

Tidal and Diel Dynamics in a Nursery Area: Patterns in Fish Migration in a Mangrove in North Brazil



Uwe Krumme

Thesis submitted in partial fulfilment of the
requirements for the degree of
Doctor of Natural Sciences

Faculty 2 (Biology/Chemistry)
University of Bremen
August, 2003

Center for Tropical Marine Ecology

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ADVISORY COMMITTEE

1. Referee: Prof. Dr. Ulrich Saint-Paul (University Bremen, Center for Topical Marine Ecology, Germany)
2. Referee: Prof. Dr. Reiner Eckmann (University Konstanz, Limnological Institute, Germany)
1. Examiner: Prof. Dr. Wilhelm Hagen (University Bremen, Germany)
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2. Member: Cand. rer. nat. Marion Kohn (University Bremen, Germany)

To Reciane, Andreas and Chico

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LIST OF PAPERS

This thesis is based on the following papers, which are referred to by their Roman numerals. All papers are reproduced with the kind permission of the copyright holder.

- Paper I** **Krumme U.**, Saint-Paul U., Rosenthal H., (Submitted). Tidal and diel changes in the structure of a nekton assemblage in small intertidal creeks in Northern Brazil. *Aquatic Living Resources*.
- Paper II** **Krumme U.** and Saint-Paul U., 2003. Observations of fish migration in a macrotidal mangrove channel in Northern Brazil using a 200-kHz split-beam sonar. *Aquatic Living Resources*, 16(3): 175-184.
- Paper III** **Krumme U.**, (Submitted) Patterns in the tidal migration of fish in a North Brazilian mangrove channel as revealed by vertical beaming using a 200 kHz split-beam sonar. *Fisheries Research*.
- Paper IV** **Krumme U.** and Liang, T.H., (In Press) Tidal induced changes in a copepod-dominated zooplankton community in a macrotidal mangrove channel in northern Brazil. *Zoological Studies*.
- Paper V** Brenner M. and **Krumme U.**, (Submitted) Tidal migration and patterns in feeding of the four-eyed fish *Anableps anableps* L. in a North Brazilian mangrove. *Marine Ecology Progress Series*.

SUMMARY

Anthropogenic degradation of mangroves - the intertidal forested wetlands on tropical and subtropical coasts - has increased dramatically in recent years. This thesis is part of a long-term project in the comparably undisturbed mangrove estuary of the Caeté River near Bragança (Pará, North Brazil), exposed to semidiurnal macrotides. The ecological investigations of the project focus on factors determining characteristic spatio-temporal patterns and the development of new methodological approaches to study such patterns.

Mangroves are considered important as fish nurseries worldwide. The tide induces large-scale exchange processes of fish between the submerged mangrove at high water (HW) and the subtidal areas at low water (LW) on a short-time scale. These short-time dynamics in the tidal migrations of the fish are yet poorly understood, albeit they likely represent one of the most direct ecological links in the system because they include the everyday survival strategies and use patterns of the fish in this amphibious environment.

Block netting in intertidal mangrove creeks at HW revealed the overwhelming significance of the factors *tide* and *time of day* and their combinations (spring tide at dusk and dawn, neap tide at midday and midnight) in structuring fish assemblages. In contrast to neap tide and daylight when nekton catches were poorest, spring tide and darkness produced the most complex fish assemblage structure when abundant species occurred with increased proportions and more rare species entered. Extreme spring tides produced extraordinary high nekton catches. Fish apparently respond with increased immigration to flood features that indicate increased HW levels. A stronger flood tide provides earlier habitat accessibility and increased resource availability for intertidal fish. Intertidal fish were juveniles or adults of small species, or juveniles of larger species. The almost complete absence of larger piscivores in the intertidal creek network suggests a low risk of predation for the juveniles, emphasizing the mangroves' great nursery function. Stomach analyses of fish showed that the intertidal movements are usually feeding migrations. Fish were concentrated in the subtidal sections at LW. However, not all intertidal species and age groups reside at LW near the areas where they feed at HW. Hence, the fish may split their migration routes intra- and interspecifically at ebb tide to return to a specific LW habitat.

Pioneer studies with a 200 kHz split-beam sonar beaming horizontally and vertically in a large mangrove channel, revealed that the entire fish community rode the first flood rise to achieve upstream transport and to enter the intertidal zone. At slack HW the fish milled around, indicating active foraging behavior. Despite low Secchi depths, diel changes in vertical distribution were apparent when fish exploited the water column only at night. Tracking parameters like direction of travel, swimming speed, track tortuosity and target strength showed tidal-related changes. The sonar provided unique high-resolution, non-invasive insights into the natural movement patterns of the fish. It has a high potential to advance the methodological approach in studying short-time patterns in fish migration.

The surface-swimming four-eyed fish *Anableps anableps* entered the intertidal creeks rapidly with the first flood rise. They fed in the submerged mangrove at HW and returned gradually after the ebb current maximum to concentrate again in the subtidal parts of the main channel at LW. The combination of high inundation at daylight (spring tide-dawn) provided optimum foraging conditions for *A. anableps* while darkness and low inundation was linked to poorest foraging conditions (neap tide-night). The tidal migration of *A. anableps* was controlled by the water level, not by time. Fish that move into the intertidal zone early and leave late in the tidal cycle most likely optimize their foraging time in this shallow water environment.

The mangrove zooplankton was dominated by copepods, an important food for juvenile fish. Zooplankton densities were higher at spring than at neap tide. In contrast to the number of zooplankton species, the densities were lowest at HW and highest at LW. Obviously, the temporal variations in abundance of fish and zooplankton are synchronized by the tide. This points to the need for simultaneous multi-disciplinary short-time sampling to comprehensively cover the range of possible functional interrelations between system compartments in areas exposed to extreme environmental conditions.

RESUMO

As degradações antropogênicas de manguezais (florestas inter-tidais de litorais tropicais e subtropicais) aumentaram dramaticamente nos últimos anos. Esta dissertação faz parte de um projeto de longo prazo, realizado em uma área de manguezal no estuário do rio Caeté, em Bragança (Pará - Norte do Brasil). Este estuário é exposto a macro-marés semi-diúrnas, e é relativamente preservado se comparado com outros estuários. As investigações ecológicas do projeto focalizam a análise dos fatores que determinam padrões espaço-temporais característicos e no desenvolvimento de novos princípios metodológicos para o estudo de tais padrões.

Mundialmente manguezais são considerados como importantes berçários de peixes. As marés induzem a processos de intercâmbios macro-espaciais de peixes, entre a área inundada durante maré alta (MA) e as áreas sub-tidais durante a maré baixa (MB), em uma curta escala de tempo. As dinâmicas a curto prazo de migrações de marés dos peixes são até o momento pouco entendidas, embora elas representem provavelmente uma das conexões ecológicas mais diretas no sistema, uma vez que, nelas estão incluídas as estratégias de sobrevivência diárias e os padrões de uso deste ambiente anfíbio pelos peixes

A tapagem nos canais de maré (durante MA) demonstrou o importante significado dos fatores *maré* e da escala temporal (*hora do dia*), bem como suas interações (maré das águas vivas durante o nascer e o por do sol e maré das águas mortas durante meio dia e meia noite) na estruturação dos grupos temporários de peixes. Contrastando com a maré das águas mortas (diária), onde a pesca de nekton se deu de forma escassa, na maré das águas vivas (noturna) tem-se uma estrutura de grupos temporários mais complexos, com o aparecimento em alta proporção de abundantes espécies, bem como, a entrada em maior quantidade de espécies raras nestes canais. Em marés de águas vivas extremas a pesca de nekton deu-se de forma extraordinariamente alta. Aparentemente os peixes reagem com elevada imigração a características de enchentes que indicam alturas de MA elevadas. Uma forte enchente oferece rápida acessibilidade ao habitat e uma alta disponibilidade de recursos para os peixes inter-tidais. Os peixes analisados através da pesca eram juvenis ou adultos, de espécies pequenas, ou juvenis de espécies grandes. A quase completa ausência de peixes ictiofagos na rede dos canais de maré sugere um nível baixo de risco de predação para os juvenis, acentuando a importante função que o mangue exerce como berçário para peixes juvenis. A análise dos estômagos dos peixes demonstrou que as migrações entre marés, na maioria das vezes são migrações com objetivos tróficos, sendo que, os peixes aglomeram-se nas zonas sub-tidais durante MB. Porém, nem todas as espécies e classes de tamanho encontram-se perto de áreas (onde eles comem durante as MA) durante a MB. Consequentemente, os peixes separaram suas rotas de migrações durante a vazante, intra- e inter-especificamente para voltar ao habitat específico de MB.

Estudos pioneiros com uso de uma Ecosonda *split-beam* de 200 kHz, emitindo sinais horizontais e verticais em um grande canal do mangue, demonstraram que toda a comunidade de peixes nada com a primeira subida da maré enchente, para conseguir transporte à montante e penetrar na zona inter-tidal. Durante a maré alta os peixes nadam em círculos, indicando um comportamento ativo de busca alimentar. Apesar da baixa visibilidade da água, os peixes demonstraram uma variação diária na distribuição vertical, em que eles usam a coluna d'água apenas à noite. Parâmetros de indícios acústicos, como direção de migração, velocidade, sinuosidade e força acústica, demonstraram mudanças relacionadas a maré. A ecosondagem forneceu conhecimentos únicos, e de alta resolução, dos padrões de movimentos naturais dos peixes, sendo que seu uso deu-se de forma não evasiva para a comunidade dos peixes. Portanto, através desta, tem-se um alto potencial de avanço dos princípios metodológicos de investigação a curto prazo dos padrões de migração dos peixes.

O tralhoto (*Anableps anableps*) que vive na superfície da água, entra rapidamente nos canais inter-tidais, com a primeira subida da maré enchente. Estes alimentam-se no manguezal inundado durante a MA, e voltam gradualmente depois da velocidade máxima da maré vazante, para se concentrarem novamente nas partes sub-tidais do canal principal durante a MB. A combinação entre alta inundação e luz solar (maré de águas vivas - por do sol) fornece condições ótimas para a busca alimentar do *A. anableps*, enquanto que a combinação entre

noite e baixa inundação é vinculada com piores condições na busca alimentar (maré de águas mortas - noturna). Quanto à migração de marés do *A. anableps*, esta foi controlada pela altura da maré, e não pela hora do dia. Peixes que entram cedo e saem tarde da zona inter-mareal durante o ciclo de maré, otimizam, provavelmente, seu tempo de busca alimentar nesses ambientes de águas pouco profundas.

O zooplankton do manguezal é dominado por Copepoda, um importantíssimo alimento para os peixes juvenis. Densidades de zooplankton são mais altas na maré de águas vivas do que na maré de águas mortas. Em contraste ao número de espécies de zooplankton, suas densidades eram baixas durante a MA, e maiores durante a MB. Tornou-se óbvio que as variações temporais de abundâncias de peixes e zooplankton são sincronizadas pela maré. Isso indica a necessidade de amostras simultâneas, multi-disciplinares e a curto prazo, para cobrir amplamente a envergadura das possíveis inter-relações funcionais entre componentes do sistema, em áreas expostas a condições ambientais extremas.

ZUSAMMENFASSUNG

Anthropogene Veränderung der Mangroven – den Gezeitenwäldern der tropischen und subtropischen Küsten – hat in den letzten Jahren dramatisch zugenommen. Diese Dissertation ist Teil eines Langzeitprojektes im vergleichsweise unberührten Mangrovenästuar des Caeté bei Bragança (Pará, Nordbrasilien), das halbtäglichen Makro-Gezeiten ausgesetzt ist. Die ökologischen Untersuchungen des Projektes richten sich auf Faktoren, die charakteristische raum-zeitliche Muster regeln, und die Entwicklung von neuen methodischen Ansätzen, um solche Muster zu untersuchen.

Weltweit werden Mangroven als wichtige Kinderstuben für Fische angesehen. Die Gezeiten führen zu großskaligen Austauschprozessen von Fischen zwischen überfluteter Mangrove bei Hochwasser (HW) und den subtidalen Bereichen bei Niedrigwasser (NW) auf kurzer Zeitskala. Diese Kurzzeitdynamik in den Gezeitenwanderungen der Fische ist bisher wenig verstanden, obwohl sie wahrscheinlich eine der direktesten ökologischen Verknüpfungen im System darstellen, denn sie enthalten die tagtäglichen Überlebensstrategien und Nutzungsmuster der Fische in dieser amphibischen Umwelt.

Die Absperrung mit Netzen von Gezeitenprielel bei HW deckte die überwältigende Bedeutung der Faktoren *Tide* und *Tageszeit* und ihrer Interaktionen bei der Strukturierung von Fischansammlungen in der Mangrove auf (Springtide in der Morgen- und Abenddämmerung, Nipptide am Mittag und um Mitternacht). Im Gegensatz zu Nipptiden und Tageslicht, wenn die Nektonfänge am dürftigsten waren, erzielten Springtiden und Dunkelheit die komplexesten Strukturen in den Fischansammlungen, wenn bereits häufige Arten mengenmäßig zunahmten und vermehrt seltene Arten einwanderten. Extreme Springtiden erbrachten außergewöhnlich hohe Nektonfänge. Offenbar reagieren die Fische mit gesteigerter Einwanderung auf Merkmale, die bei Flut auf höhere HW-Stände hindeuten. Eine stärkere Flut erlaubt eine schnellere Habitatzugänglichkeit und erhöhte Ressourcenverfügbarkeit für die Gezeitenfische. Die gefangenen Fische waren Juvenile oder Adulte von kleinen Arten, oder Juvenile größerer Arten. Die fast komplette Abwesenheit größerer fischfressender Fische in dem Netzwerk der Gezeitenpriele läßt auf ein geringes Sterblichkeitsrisiko für die Juvenilen schließen, was die bedeutende Funktion der Mangroven als Aufwuchsgebiet für Juvenilstadien unterstreicht. Magenanalysen an Fischen zeigten, dass die Gezeitenbewegungen meist Nahrungswanderungen sind. Bei NW waren die Fische in den subtidalen Bereichen konzentriert. Allerdings halten sich bei NW nicht alle Arten und Altersgruppen gezeitenwandernder Fische in der Nähe der Gebiete auf, wo sie bei HW fressen. Folglich dürften die Fische ihre Wanderrouten intra- und interspezifisch aufspalten, um bei Ebbe zu einem spezifischen NW-Habitat zurückzukehren.

Pilotstudien mit einem 200-kHz split-beam Echolot, das horizontal und vertikal abstrahlte, zeigten, dass die gesamte Fischgemeinschaft mit dem ersten Flutanstieg schwamm, um Stromaufwärtstransport zu erzielen und in die Gezeitenzone einzuwandern. Bei HW-Kenterwasser schwammen die Fische hin und her, was auf aktives Foragierverhalten hinweist. Trotz geringer Secchi-Tiefen gab es deutliche tageszeit-abhängige Veränderungen in der Vertikalverteilung, wobei die Fische die Wassersäule nur bei Nacht aussuchten. Parameter der akustischen Fischspuren wie Wanderungsrichtung, Schwimmgeschwindigkeit, Gewundenheit der Fischspuren und Echostärke zeigten gezeitenabhängige Veränderungen. Das nicht-invasive Sonar lieferte einzigartige, hochauflösende Einblicke in die natürlichen Bewegungsmuster der Fische. Es hat ein großes Potential, die methodischen Ansätze bei der Erforschung von Kurzzeitmustern der Fischwanderung voranzubringen.

Der an der Wasseroberfläche lebende Vieraugenfisch *Anableps anableps* wanderte schnell mit dem ersten Flutanstieg in die Gezeitenpriele ein. Sie fraßen in der überfluteten Mangrove bei HW und kehrten nach dem Ebbmaximum nach und nach in den Hauptkanal zurück, um sich dort bei NW anzusammeln. Die Kombination aus hoher Überflutung und Tageslicht (Springtide-Morgendämmerung) lieferte optimale Fraßbedingungen für *A. anableps*, wohingegen Dunkelheit und geringe Überflutung (Nipptide-Mitternacht) an die schlechtesten Fraßbedingungen geknüpft war. Die Gezeitenwanderung von *A. anableps* wurde vom Wasserstand kontrolliert, nicht von der Uhrzeit. Fische, die früh in die Gezeitenpriele

einwandern und spät im Tidenzyklus zurückkehren, optimieren sehr wahrscheinlich ihre Foragierzeit in diesem Flachwasserlebensraum.

Das Zooplankton der Mangrove wurde von Copepoden, einer wichtigen Nahrung juveniler Fische, dominiert. Zooplanktondichten waren größer bei Spring- als bei Nipptiden. Im Gegensatz zu der Artenzahl an Zooplanktern waren die Dichten bei HW am niedrigsten und bei NW am höchsten. Es ist klar, dass die zeitlichen Variationen in den Häufigkeiten von Fischen und Zooplankton durch die Tide synchronisiert sind. Dies weist auf die Notwendigkeit simultaner, multi-disziplinärer Beprobung mit hoher zeitlicher Auflösung hin, um die Spannweite möglicher funktionaler Wechselbeziehungen zwischen Systemkompartimenten in Gebieten mit extremen Umweltbedingungen umfassend abzudecken.

SCOPE OF THE THESIS

Mangrove ecosystems formerly covered approximately 75 % of tropical coasts and inlets (Chapman 1976). But today these tidal forests only line about 25 % of the world's tropical coastline (World Resource Institute 1996). Mangroves generate a variety of natural resources and ecosystem services that sustain economic activities in the tropics and subtropics. For example, mangroves are considered important as fish nurseries worldwide, which has been shown in several studies (e.g. Bell et al. 1984; Robertson and Duke 1987; Davis 1988; Little et al. 1988; Robertson and Duke 1990; Sasekumar et al. 1992; Laegdsgaard and Johnson 1995; Laroche et al. 1997; Nagelkerken et al. 2000; Barletta-Bergan et al. 2002). However, degradation of mangrove areas has increased in recent years, mainly due to the conversion into shrimp aquaculture ponds, but also through deforestation, overfishing, pollution, urban development and several other causes (Kjerfve and de Lacerda 1993; Mastaller 1996; Spalding et al. 1997).

This study forms part of a joint Brazilian-German long-term mangrove ecosystem project (Berger et al. 1999). The project, named MADAM (**MA**ngrove **D**ynamics **A**nd **M**anagement), started in 1996 and is situated in the macrotidal estuary of the Caeté River near Bragança (Pará) in North Brazil where extensive and comparably undisturbed mangrove forests can still be found (Krause et al. 2001). The main objective of the multi-disciplinary project is to generate the scientific basis for the sustainable management of the resources in the Caeté mangrove estuary. The ecological investigations of the project focus on the question of factors that determine spatio-temporal patterns characteristic of the mangrove system. Since the identification of such patterns and their interrelations is difficult in dynamic tidal areas, the development of new methodological approaches to conduct appropriate studies is another important project aim.

Socio-economic studies showed that the fish species perceived as most important by rural residents in the Caeté Bay are almost exclusively fished in the mangrove system and constitute the major protein source for the poorer sections of the local population (Glaser and Grasso 1999). The fisheries discipline has so far investigated seasonal dynamics in the larval, juvenile and adult fish community of the Caeté estuary system (Camargo and Isaac 1998; Barletta 1999; Barletta-Bergan 1999; Keuthen 1999; Barletta et al. 1999; Barletta et al. 2000; Schaub 2000; Barletta-Bergan et al. 2002; Barletta et al. 2003). Though it is one of the most striking features of the mangrove, the tidal-induced short-term exchange of intertidal organisms between the submerged mangrove

forest and the subtidal areas was still relatively unclear. Concurrently, conventional fishing methods are not readily able to ensure the temporal resolution necessary to reveal the short-term patterns of these migratory processes. Spatial and temporal small-scale migrations in the nursery area likely to increase survival rates of juvenile fish (Gibson et al. 1998). The ways the intertidal fish synchronize their movements and behavior to the ever-changing tide levels characterizes their everyday survival strategies. Therefore, elucidating patterns in the fishes' tidal migration is directly related to a better understanding of the use patterns in the mangrove nursery and the ecological functions the mangrove provides for the fish. Detailed insights in this interplay likely reveal one of the most tightly coupled habitat and resource use patterns in the mangrove system.

Intertidal fish are classified as either permanent resident or temporary inhabitants (Gibson 1988). Permanent resident fish species are those that stay behind at low tide, for example *Myrophis punctatus* in crab holes (Barletta et al. 2000) and continuously live in the intertidal zone (Gibson 1992). Transients or visitors are those fish species that enter the intertidal zone with the rising tide and return to the subtidal zone with the receding tide (Gibson 1988, 1992). The spatial movements of the tidal migrating fish can cover considerable distances depending on the tidal range and the local topography (Gibson 1988).

The main functions generally ascribed to the tidal migrations of fish are feeding, avoidance of predation and competitors, selection of convenient ambient conditions, and reproduction (Gibson et al. 1998). Thus, in mangroves the tidal visitors take advantage of the temporary limited accessibility to the highly productive habitat that provides favorable conditions for feeding, growth and survival of the young fish (Laegdsgaard and Johnson 2001).

This doctoral thesis is based on five scientific papers (I-V) that deal with different aspects of the tidal and diel dynamics and their interactions on the species and community level mainly for fish, but also for zooplankton in the mangrove (**Paper IV**). The prime focus is on the influence of tide height, light-dark cycle and within-tidal cycle dynamics on numbers and compositions of the tidally migrating part of the mangrove fish community. **Paper I** describes the diel and spring-neap tide variability in the high water nekton assemblage composition in the mangrove forest as determined with a block netting study. The conclusions drawn in this paper are the basis for the following studies. The first applications of shallow-water sonar in studying the

movements of fish in a Brazilian mangrove channel using horizontal and vertical beaming are dealt with in **Paper II** and **Paper III**, respectively. These field studies investigate the short-term timing and the order of magnitude of tidal-induced fish movements. The two papers further demonstrate the high potential that modern sonar provide for non-invasive, high-resolution sampling of fish populations even in an acoustically complex mangrove environment. **Paper IV** studies the tidal and diel changes in the zooplankton community in order to gain insight into the unknown dynamics of one of the most important food resources for the fish. **Paper V** is the first comprehensive study on the ecology of the surface-swimming four-eyed fish *Anableps anableps* in its natural environment. It describes the tidal migration and patterns in feeding of this conspicuous fish species.

The different aspects covered in each of the papers are presented according to the topic overview given in Figure 1.

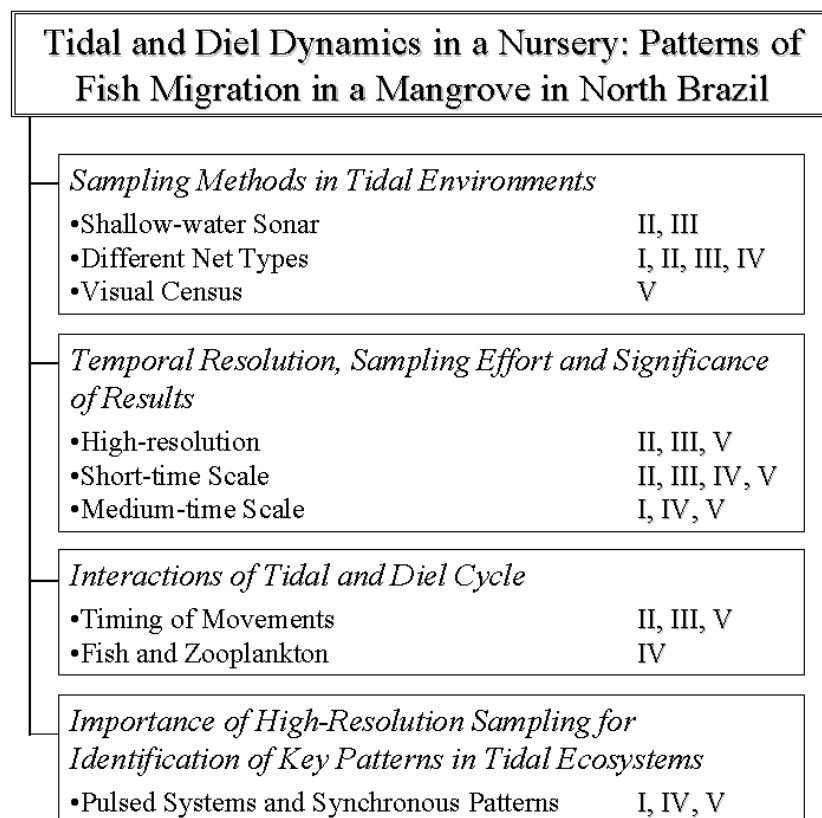


Fig. 1. An overview of the main topics covered in this thesis. The included contents of the scientific papers are referred to by Roman numerals (I-V).

Sampling Methods in Tidal Environments describes the limitations and possibilities of an array of techniques, considered suitable for gathering information about the short-

term pattern in the tidal-induced fish movements. *Temporal Resolution, Sampling Effort and Significance of Results* illustrates the inter-relationship between an increasing degree of temporal resolution, the sample effort necessary to realize it and the significance of the results provided to elucidate short-term patterns. *Interactions of Tidal and Diel Cycle* presents functional overlaps in the temporal patterns between ichthyofauna and zooplankton community. *Importance of High-Resolution Sampling for Identification of Key Patterns in Tidal Ecosystems* describes the necessity for and the resulting advantages of trying to sample on the short-term scale in complex structured environments with a regular ambient pulse.

Sampling Methods in Tidal Environments

When attempting to study short-term movements of fish both quantitatively and qualitatively, one needs a fishing methodology that provides a large number of representative samples of high, stable efficiency and sufficient validity throughout the tidal cycle. Sampling in tidal environments should consider the three dimensions plus the time scale. According to Colby (1988), a design should therefore provide a sampling frequency at least four times the frequency of the periodic influence to avoid a biased and overly simplistic representation of the dynamic system. In the mangrove of the Caeté estuary system the tide is semidiurnal, in which weak neap tides alternate with strong spring tides. Only few fishing gears can cope with these dynamics while concurrently allowing for the required high sampling resolution.

Horn et al. (1999) provide an excellent overview of the array of techniques used to sample intertidal fish. Since no one capture method is suitable for all conditions and all species, the present investigation employed different netting techniques.

Experience was gathered with a beach seine (**Paper I**) that, however, like trawls have low, variable catch efficiency (Rozas and Minello 1997; Wennhage et al. 1997). But the results are not affected when concerning only relative abundances of species and age groups (Ansell and Gibson 1990).

Regional artisanal methods often provide well-adapted approaches to catch local fish species (Batista and Rêgo 1996; Barletta et al. 1998). Setting a block net at the outlet of an intertidal creek at high tide is an inexpensive and effective fishing method since it is supposed to catch almost 100 % of the nekton community present in the creek during maximum flooding (**Paper I**; Bozeman and Dean 1980). However, block nets integrate information over space and time during the tidal cycle (Kneib and Wagner 1994).

Lift nets were tested, but the efficiency varies enormously with the tidal stage and does not allow for representative sampling during the tidal cycle (Leal-Flórez, pers. comm.; **Paper II**). Rozas and Minello (1997) reviewed the sampling design to catch fish in shallow estuarine habitats and recommended enclosure samplers, particularly a bottomless lift net (Rozas 1992), for quantitatively sampling nekton on intertidal marshes. Connolly (1994) described the advantages of a buoyant, floorless pop net over a beach seine net to sample in a shallow seagrass habitat. Considering the slope of the mangrove creeks and the strong spring tide currents, these techniques hardly fulfil the requirements to sample with high temporal resolution.

Large commercial tidal traps provided considerable insight into the tidal movements of fish in the Caeté estuary (Schaub 2000). An adapted tidal trap used in the upper reaches of a large mangrove tributary revealed useful details about the tidal migrations of mangrove fish (**Paper III**), though weak neap tides did not exert a sufficiently strong directional force on the movements and species-specific avoidance became apparent.

Likewise, fyke nets (e.g. Cattrijsse et al. 1994) do not work during weak neap tide currents and may close up at spring tide with mangrove detritus. Furthermore, strong spring tide currents hamper the realization of a regular short-term clearing schedule.

The sampling of zooplankton with a conical net appears a simple task (**Paper IV**). But in turbid mangroves considerable amounts of detritus and fine particles can rapidly obstruct fine mesh nets (e.g. 150 μm), depending on the turbidity situation in the mangrove water as determined by season and tidal stage. Therefore, the mesh size of the zooplankton nets has to be adapted to the turbidity condition encountered in a mangrove environment.

Although modern shallow-water sonar are costly (Fig. 2), they represent an invaluable tool for a unique understanding of the spatial and temporal dynamics in aquatic environments that conventional fishing gear cannot provide (MacLennan and Simmonds 1992, **Paper II**, **Paper III**). Sonar is non-invasive, non-selective and samples targets throughout the acoustic range. A body of water can thus continuously be controlled for fish movements. A sonar system is an apparatus used for obtaining information about underwater objects and events by transmitting sound waves and displaying the returning echoes (Duncan and Kuběcka 1993). All sonar work in basically the same manner: Electrical energy is converted to a pulse of sound by the transducer and emitted as a sound wave into the water. The system receives the returning echo, which is converted back to electrical energy and displayed, in the past

on paper, nowadays on a monitor. Modern split-beam systems provide estimates of the acoustic size of a target, its swimming speed, 3-D location in the water column, direction of travel and allow target tracking (MacLennan and Simmonds 1992; Ehrenberg and Torkelson 1996). One major disadvantage, however, is that fish species cannot be identified directly due to the highly variable scattering properties of a fish (MacLennan and Simmonds 1992).

Since the water clarity in the mangrove is usually low, underwater observation of the fish is not feasible (English 1994). But along the northeast coast of South America nature itself provides a unique and inexpensive opportunity to study patterns in tidal migration with high temporal resolution on the species level: In the mangrove the four-eyed fish *A. anableps* always swim on the water surface. This allows the direct observation of its behavior and counting of the abundances that change with the tide height (**Paper V**).

Temporal Resolution, Sampling Effort and Significance of Results

Semidiurnal tides represent a continuous change in the water level with a fairly high frequency of two HW (high water) and two LW (low water) each day. Hence, a quasi-continuous sampling would be desirable to describe the natural processes. At the same time the number of samples that can be taken within a tidal cycle is often restricted due to the sample method *per se*, the time necessary to handle each sample or the labor and financial effort to get and process the samples.

In the case of the present thesis it can be readily assumed that increasing the resolution to study temporal patterns is associated with an increase in the effort, i.e. the time necessary to get and process the data and the money to buy equipment and know-how (Fig. 2).

Concurrently, an increase in the temporal sample resolution increases the quality and significance of the results for understanding the everyday life of the fish. If this is true, our lack in knowledge about short-term dynamics in complex systems is often a consequence of the positive relationship between increased temporal sampling resolution and the financial and labor effort necessary to realize it.

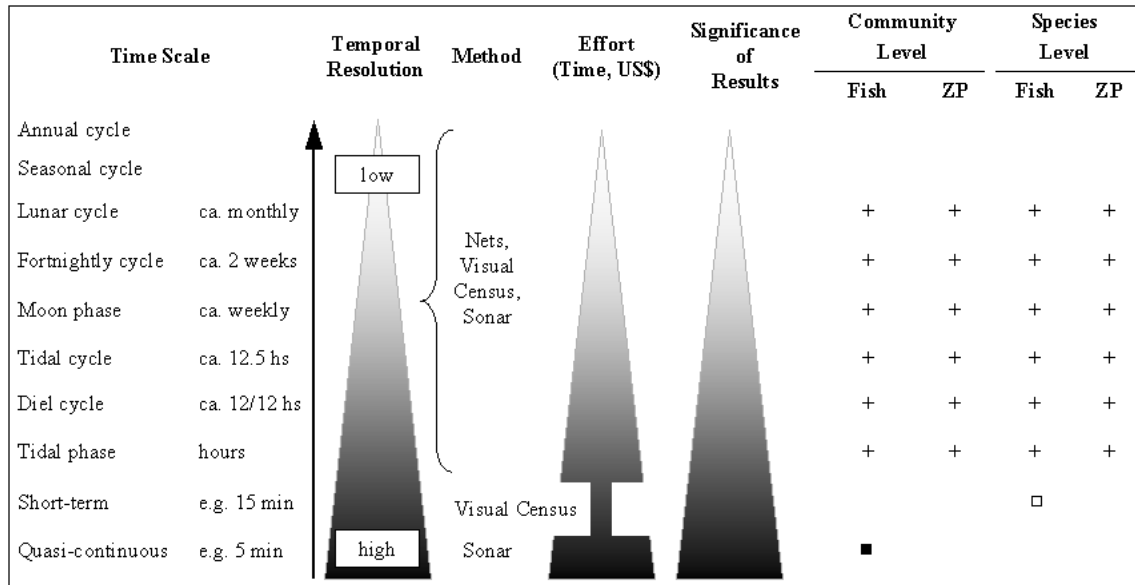


Fig. 2. Schematic overview of the time scales covered in the thesis and their temporal resolutions as related to sampling method, the effort of purchase and application of the method, and the significance of the results to the everyday life of fish. Coverage of the respective time scale for fish and zooplankton (ZP) on the community and species level are indicated by +, while the outstanding significance of the expensive sonar (■) and the low cost visual census of *A. anableps* (□) are especially emphasized.

In this thesis, sonar provided the highest temporal resolution with results that are of highest significance (Fig. 2, ■) when studying tidal-related changes in abundance (**Paper II, Paper III**). This is unfortunately linked to the fact that the effort required to purchase the equipment, acquire the know-how to handle it and finally analyze the acoustic data is considerable. But when a certain routine takes place, sonar application becomes effective, particularly when considering the unique quality of the results achieved.

The highest pay-off between effort and significance of the results was achieved in studying *A. anableps* using visual census (Fig. 2, □; **Paper V**). Both capital expenditure and time necessary for pre- and post-processing of the high-resolution sampling are very low while the significance of the results is very high. The combination of sonar and visual monitoring of *A. anableps*, i.e. sampling on the nekton community level and at a species level, respectively, provides a unique opportunity not only to gather insights into movement patterns of a dynamic system, but also to cross-check the results acquired by the two approaches.

Representative short-time samples, allowing for within-tidal cycle comparisons, were realized for tidal-phase-related zooplankton sampling (**Paper IV**). The small size of the plankton organisms already allows the coverage of both the species and community

level in the sampling. Also on the short time scale, tidal trap (**Paper III**) and lift nets (Leal-Floréz, pers. comm.; **Paper II**) were used to catch fish, though sampling was found to be highly selective and accompanied by tidal-related changes in catch efficiency.

With conventional fishing gear, the highest temporal resolution delivering results was on the medium-time scale using the HW-block net technique in intertidal mangrove creeks (**Paper I**), allowing for between-tidal cycle comparisons. A further decrease in the temporal resolution is not suitable for studying tidal and diel migration patterns. But, all lower temporal resolution scales (day-to-day, week-to week, fortnightly, moon cycle, seasonal cycle, annual cycle) can be covered by the previously mentioned methods (Fig. 2, +).

Interactions of Tidal and Diel Cycle

The activity of most fishes is synchronized with the diel cycle of the solar-day period of 24 hours (Helfman 1986). As an additional stimulus fish on tidal coasts are exposed to the tidal cycle that can vary considerable in form, amplitude and frequency according to the regional and local hydrology (Gibson 1992). Due to the lunar-day period of 24.8 hours, in a semidiurnal tidal area each tidal minimum or maximum occurs about 12 h 25 min after the previous one. The tidal cycles' amplitude is modulated on a fortnightly basis (spring tide at new and full moon, neap tide at wane and wax of the moon). This leads to a unique combination of the time of HW or LW at spring and neap tide. In the study area of this thesis HW at spring tides always coincide with approximately dusk and dawn. In contrast, HW at neap tide always coincide with approximately midday and midnight. Accordingly, the activity and movement patterns of the tidally visiting fish are synchronized with the exact nature of the relative phase of the diel and tidal cycle (Gibson 1992; **Paper I, Paper V**).

Semidiurnal tides generate the highest frequency of regular flooding and ebbing in a natural environment. Therefore, the tidal visiting fish are likely to optimize the time they can use the only temporary accessible productive intertidal zone. Each flood and ebb tide has a range of velocities from almost zero up to the maximum current speeds at some stage within the cycle. Especially in macrotidal areas certain phases are probably more advantageous for migrating or foraging than others. During the evolutionary process the fish have likely adapted their locomotory activity according to those current phases that are of most benefit to their migratory movements.

The time spent foraging in the intertidal zone can be maximized by early immigration at flood tide and late return at ebb tide (Kneib and Wagner 1994). However, visitors may readily adopt others strategies as well and stay shorter periods of time in the intertidal zone. Movements can be synchronized with other or more factors than water level; some may only enter at spring tides or at night while others are seasonal or accidental visitors (Gibson 1988). All this leads to complex patterns of utilization of the intertidal zone in space and time. In this thesis, use patterns are described on the community level (**Paper I, Paper II, Paper III, Paper IV**) and the species level (**Paper I, Paper IV, Paper V**), thus allowing to cross-check between the general and specific patterns found (Fig. 2).

Tidal height is a major factor determining the accessibility of the eulitoral and hence, the availability of intertidal resources for visitors. Consequently, increasing HW levels should be expected to generate a positive response in fish abundance (**Paper I**) and be directly reflected in a both quantitatively and qualitatively increased fish diet (**Paper V**; Brenner 2002). However, due to diel changes in prey abundance, availability and light level-related differences in the fishes foraging ability, the generally positive impact of higher water levels is likely further modulated by the light-dark cycle (**Paper V**).

Besides the tidal and diel cycles, temporal dynamics in food resources of the fish, for example in zooplankton, can likely influence fish migrations. Zooplankton is a principal component in the aquatic food web and represents one of the most important food items especially for the youngest juveniles in a nursery due to its size, high nutritious value and the ubiquitous distribution. However, the dynamics in the mangrove zooplankton community are essentially unknown. Basic information about the zooplankton community is highly necessary not only to understand its short- and medium-term variations, but also to look for similarities in the temporal changes in abundance between the fish as the predators and the zooplankton as their prey (**Paper IV**).

Importance of High-Resolution Sampling for Identification of Key Patterns in Tidal Ecosystems

A strong tidal pulse synchronizes an array of abiotic parameters (e.g. tidal height, current speed, Secchi depth, sediment transport) and biological parameters (e.g. fish and plankton abundances) that might again be inter-related and cross-linked. An

example is the population of the economically highly important mangrove crab *Ucides cordatus cordatus*, which releases billions of eggs exclusively at some nocturnal spring HWs in the wet season that are subsequently exported at ebb tide together with mangrove detritus towards coastal waters (Diele 2000). Apparently, relatively short time windows can serve e.g. for the reproduction in certain species. To detect such adaptations one has to be at the right place at the right time and sample those parameters relevant to answer an ecological question. Short, though ecologically important peaks are left out in a sample design with a too coarse temporal resolution.

In analogy to the well-known requirement for sufficient sample sizes to investigate patterns in space, a sufficiently high temporal resolution is required to describe phenomena in time.

Strong ambient pulses usually influence a series of parameter simultaneously. Therefore, different system components show synchronous patterns that functionally may or may not be linked to each other. For example in the mangrove in the wet season, HW is accompanied by the cycles' salinity maximum and LW by the cycles' salinity minimum while this relationship is reversed in the dry season (Lara and Dittmar 1999; Dittmar and Lara 2001). Consequently, any HW-LW pattern that is stable throughout the year is unlikely to be triggered by changes in salinity, but rather by tidal height (e.g. zooplankton, **Paper IV**). Apparently, short-term patterns can change in response to superordinate system components (in the case of salinity it is the precipitation pattern). Knowledge of such patterns allows the determination of super- and subordinate parameters and the opportunity to better understand inter-linkages between system components.

Flooded areas are subject to pulses with different heights and frequencies. For example the Amazon floodplains are exposed to a slow annual flood pulse where inundation heights can exceed 10 m and large areas remain submerged for several month of the year, forcing the fish to acquire flexibility in habitat demands and feeding habits (Junk et al. 1997). On tidal coasts, the rhythmic behavior exhibited by the intertidal fish reflects the relative importance of the tidal regime in their environment. Gibson and Hesthagen (1981) and Sawara (1992) found that different tidal regimes coincide with a different internal timing and behavior in gobies. The epibenthic *Arius felis* in Florida with a tidal range of 0.7 m exhibited a clear tidal migration (Sogard et al. 1989) whereas *A. felis* experiencing a very small tidal range in Texas apparently had no

entrained tidal rhythm (Steele 1985). But even in areas where tidal fluctuations are considerable, many species are strongly diurnal (Gibson 1982). Characteristic responses to day, night and twilight are exhibited by coral reef fishes (Helfman 1993).

According to different environments and ecological questions, an optimized temporal resolution is desirable where a maximum number of samples is acquired at a minimum of effort. Due to its ubiquitous impact, the coverage of the light-dark cycle is obviously the minimum requirement when interested in short-term changes irrespective of the frequency of the systems additional stimulus. Including the diel variability, automatically suggests that changes on lower temporal scales are covered (Fig. 2).

Working on the short-term scale opens the view to dynamics and inherent patterns that are masked by lower resolution designs. Being close to the natural dynamics forces the researcher to intimately go into the complexity of a system and likely increases the understanding and hence, the quality of the results.

RESULTS

Patterns in the tidal migration of mangrove fish

Tide and diel patterns. The principal medium-term pulse of the Caeté estuarine system is the alternation between spring and neap tide. According to the four different combinations of tide and time of day sampled, four significantly different HW-fish assemblage structures were found in the intertidal mangrove at spring tide-dusk, spring tide-dawn, neap tide-midnight and neap tide-midday (**Paper I**). Spring tides resulted in far greater immigration of fish than neap tides. The intertidal zone is not a *per se* favorable habitat and not all fish species, age groups or individuals necessarily enter each tide (**Paper I**, **Paper V**). High inundations coinciding with darkness produced the highest numbers of fish species and lowest evenness J' indicated that more rare species entered and already abundant species even became more dominant. Low inundation coinciding with daylight yielded lowest numbers of fish species and poorest assemblage structure complexity. It was apparent that tide height had a stronger structuring impact than the time of day while salinity and water temperature had no detectable influence on medium-term changes in the fish assemblage composition.

The clear impact of the factors tide and time of day and their combinations was also reflected in the diet of several tidal visitors (**Paper I**; **Paper V**; Leal-Flórez et al., in prep; Brenner 2002). Generally, spring tides provide better foraging conditions than neap tides since greater submergence is directly linked to an increase in accessible

intertidal resources for the fish. The impact of daylight and darkness on the feeding is related to the species-specific visual adaptations and activity patterns of their prey (**Paper V**). The fish community responded to the fortnightly turbidity minimum during the daylight flooding at neap tide with strong avoidance of the upper channel strata while the fish intensively exploited the entire water column during the nocturnal flooding (**Paper II**; **Paper III**).

At spring tides a simultaneous peak in various processes was observed: high zooplankton (**Paper IV**), strong sediment transport (own obs.; Krause and Soares, in press; **Paper II**), the export of mangrove detritus from the plateau mangrove towards the Caeté bay (**Paper II**) and the most intense visit of fish of the intertidal zone (**Paper I**).

The mean fish biomass found in the mangrove creeks at HW ($1.4 \pm 0.4 \text{ g m}^{-2}$) was at the low end of the values given for other mangroves (Blaber 1997, p. 107; **Paper I**). This is likely related to (i) the preponderance of small fish with low wet weights and (ii) the restricted coupling of terrestrial and aquatic food web via mangrove detritus export (Wolff et al. 2000).

Within-tidal cycle patterns. Besides the clear spring-neap tide pattern, the local tidal cycle exhibits stable, recurring features that were reflected in the tidal migration of the fish. The tidal cycle in the Furo do Meio is asymmetric with ca. 4 hours flood and ca. 8 hours ebb tide. However, due to higher velocities at flood than at ebb tide the system is clearly flood-dominated with a net upstream longitudinal current. The mean net upstream drift is about 0.5 km in a neap (**Paper III**) and about 1.5 km in a spring tide cycle. Besides the almost complete absence of piscivores in the complex network of intertidal creeks that minimize the incidence of predation (Laegdsgaard and Johnson 2001; **Paper I**) and the high food availability, the net upstream longitudinal current is an additional advantage, emphasizing the outstanding nursery function provided by the Furo do Meio (**Paper I**). The successful retention in the Furo do Meio from one tide to the next was apparent for copepods (**Paper IV**) and is suggested for fish, too (**Paper III**).

Figure 3 shows a schematic view of the fishes' tidal migration at neap and spring tide. During the quasi-stagnant LW phase fish are concentrated in the subtidal channel sections (**Paper I**, **Paper IV**; Fig. 3). At LW the species composition essentially was a less diverse subset of the assemblage caught in the intertidal mangrove creeks at HW,

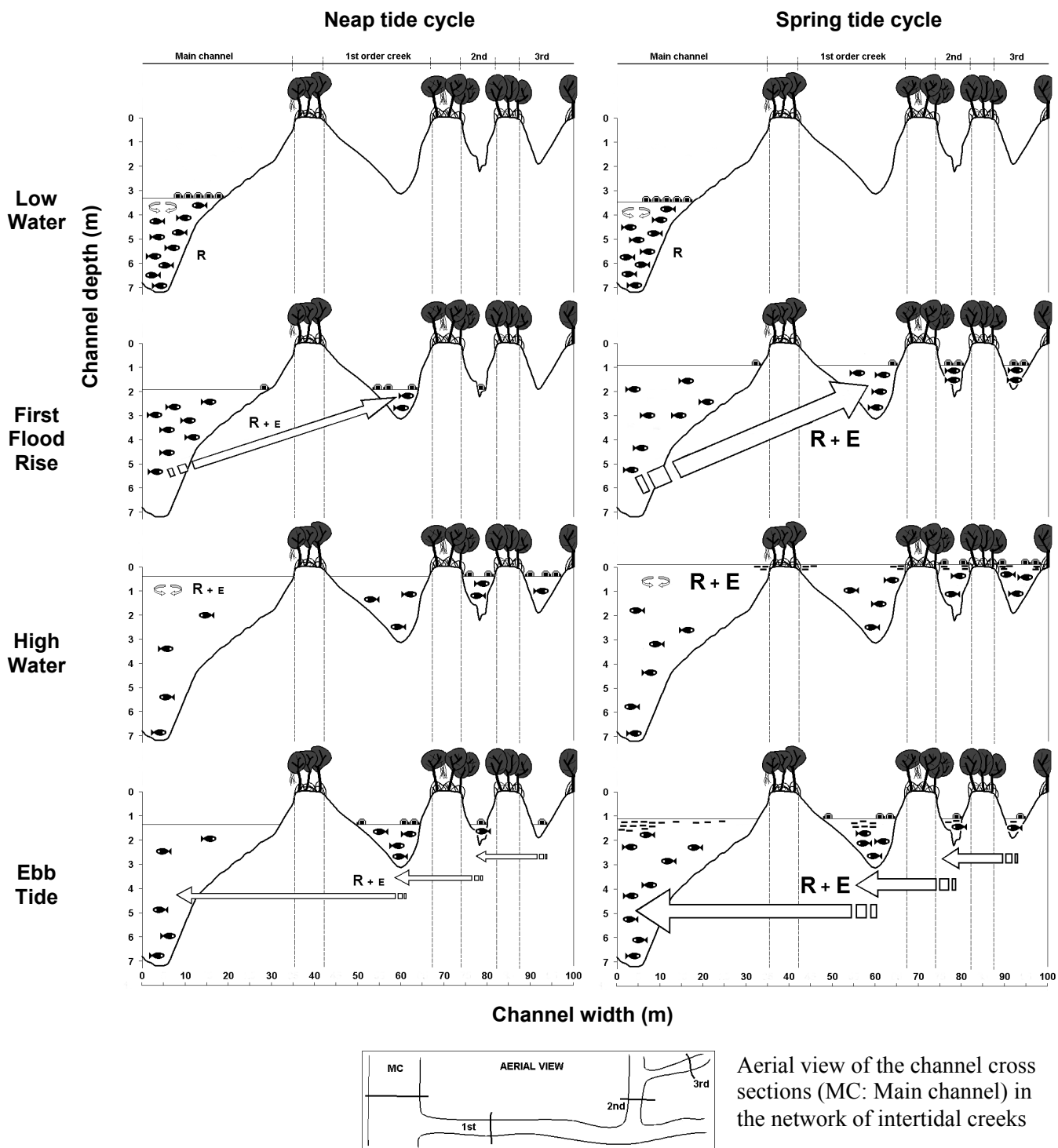




Fig. 3. Schematic drawing of the tidal migration of fish in the mangrove channel Furo do Meio at neap tides (left column) and spring tides (right column), North Brazil. Channel depths (y axis) and widths (x axis) represent the real dimensions while the two axis have different scales. Tidal stages shown are low water (LW), first flood rise, high water (HW) and strong ebb tide (from top to bottom). R: Resident fish. E: Estuarine fish. At spring tide HW mangrove detritus (—) floats up and is exported at ebb tide.  indicates fish in general;  represents the surface-swimming four-eyed fish *Anableps anableps*. The arrows indicate overall direction of fish movements (milling at LW and HW, directed immigration at first flood rise and gradual return at ebb tide).

suggesting a direct spatial linkage between the two habitats on the scale of at least several tens to hundreds of meters. It follows that not all species and sizes reside at LW near the areas where they feed at HW. This implies that fish migration at ebb tide has to be differentiated according to the specific LW habitat requirements. Hence, fish species or their respective age groups can be classified as “residents” (R in Fig. 3) when they reside in the tidal tributary at LW; or as “estuarine” when they reside outside the tidal tributary at LW (E in Fig. 3).

Both surface-swimming *A. anableps* and the entire “underwater” fish community used the first flood rise to enter the intertidal mangrove creeks (**Paper II, Paper III, Paper V**) (Fig. 3). In addition to the aforementioned positive nursery features of the Furo do Meio, riding the first rise current may be part of a strategy of the fish, especially of the juvenile stages, to save transport energy and concurrently increase surplus power that can be converted in faster growth (Miller et al. 1985). First rise coincides with lowest Secchi readings and highest seston transport during a tidal cycle. Increased turbidity reduces the visual range of predators (Grechay and Targett 1996) and thus, likely minimizes the risk of predation for first rise immigrating fish. At neap tides, the majority of the tidal visitors are resident fish and only few enter from the estuary possibly due to weak current velocities. In contrast, at spring tides both residents and estuarine fish ride the first flood rise, when water level rise can be more than 2 m in less than 1 h (**Paper II**), thus achieving a quick longitudinal and vertical lift into the intertidal mangrove zone (Fig. 3).

At slack HW low current speed and maximum Secchi depths coincide with maximum habitat accessibility for intertidal fish. The fish showed increased milling (**Paper II, Paper III**), suggesting active foraging behavior (Fig. 3). The number of zooplankton species is highest while density and biomass are lowest at HW (**Paper IV**). Likewise, in the intertidal mangrove creeks the number of nekton species and total number of individuals peak at HW while density and biomass have a minimum (**Paper I; Paper V; Krause and Krumme, in prep.**). Hence, while maximum habitat accessibility coincides with the dilution maximum of aquatic organisms, the maximum resource availability per individual is reached at slack HW. When the mangrove plateau is submerged at spring tides, the mangrove detritus agglomerated on the ground since the last flooding floats up and is subsequently exported during the phase of maximum ebb tide downstream towards the Caeté bay and coastal waters (Schories et al. 2003).

At ebb tide the fish likely returned gradually to the main channel according to inter- and intraspecific strategies and the ability to withstand the ebb current export (**Paper III**, **Paper V**, Krause and Krumme, in prep.). Estuarine fish may also utilize the ebb tide to save transport energy because their tidal migration between the bay and the upper reaches of the Furo do Meio covers at least 8 km.

With the falling tide *A. anableps* concentrated at the mouth of 1st order creeks from where they returned again to the main channel only after the ebb current maximum was over. Obviously the outlet of the 1st order creek is of strategic significance, being the bottleneck where all the exported material from the creeks' drainage area is passed through by the receding tide, and is possibly used for a migratory stopover by other fish species too (**Paper V**; Fig. 3). In view of the early first flood rise immigration of the entire fish community and the likely gradual and more specific return during ebb tide, it can be suggested that at least the resident fish optimize their stay in the intertidal zone according to species- and age-specific water level preferences (**Paper V**; Gibson 1973). The optimized temporal use of the intertidal zone by the resident mangrove fish would also explain their weight dominance in the block net catches. Optimal utilization is enabled by successful adaptations to this dynamic environment, e.g. reproductive adaptations like vivipary in *A. anableps* or mouth-breeding in Ariidae (**Paper I**).

CONCLUDING REMARKS AND RESEARCH PERSPECTIVES

This thesis demonstrates that the short-time movements and abundance changes of tidal visiting fish in a tropical mangrove system are closely related to changes in tide height, tidal current speeds and light levels while salinity and water temperature are of insignificant importance. The results generally suggest that the sampling of highly mobile taxa especially areas with strong tides has to consider the spring-neap tide alternation, day-night changes and tidal phase in the sample design. It is recommended to use a sufficiently high sample resolution to reveal the natural patterns.

Many parameters in the mangrove occur synchronized and are functionally connected to each other by the tidal pulse, emphasizing the necessity for simultaneous, interdisciplinary sampling approaches (abiotic cycles, hydrology, phytoplankton, zooplankton, sediment, nekton, etc.) to comprehensively understand the characteristic features of the mangrove system dynamics. For example, mass mortality of the anchovy *Cetengraulis edentulus* apparently occurs in the upper reaches of the tidal tributaries

each year in May/June when the rains cease, i.e. when salinities increase again and the nutrient supply is likely high. Apparently linked to neap tides (in 3 years in the wane of the moon), the species-specific mortality is probably caused by a red tide (*Peridinium* sp.) occurring from one tide to the next (own obs.). But the exact mechanism, its causes and consequences are still unknown.

It is striking that the first flood rise universally triggers the immigration of the entire fish community while no such pattern occurred at ebb tide when fish returned gradually to the subtidal parts of the main channel. Apparently, different intra- and interspecific reactions to the same ebb tide stimuli result in different temporal movement patterns at ebb (Krause and Krumme, in prep.). These specific short-term routes of the migrations of intertidal fish and the different distributions of species and size groups at ebb tide and LW are still unknown.

Furthermore, direct evidence of the connection between juvenile and adult habitats in the context of tidal-induced movement is rare (Gillanders et al. 2003). In a macrotidal area strong spring tides are most likely to serve the fish when making ontogenetically synchronized larger scale habitat shifts (Scott Taylor et al. 1998, Goch 2002)

Nowadays, improved active (echosounding) and passive systems based on acoustic emitting tags implanted in fish are able to accurately reveal the behavior of the fish as a function of space and time (Ehrenberg and Steig 2003). Ultrasonic telemetry was successfully used to study tide-related movements of e.g. *Liza ramada* (Almeida 1996), *Gadus morhua* (Arnold et al. 1994), *Paralichthys dentatus* (Szedlmayer and Able 1993), *Platichthys flesus* (Wirjoatmodjo and Pitcher 1984) and *Salmo salar* (Tytler et al. 1978) on temperate coasts, but studies on mangrove fish for e.g. larger Ariidae or pufferfish are still lacking. Ultrasonic telemetry of selected species allows the spatial extrapolation of high-resolution results gathered stationary with a sonar.

The movement patterns exhibited within a tidal cycle by the tidal visiting fish (e.g. riding the first rise current; milling at HW) ensure an optimized use of the feeding and shelter functions the submerged mangrove provides, according to the local semidiurnal tide. However, it is for example, largely unknown whether this holds for fish species and assemblages under different semidiurnal or diurnal tides.

Sonar application and studying *A. anableps* provided comprehensive high-resolution insights in the movement patterns of fish on the community and the species level,

respectively. The two approaches complement one another and allow a cross-check between the results gathered by the two methods. Hence, further research combining sonar application, studies on four-eyed fish and telemetry is highly promising to extend our knowledge about the tidal movements of mangrove fish on the northeast coast of South America.

