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Analysis of the Benthic Food Web of a Mangrove Ecosystem at Northeastern Brazil

Analyse des benthischen Nahrungsnetzes eines Mangrovenökosystems im Nordosten Brasiliens

by

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1. Summary

The benthic food web of the mangal sector of the mangrove ecosystem of the Canal de Santa Cruz estuary at northeastern Brazil (Pernambuco State) was analyzed from March 1995 until February 1996. Several field as well as tank experiments were conducted to elucidate the trophic structure of this zone. The checkered puffer, *Sphoeroides testudineus*, the southern periwinkle, *Littorina scabra angulifera*, and the brachyurans *Goniopsis cruentata*, *Aratus pisonii*, *Uca maracoani*, *U. thayeri*, *Ucides cordatus*, *Cardisoma guanhumi* and *Callinectes danae* were chosen as representative central target or trophic key species during the study. The trophic distances and the nutritional interactions between all animal species and food sources in the mangal were evaluated applying 24h-analyses of the relative weight of gastro-intestinal contents, monodietary experiments, starvation experiments and the method of stable isotopes of the chemical elements carbon, nitrogen and sulfur. Multiple transect sweep-sampling was conducted to determine the total plant and animal biomass in the area. The specific primary production rates of the mangrove species *Rhizophora mangle*, *Avicennia marina*, *Conocarpus erecta*, and *Laguncularia racemosa* (growth, litterfall), and of the epiphyte groups Chlorophyta and Phaeo-/ Rhodophyta (pooled) were obtained from additional monthly samplings.

The total standing plant biomass of the mangal (27.7 km^2) was 738 205 tonnesDW or $26.65 \cdot 10^3$ $gDW \cdot m^{-2}$ (DW = dry weight). The mangrove flora was dominated by *R. mangle* (392 509 tonnesDW or $14.17 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$) and *A. marina* (228 525 tonnesDW or $8.25 \cdot 10^3$ $gDW \cdot m^{-2}$). *L. racemosa* and *C. erecta* together contributed just 13.6 % (97 504 tonnesDW or $3.52 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$) to the total mangrove tree biomass of 718 538 tonnesDW or $25.94 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$. The standing biomass of epiphytes within the mangrove canopy was negligible at 831 tonnesDW or $0.03 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$. Insignificant biomasses were also observed for the seagrass *Halodule wrightii* (277 tonnesDW or $0.01 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$) and for diverse terrestrial plants ($20.30 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$) at the upper periphery of the mangal zone.

The annual total plant biomass production in the Canal de Sta. Cruz mangal was 117 478 tonnesDW or 49 232 tonnes of organic carbon. One outstanding result of the present study is that benthic and epiphytic algae contribute 59.4 % dry weight or 47.0 % organic carbon to this annual production although they represent only 2.4 % of the benthic total standing plant biomass in the area. The algae had a total standing biomass of 18 005 tonnesDW or $0.65 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$. The chlorophyte fraction had a standing biomass of 10 249 tonnesDW or $0.37 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$ while the phaeo-/ rhodophyte pool made up 7 756 tonnesDW or $0.28 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$. The relative annual organic carbon primary production (through litterfall) of the mangroves trees representing 53.0 % of the primary production is low compared to the enormous rate of epiphyte biomass production in relation to their standing biomass.

The average biomass of all macro-zoobenthic trophic key species in the mangal (27.7 km^2) was 20.486 $gFW \cdot m^{-2}$ or 567.5 tonnesFW (FW = fresh weight). The biomass graduation (descending) was *G. cruentata* (235.8 tonnesFW, 8.5 $g \cdot m^{-2}$), *C. danae* (162.2 tonnesFW, 5.6 $g \cdot m^{-2}$), *U. maracoani* (81.2 tonnesFW, 2.9 $g \cdot m^{-2}$), *S. testudineus* (30.5 tonnesFW, 1.1 $g \cdot m^{-2}$), *A. pisonii* (23.5 tonnesFW, 0.8 $g \cdot m^{-2}$), *C. guanhumi* (11.4 tonnesFW, 0.4 $g \cdot m^{-2}$), *U. cordatus* (10.1 tonnesFW, 0.4 $g \cdot m^{-2}$), *L.s.angulifera* (8.9 tonnesFW, 0.3 $g \cdot m^{-2}$), and *U. thayeri* (3.8 tonnesFW, 0.1 $g \cdot m^{-2}$).

The dry-weight amount of food required per year AR_{DW} (expressed as % body fresh weight, %BFW) as well as the intensity and timing of the daily feeding periods was found extremely different between species. *G. cruentata* (959 %BFW), *A. pisonii* (1 311 %BFW), and *L.s.angulifera* (868 %BFW) fed during the day and nighttime. The feeding activity of *C. guanhumi* and *U. cordatus* was restricted to nighttime. *U. maracoani* (3 216 %BFW), *U. thayeri* (7 827 %BFW), *C. danae* (1 230 %BFW), and *S. testudineus* (1 210 %BFW) were observed feeding only during the daytime. The temporal variations were mainly induced by predation response behavior. The quantitative variations were caused by general energetic requirements and different nutrient contents of the food sources. All animals displayed filling-level dependent evacuation rates of their gastro-intestinal tracts. The software-based data

analysis of the 24h-field experiments was confirmed by 24h-tank experiments under controlled environmental conditions and by starvation experiments as a secondary methodical approach to determine the individual evacuation rates of the animals.

The annual total food requirement of the benthic trophic key species was 7 827 tonnesDW or 10 819 tonnesFW. It consisted of a plant biomass of 4 080-7 268 tonnesFW and an animal biomass of 3 551-6 739 tonnesFW per year. The annual fresh-weight food requirement of all trophic key species combined was 19.8 fold their standing biomass. The provision of a sufficient plant biomass was managed without great exertion by the mangrove ecosystem because the annual plant biomass production of 117 478 tonnesDW exceeded the food requirements of the strictly herbivorous *A. pisonii* and *L.s.angulifera* by 209 fold. The annual food requirements of all carnivorous trophic key species of 3 551 tonnesFW could not be produced by the benthic mangal ecosystem alone. The blue crab, *C. danae*, as well as the fish *S. testudineus* were dependent on food sources outside the mangal ecosystem. It is concluded that the benthic food web of the Canal de Sta. Cruz mangal can be divided into a self-contained herbivorous or omnivorous and a non-self-contained carnivorous compartment.

The complete daily light cycle as well as the entire three-dimensional extension of the mangal was utilized by the zoobenthic community monitored. Vertical migrations into canopy heights of up to 7 m were observed. Morphological and behavioral adaptations to particular ecological and nutritional niches, direct predation responses as well as temporal predator avoidance strategies, particular feeding strategies and multi-individual social behavior determine the structure of the mangal macro-zoobenthos. Preferences for *R. mangle* were observed for the red mangrove crab, *G. cruentata*, *A. pisonii*, and *L.s.angulifera*. The mangrove tree crab, *A. pisonii*, showed significantly different population structures at different canopy heights. Groupwise foraging behavior was observed for *C. guanhumi*. The small fiddler crab, *U. thayeri*, displayed a much more developed social behavior than the larger *U. maracoani* which lives in isolated burrows at the muddy plains.

With the exception of *U. maracoani*, *U. thayeri*, and *L.s.angulifera*, no species displayed a restriction to one or two single food sources. Of all species tested *G. cruentata* showed the most evolved generalism concerning the utilization of potential food sources. However, the crab had a preference for benthic crustaceans within its reach. Live and moving *A. pisonii* as well as *Uca* specimens were preferred. Of the mangrove leaves, *A. marina* litter was preferred, and phaeophyte and rhodophyte benthic or epiphytic algae were selected over chlorophytes. *A. pisonii* strongly preferred a plant diet over any kind of animal prey including carrion. Live animals were never accepted. Chlorophyte algae were preferred over others, and epiphytic growth forms were preferred over benthic ones. *C. danae* showed exclusive carnivorous feeding behavior, but no cannibalism. Live *Aratus pisonii* were preferred, followed by live *U. thayeri*, *U. maracoani*, *G. cruentata*, *Penaeus schmitti* and *P. brasiliensis*. Of the fish species tested, *S. testudineus* was the least preferred. The fiddler crabs, *U. maracoani* and *U. thayeri*, accepted no other food sources than the benthic surface layer of detritus and microalgae. *C. guanhumi* strongly preferred a mango fruit mix over decayed carrion of any kind. *U. cordatus* also displayed a strong preference for the mangrove fruit mix, but accepted only fruits that were already decomposed. Other than *C. guanhumi*, *U. cordatus* was preferably herbivorous concerning the rest of its food range. *S. testudineus* fed on penaeids and live or fresh food in general. Brachyurans as food sources ranked (descending) from *U. maracoani* over *U. thayeri* and *A. pisonii* to *G. cruentata*. The periwinkle *L.s.angulifera* was preferred over *C. danae* which was accepted alive or dead depending on its size. *L.s.angulifera* itself preferred chlorophyte over phaeophyte and rhodophyte algae.

In contrast to the mangal phytobenthos of the mangrove ecosystem of the Canal de Sta. Cruz with its enormous primary production and plant biomass output to neighboring systems and its indisputable function as a nursing area, feeding ground and refuge to a variety of organisms, the zoobenthic mangal section of the ecosystem is a self-contained rim system of only minor importance concerning its animal biomass output. It is questioned whether there exists any notable export of benthic animal biomass at all. Only in combination with the open channel and the estuarine region as a whole, the ecological significance of the specific structure of the animal and plant community of the mangal segment of the Canal de Sta. Cruz mangal can be understood.

2. Introduction

For numerous reasons tropical mangrove forests are among the most valuable coastal ecosystems in the word (Lugo et *al.* 1973; Lugo & Snedaker 1974; Saenger et *al.* 1983; Hutchings & Saenger 1987; Birkeland & Grossenbaugh 1984; Bunt 1992; Robertson & Blaber 1992; Zabi & Le-Loeuff 1993; Lacerda 1994). They serve as nursing grounds for a huge number of commercial and non-commercial vertebrate (Pool 1973; Phillips 1981, 1983; Vasconcelos Filho et *al.* 1984; Pauly & Ingles 1986; Robertson & Duke 1987, 1990a, 1990b; Twilley 1988; Mastaller 1989; Blaber & Milton 1990; Flores Verdugo et *al.* 1990; Morton 1990; Dennis 1992; Thollot 1992; Tzeng & Wang 1992; Börner 1994; Teixeira 1994) as well as invertebrate marine species (Warner 1977; Bliss 1982, 1982-85; Staples et *al.* 1985; Morgan 1987; Epifanio 1988; Robertson 1988; Dittel & Epifanio 1990; Camilleri 1992; Newell et *al.* 1995). The ecological intactness of the ecosystem is of enormous socio-economical importance to the human populations in most tropical coastal regions, particularly in developing countries (Snedaker 1978; Ajana 1980; FAO 1983; Matthes & Kapetsky 1988; Hamilton et *al.* 1989; Azevedo et *al.* 1990; Aksornkoae et *al.* 1993; Kjerfve & Lacerda 1993; Ajiki 1994; Siddiqi 1994).

The coastal management of mangrove areas is highly complex (Hamilton & Snedaker 1984; Hanley & Couriel 1992). The continuous worldwide deforestation of mangrove forests for the purpose of industrial, urban and aquaculture land claiming (Davis 1938; Hutchings & Recher 1977; Rabanal 1977; Sundararaj 1978; Cintrón & Shaeffer Novelli 1983; Nogueira Paranagua & Eskinazi 1985; Mahmood 1986; Lahmann et *al.* 1987; Zamora 1988; Chua et *al.* 1989; Mastaller 1989; Aiken 1990; Larsson 1992; Pillay 1992; Rosenberry 1992; Ajiki 1994; Peng 1994) destroys the natural protection against abrasion and erosion along extended stretches of tropical coastline (Zamora 1988; Smith 1992; Diop 1993; Pernetta & Elder 1993; Othman 1994; Mastaller 1996). Today, even the function as one of our planet's most important carbon sinks diminishing the greenhouse effect has been acclaimed to the worldwide mangrove ecosystems (Wollast 1991; Twilley et *al.* 1992).

The detailed investigation of organic carbon cycling in estuarine and marine environments has stimulated the development of multidisciplinary concepts, research and sampling strategies as well as analytical tools over the last 10 years. Although intensive research has been carried out on various biological and economical aspects, integrate analyses of the ecological interaction of mangrove organisms are still sparse. While the demersal fish communities of the open water regions of channels and estuaries have received considerable scientific interest, other biotope zones of the mangrove ecosystem or even whole classes of animals have been left out. The ecological and particularly the trophic interactions in the intertidal mangrove tree zone or mangal with its benthic invertebrate animal community are still poorly understood (Boto 1982; Alongi 1987; Alongi & Sasekumar 1992). Biomass and primary production in the mangal are still reduced to and accepted as mangrove tree growth and mangrove litterfall leaving out all other sources like epiphytes and algae of the upper sediment layer (Zaninetti et *al.* 1977, 1979; Cordero 1978; Dobrovol'skiy 1978; Bunt & Williams 1980; Alongi 1988, 1990; Woodroffe et *al.* 1988; Boto et *al.* 1989; Daniel & Robertson 1990; McIvor & Smith 1995). The consumer food web and internal pathways of nutrients inside the mangal as well as the origin of animal biomass exported to neighboring biotopes are surprisingly unexplored and are thus the subject of this study.

One reason for the inadequate research on the trophic structure of the mangal benthos was the lack of applicable methods for the tracing of nutrients along food chains. This situation has

changed since the introduction of stable isotope analyses to nutritional biology. Depending on the number of chemical elements included in the analysis, the biochemical „origin" of consumer body tissue can now be determined more or less exactly. The usual homogenous gastro-intestinal contents of benthic invertebrates such as crabs and mollusks can now be ascribed to definite food sources. In combination with a quantification of food requirements of the single consumers, a conclusive model of the mangal food web could be developed stretching from different sources of primary production to the export level from the biotope. The study should nevertheless not be understood as a quantitative tool for a fishery management because numerous aspects such as population dynamics of the target species and the temporal immigration of animals from neighboring systems were not quantified but only included into the discussion of the results.

The Canal de Sta. Cruz, 55 km north of the city of Recife, Pernambuco State, northeastern Brazil, is a shallow estuarine mangrove ecosystem hydrologically influenced by six small rivers from the mainland and Itamaracá Island which forms the eastern coastline of the channel. Live mangrove trees cover 27.7 km^2 of the total area of the estuarine system of 35.0 km^2. The combination of old and new research methods developed for the experiments and the results of the study are presented in a way to be generally applicable to mangrove ecosystems in other geographical regions. The biological structure of the Canal de Sta. Cruz mangal is however immediately representative for large parts of the coastline of northeastern Brazil.

Various ecological aspects of the coastal ecosystem of Itamaracá have already been studied (Nogueira Paranagua & Eskinazi Leca 1985). Research has been conducted on the physical and chemical characteristics of the water, on the planktonic, on benthic and ichthyological communities (Cavalcanti Atunes 1978; Vasconcelos Filho 1979, 1980; Gomes de Azevedo 1980; Ramos Porto 1980; Wallner et *al.* 1986; Souza 1993; Börner 1994; Souza et *al.* 1994; Coelho & Ramos-Porto 1995; Torbohm-Albrecht 1995). Experiments on extensive fish cultures were also conducted (Macêdo et *al.* 1989). The results obtained to this date reveal that the Canal de Sta. Cruz ecosystem has broad possibilities for economic exploitation. Its hydrological (Medeiros de Queiros 1991; Medeiros & Kjerfve 1993) and planktonic characteristics demonstrate that the entire region exhibits eutrophic conditions due to the continuous input of nutrients and the consequent high concentration of planktonic organisms available, especially diatoms, phytoflagellates and copepods which, in turn, can support different fish, crustacean and mollusk populations. At the northern and southern areas of the Santa Cruz channel, Vasconçelos et *al.* (1984) conducted stomach content studies on various fish species. Costa & Macêdo (1989) and Macêdo & Costa (1990) conducted chemical and physical studies in the Timbo and Iguaraçu River Estuary at Itamaracá, near the Santa Cruz channel, and made a hydrological survey in the area to detect signs and effects of industrial pollution. The estuary showed high levels of some of the parameters monitored (alkalinity, material in suspension, silicate), but the authors concluded that the area doesn't yet reveal biologically critical conditions, because dissolved oxygen saturation was still exceeding 50 %.

The initial selection of the key organisms to be analyzed during the project was based on the apparent magnitude of their proportional standing biomass fraction as well as on the hypothesis of their prominent quality as central crossing points within the food web of the mangal segment of the Canal Sta. Cruz mangrove ecosystem. The total of 9 trophic key animal species (consumers) included organisms from different taxonomic classes e.g. one fish, seven brachyuran crabs and one gastropod species, thus covering a broad hypothetical range of feeding modes (Ellison & Farnsworth 1992). The checkered puffer, *Sphoeroides testudineus* (Tetraodontidae), and the blue crab *Callinectes danae* (Portunidae) represented a holo-aquatic division of the mangal food web (Robins & Ray 1986; Epifanio 1988). The

terrestrial or amphibious crabs *Cardisoma guanhumi* and *Ucides cordatus* (Gecarcinidae, Grapsoidea) inhabit the transition zone between the upper littoral and the adjacent coconut-tree zone (Herreid 1963; Zanders & Martelo 1984; Innes & Taylor 1986; Tuerkay 1987; Turrin et *al.* 1992; Harris et *al.* 1993; Nascimento 1993). The mangrove tree crab, *Aratus pisonii* (Grapsidae), and the southern periwinkle, *Littorina scabra angulifera* (Littorinidae, Prosobranchia, Gastropoda), extend the mangal food web into the mangrove tree canopy (Gallagher & Reid 1974; Conde & Diaz 1989a; Cook & Garbett 1989). The fiddler crabs, *Uca maracoani* and *U. thayeri* (Ocypodidae), are permanent exclusive residents of the muddy plains inside and neighboring the inner mangal zone (Salmon 1987; Ewa-Oboho 1993). The red mangrove crab, *Goniopsis cruentata* (Grapsidae), living within the mangrove root thicket and having the capability to climb the trees as well as to enter the aquatic zone was selected as the hypothetical predatory or omnivorous central trophic key species of the food web to be analyzed (Bingham 1992; Santos & Costa 1993).

After being designed for the geological, paleontological (Sternberg et *al.* 1986; MacLeod & Hoppe 1992) and paleo-climatological (Mackensen et *al.* 1989; Hertelendi & Veto 1991; Charles & Fairbanks 1992) sciences, the employment of the method of stable isotopes for the analysis of food chains is slowly becoming a new and universal standard method (Rau et *al.* 1983; Wada et *al.* 1991; Hemminga, et *al.* 1994). Some 85 % of the literature on the application of the stable isotope method are still of geological, geochemical and/ or paleontological nature. However, conclusive biological research has already been conducted on limnic systems (Raven 1990; Spiro & Pentecost 1991), on marine systems (Deegan et *al.* 1990), on aquaculture aspects (Ye et *al.* 1991), and mangrove food webs in general (Rodelli et *al.* 1984; Hoffman et *al.* 1990, 1991; Lacerda et *al.* 1986; Robertson et *al.* 1992; Rao et *al.* 1994). Nevertheless, care has to be taken not to overstress the capabilities of this new method. Most times, the indubitable identification of two single food sources is unrealizable due to a significant overlap of almost identical isotope values or due to methodical bias exceeding narrow ranges of natural isotope values to be traced. Additionally, the variability of the isotope values even between different parts of one single plant specimen (Keeley 1990; Lin et *al.* 1991) or between body organs of one single animal may be very high (Sholto Douglas et *al.* 1991). Stephenson et *al.* (1984) as well as Fenton & Ritz (1989) for example questioned the value of the stable isotope tracing in food webs containing macroalgae. However, it is generally accepted that, since very little carbon isotope discrimination occurs in aerobic food chains subsequent to the primary production process, the $\delta^{13}C$-values of aerobic heterotrophs (biophages and necrophages) reflected the values of their ultimate photosynthetic food source (Rodelli et *al.* 1984).

A combination of field observations as well as different field and tank experiments will constitute a general approach to the trophic structure of the Canal de Sta. Cruz mangal. Feeding experiments will reveal general food preferences of the animals and successive 24h-experiments analyzing the relative weight of gastro-intestinal contents will serve quantitative data. Tank experiments conducted as 24h-experiments and as starvation experiments conducted under controlled environmental conditions will permit a determination of the significance of the respective field data. Over a period of 14 months, analyses of the natural stable isotope values of carbon, nitrogen and sulfur of all primary producers and consumers will allow the creation of a basic model of trophic interactions. Monodietary tank experiments on the time-dependent conversion of stable isotopes of specific food sources to isotope values of consumer body tissue will provide information to relativize the stable isotope values in the field. The combination of innovative quantitative and qualitative methodical approaches will thus lead to a first-time integrate assessment of the trophic structure and the significance of the mangal segment of a mangrove ecosystem.

3 Materials and Methods

Table 1: Explanations of technical terms, definitions and abbreviations used in the present study. The page numbers refer to additional comments or the first appearance in the text.

technical term	comment / definition	page
AR_{DW}	dry-weight annual food ratio (0.1 %BFW): quantitative food requirement per year expressed as percentage of BFW	37
$AReq_{FW}$	fresh-weight annual food requirement (kg)	128
ATMN (standard)	atmospheric nitrogen isotope standard	51
BFW	body fresh weight (0.1 g): fresh weight of whole animal (all extremities intact), excluding adhesive dirt, including weight of the gastro-intestinal content	34
CDT (standard)	international sulfur isotope standard derived from Canon Diabolo triolite (CDT)	51
CSA	Central and South America(n)	26
DR_{DW}	dry-weight daily food ratio (0.1 %BFW): quantitative food requirement per day as percentage of BFW	37
DS	dry season at the study site: September - December*	26
DW	dry weight (0.1 g): weight of material after 48 h at 65°C, treatment corresponding to BFW	46
EHWN, EHWS, ELWN, ELWS	extreme high (low) water during neap (spring) tides: maximum or minimum annual water level including short-term wave action, but excluding the spray zone	44
$ER_{dep.}$	filling-level (GIC) dependent evacuation rate: expressed as % GIC · h^{-1}	37
$ER_{indep.}$	filling-level (GIC) independent evacuation rate: expressed as % GIC · h^{-1}	37
ERS	early rainy season at the study site: January - April*	32
f_{AR}	annual fresh-weight food requirement (BFW) ($f_{AR} = DR_{DW} \cdot 365\ d \cdot f_{DF} \cdot 100^{-1}$)	37
f_{DF}	conversion factor from dry to fresh weight of GIC	61
FW	fresh weight (0.1 g): weight excluding adhesive dirt	46
GIC, gastro-intestinal content	relative dry weight of the entire material within the complete alimentary tract from the esophagus to the anus(0.1 %BFW), including gastro-vascular and digestive fluids	34
LRS	late rainy season at the study site: May - August*	32
mangal (zone, segment)	area of mangrove tree growth that creates typical habitats (substrate, root thicket, canopy, etc.), including tidal creeks and puddles in the area, but excluding the open channel region of the Canal de Sta. Cruz	26
non-target (animal) species	animal species which were exclusively analyzed for their function as food source to the trophic key species	33
sweep-sampling	sampling strategy aiming on the complete removal of all trophic key organisms from the sampling area	45
PE	polyethylene	27

Table 1: continued. Explanations of technical terms, definitions and abbreviations used in the present study. The page numbers refer to additional comments or the first appearance in the text.

technical term	comment / definition	page
PDB (standard)	international calcium carbonate standard derived from a Cretaceous Pee Dee formation at South Carolina, USA. Its absolute $^{13}C/^{12}C$ ratio of 0.0112372 has been assigned the $\delta^{13}C$ value of 0 ‰	51
PDS	peak dry season at the study site: November*	26
PRS	peak rainy season at the study site: June - July*	26
r_B	range of (standing) biomass: relation between the maximum and minimum (standing) biomass per area	96
RS	rainy season at the study site: January - August*	26
trophic key (animal) species	animal species which were analyzed both for their function as food and consumers within the food web of the Canal de Sta. Cruz mangal; syn. "target species" see also „non-target species"	44
TRS	transect sweep-sampling: complete removal of all target animal species along a line cutting through the Canal de Sta. Cruz mangal	44
standing biomass	biomass of a particular organism within the study area at a particular time (sampling event)	41
upper intertidal zone	intertidal area above 50% of the water level range between ELWS and EHWS	53
WILCOXON-test	distribution-free non-parametric paired comparison of observations (Wilcoxon & Wilcoxon 1964)	52

*: from Medeiros & Kjerfve 1993

3.1 General Experimental Approach

From March 1995 until February 1996, several field and tank experiments were conducted to analyze the trophic structure of the benthic mangal segment of the mangrove ecosystem of the Canal de Santa Cruz estuary at northeastern Brazil (Pernambuco State). Four types of experiments were conducted:(1) standard field and tank observations of the general and nutritional behavior of the trophic key organisms monitored, (2) analyses of the population structures of the trophic key organisms monitored, (3) qualitative alimentary experiments in the field and under tank conditions, (4) quantitative alimentary experiments in the field and under controlled tank conditions. The latter two types formed the central part of the research project. A chronological schedule of all experiments conducted in the course of the project is given in Table 2. A contemporaneous analysis of the planktonic ecosystems of the Canal de Sta. Cruz area was conducted by Schwamborn (1997). The results from both research projects will later be combined for an integrated approach to the nutrient flux within the estuarine system.

In addition to standard ecological methods, the primary research strategies that are presented here were accomplished through application of the following experimental techniques: (1) 24h-analyses of gastro-intestinal contents, (2) monodietary experiments, (3) starvation experiments, (4) analyses of the stable isotopes of the chemical elements carbon $\delta^{13}C$ ($^{13}C/^{12}C$), nitrogen $\delta^{15}N$ ($^{15}N/^{14}N$), and sulfur $\delta^{34}S$ ($^{34}S/^{32}S$) within the food chains.

Table 2: Chronogramm of the field, tank and laboratory experiments conducted in the Canal d Sta. Cruz mangrove ecosystem, Pernambuco State, northeastern Brazil between February 1995 an March 1996. The tank experiments were conducted at the field station of the Department o Oceanography, Federal University of Pernambuco, Itamaracá Island. Asterisks mark experiments tha were repeated every month. These experiments are only listed at first appearance. **ERS** = early rain season; **LRS** = late rainy season; **RS** = rainy season.

month	date	experiment type	chapter in text
February 1995	[1]15. - 25.	Observations of general behavior in the field **- all trophic key species -**	3.4
	*15.	Monthly sampling for stable isotope ratios in the field: **- all trophic key species - - all food sources -**	3.5.4
	*15.	Monthly sampling for mangrove litterfall	3.6
	*15.	Monthly sampling for epiphyte biomass production	3.6
	21. - 28.	Installation and test runs of tank facility	3.3 & 3.5.1
March	01. - 06.	Observations of general feeding behavior in the field	3.5.1
	06. - 08.	Installation of tank environments and observations of general behavior under tank conditions	3.3 & 3.5.1
	09. - 14.	Observations of general feeding behavior under tank conditions	3.5.1
	16. - 21.	Starvation experiments, RS_{1995}: **- all trophic key species except -** *C. guanhumi* and *U. cordatus*	3.5.3
	24. - 25.	24h-field experiment, ERS_I: *G.cruentata*	3.5.2
	26. - 27.	24h-field experiment, ERS_I: *A.pisonii*	3.5.2
	30. - 31.	24h-tank experiment, ERS_I: *G.cruentata*	3.5.2
April	03. - 04.	24h-tank experiment, ERS_I: *A.pisonii*	3.5.2
	05. - 06.	24h-field experiment, ERS_I: *U.maracoani*	3.5.2
	09. - 10.	24h-field experiment, ERS_I: *L.s.angulifera*	3.5.2
	12. - 13.	24h-field experiment, ERS_I: *C.danae*	3.5.2
	15. - 16.	24h-tank experiment, ERS_I: *U. thayeri*	3.5.2
	18. - 19.	24h-tank experiment, ERS_I: *U.maracoani*	3.5.2
	20. - 21.	24h-tank experiment, ERS_I: *L.s.angulifera*	3.5.2
	24. - 25.	24h-field experiment, ERS_I: *S. testudineus* and *U. thayeri*3.5.2	3.5.2
	27. - 28.	24h-tank experiment, ERS_I: *C.danae*	3.5.2
May	02. - 03.	24h-tank experiment, ERS_I: *S. testudineus*	3.5.2
	08. - 09.	24h-field experiment, LRS_I: *G.cruentata*	3.5.2
	10. - 11.	24h-field experiment, LRS_I: *A.pisonii*	3.5.2
	20. - 21.	24h-field experiment, LRS_I: *U.maracoani*	3.5.2
	22. - 23.	24h-field experiment, LRS_I: *S. testudineus* and *U. thayeri*3.5.2	
	25. - 26.	24h-field experiment, LRS_I: *C.danae*	3.5.2
	03. - 30.	Monodietary experiments, RS_{1995} *G.cruentata*	3.5.5
	15.05. - 10.06.	Monodietary experiments, RS_{1995} *U.maracoani, U. thayeri, L.s.angulifera, A.pisonii*	3.5.5

Table 2: continued: Chronogramm of the field, tank and laboratory experiments conducted in the Canal de Sta. Cruz mangrove ecosystem, Pernambuco State, northeastern Brazil between February 1995 and March 1996.

month	date		experiment type	chapter in text
June	07. - 08.		24h-tank experiment, LRS_I: *G.cruentata*	3.5.2
	09. - 10.		24h-tank experiment, LRS_I: *A.pisonii*	3.5.2
	12. - 13.		24h-tank experiment, LRS_I: *U.maracoani*	3.5.2
	15. - 16.		24h-tank experiment, LRS_I: *U. thayeri*	3.5.2
	17.		Determination of standing biomass in the field (LRS_I: 4 000m^2)	3.6
	19. - 20.		24h-field experiment, LRS_I: *L.s.angulifera*	3.5.2
		+	24h-tank experiment, LRS_I: *L.s.angulifera*	3.5.2
	21. - 22.		24h-tank experiment, LRS_I: *C.danae*	3.5.2
	26. - 27.		24h-tank experiment, LRS_I: *S. testudineus*	3.5.2
July	01. - 25.		Monodietary experiments, RS_{1995} *S. testudineus, C.danae, C. guanhumi, U. cordatus*	3.5.5
August	01. - 31.		Laboratory analyses of stable isotopes	3.5.4 & 3.12
September through **December**	01. - 31.		Laboratory analyses of stable isotopes	3.5.4 & 3.12
	01. - 31.		Preliminary data analyses	3.7 & 3.13
January 1996	15. - 16.		24h-field experiment, ERS_{II}: *G.cruentata*	3.5.2
		+	24h-tank experiment, ERS_{II}: *G.cruentata*	3.5.2
	17. - 18.		24h-field experiment, ERS_{II}: *A.pisonii*3.5.2	
		+	24h-tank experiment, ERS_{II}: *A.pisonii*	3.5.2
	19. - 20.		24h-field experiment, ERS_{II}: *U.maracoani*	3.5.2
		+	24h-tank experiment, ERS_{II}: *U.maracoani*	3.5.2
	22.		Determination of standing biomass in the field (ERS_I: 4 000m^2)	3.6
	27. - 28.		24h-field experiment, ERS_{II}: *L.s.angulifera*	3.5.2
		+	24h-tank experiment, ERS_{II}: *L.s.angulifera*	3.5.2
	29. - 30.		24h-field experiment, ERS_{II}: *C.danae*	3.5.2
		+	24h-tank experiment, ERS_{II}: *C.danae*	3.5.2
	31. - 01.02.		24h-field experiment, ERS_{II}: *S. testudineus* and *U. thayeri*3.5.2	
February	02. - 03.		24h-tank experiment, ERS_{II}: *S. testudineus*	3.5.2
	04. - 05.		24h-tank experiment, ERS_{II}: *U. thayeri*	3.5.2
	07. - 12.		Starvation experiments, RS_{1996}: **- all trophic key species except -** *C. guanhumi* and *U. cordatus*	3.5.3
	13. - 14.		Determination of standing biomass in the field (ERS_{II}: 20 000m^2)	3.6
	16.02. - 10.03.		Monodietary experiments, RS_{1996} *G.cruentata*	3.5.5
	25.02. - 10.03.		Monodietary experiments, RS_{1996} *U.maracoani, U. thayeri, L.s.angulifera, A.pisonii*	3.5.5
March	01. - 25.		Monodietary experiments, RS_{1996} *S. testudineus, C.danae, C. guanhumi, U. cordatus*	3.5.5

[1]: intermediate (in the main monthly) repetitions during the entire run of the project

3.2 Geography and Climate

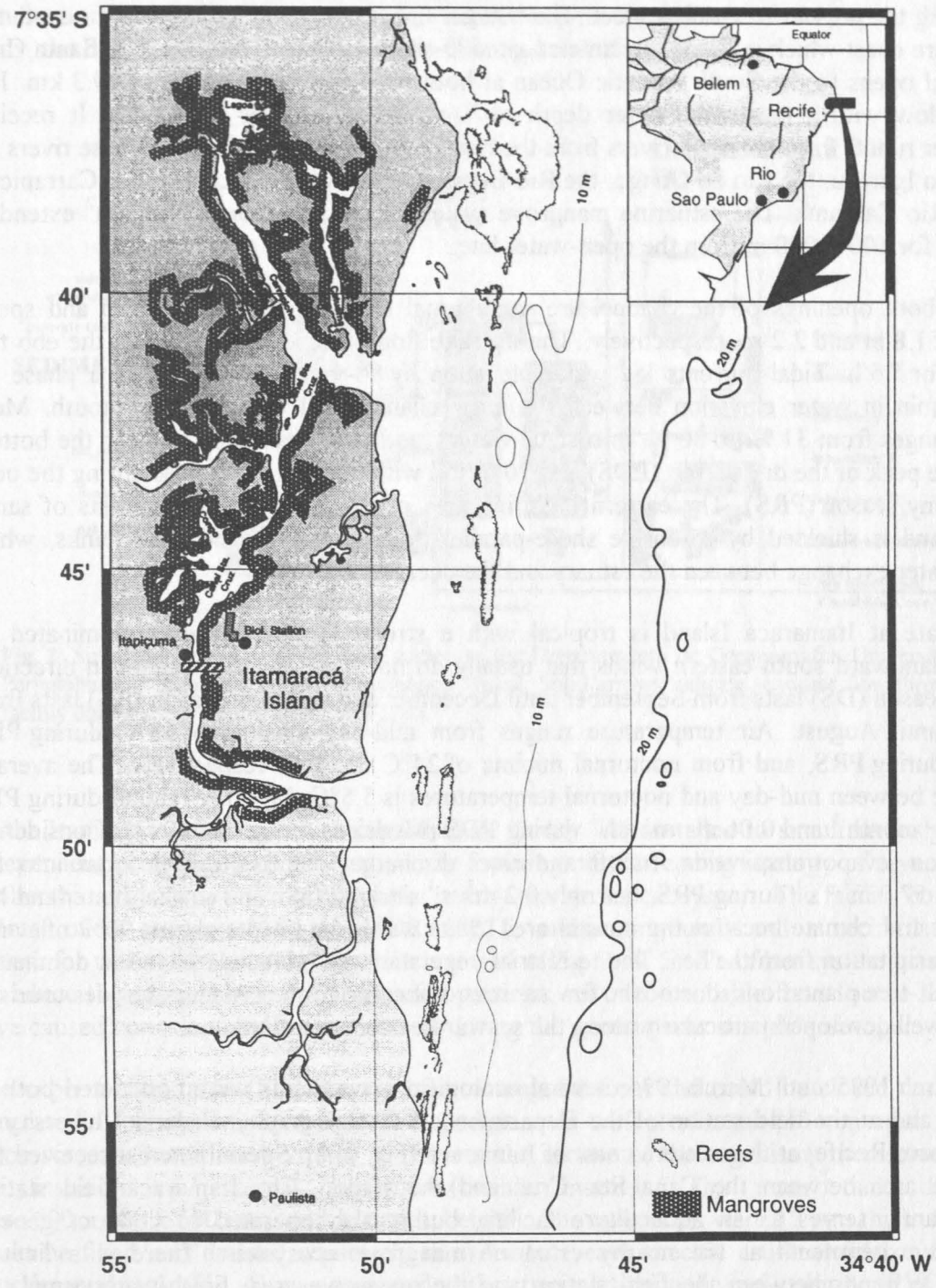


Fig. 1: Itamaracá Island (7°46' S / 34°52' W), northeastern Brazil, and the extension of the estuarine mangrove system (dotted areas = mangal areas) of the Canal de Sta. Cruz. The sweep-sampling transect for determination of standing biomass (black bar) is situated west of the field station of the Department of Oceanography, Federal University of Pernambuco (Recife).

The experimental site chosen for the field experiments in the course of the research project was the west-coast mangrove fringe encircling Itamaracá Island, 55 km north of the city of Recife, Pernambuco State, northeastern Brazil, between 7°34' S / 34°38' W and 7°55' S / 34°52' W (Fig. 1). Live mangrove trees of a maximum canopy height of 7 m cover 27.7 km^2 (= 79 %) of the Canal de Santa Cruz estuarine system. This mangal zone (Table 1) was defined as the study area during the present research project. The mangal surrounds the island's estuarine system at the western coast which is formed by an elongated U-shaped channel, the Canal de Santa Cruz. The Canal opens to the South Atlantic Ocean at both ends and has a length of 19.3 km. It is very shallow with a maximum water depth of 10 m during average high tides. It receives freshwater runoff from six small rivers from the mainland and the island itself. These rivers are the Rio do Igaraçu, the Rio do Congo, the Rio Botafogo, the Rio Arataca, the Rio Carrapicho, and the Rio Catuama. The estuarine mangrove system covers an area of 35.0 km^2 extending landward for 100-1 000 m from the open-water line.

Tides at both openings of the channel are semidiurnal in phase, and have mean and spring ranges of 1.8 m and 2.2 m, respectively. The average flood tide lasts 6.9 h while the ebb tide extends for 5.5 h. Tidal currents lag water elevation by 86-94 min and there is a phase lag of 15-20 min in water elevation between the inner channel and the estuarine mouth. Mean salinity ranges from 31 ‰ to 36 ‰ in surface waters, and may reach 38.6 ‰ near the bottom during the peak of the dry season (PDS) and 20-32 ‰ with maxima at 33.5 ‰ during the peak of the rainy season (PRS). The eastern coastline area of Itamaracá mainly consists of sandy beaches and is shielded by extensive shore-parallel sandstone reefs and sand banks, which reduce water exchange between the estuary and the ocean.

The climate at Itamaracá Island is tropical with a strong coastal influence dominated by constant landward south-eastern winds that usually do not have diurnal changes in direction. The dry season (DS) lasts from September until December and the rainy season (RS) lasts from January until August. Air temperature ranges from mid-day maxima of 38°C during PDS to 29°C during PRS, and from nocturnal minima of 24°C to 18°C, respectively. The average difference between mid-day and nocturnal temperatures is 5.5°C. Monthly rainfall during PRS is 0.34 $m \cdot month^{-1}$ and 0.06 $m \cdot month^{-1}$ during PDS (Medeiros & Kjerfve 1993). Considering evaporation, evapotranspiration, runoff and river discharge, the fresh-water input into the estuary is 57.7 $m^3 \cdot s^{-1}$ during PRS, but only 0.2 $m^3\ s^{-1}$ during PDS. The coastal hinterland has a tropical arid climate because the coastal area (5 km width) intercepts almost 90% of wind-driven precipitation from the sea. The terrestrial vegetation on Itamaracá Island is dominated by coconut-tree plantations, one of the few sources of income to the islanders besides tourism, which is well developed particularly along the seaward eastern coastline.

From March 1995 until March 1996, several ecological experiments were conducted both in the field, and at the field station of the Department of Oceanography, Federal University of Pernambuco (Recife) at the western coast of Itamaracá (Fig. 1, 2). Special interest received the mangrove area between the Canal Sta. Cruz and the station. The Itamaracá field station predominantly serves as an aquaculture facility, but is also operated to conduct general ecological experiments at the nearby estuarine mangrove ecosystem. There is a line of aquaculture ponds between the field station and the mangrove area. Fresh-water supply to these ponds is maintained through tidal flooding cycles. During the last 20 years, the outermost ponds have been abandoned, thus extending the coastal mangrove system further landward.

The field station has a sheltered roof-covered area of 200 m^2 where experimental tank facilities as well as filter systems can be installed (Fig. 2, 3, 4). There are two laboratories (Biology, Oceanography, Marine Chemistry), one combined office-/ classroom, and several storage and

service rooms. The water supply to the station is taken from the nearest aquaculture pond via an electrical centrifugal pump. The water is first stored in a 2 000 l tank for sedimentation before it enters the experimental facilities connected. For information on the specific design of the experimental facility used during the research project presented here, please refer to Chapter 3.3. Having passed the experimental facilities the water is discharged. Prior to the installation of the experimental facilities used during the experiments described in the present study, the field station did not have water filter systems of any kind.

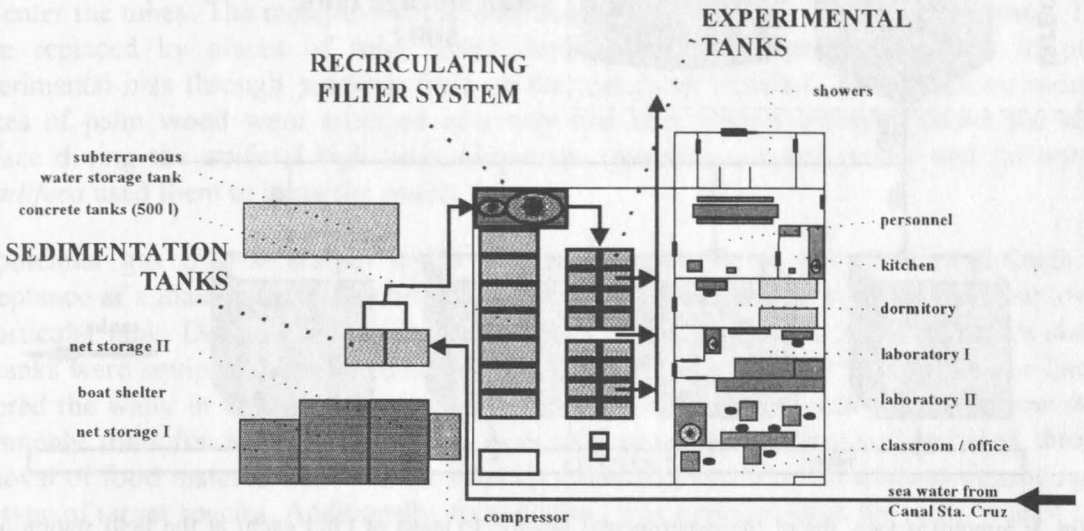


Fig. 2: Simplified top-view of the field station of the Departamento de Oceanografia, Universidade de Pernambuco at Itamaracá Island, Pernambuco, Brazil. Solid arrows indicate seawater flow through the facility during experiments from 1995-1996.

At the Itamaracá field station, an experimental facility was installed to simultaneously conduct independent ecological experiments mainly focusing on the feeding ecology of several macro-zoobenthic organisms (>1 mm) from the nearby mangrove ecosystem. The facility consisted of a total of 16 concrete 150 l tanks (BRASILIT, multi-compound) and a recirculating filter system for water supply to the experimental tanks (Fig. 3, 4, 5). The filter system was designed to reduce the concentration of suspended particles, an uncontrollable food source that would have caused considerable bias particularly during the experiments on stable isotopes.

The experimental tanks (Fig. 4) were of a rectangular form and could be closed with either a concrete lid for simulation of nighttime conditions or with steal mesh (10 mm mesh width) or nylon screens (1 mm mesh width) to prevent the escape of the organisms themselves and/ or the invasion of external organisms (mainly insects). The inner tank dimensions were 600 x 600 x 500 mm (width, depth, height). The tank walls were 15 mm thick. Each tank could be filled and drained separately in order to create specific artificial tidal cycles. Each experimental tank (Fig. 4) was equipped with a two vertical polyvinyl-chloride (PVC) siphons of 21 mm inner diameter. The water supply from the filter system entered the inflow siphon through polyethylene (PE, Table 1) tubes of 16 mm inner diameter. Each tube was equipped with a variable ball valve (EHEIM) for inflow regulation. When the filter system was completely filled and only one experimental tank was supplied with water, the maximum inflow rate of water to one tank was 7.5 $l \cdot min^{-1}$. The minimum water level in the tank was 45 mm (= 16 l) and the maximum level was 450 mm (= 162 l).

3.3 Experimental Setup during Tank Experiments

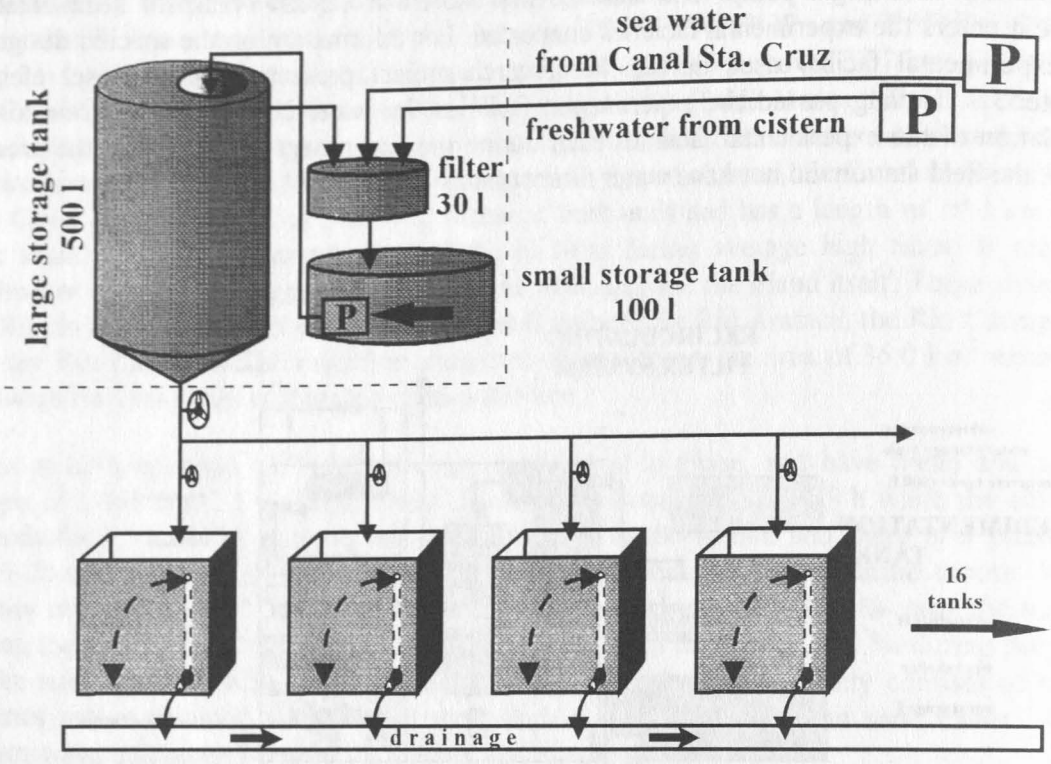


Fig. 3: Simplified view the of the experimental facility (16 tanks of 150 l each) at the field station at Itamaracá Island, Pernambuco State, Brazil. Each tank was designed to have a separate adjustable water in- and outlet to allow the installation of different environmental (tidal, salinity, water exchange rate) conditions. The dotted line separates the recirculating filter component (2 l · min^{-1} when filled completely) and the adjustable unidirectional water supply to the separate experimental tanks (maximum 7.5 l · min^{-1}).

