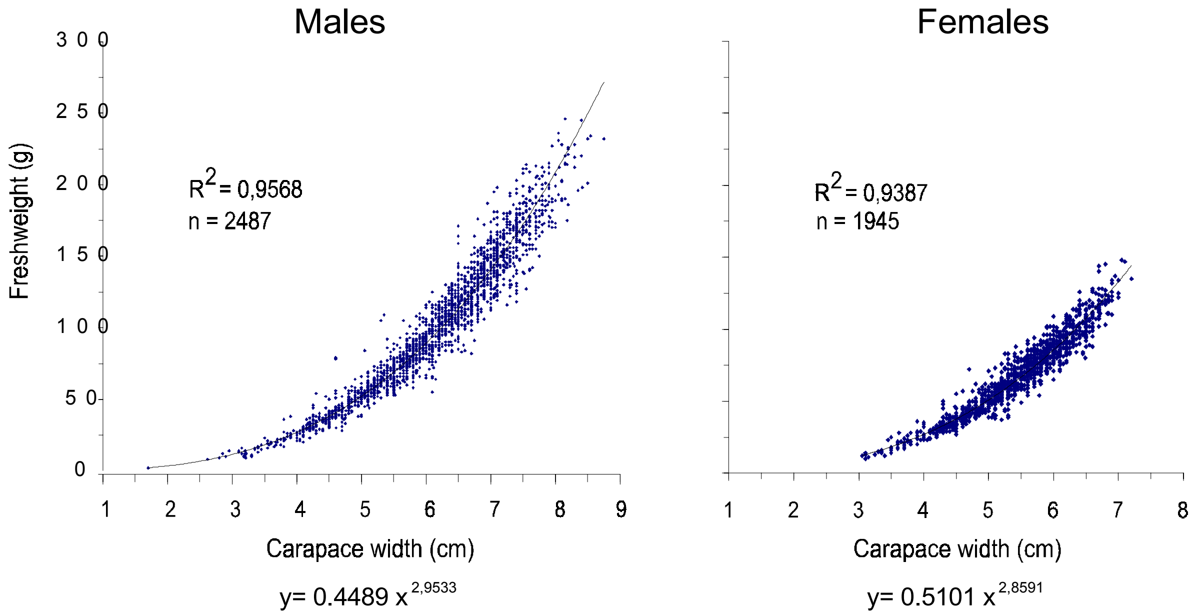


Fig. 36: Size-weight relationship in males and females.

Re-population For determining crab re-population of a formerly emptied area, 275 m² of the total area sampled during the transect program in June 1998 was re-sampled two weeks later (in-between the region remained undisturbed). By subtracting the number of crabs that had remained after transect capture (due to hampering roots, see section 5.4.2), a replacement value of 80% of the total catch removed two weeks earlier was obtained (Table. 9). Regarding commercial crab fishery, the number of re-populating market-sized males ($\geq$ 6.5 cm carapace width) is of particular interest. 69% of the initially captured large males (n = 49) had been replenished by new specimens of respective size. Small crabs ($\leq$ 4.0 cm) occurred in two and a half fold higher numbers during the second sampling occasion (1st sampling n = 8, 2nd sampling n = 21).

Table 9: Burrow number and re-population of an area where crabs were repetitively captured (275 m²).
The time span between first and second sampling was two weeks. For further explanation see text.

first sampling			second sampling	
burrows	removed crabs	remaining crabs	burrows	re-populating crabs
332	265	67	280	213

5.3.1.2 Peripheral habitats

Size-frequency distribution Compared to the inner *R. mangle* forest habitat, additionally sampled areas with peripheral character were predominated by smaller crabs (Fig. 37). So called peripheral habitats include the embankment of the road crossing the peninsula, larger forest gaps, thin stretches near tidal creeks and large islands (elevated sandy areas within the mangrove forest that are not flooded during spring tides). Unlike the inner forest habitat, peripheral areas are poorly rooted and canopy coverage is reduced or absent.

Crabs were sampled in two peripheral habitats, near the road and in a forest gap. As size frequency distributions were not significantly different (p>0.05, Appendix 5), data were combined and are plotted in Fig.37. In both sexes distributions are positively skewed and with 67% of the total catch (n=172), the proportion of crabs with a carapace width smaller than 4.0 cm is approximately twentyfold higher than for specimens captured during transect sampling within the *R. mangle* forest (5.3.1.1).

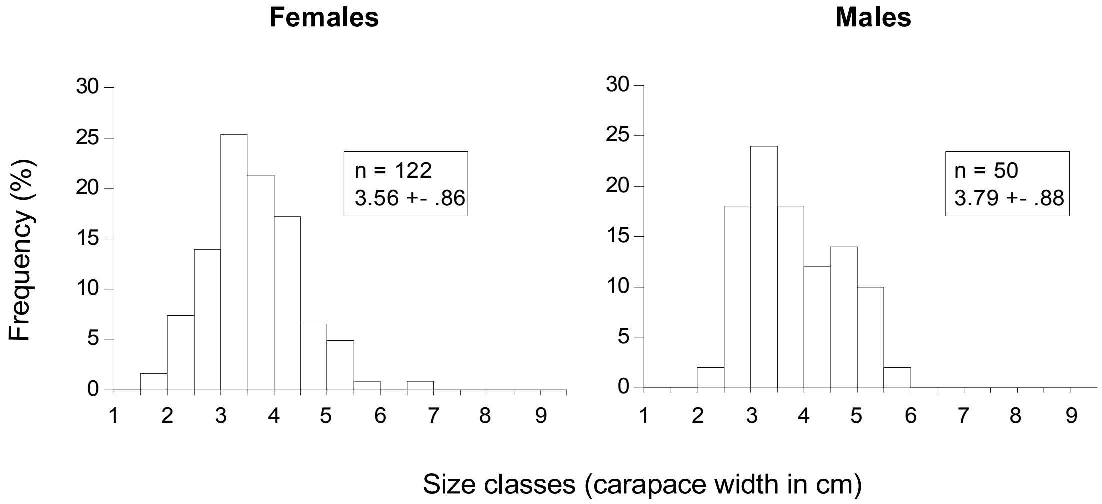


Fig. 37: Size frequency distribution of crabs sampled in peripheral habitats.
In square fields mean carapace width and standard deviation is given.

Sex ratio and abundance In peripheral habitats females were more abundant than males. Near the road they predominated with 61% of the total catch (n=76) with even higher proportions of 79% in the forest gap (n=96). Combined for both sites crab abundance was 4.38 indiv./m² (± 1.59), with 4.16 (±1.17) and 4.61 (±2.04) indiv./m² near the road and at the gap site, respectively.

5.3.2 Size of commercially landed crabs

Approximately 16700 crabs captured by traditional collectors at Furo Grande were measured between February 1998 and July 1999. Only males with a size between 5.0 and 9.1 cm carapace width had been landed and mean size of the catch was 7.3 ± 0.5 cm. Less than 4% of the crabs were smaller than 6.5 cm and in the following all specimens ≥ 6.5 cm are defined as market-sized crabs. Within this size range, the highest portion (43%) fell into the size class of 7.0 to 7.5 cm (Fig. 38).

The size frequency distribution of crabs landed from different capture locations demonstrates a relatively high variability among sites along Furo Grande (Appendix 6a-c), but when the group of near and distant sites are distinguished and compared on a spatial and temporal scale a distinct pattern arises. Pooled mean carapace width and size frequency

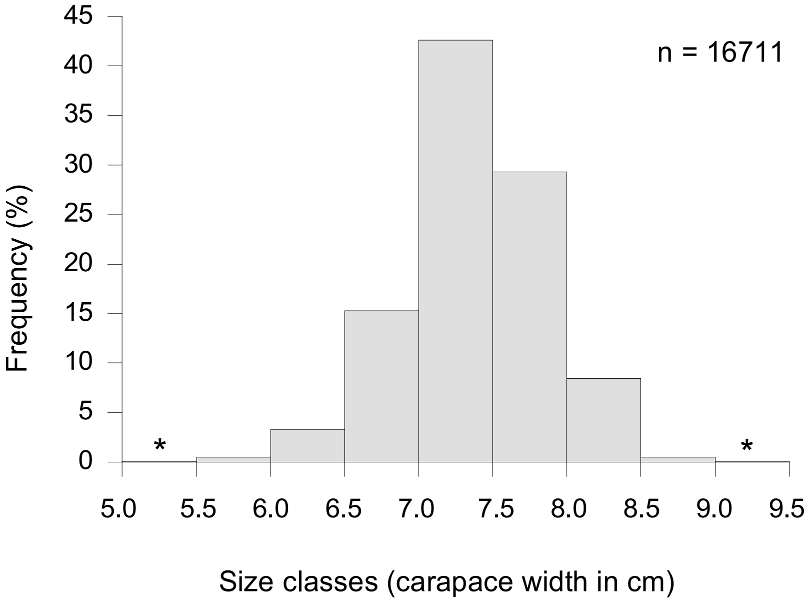


Fig. 38: Size frequency distribution of crabs landed by traditional crab collectors at Furo Grande between February 1998 and July 1999 (pooled data). *: < 0.1%.

distribution for all distant and all near site crabs within the three subsequent study seasons are shown in Fig. 39. The intra-seasonal comparison of males landed from near and distant sites demonstrates, that during the rainy season 1998, mean carapace width of near site crabs was significantly larger than of crabs captured at distant sites (Fig. 39, Appendix 6a-c, Appendix 7). The opposite was the case during the following two seasons, when distant sites yielded distinctly larger males (Fig. 39, Appendix 6a-c, Appendix 7). For both site categories, the inter-seasonal comparison shows that during the rainy season 1998 mean size of landed crabs was lowest whereas highest values were recorded during the rainy season 1999 (Fig. 39, Appendix 7). As indicated by the corresponding size frequency distributions, during the rainy season 1998 the number of small landed crabs (5.0-6.5 cm) was comparably high, which was particularly true for distant sites. The overall portion of large crabs (≥ 8.0 cm) at near sites remained relatively stable throughout the entire study period, whereas at distant bay mouth sites this size class was much stronger in the dry and rainy season 1998/1999 than during the first studied rainy season in 1998 (Fig. 39, Appendix 6a-c).