The almost complete absence of larger piscivores in the flooded mangrove creeks suggests low predation pressure. However, mortality factors and their dynamics especially in comparison to other habitats outside the mangrove are essentially unknown.

While feeding is obviously the main function for the movements of the intertidal visitors to the mangrove, much remains to be learnt about the interactions between foraging fishes and their plankton, epi- and infauna prey. Given highest within-tidal cycle concentrations of zooplankton (**Paper IV**), phytoplankton (Schories, unpubl. data) and fish in the subtidal channel sections at LW (**Paper I, Paper V**), the question arises why certain fish species or age groups should not also feed extensively during LW or whether the subtidal habitat merely serves as a refuge until the next flooding. Qualitative and quantitative determination of stomach contents of the fish with time and tidal stage that could elucidate such use patterns, are scarce or lacking at all (Reis and Dean 1981; Leal-Flórez et al., in prep.).

The high standing stock of both juveniles and adults of small species, and juveniles of larger species emphasized the overwhelming nursery function provided by the upper reaches of the Furo do Meio system. Beck et al. (2001) underline the need to compare the relative nursery values between different nursery habitats, thus allowing an identification and prioritisation of specific nursery habitat complexes for targeting fisheries management and conservation efforts. The tidal tributaries of the Furo do Meio-type with a high nursery value undoubtedly deserve a very high level of conservation and are due to highest priority in sustainable management concepts. Since the upper reaches depend both on the nature state of the downstream sites and the processes in drainage area of the estuary, the management unit should be on the level of an entire mangrove peninsula and its watershed and functional hinterland.

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LITERATURE CITED

- Almeida, P.R. (1996) Estuarine movement patterns of adult thin-lipped grey mullet, *Liza ramada* (Risso) (Pisces, Mugilidae), observed by ultrasonic tracking. J. Exp. Mar. Biol. Ecol. 202: 137-150.
- Ansell, A.D.; Gibson, R.N. (1990) Patterns of feeding and movement of juvenile flatfish on an open sandy beach, pp. 191-207. In: Barnes M.; Gibson R.N. (Eds.) "Trophic Relationships in the Marine Environment", Aberdeen University Press.
- Arnold G.P., Greer Walker M., Emerson L.S., Holford BH. (1994) Movements of cod (*Gadus morhua* L.) in relation to the tidal streams in the southern North Sea. ICES J. Mar. Sci. 51: 207-232.
- Barletta M. (1999) Seasonal changes of density, biomass and species composition of fishes in different habitats of the Caete estuary (North Brazilian coast - east Amazon). ZMT Contrib. No. 7, Zentrum fuer Marine Tropenoekologie, Bremen (FRG), 115 pp, Bremen Univ., (FRG) Fachbereich 2 (Biologie/Chemie). ISSN 0944-0143.

- Barletta M., Barletta-Bergan A., Saint-Paul U. (1998) Description of the fisheries structure in the mangrove-dominated region of Bragança (State of Pará). *Ecotropica* 4: 41-53.
- Barletta M., Barletta-Bergan A., Saint-Paul U., Hubold G. (2003) Seasonal changes in density, biomass, and diversity of estuarine fishes in tidal mangrove creeks of the lower Caeté Estuary (northern Brazilian coast, east Amazon). *Mar. Ecol. Prog. Ser.* 256: 217-228.
- Barletta M., Saint-Paul U., Barletta-Bergan A. (1999) The use of an ichthyotoxic plant in artisanal coastal cutuca (*Myrophis punctatus*, Lütken - Ophichthidae) fisheries along the North Brazilian coast. *Ecotropica* 5: 83-86.
- Barletta M., Saint-Paul U., Barletta-Bergan A., Ekau W., Schories D. (2000) Spatial and temporal distribution of *Myrophis punctatus* (Ophichthidae) and associated fish fauna in a northern Brazilian intertidal mangrove forest. *Hydrobiologia* 426(1-3): 65-74.
- Barletta-Bergan A. (1999) Structure and seasonal dynamics of larval and juvenile fish in the mangrove-fringed estuary of the Rio Caete in North Brazil, ZMT Contrib. No. 8, Zentrum fuer Marine Tropenoekologie, Bremen (FRG), 219 pp, Bremen Univ., (FRG) Fachbereich 2 (Biologie/Chemie), ISSN 0944-0143.
- Barletta-Bergan A., Barletta M., Saint-Paul U. (2002) Structure and Seasonal Dynamics of Larval Fish in the Caeté River Estuary in North Brazil. *Estuar. Coast. Shelf Sci.* 54: 193-206.
- Batista V.D.S.; Rêgo F.N. (1996) Análise de associações de peixes, em igarapés do estuário do Rio Tibiri, Maranhão. *Rev. Brasil. Biol.* 56(1): 163-176.
- Beck M.W., Heck K.L. Jr., Able K.W., Childers D.L., Eggleston D.B., Gillanders B.M., Halpern B., Hays C.G., Hoshino K., Minello T.J., Orth R.J., Sheridan P.F., Weinstein M.P. (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51(8): 633-641.
- Bell J.D., Pollard D.A., Burchmore J.J., Pease B.C., Middleton M.J. (1984) Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, New South Wales. *Austr. J. Mar. Freshwat. Res.* 35: 33-46.
- Berger U.; Glaser M.; Koch B.; Krause G.; Lara R.; Saint-Paul U.; Schories D.; Wolff M. (1999) An intergrated approach to mangrove dynamics and management. *J. Coastal Conservation* 5: 125-134.

- Blaber S.J.M. (1997) Fish and Fisheries in Tropical Estuaries. Chapman & Hall, Fish and Fisheries Series 22, 367 pp.
- Bozeman, E.L.Jr.; Dean, J.M. (1980) The abundance of estuarine larval and juvenile fish in a South Carolina intertidal creek, *Estuaries* 3(2): 89-97.
- Brenner M. (2002) Examination of the feeding ecology of *Anableps anableps*, *Arius herzbergii* and *Anchovia clupeioides* in the tidal creeks of the Caeté estuary in North Brazil. University Bremen, Germany. In German, 101 p.
- Camargo M., Isaac V.J. (1998) Population structure of fish fauna in the estuarine area of Caeté River, Bragança, Pará, Brazil. *Acta Scientiarum* 20(2): 171-177.
- Cattrijsse, A.; Makwaia, E.S.; Dankwa, H.R.; Hamerlynck, O.; Hemminga, M.A. (1994) Nekton communities of an intertidal creek of a European estuarine brackish marsh. *Mar. Ecol. Prog. Ser.* 109: 195-208.
- Chapman V.J. (1976) Mangrove vegetation. Cramer, Vaduz, Lichtenstein.
- Colby D.R. (1988) Null hypothesis, models, and statistical design in the study of larval transport. *American Fish. Soc. Symp.* 3: 149-162.
- Connolly R.M. (1994) Comparison of fish catches from a buoyant pop net and a beach seine net in a shallow seagrass habitat. *Mar. Ecol. Prog. Ser.* 109: 305-309.
- Davis T.L.O. (1988) Temporal patterns in the fish fauna entering a tidal swamp system in tropical Australia. *Env. Biol. Fish.* 21(3): 161-172.
- Diele K. (2000) Life history and population structure of the exploited mangrove crab *Ucides cordatus cordatus* (L.) (Decapoda: Brachyura) in the Caeté estuary, North Brazil. ZMT Contrib. No. 9, Zentrum fuer Marine Tropenoekologie, Bremen (FRG), 103 pp, Bremen Univ., (FRG) Fachbereich 2 (Biologie/Chemie), ISSN 0944-0143.
- Dittmar T. (1999) Outwelling of organic matter and nutrients from a mangrove in North Brazil: Evidence from organic tracers and flux measurements. Diss., Universität Bremen, Fachbereich 2 (Biologie/Chemie), ZMT Contribution 5, 229 pp.
- Dittmar, T., Lara, R.J., 2001. Driving forces behind nutrient and organic matter dynamics in a mangrove tidal creek in North Brazil. *Estuar. Coast. Shelf Sci.* 52, 249-259.
- Duncan A., Kubecka J. (1993) Hydroacoustic methods of fish surveys. Research and Development Note 196, Environmental Agency, National Rivers Authority. Order via solutions@wrcplc.co.uk.

- Ehrenberg J.E., Steig T.W. (2003) Improved techniques for studying the temporal and spatial behavior of fish in a fixed location. *ICES J. Mar. Sci.* 60: 700-706.
- Ehrenberg J.E., Torkelson T.C. (1996) Application of dual-beam and split-beam target tracking in fisheries acoustics. *ICES J. Mar. Sci.* 53: 329-334.
- English S. (1994) Survey manual for tropical marine resources. Australian Marine Science. Townsville, 368 p.
- Gibson R.N. (1973) The intertidal movements and distribution of young fish on a sandy beach with special reference to the plaice (*Pleuronectes platessa* L.). *J. Exp. Mar. Biol. Ecol.* 12:79-102.
- Gibson R.N. (1988) Patterns of movement in intertidal fishes, pp. 55-63. In: Chelazzi, G.; Vanini, M. (Eds.) "Behavioural adaptations to intertidal life". NATO ASI Series Life Sciences Vol. 151, Plenum Press, London.
- Gibson R.N. (1992) Tidally-synchronised behaviour in marine fishes, pp.63-81. In: Ali, M.A. (Ed.) "Rhythms in Fishes". NATO ASI Series Life Sciences Vol. 236, Plenum Press, New York.
- Gibson R.N., Hesthagen I.H. (1981) A comparison of the activity patterns of the sand goby *Pomatoschistus minutus* (Pallas) from areas of different tidal range. *J. Fish. Biol.* 18(6): 669-684.
- Gibson R.N., Pihl L., Burrows M.T., Modin J., Wennhage H., Nickell L.A. (1998) Diel movements of juvenile plaice *Pleuronectes platessa* in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. *Mar. Ecol. Prog. Ser.* 165: 145-159.
- Gillanders B.M., Able K.W., Brown J.A., Eggleston D.B., Sheridan P.F. (2003) Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Mar. Ecol. Prog. Ser.* 247: 281-295.
- Glaser, M., Grasso, M., 1999. Fisheries of a mangrove estuary: Dynamics and dependencies between economy and ecosystem in the Caeté Bay, Northeastern Pará, Brazil. *Boletim do Museu Paraense Emílio Goeldi, Ser. Zool.* 14, 95-125.
- Goch Y.G. (2002) A comunidade íctica de uma lagoa no manguezal de Bragança, PA. Mestrado, Universidade Federal de Para, Brasil. In Portuguese.
- Grechay P.A., Targett T. E. (1996) Effects of turbidity, light level and prey concentration on feeding of juvenile weakfish *Cynoscion regalis*. *Mar. Ecol. Prog. Ser.* 131: 11-16.

- Helfman G.S. (1993) Fish behaviour by day, night and twilight. In: Pitcher T.J. (Ed.) The behaviour of teleost fishes. Chapman & Hall, London, pp. 479-512.
- Horn M.H., Martin K.L.M., Chotkowski M.A. (1999) Intertidal fishes: Life in two worlds. Academic Press, San Diego, 399 pp.
- Junk W.J., Soares M.G.M., Saint-Paul U. (1997) The fish. In: Junk W.J. (Ed.) The central Amazon floodplain: Ecology of a pulsing system. Ecological Studies, Vol. 126, Springer, Berlin, pp. 385-408.
- Keuthen H. (1998) Nahrungsökologische Untersuchungen an ausgewählten Beispielen der Ichthyofauna der Mangrove vor Bragança (Pará, Brasilien). Diploma thesis, Universität Hamburg, 114 pp., in German.
- Kjerfve, B., de Lacerda, L.D. (1993) Mangroves of Brazil. In: de Lacerda, L.D. (Ed.) Mangrove ecosystems technical reports ITTO TS-13(2): 245-272.
- Kneib R.T. (1991) Flume weir for quantitative collection of nekton from vegetated intertidal habitats. Mar. Ecol. Prog. Ser. 75: 29-38.
- Kneib R.T., Wagner S.L. (1994) Nekton use of vegetated marsh habitats at different stages of tidal inundation. Mar. Ecol. Prog. Ser. 106: 227-238.
- Krause G., Krumme U. (in prep.) Spatial quantification of biomass and density in correlation to migratory processes of fish in intertidal mangrove creeks in North Brazil using GIS tools: A methodological case study.
- Krause G., Soares C. (In press) Analysis of beach morphodynamics on the Bragantian mangrove peninsula (Pará, Northern Brazil) as prerequisite for coastal zone management recommendations. Geomorphology.
- Krause, G., Schories D., Glaser M., Diele K., 2001. Spatial patterns of mangrove ecosystems: the bragantian mangroves of northern Brazil (Bragança, Pará). *Ecotropica* 7, 93-107.
- Laegdsgaard P., Johnson C.R. (1995) Mangrove habitats as nurseries: Unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. Mar. Ecol. Prog. Ser. 126: 67-81.
- Laegdsgaard P., Johnson C.R. (2001) Why do juvenile fish utilise mangrove habitats? *J. Exp. Mar. Biol. Ecol.* 257: 229-253.
- Lara R.J., Dittmar T. (1999) Nutrient dynamics in mangrove creek (North Brazil) during the dry season. *Mangroves and Salt Marshes* 3: 185-195.
- Laroche J., Baran E., Rasoanandrasana N.B. (1997) Temporal patterns in a fish assemblage of a semiarid mangrove zone in Madagascar. *J. Fish Biol.* 51: 3-20.

- Leal-Flórez J., Krumme U., Saint-Paul U. (In Prep.) Tidal-related patterns in feeding of the catfish *Cathorops* sp. (Ariidae) in a macrotidal mangrove channel in North Brazil. *Env. Biol. Fish.*
- Little M.C., Reay P.J., Grove S. J. (1988) The fish community of an East African mangrove creek. *J. Fish. Biol.* 32: 729-747.
- MacLennan D.N., Simmonds E.J. (1992) Fisheries acoustics. Chapman & Hall, London. 325 pp., ISBN 0442314728.
- Mastaller M. (1996) Destruction of mangrove wetlands – causes and consequences. *Natural Resources and Development*, 43/44, 37-57.
- Miller J.M., Crowder L.B., Moser M.L. (1985) Migration and utilization of estuarine nurseries by juvenile fishes: an evolutionary perspective. *Contrib. Mar. Sci. Univ. Texas* 27: 338-352.
- Nagelkerken I., Dorenbosch M., Verberk W.C.E.P., Cocheret de la Morinière E., van der Velde G. (2000) Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. *Mar. Ecol. Prog. Ser.* 202:175-192.
- Reis R.R., Dean J.M. (1981) Temporal Variation in the Utilization of an Intertidal Creek by the Bay Anchovy (*Anchoa mitchilli*). *Estuaries* 4(1): 16-23.
- Robertson A.I., Duke N.C. (1987) Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. *Mar. Biol.* 96: 193-205.
- Robertson A.I., Duke N.C. (1990) Mangrove fish-communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass and community structure. *Mar. Biol.* 104: 369-379.
- Rozas L.P. (1992) Bottomless lift net for quantitatively sampling nekton on intertidal marshes. *Mar. Ecol. Prog. Ser.* 89: 287-292.
- Rozas L.P., Minello T.J. (1997) Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: A review of sampling design with focus on gear selection. *Estuaries* 20(1): 199-213.
- Sasekumar A., Chong V.C., Leh M.U., D’Cruz R. (1992) Mangroves as a habitat for fish and prawns. *Hydrobiologia*, 247: 195-207.
- Sawara Y. (1992) Differences in the activity rhythms of juvenile gobiid fish, *Chasmichthys gulosus*, from different tidal localities. *Jap. J. Ichthyol.* 39(3): 201-210.

- Schaub, C. (2000) A study of the trap fisheries (*curral*) in the Caeté estuary, northern Brazil. University Bremen, Diploma thesis, 78p., in German.
- Schories D., Barletta-Bergan A., Barletta M., Krumme U., Rademaker V. (2003). The keystone role of leaf-removing crabs in mangrove forests of North Brazil. *Wetlands Ecology and Management*, in press.
- Scott Taylor D., Poulakis G. R., Kupschus S. R., Faunce C. H. (1998) Estuarine reconnection of an impounded salt marsh in the Indian River Lagoon, Florida: short-term changes in fish fauna. *Mangroves and Salt Marshes* 2: 29-36.
- Sogard S.M., Powell G.V.N., Holmquist J.G. (1989) Utilization by fishes of shallow, seagrass-covred banks in Florida Bay: 2. Diel and tidal patterns. *Env. Biol. Fish.* 24(2): 8-92.
- Spalding M., Blasco F., Field C.D. (Eds.) (1997) *World Mangrove Atlas*. The International Society for Mangrove Ecosystems, Okinawa, Japan.
- Steele C.W. (1985) Absence of a tidal component in the diel pattern of locomotory activity of sea catfish, *Arius felis*. *Env. Biol. Fish.* 12: 69-73.
- Szedlmayer S.T., Able K.W. (1993) Ultrasonic telemetry of age-0 summer flounder, *Paralichthys dentatus*, movements in a southern New Jersey estuary. *Copeia* 3: 728-736.
- Tytler P., Thorpe J.E., Shearer W.M. (1978) Ultrasonic tracking of the movements of Atlantic salmon smolts (*Salmo salar* L.) in the estuaries of two Scottish rivers. *J. Fish Biol.* 12(6): 575-586.
- Wennhage H., Gibson R.N., Robb L (1997) The use of drop traps to estimate the efficiency of two beam trawls commonly used for sampling juvenile flatfishes. *J. Fish. Biol.* 51: 441-445.
- Wirjoatmodjo S., Pitcher T.J. (1984) Flounders follow the tides to feed: evidence from ultrasonic tracking in an estuary. *Estuar. Coast. Shelf Sci.* 19: 231-241.
- Wolff M., Koch V., Isaac V. (2000) A trophic flow model of the Caeté mangrove estuary (North Brazil) with considerations for the sustainable use of its resources. *Estuar. Coast. Shelf Sci.* 50(6): 789-803.
- World Resources Institute (1996) *World resources 1996-97*. The World Resources Institute, UNEP, UNDP, World Bank. Oxford Univ. Press, Oxford, 365 pp.



Photo: U. Krumme

Block net sampling in an intertidal mangrove creek (*tapagem*). The creek surface is exposed to the air after total drainage at ebb tide.

Tidal and diel changes in the structure of a nekton assemblage in small intertidal mangrove creeks in northern Brazil

Uwe Krumme¹, Ulrich Saint-Paul¹ & Harald Rosenthal²

¹ Zentrum für Marine Tropenökologie (ZMT), Fahrenheitstr. 6, 28359 Bremen, Germany

² Institut für Meereskunde (IfM), Duesternbrooker Weg 20, 24105 Kiel, Germany

Corresponding author, E-mail: ukrumme@uni-bremen.de

ABSTRACT

Changes in nekton community structure in North Brazilian intertidal mangrove creeks were studied by setting block nets at high water in the wet season 1999. From a total of 47 species (27 families), the most abundant were: *Cathorops* sp. (Ariidae), *Colomesus psittacus* (Tetraodontidae), *Arius herzbergii* (Ariidae), *Pseudauchenipterus nodosus* (Auchenipteridae), the shrimp *Fenneropenaeus subtilis* (Penaeidae), *Anchovia clupeioides* (Engraulidae), *Mugil* spp. (Mugilidae), and *Anableps anableps* (Anablepidae). Diversity H' was low (0.9). Mean values of fish density and biomass (\pm S.E.) were 0.19 ± 0.05 fish m^{-3} and 2.61 ± 0.67 g m^{-3} or 1.4 ± 0.4 g m^{-2} , respectively. The high proportion of juvenile fish (87 %) and shrimps point to the significant importance of intertidal mangrove creeks for fish nurseries. The number of species was highest at spring tide-night and lowest at neap tide-day. Evenness J' was lowest at spring tide-night when more rare species entered and dominant species increased in quantitative proportions. Four different species assemblages were identified as being triggered by factor combinations such as "tide" and "time of day": spring tide-night, spring tide-day, neap tide-night and neap tide-day. High-water level influenced the species assemblages, but salinity and water temperature did not. Abundances of fourteen species correlated positively with the high water level. Strong spring tides yielded extraordinary high nekton catches, suggesting that high-water level is an important parameter in the tidal migration of fish. Most fish entered the mangrove to feed. Predation pressure was considered to be low because of the presence of only a few, mainly juvenile predators. Beach seining in the subtidal parts at low water revealed a high biomass (30 ± 14 g m^{-2}). Larger fish withdraw to depressions, small fish and juvenile shrimp were abundant near the shallow banks, suggesting inter- and intraspecific splitting of the migration routes when returning from the intertidal zone at ebb tide. To cover the entire short-term range of tidal ichthyofauna responses, a sample design should consider the spring/neap and the day/night cycle.

Keywords: Tide, Water level, Nursery, Tidal migration, Community, Fish, Shrimp, Low water, High water

INTRODUCTION

Mangroves, the impressive tidal forests covering vast stretches of tropical coastline, are considered important as supporting fish nurseries (Bell et al., 1984; Davis, 1988; Little et al., 1988; Robertson and Duke, 1987; Robertson and Duke, 1990; Sasekumar et al., 1992; Laegdsgaard and Johnson, 1995; Laroche et al., 1997; Nagelkerken et al., 2000), providing advantageous conditions for growth in a protected habitat (Miller et al., 1985; Laegdsgaard and Johnson, 2001).

Mangrove estuaries are exposed to tidal influence; clearly fish behavior has adapted to the regular inundation pattern. Four functions are ascribed to the tidal migrations of fish whose advantages are generally related to life in shallow water: feeding, predator avoidance, selection of convenient ambient conditions and reproduction (Gibson 1992, 1996; Rountree and Able, 1993; Gibson et al., 1998). Accordingly, tidal-induced spatial and temporal small-scale migration patterns between the estuary and the tidal creeks are assumed to increase survival rates of juvenile fish (Gibson et al., 1998). While lunar and diel cycles determine intertidal properties, a clear quantifying evidence of influencing migration patterns of juvenile fish is still lacking, partially due to sampling difficulties in the intertidal areas (Rozas and Minello, 1997; Horn et al., 1999).

It is well documented that fish population composition in mangroves changes seasonally according to alternations between wet and dry season (Davis, 1988; Laegdsgaard and Johnson, 1995; Louis et al., 1995; Laroche et al., 1997; Lin and Shao, 1999; Barletta et al., 2003), on a medium-term time scale by lunar periodicity (Davis, 1988; Rooker and Dennis, 1991; Laroche et al., 1997) and on a fortnightly cycle related to spring and neap tide alternations (Gibson, 1992; Blaber et al., 1995; Laroche et al., 1997; Wilson and Sheaves, 2001). Additionally, spring and neap tide cycles change current velocity (Blaber et al., 1994a; Barletta-Bergan, 1999), water turbidity (Blaber et al. 1995) and tidal height (Blaber et al., 1995; Davis, 1988) and thus, fish community structure. Various authors have reported on diel activity changes (Rooker and Dennis, 1991; Helfman, 1993; Blaber et al., 1995; Lin and Shao, 1999).

Studies from Australia, Madagascar and Taiwan (Davis, 1988; Laroche et al., 1997; Lin and Shao, 1999) have specifically focused on temporal patterns in the composition of fish communities. In Northern Brazil, Barletta-Bergan (1999) investigated the seasonal dynamics of fish larvae and juvenile fish in the Caeté estuary and its tidal channels; Barletta (1999) studied seasonal changes of density, biomass and species composition and Camargo and Isaac (1998) focused on population parameters and feeding ecology of Sciaenidae.

Little work has been done on short- and medium-term changes. Movements over short temporal and spatial scales are most likely tightly coupled with habitat and resource usage (Morrison et al., 2002). As many fish species are only temporary residents of the mangrove, spending most of their life history elsewhere, investigations with a higher temporal resolution on habitat use are necessary to understand the ecological role of the mangrove for the fish.

Robertson and Blaber (1992) assumed that fish reside in the main channel at low water (LW) from where they immigrate again into the mangrove forest at flood tide. However, the habitat utilization of juvenile fish in the subtidal mangrove parts at LW is essentially unknown (Laegdsgaard and Johnson, 1995) although intertidal fish become physically concentrated in these areas each low tide.

Therefore this paper focuses on temporal patterns in the community structure to understand tidal-induced fish migration between the subtidal parts of an estuary and its intertidal tributaries.

STUDY AREA AND SAMPLE SITE

The Caeté estuary lies within the worlds' second largest mangrove area (Kjerfve and de Lacerda 1993), located about 200 km southeast of the Amazon delta (Fig. 1). The peninsula (about 220 km²) on the western side of the Caeté River is presently under study by the interdisciplinary German-Brazilian MADAM project (Mangrove Dynamics and Management) (Berger et al., 1999).

A detailed description of the study area can be found in Krause et al. (2001). Dittmar and Lara (2001a,b), which provides information about the dynamics of abiotic parameters in the Caeté estuary. No seagrass beds or coral reefs exist near to the Caeté estuary.

The wet season (January to June) accounts for the largest part of the 2 500 mm of mean annual precipitation in the region (INMET, 1992). Salinity can fall below 5 and exceed 35 in the wet and dry season, respectively. Wet season Secchi depth is on average 20 cm \pm 0.8 S.E. at neaps and 12 cm \pm 0.35 S.E. at springs. The tide is semidiurnal with a mean tidal range of 2.5 m at neaps and 5.0 m at springs. The tide is asymmetric (Wolanski et al., 1980), flood and ebb tide lasting ca. 4 and 8 hours, respectively.

About 110 km² of the peninsula are covered by mangrove, of which parts are connected to the estuary by tidal channels (e.g. the 4.5 km long and dead-ending "Furo do Meio"; Fig. 1). The mangrove forest proper is only inundated fortnightly at spring tides ("plateau mangrove"). In the funnel-shaped network of shallow tidal creeks, wind direction and wind

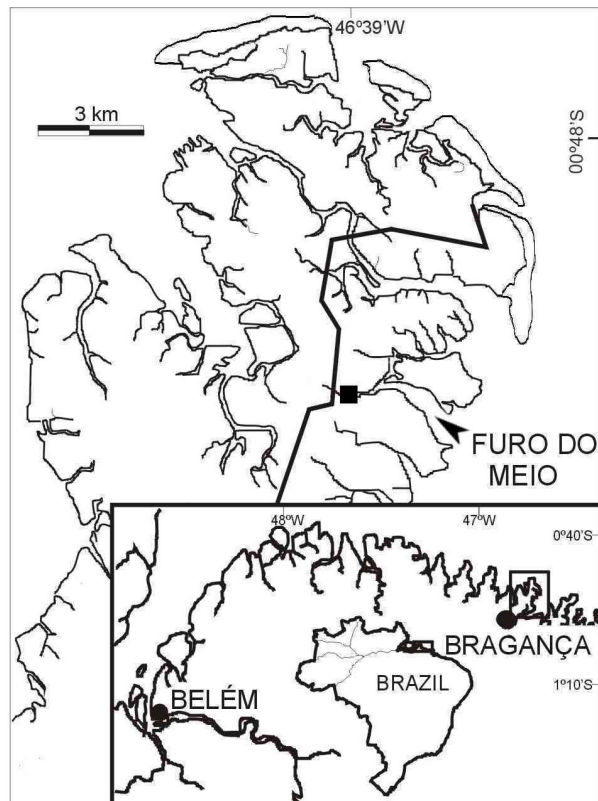


Fig. 1. Mangrove peninsula southeast of the Amazon estuary, 200 km east of Belém, North Brazil. Black square indicates the location of the study site (Fig. 2) in the Furo do Meio in the center of the mangrove peninsula near the city of Bragança. Black line indicates the road from Bragança to the beach.

strength can considerably influence tidal height on the scale of decimeters (e.g. Cain and Dean, 1976, Shenker and Dean, 1979; Jager, 1999).

The two selected tidal creeks A and B ($00^{\circ}87'40''$ S, $46^{\circ}64'50''$) were 2nd order creeks located in the muddy upper reaches of the Furo do Meio (Fig. 2). They were ca. 70 m long and completely covered by mangrove canopy. The mouth of the creeks were approximately 8 m wide; the creek bed was 2 m deep and rose gradually while progressing into the forest. The mouths of the creeks were approximately 1.1 m above the mean low water level and therefore, only inundated for ca. 6 hs 30 min each tidal cycle (Fig. 2). The sample site was dominated by *Rhizophora mangle* and single stands of *Avicennia germinans* on elevated sites, thus, was a representative vegetation subset for large parts of the mangrove on the peninsula.

MATERIAL AND METHODS

The intertidal nekton fauna in the submerged mangrove was captured using “tapagem”, a block net technique (Batista and Rêgo, 1996; Barletta et al., 1998). A 10×3 m nylon net (12 mm stretched mesh size) was set at the mouth of an intertidal creek at slack high water (HW)

along the upstream side of three to four wooden poles set firmly into the mud. The headline was moored on the poles to hold the net above the water surface. The nets lead line was pushed into the mud to prevent fish from escaping below the net. When the tide had receded to max. 1.3 m water height, the collection of fish by hand started and lasted until the creek was totally drained.

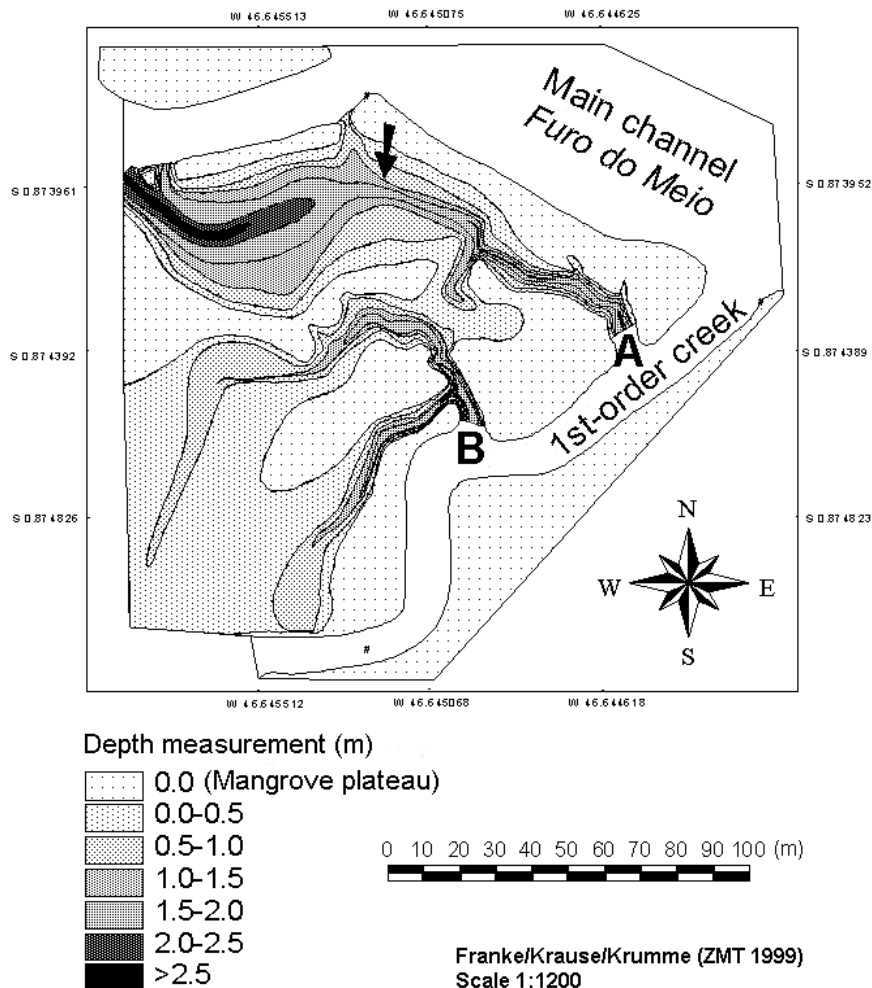


Fig. 2. Map of the two 2nd-order intertidal mangrove creeks A and B in the upper reaches of the Furo do Meio, North Brazil. The creek entrances indicated as A and B were blocked at high water. The Furo do Meio main channel drains downstream to the estuary in southeast direction. The arrow in the upper reaches of creek A indicate a strong flattening acting as a natural topographical barrier during neap tides, limiting water exchange towards the adjacent creek system.

Between February and April 1999, sixteen *tapagem* samples were taken eight times a month, to take account of the four different combinations of tide or lunar phase and daylight conditions: spring tide-night, spring tide-day, neap tide-night and neap tide-day (for the remainder of this paper we denote the factor combinations as SN, SD, NN and ND, respectively) (Table 1). However, SN is not equal to NN, nor is SD equal to ND. Due to the

lunar postponement of ca. six hours, HW at spring tide occurred after dusk (19:00) and dawn (7:00) whereas HW at neap tide occurred at approximately midnight (1:00) and midday (13:00) (Table 1).

The last sample in creek B (no. 16, SD) was followed by another sample in creek B (no. 17, SN) (Table 1). This repeated sampling (although $n = 1$) should provide i) a preliminary comparison between day and night conditions in the same creek, ii) an assessment of the potential effect of substrate disturbance on species immigration and iii) and an idea if and how consistently fish prefer a certain creek from tide to tide. Species with $n > 5$ specimens were compared using the Chi square test.

Table 1. Sample design and physical parameters of 17 high water-block net samples (*tapagem*) in intertidal mangrove creeks, North Brazil, in the wet season 1999. Tide: S (Spring tide), N (Neap tide); Time of day (time): D (Daytime), N (Night); Creek: A (creek A), B (creek B); +: Positive impact of wind on maximum water depth at high water (HW).

No.	Date	Lunar phase	Treatment factors			Max. Depth at HW (m)	Wind	Time of HW	Salinity (psu)	Temp. (°C)
			Tide	Time	Creek					
1	8 Feb	◐ Wane	N	D	B	1.46		11:00	27.8	27.5
2	9 Feb	◐ Wane	N	N	A	1.19		23:25	28.8	28.8
3	15 Feb	● New moon	S	N	B	2.64	+	18:35	30.4	29.5
4	16 Feb	● New moon	S	D	A	2.39		07:10	29.9	28.4
5	22 Feb	◐ Wax	N	D	A	2.12	+	10:45	27.3	28.2
6	22/23 Feb	◐ Wax	N	N	B	1.89		23:00	27.8	28.2
7	2 Mar	◻ Full moon	S	N	B	2.82		19:10	18.5	27.8
8	3 Mar	◻ Full moon	S	D	A	2.51		07:35	17.9	27.0
9	10 Mar	◐ Wane	N	D	A	1.36		11:55	16.4	28.4
10	11 Mar	◐ Wane	N	N	B	1.12		00:55	16.4	28.6
11	17 Mar	● New moon	S	N	A	3.11		18:55	10.7	28.2
12	18 Mar	● New moon	S	D	B	2.89		07:25	10.2	27.6
13	24 Mar	◐ Wax	N	D	B	2.01	+	11:20	8.1	27.5
14	24/25 Mar	◐ Wax	N	N	A	1.56		23:35	8.1	27.0
15	31 Mar	◻ Full moon	S	N	A	2.64		18:30	9.6	28.0
16	1 Apr	◻ Full moon	S	D	B	2.54		06:50	10.2	27.4
17	1 Apr	◻ Full moon	S	N	B	2.57		19:10	10.2	27.9

Caught fish were transported on ice to the laboratory and kept in a freezer (-20°C) between one and ten days before analysis. Defrosted fish were measured (total length (TL) in cm below), weighed (Sartorius MC 1/Laboratory LC 4200 S; ± 0.01 g) and identified to the lowest taxonomic level possible (FAO species identification sheets, 1977; Cervigón 1991,

1993, 1994, 1996; Cervigón et al., 1993; Smith, 1997). Various mullet species were collectively counted as *Mugil* spp. We use *Cathorops* sp. (Ariidae) for what is locally called "Uricica branca" and determined as *C. pleurops* in Barletta et al. (2003); apparently, *Cathorops spixii* is a species complex, probably with different valid species along its distribution in Central and South America (Higuichi, Museu Paraense Emílio Goeldi, pers. comm. in Camargo and Isaac, 1998).

Stomach fullness of three abundant benthic species (*Cathorops* sp., *Arius herzbergii*, *Pseudauchenipterus nodosus*) was determined visually and assigned to one of five fullness categories: 0, 0-25, 25-50, 50-75 and 75-100 %. We tested for differences between SN, SD, NN and ND using the Kruskal-Wallis test and the Nemenyi test for post-hoc analysis. To provide a balanced design for the Nemenyi test (Sachs, 1992), we selected representative subsamples from the three groups with larger sample sizes.

Each sampling event at HW, water temperature (± 0.1 °C), salinity (± 0.1 psu; both measured with conductivity measuring instrument (WTW LF197) equipped with a WTW Tetracon 325 sonde) and tidal height (± 1 cm) were recorded at the mouth of the creeks.

Since HW level varied each tide, catch weights and abundances were standardized to biomass (g m^{-3} or g m^{-2}) and density (number of fish m^{-3} or number of fish m^{-2}). The sample site was surveyed and relationships between HW level and the volume of water and the area inundated were established for each creek (Krumme and Krause, unpubl. data).

The fish species caught were assigned to three migratory categories according to Day et al. (1981), Blaber (1997), Barletta (1999); and to six feeding categories according to Longhurst and Pauly (1987) and own observations, based on qualitative analysis of the diet composition of the majority of species collected. The stomachs of fish larger than ca. 5 cm TL were opened and a qualitative list of the diet for each species was made. Abundant food items were identified to the lowest taxonomic level possible, others only to higher taxa (Carl Zeiss magnifying glass Stemi 2000-C). In piscivorous species, the number of prey items was counted. In rare species, all stomachs were examined. In more abundant species, a subsample of 10–20 specimens was analyzed.

We used TL from the literature and our own observations to determine the proportion of juveniles and adults in the catches. The dependence of the proportion of juveniles on salinity (correlation) and on SN, SD, NN and ND (Kruskal-Wallis test) was tested.

Adults of *Anableps anableps*, *Cathorops* sp. and *Stellifer naso* were sexed and TL at which half of the population contained mature gonads (L_{50}) was established graphically (± 0.1 cm).

For the shrimp *Palaemon northropi* the TL was determined when 50 % of the individuals caught were egg-carrying females.

Sex-specific occurrence of *Cathorops* sp. was tested by a R×C test of independence using the G-test (Sokal and Rohlf 1995). As undeveloped females and females with regressed ovaries could only be inconsistently separated from juveniles, *post-hoc* analysis [unplanned test of the homogeneity of replicates tested for goodness of fit using the simultaneous test procedure (Sokal and Rohlf, 1995)] was only applied for male *Cathorops* sp. that were recognizable as mouth-breeding specimens.

The influence of SN, SD, NN and ND on the number of species, the Shannon-Weaver diversity H' , as \log_{10} based on abundances (Shannon and Weaver, 1949) and Evenness J' (Pielou, 1969) was tested using the Kruskal-Wallis test.

Species abundances were correlated with salinity to identify seasonal migration trends; to account for the unproportional daily fluctuations between abundance (abundance at night 1.6 times higher than at daytime) and salinity (range of 0.3 psu between day and night), abundances and salinities of consecutive day-night samples were averaged.

Abundance, biomass and total catch weight were analyzed using 2-way and 3-way ANOVA. Only species with $n > 10$ individuals were considered for analysis.

The similarities in species composition between the samples were assessed using non-parametric multi-dimensional scaling (MDS) (program package Primer 5; Clarke and Warwick, 1994). We used square root transformation to generate the Bray-Curtis similarity indices. The stress of the MDS representation - a measure of how well the ordination represents the similarities between the samples - was assessed using the classification of Clarke and Warwick (1994). Significance of differences between samples was tested using the analysis of similarities (ANOSIM) (Clarke and Green, 1988; Clarke, 1993) for a 2-way crossed case with the treatment factors "tide" and "time of day".

Circles scaled in size to represent the values of abiotic parameters (high water level, salinity and temperature) were superimposed onto the faunistic 2-dimensional MDS configuration to visualize obvious concordance between arrangement of samples and changes in abiotic parameters (Field et al., 1982).

To study the structure of the nekton assemblage in the subtidal parts of the mangrove at LW, we conducted 16 scientific beach seine catches at neap tide in the main channel with the same net used for *tapagem* at both daytime and night in August 2002 during the early dry season (salinity: 26.8 psu \pm 0.0 S.E.). Two people dragged and hauled the net straight to the shore, covering areas between ca. 25 and 65 m² of the shallow channel bank for each haul

(maximum depth ca. 1.7 m). Additionally, we analyzed artisanal catches taken with a gillnet at daytime-LW in October (salinity: 31.1 psu \pm 0.0 S.E.) at spring and neap tide in the dry season 2000 (50 \times 3 m, 60 mm stretched mesh size; maximum depth ca. 3 m). Three fishermen enclosed an area with the net; one hit the water surface with a large branch while the others dived to startle the fish. All catches were taken from the subtidal parts of the Furo do Meio near the sample site (max. 100 m distance). We used the U-test to compare catch parameters between day and night samples.

RESULTS

Abiotic variables

Water temperature remained almost constant throughout the study period (28 °C \pm 0.65 S.D.). Salinity dropped off remarkably from 30 psu early in February down to a minimum of 8 psu at the end of March. Salinities increased again in April (14 psu in April, 29th).

Mean water depth at the mouths of the intertidal creeks at HW was 1.59 m \pm 0.38 S.D. (n = 8) at neaps and 2.68 m \pm 0.22 S.D. (n = 9) at springs. Variability in maximum tidal height at neap tide was 16 % higher than at spring tide. The weeks before equinox produced the lowest neap tide (1.12 m) and the highest spring tide (3.10 m) (Table 1).

Due to wind force, maximum HW levels between two consecutive samples differed from 0.22 to 0.55 m in three sample pairs (no. 5 and 6; no. 13 and 14; no. 3 and 4). The two maximum neap tide HWs (no. 5 and no. 13) could be attributed to wind influence (Table 1).

Species composition in the intertidal creeks at high water

A total of 40 fish species (22 families) were captured at HW. The following seven families dominated by weight: Ariidae, Tetraodontidae, Auchenipteridae, Engraulidae, Mugilidae, Anablepidae, and Sciaenidae.

Total catch of the entire study weighed 66 kg (fish: 62.5 kg, shrimp: 3.5 kg). Eight species produced more than 85 % of the total biomass: *Cathorops* sp. (34 %), *Colomesus psittacus* (18 %), *Arius herzbergii* (10 %), *Pseudauchenipterus nodosus* (6 %), *Fenneropenaeus subtilis* (5 %), *Anchovia clupeioides* (5 %), *Mugil* spp. (4 %), and *Anableps anableps* (4 %) (Table 2).

Most abundant species were *F. subtilis* (28 %), *Cathorops* sp. (17 %), *Mugil* spp. (7 %), *A. herzbergii* (7 %), *P. nodosus* (7 %), *C. psittacus* (7 %), *Lycengraulis grossidens* (6 %), and *A. clupeioides* (4 %) of altogether 6142 individuals captured. All other species accounted for the remaining 17 % of the total abundance, however, each with less than 2 %.

Table 2. Total weight and total abundance of species caught in 17 high-water block net samples in intertidal mangrove creeks, North Brazil, in the wet season 1999 ranked according to their total catch weight. Species codes are used in Figure 5. Abund: Abundance. MC: Migratory categories (M: Marine migrants; E: Estuarine fish; F: Freshwater migrants). TC: Trophic categories (B: Benthophage; H: Herbivorous; I: Ichthyophage; B/I: Benthophage-ichthyophage; Z: Zooplanktivorous; L: Lepidophage). No vs HW: significant positive correlations between the number of specimens and the maximum high-water level per sample are indicated; ** $p \leq 0.01$, * $p \leq 0.05$, (*) $p \leq 0.1$.

Species	Code	Weight (g)	Abund	Mean TL (min-max)	MC	TC	No vs HW
FISH							
<i>Cathorops</i> sp. (Ariidae)	Ca	23408	1030	12 (3-23)	E	B	**
<i>Colomesus psittacus</i> (Tetraodontidae)	Cp	12081	417	7 (1-27)	E	B	*
<i>Arius herzbergii</i> (Ariidae)	Ah	6312	441	10 (3-34)	E	B	
<i>Pseudauchenipterus nodosus</i> (Auchenipteridae)	Pn	3851	426	9 (5-13)	E	B	(*)
<i>Anchovia clupeioides</i> (Engraulidae)	Ac	3034	248	10 (5-17)	E	H	
<i>Mugil</i> sp. (Mugilidae)	Mu	2605	446	6 (2-29)	M	H	*
<i>Anableps anableps</i> (Anablepidae)	Aa	2320	75	13 (1-25)	E	H	
<i>Lycengraulis grossidens</i> (Engraulidae)	Lg	1354	348	7 (3-14)	M	Z	
<i>Batrachoides surinamensis</i> (Batrachoididae)	Bs	1025	4	20 (8-30)	M	B/I	*
<i>Stellifer naso</i> (Sciaenidae)	Sn	984	50	12 (6-14)	E	B	*
<i>Stellifer stellifer</i> (Sciaenidae)	Ss	788	89	7 (3-14)	M	B/I	(*)
<i>Pterengraulis atherinoides</i> (Engraulidae)		588	28	12 (2-20)	E	B/I	
<i>Macrodon ancylodon</i> (Sciaenidae)	Ma	553	46	8 (2-23)	M	B/I	(*)
<i>Cynoscion leiarchus</i> (Sciaenidae)	Cl	525	80	7 (2-16)	M	B/I	**
<i>Cynoscion acoupa</i> (Sciaenidae)		485	41	9 (2-19)	M	B/I	
<i>Bairdiella ronchus</i> (Sciaenidae)	Br	333	8	13 (7-18)	M	B	*
<i>Stellifer rastrifer</i> (Sciaenidae)	Sr	304	31	8 (3-14)	E	B	
<i>Hyporhamphus roberti</i> (Hemiramphidae)		283	35	12 (9-16)	M	Z	
<i>Genyatremus luteus</i> (Pomadasyidae)		280	30	6 (2-12)	E	B	
<i>Micropogonias furnieri</i> (Sciaenidae)		199	114	5 (3-9)	M	B	(*)
<i>Oligoplites saurus</i> (Carangidae)		197	97	5 (1-9)	M	L	
<i>Achirus achirus</i> (Soleidae)		167	4	13 (8-15)	E	B	
<i>Lutjanus jocu</i> (Lutjanidae)		143	2	(10-19)	M	I	
<i>Guavina</i> sp. (Eleotridae)		139	5	12 (10-14)	E	B	
<i>Arius passany</i> (Ariidae)		138	1	24	M	B	
<i>Centropomus parallelus</i> (Centropomidae)		126	6	11 (11-14)	M	I	
<i>Diapterus auratus</i> (Gerreidae)		115	10	9 (7-13)	M	B	
<i>Chaetodipterus faber</i> (Ephippidae)		68.6	47	3 (1-7)	M	B	(*)
<i>Cetengraulis edentulus</i> (Engraulidae)		63.5	5	10 (6-14)	M	H	
<i>Rhinosardinia amazonica</i> (Clupeidae)		33.9	18	6 (4-7)	E	H	**
<i>Anchoviella lepidentostole</i> (Engraulidae)		25.5	20	4 (2-8)	M	H	
<i>Anchoa spinifer</i> (Engraulidae)		24.9	16	5 (4-8)	M	Z	
<i>Cynoscion steindachneri</i> (Sciaenidae)		24.7	1	14	M	B/I	
<i>Odontognathus mucronatus</i> (Pristigasteridae)		16.7	8	7 (5-9)	M	Z	
c.f. <i>Bryconamericus</i> sp. (Characidae)		7.5	1	9	F	Z	
<i>Selene vomer</i> (Carangidae)		6.6	2	(5-6)	M	Z	
Poeciliidae		2.6	2	(2-5)	F	Z	
<i>Strongylura timucu</i> (Belonidae)		1.1	2	(7-8)	M	Z	
<i>Chloroscombrus chrysus</i> (Carangidae)		0.6	1	3	M	Z	
<i>Sphoeroides testudineus</i> (Tetraodontidae)		0.1	1	1	M	B	

Table 2 continued.

CRUSTACEA					
<i>Fenneropenaeus subtilis</i> (Penaeidae)	Fs	3321	1760	5 (1-14)	**
<i>Palaemon northopi</i> (Palaemonidae)		280	101	5 (3-8)	
<i>Alpheus</i> sp. (Alpheidae)		22.5	15	3 (2-6)	
<i>Xiphopenaeus kroyeri</i> (Penaeidae)		18.7	24	5 (4-6)	
<i>Squilla</i> sp. (Scyllidae)		8.3	1	9	
<i>Nematopalaemon schmitti</i> (Palaemonidae)		2.3	5	5 (4-5)	
<i>Callinectes</i> sp. (Portunidae)		-	3	-	
Σ Fish		62613	4236		
Σ Crustacea		3653	1909		
ΣΣ		66266	6145		

Juvenile fish consistently accounted for 87 % of the total catch. Mean TL and weight \pm S.D. of all fish ($n = 4236$) was 9.11 cm \pm 4.25 and 14.8 g \pm 28, respectively. Mean diversity H' was low (0.91 ± 0.13 S.D.; range: 0.5 to 1.0).

The migratory category of estuarine fish accounted for almost 85 % of the total catch weight (Table 2). Marine and freshwater migrants accounted for nearly 15 % and less than 1 %, respectively. However, on the species level marine migrants dominated with 63 % while estuarine fish accounted for 32 % and freshwater migrants for only 5 % of the total species number.

Benthophage fishes (77 %) dominated the catch weight (Table 2). Herbivorous, benthophilic, zooplanktivorous, ichthyophage, and lepidophage species accounted for 13, 5, 4, 0.4, and 0.3 %, respectively. In contrast, benthophage fish species accounted only for 37 % of all fish species captured. Zooplanktivorous, herbivorous and benthophilic-ichthyophage accounted for 24, 17 and 15 % of the total species number. Only two species were entirely ichthyophage (5 %) and *Oligoplites saurus* was lepidophage (2 %).

Biomass and Density

Mean values of fish density and biomass of all species (\pm S.E.) were 0.19 fish $m^{-3} \pm 0.05$ (range: 0.04 to 0.77) or 0.10 fish $m^{-2} \pm 0.02$ (range: 0.04 to 0.28) and 2.61 g $m^{-3} \pm 0.67$ (range: 0.55 to 11.40) or 1.38 g $m^{-2} \pm 0.28$ (range: 0.49 to 4.25), respectively.

Mean values of shrimp density and biomass (\pm S.E.) were 0.06 shrimp $m^{-3} \pm 0.02$ (range: 0.004 to 0.24) or 0.03 fish $m^{-2} \pm 0.01$ (range: 0.002 to 0.12) and 0.14 g $m^{-3} \pm 0.04$ (range: 0.01 to 0.62) or 0.08 g $m^{-2} \pm 0.02$ (range: 0.01 to 0.23), respectively.

Life history features

L_{50} of *A. anableps* was between 10 and 12 cm TL ($n = 75$; few specimens within the L_{50} range). Adult *S. naso* had clearly developed gonads. Females predominated. L_{50} for *S. naso* was 10.7 cm ($n = 50$). L_{50} for *Cathorops* sp. was 13.6 cm ($n = 1030$). 34 % of the shrimp *Palaemon northropi* captured carried eggs. The length at which 50 % of female *P. northropi* were carrying eggs was between 6.0 and 6.5 cm TL ($n = 101$).

For *Cathorops* sp., the proportions of the groups "juvenile", "female" and "male" were inhomogeneous in the 17 samples. *Post hoc*-analysis for males revealed two homogenous non-overlapping groups of samples: (i) five samples at spring tide both at night and day (5 to 20 % of males in the catch); (ii) the remaining 12 samples at neap and spring tides (0 to 2 % of male in the catch). Male *Cathorops* sp. entered the mangrove creeks exclusively at spring tide, rather at night and rarely at daytime. At neap tides not a single male *Cathorops* sp. was caught. Up to 17 embryos were found in the mouth of one male (15 cm TL). Ripe female *Cathorops* sp. were caught throughout the study period in the mangrove creeks. Only one male *A. herzbergii* (33 cm TL) was caught at SN which incubated 24 embryos.

Stomach fullness

Cathorops sp. stomachs were constantly filled by at least 50 to 75 %. *Cathorops* sp. exhibited no periodicity in stomach fullness. In the creeks *Cathorops* sp. fed especially on polychaeta, and small brachyuran crabs.

Stomachs of *A. herzbergii* were generally 50 to 75 % full throughout the samples. Stomachs were emptiest at NN ($p \leq 0.001$). Stomachs at ND and SD were fuller than at NN ($p \leq 0.05$ and $p \leq 0.05$, respectively). Considering that stomachs of *A. herzbergii* were still remarkably filled at NN (see above), the proven significance may only indicate a more successful feeding at daytime than at night. *Arius herzbergii* mainly fed on small brachyuran crabs like *Uca* sp. and polychaeta.

Pseudauchipterus nodosus exhibited a marked day-night activity pattern, superimposed by a strong fortnightly cycle ($p \leq 0.001$) with intense feeding at SN only. Stomachs of *P. nodosus* were fullest at SN (at least 75 % filled) and emptiest at SD (fullness not exceeding 25 %) ($p \leq 0.05$). Stomach fullness at neap tide was intermediate, but stomachs at night were again fuller than those at daytime. The stomachs contained hymenoptera, cicada, rests of chitin in general, small crabs and woodlouses that probably were captured in the mangrove forest.

Intestines of *C. psittacus* (the stomachs are usually empty; H. Keuthen, pers. comm.) in the intertidal creeks were generally full. The stomachs contained barnacles and brachyuran crabs.

All mullets examined had an intestine darkened by ingested substrate, indicating iliophagous feeding in the creeks.

Temporal variations in assemblage structure

Diversity was not a good measure to describe the short-term changes in the nekton fauna. The index did not differ significantly between creeks and the treatment combinations of SN, SD, NN and ND. Evenness J' differed significantly between SN, SD, NN and ND ($p \leq 0.05$). Species at NN were present more even than at the J' minimum at SN ($p \leq 0.01$) when more rare species such as members of the Sciaenidae entered the creeks with low abundances and the dominance of a few species like *Cathorops* sp. increased remarkably, both in numbers and weight.

The number of species and hence, the number of available niches was highest at SN, declined gradually from SD and NN down to minimum species numbers at ND (Fig. 3). The number of species at spring tide was significantly higher than at neap tide ($p \leq 0.01$). At the 10 % level, the number of species at night was higher than at daytime ($p \leq 0.085$). The ratio of fish species to families (S/F), characterizing the diversity within families, exhibited a pattern similar to the one found for total number of species.

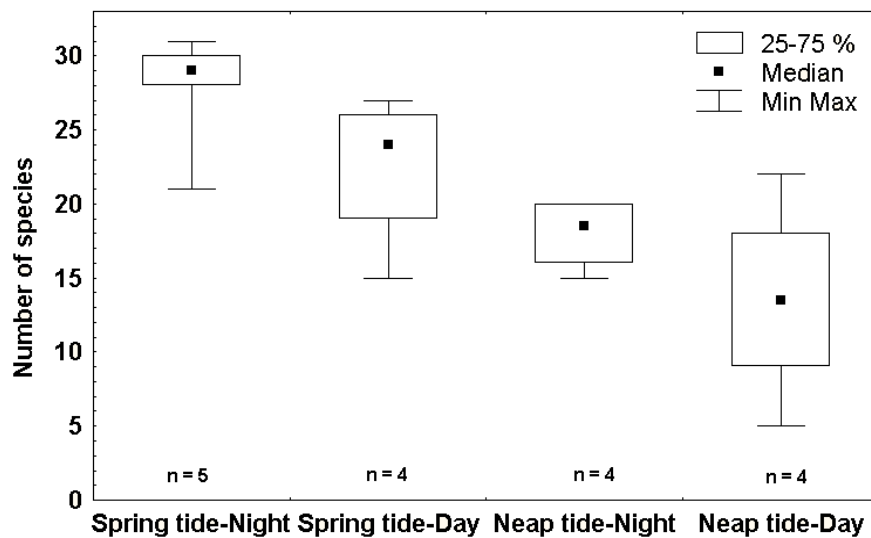


Fig. 3. Median number of nekton species captured at spring tide-night, spring tide-day, neap tide-night and neap tide-day in intertidal mangrove creeks at high water. The 25 to 75 % quartiles and minimum and maximum values are shown.