The siphon used for water inflow was centrally fixed to one tank wall and stretched from 50 mm above tank rim to a point 20 mm above tank bottom. The siphon used for water outflow had a rectangular connection at its lower end which was attached to a 50 mm pipe perforating the tank wall at an internal level of 45 mm. This connection consisted of a thread of 25 mm length which allowed a lateral rotation of the siphon around its lower end and thus the creation of a variable water level inside the tank. The length of the thread granted a leakproof coupling between the two pipes.

During the tank experiments that required the creation of specific bottom substrates, the inflow siphon ended within a 10 x 10 cm area consisting of washed granite pebbles of 5-30 mm diameter which served as a water dispersion layer in order to prevent a washing effect of the water entering the tank. Around this area, the actual experimental substrate filled the tank to a level depending on the type of experiment and the burrowing activity of the particular organism during the experiment. Any vertical water movement through the substrate was avoided to prevent the expansion of the anaerobe environment to the upper surface level. Additionally, a filling of the air chambers (burrows) of the *Uca* species had to be avoided. Care was taken to implement the substrate stratification found at the field area the material was taken from. For this purpose, a surface layer of 20 mm thickness and two consecutive substrate layers from a substrate depth of 20-75 mm and 75-150 mm, respectively, were defined and correspondingly transferred to the tanks. No bottom substrate was provided during most

experiments on *Sphoeroides testudineus* and during the monodietary experiments on *Goniopsis cruentata*, *Aratus pisonii*, *Callinectes danae*, and *Littorina s. angulifera*.

With the exception of the experiments on *Uca maracoani* and *U. thayeri*, all tanks were equipped with additional hard substrates consisting of live mangrove roots or pieces of decorticated palm wood, as well as with pieces of PVC-tubes of 300 mm length and 50, 75 or 100 mm diameter. The latter substrate only served as shelter and reduced stress effects on the animals caused by territorial behavior and human disturbance. To the smaller specimens inside the tank the different tube diameters provided a refuge from larger specimens that could not enter the tubes. The mangrove roots were supplied during the 24h-experiments only. They were replaced by pieces of palm wood during the monodietary experiments to avoid experimental bias through potential frass on the mangrove material. The mangrove roots or pieces of palm wood were arranged in a way that they always extended above the water surface during the artificial high tides. *Goniopsis cruentata*, *Aratus pisonii* and *Littorina s. angulifera* used them to leave the water.

A potential gas over-saturation inside the experimental tanks was avoided through the acceptance of a maximum temperature difference of 2°C between the water in- and outflow of a particular tank. During the experiments on *Sphoeroides testudineus* and *Callinectes danae*, all tanks were equipped with an additional aeration from an electric membrane pump. The air entered the water in an adjustable stream of fine bubbles through a calcareous outflow stone commonly used for aquaristic purpose. A detrital oxygen depletion was avoided through removal of food material that was not used up within defined short time spans depending on the type of target species. Additionally, fecal detritus was siphoned from the tanks at least once a day. Water leaving the tanks was always discharged.

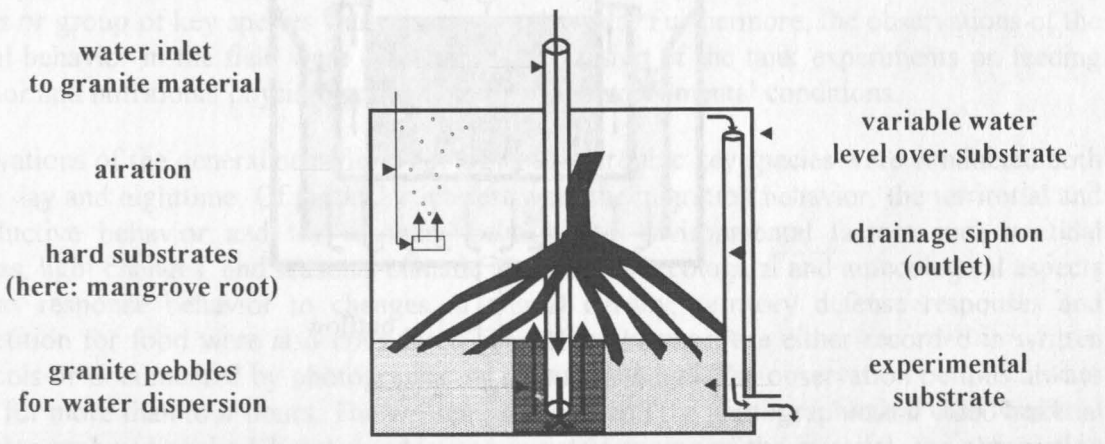


Fig. 4: General design of experimental tanks.

The recirculating filter system (Fig. 3, 5) contained a total of 630 l of seawater and consisted of three coupled units: (1) a large cylindrical glass-fiber storage tank (500 l) and (2) a small concrete storage tank to allow circulation through (3) a polyethylene two-level cascade filter (30 l). The external water supply came from the nearest aquaculture pond through an intermediate 2 000 l pre-sedimentation tank to reduce the concentration of suspended particles (SP). The water entered the system through the filter unit. All units except the filter unit were closed by concrete lids to prevent algal growth enhanced by illumination. The

filtration rate of the system was 4 l · min^{-1} when filled completely. Thus, the minimum theoretical complete filtration cycle of the water lasted 157 min, not considering mixing processes within the units. Inside the system, the sedimentation of suspended particles was additionally enhanced through the creation of a spinning water movement inside the cylindrical large storage tank and the elevated above-ground installation of the system's pump inside the small storage tank (submersible centrifugal pump EHEIM, model 1056 , max. 300 l · h^{-1}, max. 2.0 m). Particles having settled in the apical area of the large storage tank could not enter the outflow siphon which protruded 20 cm above ground level. They were discharged in 24h-intervals. Particles having settled inside the small storage tank were discharged in 72h-intervals. Through continuous re-filling from the 2 000 l pre-sedimentation tank, the filter system was kept completely filled during most of the experiments. Whenever possible, the water was allowed at least four complete filtration cycles before it was used in the experiments. However, during some experiments, when the artificially installed environmental conditions required a higher rate of water exchange the water was filtered only once at minimum.

The water was filtered through two separate materials arranged in a cascade system (Fig. 5). The time required to pass the filter was 7 min The first material to be passed through was a mixture of 75 % granite rubble (5-10 mm diameter) and 25 % sand (0.5-2.0 mm diameter). The second filter material consisted of dead coralline shreds (0.5-2.0 mm diameter). The volumetric proportion between the two filter materials was 1 : 1 and total volume was 20 l allowing an additional water volume of 30 l inside the filter.

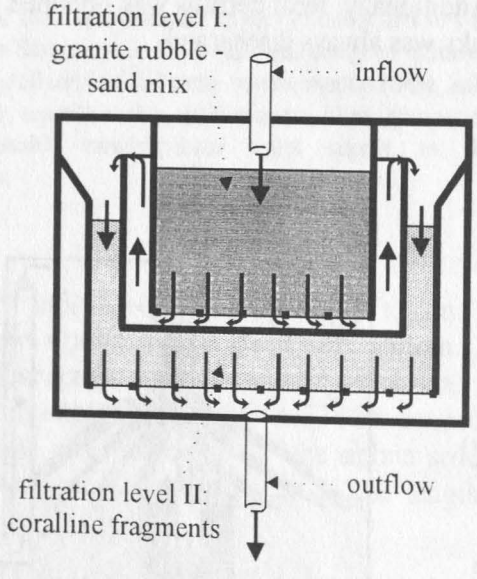


Fig. 5: Filter design.

The most critical environmental factors to be adjusted to natural settings were the composition and stratification of the substrate, the adjustment to natural tidal rhythms and light cycles, the creation of the natural density of the organisms themselves and the provision of appropriate food sources at densities found in the field. A particular problem was the installation of the specific salinity level with respect to the values at the habitat of each species or group of associated species. Whenever necessary, the particular technical and/ or strategic solutions to these problems are given within the Chapters following below.

3.3.1 Diurnal Cycles under Tank Conditions

Two environmental diurnal cycles had to be simulated inside the tanks. Those were the tidal rhythms and the light cycles. The simulation of the natural tidal rhythms of the surrounding mangrove system was adjusted by hand using the variable outflow pipes of the experimental tanks. Particularly during the numerous 24h-experiments this meant exhaustive continuous attention to the tanks. The pipes were adjusted in 20 min-intervals during the ebb and flood periods. The duration of high and low tide was prolonged to a period of one hour to allow a short pause to the personnel involved in the experimental process. By slightly speeding up the interim phases of tidal changes, the total tidal periodicity was kept synchronized to the natural tidal cycles at the mangrove area.

The creation of the natural light cycles was managed by covering the tanks using concrete lids during the night. In case the tanks had to be opened during the night time, the surrounding illumination was kept low. The tanks were never exposed to direct sunlight which may have been closer to natural conditions at certain experimental phases, but may have caused an increase of the substrate temperature to lethal levels due to the lack of ventilation inside the tanks. Instead, the tanks were shaded to the extend that the diurnal changes of light intensity were still susceptible to the organisms. Those light conditions were considered very similar to the natural conditions within the thicket of the natural mangal system monitored.

3.4 General Behavior

To provide additional means for the interpretation of the quantitative and qualitative results from the food web analyses the autecological and synecological behavior of each trophic key species or group of key species was observed in the field. Furthermore, the observations of the general behavior in the field were essential for the design of the tank experiments on feeding behavior and nutritional physiology under controlled environmental conditions.

Observations of the general behavioral ecology of the trophic key species were conducted both during day and nighttime. Of particular interest were the migration behavior, the territorial and reproductive behavior and the response behavior to environmental factors such as tidal changes, light changes, and seasonal climatic changes. Synecological and autecological aspects such as response behavior to changes of animal density, territory defense responses and competition for food were also considered. The observations were either recorded in written protocols or documented by photographic or video coverage. The observation periods always lasted for more than four hours. The written protocols and the photographic and video material was later analyzed at the laboratory. After an initial screening of the material, the observation strategies were frequently fine-tuned in order to intensify coverage of behavioral aspects that seemed to be of particular significance to other parts of the research project.

Based on the ecological observations in the field, the autecological and synecological effects on the behavior of the organisms under tank conditions were examined for perceptible and principal differences. All tank experiments were initiated after acclimatization periods suitable to the specific experimental type. The tank environments were optimized to create the most appropriate adaptation to the natural environmental situation workable with respect to the limited logistic and technical potential at the field station. The minimum observation period during all experiments was four hours. All experiments were repeated at least two times.

Written protocols, black-and-white photographs and video coverages were prepared, both during the acclimatization phases and during the actual experimental phases. The use of video equipment during the field and tank experiments proved to be most appropriate because it caused minimum disturbance to the organisms and because repeated observations of the same scene were possible under various observation criteria.

3.5 Food Web Analysis and Turn-Over Rates

Two general methodical approaches were followed to obtain information on food chain structures and turn-over rates between the main trophic key organisms in the field. (1) The quantitative analysis of gastro-intestinal contents, conducted as 24h-experiments, was combined with (2) the analysis of stable isotope ratios of organic carbon, nitrogen and sulfur of ingested material and muscle tissue of the organisms. All results from the field experiments were conclusively interpreted only after three types of additional tank experiments had provided further data under controlled conditions e.g. (1) 24h-experiments, (2) starvation experiments. Both tank experiment types were conducted under close-to natural conditions in terms of food availability as well as under (3) monodietary conditions.

Monthly sampling of all trophic key species and food sources was conducted on the 15th (± 2 days) of each month from February 1995 until March 1996. This sampling strategy was chosen to acquire data on possible annual periodicities concerning food selectivity of the organisms as well as concerning possible oscillations of the stable isotope ratios of the food sources. This sampling strategy provided qualitative information but no data on specific quantitative alimentary interactions between the different organisms and their food sources. In order to obtain these quantitative data sets, which would be later combined with the qualitative results from the gastro-intestinal content and tissue analyses of stable isotope ratios, multiple 24h-experiments on gastro-intestinal content changes were conducted as field and tank experiments. Each organism was analyzed three times with two experiments during the early rainy season (ERS) and one experiment during the late rainy season (LRS).

3.5.1 General Feeding Behavior in the Field

Observations of the general feeding behavior in the field as part of the observations of the general behavior of the animals (Chapter 4.2.1) were conducted in order to develop particular experimental strategies that would yield an optimum coverage of the central nutritional pathways within the mangal segment of the Canal Sta. Cruz mangrove ecosystem. Initial questions were (1) the potential periodicities of the diurnal feeding behavior and (2) their dependency on environmental factors in the area. Of further interest was (3) the primary identification of food sources of the trophic key species. For this purpose, different types of potential prey were offered within the territory boundaries of single undisturbed specimens. Observed preferences during a progressive downgrading of the food sources offered led to an initial hypothetical graduation of selectivity. All animal prey species were offered as live or fresh and as slightly or strongly decayed food. Correspondingly, plant material was offered as fresh, slightly decomposed and strongly decomposed material. Quantitative conclusions on relative food preferences were not made at this point. They would be part of later field- and tank experiments under controlled quantitative conditions.

Table 3: Preliminary testing of food sources at the initiation of the food web analysis of the mangal segment of the Canal Sta. Cruz mangrove ecosystem, Pernambuco State, northeastern Brazil, between April 1995 and March 1996. **L** = live, **F** = fresh, **d** = slightly decayed/ decomposed, **D** = strongly decayed/ decomposed. For further details on species taxonomy see Chapter 3.9.

food source	component used as prey to other organisms
Goniopsis cruentata[1]	whole: L, d, D
Aratus pisonii[1]	whole: L, d, D
Uca maracoani[1]	whole: L, d, D
Uca thayeri[1]	whole: L, d, D
Callinectes danae[1]	whole: L, d, D
Cardisoma guanhumi[1]	whole: L, d, D
Ucides cordatus[1]	whole: L, d, D
Littorina scabra angulifera[1]	whole: L, d, D
Sphoeroides testudineus[1]	whole: L, d, D
Halodule wrightii	leaves, roots: F, d, D
Avicennia marina	leaves, branches, roots: F, d, D
Rhizophora mangle	leaves, branches, seedlings, roots: F, d, D
Laguncullaria racemosa	leaves, branches, flowers, roots: F, d, D
Conocarpus erecta	leaves, branches, roots: F, d, D
chlorophyte mix	whole: F
phaeo- /rhodophyte mix	whole and pieces: F
mango fruit mix	whole: F, d, D
Centropomus undecimalis[2]	whole: L, d, D
Eugerres brasilianus[2]	whole: L, d, D
Opisthonema oglinum[2]	whole: L, d, D
Mugil gairmardianus[2]	whole: L, d ,D
Penaeus schmitti[2]	whole: L,d ,D
Penaeus brasiliensis[2]	whole: L, d, D

[1]: primary trophic key animal species during the research project; [2]: non-target animal species

The aquatic species *Sphoeroides testudineus* and *Callinectes danae* were excluded from initial observations of feeding behavior because of the limited access to their habitats. However, this meant a more extensive initial range of food sources to be offered to this two species during the tank experiments. In spite of the in some cases seemingly unrealistic combinations of consumers and food sources, all trophic key animal species were initially offered the entire range of food sources tested during the research project. All food sources tested are given in Table 3. All trophic key species were tested as prey species as well. The food material was separated (e.g. mostly from epiphytes), but was not washed or cleaned.

The grade of decomposition of the mangrove leaves and seagrass material was defined as yellow coloration for slight and brown coloration for advanced decomposition. The epiphyte material was not sub-grouped into grades of decomposition. The grade of decomposition of the mangrove branches and roots was defined via the hardness of the material e.g. hard wood stood for a short decomposition period and soft wood was classified as wood that had undergone a prolonged period of decomposition. The level of decayment of the animal key

organisms was initially tested by their smell of the material. The decayment levels of the fish specimens was additionally defined via the intactness of their outer body tissue. Unseizured tissue meant slight decayment and seizured tissue was defined as an advanced state of decayment. Crustaceans were additionally tested for the flexibility of their extremities e.g. inflexibility standing for slight and flexibility standing for advanced decayment levels.

3.5.2 24h-Experiments

Information on the daily food requirements of *Sphoeroides testudineus*, *Goniopsis cruentata*, *Aratus pisonii*, *Uca maracoani*, *U. thayeri*, *Callinectes danae* and *Littorina s. angulifera* was acquired via 24h-field and tank experiments conducted two times each for each species during the early rainy seasons of 1995 and 1996 and once for each species during the late rainy season of 1995 (Table 2). All results were obtained as dry weight of the gastro-intestinal content in relation to the body fresh weight (BFW, Table 1) of the animals and were later interpreted in combination with the results the monodietary experiments, the starvation experiments and the biomass analyses in the field (Chapter 3.6). The combined results led to a species-specific modelling of the food-web structures and the annual nutrient flux of the mangal segment of the Canal de Sta. Cruz ecosystem. The 24h-experiments in the field exclusively delivered quantitative data on daily food requirements under specific environmental conditions. Information on the type and composition of the food ingested had to be obtained from stable isotope analyses of the gastro-intestinal contents under controlled environmental conditions in tank experiments., The methodological bias of the iteration of the daily relative weight of the gastro-intestinal contents had to be specified via additional starvation (tank-) experiments. These experiments also provided valuable information on evacuation rates of particular food sources which could be compared with the results from the 24h-field experiments.

The experiments on *Goniopsis cruentata*, *Aratus pisonii*, *Uca maracoani*, *Callinectes danae* and *Littorina s. angulifera* were conducted on separate days because of the more laborious and time-consuming dissection of these organisms at the laboratory in relation to the other trophic key species. The sampling of *Sphoeroides testudineus* and *U. thayeri* was combined on the same days because of the less laborious dissection of the fish and the relatively easy access to the crab's habitat compared to the other organisms. For all trophic key species the gastro-intestinal content was defined as the entire ingested material within the complete gastro-intestinal tract from the esophagus to the anus (Table 1). The gastro-vascular and digestive fluids were included, but their dry weight was negligible compared to the ingested material.

Sampling was conducted in approximate one-hour intervals (± 10 min). Although deviations from this periodicity did not influence later data processing, a continuous coverage of the 24h-period was outlined. All experiments were initiated during low tides. The second experimental run on each key species was conducted on a date showing a reversed rhythm of illumination e.g. starting at daytime low tide instead at nighttime lot tide. Spring and neap tides were avoided as sampling dates because of their hypothetical non-representative character with respect to food uptake. During the repetition experiment of the same climatic season, the sampling frequencies around periods of intensified feeding activity that had been detected during the first season run of the experiment were increased. After being captured or sampled and instantly being transported to the laboratory, all animals were killed by deep-freezing them at -20°C for 3 h. This procedure ensured comparatively relaxed expiration of the animals. The use of chemical anestheica would have caused stress-induced evacuation of the gastro-

intestinal tracts (Wiedemeyer 1992) and would have thus caused an unnecessary and moreover incorrigible methodological bias.

The sampling methods differed between species according to the initial observations of their specific feeding behavior in the field. Between the target key species, the numbers of specimens per sample differed as well. Sampling was not absolutely representative with respect to the size frequencies of particular target species. However, care was taken to sample both sexes (excluding *Sphoeroides testudineus* and *Littorina s. angulifera*) at equal numbers and to sample specimens covering the whole size or weight range of the species. This non-representative sampling was acceptable because all gastro-intestinal weight data was processed as percentages of fresh body weight of the animals. A conversion to the scale of the entire Canal de Sta. Cruz mangal was facilitated via the separate determination of animal and plant biomass in the area (Chapter 3.6).

Two methods were applied to catch *Sphoeroides testudineus*. The first method, which was mainly applied within the thicket of the mangrove roots, was line fishing using empty abdominal exoskeletons of *Penaeus schmitti* as bait on small steel hooks of 8 mm arch width. During initial tests, this method proved to be successful for specimens larger than 50 mm during day and nighttime. Prior to the experiment, the exoskeletons were marked with a black grid using a waterproof text marker. The ingested material derived from the bait was thus easily detected and excluded from gastro-intestinal weight analyses during the dissection of the animals. The second sampling method for *S. testudineus* was closing tidal creeks using 5 mm-nylon enclosure-nets. By this method all fish including those below 50 mm total body length were sampled. The net was never set twice at the same spot and never set for periods of more than 5 min and care was taken to instantly remove the fish before they were attacked by *Callinectes danae*. *C. danae* itself was caught using 5 mm enclosure nets.

Littorina s. angulifera was collected by hand from the roots, stems and branches of the mangrove trees in the area. Care was taken to sample individuals from the entire vertical distributional range at a particular sampling interval because the animals moved up and down the mangrove vegetation in the course of the tidal cycles. The same strategy was applied while sampling *Aratus pisonii* which was encountered between the root area to the upper canopy regions of the mangrove trees. To collect the specimens from the latter region, one person had to bend a branch to the ground and the other had to pick the animals from the vegetation. Detecting the effectively camouflaged animals during the night was extremely difficult and only possible through the use of strong hand torches.

Goniopsis cruentata was caught using live *Aratus pisonii* as bait which were strapped to a nylon line on a long rod held with one hand. The bait was offered in front of *G. cruentata* and readily grabbed by the predators. Because the animals did not let loose of their prey, they could be easily transferred into a bucket held with the other hand. This method was successfully used to probe the entire size and weight range of the species. To catch smaller or larger specimens, the bait size was reduced and vice versa.

Uca maracoani and *U. thayeri* were sampled by hand which was comparatively easy during the day and low tide but very difficult at night and/ or during high tides when the animals had retreated to their burrows. During high tides, the locations of the burrows of *U. maracoani* were detected by carefully probing the substrate surface with one finger boring into the ground. Detected burrows were than entered with the hand and the retreating animal was grabbed before it could escape the entire arm's range. In some cases this meant skin diving while having no visibility and one arm completely sticking in a muddy whole. The burrows of

the smaller *U. thayeri* were less deep. Detected burrows were closed beneath the animal by a lateral protrusion of one hand into the substrate at an angle it would meet the burrow at a depth of 25-30 cm. Than the surface lid of the burrow was removed with the other hand. With both hands vertically closing in on each other the animal was than grabbed. During the sampling on both *Uca* species, care was taken not to unnecessarily destroy burrows that were not probed because their destruction would have caused pathological problems to the air breathing crustaceans being dependent on their gas reservoirs during the stay below the surface.

The gastro-intestinal contents of the defrosted animals of one sampling interval, weight class and sex were pooled. The material was prepared using the following methods. The body cavity of *Sphoeroides testudineus* was ventrally opened by cutting craniad from a point 5 mm in front of the anus over the entire length of the cavity using a blunt-ended pair of dissection scissors. Than both parts of the now divided ventral flaps were removed by cutting along the lateral borders of the body cavity. After this, the entire gastro-intestinal tract from the end of the esophagus to the anus was carefully removed without rupturing the tissue. On a clean tray, the gastro-intestinal tract was than opened by a lateral cut over the entire length of the organs. The stomach and intestinal content was than rinsed from the organs tract using a small glass pipette filled with fresh-water that had been filtered through an earthenware filter commonly used by the local people to produce drinking-water. Care was taken not to detach the mucous layer covering the inner side of the gastro-intestinal tract. However, a small amount of this material always contaminated the ingested material desired for analysis.

Hard materials such as calcareous or silicate fragments of shells, clams and crustaceans were separated from the rest of the material and not included in the later weight analysis of the material. This preparation strategy was later taken account of through the conversion of dry weight to fresh weight of the food organisms being reduced to their soft-part weight at this point. The hard material was not disposed but analyzed separately instead. It would provide valuable information on the type of prey ingested. Additionally, it allowed a verification of the results obtained from the analyses of the stable isotope ratios. Representative fragments were photographed.

The gastro-intestinal content was dispensed in 100 ml of filtered fresh-water in a 500 ml beaker and than filtered through pre-weighted (0.01 g) glass-fiber filters of 63 mm diameter (SCHLEICHER & SCHUEL GF 6) at an adjusted vacuum of $-0.5 \pm 0.1 \cdot 10^{-5}$ Pa ($\approx -0.5 \pm 0.1$ atm) created by an in-row double-cylinder vacuum pump (KNF NEUENBERGER MW 63/4, Germany, max. $1.4\ l \cdot min^{-1}$, $\cos \varphi = 0.93$). To avoid clogging of the filter, more extensive amounts of material were filtered through more than one filter. The filters were than dried at 65°C for 48 h, weighted and the dry weight of the ingested material (0.1 g) was calculated as weight difference to the initial dry weight of the filter.

To avoid contamination by dirt attached to the animals, the gastro-intestinal contents of *Goniopsis cruentata*, *Aratus pisonii*, *Uca maracoani* and *U. thayeri* were obtained after washing the animals. The hind gut stretching along the inner side of the abdomen was cut slightly lateral over its entire length to the ventral transition zone between the stomach and the abdominal gastro-intestinal tract. The cut was not made ventrally because of the location of blood vessels in this region. After entering the stomach with the very tip of a small blunt pipette, filtered seawater was injected into this cavity. Care was taken not to puncture the dorsal wall of the stomach which would have caused an irreversible contamination of the gastro-intestinal content with haemal fluid from the neighboring heart of the animal. The water

pressure in the stomach was kept low allowing the water to leave the stomach through the artificial opening. After this procedure, the rest of the gastro-intestinal tract to the anus was rinsed as described for *Sphoeroides testudineus*. All water and dispensed material was gathered in a 500 ml beaker and was allowed a sedimentation period of 10 min. After this, the surface water was pipetted until a volume of 100 ml remained in the beaker. This volume was filtered as described above.

Littorina s. angulifera was dissected after the shell had been carefully crushed and removed. A household nutcracker was used to crush the animals' shells. The stomach and intestine were than carefully opened with a small needle not perforating the neighboring digestive gland. Using the ball-shaped blunt end of the needle the gastro-intestinal content was than pushed out of the intestine and transferred into small pre-weighted laboratory watch glasses filled with filtered fresh-water (see above). The esophageal content was not sampled because it was impossible to open this part of the gastro-intestinal tract without perforation of the neighboring organs. After finishing the dissection of all animals of one sampling interval, the excess water was removed from the watch glasses using a pipette and the remaining gastro-intestinal content was dried for 48 h at 65°C. The dry weight of the gastro-intestinal content was calculated as described for the other organisms.

Several mathematical methods were applied to calculate the food requirements of the organisms on a daily and annual scale. The daily food ratios of specific sex, weight or length class of a particular trophic key species were computed from the data from 24h-field experiments, applying MAXIMS, a multiple-iteration software published by ICLARM (Pauly 1986; Jarre, 1990; Jarre-Teichmann 1992). This software was initially developed for the estimation of daily food requirements from stomach content data in fish, but is also applicable to invertebrate digestive physiology (Wiedemeyer 1993, 1994). All weight data on the gastro-intestinal contents was processed as dry weight percentages of the total fresh weight of the respective organism. Thus, morphology-dependent influences could be excluded during the primary calculation of food requirements and the final results would be readily applicable to populations at other locations within the distributional range of the organisms. To calculate the food requirements of the trophic key species in the entire mangal zone of the Canal de Sta. Cruz, additional information was needed on (1) the sex-ratio of the organism, (2) principal differences of food types or selective feeding between sex and weight or length classes of the organisms, (3) principal differences of the diurnal feeding cycles between sex and weight or length classes of the organisms. This information was acquired throughout the experimental routine itself as well as through specific analyses of the stable isotope ratios within sex, weight and/ or length classes.

The parameters computed by MAXIMS were (1) the average ingestion rate (IR) per hour during feeding periods as % body fresh weight $\cdot h^{-1}$, (2) the average evacuation rate (ER) of the gastro-intestinal content (GIC) per time as % GIC $\cdot h^{-1}$, (3) and the beginning and the end of the daily feeding periods (t_0, t_x) of the organisms in hours. The equations describing the ingestion rate and the evacuation rate of a specific sex, weight or length class of the organism were simultaneously iterated from the average relative weight of the gastro-intestinal contents at definite sampling intervals. Filling-level dependent ($ER_{dep.}$, Table 1) and filling-level independent evacuation rates ($ER_{indep.}$) were tested as initial hypotheses depending on the type of organism. The existence of one or two daily feeding periods was tested depending on the shape of the observed time series. The resulting daily dry-weight food ratios DR_{DW} (Table 1) were expressed as dry-weight percentage of the body fresh weight and later converted to the annual scale (AR_{DW}, f_{AR}, Table 1). The accuracy of the software-based calculation of DR_{DW} was evaluated by two additional tank experiment types under controlled environmental

conditions. (1) The evacuation rates per time (ER) were analyzed during individual starvation experiments (Chapter 3.5.3). (2) The potential influence of particular food source types was tested during 24h-tank experiments under monodietary conditions (Chapter 3.5.5).

Each 24h-tank experiment was based on the respective field experiment. Thus, some experimental settings were based on findings from the field experiments. The specimens were weighted and individually tagged prior to the start of the experiment. This allowed a determination of changes of the organism's fresh weight during the experiment which were not dependent on food uptake. The dry weight of the gastro-intestinal content was later set into relation to the average fresh weight of the animal basing on the initial fresh weight and the fresh weight at the time of dissection. All other preparation techniques and methods of analyses of the gastro-intestinal contents were similar to those described for the respective field experiments. No 24h-experiments were conducted on *Cardisoma guanhumi* and *Ucides cordatus* because of their low density in the field and the lack of representative sampling methods with respect to their population structure in the area.

With respect to the installation of a near-to natural density of the particular key organisms to be analyzed, the initial number of individuals per tank differed between the experiments on different species. For each separate experiment it was however set constant. The tanks were sampled one after another. Thus, the density of the animals was held constant over the entire experimental period. The most important experimental settings are given in Table 3. Each experiment was initiated after two pre-experimental phases: (1) An adjustment phase of the tank conditions to the natural abiotic environmental factors, and (2) the acclimatization phase of the organisms to be monitored. During the adjustment phase, the diurnal cycles (Chapter 3.3.1) were synchronized and salinity and temperature were calibrated. This phase lasted twelve hours in order to cover a complete tidal cycle. The sampling frequency around the prominent ingestion periods detected during the field experiments was increased by two fold. The basic sampling frequency was set at one-hour intervals.

Except for the first run of the 24h-tank experiments, the densities of the food organisms were kept constant and close to the approximate food availabilities in the field. Each type of food was offered only during the appropriate daytime and/or tidal phase during which it would be accessible in the field. During the experiments on species having multiple food sources, a continuous replacement and substitution of particular food sources was conducted and the environmental conditions (tide induced) were altered at the same time. Food organisms offered were always fresh or had been deep-frozen at -18°C. During the 24h-experiments, only life food organisms were offered. At the beginning of the starvation experiments, only dead food organisms were supplied to accelerate and synchronize the food uptake of all specimens to be monitored.

To simultaneously conduct the continuous transformation of experimental conditions in several tanks containing different species at the same time, a detailed chronological schedule of activities was prepared prior to each experimental run. This schedule was explained and discussed with the staff members involved in the experimental sequence and responsibilities for specific activities were assigned.

The 24h-tank experiments were conducted two times during ERS and once during LRS, respectively. During the first run, all food sources found in the specific ecological zone in the field were given in excess quantity. The results from this experiment type allowed the identification of filling-level dependent or filling-level independent feeding of the organisms. This information was essential for the accurate application of the software-based calculation of

the daily food requirements of the particular organism during the 24h-field experiments. During the second run during one climatic season, the experiment was conducted offering just one type of food to the animals. Depending on the trophic key species, this meant a reduction to plant material, to a specific group of animal prey species or the reduction to one single plant or animal species. This particular type of experiment provided valuable information on the influence of the type of food ingested on feeding rates. This aspect was of essential importance for the interpretation of the field experiments and the application of the final results to specific food availabilities and food chain structures at other geographical locations within the distributional range of the particular organism.

Table 4: Basic experimental settings during the 24h-tank experiments conducted during the early rainy season (ERS) and the late rainy season (LRS) between April 1995 and March 1996 at the field station of the Universidade Federal de Pernambuco at Itamaracá Island, northeastern Brazil. The substrate/ ground surface area within each tank was 0.36 m^2. n = number of specimens.

species	tanks	n · tank^{-1}	n ·m^{-2}	n · sample^{-1}	∑n
Sphoeroides testudineus	8	11	31	4	88
Goniopsis cruentata	8	12	33	4	96
Aratus pisonii	8	24	67	8	192
Uca maracoani	12	12	33	8	144
Uca thayeri	8	24	67	8	192
Callinectes danae	12	8	22	4	96
Littorina s. angulifera	4	48	133	8	192
Cardisoma guanhumi		not conducted with this species			
Ucides cordatus		not conducted with this species			

The acclimatization phase of the organisms lasted five hours and was always initiated at the beginning of the particular tidal phase which had been identified as the phase of reduced food uptake during the 24h-experiments conducted in the field. This strategy minimized the disturbance of the alimentary cycle of the animals which were transferred directly from the field into the tanks. In one or two separate tanks, the food organisms and/ or plant material to be supplied as food sources went through an identical acclimatization phase under synchronized tidal conditions. One hour before the start of the natural main feeding period identified from the field experiments, these food organisms were transferred to the experimental tanks and the experimental phase started. Sample intervals and number of specimens per sample differed between species (Table 4). The sex ratio within the Crustacea samples was balanced. This was not workable for *Littorina scabra angulifera* and *Sphoeroides testudineus* because of hermaphroditism of the former and the lack of sexual dimorphism of the latter species. However, as all specimens were collected haphazardly in the field, close-to natural sex ratios were to be expected for the latter two species, too.

3.5.3 Starvation Experiments

Two additional starvation experiments were conducted on each trophic key species of the 24h-experiments. This tank experiments served as a secondary method to verify the results on the

animals' daily food requirements from the 24h-field and tank experiments. The main physiological factor tested during the starvation experiments was the average evacuation rate during the digestion process.

The animals were sampled in the field and transferred to the tanks at the beginning of their particular period of reduced feeding activity as analyzed during the 24h-field experiments. This strategy reduced disturbance effects on activity levels. The animals were then allowed an acclimatization phase of 24 h without food but under a synchronized cycle of all abiotic factors e.g. tide, temperature, light, substrate with respect to the natural conditions at the sampling site they had been taken from. All specimens were individually tagged using colored pieces of PE-coated steal wire. The numbers of animals per tank as well as some other additional information on the experimental settings are presented in Table 5.

Table 5: Basic experimental settings during the starvation tank-experiments conducted during the early rainy season (ERS) and the late rainy season (LRS) between April 1995 and March 1996 at the field station of the Universidade Federal de Pernambuco at Itamaracá, northeastern Brazil. The substrate/ ground surface area within each tank was 0.36 m^2. n = number of specimens.

species	tanks	n · $tank^{-1}$	n · m^{-2}	n · $sample^{-1}$	Σn
Sphoeroides testudineus	8	8	22	2	64
Goniopsis cruentata	12	10	28	4	120
Aratus pisonii	12	16	44	6	192
Uca maracoani	12	10	28	4	120
Uca thayeri	12	20	56	8	240
Callinectes danae	12	10	28	4	120
Littorina s. angulifera	12	20	56	8	240
Cardisoma guanhumi		not conducted with this species			
Ucides cordatus		not conducted with this species			

Each 24h-tank experiment was started at the beginning of the natural main feeding period of the particular trophic key species in the field. All food sources of the particular consumer that had been identified during the field experiments were offered dead, but fresh and in excess quantity. The animals were allowed to feed for a definite timespan. This timespan was 15 min for *Sphoeroides testudineus*, 30 min for all crustacean species, and 60 min for *Littorina s. angulifera*. After this feeding period, all food sources were removed and the animals were individually analyzed for their fresh weight (0.1 g). A definite number of specimens (Table 5) was sampled at intervals of 15 min during the first three hours of the experiment and at intervals of 30 min during the rest of the experiment. The experiment was terminated after eight hours or two hours after the beginning of the next natural feeding period of the species the field. As during the 24h-experiments, the relative weight of the gastro-intestinal content was defined as percentage dry weight of the fresh weight of the respective animal.

In order to avoid density dependent bias on the results, the tanks were sampled one after the other. As during the other field and tank experiments on nutritional aspects, all animals were killed by deep-freezing them at -20°C for 3 h. Avoiding the use of chemical anestheica this procedure ensured comparatively relaxed expiration of the animals. The later determination of

the relative dry weight of the gastro-intestinal contents was conducted as described for the 24h-field experiments.

For each trophic key species the average filling-level independent evacuation rate $\mathbf{ER}_{indep.}$ (% GIC · h^{-1}) of the gastro-intestinal content GIC was determined for the period $\mathbf{t} = \mathbf{t}_x - \mathbf{t}_0$ (h) between a maximum filling level of the gastro-intestinal tract $\mathbf{W}_{max}$ at $\mathbf{t}_0$ and reaching the average filling level $\mathbf{W}_{rest.}$ at $\mathbf{t}_x$ when not feeding. The average filling-level independent evacuation rate during the starvation tank-experiments was calculated as:

$$ER_{indep.} = 100-(W_{rest.} / W_{max})^{1\,h} \cdot 100$$

In order to permit a direct comparison between the results from the different experiments types, the filling-level independent evacuation rate $ER_{indep.}$ from the starvation experiments had to be transformed into a filling-level dependent evacuation rate $ER_{dep.}$ as computed for the 24h-experiments in the field. For this purpose, the evacuation rate from the starvation experiments $ER_{indep.}$ and the feeding period(s) (t_0, t_x) were set constant while the average ingestion rate (IR) and the dry-weight daily food ratio (DR_{DW}) were computed for a filling-level independent feeding mode applying the MAXIMS software. The results were than vice versa set constant and the respective filling-level dependent evacuation rate $ER_{dep.}$ was computed.

3.5.4 Stable Isotope Ratios

Stable isotope ratios of all trophic key species and food sources were monitored from monthly samples of organisms and plant material during the period from February 1995 until March 1996. The isotope monitoring in the field was intended to provide additional means for the conclusive interpretation of the quantitative field experiments on a diurnal and annual scale. The monthly sampling strategy was chosen to detect potential annual fluctuations of the stable isotope values of the organisms that would have influenced the interpretation of the experiments on the food-web structure.

Additional monodietary tank experiments (Chapter 3.5.5) were conducted to provide the basis for the determination of isotope shifts of the animals muscle tissue detected in the field. The information on the specific relationships between isotope values of the consumer's muscle tissue a particular type of food was essential for the interpretation of the field data on the natural mixed diet. At the same time, the monodietary experiments provided valuable data on the speed of isotope shifts of consumer muscle tissue. This information was used to define a specific speed of shift per time as minimum speed caused by nutritional changes.

A definite amount of material or a definite number of specimens of each target or food species (Table 6) was sampled on the 15th (± 2 days) of each month. Sampling spots were haphazardly chosen at sites of high densities of the organisms during food uptake. Except for *Uca maracoani* and *U. thayeri*, those sites were situated within the 20 000 m^2 sampling area along the transect line defined for sampling for standing biomass in the mangal ecosystem (Chapter 3.6). *U. maracoani* was sampled at a fish pond that had been abandoned for several years at the northern end of the experimental mangrove area. This pond had an opening to the Canal de Sta. Cruz and fully participated in the tidal changes of water level. During low tides, this pond was exclusively inhabited by *U. maracoani* and showed very high

densities of the animals. During high tides, all common fish species of the area as well as *Callinectes danae* entered the pond. *U. thayeri* was sampled within the upper tidal zone in front of the field station which showed high densities of this small fiddler crab.

Table 6: Sampling strategy during the monthly monitoring of the stable carbon, nitrogen and sulfur isotope ratios of the trophic key organisms and food sources in the mangal segment of the Canal Sta. Cruz mangrove ecosystem, Pernambuco State, northeastern Brazil, between March 1995 and March 1996. The animal sex ratio was 1 : 1 (except*). n = number of samples, specimens or pieces pooled each month, gDW = average dry weight (g) of monthly material.

taxa	n · month^{-1}	gDW · month^{-1}
*Sphoeroides testudineus**	4	6.2^{m}
Goniopsis cruentata	8	3.2^{cm}
Aratus pisonii	16	1.3^{cm}
Uca maracoani	8	2.9^{cm}
Uca thayeri	16	2.1^{cm}
Callinectes danae	4	4.1^{cm}
*Littorina s. angulifera**	16	1.2^{fm}
Cardisoma guanhumi	4	5.1^{cm}
Ucides cordatus	4	5.4^{cm}
gastro-intestinal contents	4-16	0.6-6.9^{e}
green mangrove leaves (mix)	20	14.5^{e}
yellow mangrove leaves (mix)	20	10.4^{e}
brown mangrove leaves (mix)	20	8.4^{e}
mangrove flowers (*L. racemosa*)	20	7.2^{e}
mangrove zone sediment	1	50.0^{e}
non-mangrove zone sediment	1	50.0^{e}
chlorophyte mix	1	5.0^{e}
phaeo-/ rhodophyte mix	1	5.0^{e}
mango fruits	5	5.0^{e}

^{m}: muscle tissue mix; ^{cm}: coxal muscle tissue, ^{fm}: foot muscle tissue; ^{e}: entire material

The plant material was washed using fresh-water for the fresh mangrove tree material and seawater for the other plant material. All plant material was than dried at 65°C for 72 hours. The entire material of one particular type was than grinded and at the same time homogenized using an agate grinder. The maximum particle diameter after grinding was 0.02 mm. For the later determination of the stable isotope ratios of organic carbon and nitrogen subsamples of 2-3 g were transferred to small glass vials. Selected samples were sealed as a whole in larger glass vials for later determination of the stable isotope ratios of sulfur. All material was protected from humidity influences through airtight aluminum lids covering the vials and the continued storage of the material in the dryer-oven at 65°C. After grinding of the samples, any contact of the probes to plastic materials like Kautex-flasks was avoided to minimize a potential contamination through artificial carbon sources.

The stable isotope samples of the animals consisted of muscle tissue excluding tendons and other external connective tissue. For the crustaceans the entire muscle mass of all extremities excluding the antennae was homogenized after drying. For *Littorina scabra angulifera*, the

entire muscle mass of the foot was used accordingly. Muscle tissue from the ventral lateral flaps as well as from the skeletal musculature of the dorsal and the tail area of *Sphoeroides testudineus* was combined in equal percentages. As far as workable, connective tissue of any kind was always removed from the material. Definite subsample weights were sealed according to handling of the plant material. After the transfer of the material to Germany, the samples were acidified using 4 %-HCl and than dried again for 48h at 65°C at the laboratory of the Center for Tropical Marine Ecology, University of Bremen. Subsamples of appropriate specific weight were filled into silver trays and again sealed in small glass vials. These samples were later analyzed for their stable carbon and nitrogen isotope ratios (Chapters 3.5.4 & 3.12).

Primary food sources or variable groups of pooled primary food sources were later identified using multiple WILCOXON-tests to analyze the correlation between paired single observations or means of similar or not similar numbers of observations of stable isotope values of muscle tissue and (the) food source(s) in identical time intervals. The "pooling" of food sources was conducted as a strictly additive process and has to be understood as an approximation without any reflection of a quantitative representation of single food sources within natural mixed diets in the field. The strategy was however acceptable because the experimental results were almost exclusively interpreted based on the analyses of single non-pooled food sources in the first place. On the remaining data sets, in order to provide at least an initial idea of a qualitative feeding strategy, "pooling" was only conducted when no conclusive relationships between the stable isotope values of the consumer's muscle tissue and any single food source could be detected.

3.5.5 Monodietary Experiments

Monodietary tank experiments on each trophic key species were conducted twice during ERS and LRS. The experiments provided essential basic values for the evaluation and interpretation of the stable isotope ratios found in the field (Chapter 3.5.4). Each monodietary experiment lasted 20-25 days depending on the type of target species. The number of animals per sample and further information on the particular experiment settings are presented in Table 7. The specific food sources offered to the animals were dependent on the results of the respective field and tank experiments.

Table 7: Basic experimental settings during the monodietary tank experiments conducted during the early rainy season (ERS) and the late rainy season (LRS) between April 1995 and March 1996 at the field station of the Universidade Federal de Pernambuco at Itamaracá, northeastern Brazil. The substrate/ ground surface area within each tank was 0.36 m^2. n = number of specimens.

species	duration	tanks	n · tank^{-1}	frequency	n · sample^{-1}	Σn
S. testudineus	25 d	3	5	5 d	2	10
G. cruentata	24 d	4	5	3 d	2	16
A. pisonii	24 d	4	12	3 d	4	32
U. maracoani	21 d	2	10	3 d	2	14
U. thayeri	21 d	2	20	3 d	4	28
C. danae	25 d	3	5	5 d	2	10
L. s. angulifera	21 d	2	20	3 d	4	28
C. guanhumi	25 d	6	2	5 d	2	10
U. cordatus	25 d	6	2	5 d	2	10

All environmental settings of the tank environment were adjusted to and synchronized with the environmental factors in the field. With the exception of the experiments on *Uca maracoani* and *U. thayeri*, the tanks did not contain any substrate except those substrate types desired for monodietary testing. The tanks were however equipped with PVC-tubes, which served as refuge shelter to the animals (Chapter 3.3). During the experiments on *Goniopsis cruentata*, *Aratus pisonii*, and *Littorina s. angulifera*, the tanks were additionally equipped with pieces of decorticated palm wood to provide the animals a possibility to leave the water. No tidal cycles were simulated during the experiments on *Cardisoma guanhumi* and *Ucides cordatus* because of their distributional range above the eulittoral zone (Fig. 7).