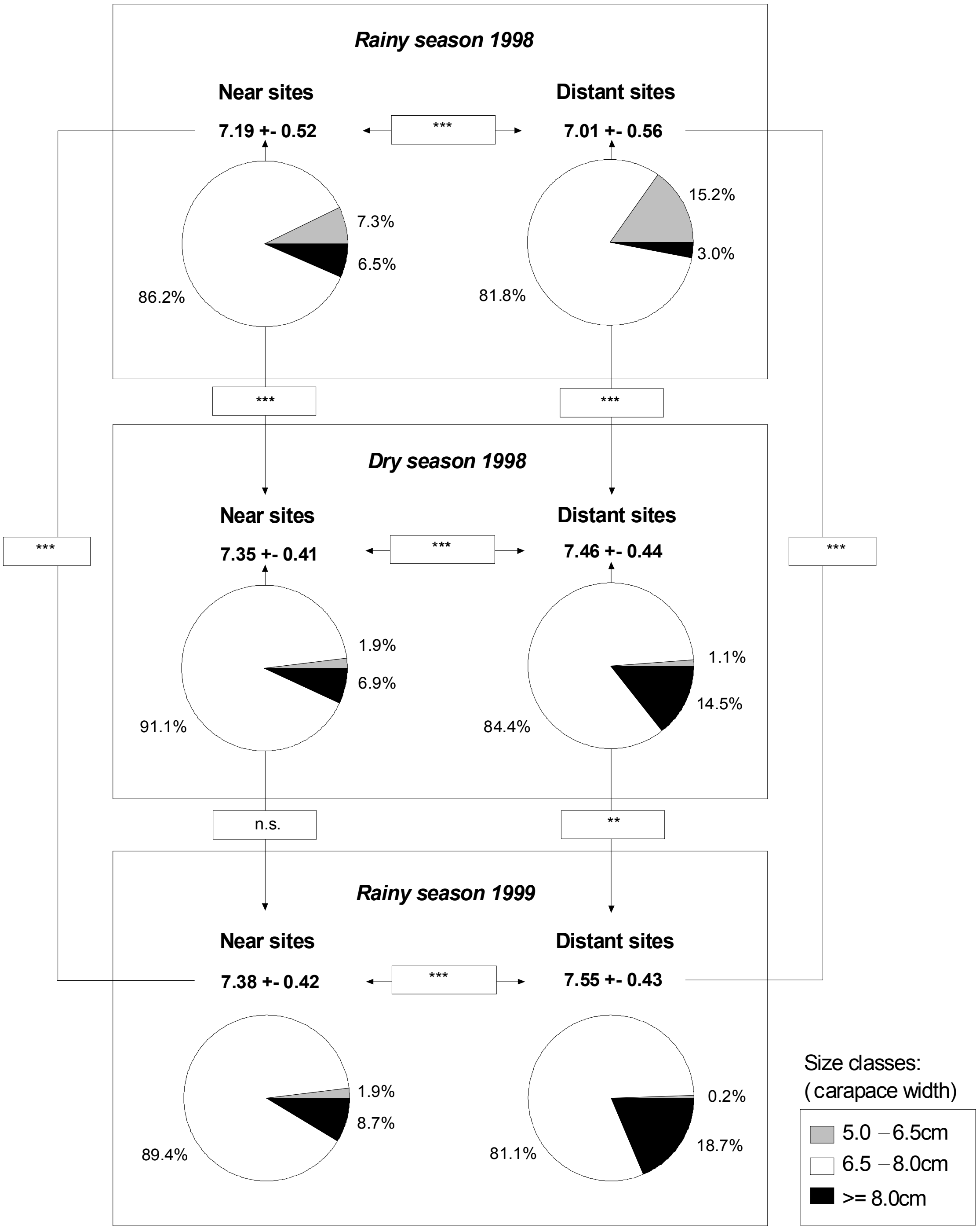


Fig. 39: Mean carapace width and size frequency distribution of crabs landed from near (n = 15) and distant sites (n = 15) during the rainy and dry season in 1998 and rainy season in 1999. Data pooled over replicate sites, n = 630 crabs per site category and season). **: < 0.01; ***: p< 0.001 (statistical analyses: Appendix 7).

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5.4 Discussion

5.4.1 Population structure

For resource evaluation purposes the primary objective was to determine overall size-frequency distribution, sex ratio, abundance and biomass of *U. cordatus* in the *R. mangle* forest habitat, the predominating vegetation type of the Caeté peninsula. As crabs are commercially exploited in the entire mangrove area of the peninsula, it was impossible to study an undisturbed control population. However, beside two relatively fast accessible sampling locations near the starting point of professional crab collectors at Furo Grande, a comparably more distant and thus less easy accessible site was included to the study in order to see whether the population structure at the sites differed as expected by the reportedly differential fishing pressure. This aspect will be addressed after the primary objective – the overall pattern in population structure – has been discussed.

Size frequency distribution and habitat partitioning During the bimonthly sampling in the *R. mangle* forest habitat (August 1997 until August 1998) the size of the crabs ranged between 1.4 cm and 8.8 cm (males) and 7.3 cm (females) carapace width for the combined catch. The high proportion of large crabs at all three study sites throughout the entire study period is striking. This is particularly true for market-sized males which provide almost 40% of the pooled male catch at the three study sites. This finding indicates, that despite many years of exploitation *U. cordatus* has not yet been growth overfished, a point that will be further discussed in section 5.4.2.

A predominance of large crabs in *R. mangle* forests has also been reported from *U. cordatus* populations in Ceará (Alcântara-Filho 1978), Maranhão (Castro 1986) and Sergipe (Nascimento et al. 1982). In the here presented study less than 4% of all specimens captured in the *R. mangle* forest had a carapace width between 1.0 and 4.0 cm. The underepresentation in small size groups can be explained by spatial segregation of different sized crabs, rather than by size biased sampling (except for young of the year crabs, see below). This was shown by additional crab capture outside the *R. mangle* forest. With 67% of the total catch smaller crabs predominated in so called peripheral habitats, e.g. along the embankment of the road crossing the peninsula and in large forest gaps. The observed heterogeneous size distribution and habitat partitioning is likely to be directly or indirectly caused by displacement of smaller by larger crabs. An indication for competitive dominance of larger crabs was given by the fact, that small crabs were two and a half fold more abundant in repopulated areas, from which most crabs had formerly been experimentally removed. Furthermore, it was frequently observed that smaller *U. cordatus* quickly retreat when large conspecifics emerge from neighbouring burrows. Above ground activity of smaller crabs and therewith foraging may thus be hampered in areas with abundant adults, whereas small crabs are likely to be less disturbed in peripheral habitats where large dominating specimens are rare or absent. In these areas with typically poorer canopy coverage than the inner forest habitat, leaf litter – as the presumably most important food source - is provided by wind from trees in the vicinity and by accumulations after tidal inundation. The exploitation of food resources in *U. cordatus* is subject of current research (Nordhaus in prep.).

Neither in peripheral habitats nor during the bimonthly sampling in the *R. mangle* forest newly recruted subjuveniles were captured, despite the large number of megalopae entering the estuary during the rainy season (3.3.2.4). Clearly, due to their small size and cryptic lifestyle young recruits are easily overseen (4.4.1). However, one 2.5 mm crab was captured between *R. mangle* trees near the bridge of Furo Grande, indicating that settlement of first crab stages does occur in areas predominated by adult crabs. Unlike older juveniles young recruits do not compete for food with adults and remain underground most of the time (4.3.1). The majority of juveniles may migrate to peripheral habitats when they begin to forage above ground (see above). As indicated by the low number of large specimens, crabs obviously re-invade back into the *R. mangle* forest when they have reached a certain size and competitive strength.

Sex ratio Despite the fact that only males are exploited by traditional crab collectors since many years, the overall sex ratio was biased towards males with proportions ranging between 53 and 62% at the three study sites in the *R. mangle* forest habitat. A preponderance of males was also reported for exploited populations of *U. cordatus* in Ceará and Sergipe (Castro 1986, Nascimento et al. 1982). When sex ratio was plotted as a function of size, a pattern called anomalous (Wenner 1972) emerged. Females clearly predominated in intermediate size classes with a peak in the 5.0 to 5.5 cm class. From off a carapace width of 6.0 cm males were more frequent. The decrease of males in lower size classes and their preponderance in larger classes is probably related to the diverging growth rate of the two sexes. At a carapace width of approximately 4.5 cm males grow more rapidly than females (Fig. 26, 4.3.2), which reduces the probability of obtaining males at this size. At the same time females accumulate in intermediate size classes due to their smaller maximum body size. When regarding the overall sex ratio, a shift towards equal proportions between sexes or a preponderance of females is expected should the number of market-sized males in the upper size classes of the population be drastically reduced by commercial fishery.

Abundance and biomass In the *R. mangle* forest habitat total mean annual crab density and biomass was 1.7 indiv./m² and 142 g/m², respectively. Rademaker (1998) and Koch (1999) found similar values in *R. mangle* forests stand at Furo do Meio 7 km south of Furo Grande. In Jamaican *Rhizophora* forests mean density was 50% lower than in the Caeté estuary (Warner 1969), but in many other exploited Brazilian *U. cordatus* populations much higher values were observed. For example in Maranhão, Castro (1986) recorded a mean density of 2.9 crabs per m² in habitats predominated by large adults and due to a higher proportion of males (80% of total catch) biomass was even 2.5 times higher (350 g/m²) than in the Caeté area. In Ceará mean crab density was 4.75 indiv./m² (Alcântara-Filho 1978). The reason for the comparably higher crab abundance in other regions – e.g. lower exploitation rate or more favourable environmental factors – are not known. In the Caeté estuary high crab densities of more than 4 indiv./m² were observed in juvenile dominated peripheral habitats. The higher density of smaller versus larger crabs probably reflects their lower degree of territorialism and action radius.

Indication for differential fishing impact and overfishing All three compared study sites were located in old dense forest stands with similar rootage, canopy coverage and silt/clay content of the sediment. One site has easy access from the tarred road and has been subject to crab exploitation since many years. The other two sites can only be reached by boat. Based upon the assumption, that fishing impact declines along with decreasing accessibility, it was expected that the distant site would yield more market-sized males than the nearer sites. For evaluating whether eventual differences are indeed related to differential fishing impact the unexploited female population (compare 5.4.2) was regarded as a control group.