Catch weights of three species (*Rhinosardinia amazonica*, *Anchoa spinifer*, *A. clupeioides*) were higher at night than at daytime (Table 3), suggesting rather nocturnal activity. The only diurnal species with higher catches at daytime than at night was *C. psittacus*.

Spring tides yielded higher catches than neap tides for nine fish (*Cathorops* sp., *R. amazonica*, *A. spinifer*, *Chaetodipterus faber*, *Mugil* spp., *C. psittacus*, *C. leiarchus*, *Macrodon ancylodon*, *Micropogonias furnieri*) and two crustacean species (*F. subtilis*, *Alpheus* sp.) (Table 3). No species was more abundant at neap tide.

Table 3. Table 3: Results of 3-way ANOVA (n = 16; no. 1-16) for catch weights of 23 species with n>10 specimens calculated as a mixed model ANOVA, creek being the unplanned factor. Only significant species are shown. Significance abbreviations: p≤0.05: *; p≤0.1: trend. Significance for "Tide" means: Spring tide > Neap tide; significance for "Time of day" is indicated with (D) for "higher catches at daytime than at night" and (N) for "higher catches at night than at daytime"; Creek: Creek A and creek B. Interactions are explained below (see i-viii).

Species	Treatment			Interaction			
	Tide	Time	Creek	Tide vs Time	Tide vs Creek	Time vs Creek	Tide vs Time vs Creek
<i>A. anableps</i>							* (i)
<i>Cathorops</i> sp.	trend			* (ii)	trend (iv)	* (iii)	
<i>O. saurus</i>							* (i)
<i>R. amazonica</i>	*	trend (N)					
<i>A. clupeioides</i>		* (N)					
<i>A. spinifer</i>	* (v)	* (v)		* (v)			
<i>C. faber</i>	*						
<i>Mugil</i> spp.	trend						* (i)
<i>C. leiarchus</i>	*			trend (vii)		* (vi)	
<i>M. ancylodon</i>	*						
<i>M. furnieri</i>	*						
<i>S. stellifer</i>							* (v)
<i>C. psittacus</i>	trend	* (D)		trend (viii)			
<i>F. subtilis</i>	*						
<i>Garnele 2</i>	trend						

(i) The multiple interactions cannot be explained.

(ii) At spring tide, catches at night were higher than those at daytime; at neap tide catches at night were only slightly higher than those at daytime.

(iii) Creek A yielded higher catches at night than at daytime. Creek B yielded lower catches at night than at daytime.

(iv) At neap tide, creek B yielded almost as low catches as did creek A; at spring tide, however, creek B yielded clearly higher catches than creek A.

(v) This species only occurred at spring tide-night in creek A.

(vi) In creek B, catches were higher at night than at daytime. In creek A catches were lower at night than at daytime.

(vii) At spring tide, catches at night yielded only slightly more than catches at daytime. At neap tide the difference between day and night was highly pronounced.

(viii) At neap tide, in the night catches were insignificant whereas the other three factor combinations yielded almost equal catches.

Four species occurred with highest catch weights at SN (*Cathorops* sp., *R. amazonica*, *A. spinifer* and *Stellifer stellifer*). Only *C. psittacus* was captured with highest catch weights at SD.

Sciaenidae were especially abundant at SN (2-way ANOVA; tide: $p \leq 0.01$; time of day: $p \leq 0.05$).

The mean total spring tide catch (5.7 kg) exceeded three times the catch at neap tide (1.9 kg) ($p \leq 0.01$). On the 10 % level, fish abundance and catch weight were significantly higher at spring than at neap tide ($p \leq 0.065$ and $p \leq 0.086$, respectively) (Fig. 4). Night catches were 1.6 times higher than those at daytime. Catches in creek B (the larger creek) were 1.4 times higher than those in creek A. However, the difference in the latter two factors lacked statistical significance.

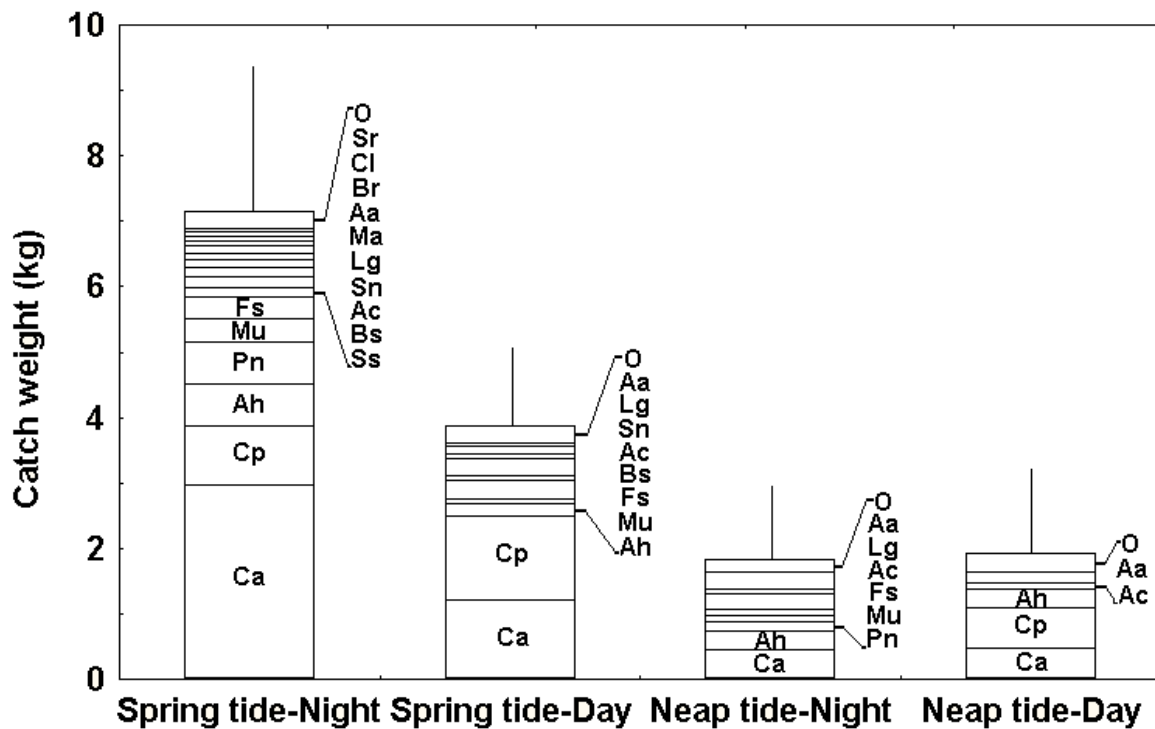


Fig. 4. Mean (\pm 1S.E.) catch weight of nekton species captured in intertidal mangrove creeks by block nets set at high water at spring tide-night ($n = 5$), spring tide-day ($n = 4$), neap tide-night ($n = 4$) and neap tide-day ($n = 4$). Stacked columns consider species contributing on average >0.05 kg to the mean catch weight. The species code letters are given in Table 2; O: Others.

Neither changes in biomass nor in density followed a significant pattern. Fish abundance in creek B showed no diel difference. In creek A catches were significantly higher at night ($p \leq 0.05$), however, only due to extreme yields before equinox ranging between 0.3 kg and 10.3 kg at ND and SN, respectively (factor 38).

The assemblage structure of the catches differed in the species composition and the proportions between the species for SN, SD, NN and ND (Fig. 4). *Cathorops* sp. and *A. herzbergii* always dominated the catch weights. *Anableps anableps* and *A. clupeioides* were abundant throughout SN, SD, NN and ND. *Mugil* spp., *L. grossidens* and *F. subtilis* were rare only at ND. *Pseudauchenipterus nodosus* produced considerable catch weights in night catches only (SN, NN). At neap tides, the daytime assemblage was a subset of the night assemblage. However, *C. psittacus* being the dominant species at ND, was almost completely absent at NN. At spring tides, dominant species altered their proportions between day and night. Ichthyophage fish species entered the creeks particularly at SN, e.g. *Batrachoides surinamensis*, *M. ancylodon*, *Bairdiella ronchus*, *C. leiarchus* and *Stellifer* spp.

Multi-dimensional scaling revealed that the factor combinations SN, SD, NN and ND exhibited a significant influence on the composition of the fish assemblage structures in the intertidal mangrove creeks (Fig. 5).

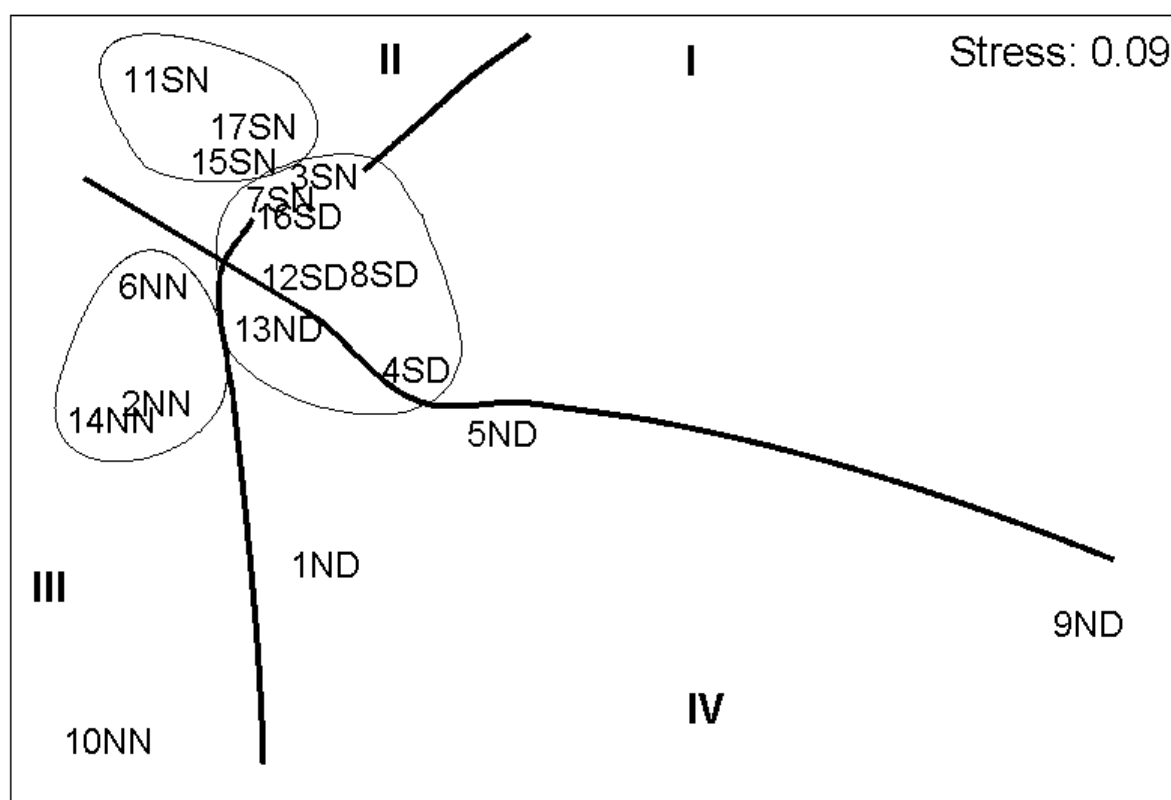


Fig. 5. Multidimensional scaling (MDS) plot of 17 nekton samples taken in intertidal mangrove creeks in the wet season 1999, North Brazil. The mouth of the creeks was blocked at high water according to the factor combinations of tide and time of day: spring tide-night (SN), spring tide-day (SD), neap tide-night (NN) and neap tide-day (ND). The MDS grouped the nekton assemblages caught according to similarities between the catch weights for each species in each sample among all 17 block net samples. Previous to each factor combination is its respective sample number 1 to 17 (see Table 1). Two bold axis separate the plot in four quadrants where quadrant I contains nekton assemblages from SD, quadrant II from SN, quadrant III from NN and quadrant IV from ND. The clusters SN, SD and NN according to the dendrogram in figure 7 are encircled.

Catches at SN were grouped in the second quadrant (upper left), those at SD in the first (upper right), those at NN in the third quadrant (below left) and those at ND in the first quadrant (lower right). Daytime catches were arranged in the first and fourth quadrant. Night catches were arranged in the second and third quadrant. The first and second quadrant contains spring tide catches. The third and fourth quadrant contains neap tide catches.

The distances between subsequent samples increased towards the lower margin, indicating that subsequent samples at spring tide (upper quadrants) had greater similarity and hence, less variability in their species composition than samples taken at neap tide (Fig. 5). The combination of "tide" and "time of day", i. e. SN, SD, NN and ND had a significant effect on the species assemblage in the mangrove creeks (2-way cross-ANOSIM, tide: $p \leq 0.001$; time of day: $p \leq 0.01$) as displayed in the MDS ordination (Fig. 5).

Considering that a MDS stress value of 0.09 corresponds to a good ordination with no real prospect of a misleading interpretation, we may use sample no. 13 (highest neap tide HW) and no. 14 to illustrate a possibility that wind-induced changes in HW level may have been reflected in the composition of the fish assemblages (Figs. 5 and 6a, Table 1). No. 13 (ND) had a wind-induced 55 cm higher HW and was assigned to the SD group (1st instead of 4th quadrant). The subsequent no. 14 (NN) was readily arranged as expected in the 3rd quadrant. Likewise, the lowest spring tide-HW no. 4 (SD) yielded an almost ND-like fish assemblage (close to 4th quadrant) whereas the previous no. 3 (SN) with 25 cm higher HW level was readily arranged in the 2nd quadrant. However, apparently no response in assemblage structure occurred at no. 5 (ND) where wind caused a 22 cm higher HW level compared to subsequent no. 6 (NN).

The abundance per species in the repetition trial no. 16/no. 17 was significantly higher at SN (second sample) than at SD (first sample) (10 species; $p \leq 0.001$), suggesting unbiased immigration from one tide to the next. Accordingly, the samples 16 and 17 yielded different assemblage characteristics typical for SD and SN (Fig. 5).

The superimposed circles in Figures 6a, b and c show that HW level (Fig. 6a) had a clear impact on the fish assemblage structure; low and high HW levels occurred at neap tides (lower margin) and spring tides (upper margin), respectively, indicating that assemblage complexity is positively related to HW level. Neither changes in salinity nor water temperature showed a relationship to the MDS ordination (Figs. 6b,c).

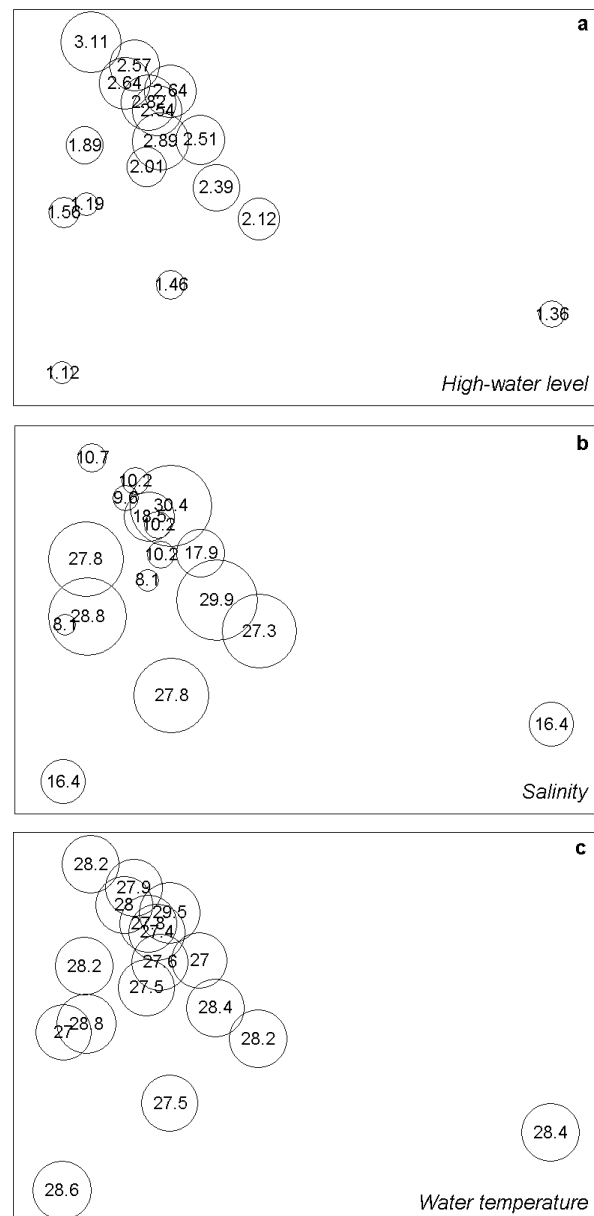


Figure 6a-c. The same MDS as in Fig. 6, but with superimposed circles, sized according to changes in high-water level (a), salinity (b) and water temperature (c). Abiotic values are also given in Table 1.

Out of 46 species tested, the numbers of 14 correlated positively with HW level (*Cathorops* sp., *P. nodosus*, *B. surinamensis*, *R. amazonica*, *C. faber*, *Mugil* spp., *B. ronchus*, *C. leiarchus*, *M. ancyllodon*, *M. furnieri*, *S. naso*, *S. stellifer*, *C. psittacus* and *F. subtilis*) (Table 2). Consequently, total weights and abundances of fish ($p \leq 0.001$) and shrimp (not shown, but $p \leq 0.01$) correlated positively with HW level; the higher the HW level of a tidal cycle in the mangrove creeks was, the more fish entered, leading to higher catches (Fig. 7). This relationship was best described by a power function. Neither abundances nor catch weights

form a linear function with increasing HW levels, but extraordinary high abundances of fish and shrimp moved into the mangrove creeks at extreme spring tides.

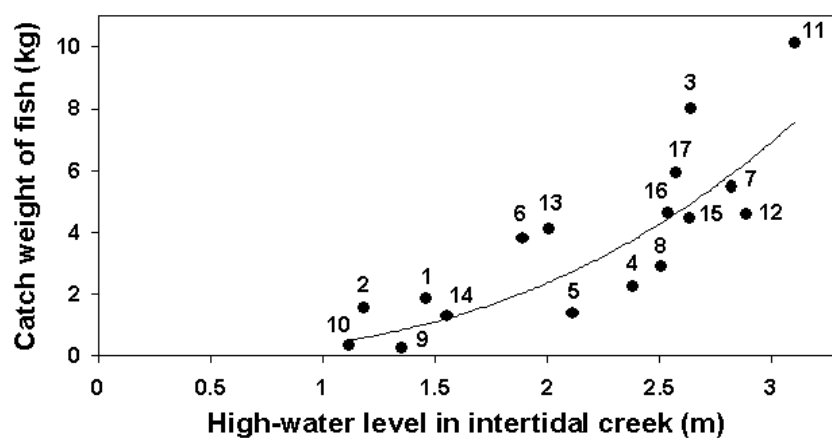


Fig. 7. Relationship between high-water level in the intertidal mangrove creek and fish catch weight of 17 block net samples. Sample number (see table 1) is assigned to each catch. A power function ($y = 2 \times 10^{-6} x^{2.6678}$, $R^2 = 0.70$) was fitted to the data.

The four moon phases had no apparent influence on the grouping of the species assemblages in Figure 5 (see together with Table 1). Significantly higher catch weights in the wane of the moon than at the three other moon phases (3-way ANOVA; $p \leq 0.05$) is readily explained by lowest HW levels coinciding with the samples at the wane of the moon (Table 1). With the replicate size of $n = 2$ (each moon phase-time of day-creek combination), the power of the analysis is too low to resolve patterns obscured by high variability and Type II errors may occur (Sokal and Rohlf 1995).

Longer-term changes were detected only for *Anchoviella lepidentostole* where abundances increased with decreasing salinity ($p \leq 0.05$). At the 10% level, abundances of *C. faber* and *C. acoupa* correlated negatively with salinity ($p \leq 0.078$ and $p \leq 0.094$, respectively), suggesting post larval recruitment processes into the mangrove during the wet season. No relationship was detectable between decreasing salinities and the relative abundance of juvenile fish.

Species composition in the subtidal zone at low water

A total of 25 species were caught in scientific seine catches in the subtidal parts of the Furo do Meio main channel at LW (Table 4). The mean number of fish species, catch weight, abundance, evenness J' and diversity H' (\pm S.E.) was 7 ± 1 , 0.7 ± 0.3 kg, 52 ± 22 , 0.5 ± 0.1 , 0.4 ± 0.1 , respectively. The parameters lacked any statistical difference between daytime and night samples.

Table 4. Abundance of species caught at low water using a scientific (12 mm stretched mesh size; daytime and night, neap tide in August in the early dry season 2002; n = 16) and an artisanal beach seine (60 mm stretched mesh size; daytime at neap and spring tide in October 2000 in the dry season) in the Furo do Meio main channel.

Species	Scientific beach seine		Artisanal beach seine	
	N	Mean TL (min-max)	N	Mean TL (min-max)
<i>C. edentulus</i> (Engraulidae)	519	11 (7-12)		
<i>A. herzbergii</i> (Ariidae)	144	10 (5-34)	60	31 (27-50)
<i>A. archirus</i> (Soleidae)	28	4 (3-9)	4	20 (15-23)
<i>C. psittacus</i> (Tetraodontidae)	28	3 (2-7)		
<i>P. atherinoides</i> (Engraulidae)	23	8 (7-12)		
<i>S. naso</i> (Sciaenidae)	21	9 (7-12)		
<i>Symphurus plagusia</i> (Cynglossidae)	20	4 (3-9)		
<i>Citarichthys spilopterus</i> (Bothidae)	15	6 (4-10)		
<i>B. surinamensis</i> (Batrachoididae)	8	13 (9-15)	7	36 (28-41)
<i>Cynoscion</i> spp. (Sciaenidae)	8	5 (4-5)		
<i>Cathorops</i> sp. (Ariidae)	6	13 (10-16)		
<i>S. stellifer</i> (Sciaenidae)	6	9 (8-10)		
<i>M. furnieri</i> (Sciaenidae)	4	6 (4-11)		
<i>O. saurus</i> (Carangidae)	4	7 (6-10)		
<i>S. vomer</i> (Carangidae)	4	8 (6-10)	1	20
<i>Mugil</i> spp. (Mugilidae)	3	7 (7-8)	1	39
<i>A. anableps</i> (Anablepidae)	2	(6-7)		
<i>G. luteus</i> (Pomadasyidae)	2	(4-5)		
<i>Guavina</i> sp. (Eleotridae)	1	10		
<i>Caranx</i> sp. (Carangidae)	1	3		
<i>D. auratus</i> (Gerreidae)	1	6		
<i>S. testudineus</i> (Tetraodontidae)	1	3		
Diodontidae	1	3		
<i>Epinephelus itajara</i> (Serranidae)			1	24
<i>F. subtilis</i> (Penaeidae)	252	6 (3-14)		

However, the fish assemblage structure based on catch weights differed significantly between day and night (1-way ANISOM, $p \leq 0.01$), suggesting the presence of a uniform species composition with actively changing proportions and hence catchable with the beach seine during the daytime and the night LW. Cluster and MDS essentially separated catches with heavy schools of *Cetengraulis edentulus* at night (N1, N7, N8) from two groups predominated by daytime samples (Fig. 8). *C. edentulus* accounted for 64 % of the total catch weight. The MDS stress of 0.13 indicates that the ordination still gives a useful picture when e.g. superimposing cluster groups (Clarke and Warwick 1994) (Fig. 8). Consecutive samples were often grouped far from each other, suggesting high spatial variability in the small catches and pointing to a patchy fish distribution at LW.

Shrimp were abundant and exhibited a wide range in size (Table 4). Mean values of fish density and biomass were 1.4 ± 0.4 fish m^{-2} and 30 ± 14 g m^{-2} , respectively. Mean shrimp

biomass was $2.12 \pm 0.25 \text{ g m}^{-2}$. Thus, density and biomass values of fish in the Furo do Meio main channel at LW were 14 and 22 times higher, respectively; the shrimp biomass was 27 times higher at LW than in the adjacent intertidal mangrove creeks at HW, clearly emphasizing the agglomeration of fish and shrimp in the subtidal channel parts.

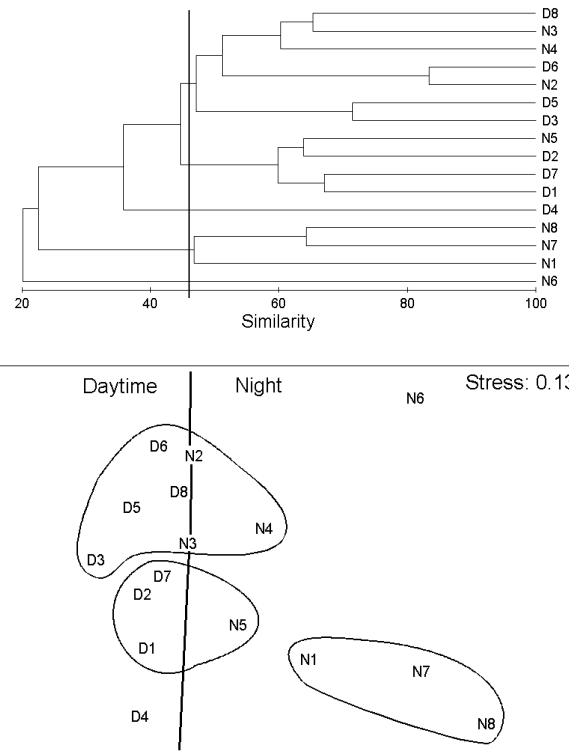


Fig. 8. Cluster (upper figure) and MDS plot (lower figure) of eight daytime (D) and eight night (N) beach seine hauls at LW in the subtidal parts of the Furo do Meio at neap tide in August 2002 (early dry season). Three groups and two single samples were separated at 47 % similarity.

The catches yielded mainly juvenile fish near to the shallow channel banks whereas larger fish (*A. herzbergii*, *Cathorops* sp.) usually were caught only when the seining covered deeper areas and/or when it passed near to branches or trunks (Table 4). The artisanal catches covering deeper parts of the main channel, were very efficient and caught exclusively large-sized fish (Table 4). The artisanal catches showed no difference between spring and neap tide. *Cathorops* sp. was absent from the artisanal catches due to escape through the large mesh size (pers. comm. with fishermen).

DISCUSSION

Sample Technique and sampling Design

Block netting is an inexpensive and effective method for studies in intertidal creeks. Bozeman and Dean (1980) caught all fish, i. e. 100 %, using a block net. Although not tested experimentally, we assume a high catch efficiency of the tapagem method. At extreme spring tides when the entire mangrove plateau is flooded, some fish could have escaped to adjacent creeks. Since extreme tides produced extremely high catches, such bias is probably negligible.

Compared to e.g. coral reefs, the low habitat diversity limits the number of fish species inhabiting tidal mangrove creeks; Davis (1988) caught 38, Wright (1986) only nine fish species. In two months, we caught 4236 fish, 40 fish species belonging to 22 fish families in two 2nd order creeks. A one-year study with monthly sampling at ND (mesh size: 10 mm between knots), in three 1st order creeks of the Furo do Meio, yielded about 29 000 fish, 49 fish species belonging to 26 fish families (Barletta et al., 2003). Compared to these authors our more "effective" sampling methodology can mainly be attributed to the sample design that covered SN, SD, NN and ND more completely. Moreover, Barletta et al. (2003) caught more than a dozen species, mainly dry season visitors like Carangidae or Megalopidae that did not occur in our samples. Barletta et al. (2003) sampled creeks located only 0.4 to 0.6 km upstream from our sample site. However, a longitudinal decrease in species richness with increasing distance from the mouth of the main channels (Quinn, 1980) is unlikely because Brenner (unpubl. data) found no significant difference in species composition between two 1st order creeks of the Furo do Meio which were 1 km apart from each other. Consequently, to cover the entire short- to medium-term range of responses of a highly mobile ichthyofauna in dynamic tidal areas, it is recommended that the sample design includes the spring tide/neap tide cycle and the day/night cycle. Two alternative sample designs are suggested to sample highly mobile fish communities (Shenker and Dean, 1979): (i) Many samples in short intervals during one tidal cycle or over a 24 h period (Livingston, 1976; Ansell and Gibson, 1990; Krumme and Saint-Paul, 2003); (ii) Time series sampling (Kleypas and Dean, 1983; Shenker and Dean, 1979; present study), with sampling at several successive blocks according to tide and time of day.

The repeated samplings showed that at each tide, fish and shrimp re-colonized the intertidal mangrove creeks. Apparently, creek fidelity towards 2nd order intertidal creeks is not a common behavior. However, several repeated samplings in the same creek led to decreased

catches (own obs.). Kleypas and Dean (1983) and Rönnbäck et al. (1999) also detected an impact of repetitive sampling on fish abundance.

Composition of the intertidal nekton fauna

Our results confirm the significant importance of the nursery function for fish and shrimp provided by mangrove habitats. Barletta (1999) determined that 85 % the fish caught were juveniles. A nursery in Martinique had a mean fish weight of 9 g (Louis et al. 1995). Most fish in tropical Australian mangrove creeks were than 10 cm in length (Blaber et al., 1989). The minimum TL of *F. subtilis* at first maturity is 8.3 and 7.2 cm for females and males, respectively (Lum Young et al., 1992), indicating that the population of *F. subtilis* in the creeks (mean TL: 5 cm \pm 2 S.D.; n = 1760) was almost exclusively composed of juveniles or sub-adults. During a one-year study in a tropical mangrove estuary, Robertson (1988) caught only one adult *Penaeus merguensis*. TL of *Xiphopenaeus kroyeri* at first maturity for females and males is 6.5 and 6.1 cm, respectively (Lum Young et al., 1992), indicating a population of mainly sub-adult specimens in the intertidal mangrove creeks (mean TL: 5 cm \pm 1 S.D.; n = 24).

The low wet season diversity agreed with Barletta et al. (2003) and Batista and Rêgo (1996). Both studies found a maximum diversity in the dry season ($H' = 1.95$ and 1.74 , respectively).

Biomass and density

Mean values of fish density and biomass at HW were close to the annual mean of 0.11 fish m⁻² or 2.06 g m⁻² as determined by Barletta et al. (2003). Densities and biomasses lacked any significance due to high variances. Biomass (3.5 ± 2.4 ind. m⁻³) and density (10.9 ± 4.5 g m⁻³) in tropical Australian mangrove creeks were greater than our values. However, standard deviations were of similar range, veiling any seasonal pattern (Robertson and Duke, 1990). Fish biomass in tropical and subtropical estuaries usually ranges between 5 and 15 g m⁻², commonly not exceeding 30 g m⁻² (Blaber 1997, p. 107).

The nekton biomass in the mangrove creeks was mostly produced by high numbers of small fish with low wet weights, thus being per se unlikely to yield high biomasses. The biomass flow through the fish compartment of the Caeté mangrove estuary is of low importance for the trophic flow within the mangrove system, likely related to the exclusive flooding of the mangrove plateau at spring tides that prevents extensive material export (Wolff et al., 2000). The periodic moth plague on *Avicennia*, when large amounts of faeces is washed out by spring tides usually leads to increased shrimp catches in the subsequent year, emphasizing the

significance of the connection “mangrove detritus export-aquatic food web productivity” (Wolff et al., 2000). Moreover, weak neap tides may not suffice to support the growth of a more productive intertidal fauna and flora, while spring tide currents are very strong and resuspend and transport massive quantities of inorganic sediment, creating too much clogging to allow for the growth of e.g. an extensive filter feeding fauna in the mangrove creeks that again could support a higher nekton biomass. Additionally, the strong tidal mixing and low turbidity restricts the pelagic phytoplankton production (Wolff et al., 2000).

Trophic relations and residence status

The importance of detritus-based food chains in mangroves is emphasized by our result that 15 benthophage fish species produced 77 % of the total catch weight. Accordingly, Koch (1999) and Koch and Wolff (2002) found the highest number of epibenthos organisms in the intertidal mangrove creeks. This agrees with studies from Florida and Australia that most food webs of mangrove systems are based on the detritus consumption (Odum and Heald, 1972; Blaber 1997, p. 176).

The majority of species in subtropical and tropical estuaries are marine migrants (Blaber 1997, p. 46) representing 63 % of the species. However, 13 estuarine fish species (32 %) produced 84 % of the total catch weight, emphasizing the important ecological role that estuarine fish species play in the Caeté mangrove system. In mangrove creeks in tropical Australia, 27 species (41 %) of estuarine fish produced a total biomass of only 43 % (Blaber et al., 1989).

Tidal migrations of fish represent a principal means of energy transfer from intertidal areas towards the sea. The main fish biomass in our study was bound in estuarine fish. Tidal-migrating fish species like *A. anableps*, *Cathorops* sp., *C. psittacus*, *B. surinamensis* and *S. naso* spend their entire life in the mangrove environment as indicated by the presence of all sizes in the catches throughout the year (own obs.). Hence, considerable quantities are not lost due to seasonal emigration, but rather remain in the system. Mulletts, shrimp and marine migrants like some predatory Sciaenidae and Carangidae may feed vigorously, thereby exporting biomass to the sea. However, during the wet season their share in the total biomass was low. Likewise, in New Caledonia, resident species were usually at low trophic level and only transient species contributed to net export of energy to coastal waters (Thollot et al., 1999). Conversely, for the temperate US east coast Bozeman and Dean (1980), Kleypas and Dean (1983) and Weinstein et al. (1980) proposed that tidal fish migrations are an important mechanism of seasonal energy transfer from the intertidal zone towards the sea.

As many species left with clearly filled stomachs, feeding is considered a principle function for fish immigration into the intertidal mangrove creeks. The intertidal mangrove benthos is rich in *Uca* spp. (Koch, 1999; Koch and Wolff, 2002), polychaeta (Acheampong, pers. comm.) and oligochaeta (Dittmann, 2001; Dittmann pers. comm.).

According to Leal-Flórez et al. (in prep.) and Oliveira-Santos (pers. comm.), *Cathorops* sp. is a polychaete-eater (Blaber et al., 1994b), also feeding on vegetal material, copepods, crabs and diatoms. The dominance of *Cathorops* sp. in the mangrove creeks is probably closely related to the specialized feeding on abundant polychaeta and special adaptations like mouth-breeding and the arming with lateral and dorsal spines.

Brenner (unpubl. data) found *A. herzbergii* feeding on *Uca* sp., Grapsidae, Gamaridae, *Eurytium limosum*, arthropoda, polychaeta (Capitellidae, Nereidae) and snails (Littorinidae, Mytilidae); SD provided the best conditions for feeding of *A. herzbergii* which might be linked to diurnal activity patterns of the brachyuran crab species in the mangrove creeks (Koch, 1999).

In the dry season 1997, about 70 % of *C. psittacus* left intertidal mangrove creeks with medium to totally filled intestines (Keuthen, unpubl. data), suggesting intense feeding in the intertidal zone (Krumme, subm.). The principal food items were Balanidae, brachyuran crabs, teleostei, bivalves, insecta, and polychaeta (Keuthen, unpubl. data). The diurnal activity pattern of *C. psittacus* is probably related to a fairly visual search for prey (own obs.) and the fact that all *Uca*-species are diurnal and cease feeding in the evening (Koch 1999).

Brenner and Krumme (subm.) found that *A. anableps* feed on red algae, Insecta, and Grapsidae. Best foraging conditions for *A. anableps* occurred at SD when daylight and maximum intertidal accessibility coincided.

Engraulidae clearly entered the creeks to feed. Although Brenner (unpubl. data) caught more *A. clupeioides* at daytime than at night, stomachs were fuller at night (more copepoda) than at daytime (more diatoms). Since abundance of both phytoplankton (Schories, unpubl. data) and zooplankton (Krumme and Liang, in press) in the Furo do Meio are highest at spring tide and essentially lack a significant diel cycle, their nocturnal immigration at spring tides can be readily explained by feeding migrations. Predatory *P. atherinoides* preyed upon Penaeidae, Caridae, the copepod *Pseudodiaptomus marshii*, juvenile fish and fish larvae (Sciaenidae, Mugilidae) in the mangrove creeks (Keuthen, unpubl. data). 50 % of *P. atherinoides* left intertidal mangrove creeks with stomachs that were more than 50 % full. Stomachs of intertidal *C. edentulus* were uniformly full, mainly with phytoplankton (diatoms) (Keuthen, unpubl. data; Krumme, subm.). In tropical Australia post-larval and juvenile Engraulidae and

Clupeidae foraged on high zooplankton abundances in mangrove creeks (Robertson et al., 1988).

Insecta occurred in the stomachs of intertidally foraging *A. anableps* (Brenner and Krumme, *subm.*), *P. nodosus* and *C. psittacus* (Keuthen, *pers. comm.*) and were also found in the stomachs of different fish species in Australia (Robertson, 1988), suggesting that Insecta may provide an important protein source in some intertidal mangrove fish species.

Life cycles

In the wet season when the river run-off is maximal, the longitudinal turbidity gradient is most pronounced and serves as a cue for the orientation of immigrating fish, especially of juveniles (Blaber and Blaber, 1980; Cyrus and Blaber, 1987; Barletta-Bergan et al., 2002). However, the salinity decrease was neither expressed in the general species composition (Fig. 6b) nor in the abundances, except for three species. Mean TL of *A. lepidentostole* caught was 4 ± 2 cm and maximum 8 cm ($n = 20$) (Table 2). In the Orinoco delta, *A. lepidentostole* migrated towards freshwater in May in the wet season to spawn; L_{50} values were 4.8 cm and 7.2 cm for males and females, respectively (Cervigón, 1991). Unfortunately, we did not analyze gonads, but Barletta-Bergan (1999) caught *A. lepidentostole* larvae exclusively in the middle and upper Caeté estuary. Hence, *A. lepidentostole* obviously was caught in the intertidal mangrove creeks during the spawning migration towards the Caeté River.

Cynoscion acoupa probably spawn in the lower estuary or near the coast (Barletta-Bergan 1999). In 1997, *C. acoupa* larvae entered the tidal mangrove creeks with high abundances in April (Barletta-Bergan 1999, p. 155). Adult *C. faber* spawn near the coast. In 1997, larvae entered the mangrove habitats with highest abundances in February (Barletta-Bergan, 1999).

Barletta et al. (2003) assumed that *P. nodosus* had moved from the upper estuary towards the lower estuary with the start of the wet season where they were caught in the intertidal creeks between January and April. Apparently, the *P. nodosus* population was already fully established when our sampling started, and therefore lacked any abundance trend.

Anger and Moreira (1998) found female *P. northropi* with eggs whose minimal carapax lengths ranged between 20 and 22 mm, indicating the presence of a mainly adult population in the mangrove creeks (Table 2).

The utilization of the intertidal creeks differed not only inter- but also intraspecifically, as indicated by the sex-specific occurrence in *Cathorops* sp. Since buccal-incubating male Ariidae stop feeding (Burgess, 1989), the presence of male *Cathorops* sp. was certainly not related to feeding migrations, but likely linked to predator avoidance. Unlike females and

juveniles that occurred in the intertidal creeks each tide, male *Cathorops* sp. were mainly caught at nocturnal spring tides when predation is supposed to be highest and probably higher in the deeper main channel than in the shallow mangrove creeks of the Furo do Meio. Even assuming that male *Cathorops* sp. required a minimum water height to enter the mangrove creeks, the preference for SN is still not explained. Rountree and Able (1993) suggested that nocturnal immigration of *Menidia menidia* in salt marsh creeks was caused by avoidance movements related to the presence of predators.

The L_{50} value of *Cathorops* sp. was below those estimated for *C. spixii* in Venezuela: 19.3 cm, minimal 14.9 cm (Cervigón, 1991). Melo and Texeira (1992) provided L_{50} values of 12.6 cm for female and 11.9 cm for male *C. spixii*. In the Caeté estuary, mature *C. spixii* were caught at only 6.5 cm TL, suggesting *C. spixii* to be a species complex (Camargo and Isaac, 1998).

Tidal and diel variations in species composition

The interplay of the fortnightly pulse of the spring/neap tide alternation together with the superimposed impact of the day/night cycle significantly determined fish assemblage compositions. The tide determines the habitat accessibility for tidal migrating fish species while the diel cycle controls the visual conditions and diel changes in the organisms' activity. However, the tide had a stronger influence on the catch weights and assemblage compositions than the diel cycle.

The numbers of species and the S/F ratio showed that more niches were available at spring tide. This is likely linked to greater habitat accessibility and food availability at spring tides, e.g. in zooplankton (Krumme and Liang, in press).

Besides the qualitative aspect of presence or absence of species, it was the quantitative change in the proportions between abundant species that determined significant changes in assemblage composition. Differences in the estuarine fish community in Florida were mainly due to quantitative changes caused by immigration of agglomerations of particular species (Livingston, 1976).

Although the influence of the tidal and diel cycle on the movements of tidal migrating fish is established (Gibson 1988), we present evidence for distinct assemblages resulting from such movements. Brenner (unpubl. data) repeated our sample design in two 1st order creeks in the wet season 2001 and found the same interplay of tide and time of day, underlining that these patterns recur annually, and most likely even is a typical fortnightly feature of the system year-round. Schaub (unpubl. data) analyzed the early dry season-catches of tidal-migrating

fish in large commercial tidal traps in the Caeté bay. Catches were higher at night than at daytime with night assemblages dominated by Arridae and Sciaenidae whereas daytime assemblages were more diverse in terms of family composition. Interestingly, he observed a pronounced species shift from neap to spring tide (wax to full moon), with species proportions changing one day before full moon. Laroche et al. (1997) and Lin and Shao (1999) observed similar temporal assemblage changes.

The lunar cycle is likely of minor importance in the mangrove ichthyofauna. In the wet season, minimal water clarity and heavy clouding may severely limit the impact of lunar light levels to control fish behavior. Quinn and Kojis (1981) found no significant differences between full and new moon in nocturnal fish assemblages in subtropical Australia.

Barletta (1999, p. 83) showed that seasonal salinity alterations were related to changes in the structure of the fish communities in the Caeté estuary system. However, almost all fish living in subtropical and tropical estuaries are euryhaline (Blaber 1997, p. 125) and salinity changes on a scale of days to weeks - even though severe - may not cause major disturbances in the structure of a tropical estuarine fish community. Variations in water temperature are recognized as insignificant in triggering changes in the fish community (Barletta-Bergan, 1999).

Tidal migration

The tide based on the lunar cycle is modified by topographical, meteorological (wind, atmospheric pressure) and hydrological phenomena. Species composition structures at spring tides are more similar and can be attributed to less variable HW levels at spring than at neap tide (Table 1). We suppose that at spring tides, the strong currents lead to a more homogenous species structure, whereas at neap tides, when the creek environment is less subjected to harsh environmental pressures, the species composition becomes more heterogeneous. In general, extreme environmental conditions produce clear-cut responses in nature whereas a wider range of responses can occur under less stressful conditions. Accordingly, the rhythmical behavior of fish species distributed in both tidal and non-tidal environments like *Pomatoschistus minutus* or *Platichthys flesus* reflected the relative importance of the tidal regime in their environment (Gibson 1982, p. 399).

Spatio-temporal movements are closely linked to the accessibility of resource-rich and large intertidal habitats. The topography of the plateau mangrove of the Caeté estuary leads to a 51 % increase in inundated mangrove area, with just 20 cm water level increase above mean HW (4 %) (Cohen et al., 2000). Similar Robertson and Duke (1990), we observed that such

extreme HW levels produced exceptionally high catches. Moreover, the maximum HW level also had a clear influence on the structure of the fish assemblages (Fig. 6a). Laegdsgaard and Johnson (1995) suggested that structure and number of species in muddy areas in the mangrove habitat depend on the tidal height. Davis (1988) found that tidal height determined the movements of the entire fish community in a tropical Australian salt marsh creek. Water height or the requirement of a minimum water level seem to be important for the occurrence of certain fish species in shallow-water environments, especially in piscivorous fish (Davis, 1988; Blaber et al., 1995; Laroche et al., 1997).

The maximum HW level is an important parameter in intertidal migration patterns influenced by the status of the tidal cycle, e.g. current speed at flood tide, and cumulatively captures the accessibility of the intertidal area. It is generally agreed that fish perceive pressure changes (Gibson, 1973). This author proposed the selection and maintenance of a particular depth range by a fish species throughout the tidal cycle, thereby functioning as a possible mechanism to control the tide-related movements and size-depth relationships. Our results suggest that following increased HW levels, an earmark of flooding, fish respond with increased immigration.

Resident fish species in the intertidal mangrove zone (Gibson, 1992; Barletta et al., 1999; Barletta et al., 2000) were virtually absent from the block net catches during LW and did not cover larger spatial scales in their tidal migration (Horn et al., 1999). In contrast, almost all species caught in the subtidal parts of the Furo do Meio at LW were also present in the intertidal mangrove at HW. Barletta (1999) caught thirteen species with the same beach seine used in the present study in the subtidal parts of the Furo do Meio at ND in April, the majority of which were again caught in the intertidal mangrove at HW with block nets (*Cathorops* sp., *C. psittacus*, *A. clupeioides*, *G. luteus*, *Mugil* spp., *C. acoupa*, *P. atherinoides*, *A. herzbergii*, *A. anableps*, *S. naso*). This suggests a direct spatial linkage between the two habitats on the scale of at least several tens to hundreds of meters. However, diversity at LW was poorer than at HW, probably related to quantitative and qualitative absence of species and to the low catch efficiency of the beach seine (net avoidance). This and the large fish caught by artisanal seining in the deeper subtidal zone indicate that our biomass values are likely underestimations of the huge biomass that agglomerates in the main channel at each LW.

Significant diel changes in the fish assemblage structure at LW affirmed the distribution patterns observed at LW using shallow-water sonar (Krumme and Saint-Paul, 2003).

At LW, juvenile fish were abundant in the shallow water whereas larger fish withdraw to deeper areas and close to wooden debris at LW (pers. comm. with fishermen). This distribution may likely be an effort by juveniles and shrimp to avoid predation from larger fish (Clark et al., 2003). Further, juvenile fish may feed on zooplankton that is close to the surface at LW (Krumme and Liang, in press). Finally, staying in shallow waters close to the channel bank at LW may facilitate an early immigration into the intertidal zone for the juveniles at the start of the flood tide (Krumme and Saint-Paul, 2003; Brenner and Krumme, *subm.*; Krumme, *subm.*).

Many fish foraging in the mangrove creeks at high tide moved into shallow subtidal creeks at ebb tide leading to higher biomasses in these habitats (Robertson and Duke 1990; Barletta 1999). Pelagic fish species, however, stayed in the central channel of the estuary (Robertson and Duke, 1990) during LW. Pelagic *C. edentulus* may undertake large-scale movements between the mangrove and the estuary, but large schools constantly become trapped in the tidal tributaries during ebb tide as indicated by the beach seine catches.

In tropical Australia, *Penaeus merguensis* were concentrated in the main channel in the turbid shallows near the banks from where they entered the mangrove creeks during flood tide (Vance et al., 1990). A similar distribution of shrimp is exploited in North Brazil by artisanal fishermen that hand-trawl for shrimp, mainly *F. subtilis*, in the muddy upper reaches of the mangrove channels during nocturnal LW, especially during the dry season when shrimp abundances are higher (own obs.; pers. comm. with fishermen).

It can be assumed that the fish returning from the intertidal feeding grounds, split their routes towards the subtidal zone both inter- and intraspecifically; e.g. juvenile *C. psittacus* were abundant at LW in the subtidal parts of the Furo do Meio but not one adult specimen was caught at any occasion although both sizes occur in the mangrove creeks at HW. The adults may return further downstream at ebb tide, probably even to the Caeté bay where they were frequently caught in large commercial tidal traps (Schaub, unpubl. data). Such larger-scale tidal migrations (probably several km per tide) also take place in species like *C. edentulus*, *M. ancylodon*, *C. acoupa* and *Mugil* spp. (pers. comm. with fishermen; Schaub unpubl. data). It is essentially unknown where the fish stay when they are absent from the flooded mangrove creeks at HW, e.g. at neap tides or *C. psittacus* at night.

Piscine predation

We have evidence to assume that the nekton experienced reduced mortality when foraging in the shallow submerged creeks. Ichthyophage fish were almost completely absent from the intertidal mangrove creeks. The ichthyophage fish were usually small-sized juveniles, hence unlikely to prey upon similarly sized juveniles of other species. The stomach fullness of the few larger ichthyophage specimens was highly variable and only about 25 % \pm 18 S.D. had at least one prey item in their stomach (own obs.).

Paterson and Whitfield (2000) showed that both juvenile and adult piscivorous fish species avoided intertidal creeks and shallow-water habitats, indicating that shallow estuarine areas provide refugia for juvenile life-stages. Likewise, Blaber (1980) and Rönnbäck et al. (1999) found a spatial decrease in the proportions of piscivorous fish towards shallow-water areas. Even on small scales (1-95 cm depth), an increase in the risk of predation with depth is detectable (Ruiz et al., 1993).

Predatory fish preyed upon Mugilidae, *R. amazonica* (Clupeidae), *A. spinifer* (Engraulidae) and especially *F. subtilis*. Shrimp, due their numerical abundance and the wide spectrum of available sizes, were of special importance as prey items for predatory fish.

Both predators and their prey were more abundant at spring tides (Table 2; Fig. 4), suggesting that (i) that the tide synchronized abundance patterns in the predators and their prey and (ii) that predators are fairly unspecific feeders and feed on what is abundant (Blaber 1986).

Piscine predation was most likely to occur at SN when predatory fish were most abundant. Although light levels are lowest at SN, the fish still feed efficiently on their prey even under high turbidity conditions and low light levels (Grechay and Targett, 1996). Mainly nocturnal feeding of piscivorous fish was demonstrated by Kleypas and Dean (1983) and Blaber et al. (1995).

CONCLUSIONS

The intertidal mangrove creeks provided an important nursery habitat for juvenile fish and shrimp at HW. The fish extensively fed in this habitat and likely experienced reduced predation due to the almost complete absence of larger-sized piscivores.

Benthophage, estuarine fish dominated the intertidal mangrove ichthyofauna, emphasizing the importance of a detritus-based food chain and suggesting that considerable biomass remains in the mangrove system.

The HW-nekton assemblages at SN, SD, NN and ND were significantly different in their species compositions, indicating that the interplay between tide and time of day determined

the tidal-related movements of fish and shrimp. The tide is the principal pulse of the mangrove system, synchronizing changes in abundance of fish, shrimp, zooplankton (Krumme and Liang, in press), detritus export (Schories et al., 2003) and biogeochemical parameters (Lara and Dittmar, 1999; Dittmar and Lara, 2001a,b). The strongest coupling of and exchange between aquatic system compartments most likely occurs at spring tides when abundances, richness and assemblage complexity of the nekton were greatest.

Species-specific studies on tidal-related patterns in feeding showed that the interaction of HW height and time of day influence the degree of foraging success of the fish (Brenner and Krumme, *subm.*; Brenner, *unpubl. data*).

The tidally migrating fish responded positively to higher submergence levels. Consequently, a rise in sea level would probably increase habitat and resource availability for intertidal fish at first glance, but anthropogenic and rapid changes in tidal regime would most likely aggravate the conditions for intertidal fish on a longer-term scale due to dramatic large-scale changes in the mangrove environment.

At LW, fish concentrated in the subtidal parts of the channel. The species structure in the subtidal parts of the channel at LW essentially was a less diverse subset of the assemblage caught in the intertidal mangrove creeks at HW. This indicates that not all species and sizes reside at LW near the areas where they feed at HW and that hence, fish split the routes of migration at ebb tide to return to a specific LW habitat. Thus, the foraging ranges, destinations of travel and depth distributions of fish movements may not only differ interspecifically, but may also ontogenetically change while juveniles grow to adults (Gillanders et al., 2003).

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REFERENCES

- Ansell, A.D., Gibson, R.N., 1990. Patterns of feeding and movement of juvenile flatfish on an open sandy beach, pp. 191-207. In: Barnes, M., Gibson R.N. (Eds.), *Trophic Relationships in the Marine Environment*. Aberdeen University Press.
- Barletta, M., 1999. Seasonal changes of density, biomass and species composition of fishes in different habitats of the Caete estuary (North Brazilian coast - east Amazon). Diss. Bremen Univ., Germany, Fachbereich 2 (Biologie/Chemie), ZMT Contrib. No. 7, Zentrum fuer Marine Tropenoekologie, Bremen, Germany, 115 pp., ISSN 0944-0143.
- Barletta, M., Barletta-Bergan, A., Saint-Paul, U., 1998. Description of the fisheries structure in the mangrove-dominated region of Bragança (state of Pará, North Brazil). *Ecotropica* 4, 41-53.
- Barletta, M., Barletta-Bergan, A., Saint-Paul, U., Hubold G., 2003. Seasonal changes in density, biomass, and diversity of estuarine fishes in tidal mangrove creeks of the lower Caeté Estuary (northern Brazilian coast, east Amazon). *Mar. Ecol. Prog. Ser.* 256, 217-228.
- Barletta, M., Saint-Paul, U., Barletta-Bergan, A., 1999. The use of an ichthyotoxic plant in artisanal coastal cutuca (*Myrophis punctatus*, Lütken - Ophichthidae) fisheries along the North Brazilian coast. *Ecotropica* 5, 83-86.
- Barletta, M., Saint-Paul, U., Barletta-Bergan, A., Ekau, W., Schories, D., 2000. Spatial and temporal distribution of *Myrophis punctatus* (Ophichthidae) and associated fish fauna in a northern Brazilian intertidal mangrove forest. *Hydrobiologia* 426, 65-74.
- Barletta-Bergan, A., 1999. Structure and seasonal dynamics of larval and juvenile fish in the mangrove-fringed estuary of the Rio Caete in North Brazil. Diss. Bremen Univ., Germany, Fachbereich 2 (Biologie/Chemie), ZMT Contrib. No. 8, Zentrum fuer Marine Tropenoekologie, Bremen, Germany, 219 pp., ISSN 0944-0143.
- Barletta-Bergan, A., Barletta, M., Saint-Paul, U., 2002. Structure and Seasonal Dynamics of Larval Fish in the Caeté River Estuary in North Brazil. *Estuar. Coast. Shelf Sci.* 54, 193-206.