Equal numbers of individuals of both sexes were haphazardly sampled at definite time intervals, except during the experiments on *Sphoeroides testudineus* and *Littorina scabra angulifera*. Due to the lack of external sexual dimorphism of *S. testudineus* and hermaphroditism of *L. s. angulifera*, the sex criterion was not workable for both species. After sampling, all animals were instantly deep-frozen at -20°C. The tissue samples were later prepared as described in Chapter 3.5.4 and analyzed for stable isotope ratios as described in Chapter 3.12.

3.6 Total Biomass and Biomass Production

Information on the size and structures of the standing stocks of the main animal target species *Sphoeroides testudineus*, *Goniopsis cruentata*, *Aratus pisonii*, *Cardisoma guanhumi*, *Ucides cordatus*, *Uca maracoani*, *Uca thayeri*, *Callinectes danae*, *Littorina scabra angulifera* was congregated via transect sweep-sampling (TRS, Table 1) and morphological analysis of all live specimens within an area of 4 000 m^2 (TRS_I, TRS_{II} = 2 x 500 m x 4 m) on 17 June, 1995 (RS) and 22 January, 1996 (DS). An additional more extensive transect sweep-sampling screening a mangal area of 20 000 m^2 (TRS_{III} = 2 x 500 m x 20 m) was conducted from 13 to 14 February, 1996 (DS). The location of the transect is shown in Fig. 1. It stretched as a straight line from the extreme low water level during spring tides (ELWS, Table 1), which was approximately 100 min front of the seaward extention of the mangrove trees, to a point 5 m into the supralittoral coconut-tree zone. The representative character of the TRS-location was tested by probing comparable areas at other locations of the Canal de Sta. Cruz mangal.

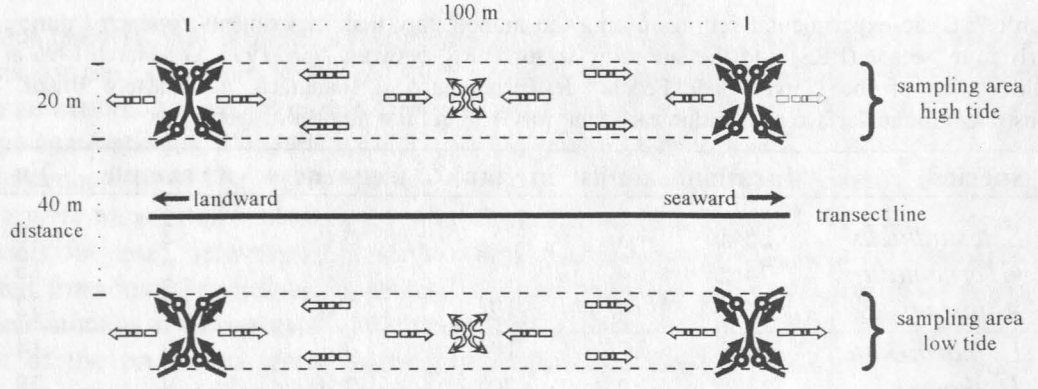


Fig. 6: Schematic description of the sweep-sampling strategy along a transect line for evaluation of standing biomass in the mangal area of the Canal Sta. Cruz, Itamaracá Island, Pernambuco State, northeastern Brazil from February 1995 until March 1996.

The location of the transect was chosen with respect to two criteria: (1) portrayal of all faunal and floral species of the mangal segment of the Canal de Sta. Cruz ecosystem and (2) a live mangrove tree coverage of 79 % representing the average coverage of the entire system. Two sampling periods within two areas situated parallel to each other were initiated at high and low tide of the same tidal cycle and all data obtained were later combined to one data set. These data combinations were made in the appropriate statistical ways regarding the specific type of data (Chapter 3.13) and led to averages for the entire tidal cycle. During high and low tide, simultaneous sweep-sampling took place in sub-sections of 100 m length as described in Fig. 6. The two sweep-sampling areas (high tide, low tide) were situated at different sides along the transect line and had a lateral distance to each other of two times their width e.g. 8 m and 40 m, respectively.

Each 100m-subsection was sampled by two persons during sampling of the 4 000 m^2 -area and four persons during sampling of the 20 000 m^2 -area. The required minimum personnel of 10 and 20 persons consisted of staff of the field station and local fishermen from Itapissuma Village. All personnel was introduced into the specific methodical requirements of the sweep-sampling and the importance of a uniform and constant procedure of the gathering of specimens for scientific purpose in general and for statistical purpose in particular. The two (four) persons responsible for the sampling within one sub-section started sampling at the opposite ends of the 100m-stretches. They slowly moved towards each other while conducting semi-circular lateral movements between the sidelong boundaries of the area. After 50 m, the teams met each other, turned around and started sampling again into the opposite direction. After 50 m the team met the team from the neighboring sub-section, turned around and started again. This oscillation movement was continued for the entire tidal period, thus sampling the area three to four times (sweep-sampling). Using 50 l-buckets and PE-trays, all animals sampled were instantly transferred to the nearby laboratory and analyzed for their morphological data. All animals not required for further analyses with respect to other parts of the project were later released to the specific areas they had been taken from.

Sampling was continuous during the complete tidal cycle, minimizing a lateral immigration of organisms from the neighboring areas through constant disturbance by human activity. To further avoid sampling of specimens that may have immigrated into the sampling area via the lateral boundary between runs, organisms that were encountered within an outward distance of 0.5 m from this border were not counted but transferred into separate buckets from the first sampling run onwards. These organisms were not recorded for experimental purpose.

Sphoeroides testudineus was caught by net fishing using 5 mm-nylon enclosure nets. Large *Goniopsis cruentata* were caught using live *Aratus pisonii* attached to the end of a nylon line as prey. This method was adopted from the local fishermen in the area. Small *G. cruentata* were collected by hand. *A. pisonii* was caught by hand which proved to be extremely laborious because of the animals tendency to flee into the upper regions of the mangrove canopy which reached up to 7 m in the sampling area. *Littorina scabra angulifera* was collected by hand from the roots, stems and branches of the mangrove trees. *Callinectes danae* was sampled using 15 mm-nylon nets encircling and closing in on the animals which aggregated in tidal puddles beneath mangrove roots. *Uca maracoani* and *U. thayeri* were sampled on the surface and to a substrate depth of 0.75 m for *U. maracoani* and 0.20m for *U. thayeri* entering their burrows by hand. To avoid the escape of highly apprehensive animals from the sampling area the area boundaries were closed during the high tide preceding the sampling period using a 5 mm-net of 0.5 m height as a fence. The animals were found not to climb this barrier even in stress situations.

Cardisoma guanhumi and *Ucides cordatus* were sampled in traps built of tin cans having a closing mechanism driven by a strong rubber band. As shown by the local fishermen, a fruit mixture mainly consisting of mango meat was used as prey for both species. The traps were installed nearby the openings of the animals' burrows above EHWS (extreme high water during spring tides). Because both species almost exclusively exhibit nocturnal feeding activity and are very susceptive to any kind of disturbance within their territory, sweep-sampling of *C. guanhumi* and *U. cordatus* was conducted during the two nights prior to the actual sweep-sampling date for the rest of the organisms in the sweep-sampling area. Burrows that had been successfully sampled were closed using rugs to avoid reclaiming by other crabs during the absence of the initial inhabitants. After a maximum duration of captivity of two days at the field station, the crabs were re-transferred to their original burrows.

The total standing plant biomass of the area consisting of mangrove material, seagrass and epiphytes within the canopy, on the mangrove roots and on the substrate was determined through a combination of metric measurements and standard mathematical conversion methods. During the three transect sweep-samplings, 60 squares of 1 m^2(= 60 m^2) were analyzed for their standing mangrove tree biomass e.g. number of leaves, their number and thickness of branches and pneumatophores. Sub-surface root material was not quantified, but assessed under application of respective relationships to above-surface material taken from literature. Additionally, all other plant material, mainly consisting of mangrove litterfall and benthic and epiphytic algae, was analyzed for its dry weight. Commonly supralittoral euryhaline plants like salt and beach grass species that were encountered as whole plants or as plant fragments within the eulittoral zone were neglected during all determinations of plant biomass in the mangal area. Macroepiphytes within the mangrove canopy were quantified via weight determination of subsamples and consecutive counting of the epiphyte stands.

All animal and plant material sampled during the three sweep-sampling events was analyzed for the following morphometrical measures. Fish were analyzed for their total body length (1.0 mm), fresh weight (FW, Table 1) (1.0 g), age, and sex. Crustaceans were analyzed for their carapace width (1.0 mm), weight (0.1 g) and sex. Mollusks were analyzed for their shell height (1.0 mm), fresh weight including shell (0.1 g), and dry weight of their shell (0.1g). All organisms sampled were counted and their numbers provided the basis for the determination of the specific standing biomass. However, only morphologically intact specimens were used for the determination of metric dimensions or weight of the species in the area. Plant standing biomass was determined as dry weight (DW, Table 1) (0.1g) after 48 h at 65°C after the material had been washed and cleaned from epiphytic material. All chlorophytes were combined into one epiphyte pool separate from the phaeophytes and rhodophytes that were combined into a second one. A further subdivision of the epiphytes into taxonomic groups was not undertaken. The mangrove plant material collected as litterfall was subdivided into leaves, woody material, flowers and seeds which were analyzed separately.

In addition to the three sweep-sampling events for standing biomass, the annual litterfall of the dominant mangrove tree species in the area, e. g. *Avicennia marina*, *Rhizophora mangle*, *Laguncularia racemosa* and *Conocarpus erecta* was analyzed through monthly samplings of ten squares of 1 m^2 (= 10 m^2) located at 30 m-distance from each other along the 300 m section of the sweep-sampling transect cutting through the mangal zone. The term "litterfall" covered all mangrove tree material that had become distached from live and dead trees including leaves, flowers, parts for reproductive dispersion and all kind of fragments from the trees. Not included was any kind of epiphyte material attached to the actual mangrove tree litter. This dirt or epiphyte material was removed and analyzed separately. The tidal transport

effect of plant material by water currents was ignored for statistical analysis because of the hypothetical assumption of quantitative homogeneity within the area.

The biomass production rates of the benthic epiphytes to a substrate depth of 1 cm consisting of chlorophyte and phaeophyte/ rhodophyte communities was also determined through monthly sampling of ten squares of 1 m^2 (= 10 m^2) located at distances of 30 m along the sweep-sampling transect. Each month, stripes of 2 cm width, 1 m length and at lateral distances of 5 cm were cleaned of all epiphytes. The dry weight of the remaining epiphyte flora was determined in 10 subsquares of 100 cm^2. The following month, the dry weight including the epiphytes that had re-grown inside the cleaned stripes was determined accordingly. The differences were defined as production. Samples of epiphytes on mangrove roots at ten squares of 1 m^2 (= 10 m^2) along the same transect were collected as well. Stripes of 2 cm width in distances of 5 cm were analyzed according to the method applied on the mangrove floor.

3.7 Combined Data Analysis and Interpretation of Field and Tank Experiments

In order to develop a model of the food web structure of the mangal segment of the Canal de Sta. Cruz mangrove ecosystem over the period of one year, the results from the 24h-field and tank experiments on all species during ERS and LRS were combined with the results from the determination of standing biomass. Additionally, all data derived from the stable isotope analyses of the trophic key and food species were integrated for the same purpose. A flow chart of the qualitative and quantitative interactions of the species was developed. To admit easy applicability of the model to tropical mangrove ecosystems having a comparable ecological structure, this model was simplified to the degree requiring just standing biomass data on species. A second even more simplified model was developed requiring standing biomass data only on groups of species such as crustaceans, fish, epiphytes and plants.

3.8 Taxonomy of Species Monitored

3.8.1 Fish

Sphoeroides testudineus (L. 1758) [syn.: *Tetr(a)odon testudineus*, *Sphoeroïdes testudinëus*, *Sphaeroides testudineus*], Tetraodontidae, Tetraodontiformes, checkered puffer, in Portuguese: "Baiacu"

3.8.2 Crustaceans

Goniopsis cruentata (Latreille 1803), Grapsidae, Grapsoidea, Brachyura, Reptantia, Decapoda, red mangrove crab, in Portuguese: "Aratu"

Aratus pisonii (H. Milne Edwards 1837), Grapsidae, Grapsoidea, Brachyura, Reptantia, Decapoda, mangrove tree crab, in Portuguese: "Mofada"

Cardisoma guanhumi (Latreille 1852), Gecarcinidae, Grapsoidea, Brachyura, Reptantia, Decapoda, in Portuguese: "Guaiamum"

Ucides cordatus (L. 1763), Gecarcinidae, Grapsoidea, Brachyura, Reptantia, Decapoda, in Portuguese: "Caranguéju"

Uca maracoani (Latreille 1802), Ocypodidae, Ocypodoidea, Brachyura, Reptantia, Decapoda, fiddler crab, in Portuguese: "Chama-maré"

Uca thayeri (Rathbun 1900), Ocypodidae, Ocypodoidea, Brachyura, Reptantia, Decapoda, small fiddler crab, in Portuguese: "Xié"

Callinectes danae (Smith 1869), Protunidae, Protunoidea, Brachyura, Reptantia, Decapoda, blue crab, in Portuguese: "Siri azul"

3.8.3 Mollusks

Littorina scabra angulifera (Lamarck 1822), Littorinidae, Littorinacea, Mesogastropoda, Prosobranchia, Gastropoda, southern periwinkle

3.8.4 Mangrove Trees

Avicennia marina (Forsk.) Vierh., black mangrove, in Portuguese: "mangue canoé"

Rhizophora mangle (L.), red mangrove, in Portuguese: "mangue casco"

Laguncularia racemosa (Gärtn.), white mangrove, in Portuguese: "mangue manso"

Conocarpus erecta (L.), buttonwood mangrove, in Portuguese: "mangue botão"

3.8.5 Seagrass

Halodule wrightii (Aschers. 1868), Cymodoceoideae, Potamogestonaceae, seagrass (after Den Hartog 1970)

3.8.6 Epiphytes

Rhodophyta, Phaeophyta, Chlorophyta: not further classified

3.9 Taxonomy of Additional Food Species During Tank Experiments

3.9.1 Fish

Centropomus undecimalis (Bloch 1792), Centropominae, Centropomidae, Perciformes, Actinopterygii, common snook, in Portuguese: "Camurim"

Eugerres brasilianus (Cuvier 1830), Gerreidae, Perciformes, Actinopterygii, Brazilian mojarra, in Portuguese: "Carapeba"

Mugil gaimardianus (Desmarest 1831), Mugilidae, Perciformes, Actinopterygii, (mangrove) mullet, in Portuguese: "Curimá"

Opisthonema oglinum (Le Sueur 1818), Clupeidae, Clupeiformes, Actinopterygii, striped sardine, in Portuguese: "Sardinha Bandeira"

3.9.2 Crustaceans

Penaeus schmitti (Burkenroad 1936), Penaeidae, Penaeoidea, Penaeidea, Natantia, Decapoda, white shrimp, in Portuguese: "Camarão-Branco"

Penaeus brasiliensis (Latreille 1817), Penaeidae, Penaeoidea, Penaeoidea, Penaeidea, Natantia, Decapoda, pink shrimp, in Portuguese: "Camarão-Rosa"

3.10 Technical Equipment at Brazil

The following technical equipment was used during the project phase at Brazil and installed at the Itamaracá field station of the Universidade Federal de Pernambuco. The equipment was supplied by the Departamento de Oceanografia, Recife, Brazil, the Center for Tropical marine Ecology at Bremen, Germany, the Institute of Marine Science, Kiel, Germany, and by myself. Additional laboratory equipment used at Germany is described within the respective chapters on the analysis of stable isotope ratios and mass-spectrometry.

1) Microprocessor conductivity meter WTW LF 96 using the equation

$$S = 0.023164500305 + 0{,}49202922521 \cdot cond + 0.006026301657 \cdot cond^2 - 7.7207053511 \cdot 10^{-5} \cdot cond^3 + 4.37090937 \cdot 10^{-7} \cdot cond^4$$

for the calculation of water salinity at 25°C.

2) Binocular ZEISS Stemi SV 6: 10 x 0.8-5.0 x 0.63; the connectable photographic unit CONTAX 167 MT increased the magnification by the factor 2.5

3) Electric furnace LBC, temperature range: 0-300°C, sensor interval = 6°C

4) Electronic balance SARTORIUS PT 210 , weight range: 0-200 g, precision: 0.01 g

5) In-row double cylinder vacuum pump KNF NEUENBERGER MW 63/4, maximum volume: 1.4 $l \cdot min^{-1}$, $\cos \varphi = 0.93$

6) Custom made filter unit, throughpass diameter: 55 mm; glass-fiber filters SCHLEICHER & SCHUEL GF 6: diameter: 63 mm, all filters had been combusted at 475°C for 1h to remove adherent organic material

7) Reflex-Camera RICOH XR-X for macro and field photography; lenses RICOH: 80-200 mm, f 4.5-5.6; RICOH: 1/4-24 macro, f 2.0-4.0; SIGMA: 28-80 mm, f 3.5-4.5; black and white films ILFORD FP 4, 125 ASA; color print films KODAK GOLD, 200 ASA and FUJICOLOR SUPER G PLUS, 100 ASA; color slide films FUJICHROME SENSIA, 100 ASA

8) Hand torches MAG LITE, 6.0 Volt

3.11 Mass-Spectrometry

Biochemical fixation of atmospheric carbon differs between primary producers out of the groups of C3 and C4-plants regarding the stable carbon isotope ratio transduced to the

chemical products. This fraction that results into a distinctive ratio of ^{12}C and ^{13}C-isotopes can be traced over long biochemical distances inside progressive food webs. There are considerable differences between phyto- and zooplankton, epiphytic algae, macroalgea, higher and terrestrial plants, lower and higher animals. As an example, the particular peak of the carbon isotope ratio of a gastropods muscle tissue will provide information whether the organism has fed on detritus, epiphytes or plant tissue. Nevertheless, the results will be just qualitative and deliver just relative values. Here, the method of stable nitrogen isotope ratios provides valuable additional information. Different from the carbon isotope ratio, the nitrogen isotope ratio $\delta^{15}N$ ($^{15}N/^{14}N$) is far less stable due to permanent exchange with atmospheric nitrogen via the metabolism of bacteria. This fact implies the great possibility to determine trophic levels of food usage or disintegrations of the primarily assimilated food source (Harrigan et *al.* 1989; Coleman 1991; Lacerda et *al.* 1991). For further details on the method of stable isotopes refer to Coleman 1991.

The combination of stable isotope ratios from three chemical elements provided the possibility to create a basic three-dimensional display of the main pathways of biomass within the benthic food web analyzed during the project. At the same time, this three-dimensionality of a restricted number of results enabled the more accurate interpretation of the remaining isotope samples that were analyzed for their stable ratios of organic carbon and nitrogen only. A three-dimensional analysis of the entire number of samples was not performable due to the very high costs of the analyses of the sulfur isotopes. The analyses of the stable isotope ratios of the elements carbon and nitrogen were conducted at the Institute of Baltic Sea Research (Institut für Ostseeforschung Warnemünde IOW) at Warnemünde, Germany and the Research Institute of Geology for Mineral Resources (CNNC) at Sanlidian Guilin, China. Additionally, selected samples were analyzed for their stable sulfur isotope ratios at the Institute of Geological Chemistry, University of Göttingen, Germany. All samples had been prepared as described in Chapter 3.5.4.

A double-inlet gas isotope mass spectrometer was used for the analyses of the stable isotope ratios of organic carbon and nitrogen. The samples were combusted in a Carlo-Erba 1108 CN-analyzer connected to a Finnigan MAT mass spectrometer (model Delta-S). The stable isotope ratios of sulfur were analyzed using a triple-inlet centrifugal gas spectrometer (KORDT). All samples were measured under a continuous helium flow. The use of multiple-inlet spectrometers reduced the risk of contamination between separate samples. The mass-spectrometers consisted of six basic technical assembly groups: 1) a dual-inlet system for the separate handling of the sample and standard gas, 2) an ion source where the gases were ionized at a hot filament, 3) a curved (90°) flight tube within a variable magnetic field to resolve ions of different masses, 4) a set of Faraday cup detectors connected to an amplification unit for collection and amplification of the separate ion beams, 5) a vacuum pump to maintain a high vacuum of approximately 10^{-8} torr inside the flight tube and 10^{-3} torr inside the gas inlet system, 6) a computer unit for data acquisition and instrument control.

At the ion source, the elements to be analyzed for their stable isotope ratios were converted into on of their gas forms that had to be unreactive at room temperature. Depending on the complexity of the chemical structure of those gases, different compositions of ions of all elements inside the molecule caused difficulties during the determination of the isotope ratios of the element of central interest. For example, the isotope ratios of organic carbon are calculated from the mass-ratios 45/44 and 46/44 of the molecule carbon dioxide CO_2. Unfortunately, those mass-ratios may result from the following different combination of isotopes of the elements oxygen and carbon inside the CO_2-molecule: 1) $^{12}C^{16}O^{16}O$ (atom mass 44), 2) $^{13}C^{16}O^{16}O$ or $^{12}C^{17}O^{16}O$ (atom mass 45), and 3) $^{12}C^{18}O^{16}O$ (atom mass 46).

With respect to international convention, values of $\delta^{13}C$ were measured against a peptone laboratory standard (Merck), which had been calibrated in relation to NBS standards (U.S. National Bureau of Standards no. 18, 20) They were however expressed as deviation from the PDB calcium carbonate standard (PDB, Table 1). This standard was derived from the limestone fossil *Belemnitella americana* from the Cretaceous Pee Dee formation at South Carolina, USA. This standard having the absolute $^{13}C/^{12}C$ ratio of 0.0112372 has been assigned the $\delta^{13}C$ value of 0 ‰. The stable isotope ratios of nitrogen and sulfur were expressed as deviations from atmospheric nitrogen (ATMN) and Canon Diabolo triolite (CDT), respectively.

The measurement precision, as calculated from differences between multiple measurements of laboratory standards, was ±0.15 ‰ for $\delta^{13}C$, ±0.20 ‰ for $\delta^{15}N$, and ±0.3 ‰ for $\delta^{34}S$ measurements. Several studies have shown the existence of an additional $\delta^{13}C$ shift of ~ 1‰ during digestion and during the assimilation processes in consumer muscle tissues (Teeri & Schoeller 1979). Whether the assimilatory shift was of summative (Harrigan et *al.* 1989) or multiplicative character with respect to the entire length of the food chains analyzed in the run of the project, was tested by cross comparison of the stable isotope results from the monodietary experiments. One principal methodological restriction of the analysis of the origin of stable isotope ratios in consumer tissue is the mathematical fact that the contribution of only two food sources is distinguishable from one experiment. Thus, multiple individual experiments on specific food-consumer combinations and, at some times, experiments on pooled food sources of comparable stable isotope ratios had to be conducted separately and were later combined to a conclusive model of the entire system. The monodietary tank experiments provided particular basic information on theoretical unbiased food-consumer shifts of the stable isotope ratios.

The ratio of a chemical element's heavy to the respective light isotopes was expressed according to the standard δ notation (Craig 1957), where positive values indicate enrichment and negative values indicate depletion of the heavy isotope relative to the standard sample. In general, the stable isotope values in the present study were calculated according to the equation:

$$\delta X = (R_{sample} / R_{standard} - 1) \cdot 1\,000$$

where X (0.1 ‰) is either $\delta^{13}C$, $\delta^{15}N$, or $\delta^{34}S$, and R is the ratio of heavy to the respective light isotopes $\delta^{12}C$, $\delta^{14}N$, or $\delta^{32}S$.

3.12 Methods of Statistical Analysis

Non-parametric **WILCOXON Tests** were applied to analyze the correlation between paired single observations or means of similar or not similar numbers of observations within samples or data sets in identical time intervals (Miller 1956; Wilcoxon & Wilcoxon 1964; Lozán 1992; Sachs 1992).

χ^2-Tests were preferred to test normal distributed samples against expected or known distributions (Fisher & Yates 1963; Lancaster 1969). Parametric **t-Tests** (Student-test) were

applied to dependent or independent samples consisting of normal distributed or almost normal distributed paired observations or parameters. Aspects tested were: general (normal) distribution fitting of samples, comparison of averages, and/or comparison of variances (Hill 1972). **Analyses of Variances ANOVA (F-test**: H_0 ($\mu_i = \mu$)) of averages were evaluated by **Least Significant Difference Tests (LSD-test)** in cases when H_0 had to be rejected. The LSD-test revealed similarities of averages of neighboring groups arranged in ascending order.

The **Friedman-test** was used to test the similarity of variances of two or more dependent non-parametric (not necessarily normal distributed) treatments or samples and replaced the ANOVA F-test in these cases (Friedman 1937). The Friedman-test using the critical values $\chi^2_{R(\alpha)}$ is very conservative. Whenever feasible, the more liberal variation using the linear combination $\mathbf{J}_{(\alpha)}$ of the critical values $\mathbf{F}_{(\alpha)}$ (parametric) and $\chi^2_{R(\alpha)}$ (non-parametric) was chosen. **Hartley's test** of similarity of variances was used for samples of equal numbers of observations (Hartley 1950). Alternative tests would have been Corchan's test and Barlett's test of similarity of variances (Corchan 1941; Barlett 1937). Corchan's test was not chosen because of the relative small magnitude of differences expected between class variances during most of the experiments conducted. Barlett's test was not chosen because of its low sensitivity to variance similarities. Its high sensitivity to a normal distribution of variances was of minor importance during the evaluation and interpretation of most experiments or was tested using other statistical methods.

4 Results

4.1 General Behavior

Cardisoma guanhumi (Plate 2.4) exclusively exhibited nocturnal activity and was hard to detected in the shrub and beach grass of the supralittoral zone (Fig. 7). A few times only, animals were observed while foraging for food. During these occasions, *C. guanhumi* was always encountered in groups. Single specimens were never found. The animals were feeding on mango or fig fruits, on larger insects like grasshoppers, as well as on all kinds of carrion like dead frogs or fish that had been washed ashore by the tide. Only during nocturnal ELWS, they were occasionally encountered within the upper intertidal zone (Table 1) while feeding on mangrove leaves and benthic algae. The species was never found entering the water. Information on reproductive biology of the species was not obtainable. The animals were too scarce and too valuable to the local fishery communities to be sacrificed just for identification of their reproductive status. *C. guanhumi* was always encountered living in couples within their burrows that were always equipped with a minimum of three openings. The burrows were always built within a maximum horizontal distance of 5 m from the EHWS-border but never directly into the final wash-out terrace separating the intertidal from the coconut-tree zone.

Those final terraces were preferred by *Ucides cordatus* (Plate 2.2, 2.3), particularly when situated near muddy plains, tidal creeks or puddles. Compared to *C. guanhumi*, the burrows of *U. cordatus* were always closer to and most times even below the EHWS-border and they were always inhabited by single specimens. During spring tides, most of the burrows were completely covered by water. The burrows were up to 2 m deep ensuring a sufficiently high humidity even during ELWS, because the animals did not move their burrows following the lunar cycle of the high tide elevation level as did *Uca maracoani* or *U. thayeri*. Only during nighttime, *U. cordatus* was encountered outside the burrows. The animals were never found within the coconut-tree zone. Unlike *C. guanhumi*, *U. cordatus* did not move in groups. As for *C. guanhumi*, no specimens of *U. cordatus* were sacrificed for the purpose of identification of their reproductive status because density of the animals was too low to derive at sufficient numbers.

The small fiddler crab, *Uca thayeri* (Plate 1.8, 2.1), lived in the upper intertidal zone at areas having a more sandy substrate than in the areas where *U. maracoani* occurred (Fig. 7; Plate 1.1). While following the tidal rim, the animals moved distances of up to 150 m during the monthly lunar cycle. The average grain diameter of the surface sediments at *U. thayeri* sites was always > 0.2 mm. The flooding period at the sites never exceeded 1.5 h. No other brachiuran species was found within the distribution range of the species. The burrows of *U. thayeri* had a maximum depth of 0.25 m and, unlike the almost exclusively separate burrows of *U. maracoani*, they formed a system of interconnected tunnels that were shared by several animals of different size and sex at the same time. Females carrying eggs were found during the entire year.

Uca maracoani (Plate 1.1) lived at great densities at muddy substrates having an average grain diameter of < 0.063 mm and a maximum duration of the tidal flooding period of 4.5 h (Fig. 7). These substrates were found within almost the entire intertidal zone of the mangrove ecosystem, e.g. at open areas within the live mangal zone, at shallow intertidal areas below the mangal zone, and at some of the abandoned aquaculture ponds in front of the Itamaracá field station that were lacking mangroves. At each site, *U. maracoani* showed different behavioral adaptations to predation pressure. During low tide, no other brachiuran species was found

within the distribution range of *U. maracoani*. The animals' burrows had a maximum depth of 1.2 m and were inhabited by single specimens except for short periods of mating. Female fiddler crabs carrying eggs were found during the entire year. As long as the burrows were covered by a minimum of 0.2 m of water during high tide and the period without water coverage had a minimum duration of 8 h, the burrows were not moved.

During high tide, several fish species including *Sphoeroides testudineus* as well as the brachiurans *Callinectes danae* and, to a low extent, *Goniopsis cruentata* immigrated to the area while the *Uca maracoani* specimens rested inside their burrows to prevent predation from these and other organisms. During low tide and at the open muddy plains within the live mangrove zone, the fiddler crabs kept a minimum average distance of 5 m to hard substrates such as roots or rocks inhabited by *G. cruentata*. The same distance was kept to tidal creeks inhabited by *C. danae* during low tides. The potential predator *G. cruentata* showed great difficulty to move when placed on wet muddy substrate. Normally they stayed close to or on hard substrates in the zone. The potential predator *C. danae* is not able to leave the aquatic environment where *U. maracoani* was never detected during the entire project phase.

Goniopsis cruentata (Plate 1.1, 1.2) was found in all benthic zones of the Canal de Sta. Cruz ecosystem having either a live or dead mangrove tree coverage (Fig. 7). In the dead mangrove tree zone, *G. cruentata* stayed close to water sources such as tidal creeks or puddles. The species was very territorial. Females carrying eggs were found during the entire year. Within the live mangrove tree zone, the specimens preferred areas dominated by *Rhizophora mangle* over areas dominated by *Avicennia marina* or other mangrove species. In general, *G. cruentata* always stayed close to or on hard substrates preferring the shaded more solid substrate between the roots and the stalk roots themselves. As an escape behavior *G. cruentata* flees into the narrow thicket of the roots or into the water depending on the distance to the particular refuge. However, the mangrove thicket was preferred when distances were equal. The animals were able to climb mangrove trees up to the canopy. In contrast to *Aratus pisonii* however, they had to move very slowly and were not able to access the underside of branches their legs couldn't embrace. Due to their higher weight, *G. cruentata* was likewise unable to move into the very apical tips of mangrove branches. Consequently these two spots were used as refuges by *A. pisonii*.

Aratus pisonii (Plate 1.1, 1.4) inhabited the entire live mangal zone (Fig. 7) with a slight preference for *Rhizophora mangle* over *Avicennia marina*. The animals were almost exclusively encountered on the stems and branches of the mangrove trees from a few centimeters above ground to the very tips of the trees' canopy at heights of up to 7 m. Having very pointed and inward bent dactyls at the end of its legs, *A. pisonii* is able to firmly attach itself to the mangrove tree bark and to move very fast on this surface. The animals were rarely detected on the mangrove floor which may have been a result of their very sensitive escape behavior when being disturbed during sampling. *A. pisonii* constructed no burrows or housings of any kind. The only shelters the animals fled to were the underside of horizontal branches of a diameter and the very apical tips of the mangrove branches. Both spots were sufficient for protection against *G. cruentata* (see above). The animals and the male specimens in particular showed an expressed territoriality and a decrease in average body weight with canopy height (Fig. 43). Females carrying eggs were found during the entire year. *A. pisonii* had no obvious daily activity oscillations but the animals moved higher into the mangrove canopy during nighttime.

Fig. 7. Distribution of selected key benthic animal species in the Canal de Sta. Cruz mangrove ecosystem, Itamaracá Island, Pernambuco State, northeastern Brazil.

Littorina scabra angulifera (Plate 2.5) was found in the live mangrove zone below EHWN (Fig. 7). On mangrove trees, the animals were vertically distributed only between the ground level and 2.0 m above ground. Other hard substrates were avoided. *Rhizophora mangle* was preferred over *Avicennia marina* (ratio 7.2 : 1) between trees of equal height. In correlation to the tidal cycles, the gastropods showed vertical migrations between these two levels (WILCOXON-test, $\alpha = 0.05$). *L.s.angulifera* always followed or moved ahead of the water level at a minimum distance of 0.4 m. No animals were observed closer than 0.4 m to the ground at any time although the algal density was higher here. No general behavioral differences were detected between day and nighttime.

The marine blue crab, *Callinectes danae* (Plate 1.6, 1.7), was observed within the entire intertidal zone during high tides but was restricted to tidal creeks, puddles and stalk root areas of *Rhizophora mangle* that were filled with water during low tide. The average size of the animals was correlated to the volume of those limited water bodies. Large *C. danae* stayed in the tidal creeks. The animals never left the water even when there was seemingly reachable prey close to the water line. Most times, *C. danae* was found in the open water not showing any expressed need for shelter although the animals were also encountered preying under hard substrates. When disturbed, the blue crabs displayed aggressive defense response. However, a territorial behavior was not observed. Specimens within the reproductive phase were scarce but found over the entire year. During nighttime, the activity level of the animals declined.

Sphoeroides testudineus (Plate 2.6, 2.7) was found in all aquatic zones of the Itamaracá Estuary (Fig. 7). Activity levels were higher during the daytime and tide-induced migrations into the flooded inner mangrove areas were observed during high tides. Here, the animals preferred the zone of higher *Rhizophora mangle* density over zones dominated by *Avicennia marina*. The migration was reduced during high tides at nights. During low tides, *S. testudineus* did not stay inside tidal creeks or puddles, but migrated back to the open water of the Canal de Sta. Cruz. Surprisingly, the average relationship between female and male *S. testudineus* at all locations was 28 : 1. There were only minor changes in this situation with a relationship of 34 : 1 during PDS and 25 : 1 during PRS. Reproduction showed a small peak during the rainy season, but continued over the entire year.

4.2 Food Web Analysis and Turn-Over Rates

The analysis of the food web in the mangal segment of the mangrove ecosystem of the Canal de Sta. Cruz required a combination of field and tank experiments. Tank experiments under controlled environmental conditions contributed valuable information on the feeding behavior, general food acceptances and food requirements per unit time essential for the analysis of the food web relationships in the field. Starvation tank experiments were essential for the evaluation of the gastro-intestinal filling-level dependent evacuation rates computed from data from the 24h-field experiments. The additional 24h-tank experiments were necessary to elucidate the influence of specific food sources on the total food requirement of a particular trophic key species (Table 1). Monodietary tank experiments were conducted to obtain stable isotope relations of the body tissue of the trophic key species resulting from single food sources. The experiment type also provided important information on the theoretical maximum speed of the shift of stable isotope relations within the body tissue of the animals after a complete change of diet. Without the latter two types of information an interpretation of the qualitative isotope data from the field would not have been possible. The results presented below are structured under physiological aspects and sometimes combine field and tank

experiments. An explicit additional subdivision into experiment types (as explained in Materials and Methods) was not made in order to avoid an unnecessary complexity of the presentation.

4.2.1 General Feeding Behavior

Showing only minor differences of activity levels, *Goniopsis cruentata*, *Aratus pisonii*, and *Littorina scabra angulifera* fed during day and nighttime. The feeding activity of *Cardisoma guanhumi* and *Ucides cordatus* was restricted to nighttime. *Uca maracoani*, *U. thayeri*, *Callinectes danae*, and *Sphoeroides testudineus* were observed feeding only during the daytime. The initial analysis of the latter two species was conducted as tank experiments.

Table 8: Results of the preliminary testing (field experiments) of food sources at the initiation of the food web analysis in the benthic Canal Sta. Cruz mangrove ecosystem, northeastern Brazil, between April 1995 and March 1996. Food sources are arranged in descending order corresponding to the observed preference graduation for the specific live/ fresh food source. Parentheses enclose similar acceptances (no statistical testing). **L** = live, **F** = fresh, **d** = slightly decayed/ decomposed, **D** = strongly decayed/ decomposed. Food source numbers without literal notation were accepted in any condition.

trophic key animal species	food source corresponding to the index (1-24) of the target and non-target species[b]
Goniopsis cruentata[1]	(2-4, 1Dd, 5-7Dd), (22Dd, 23Dd), (9Dd, 18-21Dd), 8Dd, 11, 12, 14, 13, 16, 15, 17
Aratus pisonii[2]	15, 16, 12, 11, 14, 13, 17, (22Dd, 23Dd), (9Dd, 18-21Dd), (1-7D), 8D
Uca maracoani[3]	24
Uca thayeri[4]	24
[a]*Callinectes danae*[5]	2, 4, 3, 1, (22, 23), (18-21LDd*),(9LDd*), 6Dd, 7Dd, 8, 5Dd
Cardisoma guanhumi[6]	17, (22Dd, 23Dd), (9Dd, 18Dd-21Dd), (1-7Dd), 8Dd, 10, (11-14), (15, 16)
Ucides cordatus[7]	17Dd, 15, 16, 24, (11-14Dd), 10Dd, 22Dd, 23Dd, (9Dd, 18-21Dd), (1-7D), 8D
Littorina scabra angulifera[8]	15, 16
[a]*Sphoeroides testudineus*[9]	(22, 23), (3, 4), 2, 1, 8, 6Dd, 7Dd, 5LDd* (9Dd, 18-21Dd), 10F

plant species and non-target animal species: *Halodule wrightii* foliage [10], *Avicennia marina* leaves[11], *Rhizophora mangle* leaves [12], *Laguncularia racemosa* leaves [13], *Conocarpus erecta* leaves [14], benthic or epiphytic chlorophyte mix[15], benthic or epiphytic phaeo-/ rhodophyte mix[16], mango fruit mix[17], *Centropomus undecimalis*[18], *Eugerres brasilianus*[19], *Opisthonema oglinum*[20], *Mugil gaimardianus*[21], *Penaeus schmitti* [22], *P. brasiliensis*[23], sediment/ benthic microalgae[24]

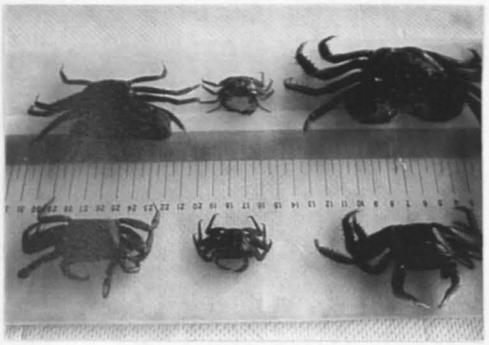
*: L, D, d depending on prey size; [a]: results from tank experiments; [b]: for definition refer to Table 1

Aside the accessible food sources, the results on food sources not naturally existing within the specific habitat ranges of the trophic key animal species, had to be interpreted on a theoretical nutritional basis. *Goniopsis cruentata* showed a preference for all other benthic crustaceans within reach (Table 8; Plate 2.3). Live and moving *Aratus pisonii* as well as *Uca* specimens were preferred over dead animals of all species. All other animal prey species were only accepted dead. The penaeids *Penaeus schmitti* and *P. brasiliensis* were preferred over dead

fish specimens and *Littorina scabra angulifera*. Of the mangrove leaves, *Avicennia marina* litter was preferred over *Rhizophora mangle*, *Conocarpus erecta*, and *Laguncularia racemosa*. Phaeophyte and rhodophyte benthic or epiphytic algae were preferred over chlorophytes. Mango fruit mix was only accepted when no other food source was offered. *A. pisonii* strongly preferred a plant diet over any kind of animal prey including carrion (Table 8; Plate 2.5). Live animals were never accepted. Chlorophyte algae were preferred over phaeophyte and rhodophyte algae, and epiphytic growth forms were preferred over benthic ones. The preference graduation for mangrove leaves was *R. mangle* over *A. marina*, *C. erecta*, and *L. racemosa*. Dead penaeids were preferred over fish and other crustacean species. All brachyuran species were only consumed when being strongly decayed. All food sources were only accepted, when offered either on the branches or in close reach of the roots of the mangrove trees *A. pisonii* lived on.

Callinectes danae showed exclusive carnivorous feeding behavior and even preferred some live moving species over seemingly more easily accessible dead prey species offered (Table 8). Live *Aratus pisonii* were preferred over all other food sources, followed by live *Uca thayeri*, *U. maracoani*, *Goniopsis cruentata*, *Penaeus schmitti* and *P. brasiliensis*. Of the fish species tested, *Sphoeroides testudineus* was the least preferred. The physical condition in which the fish species were accepted was depending on their size. Larger fish specimens were only consumed when dead. *Cardisoma guanhumi* and *Ucides cordatus* were also accepted only when dead. *Littorina scabra angulifera* was accepted live only when being artificially offered as moving food source by dropping the snails into the water. Snails slowly moving on the tank walls were not attacked. Dead *L.s.angulifera* were however accepted. *C. danae* showed no acceptance for live specimens of its own species even when very small compared to the predator. Only dead animals were consumed and only when no other food source was offered. The fiddler crabs *U. maracoani* and *U. thayeri* accepted no other food sources than the benthic surface layer of detritus and microalgae (Table 8). *C. guanhumi* strongly preferred the mango fruit mix over all other food sources offered. However, this food source was followed up by carnivorous preference for dead penaeids, fish, brachyurans and *L.s.angulifera*. Live animals were never accepted. Of the plant diet, the sea grass *Halodule wrightii* was preferred over mangrove leaves. The benthic or epiphytic algae were the food source least accepted. *U. cordatus* also displayed a strong preference for the mangrove fruit mix, but accepted only material that was already decayed. Other than *C. guanhumi*, *U. cordatus* was preferably herbivorous concerning the rest of its food range. Benthic or epiphytic chlorophytes were preferred over phaeophytes, rhodophytes, and mangrove zone sediment/ microalgae. *H. wrightii*, Penaeids and fish were only consumed at least slightly decomposed or decayed. All brachyuran species and *L.s.angulifera* had to be strongly decayed before being consumed. *L.s.angulifera* itself exclusively fed on benthic or epiphytic algae preferring chlorophyte species over phaeophytes and rhodophytes and only fed when placed on the mangrove tree roots and stems. When placed on stones, the animals exhibited a vertical escape response even when the substrate was covered by epiphytes.

The experiments revealed a prominent preference of *Sphoeroides testudineus* for the penaeids *Penaeus schmitti* and *P. brasiliensis* and for live or fresh food in general (Plate 2.8). The brachyuran species that followed next in acceptance were ranked from *Uca maracoani* over *U. thayeri* and *Aratus pisonii* to *Goniopsis cruentata*. *Littorina scabra angulifera* was preferred over *Callinectes danae* which was accepted alive or dead depending on its size. All fish species that followed in acceptance (including *S. testudineus* itself) were consumed only when being already dead and at least slightly decayed. The acceptance was however very low on the latter food source. The seagrass *Halodule wrightii* was the least accepted food source and the only plant species. It was only consumed fresh.



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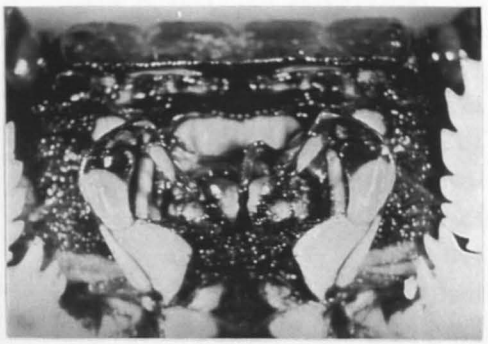

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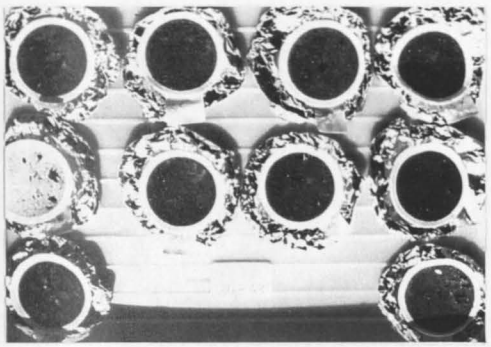

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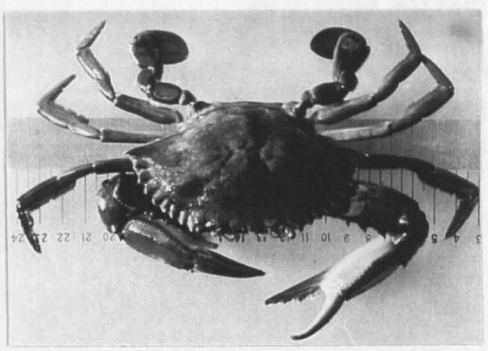

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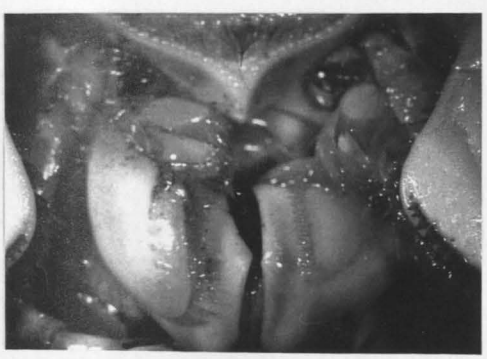

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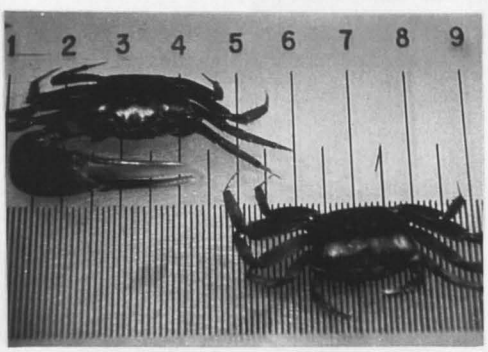

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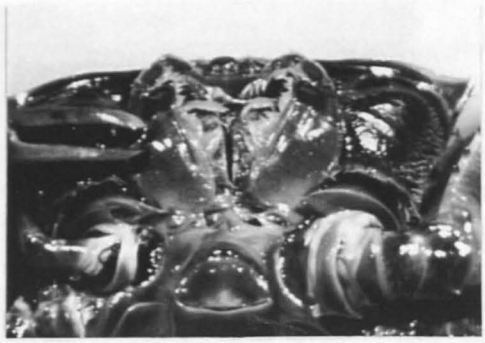
Plate 1. ❶ *Uca maracoani* (top left =♂, bottom =♀), *Aratus pisonii* (top middle =♂, bottom =♀), *Goniopsis cruentata* (top right =♂, bottom =♀),❷ mandibular region of *G. cruentata*, ❸ filtered digestive contents of *G. cruentata* from (10) serial samplings during 24h, ❹ *A. pisonii* (♂),ventral view and mandibular region ❺ filtered digestive contents of *A. pisonii* from (10) serial samplings during 24h, ❻ *Callinectes danae* (♂), ❼ inner mandibular region of *C. danae*, ❽ *Uca thayeri* (top =♂, bottom =♀). All animals were sampled in the mangal ecosystem of the Canal Sta. Cruz, northeastern Brazil between February 1995 and March 1996.