Crab populations at the three sampling locations differed in regard to their size-frequency distribution. In both males and females the proportion of large crabs was higher at the distant than at the nearer sites. However, as both sexes showed a similar site-specific pattern, the different mean size of males cannot be automatically attributed to higher fishing pressure at the one and a lower pressure at the other site. The fact that mean size in females varied accordingly indicates that factors other than fishery must be responsible for these overall dissimilarities. The higher proportion of large crabs at the distant site may reflect older age or – as an alternative – faster growth of the population. Differential growth rates between areas could be caused by differences in food availability (McKoy and Esterman 1981). Leaf litter fall was not determined for the three study areas, but due to similar canopy coverage it is not very likely that different quantities in available food have accounted for the observed differences. Whether differences in the quality of food exist is not known. However, despite the "natural" variation in mean crab size at the three sampling locations, evidence for site specific differential fishing impact was found when male and female class strength in uppermost size classes was compared. Due to market demand professional crab collectors catch only the largest males (see section 5.4.2) and accordingly reduce the number of males in the uppermost size classes. Therefore, if fishing pressure at the near-road and near-upstream site was higher than at the distant site, the number of large males should be over-proportionally lower when compared to the unexploited female control group, regardless of the overall site specific variations. This assumption was exactly confirmed by the data which showed decreasing proportions of larger crabs from the distant to the near-upstream and near-road site, but in males this trend was distinctly more pronounced than in females (Fig. 33). A further indication for differential fishing impact and its consequences was obtained by comparing capture frequencies of the upper size classes over the course of the seven sampling months. For example males falling into the second highest size class were encountered at all seven sampling occasions at the distant site, whereas at the near-road location they were only met in one month. Contrarily, females of corresponding size class were captured in all months at the near-road site. Hence, although the overall differences in size-frequency distributions of the *U. cordatus* populations at the three sites must be attributed to factors other than fishery, the analyses of the uppermost size classes strongly suggests that higher fishing pressure is responsible for the comparably lower abundance and biomass of market-sized males at the near and thus more accessible site. Thus, within the size range of market sized males the uppermost classes seem to be subject to overfishing. This is further evidenced by the different size structure of commercially landings from near and distant sites, which is discussed in the following section (5.4.2).

5.4.2 Size of commercially landed crabs

The size monitoring of crabs landed at Furo Grande has shown, that traditional crab collectors preferentially capture large males. Not a single females was encountered and 96% of the measured specimens had a carapace width of 6.5 cm or larger with a mean landing size of 7.3 cm. The reason for the size and sex selective fishery is market demand. Crabs are sold in strings of 14 living crabs (cambadas, see 5.1.2 Fig. 29 d) and cambadas with large specimens yield the highest market price. Females are rejected as they attain a smaller maximum body size and have distinctly smaller chelae than males.

When considering the many years of crab exploitation in the Caeté estuary, it is astonishing that the *U. cordatus* population still yields so many large males (5.4.1). However, in addition to the population structure analyses (5.3.1), an indication for the impact of fishery was obtained by investigating whether traditional crab collectors landed larger crabs from distant sites than from easier accessible sites close to the bridge crossing the tidal channel Furo Grande. From the bridge, traditional crab collectors travel by canoe to the various capture locations along the channel. As remote up- or downstream sites are more difficult to reach, the hypothesis was that distant sites - due to lower fishing pressure - yield larger crabs. At first sight the results are controversial: Whereas the pattern found during the dry season in 1998 and rainy season 1999 accorded to the hypothesis, the opposite was the case in the rainy season 1998. Here, mean carapace width of distant site crabs was smaller than for crabs landed from near sites. Natural environmental factors responsible for this situation are unknown. But unlike former times and subsequent seasons, during the rainy season 1998 modern crab collectors entered Furo Grande with motorised boats via the northern and southern bay mouths of the channel (5.1.2). They worked primarily far away from the bridge hereby increasing the fishing pressure that the group of traditional collectors already exerted upon distant sites. This may explain why - during the rainy season 1998 - crabs landed from remote sites were smaller than those from near sites. Traditional crab collectors reported that the modern group not only captures large males, but frequently retains smaller specimens as well as some females (see below). The working style of modern collectors is disliked by traditional collectors and at Furo Grande they feared an overfishing of "their" area. This led to a conflict between the two groups and traditional crab collectors hindered the unloading of the motorised boats at the bridge. As a consequence modern collectors ceased working at Furo Grande during the dry season 1998 and rainy season 1999 (information provided by traditional crab collectors) and overall fishing pressure upon distant sites decreased. Subsequently traditional crab collectors landed larger crabs from distant than from near sites. The temporal accordance of the two observations - decreasing fishing pressure and increasing size of landed crabs - strongly suggests a causal relationship. However, as neither frequency and quantity of crab capture nor the exact localities visited by modern collectors could be assessed during the present study, this assumption can not be proved.

Beside the intra-seasonal differences between near and distant sites, an overall increase in mean size of landed crabs irrespective of site category was determined after the rainy season 1998, which may have also been related to the decreasing fishing pressure after the departure of modern collectors. However, the rise in mean landing size was probably also caused by the moulting of crabs during the dry season (4.1). Additionally, our research may have biased the size selection of traditional crab collectors towards larger capture sizes. They became increasingly aware of our crab-size monitoring and some feared that our results could encourage environmental institutions to implement capture restrictions. As a result some traditional crab collectors may have begun to retain less males of smaller size (5.0-6.5 cm carapace width) than formerly.

The central question is whether the *U. cordatus* population in the Caeté estuary is threatened by overfishing, as the relatively slow growth rate of the species (4.4.2) suggests a high vulnerability to fishery. However, traditional crab capture with its current sex and size selectivity yields a high potential for sustainability. As females are unexploited and males mature well before attaining market-size, present traditional fishery does not endanger the reproductive potential of the *U. cordatus* population. The latter is also assumed for modern crab capture for which research upon sex and size of landed crabs is currently in progress (Diele and Glaser in prep.). Preliminary results confirm the statement of traditional crab collectors, that modern fishery is less size and sex selective, but only a small percentage of the yield are females, and males – although smaller – are still captured well above the size where they are likely to reach maturity. Hence, at present there is no indication for a reduction of the spawning stock to levels that may result in lowered recruitment. However, whether recruitment in the *U. cordatus* population of the Caeté estuary is at all a function of its spawning stock is not yet clear. Larvae were shown to be exported and may be dispersed away over long distance, whereas the Caeté population may depend upon recruits originating from other coastal regions (3.4.1).

As indicated by the population structure (5.3.1) and size of landed crabs, until today the male *U. cordatus* population has not been growth overfished. There is no fishing pressure upon smaller individuals that would prevent fishery to produce its maximal yield. However, in section 5.4.1 it was concluded that the targeted uppermost size classes are subject to overfishing, which is also evidenced by the comparably smaller size of crabs landed from easy accessible sites than from distant locations. Furthermore, the overall mean size of landed males (7.3 cm carapace width for traditional fishery) is well below their observed maximum size (9.1 cm). That only a small portion of males naturally reaches a size above 8 cm seems unlikely. Both crab collectors and consumers reported that at former times males landed from the Caeté estuary were distinctly larger than today. Unfortunately, this statement can not be proved as size measurements are unavailable from the past. However, at the market of Bragança cambadas entirely consisting of crabs between 8 and 9 cm carapace width were occasionally offered. These specimens had been captured approximately 40 km north west of Bragança, in an area called Campo 60. The site is well known for its high number of very large males, but due to the inaccessibility by public transport it is only occasionally visited by crab collectors. This probably explains the large size of the captured males. Contrarily, since the construction of the road 15 years ago the Caeté estuary is easily accessible and constantly exploited by a large number of crab collectors. This must have led to an overall decrease in mean size of landed crabs over time, when considering the slow growth rate of the species. However, at Furo Grande mean landing size did not decline during the 1.5 year lasting size monitoring program which indicates that overfishing in the uppermost size classes must be a gradual rather than rapid process.

Thus, the question arises how it is possible that market-sized males are still so frequent despite the over 15 years lasting exploitation and slow growth rate. At first sight this situation seems to be contradictory, but it becomes comprehensive when the structural constraints on crab capture in the mangrove forest are considered. First of all, crab capture is only possible where burrow entrances are accessible and not blocked by roots or dead wood. Secondly, the surrounding sediment must be soft enough to allow the collector to push in his arm or "gancho" (hooked stick) (Fig. 29 a, b) such that the crab can be reached in the depth of its burrow (between 0.9 and 1.8 metres). Finally, underground rooting needs to be absent or rare as it frequently blocks the way to the crab. In many areas these prerequisites for successful capture are not given, as for example around *A. germinans* trees. Here the sediment is comparably sandy as well as dry and a dense carpet of prop roots covers the ground. Therefore *A. germinans* dominated forests - which only cover a small part of the Caeté peninsula - are often neglected by crab collectors.

Contrarily, the widely distributed *Rhizophora* dominated forest stands are regularly exploited as they are more suitable for crab fishing due to overall softer sediment and different root structure. However, on several occasions when crab collectors were followed during their normal work, it was realised that even in this forest type only a part of the actually existing number of large crab burrows is suitable for a capture attempt. These are burrows that are located in patches with few or medium dense stilt roots, whereas those in-between dense stilt roots remain untouched. Hence, in the mangrove fringed Caeté estuary, blanket coverage capture of *U. cordatus* is prevented by small-scale environmental factors. The resulting mosaic of naturally protected patches acts as a buffer or refuge for market-sized crabs. Unless they move to more accessible and thus fishable areas (see below), crabs inhabiting these refuge habitats are not affected by fishery. The total surface area occupied by refugia is difficult to determine. Visual inspection suggests a value of 40% in *R. mangle* dominates forests, an estimation which will be ascertained during a large-scale forest structure monitoring (Schories in prep.). However, already after visual inspection alone, it seems reasonable to postulate that the total area of naturally fishery protected patches within the Caeté peninsula is remarkably large. It is concluded that these refugia have played a major role in delaying severe overfishing of large males up to the present. Their existence may also explain the fact that experimentally emptied sampling areas were re-inhabited by crabs within few days (5.3.1.1). Accordingly, crab collectors have reported that freshly exploited areas yield considerable numbers of market-sized specimens after two to three weeks without fishery impact. This indicates a relatively high buffer capacity, mobility and consequently burrow turn over of the population.