- Batista, V.D.S., Rêgo, F.N., 1996. Análise de associações de peixes, em igarapés do estuário do Rio Tibiri, Maranhão. Rev. Brasil. Biol. 56(1), 163-176. In Portuguese.
- Bell, J.D., Pollard, D.A., Burchmore, J.J., Pease, B.C., Middleton, M.J., 1984. Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, New South Wales. Austr. J. Mar. Freshwat. Res. 35, 33-46.
- Berger, U., Glaser, M., Koch, B., Krause, G., Lara, R., Saint-Paul, U., Schories, D., Wolff, M., 1999. An intergrated approach to mangrove dynamics and management. J. Coastal Conservation 5, 125-134.
- Blaber, S.J.M., 1980. Fish of the Trinity Inlet system of North Queensland with notes on the ecology of fish faunas of tropical Indo-Pacific estuaries. Austr. J. Mar. Freshwat. Res. 31, 137-145.
- Blaber, S.J.M., 1986. Feeding selectivity of a guild of piscivorous fish in mangrove areas of north-west Australia. Aust. J. Mar. Freshwat. Res. 37, 329-336.
- Blaber, S.J.M., 1997. Fish and Fisheries in Tropical Estuaries. Chapman & Hall, Fish and Fisheries Series 22, London, 367 pp., ISBN 0412785005.
- Blaber, S.J.M., Blaber, T.G., 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. J. Fish. Biol. 17, 143-162.
- Blaber, S.J.M., Brewer, D.T., Salini, J.P., 1989. Species composition and biomasses of fishes in different habitats of a tropical northern Australian estuary: Their occurrence in the adjoining sea and estuarine dependence. Estuar. Coast. Shelf Sci. 29, 509-531.
- Blaber, S.J.M., Brewer, D.T., Salini, J.P., 1994a. Comparisons of the fish communities of tropical estuarine and inshore habitats in the Gulf of Carpentaria, northern Australia. International Symposium Series, ECSA 22, Olsen & Olsen, Fredensborg, pp. 363-372.
- Blaber, S.J.M., Brewer, D.T., Salini, J.P., 1994b. Dentition and diet in tropical ariid catfish from Australia. Environ. Biol. Fish. 40, 159-174.
- Blaber, S.J.M., Brewer, D.T., Salini, J.P., 1995. Fish communities and the nursery role of the shallow inshore waters of a tropical bay in the Gulf of Carpentaria, Australia. Estuar. Coast. Shelf Sci. 40, 177-193.
- Bozeman, E.L.Jr., Dean, J.M., 1980. The abundance of estuarine larval and juvenile fish in a South Carolina intertidal creek, Estuaries 3(2), 89-97.
- Brenner, M., Krumme, U., (Submitted) Tidal migration and patterns in feeding of *Anableps anableps* L. (Anablepidae) in a North Brazilian mangrove. Mar. Ecol. Prog. Ser.
- Cain, R.L., Dean, J.M., 1976. Annual occurrence, abundance and diversity of fish in a South Carolina intertidal creek. Mar. Biol. 36, 369-379.

- Camargo, M., Isaac, V.J., 1998. Population structure of fish fauna in the estuarine area of Caeté River, Bragança, Pará, Brazil. *Acta Scientiarum* 20(2), 171-177.
- Cervigón, F., 1991. Los peces marinos de Venezuela, Vol. I, 2ª Ed., Fundación científica Los Roques, Caracas, Venezuela, 425 pp. Cervigón, F., 1991. Los peces marinos de Venezuela, Vol. I, 2ª Ed., Fundación científica Los Roques, Caracas, Venezuela, 425 pp.
- Cervigón, F., 1993. Los peces marinos de Venezuela, Vol. II, 2ª Ed., Fundación científica Los Roques, Caracas, Venezuela, 497 pp.
- Cervigón, F., 1994. Los peces marinos de Venezuela, Vol. III, 2ª Ed., Fundación científica Los Roques, Caracas, Venezuela.
- Cervigón, F., 1996. Los peces marinos de Venezuela, Vol. IV, 2ª Ed., Fundación científica Los Roques, Caracas, Venezuela.
- Cervigón, F., Cipriani, R., Fischer, W., Garibaldi, L., Hendrickx, M., Lemus, A.J., Márquez, R., Poutiers, J.M., Robaina, G., Rodríguez, B., 1993. FAO species identification sheets for fishery purposes: Field guide to the commercial marine and brackish-water resources of the northern coast of South America. Rome, FAO, 513 pp.
- Clark, K.L., Ruiz, G.M., Hines, A.H., 2003. Diel variation in predator abundance, predation risk and prey distribution in shallow-water estuarine habitats. *J. Exp. Mar. Biol. Ecol.* 287, 37-55.
- Clarke, K.R., Green, R.H., 1988. Statistical design and analysis for a 'biological effects' study. *Mar. Ecol. Prog. Ser.* 46, 213-226.
- Clarke, K.R., Warwick, R.M., 1994. Changes in marine communities: An approach to statistical analysis and interpretation. Plymouth Marine Laboratory. Natural Environment Research Council, U.K. 144 pp.
- Clarke, R.M., 1993. Non-parametric multivariate analysis of changes in community structure. *Aust. J. Ecol.* 18, 117-143.
- Cohen, M.C., Lara, R.J., Szlafsztein, C.F., Dittmar, T., 2000. Digital elevation models as a GIS tool for the analysis of mangrove coasts. Amazon Region, Brazil. *J. Internat. Environ. Creat.* 3(1), 31-41. ISSN 13439863.
- Cyrus, D.P., Blaber, S.J.M., 1987. The influence of turbidity on juvenile marine fishes in estuaries. Part 2, laboratory studies. *J. Exp. Mar. Biol. Ecol.* 109, 53-70.
- Daniel, P.A., Robertson, A.I., 1990. Epibenthos of mangrove waterways and open embayments: Community structure and the relationship between exported mangrove detritus and epifaunal standing stocks. *Estuar. Coast. Shelf Sci.* 31, 599-619.

- Davis, T.L.O., 1988. Temporal patterns in the fish fauna entering a tidal swamp system in tropical Australia. *Env. Biol. Fish.* 21(3), 161-172.
- Day, J.H., Blaber, S.J.M., Wallace, J.H., 1981. Estuarine fishes. In: Day, J.H. (Ed.), *Estuarine ecology with particular reference to South Africa*. Rotterdam, Balkema. pp. 197-223.
- Dittmann, S., 2001. Abundance and distribution of small infauna in mangroves of Missionary Bay, North Queensland, Australia. *Rev. Biol. Trop.* 49, 535-544.
- Dittmar, T., Lara, R.J., 2001a. Do mangroves rather than rivers provide nutrients to coastal environments south of the Amazon River? Evidence from long-term flux measurements. *Mar. Ecol. Prog. Ser.* 213, 67-77.
- Dittmar, T., Lara, R.J., 2001b. Driving forces behind nutrient and organic matter dynamics in a mangrove tidal creek in North Brazil. *Estuar. Coast. Shelf Sci.* 52, 249-259.
- Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.* 8, 37-52.
- Gibson, R.N., 1973. The intertidal movements and distribution of young fish on a sandy beach with special reference to the plaice (*Pleuronectes platessa* L.). *J. Exp. Mar. Biol. Ecol.* 12, 79-102.
- Gibson, R.N., 1982. Recent studies of the biology of intertidal fishes. *Oceanogr. Mar. Biol. Ann. Rev.* 20, 363-414.
- Gibson, R.N., 1988. Patterns of movement in intertidal fishes. In: Chelazzi, G., Vanini, M. (Eds.), *Behavioural adaptations to intertidal life*. NATO ASI Series Life Sciences Vol. 151, Plenum Press, London. pp. 55-63.
- Gibson, R.N., 1992. Tidally-synchronised behaviour in marine fishes. In: Ali, M.A. (Ed.), *Rhythms in Fishes*. NATO ASI Series Life Sciences Vol. 236, Plenum Press, New York. pp. 63-81.
- Gibson, R.N., 1996. Tidal, diel and longer term changes in the distribution of fishes on a Scottish sandy beach. *Mar. Ecol. Prog. Ser.* 130, 1-17.
- Gibson, R.N., Pihl, L., Burrows, M.T., Modin, J., Wennhage, H., Nickell, L.A., 1998. Diel movements of juvenile plaice *Pleuronectes platessa* in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. *Mar. Ecol. Prog. Ser.* 165, 145-159.
- Gillanders, B.M., Able, K.W., Brown, J.A., Eggleston, D.B., Sheridan, P.F., 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Mar. Ecol. Prog. Ser.* 247, 281-295.

- Helfman, G.S., 1993. Fish behaviour by day, night and twilight. In: Pitcher, T.J. (Ed.) Behaviour of teleost fishes. Second ed., Chapman & Hall, Fish & Fisheries Series 7, London, 715 pp., pp. 479-512.
- Horn, M.H., Martin, K.L.M., Chotkowski, M.A., 1999. Intertidal Fishes: Life in Two Worlds. Academic Press, San Diego, 399 pp.
- INMET (Instituto Nacional de Meteorologia), 1992. Normais climatológicas (1961-1991). Tech. Rep. Instituto Nacional de Meteorologia, Brasilia DF, Brasil.
- Jager, Z., 1999. Selective tidal stream transport of flounder larvae (*Platichthys flesus* L.) in the Dollard (Ems estuary). Estuar. Coast. Shelf Sci. 49, 347-362.
- Kjerfve, B., de Lacerda, L.D., 1993. Mangroves of Brazil. In: de Lacerda, L.D. (Ed.) Mangrove ecosystems technical reports ITTO TS-13(2), 245-272.
- Kleypas, J., Dean, J.M., 1983. Migration and feeding of the predatory fish, *Bairdiella chrysura* Lacépède, in an intertidal creek. J. Exp. Mar. Biol. Ecol. 72, 199-209.
- Koch, V., 1999. Epibenthic production and energy flow in the Caeté mangrove estuary, North Brazil. Diss. Bremen Univ., Germany, Fachbereich 2 (Biologie/Chemie), ZMT Contrib. No. 6, Zentrum fuer Marine Tropenökologie, Bremen, Germany, 97 pp., ISSN 0944-0143.
- Koch, V., Wolff M., 2002. Energy budget and ecological role of mangrove epibenthic in the Caeté estuary, North Brazil. Mar. Ecol. Prog. Ser. 228, 119-130.
- Krause, G., Schories, D., Glaser, M., Diele, K., 2001. Spatial patterns of mangrove ecosystems: the bragantinian mangroves of northern Brazil (Bragança, Pará). Ecotropica 7, 93-107.
- Krumme U., (Submitted) Patterns in the tidal migration of fish in a North Brazilian mangrove channel as revealed by vertical beaming using a 200 kHz split-beam sonar. Fish. Res.
- Krumme, U., Liang, T.H. (In Press) Tidal induced changes in a copepod-dominated zooplankton community in a macrotidal mangrove channel in northern Brazil. Zool. Stud.
- Krumme, U., Saint-Paul, U., 2003. Observation of fish migration in a macrotidal mangrove channel in Northern Brazil using 200-kHz split-beam sonar. Aquat. Living Resour. 16(3), 175-184.
- Laegdsgaard, P., Johnson C.R., 1995. Mangrove habitats as nurseries: Unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. Mar. Ecol. Prog. Ser. 126, 67-81.

- Laegdsgaard, P., Johnson C.R., 2001. Why do juvenile fish utilise mangrove habitats? *J. Exp. Mar. Biol. Ecol.* 257, 229-253.
- Lara R.J., Dittmar T., 1999. Nutrient dynamics in mangrove creek (North Brazil) during the dry season. *Mangroves and Salt Marshes* 3, 185-195.
- Laroche, J., Baran, E., Rasoanandrasana, N.B., 1997. Temporal patterns in a fish assemblage of a semiarid mangrove zone in Madagascar. *J. Fish Biol.* 51, 3-20.
- Leal-Flórez, J., Krumme, U., Saint-Paul, U., (In prep.) Tidal-related changes in feeding of *Cathorops* sp. (Ariidae) in a macrotidal mangrove in North Brazil. *Env. Biol. Fish.*
- Lin, H.J., Shao, K.T., 1999. Seasonal and diel changes in a subtropical mangrove fish assemblage. *Bull. Mar. Sci.* 65, 775-794.
- Little, M.C., Reay, P.J., Grove, S.J., 1988. The fish community of an East African mangrove creek. *J. Fish. Biol.* 32, 729-747.
- Livingstone, R.J., 1976. Diurnal and seasonal fluctuations of organisms in a north Florida estuary. *Estuar. Coast. Shelf Sci.* 4, 373-400.
- Longhurst, A.R., Pauly, D., 1987. *Ecology of Tropical Oceans*. Academic Press, San Diego, 407 pp.
- Louis, M., Bouchon, C., Bouchon-Navaro, Y., 1995. Spatial and temporal variations of mangrove fish assemblages in Martinique (French West Indies). In: Wong, Y.S., Tam, F.Y. (Eds.), *Asia-Pacific Symposium on Mangrove Management*. pp. 275-284.
- Lum Young, P., Ferreira, L., Maharaj, L., 1992. Stock assessment parameters of five species of Western Atlantic tropical shrimp. Technical Report of the Project for the Establishment of Data Collection Systems and Assessment of the Fisheries Resources. FAO/UNAP:TRI/91/001/TR1. Port of Spain (Trinidad). July, 1992, 43 pp.
- Melo, S.C., Texeira, R.L., 1992. Distribuição, reprodução e alimentação de *Cathorops spixii* e *Arius rugispinis* (PISCES: Ariidae) do complexo Mundaú/Maceió-Al. *Rev. Brasil. Biol.* 52(1), 169-180.
- Miller, J.M., Crowder, L.B., Moser, M.L., 1985. Migration and utilization of estuarine nurseries by juvenile fishes: an evolutionary perspective. *Contrib. Mar. Sci. Univ. Texas* 27, 338-352.
- Morrison, M.A., Francis, M.P., Hartill, B.W., Parkinson, D.M., 2002. Diurnal and tidal variation in the abundance of the fish fauna of a temperate tidal mudflat. *Estuar. Coast. Shelf Sci.* 54, 793-807.
- Nagelkerken, I., Dorenbosch, M., Verberk, W.C.E.P., Cocheret de la Morinière, E., van der Velde G., 2000. Importance of shallow-water biotopes of a Caribbean bay for juvenile

- coral reef fishes: patterns in biotope association, community structure and spatial distribution. *Mar. Ecol. Prog. Ser.* 202, 175-192.
- Odum, W.E., Heald, E.J., 1972. Trophic analyses of an estuarine mangrove community. *Bull. Mar. Sci.* 22(3), 671-738.
- Paterson, A.W., Whitfield, A.K., 2000. Do shallow-water habitats function as refugia for juvenile fishes? *Estuar. Coast. Shelf Sci.* 51, 359-364.
- Perez-Farfante, I., Kensley, B., 1997. Penaeoid and sergestoid shrimps and prawns of the world. Keys and diagnoses for the families and genera. *Mem. Mus. Natl. Hist. Nat. (France)*, 175, 233 pp., ISBN 2856535100.
- Pielou, E.C., 1969. *An introduction to mathematical ecology*. Wiley, New York.
- Quinn, N.J., 1980. Analysis of temporal changes in fish assemblages in Serpentine creek, Queensland. *Environ. Biol. Fish.* 5(2), 117-133.
- Quinn, N.J., Kojis, B.L., 1981. The lack of changes in nocturnal fish assemblages between new and full moon phases in Serpentine creek, Queensland. *Environ. Biol. Fish.* 6(2), 213-218.
- Robertson, A.I., 1988. Abundance, diet and predators of juvenile banana prawns, *Penaeus merguensis*, in a tropical mangrove estuary. *Aust. J. Mar. Freshwat. Res.* 39, 467-478.
- Robertson, A.I., Blaber, S.J.M., 1992. Plankton, Epibenthos and Fish Communities. In: Robertson, A.I., Alongi, D.M. (Eds.), *Tropical Mangrove Ecosystems. Coastal and Estuarine Studies 41*, American Geophysical Union, Washington, DC, 329 pp., pp. 173-224.
- Robertson, A.I., Duke, N.C., 1987. Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. *Mar. Biol.* 96, 193-205.
- Robertson, A.I., Duke, N.C., 1990. Mangrove fish-communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass and community structure. *Mar. Biol.* 104, 369-379.
- Robertson, A.I., Dixon P., Daniel P.A., 1988. Zooplankton dynamics in mangrove and other nearshore habitats in tropical Australia. *Mar. Ecol. Prog. Ser.* 43, 139-150.
- Rönnbäck, P., Troell, M., Kautsky, N., Primavera, J.H., 1999. Distribution patterns of shrimp and fish among *Avicennia* and *Rhizophora* microhabitats in the Pagbilao mangroves, Philippines. *Estuar. Coast. Shelf Sci.* 48, 223-234.
- Rooker, J.R., Dennis, G.D., 1991. Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bull. Mar. Sci.* 49, 684-698.

- Rountree, R.A., Able, K.W., 1993. Diel variation in decapod and fish assemblages in New Jersey polyhaline marsh creeks. *Estuar. Coast. Shelf Sci.* 37, 181-201.
- Rozas, L.P., Minello, T.J., 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: A review of sampling design with focus on gear selection. *Estuaries* 20(1), 199-213.
- Ruiz, G.M., Hines, A.H., Posey, M.H., 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: An example from Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 99, 1-16.
- Sachs, L., 1992. *Angewandte Statistik - Anwendung statistischer Methoden*. 7. Aufl., Springer, Berlin.
- Sasekumar, A., Chong, V.C., Leh, M.U., D'Cruz, R., 1992. Mangroves as a habitat for fish and prawns. *Hydrobiologia* 247, 195-207.
- Schories, D., Barletta-Bergan, A., Barletta, M., Krumme, U., Rademaker, V., 2003. The keystone role of leaf-removing crabs in mangrove forests of North Brazil. *Wetlands Ecology and Management*, in press.
- Schwammborn, R., Bonecker, A.C.T., 1996. Seasonal changes in the transport and distribution of meroplankton into a Brazilian estuary with emphasis on the importance of floating mangrove leaves. *Arq. Biol. Technol.* 39(2), 451-462.
- Shannon, C.E., Weaver, W., 1949. *The mathematical theory of communication*. Urbana: University of Illinois Press.
- Shenker, J.M., Dean, J.M., 1979. The utilization of an intertidal salt marsh creek by larval and juvenile fishes: abundance, diversity and temporal variation. *Estuaries* 2(3), 154-163.
- Smith, C.L., 1997. *Field Guide to Fishes of the Caribbean, the Gulf of Mexico, Florida, the Bahamas, and Bermuda*. Alfred A. Knopf, New York.
- Sokal, R.R., Rohlf F.J., 1995. *Biometry: Principles and practice of statistics in biological research*, 3rd Ed., W.H. Freeman and Company, New York, 887 p.
- Thollot, P., Kulbicki, M., Harmelin-Vivien M., 1999. Réseaux trophique et fonctionnement trophodynamique de l'ichtyofaune de mangroves de Nouvelle-Calédonie. *C. R. Acad. Sci. Paris, Sciences de la vie* 322, 607-619.
- Vance, D.J., Haywood, M.D.E., Staples, D.J., 1990. Use of a mangrove estuary as a nursery area by postlarval and juvenile banana prawns, *Penaeus merguensis* de Man, in northern Australia. *Estuar. Coast. Shelf Sci.* 31, 689-702.

- Weinstein, M.P., Weiss, S.L., Walters, M.F., 1980. Multiple determinants of community structure in shallow marsh habitats, Cape Fear River estuary, North Carolina. *Mar. Biol.* 58, 227-243.
- Wilson, J.P., Sheaves M., 2001. Short-term temporal variations in taxonomic composition and trophic structure of a tropical estuarine fish assemblage. *Mar. Biol.* 139, 787-796.
- Wolanski, E., Jones, M., Bunt, J.S., 1980. Hydrodynamics of a tidal creek-mangrove swamp system. *Austr. J. Mar. Freshwat. Res.* 31, 431-450.
- Wolff, M., Koch, V., Isaac, V., 2000. A trophic flow model of the Caeté mangrove estuary (North Brazil) with considerations for the sustainable use of its resources. *Estuar. Coast. Shelf Sci.* 50(6), 789-803.
- Wright, J.M., 1986. The ecology of fish occurring in shallow water creeks of a Nigerian mangrove swamp. *J. Fish. Biol.* 29, 431-441.



Photo: U. Krumme

The sonar beaming horizontally across the Furo do Meio main channel at spring tide high water.



Photo: U. Krumme

Sonar equipment with transducer mounted on the floating device.



Photo: A. Hanning

Export of mangrove detritus at spring ebb tide in the main channel.

**Observations of fish migration in a macrotidal mangrove channel
in Northern Brazil using a 200-kHz split-beam sonar**

Uwe Krumme* & Ulrich Saint-Paul

Zentrum für Marine Tropenökologie (ZMT), Fahrenheitstr. 6, 28359 Bremen, Germany

* Corresponding author. Email address: uwe.krumme@zmt.uni-bremen.de (U. Krumme).

ABSTRACT

A 200-kHz split beam echosounder (BioSonics, DT6000) with a 6° circular-beam transducer was applied in a mangrove channel in Northern Brazil to study the migratory patterns of intertidal fish. Acoustic sampling was conducted horizontally across the channel perpendicular to the tidal current during two lunar cycles in the dry season 2000 and the wet season 2001. The complex acoustic environment of the mangrove channel was characterized by small target sizes (juvenile fish), multiple targets (aggregated fish), high reverberation and background noise levels due to sediment loads, planktons and mangrove litter transport. Dry seasons provided less noisy acoustic conditions resulting in clearer echo data than wet seasons. Neap tide data were less complex than spring tide data. During a tidal cycle, low water provided the clearest acoustic conditions. Mangrove leaves generated fish-like echoes. Analysis of two dry season wax moon cycles revealed fish flux maxima at low water, flood start and high water in the daytime and the night cycle. Night fish fluxes were significantly higher than at daylight. Throughout the tidal cycles, 60% of the fish traveled with the tide and 40% against, suggesting active foraging against the tide to be a major component of fish movements. Resident mangrove fish entered the intertidal creeks at early flood tide, leaving at late ebb tide at fairly shallow water depths. Estuarine fish required a minimum water depth (about 2 m) for tidal migration. Since time delays during spring tides between immigration of resident and estuarine fish were reduced, foraging time and habitat accessibility would be enhanced and fish catches and fishes' feeding success would be greater.

Keywords: Shallow-water echosounder; Mangrove; Fish migration; Tide; Tidal cycle

INTRODUCTION

Mangroves - the highly productive evergreen tidal forests - are considered important nursery areas for young fish throughout the tropical and subtropical coasts of the world (Bell et al., 1984; Robertson and Duke, 1987; Louis et al., 1995; Laroche et al., 1997; Barletta-Bergan et al., 2002). Interannual, seasonal, lunar and diel changes have been observed in mangrove ichthyofauna (Davis, 1988; Laegdsgaard and Johnson, 1995; Laroche et al., 1997; Barletta, 1999). These changes are caused by active movements of the fish in response to variations in food availability, presence of competitors, predation risk and environmental suitability (Gibson et al., 1998) on short -, medium - and long-term scales.

Since tidal-related short-time movements may play a large part in the everyday survival strategies of juvenile fish, comprehensive information about such movements is essential for understanding the life of the young fish in their nursery habitats. Optimized small-scale movements within a nursery probably enhance growth, survival and thus recruitment success. Although short-time changes in intertidal fish communities have been the focus of several studies (Davis, 1988; Laroche et al., 1997; Gibson et al., 1998; Krumme, own obs.), there is a considerable lack of detailed investigations on this particular time scale.

However, sampling in tidal habitats is often difficult to carry out (Horn et al., 1999). Generally, high tidal dynamics require high sample resolution and thus, sampling soon becomes labor-intensive. Additionally, strong tides and floating mangrove litter can considerably impede sampling with conventional fishing gear. Finally, low water- clarity prevailing in many mangroves, hampers visual observations of fish movements.

Modern hydroacoustic equipment allows for non-intrusive, high-resolution sampling even in shallow-water environments. The tidally influenced fish behavior has been commonly observed in many estuaries and tidally influenced rivers (e.g. Levy and Cadenhead, 1995), albeit we found only one study which was conducted in a tropical mangrove environment (Guillard, 1998).

Within the scope of the MADAM project (Mangrove Dynamics and Management; Berger et al., 1999) we could apply a 200-kHz split-beam sonar (BioSonics) in a macrotidal mangrove channel in Northern Brazil. Here, we present results about the tidal-related migratory dynamics of mangrove fish; critical phases for data acquisition in a mangrove environment are discussed.

MATERIAL AND METHODS

Study Area and Study Site. The study area, a 180 km² peninsula located in the second largest mangrove area in the world (Spalding, 1997), is situated about 200 km east of Belém in the estuary of the Caeté river (Fig. 1). More than 4/5 of the mangrove peninsula is covered by mangroves, predominantly *Rhizophora mangle*, *Avicennia germinans* on the more elevated sites, and rarely *Laguncularia racemosa*. A detailed description of the study area can be found in Krause et al. (2001).

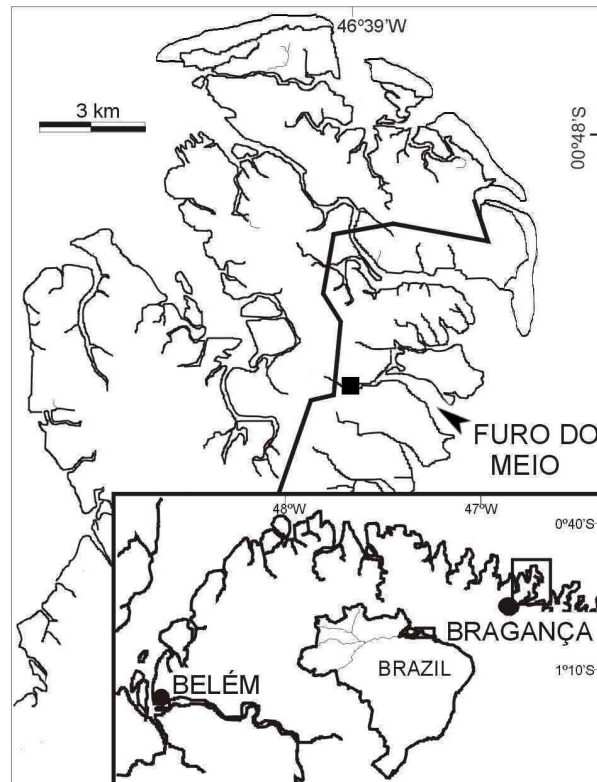


Fig. 1. Mangrove peninsula southeast of the Amazon estuary, 200 km east of Belém, North Brazil; location of the study site (Furo do Meio) in the center of the mangrove peninsula (black square) near the city of Bragança. Black line indicates road from Bragança to the beach.

The tidal regime is semidiurnal, ranging between 2.5 m and 5 m at neap tides and spring tides, respectively. The region receives about 2 500 mm of rainfall per year (INMET, 1992), mainly from January to June. Salinities (psu) can be below 5 in April and exceed 35 in November. Air and water temperature are high year-round, ranging from 25 °C to 33 °C and 27 °C to 30 °C, respectively. Water clarity is low (5 to 30 cm, max. 100 cm Secchi depth). Dittmar and Lara (2001a, b) provide further details about the dynamics of abiotic parameters. The study site was located in the Furo do Meio, a large creek in the central part of the peninsula (Fig. 1) that has already been the sample site for several fisheries studies (Barletta, 1999; Barletta-Bergan, 1999; Krumme, own obs.; Leal-Flórez, pers. comm.; Brenner, pers.

comm.). The Furo do Meio is a cul-de-sac channel with a length of about 4.5 km. An extensive sand bank characterises the lower reaches until 2.5 km upstream of the mouth. The upper reaches are composed entirely of mud providing an acoustically absorptive bottom boundary. Both the extreme upper and the entire lower reaches of the Furo do Meio are almost completely exposed to the air during low water (LW) (the deepest channel holds less than 5 m of water at LW). The sonar site was situated in the upper sector of the extensive subtidal section (1 km length) that extended to where the sand-dominated lower reaches started. Water depth at the sample site was 4 m at LW and could exceed 8 m at high water (HW). The channel width at the sonar site was 30 m at LW and about 50 m at HW (Fig. 2).

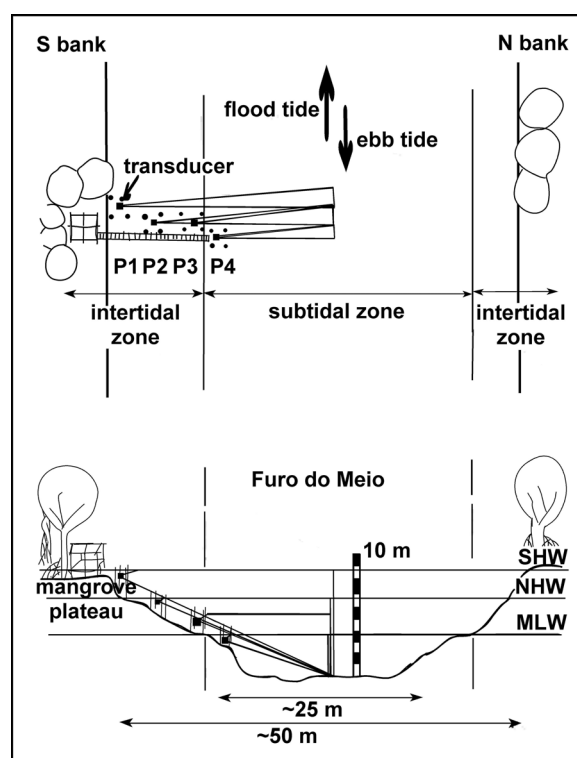


Fig. 2. Tidal related acoustic sampling in the Furo do Meio. Aerial (above) and cross-sectional view (below) of sonar site. Insonified portions of the channel at different tidal stages (schematic drawing). P1: transducer high water position, P2 and P3: intermediate positions, P4: low water position. SHW = spring tide high water; NHW = neap tide high water; MLW = mean low water.

Tidal-related acoustic sampling. The 200-kHz split-beam sonar (Biosonics, DT6000) with a 6° circular-beam transducer was employed horizontally across the channel perpendicular to the tidal flux (Fig. 2) with acoustic ranges at neap tide between 14 m at LW and 23 m at HW. The transducer was fixed to an aluminum frame (35 cm below the water surface), which was attached on two plastic floating bodies ($130 \times 25 \times 25$ cm each). The horizontal position of the floating device was adapted to the changing water levels using four different positions (P1: HW, P2 and P3: intermediate, P4: LW). At each position, the four corners of the floating

device were moored on four wooden sticks that determined the position. Thus, the transducer could float within each position while the transducer's orientation remained steady (no pitch and roll).

Data acquisition. Acoustic data were collected during two successive lunar cycles: a dry season from September to November 2000, and a wet season from March to May 2001. For each lunar phase data were continuously acquired for 50 hours, thus covering four consecutive tidal cycles. The transmission rate of the sound pulses was four pings per second. A narrow pulse-width of 0.2 ms was chosen to maximize the range-resolution of individual fish, and to minimize reverberation levels. Low ambient noise (beyond -80 dB) allowed for a threshold of -70 dB. The acquisition software (Visacq 4.0.2, BioSonics) run 5 min on, 5 min off continuously throughout the 50 hours.

Abiotic cycles were measured constantly during each sonar sampling (water level, salinity, Secchi depth, water temperature, wind). We inferred current velocities from a relationship established between current velocity (m s^{-1}) and water level change (height change min^{-1}) during sixteen neap tide tidal cycles in the Furo do Meio in October and November 2002. The neap tide tidal curve was subdivided in five different parts and five linear or polynomial regressions were calculated fitting best the relationship between water level change and current velocity: (1) LW until about 1.1 m after start of flood tide, (2) >1.1 m until HW, (3) HW until maximum ebb tide, (4) maximum ebb until about 1.1 m, (5) <1.1 m until LW. Approximately 1.1 m above LW corresponds to the topographical height where the lateral mangrove creeks enter the main channel.

Calibration. The DT6000 was professionally calibrated by BioSonics (Seattle, USA). Since *in situ* calibration was uncorroborated by the tidal current and in the occasionally strong wind, calibration (tungsten carbide sphere) was performed in a black water pool (0 psu, 28°C) in Bragança (Pará, Brazil) and in a brackish water mangrove lagoon (10 psu, 29°C) near the sample site. The mean target strength (TS) value for the sphere of -39.8 dB (± 2.59 S.E., $n = 229$ echoes; pool) and -40.5 dB (± 1.00 S.E., $n = 1\ 727$ echoes, lagoon) corresponded closely with the theoretical value of -40.0 dB (both calibration files analysed with VisAnal4.0.2).

Data processing. Two dry season wax moon tidal cycles (October 6-7 and November 5-6) were analyzed for fish tracks using Vtrack1.0.1 (BioSonics software). Since different acoustic conditions occurred at different tidal stages, we adopted an analysis strategy in which each 5-

min-file was run several times with varying parameter sets. Thus, we tried to minimize the noise and maximize fish echo recognition performance. The Vtrack software showed the track formation results visually, and track formation parameters were selected to optimize the formation of fish tracks. Thus, different minimum TS limits were used for different files acquired during a tidal cycle. One single TS limit would have provided a better inter-file-comparability in terms of target size. The median Vtrack TS limits applied during tracking analysis for the neap tide cycles in October and November were -52 dB (S.D. 4, S.E. 0.3, min -60 dB, max -43 dB) and -55 dB (S.D. 4, S.E. 0.3, min -63 dB, max -43 dB), respectively. We found a range-dependent bias in the TS measurements between Vtrack and VisAnal (both programs BioSonics) that followed a power function ($y = 7.8906 \cdot x^{-0.7481}$) with highest bias in less than 5 m range (e.g. Vtrack TS was 6 dB higher at 3.5 m range) and decreasing bias with increasing range (>1 dB beyond 15 m; J. Dawson, pers. comm.). All other parameters like range, angles or beam pattern correction values were calculated the same by the two programs (J. Dawson, pers. comm.). Given the TS difference, we decided to leave out a detailed analysis of the TS values.

To determine the fish flux in front of the transducer, we calculated the cross-section intercepting the movements of the fish; dividing the number of up- and downstream fish tracks by the cross section area per unit time provided a straightforward algorithm in the form number of fish $\text{m}^{-2} \text{min}^{-1}$.

RESULTS

Acoustic characterization

Season. The dry season provided better acoustic conditions than the wet season, when terrestrial run-off in the catchment area increased sediment loads in the entire Caeté estuary and in the mangrove channels. In the mangrove proper, rains eroded fine sediments from the forest floor into the channels, with poorest acoustic conditions in the channels' upper reaches (increased background reverberation, decreased signal-to-noise ratio). During wet season neap tide-LW, when the tide was almost stagnant, the water had quasi-viscose properties due to the high concentrations of fine sediment particles. Sound was completely absorbed for hours (white sonar files) until the next flood tide. This phenomenon disappeared when the rains retreated. During rain showers ambient noise levels in the water increased and occasionally completely concealed targets, thus generating phases of missing data.

Tide. Acoustic conditions at spring tide were by far more complex and hence poorer than at neap tide. At spring flood tides the water level rose more than 2 m in less than 1 hour (Fig. 6). Extreme tidal rise or fall at spring tide always correlated with minimum Secchi readings and maximum seston transport, thus deteriorating acoustic conditions (see above). At spring tide HW, the mangrove floor was usually inundated. About $\frac{3}{4}$ hour after HW, the export of huge amounts of mangrove litter (particularly buoyant leaves) started and lasted for about $1\frac{1}{2}$ hour. During each spring ebb tide this phenomenon was observed on the channel surface as concrete convergence-like surface bands at the zone where the ebb current was supposed to be strongest, and on the echogram as undulating bands with high TS values. Common software cannot analyze the increased structural complexity in the channel.

Tidal phase. The tide was asymmetric, flood and ebb tide lasting between 4 and 8 hours, respectively. In the last 4 hours, ebb tide was extremely weak with an almost negligible fall in the water level. Consequently, different acoustic conditions occurred at different tidal stages. The best acoustic conditions prevailed during weak ebb tide when the tidal impact was insignificant (signal-to-noise ratio (SNR) at LW: ca. 15 dB).

Acoustic conditions at strong flood tide and strong ebb tide were poorest due to increased background reverberation. Weak flood tide, HW and weak ebb tide provided intermediate acoustic conditions (SNR at HW: ca. 7 dB).

Abiotic parameters

Secchi disc readings at dry season-neap tide were positively correlated with water level (LW 20-30 cm; HW 70-90 cm). Extreme tidal rise or fall coincided with minimum Secchi readings, maximum seston transport and current velocity maxima. Neap tide current velocities were asymmetric. Flood and ebb tide speeds reached maxima of almost 25 cm s^{-1} and 15 cm s^{-1} , respectively (Fig. 3, upper figures). Current velocities were highly dynamic, with irregular and strong changes in speed within a few minutes. During weak flood tide intervals, even complete changes to ebb direction occurred. Salinity (psu) increased from 29 in October to 33 in November. Salinity was negatively correlated with water level (cycle maxima at LW, minima at HW). Oxygen and water temperature followed a 24 h cycle, reaching highest values in the late afternoon at ebb tide (9.5 mg l^{-1} and $30 \text{ }^{\circ}\text{C}$, respectively). Lowest water temperatures were recorded during the night-HW ($28 \text{ }^{\circ}\text{C}$). Lowest oxygen values were recorded at 7:30 (6 mg l^{-1}). Wind consistently blew in from the northeast with stronger periods both in the afternoon and in the night.

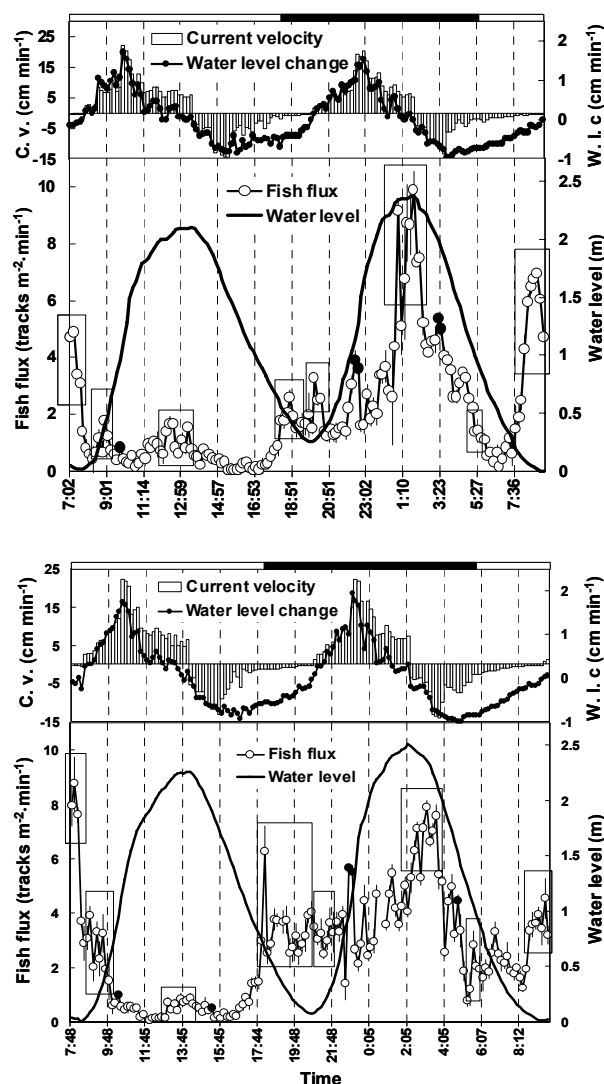


Fig. 3. Mean fish flux (fish $m^{-2} min^{-1}$) \pm 1 S.E. and tidal curve (lower figure) and current velocities (bars) derived from the water level change (upper figure) at two wax moon cycles (neap tide), October 6-7 (above) and November 5-6 (below), during dry season 2000, in the Furo do Meio. Horizontal bars on top indicate night (18 h 00 – 5 h 45). Lower figure: Rectangles indicate fish flux peaks at daytime-LW, daytime-flood start, daytime-HW, night-LW, night-flood start, night-HW, dawn and again daytime-LW (from left to right). Closed circles indicate distinct fish flux peaks at increased current velocities.

Fish tracking

About 30 000 fish were detected during each neap tide cycle. Assuming that half of the channel cross-section was insonified and considering only fish moving upstream, we calculated a mean of 6 000 and 28 000 fish immigrating into the mangrove during the daytime and the night flood tide, respectively.

The fish flux curves of both dry season neap tide cycles had seven peaks: at daytime-LW, the start of daytime flood, daytime-HW, night-LW (starting at dusk), the start of night flood, night-HW and at dawn (Fig. 3). The daytime-LW peak occurred in the morning (five to nine

fish $\text{m}^{-2} \text{min}^{-1}$) with highest values at slack low tide just before the water level started to rise again. A unique migratory pattern was observed during the daytime-LW peak when many targets occurred in a near-range corridor along the southern side of the channel and several tracks were visible in the far range (Fig. 4a).

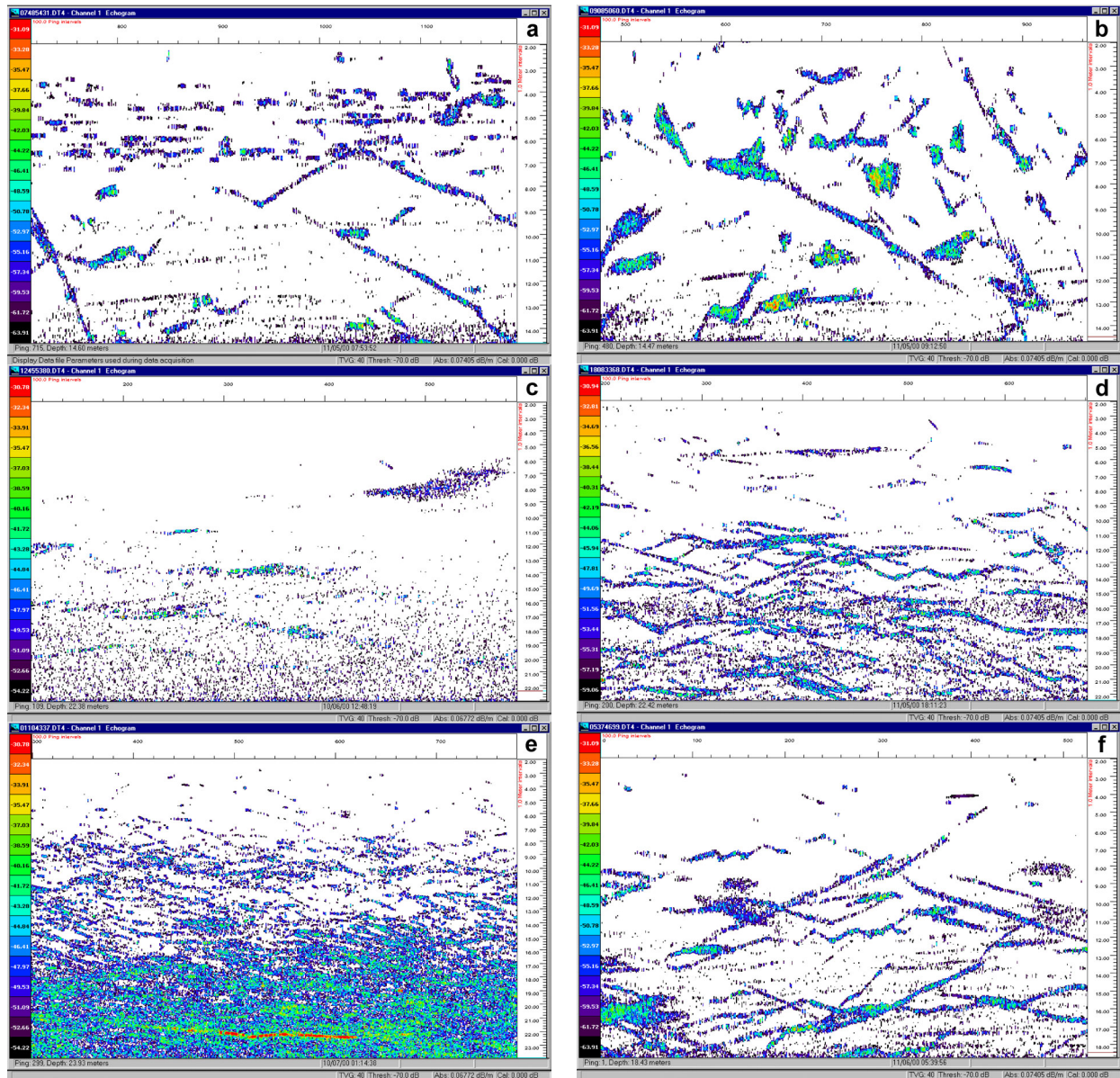


Fig. 4. Examples of echograms from fish flux peaks in the mangrove channel Furo do Meio near Bragança, PA, North Brazil, neap tides, during dry season 2000, at (a) daytime-low water, 7 h 54, November 5, 2000; (b) flood tide start at daytime, 9 h 13, November 5, 2000; (c) daytime-high water, 12 h 48, October 6, 2000; (d) night-low water at sunset, 18 h 11, November 5, 2000; (e) night-high water, 1 h 14, October 7, 2000 and (f) sunrise, 5 h 40, November 6, 2000. Echogram axis, left: echo intensity (dB; red strongest); right: range in front of transducer (m); top: time (2 min period or about 480 pings at a ping rate of 4 pings s^{-1}); bottom: first bottom echo. Note different scales for range and echo intensity between echograms.

At the start of daytime flood tide when current velocity increased sharply fish fluxes peaked to about $2 \text{ fish m}^{-2} \text{ min}^{-1}$ showing an upsurge in activity with many multiple targets occurring and crisscrossing throughout the range (Figs. 3 and 4b). At the end of the daytime flood tide, fish flux increased slightly to form the daytime-HW peak, albeit reaching only about $1 \text{ fish m}^{-2} \text{ min}^{-1}$ (Figs. 3 and 4c). The night-LW peak started at dusk. The fish flux remained high throughout the night low water phase and ended when the night-flood tide started (about 2 to 3 $\text{fish m}^{-2} \text{ min}^{-1}$; Figs. 3 and 4d). The night flood start peak occurred at a fish flux level similar to the previous night-LW peak (about 2 to 3 $\text{fish m}^{-2} \text{ min}^{-1}$). The distribution pattern of target tracks resembled the night-LW situation; unlike the start of daytime flood tide, night flood start lacked multiple targets. The night-HW peak also started at the end of flood tide (5 to 10 $\text{fish m}^{-2} \text{ min}^{-1}$); many target tracks occurred throughout the range (Figs. 3 and 4e). At dawn fish fluxes increased briefly (Fig. 4f). After sunrise fish flux was low until the daytime-LW was formed again towards the end of weak ebb tide. In contrast to the clear fish flux increase at dusk, fish flux increase at dawn was weak (Figs. 3 and 4d,f). Individual fish flux maxima coincided with strong flood and ebb tide intervals (Fig. 3). Mean fish flux was $2.4 \text{ fish m}^{-2} \text{ min}^{-1} \pm 2.1 \text{ S.D.}$ The night fish fluxes, especially at HW were several times higher than those at daytime. Due to the particular flux patterns at daytime-LW, however, the LW fish flux peak was usually higher at daytime than at night.

Target sizes were generally small ($-43 \pm 4 \text{ dB}$, $n = 55\,727$; results from Vtrack), indicating the presence of mainly juvenile or small-sized fish. Larger echoes ($>-30 \text{ dB}$) were usually only caused by multiple targets.

Throughout the tidal cycles, about 60% of the fish tracks were directed with and about 40% against the tide (Fig. 5), with higher variability in the proportions occurring during the daytime cycle. A tidal periodicity was not apparent.

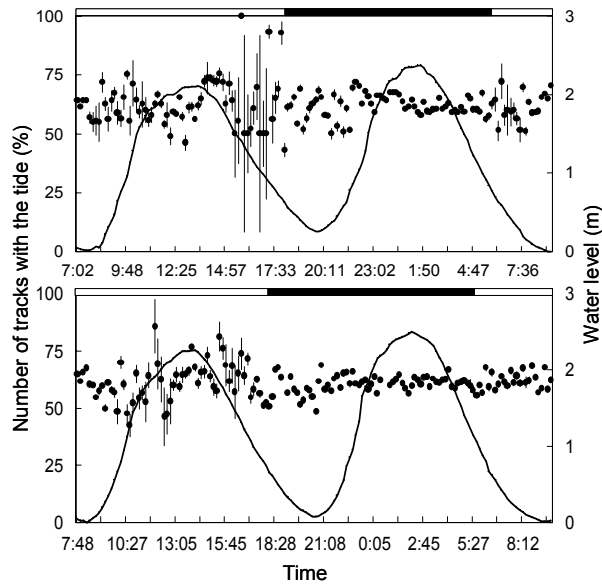


Fig. 5. Proportion of fish tracks going with the tide (solid circle \pm 15 S.E.) and tidal cycle (solid line) for two neap tide cycles, October 6-7 (above) and November 5-6 (below). Black bars on top indicate night (18 h 00 until 5 h 45). High se is related to low sample size (number of fish tracks) since variance was $p \times [(1-p) \times n^{-1}]$ with p = proportion of fish tracks going with the tide.

DISCUSSION

Acoustic characterization

It was a clear advantage that the sampling period started in the dry season. Thus, we became acquainted with the yet unknown acoustic conditions in the mangrove environment under a minimum of external influences. The poor acoustic conditions encountered in the wet season might hold true for turbid shallow-water environments on tropical coasts in general. Experiments using vertical transducer orientation or the use of a lower frequency echosounder (120 kHz instead of 200 kHz) could be worthwhile alternatives.

When studying intertidal migration patterns of fish acoustically, it is very problematic when the clearest conditions for sonar application occur at weak ebb tide when tidal impact is negligible. Fortunately, weak neap tide currents allowed for sonar file analysis throughout the tidal cycles.

Fish Tracking

Considerable numbers of fish entered the upper reaches of the mangrove during flood tides. The high numbers can be attributed to the high abundances of juvenile fish commonly found in mangroves (Sasekumar, 1992; Laedgsgaards and Johnson, 1995; Barletta, 1999).

The high number of target tracks, their relatively low TS values and a mean fish size of 14 cm in the mangrove channels (Krumme, own obs.) clearly emphasized the importance of this habitat as a fish nursery.

The hypothesis that intertidal fish behave like passive particles can be readily rejected since a considerable proportion of the tracks (about 40%) were directed against the tidal current irrespective of flood or ebb tide. However, the high background noise levels observed in the channel may have added higher variability to the positional data of the split-beam system (Kieser et al., 2000; Fleischman and Burwen, 2000) and could have led to incorrect results when assigning the track directions. It is nevertheless clear that the fish are not passively transported by the tides but may in fact actively move to, and concentrate in resource-rich intertidal habitats when accessible. Obviously, swimming against the direction of the tide was a major component of fish movements in the mangrove channel at neap tide. Thus, surface and midwater fish may take advantage of the fact that food is passively transported towards their mouth. *Colomesus psittacus* (Tetraodontidae) was observed maintaining its relative position in the channel while actively swimming against the current near the water surface. Thus, they patrolled a certain corridor for several minutes searching for prey. This particular swimming behavior of *C. psittacus* was reflected on the echogram as extraordinarily long tracks. Position shifts to the left or to the right may have caused the zick-zack tracks visible on the echograms (Figs. 4a,f).

We assume that the fish swam and crisscrossed in the flooding and ebbing water body to inter- and intra-specifically increase their particular foraging areas while taking advantage of the tidal transport into and out of the intertidal area. Weak neap tide current speeds did not constrain fish to show strong directional movements. Nevertheless did fish fluxes noticeably increase during short intervals of increased current speed suggesting a positive response of the fish to increased tidal current speeds (Fig. 3).

Tidal stage

LW and HW phases represented stable stages with established fish assemblages at increased fish fluxes; unlike flood and ebb tides that can be considered as transitional stages during the tidal migration of fishes. Detailed stomach analysis of the catfish *Cathorops* sp., predominant in the upper reaches of the channels (Barletta, 1999), revealed that flood tide stomachs were generally empty, whereas ebb tide stomachs were already well filled briefly after HW (Leal-Flórez, pers. comm.). Apparently the tidal stages before and around HW were the principal phases for catfish feeding. This pattern corresponded well with the fish flux peaks around

HW in the channel. Although benthic catfish may not have been well represented by horizontal beaming, their foraging pattern can serve as a general rule for more pelagic fish species as well since the water level likewise determines the degree of habitat accessibility for other intertidal fish.

It seems contradictory that fish fluxes increased at HW when the water volume was greatest. However, we assume that the immigration and import of organisms from downstream was maximum at HW. Both nekton abundance and species richness was significantly greater at slack high tide than either flood or ebb tide on a temperate marsh surface (Kneib and Wagner, 1994). HW is the short period where insignificant current speed and maximum intertidal accessibility coincide. Water transparency was highest at and after HW. Fish that actively immigrated into the mangrove during flood tide probably milled around at HW in the main channel, especially during the night-HW (Fig. 4e). The increased fish flux at HW clearly indicates that active movements in the water column increased. We assume that negligible current speed and high water transparency around HW favored visual focusing of pelagic prey by the fish in the mangrove water, both at day and night. Insignificant current speeds at slack HW probably favored localisation and oral fixing of benthic prey in the mud.

The high fish fluxes at LW resulted from the resident fishes' active swimming in the subtidal parts of the channel. The population of resident mangrove fish probably achieved successful maintenance in the channels' upper reaches by late emigration out of the intertidal mangrove creeks. Thus, they would both achieve avoidance of undesirable downstream transport and optimize the time for feeding in the intertidal creeks. Staying horizontally in distance to the main channel is probably linked to rather bottom-oriented movements at ebb tide. Interconnected to the fish community, similar temporal patterns with stable assemblage structures during HW and LW can be proposed for other tidally influenced nekton communities, e.g. zooplankton (Krumme and Liang, in press) and phytoplankton organisms (Schories et al., unpubl.).

Migratory cycle

The course of the flux curve and the series of sonar files suggest a schematic migratory cycle for intertidal mangrove fish. The migratory pattern found for the two wax moon cycles to all appearances also applies to wane moon cycles, thus reflecting a typical dry season neap tide pattern in 2000.

1. Resident mangrove fish were clearly concentrated in the subtidal parts of the channel forming both the LW peak at daytime and at night (Fig. 3).

2. As soon as the water level started to rise at the start of flood tide, fish flux first peaked and then decreased. Resident fish either left the channel horizontally entering the shallow (less than 50 cm) intertidal creeks, or went down towards the channel bottom. We assume early horizontal immigration into the mangrove creeks since a clear upsurge in fish activity during the first 30 minutes after slack low tide was observed on the echograms (Fig. 4b). Cattrijsse et al. (1994), using a fyke net in a Dutch marsh, found that most species migrate during the first and the last hours of the tidal cycle when the current velocities were low; gill net catches of summer flounder in New Jersey were greatest in early flood tides and in mid and late ebb (Rountree and Able, 1992).
3. During flood tide, distinct fish flux maxima coincided with current speed maxima. The mangrove fish community apparently directly responded to the tidal current regime on a very short time scale.
4. During flood tide, the fish fluxes increased towards HW. Many resident mangrove fish were probably foraging in the intertidal mangrove creeks at this time and hence absent from the main channel. Fish fluxes in the mangrove channel did not increase until the flood tide water level had risen about 2 m above the previous LW level and flood current speeds had fallen below 10 cm s^{-1} (upper figures in Fig. 3). Estuarine fish that immigrated with the flood tide from the Caeté estuary to the upper reaches (a distance of at least 4 km) probably contributed to the HW fish flux peak. Several other authors have assumed that some estuarine fish require a minimum water level to enter an intertidal area (Davis, 1988; Blaber et al., 1994). Interestingly, Gibson (1973) counted most fish in an intertidal Scottish sandy beach when the water was 1 to 2 m deep. Prey search of pelagic and benthic fish in the channel was probably facilitated (see above) and hence resulted in increased milling in front of the transducer around HW.
5. When the water levels in the mangrove channel started to fall with the receding tide, fish flux decreased again. The decrease in fish flux during ebb tide occurred at water depths apparently symmetrical to those at flood tide (Fig. 3). When we assume that estuarine fish returned to the start points of their tidal migration, they covered distances of at least 8 km each tidal cycle between the estuary and the upper mangrove reaches. The emigration of estuarine fish out of the mangrove channels during ebb tide is exploited by local fishermen with large fish traps (*corrals*) on the sand banks of the lower reaches of the channels and in the estuary (Barletta et al.,

1998; Schaub, pers. comm.). Resident mangrove fish may have returned from the intertidal creeks to the channel at mid or late ebb tide as observed by Rountree and Able (1992) for summer flounder where they stay until the next flood tide enters again. A signal from this emigration was not apparent in the sonar files, possibly due to more bottom-oriented movements. The fish flux rather showed a continuous decrease. However, like at flood tide did distinct ebb fish flux maxima coincide with ebb current speed maxima.