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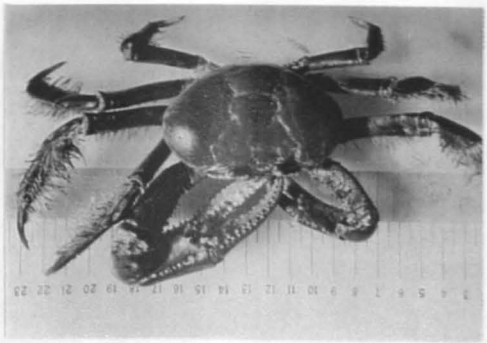

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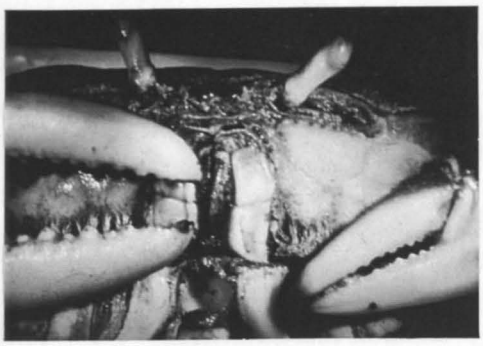

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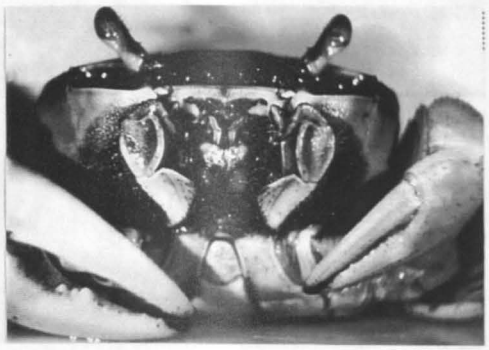

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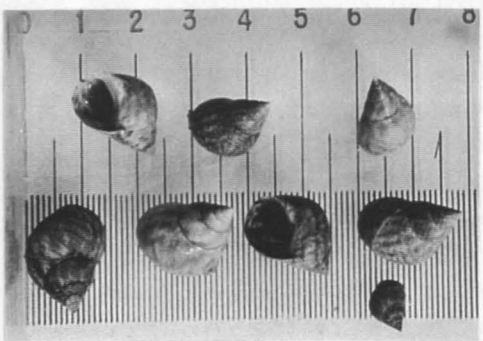

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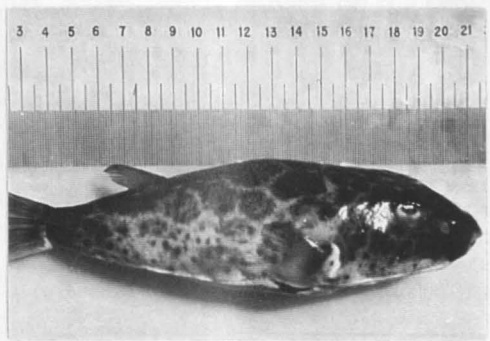

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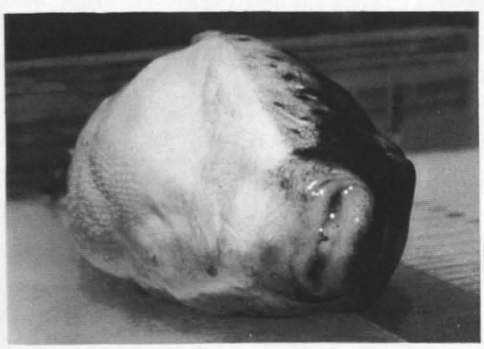

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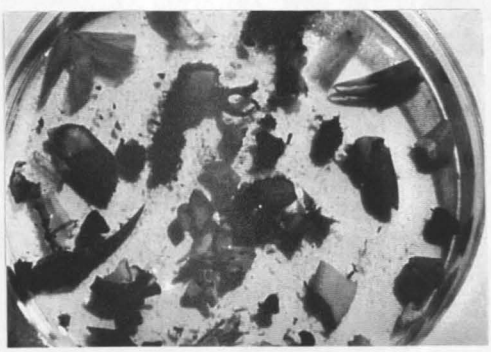

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Plate 2. ❶ ***Uca thayeri*** (♂), left feeding claw; ❷ ***Ucides cordatus*** (♀); ❸ frontal view and mandibular region of ***U. cordatus***; ❹ ***Cardisoma guanhumi*** (♂, carapace width = 56 mm), frontal view and mandibular region; ❺ ***Littorina scabra angulifera*** (scale = cm); ❻ ***Sphaeroides testudineus***, lateral view; ❼ frontal view and dental region of ***S. testudineus***; ❽ digestive content of ***S. testudineus,*** fragments of: *L.s.angulifera* (l), *Callinectes danae* (c), *Penaeus spp.* (p), *Goniopsis cruentata* (g), div. bivalves (b), *Halodule wrightii* (h). Samples from the mangal ecosystem of the Canal Sta. Cruz, northeastern Brazil (1995-1996).

4.2.2 24h-Experiments

Goniopsis cruentata had a complex sex specific daily feeding cycle (Fig. 8). With the exception of the ERS_2 (1996), the female animals had a daily dry-weight food ratio (DR_{DW}) of 3.8 % of their body fresh weight (BFW) which was three-fold higher than the respective food requirement of 1.3-1.8 %BFW · d^{-1} of the male specimens (Table 9; Plate 2.3). Both sexes displayed just one prominent feeding period per day. The gastro-intestinal filling level was not influenced by BFW (non-linear test for randomness, $\alpha = 0.01$). The female *G. cruentata* had their main feeding period during the phase of daylight between 6 a.m. and 6 p.m. during all experiments. The males had a much shorter and less intense feeding period during different times of the day. During 20 hours of the day the relative weight of the gastro-intestinal content of the males stayed close to 0.9 %BFW while the females reached 1.8 %BFW at the peak of the contemporaneous feeding period. As a result of the shorter feeding periods of the males, their ingestion rates of food and their filling-level dependent evacuation rates of material from their digestive tracts were comparatively higher than the rates of the female *G. cruentata*. During LRS (1995) and ERS_1 (1996), both sexes had the highest gastro-intestinal filling levels during ebb tide (females) or low tides (males). During the ERS_2-experiment, both daily low tides coincided with the changes of daylight. The response of the male *G. cruentata* was intense feeding before daylight. This behavior was not observed during LRS although the low tide here happened just two hours earlier. During LRS, the male specimens consequently used the two hours shift at the end of the daylight period for feeding. The filling level of the gastro-intestinal tract of both sexes of *Goniopsis cruentata* was correlated to the periods of daylight and the tidal rhythm (WILCOXON-test, $\alpha = 0.05$). The individual BFW of the animals had no significant influence on the relative weight of the gastro-intestinal content (statistical variance) at a particular daytime (ANOVA, Friedman-test: $\alpha = 0.05$, d.f. = 194). The average daily food ratio of *G. cruentata* over one year was 2.6 %BFW. The annual food requirement was thus 959 %BFW.

Table 9: Results from 24h-field experiments conducted during two early rainy seasons **ERS_1** (1995) and **ERS_2** (1996), and one late rainy season **LRS** (1995) in the benthic mangal segment of the mangrove ecosystem of the Canal Sta. Cruz, Itamaracá Island, northeastern Brazil. The average dry-weight daily food ratio **DR_{DW}** was calculated as ((((ERS_1+ERS_2):2) + LRS):2 under consideration of the average sex ratio of the species. **n** = total number of specimens in all experiments. **f_{DF}** = conversion factor from dry weight DW to fresh weight of the gastro-intestinal content (Table 1, not applied here). **GIC** = gastro-intestinal content. All evacuation rates were filling-level dependent.

species / experiment / feeding periods per day		ingestion rate [% body fresh weight · h^{-1}]	evacuation rate [% GIC · h^{-1}]	DR_{DW} [% body fresh weight · d^{-1}] / $\sum$residuals^2
Sphoeroides testudineus (n = 204), f_{DF} = 1.46				
ERS_1 ♀♀	2	0.129	14.4	**6.780** (3.267)
ERS_1 ♂♂	2	0.093	8.1	**1.973** (6.875)
LRS ♀♀	2	0.168	18.6	**2.062** (6.229)
LRS ♂♂	2	0.218	15.5	**1.551** (5.162)
ERS_2 ♀♀	2	0.250	12.5	**2.502** (6.795)
ERS_2 ♂♂	2	0.280	12.2	**2.925** (2.768)
		annual averages:		♀♀ **3.462** (5.772)
				♂♂ **2.344** (4.393)
			♀♀ : ♂♂ = **1 : 0.15** ⇒	DR_{DW} = **3.3** (5.6)

continued next page

Table 9: continued: Results from 24h-field experiments conducted in the benthic mangal segment of the mangrove ecosystem of the Canal Sta. Cruz, Itamaracá Island, northeastern Brazil.

species / experiment / feeding periods per day		ingestion rate [% body fresh weight · h^{-1}]	evacuation rate [% GIC · h^{-1}]	DR_{DW} [% body fresh weight · d^{-1}] / $\sum$residuals^2
Goniopsis cruentata (n = 195) , f_{DF} = 1.41				
ERS_1 ♀♀	1	0.037	10.6	**3.784** (0.456)
ERS_1 ♂♂	1	0.045	12.8	**1.294** (0.495)
LRS ♀♀	1	0.012	6.5	**3.780** (0.501)
LRS ♂♂	1	0.076	12.3	**1.789** (0.362)
ERS_2 ♀♀	1	0.020	12.7	**2.999** (0.304)
ERS_2 ♂♂	1	0.018	10.8	**2.298** (0.417)
	annual averages:			♀♀ **3.391** (0.391)
				♂♂ **1.920** (0.423)
			♀♀ : ♂♂ = **1 : 1.08** ⇒	DR_{DW} = **2.6** (0.4)
Aratus pisonii (n = 528), f_{DF} = 1.49				
ERS_1 ♀♀	1-2	0.025	14.9	**4.762** (2.051)
ERS_1 ♂♂	1-2	0.018	12.0	**3.068** (3.033)
LRS ♀♀	1-2	0.094	12.0	**3.570** (1.468)
LRS ♂♂	1-2	0.016	11.3	**3.308** (2.580)
ERS_2 ♀♀	1-2	0.015	12.9	**3.671** (3.321)
ERS_2 ♂♂	1-2	0.037	11.9	**3.255** (2.511)
	annual averages:			♀♀ **3.919** (2.540)
				♂♂ **3.222** (2.659)
			♀♀ : ♂♂ = **1 : 0.89** ⇒	DR_{DW} = **3.6** (2.6)
Uca maracoani (n = 384), f_{DF} = 1.22				
ERS_1 ♀♀	2	0.044	28.8	**12.905** (15.601)
ERS_1 ♂♂	1	0.371	69.1	**8.936** (1.775)
LRS ♀♀	2	0.033	30.0	**15.273** (11.977)
LRS ♂♂	1	0.031	23.8	**6.376** (7.130)
ERS_2 ♀♀	1	0.050	30.0	**7.566** (9.713)
ERS_2 ♂♂	2	0.358	41.4	**6.145** (3.999)
	annual averages:			♀♀ **10.828** (11.751)
				♂♂ **6.901** (4.226)
			♀♀ : ♂♂ = **1 : 1.11** ⇒	DR_{DW} = **8.8** (7.8)

continued next page

Table 9: continued: Results from 24h-field experiments conducted in the benthic mangal segment of the mangrove ecosystem of the Canal Sta. Cruz, Itamaracá Island, northeastern Brazil.

species / experiment / feeding periods per day		ingestion rate [% body fresh weight · h^{-1}]	evacuation rate [% GIC · h^{-1}]	DR_{DW} [% body fresh weight · d^{-1}] / $\sum$residuals^2
Uca thayeri (n = 416), f_{DF} = 1.18				
ERS_1 ♀♀	2	0.116	27.0	**18.503** (30.167)
ERS_1 ♂♂	2	0.150	35.2	**17.555** (11.510)
LRS ♀♀	2	0.110	32.1	**16.064** (27.132)
LRS ♂♂	2	0.117	15.7	**13.541** (18.517)
ERS_2 ♀♀	2	0.135	41.4	**29.123** (15.590)
ERS_2 ♂♂	2	0.137	40.0	**23.929** (17.510)
	annual averages:			♀♀ **23.203** (22.120)
				♂♂ **19.739** (16.262)
			♀♀ : ♂♂ = **1 : 1.03** ⇒	DR_{DW} = **21.4** (19.1)
Callinectes danae (n = 260), f_{DF} = 1.51				
ERS_1 ♀♀	2	0.237	31.2	**3.286** (0.845)
ERS_1 ♂♂	2	0.259	33.2	**3.091** (0.890)
LRS ♀♀	2	0.115	29.7	**3.403** (0.735)
LRS ♂♂	2	0.184	30.1	**3.213** (0.796)
ERS_2 ♀♀	2	0.142	39.2	**3.373** (0.367)
ERS_2 ♂♂	2	0.024	37.4	**3.607** (0.398)
	annual averages:			♀♀ **3.359** (0.579)
				♂♂ **3.380** (0.621)
			♀♀ : ♂♂ = **1 : 1.47** ⇒	DR_{DW} = **3.4** (0.6)
Littorina scabra angulifera (n = 440), f_{DF} = 1.34				
ERS_1	2	0.026	30.0	**2.753** (0.159)
LRS	2	0.009	21.5	**2.136** (0.167)
ERS_2	2	0.054	31.1	**2.482** (0.303)
	annual average:			
				DR_{DW} = **2.4** (0.2)
Cardisoma guanhumi		not conducted with this species		
Ucides cordatus		not conducted with this species		

The additional 24h-tank experiments (Fig. 15) showed no differences to the respective field experiments. The daily ratios (average = 2.4 %BFW), ingestion rates and filling-level dependent evacuation rates were almost similar to those found in the field. Tagging of the individual specimens of *Goniopsis cruentata* revealed no significant influence of changes in BFW not caused by food uptake. The oscillation of feeding-independent changes of BFW had a maximum amplitude of ±5.1 %BFW. It was not related to the daily periodicity of food

uptake itself and resulted in a maximum shift of the DR_{DW} of 0.1 % (WILCOXON-test, $\alpha = 0.05$).

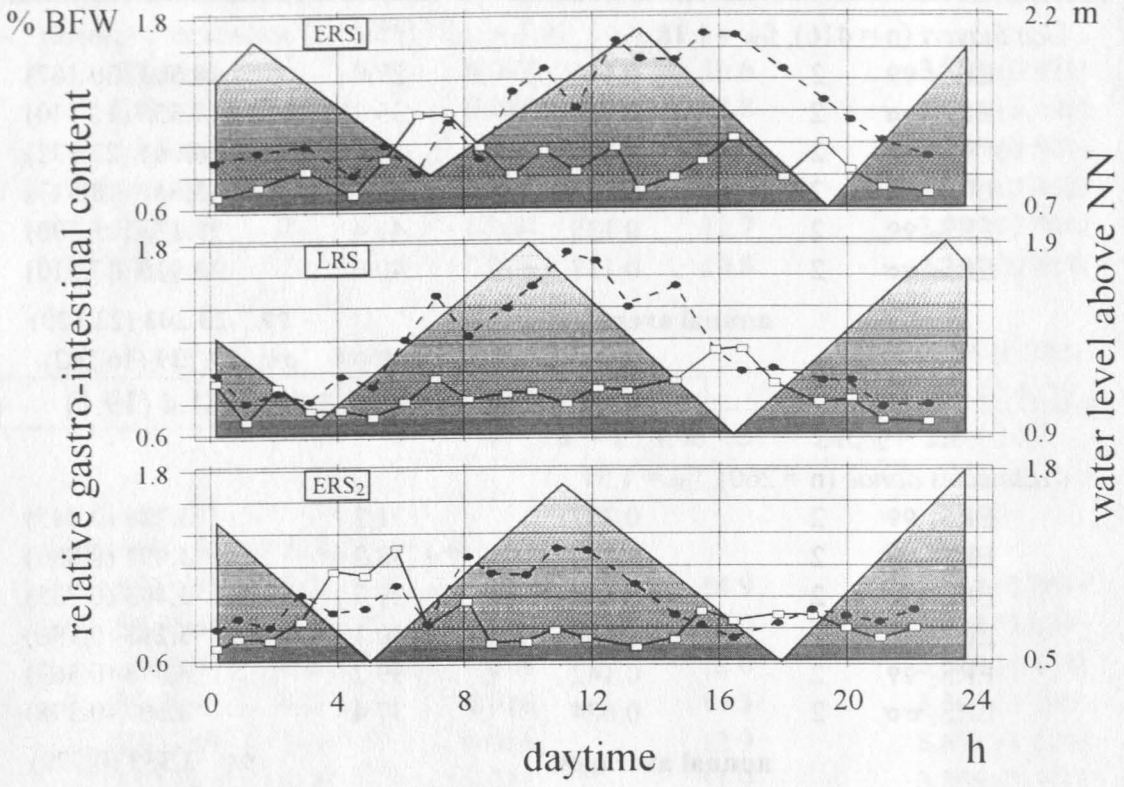

Fig. 8: Relative weight of the gastro-intestinal contents of the brachyuran red mangrove crab *Goniopsis cruentata* during three 24h-field experiments conducted at two early rainy seasons **ERS_1** (1995), **ERS_2** (1996), and one late rainy season **LRS** (1995) in the benthic mangal segment of the mangrove ecosystem of the Canal de Sta. Cruz, Itamaracá Island, northeastern Brazil. The results are presented as the average relationship of content dry weights to the specimen's body fresh weights **BFW** at specific daytimes. The dark areas represent the tidal water level during each experiment (n = 2♀♀+2♂♂ per sample; ERS_1: $n_{total} = 84$; LRS, ERS_2: $n_{total} = 88$). ● = ♀♀; □ = ♂♂.

During all experiments, *Aratus pisonii* showed one major feeding period during the daylight period (Fig. 9) which was correlated to the tidal cycle with peak relative weights of the gastro-intestinal contents (Plate 2.5) during high tides (WILCOXON-test, $\alpha = 0.05$). No significant differences were detected between sexes (WILCOXON-test, $\alpha = 0.01$). A second short but intense period of enhanced feeding activity was observed during the first two hours of daylight at low tides. A third less intense but prolonged feeding period happened during the last two hours of daylight. The individual BFW had no significant influence on the gastro-intestinal filling level of a particular specimen (non-linear test for randomness, $\alpha = 0.01$). The average daily dry-weight food ratio (DR_{DW}) of the *A. pisonii* was 3.6 %BFW during the entire experimental period from April 1995 until March 1996 (Table 9). The resulting annual food ratio was 1 311 %BFW. Male specimens consumed 3.9 %BFW $\cdot$ d^{-1} and females required 3.2 %BFW $\cdot$ d^{-1}.

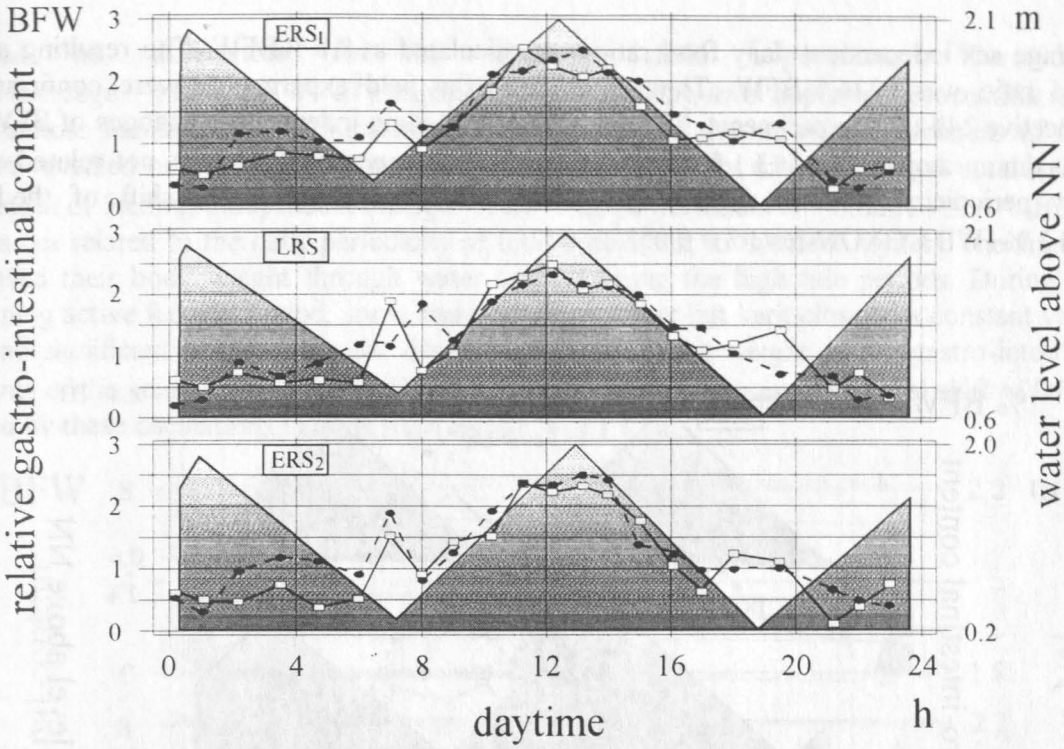

Fig. 9: Relative weight of the gastro-intestinal contents of the brachyuran crab *Aratus pisonii* during three 24h-field experiments conducted at two early rainy seasons **ERS$_1$** (1995), **ERS$_2$** (1996), and one late rainy season **LRS** (1995) in the benthic mangal segment of the mangrove ecosystem of the Canal de Sta. Cruz, Itamaracá Island, northeastern Brazil. The results are presented as the average relationship of content dry weights to the specimen's body fresh weights **BFW** at specific daytimes. The dark areas represent the tidal water level during each experiment (n = 4♀♀+4♂♂ per sample; n_{total} = 176 for each experiments). ● = ♀♀; □ = ♂♂.

The results from the 24h-tank experiments on *Aratus pisonii* (Fig. 16) corresponded with the findings from the respective field experiments in the mangal. The quantitative food requirements (3.4 %BFW · d^{-1}) and the existence of one major feeding period were comparable. However, from the findings of the ERS$_1$-experiment, the assumed correlation between the tidal cycle and the relative weight of the gastro-intestinal content had to be rejected and to be replaced by a correlation between daylight and gastro-intestinal filling levels. No secondary feeding periods were detected during the tank experiments. The oscillation of feeding-independent changes of BFW had a maximum amplitude of ±4.3 %BFW during the tank experiments. It was not related to the daily periodicity of food uptake itself and resulted in a maximum shift of DR_{DW} of 0.2 % (WILCOXON-test, $\alpha = 0.05$).

Feeding periods of the fiddler crab *Uca maracoani* were observed during daylight low tides only (Fig. 10). Their duration and intensity was dependent on the duration of concurrence of these two environmental factors. The animals did not feed when retreated into their burrows. The daily feeding mode in the field differed between sexes (WILCOXON-test, $\alpha = 0.05$). Male specimens showed a slight decrease of their food uptake between two peaks of feeding activity while the females uninterruptedly continued feeding at a higher rate. Consequently, the resulting average daily food ratio of the females of 11.8 %BFW was two-fold higher than the males' daily food ratio of 6.9 %BFW (Table 9). The individual BFW of a particular specimen had no significant influence on the gastro-intestinal filling level of *U. maracoani* (non-linear test for randomness, $\alpha = 0.01$). Under consideration of the sex ratio of 1 : 1.11 (♀♀:♂♂) the

average sex-independent daily food ratio was calculated as 8.8 %BFW. The resulting annual food ratio was 3 216 %BFW. The results from the field experiments were confirmed by respective 24h-tank experiments. The oscillation of feeding-independent changes of BFW had a maximum amplitude of ±3.1 %BFW during the tank experiments. It was not related to the daily periodicity of food uptake itself and resulted in a maximum shift of the DR_{DW} of 0.3 % (WILCOXON-test, $\alpha = 0.05$).

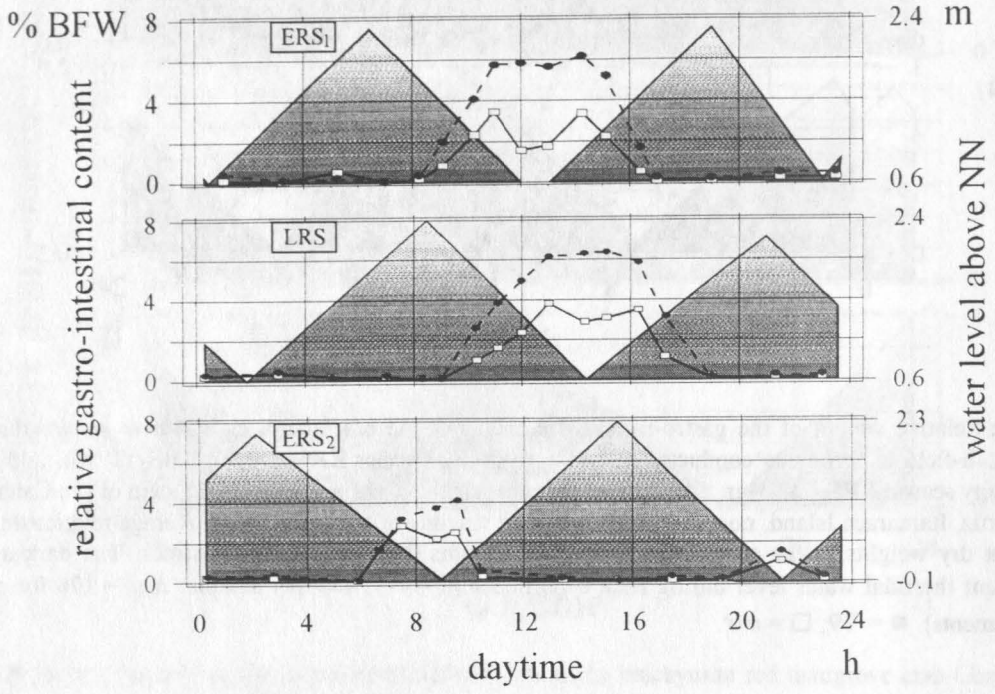

Fig. 10 Relative weight of the gastro-intestinal contents of the brachyuran crab *Uca maracoani* during three 24h-field experiments conducted at two early rainy seasons **ERS_1** (1995), **ERS_2** (1996), and one late rainy season **LRS** (1995) in the benthic mangal segment of the mangrove ecosystem of the Canal de Sta. Cruz, Itamaracá Island, northeastern Brazil. The results are presented as the average relationship of content dry weights to the specimen's body fresh weights **BFW** at specific daytimes. The dark areas represent the tidal water level during each experiment (n = 4♀♀+4♂♂ per sample; ERS_1, LRS: n_{total} = 136; ERS_2: n_{total} = 112). ● = ♀♀; □ = ♂♂.

The almost continuous feeding activity of *Uca thayeri* was only interrupted by the short periods when the flood entered the upper intertidal zone (Fig. 11). The animals fed during day and nighttime on the detrital and microalgal surface material of the upper intertidal zone. However, feeding intensity was higher during the daytime. No differences were detected between the daily feeding activity cycles of the sexes (WILCOXON-test, $\alpha = 0.05$). The individual BFW had no significant influence on the gastro-intestinal filling level of the animals (non-linear test for randomness, $\alpha = 0.01$). As for *U. maracoani*, *U. thayeri* did not feed while retreated into its burrows. Females had a higher average daily dry-weight food ratio (DR_{DW}) of 23.2 %BFW compared to the ratio of 19.7 %BFW · d^{-1} of the males (Table 9). Balanced by sex ratio, the average daily food ratio was calculated as 21.5 %BFW. The resulting annual ratio was 7 827 % of the standing biomass of *U. thayeri* in the benthic mangal zone of the Canal de Sta. Cruz (27.7 km^2). The additional 24h-tank experiments (Fig. 17, 18)

showed no differences to the respective field experiments. The daily ratios (average = 19.7 %BFW · d^{-1}), ingestion rates and filling-level dependent evacuation rates were almost similar to those found in the field. Tagging of the individual specimens of *Uca thayeri* revealed no significant influence of changes in BFW not caused by food uptake. The oscillation of feeding-independent changes of BFW had a maximum amplitude of ±6.1 %BFW. It was not related to the daily periodicity of food uptake but to the tidal rhythm. The animals increased their body weight through water uptake during the high tide periods. During the remaining active feeding period, some body weight was lost but kept close to a constant value with no significant influence on the determination of relative weight of the gastro-intestinal contents of the animals (WILCOXON-test, $\alpha = 0.05$). The maximum theoretical shift of DR_{DW} caused by these oscillations in body fresh weight was 1.1 %.

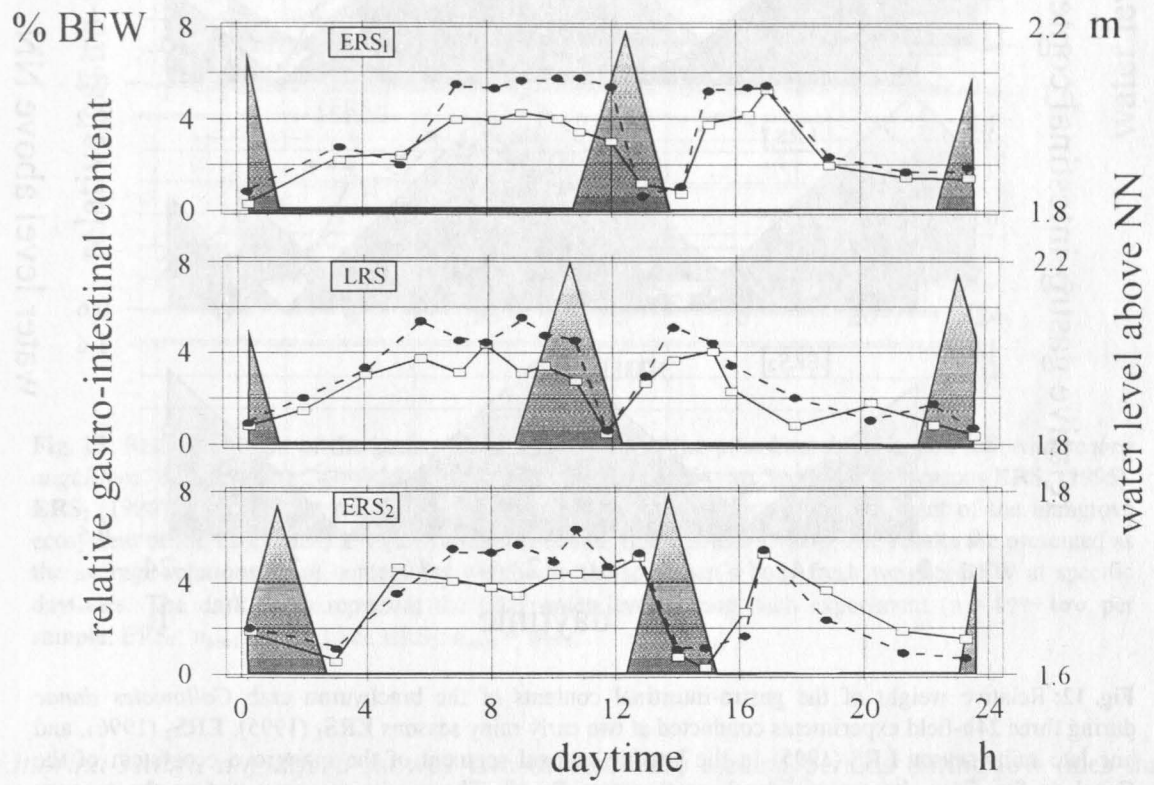

Fig. 11: Relative weight of the gastro-intestinal contents of the brachyuran crab *Uca thayeri* during three 24h-field experiments conducted at two early rainy seasons **ERS$_1$** (1995), **ERS$_2$** (1996), and one late rainy season **LRS** (1995) in the benthic mangal segment of the mangrove ecosystem of the Canal de Sta. Cruz, Itamaracá Island, northeastern Brazil. The results are presented as the average relationship of content dry weights to the specimen's body fresh weights **BFW** at specific daytimes. The dark areas represent the tidal water level during each experiment (n = 4♀♀+4♂♂ per sample; ERS$_1$, ERS$_2$: n_{total} = 136; LRS: n_{total} = 144). ● = ♀♀; □ = ♂♂.

One prominent feeding period during the daytime and one secondary feeding period during the nighttime were observed during the 24h-field experiments on *Callinectes danae* (Fig. 12). With the exception of the ERS$_2$-experiment when no prominent feeding period could be detected, all feeding periods coincided with the high tides in the area. The quantitative feeding behavior of male and female *C. danae* was significantly similar (WILCOXON-test, $\alpha = 0.01$). The individual BFW of a particular specimen had no significant influence on the gastro-intestinal filling level of the animals (non-linear test for randomness, $\alpha = 0.01$). A possible reason for the different feeding pattern during the ERS$_2$-experiment compared to the ERS$_1$-experiment may

have been the high percentage of molting individuals that was observed at the sampling spots. The average daily dry-weight food ratio (DR_{DW}) required by *C. danae* was calculated as 3.4 %BFW · d^{-1}. Female specimens consumed 3.4 %BFW · d^{-1}. The male blue crabs had an almost identical food ratio of 3.4 %BFW · d^{-1}. On an annual basis, the amount (DW) of food consumed was calculated as 1 230 %BFW.

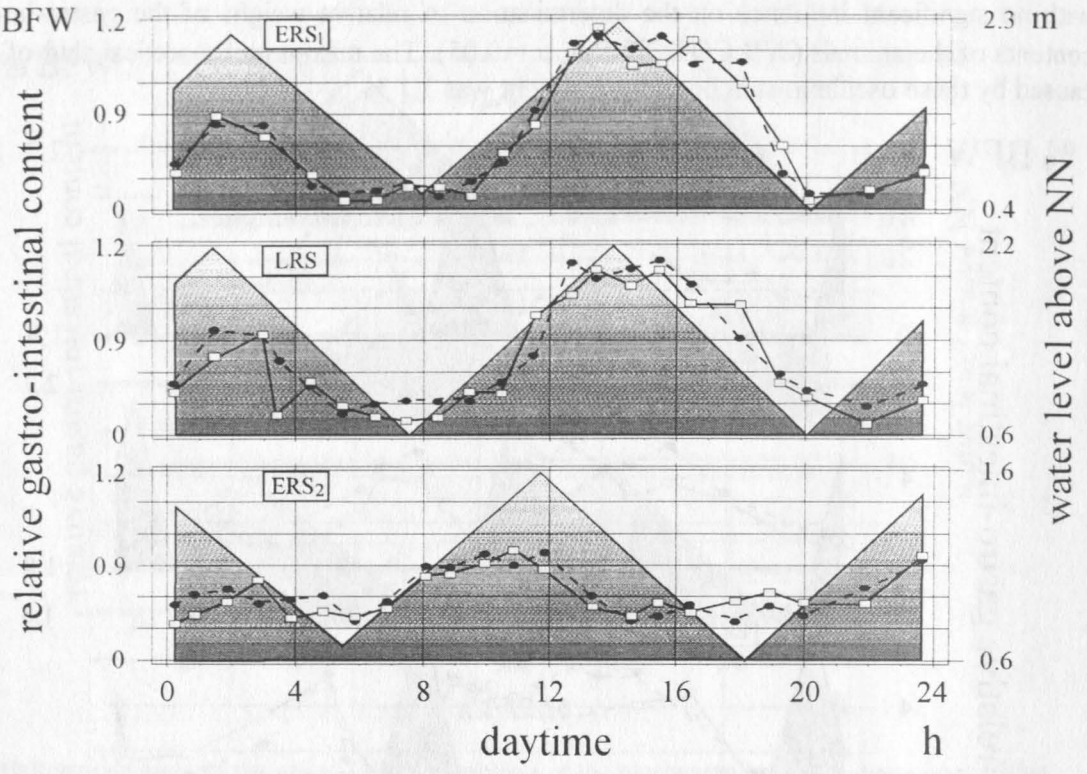

Fig. 12: Relative weight of the gastro-intestinal contents of the brachyuran crab *Callinectes danae* during three 24h-field experiments conducted at two early rainy seasons **ERS_1** (1995), **ERS_2** (1996), and one late rainy season **LRS** (1995) in the benthic mangal segment of the mangrove ecosystem of the Canal de Sta. Cruz, Itamaracá Island, northeastern Brazil. The results are presented as the average relationship between the content dry weights and specimen's body fresh weights **BFW** at specific daytimes. The dark areas represent the tidal water level during each experiment (n = 2♀♀+2♂♂ per sample; ERS_1: n_{total} = 84; LRS, ERS_2: n_{total} = 88). ● = ♀♀; □ = ♂♂.

The results from the field experiments on *Callinectes danae* were confirmed by 24h-tank experiments under close-to natural conditions (Fig. 19). During the ERS_2-tank experiment, a representative percentage of molting individuals was included and the observation of a different integrated feeding activity during the field experiments at different seasons was repeated. In general, the oscillation of feeding-independent changes of BFW had a maximum amplitude of ±1.4 %BFW during the tank experiments. A correlation to the daily periodicity of food uptake itself was not detected (WILCOXON-test, $\alpha = 0.01$) and the maximum theoretical shift of DR_{DW} caused by this amplitude was calculated as 0.02 %.

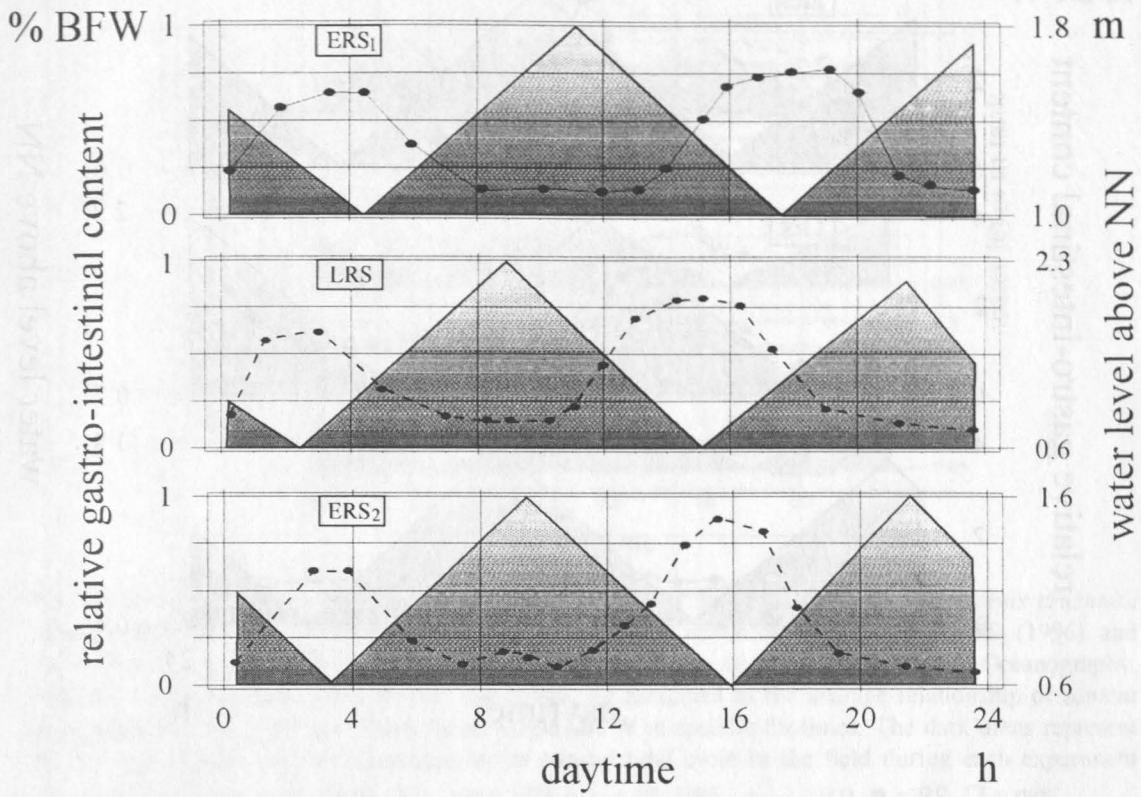

Fig. 13: Relative weight of the gastro-intestinal contents of the prosobranch gastropod *Littorina scabra angulifera* during three 24h-field experiments conducted at two early rainy seasons **ERS$_1$** (1995), **ERS$_2$** (1996), and one late rainy season **LRS** (1995) in the benthic mangal segment of the mangrove ecosystem of the Canal de Sta. Cruz, Itamaracá Island, northeastern Brazil. The results are presented as the average relationship of content dry weights to the specimen's body fresh weights **BFW** at specific daytimes. The dark areas represent the tidal water level during each experiment (n = 4♀♀+4♂♂ per sample; ERS$_1$: n_{total} = 152; LRS, ERS$_2$: n_{total} = 144).

Littorina scabra angulifera showed two evident daily feeding periods during low tides that were not influenced by the change of daylight (Fig. 13). The slightly shorter and less intense feeding activity during nighttime low tides was not significantly different from the feeding activity during other periods (WILCOXON-test, $\alpha = 0.05$). The animals did never completely stop feeding during any time of the day. The minimum filling level of the digestive tract was 0.1 %BFW. No significant internal differences were detected neither between the three field and tank experiments nor between field and tank experiments (Fig. 20) in general (WILCOXON-test, $\alpha = 0.05$). The individual BFW of a particular specimen had no significant influence on the gastro-intestinal filling level of the animals (non-linear test for randomness, $\alpha = 0.01$). The daily food ratio (DW) of *L.s.angulifera* was 2.4 %BFW and led to the annual food ratio (DW) of 868 %BFW. The oscillation of feeding-independent changes of BFW, observed during the additional tank experiments, had a maximum amplitude of ±2.0 %BFW. A correlation to the daily periodicity of food uptake itself was not detected and the maximum theoretical shift of the daily dry-weight food ratio (DR_{DW}) caused by this amplitude was calculated as 0.05 % (WILCOXON-test, $\alpha = 0.01$).

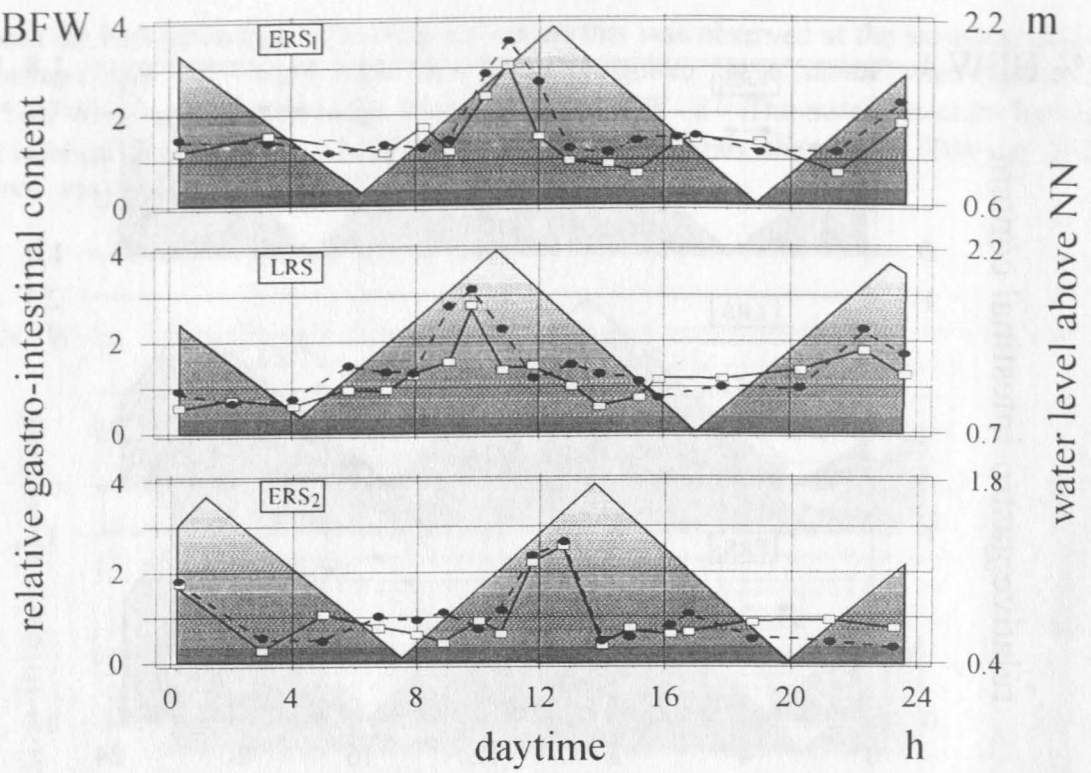

Fig. 14: Relative weight of the gastro-intestinal contents of the tetraodontid fish *Sphoeroides testudineus* during three 24h-field experiments conducted at two early rainy seasons **ERS$_1$** (1995), **ERS$_2$** (1996), and one late rainy season **LRS** (1995) in the benthic mangal segment of the mangrove ecosystem of the Canal de Sta. Cruz, Itamaracá Island, northeastern Brazil. The results are presented as the average relationship of content dry weights to the specimen's body fresh weights **BFW** at specific daytimes. The dark areas represent the tidal water level during each experiment (n = 2♀♀+2♂♂ per sample; n_{total} = 68 for each experiment). ● = ♀♀; □ = ♂♂.