In summary, the sustainable size and sex selective crab fishery together with the numerous natural refugia are assumed to be responsible for the fact, that *U. cordatus* in the Caeté estuary has neither been recruitment- nor growth overfished - despite the many years of exploitation and slow growth rate of the species. Nevertheless, the low abundance of very large males (≥ 8.0 cm carapace width) indicates that overfishing does occur – at least in the uppermost size classes.

If future fishing pressure remains at its present state or even increases, it seems likely that the buffer capacity eventually becomes depleted and the number of large crabs distinctly declines. This would result in a decrease in size as well as in numbers of landed specimens. Consumers purchasing traditionally landed livestock will either accept smaller market sizes, or – if offered for sale – buy larger crabs from other regions. In response to sinking earning prospects, the number of traditional crab collectors exploiting the Caeté estuary will probably decline. Some will move to better fishing areas, others will change to more profitable occupations, but when regarding the economical situation of the region as well as the poor education of crab collectors (Glaser 1999), the latter seems little realistic. Modern collectors will be similarly affected by a future decline in landing sizes and quantities, although purchasing meat processors – already today - accept smaller crabs than livestock consumers. However, latest when the majority of landed legs and chelae are derived from small specimens around 4.5 cm carapace width, meat processing will become unprofitable. Due to these self-regulating market mechanisms and the high number of refugia it is most unlikely that the survival of the *U. cordatus* population as a whole can ever be seriously endangered by traditional or modern fishery.

6 CONCLUSIONS AND PERSPECTIVES

Environmental organisations and user groups are increasingly concerned about the future abundance of *U. cordatus* in the Caeté estuary as presently more than 50% of the rural households directly depend on crab fishery (Glaser 1999). Recent conflicts between traditional and modern crab collectors, who compete for fishing grounds, demonstrate their fear that this resource may not be unlimited and that future yields may decrease. In addition to professional crab collectors exploiting the Caeté peninsula since many years, unprofessional locals and villagers from the hinterland supply themselves with large amounts of crabs during mate searching times. At these so called andança events, trucks from as far as Belém (210 km) enter the peninsula and are quickly loaded as mate searching crabs leave their burrows in large numbers and are thus very easy to catch. Particularly in view of this mass capture events national government organisations began to consider the implementation of management plans for *U. cordatus*.

The present work, which focussed on reproduction and growth of *U. cordatus* as well as on the state of the exploited population in the Caeté estuary, provides new knowledge on the biology of these crabs, which forms an essential base for sustainable management plans. Both phases of the life cycle of *U. cordatus* were studied, the pelagic larvae as well as the semiterrestrial juveniles and adults that inhabit the mangrove forest. A schematic view of the life history of *U. cordatus* is given in Fig. 40. In adult crabs moulting was confined to the dry season, whereas reproduction occurred in the rainy season with larval output between January and June (Fig. 40). During the three study years a strict lunar rhythm was found for both mass mate searching activities (andança) and subsequent spawning which exclusively took place once per month around new moon. The onset of sexual maturity as indicated by the smallest female found with eggs occurs at a carapace width of 3.1 cm, which corresponds to an age of approximately 2.1 to 3 years (Fig. 40). Andança events lasted for up to 4 days and a distinct peak occurred in either January or February. If mass capture of mate searching crabs is to be prevented, a short-term capture restriction covering the few days of andança would suffice instead of closing the Caeté peninsula for several months during the reproductive season as was outlined by a legislation framework in 1997 ("Programa de preservação do caranguejo Uça no estado do Pará, Lei 6.082", 13.11.1997). Its implementation would render the crab collector community without income for 1/3 of the year, a point that was disregarded by decision makers.

The time span of one complete reproductive cycle from mate searching over breeding, spawning and subsequent post-larval return was determined for the first time and encompassed approximately two months (Fig. 40). Precisely timed larval release around slack spring high tides promoted rapid export of the zoeae with the ebbing water masses from the

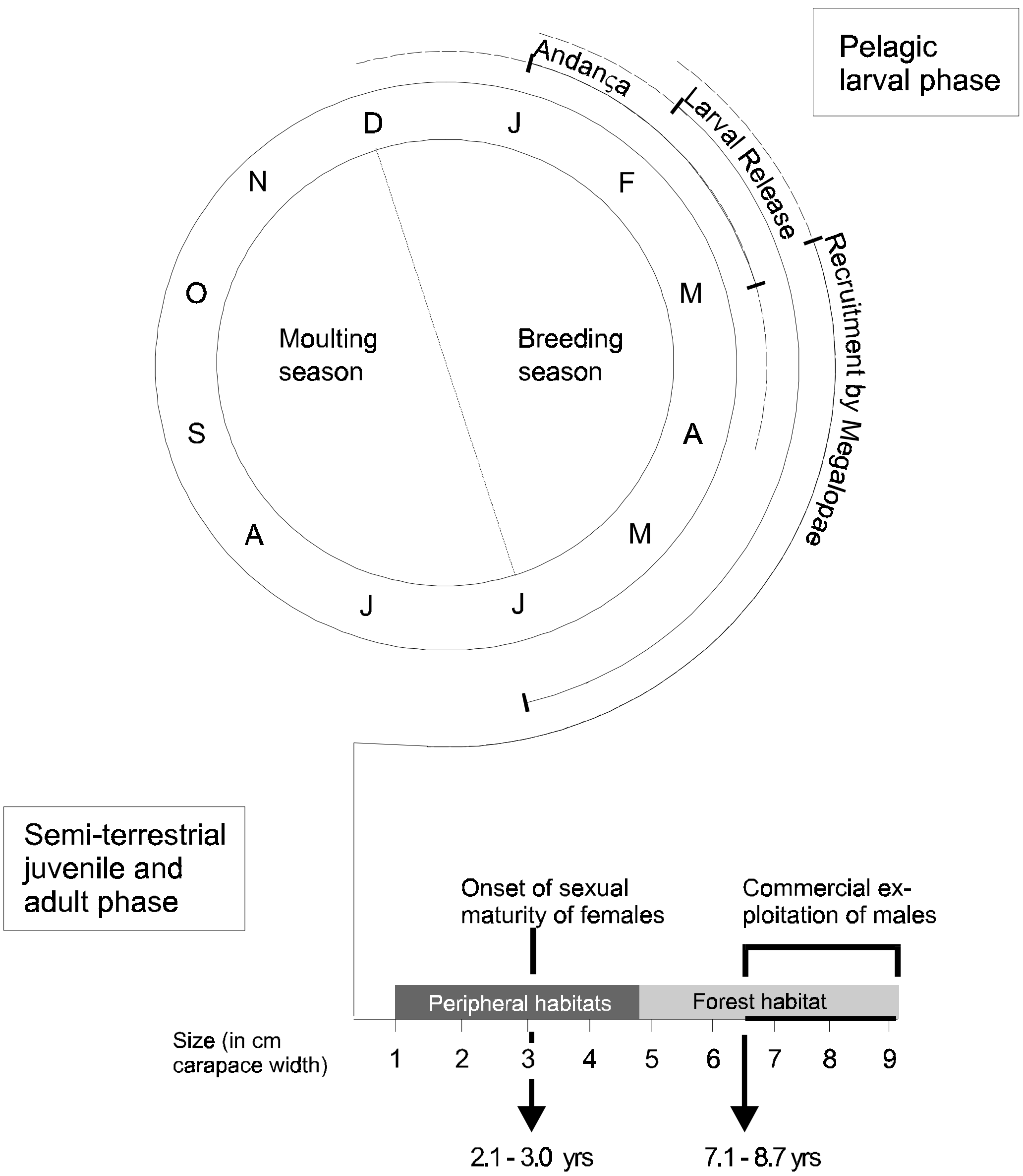

Fig. 40: Schematic of the life history of *U. cordatus*.
Hatched parts of curves indicate inter-annual variability. "Peripheral habitats" and "Forest habitat" refer to the dominance of respective sized crabs in each habitat. Arrows highlight estimated age in years at given size. (Layout modified after Botsford et al. 1989).

inner estuary to off-shore waters. Absence of later stage zoeae in tidal channels indicated that the larvae remained offshore throughout their approximately three to four weeks of development. The finding that zoea larvae are exported gave rise to the hypothesis that *U. cordatus* populations of possibly distant localities are interconnected as coastal or oceanic currents may disperse the offspring over a wide geographical area (3.3.2.2). Thus, future stock of the population of the Caeté peninsula may be influenced by- or even dependent on returning recruits expelled from another. In this case management considerations for the crab population of the Caeté estuary could not rely upon spawning stock recruitment relationships (McConnaughey et al. 1992). As long as the above mentioned hypothesis has not been disapproved, protection and management plans should consider a regional rather than local frame. Interconnected coastal crab populations could be managed by preserving specific areas as refugia from environmental degradation and harvest - such as presently still undeveloped mangrove regions - to provide sources of larvae to seed other areas in the future. A growing interest for such management considerations exists for dungness crab populations (*Cancer magister*) from northern California to the Canada border (Botsford et al. 1994).

Recruitment into the Caeté crab population was accomplished by discrete pulses of re-invading megalopae three to four weeks after former larval release (Fig. 40), again with a peak near new moon. As the timing of megalopal re-invasion is now accurately known future research should aim for the determination of recruit supply over the course of several years. The importance of this relies upon the fact, that inter-annual variations in larval/postlarval numbers may be large (3.4.2) and that attempts to conserve or manage exploited populations are dependent upon the precision of predictions made about future numbers in the population (Underwood & Fairweather 1989). Post-larval supply, in setting the upper limit of recruitment, clearly is one factor that influences the eventual demographic of a population.

A recently settled young-of-the-year crab (2.5 mm carapace width) was encountered in the mangrove forest for the first time. Due to the small size and the cryptic life style of settling crabs, even now as the time of arrival in the forest is known, it remains difficult to study their behaviour and abundance in the field. In the laboratory young recruits spent most of the time underground in minute burrows and they were observed to feed upon infauna. This explains why early settlers are difficult to encounter, but even larger juveniles that feed upon leaf litter and consequently spend considerable time above ground, were rarely met during the population structure analyses in the *R. mangle* forest habitat (Fig. 40). Less than 4% of all captured specimens had a carapace width between 1 and 4 cm. The paucity of smaller versus large crabs inside *R. mangle* forest stands was not caused by cryptic behaviour or size-biased sampling. Instead, later juveniles were very abundant in peripheral areas such as for example near the embankment of the road or in large forest gaps, probably due to competitive displacement by larger crabs. The latter were scarce in peripheral habitats which suggests that crabs migrate back into the presumably more favourable inner Rhizophora forest when they have reached a certain size and competitive strength (Fig. 40).