6. At neap tides, twilight coincided with the semi-stagnant LW phase. Especially at dusk fish flux increased significantly whereas sunrise only produced a weak signal in the fish flux curves. Most mangrove fish are rather nocturnal or show at least negative phototaxis (own obs.); only *C. psittacus* is a clear diurnal species (Table 1).

Table 1. Lift net catches in main channel of the mangrove creek Furo do Meio, dry season 2000; sunrise was at 5 h 45, sunset at 18 h 00; data from Leal-Flórez (pers. comm.).

Species	Total	%	Day	Night
<i>Cathorops</i> sp.	735	39	316	419
Sciaenidae	468	25	158	310
<i>Colomesus psittacus</i>	229	12	192	37
Engraulidae	137	7	81	56
others	312	17	169	143
Sum	1881	100	916	965

Delay in accessibility

The accessibility of the intertidal area is determined by the water level, i.e. the height of the tide. Since resident and estuarine fish apparently accessed the intertidal mangrove area at different water levels, the time delay between the two access levels determines the time available for mangrove foraging. Fig. 6 shows the extremely short time delay between habitat accessibility for resident and estuarine fish at spring tide and the rather marked time delay for neap tides. Resident mangrove fish may spend more time feeding in the mangrove than estuarine fish whose foraging activity is more restricted in time, especially at neap tide (Fig. 6). The high standing stocks of resident *Cathorops* sp. and *Anableps anableps* (Barletta, 1999; Krumme, own obs.) compared to other fish species captured in the upper reaches of the mangrove channel at HW support this argument. For estuarine fish, the time delay between the start of flood tide until a minimum water depth provides access to the intertidal area, may be a crucial parameter for intertidal migration of estuarine fish. Hence, the hydrodynamics at

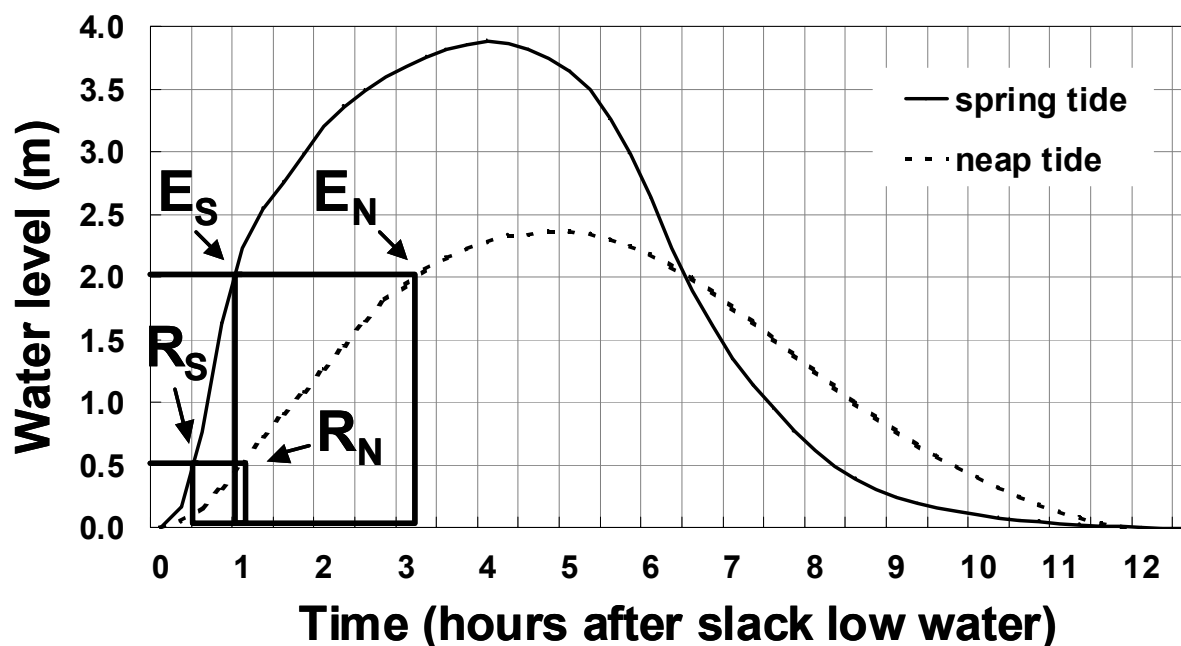


Fig. 6: Time delay threshold between spring tide and neap tide in mangrove accessibility at two water levels; E_S : Estuarine fish at spring tide, E_N : Estuarine fish at neap tide, R_S : Resident fish at spring tide, R_N : Resident fish at neap tide.

spring tide provide excellent conditions for immigration of estuarine fish since the mangrove becomes accessible in less than an hour after slack LW, unlike more than 3 hours during neap tides (Fig. 6). The numbers of eleven fish species were greater at spring tides (Krumme, own obs.) when both the period available for foraging and the habitat accessibility in the mangrove are increased (Fig. 6). Foraging success of *A. anableps*, *Arius herzbergii* and *Anchovia clupeioides* was clearly greater at spring than at neap tide (Brenner, pers. comm.).

Four assemblages

We assume that different fish assemblages caused each of the fish flux peaks at LW and HW during a neap tide cycle. Krumme (own obs.) already found that HW assemblages of mangrove fish at neap tide differ significantly between day and night with the neap tide-daytime assemblage being poorest in both biomass and diversity. This might explain the marked increase of fish tracks throughout the night cycle compared to the desolated track situation during the daytime cycle. Morrison et al. (2002) found clear differences in the fish fauna composition between both low and high tide and day and night samples in a temperate New Zealand tidal mudflat. Simultaneously to the sonar application during the dry season 2000, Leal-Flórez (pers. comm.) caught migrating fish 500 m upstream of the sonar site in the open channel from a bridge using lift nets. Day and night catches were similar in terms of

abundance but differed clearly in their species composition (Table 1). *Cathorops* sp. was constantly present in the catches. Sciaenidae, a mainly nocturnal family (Helfman, 1993) was more abundant at night and may have caused the high numbers of targets at night-HW. The diurnal pufferfish *C. psittacus* was mainly caught during daylight. Engraulidae tended to be more abundant at daytime as well. These species may have contributed to the daytime-HW fish flux peak. Unfortunately, there was no relationship between the number of fish caught (lift nets) and the number of fish tracked (counting of acoustic traces). The lift net did not produce representative catches. It suffered from several shortcomings: During strong spring flood and ebb tide the lift nets flouted. They became frequently entangled in the channel bottom near the bridge and clearing of the net might have expelled fish from the area. LW depth at the Furo do Meio bridge was less than 1 m, hence complicating lift net use.

Our findings suggest that different assemblages also existed for LW day and LW night during neap tide. Increasing fish fluxes at the night-LW coincided with sunset and remained high throughout the LW phase (Fig. 3, 4d). During the daytime LW phase fish fluxes peaked weakly at sunrise. This was probably caused by an activity upsurge of *C. psittacus*. At dawn, lift nets again caught *C. psittacus* (Leal-Flórez, pers. comm.). Fish fluxes then only increased after 7:00, peaking towards 9:00 at slack low tide. Maybe the formation of the near-range corridor at LW, i.e. increasing fish fluxes, was related to the increased oxygen concentrations after the oxygen minimum at around 7:00 (start of phytoplankton activity during the stable weak ebb tide). Barletta-Bergan (1999) found at neap tide in the same mangrove area, high densities of five fish species: early larval stages of <10 mm of *A. clupeioides* (Engraulidae), *Stellifer* sp. (Sciaenidae), *Rhinosardinia amazonica* (Clupeidae), *Archirus* sp. and *Guavina guavina* (Eleotridae) in the morning (9:00), predominantly occurring at the surface, probably feeding on plankton. Densities of larval and juvenile fish were significantly lower during the night-LW (21:00) for most taxa except for *Stellifer rastrifer*, which showed significantly higher values at night (Barletta-Bergan, 1999). Furthermore, Fig. 4d shows clearly that the horizontal distribution and movement pattern of targets was different between the daytime and the night LW situation. During the night-LW, multiple targets did not occur and the near-range corridor was absent, suggesting different assemblages to be active at these periods. However, it remains unclear whether the near-range band of targets at daytime-LW represented a typical feature of the system or whether it was merely caused by an extraordinary abundant cohort in its nursery ground. Spring tide LW lacked any similar horizontal pattern in the target distribution.

CONCLUSIONS

The observation of fish movements using shallow-water acoustics was feasible in a mangrove environment. Shallow-water acoustics provided a reasonable approach to obtain high-resolution samples in a dynamic environment where conventional fishing methods have become limited. For acoustic studies in tropical estuarine environments we recommend sampling during the dry season and at weaker tides, that is, at neap tide and/or during LW.

Fisheries studies conducted under meso- or macrotidal regimes should consider the importance of temporal changes on the short-term scale determined by the factors “tide”, “photoperiod” and “tidal stage” in both the survey design and choosing a sampling method.

The tidal-induced fish flux changes together with the considerable proportion of fish tracks directed against the tide indicate clearly that tidal migration of fish was an active movement to and from intertidal areas promoted by the tide.

Our data suggest that resident mangrove fish enter the intertidal mangrove creeks at early flood tide and leave them at late ebb tide at fairly shallow water depths. The estuarine fish enter and leave the upper reaches of the mangrove channel when water level was about 2 m above the previous LW level, thus requiring a minimum water depth for tidal migration. At HW, maximum habitat accessibility reduced current speeds and maximum visibility probably helped in the foraging of pelagic and benthic fish in the channel and hence resulted in high fish fluxes due to increased milling in front of the transducer. The time delay between immigration of resident and estuarine fish is shorter at spring than at neap tide (Fig. 6). Hence, the period available for foraging and the habitat accessibility is enhanced at spring tide; both catches of fish (Davis, 1988; Laroche et al., 1997; Krumme, own obs.) and the fishes' feeding success are greater at spring tide (Colombini et al., 1996; Brenner, pers. comm.).

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REFERENCES

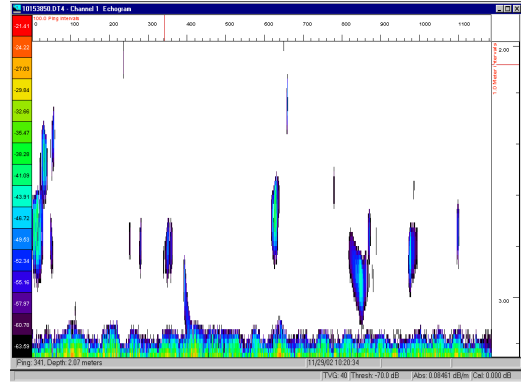
- Barletta, M., 1999. Seasonal changes of density, biomass and species composition of fishes in different habitats of the Caeté estuary (North Brazilian coast - east Amazon). ZMT Contrib. No. 7, Zentrum fuer Marine Tropenoekologie, Bremen (FRG), 115 pp, Bremen Univ., (FRG) Fachbereich 2 (Biologie/Chemie). ISSN 0944-0143.
- Barletta, M., Barletta-Bergan, A., Saint-Paul, U., 1998. Description of the fisheries structure in the mangrove-dominated region of Bragança (state of Pará, North Brazil). *Ecotropica* 4, 41-53.
- Barletta-Bergan, A., 1999. Structure and seasonal dynamics of larval and juvenile fish in the mangrove-fringed estuary of the Rio Caeté in North Brazil, ZMT Contrib. No. 8, Zentrum fuer Marine Tropenoekologie, Bremen (FRG), 219 pp, Bremen Univ., (FRG) Fachbereich 2 (Biologie/Chemie), ISSN 0944-0143.
- Barletta-Bergan, A., Barletta, M., Saint-Paul, U., 2002. Structure and Seasonal Dynamics of Larval Fish in the Caeté River Estuary in North Brazil. *Estuar. Coast. Shelf Sci.* 54, 193-206.
- Bell, J.D., Pollard, D.A., Burchmore, J.J., Pease, B.C., Middleton, M.J., 1984. Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, New South Wales. *Austr. J. Mar. Fresh. Res.* 35, 33-46.
- Berger, U., Glaser, M., Koch, B., Krause, G., Lara, R., Saint-Paul, U., Schories, D., Wolff, M., 1999. An integrated approach to mangrove dynamics and management. *J. Coast. Cons.*, 5, 125-134.
- Blaber, S.J.M., Brewer, D.T., Harris, A.N., 1994. Distribution, biomass and community structure of demersal fishes of the Gulf of Carpentaria, Australia. *Aust. J. Mar. Fresh. Res.* 45, 375-396.
- Cattrijsse, A., Makwaia, E.S., Dankwa, H.R., Hamerlynck, O., Hemminga, M.A., 1994. Nekton communities of an intertidal creek of a European estuarine brackish marsh. *Mar. Ecol. Prog. Ser.* 109, 195-208.

- Colombini, I., Berti, R., Nocita, A., Chelazzi, L., 1996. Foraging strategy of the mudskipper *Periophthalmus sobrinus* Eggert in a Kenyan mangrove. *J. Exp. Mar. Biol. Ecol.* 197(2), 219-235.
- Davis, T.L.O., 1988. Temporal patterns in the fish fauna entering a tidal swamp system in tropical Australia. *Env. Biol. Fish.* 21(3), 161-172.
- Dittmar, T., Lara, R.J., 2001a. Do mangroves rather than rivers provide nutrients to coastal environments south of the Amazon River? Evidence from long-term flux measurements. *Mar. Ecol. Prog. Ser.* 213, 67-77.
- Dittmar, T., Lara, R.J., 2001b. Driving forces behind nutrient and organic matter dynamics in a mangrove tidal creek in North Brazil. *Estuar. Coast. Shelf Sci.* 52, 249-259.
- Fleischman, S.J., Burwen, D.L., 2000. Correcting for positional-related bias in estimates of the acoustic backscattering cross-section. *Aquat. Living Resour.* 13(5), 283-290.
- Gibson, R.N., 1973. The intertidal movements and distribution of young fish on a sandy beach with special reference to the plaice (*Pleuronectes platessa* L.). *J. Exp. Mar. Biol. Ecol.* 12, 79-102.
- Gibson, R.N., Pihl, L., Burrows, M.T., Modin, J., Wennhage, H., Nickell, L.A., 1998. Diel movements of juvenile plaice *Pleuronectes platessa* in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. *Mar. Ecol. Prog. Ser.* 165, 145-159.
- Guillard, J., 1998. Daily migration cycles of fish populations in a tropical estuary (Sine-Saloum, Senegal) using a horizontal-directed split-beam transducer and multibeam sonar. *Fish. Res.* 35, 23-31.
- Helfman, G.S., 1993. Fish behaviour by day, night and twilight. In: Pitcher, T.J., (Ed.), *Behavior of teleost fishes*. Chapman & Hall, Fish & Fisheries Series 7, London, pp. 479-512.
- Horn, M.H., Martin, K.L.M., Chotkowski, M.A., 1999. *Intertidal Fishes: Life in Two Worlds*. Academic Press, San Diego, 399 pp.
- INMET (Instituto Nacional de Metereologia), 1992. Normais climatológicas (1961-1991). Tech. Rep. Instituto Nacional de Metereologia, Brasilia DF, Brasil.
- Kieser, R., Mulligan T., Ehrenberg J., 2000. Observation and explanation of systematic split-beam angle measurement errors. *Aquat. Living Resour.* 13(5), 275-281.
- Kneib, R.T., Wagner S.L., 1994. Nekton use of vegetated marsh habitats at different tidal stages of tidal inundation. *Mar. Ecol. Prog. Ser.* 106, 227-238.

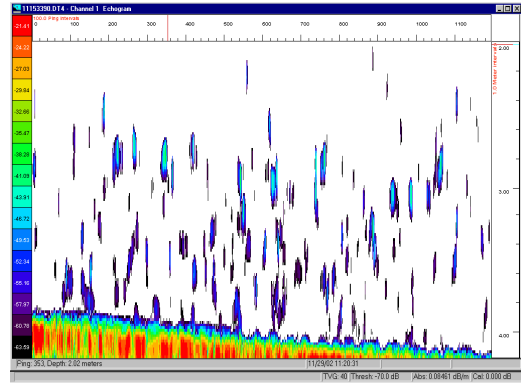
- Krause, G., Schories D., Glaser M., Diele K., 2001. Spatial patterns of mangrove ecosystems: the bragantinian mangroves of northern Brazil (Bragança, Pará). *Ecotropica* 7, 93-107.
- Krumme, U., Liang, T.S., (In press). Tidal induced changes in a copepod-dominated zooplankton community in a macrotidal mangrove channel in northern Brazil. *Zoological Studies*.
- Laegdsgaard, P., Johnson, C.R., 1995. Mangrove habitats as nurseries: unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. *Mar. Ecol. Prog. Ser.* 126, 67-81.
- Laroche, J., Baran, E., Rasoanandrasana, N.B., 1997. Temporal patterns in a fish assemblage of a semiarid mangrove zone in Madagascar. *J. Fish Biol.* 51, 3-20.
- Levy, D.A., Cadenhead, A.D., 1995, Selective tidal stream transport of adult sockeye salmon (*Oncorhynchus nerka*) in the Fraser River Estuary. *Can. J. Fish. Aquat. Sci.* 52(1), 1-12.
- Louis, M., Bouchon, C., Bouchon-Navaro, Y., 1995. Spatial and temporal variations of mangrove fish assemblages in Martinique (French West Indies). In: Wong, Y.S., Tam, F.Y., (Eds.), *Asia-Pacific Symposium on Mangrove Management*, pp. 275-284.
- Morrison, M.A., Francis, M.P., Hartill, B.W., Parkison, D.M., 2002. Diurnal and tidal variation in the abundance of the fish fauna of a temperate tidal mudflat. *Estuar. Coast. Shelf Sci.* 54, 793-807.
- Robertson, A.I., Duke, N.C., 1987. Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. *Mar. Biol.* 96, 193-205.
- Rountree R.A., Able K.W., 1992. Foraging habits, growth, and temporal patterns of salt-marsh creek habitat use by young-of-year summer flounder in New Jersey. *Trans. Am. Fish. Soc.* 121, 765-776.
- Sasekumar A., Chong V.C., Leh M.U., D'Cruz R., 1992. Mangroves as a habitat for fish and prawns. *Hydrobiologia* 247, 195-207.
- Spalding, M., Blasco F., Field C.D., (Eds.) 1997. *World mangrove atlas*. International Society for Mangrove Ecosystems, Okinawa.

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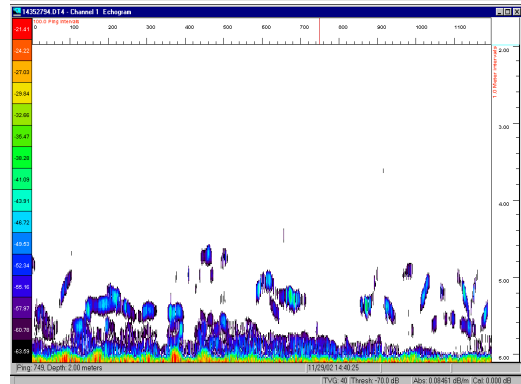
Low
Water



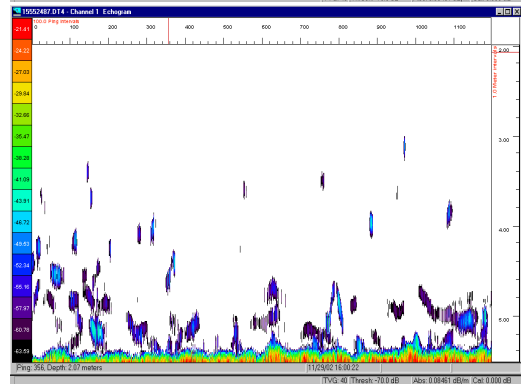
First
Flood
Rise



High
Water



Ebb
Tide



Time series of submergence levels of the Furo do Meio at spring tide (left column) and echograms with migrating fish acquired at comparable tidal stages using vertical beaming at neap tide (right column). Echogram axis, left: echo intensity (dB; red strongest); right: depth below the transducer (m); top: time (5 min period or 1200 pings at a ping rate of 4 pings s^{-1}); bottom: bottom echo. Note different depths between echograms.

**Patterns in the tidal migration of fish in a North Brazilian
mangrove channel as revealed by vertical beaming
using a 200 kHz split-beam sonar**

Uwe Krumme

Center for Marine Tropical Ecology (ZMT), Fahrenheitstr. 6, 28359 Bremen, Germany
Tel.: +49 421 2380029; fax: +49 421 2380030; e-mail: ukrumme@uni-bremen.de

ABSTRACT

A 200-kHz circular split-beam echosounder (BioSonics, DT 6000) was placed in the center of a macrotidal mangrove channel in North Brazil to study the movement patterns of tidal migrating fish. Vertical beaming operated at high signal-to-noise ratios (21 dB) during neap tides in the dry season 2002. Despite low Secchi depths, a diel change in the vertical target distribution was apparent when fish exploited the water column only during the night flooding. Moreover, responses in vertical distribution occurred at dusk and dawn. The tropical multispecies population simultaneously caught with a tidal trap consisted of juveniles and adults of small species, and juveniles of larger species (mean total length of fish: 14 cm), being reflected in target strength values ranging from -60 to -40 dB. Nekton organisms usually traveled with the tide. At low water fish concentrated in the subtidal channel sections, swam slowly and meandered in different directions. At first flood rise - the strongest ambient change - the entire fish population 'rode the tide' to immigrate into the intertidal zone, indicated by fast, linear, upstream tracks throughout the water column. At slack high water fish milled around (likely *Cetengraulis edentulus* and *Anchovia clupeioides* at night and epibenthic fish at daytime). Fish returned from the mangrove creeks gradually. The tidal migration of the fish was often characterized by temporal and spatial patchiness, being heterogeneous in 3-D and on the time scale. Boyle's law was not consistently reflected in the tidal-related TS alternations observed, suggesting interactions with factors other than depth (fish size, stomach fullness, tilt angle). A net upstream longitudinal current together with a regular first flood rise likely promoted retention of fish in this mangrove nursery from one tide to the next. In well-mixed shallow-water environments with a dominant epibenthic fish population, horizontal and vertical beaming should be combined since deeper sections may serve as a refuge for the fish.

Keywords: STST, 3-D tracks, Catfish, Tortuosity, Swimming speed

INTRODUCTION

On tropical and subtropical coasts mangroves provide important nursery grounds for fish as has been shown in several studies throughout the world (e.g. Sasekumar et al., 1992; Laegdsgaard and Johnson, 1995; Blaber, 1997; Barletta-Bergan et al., 2002). Tidal visiting fish enter the intertidal mangrove habitat during the rising tide and return to the subtidal parts with the receding tide (Sasekumar et al., 1984; Robertson and Duke, 1990; Leh and Sasekumar, 1991; Vance et al., 1996; Krumme et al., *subm.*). However, most insights into the tidal migration movements of fish come from studies done in the temperate zone (Gibson 1982, 1988, 1992, 1993). These investigations of fish movement over only shorter periods of time have revealed important patterns and mechanisms in the everyday life of the fish in their nurseries.

It remains largely unknown however, how fish time their migration on short temporal and spatial scales according to the local tidal regime. This lack of data can often be attributed to problems in representative short-time sampling of highly mobile ichthyofauna in tidal areas (Horn et al., 1999). Improved knowledge of the dynamics in natural fish behavior is essential to understand changes in fish abundance, their vulnerability to anthropogenic disturbances and hence, an improved management of the aquatic resources.

Although relatively costly, modern shallow-water sonar provides a non-invasive method to obtain new, high-resolution information on short-term movement patterns of fish. In particular, split-beam systems provide estimates of swimming speed, location within the water column, direction of travel and allow target tracking (Thorne et al., 1989; MacLennan and Simmonds, 1992; Ehrenberg and Torkelson, 1996; Arrhenius et al., 2000).

Hydroacoustics have as yet been rarely applied in shallow, turbid mangrove environments (Guillard, 1998; Krumme and Saint-Paul, 2003). Particularly, vertical beaming may be of only minor benefit in very shallow waters due to the hydroacoustical blind-zone (Knudsen and Sægrov, 2002). Nevertheless, a combination of horizontal and vertical beaming in acoustic fish stock surveys in shallow water environments is clearly recommended (Kubečka and Wittingerova, 1998; Knudsen and Sægrov, 2002).

In essentially non-stratified tidal areas, deeper subtidal sections may provide an important sheltering function, especially for epibenthic fish. In the mangroves of Northern Brazil, epibenthic fish usually dominate the fish community (Batista and Rêgo, 1996; Barletta et al., 2003; Krumme et al., *subm.*), but little is known about their tidal movements. Vertical beaming could reveal movement patterns characteristic for epibenthic fish.

Tidal patterns in vertical distribution of fish are often studied to explain immigration and retention of juvenile fish in a nursery in terms of selective tidal stream transport (STST) (e.g. Forward Jr. et al., 1999; Jager, 1999; Schultz et al., 2000). Vertical beaming could unequivocally reveal patterns in vertical distribution of targets that may be more difficult to recognize in horizontal beaming using split-beam systems due to noise (Fleischman and Burwen, 2000; Kieser et al., 2000).

Given the experience acquired in previous horizontal samplings (Krumme and Saint-Paul 2003), the general objective of this study was to evaluate the usefulness of vertical beaming in the shallow upper reaches of the macrotidal mangrove channel Furo do Meio (North Brazil). The study centers on the observation of temporal changes in abundance, vertical distribution and fish track parameters, and relates them to changes in physical parameters (water level, current speed, water transparency), while concurrently catching migrating fish with a tidal trap.

MATERIAL AND METHODS

Sample site. The blind cul-de-sac channel Furo do Meio is one of the principal mangrove tributaries channeling the tides into the mangrove peninsula and out to the Caeté Bay, and is located about 200 km southeast of the mouth of the Amazon River (see Krumme and Saint-Paul, 2003). Due to its high elevation, the mangrove peninsula is flooded only during spring tides while the network of creeks running through the mangrove is flooded twice daily by the semidiurnal tide. Mean tidal ranges are 2.5 m on neaps and 5 m on springs. The tide is asymmetric; flood and ebb tide last 4 and 8 hours, respectively. In the last 4 hours, ebb tide is extremely weak with an almost negligible fall in the water level. An extended sand bank in the lower reaches of the Furo do Meio dams up the flood tide that enters from the bay that itself is guarded by sand banks against the coast. The moment the sand bank is inundated, the tidal gradient built up between the bay and the Furo do Meio is balanced by a pronounced flood wave channeled along the main channel. This feature is weak at neaps, but of impressive velocity at springs. Maximum flood current speeds can exceed 1.5 m s^{-1} at springs and are usually below 0.5 m s^{-1} at neaps (Krumme, unpubl. data). Due to the macrotidal regime and its shallowness (maximum depth in the Furo do Meio at high water (HW): 10 m) the water body is usually well mixed. Water temperature ranges between 25 and 31 °C.

Apparatus. Vertical acoustic sampling was conducted in the center of the Furo do Meio main channel at the same mangrove site in the muddy upper reaches as described in Krumme

and Saint-Paul (2003). A 200-kHz split-beam sonar (Biosonics, DT6000) with a 6° circular-beam transducer was fixed to a 90° metal angle and attached to the floating device described in Krumme and Saint-Paul (2003). The floating device was moored on the upstream side of a canoe set perpendicular to the current direction. When the deepest part of the channel cross-section with a smooth bottom structure was determined acoustically at low water (LW), both ends of the canoe were fixed to a wooden pole (6 m high) in a way that allowed the canoe to freely rise at flood and sink at ebb tide. The canoe housing the entire equipment (surface unit, batteries, cable etc.) was very stable and no pitch or roll occurred at any one tidal phase.

A neap tide data set was acquired during the wane of the moon for four consecutive tidal cycles between November 27 and 29, 2002 (dry season). Days were characterized by sunshine with absolutely no clouding. Moonrise was at approximately 1:15 in the night. Due to battery problems, the neap tide cycle had to be made up of three separate data sets. The data sets were tied together at equal water levels.

Calibration. Since tidal current and strong wind hindered *in situ* calibration in the Furo do Meio, calibration (tungsten carbide sphere) was performed in a brackish water mangrove lagoon (16 psu, 29 °C) 5 km away from the sample site. The mean target strength (TS) value for the sphere of -39.8 dB (± 1.46 se, $n = 928$ echoes) corresponded closely with the theoretical value of -40.0 dB (calibration file analysis with VisAnal 4.0.2).

Data acquisition settings. Acoustic data were acquired using a pulse rate of four pings per second. Pulse duration was 0.2 ms. Data acquisition threshold was -70 dB. The acquisition software (Visacq 4.0.2, BioSonics) runs 5 min on, 15 min off continuously throughout the sampling periods. The transducer's blind zone extended from 0 to 2 m.

Data analysis. Acoustic data were analyzed for fish tracks using Vtrack 1.0.1 (BioSonics). Vertical beaming was associated with a high SNR of 21 dB. This allowed for the use of one single set of analysis parameters for all data files, thus ensuring maximum inter-file-comparability. The minimum TS limit was -65 dB. In the fish tracking configuration, maximum velocity was set at 1.4 m s⁻¹ (sphere size in that a single track can move, from ping to ping); ping gap was set at three pings (maximum amount of missing pings that a track can skip).

A range-dependent bias in the TS measurements between Vtrack and VisAnal was found (both programs BioSonics). However, all other parameters such as range, angles or beam

pattern correction values were calculated in the same manner by the two programs (J. Dawson, personal communication). A power function ($y = 18.9262 \times x^{-0.735}$, $n = 1147$, $r^2 = 0.98$) was established where x is the mean range of a track (m) and y is the TS deviation ($ESn_{Vtrack} - ESn_{VisAnal}$; in dB) between $Vtrack$ and $VisAnal$, which covered the entire acoustical range encountered during the sampling (2.0 m to 5.6 m). Using the above power function, all $Vtrack$ TS values were corrected according to their specific range to the correct $VisAnal$ TS values (J. Dawson, personal communication).

The fish flux below the transducer was expressed in number of fish $m^{-2} min^{-1}$, calculated by dividing the number of up- and downstream fish tracks by the cross section area intercepting the movements of the fish per unit time.

Given the high SNR, the number of fish tracks were counted visually on the echograms and compared with the numbers generated by the automatic tracking ($Vtrack$) using the Chi-square test (Statistica).

A tortuosity index was calculated to quantify track characteristics. The calculations of the target track characteristics relied on a proper tracking performance of $Vtrack$. The tortuosity index is the quotient of the net distance (distance between start and end ping of a track) divided by the total distance (inter-ping distance of a track). The tortuosity index ranges between 1 and >0 . A fish traveling in a straight line has a tortuosity index of 1; the more a fish track criss-crosses, the higher is its inter-ping distance and the smaller will be its tortuosity index.

In vertical beaming the dorsal aspect angle is one of the most important factors influencing *in situ* TS estimates (McQuinn and Winger, 2003). To provide an estimate of the tilt of the fish tracks, the positive or negative tilt angle of each target track was calculated, assuming a right-angled triangle to describe the tilt of a fish track (Fig. 1). The opposite leg, the difference in height (m) between the start (A) and the end ping (C), was divided by the adjacent leg, the distance (m) between the start (A) and the end ping (B), thus providing the tangent of the tilt angle between the start and the end point of the fish track.

The swimming speed of a fish track was calculated as the total distance (m) divided by the time the fish was in the beam (sec). Targets tracks usually occurred well separated one from the other.

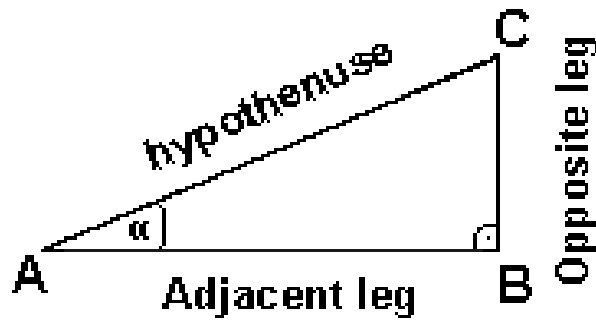


Fig. 1. Determination of the tilt angle of a target track. The distance AB is the linear distance between start and the end ping of a fish track. The distance BC corresponds to the height difference between the start and end ping of a track. Tilt angle = tangent $\alpha = (\text{opposite leg}) \times (\text{adjacent leg}^{-1})$.

When relating a target at a depth of e.g. 2.5 m to the total insonified range of e.g. 3 m at LW and 5 m at HW, the target would be at $2.5/3 = 0.83$ of the channel depth at LW and at half ($2.5/5$) at HW. When, however, related to the actual sampled volume (2+ m depth) and excluding the blind zone (0-2 m), the target would be at half ($0.5/1$) of the sampled depth at LW and at $0.5/3 = 0.16$ at HW. Thus, considering the acoustically sampled depth, a target in the center of the water column at HW is converted to its upper strata position and, a target in the lower water column at LW is converted to its central position. Converting the real target depth to the relative target depth increases the comparability in vertical distribution of targets between different tidal stages. Therefore, TS, tortuosity index and swimming speed were correlated with the relative depth ($[\text{depth of the target} - \text{blind zone range}] \times [\text{maximum insonified depth} - \text{blind zone range}]^{-1}$). The significance of the correlation coefficient ($n = 1262$ fish tracks) was assessed using Rohlf and Sokal (2003).

Physical parameters. Water level (± 1 cm) and tidal current speed (m s^{-1}) were measured every 15 min; the former on a tidal gauge in the Furo do Meio main channel. The latter was determined by measuring the time (stopwatch) it took the tidal current to stretch a 10 m long tape attached to a weight with a buoy. Each current velocity was converted into the distance the water traveled within the 15 min time interval $[(\text{m s}^{-1}) \times 60 \text{ s} \times 15 \text{ min}]$. The sum of the distances at flood and ebb tide intervals were used to generate an estimate for the mean tidal excursion at flood and ebb tide.

Secchi depth (± 1 cm) was measured hourly during daylight hours (6:00 – 18:00). Surface salinity (± 0.1 psu) was measured hourly throughout the sample periods using a conductivity-measuring instrument (WTW LF197) equipped with a sonde (WTW Tetracon 325). Secchi depth and salinity were correlated with water level (Spearman rank correlation).

Fish capture with a tidal trap. To study the tidal migration of fish, live fish were captured with a specially designed tidal trap (Barletta et al. 1998) ca. 400 m upstream of the sonar site during eight neap tide cycles in the dry season 2002 (Nov. 11-13; Nov. 27-29 simultaneously to the acoustic sampling). The tidal trap consisted of a net barrier (fence) placed perpendicular to the current direction (length: 25 m), blocking the southern side of the channel from the mangrove plateau down to the subtidal part of the channel (mesh size between knots: 25 mm, height: 2.6 m). The subtidal end of the net fence entered into two separate heart-shaped traps (diameter: 1.5 m), one on the flood and the other on the ebb side end of the fence. The traps were cleared hourly for fish by hands using a heart-shaped lift net laid on the bottom of each trap (mesh size between knots: 15 mm) during the phase of detectable current speed, four times at flood tide and five times at ebb tide. At flood tide, the flood trap was cleared before the ebb trap whereas at ebb tide, the ebb trap was cleared before the flood trap. Preliminary tests had shown that almost no fish entered the traps during the four hours of quasi-stagnant LW phase. To ensure empty traps before the next flood tide, traps were cleared once shortly before the next estimated slack LW. The hourly clearing schedule was re-started each slack LW. Sampling at neap tides ensured that the headline was above the HW level throughout the samples. In the field, fish were measured (TL to cm below) and the stomach fullness was assigned to a scale ranging from 1 (0-25 %) to 4 (75-100 %). The Kruskal-Wallis test was used to look for significant changes in abundance and stomach fullness of the most abundant species for the four groups daytime-flood, daytime-ebb, night-flood and night-ebb tide. The Nemenyi test was used for post-hoc analysis to test which groups differed significantly from the others (Sachs, 1992).

RESULTS

Abiotic parameters

During the neap tide period when acoustic data were acquired, abiotic parameters showed patterns typical for the dry season in the Furo do Meio. Secchi disc readings (LW 15 cm; HW 45 cm) were positively correlated with water level ($p \leq 0.0001$). Maximum salinity range within a tidal cycle was 1.4 psu. Salinity correlated negatively with water level ($p \leq 0.0001$) and increased slightly from 35.3 to 37.2 during the November sampling. Maximum current speed was 29 cm s^{-1} at flood and 22 cm s^{-1} at ebb tide (Fig. 3b). Current maxima occurred about 50 min after slack LW at flood (in the remainder of the text called “first rise”) and about 90 min after slack HW at ebb tide. Current velocities were highly dynamic, with irregular and strong changes in speed occurring within a few minutes. During weak flood tide

intervals, even complete changes in ebb direction occurred. The mean neap tide tidal excursion \pm SD was 1.75 km \pm 0.98 at flood and 1.30 km \pm 0.88 at ebb tide. The mean net longitudinal current was upstream: 0.41 km \pm 0.29 (n = 11 neap tide cycles).

Tidal trap catches

The tidal traps caught 257 nekton individuals belonging to 20 fish species (12 families) and two crustacean species (Table 1), clearly reflecting the presence of a tropical multispecies population. The top five fish species produced $\frac{3}{4}$ of the total abundance. In general, the catches consisted of juveniles and adults of small species and juveniles of larger species. Mean TL \pm SD of fish was 14 cm \pm 4. Fish were almost exclusively caught during the phase of inundation when current speeds were detectable (Fig. 2).

Table 1. Number of nekton species caught with a tidal trap during eight neap tide cycles in the upper reaches of the mangrove channel Furo do Meio (North Brazil) in November 2002 (dry season). Mean, minimum and maximum total length (TL) per species captured are given. Significant differences between the four groups night flood, night ebb, day flood, and day ebb tide (Kruskal-Wallis test, $p \leq 0.05$) are indicated with *.

Nekton species	Total Number	Night Flood	Night Ebb	Day Flood	Day Ebb	Mean TL (Min-Max)
<i>Cetengraulis edentulus</i> (Engraulidae)	60	5	41 *	2	12	12 (10-14)
<i>Colomesus psittacus</i> (Tetraodontidae)	49	1	1	26 *	21 *	14 (11-30)
<i>Anableps anableps</i> (Anablepidae)	46	13	11	7	15	17 (15-26)
<i>Anchovia clupeioides</i> (Engraulidae)	25	6	15 *	2	2	14 (12-16)
<i>Cathorops</i> sp. (Ariidae)	17	6	3	5	3	16 (12-22)
<i>Calinectes</i> sp. (Portunidae)	14	2		9	3	-
<i>Fenaeropenaeus subtilis</i> (Penaeidae)	12	5	1	4	2	10 (9-14)
<i>Genyatemus luteus</i> (Pomadasyidae)	6	2		3	1	9 (7-11)
<i>Stellifer naso</i> (Sciaenidae)	6	3	2		1	13 (12-14)
<i>Pterengraulis atherinoides</i> (Engraulidae)	6	1	4		1	17 (15-21)
<i>Mugil</i> sp. (Mugilidae)	3	1	2			15 (14-16)
<i>Stellifer stellifer</i> (Sciaenidae)	2		1		1	(10-14)
<i>Archirus archirus</i> (Soleidae)	2		1	1		(6-12)
<i>Oligoplites saurus</i> (Carangidae)	1			1		11
<i>Symphyrus plagusia</i> (Cynglossidae)	1	1				7
<i>Bairdiella ronchus</i> (Sciaenidae)	1				1	11
<i>Cynoscion leiarchus</i> (Sciaenidae)	1		1			18
<i>Stellifer rastrifer</i> (Sciaenidae)	1		1			11
<i>Cathorops spixii</i> (Ariidae)	1				1	12
<i>Batrachiodes surinamensis</i> (Batrachiodidae)	1				1	27
<i>Chaetodipterus faber</i> (Ephippidae)	1				1	9
<i>Cynoscion acoupa</i> (Sciaenidae)	1		1			29
Total abundance	257	46	85 *	60	66	
Number of species		12	14	10	16	

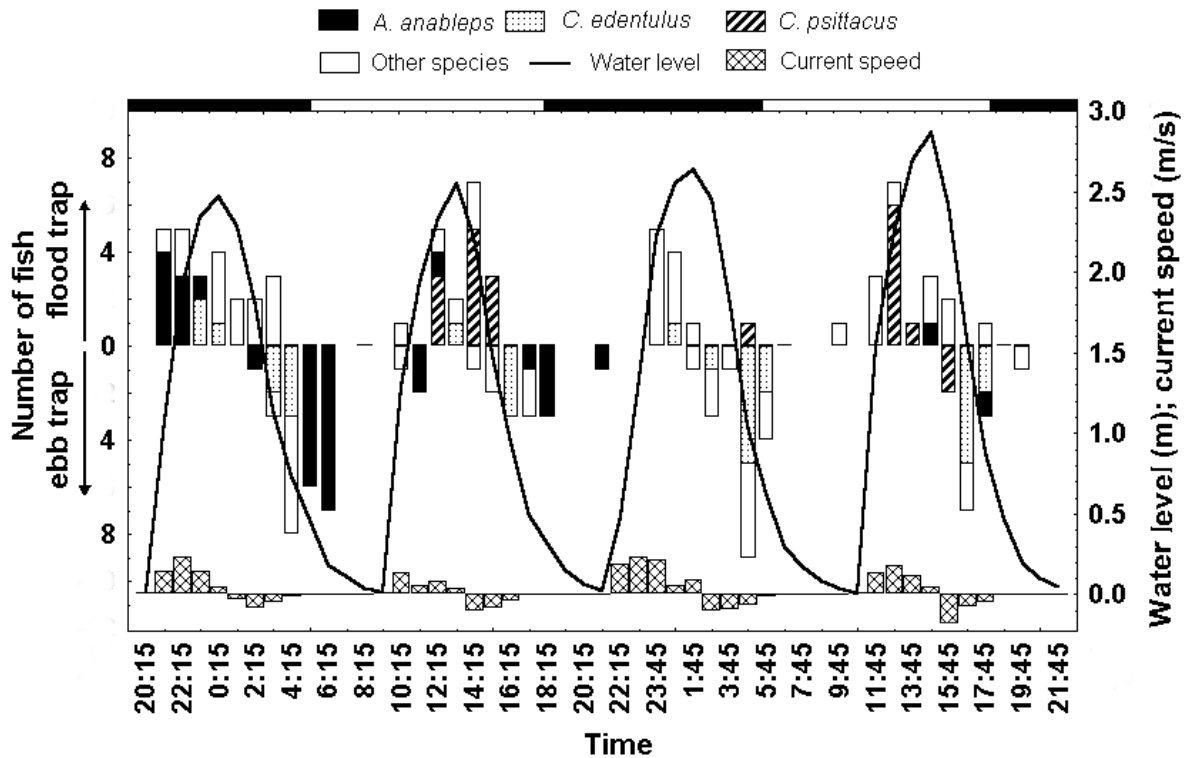


Fig. 2. Number of fish caught with a tidal trap during four consecutive neap tide cycles in the dry season (November 27-29, 2002) in the mangrove channel Furo do Meio. Water level and current speeds are shown. The number of fish is classified according to the three most abundant species and others. The upward bars indicate fish caught in the flood side of the trap; the downward bars indicate fish caught in the ebb side of the trap.

The flood trap generally caught fish at flood tide, the ebb trap caught fish at ebb tide, suggesting that fish usually traveled with the tide. Only *Colomesus psittacus*, *Callinectes* sp., rarely *Anableps anableps* and Sciaenidae were captured in a trap opposite to the respective tidal direction, indicating that these species were actively swimming against the tide. Concurrent artisanal line fishing frequently caught *Arius herzbergii* whereas not a single specimen was captured in the tidal traps, suggesting species-specific avoidance of the traps. Direct net avoidance and even escape out of the trap was likely since weak neap tide currents failed to exert a strong directional force on the fish movements. The traps unfortunately failed to reveal a pattern in the within-tidal cycle timing of the fish migration, due to low sample sizes. The Engraulidae *Cetengraulis edentulus* and *Anchovia clupeioides* were significantly more abundant at night-ebb tide than at any other of the three time-tidal cycle combinations (Kruskal-Wallis test, $p \leq 0.05$; $p \leq 0.05$, Table 1). The same pattern for total fish (Kruskal-Wallis test, $p \leq 0.05$) is strongly reflective of the abundance of the two Engraulidae species. The pufferfish *Colomesus psittacus* was diurnal, almost exclusively occurring at daylight hours (Kruskal-Wallis test, $p \leq 0.05$).

Stomach fullness

Diurnal *C. psittacus* had significantly fuller intestines (the stomachs are usually empty; H. Keuthen, pers. comm.) at ebb than at flood tide (Kruskal-Wallis test, $p \leq 0.0001$). The stomach fullness in *A. anableps* differed significantly between the groups (Kruskal-Wallis test, $p \leq 0.01$). Although the Nemenyi test failed to indicate which groups differed from the others, it was apparent that daytime stomachs of *A. anableps* were fuller than night stomachs. *Cetengraulis edentulus* stomachs were full at all different times, suggesting continuous feeding throughout the tidal cycle.

Fish flux and patterns in the tidal migration of mangrove fish

Considering both the course of the fish flux curve based on the number of fish tracks counted automatically (Fig. 3a) and the vertical distribution (Fig. 4), seven peaks during a neap tide cycle were apparent: at sunset, night-flood start, night-HW, sunrise, daytime-flood start, daytime-HW and daytime-ebb.

At sunset during quasi-stagnant ebb tide an upsurge in fish flux occurred (ca. $12 \text{ fish m}^{-2} \text{ min}^{-1}$) and lasted until total darkness (18:00-18:40). Fish tracks were orientated rather downward (tilt angle < 0) (Fig. 3e), characterized by slow milling (Figs. 3f,g) and directed in all directions as visualized in the 3-D tracks in Figure 5 (Low water) where some tracks seemed to stop briefly in-between before continuing again. Tracks were distributed throughout the small insonified range with most fish in the 0.5-1 m layer above the bottom (Fig. 4). TS values shortly decreased (Fig. 3d), suggesting that smaller fish descended from the near-surface zone downwards.

The moment the nocturnal flood tide started and current speeds rose noticeably (max. 24 cm s^{-1} ; Fig. 3b), fish fluxes increased dramatically for a period of ca. one hour (max. $12 \text{ fish m}^{-2} \text{ min}^{-1}$). Fish tracks were positioned well off-bottom throughout the water column (Figs. 4a and 5, flood start). The preponderance of tracks were directed in the upstream direction (Fig. 3c, 65 % of the tracks going with the flood tide), swimming speeds increased and tracks passed horizontally and mostly linear with high tortuosity indices (Figs. 3f,e,g and 5, flood start). TS values decreased sharply, suggesting active and directed immigration of smaller fish that were riding the first flood rise in the upper channel strata to achieve upstream transport and enter the intertidal zone.

The rest of the nocturnal flood tide fish fluxes continued alternating at ca. $2 \text{ fish m}^{-2} \text{ min}^{-1}$ and were very low before the nocturnal HW. Likewise TS values alternated up and down. Off-bottom movements of fish were abundant though very dynamic in time and space.

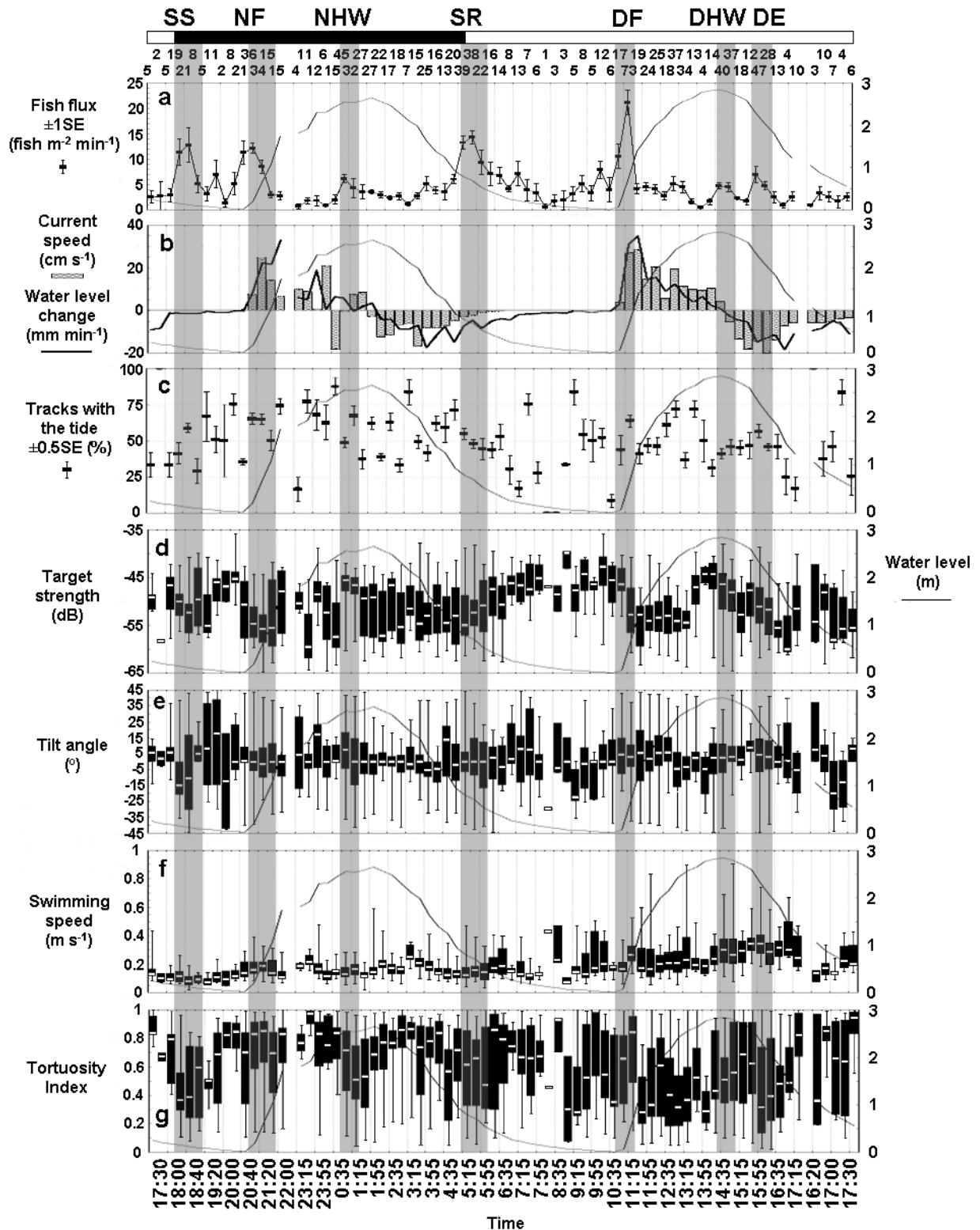


Fig. 3. 24-h time-series of fish flux (a), tidal parameters (b) and fish track characteristics (c-g) at neap tide, dry season, in the mangrove channel Furo do Meio, North Brazil. The box plots (d-g) are given with median (\square), 25-75 % quartile (\blacksquare) and min-max whiskers. On top fish flux peaks are indicated with SS (sunset), NF (night-first rise), NHW (night-high-water), SR (sunrise), DF (daytime-first rise), DHW (daytime-high water) and DE (daytime-ebb). The black horizontal bar indicates night. The series of alternating numbers provides the sample size of fish automatically tracked per 5-min sample interval. Three data sets acquired on November 27-29, 2002, were tied together at equal water levels and are separated by a gap while real times are given in the x-axis.

However, a second strong flood tide interval clearly coincided with fish swimming in the upper stratum (Fig. 4b). Fish tracks continued linearly as indicated by high tortuosity indices (Fig. 3g).

Around the nocturnal slack HW, a distinct fish flux peak occurred (max. 6 fish m⁻² min⁻¹) while all fish tracks occurred off-bottom. TS values went up again. Tortuosity indices were decreased and swimming speeds dropped briefly, likely indicating active milling behavior of larger fish around slack HW in the main channel.

The fish flux levels at night ebb were similar to night flood, but showed a weak minimum during the phase of maximum ebb current speeds. Many fish tracks continued off-bottom even during the start of night-ebb tide; however, fish descended during the ebb current maximum (Fig. 4c). Tracks became very linear again. While the tide receded, TS values tended to slightly decrease with the progressing ebb tide, suggesting the gradual return of smaller fish with most small fish passing after the ebb current maximum.

While sunrise coincided with the end of the phase with stronger ebb current speeds, fish fluxes peaked at dawn (5:15-5:35; 14 fish m⁻² min⁻¹) and decreased gradually to a minimum at 8:15. For the rest of the diurnal LW phase, fish fluxes again increased slightly towards slack LW. At dawn fish tracks were distributed shortly throughout the water column (Fig. 4d) while TS values started to increase gradually to reach the highest cycle values at daytime-LW (Fig. 3d). The tortuosity indices were very variable indicating that both linear and directional tracks were equally likely to occur (Fig. 3g).

As soon as the daytime flood started (max. current speed: 27 cm s⁻¹), fish fluxes again increased dramatically for ca. half an hour with a maximum of 21 fish m⁻² min⁻¹, thus numerically even surpassing the nocturnal first rise. While high tortuosity indices with mostly linear, fast upstream tracks throughout the acoustic range (Fig. 5, flood start) occurred only during the first two samples right after daytime slack LW (Figs. 3f,g and 4e), TS values continued to be low for ca. 2½ hours (Fig. 3d).

The rest of the daytime flood tide fish fluxes continued on a lower level similar to the night flood tide (on average 3 fish m⁻² min⁻¹) and reached a minimum before HW while TS suddenly shifted to higher values again. The preponderance of smaller fish had probably left the main channel during the first part of the flood tide as reflected in increased TS values towards the end of flood tide in both tidal cycles (Fig. 3d).

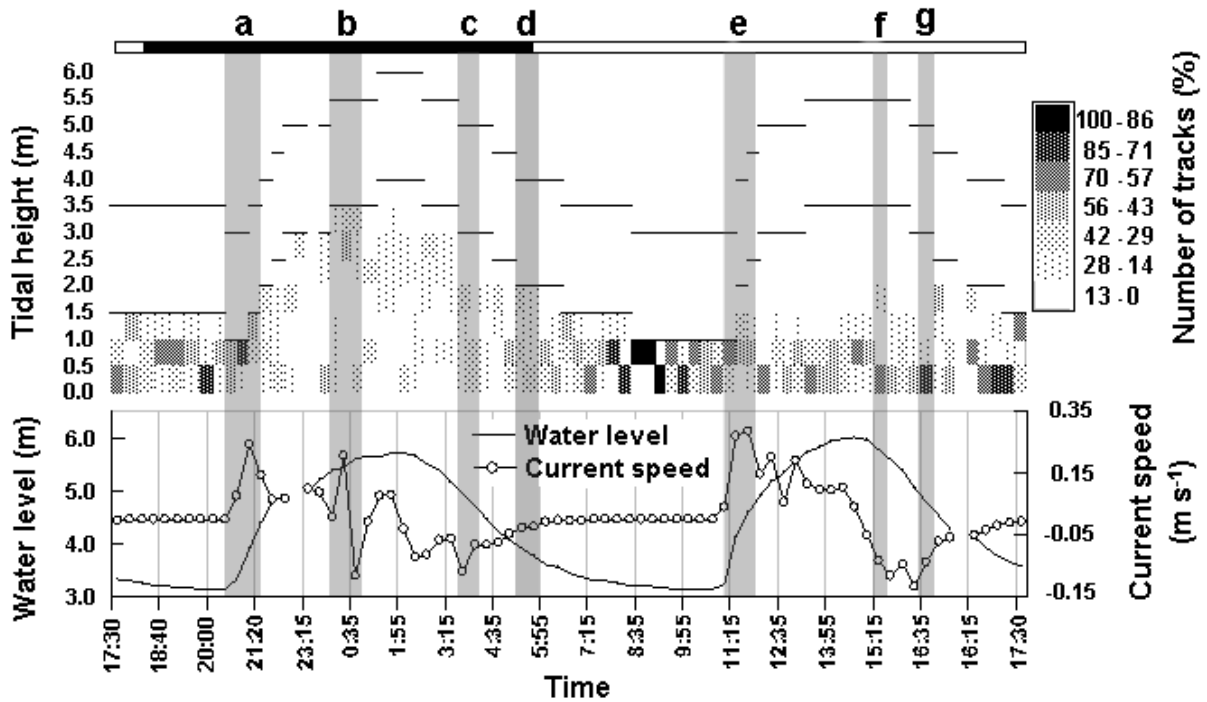


Fig. 4. 24-h times series showing vertical distribution of fish tracks and current speeds at neap tide cycles in the mangrove channel Furo do Meio (North Brazil). Upper figure: Discrete contour graph with fish abundance per depth cell (%) vs time. Depth between the two parallel horizontal lines corresponds to the transducers' blind zone (0-2 m). The channel bottom is the reference line for the depth cells. The sum of the cells below the blind zone until the bottom corresponds to 100 % of the fish tracks automatically recognized during a 5-min sample interval. The legend on the right represents the percent of tracks in each 0.5 m-depth cell in seven pattern categories. Lower figure: Concurrent water level and tidal current speed. Top horizontal bar indicates day and night. The number from 1 to 6 highlights coincidences between current speed and vertical distribution patterns: a, e: First flood rise; b: Intermediate flood current peak; c, g: Ebb current maximum; d: sunrise; f: Daytime high water. The cycle consists of three data sets acquired from Nov 27-29, dry season 2002, lined up at equal water levels.