The 24h-field experiments on *Sphoeroides testudineus* showed one major feeding period during the daylight flood interval and one secondary less expressed feeding period during the nighttime flood interval at each climatic season (Fig. 14). The secondary feeding period was however not observed during the ERS$_2$ and the LRS-24h-tank experiments (Fig. 21). The food uptake was always reduced before the water level reached high tide in the area or within the experimental tanks. However, the animals did not entirely stop feeding at any time of the day during all experiments. Differences between sexes were not significant (WILCOXON-test, $\alpha = 0.05$). The average dry-weight food ratio (DR_{DW}) independent from sex was 3.3 %BFW · d^{-1}. The specific average food ratio (DW) of the males was 2.3 %BFW · d^{-1}, while the females consumed 3.5 %BFW · d^{-1} (DW). The average annual food ratio of *S. testudineus* was calculated as 1 210 %BFW. The individual BFW of a particular specimen had no significant influence on the gastro-intestinal filling level of the animals (non-linear test for randomness, $\alpha = 0.01$). The oscillation of feeding-independent changes of BFW, observed during the tank experiments, had a maximum amplitude of ±1.9 %BFW. A correlation to the daily periodicity of food uptake itself was not detected (WILCOXON-test, $\alpha = 0.01$) and the maximum theoretical shift of DR_{DW} caused by this amplitude was calculated as 0.06 %.

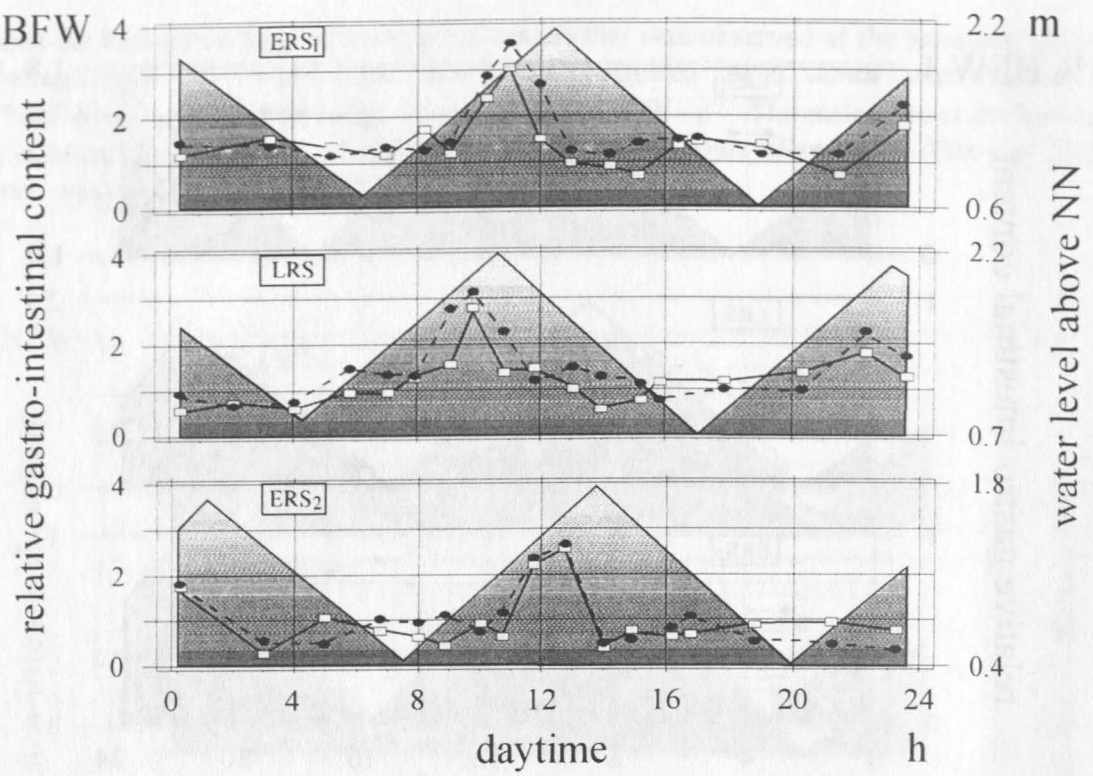

Fig. 14: Relative weight of the gastro-intestinal contents of the tetraodontid fish *Sphoeroides testudineus* during three 24h-field experiments conducted at two early rainy seasons **ERS$_1$** (1995), **ERS$_2$** (1996), and one late rainy season **LRS** (1995) in the benthic mangal segment of the mangrove ecosystem of the Canal de Sta. Cruz, Itamaracá Island, northeastern Brazil. The results are presented as the average relationship of content dry weights to the specimen's body fresh weights **BFW** at specific daytimes. The dark areas represent the tidal water level during each experiment ($n = 2♀♀+2♂♂$ per sample; $n_{total} = 68$ for each experiment). ● = ♀♀; □ = ♂♂.

The 24h-field experiments on *Sphoeroides testudineus* showed one major feeding period during the daylight flood interval and one secondary less expressed feeding period during the nighttime flood interval at each climatic season (Fig. 14). The secondary feeding period was however not observed during the ERS$_2$ and the LRS-24h-tank experiments (Fig. 21). The food uptake was always reduced before the water level reached high tide in the area or within the experimental tanks. However, the animals did not entirely stop feeding at any time of the day during all experiments. Differences between sexes were not significant (WILCOXON-test, $\alpha = 0.05$). The average dry-weight food ratio (DR_{DW}) independent from sex was 3.3 %BFW · d^{-1}. The specific average food ratio (DW) of the males was 2.3 %BFW · d^{-1}, while the females consumed 3.5 %BFW · d^{-1} (DW). The average annual food ratio of *S. testudineus* was calculated as 1 210 %BFW. The individual BFW of a particular specimen had no significant influence on the gastro-intestinal filling level of the animals (non-linear test for randomness, $\alpha = 0.01$). The oscillation of feeding-independent changes of BFW, observed during the tank experiments, had a maximum amplitude of ±1.9 %BFW. A correlation to the daily periodicity of food uptake itself was not detected (WILCOXON-test, $\alpha = 0.01$) and the maximum theoretical shift of DR_{DW} caused by this amplitude was calculated as 0.06 %.

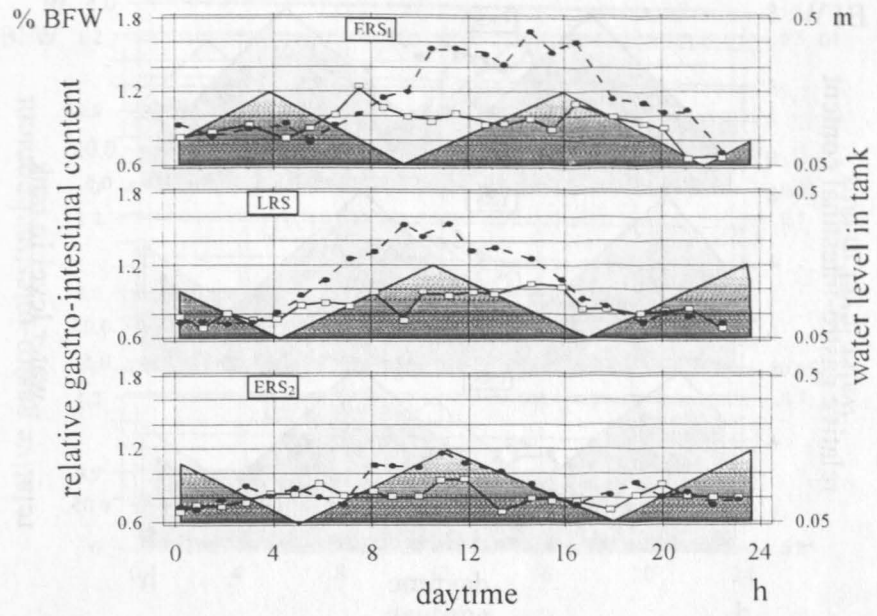

Fig. 15: Relative weight of the gastro-intestinal contents of the brachyuran crab *Goniopsis cruentata* during three 24h-tank experiments conducted at two early rainy seasons **ERS$_1$** (1995), **ERS$_2$** (1996), and one late rainy season **LRS** (1995) at the field station of the Department of Marine Oceanography, Itamaracá Island, northeastern Brazil. The results are presented as the average relationship of content dry weights to the specimen's body fresh weights **BFW** at specific daytimes. The dark areas represent the simulated tidal cycle synchronized to the natural tidal cycle in the field during each experiment (n = 4♀♀+4♂♂ per sample; ERS$_1$: n_{total} = 84; LRS n_{total} = 88; ERS$_2$: n_{total} = 92). ● = ♀♀; □ = ♂♂.

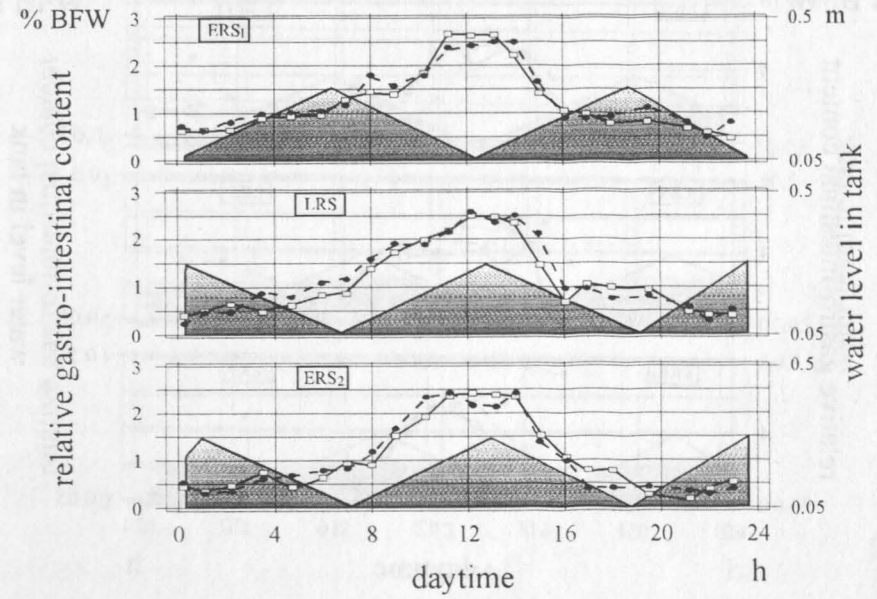

Fig. 16: Relative weight of the gastro-intestinal contents of the brachyuran crab *Aratus pisonii* during three 24h-tank experiments conducted at two early rainy seasons **ERS$_1$** (1995), **ERS$_2$** (1996), and one late rainy season **LRS** (1995) at the field station of the Department of Marine Oceanography, Federal University of Pernambuco, Itamaracá Island, northeastern Brazil. The results are presented as the average relationship of content dry weights to the specimen's body fresh weights **BFW** at specific daytimes. The dark areas represent the simulated tidal cycle which was synchronized to the natural tidal cycle in the field during each experiment period (n = 4♀♀+4♂♂ per sample; n_{total} = 176 for each experiment). ● = ♀♀; □ = ♂♂.

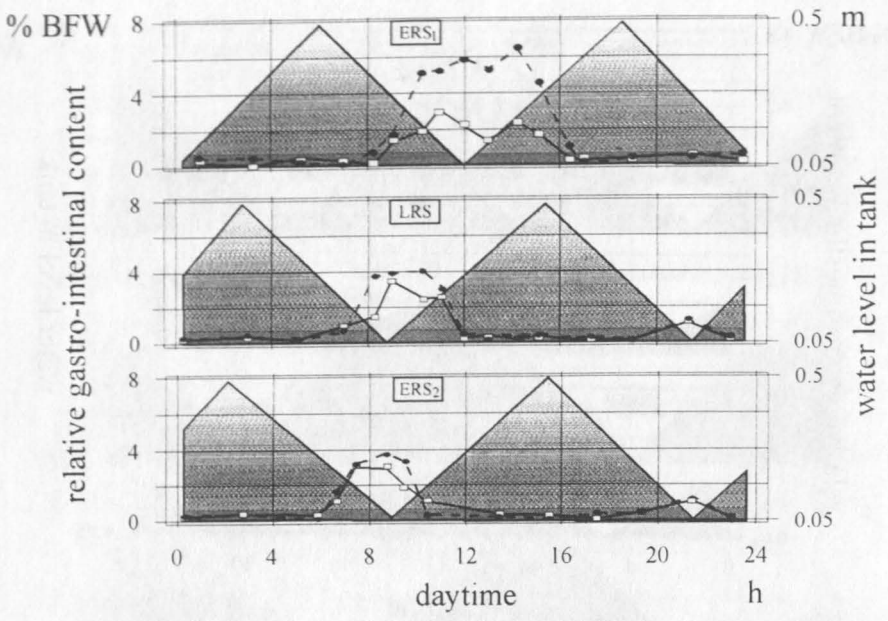

Fig. 17: Relative weight of the gastro-intestinal contents of the brachyuran crab *Uca maracoani* during three 24h-tank experiments conducted at two early rainy seasons **ERS$_1$** (1995), **ERS$_2$** (1996), and one late rainy season **LRS** (1995) at the field station of the Federal University of Pernambuco, Itamaracá Island, northeastern Brazil. The results are presented as the average relationship of content dry weights to the specimen's body fresh weights **BFW** at specific daytimes. The dark areas represent the simulated tidal cycle which was synchronized to the natural cycle in the field during each experiment period (n = 4♀♀+4♂♂ per sample; ERS$_1$, LRS: n_{total} = 136; ERS$_2$: n_{total} = 112). ● = ♀♀; □ = ♂♂.

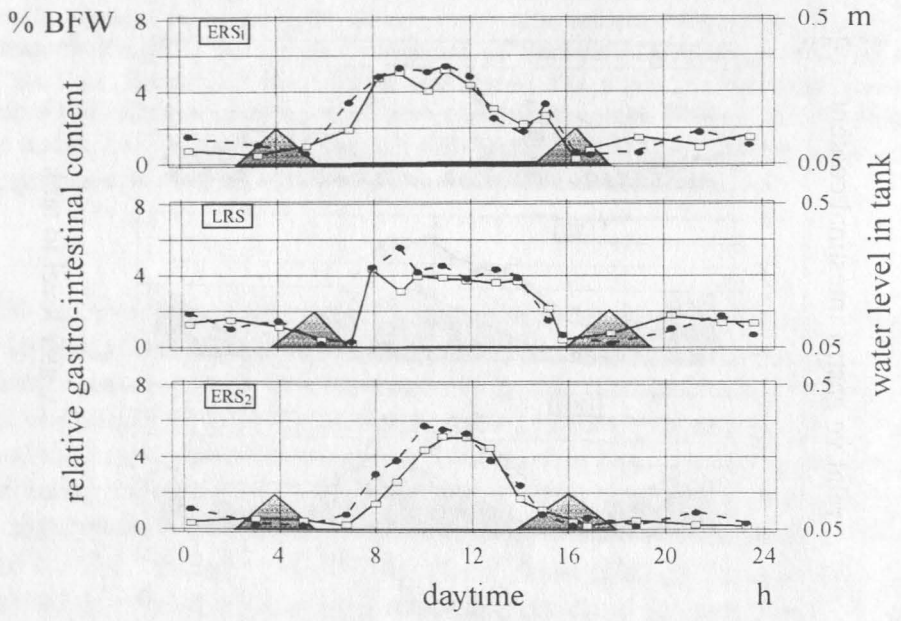

Fig. 18: Relative weight of the gastro-intestinal contents of the brachyuran crab *Uca thayeri* during three 24h-tank experiments conducted at two early rainy seasons **ERS$_1$** (1995), **ERS$_2$** (1996), and one late rainy season **LRS** (1995) at the field station of the Department of Marine Oceanography, Federal University of Pernambuco, Itamaracá Island, northeastern Brazil. The results are presented as the average relationship of content dry weights to the specimen's body fresh weights **BFW** at specific daytimes. The dark areas represent the simulated tidal cycle which was synchronized to the natural cycle in the field during each experiment period (n = 4♀♀+4♂♂ per sample; ERS$_1$, ERS$_2$: n_{total} = 136; LRS: n_{total} = 144). ● = ♀♀; □ = ♂♂.

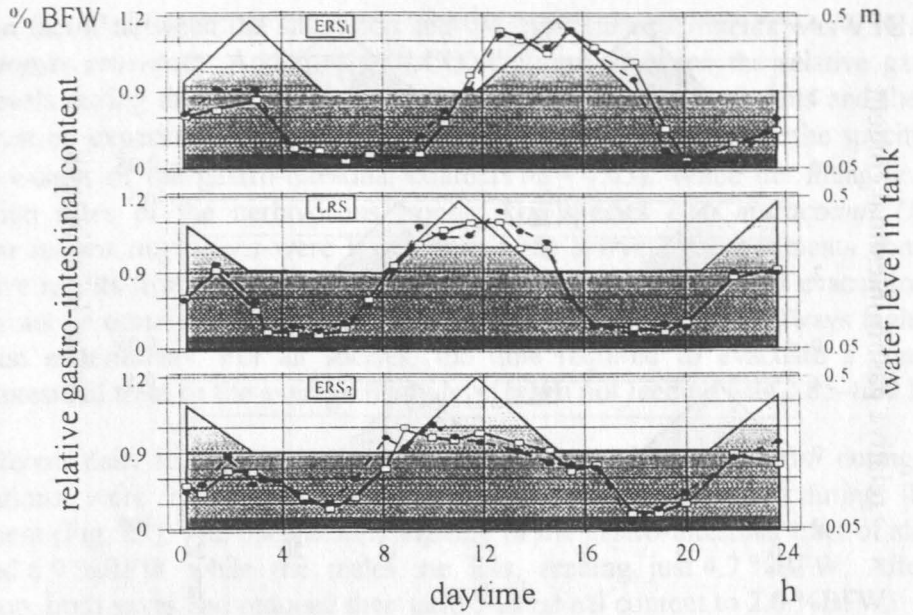

Fig. 19: Relative weight of the gastro-intestinal contents of the brachyuran crab *Callinectes danae* during three 24h-tank experiments conducted at two early rainy seasons **ERS$_1$** (1995), **ERS$_2$** (1996), and one late rainy season **LRS** (1995) at the field station of the Federal University of Pernambuco, Itamaracá Island, northeastern Brazil. The results are presented as the average relationship of content dry weights to the specimen's body fresh weights **BFW** at specific daytimes. The dark areas represent the simulated tidal cycle which was synchronized to the natural tidal cycle in the field during each experiment (n = 2♀♀+2♂♂ per sample; ERS$_1$: n_{total} = 84; LRS, ERS$_2$: n_{total} = 88). ● = ♀♀; □ = ♂♂.

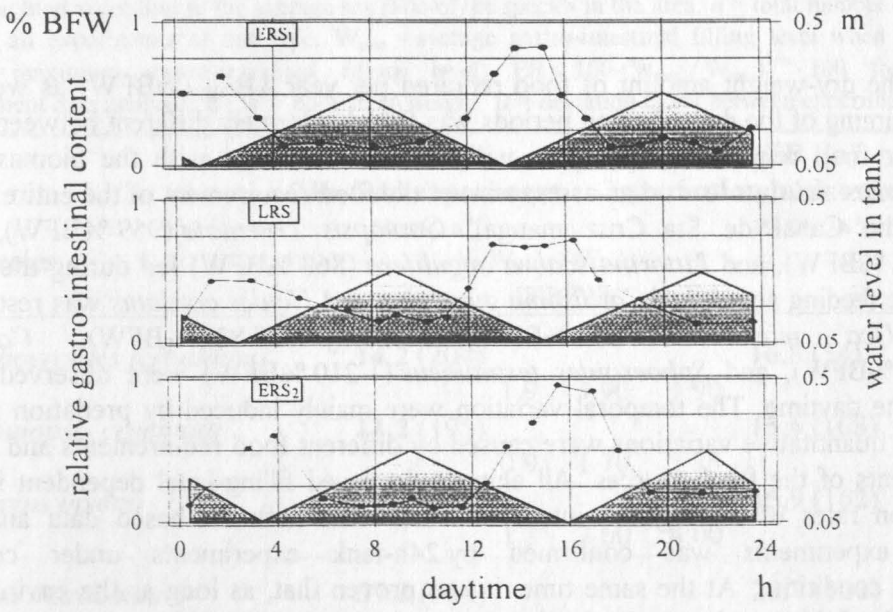

Fig. 20: Relative weight of the gastro-intestinal contents of the prosobranch gastropod *Littorina scabra angulifera* during three 24h-tank experiments conducted at two early rainy seasons **ERS$_1$** (1995), **ERS$_2$** (1996), and one late rainy season **LRS** (1995) at the field station of the Department of Marine Oceanography, Federal University of Pernambuco, Itamaracá Island, northeastern Brazil. The results are presented as the average relationship of content dry weights to the specimen's body fresh weights **BFW** at specific daytimes. The dark areas represent the simulated tidal cycle which was synchronized to the natural tidal cycle in the field during each experiment (n = 4♀♀+4♂♂ per sample; ERS$_1$: n_{total} = 152; LRS, ERS$_2$: n_{total} = 144).

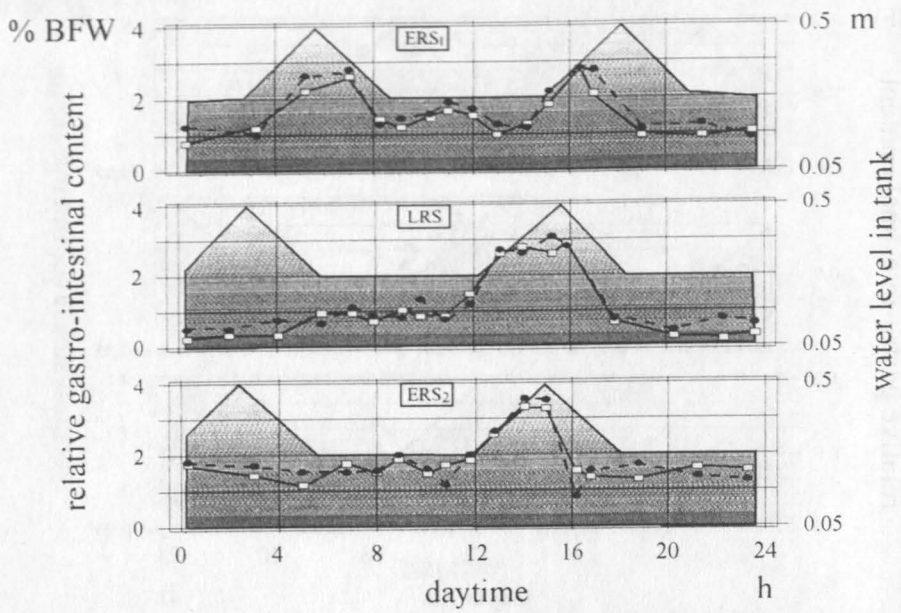

Fig. 21: Relative weight of the gastro-intestinal contents of the tetraodontid fish *Sphoeroides testudineus* during three 24h-tank experiments conducted at two early rainy seasons **ERS$_1$** (1995), **ERS$_2$** (1996), and one late rainy season **LRS** (1995) at the field station of the Federal University of Pernambuco, Itamaracá Island, northeastern Brazil. The results are presented as the average relationship of content dry weights to the specimen's body fresh weights **BFW** at specific daytimes. The dark areas represent the simulated tidal cycle which was synchronized to the natural tidal cycle in the field during each experiment (n = 2♀♀+2♂♂ per sample; ERS$_1$, ERS$_2$: n_{total} = 17; LRS: n_{total} = 18). ● = ♀♀; □ = ♂♂.

In summary the dry-weight amount of food required per year $\mathbf{AR_{DW}}$ (%BFW) as well as the intensity and timing of the daily feeding periods was found extremely different between species. The particular food requirement per year will later be combined with the biomass of the respective species and thus lead to an assessment of the food requirement of the entire standing biomass in the Canal de Sta. Cruz mangal. *Goniopsis cruentata* (959 %BFW), *Aratus pisonii* (1 311 %BFW), and *Littorina scabra angulifera* (868 %BFW) fed during the day and nighttime. The feeding activity of *Cardisoma guanhumi* and *Ucides cordatus* was restricted to nighttime. *Uca maracoani* (3 216 %BFW), *U. thayeri* (7 827 %BFW), *Callinectes danae* (1 230 %BFW), and *Sphoeroides testudineus* (1 210 %BFW) were observed feeding only during the daytime. The temporal variation were mainly induced by predation response behavior. The quantitative variations were caused by different food requirements and different nutrient contents of the food sources. All animals displayed filling-level dependent ingestion and evacuation rates of their gastro-intestinal tracts. The software-based data analysis of all 24h-field experiments was confirmed by 24h-tank experiments under controlled environmental conditions. At the same time, it was proven that, as long as the environmental conditions in the field are adequately simulated, quantitative nutritional experiments on benthic organisms of the mangal zone can be conducted as tank experiments without causing considerable bias on the results. This gives way to more detailed research on particular physiological questions that require control or active alteration of experimental settings.

4.2.3 Starvation Experiments

The starvation experiments on the trophic key species (Table 1) were conducted to verify the results from the 24h-field and tank experiments (Table 9, 10; Fig. 22, 23). The maximum

deviation factor between the starvation and the 24h-field experiments was 1.39 for the DR_{DW} of *Goniopsis cruentata*. Additional WILCOXON-tests between the relative gastro-intestinal filling levels during the non-feeding periods of the 24h-field experiments and the results from the starvation experiments showed no significant differences between the specific declines of relative weight of the gastro-intestinal contents ($\alpha = 0.05$). While the filling-level dependent evacuation rates of the herbivorous trophic key species *Uca maracoani*, *U. thayeri* and *Littorina scabra angulifera* were lower during the starvation experiments compared to the respective results from the 24h-experiments, the filling-level dependent evacuation rates of the carnivorous or omnivorous species except *Callinectes danae* were always higher during the starvation experiments. For all species, the time required to evacuate a completely filled gastro-intestinal tract to the average filling level when not feeding was 2.85-4.00 h.

The different daily feeding patterns of male and female *Uca maracoani* during the 24h-field observations were reflected in the evacuation rates determined during the starvation experiment (Fig. 23). The maximum filling rate of the gastro-intestinal tract of all female crabs averaged 6.9 %BFW while the males ate less, reading just 4.7 %BFW. After 270 min of starvation, both sexes had reduced their gastro-intestinal content to 2.0 %BFW.

Table 10: Comparison of the average filling-level dependent evacuation rates $\mathbf{ER}_{dep.}$ (% GIC · h^{-1}) of the gastro-intestinal contents (**GIC**) obtained from two types of experiments conducted in the benthic mangal of the Canal Sta. Cruz, northeastern Brazil: 1) Three 24h-field experiments conducted during the early rainy seasons $\mathbf{ERS}_1$ (1995) and $\mathbf{ERS}_2$ (1996), and the late rainy season **LRS** (1995) and 2) two starvation tank-experiments. The averages from the 24h-experiments were $(((ERS_1+ERS_2):2)+LRS):2$ and weighted according to the average sex ratio of the species in the area. **n** = total number of specimens during all experiments of one type; $\mathbf{W}_{rest}$ = average gastro-intestinal filling level when not feeding; $\mathbf{W}_{max}$ = maximum gastro-intestinal filling level; $ER = 100-(W_{rest.} / W_{max})^{1/h} \cdot 100$ for starvation experiment data analysis; **BFW** = body fresh weight. **D** = deviation factor between experiment types.

species	ER (n) 24h-field experiment [% GIC · h^{-1}]	W_{rest} [%BFW]	W_{max} [%BFW]	t [h]	ER (n) starvation tank experiment [% GIC · h^{-1}]	D
Sphoeroides testudineus	**14.2** (204)	1.9	3.90	3.90	**16.8** (54)	**1.18**
Goniopsis cruentata	**11.2** (195)	0.9	1.70	3.75	**15.6** (108)	**1.39**
Aratus pisonii	**12.5** (528)	1.3	2.60	4.00	**15.9** (162)	**1.27**
Uca maracoani	**37.2** (384)	2.1	5.80	3.00	**28.7** (108)	**0.77**
Uca thayeri	**34.1** (416)	2.0	5.60	3.00	**29.8** (216)	**0.87**
Callinectes danae	**34.7** (260)	0.4	1.15	2.85	**31.0** (108)	**0.89**
Littorina s. angulifera	**28.4** (440)	0.3	0.80	3.00	**27.9** (216)	**0.98**
Cardisoma guanhumi	not conducted with this species					
Ucides cordatus	not conducted with this species					

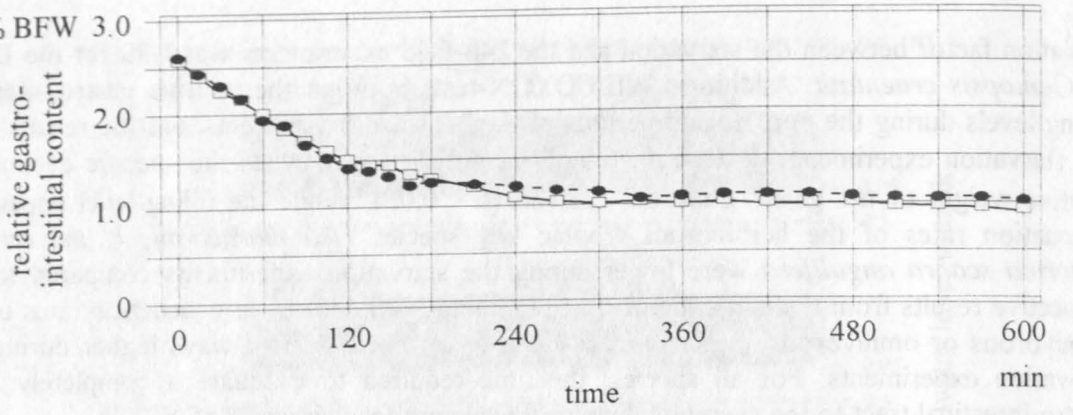

Fig. 22: Decline of the relative weight of the gastro-intestinal contents of *Aratus pisonii* during a starvation period of 10 h (tank experiment) during the early rainy season ERS_1 of 1995 at the field station on Itamaracá Island, northeastern Brazil. The results are presented as the average relationship of content dry weights to the specimen's body fresh weights **BFW**. n = 162; ● = ♀♀; □ = ♂♂.

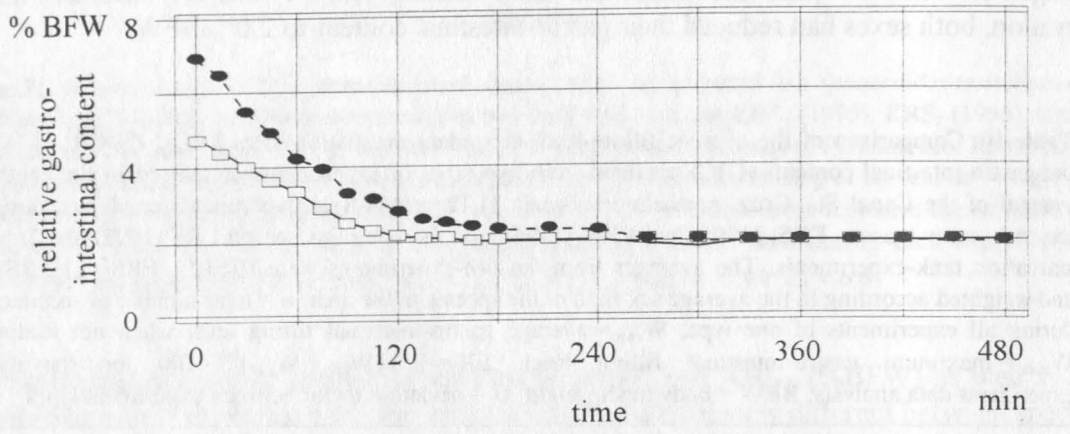

Fig. 23: Decline of the relative weight of the gastro-intestinal contents of *Uca maracoani* during a starvation period of 10 h (tank experiment) during the early rainy season ERS_1 of 1995 at the field station on Itamaracá Island, northeastern Brazil. The results are presented as the average relationship of content dry weights to the specimen's body fresh weights **BFW**. n = 162); ● = ♀♀; □ = ♂♂.

4.2.4 Stable Isotope Ratios

The benthic animal key species of the Canal de Sta. Cruz mangal ecosystem showed a wide range of $\delta^{13}C$-values of their muscle tissue reaching from -10.1 ‰ PDB of *Ucides cordatus* to -26.2 ‰ PDB of *Aratus pisonii* (Fig. 24). Because of the direct biochemical dependency of the tissue values on the $\delta^{13}C$-values of ingested organic material, the reason for this wide range had to be a specific selectivity of all species for particular food sources. At the same time, the sole existence of very different $\delta^{13}C$-values of body tissues would allow a high resolution while trying to separate the species into consumer groups.

The following figures (Fig. 24-33) display the average stable carbon isotope values of the muscle tissue, the gastro-intestinal content and the main food sources of a particular consumer as observed during the initial field experiments on food preferences. Matching $\delta^{13}C$-values of a food source and the gastro-intestinal content indicate a high probability that the consumer feeds on the respective material. To this point, biochemical assimilation and selective

fractionation in the process of digestion were of no importance. The $\delta^{13}C$-values of the gastro-intestinal content are however a sum of all food sources ingested at unknown quantities. Multiple correlation tests had to elucidate whether single or combined groups of food sources were more influential than others. The $\delta^{13}C$-value of the body muscle tissue of the consumers primarily is a result of the initial $\delta^{13}C$-value of the gastro-intestinal content, but is also dependent on biochemical fractionation of isotopes in the course of assimilation. A significant influence of the gastro-intestinal $\delta^{13}C$-values on the isotope fractionation of the muscle tissue may be instantaneous or may be delayed even for a month or more depending on the speed of biochemical processes which were not determined in the present study.

The carnivorous *Callinectes danae*, the omnivorous *Goniopsis cruentata*, and the carnivorous fish *Sphoeroides testudineus* were found in the center of the range of isotope values. The individual ranges of the species were narrow (1-2 ‰) and had only small oscillations with the exception of *Uca maracoani* that showed a range of 6 ‰ and *Aratus pisonii* that showed a range of 4 ‰. Species that inhabited adjacent or equal habitats like *Ucides cordatus* and *Uca thayeri* or *A. pisonii* and *Littorina scabra angulifera* had very similar $\delta^{13}C$-values. All species showed higher $\delta^{13}C$-values of their muscle tissues than were analyzed for their gastro-intestinal contents (Fig. 25-33).

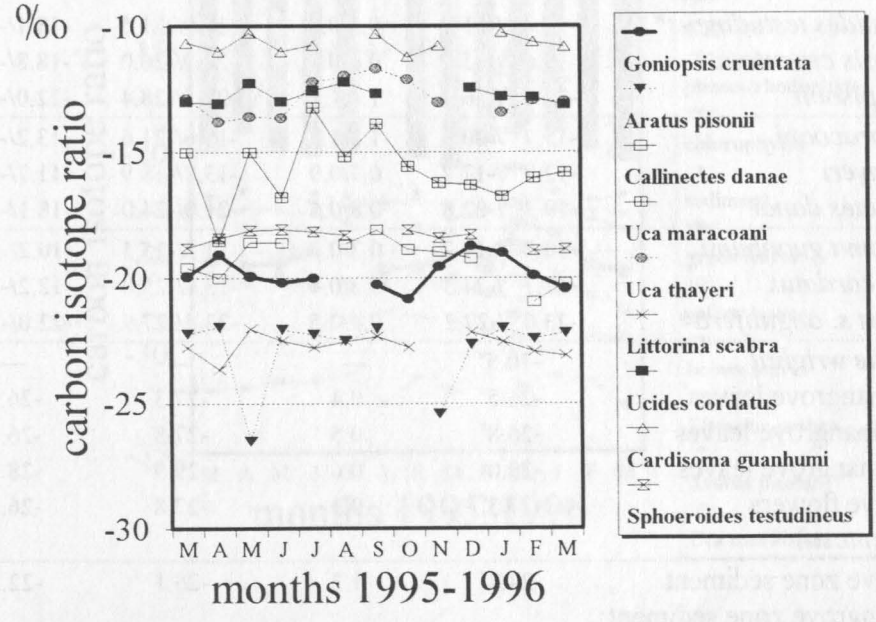

Fig. 24: Monthly average stable carbon isotope values $\delta^{13}C$ (‰ PDB) of muscle tissue of seven crustacean, one fish, and one gastropod species analyzed in the mangal segment of the Canal de Sta. Cruz mangrove ecosystem, Itamaracá Island, Pernambuco State, northeastern Brazil, from March 1995 until March 1996. *G. cruentata*, *U. maracoani*: $n = 8 \cdot month^{-1}$; *A. pisonii*, *U. thayeri*, *L.s.angulifera*: $n = 16 \cdot month^{-1}$; *U. cordatus*, *C. guanhumi*, *S. testudineus*, *C. danae*: $n = 4 \cdot month^{-1}$.

While the green and yellow leaf fraction of the mixed mangrove litterfall of *Rhizophora mangle*, *Avicennia marina*, *Laguncularia racemosa* and *Conocarpus erecta* had almost equal $\delta^{13}C$-values (Table 11) of -26.5 and -26.8 ‰ PDB, respectively, the brown fraction of already decomposed leaves showed much lower $\delta^{13}C$-values with an average of -29.0 ‰ PDB. A big difference was observed between the average $\delta^{13}C$-values of the chlorophyte and the

phaeo-/ rhodophyte benthic or epiphytic algae that were -23.1 and -31.7 ‰ PDB, respectively. In order to check whether or not the strong oscillations (Fig. 25) of the monthly $\delta^{13}C$-values of the mangrove zone sediment/ microalgae (range = 3.8: -26.1 to -22.3 ‰ PDB) may have been caused by methodological bias, they were tested against the contemporaneous $\delta^{13}C$-values of sediment/ microalgae samples at the *Uca maracoani* (Fig. 28) and the *U. thayeri* (Fig. 29) locations. All WILCOXON-tests between the three types of sediments revealed significant similarities of the annual oscillations of values after the elimination of the differences between the specific annual averages ($\alpha = 0.05$). Consequently, the oscillations were accepted as natural and the hypothetical methodological bias was rejected.

Table 11: Mean annual carbon isotope values $\delta^{13}C$ (‰ PDB) of the muscle tissue and the gastro-intestinal content of benthic animal key species and food sources in the mangal segment of the Canal de Sta. Cruz mangrove ecosystem, Itamaracá Island, Pernambuco State, northeastern Brazil, from March 1995 until March 1996. The animal sex ratio was 1 : 1 (except*). n = 48-192 · month^{-1} (see text). **m** = muscle tissue, **GIC** = gastro-intestinal content.

	weighted arithmetic mean $\delta^{13}C$		SD		minimum		maximum	
taxa	m	GIC	m	GIC	m	GIC	m	GIC
*Sphoeroides testudineus**	-18.4[m]	-21.0	0.3	0.3	-18.9	-21.5	-18.1	-20.6
Goniopsis cruentata	-19.6[cm]	-25.3	0.6	0.7	-20.9	-26.0	-18.8	-23.6
Aratus pisonii	-22.9[cm]	-26.1	1.4	1.1	-26.5	-28.4	-22.0	-24.5
Uca maracoani	-15.7[cm]	-20.4	1.3	1.0	-18.6	-21.6	-13.2	-18.1
Uca thayeri	-12.9[cm]	-17.7	0.7	0.9	-13.8	-18.9	-11.7	-15.4
Callinectes danae	-19.3[cm]	-22.8	0.8	0.6	-21.0	-24.0	-18.1	-22.1
Cardisoma guanhumi	-10.7[cm]	-14.7	0.3	0.3	-11.2	-15.1	-10.2	-14.1
Ucides cordatus	-12.7[cm]	-24.3	0.3	0.4	-13.1	-25.0	-12.2	-23.7
*Littorina s. angulifera**	-23.0[fm]	-27.2	0.4	0.5	-23.7	-27.9	-22.0	-25.9
Halodule wrightii	-10.5[e]		---		---		---	
green mangrove leaves	-26.5[e]		0.4		-27.3		-26.0	
yellow mangrove leaves	-26.8[e]		0.5		-27.8		-26.1	
brown mangrove leaves	-29.0[e]		0.6		-29.9		-28.1	
mangrove flowers (*L. racemosa*)	-27.3[e]		0.3		-27.8		-26.9	
mangrove zone sediment	-24.8[e]		1.2		-26.1		-22.3	
non-mangrove zone sediment:								
U. maracoani zone	-18.7[e]		0.9		-19.8		-16.5	
U. thayeri zone	-19.6[e]		0.9		-20.8		-17.2	
benthic or epiphytic macroalgae:								
a) chlorophytes	-23.1[e]		0.4		-23.9		-22.8	
b) phaeo-/ rhodophyte mix	-31.7[e]		0.5		-32.8		-31.1	
mango fruits	-18.9[e]		0.3		-19.2		-18.3	

[m]: muscle tissue mix; [cm]: coxal muscle tissue; [fm]: foot muscle tissue; [e]: entire animal or plant

Goniopsis cruentata as the most central species with respect to its food acceptance had a $\delta^{13}C$-range (Fig. 25; Table 11) of its coxal muscle tissue of 2.1 ‰ PDB (-20.9 to -18.8). The average $\delta^{13}C$-value was -19.9 ‰ PDB . The average $\delta^{13}C$-value of its gastro-intestinal content

was 5.5 ‰ lower at -25.3 ‰ PDB. A WILCOXON-test revealed a significant ($\alpha = 0.05$) influence of the $\delta^{13}C$-values of the gastro-intestinal content on the $\delta^{13}C$-values of the muscle tissue observed one month later. No significant correlations were detected between the $\delta^{13}C$-values of any single food source and the gastro-intestinal content. However, a weak correlation (WILCOXON-test, $\alpha = 0.1$) was found between the pooled (strictly additive, see Chapter 3.5.4) food sources [*Littorina scabra angulifera* + *Aratus pisonii* + mangrove zone sediment + benthic or epiphytic phaeo-/ rhodophytes] and the gastro-intestinal content. Because all these pooled food sources together had a $\delta^{13}C$-value lower than the $\delta^{13}C$-value of the gastro-intestinal content, it was concluded that the remaining food sources had to influence those values at a constant rate. This balancing effect was found for the entire leaf fraction of the diet of *G. cruentata*. After elimination of the average distance between paired $\delta^{13}C$-values, the inclusion of this fraction did not influence the WILCOXON-testing of the other food sources.

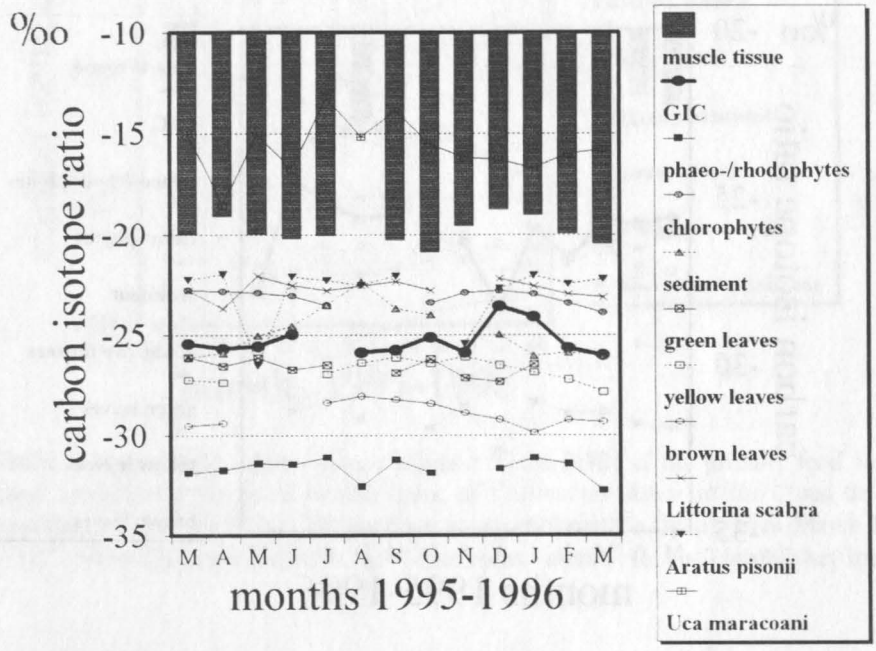

Fig. 25: Monthly average stable carbon isotope values $\delta^{13}C$ (‰ PDB) of the primary food sources, the gastro-intestinal content and the coxal muscle tissue of *Goniopsis cruentata* in the mangal segment of the Canal de Sta. Cruz mangrove ecosystem, Itamaracá Island, Pernambuco State, northeastern Brazil, from March 1995 until March 1996. GIC = gastro-intestinal content. n = 8 specimens · month^{-1} for each trophic key species.