Whereas peripheral habitats are unaffected by commercial exploitation, the inner *R. mangle* forest with its abundant large crabs, is the most important working fishing ground of traditional and modern crab collectors (5.1.2). Mean crab abundance and biomass in this habitat was 1.7 individuals and 142 g per m², respectively. Due to market demand extraction is confined to the upper size classes of the population. As females attain a smaller maximum body size they are mostly rejected, whereas large males are harvested in high numbers since many years. It is therefore remarkable, that still 40% of all males sampled in the *R. mangle* forest had commercial size (≥ 6.5 cm carapace width). At the same time it was shown that *U. cordatus* is a relatively slow growing species and that males at a size of 6.5 cm are approximately 7.1 to 8.7 years old (Fig. 40). The most frequently harvested specimens with 7.0 to 7.5 carapace width have an approximate age between 8.5 and 12.4 years. These age at size estimates base upon more than 200 growth increment data of a wide range of different sized specimens, of which the majority was kept in a field enclosure. The importance of obtaining field data was emphasised by the twofold higher relative size increment of crabs similar in size as specimens considered in former laboratory studies (Ostrensky et al. 1995).

The slow growth of *U. cordatus* suggests a high vulnerability to overfishing. However, despite the many years of exploitation in the Caeté estuary, the population structure analyses and monitoring of the size of landed crabs revealed that the population in the Caeté estuary has not been growth overfished. At present there is no fishing pressure upon smaller crabs that would prevent fishery to produce its maximal yield. Although only large males are exploited they are still considerable abundant. This points to a high buffer capacity of the system which may result from mosaic refugia that prevent blanket coverage exploitation. Refugia are patches unsuited to crab capture, for example areas with dense stilt roots, and may act as source for replenishment of fishable patches. However, the reduced number of males in the uppermost size classes in frequently exploited areas indicates that the puffer capacity at these sites is becoming depleted. In future times this may result in a distinct drop in numbers of large males and as a consequence smaller crabs may be affected by fishery.

Due to self-controlling market mechanisms (5.4.2) and the natural prevention of blanket coverage fishery in the mangrove forest habitat it seems unlikely that the persistence of the *U. cordatus* population as a whole can be endangered by fishery, even if future fishing pressure increases. Although at present the number of large males still sustains the crab collectors in the Caeté estuary, this study also provided results suggesting a decline of the future yield, which underlines a need for management plans. During meetings with user communities first results of the socioeconomical and biological work of the MADAM proj??ect were presented with considerable feed-back. Further activities included bringing together local user groups with governmental decision makers. Since August 1999 the Ministry of Agrarian Reform and Development examines the possibility to implement extractive reserves ("reservas extrativista"). The idea is to prevent increasing fishing pressure by "freezing" the present number of crab collectors by prohibiting the extraction of *U. cordatus* to newcomers. The approach integrates local user communities who are actively taking part in the process of decision making and managing of the exploited areas. Traditional crab collectors support the plan of prohibiting capture during the few days of mate searching activities and modern crab collectors offered to refrain from the capture of females and to respect a "reasonable" minimum capture size which is currently under discussion (Glaser, pers. comm.). The joint concern and approach of government and user groups is a very positive step towards ecologically, economically and socially sustainable policy development.

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8 APPENDICES

Appendix 1: Comparison of environmental factors of the three transect-sampling sites

Canopy coverage

a) Test for homogeneity of variances

Hartley´s F-max = 1.1847, $p>0.05$

b) F-Test

	df effect	MS effect	MS error	df error	F	p-level
site	2	175.1676	611.2680	148	0.2865	0.7513

R. mangle rootage

a) Test for homogeneity of variances

Hartley´s F-max = 1.7154, $p>0.05$

b) F-Test

	df effect	MS effect	MS error	df error	F	p-level
site	2	1532.863	646.6841	159	2.3703	0.0967

A. germinans rootage

a) Test for homogeneity of variances

Hartley´s F-max = 1.2826, $p>0.05$

b) F-Test

	df effect	MS effect	MS error	df error	F	p-level
site	2	244.4364	338.0005	159	0.7232	0.4868

Silt/clay content

a) Test for homogeneity of variances

Hartley´s F-max = 1.7916, $p>0.05$

b) F-Test

	df effect	MS effect	MS error	df error	F	p-level
site	2	3104.244	491.1302	156	6.3206	0.0023