When water depth was maximal, fish tracks were concentrated in only 0.5 m above the channel bottom (Fig. 5, high water) while in the previous and next sample intervals fish tracks were distributed in the 1.5 m above the channel bottom (Fig. 4f). Fish tracks were long, sometimes criss-crossing and orientated in all directions but in contrast to LW, very close to the substrate, suggesting active foraging behavior of epibenthic fish.

Ebb tide fish flux levels were similar to daytime flood tide except for a distinct maximum coinciding with maximum ebb current speeds ($7 \text{ fish m}^{-2} \text{ min}^{-1}$) when most fish tracks occurred close to the bottom (Fig. 4g). Some fish tracks meandered diagonal to the tide (Fig. 5, ebb tide) suggesting that some epibenthic fish were still involved in increasing the area searched for prey during the ebb migration. Swimming speeds reached a maximum coinciding with the phase of ebb current maximum. The gradual decrease in TS values was

more apparent with the progressing ebb tide at daytime than at night. The mean fish flux \pm SD during the 24-h series was $4.7 \text{ fish m}^{-2} \text{ min}^{-1} \pm 3.7$ (Fig. 3a).

When relating the numbers of fish to cubic meter of water run through the cross-section of the beam min^{-1} , values during the quasi-stagnant LW phase (current speed $<0.01 \text{ m s}^{-1}$) when fish were concentrated in the subtidal channel section, were 100 to 200 times higher than those during the period of inundation of the intertidal zone (median during inundation \pm SD: $1.0 \text{ fish m}^{-3} \text{ min}^{-1} \pm 5.7$).

TS distribution

The corrected TS values ranged between -40 and -60 dB (Fig. 3d), pointing to the presence of small fish, typical for a nursery area. During LW (water height: $<25 \text{ cm}$ above slack LW), TS values were significantly greater than during the period of inundation (mean \pm SE: -48.6 ± 0.4 vs -51.6 ± 0.2 , respectively; U-test; $p \leq 0.0001$), suggesting the presence of larger fish at LW. TS increased towards the bottom ($p \leq 0.01$), suggesting smaller fish passing in the upper stratum and larger fish in the near-bottom stratum. Swim speed and TS did not correlate.

Tilt angle

Tilt angles ranged between -45° and $+45^\circ$ with a median of $0^\circ \pm 0.5 \text{ SE}$ and a mean of $+1.2^\circ \pm 17.5 \text{ SD}$ ($n = 1262$). The temporal distribution of the tilt angles of the fish tracks was subject to significant variability, though angles essentially centered around a tilt angle of zero degrees (Fig. 3e), i.e. the majority of the fish tracks passed horizontally through the beam. In contrast to downward orientated tracks at sunset, no such pattern occurred at sunrise, suggesting that the sunrise fish flux peak was not caused by a rise of fish from the bottom, but rather by fish that entered the center of the channel more or less horizontally from the sides.

Swimming speed

Swimming speeds in the mangrove channel essentially ranged between 0.1 to 0.5 m s^{-1} . Considering 14 cm as the mean TL of fish, swimming speed ranged between 1 and 3.5 length s^{-1} . The swim speeds at LW (water height: $<25 \text{ cm}$ above next slack LW) were significantly lower than during the phase of inundation (mean \pm SE: 0.15 ± 0.01 vs $0.21 \text{ m s}^{-1} \pm 0.004$, respectively; U-test, $p \leq 0.0001$), suggesting relaxed swimming during the quasi-stagnant LW phase, as also indicated in Figure 5 (low water). At LW an unknown portion of the fish population was actively swimming around in the subtidal zone instead of resting stationary on the channel bottom.

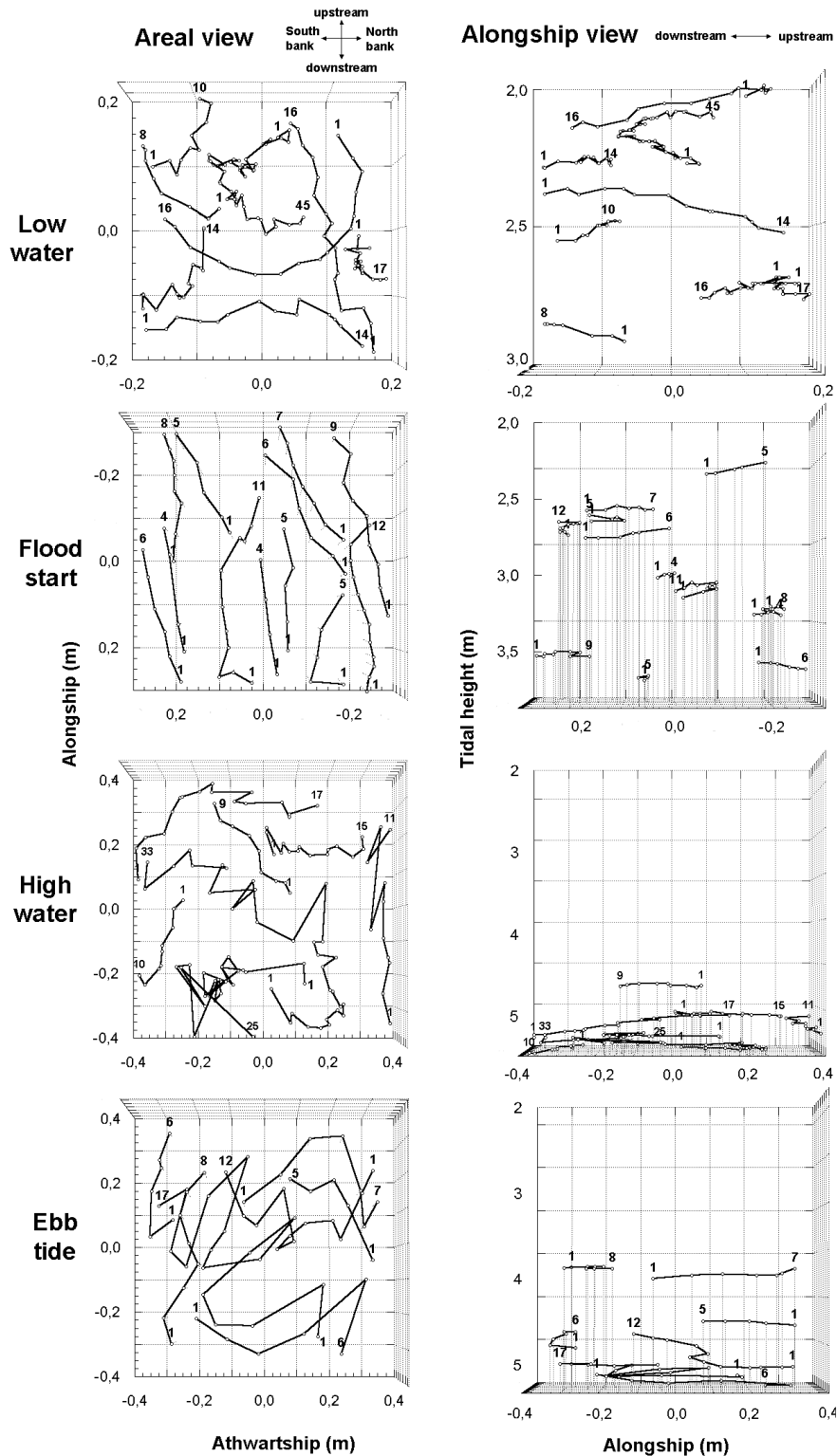


Fig. 5. Selected fish tracks - from top to bottom – at low water (18:20, sunset, Nov. 27), first rise at flood start (11:15, Nov. 29.), high water (14:35, Nov. 29) and ebb tide (15:55, current peak, Nov. 29) during neap tide, beaming vertically in the center of the mangrove channel Furo do Meio, North Brazil, with a 200 kHz split-beam sonar. The transducer's blind zone was 0-2 m. The left column shows the tracks' aerial view (athwart range vs. alongship range); the right column shows the tracks' alongship view (alongship range vs. tidal height). Note that different along- and athwartship ranges correspond to changes in tidal height and hence, maximum beam width. The start and end point of each track is indicated by 1 and the number of the end ping, respectively.

The mean swimming speed (averaged over the entire water column) was usually greater than the current speed at any one tidal phase, suggesting active swimming in the tidal current. It is apparent in Figure 3f that stronger current phases at flood and ebb tide coincided with increased swim speeds. However, swimming speeds did not significantly change with depth nor correlate with tidal current speeds.

Tortuosity index

The temporal distribution of the tortuosity indices showed a consistent tidal-related pattern during the night cycle while no clear temporal correlation was apparent in the daytime cycle (Fig. 3g). Tortuosity indices were higher towards the bottom ($p \leq 0.01$), suggesting more linear movements towards the surface and more milling in the near-bottom stratum.

Vertical distribution of fish tracks

The vertical distribution of fish tracks showed a remarkable difference between the daytime and the night cycle: At daytime fish remained in a near-bottom zone, extending to about 1.5 m above bottom and there was virtually no fish in the water column, whereas during the nocturnal inundation fish extensively exploited the entire water column (Fig. 4).

STST was most apparent during the first rise, both at daytime and at night. Current speed-related shifts in vertical distribution occurred only during short time intervals. The ebb maximum coincided with a fish flux minimum at night and a maximum at daytime, suggesting two different fish groups were active at these times.

Automatic vs visual target counting

Visual counting of target tracks on the echograms produced passage numbers that were on average two times higher than the automatic tracking, principally due to near-bottom targets that were readily recognized visually but not detected by Vtrack ($p \leq 0.0001$; daytime cycle: automatic 696, visual 911; night cycle: automatic 566, visual 1135). 50 % of the fish tracks detected automatically occurred in the lower 30 % of the relative water depth. Considering the results of the visual track counting and the diurnal distribution, it is clear that the majority of the fish traveled in the lower strata of the channel.

Total estimate

Applying the proportion of upstream migrating fish provided by Vtrack to the number of fish visually counted from the echograms produced an estimate of 29 300 and 30 000 upstream

fish tracks at flood tide that passed the sonar site at daytime and at night, respectively. Two assumptions underlie this estimate: (i) Vertical beaming insonified on average 1/30 of the channel cross-section with more than 2 m water depth at any one tidal phase; (ii) A homogenous water body was assumed; and due to lack of biological data, fish distribution was considered to continue uniformly from the deepest channel section towards the banks.

DISCUSSION

This paper shows that in well-mixed shallow-water environments with a dominant epibenthic fish population, horizontal beaming should be combined with vertical beaming when attempting to generate reliable passage estimates. Under certain ambient conditions deeper sections may serve as a refuge for fish. Even though the benthic and pelagic zone are close to each other in shallow water, spatiotemporal changes in separation and fusion between the strata may occur and hence, lead to considerable changes in fish abundance. Due to avoidance of the sub-surface layer by the fish at daytime, the sole use of horizontal beaming (Krumme and Saint-Paul, 2003) only included about one fifth of the total estimate of immigrated fish during the daytime flood when the estimates of horizontal and vertical beaming were combined (Table 2). During the night flood cycle approximately half of the fish immigrated in the sub-surface layer whereas the other half used the deeper strata of the channel cross-section.

Despite the low sample volume, vertical beaming generally dealt on average with fish fluxes that were twice as high compared to the horizontal beaming (Krumme and Saint-Paul, 2003), suggesting that the fish abundance in the mangrove channel is usually higher near creek bottom and lower near the surface, thus reflecting the dominance of epibenthic fish in the intertidal mangrove fish community (Krumme et al., *subm.*).

Table 2. Estimated numbers of upstream fish during the daytime and the night flood using stationary horizontal (Krumme and Saint-Paul 2003) and vertical beaming (present study) at neap tides in the dry season in the mangrove channel Furo do Meio (North Brazil). The number of immigrated fish at flood tide was determined as the mean number of upstream fish tracks min^{-1} during a 5 min sample interval, multiplied by the time (min) between successive sample intervals (10 min in horizontal and 20 min vertical beaming) and finally adding up the number of upstream fish tracks of all flood intervals. Assumptions to extrapolate the sum of the number of upstream fish tracks detected in the beam to the entire channel cross-section: Horizontal beaming insonified half the channel width and vertical beaming insonified 1/30 of the channel width in any one tidal phase.

Flood Cycle	Horizontal beaming		Vertical beaming		Sum	
	Numbers	% of sum	Numbers	% of sum	Numbers	%
Daytime	6 000	17	29 300	83	35 300	100
Night	28 000	48	30 000	52	58 000	100

Fish Abundance Estimates

Combining the fish passage estimates of vertical and horizontal beaming reveals several tens of thousands of upstream fish immigrating into the mangrove during flood tide at dry season-neaps in the Furo do Meio (Table 2). However, fish abundances are much higher at spring tides and outside of the dry season. At springs, fish abundances increase on average roughly three times compared to neaps (factor extracted from Krumme et al., subm.). Fish abundances in the wet season (Barletta et al., 2003) and during the wet-dry season transition when the period of maximum *C. edentulus* abundance triggers the entrance of predatory coastal fish, are even greater than during the dry season (personal communication with fishermen). It is hence apparent that the mangrove supplies an enormous number of fish, by both providing a support function for juvenile fish nurseries, and providing a suitable habitat for adults.

The fish species perceived as most important by rural residents in the Caeté Bay are almost exclusively fished in the mangrove system and constitute the major protein source for the poorer sections of the local population (Glaser and Grasso, 1999). Juveniles in the mangroves such as *Cynoscion acoupa* and the shrimp *Fenaeropenaeus subtilis* (Krumme et al., subm.) are taken as adults by the regional offshore industrial fisheries (Barletta et al., 1998).

Diel Variations

Vertical beaming confirmed the poor fish abundance beneath the surface zone at neap tide-daytime as observed by Krumme and Saint-Paul (2003). Krumme et al. (subm.) caught the poorest fish assemblages in terms of abundance and diversity at neap tide-day in intertidal mangrove creeks in the wet season, suggesting that the daytime absence of fish in the pelagic zone of the main channel at neaps not only continues spatially into the intertidal zone, but that it is also a temporal pattern recurring fortnightly year-round in the mangrove system.

The use of the water column during the phase of inundation apparently depends strongly on the presence of Engraulidae and changes in their foraging behaviour. The rather nocturnal occurrence of *C. edentulus* in the traps cannot be readily considered as their typical diel activity pattern. Horizontal beaming revealed huge schools beneath the surface appearing during both the daytime and the night HW phase from May to September in the Furo do Meio (Krumme, unpubl. data). In November, remains of the previously huge *C. edentulus* biomass likely exhibited a different behaviour than during the abundance peak. Maes et al. (1999) working in the highly turbid, tidally dominated Zeeschelde estuary (Belgium) found that pelagic fish maintained their position underneath the water surface throughout the day.

It is not known to what extent epibenthic mangrove fish exhibit off-bottom movements in the channels. The tidal-related patterns in feeding of *Cathorops* sp. do not suggest any pelagic excursions that were reflected in the catfishes' diet (Leal-Flórez et al., in prep.). However, *Cathorops* sp. is supposed to occur in schools of more than 20 individuals while undertaking tidal movements (personal communication with fishermen). Maes et al. (1999) found that demersal fish remained on the bottom during the day while at least a part of the population exploited surface waters at night. Several flatfish species spend considerable periods in the water column, usually during the night, indicating that they are by far not as bottom orientated as their morphology might suggest (Gibson, 1997).

Poor fish abundance during the daytime flooding might be related to a combination of avoidance of light by the fish during the fortnightly water clarity maximum, together with poor food availability at neaps. The strong response to the photoperiod is thus somewhat surprising as Secchi depths in the mangrove water are usually below 0.5 m. However, the real light attenuation and visual sense of the fish is unknown. The eyes of Ariidae, Sciaenidae, Engraulidae and other mangrove fish species reflect light when caught at night and are hence likely to have a tapetum (own observation), in adaptation to the low light levels. Grecey and Targett (1996) showed that fish still feed efficiently on their prey even under high turbidity conditions. At neap tide zooplankton abundance and biomass are lowest (Krumme and Liang, in press), the accessibility to the intertidal zone and its resources is minimum and increased water clarity renders it more likely for the prey to escape or avoid attacks of predatory fish.

Avoidance of piscine and avian predation by the fish is unlikely to be a major cause for the lack of fish in the water column during daytime flooding at neap tides. The tidal trap caught only one larger piscivorous fish (Table 1, *C. acoupa*, 25-50 % filled stomach). Large piscivores are almost totally absent from the intertidal creeks of the Furo do Meio at neap tides (Barletta et al., 2003; Krumme et al., subm.; Brenner, unpubl. data). Individuals or groups of three to six cormorants were observed flying over the Furo do Meio exclusively at daytime-neaps around HW, but they were observed diving for fish only once (n > 30 daytime neap cycles, own observation). Egrets can be observed at daylight hours throughout the tidal cycle but are rare and their impact is restricted to the channel banks.

The abundance peaks at twilight have already been demonstrated by Krumme and Saint-Paul (2003). Since at neap tides the twilight periods coincide with late ebb tide, the tidal trap catches failed to provide information on the twilight species composition. The abundance

peak at sunrise was probably linked to an activity upsurge in diurnal *C. psittacus* as also suggested by lift net catches in the main channel (Leal-Flórez, unpubl. data; Krumme and Saint-Paul, 2003).

At sunset *C. edentulus* may have contributed to the abundance peak. Concurrent to the sampling, *C. edentulus* was a frequent bycatch in artisanal shrimp nets that are trawled by two fishermen along the shallow banks until ca. 1.5 m depth during the night LW phase (own observation). Engraulidae that filter the water for ubiquitous plankton may feed continuously and depend less on feeding in the intertidal creeks, therefore lacking a pronounced tidal-related pattern in feeding. Probably they even profit from LW-feeding when highest abundances in zoo- and phytoplankton occur in the Furo do Meio (Krumme and Liang, in press; Schories, unpubl. data).

Patterns in the Tidal Migration

Target strength “behaviour”. It is not clear how the interplay of different possible factors exactly influenced the TS behavior during the tidal cycle. The swim bladder, which is proportional to fish size and water depth (TeWinkel and Fleischer, 1988; Hazen and Horne, 2003), is recognized as having the most important effect on the TS. There is evidence that higher TS values at LW were related to the concentration of mainly larger fish of only a few species. At LW larger fish, especially catfish, withdrew to subtidal deepenings of the Furo do Meio whereas smaller fish occurred more often in the shallow banks (Krumme et al., subm.). Volume changes in a swim bladder are strongest in shallow waters (Bone and Marshall, 1985). According to Boyle’s law, when a demersal fish swims in a tidal area that is in 6 m depth at HW, or conversely at 3 m depth at LW, the volume of the swim bladder changes by 1/3. Hence, on shallow tidal coasts TS should exhibit a regular alternation with higher TS values at LW and lower TS values at HW. Mukai and Iida (1996) found depth dependence in TS in *Oncorhynchus nerka* to be in accordance with Boyle’s law covering depths from 5 to 40 m. In the present study, Boyle’s law was not consistently reflected in the TS patterns observed. While TS values were high during LW, remarkable TS increases occurred at the night slack HW and particularly before and at the daytime slack-HW (Figs. 3d and 4). Tidal traps failed to provide information concerning this pattern. However, it is not unlikely that large fish use the upper reaches of the Furo do Meio main channel during the highest water levels of a tidal cycle when the conditions are most favorable for them to forage. Particularly larger piscivores apparently require a minimum water level to access shallow water environments (Blaber, 1980; Rönnbäck et al., 1999; Paterson and Withfield, 2000).

Also inconsistent with Boyle's law was the observation that TS values generally showed an increase towards the bottom instead of a decrease. This suggests that fish size increased towards the bottom. Moreover, first rise (when fish entered the water column) coincided with a decline instead of an increase in TS values, again suggesting the passage of smaller fish in the upper strata. Gee (1983) found that freshwater fish living in fast currents presumably improved the frictional grip by having reduced swim bladder volumes compared to the same species living in slower waters. Unfortunately, the author found no studies dealing with special adaptations in swim bladder morphology of fish species living in macrotidal areas, or concerning depth dependence in swim bladder size and its relationship to TS in very shallow water.

At the same time, it is worth mentioning that changes in hydrostatic pressure, or swim bladder size, may in fact be a cue for the timing of fish movement in and out of the intertidal zone (Gibson, 1973; Ruiz et al., 1993; Gibson, 1997).

In addition to fish size and depth, biological factors such as orientation (Love, 1971; Blaxter and Batty, 1990; Čech and Kubečka, 2002; Hazen and Horne, 2003; McQuinn and Winger, 2003) and physiology (Ona, 1990) are known to influence TS. Since fish usually passed more or less horizontally through the beam, tilt angle showed no consistent relationship to the tidal cycle. Therefore, temporal changes in TS cannot be attributed to a systematic tilting of the aspect angles of the fish.

Tidally visiting mangrove fish like *C. psittacus* or *Cathorops* sp. (Leal-Flórez, in prep.) exhibited a recurring pattern with emptier stomachs at flood than at ebb tide. These gradual changes in the fullness of the digestion tract and the likely consequences for the reflection properties of the fish can hardly explain rapid alternations in the TS behavior, like the sudden drop in TS at nocturnal and daytime first rise, the temporary decrease at sunset (Fig. 3d), and the gradual decline followed by an increase at daytime ebb tide.

Immigration at first flood rise. The most remarkable feature in the intertidal migration of fish was the activity upsurge at first rise in both tidal cycles. First rise immigration of the entire fish community was also apparent in horizontal beaming (Krumme and Saint-Paul, 2003). On the species level the pattern was observed in the tidal migration of surface-dwelling *A. anableps* (Brenner and Krumme, subm.), suggesting that first-rise immigration is a typical constituent of the tidal migration of many mangrove fish in the Furo do Meio.

While the slightly stronger diurnal first rise resulted in a flux peak two-times higher than in the nocturnal first rise, the first rise pattern occurring at spring tides (Krumme, unpubl. data)

is accompanied by even greater fluxes of fish entering the intertidal zone. The correlation between stronger first rise velocities and stronger fish immigration could explain why extraordinary strong equinox spring tides yield extraordinary high mangrove fish catches (Krumme et al., *subm.*).

First rise did not coincide with strong upward-orientated tracks, suggesting the absence of a sudden ascent of fish from the bottom into the water column in the upper reaches. When responding to continuous changes in e.g. current speed or light levels, the fish likely adapt their vertical position gradually on a scale of minutes and meters. Therefore, the small sample volume was unlikely to clearly reflect these patterns, except for sunset. To ride the tide at first rise the mostly juvenile fish may (1) more or less horizontally head from the sides towards the channel center where highest current speeds occur (Wolanski et al., 1980). The migrating fish may either entirely rely on the tide or, after some distance of upstream travel, use lateral movements to enter the intertidal creeks. Or (2) fish may gather close to the bank, thus using the lateral widening of the channel with the rising tide to achieve early intertidal access like observed for *A. anableps* (Brenner and Krumme, *subm.*). It is, however, rather unlikely that (3) fish may ascend into the water column only further downstream.

In the Furo do Meio first rise coincides with lowest Secchi readings and highest seston transport during a tidal cycle (Krumme and Saint-Paul, 2003). Increased turbidity reduces the visual range of predators (Greay and Targett, 1996) and may hence, further promote migratory activity during first rise.

Although flood lasts only half the time of ebb, the Furo do Meio clearly is a flood-dominated system with a net upstream longitudinal current (Wolanski et al. 1980). This not only results in sediment deposition (own observation; Furukawa et al., 1997) in the tidal tributaries, but also facilitates retention of plankton organisms (Krumme and Liang, *in press*). Hence, even without selective vertical movements, fish are readily capable of achieving retention, once in the channel, while first rise immigration may additionally improve the conditions for intertidal foraging and sustenance in the mangrove nursery.

Fish unequivocally swam actively in the tidal current as indicated by trap catches, the up-downstream relationship and swimming speeds usually exceeding current speeds. It is a common migratory strategy of juvenile fish to use tidal currents as a mode of transport (Boehlert and Mundy, 1988). Riding the tide likely enables fish to avoid significant expenditure of energy for movement, thereby gaining capacity for faster growth (Miller et al., 1985).

The principal time window for immigration was the first rise. The remainder of the tidal movements of the fish in the main channel was characterized by temporal and spatial patchiness, thus being heterogeneous in the three dimensions plus the time scale. The correlation between physical and behavioral parameters often only lasted for short time periods. When sampling the vertical and temporal distribution of juvenile fish in intertidal environments, the 3-D heterogeneity vs time should be seriously considered.

Usually STST is considered as a continuous process where fish larvae supposedly ascend actively in the water column during flood and return to the bottom when the tide turns to prevent being flushed back at ebb tide (Creutzberg, 1961). Taking a series of vertical samples during specified intervals at flood and ebb tide (e.g. Colby, 1988; Jager, 1999) involved a fairly abstract approach to the naturally dynamic tidal current features. The fish may readily be able to synchronize their swimming behavior to short-term changes in tidal current features as revealed in this study. Moreover, in channels with strong tidal mixing, selective positioning in the water column is likely difficult for the smallest juveniles. Hence, a clear understanding of the hydrological dynamics underlying the fish migration and an appropriate sample design are essential for studying the tidal-related movements of fish (Colby, 1988). Here, sonar application provides a useful non-intrusive, high-resolution tool to study the natural patterns.

High Water. The increase in fish flux at slack HW is likely related to increased milling of foraging fish and not caused by new fish, either from downstream or those already returning from the intertidal zone. Sogard et al. (1989) found that the most abundant species centered their activity on seagrass-covered banks around high tide. At high tide *Platichthys flesus* made meandering searches for food and showed highest turn rates (Wirjoatmodjo and Pitcher, 1984).

Around the night-HW, both vertical and horizontal beaming (Krumme and Saint-Paul, 2003) showed intense nocturnal use of the pelagic zone, coinciding with higher catches of two anchovy species during first ebb fall at moonrise. At HW zooplankton diversity reaches a maximum while abundance reaches a minimum irrespective of time of day (Krumme and Liang, in press). Moonlight may enable filter feeders to shift to more efficient visual feeding on plankton items in the upper water column that may again facilitate trap entrance. Reis and Dean (1981) mentioned that maximum numbers of *Anchoa mitchilli* occurred in large creeks in the sub-surface at night to feed.

At daytime-slack HW, epibenthic fish milled close to the channel bottom (Fig. 4), suggesting intense infauna feeding. Leal-Flórez et al. (in prep.) caught the catfish *Cathorops* sp. in the main channel with well-filled stomachs briefly after HW, suggesting high feeding activity during the HW period.

Although the short no-current interval at slack HW renders it a unique period for catfish to forage for intertidal infaunal prey, subtidal resources are accessible to fish throughout the tidal cycle; and subtidal infauna is unlikely to exhibit extensive tidal-related changes in their availability to predatory fish (S. Dittmann, personal communication). Hence, a reason why epibenthic fish should forage in the subtidal zone particularly around slack HW is not known.

Ebb tide. Decreasing TS values during ebb tide suggest that smaller fish returned gradually from the intertidal creeks back into the main channel with lowest TS values and hence, highest proportions of smaller fish at the end of the phase with detectable current speeds. Early immigration using the first rise into and late return from the intertidal zone maximizes the time spent foraging. Surface-swimming *A. anableps* showed a similar pattern of gradual ebb tide return in the Furo Meio that was controlled by the falling water level (Brenner and Krumme, subm.).

The daytime ebb current maximum coincided with a fish flux peak and high swimming speeds, suggesting directed downstream movements in particular species. Similarly, downstream movements of *P. flesus* were accompanied by the highest recorded swimming speeds at ebb tide (Wirjoatmodjo and Pitcher, 1984).

Swimming. Tidal trap catches supported the assumption that the net direction of travel is supposedly upstream at flood and downstream at ebb tide, while the upstream-downstream relationship (Fig. 3c), except for first rise, was subject to considerable variance due to low sample volume and occasionally low sample sizes. But, a certain amount of movement against the tide is apparently common in tidally migrating fish. Ultrasonic telemetry on *P. flesus* (Wirjoatmodjo and Pitcher, 1984) showed that the flounders essentially followed the tide, but only about 70 % of the tracks were movements with the tide. Directional and meandering movements and halts occurred while foraging in the intertidal zone. Szedlmayer and Able (1993) calculated that ultrasonically tracked *Paralichthys dentatus* moved about 60 % of the time in the same direction as the tidal current.

According to theoretical considerations, the optimum swimming speed of fish should be 1 L s^{-1} (Videler, 1993) as actually found by Quinn (1988) in ultrasonic tag experiments with

migrating *O. nerka*. In the mangrove channel fish swam probably at about 1 L s^{-1} during LW. At first rise, swimming speed in terms of L s^{-1} was likely to have increased considerably due to the preponderance of small targets.

Arrhenius et al. (2000) concluded that split-beam sonar is an appropriate method to estimate swimming speeds of fish, however, he also stated that swimming speeds of smaller targets (<5 cm) appeared to be over-estimated. But since low swimming speeds coincided with low TS values e.g. at sunset and sunrise (Figs. 3d,f), such a bias is unlikely to have occurred.

The swimming speeds detected acoustically corresponded well with the range of routine swimming speeds available for tropical estuarine fish species like *Liza macrolepis* (2 L s^{-1}), *C. nebulosus* (2.7 L s^{-1}) and *Sciaenops ocellata* (3.0 L s^{-1}) in Videler (1993).

CONCLUSIONS

Vertical beaming in the macrotidal mangrove channel Furo do Meio operated at a high SNR of 21 dB compared to 7 to max. 15 dB in horizontal beaming (Krumme and Saint-Paul, 2003).

The considerable number of fish tracks detected in the small acoustic sample volume emphasizes the high abundance of fish present in the mangrove nursery area even at neaps in the dry season.

The fortnightly maximum in water transparency was accompanied by a pronounced diel change in vertical distribution where fish exploited the water column only during the night flooding, likely due to a combination of a general negative phototaxis of the fish and poor prey availability.

The most conspicuous feature was the first rise immigration peak at flood start each tidal cycle when the strongest environmental cue caused a clear response in the movements of the entire mangrove fish population. The first rise immigration is a strong and regular directional vector that, together with the net upstream longitudinal current, is likely sufficient for the fish to achieve retention in the Furo do Meio from one tidal cycle to the next, emphasizing the importance of the channel in providing a significant nursery function. It seems promising to study migratory patterns of fish in areas with different tidal signatures to better understand universal patterns and particular adaptations exhibited by fish assemblages in their shallow-water environment.

Non-intrusive shallow-water sonar has provided valuable temporal and spatial evidence of the natural movement and behavioral patterns of tidally migrating fish, predominantly epibenthic, in a highly turbid mangrove environment. In contrast, fishing techniques to

quantitatively and qualitatively catch tidally migrating fish on high temporal resolution such as tidal traps still have to be improved (Rozas and Minello, 1997; Horn et al., 1999). As the sonar technique does not show variations between species, the detailed evidence of changes in fish abundance and composition in time and space simultaneously provided by fishing is essential, in particular for tropical multispecies populations.

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REFERENCES

- Arrhenius, F., Benneheij, B.J.A.M., Rudstam, L.G., Boisclair, D., 2000. Can stationary bottom split-beam hydroacoustics be used to measure fish swimming speed in situ? *Fish. Res.* 45, 31-41.
- Barletta, M., Barletta-Bergan, A., Saint-Paul, U., 1998. Description of the fisheries structure in the mangrove-dominated region of Bragança (state of Pará, North Brazil). *Ecotropica* 4, 41-53.
- Barletta, M., Barletta-Bergan, A., Saint-Paul, U., Hubold, G., 2003. Seasonal changes in density, biomass, and diversity of estuarine fishes in tidal mangrove creeks of the lower Caeté Estuary (northern Brazilian coast, east Amazon). *Mar. Ecol. Prog. Ser.* 256, 217-228.
- Barletta-Bergan, A., Barletta, M., Saint-Paul, U., 2002. Structure and Seasonal Dynamics of Larval Fish in the Caeté River Estuary in North Brazil. *Estuar. Coast. Shelf Sci.* 54, 193-206.

- Batista, V.D.S., Rêgo, F.N., 1996. Análise de associações de peixes, em igarapés do estuário do Rio Tibiri, Maranhão. *Rev. Brasil. Biol.* 56(1), 163-176, in Portuguese.
- Blaber, S.J.M., 1980 Fish of the Trinity Inlet system of North Queensland with notes on the ecology of fish faunas of tropical Indo-Pacific estuaries. *Austr. J. Mar. Freshwat. Res.* 31, 137-145.
- Blaber, S.J.M., 1997. *Fish and Fisheries in Tropical Estuaries*. Chapman and Hall, Fish and Fisheries Series 22, London.
- Blaxter, J.H.S., Batty, R.S., 1990. Swim bladder "behaviour" and target strength. *Int. Symp. on Fisheries Acoustics, Seattle, WA (USA), 22-26 Jun 1987, Developments in fisheries acoustics, Rapp. P.-V. Reun. Ciém., vol. 189, pp. 233-244.*
- Boehlert, G.W., Mundy, B.C., 1988. Roles of behavioural and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *Am. Fish. Soc. Symp.* 3, 51-67.
- Bone, Q., Marshall, N.B., 1985. *Biologie der Fische*. Fischer, Stuttgart.
- Brenner, M., Krumme, U. (Submitted) Tidal migration and patterns in feeding of the four-eyed fish *Anableps anableps* L. in a North Brazilian mangrove. *Mar. Ecol. Prog. Ser.*
- Čech, M., Kubečka, J., 2002. Sinusoidal cycling swimming pattern of reservoir fishes. *J. Fish. Biol.* 61, 456-471.
- Colby, D.R., 1988. Null hypothesis, models, and statistical design in the study of larval transport. *Am. Fish. Soc. Symp.* 3, 149-162.
- Creutzberg F. (1961) On the orientation of migrating elvers (*Anguilla vulgaris* Turt.) in a tidal area. *Netherlands J. Sea Res.* 1, 257-338.
- Ehrenberg, J.E., Torkelson, T.C., 1996. Application of dual-beam and split-beam target tracking in fisheries acoustics. *ICES J. Mar. Sci.* 53, 329-334.
- Fleischman, S.J., Burwen, D.L., 2000. Correcting for positional-related bias in estimates of the acoustic backscattering cross-section. *Aquat. Living Res.* 13, 283-290.
- Forward, Jr., R.B., Reinsel, K.A., Peters, D.S., Tankerslev, R.A., Churchill, J.H., Crowder, L.B., Hettler, W.F., Warlen, S.M., Green, M.D., 1999. Transport of fish larvae through a tidal inlet. *Fish. Oceanogr.* 8 (Suppl. 2), 153-172.
- Furukawa, F., Wolanski, E., Mueller, H., 1997. Currents and sediment transport in mangrove forests. *Estuar. Coast. Shelf Sci.* 44, 301-310.
- Gee, J.H., 1983. Ecological implications of buoyancy control in fish. In: Webb, P.W., Weihs, D., (Eds.) *Fish Biomechanics*. Praeger Publishers, New York, p. 140.

- Gibson, R.N., 1973. The intertidal movements and distribution of young fish on a sandy beach with special reference to the plaice (*Pleuronectes platessa* L.). *J. Exp. Mar. Biol. Ecol.* 12,79-102.
- Gibson, R.N., 1982. Recent studies of the biology of intertidal fishes. *Oceanogr. Mar. Biol. Ann. Rev.* 20, 363-414.
- Gibson, R.N., 1988. Patterns of movement in intertidal fishes. In: Chelazzi, G., Vanini, M., (Eds.) Behavioural adaptations to intertidal life. NATO ASI Series Life Sciences Vol. 151, Plenum Press, London. pp. 55-63.
- Gibson, R.N., 1992. Tidally-synchronised behaviour in marine fishes, In: Ali, M.A., (Ed.) Rhythms in Fishes. NATO ASI Series Life Sciences Vol. 236, Plenum Press, New York. pp.63-81.
- Gibson, R.N., 1993. Intertidal teleosts: life in a fluctuating environment, In: Pitcher, T.J., (Ed.) Behaviour of teleost fishes. 2nd Ed., Fish and Fisheries Series 7, Chapman and Hall, London, pp. 513-536.
- Gibson, R.N., 1997. Behaviour and the distribution of flatfishes. *J. Sea Res.* 37, 241-256.
- Glaser, M., Grasso, M., 1999. Fisheries of a mangrove estuary: Dynamics and dependencies between economy and ecosystem in the Caeté Bay, Northeastern Pará, Brazil. *Boletim do Museu Paraense Emílio Goeldi, Ser. Zool.* 14, 95-125.
- Greccay, P.A., Targett, T.E., 1996. Effects of turbidity, light level and prey concentration on feeding of juvenile weakfish *Cynoscion regalis*. *Mar. Ecol. Prog. Ser.* 131, 11-16.
- Guillard, J., 1998. Daily migration cycles of fish populations in a tropical estuary (Sine-Saloum, Senegal) using a horizontal-directed split-beam transducer and multibeam sonar. *Fish. Res.* 35, 23-31.
- Hazen, E.L., Horne J.K., 2003. A method for evaluating the effects of biological factors on fish target strength. *ICES J. Mar. Sci.* 60, 555-562.
- Horn, M.H., Martin, K.L.M., Chotkowski, M.A., 1999. Intertidal Fishes: Life in Two Worlds. Academic Press, San Diego.
- Jager, Z., 1999. Selective tidal stream transport of flounder larvae (*Platichthys platessa* L.) in the Dollard (Ems estuary). *Estuar. Coast. Shelf. Sci.* 49, 347-362.
- Kieser, R., Mulligan T., Ehrenberg J., 2000. Observation and explanation of systematic split-beam angle measurement errors. *Aquat. Living Resour.* 13, 275-281.
- Knudsen, F.R., Sægvog, H. 2002. Benefits from horizontal beaming during acoustic survey: application to three Norwegian lakes. *Fish. Res.* 56, 205-211.

- Krumme, U., Liang, T.H., (In press). Tidal induced changes in a copepod-dominated zooplankton community in a macrotidal mangrove channel in northern Brazil. *Zool. Stud.*
- Krumme, U., Saint-Paul, U., 2003. Observations of fish migration in a macrotidal mangrove channel in Northern Brazil using a 200-kHz split-beam sonar. *Aquat. Living Resour.* 16(3), 175-184.
- Krumme, U., Saint-Paul, U., Rosenthal, H. (Submitted) Tidal and diel changes in the structure of a nekton assemblage in small intertidal creeks in Northern Brazil. *Aquat. Living Resour.*
- Kubečka, J., Wittingerova, M., 1998. Horizontal beaming as a crucial component of acoustic fish stock assessment in freshwater reservoirs. *Fish. Res.* 35, 99-106.
- Laegdsgaard, P., Johnson, C.R., 2001. Why do juvenile fish utilise mangrove habitats? *J. Exp. Mar. Biol. Ecol.* 257, 229-253.
- Leh, M.U.C., Sasekumar, A., 1991. Ingression of fish into mangroves creeks in Selangor, Malaysia. *Proceedings of the Regional Symposium on Living Resources in Coastal Areas, Manila, Philippines.* pp. 495-501. ISBN 9711050633.
- Love, R.H., 1971. Measurements of fish target strength: a review. *Fisheries Bulletin* 69, 703-715.
- MacLennan, D.N., Simmonds, E.J., 1992. *Fisheries Acoustics.* Chapman and Hall, London.
- McQuinn I.H., Winger P.D. (2003) Tilt angle and target strength: target tracking of Atlantic cod (*Gadus morhua*) during trawling. *ICES J. Mar. Sci.* 60, 575-583.
- Miller, J.M., Crowder, L.B., Moser, M.L., 1985. Migration and utilization of estuarine nurseries by juvenile fishes: an evolutionary perspective. *Contrib. Mar. Sci. Univ. Texas* 27, 338-352.
- Mukai, T., Iida, K., 1996. Depth dependence of target strength of live kokanee salmon in accordance with Boyle's law. *ICES J. Mar. Sci.* 53, 245-248.
- Ona, E., 1990. Physiological factors causing natural variations in acoustic target strength of fish. *J. Mar. Biol. Assoc. U.K.* 70(1), 107-127.
- Paterson, A.W., Whitfield, A.K., 2000. Do shallow-water habitats function as refugia for juvenile fishes? *Estuar. Coast. Shelf Sci.* 51, 359-364.
- Quinn, T.P., 1988. Estimated swimming speeds of migrating sockeye salmon. *Can. J. Zool.* 66, 2160-2163.
- Reis, R.R., Dean, J.M., 1981. Temporal Variation in the Utilization of an Intertidal Creek by the Bay Anchovy (*Anchoa mitchilli*). *Estuaries* 4(1), 16-23.

- Robertson, A.I., Duke, N.C., 1990. Mangrove fish-communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass and community structure. *Mar. Biol.* 104, 369-379.
- Rohlf, F.J., Sokal, R.R., 2003. *Statistical Tables*. Freeman, New York, 199 p., 3rd ed., ISBN 071672412.
- Rönnbäck, P., Troell, M., Kautsky, N., Primavera, J.H., 1999. Distribution patterns of shrimp and fish among *Avicennia* and *Rhizophora* microhabitats in the Pagbilao mangroves, Philippines. *Estuar. Coast. Shelf Sci.* 48, 223-234.
- Rozas, L.P., Minello, T.J., 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: A review of sampling design with focus on gear selection. *Estuaries* 20(1), 199-213.
- Ruiz, G.M., Hines, A.H., Posey, M.H., 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: An example from Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 99, 1-16.
- Sachs, L., 1992. *Angewandte Statistik: Anwendung statistischer Methoden*. 6. Auflage, Springer, Berlin.
- Sasekumar, A., Chong V.C., Leh, M.U., D'Cruz, R., 1992. Mangroves as a habitat for fish and prawns. *Hydrobiologia* 247, 195-207.
- Sasekumar, A., Ong, T.L., Thong, K.L., 1984. Predation of mangrove fauna by marine fishes. *Proc. As. Symp. Mangr. Env. – Res. and Manag.*, p. 378-384.
- Schultz, E.T., Cowen, R.K., Kamazima, M.W., Lwiza, M., Gospodarek, A.M., 2000. Explaining advection: do larval bay anchovy (*Anchoa mitchilli*) show selective tidal-stream transport? *ICES. J. Mar. Sci.* 57, 360-371.
- Sogard, S.M., Powel, G.V.N., Holmquist, J.G., 1989. Spatial distribution and trends in abundance of fishes residing in seagrass meadows on Florida Bay mudbanks. *Bull. Mar. Sci.* 44, 179-199.
- TeWinkel, L.M., Fleischer, G.W., 1998. Pressure as a limit to bloater (*Coregonus hoyi*) vertical migration. *Copeia* 4, 1060-1063.
- Thorne, R.E., Hedgepeth, J.B., Campos J., 1989. Hydroacoustic observation of fish abundance and behavior around an artificial reef in Costa Rica. *Bull. Mar. Sci.* 44(2), 1058-1064.
- Vance, D.J., Haywood, M.D.E., Heales, D.S., Kenyon, R.A., Loneragan, N.R., Pendrey, R.C., 1996. How far do prawns and fish move into mangroves? Distribution of juvenile banana

- prawns *Penaeus merguensis* and fish in a tropical mangrove forest in northern Australia. Mar. Ecol. Prog. Ser. 131, 115-124.
- Videler, J.J., 1993. Fish Swimming. Chapman and Hall, Fish and Fisheries Series 10, London.
- Wirjoatmodjo, S., Pitcher, T.J., 1984. Flounders follow the tides to feed: Evidence from ultrasonic tracking in an estuary. Estuar. Coast. Shelf Sci. 19, 231-241.
- Wolanski, E., Jones, M., Bunt, J. S., 1980. Hydrodynamics of a tidal creek-mangrove swamp system. Aust. J. Mar. Freshwat. Res. 31, 431-450.



Photos: F. Porto

Copepod *Pseudodiaptomus marshi*, male (left) and female (above).

**Tidal induced changes in a copepod-dominated zooplankton community
in a macrotidal mangrove channel in northern Brazil**

Krumme, Uwe¹ & Liang, Tsui Hua²

¹ Center for Tropical Marine Ecology (ZMT), Fahrenheitstr. 6, 28359 Bremen, Germany.

² Universidade Federal do Pará – Campus Universitario de Bragança, Alameda Leandro Ribeiro s/n, Bragança, Para, Brazil.

E-mail address: uwe.krumme@zmt.uni-bremen.de

Tel: 0049 421 23800-29, Fax: 0049 421 23800-30

ABSTRACT

The zooplankton community of the muddy upper reaches of the Furo do Meio, Caeté system, Pará, Brazil, was studied between March and May 2001 (wet season). Zooplankton samples were taken during two lunar cycles; at each lunar phase in four consecutive tidal cycles and at each tidal cycle four hauls (flood, high water [HW], ebb, low water [LW]). Short-term changes in species number, abundance and biomass were studied. Salinity (mean: 7 ± 3 psu) and water level were positively correlated. Copepods dominated the zooplankton community. The number of total zooplankton and copepod species was high at HW and low at LW, irrespective of time of day and tide. In contrast, abundance and biomass of both total zooplankton and copepods were high at LW and low at HW. Copepod species number and abundance of total zooplankton and copepods were greater at spring than at neap tide. The calanoid copepod *Pseudodiaptomus marshi* dominated the copepod community in terms of abundance and biomass. Highest abundance occurred at LW, suggesting retention in the cul-de-sac channel. The *P. marshi* population was composed of ovigerous females, adult males and copepodite stages 4 and 5. Copepod biomass ranged from 0.46 to 6.9 mgDWm⁻³, with an overall mean of 2.63 mgDWm⁻³. Non-parametric multi-dimensional scaling revealed that spring tide-neap tide together with HW-LW were important factors structuring the zooplankton community. Time of day had no effect on the community structure. We suggest a positive relationship between increased copepod abundances, high sediment loads and decreased salinities during the wet season. Synchronous temporal patterns between zooplankton and fish abundance are discussed.

Keywords: Tropical estuary, Tide, *Pseudodiaptomus marshi*, Fish predation, Amazonia.

INTRODUCTION

Mangrove forests are the predominant type of vegetation covering 60-75% of the tropical coastline (Clough 1998). The mangrove ecosystem provides an important nursery ground for fish and shellfish throughout the world (Robertson and Duke 1987, Little et al. 1988, Chong et al. 1990, Laegdsgaard and Johnson 1995, Louis et al. 1995, Barletta-Bergan et al. 2002). The complex spatial structure of the mangrove habitat that provides maximum food availability and minimises the risk of predation apparently is an important aspect for small juvenile fish (Laegdsgaard and Johnson 2001), thus optimising conditions for growth and survival of juvenile fish (Miller et al. 1985). Since mangroves support valuable fisheries in many parts of the world, considerable effort has been undertaken to elucidate life history patterns of fish and prawns in mangroves (Robertson and Blaber 1992, Sasekumar et al. 1992). However, the knowledge about the dynamics of the food preyed upon by juvenile mangrove fish is comparatively poor (Robertson et al. 1988).

Zooplankton, particularly copepods, are of paramount importance as prey for many juvenile mangrove fish due to their ubiquitous dominance, the wide range of relatively small sized organisms and their ready availability (Turner 1984). In mangrove ecosystems, zooplankton forms a fundamental trophic link in the aquatic food webs as well (Godhantaraman 2001). On tidal coasts, the zooplankton community has to cope with continual changes of water level, current strength and direction. Variations in zooplankton composition and abundance have been correlated to the spring/neap tide alteration and to the tidal cycle (Wang et al. 1995, Morgan et al. 1997, Villate 1997). These short/medium-term patterns of zooplankton abundance probably determine the availability of food for their predators and may thus have significant implications for the foraging strategies of juvenile fish preying upon zooplankton. Macrotides characterise the northern and southern coastline of the Amazon estuary. The coast is covered by the second largest mangrove area in the world (Spalding et al. 1997). However, few zooplankton studies have been conducted in this extensive mangrove ecosystem (Magalhães 1998, Peres 1999). Tidal creeks connect the mangrove with adjacent areas and build well-defined pathways for aquatic organisms, water and material exchange (Dittmar and Lara 2001). We studied the zooplankton community of a macrotidal mangrove channel in northern Brazil to determine the extent of temporal variability in terms of the number of species, abundance and biomass on three temporal scales: the spring/neap tide alternation, the tidal cycle (flood, high water [HW], ebb, low water [LW]), and the light/dark cycle.

MATERIALS AND METHODS

Sampling site. The sampling site is located in the upper reaches of the macrotidal cul-de-sac mangrove channel, the Furo do Meio, in the Caeté River estuary (Caeté Bay) (Fig. 1). At the sampling site, the width and depth of the Furo do Meio are 30 m and 4 m at LW, and 50 m and 8 m at HW, respectively. The area is located about 200 km east of Belém on the southeast margins of the Amazon estuary.

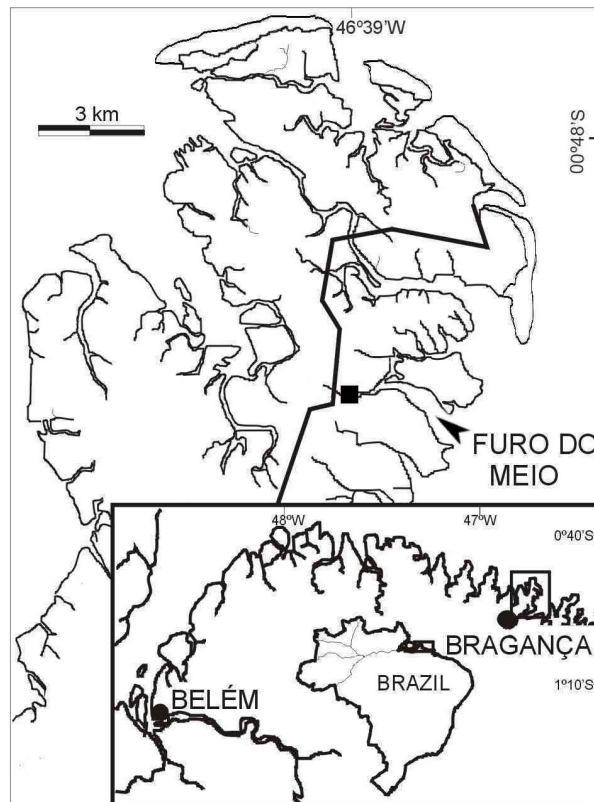


Figure 1. Location of the study site (square) in the upper reaches of the mangrove channel “Furo do Meio” near Bragança, northern Brazil.

The tidal regime is semidiurnal, with a range at neap and spring tides of 2.5 and 5 m, respectively. The tide is asymmetric, flood and ebb tide lasting 4 and 8 hours, respectively. In the last 4 hours, ebb tide is extremely weak with an almost negligible fall in the water level. However, due to higher velocities at flood than at ebb tide the Furo do Meio is clearly flood-dominated with a net upstream longitudinal current. The mean net upstream drift is about 0.5 km in a neap (Krumme, *subm.*) and about 1.5 km in a spring tide cycle. Salinities can fall below 5 psu and exceed 30 psu in the wet and in the dry season, respectively. Secchi depth is low (range: 5-100 cm). For a more detailed description of the study area, refer to Krause et al. (2001).

Field methods and data analysis. Mesozooplankton samples were taken in the Furo do Meio (Fig. 1) during two consecutive lunar cycles between March and May 2001, using a conical plankton net (mouth diameter: 0.32 m; mesh opening: 300 μm), provided with a flowmeter. Each lunar phase sampling started at LW and covered four consecutive tidal cycles. Spring tide hauls were taken at 3:00, 5:00, 7:00, 10:00 a.m. and p.m. (corresponding to LW, flood, HW, ebb). Neap tide hauls were taken at 1:00, 4:00, 8:00, 11:00 a.m. and p.m. (corresponding to HW, ebb, LW, flood). Thus, at each lunar phase 17 surface hauls were made against the tidal current. In one spring tide cycle 6 hauls could not be taken due to technical problems, yielding a total of 130 hauls. Net samples were immediately preserved in 5% buffered formalin seawater solution.

At each sampling time surface temperature and salinity were recorded using a conductivity-measuring instrument (WTW LF197) equipped with a sonde (WTW Tetracon 325). Water level was recorded at a tidal gauge.

Zooplankton was identified and counted; copepod species were sorted, counted and staged. Prosome lengths of copepodite stages were measured with an eyepiece micrometer. Groups of 20-100 individuals of comparable lengths were weighed on a microbalance ($\pm 0.1 \mu\text{g}$) after drying in an electric oven at 60 °C for 48 h and cooled in a dessicator. Each weighing was repeated 3-6 times until a constant weight was obtained. All measurements were made on material preserved for at least 3 months, but not exceeding one year. Biomass was estimated by the product of mean dry weight of each individual belonging to a certain size/maturity class and the abundance of the class.

We used 3-way analysis of variance (ANOVA) to test for the separate and interactive effects of tide (spring tide, neap tide), time of day, and tidal cycle (low water, flood, high water and ebb) on $\log(x+1)$ -transformed values of abundance and the number of copepod species. When the multifactor ANOVA detected significant effects, the Least Significant Differences (LSD) test ($\alpha=0.05$) was applied to determine which means differed from the others. If the transformed abundance values did not conform with the ANOVA assumptions, (as was the case of biomass values), we used the non-parametrical Kolmogorov-Smirnoff two-sample test (KS test) (Sokal and Rohlf 1995).

The relationships between salinity, water level and species numbers and abundances were tested using Spearman's rank correlation. Similarity of species composition between samples was determined by non-parametric multi-dimensional scaling (MDS) using the program package Primer 5 (Clarke and Warwick 1994). We used square root transformation to generate the Bray-Curtis similarity matrix. A stress value of the MDS representation of 0.1

indicated a fairly accurate and useful two-dimensional representation of the inter-haul similarities (Clarke and Warwick 1994).

RESULTS

Environmental parameters

During the sampling period, temperature varied from 27.5 to 28.3 °C. All salinities were below 10 psu (mean: 7 psu \pm 3 SD; range: 1 to 14 psu), except in the last sampling campaign in May. Salinity was positively correlated to water level (Fig. 2; Spearman rank correlation, spring tide, $R=0.679$, $p<0.001$; neap tide, $R=0.285$, $p<0.01$). Salinity changes during a tidal cycle ranged between 3.5 ± 2.0 psu (average \pm SD) and 1.8 ± 1.1 psu at neap and spring tide, respectively. Especially at neap tide-LW, measurement variability of salinity was high. Lowest salinities occurred during the first sample campaign (neap tide, March, 16-18).