The average $\delta^{13}C$-value of the coxal muscle tissue of *Aratus pisonii* (Fig. 26; Table 11) was -22.9 ‰ PDB. In comparison to *Goniopsis cruentata*, it had a wide range of 4.5 ‰ PDB (-26.5 to -22.0). The average $\delta^{13}C$-value of its gastro-intestinal content was 3.3 ‰ lower at -26.1 ‰ PDB with a range of 3.9 ‰ (-28.4 to -24.5). The $\delta^{13}C$-value of the coxal muscle tissue showed noticeable peaks during the months May and November

of 1995. These peaks were matched by the δ^{13}C-values of the gastro-intestinal content three months prior to the respective months. A WILCOXON-test revealed a significant ($\alpha = 0.05$) correlation after this three-months delay and an approximation between the averages. A significant correlation was observed between the contemporaneous δ^{13}C-values of the gastro-intestinal content and the δ^{13}C-values of the benthic or epiphytic phaeo-/ rhodophyte food source (WILCOXON-test, $\alpha = 0.1$). No correlation was found for the benthic or epiphytic chlorophyte food source. The pooled (see above) food sources [mangrove zone sediment + mangrove flowers + mangrove leaves] showed no correlation as well. However, the big difference (5.6 ‰ PDB) between the average δ^{13}C-values of the gastro-intestinal content (-26.1 ‰ PDB) and the average δ^{13}C-values of the benthic or epiphytic phaeo-/ rhodophytes (3.3 ‰ PDB) had to be caused by a balanced ingestion of all food sources with the exception of mangrove zone sediment. It was concluded that the latter food source was of minimum or no importance for the alimentation of *A. pisonii* because of its negative effect when combined to various pools of other food sources during multiple WILCOXON-testing.

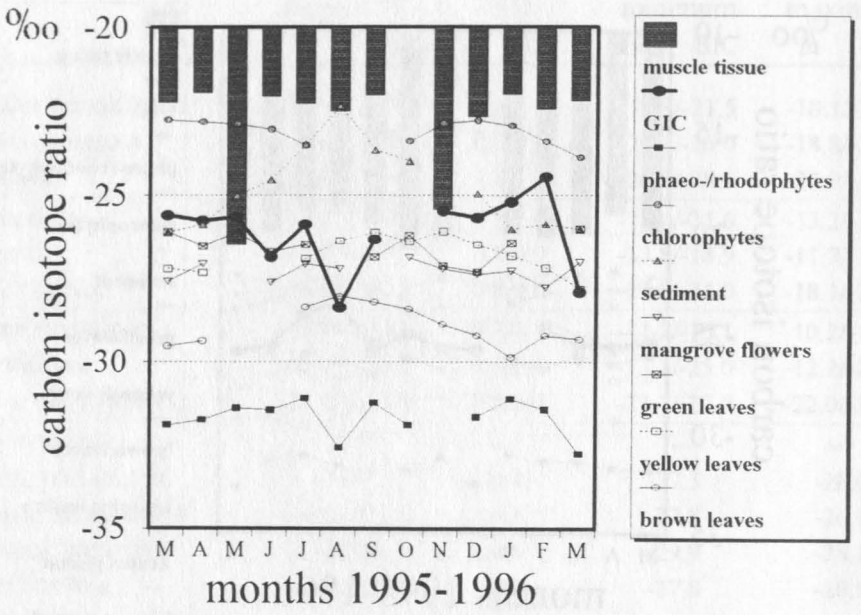

Fig. 26: Monthly average stable carbon isotope values δ^{13}C (‰ PDB) of the primary food sources, the gastro-intestinal content and the coxal muscle tissue of *Aratus pisonii* in the mangal segment of the Canal de Sta. Cruz mangrove ecosystem, Itamaracá Island, Pernambuco State, northeastern Brazil, from March 1995 until March 1996. GIC = gastro-intestinal content. n =16 specimens · month^{-1} for each trophic key species (Table 1).

Callinectes danae had a δ^{13}C-range (Fig. 27; Table 11) of its coxal muscle tissue of 2.9 ‰ PDB (-21.0 to -18.1). The average δ^{13}C-value was -19.3 ‰ PDB. The average δ^{13}C-value of its gastro-intestinal content was 3.5 ‰ lower at -22.8 ‰ PDB. A WILCOXON-test revealed a significant ($\alpha = 0.05$) influence of the δ^{13}C-values of the gastro-intestinal content on the δ^{13}C-values of the muscle tissue without a temporal delay that was observed for several other target species. No significant correlations were detected between the δ^{13}C-values of any single food source and the gastro-intestinal content. However, a significant

correlation (WILCOXON-test, $\alpha = 0.1$) was found between the $\delta^{13}C$-values of the pool (see above) of all food sources tested and the gastro-intestinal content. *Littorina scabra angulifera* and *Aratus pisonii* had to be the most important food sources of *C. danae* because their average annual $\delta^{13}C$-values of tissue were almost similar (-23.0 ‰ PDB; -22.9 ‰ PDB) to the average annual $\delta^{13}C$-values of the gastro-intestinal content of the species (-22.8 ‰ PDB). All other food sources of the species had average annual $\delta^{13}C$-values much higher (Table 11) than those of the gastro-intestinal content. The strong oscillations of the $\delta^{13}C$-values of the muscle tissue of *Uca maracoani* and *U. thayeri* were not found to influence the $\delta^{13}C$-values of the gastro-intestinal content of *C. danae* (WILCOXON-test, $\alpha = 0.1$). Fiddler crabs were no important food source for the blue crabs in the Canal de Sta. Cruz ecosystem.

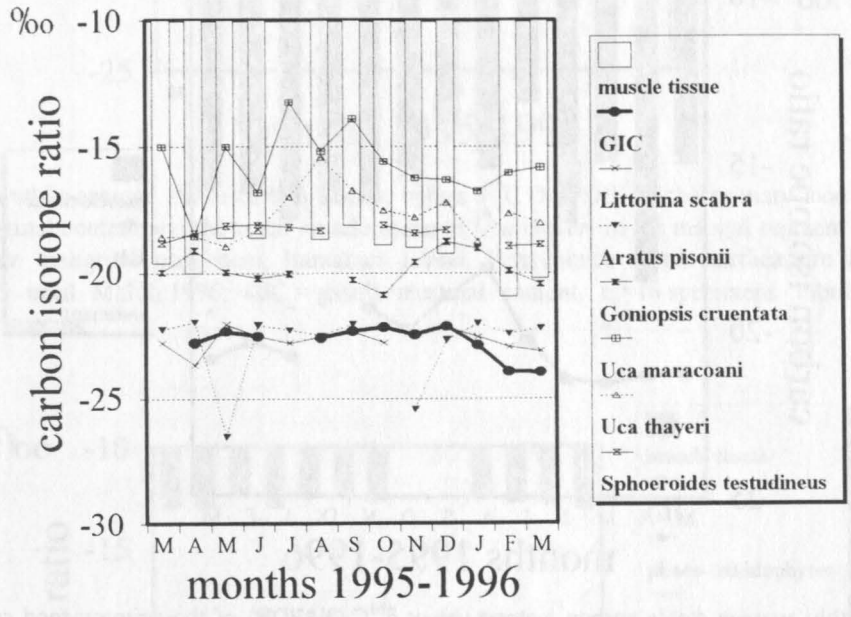

Fig. 27: Monthly average stable carbon isotope values $\delta^{13}C$ (‰ PDB) of the primary food sources, the gastro-intestinal content and the coxal muscle tissue of *Callinectes danae* in the Canal de Sta. Cruz mangrove ecosystem, Itamaracá Island, Pernambuco State, northeastern Brazil, from March 1995 until March 1996. GIC = gastro-intestinal content. n =4 specimens · month^{-1} for each trophic key species.

Uca maracoani and *U. thayeri* showed comparable progressions of the monthly average $\delta^{13}C$-values of their muscle tissue as well as of their gastro-intestinal content (Fig. 28, 29; Table 11) although, on a monthly scale, *U. maracoani* had more expressed oscillations of its $\delta^{13}C$-values than *U. thayeri*. The average $\delta^{13}C$-value of the coxal muscle tissue of *U. maracoani* was -15.7 ‰ PDB. *U. thayeri* had an average of -12.9 ‰ PDB. Both values were much higher than the average values of all other target species except *Ucides cordatus* (-12.7 ‰ PDB). The average $\delta^{13}C$-value of the gastro-intestinal content of *U. maracoani* of -20.4 ‰ PDB was 4.7 ‰ lower than that of the muscle tissue with a range of 3.4 ‰ (-21.6 to -18.1). The average $\delta^{13}C$-value of the gastro-intestinal content of *U. thayeri* of -17.7 ‰ ‰ PDB was 4.8 ‰ lower than that of the muscle tissue with a range of 3.5 ‰ (-18.9 to -15.4). For both species, significant correlations were observed for all contemporaneous combinations the $\delta^{13}C$-values of the gastro-intestinal content, the $\delta^{13}C$-values of the coxal muscle tissue, and the $\delta^{13}C$-values of the surface detritus and microalgae in the area (WILCOXON-test, $\alpha = 0.05$). The main difference between the feeding physiology of both species was that

the average monthly δ^{13}C-values of the gastro-intestinal content of *U. maracoani* were lower than the average values of detritus and microalgae in the area while the average monthly δ^{13}C-values of the gastro-intestinal content of *U. thayeri* were higher than the respective sediment values. The wide range of the average δ^{13}C-values of the monthly sediment samples in both areas had already been tested for in combination with the values of the mangrove zone sediment (Fig. 26) during data analysis concerning *Aratus pisonii* (see above) and a hypothetical methodological bias had been rejected. The ranges of values were 3.3 ‰ PDB (-19.8 to -16.5 ‰) with an average of -18.7 ‰ in the zone exclusively inhabited by *U. maracoani* and 3.5 ‰ PDB (-20.8 to -17.2 ‰) with an average of -19.6 ‰ PDB in the zone exclusively inhabited by *U. thayeri*.

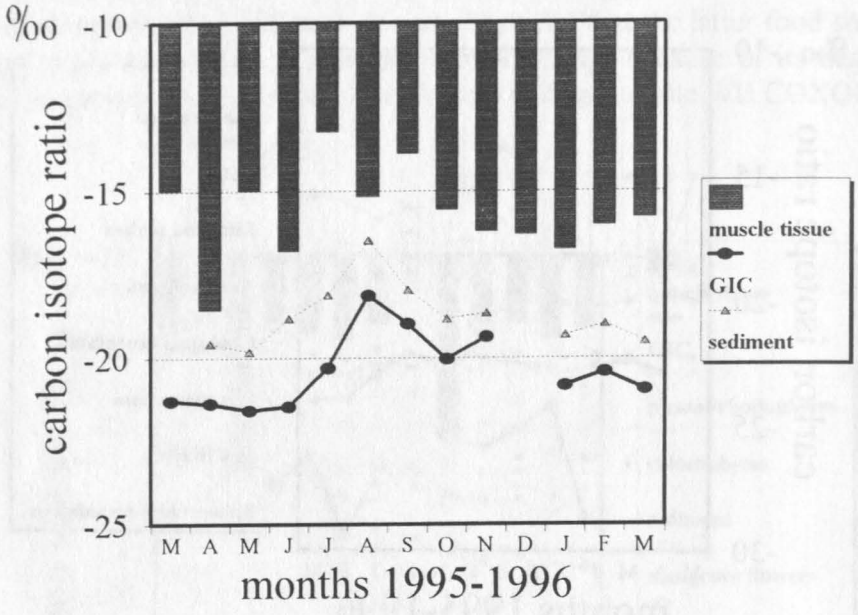

Fig. 28: Monthly average stable carbon isotope values δ^{13}C (‰ PDB) of the primary food sources, the gastro-intestinal content and the coxal muscle tissue of *Uca maracoani* in the mangal segment of the Canal de Sta. Cruz mangrove ecosystem, Itamaracá Island, Pernambuco State, northeastern Brazil, from March 1995 until March 1996. GIC = gastro-intestinal content. n =8 specimens · month^{-1} for each trophic key species.

Ucides cordatus had an average δ^{13}C-value (Fig. 30; Table 11) of its coxal muscle tissue of -12.7 ‰ PDB with a narrow δ^{13}C-range of 0.9 ‰ (-13.1 to -12.2) compared to most other trophic key species. The most prominent difference however was that the average δ^{13}C-value of its gastro-intestinal content (-24.3 ‰ PDB) was 11.6 ‰ lower than the respective muscle tissue value (-12.7 ‰ PDB). A WILCOXON-test revealed no significant ($\alpha = 0.1$) influence of the δ^{13}C-values of the gastro-intestinal content on the δ^{13}C-values of the muscle tissue even under consideration of various temporal shifts. No significant correlations were detected between the δ^{13}C-values of any single food source and the gastro-intestinal content. However, a significant correlation (WILCOXON-test, $\alpha = 0.05$) was found between the δ^{13}C-values of the pool of all food sources tested concerning *U. cordatus* (strictly additive, see Chapter 3.5.4) and the gastro-intestinal content of the species. A balanced influence of all food sources was assumed because of the central position of the δ^{13}C-values of the gastro-intestinal within the δ^{13}C-values of the food sources and the, -with respect to the entire δ^{13}C-range of the biotic sphere of the ecosystem-, comparatively large difference to the δ^{13}C-values of the coxal muscle tissue. The expected dominance of the surface detritus and microalgal fraction within the diet of *U. cordatus* had to be rejected.

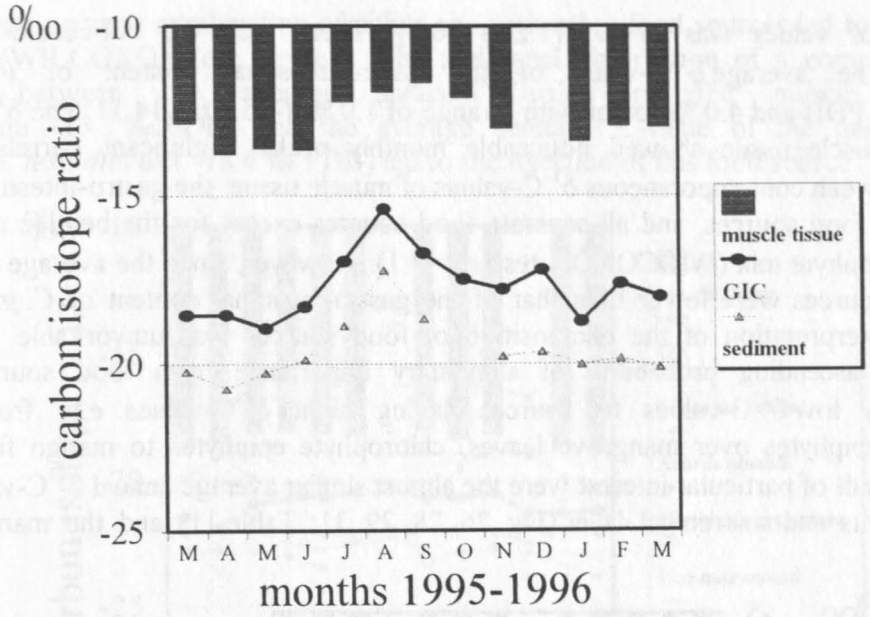

Fig. 29: Monthly average stable carbon isotope values $\delta^{13}C$ (‰ PDB) of the primary food sources, the gastro-intestinal content and the coxal muscle tissue of *Uca thayeri* in the mangal segment of the Canal de Sta. Cruz mangrove ecosystem, Itamaracá Island, Pernambuco State, northeastern Brazil, from March 1995 until March 1996. GIC = gastro-intestinal content. n =16 specimens · month^{-1} for each trophic key species.

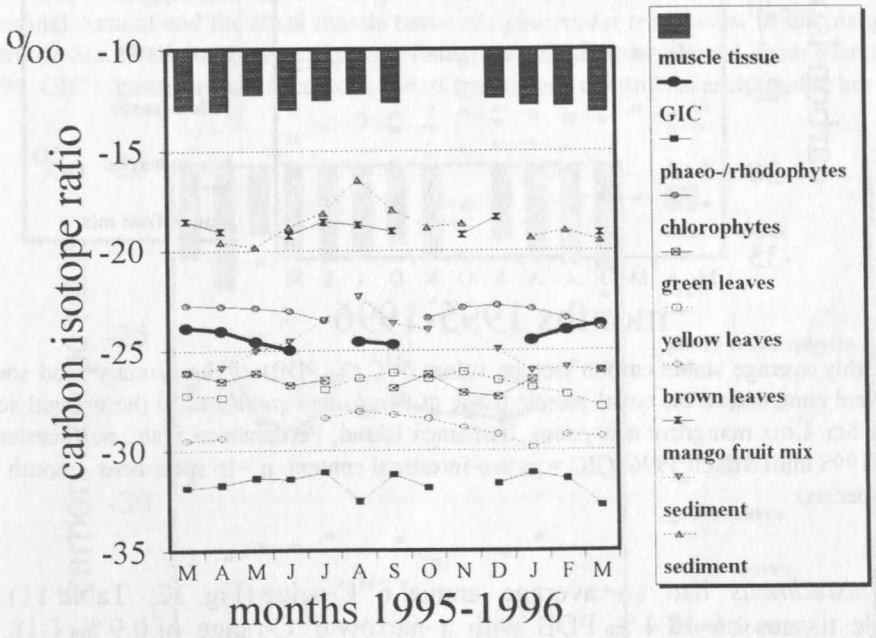

Fig. 30: Monthly average stable carbon isotope values $\delta^{13}C$ (‰ PDB) of the primary food sources, the gastro-intestinal content and the coxal muscle tissue of *Ucides cordatus* in the mangal segment of the Canal de Sta. Cruz mangrove ecosystem, Itamaracá Island, Pernambuco State, northeastern Brazil, from March 1995 until March 1996. GIC = gastro-intestinal content. n =16 specimens · month^{-1} for each trophic key species.

The average $\delta^{13}C$-value of the coxal muscle tissue of *Cardisoma guanhumi* (Fig. 31; Table 11) was -10.7 ‰ PDB and the highest within the entire biotic zone of the mangrove ecosystem.

Littorina scabra angulifera had an average annual $\delta^{13}C$-value (Fig. 33; Table 11) of its foot musculature of -23.0 ‰ PDB with a range of 1.6 ‰ (-23.7 to -22.0). The average $\delta^{13}C$-value of its gastro-intestinal content was 4.3 ‰ lower at -27.2 ‰ PDB. A WILCOXON-test revealed no significant ($\alpha = 0.05$) contemporaneous or temporal shifted influences of the $\delta^{13}C$-values of the gastro-intestinal content on the $\delta^{13}C$-values of the foot muscle tissue. A significant correlation was detected between the course of the monthly $\delta^{13}C$-values of the pooled food sources [mangrove leaves + benthic or epiphytic phaeo-/ rhodophytes + benthic or epiphytic chlorophytes] and the course of the monthly $\delta^{13}C$-values of the gastro-intestinal content of *L.s.angulifera* (WILCOXON-test, $\alpha = 0.05$). No correlation effect was observed for the mangrove zone surface sediment layer (WILCOXON-test, $\alpha = 0.1$). It is most unlikely that this food source was important to the gastropod. The location of the average annual $\delta^{13}C$-value of the gastro-intestinal content of *L.s.angulifera* (-27.2 ‰ PDB) close to the average $\delta^{13}C$-value of the combination of benthic or epiphytic chlorophytes and phaeo-/ rhodophytes (-27.4 ‰ PDB) indicated an outstanding importance of these two food sources.

Table 12: Mean annual stable nitrogen isotope values $\delta^{15}N$ (‰ ATMN) of the muscle tissue and the gastro-intestinal content of benthic animal key species and food sources in the mangal segment of the Canal de Sta. Cruz mangrove ecosystem, Itamaracá Island, Pernambuco State, northeastern Brazil, from March 1995 until March 1996. The sex ratio was 1 : 1 (except*). Except for "---", where only single or a maximum of two samples were analyzed: n = 48-192 · month^{-1} depending on type of trophic key animal species (see text). **m** = muscle tissue, **GIC** = gastro-intestinal content.

taxa	weighted arithmetic mean $\delta^{15}N$ m GIC	SD m GIC	minimum m GIC	maximum m GIC
*Sphoeroides testudineus**	12.8^{m}/8.4	0.2/0.6	12.5/7.6	13.1/9.0
Goniopsis cruentata	7.6^{cm}/5.2	0.4/1.7	7.0/2.7	8.2/7.5
Aratus pisonii	5.3^{cm}/4.6	0.2/2.2	5.1/2.9	5.7/8.2
Uca maracoani	5.6^{cm}/5.8	1.0/0.5	4.0/5.3	6.4/6.5
Uca thayeri	5.8^{cm}/6.0	---/0.1	---/5.8	---/6.1
Callinectes danae	7.6^{cm}/10.5	0.4/0.6	7.2/9.9	8.2/11.2
Cardisoma guanhumi	6.2^{cm}/3.4	0.3/0.1	5.9/3.3	6.4/3.5
Ucides cordatus	5.4^{cm}/3.4	0.1/0.1	5.4/3.3	5.4/3.5
*Littorina s. angulifera**	2.8^{fm}/2.6	0.4/0.5	2.2/1.9	3.1/3.0
Halodule wrightii	---	---	---	---
green mangrove leaves	4.4^{e}	---	---	---
yellow mangrove leaves	4.4^{e}	---	---	---
brown mangrove leaves	4.9^{e}	---	---	---
mangrove flowers (*L. racemosa*)	4.8^{e}	---	---	---
mangrove zone sediment	4.9^{e}	---	---	---
non-mangrove zone sediment:				
U. maracoani zone	6.1^{e}	---	---	---
U. thayeri zone	4.3^{e}	---	---	---
benthic or epiphytic macroalgae:				
a) chlorophytes	5.3^{e}	0.2	5.0	5.5
b) phaeo-/ rhodophyte mix	4.7^{e}	0.1	4.4	5.0
mango fruits	---	---	---	---

^{m}: muscle tissue mix; ^{cm}: coxal muscle tissue, ^{fm}: foot muscle tissue; ^{e}: entire material

Summarizing the information presented in this chapter, one can conclude that *Callinectes danae* and *Goniopsis cruentata* formed a trophic group as did the five species *Cardisoma guanhumi*, *Ucides cordatus*, *Uca maracoani* (mangrove zone), *U. maracoani* (outside mangrove zone), and *U. thayeri* (Fig. 34). The fish species *Sphoeroides testudineus*, the gastropod *L.s.angulifera* and *Aratus pisonii* belonged to none of the possible trophic groups. *L.s.angulifera* was the only consumer that had δ^{15}N-values lower than those of all food sources tested. The hypothesis of a progressive increase of δ^{15}N-values in the food chain was confirmed. The preferable herbivorous species *L.s.angulifera* showed lower δ^{15}N-values than the omnivorous/ detrivorous species *C. guanhumi*, *U. cordatus*, *U. maracoani*, and *U. thayeri*. The portunid species *C. danae* and the grapsid *G. cruentata* were next in line of progression. The carnivorous fish species *S. testudineus* showed a δ^{15}N-value (12.8 ‰) much higher than all other consumers.

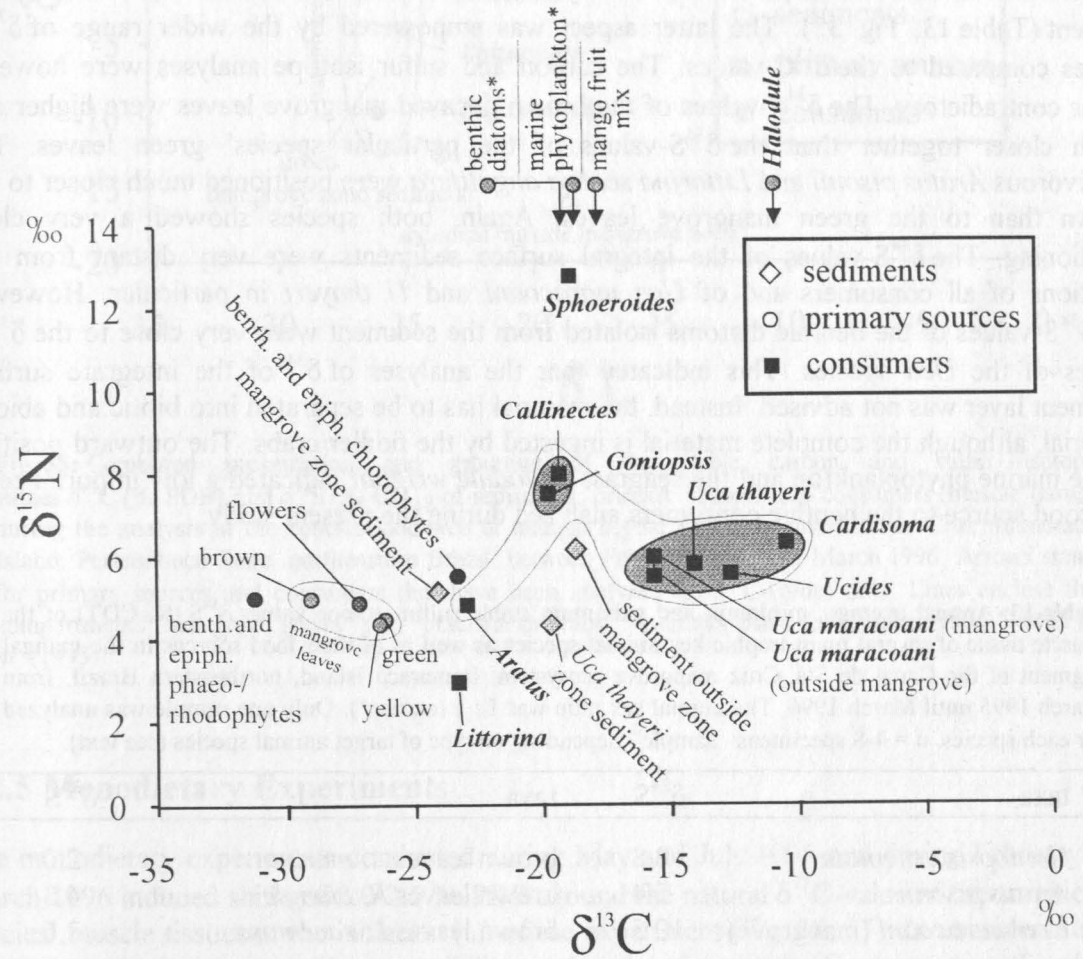

Fig. 34: Combined presentation and grouping of the stable carbon and nitrogen isotope values δ^{13}C (‰ PDB) and δ^{15}N (‰ ATMN) of sediments, primary sources and consumers (muscle tissue) during the analysis of the benthic food web of the benthic mangal segment of the Canal de Sta. Cruz, Itamaracá Island, Pernambuco State, northeastern Brazil, between February 1995 and March 1996. Arrows stand for primary sources that have been analyzed for δ^{13}C-values only. Lines enclose the compartments "mangrove leaves and flowers" and "brachyuran crabs". Shaded areas are non-statistical trophic groupings. Asterisks mark values taken from Newell et *al.* (1995).

As expected, the stable carbon and nitrogen isotope values of all mangrove tree material were close together. Brown mangrove leaves showed slightly higher $\delta^{15}N$-values (4.9 ‰ ATMN) than green leaves (4.4 ‰ ATMN). The difference between green and yellow leaves(4.4 ‰ ATMN) was not significant (t-test, $\alpha = 0.05$). The benthic or epiphytic chlorophytes and phaeo-/ rhodophytes showed dissimilar $\delta^{13}C$-values but comparable $\delta^{15}N$-values of 5.3 ‰ ATMN and 4.7 ‰ ATMN, respectively. The difference of $\delta^{15}N$-values of the surface sediments inside (4.9 ‰) and outside (6.1 ‰) the mangal zone was 1.2 ‰. The $\delta^{13}C$-value of the benthic diatoms (-19.6 ‰ PDB) was very close to the $\delta^{13}C$-value of the surface sediment outside (-18.7 ‰ PDB) the mangal zone. It was concluded that the *Uca* species were most probably almost exclusively feeding on this food source.

While the results of the analyses of $\delta^{34}S$ ($^{34}S/^{32}S$) did only add limited information to the results of the carbon isotope analyses from the first consumer level upwards, they provided a more definite identification and separation of closely related food sources within the gastro-intestinal content (Table 13; Fig. 35). The latter aspect was empowered by the wider range of $\delta^{34}S$-values compared to the $\delta^{13}C$-values. The carbon and sulfur isotope analyses were however never contradictory. The $\delta^{34}S$-values of the brown decayed mangrove leaves were higher and much closer together than the $\delta^{34}S$-values of the particular species' green leaves. The herbivorous *Aratus pisonii* and *Littorina scabra angulifera* were positioned much closer to the brown than to the green mangrove leaves. Again, both species showed a very close positioning. The $\delta^{34}S$-values of the integral surface sediments were very distant from the positions of all consumers and of *Uca maracoani* and *U. thayeri* in particular. However, the $\delta^{34}S$-values of the benthic diatoms isolated from the sediment were very close to the $\delta^{34}S$-values of the *Uca* species. This indicated that the analyses of δ^{34} of the integrate surface sediment layer was not advised. Instead, the material has to be separated into biotic and abiotic material, although the complete material is ingested by the fiddler crabs. The outward position of the marine phytoplankton and the seagrass *Halodule wrightii* indicated a low importance of this food source to the benthic consumers analyzed during the present study.

Table 13: Annual average, minimum and maximum stable sulfur isotope values $\delta^{34}S$ (‰ CDT) of the muscle tissue of several main trophic key animal species as well as of their food sources in the mangal segment of the Canal de Sta. Cruz mangrove ecosystem, Itamaracá Island, northeastern Brazil, from March 1995 until March 1996. The animal sex ratio was 1 : 1 (except*). Only one sample was analyzed for each species. n = 4-8 specimens · sample^{-1} depending on type of target animal species (see text).

taxa	$\delta^{34}S$	taxa	$\delta^{34}S$
Goniopsis cruentata	8.8	brown leaves *A. marina*	2.0
Aratus pisonii	5.4	brown leaves *R. mangle*	4.3
Uca maracoani (mangrove)	10.5	brown leaves *L. racemosa*	3.6
Uca maracoani (outside mangrove)	9.0	mangrove zone sediment	-12.6
		non-mangrove zone sediment:	-16.1
*Littorina s. angulifera**	7.8	*U. maracoani* zone	
Halodule wrightii	17.3	benthic diatoms^{N}	6.5
green leaves *A. marina*	0.2	marine phytoplankton^{N}	17.9
green leaves *R. mangle*	-9.1	benthic or epiphytic macroalgae:	
green leaves *L. racemosa*	-4.1	a) chlorophytes	12.6
		b) phaeo-/ rhodophyte mix	13.4

^{m}: muscle tissue mix; ^{cm}: coxal muscle, ^{fm}: foot muscle; ^{e}: entire material; N: Newell et *al.* 1995

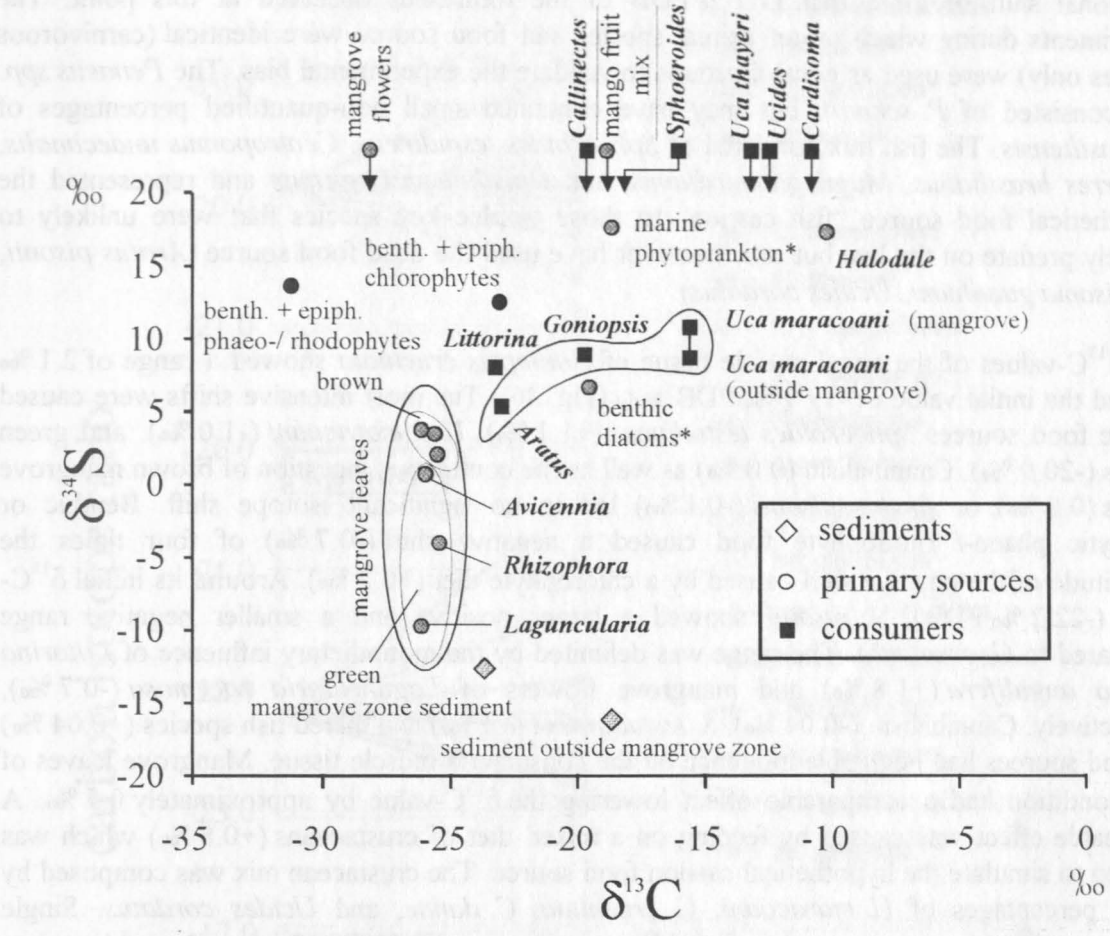

Fig. 35: Combined presentation and grouping of the stable carbon and sulfur isotope values $\delta^{13}C$ (‰ PDB) and $\delta^{34}S$ (‰ CDT) of sediments, primary sources and consumers (muscle tissue) during the analysis of the benthic food web of mangal segment of the Canal de Sta. Cruz, Itamaracá Island, Pernambuco State, northeastern Brazil, between February 1995 and March 1996. Arrows stand for primary sources and consumers that have been analyzed for $\delta^{13}C$-values only. Lines enclose the compartments "mangrove leaves" and "brachyuran crabs". Asterisks mark values taken from Newell et *al.* (1995).

4.2.5 Monodietary Experiments

The monodietary experiments conducted during May and July 1995 and during February and March 1996 induced shifts of 2.0-2.5 ‰ PDB around the natural $\delta^{13}C$-value of the trophic key species' muscle tissues at the initiation (t_0) of the experiment (Fig. 36, 37). In consideration of other autecological aspects like accessibility or density of particular food sources offered, the smallest changes of the trophic key species' $\delta^{13}C$-values were interpreted as indicators for preferred natural food sources. All plant material and sediment samples were fresh. All animal food sources were offered dead but fresh. The quantity of food ingested was not evaluated but all food sources displayed in Fig. 36 and 37 were accepted. For the purpose of comprehensibility, all results are presented as $\delta^{13}C$-values at the initiation of the experiments at t_0 and after 20 days although the isotope shift never was a linear but an asymptotic function of time. After 20 days, the animals had always reached the 90 %-plateau level of their $\delta^{13}C$-shift and a continuation of the particular monodietary experiment would not have resulted in an

additional shift of more than 11.1 % PDB of the total shift observed at this point. The experiments during which target animal species and food source were identical (carnivorous species only) were used as control groups to validate the experimental bias. The *Penaeus spp.* mix consisted of *P. schmitti* but may have contained small non-quantified percentages of *P. brasiliensis*. The fish mix consisted of *Sphoeroides testudineus*, *Centropomus undecimalis*, *Eugerres brasilianus*, *Mugil gaimardianus*, and *Opisthonema oglinum* and represented the hypothetical food source "fish carrion" to those trophic key species that were unlikely to actively predate on the live but may however have used the dead food source (*Aratus pisonii*, *Cardisoma guanhumi*, *Ucides cordatus*).

The δ^{13}C-values of the coxal muscle tissue of *Goniopsis cruentata* showed a range of 2.1 ‰ around the initial value of -19.9 ‰ PDB at t_0 (Fig. 36). The most intensive shifts were caused by the food sources *Sphoeroides testudineus* (+1.1 ‰), *Uca maracoani* (-1.0 ‰), and green leaves (-20.9 ‰). Cannibalism (0.0 ‰) as well as the continuous ingestion of brown mangrove leaves (0.0 ‰) or *Aratus pisonii* (-0.1 ‰) led to no significant isotope shift. Benthic or epiphytic phaeo-/ rhodophyte food caused a negative shift (-0.7 ‰) of four times the magnitude of the positive shift caused by a chlorophyte diet (+0.2 ‰). Around its initial δ^{13}C-value (-22.2 ‰ PDB), *A. pisonii* showed a larger positive and a smaller negative range compared to *G. cruentata*. The range was delimited by the monodietary influence of *Littorina scabra angulifera* (+1.8 ‰) and mangrove flowers of *Laguncularia racemosa* (-0.7 ‰), respectively. Cannibalism (-0.04 ‰), *S. testudineus* (-0.1 ‰) and mixed fish species (+0.04 ‰) as food sources had negligible influence on the consumer's muscle tissue. Mangrove leaves of any condition had a comparable effect lowering the δ^{13}C-value by approximately 0.5 ‰. A noticeable effect was caused by feeding on a mixed diet of crustaceans (+0.8 ‰) which was offered to simulate the hypothetical carrion food source. The crustacean mix was composed by equal percentages of *U. maracoani*, *G. cruentata*, *C. danae*, and *Ucides cordatus*. Single crustacean food sources were not offered because it was unlikely that *A. pisonii* would predate on any of the other much larger crab species. *U. thayeri* and *Cardisoma guanhumi* were excluded from the crustacean mix because they were rarely encountered in the mangal zone.

After 20 days of monodietary feeding, the range of the δ^{13}C-shift (Fig. 36) of *Callinectes danae* muscle tissue was outlined by the food sources *Uca maracoani* (+0.8 ‰) and *Aratus pisonii* (-1.4 ‰). The initial stable carbon isotope value had been -18.2 ‰ PDB at t_0. The effect of *U. thayeri* (+0.7 ‰) was only slightly smaller than that of the larger fiddler crab species. *Goniopsis cruentata* caused a comparable but negative shift of -0.5 ‰. Continuous feeding on *Sphoeroides testudineus* resulted in a carbon isotope shift of (+0.7 ‰) As during the experiments on *A. pisonii*, cannibalism (+0.1 ‰) had almost no effect.

Sphoeroides testudineus showed the widest range of δ^{13}C-shift of all species tested (Fig. 36). The initial δ^{13}C-value of its skeletal muscles (-18.2 ‰ PDB) was most intensely altered by the food sources *Uca maracoani* (+0.7 ‰), *U. thayeri* (+0.7 ‰) and *Littorina scabra angulifera* (-1.9 ‰). A significant negative shift was also caused by exclusively feeding on *Aratus pisonii* (-1.2 ‰). Of all trophic key species, cannibalism caused the strongest, -but still small-, effect on the muscle tissue of *S. testudineus* (+0.2 ‰). The effect of a *Callinectes danae* monodiet was only slightly stronger (+0.3 ‰). The shifts caused by exclusively feeding on *Goniopsis cruentata* (-0.3 ‰), on the *Penaeus spp.* mix (-0.1 ‰) and on *Halodule wrightii* (+0.5 ‰) were small and indicated a preferential feeding on these food sources.

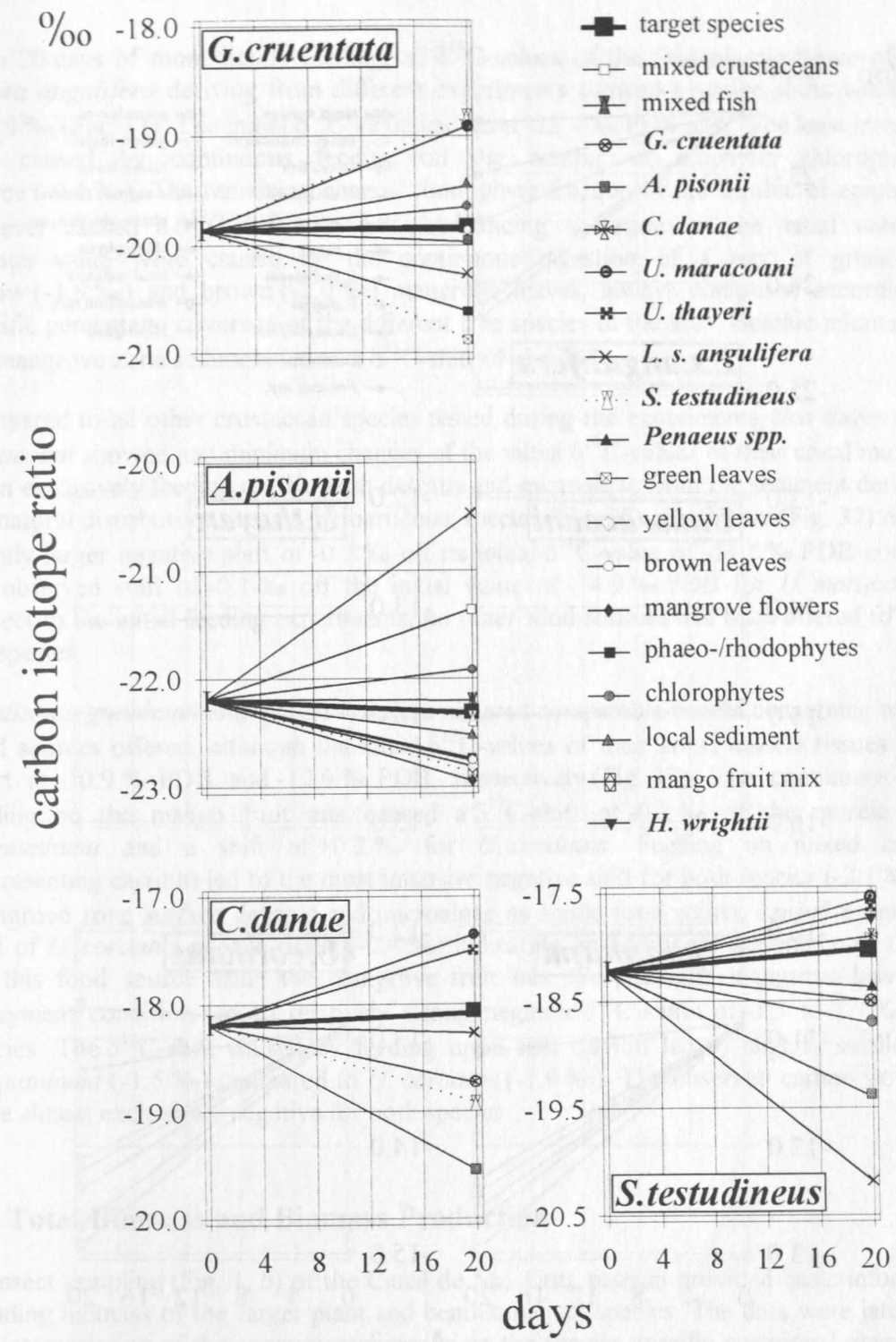

Fig. 36: Shift of the stable carbon isotope values $\delta^{13}C$ (‰ PDB) of the coxal (crustaceans) or skeletal (fish) muscle tissue of *Goniopsis cruentata* (n = 84), *Aratus pisonii* (n = 168), *Callinectes danae* (n = 84), and *Sphoeroides testudineus* (n = 84) during monodietary experiments while exclusively feeding on the food sources indicated by symbols over a period of 20 days. The experiments were conducted at the field station of the Department of Marine Oceanography, Federal University of Pernambuco, Itamaracá Island, northeastern Brazil during May and July 1995 and during February and March 1996. Note that lines between points are intended to simplify the presentation and do NOT symbolize linear functions.

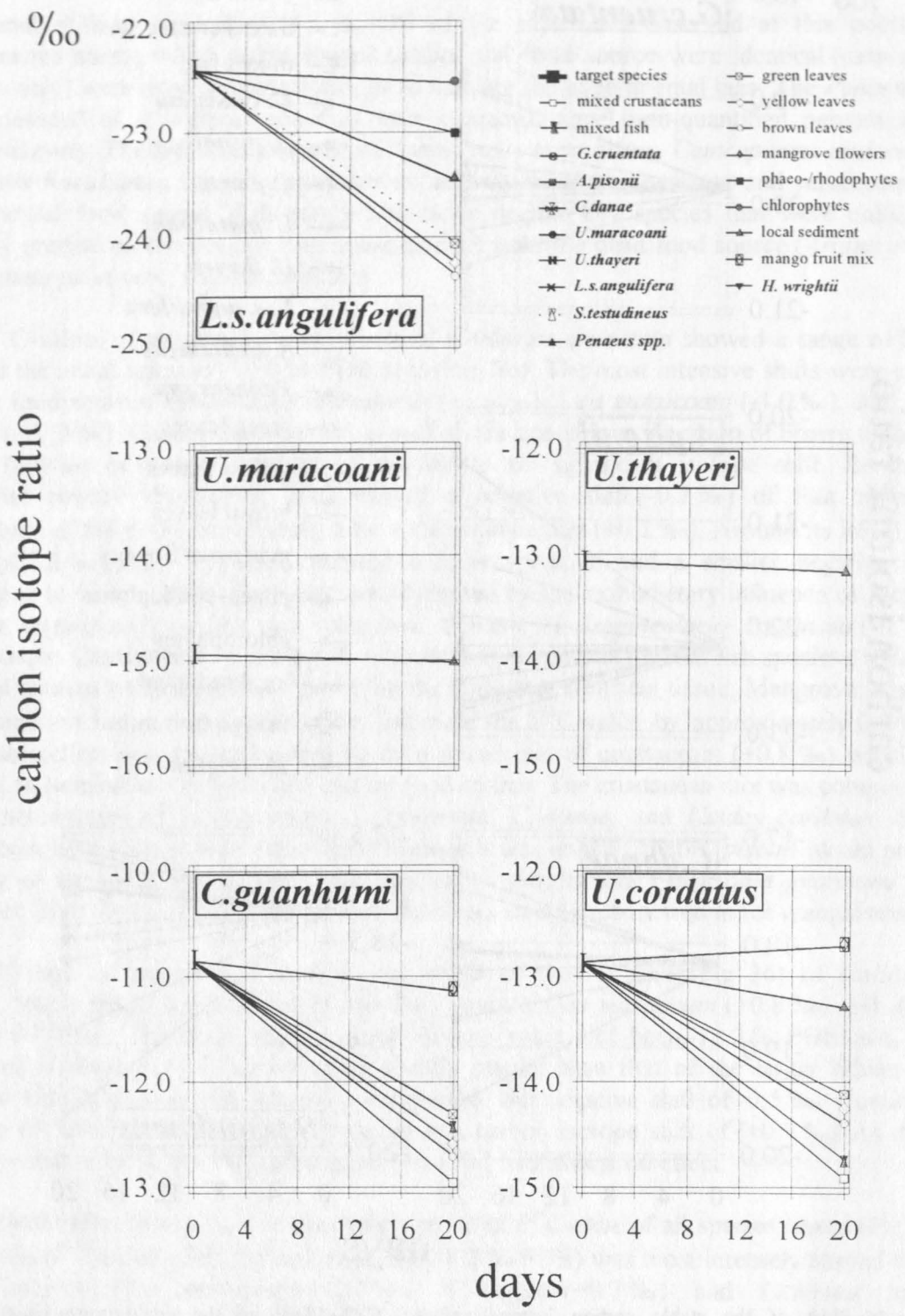

Fig. 37: Shift of the stable carbon isotope values $\delta^{13}C$ (‰ PDB) of the coxal (crustaceans) or skeletal (fish) muscle tissue of *Littorina scabra angulifera* (n = 168), *Uca maracoani* (n = 84), *U. thayeri* (n = 168), *Cardisoma guanhumi* (n = 84), and *Ucides cordatus* (n = 84) during monodietary experiments while exclusively feeding on food indicated by symbols over a period of 20 days. The experiments were conducted at the field station of the Department of Marine Oceanography, Itamaracá Island, northeastern Brazil during May and July 1995 and during February and March 1996. Note that lines between points are intended to simplify the presentation and do NOT symbolize linear functions.