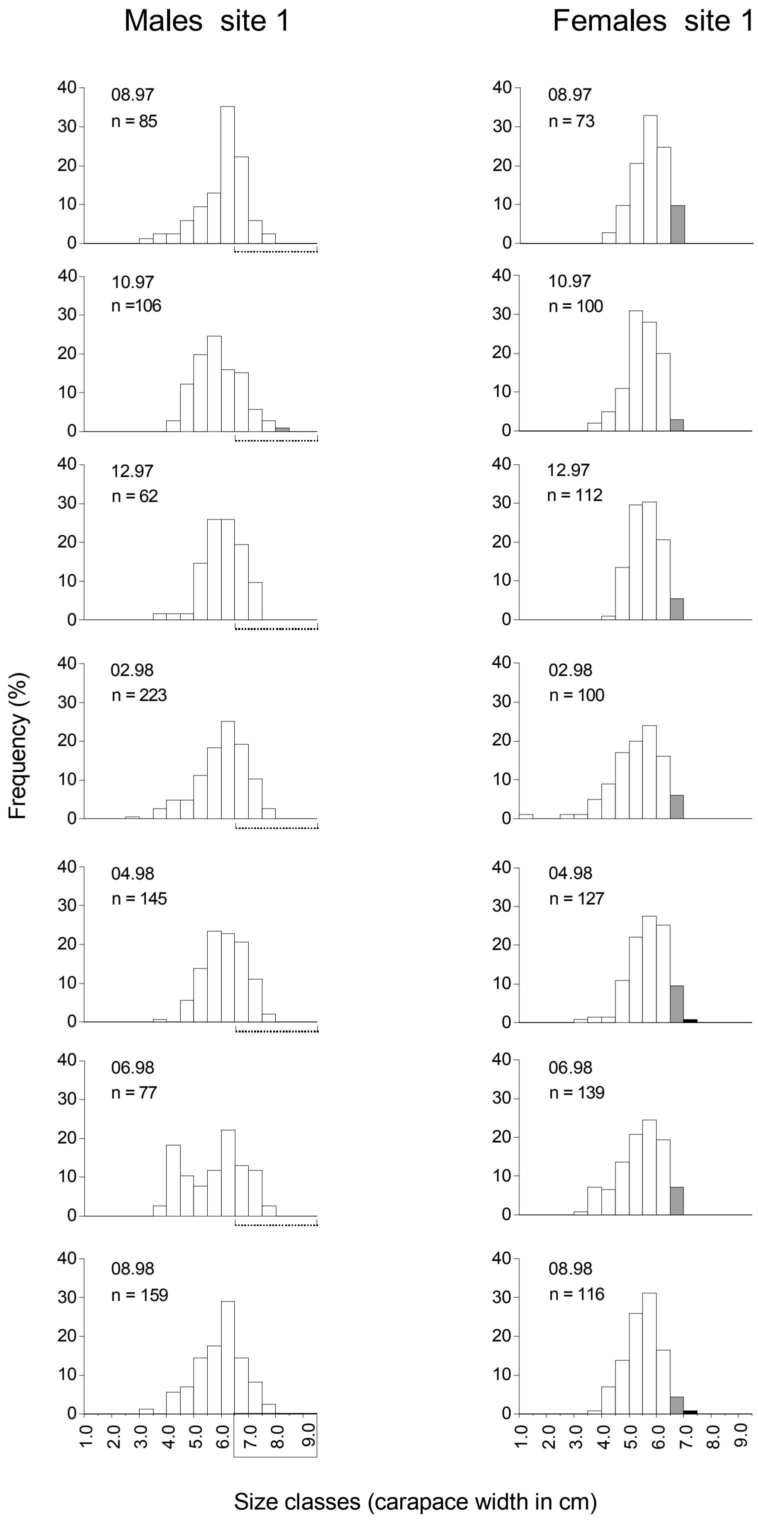
c) post hoc comparison

Tukeys HSD-Test

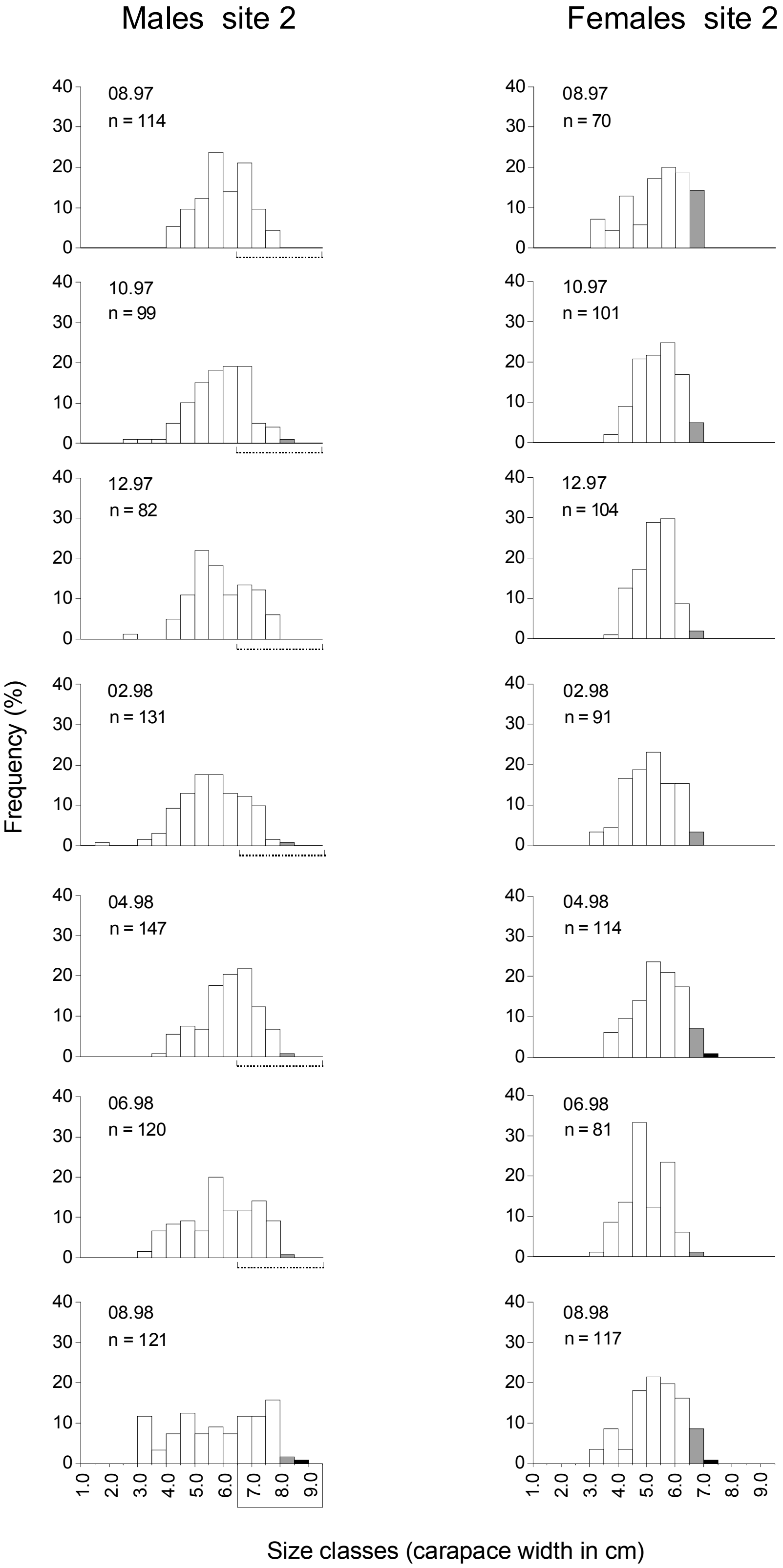
		{1}	{2}	{3}
mean		60.91154	75.58679	72.26667
site 1	{1}	-	0.002128	0.024396
site 2	{2}	0.002128	-	0.720719
site 3	{3}	0.024396	0.720719	-

Appendix 2: Bimonthly size frequency distribution of crabs sampled in the *R. mangle* forest (08.97-08.98)

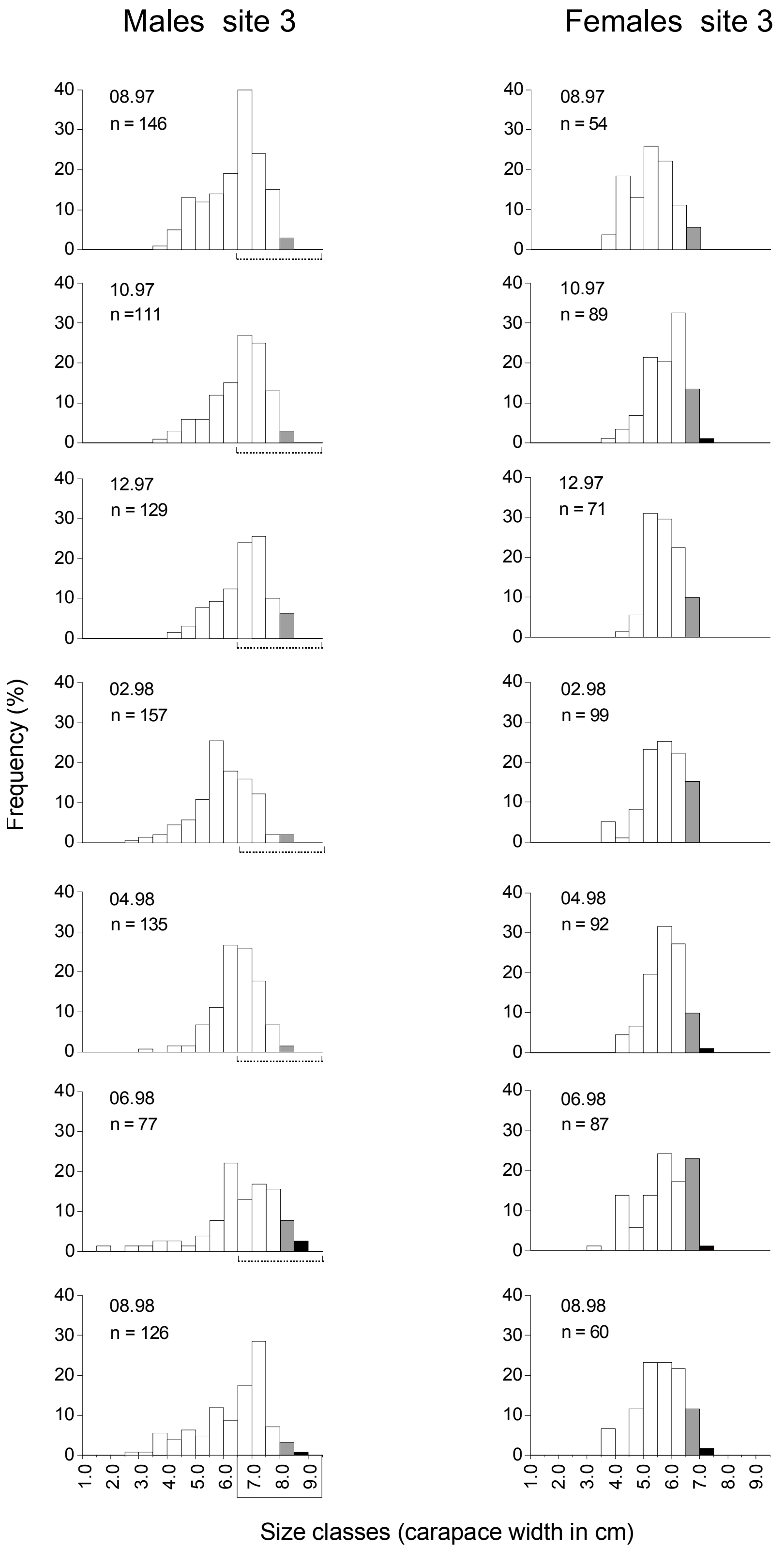
2a) Near road site: Brackets indicate commercially exploited size classes. Catch falling into the highest (black) and second highest classes (grey) that were found over the entire sampling period at the three study sites (see 2b and c) is highlighted by filled bars.



2b) Bimonthly size frequency distribution of crabs sampled in the *R. mangle* forest (08.97-08.98) at the **near-upstream site**. For further explanation see Appendix 2a.



2c) Bimonthly size frequency distribution of crabs sampled in the *R. mangle* forest (08.97-08.98) at the **distant-upstream site**. for further explanation see Appendix 2a.



Appendix 3: Chi^2 test for size frequency independence of site at three *R. mangle* forest sampling sites
1: near-road site; 2: near-upstream site; 3: distant upstream-site

App. 3 a **Males** chi^2 = 224.85 $p < 0.0001$ 20 df

Size class (cm carapace width)	Observed Frequencies			Expected frequencies			Observed - expected			Cell chi^2		
	site 1	site 2	site 3	site 1	site 2	site 3	site 1	site 2	site 3	site 1	site 2	site 3
< 3.5	4	22	9	12	11	12	-8	11	-3	5.12	10.52	0.79
3.5 - 4.0	12	18	14	15	14	15	-3	4	-1	0.52	1.12	0.09
4.0 - 4.5	40	54	26	40	38	41	0	16	-15	0.00	6.46	5.74
4.5 - 5.0	57	84	43	62	59	64	-5	25	-21	0.37	10.92	6.63
5.0 - 5.5	112	97	63	91	87	94	21	10	-31	4.67	1.21	10.17
5.5 - 6.0	165	144	114	142	135	146	23	9	-32	3.71	0.61	7.03
6.0 - 6.5	215	114	142	158	150	163	57	-36	-21	20.42	8.74	2.61
6.5 - 7.0	153	130	190	159	151	163	-6	-21	27	0.22	2.89	4.37
7.0 - 7.5	78	88	174	114	108	117	-36	-20	57	11.46	3.86	27.32
7.5 - 8.0	20	56	74	50	48	52	-30	8	22	18.31	1.39	9.53
≥ 8.0	1	7	32	13	13	14	-12	-6	18	11.51	2.60	23.97

App. 3 b **Females** chi^2 = 111.76 $p < 0.0001$ 14 df

Size class (cm carapace width)	Observed Frequencies			Expected frequencies			Observed - expected			Cell chi^2		
	site 1	site 2	site 3	site 1	site 2	site 3	site 1	site 2	site 3	site 1	site 2	site 3
< 3.5	5	13	1	7	6	5	-2	7	-4	0.72	6.65	3.44
3.5 - 4.0	20	34	12	25	22	18	-5	12	-6	1.13	6.00	2.14
4.0 - 4.5	36	72	31	53	47	38	-17	25	-7	5.66	13.04	1.43
4.5 - 5.0	99	124	43	102	90	74	-3	34	-31	0.10	12.57	12.67
5.0 - 5.5	186	147	122	175	154	126	11	-7	-4	0.72	0.36	0.11
5.5 - 6.0	215	150	140	194	171	140	21	-21	0	2.28	2.68	0.00
6.0 - 6.5	155	97	126	145	128	104	10	-31	22	0.66	7.65	4.43
6.5 - 7.0	51	41	77	65	57	47	-14	-16	30	2.98	4.67	19.64

Appendix 4: Comparison of crab biomass and crab abundance between sites

Total crab abundance

a) Test for homogeneity of variances

Hartley´s F-max = 80.49426, $p < 0.0001$

b) F-Test (nested Anova)

	Sum of squares	Degrees of freedom	Mean square	F-ratio	
site (n = 3)	5.385	2	2.648761	4.994561	$p < 0.05$
months (n = 7)	9.5459	18	0.530329		
quadrats (n = 162)	23.7510	141	0.168447		

c) Post hoc comparison
Tukeys HSD-Test

		{1} 1.910476	{2} 1.534388	{3} 1.510000
near road site	{1}	-	0.000030	0.000023
near upstream site	{2}	0.000030	-	0.947886
distant upstream site	{3}	0.000023	0.947886	-