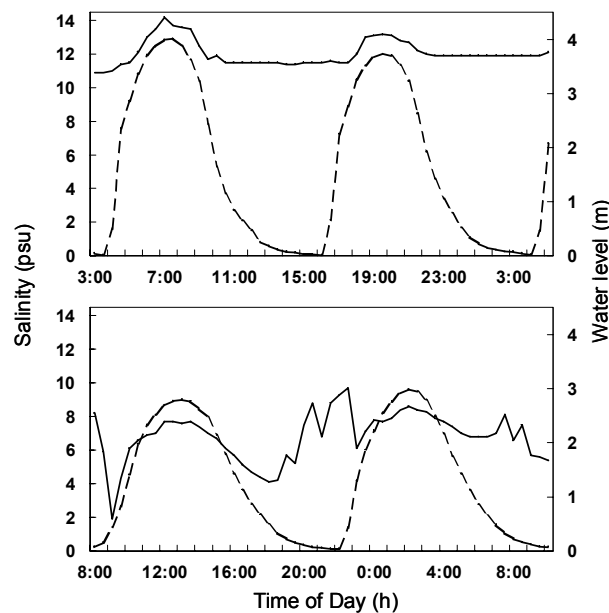


Figure 2. 26 h series of salinity (solid line) and water level (dashed line) at spring tide (upper, May 7-8) and neap tide (lower, April 30 to May 1) at the Furo do Meio in the wet season 2001.

Zooplankton composition

Copepods, appendicularia, chaetognaths, ostracods, hydromedusa as well as zoea of Brachyura, fish larvae and larvae of polychaetes composed the zooplankton community of the Furo do Meio during the wet season 2001 (Table 1).

Table 1. Mean, maximum (ind. m⁻³) and relative abundance and percent presence of the zooplankton taxa found in the mangrove channel Furo do Meio in the wet season 2001. +: present, but <0.1% of the total abundance.

TAXON	Abundance (ind. m ⁻³)			Presence				
	Mean	Max.	%	%				
CRUSTACEA	Copepoda	<i>Pseudodiaptomus marshi</i>	198.04	3621.50	56.9	92.31		
		<i>Pseudodiaptomus richardi</i>	236.03	1983.70	22.8	32.31		
		<i>Acartia tonsa</i>	40.93	1397.50	11.6	86.15		
		<i>Acartia lilljeborgi</i>	15.22	283.00	3.3	71.54		
		<i>Eucalanus pileatus</i>	0.05	0.05	+	0.77		
		<i>Paracalanus aculeatus</i>	1.17	2.97	+	4.62		
		<i>Centropages furcatus</i>	0.24	0.24	+	0.77		
		<i>Temora turbinata</i>	7.65	7.65	+	0.77		
		<i>Oithona hebes</i>	0.04	0.10	+	1.54		
		<i>Hemicyclops</i> sp.	0.21	0.47	+	6.15		
		<i>Caligus</i> sp.	0.01	0.01	+	0.77		
		Harpacticoida	1.67	3.32	+	2.31		
		Decapoda	Brachyura, Ocypodidae	Zoea	8.25	276.87	1.4	55.38
			Brachyura, Ocypodidae	Megalopa	1.97	17.69	0.1	23.08
			Penaeidae		0.49	3.82	+	16.15
			Mysidacea		0.48	1.72	+	3.08
			Ostracoda		5.97	76.53	1.1	63.85
			Cirripectida	Nauplii	2.83	35.37	0.3	35.38
			Isopoda		0.31	0.95	+	5.38
Amphipoda			0.04	0.06	+	2.31		
Unidentified			0.02	0.02	+	0.77		
POLYCHAET			1.12	5.31	+	12.31		
MOLLUSC	Bivalve	Larvae	5.15	88.45	0.4	25.38		
	Gastropoda	Larvae	4.49	23.88	0.3	20.00		
CHAETOGNAT		<i>Sagitta friderici</i>	2.11	17.69	0.1	23.07		
CNIDARI	Hydromedusae	<i>Clytia</i> sp.	2.44	25.27	0.3	36.15		
UROCHORDAT	Appendicularia	<i>Oikopleura dioica</i>	0.65	4.54	+	18.46		
CHORDAT	Pisces	Eggs and larvae	27.17	566.06	1.3	16.15		
PROTOZO	Foraminifera		0.08	0.17	+	1.54		
INSECT			0.01	0.01	+	0.77		

Copepods dominated the zooplankton community contributing on average 85% to the total abundance. Twelve species of copepods occurred: *Pseudodiaptomus marshi*, *P. richardi*, *Acartia tonsa*, *A. lilljeborgi*, *Eucalanus pileatus*, *Paracalanus aculeatus*, *Centropages furcatus*, *Temora turbinata*, *Oithona hebes*, *Tisbe* sp. and unidentified Harpacticoida.

Tidal and diel variations

The total number of zooplankton species at HW was always greater than at all other tidal phases, with lowest numbers at LW (KS-test, $p < 0.001$). The positive correlation between species number and water level recurred each tidal cycle irrespective of the time of day, and the spring-neap tide alternation (KS-test, $p > 0.1$; Fig. 3, Table 2).

Table 2. Kolmogorov-Smirnov two-sample test results: differences in the distributions of spring and neap tide (S and N), night and day (N and D) and all combinations of the tidal stages high water (HW), low water (LW), ebb tide (ebb) and flood tide (flood) in terms of abundance (ind. m⁻³) and the number of species (two bottom rows). C5, C4 and C3/C2/C1 are copepodite stages of *P. marshi*. Significant levels: (*) 0.01<*p*<0.05; (**) 0.001<*p*<0.01; (***) *p*<0.001.

Variable	Treatment						
	Tide	Time of day	Tidal cycle				ebb vs flood
			HW vs LW	HW vs ebb	HW vs flood	LW vs ebb	
Zooplankton	**S		**LW	*ebb	**flood	**LW	*LW
Copepoda	**S		**LW	*ebb	**flood	*LW	*LW
Total <i>P. marshi</i>	*S	*N	**LW	**ebb	**flood	*LW	**LW
Females		*N	**LW	**ebb	**flood	*LW	*LW
Males	*S		**LW	**ebb	**flood		*LW
C5	*S		**LW	**ebb	**flood	**LW	**LW
C4	*S		**LW	**ebb	**flood	**LW	**LW
C3/C2/C1	*S		**LW	**ebb	**flood	**LW	**LW
<i>P. richardi</i>			*LW				
<i>A. tonsa</i>	**S		*LW	**ebb		*ebb	*flood *ebb
<i>A. liljeborgi</i>	**S		**LW	*ebb		**ebb	**flood
Zooplankton			**HW	**HW	**HW	**ebb	**flood
Copepoda	*S		*HW				

Table 3. Mean squares and significance levels for three-way ANOVAs of log(x+1)-abundance of five zooplankton community variables of surface hauls in the macrotidal mangrove channel Furo do Meio during the wet season 2001. S: Spring tide; N: Neap tide. LW: Low water; E: Ebb tide; F: Flood tide; HW: High water. SD: Spring tide-Day; SN: Spring tide-Night; NN: Neap tide-Night; ND: Neap tide-Day. Three-way interactions are not considered due to high complexity. The interactions are listed from highest mean (left) to lowest mean (right) in the *post hoc* LSD test. Significant levels: (*) 0.01<*p*<0.05; (**) 0.001<*p*<0.01; (***) *p*<0.001. d.f.=degrees of freedom. # Cop. spec.: Number of copepod species.

Variables	Main Effects		3-way interaction			LSD				
	Tide (1)	Time of day (2)	Tidal cycle (3)	(1)×(2)	(1)×(2)×(3)	Residual	-1	-3	(1)×(2)	(1)×(2)×(3)
	(1 d.f.)	(1 d.f.)	(3 d.f.)	(1 d.f.)	(3 d.f.)	(d.f. 114)				
Zooplankton	8.54***		4.91***	2.56*	1.60*	0.41	S N	LW E F HW	SD SN NN ND	...
Copepoda	9.11***		5.51***	2.20*	1.99**	0.45	S N	LW E F HW	SD SN NN ND	...
<i>P. richardi</i>	4.10*		2.98*			0.81	S N	LW E F HW		
<i>A. tonsa</i>	9.07***					0.41	S N			
# Cop. spec.	0.08**		0.03*			0.01	S N	HW E F LW		

At spring tides, the copepods provided most of the zooplankton species collected, except for daytime-HW and ebb when other taxa were abundant in the plankton samples. At neap tides, on average only three copepod species were present throughout the tidal cycle (Fig. 3). The number of copepod species was significantly lower at LW than that at HW (3-way ANOVA, *p*<0.01).

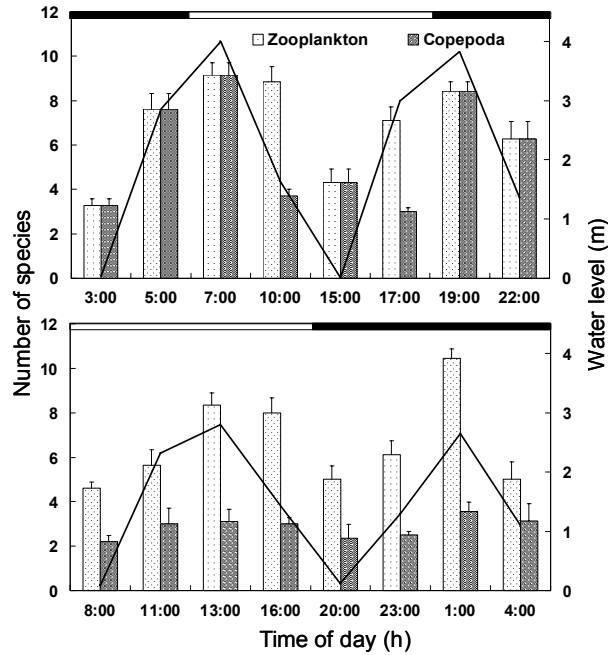


Figure 3. Mean number of zooplankton and copepod species (\pm SE) at low water, flood, high water, ebb tide etc. during 25 hs at spring tide (upper) and neap tide (lower), wet season 2001, Furo do Meio (n=130). The line indicates the tidal water level. Horizontal bars on top indicate night (6:00 – 18:00).

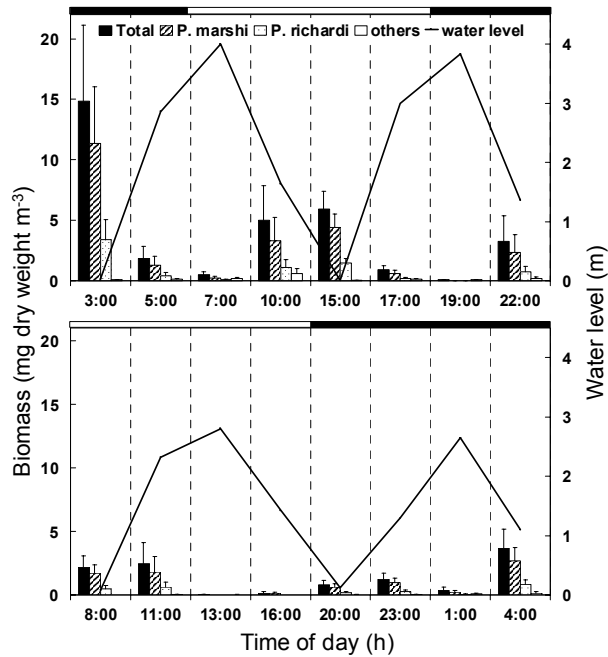


Figure 4. Mean biomass of total zooplankton, *P. marshi*, *P. richardi* and the remaining other species (\pm SE) at low water, flood, high water, ebb tide etc. for spring tide (upper) and neap tide (lower), wet season 2001, Furo do Meio (n=130). Horizontal bars on top indicate night (6:00 – 18:00).

Abundance of zooplankton and copepods was highly variable, ranging from 0.5 to 5434 ind. m⁻³ (mean: 335 \pm 55 SE) and 0.2 to 5434 ind. m⁻³ (mean: 317 \pm 5 SE), respectively.

Zooplankton and copepod abundances were greater at LW than at all other tidal phases (Table 2). The correlation of tide and tidal cycle on mean copepod biomass is shown in Fig. 4. Zooplankton and copepods occurred at significantly greater abundances at spring than at neap tide (3-way ANOVA, $p < 0.001$; Fig. 4). Furthermore, abundances of zooplankton and copepods significantly correlated with the tidal cycle (3-way ANOVA, $p < 0.001$), whereas the time of day was not significantly correlated with abundances (3-way ANOVA, $p > 0.05$; Fig. 4). Finally, the interaction of tide versus time of day had a significant correlation, since neap tide-day abundances were clearly lower than at the three other factor combinations (3-way ANOVA, $p < 0.05$).

The calanoid copepod *P. marshi* dominated the zooplankton community throughout the wet season. The highest abundance of *P. marshi* was recorded on 25 March at new moon-night-LW (3622 ind. m⁻³). On average, *P. marshi* accounted for approximately 50% of the total copepod abundance. The total abundances of *P. marshi* were significantly higher at spring than at neap tide and higher at night than at day (KS-test, $p < 0.05$). The tidal cycle variation in abundance was reflective of the patterns revealed for total copepoda (Table 2).

The *P. marshi* population was mainly composed of ovigerous females and adult males (Fig. 5). Adult females were present during the entire study period. Unlike the total abundance of *P. marshi*, the abundance of female *P. marshi* was not correlated with the tide (KS-test, $p > 0.1$), whereas time of day (KS-test, $p < 0.05$) and tidal cycle had a significant correlation with abundances (KS-test, $p < 0.05$). In contrast to female *P. marshi*, abundances of male *P. marshi* and C5, C4 and C3-C1 copepodite stages were correlated with the tide and the tidal cycle, and lacked correlation with time of day (Table 2).

At spring tide, the proportions between adults and copepodite stages of *P. marshi* were fairly homogenous throughout the tidal cycle. At neap tide, copepodite stages C1–C5 occurred with increased proportions at flood tides, whereas females were more numerous at LW (Fig. 5).

Abundances of *P. richardi* were greater at spring than at neap tide (3-way ANOVA, $p < 0.05$). Within a tidal cycle, lowest abundance of *P. richardi* occurred at HW compared to all other tidal phases (3-way ANOVA, $p < 0.05$).

Abundances of *A. tonsa* and *A. lilljeborgi* were greater at spring tides (Tables 2, 3). In contrast to all other species, ebb tide abundances of *A. tonsa* were greater than those at flood tide (KS-test, $p < 0.05$); and ebb and flood tide abundances of *A. tonsa* and *A. lilljeborgi* were greater than those at LW (KS-test, $p < 0.05$ and $p < 0.001$, respectively).

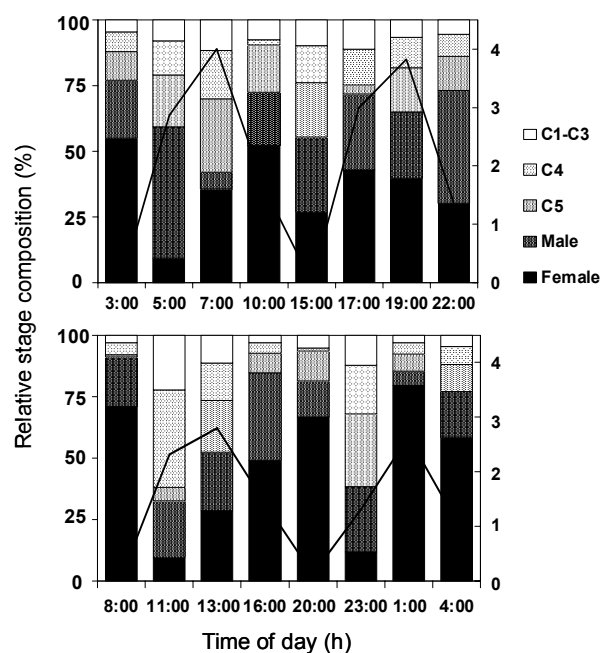


Figure 5. Proportions of mean abundance (ind. m^{-3}) of adult females, males, copepodites C5, C4 and C1–C3 of the copepod *Pseudodiaptomus marshi* during a complete tidal cycle at spring tide (upper) and neap tide (lower), Furo do Meio, wet season 2001 (n=130). The time axis corresponds to the tidal phases (from left to right) low water, flood, high water, ebb tide etc. in both graphs. Night was between 18:00 and 6:00.

Salinity was negatively correlated to zooplankton and copepod abundance ($p < 0.05$), and the abundances of *P. marshi* females ($p < 0.05$) and males ($p < 0.01$) (Table 4).

Table 4. Spearman rank correlation analysis between salinity (psu) and several zooplankton community variables, Furo do Meio, wet season 2001; R=Spearman's coefficient, n=129 for all variables; significant levels: (*) $0.01 < p < 0.05$; (**) $0.001 < p < 0.01$.

Factor	Variable	R	p
Salinity	Zooplankton abundance	-0.182	*
	Copepod abundance	-0.197	*
	Number of zooplankton species	0.089	
	Number of copepod species	-0.018	
	Abundance of total <i>P. marshi</i>	-0.217	*
	Abundance of <i>P. marshi</i> females	-0.226	*
	Abundance of <i>P. marshi</i> males	-0.230	**
	Abundance of <i>P. marshi</i> C5	-0.124	
	Abundance of <i>P. marshi</i> C4	-0.108	
	Abundance of <i>P. marshi</i> C1-C3	-0.090	
	Abundance of <i>P. richardi</i>	-0.114	
	Abundance of <i>A. tonsa</i>	-0.019	
	Abundance of <i>A. lilljeborgi</i>	0.022	

Copepod biomass varied from 0.46 to 6.91 mgDWm⁻³ with a mean of 2.63 mgDWm⁻³. *Pseudodiaptomus marshi* accounted for 66% of the mesozooplanktonic copepod biomass (range: 0.46-6.82 mgDWm⁻³). *Pseudodiaptomus richardi*, *A. tonsa* and *A. lilljeborgi* on average comprised 22, 19 and 9% of the biomass in the channel, respectively.

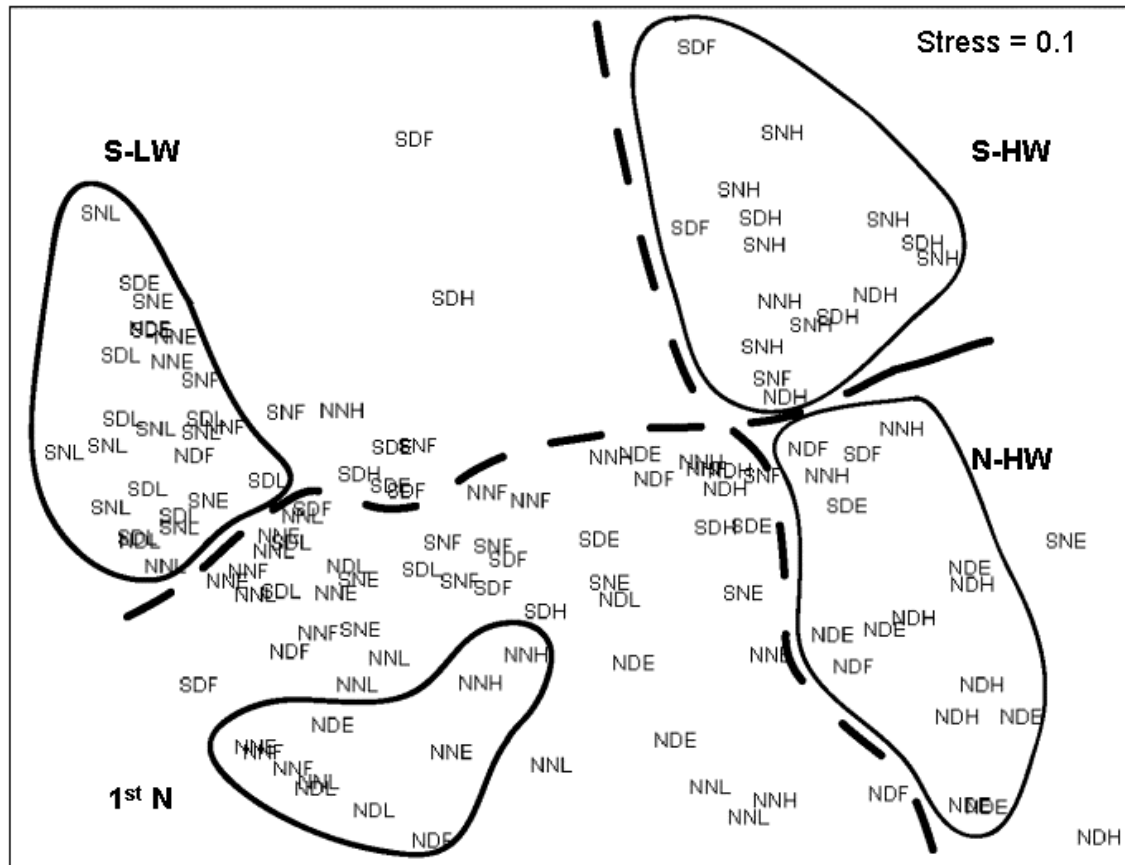


Figure 6. Multidimensional scaling plot of the copepod community (biomass, mg DW m⁻³) in the Furo do Meio, wet season 2001 (n=129 hauls). Three-letter abbreviations: 1st letter N: Neap tide, S: Spring tide; 2nd letter: D: Daytime, N: Night; 3rd letter: L: Low water, F: Flood, H: High water, E: Ebb tide. Broken horizontal axis divides between copepod hauls at spring (upper) and neap tide (lower). Broken vertical axis separates HW hauls (on the right) from the rest. Frames show distinct groups at spring tide-LW, spring tide-HW, first neap tide sample campaign (March 16-18; lowest salinities) and neap tide-HW.

Temporal variations in copepod assemblage structure

Multi-dimensional scaling (Fig. 6) revealed that spring tide/neap tide together with HW/LW were important factors determining the changes in the structure of the copepod community (biomass of copepod species for n=129; exclusion of one outlier, a nearly empty haul). Combining the ordination and clustering analysis revealed four distinct groups of copepod assemblages (frames in Fig. 6). The S-LW group (upper left) contained hauls taken at spring tide-LW; the S-HW group (upper right) contains hauls at spring tide-HW. The 1st N group

(lower left) comprised mainly hauls from the first neap tide sampling (March 16-18); the N-HW group (lower left) contains hauls at neap tide-HW. The broken horizontal axis separates the copepod assemblages at spring tide (above) from neap tide (below). The broken vertical axis divides HW assemblages (on the right) from the rest. Diel variations were not significantly associated with changes in the community structure. Separation between the two spring tide groups was more marked than between the two neap tide groups. At spring tide, the hauls at HW (high number of species, low biomass) were markedly different from those at LW (low number of species, high biomass) (Figs. 3, 4). At neap tide, few copepod species and generally low biomass caused neap tide hauls to be rather uniform. Only the neap tide-HW hauls distinctly grouped together and no clear neap tide-LW group was formed (Fig. 6). However, similar hauls taken during the first neap tide sampling when tidal range was small (2.2 m) and salinity extremely low (5 ± 2 psu) grouped together irrespective of the tidal stage (1st N).

DISCUSSION

Zooplankton composition

The use of a coarse mesh size undoubtedly influenced the composition of zooplankton and copepod species and stages caught. The small copepodite stages C1-C3 of *P. marshi* probably occurred in the samples only because high sediment loads partially plugged the net and, hence, hold back even these small stages. Moreover, the very small species of the families Oncaeidae and Oithonidae could also have been undersampled. Lopes (1994) collecting zooplankton in the Guaraú estuary with a bottle and filtering with a 75 μm mesh net showed that copepodites and nauplii of *P. richardi* were almost the only species in the inner estuary, whereas in the middle estuary this species co-existed with *A. lilljeborgi* and *O. hebes*. Thus, we believe that the composition patterns found in the Furo do Meio with a 300 μm mesh are representative of the mesozooplankton community except for the younger copepodite stages C1-C3 of *P. marshi*.

In the wet season, the mesozooplankton community of the macrotidal mangrove channel Furo do Meio was characterised by low numbers of species and by the dominance of copepods, particularly *P. marshi*. Björnberg (1981) characterised *P. marshi* as a typical species of the estuaries and mangrove systems off the northern and north-eastern coast of Brazil, with high abundances at low tide. Seasonal changes in the zooplankton composition in the Furo do Meio are not apparently severe since the wet season community generally resembled the one found during a dry season study (Peres 1999).

The zooplankton composition of the semi-enclosed Furo do Meio differed from the communities found in e.g. the open mangrove channel Furo Grande (located further to the coast) and in samples taken at the lower reaches of the Caeté estuary system (Liang, unpublished data). The dominant species in the Caeté estuary are *A. tonsa* and *A. lilljeborgi* (Liang, unpublished data). In the Furo do Meio, these two species exhibited typical features of estuarine copepod species that are imported at strong rising tides and exported with the receding tide in that only *A. tonsa* and *A. lilljeborgi* were caught with higher abundances at flood and ebb tide than at LW.

Our wet season-copepod abundances were higher than those found by Peres (1999) during the dry season ($0.2 - 1\,382$ ind. m^{-3} , mean: 91 ind. m^{-3}), suggesting seasonal fluctuations in abundance related to rainfall and, hence, to alternations in salinity. A marked seasonality with higher wet season zooplankton densities is apparently a general pattern of tropical mangrove estuaries (Robertson et al. 1988).

Tidal variations in abundance and biomass

On the medium-time scale temporal variations within the zooplankton community were related to the spring/neap tide pulse that is the key factor determining the fortnightly differences in the zooplankton composition. At spring tides, current velocities in the Caeté estuary system can exceed 1.5 m s^{-1} . At neap tides, estuarine copepod species apparently were not carried into the channel, most likely because of the weak neap tide current speeds that may not suffice to suspend and then transport them to the upper reaches of the mangrove channel (at least 4 km from the estuary). The copepod assemblages at neap tide exhibited a rather uniform structure. We assume that the similarity of the copepod community during the first sample campaign was related to the combined effects of a fairly weak neap tide cycle, very low salinities throughout the tidal cycle and extraordinary high sediment loads.

On the short-time scale the tidal cycle additionally determined changes in the zooplankton composition. It remains, however, unclear if water level or salinity determines the short-term changes in the zooplankton community, and whether high abundance of *P. marshi* is rather related to low salinities or to the tidal situation at LW *per se*. Peres (1999) surprisingly found no significant tidal-related correlation during the dry season, when inversely to the wet season, salinity is lower at HW and higher at LW (Lara and Dittmar 1999).

Abundance and biomass were greatest at LW when the number of species was lowest and conversely, lowest at HW (“highest dilution”) when the number of species was greatest. This is in contrast to Robertson et al. (1988) and Wang et al. (1995) who found higher densities

and total abundances at high tide than at low tide, respectively. Unlike open estuarine environments, the semi-enclosed Furo do Meio with a net upstream drift due to higher flood tide velocities apparently promotes the retention of copepods from one tide to the next. Since the retention is species-specific (dominance of *P. marshi* at LW), a simple mechanism similar to tidal pumping (Pethick 1984) must, however, be ruled out.

Our data lack direct evidence for a pattern of tidal-related vertical migration since the sampling dealt with surface hauls only. Selective tidal stream transport in layers of different salinities is unlikely to occur in a well-mixed shallow estuary exposed to macrotides. It is rather likely that *P. marshi* may take advantage of its weight, the net upstream longitudinal current and hydrodynamic processes that trap fine particulate matter (Castel and Veiga 1990) in the upper reaches of the mangrove channels to ensure population maintenance in the Furo do Meio. Adult and late copepodite stages of *P. richardi* (Lopes 1994) and *P. hessei* (Wooldridge and Erasmus 1980, Kouassi et al. 2001) were found in higher abundances near the bottom at ebb tide, showing that selective avoidance of stronger surface currents during the receding tide also occurs in other Pseudodiaptomidae.

We hypothesise a retention mechanism for copepods resident in the Furo do Meio where they are imported into the intertidal area during flood tide; at HW they may tend to sink to ground-level preventing horizontal export out of the intertidal creeks within the upper strata during the strong ebb tide current, and return later to the main channel during the weak receding tide to resurface at LW. Whether such a mechanism of accumulation operates for copepods in mangrove channels awaits further work on the vertical migratory behavior of individual copepod species.

Retention in lateral, high-turbidity appendices of the estuary during LW may be advantageous when considering the detritivorous feeding habits of estuarine copepods, especially of the family Pseudodiaptomidae. In the wet season, the lowest water clarity was found in the upper reaches of the Furo do Meio. High turbidity is not only linked to reduced visual range of predators (Grecoy and Targett 1996), but also to high concentrations of detritus and associated microbes that provide an important source of energy for copepods, as suggested for *P. inopinus* that apparently maintain the population over time in the estuarine turbidity maximum of the Columbia River (Morgan et al. 1997).

Synchronous pattern between zooplankton and fish

At the moment, we cannot assess the predatory impact of fish on the zooplankton community due to the lack of studies that simultaneously address temporal changes in zooplankton and

fish larvae abundances and the larval predation. It is, however, striking that the short- to medium-term changes in abundance of zooplankton (spring > neap; LW > HW) mirror those of tidal migrating fish, including copepod feeding species and age groups (Krumme and Saint-Paul 2003; Krumme et al., *subm.*), suggesting that the tidal pulse synchronizes their temporal patterns and most likely tightly couples their interplay. The stomachs of several fish species so far studied in the Caeté system, especially in the Furo do Meio, contained copepods. Specimens of the 7-9 cm standard length size class of the predatory anchovy *Pterengraulis atherinoides* were specialized on copepods, particularly *P. marshi*, that contributed 40% to the dry weight and 85% to the abundances of the stomach contents (Keuthen 1998). Further, adult *Anchovia chupeoides* (Brenner 2002), *Cathorops* sp. (<12 cm) (Leal-Flórez 2001), *C. spixii* (Espírito-Santo and Isaac 1999), *Stellifer naso* (4 cm), and *S. rastrifer* (1-3 cm) (Camargo-Zorro 1999) have been recorded as copepod feeders. All these species, except *C. spixii*, occur at all ages in the Furo do Meio throughout the year (Barletta et al. 2003; Krumme et al., *subm.*).

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REFERENCES

- Barletta M, A Barletta-Bergan, U Saint-Paul, G Hubold. 2003. Seasonal changes in density, biomass, and diversity of estuarine fishes in tidal mangrove creeks of the lower Caeté Estuary (northern Brazilian coast, east Amazon). *Mar. Ecol. Prog. Ser.* **256**: 217-228.
- Barletta-Bergan A, M Barletta, U Saint-Paul. 2002. Structure and seasonal dynamics of larval fish in the Caeté river estuary in North Brazil. *Estuar. Coast. Shelf Sci.* **54(2)**: 193-206.
- Björnberg TKS. 1981. Copepoda. In: D Boltovskoy, ed. *Atlas del zooplancton del Atlantico Suboccidental*. Mar del Plata, INIDEP, pp. 587-679.

- Brenner M. 2002. Feeding ecology of *Arius herzbergii* (Pisces: Ariidae), *Anableps anableps* (Pisces: Anablepidae) and *Anchovia clupeioides* (Pisces: Engraulidae) in the tidal mangrove channels of the Caeté estuary, Pará, Brazil. Diploma thesis University Bremen/Center for Tropical Marine Ecology, Bremen, Germany, 101 p., in German.
- Camargo-Zorro M. 1999. Biologia e estrutura populacional das espécies da família Sciaenidae (Pisces: Perciformes), no estuário do Rio Caeté Município de Bragança-Brasil. M.Sc. Thesis. Mus. Paraense Emílio Goeldi, UFPA, Belém.
- Castel J, J Veiga. 1990. Distribution and retention of the copepod *Eurytemora affinis hirundoides* in a turbid estuary. Mar. Biol. **107**: 119-128.
- Chong VC, A Sasekumar, MUC Leh, RD Cruz. 1990. The fish and prawn communities of a Malaysian coastal mangrove system, with comparison to adjacent mudflats and inshore water. Estuar. Coast. Shelf Sci. **31**: 703-722.
- Clarke KR, RM Warwick. 1994. Changes in marine communities: An approach to statistical analysis and interpretation. Plymouth Marine Laboratory. Natural Environment Research Council, U.K., 144 p., ISBN 1855311402.
- Clough B. 1998. Mangrove forest productivity and biomass accumulation in Hinchinbrook Channel, Australia. Mangroves and Salt Marshes **2**: 191-198.
- Dittmar T, RJ Lara. 2001. Driving forces behind nutrient and organic matter dynamics in a mangrove tidal creek in North Brazil. Estuar. Coast. Shelf Sci. **52(2)**: 249-259.
- Espirito-Santo RV, VJ Isaac. 1999. Alimentação e aspectos da reprodução da *Uricica Cathorops spixii* (AGASSIZ, 1829) (Osteichthyes, Siluriformes, Ariidae), no estuário do rio Caeté (Município de Bragança – PA). Bol. Mus. Para. Emilio Goeldi, sér. Zool. **15**: 95-111.
- Godhantaraman N. 2001. Seasonal variations in taxonomic composition, abundance and food web relationship of microzooplankton in estuarine and mangrove waters, Parangipettai region, southeast coast of India. Indian J. Mar. Sci. **30**: 151-160.
- Greay PA, TE Targett. 1996. Effects of turbidity, light level and prey concentration on feeding of juvenile weakfish *Cynoscion regalis*. Mar. Ecol. Prog. Ser. **131**: 11-16.
- Kouassi E, M Pagano, L Saint-Jean, R Arfi, M Bouvy. 2001. Vertical migrations and feeding rhythms of *Acartia clausi* and *Pseudodiaptomus hessei* (Copepoda: Calanoida) in a tropical lagoon (Ebrié, Côte d'Ivoire). Estuar. Coast. Shelf Sci. **52**: 715-728.
- Krause G., D Schories, M Glaser, K Diele. 2001. Spatial patterns of mangrove ecosystems: the bragantinian mangroves of northern Brazil (Bragança, Pará). Ecotropica **7**: 93-107.

- Krumme U. (Submitted). Patterns in the tidal migration of fish in a North Brazilian mangrove channel as revealed by vertical beaming using a 200 kHz split-beam sonar. *Fish. Res.*
- Krumme U, U Saint-Paul. 2003. Observation of fish migration in a macrotidal mangrove channel in Northern Brazil using 200kHz split-beam sonar. *Aquat. Living Resour.* **16(3)**: 175-184.
- Krumme U, U Saint-Paul, H Rosenthal. (Submitted) Tidal and diel changes in the structure of a nekton assemblage in small intertidal creeks in Northern Brazil. *Aquat. Living Resour.*
- Laegdsgaard P, CR Johnson. 1995. Mangrove habitats as nurseries: unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. *Mar. Ecol. Prog. Ser.* **126**: 67-81.
- Laegdsgaard P, CR Johnson. 2001. Why do juvenile fish utilise mangrove habitats? *J. Exp. Mar. Biol. Ecol.* **257**: 229-253
- Lara RJ, T Dittmar. 1999. Nutrient dynamics in a mangrove creek (North Brazil) during the dry season. *Mangroves and Salt Marshes* **3**: 185-195.
- Leal-Flórez J. 2001. Feeding ecology of *Uricica branca*, *Cathorops agassizii* (Pisces: Ariidae), in an intertidal channel of the Caeté estuary, northern Brazil. MSc thesis University Bremen/Center for Tropical Marine Ecology, Bremen, Germany, 64 p.
- Little MC, PJ Reay, SJ Grove. 1988. The fish community of an East African mangrove creek. *J. Fish. Biol.* **32**: 729-747.
- Lopes RM. 1994. Zooplankton distribution in the Guaraú River estuary (South-eastern Brazil). *Estuar. Coast. Shelf Sci.* **39**: 287-302.
- Louis M, C Bouchon, Y Bouchon-Navaro. 1995. Spatial and temporal variations of mangrove fish assemblages in Martinique (French West Indies). *In* YS Wong, FY Tam, eds. Asia-Pacific Symposium on Mangrove Management. pp. 275-284.
- Magalhães ALP. 1998. Aspectos ecológicos do macrozooplâncton no estuário do rio Caeté, Bragança (Pará, Brasil). Trabalho de conclusão de curso, Universidade Federal do Pará. 42 p.
- Miller JM, LB Crowder, ML Moser. 1985. Migration and utilization of estuarine nurseries by juvenile fishes: an evolutionary perspective. *Contrib. Mar. Sci. Univ. Texas* **27**: 338-352.
- Morgan CA, JR Cordell, CA Simenstad. 1997. Sink or swim? Copepod population maintenance in the Columbia River estuarine turbidity-maxima region. *Mar. Biol.* **129**: 309-317.

- Peres AC. 1999. A comunidade zoolânctônica em um canal de maré no estuário do rio Caeté, Bragança (Pará, Brasil). Dissertação de Mestrado. Universidade Federal do Pará/Museu Paraense Emílio Goeldi. 121 p.
- Pethick J. 1984. An introduction to coastal geomorphology. Edward Arnold, London, 260 p.
- Robertson AI, NC Duke. 1987. Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. *Mar. Biol.* **96**: 193-205.
- Robertson AI, P Dixon, PA Daniel. 1988. Zooplankton dynamics in mangrove and other nearshore habitats in tropical Australia. *Mar. Ecol. Prog. Ser.* **43**: 139-150.
- Robertson AI, SJM Blaber. 1992. Plankton, epibenthos and fish communities. *In* AI Robertson, DM Alongi, eds. Coastal and Estuarine Studies 41, Tropical Mangrove Ecosystems, American Geophysical Union, 329 p., pp. 173-224.
- Sasekumar A, VC Chong, MU Leh, RR D´Cruz. 1992. Mangroves as a habitat for fish and prawns. *Hydrobiologia* **247**: 195-207.
- Sokal RR, FJ Rohlf. 1995. Biometry: Principles and practice of statistics in biological research, 3rd ed., WH Freeman and Company. 887 p., ISBN 0716724111.
- Spalding M, F Blasco, CD Field, eds. 1997. World mangrove atlas. International Society for Mangrove Ecosystems, Okinawa.
- Turner JT. 1984. The feeding ecology of some zooplankters that are important prey items of larval fish. NOAA Tech. Rept. NMFS **7**: 1-28.
- Villate F. 1997. Tidal influence on zonation and occurrence of resident and temporary zooplankton in a shallow system (estuary of Mundaka, Bay of Biscay). *Sci. Mar.* **61**: 173-188.
- Wang Z, E Thiebaut, JC Dauvin. 1995. Short-term variations of zooplankton in a megatidal estuary (Seine, eastern English Channel). Proc. of the 20th symp. Union des Océanographes de France, Paris, 24-25 November 1994: Spatial and temporal scales of the ocean. Methods and problems. Union des Oceanographes de France, Paris (France), 1995, *J. Rech. Oceanogr.* **20(3-4)**: p. 152.
- Wooldridge T, T Erasmus. 1980. Utilization of tidal currents by estuarine zooplankton. *Estuar. Coast. Shelf Sci.* **11**: 115-118.

Photo: A. Hanning



A. anableps close to the bank at low water in the Furo do Meio main channel

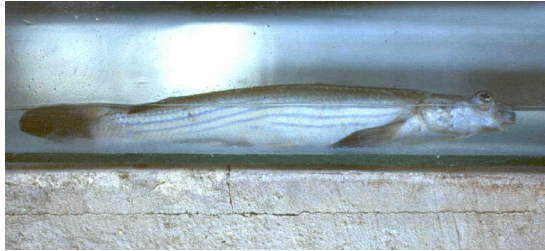


Photo: U. Krumme

Four-eyed fish *Anableps anableps* (Female with 17 cm total length).

Photo: A. Hanning



Burst-and-coast (or kick-and-glide) swimming behavior of *A. anableps* to escape an approaching canoe.



Tidal migration and patterns in feeding of the four-eyed fish *Anableps anableps* L. in a north Brazilian mangrove

Matthias Brenner & Uwe Krumme

Center for Marine Tropical Ecology (ZMT), Fahrenheitstr. 6, 28359 Bremen, Germany
E-mail: MatthiasBrenner@gmx.de

ABSTRACT

The surface-swimming four-eyed fish *Anableps anableps* on the northeast coast of South America provides the unique opportunity to study the migration patterns and feeding ecology of a tidal visiting mangrove fish in a turbid environment. We counted tidal-related changes in abundance and studied the diet composition of *A. anableps* in a macrotidal mangrove channel in North Brazil. Main channel abundances were high at low water (LW) and low at high water (HW). *A. anableps* entered the intertidal creeks rapidly with the first flood rise. They fed in the submerged mangrove at HW and returned gradually after the ebb current maximum to concentrate again in the subtidal parts of the main channel at LW. This pattern occurred at neap, mid and spring tides throughout the year. The tidal migration was triggered by water level, not by time. In our study area *A. anableps* exhibited a generalized feeding strategy (Insecta, Grapsidae), the most important food component being *Catanella* sp. which grows on the prop roots of *Rhizophora mangle*. Mud only taken at neaps is likely an evasive food item. The combination of high inundation at daylight (spring tide-day) provided optimum foraging conditions while darkness and low inundation was linked to poorest foraging conditions (neap tide-night). Spring tide-night and neap tide-day were intermediate. Improved foraging at daylight emphasized the importance of the above-water eye. Diet composition was not influenced by size, sex, tide and time of day, but differed in the proportions of the food items according to the combination of the factors tide and time of day. The presence of a gastrointestinal tract and its relative length (1.95) reflected the herbivorous-omnivorous diet. The elongated body (length-weight relationship) is likely an evolutionary adaptation to escape swimming and prey attacks. *A. anableps* successfully occupy the outermost niche of the coastal ecotone between aquatic and terrestrial habitat.

Keywords: Stomach fullness, foraging time, tide, distribution, shallow water, movements

INTRODUCTION

The northeast coast of South America is covered by one of the largest continuous mangrove areas of the world (Spalding et al. 1997). The direct observation of fish, their movements and behavior is strongly hampered by the very turbid waters prevailing along the coastline. The four-eyed fish *Anableps anableps* is a viviparous cyprinodontiform fish that always swims at the surface and occurs in very shallow waters close to the water edge (Wothke & Greven 1998), where its movements and behavior can be readily observed.

The northernmost occurrence of *A. anableps* is at the Gulf of Paria (East Venezuela) (Cervigón et al. 1993) and the Caroni Swamps in Trinidad with a maximum tidal range of 0.8 m (Wothke & Greven 1998). Southwards *A. anableps* has been documented in French-Guyana (Boujard & Rojas Beltran 1988) to well south of the mouth of the Amazon, at least to São Luís, Maranhão, Brazil (Batista & Rêgo 1998) with a maximum tidal range of almost 7 m.

A. anableps has long attracted the attention of scientists due to its unique eye morphology; the eye is divided horizontally by a band of opaque tissue into an upper and lower half, each with a separate retina. The division coincides with the water meniscus in swimming *A. anableps* and allows for simultaneous vision in air and water (Sivak 1976). The peculiarity of “sexual rights and lefts” in *Anableps* stimulated behavioral studies (Mattig & Greven 1994a,b). In the international aquarium trade, *A. anableps* is a well-known species. However, knowledge about the general ecology of this conspicuous fish species in its natural environment is rare (Miller 1979; Wothke & Greven 1998). Research on the diet of *A. anableps* is at best anecdotal, and comprehensive studies about the feeding ecology are not found in the literature.

Surface swimming *A. anableps* on the northeast coast of South America allow the unique opportunity to track visually the tidal movements during a tidal cycle as Schwassmann (1967, 1971) already observed for *A. microlepis* in a coastal lagoon in Salinópolis (Pará, Brazil). *A. microlepis* exhibited a regular tidal periodicity according to the semidiurnal tidal regime superimposed by the fortnightly alternation between spring and neap tides; *A. microlepis* moved up on the beaches each rising tide, day or night, and left before the water level receded (Schwassmann 1971).

Wothke & Greven (1998) found that *A. anableps* in Trinidad (microtidal regime) moved with the tidal edge while remaining mostly inactive between the mangrove pneumatophores at flood and high tide, and feeding at ebb tide. There, *A. anableps* fed on algae and arthropods that were

occasionally captured by a leaping action into the air. They suggested that the fish were taking food from the bottom of largely exposed flat mud banks at low tide. Zahl et al. (1977) assumed that *A. anableps* were feeding on mud on the exposed shoreline. Greven et al. (2002) inferred from their observations and the mouth morphology that *A. anableps* take food from the ground in shallow waters because they have severe difficulties in diving and their appearance clearly reminds one of a surface-swimming fish.

In fish that undergo regular intertidal migrations, however, feeding is considered a major function, besides avoidance of predators and competitors and, the selection of appropriate environmental conditions (Gibson et al. 1998). Fish that move into the intertidal zone early and leave late in the tidal cycle maximize foraging time in this productive shallow water environment (Kneib & Wagner 1994). Factors affecting the accessibility and foraging time in the intertidal habitats are likely determinants of the use patterns exhibited by the fish.

The macrotidal regime around the Amazon delta is likely to synchronize the tidal periodicity in many of the fish species, both juveniles and adults, co-occurring with *A. anableps* and undergoing intertidal movements into and out of the mangrove each tidal cycle (Krumme et al., *subm.*). Therefore, despite its specialized morphological and behavioral adaptations, *A. anableps* may serve as an exemplary intertidal visitor to elucidate tide-related patterns in movements in a turbid environment that regularly expands and shrinks with the flow and ebb of the tides.

To study the tidal migration and patterns in feeding, we ascertained temporal changes in abundance and feeding of *A. anableps* in a macrotidal mangrove channel in Northern Brazil according to the factors: tide (spring and neap tide), time of day (day and night) and tidal cycle (flood and ebb tide). This study is the first comprehensive investigation into the ecology of *A. anableps* in a natural macrotidal environment, offering insight into the general movements and behavioral patterns of shallow-water living fish.

STUDY AREA

The study was conducted in the macrotidal blind cul-de-sac channel Furo do Meio, a tidal tributary of the Caeté Bay, situated north of Bragança (Pará, Brazil). The Furo do Meio is approximately 4.5 km long, draining the central part of a 180 km² mangrove peninsula dominated by *Rhizophora mangle*, intermixed with *Avicennia germinans* at more elevated sites.

In the muddy upper reaches of the Furo do Meio, the main channel width is ca. 50 m at high water (HW) and ca. 25 m at low water (LW). At LW only the main channel holds water. In the basin-like lower section of the upper reaches, maximum water depth at LW can be 5 m. The rest of the branching network of 1st, 2nd and 3rd order creeks that channel the tidal flow into the mangrove, are intertidal and essentially empty at LW, except for a degree of nutrient-rich seepage water from mangrove sediments (Lara & Dittmar 1999; Dittmar & Lara 2001a,b) in the thalwegs. The mouths of the 1st order creeks where seepage water flows into the subtidal parts of the main channel remain covered by very shallow water even during LW.

In the sandy lower reaches of the Furo do Meio, channel width is 400 m at HW. At LW, it is however only about 30 m wide and maximally ca. 3.5 m deep. An extended sand bank in the lower reaches dams up the flood tide that enters from the estuary that itself is guarded by sand banks against the coast. The moment the sand bank is inundated, the tidal gradient built up between estuary and the Furo do Meio is balanced by a pronounced flood wave channeled along the main channel ("first rise"). This feature is weak at neaps, but of impressive velocity at springs. Maximum flood current speeds can exceed 1.5 m s^{-1} at springs and are usually below 0.5 m s^{-1} at neaps (Krumme, unpubl. data).

The tide is semidiurnal and asymmetric; flood and ebb tide last 4 and 8 hours, respectively. In the last 4 hours, ebb tide is extremely weak with an almost negligible fall in the water level. At neaps, tidal inundation is restricted to the intertidal mangrove creeks and the mangrove plateau remains dry. The mangrove peninsula is flooded only during spring tides (6 to 8 times each spring tide) and remains dry for 10-12 days at a time. On a yearly basis, the percentage of time the mangrove floor is submerged is approximately 3.3 % (mean submerged time during spring tides: $1 \text{ h } 42 \text{ min} \pm 18 \text{ min SD}$; $n = 9$; on average seven submergences spring tide⁻¹ and 24 spring tides y^{-1}). The mangrove receives freshwater only through precipitation. Water temperatures range between 25 and 31°C. Salinity can fall below 5 psu in the wet season (January to June) and exceed 35 psu in the dry season (July to December). Annual Secchi depth range is between <5-100 cm at neaps and <5-40 cm at springs, respectively. During a tidal cycle, Secchi depth maximum occurs around HW (Krumme, unpubl. data). For a detailed description of the study area and study site refer to Krause et al. (2001) and Krumme et al. (subm), respectively.

MATERIAL AND METHODS

Censuses. We counted the number of *A. anableps* present in a section of the Furo do Meio main channel (upper reaches) every 15 min during daylight hours (6:00 to 18:00 h) by eye and with binoculars (10×40). As *A. anableps* quickly eluded the light from flashlights, we did not count at night. The section of the Furo do Meio covered a rectangular area of about 40 m length on both banks, marked off by conspicuous landmarks. *A. anableps* in the Furo do Meio main channel usually were distributed in a band not further than 1 m away from the water edge on both banks throughout the tidal cycles. We divided the channel in the middle and counted each side separately, thus generating $n = 2$ for each count (left and right channel side). Due to the band-like distribution close to the water edge, we standardized the abundances to “number of *A. anableps* m^{-1} channel bank”. We conducted the various censuses at two different channel sections, 500 m apart from each other (three cycles in the wet season 2001 and 2003, section length: 40m, counting from the southern channel bank; six cycles in the dry season 2002, section length: 36 m, counting from a bridge crossing the Furo do Meio).

Simultaneously to a census, the water level was taken at a tidal gauge in the main channel (± 1 cm). The difference in topographical altitude between the main channel and 2nd order intertidal mangrove creeks was determined by simultaneous water level measurements at both sites. We determined the tidal current speed by measuring the time (stopwatch) it took the tidal current to stretch a 10 m long tape attached to a weight with a buoy. To compare for differences between LW (water levels < 1 m above mean LW [mLW]) and HW (water levels ≥ 1 m above mLW), we used the U-test.

***A. anableps* catches in the mangrove.** To study tidal-related changes in abundance of *A. anableps* in the intertidal mangrove habitat, we blocked the mouth of two neighboring 2nd order mangrove creeks (12 mm stretched mesh size) at flood tide (0.5-1.0 m water depth), slack HW and ebb tide (1.0-0.5 m water depth). The numbers of *A. anableps* left by the receding tide were compared using the Kruskal-Wallis test. We only used neap tides to ensure that *A. anableps* were unable to escape to adjacent creeks. Flood ($n = 6$), ebb ($n = 8$) and two HW samples were taken in the dry season 2002. Additionally, eight HW samples taken in the wet season 1999 were included to increase sample size (Krumme et al., *subm.*)

To study temporal changes in feeding of *A. anableps*, we blocked two 1st order intertidal creeks at HW, one in the upper and the other in the lower reaches of the Furo do Meio (1 km apart), using the same block net technique although with a larger net (30 × 3 m, 50 mm stretched mesh size) in the wet season 2001. Seven, 6, 8 and 8 samples were conducted at spring tide-night, spring tide-day, neap tide-night and neap tide-day in the wet season 2001, respectively (for the remainder of this paper we denote this as SN, SD, NN and ND). At three strong spring tides, the sampling was interrupted to save the net. However, *A. anableps* already entangled in the net were used for stomach analyses. HW at SN, SD, NN and ND occurred at ca. 19:00, 07:00, 01:00 and 13:00 h, respectively. Though an alternating sampling schedule would have been more beneficial, at each lunar phase each creek was first blocked at the night slack HW, then at the daytime slack HW due to logistical considerations. Fish were collected at LW. Most *A. anableps* were caught alive agglomerated in small puddles upstream of the net.

Samples were taken from two 1st order creeks to test whether increasing distance from the Furo do Meio mouth influenced fish assemblage structures, abundance and biomass (Brenner, unpubl. data).

Since the sampling failed to show a significant “site” influence on the catch compositions, the data were pooled for further analyses. For details on the sample design refer to Krumme et al. (subm.). After the sampling the creeks were surveyed to provide an estimate of the area (m²) submerged at neap tides.

In the field, sex, total length (TL) to cm below and total wet weight (WEDO/DIGI 2000; ± 1 g) were determined.

The length-weight relationship ($W = a \cdot L^b$) for males and females was investigated and the parameters a (W in gram; L in cm TL [Xiao 1998]) and b , and the condition factor c.f. ($c.f. = (\sum(W \cdot 100/L^3))/n$) for both sexes were calculated (Ricker 1975; Cinco 1982).

Analysis of *A. anableps* stomachs. Since a separation between stomach and intestine in *A. anableps* was not visible when dissecting fish in the field, the entire gastro-intestinal tract (GIT) from the esophagus to the anus was removed, each put in a teabag, numbered and conserved in 10 % formol.

The length of the uncoiled GIT of 56 defrosted specimens (22 males, 77 to 191 mm TL; 34 females, 63 to 231 mm TL) was measured from the esophagus to the anus (± 1 mm). Relative length of the GIT for males and females was calculated ($TL_{GIT} \cdot TL^{-1}$).

In the laboratory, GITs were washed, drained on an absorbent paper and weighed (Sartorius MC 1/Laboratory LC 4200 S; ± 0.01 g). GITs were opened and GIT fullness was assigned to five categories according to Dalpado & Gjøsæter (1988): empty; filled to 30 %; filled 30-70 %; filled 70-100 %; 100 % full with a stretched GIT and thin walls.

The digestion stage of the entire GIT content was assigned to four categories according to Dalpado & Gjøsæter (1988): recently eaten; <30 % digested; 30-70 % digested; >70 % digested. We tested for significant differences of the categories of GIT fullness and digestion stage between the four factor combinations SN, SD, NN and ND using the Kruskal-Wallis test (Statistica).

Subsequently GIT contents were washed out onto a sieve (63 μ m) and transferred to 50 ml Kautex bottles (4 % formol) for content analysis. Empty GITs were drained and weighed. The weight of the contents of the GIT ($W_{GIT\ C}$) was calculated as $W_{GIT\ C} = W_{GIT\ F} - W_{GIT\ E}$; where $W_{GIT\ F}$ is the weight of the removed GIT (g); $W_{GIT\ E}$ is the weight of the empty GIT (g).

Contents were determined to the lowest possible taxon with a ZEISS-STEMI SV-11 stereo magnifying glass (formol substituted by distilled water) using Dixon & Irvine (1997), Tucker & Dance (1986), Schmidt de Melo (1996), Drebes (1974), Ricard (1987), Boltovskoy (1999), Hayward & Ryland (2000), Kaestner (1967) and Hennig (1986).

In Athropoda, only Crustacea were determined in detail. Araneae and Insecta were not further determined. Each taxon was briefly drained and then weighed (Sartorius basic plus; ± 0.00001 g). Items with less than 0.00001 g were included as 0.00001 g. Whenever possible fragments were assigned to the according taxon and weighed together. Unidentifiable fragments were weighed separately and assigned as “others”.

To determine the number of the items eaten, heads, eyes, carapace and thorax were considered as units. When fragments failed to provide numerical information, they were counted as 1; thus, the numbers given are the minimums of items eaten.

The numerous algae fragments eaten were not counted, but like all other items wet weight (g) was determined.

Forty-three GITs ($n = 33$ at ND; $n = 10$ at NN) contained great amounts of mud. These samples were separated, dried (72 hs at 60°C) and weighed (dry weight = dw). Then the samples were burned (5 hs at 530°C in a muffle furnace) and weighed (ash free dry weight = afdw). The difference between dw and afdw gives the amount of organic carbon (g), which should be available for an animal feeding on mud.

To look for ontogenetic changes in feeding, fish were assigned to four size classes: 12-14 cm; 15-17 cm; 18-20 cm; >21 cm.