After 20 days of monodietary feeding, all $\delta^{13}C$-values of the foot muscle tissue of *Littorina scabra angulifera* deriving from different experiments showed negative shifts within a range of 1.9 ‰ (Fig. 37). The initial $\delta^{13}C$-value had been -22.4 ‰ PDB at t_0. The least intensive shift was caused by continuous feeding on the benthic or epiphytic chlorophyte food source (-0.1 ‰). The remaining phaeo-/ rhodophyte fraction of the benthic or epiphytic algae however caused a $\delta^{13}C$-shift of -0.6 ‰. Advancing alterations of the initial stable carbon isotope value were caused by the continuous ingestion of a mix of green (-1.7 ‰), yellow (-1.9 ‰) and brown (-2.0 ‰) mangrove leaves, always composed according to the specific percentage coverage of the different tree species in the area. Benthic microalgae from the mangrove zone sediment led to a $\delta^{13}C$-shift of -1.0 ‰.

Compared to all other crustacean species tested during the experiments *Uca thayeri* and *Uca maracoani* showed just minimum changes of the initial $\delta^{13}C$-values of their coxal muscle tissue when exclusively feeding on the fresh detritus and microalgae from the sediment deriving from the natural distribution sites of the particular species (Fig. 37). *U. thayeri* (Fig. 37) displayed a slightly larger negative shift of -0.2 ‰ off its initial $\delta^{13}C$-value of -13.1 ‰ PDB compared to the observed shift of -0.1 ‰ off the initial value of -14.9 ‰ PDB for *U. maracoani*. With respect to the initial feeding experiments, no other food sources had been offered to neither of the species.

Cardisoma guanhumi and *Ucides cordatus* showed comparable results concerning most of the food sources offered, although the initial $\delta^{13}C$-values of their coxal muscle tissues were 2 ‰ apart at -10.9 ‰ PDB and -12.9 ‰ PDB, respectively (Fig. 37). The continuous exclusive feeding on the mango fruit mix caused a $\delta^{13}C$-shift of -0.2 ‰ of the muscle tissue of *C. guanhumi* and a shift of +0.2 ‰ for *U. cordatus*. Feeding on mixed crustaceans (representing carrion) led to the most intensive negative shift for both species (-2.1 ‰, -2. ‰). Mangrove zone surface detritus and microalgae as single food source caused a modest $\delta^{13}C$-shift of *U. cordatus* muscle tissue (-0.4 ‰) indicating an additional preference of the species for this food source aside the mangrove fruit mix. Surprisingly, mangrove leaves of any decayment condition led to relatively strong negative $\delta^{13}C$-shifts of -1.3 to-1.7 ‰ for both species. The $\delta^{13}C$-shift caused by feeding upon fish carrion led to slightly smaller shift of *C. guanhumi* (-1.5 ‰) compared to *U. cordatus* (-1.9 ‰). The observed carbon isotope shifts were almost exclusively negative for both species.

4.3 Total Biomass and Biomass Production

Transect sampling (Fig. 1, 6) of the Canal de Sta. Cruz mangal provided basic information on standing biomass of the target plant and benthic animal species. The data were later used for the interpretation of the experimental results on the species-specific nutritional physiology and on the general food web structure of the benthic macrofauna (>1 mm) of the mangal ecosystem (Chapter 4.4). A total of 30 099 animal specimens were sampled during the three sampling events. The estimated total standing biomass of the trophic key animal species accounted for 20.4 $g \cdot m^{-2}$ which is equivalent to 567.4 tonnesFW (Table 14) in the mangal segment of the Canal de Sta. Cruz ecosystem from a line 100 m in front of the outermost extension of the mangroves to a line 5 m into the supralittoral landward coconut-tree zone. This mangal zone has an extention of 27.7 km^2 and was defined as study area during the research project.

The holo-aquatic channel zone of the Canal de Sta. Cruz in general and the temporal exchange of the migratory trophic key animal species *Callinectes danae* and *Sphoeroides testudineus* and other fish species between this two zones in particular were not analyzed during the present study. The meio- and microfaunal biomass as well as the biomass of the mangrove oyster *Crassostrea rhizophorae* were also not analyzed. The inhomogeniety of distribution of the trophic key animal species within the mangrove zone has already been described in the chapter on general behavior.

Table 14: Average standing biomass per unit area and total standing biomass (fresh weight) of selected benthic animal key species in the mangal segment (27.7 km^2) of the Canal Sta. Cruz mangrove ecosystem, Itamaracá Island, northeastern Brazil, during three transect sweep-sampling events (TRS_I, TRS_{II}, TRS_{III}) from February 1995 until March 1996. TRS_I, TRS_{II} = 4 000 m^2, TRS_{III} = 20 000 m^2.

species	TRS	averages [$g \cdot m^{-2}$]		maximum [$^a g_{max} \cdot m^{-2}$]	entire mangal [10^3 kg]	sample size [n]
G. cruentata	I	**10.4**				
	II	**8.1**	$\bar{x}$ = **8.5**	121.8	**235.8**	7 503
	III	**7.0**				
A. pisonii	I	**0.9**				
	II	**0.5**	$\bar{x}$ = **0.8**	37.2	**23.5**	9 287
	III	**1.0**				
C. danae	I	**6.3**				
	II	**4.9**	$\bar{x}$ = **5.6**	845.2	**162.2**	2 325
	III	**6.4**				
U. maracoani	I	**2.8**				
	II	**3.5**	$\bar{x}$ = **2.9**	1 634.9	**81.2**	4 481
	III	**2.5**				
U. thayeri	I	**0.1**				
	II	**0.2**	$\bar{x}$ = **0.1**	161.3	**3.8**	1 297
	III	**0.1**				
C. guanhumi	I	**0.3**				
	II	**0.5**	$\bar{x}$ = **0.4**	282.3	**11.4**	163
	III	**0.3**				
U. cordatus	I	**0.4**				
	II	**0.5**	$\bar{x}$ = **0.4**	351.1	**10.1**	121
	III	**0.4**				
L. s. angulifera[b]	I	**0.3**				
	II	**0.5**	$\bar{x}$ = **0.3**	78.5	**8.9**	4 518
	III	**0.3**				
S. testudineus	I	**0.8**				
	II	**1.7**	$\bar{x}$ = **1.1**	232.2	**30.5**	404
	III	**0.8**				
	Σ		**20.4**		**567.4**	30 099

[a]: average for 10 m^2 of highest density of all samples; [b]: including shell

Table 15: Average standing biomass per unit area and total standing biomass (dry weight) of selected key plant species in the mangal segment (27.7 km^2) of the Canal Sta. Cruz mangrove ecosystem, Itamaracá Island, Pernambuco State, northeastern Brazil, during three transect sweep-sampling events (TRS_I, TRS_{II}, TRS_{III}) from February 1995 until March 1996. TRS_I, TRS_{II} = 4 000 m^2, TRS_{III} = 20 000 m^2.

		average		maximum	entire mangal	sample size
taxa	TRS	[g · 10^3·m^{-2}]		[^{a} g_{max} · 10^3·m^{-2}]	[10^3 kg]	[10^3 g]
A. marina[b]	I	**7.95**				
	II	**8.44**	$\bar{x}$ = **8.25**	21.12	**228 525**	521
	III	**8.36**				
R. mangle[b]	I	**14.02**				
	II	**13.78**	$\bar{x}$ = **14.17**	25.11	**392 509**	887
	III	**14.71**				
L. racemosa[b]	I	**2.89**				
	II	**2.98**	$\bar{x}$ = **2.81**	19.53	**77 837**	174
	III	**2.56**				
C. erecta[b]	I	**0.68**				
	II	**0.73**	$\bar{x}$ = **0.71**	19.71	**19 667**	45
	III	**0.72**				
H. wrightii	I	**0.01**				
	II	**0.01**	$\bar{x}$ = **0.01**	0.48	**277**	3
	III	**0.01**				
epiphytes in mangrove canopy (height >1m above EHWS)						
	I	**0.03**				
	II	**0.03**	$\bar{x}$ = **0.03**	0.12	**831**	2
	III	**0.03**				
benthic and epiphytic algae (intertidal zone)						
a) phaeo-/ rhodophytes						
	I	**0.25**				
	II	**0.29**	$\bar{x}$ = **0.28**	0.81	**7 756**	26
	III	**0.30**				
b) chlorophytes						
	I	**0.39**				
	II	**0.39**	$\bar{x}$ = **0.37**	1.62	**10 249**	28
	III	**0.33**				
terrestrial plants						
	I	**0.02**				
	II	**0.02**	$\bar{x}$ = **0.02**	20.30	**554**	4
	III	**0.02**				
Σ			**26.65**		**738 205**	1 726

[a]: average for 4 m^2 of highest density of all samples; [b]: including litterfall; ELWS = extreme low water during spring tides

The semi-terrestrial *Goniopsis cruentata* and the blue crab *Callinectes danae* showed the highest standing biomass in the area. These species were followed by the fiddler crab *Uca maracoani* and the puffer fish *Sphoeroides testudineus*. Thus, two of the four species of highest standing biomass in the area were migratory between the mangrove ecosystem itself and the adjacent area of the Canal de Sta. Cruz open channel. *Aratus pisonii* and *Littorina scabra angulifera* conjointly had a standing biomass of 1.2 $g \cdot m^{-2}$ or 32.4 tonnesFW within the entire system. This means a temporary vertical expansion of 5.7 % of the benthic biomass into the mangrove canopy.

All species studied were more or less restricted to a specific habitat type or mangrove zone as shown in Fig. 7. The terrestrial *Cardisoma guanhumi* and *Ucides cordatus* were both restricted to the coconut-tree zone and only temporarily entered a few meters into the upper intertidal zone during low tides and at night. The small fiddler crab, *Uca thayeri*, was found only in the sandy upper intertidal zone to a maximum water depth of 0.4 m during high tides. *Uca maracoani* inhabited all muddy areas between the extreme low water during spring tides (ELWS) and the extreme high water during neap tides (EHWN) that had minimum distances of 2.5 m to mangrove channels and 5.0 m to mangrove trees and a substrate depth sufficient for burrowing. *Aratus pisonii* and *Littorina scabra angulifera* were found only in the mangal zone, but while *L.s.angulifera* inhabited a zone from the seaward extension of the zone to a line of minimum water depth of 0.5 m during EHWN, *A. pisonii* was found to neighbor this distributional range landward to a minimum water depth of 0.2 m during EHWN. All species displayed density and biomass differences over their complete distributional ranges. Widest ranges of biomass per square meter (r_B = maximum factor of range of biomass,) were found for *U. thayeri* (r_B = 1 177), *U. cordatus* (r_B = 964), *C. guanhumi* (r_B = 685), and *U. maracoani* (r_B = 560). Lowest differences showed *G. cruentata* (r_B = 14) and *A. pisonii* (r_B = 44).

Statistical analyses via WILCOXON-tests revealed no significant differences of paired observations of standing biomass per unit area (40 m^2) along the sampling transect line at a resolution of 10 m sub-sections between the three sampling events. The 5-fold larger screening area during the sampling event from 13 to 14 February, 1996 had no significant influence on the results on species-specific standing biomass ($\alpha = 0.5$). Mortality rates caused by the sampling methods or the determination of body size and weight at the laboratory were kept under 10 % except for *Sphoeroides testudineus* (18.5 %). The later careful releasing of the animals to the sampling area caused no or negligible additional mortality which was ensured through successive sampling for dead animals in the area for 2 hours.

The Canal de Sta. Cruz mangrove ecosystem is dominated by the two mangrove tree species *Rhizophora mangle* and *Avicennia marina*. *R. mangle* covers 49 % and *A. marina* covers 36 % of the mangal zone of the ecosystem. The mangrove species *Laguncularia racemosa* and *Conocarpus erecta* contribute just 5 %, respective 1 % to the coverage. The remaining 9 % are muddy plains, slopes and tidal creeks.

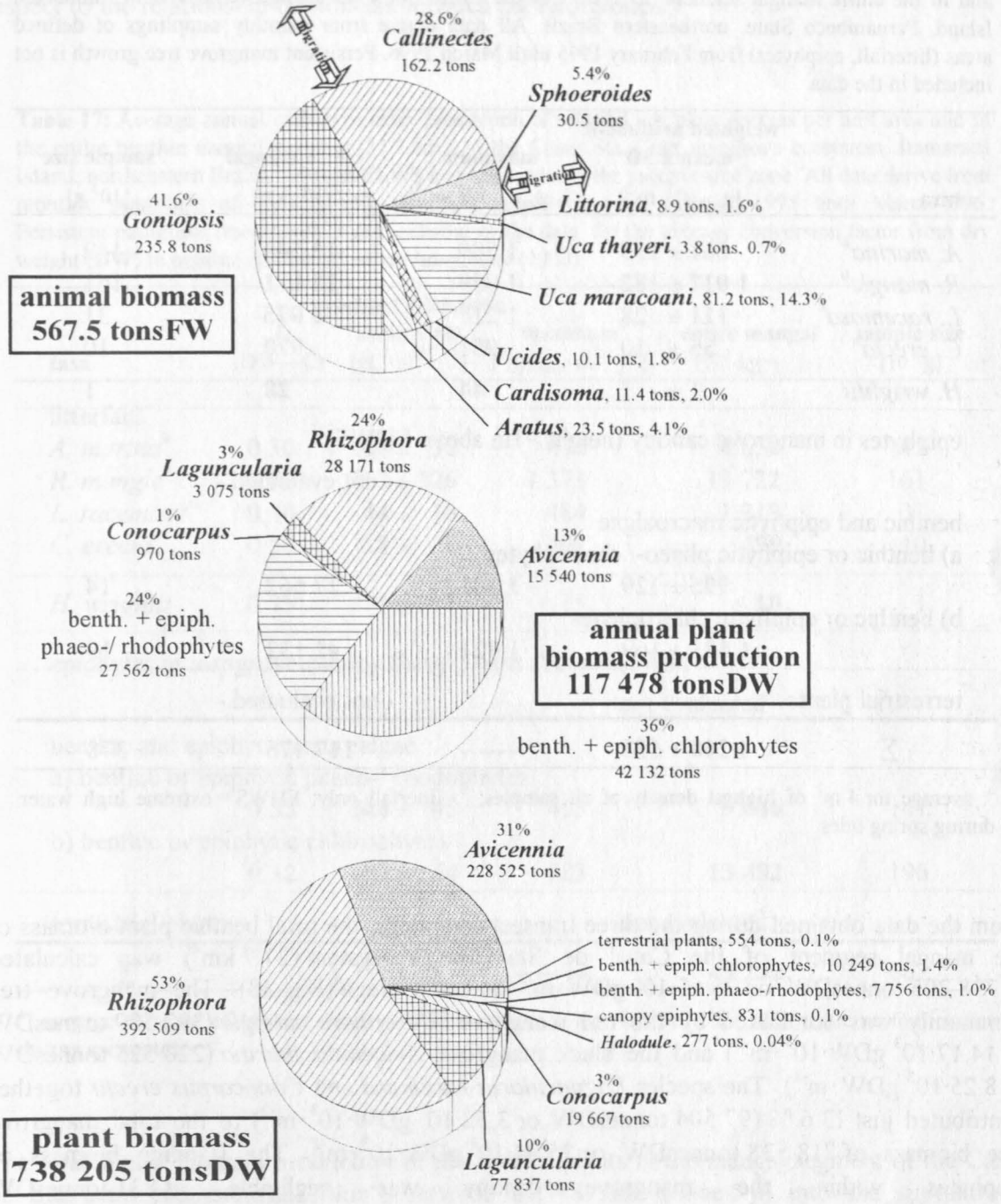

Fig. 38: Relative standing stocks (% biomass fresh weight) of selected benthic animal key species, relative total standing biomass (% dry weight) and annual biomass production (% dry weight) of selected key plant species in the benthic mangal segment (27.7 km^2) of the ecosystem of the Canal de Sta. Cruz, Pernambuco State, northeastern Brazil. All data derive from monthly samplings of defined areas (litterfall, epiphytes) from February 1995 until March 1996. Persistent mangrove tree growth is not included in the data.

Table 16: Average annual biomass production (dry weight) of selected key plant species per unit area and in the entire mangal segment (27.7 km^2) of the Canal Sta. Cruz mangrove ecosystem, Itamaracá Island, Pernambuco State, northeastern Brazil. All data derive from monthly samplings of defined areas (litterfall, epiphytes) from February 1995 until March 1996. Persistent mangrove tree growth is not included in the data.

taxa	weighted arithmetic mean ± SD [$g \cdot 10^3 \cdot m^{-2}$]	maximum [$^a g_{max} \cdot 10^3 \cdot m^{-2}$]	entire mangal [10^3 kg]	sample size [10^3 g]
A. marina[b]	**561** ± 139	1 589	**15 540**	142
R. mangle[b]	**1 017** ± 182	1 959	**28 171**	161
L. racemosa[b]	**111** ± 28	1 211	**3 075**	31
C. erecta[b]	**35** ± 10	981	**970**	10
H. wrightii	**1** ± 1	44	**28**	1
epiphytes in mangrove canopy (height >1m above EHWS)		- not evaluated -		
benthic and epiphytic macroalgae				
a) benthic or epiphytic phaeo-/ rhodophytes	**995** ± 129	1 301	**27 562**	14
b) benthic or epiphytic chlorophytes	**1 521** ± 169	1 821	**42 132**	19
terrestrial plants		- not evaluated -		
Σ	**4 240** ± 658	--------	**117 478**	378

[a]: average for 4 m^2 of highest density of all samples; [b]: litterfall only; EHWS = extreme high water during spring tides

From the data obtained during the three transect samplings, the total benthic plant biomass of the mangal segment of the Canal de Sta. Cruz ecosystem (27.7 km^2) was calculated as 738 205 tonnesDW or $26.65 \cdot 10^3$ $gDW \cdot m^{-2}$ as an average (Fig. 38). The mangrove tree community was dominated by the red mangrove *Rhizophora mangle* (392 509 tonnesDW or $14.17 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$) and the black mangrove *Avicennia marina* (228 525 tonnesDW or $8.25 \cdot 10^3$ $gDW \cdot m^{-2}$). The species *Laguncularia racemosa* and *Conocarpus erecta* together contributed just 13.6 % (97 504 tonnesDW or $3.52 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$) to the total mangrove tree biomass of 718 538 tonnesDW or $25.94 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$. The standing biomass of epiphytes within the mangrove canopy was negligible at 831 tonnesDW or $0.03 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$. Terrestrial plants had a standing biomass of $20.30 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$ at the supralittoral border to the coconut tree zone. At the seaward end of the sampling transect, the seagrass *Halodule wrightii* contributed 277 tonnesDW or $0.01 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$.

Benthic or epiphytic algae had a standing biomass of 18 005 tonnesDW or $0.65 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$ below a horizontal line at 0.1 m above EHWS (Table 1). The fraction of chlorophyte algae having a standing biomass of 10 249 tonnesDW or $0.37 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$ contributed 56.9 % to this phytal subsection of the system. The remaining benthic or epiphytic phaeo-/ rhodophyte pool had a slightly lower standing biomass of 7 756 tonnesDW or $0.28 \cdot 10^3$ $gDW \cdot 10^3 \cdot m^{-2}$. However, either of the groups dominated the benthic algal community at certain vertical zones of the ecosystem with an increase of

chlorophyte biomass above ELWN (Table 1) which functioned as the equilibrium point with respect to the relationship of biomass between the two groups.

Table 17: Average annual carbon primary production of selected key plant species per unit area and in the entire benthic mangal segment (27.7 km^2) of the Canal Sta. Cruz mangrove ecosystem, Itamaracá Island, northeastern Brazil, between ELWS and the border of the coconut-tree zone. All data derive from monthly samplings of defined areas (litterfall, epiphytes) from February 1995 until March 1996. Persistent mangrove tree growth is not included in the data. f = the average conversion factor from dry weight (**DW**) to organic carbon (**C**) after Vinogradov (1953).

taxa	f (DW→C)	weighted arithmetic mean ± SD [$gC \cdot m^{-2} \cdot y^{-1}$]	maximum [$^a gC_{max} \cdot m^{-2} \cdot y^{-1}$]	entire mangal [$10^3 kg \cdot y^{-1}$]	sample size [10^3 g]
litterfall:					
A. marina[b]	0.30	**168** ± 36	476	**4 654**	142
R. mangle[b]	0.70	**712** ± 126	1 371	**19 722**	161
L. racemosa[b]	0.40	**44** ± 16	484	**1 219**	31
C. erecta[b]	0.50	**18** ± 4	491	**499**	10
H. wrightii	0.35	< 1 ± < 1	15	< **10**	1
epiphytes in mangrove canopy (height >1m above EHWS)					
			- not evaluated -		
benthic and epiphytic macroalgae					
a) benthic or epiphytic phaeo-/ rhodophytes					
	0.35	**348** ± 45	455	**9 646**	141
b) benthic or epiphytic chlorophytes					
	0.32	**487** ± 54	583	**13 482**	196
terrestrial plants			- not evaluated -		
Σ		**1 777** ± 281	--------	**49 232**	682

[a]: average for 4 m^2 of highest density of all samples; [b]: litterfall only; EHWS = extreme high water during spring tides

The total annual biomass production of the benthic plants in the mangal segment of the Canal de Sta. Cruz ecosystem (27.7 km^2) between ELWS and a line 5 m into the supralittoral coconut-tree zone was 117 478 tonnesDW or 49 232 tonnes of organic carbon (Tables 15, 16, 17). The average annual production per square meter was 4 240 gDW or 1 777 gC. The biomass production by terrestrial plants and by epiphytes above a horizontal line at 0.1 m above EHWS were not evaluated and, from their biomass data, were presumed negligible compared to other sources of biomass production. Mangrove tree litterfall (1 724 $gDW \cdot m^{-2} \cdot y^{-1}$) and benthic or epiphytic macroalgae below a horizontal line at 0.1 m above EHWS (2 516 $gDW \cdot m^{-2} \cdot y^{-1}$) contributed approximately 41 and 59 % to the annual dry weight biomass production. The mangrove litterfall of all tree species combined was composed of 86 % leaves, of 12 % woody material, and of 2 % flowers and seeds. Because mangrove litterfall and epiphytic algae have different conversion factors (Table 17) from dry to carbon weight, all mangrove tree species combined contributed 53.0 % (942 $gC \cdot m^{-2} \cdot y^{-1}$) to

the total annual benthic primary carbon production of the system. The benthic algal community contributed an almost equal portion of 47.0 %.

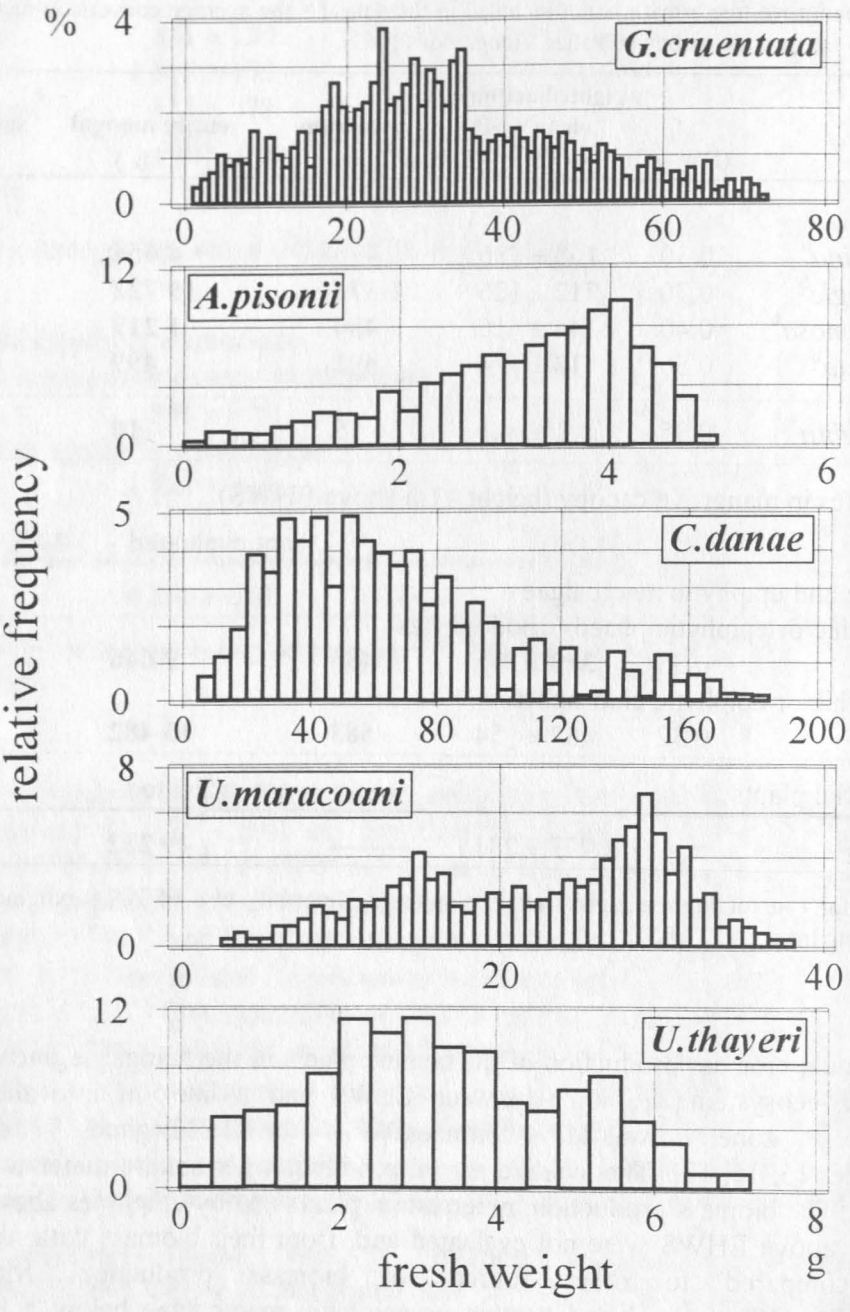

Fig. 39: Relative fresh weight frequencies of the standing stocks of *Goniopsis cruentata* (n = 7 503), *Aratus pisonii* (n = 9 287), *Callinectes danae* (n = 2 325), *Uca maracoani* (n = 4 481), and *U. thayeri* (n = 1 297) in the benthic mangal segment of the Canal de Sta. Cruz mangrove ecosystem, Itamaracá Island, Pernambuco State, northeastern Brazil, from June 1995 until February 1996.

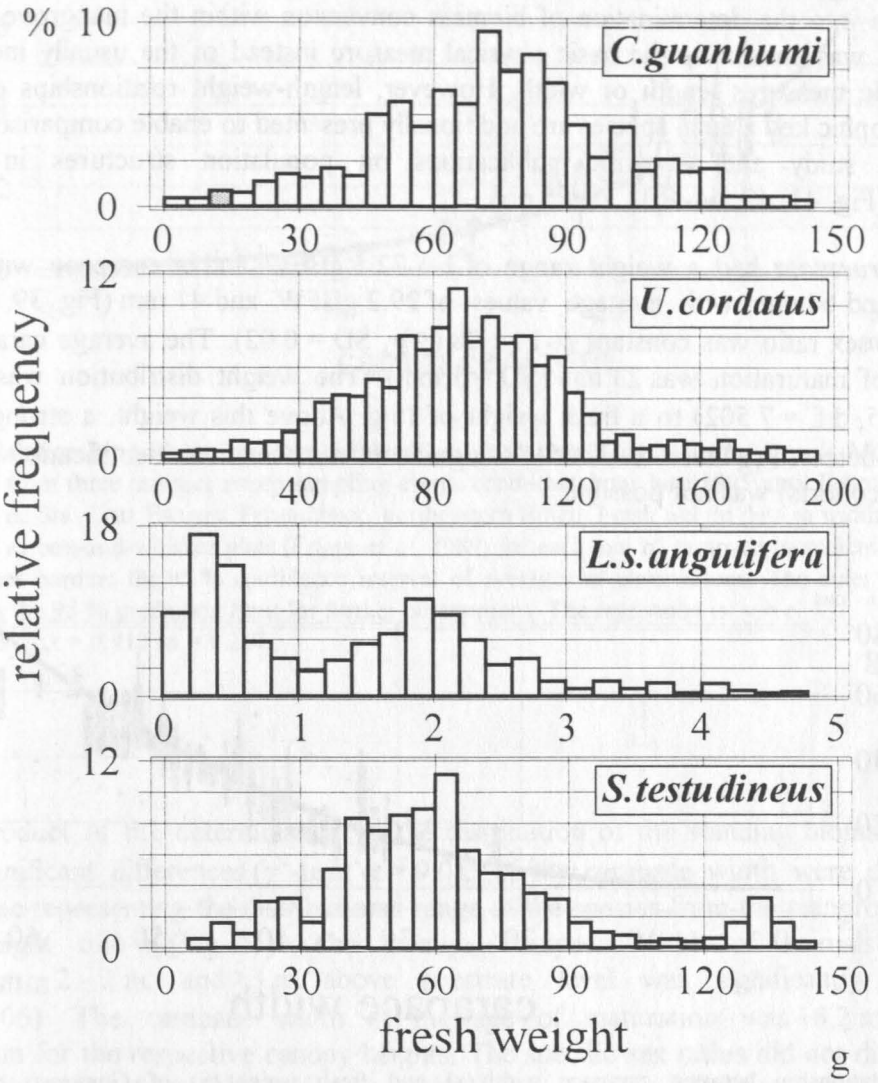

Fig. 40: Relative fresh weight frequencies of the standing stocks of *Cardisoma guanhumi* (n = 163), *Ucides cordatus* (n = 121), *Littorina scabra angulifera* (n = 4 518), and *Sphoeroides testudineus* (n = 404) in the benthic mangal segment of the Canal de Sta. Cruz mangrove ecosystem, Itamaracá Island, Pernambuco State, northeastern Brazil, from June 1995 until February 1996.

The average annual quantitative (dry weight) composition of the litterfall was 35.3 % *Avicennia marina*, 51.9 % *Rhizophora mangle*, 9.2 % *Laguncularia racemosa*, and 3.6 % *Conocarpus erecta* material. Although the annual dry weight biomass production of *R. mangle* and *A. marina* was comparable (Table 16), the respective annual carbon primary production (Table 17) of *R. mangle* (712 $gC \cdot m^{-2} \cdot y^{-1}$) was 4.2 fold higher than that of *A. marina* (168 $gC \cdot m^{-2} \cdot y^{-1}$). This divergence was a result of the species' very dissimilar average conversion factors from dry weight to organic carbon which was 0.30 for *A. marina* and 0.7 for *R. mangle*. The mangrove species *L. racemosa* and *C. erecta* together showed a primary production of 62 $gC \cdot m^{-2} \cdot y^{-1}$ which represented 6.6 % of the respective primary production.

All trophic key animal species showed normal or log-normal distributions of weight classes of body fresh weights (BFW) (Fig. 39, 40). With respect to the intended later integration of the biomass data into the determination of biomass conversion within the mangrove ecosystem, fresh weight was chosen as the basic physical measure instead of the usually more popular morphometric measures length or width. However, length-weight relationships of the most important trophic key animal species are additionally presented to enable comparisons between the present study and scientific publications on population structures in mangrove ecosystems (Fig. 41, 42, 44-46).

Goniopsis cruentata had a weight range of 1.4-72.5 gBFW and a carapace width ranging between 7 and 64 mm with average values of 29.2 gBFW and 41 mm (Fig. 39, 41). In all samples, the sex ratio was constant at 1 : 1.08 (♀/♂, SD = 0.02). The average carapace width at the age of maturation was 23 mm (SD = 3 mm). The weight distribution was normal (t-test: $\alpha = 0.05$, d.f. = 7 502) to a fresh weight of 35 g. Above this weight, a strong frequency decline was detected (χ^2-test: $\alpha = 0.05$). A significant mathematical identification of separate age classes (cohorts) was not possible.

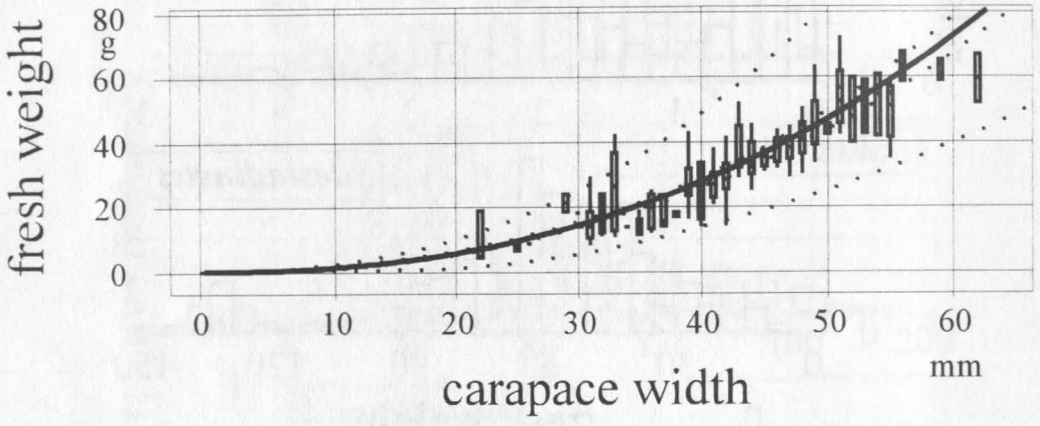

Fig. 41: Relationship between carapace width (**x**) and fresh weight (**y**) of *Goniopsis cruentata*. Morphometric field data from three transect sweep-sampling events conducted from June 1995 until February 1996 at the Canal de Sta. Cruz Estuary, Pernambuco, northeastern Brazil. Fresh weight data in width classes are presented as box-and-whisker plots (Frigge et *al.* 1989) for each mm of carapace increment. The inner dotted line borders the 95 % confidence interval of averages of observations. The outer dotted line represents the 95 % prediction limit for further observations. The regression is: $y = e^{0.6555 + 0.062182 x}$. The correlation is: r = 0.927 (n = 7 503).

Aratus pisonii showed a weight range of 0.2 - 4.9 gBFW and a carapace width between 5 and 28 mm with average values of 2.5 gBFW and 21 mm (Fig. 39, 42). The sex ratio was constant at 1 : 0.89 (♀/♂, SD = 0.02) in all samples. The average carapace width at the age of maturation was 15 mm (SD = 4 mm). The weight distribution was positive log-normal (t-test: $\alpha = 0.05$, d.f. = 9 286) as indicated by the average carapace width in the upper quarter of the range of values. A significant mathematical identification of three separate age classes having average fresh weights of 3.8 g, 2.2 g, and 1.4 g (χ^2-test: $\alpha = 0.05$) was possible.

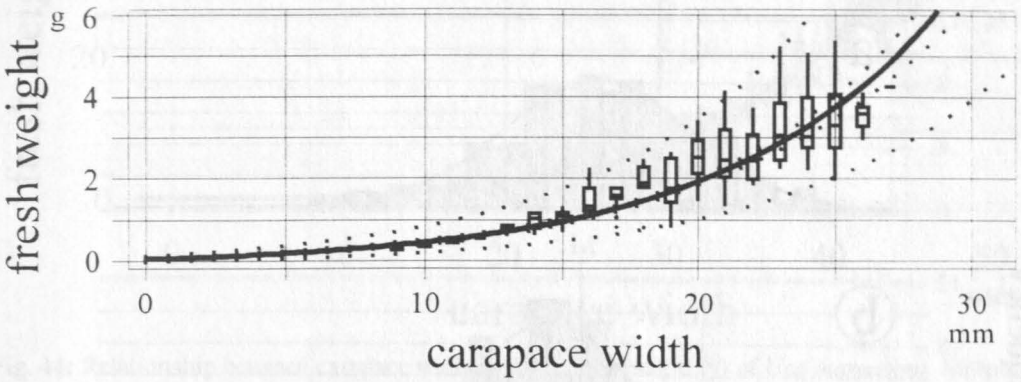

Fig. 42: Relationship between carapace width (**x**) and fresh weight (**y**) of *Aratus pisonii*. Morphometric field data from three transect sweep-sampling events conducted from June 1995 until February 1996 at the Canal de Sta. Cruz Estuary, Pernambuco, northeastern Brazil. Fresh weight data in width classes are presented as box-and-whisker plots (Frigge et *al.* 1989) for each mm of carapace increment. The inner dotted lines borders the 95 % confidence interval of averages of observations. The outer dotted line represents the 95 % prediction limit for further observations. The regression is: $y = e^{-1.8681 + 0.129457 x}$. The correlation is: r = 0.912 (n = 9 287).

As a by-product of the determination of the distribution of the standing biomass of *Aratus pisonii*, significant differences (χ^2-test: $\alpha = 0.05$) of the carapace width were detected at a vertical scale representing the distributional range of the species from the mangrove floor to a canopy height of 6 m (Fig. 43). The average carapace width of animals at canopy heights <2 m, 2 - 3 m, and >3 m above substrate level was significantly different (F-test: $\alpha = 0.05$). The carapace width at the age of maturation was 16.2 mm, 16.3 mm, and 12.0 mm for the respective canopy heights. The specific sex ratios did not differ from the figures for the entire *Aratus* stock in the mangal.

The fresh weight range of *Callinectes danae* was 8.8 - 184.2 g and the animals had a carapace width range between 7 and 117 mm with average values of 69.8 g and 86 mm (Fig. 39). The weight distribution was negatively log-normal (t-test: $\alpha = 0.05$, d.f. = 2 324) to a fresh weight of 90 g. Above this weight, a strong frequency decline was detected (χ^2-test: $\alpha = 0.05$). A significant mathematical identification of separate age classes was not possible. The sex ratio was unbalanced at 1 : 1.47 (♀/♂, SD = 0.27) in all samples. The maturation age of *C. danae* could not be determined exactly because the females do not carry egg masses as the other target animal species of the present study. Based on the dissection of the animals' gonads the average carapace width at the age of maturation was assumed to be approximately 51 mm. The regression of the length-weight relationship led to the equation $y = e^{0.0008 + 0.0473 x}$. The correlation was r = 0.978 (n = 2 325).

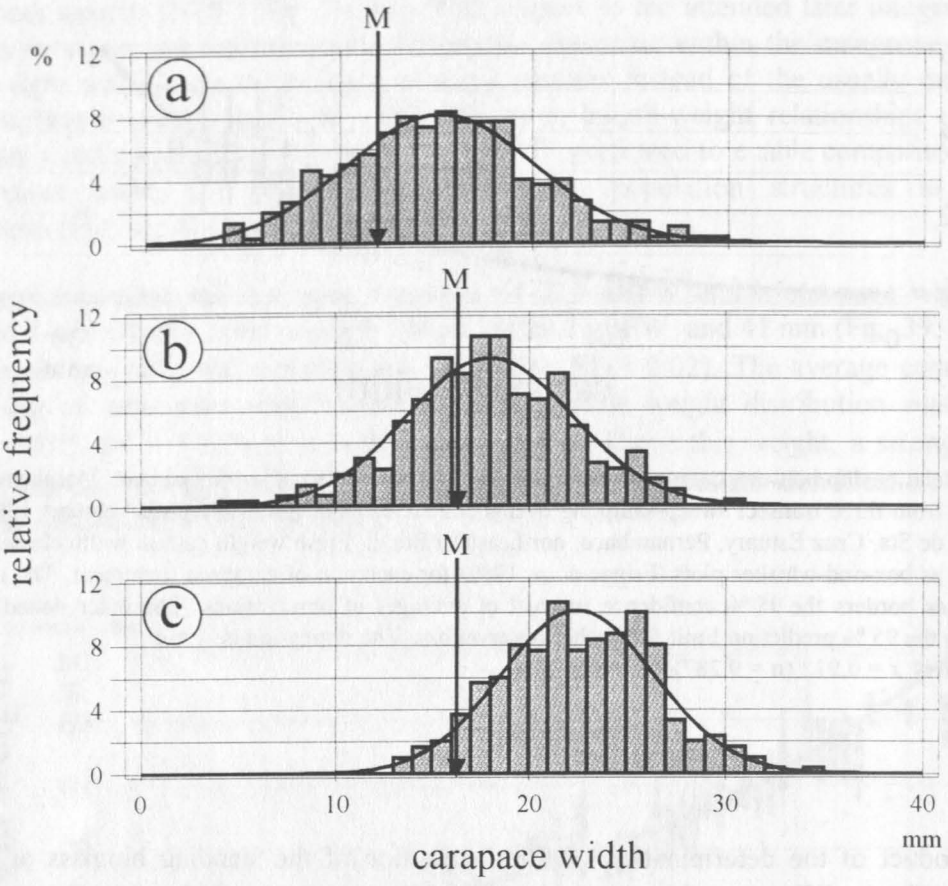

Fig. 43: Relative frequencies of *Aratus pisonii* (carapace width) in the mangal segment of the mangrove ecosystem of the Canal de Sta. Cruz Estuary, northeastern Brazil, between June 1995 and February 1996. (a) canopy height of mangrove trees = 301-400 mm, (b) 201-300 mm, (c) 0-200 mm above substrate level. Note the dissimilar carapace width at the age of maturation of *A. pisonii* (♂/♀ pooled). Width classes include frequencies at or below tic-mark value. All groups are part of the log-normal distribution of the integral *Aratus* stock in the mangal area presented in Fig. 42. Highly significant (α =0.01) t-tests for (a), (b), and (c); n_{total} = 3 x 3.096 = 9 288.

Uca maracoani showed a weight range of 3.4 - 37.1 gBFW and a carapace width range between 4 and 46 mm with average values of 17.1 gBFW and 34 mm (Fig. 39, 44). The sex ratio was constant at 1 : 1.11 (♀/♂, SD = 0.04) in all samples. The average carapace width at the age of maturation was 16 mm (SD = 2 mm). *U. maracoani* was normal distributed in two age classes having a significantly different body fresh weight (F-test: $\alpha = 0.05$) of 16.2 and 29.6 g, respectively. Otherwise the normal distributions were significantly similar (χ^2-test: $\alpha = 0.01$). The two normal distributions (t-test: $\alpha = 0.05$, $d.f._1 = 2\,000$; $d.f._2 = 2\,000$) were of identical statistical shape (χ^2-test: $\alpha = 0.05$) but had highly significantly different averages (F-test: $\alpha = 0.01$).

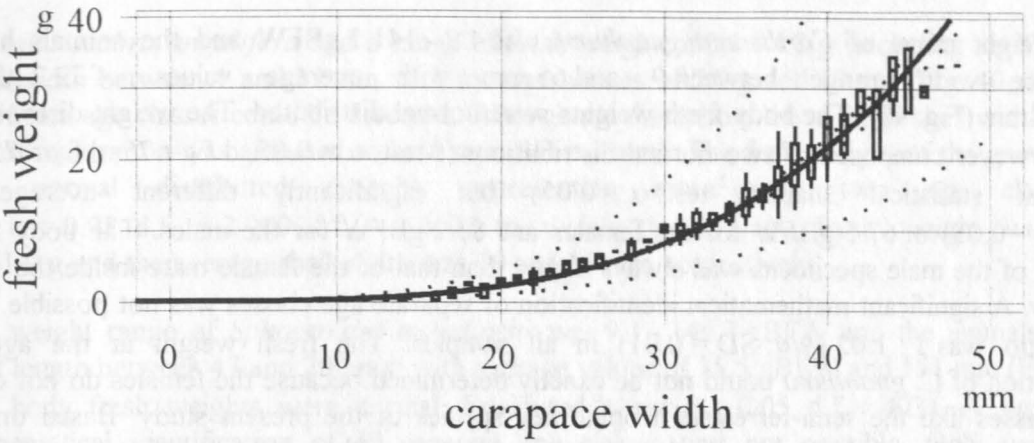

Fig. 44: Relationship between carapace width (**x**) and fresh weight (**y**) of *Uca maracoani*. Morphometric data from three transect sweep-sampling events conducted from June 1995 until February 1996 at the Canal de Sta. Cruz Estuary, Pernambuco, northeastern Brazil. Fresh weight data in width classes are presented as box-and-whisker plots (Frigge et *al.* 1989) for each mm of carapace increment. The inner dotted line borders the 95 % confidence interval of averages of observations. The outer dotted line represents the 95 % prediction limit for further observations. The corresponding exponential regression is: $y = e^{-2.5144 + 0.145926\,x}$. The correlation is: r = 0.9244 (n = 4 481).