Female abundance

a) Test for homogeneity of variances

Hartley´s F-max = 171.5675, $p < 0.0001$

b) F-Test (nested Anova)

	Sum of squares	Degrees of freedom	Mean square	F-ratio	
site (n = 3)	3.485624	2	1.742812	15.13291	$p < 0.0001$
months (n = 7)	2.073006	18	0.115167		
quadrats (n = 162)	107.3574	141	0.76140		

c) Post hoc comparison
Tukeys HSD-Test

		{1} 0.923028	{2} 0.698999	{3} 0.574080
near road site	{1}	-	0.000074	0.000022
near upstream site	{2}	0.000074	-	0.042824
distant upstream site	{3}	0.000022	0.042824	-

Male abundance

a) Test for homogeneity of variances
Transformation: log (x+1)

Hartley´s F-max = 18.82978, $p < 0.05$

b) F-Test

		Sum of squares	Degrees of freedom	Mean square	F-ratio	
site	(n = 3)	0.107036	2	0.053518	0.419085	$p > 0.05$
months	(n = 7)	2.298636	18	0.127702		
quadrats	(n = 162)	3.072249	141	0.021789		

Abundance of market sized males

a) Test for homogeneity of variances
Transformation: log (x+1)

Hartley´s F-max = 12.45123, $p < 0.05$

b) F-Test

log(x+1)		Sum of squares	Degrees of freedom	Mean square	F-ratio	
site	(n = 3)	0.808832	2	0.404416	8.26013	$p < 0.01$
months	(n = 7)	0.88128	18	0.048960		
quadrats	(n = 162)	3.779223	141	0.026803		

c) post hoc comparison
Tukeys HSD-Test

log (x+1)		{1} 0.2357134	{2} 0.2341121	{3} 0.3843631
near road site	{1}	-	0.998630	0.000032
near upstream site	{2}	0.998630	-	0.000026
distant upstream site	{3}	0.000032	0.000026	-

Total crab biomass

a) Test for homogeneity of variances
Transformation: log(x+1)

Hartleys´s F-max = 42.42879, $p < 0.05$

b) F-Test (nested Anova)

log(x+1)	Sum of squares	Degrees of freedom	Mean square	F-ratio	
site (n = 3)	1.919506	2	0.959753	4.59165	$p < 0.05$
months (n = 7)	3.762378	18	0.209021		
quadrats (n = 162)	11.36093	141	0.080574		

c) Post hoc comparison
Tukeys HSD-Test

log(x+1)		{1} 5.001210	{2} 4.755950	{3} 4.968966
near road site	{1}	-	0.000051	0.831239
near upstream site	{2}	0.000051	-	0.000261
distant upstream site	{3}	0.831239	0.000261	-

Female biomass

a) Test for homogeneity of variances
Tranformation: sqrt (x+1)

Hartley´s F-max =20.53138, $p < 0.01$

b) F-Test

sqrt(x+1)	Sum of squares	Degrees of freedom	Mean square	F-ratio	
site (n = 3)	65.97658	2	32.98829	8.66227	$p < 0.01$
months (n = 7)	68.54886	18	3.80827		
quadrats (n = 162)	267.40495	141	1.896489		

c) Post hoc comparison
Tukeys HSD-Test

sqrt(x+1)		{1} 0.9300538	{2} 0.6984088	{3} 0.5719012
near road site	{1}	-	0.00074	0.000022
near upstream site	{2}	0.000074	-	0.042824
distant upstream site	{3}	0.000022	0.042824	-

Male biomass

a) Test for homogeneity of variances
Transformation: log(x+1)

Hartley´s F-max = 5.856671, p > 0.05

b) F-Test

log(x+1)	Sum of squares	Degrees of freedom	Mean square	F-ratio	
site (n = 3)	2.5069	2	1.253450	1.93130	p > 0.05
months (n = 7)	11.682324	18	0.649018		
quadrats (n = 162)	24.203214	141	0.171654		

Biomass of market sized males

a) Test for homogeneity of variances

Hartley´s F-max = 61.79760, p < 0.0001

b) F-Test (nested Anova)

	Sum of squares	Degrees of freedom	Mean square	F-ratio	
site (n = 3)	42212.76	2	21106.38	8.37039	p < 0.01
months (n = 7)	45387.9	18	2521.55		
quadrats (n = 162)	250876.93	141	1779.269		

c) Post hoc comparison
Tukeys HSD-Test

		{1} 44.06117	{2} 39.92325	{3} 75.55592
near road site	{1}	-	0.894501	0.000325
near upstream site	{2}	0.894501	-	0.000045
distant upstream site	{3}	0.000325	0.000045	-

Appendix 5: Chi² test for size frequency independence of site in peripheral habitats
G: gap; R: near-road

Appendix 5a **Females** chi² = 3.446 $p > 0.05$ 4 df

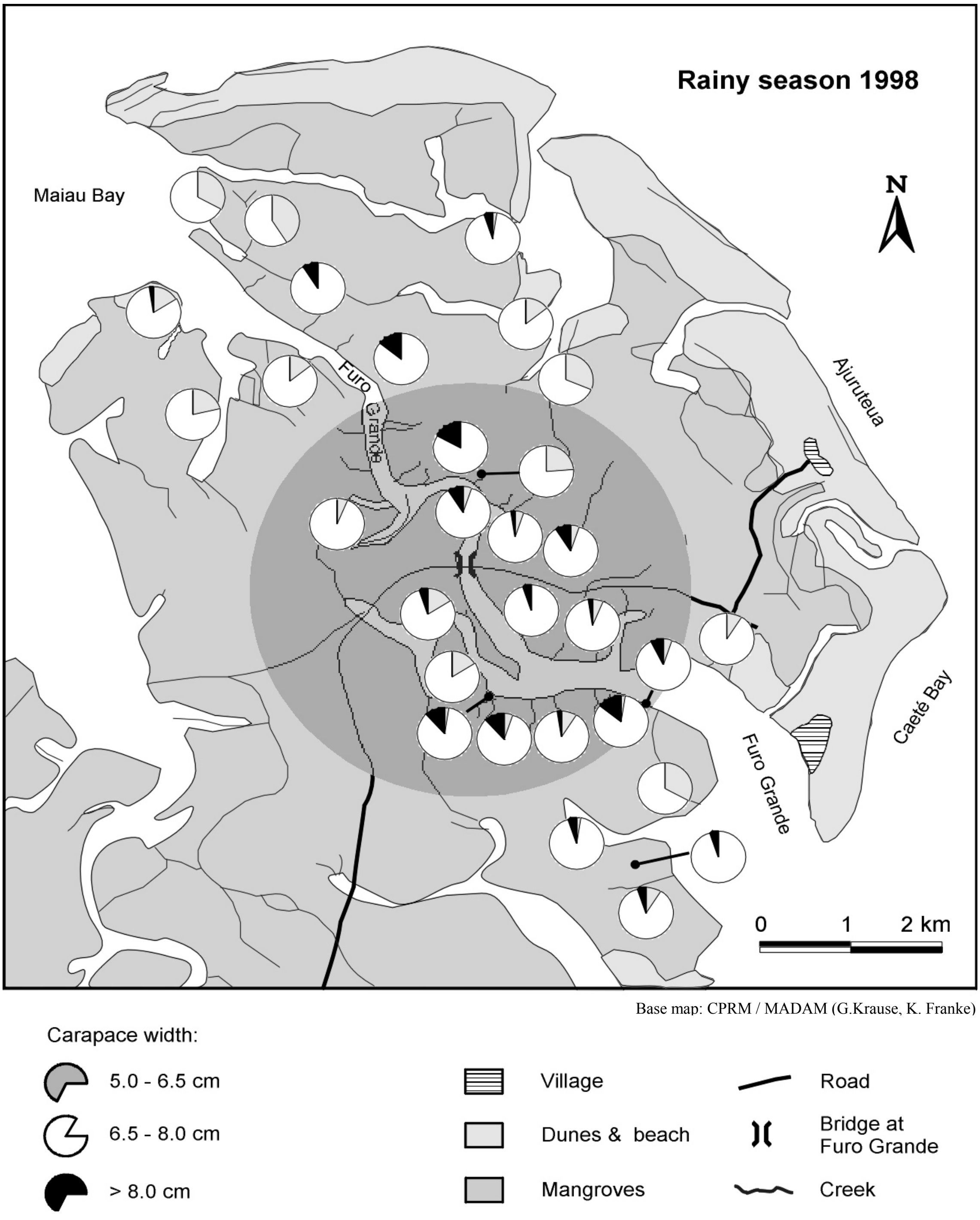
size class (cm)	Observed Frequencies		Expected frequencies		Observed - expected		Cell chi²	
carapace width	**G**	**R**	**G**	**R**	**G**	**R**	**G**	**R**
<3.0	19	9	17.443	10.557	1.557	-1.557	0.139	0.230
3.0-3.5	21	10	19.311	11.698	1.689	-1.698	0.148	0.244
3.5-4.0	17	9	16.197	9.803	0.803	-0.803	0.040	0.066
4.0-4.5	12	9	13.082	7.918	-1.082	1.082	0.089	0.148
≥4.5	7	9	9.967	6.033	-2.967	2.967	0.883	1.459

Appendix: 5b **Males and females combined** chi² = 3.417 $p > 0.05$ 6 df

size class (cm)	Observed Frequencies		Expected frequencies		Observed - expected		Cell chi²	
carapace width	**G**	**R**	**G**	**R**	**G**	**R**	**G**	**R**
<2.5	7	5	6.698	5.302	0.302	-0.302	0.014	0.017
2.5-3.0	15	11	14.512	11.488	0.488	-0.488	0.016	0.021
3.0-3.5	27	16	24.000	19.000	3.000	-3.000	0.375	0.474
3.5-4.0	20	15	19.535	15.465	0.465	-0.465	0.011	0.014
4.0-4.5	15	12	15.070	11.930	-0.070	0.070	3.2E-4	4.1 E-4
4.5-5.0	6	9	8.372	6.628	-2.372	2.372	0.672	0.849
≥5.0	6	8	7.814	6.186	-1.814	1.814	0.421	0.532