Standardization of numbers and weights of food items. The effect of fish size within the different size classes was removed from further analysis by standardizing GIT content weights to the geometrical mean weight of all investigated fishes of one size class according to Brenner et al. (2001): A linear regression between fish weight (WF) and weight of empty GIT (WEG) was established:

$$\text{WEG} = a + b \cdot \text{WF}$$

Subsequently, number ($\text{NP}_{j,i}$) and weight ($\text{WP}_{j,i}$) of each prey item j found in the GIT of a fish i of weight WF_i was standardized (SF) using the geometrical mean weight (GM) for the size class the fish WF_i was stated as:

$$\text{NP (SF)}_{j,i} = \text{NP}_{j,i} \cdot (a + b \cdot \text{GM}) / (a + b \cdot \text{WF}_i)$$

$$\text{WP (SF)}_{j,i} = \text{WP}_{j,i} \cdot (a + b \cdot \text{GM}) / (a + b \cdot \text{WF}_i)$$

Using $y = 0.0422 x - 0.1572$ ($r^2 = 0.82$; $n = 255$) we converted the original GIT content weights into standardized GIT content weights (Brenner et al. 2001).

The similarities in diet composition between sample combination and size class were displayed using non-parametric multi-dimensional scaling (MDS) [program package Primer 5; Clarke & Warwick (1994)]. In the original species-sample Table, each cell contained the mean standardized weight of food item (g) per size class and factor combination (e.g. NN1 = neap tide-night, smallest size class). We used square root transformation to generate the Bray-Curtis similarity indices. The stress of the MDS representation - a measure of how well the ordination represents the similarities between the samples - was assessed using the classification of Clarke & Warwick (1994).

RESULTS

Censuses

The censuses in the Furo do Meio main channel revealed a clear tidal-related alternation in abundances of *A. anableps* with high abundances at LW and low abundances at HW (U-test; $p \leq 0.001$) irrespective of neap, mid or spring tide (Fig. 1).

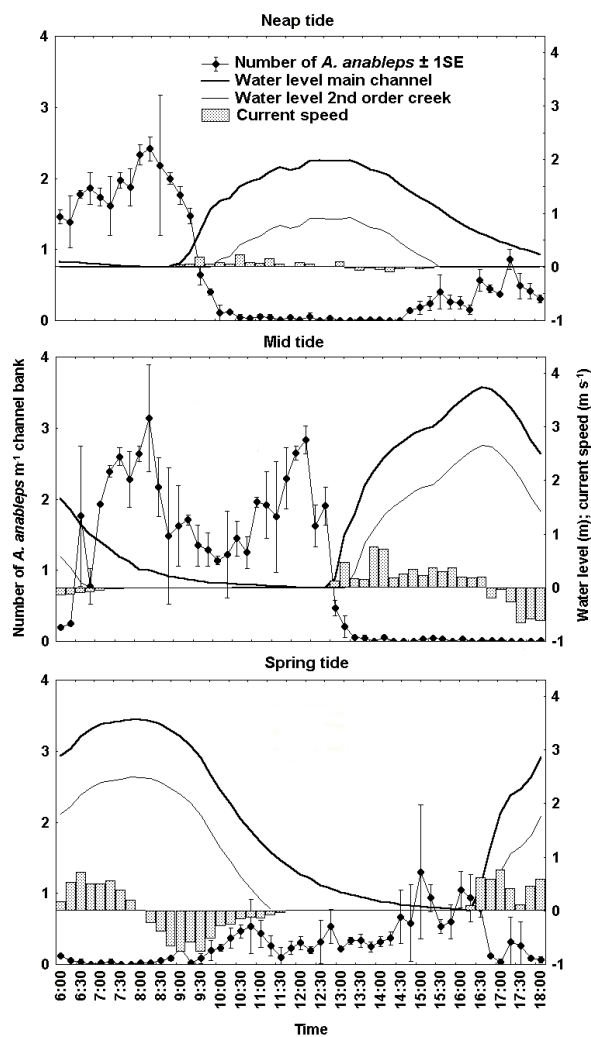


Figure 1. Number of *A. anableps* \pm 1SE per meter of bank in the main channel of the Furo do Meio (North Brazil) at neap, mid and spring tide during daylight hours. Tidal curves for the subtidal main channel and intertidal 2nd order mangrove creeks are shown. Positive and negative current speeds correspond to flood and ebb tide, respectively.

As soon as the flood tide started, abundances of *A. anableps* started to decrease, suggesting that *A. anableps* were riding the tide with the first rise to enter the intertidal mangrove zone each tidal

cycle. Within an hour after slack LW, *A. anableps* were almost completely absent from the main channel. Only very few *A. anableps* remained close to the main channel banks throughout the phase of inundation of the mangrove at daytime.

Flood tide swimming was not necessarily uni-directional; larger sizes readily left 2nd order creeks against the flood current and returned to the 1st order creek where they continued to swim further into the mangrove. In the mangrove *A. anableps* usually swam close to the tidal margin while foraging and maneuvering for food in the rising tide. By usually swimming with the tide *A. anableps* may save considerable transport costs during its tidal migration. Thus, *A. anableps* penetrate deep into the creek network in the mangrove forest (>1 km distance to the main channel) during the flood tide. Only the smallest individuals were observed foraging in very shallow water (<10 cm deep) on the mangrove plateau at spring tide HW, suggesting an ontogenetic separation in habitat use. This can also be observed in captivity where the juveniles select the shallow-water zones to search for mosquito larvae (H Greven, pers. comm.).

When returning downstream during ebb tide, *A. anableps* swam alone or in groups of 3 to 8 or more, using the tide in the more central parts of the mangrove creeks until they maneuvered to an appropriate site close to the shallow bank to stop and prevent further downstream transport. At ebb tide *A. anableps* movements were mostly uni-directional, swimming with the receding tide, except during escape behavior. When a group encountered the block net on their downstream travel, only one or two individuals jumped several times against the net, however without getting entangled in the net, while the others stayed at a distance. Then the group swam upstream against the ebb current, apparently looking for exits in the upper reaches of the creek (Krumme, own obs.; pers. comm. with fishermen). While the 2nd order creeks drain, *A. anableps* retreated to the 1st order creek.

With the falling tide *A. anableps* concentrated at the mouth of the 1st order creek from where they finally returned to the main channel. The abundances of *A. anableps* in the main channel started to increase again only after the ebb current speed maximum was over (Fig. 1). Thus, *A. anableps* are likely to avoid longitudinal downstream displacement in the main channel at least during neap tides. Maximum abundances occurred during the quasi-stagnant LW phase in the subtidal parts of the main channel.

Considering the entire width of the channel, mean abundance (\pm SE) at slack LW at neap tides was 0.127 ± 0.003 *A. anableps* m^{-2} . However, correlating the abundance to the real distribution corridor of 1 m width along each bank, mean abundance was 1.91 ± 0.05 *A. anableps* m^{-2} .

When related to water level, the tidal migration of *A. anableps* proceeded symmetrically to slack high water; fish abundance decline at flood tide is paralleled by the increase at ebb tide (Fig. 2).

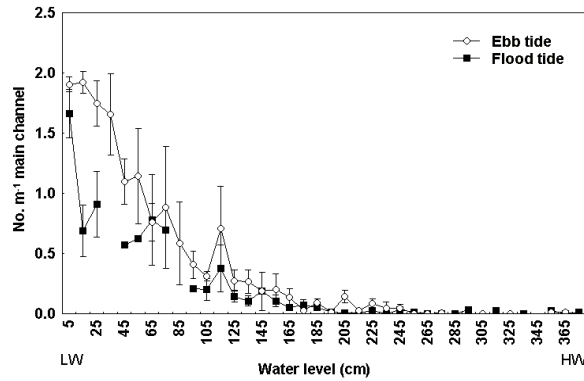


Figure 2. Mean number of *A. anableps* m^{-1} channel bank in the main channel of the Furo do Meio (North Brazil) at flood and ebb tide at increasing and decreasing water levels above mean low water, respectively (n = six neap tide cycles). LW: slack low water; HW: slack high water.

Only at the end of ebb tide (water level ca. 0.5 m above mLW) did the numbers surpass those at flood tide since many *A. anableps* left the mouths of the 1st order creeks to agglomerate in the main channel. In contrast, when related to time after HW, the migratory patterns proceeded

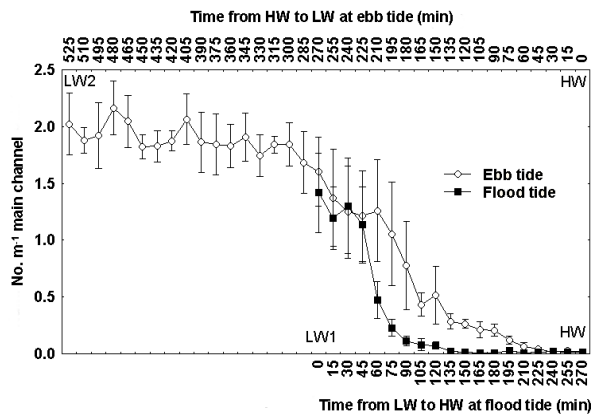


Figure 3. Mean number of *A. anableps* m^{-1} channel bank in the main channel of the Furo do Meio (North Brazil) related to the time from slack low water (LW1) to slack high water (HW) at flood tide lasting max. 270 min (lower abscissa) and the time from slack high water (HW) to the next slack low water (LW2) at ebb tide lasting max. 525 min (upper abscissa) (n = six neap tide cycles). Note asymmetry in the flood and ebb curve due to earlier emigration out of the intertidal mangrove creeks at ebb tide.

asymmetrically (Fig. 3), indicating that tidal migration of *A. anableps* is controlled by water level and not by time. Although only shown for neap tide, the same water level-controlled movement pattern occurred at spring tides.

Abundance patterns in the submerged mangrove

Although samples were always taken first at night HW, highest abundances of *A. anableps* occurred in the second sampling at daytime HW, both at spring and neap tides (Fig. 4). However, high variances in catches masked any significant differences between the four treatment groups

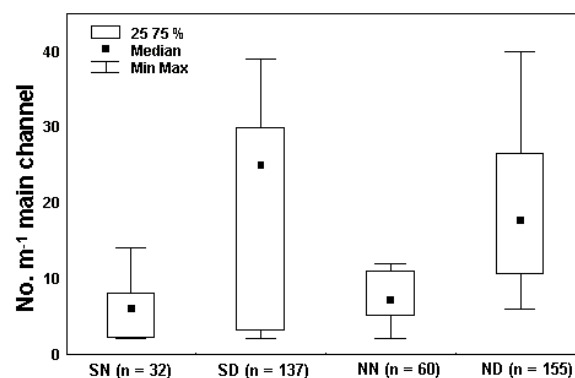


Figure 4. Box Whisker plots of the median numbers of *A. anableps* caught in 1st order mangrove creeks using block nets set at high water (HW) at spring tide-night (SN), spring tide-day (SD), neap tide-night (NN) and neap tide-day (ND) with $n = 5, 7, 8,$ and 8 block net samples, respectively. Below each group the total number of specimens caught is indicated.

(Kruskal-Wallis test, $0.1 > p > 0.05$). An estimated area of $15\,566\text{ m}^{-2}$ and 7693 m^{-2} was submerged at HW at neap tides in the 1st order creeks in the upper and lower reaches, respectively. Mean HW abundance (\pm SE) in the flooded mangrove creeks was 0.002 ± 0.0003 *A. anableps* m^{-2} , thus being about 65 times lower compared to the concentration of *A. anableps* at LW.

At rising tide (water depth: 0.5 to 1.0 m) *A. anableps* were generally already present in the 2nd order mangrove creeks (Fig. 5). Abundances at HW were slightly higher than at flood and ebb tide. At falling tide (water depth: 1.0 to 0.5 m) *A. anableps* were often still present in the creeks. However, the numbers of *A. anableps* at flood, HW and ebb tide were not significantly different (Kruskal-Wallis test, $p > 0.05$), mainly due to high variability in the catches that was caused by the patchy distribution of groups of foraging *A. anableps* in the network of submerged creek. A size-specific pattern was obscured as well.

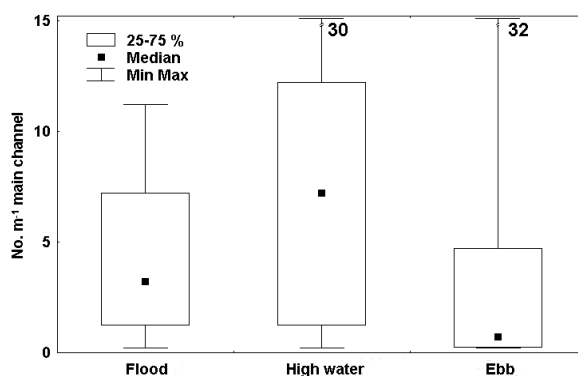


Figure 5. Box Whisker plots of the median number of *A. anableps* caught in 2nd order mangrove creeks with block nets set at flood tide, high water and ebb tide. N = 6, 10 and 8 neap tide cycles for flood tide, high water and ebb tide, respectively.

Figure 1 shows that *A. anableps* were in the mangrove about 3 hs at flood and 2 hs at ebb tide, totaling about 5 hs that *A. anableps* were likely to be foraging in the mangrove creeks. Neap, mid and spring tides resulted in very similar periods of time of inundation of 2nd order intertidal creeks (on average 6 hs tide⁻¹) (Fig. 6). Likewise the period of time *A. anableps* were likely to forage in the intertidal zone (on average 5 hs tide⁻¹) showed no clear relationship to increasing HW levels, i.e. higher HW levels did not result in longer foraging times of *A. anableps* in the mangrove.

Interestingly, Figure 6 shows that at strong mid tides (with increasing HW levels towards spring tides) *A. anableps* stayed particularly long in the intertidal zone, suggesting that *A. anableps* used the opportunity of first access to previously inaccessible and unused food resources in the higher

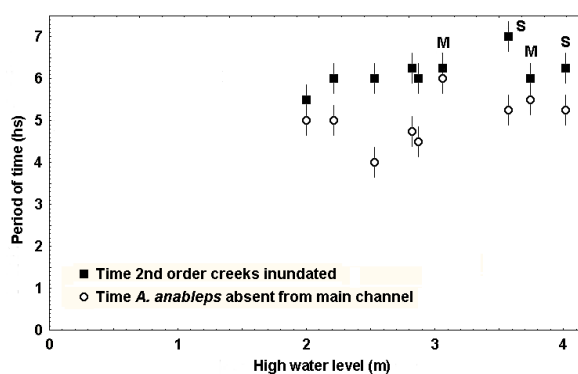


Figure 6. Relationship (n = 9 censuses) between high water level, the period of time a 2nd order intertidal mangrove creek was inundated (black squares) and the period of time *A. anableps* was absent from the main channel (<0.15 fish m⁻¹ bank) and is hence likely to forage in the mangrove (open circles) (± 0.25 h). M: Mid tide; S: Spring tide; all other censuses at neap tide.

intertidal zone. At spring tides, ready access to the highest intertidal zone, stronger ebb current and avoidance of stranding may prevent *A. anableps* from staying exceptionally long periods of time in the mangrove. *A. anableps* may use the tide as a horizontal and vertical lift to the food resources in the intertidal zone, probably responding immediately to tidal characteristics indicating high levels of inundation after the neap tide phase.

Fortnightly and seasonal patterns in LW abundance

During LW (water level <1 m above mLW) at neap tides *A. anableps* occurred at similar abundances in the dry and in the wet season (mean number of fish m⁻¹ mangrove channel bank ± SD: 1.6 ± 0.7 (n = 148) and 1.7 ± 1.4 (n = 7), respectively; Kruskal-Wallis test, p>0.05). Although wet season LW abundances seemed to be greater at neap than at spring tide (1.7 ± 1.4 vs. 0.6 ± 0.3; n = 44), no significant difference was determined (Kruskal-Wallis test, p>0.05), likely due to the high variation in the neap tide abundances. However, LW abundances at neap tide-dry season were significantly greater than at spring tide-wet season (Kruskal-Wallis test, p≤0.0001). Though our observations lack a direct dry season comparison between LW neap and spring tide, it is likely that the weekly alternation with greater LW abundances at neap than at spring tide is not only a seasonal but an annual pattern.

Population parameters

We caught a total of 384 *A. anableps* in the 1st order creeks with a female:male relationship of 2.2:1, of which 255 specimens were used for stomach analyses. The size range for males and females was 12-18 cm (n = 79) and 12-25 cm (n = 173), respectively while three individuals were left unsexed due to damage by *Callinectes* sp. The two smallest size classes contained both males and females (12-14 and 15-17 cm), whereas all other size classes >18 cm consisted entirely of females.

The parameters of the length-weight relationship for male *A. anableps* were a = 0.1229 and b = 2.144, (r² = 0.72; n = 79) and for females were a = 0.0516 and b = 2.517 (r² = 0.91; n = 173). Females were heavier at a given length and increased faster in weight than males. Females had a larger condition factor (1.307) than males (1.256).

Relative GIT length

The mean relative length of the GIT was 1.95 ± 0.30 SD ($n = 56$). The relative length of the GIT in females (2.03 ± 0.06 SE) was significantly greater than in males (1.83 ± 0.05 SE) (Kruskal-Wallis test, $p \leq 0.05$). There was a clear positive relationship between GIT length (y) and TL (x) that was best described by a power function ($y = 1.1154 \cdot x^{1.2128}$, $r^2 = 0.88$ for females, and $y = 2.3001 \cdot x^{0.9146}$, $r^2 = 0.70$ for males).

GIT fullness

Spring tide GITs were clearly fuller than GITs at neap tide (Fig. 7). SD GITs were fuller than SN GITs. ND GITs were fuller than NN GITs, clearly indicating better foraging conditions when HW coincided with daylight (SD, ND). Kruskal-Wallis test revealed a significant difference between the fullness groups within the category of 100 % filled and stretched GITs ($p \leq 0.05$).

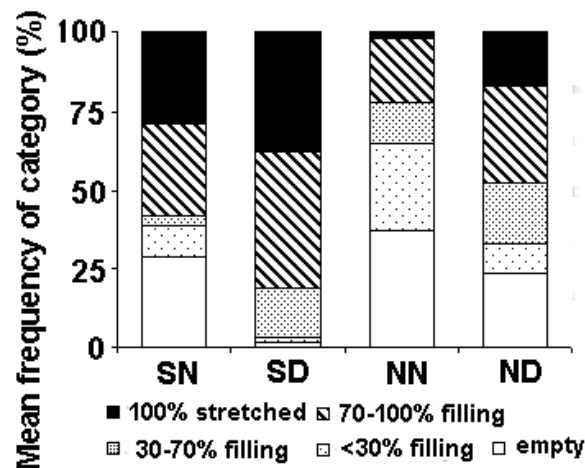


Figure 7. Mean gastrointestinal tract fullness of *A. anableps* caught in 1st order mangrove creeks of the Furo do Meio at high water (North Brazil) in the wet season 2001 according to the five fullness categories indicated, at spring tide-night (SN), spring tide-day (SD), neap tide-night (NN) and neap tide-day (ND) with $n = 31, 69, 54$ and 101 , respectively.

On the 10 % level percent values at SD were significantly higher than at NN (Nemenyi test, $0.1 > p > 0.05$), indicating that feeding was most successful at SD and poorest at NN.

Digestion stage

At spring tides, more food had been recently ingested and only weakly digested than at neap tides (Fig. 8). Digestion stage at SD was lower than at SN. Digestion stage at ND was lower than

at NN, thus emphasizing the pattern revealed by GIT fullness. Kruskal-Wallis test revealed a significant difference between the digestion stage groups within the category of “>70 % digested” ($p \leq 0.05$). Percent values at SD were significantly higher than at NN (Nemenyi test, $p \leq 0.05$), indicating that these two groups provided the most opposite foraging conditions for *A. anableps*. The best feeding conditions for *A. anableps* occurred at SD when high water levels and daylight coincided. Worst conditions occurred at NN when darkness coincided with HW. ND and SN achieved fairly similar proportions between the fullness categories whereas digestion stage categories showed that food at ND was more digested than at SN.

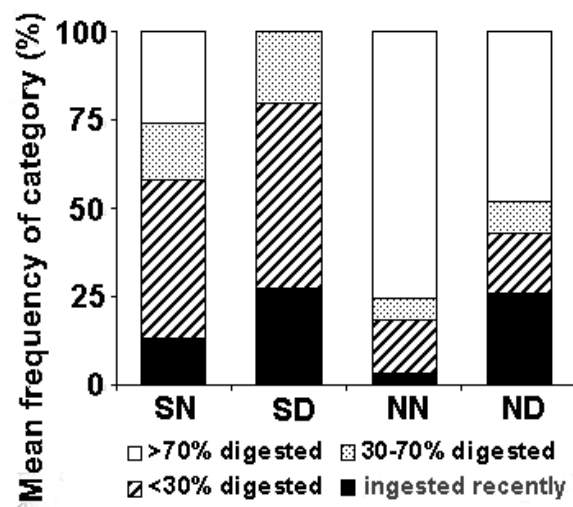


Figure 8. Mean digestion stage of *A. anableps* caught in 1st order mangrove creeks of the Furo do Meio at high water (North Brazil) in the wet season 2001 according to the four digestion categories indicated, at spring tide-night (SN), spring tide-day (SD), neap tide-night (NN) and neap tide-day (ND) with $n = 31, 69, 33$ and 77 , respectively.

Food analysis

A. anableps fed mainly on red macroalgae of the genus *Catanelia* sp. and *Bostrychia* sp., that grow as dense cover on prop roots of *Rhizophora mangle* around the mean HW level. Other important food items were Insecta, small crabs of the family Grapsidae (probably most of them *Grapsidae cruentata*) and at neap tides also mud. Less important diet components were Gammaridae, Polychaeta, Capitellidae, Araneae, Littorinidae and Mytellidae. The latter two occurred within the epiphytic prop root cover (pers. obs.). The food items *Catanelia* sp. and Insecta were always present in the GIT contents irrespective of sex, size class, tide and time of day.

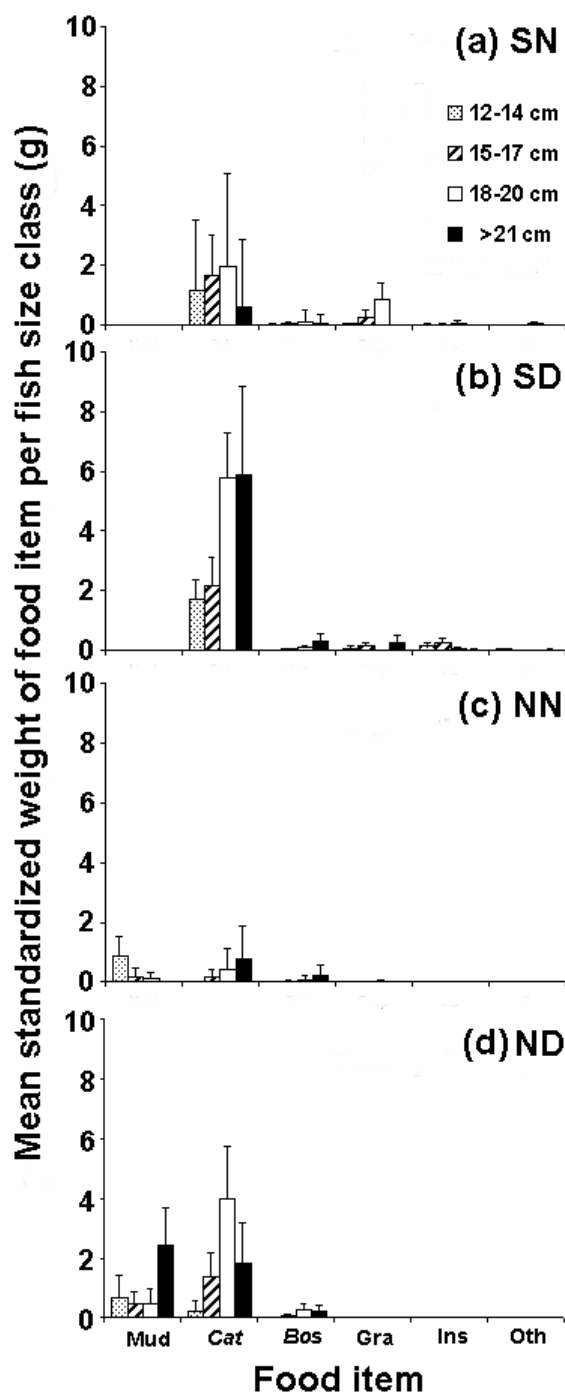


Figure 9. Food composition of the four size classes of *A. anableps* in terms of weight (g + 95 % confidence interval) according to the combination of the factors tide and time of day: Spring tide-night (a, SN), spring tide-day (b, SD), neap tide-night (c, NN) and neap tide-day (d, ND). According to the four size classes (12-14 cm; 15-17 cm; 18-20 cm; >21 cm) $n = 31$ (7, 19, 3, 2) specimens were analysed at SN, $n = 69$ (32, 26, 3, 8) at SD, $n = 54$ (10, 20, 12, 12) at NN and $n = 101$ (16, 36, 26, 23) at ND. Weights of food items were standardized per fish size class. Food items are abbreviated; Mud: Mud; Cat: *Catantella* sp.; Bos: *Bostrychia* sp.; Gra: Grapsidae; Ins: Insecta; Oth: Others. Specimens were caught in 1st order mangrove creeks of the Furo do Meio (North Brazil) in the wet season 2001.

At spring tides, the major diet components of *A. anableps* were essentially equal between day and night (Fig. 9). However, the total GIT weight was higher at daytime than at night irrespective of size and sex. In terms of weight the algae *Catanella* sp. dominated the diet at SD. At SD Insecta occurred in significant amounts (e.g. on average 23 Insecta per GIT in the size class 15-17 cm at SD). Other food items occurring were *Bostrychia* sp. and Grapsidae. At SN the dominance of *Catanella* sp. clearly declined, Insecta declined while Grapsidae gained in weight. At neap tides, algae and mud were the first and second most important food components of the diet, respectively. In contrast, not a single spring tide GIT contained mud. Like at spring tides, GIT weight was higher at daytime than at night. At ND the amount of food taken was higher than at NN, particularly *Catanella* sp. and mud. While Insecta were important in the SD diet both in terms of weight and abundance, insignificant amounts of Insecta were found at neap tides.

Almost all size classes fed on the same major diet components at spring and neap tide, however in different proportions. Only the diet of the smallest size class was dominated by mud at neap tide as reflected in the separation of these two size classes in the group on the right in the MDS plot (Fig. 10).

ND and NN GITs contained on average (\pm SD) 0.16 ± 0.13 and 0.07 ± 0.06 g organic carbon in the mud ingested, respectively, while mud constituted on average (\pm SD) $12 \% \pm 32$ of the GIT wet weight in the specimens that had ingested mud ($n = 43$). The high variation points to strong intra-specific differences in mud consumption.

Similarities in diet composition

The MDS plot in Figure 10 shows that the diet composition at spring tides (left group) was clearly different from the one at neap tides (middle group) and the smallest size class at neap tides (right group). The good stress value of 0.09 allowed for the interpretation of ordination details: At neap tides (middle group), the diet composition at daytime (lower group) was clearly separated from the one at night (upper group) whereas diet composition at SN and SD was homogenous.

Except for the smallest size class at neap tides (right group, NN1 and ND1) that mainly fed on mud (see above), diet composition did not differ between size classes and hence between sexes. Irrespective of the factors tide and time of day the two smallest, mixed size classes (12-17 cm) fed on the same food items as the three larger, “female” classes (>18 cm). It was the changing proportions of the food items that resulted in clearly different GIT content compositions between tide and time of day, indicated by highest GIT content weights at spring tide on the left corner of the plot and lower weights towards the right corner (Fig. 9, 10).

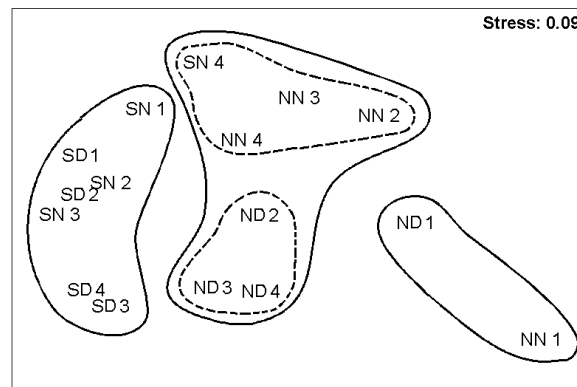


Figure 10. MDS plot of the similarities in food composition of *A. anableps* caught at high water in 1st order mangrove creeks of the Furo do Meio (North Brazil) in the wet season 2001 at the four tide-time of day combinations (SN: spring tide-night; SD: spring tide-day; NN: neap tide-night; ND: neap tide-day) and of the four size classes (1:12-14 cm; 2: 15-17 cm; 3: 18-20 cm; 4: >21 cm).

Feeding strategy

Figure 11 shows that *A. anableps* subsisted primarily on *Catanella* sp. which was eaten by 62 % of the fish, while its average contribution to the GIT weight was 55 %. Insecta was consumed by 63 % of the fish while, however, only contributing <2 % to the GIT weight. The other prey taxa occurred in 22 to 50 % of the GITs, but their average contribution to the GIT weights of the fish was low, indicating a generalized feeding strategy for these food items. *A. anableps* exhibited a high within-phenotype component where most of the individuals used many resource types simultaneously. Mud was clearly of minor importance in the feeding strategy of *A. anableps*. Although mud was the second most important food item in terms of weight, mud was eaten by only 16 % of the fish, which was by far the lowest value of occurrence found for all food items.

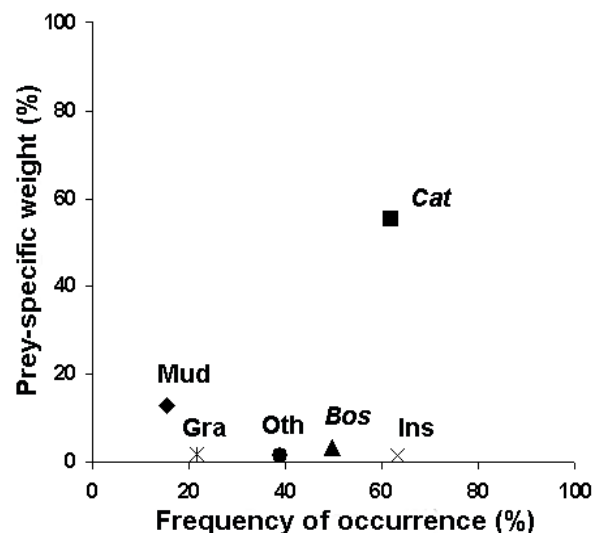


Figure 11. Feeding strategy plot (Amundsen et al. 1996) of *A. anableps* (n = 255) caught in the mangrove channel Furo do Meio (North Brazil) in the wet season 2001. The points represent the food items *Cat*: *Catanella* sp.; Mud: Mud; Gra: Grapsidae; Oth: Others; Bos: *Bostrychia* sp.; Ins: Insecta. See text for further explanation.

DISCUSSION

Geographical distribution

While the northernmost occurrence of *A. anableps* on the Atlantic coast of South America is well documented (Cervigón et al. 1993; Wothke & Greven 1998), knowledge about its distribution to the south relies on few geographical points lacking the area perspective (Boujard & Rojas Beltran 1988; Batista & Rêgo 1998). However, the distribution likely goes beyond the evidence for São Luís, Maranhão, Brazil (Batista & Rêgo 1998) because *A. anableps* is still abundant at

the mouth of Rio Parnaíba in Piauí (A. Morais, pers. comm.). However *A. anableps* was neither caught in the mouth of the Rio Jaguaribe, east Ceará (Oliveira 1976) nor along the northeast coast of Brazil (Paraíba to Sergipe) (Oliveira 1972) and does not occur in Fortaleza (AR Araújo, pers. comm.). We assume that the distribution of *A. anableps* coincides with the world's second largest mangrove area in the humid tropical zone along the northeast coast of South America (Kjerfve & de Lacerda 1993) that is characterized by high precipitation, high water turbidity, strong salinity changes and tidal influence. The southernmost populations of *A. anableps* likely occur between Bareirinhas (Piauí) and the western Ceará coast, where the mangrove-fringed coastline is cleaved by large sand dunes kilometers in length. There the climate is arid, the water clarity is high (coral reefs) while the tidal range is still 2 to 3 m. Unfortunately, we were unsuccessful in obtaining detailed information about *A. anableps* occurrence in west Ceará (Camocim, Rio Acaraú).

Tidal migration

A. anableps exhibited a regular tidal periodicity following the semidiurnal tidal regime. The fish moved rapidly into the intertidal mangrove creeks with the first rise at the start of flood tide, but left the creeks gradually after the ebb current maximum to finally concentrate in the subtidal parts of the main channel. Thus, *A. anableps* likely maximized foraging time and use of the intertidal mangrove zone (Kneib & Wagner 1994). On the Pará coast Schwassmann (1971) observed similar patterns for *A. microlepis*.

A. anableps always gathered close to the bank, thus using the lateral widening of the channel with the rising tide to achieve early access into the intertidal creeks. Riding the tide with the first rise enables the fish swimming on the edge of the water-air ecotone to be the first to encounter the resources which have fallen on the previously exposed creek grounds e.g. arthropods, and to capture prey items by surprise while the intertidal zone is being flooded.

A. anableps generally stayed in the shallowest water on the tide edge, particularly at LW. By this means *A. anableps* likely not only reduced the risk of piscine attacks since a silhouette on the open water is readily visible when looking up to the surface, but also ensured proximity to potential prey when foraging. Since HW always coincides with maximum Secchi readings in the tidal cycle, *A. anableps* foraged during the periods of highest water clarity in the shallow mangrove creeks. Thus, they not only encounter optimal visual conditions for underwater vision

(food search e.g. Grapsidae, algae), but also avoid predators because large piscivores are more likely to occur at high water levels in the main channel (Paterson & Whitfield 2000). Furthermore, Lawrie et al. (1999) showed that *Neomysis integer* were concentrated in a band toward the moving tide edge to avoid areas of high flow. The usually orderly close-to-the-bank swimming of *A. anableps* in the main channel during strong tidal phases suggests that the avoidance of higher current speeds is another primary reason for the shallow-water preference during intertidal flooding.

At ebb tide *A. anableps* concentrated in the mouths of the 1st order creeks, i.e. the bottleneck where all the exported material from the creek drainage areas are passed through by the receding tide. Due to the general strategic feature of 1st order creek mouths at ebb tide, other fish species may behave similarly to *A. anableps* and search for potential prey organisms brought by the receding tide at the creeks outlets. Hoeninghaus et al. (subm.) caught piscivores almost exclusively at mouth or mid-stream sites of floodplain creeks in Venezuela in the dry season where they were likely waiting for emigrating fish.

The tidal migration of *A. anableps* was triggered by the water level, not by the relative time after LW or HW, clearly suggesting that the sample design in tidal-related studies on nekton species should be oriented according to equal flood and ebb water levels instead of equal times after LW or HW.

Since surface-dwelling *A. anableps* visited the intertidal mangrove zone each tidal cycle like many other even more abundant fish species, e.g. Ariidae and Sciaenidae (Krumme et al., subm.), the migratory patterns exhibited by *A. anableps* may serve as an exemplary model for the tidal migration of the “invisible” intertidal fish species as well. Krumme and Saint-Paul (2003) and Krumme (subm.), using sonar, found that first rise was the universal immigration trigger for the entire fish community in the Furo do Meio. The tidally visiting mangrove fish resident in the Furo do Meio seem to be optimally adapted to the local tidal regime in that the species optimized the temporal use of the rich intertidal habitat each flooding, partially explaining their dominance in weight and abundance (Krumme et al., subm.).

At LW *A. anableps* were generally concentrated close to the main channel banks. Wothke & Greven (1998) observed groups of 4-13 individuals. Similar group sizes were typical during the intertidal migration of *A. anableps* in the Furo do Meio. We observed large synchronized

swimming schools in the center of the main channel in May in the wet season at LW (170–270 individuals), never in the dry season.

The Furo do Meio drainage system is connected to the adjacent drainage systems only at high spring tides, thus enabling transversal exchange of aquatic organisms while the numerical gains and losses are suggested to be equal between adjacent systems. Therefore, the higher LW abundances of *A. anableps* at neap compared to spring tide found in the wet season suggest a longitudinal downstream displacement of a part of the population by the strong spring ebb tide towards the lower reaches of the Furo do Meio. Consequently, the return to previous neap tide abundances can only be explained by the return of *A. anableps* from downstream. However, our sample design failed to directly test for this temporal feature.

Feeding ecology

The most important food items in the diet of *A. anableps* are usually found at or above the water surface. Within its distributional range, *A. anableps* occupy the outermost niche on the coastal ecotone between aquatic and terrestrial habitat. Changes in GIT fullness and diet composition indicate that good vision at daylight provides better foraging conditions for *A. anableps* than darkness, clearly emphasizing the importance of the above-water eye in foraging.

While immigrating at similar HW levels at daytime and night, nocturnal feeding was less successful. But independently of time of day, tidal migration represents a useful strategy to increase accessibility to potential prey resources for *A. anableps*. Although nocturnal samples were always taken previous to the daytime samples, three times more *A. anableps* were captured at daytime HWs, both at neaps and springs. This suggests that nocturnal immigration into the mangrove is less important because darkness equally limits foraging conditions for a visual predator both in the main channel and in the flooded mangrove creeks.

One can assume that higher water levels provide greater foraging habitat for fish on intertidal coasts. The topography of the mangrove peninsula (plateau mangrove) leads to a relationship between tidal height and inundated area where a water level increase of 20 cm above mean HW (4 %) causes an increase of 51 % of inundated mangrove area (Cohen et al. 2000). Although on a yearly basis the plateau mangrove is rarely completely flooded, submergence involves an extraordinary increase in surface area and foraging habitat for *A. anableps*, which is clearly

reflected in the fuller GITs and lower digestion stages. These circumstances apparently favor the strategy of a fish species foraging on the tide edge in very shallow water.

The combination of the factors considered in this study (tide and time of day) yields a positive interplay with best foraging conditions at SD and a neutral interplay at SN when habitat accessibility was high, but darkness hampered visual foraging and fish immigrated with lower abundances. In contrast, at ND daylight provided reasonable conditions although habitat accessibility was low, whereas at NN, when low water levels coincide with darkness, a negative interplay of the ambient factors result.

However, the condition of the prey items in the GITs did not allow species-specific determination and hence, the inference to diel activity patterns. Consequently, it cannot be ruled out that diel changes in prey activity had an influence on better foraging conditions encountered at daylight.

Diet composition

The structure of the alimentary tract reflects fish diets (Al-Hussaini 1947). According to Al-Hussaini (1947) relative gut length of carnivorous, omnivorous and herbivorous fish are 0.6-2.4, 1.3-4.2 and 3.7-6.0, respectively. Odum (1970) suggested relative gut lengths of <1, 1-3 and >3 for carnivorous, omnivorous and herbivorous fishes, respectively. In both approaches, *A. anableps* (1.95) would be considered an omnivorous fish species. As shown in the feeding strategy plot (Fig. 11), *A. anableps* in the Furo do Meio actually had an omnivorous diet, however, dominated by the red algae *Catanelia* sp. Additionally, the long, thin and weak-muscular GIT emphasizes the herbivorous-omnivorous feeding of *A. anableps*, compared e.g. to the compact, strong-muscular stomach of brachyuran crab-feeding *Arius herzbergii* (Brenner, unpubl. data).

Greven et al. (2002) showed that the mouth of *A. anableps* is terminal, orientated slightly downwards and assumed that the genus *Anableps* mainly takes food from the bottom. However, our results render the suggestion of bottom-orientated feeding unlikely due to the clear specialization on the near-surface food resources, the phylogenetic development of the above-water eye, the poor diving capacity (Greven et al. 2002) and the obvious surface swimmer shape of *A. anableps*. In the Furo do Meio *A. anableps* grazed on the epiphyte flora and was observed

foraging for insects fallen from the canopy and skillfully attacking prey (e.g. ants) by jumps on prop roots in the forest around HW, similar to the behavior observed by Wothke & Greven (1998). *G. cruentata* became available when moving on the prop roots close above the water surface during mangrove submergence. Likewise, other prey items (Insecta, Aranae, Littorinidae, Mytilidae) occurred near the water surface. At LW adult *A. anableps* were observed feeding on fish carcasses and making jumps on the mud to catch insects (S Peterhaensel, pers. comm.).

The macroalgae flora attached to the prop roots and pneumatophores of the mangrove trees is dominated by red algae, particularly *Catanelia* sp. co-occurring with *Bostrychia* sp. Red algae was the predominant food item in *A. anableps*, but the average dry weight of the epiphyte flora does not exceed 1 g DW m⁻² (Schories, unpubl. data, in Krause et al. 2001). Considering the different nutritional values of the food items, the arrangement in Figure 11 may distort the real importance of the food items in the diet of *A. anableps*. There is a great difference between weight, number and the nutritional value of the food items found in the GITs of *A. anableps*, e.g. the GITs often contained only the empty, low-weight chitin carapaces of Insecta. A calorimetric estimate instead of a prey-specific weight for the food items would likely facilitate our understanding of the real importance of food items in a fish diet (Amundsen et al. 1996). Such an approach would likely change the interpretation of Figure 11 where *A. anableps* exhibited a generalized feeding strategy with specialization on *Catanelia* sp. to a more mixed feeding strategy with varying degrees of generalization and specialization on prey types like Insecta and Grapsidae (Amundsen et al. 1996). Insecta likely represent an abundant and nutrient-rich food resource for many mangrove fish (Robertson 1988; Krumme et al., subm.).

A. anableps apparently relied entirely on intertidal prey, except when feeding on ubiquitous mud at neap tides. Zahl et al. (1977) and Greven et al. (2002) have suggested that *A. anableps* feed as well on substrate and mud from the water edge. Our results suggest that mud is of minor importance in the diet. It can be assumed that the main food items eaten under the best conditions (at SD) are likely to be the preferred food items for a species (*Catanelia* sp., Insecta, Grapsidae). Furthermore, mud is permanently available throughout time and water level, but was only taken up at neap tides. The sediment surface of the intertidal mangrove slopes contained on average 2.5 % organic carbon per g sample wet weight (Koch 1999), suggesting that mud is just an evasive food item under poor foraging conditions, likely having only poor nutritive value for the fish. However, due to its generalized feeding strategies, it seems *A. anableps* have developed

considerable adaptive elasticity in coping with characteristics of the local food supply and availability.

Population parameters

The preponderance in females does not necessarily reflect a heterogeneous sex relationship in the population. The mesh size suggests the likelihood that smaller males often passed through the net. Although larger females also occur in oviparous fish species, the sex dimorphism in *A. anableps* with females being larger, growing faster and having higher condition factors than males might be linked to the viviparity.

The length-weight relationship for male *A. anableps* was subject to considerable variation (low r^2), due to the small size range covered. However, *A. anableps* clearly showed negative allometric growth with the parameter b being smaller than 3, indicating a fish species that increases more in length than predicted by their increase in weight. We assume that the elongated body is related to acceleration during burst-and-coast escape swimming and active jump attacks toward above-water prey items such as Insecta and Grapsidae. Surface swimmers lose a considerable portion of their swimming energy by generating waves (Videler 1993, p. 195). But burst-and-coast swimming is predicted to save energy by up to 50 % compared to steady swimming at the same average speed (Videler 1993, p. 127). Usually *A. anableps* covered 5-10 m with escape burst-and-coast jumps on the water surface, but in extreme situations several tens of meters were covered (own obs.).

Natural and fishing mortality

In northern Brazil, *A. anableps* is of insignificant commercial importance, though artisanal fishermen occasionally capture *A. anableps* with beach seines at LW in the mangrove channels and with net barriers blocking intertidal creeks at HW for their own use (own obs.). In particular the former method can temporarily cause a significant decrease in population size of a tidal channel like the Furo do Meio (Krumme, own obs.). Natural mortality is likely highest in recently born *A. anableps* (ca. 4 cm TL), mainly due to piscine predation as revealed in stomach analysis of Krumme et al. (subm.). While foraging in the mangrove creeks, *A. anableps* may experience reduced risk of avian predation in the creek network due to the steep creek slopes, and closed canopy. In daylight, egrets (*Casmerodius albus*, *Egretta thula*) may sometimes

capture the smallest sizes while during the nocturnal LW we observed *A. anableps* startled by attacks from fishing bats (*Noctilio leprinus*) that may readily be able to capture even adult *A. anableps*. A recent study by Peterhaensel (pers. comm.) assumes that *A. anableps* exhibit considerable site fidelity on the level of 1st order creeks. Hence, an increase in local artisanal fishery pressure could readily decrease local stock sizes (de Boer et al. 2001).

CONCLUSIONS

The four-eyed fish *A. anableps* exhibited appropriate adaptations to the tidal pulse in the Furo do Meio. At each first rise at flood tide most *A. anableps* rode the tide to enter the intertidal mangrove creeks where they forage for food items at or above the water surface. The HW level determined the accessibility of the intertidal habitat and hence, the quantitative and qualitative composition of the diet.

The combination of spring tide and daytime flooding (SD) clearly provided the best foraging conditions. In contrast, nocturnal flooding at neap tide (NN) provided poorest foraging conditions. Intermediate foraging conditions occurred at SN and ND where darkness diminished the positive effects of high water levels in the former, and daylight increased the poor conditions caused by low water levels in the latter case. Independent of water level, daylight always improved the foraging conditions and creek block net catches produced highest abundances at SD and ND, thus emphasizing the significance of the above-water eye for the successful foraging of *A. anableps*.

Based on prey-specific weight *A. anableps* in the Furo do Meio exhibited an omnivorous feeding strategy with strong specialization on *Catanella* sp. irrespective of size, sex, tide and time of day. The relative length of the GIT further emphasized the adaptation to an herbivorous-omnivorous diet.

Most of the individuals used many resource types simultaneously and differences in the diet compositions were only related to changes in the proportions between the food items. Mud only occurred at neap tides in the GITs and was just an evasive food item.

Further research on *A. anableps* is recommended to extend our knowledge about the tidal movements of mangrove fish on the northeast coast of South America. *A. anableps* provides excellent prerequisites in that it is a relatively resistant species (e.g. for tagging or telemetry), occurs under different tidal regimes, and motion and behavioral patterns can be readily observed.

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REFERENCES CITED

- Al-Hussaini AH (1947) The feeding habits and the morphology of the alimentary tract of some teleosts living in the neighbourhood of the Marine Biological Station, Ghardaqa, Red Sea. *Publ Mar Biol Stat Ghardaqa* 5:1-61
- Amundsen PA, Gabler HM, Staldvik FJ (1996) A new approach to graphical analysis of feeding strategy from stomach contents data - modification of the Costello (1990) method. *J Fish Biol* 48(4):607-614
- Batista VDS, Rêgo FN (1996) Análise de associações de peixes, em igarapés do estuário do Rio Tibiri, Maranhão. *Rev Brasil Biol* 56(1):163-176
- Boltovskoy D (1999) South Atlantic zooplankton. Vol. 1, Vol. 2. Backhuys, Leiden
- Boujard T, Rojas Beltran R (1988) Zonation longitudinale du peuplement ichthyique du fleuve Sinnamary (Guyane Française). *Rev Hydrobiol Trop* 21(1):47-61
- Brenner M, Buck BH, Cordes S, Dietrich L, Jacob U, Mintenbeck K, Schröder A, Brey T, Knust R, Arntz WE (2001) The role of iceberg scours in niche separation within the Antarctic fish genus *Trematomus*. *Polar Biol* 24:502-507
- Cervigón F, Cipriani R, Fischer W, Garibaldi L, Hendrickx M, Lemus AJ, Márquez R, Poutiers JM, Robaina G, Rodriguez B (1993) FAO species identification sheets for fishery purposes:

- Field guide to the commercial marine and brackish-water resources of the northern coast of South America. FAO species catalogue. NORAD & FAO, Rome
- Cinco E (1982) Length-weight relationships of fishes. In: Pauly D, Mines AN (eds) Small-scale fisheries of San Miguel Bay, Philippines: Biology and stock assessment. ICLARM Techn Rep 7, p 34-37
- Clarke KR, Warwick RM (1994) Changes in marine communities: An approach to statistical analysis and interpretation. Plymouth Marine Laboratory. Natural Environment Research Council, U.K.
- Cohen MC, Lara RJ, Szlafsztein CF, Dittmar T (2000) Digital elevation models as a GIS tool for the analysis of mangrove coasts. Amazon Region, Brazil. J Int Environ Creat 3(1):31-41. ISSN 13439863
- Dalpado P, Gjøsæter J (1988) Feeding ecology of the lanternfish *Benthosema pterotum* from the Indian Ocean. Mar Biol 99:555-576
- De Boer WF, Van Schie AMP, Jocene DF, Mabote ABP, Guissamulo A (2001) The impact of artisanal fishery on a tropical intertidal benthic fish community. Environ Biol Fish 61:213-229
- Dittmar T, Lara RJ (2001a) Do mangroves rather than rivers provide nutrients to coastal environments south of the Amazon River? Evidence from long-term flux measurements. Mar Ecol Prog Ser 213:67-77
- Dittmar T, Lara RJ (2001b) Driving forces behind nutrient and organic matter dynamics in a mangrove tidal creek in North Brazil. Estuar Coast Shelf Sci 52:249-259
- Dixon PS, Irvine LM (1997) Seaweeds of the British Isles. British Museum of History, London, Vol 1, 190-191; Vol. 2, 286-289
- Drebes G (1974) Marines Phytoplankton. Thieme Verlag, Stuttgart
- Gibson RN, Pihl L, Burrows MT, Modin J, Wennhage H, Nickell LA (1998) Diel movements of juvenile plaice *Pleuronectes platessa* in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. Mar Ecol Prog Ser 165:145-159
- Greven H, Götz A, Kervath S, Mattig S, Wothke A (2002) Beobachtungen zur Nahrungsaufnahme und zum Fluchtverhalten der Vieraugenfische *Anableps microlepis* and *A. anableps* (Anablepidae, Cyprinodontiformes). In: Riehl R, Greven H (eds) Verhalten der Aquarienfische (2). Birgit Schmettkamp Verlag, Bornheim, p 55-62

- Hayward PJ, Ryland JS (2000) Handbook of the marine fauna of north-west Europe. 4. ed, Oxford University Press
- Hennig W (1986) Taschenbuch der Zoologie, Band 3, Wirbellose. Gustav Fischer Verlag, Jena
- Hoeinghaus DJ, Layman CA, Arrington DA, Winemiller KO (Submitted) Spatiotemporal variation in fish assemblage structure in tropical floodplain creek. Environ Biol Fish
- Kaestner A (1967) Lehrbuch der Speziellen Zoologie, Band 1: Wirbellose. Gustav Fischer Verlag, Stuttgart
- Kjerfve B, de Lacerda LD (1993) Mangroves of Brazil. In: de Lacerda LD (ed) Mangrove ecosystems technical reports ITTO TS-13(2), p 245-272
- Kneib RT, Wagner SL (1994) Nekton use of vegetated marsh habitats at different stages of tidal inundation. Mar Ecol Prog Ser 106:227-238
- Koch V. (1999) Epibenthic production and energy flow in the Caeté mangrove estuary, North Brazil. ZMT Contrib. No. 6, Zentrum fuer Marine Tropenoekologie, Bremen, Germany
- Krause G, Schories D, Glaser M, Diele K (2001) Spatial patterns of mangrove ecosystems: the bragantinian mangroves of northern Brazil (Bragança, Pará). Ecotropica 7:93-107
- Krumme U (Submitted) Patterns in the tidal migration of fish in a North Brazilian mangrove channel as revealed by vertical beaming using a 200 kHz split-beam sonar. Fish Res
- Krumme U, Saint-Paul U (2003) Observations of fish migration in a macrotidal mangrove channel in Northern Brazil using a 200-kHz split-beam sonar. Aquat Living Resour 16(3):175-184
- Krumme U, Saint-Paul U, Rosenthal H (Submitted) Tidal and diurnal changes in the structure of a nekton assemblage in small intertidal mangrove creeks in northern Brazil. Aquat Living Resour
- Lara RJ, Dittmar T (1999) Nutrient dynamics in a mangrove creek (North Brazil) during the dry season. Mangroves Salt Marshes 3:185-195
- Lawrie SM, Speirs DC, Raffaelli DG, Gurney WSC, Paterson DM, Ford R (1999) The swimming behaviour and distribution of *Neomysis integer* in relation to tidal flow. J Exp Mar Biol Ecol 242(1):95-106
- Mattig S, Greven H (1994a) Observations on the agonistic behaviour of the four-eyed fish *Anableps anableps* (Linne, 1758) (Anablepidae, Cyprinodontiformes). Z Fischkd 2(2):113-149

- Mattig S, Greven H (1994b) Observations on courtship and mating behaviour of the four-eyed fish *Anableps anableps* (Linne, 1758) (Anablepidae, Cyprinodontiformes). *Z Fischkd* 2(2):167-192
- Miller RR (1979) Ecology, habits and relationships of the middle America cuatro ojos, *Anableps dowi* (Pisces: Anablepidae). *Copeia*, 1:82-91
- Odum WE (1970) Utilization of the direct grazing and plant detritus food chains by the striped mullet *Mugil cephalus*. In Steele JH (ed) *Marine food chains*. Oliver and Boyd, Edinburgh, p 222-240
- Oliveira AME (1972) Peixes estuarinos do nordeste oriental brasileiro. *Arq Cien Mar* 12:35-41
- Oliveira AME (1976) Composicao e distribuicao da ictiofauna nas aguas estuarinas do rio Jaguaribe (Ceara - Brazil). *Arq Cien Mar* 16:9-18
- Paterson AW, Whitfield AK (2000) Do shallow-water habitats function as refugia for juvenile fishes? *Estuar Coast Shelf Sci* 51:359-364
- Ricard M (1987) *Atlas du phytoplancton marin, Vol 2*. Ed du CNRS, Paris
- Ricker WE (1975) Computation and interpretation of biological statistics of fish population. *Bulletin of the Fisheries Research Board of Canada*, 191
- Robertson AI (1988) Abundance, diet and predators of juvenile banana prawns, *Penaeus merguensis*, in a tropical mangrove estuary. *Aust J Mar Freshwat Res* 39:467-478
- Schmidt de Melo GA (1996) *Manual de identificação dos brachyura (caranguejos e siris) do litoral brasileiro*. Museo de Zoologia, Universidade de São Paulo
- Schwassmann HO (1967) Orientation of Amazonian fishes to the equatorial sun. In: Lent H (ed.) *Atlas do Simpósio sobre a Biota Amazônica (Belém, Brazil)*, p 201-220.
- Schwassmann HO (1971) Biological rhythms. In: Hoar WH, Randall DJ (eds) *Fish physiology* VI. Academic Press, New York, p 371-428
- Sivak J (1976) Optics of the eye of the "four-eyed fish" (*Anableps anableps*). *Vision Res.* 16(5): 531-534.
- Spalding M, Blasco F, Field CD (1997) *World mangrove atlas*. International Society for Mangrove Ecosystems, Okinawa
- Tucker R, Dance SP (1986) *Compendium of seashells*. American Malacologists. Inc, 5. Aufl., Melbourne, Florida
- Videler JJ (1993) *Fish swimming*. Fish and Fisheries Series 10, Chapman & Hall, London

- Wothke A, Greven H (1998) Field observations on four-eyed fishes, *Anableps anableps* (Anablepidae, Cyprinodontiformes), in Trinidad. *Z Fischkd* 5(1):59-75
- Wright JM, Clayton DA, Bishop JM (1990) Tidal movements of shallow water fishes in Kuwait Bay. *J Fish Biol* 37:959-974
- Xiao Y (1998) What are the units of the parameters in the power function for the length-weight relationship? *Fish Res* 35:247-249
- Zahl PA, McLaughlin JJA, Gomprecht RJ (1977) Visual versatility and feeding of the four-eyed fishes, *Anableps*. *Copeia* 4:791-793

Erklärung:

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

Bremen, den 28. August 2003

Uwe Krumme