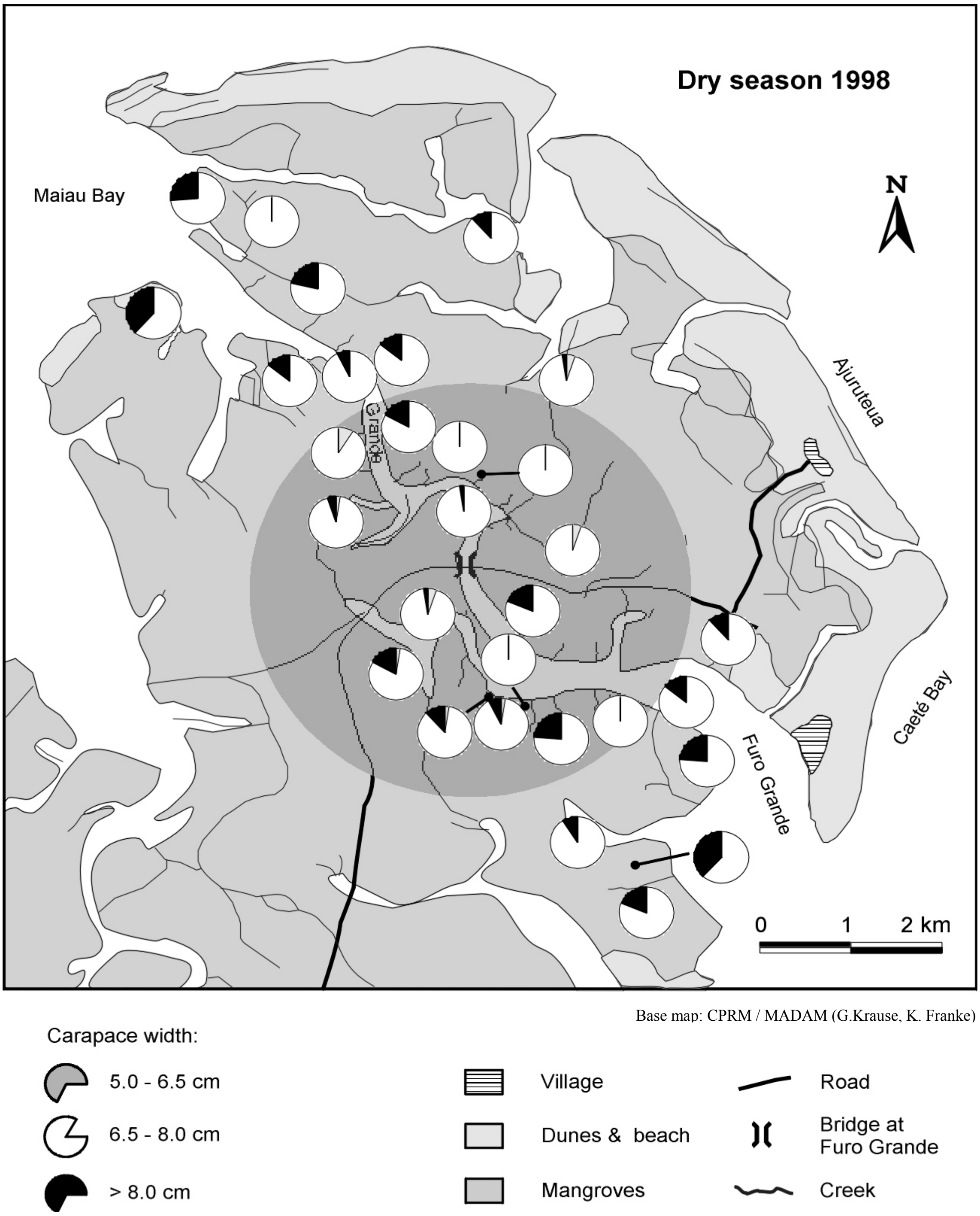
Appendix 6: Size frequency distribution for crabs landed from different capture localities along Furo Grande. a) Rainy season 1998; b) Dry season 1998; c) Rainy season 1999. Inner grey circle marks distance to bridge, sites located within and outside the circle represent the category "near" and "distant", respectively. n = 15 replicate sites per category; n = 42 crabs per replicate site.

Appendix 6a:



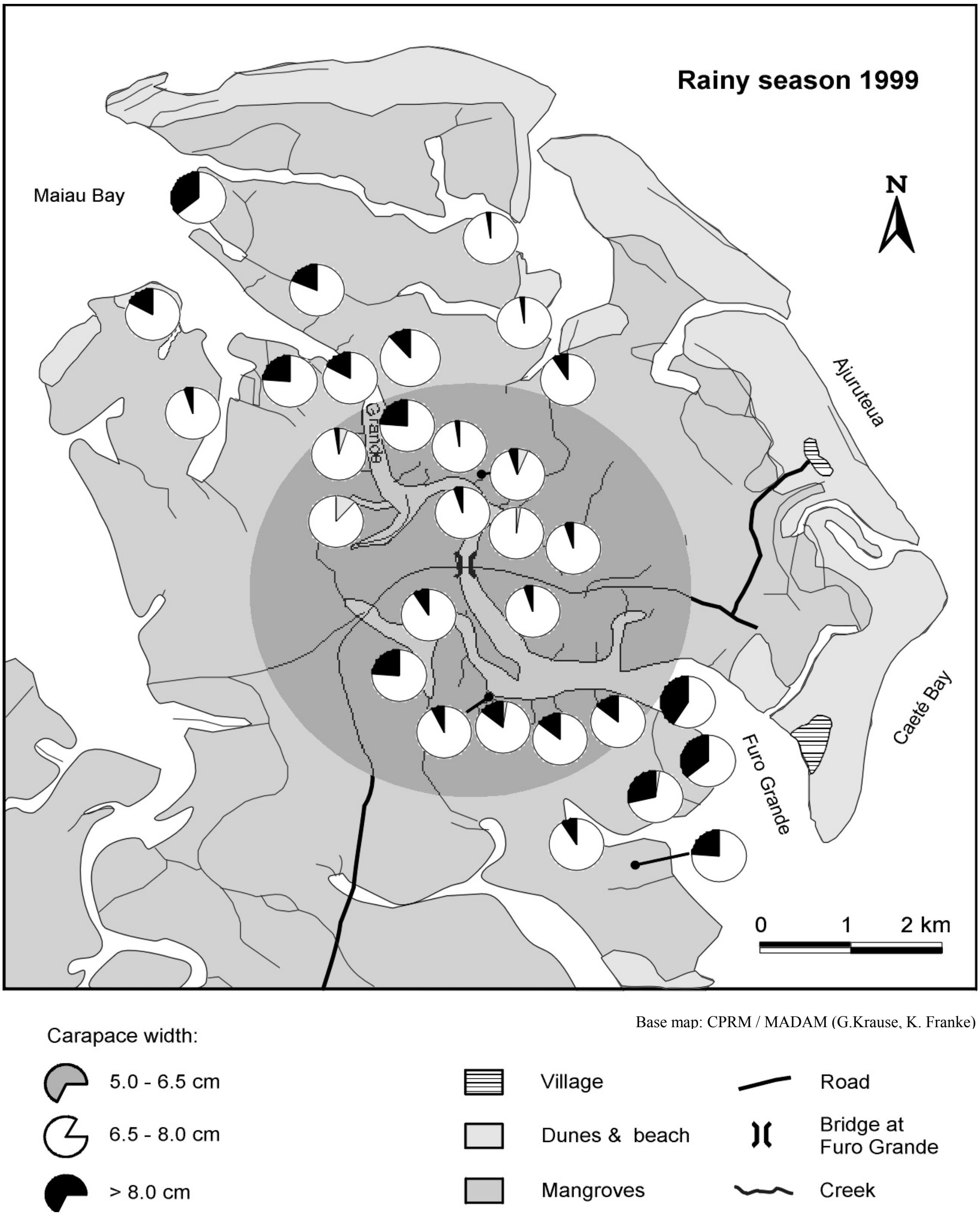
Base map: CPRM / MADAM (G.Krause, K. Franke)

Appendix 6b:



Base map: CPRM / MADAM (G.Krause, K. Franke)

Appendix 6c:



Base map: CPRM / MADAM (G.Krause, K. Franke)

Appendix 7: Comparison of mean carapace widths between crabs landed from near and distant sites

Appendix 7.1: Intra-seasonal comparison

Rainy season 1998

a) Test for homogeneity of variances

Hartley´s F-max: 1.173948; p<0.05

b) F-Test

	df effect	MS effect	MS error	df error	F	p-level
site category	1	9.516071	0.291630	1258	32.63064	0.000000...

Dry season 1998

a) Test for homogeneity of variances

Hartely´s F-max= 1.120531; p>0.05

b) F-Test

	df effect	MS effect	MS error	df error	F	p-level
site category	1	4.183143	0.181499	1258	23.04771	0.000002

Rainy season 1999

a) Test for homogeneity of variances

Hartley´s F-max = 1.049705; p>0.05

b) F-Test

	df effect	MS effect	MS error	df error	F	p-level
site category	1	8.733341	0.182226	1258	47.92585	0.000000...

Appendix 7.2: Inter-seasonal comparison

Near sites

a) Test for homogeneity of variances

Hartley´s F-max = 1.567303, p>0.0001
b) F-Test

	df effect	MS effect	MS error	df error	F	p-level
season	2	6.577339	0.205762	1887	31.96580	0.000000...

c) Post hoc comparison
Tukeys HSD-Test

	{1}	{2}	{3}
mean carapace width	7.1888571	7.348730	7.378572
Rainy season 1998 {1}	-	0.000022	0.000022
Dry season 1998 {2}	0.000022	-	0.472617
Rainy season 1999 {3}	0.000022	0.472617	-

Distant sites

a) Test for homogeneity of variances

Hartleý F-max = 1.567303; p > 0.0001

b) F-Test

	df effect	MS effect	MS error	df error	F	p-level
season	2	51.40821	0.231142	1887	222.4098	0.0000...

c) Post hoc comparison
Tukeys HSD-Test

	{1}	{2}	{3}
mean carapace width	7.014762	7.463968	7.545079
Rainy season 1998 {1}	-	0.000022	0.000022
Dry season 1998 {2}	0.000022	-	0.007753
Rainy season 1999 {3}	0.000022	0.007753	-

Erklärung:

Hiermit erkläre ich, dass ich die vorliegende Dissertationsschrift selbständig verfasst und keine anderen als die angegebenen Hilfsmittel verwendet habe.

Bremen, den 25. Februar 2000

Karen Diele