Uca thayeri had a fresh weight range of 0.6 - 6.5 g and a carapace width range between 4 and 31 mm with average values of 3.1 g and 24 mm (Fig. 39, 45). The sex ratio was constant at 1 : 1.03 (♀/♂, SD = 0.03) in all samples. The average carapace width at the age of maturation was 9 mm (SD = 3 mm). Two significant age classes were detected. Both were normal distributions (t-test: $\alpha = 0.05$, $d.f._1 = 500$; $d.f._2 = 500$) of identical statistical shape (χ^2-test: $\alpha = 0.05$) but highly significantly different averages (F-test: $\alpha = 0.01$) of 2.4 and 5.3 g, respectively.

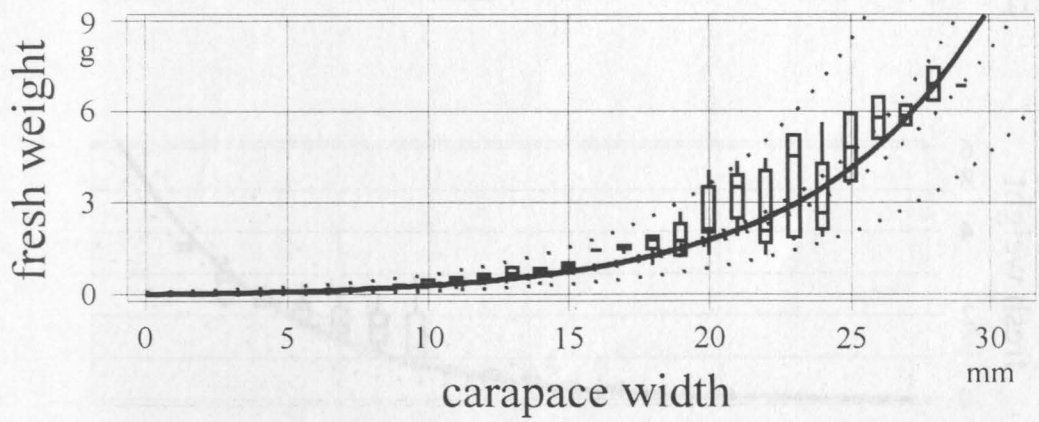

Fig. 45: Relationship between shell width (**x**) and fresh weight (**y**) of *Uca thayeri*. Morphometric field data from three transect sweep-sampling events conducted from June 1995 until February 1996 at the Canal de Sta. Cruz Estuary, Pernambuco, northeastern Brazil. Fresh weight data in width classes are presented as box-and-whisker plots (Frigge et *al.* 1989) for each mm of carapace increment. The inner dotted line borders the 95 % confidence interval of averages of observations. The outer dotted line represents the 95 % prediction limit for further observations. The regression: $y = e^{-2.6782 + 0.171105\,x}$. The correlation is: r = 0.9236 (n = 1 297).

The weight range of *Cardisoma guanhumi* was 4.9 - 141.1 gBFW and the animals had a carapace width range between 9 and 65 mm with average values of 72.2 gBFW and 51 mm (Fig. 40). The body fresh weights were normal distributed. The weight distribution was however composed of two normal distributions (t-test: $\alpha = 0.05$, $d.f._1 = 75$; $d.f._2 = 75$) of identical statistical shape (χ^2-test: $\alpha = 0.05$) but significantly different averages (F-test: $\alpha = 0.05$) of 67.5 gBFW for the females and 81.2 gBFW for the males. The body fresh weight of the male specimens was always higher than that of the female mate inside the same burrow. A significant mathematical identification of separate age classes was not possible. The sex ratio was 1 : 1.02 (♀/♂, SD = 0.01) in all samples. The fresh weight at the age of maturation of *C. guanhumi* could not be exactly determined because the females do not carry egg masses like the semi-terrestrial trophic key species of the present study. Based on the dissection of the animals' gonads the average carapace width at the age of maturation was assumed to be approximately 31 mm. The regression of the length-weight relationship led to the equation $y = e^{0.7072 + 0.0663\,x}$. The correlation was r = 0.972 (n = 163).

Ucides cordatus displayed a fresh weight range of 4.9 - 193.8 g and the animals had a carapace width range between 9 and 72 mm with average values s of 85.5 g and 56 mm (Fig. 40). Up to a value of approximately 130 gBFW, body fresh weight were normal distributed (t-test: $\alpha = 0.05$; $d.f._1 = 50$; $d.f._2 = 50$) in two distributions of identical statistical shape (χ^2-test: $\alpha = 0.05$) but significantly different averages (F-test: $\alpha = 0.05$) at 80.6 gBFW for the females and 88.6 gBFW for the male crabs. The body fresh weight of the male specimens was always higher than that of the females of same carapace width. Above a fresh weight of 130 g a frequency decline was detected (χ^2-test: $\alpha = 0.05$). A significant mathematical identification of separate age classes within the standing stock of *U. cordatus* was not possible. The sex ratio constant at 1 : 1.04 (♀/♂, SD = 0.01) in all samples. The carapace width at the age of maturation of the species could not be exactly determined because the females do not carry egg masses like the semi-terrestrial trophic key species of the present study. Based on the dissection of the animals' gonads it was assumed to be approximately 26 mm. The regression of the width-weight relationship led to $y = e^{0.4250 + 0.0694\,x}$. The correlation was r = 0.966 (n = 121).

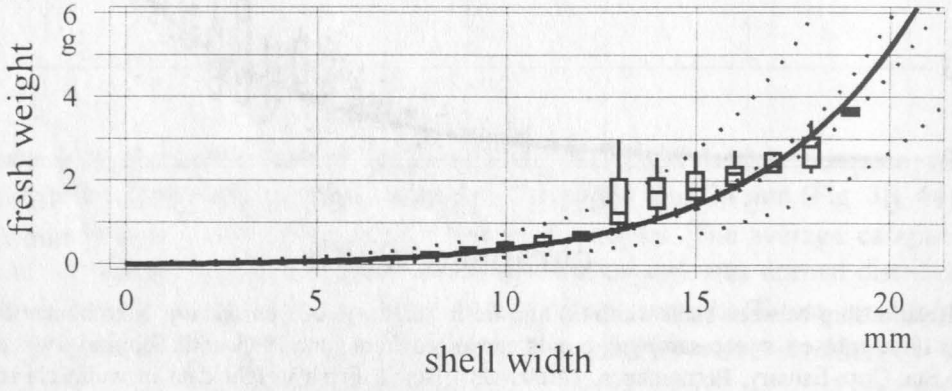

Fig. 46: Relationship between shell width (**x**) and fresh weight (**y**) (including shell) of *Littorina scabra angulifera*. Morphometric field data from three transect sweep-sampling events conducted from June 1995 until February 1996 at the Canal de Sta. Cruz Estuary, Pernambuco, northeastern Brazil. Fresh weight data in width classes are presented as box-and-whisker plots (Frigge et *al.* 1989) for each mm of carapace increment. The inner dotted line borders the 95 % confidence interval of averages of observations. The outer dotted line represents the 95 % prediction limit for further observations. The regression is: $y = e^{-0.0708 + 0.048802\,x}$. The correlation is: r = 0.982 (n = 4 518).

Littorina scabra angulifera had a range of fresh weight of 0.1 - 4.8 g (including shell) and a shell width between 4 and 19 mm with average values of 2.0 g and 13 mm (Fig. 40, 46). No significant age classes could be detected. From gonad dissection, the average shell width at the age of maturation was assumed to be 8 mm (SD = 1 mm). The fresh weight of the gastropods was normal distributed probably representing more than two age classes (t-test: $\alpha = 0.05$, $d.f._1 = 2\,000$; $d.f._2 = 2\,000$) in which the average fresh weight was 0.5 g and 1.9 g and the average shell width was 10 and 15 mm, respectively.

The weight range of *Sphoeroides testudineus* was 9.1 - 144.7 gBFW and the animals had a total length between 47 and 200 mm with average values of 75.5 gBFW and 151 mm (Fig. 40). The body fresh weights were normal distributed (t-test: $\alpha = 0.05$, d.f. = 403). A significant mathematical identification of all separate age classes was not possible. Only two non-neighboring age classes could be identified (t-test: $\alpha = 0.05$, $d.f._1 = 350$; $d.f._2 = 20$). Those age classes were specified by their respective average fresh weight of 57.1 g and 133.2 g and their average total body length of 139 and 180 mm, respectively. The average sex ratio was highly unbalanced at 1 : 0.15 (♀/♂, SD = 0.08) in all samples. The average fresh weight at the age of maturation was determined as 66 g (SD = 4 g) at an average total body length of 142 mm. The regression of the length-weight relationship led to the equation $y = e^{0.6541 + 0.0230\,x}$. The correlation was r = 0.948 (n = 403).

5 Discussion

5.1 General Behavior

The field experiments revealed a highly specialized general behavior of the species monitored in the mangal segment of the Canal de Sta. Cruz mangrove ecosystem. Prominent aut- and synecological behavioral differences were found that are dependent on the topographic position of the organisms within the three-dimensional ecosystem both horizontally and vertically. This three-dimensionality extends vertically from 1.5 m below substrate surface (which is the burrow depth of *Uca maracoani*) to a height of 7 m above ground which is the upper distribution limit of *Aratus pisonii* within the canopy of the mangrove trees. Horizontally the extended mangrove system stretches from the subtidal seaward mud plains with species exhibiting diurnal migrations into the channel region of the system like *Sphoeroides testudineus* or *Callinectes danae* to the supralittoral zone being dominated by brachiurans like the terrestrial *Cardisoma guanhumi* or the amphibious *Ucides cordatus*.

The mangrove rhizosphere creates an optimum habitat climate for crustacean life. Several authors found that pH and salinity of rhizospheres of mangroves are lower than of non-rhizosphere mud while the organic matter and moisture content are higher in the rhizosphere mud of the plants (Chowdherry et *al.* 1982; Andersen & Kristensen 1988; McKee et *al.* 1988; Nair et *al.* 1991). Even at shaded spots, water loss on land in was estimated as 0.43 g · 100 gFW^{-1} · h^{-1} for *Ucides cordatus* and as 0.53 g · 100 gFW^{-1} · h^{-1} for *Goniopsis cruentata* (Martelo & Zanders 1986; Santos et *al.* 1986).

The general behavior of all target species in the present study showed specific adaptations mainly caused by two factors, the effective utilization of particular distributional or nutritional niches and the avoidance of predation. The entire three-dimensional extension as well as the entire daily light cycle was continuously or temporarily filled with activities by particular species. Nocturnal activity was exhibited by the species *Cardisoma guanhumi* and *Ucides cordatus*. During the daytime, the animals rested in their burrows. This behavior is typical for crabs living at or above the transition area between the upper intertidal and the coconut-tree zone (Zanders & Martelo 1984; Santos et *al.* 1985, 1986; Turrin et *al.* 1992; Harris et *al.* 1992, 1993). It has been interpreted as an adaptation to avoid avian and mammal predation during the daytime (Formanowicz & Brodie 1988; Teixeira 1994). The groupwise foraging observed for *C. guanhumi* enhances the chance of a single animal to be warned of potential predators. The at least temporary binding of couples minimizes the predation risk during extensive and continuous mating behavior. At the same time, it increases the probability of successful mating of the animals.

Neighboring the distribution range of *Cardisoma guanhumi* in seaward direction, *Ucides cordatus* builds its burrows into the slopes and terraces separating the intertidal from the coconut-tree zone. The very limited width of this distribution belt as well as the less expressed migration behavior compared to *C. guanhumi* ensure a contact frequency between the sexes sufficient for the reproduction of *U. cordatus*. Inhabiting the burrows in couples is thus not necessary for the species. A wide range of salinity tolerance of 2-34 S (Harris et *al.* 1992, 1993; Queiroz et *al.* 1992) as well as the large branchial chamber for air breathing (Santos et *al.* 1985) enable the species to inhabit the extreme environment of the supralittoral zone.

The two species of fiddler crabs, *Uca maracoani* and *U. thayeri*, show distinct behavioral differences. Their distribution zones were completely separated with *U. maracoani* living on the muddy plains and *U. thayeri* inhabiting the upper sandy intertidal areas. *U. maracoani* specimens showed a more individual social behavior expressed by a certain territoriality of the males and a construction of solitary burrows. Having its own burrow, each individual is responsible for its survival during high tide. The interconnected burrows of *U. thayeri* require a social responsibility because all openings have to be closed to ensure the survival of the whole group of animals living within one system of burrows. In general, territoriality and consequently intraspecific aggression is less expressed in *U. thayeri*. Avian predation pressure on the species (Bildstein et *al.* 1989; Pennycuick & De Santo 1989; Thibault & McNeil 1994) is considerably reduced because the animals can retreat into any burrow opening within their immediate reach. This allows a substantial expansion of the individual feeding area of *U. thayeri* the animals. This social behavior of the species may be a result of the less favorable environmental conditions in the upper intertidal zone compared to the distribution zone of *U. maracoani*. During low tides, the distribution areas of *U. maracoani* and *U. thayeri* were almost exclusively inhabited by these two species. The invasion of other species during high tides and the resulting temporarily isolated utilization of each fiddler crab's habitat adds to the ecological complexity of the intertidal mangrove zone. Almost all animal species entering the two zones are potential predators of the two fiddler crab species, but none of the predators showed any kind of direct substrate utilization.

The genus *Uca* has by far received the most extensive scientific interest of all intertidal brachiurian crustaceans. However, few literature exists on ecological and particularly on synecological aspects of the fiddler crabs. The genus has proven very potent concerning the research on complex behavioral communication of invertebrate animals (Murai et *al.* 1987; Christy 1988; Takeda & Murai 1993; Christy & Schober 1994) and on the response to predation pressure in general (Frix et *al.* 1991). Avian predation on the crabs has also been studied to obtain information on the life cycles of nematode parasites. *Uca* serves as the intermediate host to the larvae of some nematode species infesting tropical birds (Dunn et *al.* 1990; Wong & Anderson 1990). In the present study, the specific position of the species within the mangrove ecosystem and within the food web of the system has been elucidated for the first time.

The blue crab *Callinectes danae* and the pufferfish *Sphoeroides testudineus* show a general behavior that is mainly determined by their predation on other species in the mangal area. Both species are restricted to the aquatic zones and consequently their activity is intensified during the high tides. During low tides, the majority of the *C. danae* specimens remains in the tidal creeks and puddles, particularly those individuals in the upper littoral region. No significant differences were observed between the total biomass of the species during high and low tides. Del-Castillo et *al.* (1992) observed a comparable behavior of *C. arcuatus* and *C. bellicosus* at the Mexican Pacific coast. The distribution and population structure of *C. sapidus*, *C. bocourti*, *C. danae*, and *C. ornatus* showed reproduction induced migrations at Terminos Lagoon, Atlantic coast, Mexico (Roman-Contreras 1986). It is concluded that the biomass exchange of *C. danae* with the Canal de Sta. Cruz channel region has to be a long-term process and is not governed by daily cycles. *S. testudineus* completely leaves the mangal zone during low tide period. This behavior is typical for most fish species in the area (Nogueira Paranagua & Eskinazi Leca 1985). It is caused by the lower tolerance of high water temperatures, reduced oxygen levels and extensive salinity fluctuations of the fish compared to most of the invertebrate animals in the same intertidal area. Marques et *al.* (1992) identified the reduction of physiological digestion processes of fish as the main cause for the avoidance of the mangrove littoral zone during low tides. During high tides, *S. testudineus* prefers the

regions of mangrove roots over the open water areas. *C. danae* does not show any particular preference and can be encountered predating at all zones in the mangrove ecosystem. In contrast to the present study, Roman-Contreras (1986) observed no significant differences of the day and nighttime activity levels of *C. danae* at Terminos Lagoon, Mexico. At the Canal de Sta. Cruz, *C. danae* and *S. testudineus* have significantly higher activity levels during the daytime which may be due to their primarily visual target pick-up (Johnson 1980; Cameron 1985). The reduction of activity is however more expressed in *S. testudineus*.

Goniopsis cruentata is the benthic species with the widest range of behavioral adaptations in the mangal ecosystem of the Canal de Sta. Cruz. The main activity period of the species is during the daytime. Tidal rhythms do not have significant influence on the overall activity level but on the type of activity. With the exception of the muddy and the sandy plains, which are inhabited by *Uca maracoani* and *U. thayeri*, *G. cruentata* can be found at any location of the mangrove ecosystem. Hard substrates in general and the roots of *Rhizophora mangle* in particular are the preferred distribution areas of the species. Although Teixeira (1994) focused on fish predation on the species, his results support a generalization of this distribution pattern. *G. cruentata* vertically expands its distribution range by climbing the mangrove trees while predating for *Aratus pisonii*. At the same time, this behavior serves as an escape response to the predation by *Callinectes danae* and *Sphoeroides testudineus*. A determination of the importance of predation escape in relation to active predation was not possible for *G. cruentata*. The species does not show intense territoriality and specimens of the same size may share one single mangrove root at a high density. Within the complex root thicket, the red coloration of the species enhances the perceptibility of the individuals to each other and may be of importance during mating behavior. A high sensitivity for the red light spectrum was reported by Fein & Szuts (1982) for *G. cruentata*. The toleration of high local densities is contradictory to the slight cannibalism tendency of the species observed during the feeding experiments which will be discussed later.

Aratus pisonii strongly prefers the mangrove canopy and is rarely found on the mangrove floor. Its behavior is predominantly determined by its feeding pattern in the lower and its escape behavior into the upper mangal regions. Because of its small size and the morphological adaptations of its legs to a life within the mangrove canopy, *A. pisonii* is able to survive at a habitat dominated by potential predators. Analyses of the distribution and vertical migrations of *A. pisonii* were conducted by Conde & Díaz (1989a, 1989c, 1992a, 1992b), by Chow & Bacon (1992), and by Del-Castillo et *al.* (1992). Their descriptions match the findings of the present study. A comparable distribution pattern within the mangrove canopy was observed for the grapsid *Sesarma leptosoma* at East Africa (Vannini & Ruwa 1994). Although *Goniopsis cruentata* is also able to climb the trees, the individuals have to move very slow and they have no access to the upper canopy regions because of their weight. Under normal circumstances, *G. cruentata* has great difficulties to catch *A. pisonii*. As a final escape response, *A. pisonii* jumps off the tree as soon as the red mangrove crab traverses a critical distance to the animal.

The general behavior of the adult *Littorina scabra angulifera* and their daily vertical migration in particular is correlated to the tidal rhythms and is dependent on food availability. The snails are exclusively living on mangrove trees and move up and down the stems and roots between 0.4 m and 2.0 m above ground or water level. Juvenile *L.s.angulifera* are reported to live intertidally (Hughes & Jones 1985). The reason of the preference of *Rhizophora mangle* over *Avicennia marina* may be the larger surface area of the species' roots and the consequential larger food availability (Murty & Rao 1977). Physical environmental factors can be excluded because of the large tolerance of the species against those factors (Underwood 1979; Pinto & Ledesma 1986). A correlation between the coloration of

the shells and the vertical position of the animals was not observed. Hughes & Jones (1985) however, found more yellow shells in the foliage and more brown shells on the trunks of mangrove trees at Queensland, Australia. *L.s.angulifera* avoids its main predators *Sphoeroides testudineus* and *Callinectes danae* by keeping a minimum distance of 0.4 m to the water level. As long as they are firmly attached to the tree, *Goniopsis cruentata*, the third predator on *L.s.angulifera*, is however not able to crush the hard shell of the animals. The crab can open the shell only by chipping away the material starting from the opening. While attached to the tree, *L.s.angulifera* is not recognized as prey by *G. cruentata* although the crab should be capable of removing the snail from the substrate. The crabs may not be able to detect the snail because of a chemical camouflage created by the epiphyte growth on the shell's surface.

5.2 Food Web Analysis and Turn-Over Rates

Not surprising, in some way, either via the direct food chain or indirectly via detrital or other chemical processes, all species monitored in the course of the project have shown ecological and, more important to the aim of the study, nutritional interrelationships. It was possible to qualify and quantify most of these pathways and to develop a basic integrated model of the relative nutrient flux through the mangal segment of the Canal de Sta. Cruz mangrove ecosystem.

5.2.1 General Feeding Behavior

The entire spectrum of 24 potential experimental food sources was accepted by either one of the nine target species (Table 8) during the initial testing of food acceptance. With the exception of *Uca maracoani*, *U. thayeri*, and *Littorina scabra angulifera*, no species displayed a restriction to one or two food sources. Of all species tested *Goniopsis cruentata* showed the most evolved generalism concerning the utilization of potential food sources in the Canal de Sta. Cruz mangal zone. This result supports the hypothetical central position of the species within the local food web. The preferred food source of *G. cruentata* is *Aratus pisonii*. The similar selectivity grade for the fiddler crab species originates from the artificial character of the experiment design during the initial testing of food sources. *U. maracoani* and *U. thayeri* rarely encounter *G. cruentata* under natural conditions as was established during the analysis of the distribution of biomass in the mangrove ecosystem.

The exceptional specialization of the feeding behavior of *Uca maracoani* and *U. thayeri* had to be expected, although feeding experiments on the particular species were never conducted. Numerous experiments on the eyestalk factor, a term defined for the integrate biochemical effects caused by the endocrine gland in this area, have been studied using different species of the genus *Uca* (Rao & Rao 1982; Hopkins 1986, 1988, 1992; Kleinholz et *al.* 1986; Kulkkarni & Fingerman 1987; Dircksen et *al.* 1988; Mangerich et *al.* 1987; Rao & Riehm 1988, 1989; Lueschen et *al.* 1991; Rittschof & Buswell 1989; Sears & Rittschof 1991). Its relation to feeding behavior, neuropeptides and other hormones, there chemical structure and capacities were analyzed. Intensive research on the fiddler crab species *U. pugnax* (Palmer 1988; Weissburg 1991, 1992, 1993), on *U. pugilator* (Sears & Rittschof 1991; O'Connor 1992), on the European fiddler crab, *U. tangeri* (Hagen 1987; Wolfrath 1992, 1993), and other species (Dye & Lasiak 1987; Rittschof & Biswell 1989; Genoni 1991) has never detected any other food sources than the algal and microbial substrate surface layer.

The acceptance of *Aratus pisonii* for animal carrion (Table 8) was surprising but supports the brief description of reduced predation behavior and even cannibalism by the species published by Beever et *al.* (1979). The strict carnivory of *Callinectes danae* was already described by Stoner & Buchanan (1990) and Netto & Da Cunha Lana (1994). The observed rejection of animals of its own species during the present study leads to the assumption of a behavioral suppression mechanism of the usually highly aggressive species in order to avoid cannibalism. This behavior seems to be advantageous concerning the temporal high density of the holoaquatic animals in puddles and creeks during low tide periods.

The observed food selectivity of *Littorina scabra angulifera* for epiphytic algae on *Rhizophora mangle* (Table 8) supports the results by Kohlmeyer & Bebout (1986). The additional feeding on the epidermal tissue of *R. mangle* observed by the authors had to be tested during later carbon isotopic experiments of the present study. No information existed so far on the feeding pattern of *Sphoeroides testudineus*. The fish species proved to be almost exclusively carnivorous and to prefer small and soft-shelled rather defenseless animals over armed or larger animal species. The broad spectrum of potential food sources of *Cardisoma guanhumi* and *Ucides cordatus* has to be regarded as theoretical because the animals rarely come into contact to most of the sources tested. As for all other target species, it is however very interesting to get an idea of the individual range of alimentary opportunism possible to the crabs. The further experiments of the present study had to demonstrate whether the target species display similar selectivities under close-to natural conditions.

5.2.2 24h-Experiments

Several authors conducted feeding experiments based on mathematical models for the ingestion and evacuation rates of fish and invertebrate species (Downing & El-Zahr 1987; Getachew 1989; Sarda & Valladares 1990). The applicability of 24h-experiments in combination with a software-based calculation of food requirements has however only recently been tested for invertebrate organisms. Wiedemeyer (1993, 1994) successfully analyzed the daily and annual food requirements of three bioturbating holothurian species at southern Japan.

During the present study, the applicability of a software-based analysis to crustacean and gastropod digestive physiology was confirmed for the first time. The direct comparison of the computed gastro-intestinal evacuation rates ($ER_{dep.}$; Table 1) to the respective parameters derived from the starvation experiments (Fig. 22, 23; Table 10) revealed no significant differences between the two methodical approaches. Anticipated methodical problems caused by the dissimilar structure and function of invertebrate organs responsible for ingestion, digestion and absorption compared to fish organs (Gabaudan 1987) were not detected. It is concluded that the software MAXIMS (Jarre 1990; Jarre-Teichmann 1992) allows the estimation of daily ration and population food consumption of invertebrates based on a diel cycle of stomach content weights. Ingestion and evacuation rates as well as feeding times can be estimated simultaneously using nonlinear least-squares algorithms. The food consumption of the invertebrate target populations can be determined in combination with the respective biomass data. During the present study, the representative sampling of body weight classes already during the 24h-experiments made the integration of weight-specific differences of food requirements (Zalachowski 1985) obsolete.

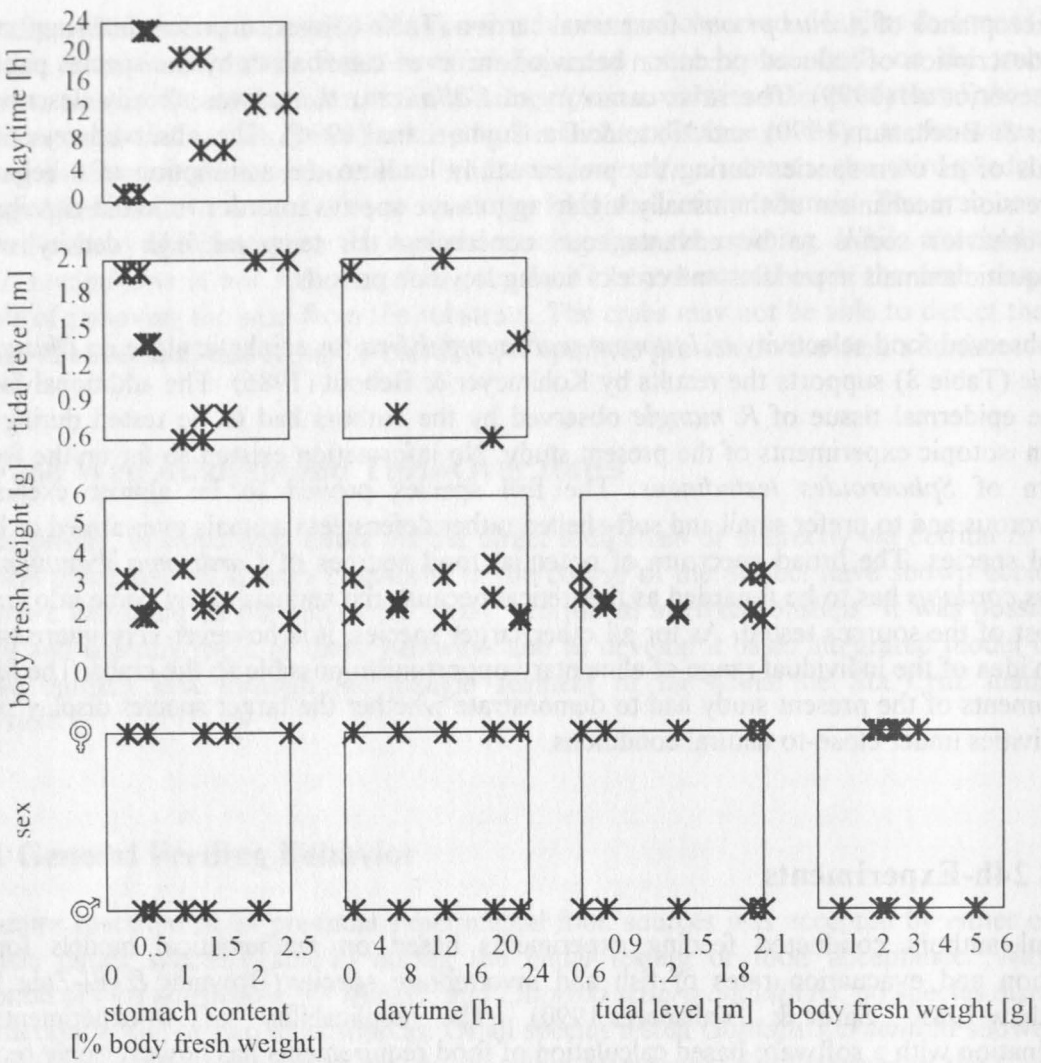

Fig. 47: Simplified presentation of the relationships between the relative weight of the gastro-intestinal content of *Aratus pisonii*, two environmental factors, and two biological measures during a 24h-field experiment conducted in the benthic mangal segment of the mangrove ecosystem of the Canal de Sta. Cruz, Itamaracá Island, northeastern Brazil. The crosses represent different numbers of pooled observations around local averages. The gastro-intestinal content is presented as the average percent relationship of content dry weights to the specimen's fresh body weights at specific daytimes (n = 176 specimens). ● = ♀♀; □ = ♂♂.

The results from each 24h-field and tank experiment were checked for individual influences of the abiotic environmental factors tidal level and daytime and the biological factors body fresh weight BFW and sex on the daily feeding routine of the particular target species. An exemplary diagram for the ERS_1-field experiment on the target species *Aratus pisonii* is presented as Fig. 47. Several kinds of information can be extracted from the diagram, for example: 1) During all daytimes and at all tidal levels, the sampling procedure was representative concerning the entire range of "BFW" of *A. pisonii*. 2) "Sex" had a minor influence on the feeding routine showing a reduced range of gastro-intestinal filling levels for the male compared to the female specimens. 3) The environmental factors "tidal level" and "daytime" had the strongest influence on the daily feeding behavior of *A. pisonii*. 4) The most important finding was that "BFW" had no influence on the relative weight of the gastro-

intestinal content and notable age dependent quantitative differences of food requirements are probably not existent for the species. However, the existence of qualitative differences remains to be analyzed during future experiments. The unbalanced representation of the entire BFW range of the female animals was thus not influential on the gastro-intestinal filling levels as well. 1, 3 and 4) were observed for all target species during all experiments and were confirmed through statistical testing specified within the text paragraphs on the particular species. The influence of the animals' sex on the gastro-intestinal filling levels varied between target species.

All target species showed distinct daily feeding periods depending on the light cycle and/ or on the tidal cycles in the area. On the diurnal scale however, foraging and thus biomass conversion caused by the animals was higher during the period of daylight. *Callinectes danae*, *Aratus pisonii* and *Littorina scabra angulifera* were the only species that showed feeding activity during the night (Fig. 12, 9, 13). The nighttime activity levels of *C. danae* and *A. pisonii* however were low compared to their activity during the day. Feeding of *C. danae* during the night was observed before and may reduce the anticipated exclusive dependency of the predatory crab species on an optical target pick-up. Nye (1990) used ultrasonic transmitters to measure feeding activity of free-ranging blue crabs at central Chesapeake Bay, USA. The results showed that the crabs feed throughout a 24-hour period. From the present study it can be concluded *C. danae* is probably also dependent on a sufficient water level during high tides and does not feed while restricted to tidal creeks and puddles during low tides. The feeding activity of *A. pisonii* may be a behavioral response to the reduced predation pressure within the mangrove canopy caused by the comparatively inactive *Goniopsis cruentata* during the night. The observed reduced nighttime feeding of the latter species during low tides (Fig. 8) took place on the mangrove floor. *L.s.angulifera* has no need to reduce feeding behavior during the night because the species' main predator *Sphoeroides testudineus* shows only very limited feeding activity during this period (Fig. 14). The fiddler crabs *Uca maracoani* and *U. thayeri* displayed no feeding when retreated into their burrows (Fig. 10, 11). During high tides, this behavior reduces the critical depletion of the limited oxygen supply.

The daily dry weight food rations DR_{DW} of the target species were very dissimilar (Table 9) and may be influenced by nutrient contents of particular food sources as well as by general activity levels of the species. The predatory species *Sphoeroides testudineus* (DR_{DW} = 3.3 %BFW), *Callinectes danae* (DR_{DW} = 3.4 %BFW) and the facultative predatory *Goniopsis cruentata* (DR_{DW} = 2.6 %BFW) had low daily ratios compared to the herbivorous, detrivorous or omnivorous species. The comparatively low daily food ratio of *Aratus pisonii* (DR_{DW} = 3.6 %BFW) is surprising with respect to the intense daily migration behavior and constant motility of the species. The low food requirements of *Littorina scabra angulifera* (DR_{DW} = 2.4 %BFW) are sufficient for the comparatively inactive gastropod species. As expected, the fiddler crabs showed highest daily requirements. The 2.5-fold higher daily food requirement of *Uca thayeri* (DR_{DW} = 21.4 %BFW) compared to *U. maracoani* (DR_{DW} = 8.8 %BFW) is probably caused by the much lower nutrient content of the substrate surface layer in the distributional range of the species. Corresponding results were reported by Wolfrath (1992, 1993) concerning and by Wiedemeyer (1992; 1993) concerning bioturbating tropical holothurians. *U. tangeri*. Klaassen & Ens (1993) presented a detailed study on the distribution pattern of different size classes of *Uca tangeri* in correlation to several environmental factors, particularly the average substrate grain diameter.

Goniopsis cruentata (Fig. 8, 15) and *Uca maracoani* (Fig. 10, 17) showed significantly different daily feeding cycles and daily food requirements between sexes. These findings from the field were confirmed during the corresponding tank experiments. The reason for these

differences are speculative for *G. cruentata*. No reproduction peaks were observed during the sampling periods. The female crabs may have a food composition of a lower energy content. With respect to their intensified feeding behavior during high tides (Fig. 8) a higher percentage of mangrove material is most probable. However, due to the limited number of isotope analyses of stomach contents, sex dependent qualitative food differences between sexes were not analyzed during the present study.

The different quantitative food requirements of the male and female *Uca maracoani* are probably caused by dissimilar energy requirements for reproduction. Reinsel (1991) described that female *U. pugilator* carrying eggs showed clearly reduced feeding behavior. The intensity of the feeding activity of *U. maracoani* during particular daytimes and in terms of consumption per time is influenced by its sex-specific territorial behavior. Particularly during a two-hour period around low tide, the male *U. maracoani* were more occupied by waving activity, territory defense and mating behavior than by the ingestion of surface substrate. During a former study on *U. panacea* the percentage of male individuals involved in construction of burrows was always found higher than that of the females (Caravello & Cameron 1991). Surprisingly the males do not compensate this reduced feeding during other periods. Less intense feeding of male crabs of the genus *Uca* has been described several times. Conclusive causalities have however not jet been found. Two feeding activity peaks per day were found in *U. pugnax* and *U. pugilator* (Palmer 1988). These peaks showed significant differences in period and intensity. This finding can be confirmed for *U. maracoani*, although the observed second feeding period during ERS_2 was very weak.

The feeding activity of the fiddler crabs in the present study is regulated by an internal clock tuned by the tidal rhythms in the area. From the literature, a direct influence of the lunar phase has to be rejected. Palmer (1989a) conducted experiments where fiddler crabs were translocateed to artificial constant tidal conditions. The activity rhythm of the sample abandoned the phase of the tidal cycle influencing the crabs activity. *Uca minax* displayed persistent, circalunidian rhythms of its locomotor-activity, i.e., cycles which were approximately the length of the lunar day (Palmer 1989b). The same endocrinological clock type may govern both circadian and circa-lunar rhythms in *Uca pugilator*. Animals being injected deuterium-oxide and/or azadirachtin showed simultaneous arrhythmic behavior regarding both time scales (Palmer 1990). On the other hand, the feeding intensity of fiddler crabs is to some extent mediated by dactyl chemoreceptors and stimulated by hexose sugars (Lueschen et *al.* 1991; Reinsel 1991; Sears & Rittschof 1991; Sears et *al.* 1991; Hopkins 1992). The eyestalks are directly involved in vision and overall neural integration as well as with chemosensory and metabolic pathways associated with feeding in *Uca minax*, *U. pugnax* and *U. pugilator* (Rittschof & Biswell 1989). Weissburg (1991) contributed the smaller quantity of sediment ingested by male *U. pugnax* compared to the female animals to a lower digestive speed of the sex an the consequential higher efficiency of nutrient extraction. The present author agrees with the conclusion, but in the vice-versa direction. Surprisingly, two years later, the same author (Weissburg 1992) described that female *U. pugnax* extract more chlorophyll-a from the surface sediments than male animals of the same species. At chlorophyll-a concentrations of 50-200 µg $Chl_a \cdot gDW\ sediment^{-1}$ the animals extract an average of 50- 100 µg $Chl_a \cdot g\ DW$ sediment. With decreasing chlorophyll-a concentrations in the sediment, the relative extraction capacity between females and males increases from 1.3 : 1 to 2.3 : 1.

Aratus pisonii showed a complex structure of daily feeding periods (Fig. 9). In addition to one main feeding period during daylight high tides, the animals displayed short but intense feeding periods during daylight peak low tides. In combination with the general field observations it is

concluded that *A. pisonii* feeds within the mangrove canopy during high tides but prefers the algal layer on the mangrove stems and roots during low tides. This food source of probably higher quality to the species is accessible only during low tide. This conclusion is supported by the non-appearance of secondary feeding periods during the 24h-tank experiments when this particular diversity of food sources was not adequately installed. *Callinectes danae* was the target species showing the smallest sex-dependent differences of relative weight of the gastro-intestinal contents (Fig. 12). The filling levels were almost identical throughout the entire 24h-periods. This finding supports the conclusion that sex-dependent differences observed for other target species were caused by different energy requirements for reproduction. Reproductive stages of *C. danae* were never observed in the mangal area during the entire study. The two daily feeding periods of *Littorina scabra angulifera* were exclusively dependent on the tidal cycle and always happened during low tides. This feeding pattern ensures both the sufficient provision of food at the intertidal root and stem segments of the mangrove trees and the protection against predation by *Sphoeroides testudineus*.

The results from all 24h-field experiments were supported or confirmed by the additional 24h-tank experiments conducted on each species. As a consequence, qualitative and quantitative experiments on the daily feeding behavior of crustaceans within mangrove ecosystems may be conducted as tank or field trials depending on the scientific aim and local logistics. Tank experiments will also allow the alteration of selected environmental factors and the analysis of their influence on the periodicity and intensity of feeding. A conclusion concerning benthic fish and gastropod species seems unfeasible with respect to the limited number of experiments during the present study.

5.2.3 Starvation Experiments

The starvation experiments clearly supported the methodical application of the otherwise software-based calculation of food requirements from 24h-experiments (Table 10). The observed maximum deviation factor between the two experiment types of 1.39 for the daily dry-weight food ratio DR_{DW} of *Goniopsis cruentata* may have been caused by differences of food compositions in the field and during the tank experiments. The wide food range of the omnivorous species may not have been matched adequately. The slightly lower evacuation rates of the herbivorous as well as the higher evacuation rates of the carnivorous species during the starvation experiments have been observed before for these feeding regimes (Gabaudan 1986; Getachew 1989; Sarda & Valladares 1990). They have been attributed to the usually lower digestive speed of herbivorous organisms and the less expressed influence of the gastro-intestinal filling level on evacuation rates (Fields & Ellington 1991, 1992).

5.2.4 Stable Isotope Ratios

The method of stable isotopes has been successfully applied to a high number of aquatic ecosystems worldwide (Macko et *al.* 1984; Gleason 1986; Forsberg et *al.* 1993; Simenstad et *al.* 1993; Fry & Quiñones 1994; Heminga et *al.* 1994; Matsuura & Wada 1994; Risk et *al.* 1994; Wiedemeyer & Schwamborn 1996). Extensive stable isotope studies have also been conducted on selected species in mangrove food webs (Odum & Heald 1972;

Haines 1976a, 1976b; Haines & Montague 1979; Rodelli et *al.* 1984; Zieman et *al.* 1984 Harrigan et *al.* 1989; Newell et *al.* 1995).

During the present study, the wide range of the $\delta^{13}C$-values of the trophic key species' muscle tissues (-10.1 to -26.2 ‰ PDB) allowed conclusions on qualitative nutritional interactions at a high resolution. During the research period, the oscillations of the monthly $\delta^{13}C$-values in the field were small for all species except for *Aratus pisonii* and *Uca maracoani* (Fig. 24, 26, 28; Table 11). The $\delta^{13}C$-values of the muscle tissues were always higher than the values of the corresponding integrate stomach contents. Spiro et *al.* (1986) described increasing $\delta^{13}C$-values in the path of assimilation of body biomass. Particular biochemical assimilation processes prefer heavier ^{13}C over the lighter ^{12}C isotopes. A conclusive biochemical explanation has not yet been discovered but dissimilar bound affinities of enzymes to organic molecules are discussed. Elevated $\delta^{13}C$-values of body tissue have also been interpreted as a result of an unbalanced oxidation of body-CO_2 (McConnaughey & McRoy 1979). However, a coupled analysis of $\delta^{13}C$ and $\delta^{18}O$-values did not support this hypothesis. Due to the less complex physiology of the organisms, almost all research on the fractionation of carbon isotopes has been conducted on phytoplankton. The fractionation of atmospheric carbon isotopes by phytoplankton is strongly correlated to the activity of 1,5-bisphosphate carboxylase, phosphoenolpyruvate and phosphoenolpyruvat-carboxylase (Descolas-Gros 1985; Descolas-Gros & Fontugne 1988; Falkowski 1991). The phytoplankton carbon metabolism has been identified as a main factor governing variations in the stable isotopic composition of organic matter in the euphotic layer of the Antarctic Indian and of the Atlantic Ocean (Fontugne et *al.* 1991). Interrelationships between light intensity, RUBISCO activity and $\delta^{13}C$ as well as an effect of the meridional temperature gradient were also verified.

A very interesting observation during the present study was the almost identical average $\delta^{13}C$-values of the muscle tissue of the herbivorous crab *Aratus pisonii* and the gastropod *Littorina scabra angulifera* and between the carnivorous crab *Callinectes danae* and the fish *Sphoeroides testudineus* (Table 11). A similarity of muscle carbon isotope values this obvious has never been reported for two organisms from completely different taxa inhabiting identical or neighboring habitats. This particular finding supports the study hypothesis of a strong and direct influence of food source $\delta^{13}C$-values on consumer tissue. Since very little carbon isotope discrimination occurs in aerobic food chains subsequent to the primary production process (Schein et *al.* 1991), the two pairs of species probably each feed upon the same food sources. As expected, a conclusive grouping of the remaining detrivorous or herbivorous trophic key species was not feasible. The combined discussion of ^{13}C-values of feces and detritus is very difficult in the first place because bacteria reduce the sulfur compounds while obtaining the CO_2 needed from the water body. This increases the amount of ^{12}C in the detritus (Peterson et *al.* 1980).

The temporal delay of correlations between the ^{13}C-values of the stomach contents and the muscle tissue observed for some consumers allowed an assessment of the assimilation speed of body muscle tissue from ingested food. While *Ucides cordatus* (Table 11; Fig. 24, 30) and the gastropod species *Littorina scabra angulifera* (Fig. 33) showed no correlation at all, *Uca maracoani* (Fig. 24, 28), *U. thayeri* (Fig. 24, 29), *Cardisoma guanhumi* (Fig. 24, 31), *Callinectes danae* (Fig. 24, 27) and the fish *Sphoeroides testudineus* (Fig. 32) showed contemporary correlations. A temporal delay of one month was observed for *Goniopsis cruentata* (Fig. 24, 25) and the delay for *Aratus pisonii* (Fig. 24, 26) was the largest at three months. A conclusive interpretation of these differences is not possible because the three animal groups belong to very different zoological taxa and food acceptances were not

comparable. The three-months delay of the correlation of values of *A. pisonii* seems not explainable on a biochemical basis and may be an artifact although it was highly significant.

The tests of correlation between the ^{13}C-values of the consumers' single or combined food sources and stomach contents revealed first insights into the structure of particular food webs. The stepwise exclusion of particular food sources led to initial assessments of their relative importance to the nutrition of a particular consumer. The later combination of the results from those monthly field samplings for isotope values with the monodietary tank experiments would further clarify the nutritional pathways.

The wide range of food sources accepted by *Goniopsis cruentata* during the initial field experiments (Table 8) on general feeding behavior found its reflection in the central position of the monthly ^{13}C-values of the species' muscle tissue (Table 11; Fig. 24, 25). Compared to *G. cruentata*, *Aratus pisonii* showed strong oscillations of its monthly stomach and muscle tissue ^{13}C-values that can only be explained by a significant selectivity for benthic and epiphytic phaeophyte and rhodophyte algae during peak daylight low tides. This food source was the only one showing comparable monthly oscillations of ^{13}C-values. A dependency of the crab species on this particular food source was already concluded by Beever et *al.* (1979). The monthly ^{13}C-values of the stomach content of *Callinectes danae* were almost similar to the values of the muscle tissue of *A. pisonii*. It can be expected that the other food sources of the blue crab are probably of minor importance. Stoner & Buchanan (1990) reported the preference of *C. danae* for mangrove crabs, but did not detect a high selectivity for *A. pisonii*.

As expected from the exclusive selectivity for the particular food source, the direct correlation between the ^{13}C-values of the surface sediment layer, the stomach content and the muscle tissue of *Uca maracoani* and *U. thayeri* was highly significant (Table 11; Fig. 24, 25). The contemporary character of all correlations however was an interesting new aspect. A future determination of the different components within the detrital material seems to be advisable in order to gather more information on a possible nutritional selectivity of fiddler crabs. The deposit-feeding worm *Capitella spp.* exhibited distinctive $\delta^{13}C$-values of its tissue depending on the type of organic matter within the sediment (Spies et *al.* 1989). The comparison of the monthly carbon isotope values of *Ucides cordatus* and *Cardisoma guanhumi* revealed no obvious correlations between their stomach contents and any single food source tested. However, all food sources pooled had a significant correlation. This finding supports the assumed opportunistic feeding pattern and, at the same time, the low selectivity of the two scavenging species. An important finding is that both species by far exceed the range of $\delta^{13}C$-values for benthic invertebrates described by Spiro et *al.* (1986). During his worldwide studies, the author found $\delta^{13}C$-values of benthic invertebrates between -16 to -20 ‰ PDB. Invertebrates living on anaerobe sediments showed more negative values e.g. -23 to -31 ‰ PDB for bivalves and -35 to -46 ‰ PDB for pogonophores. It can thus be concluded that terrestrial plant food sources have a positive effect on the $\delta^{13}C$-values of the muscle tissue of *U. cordatus* and *C. guanhumi*.

Concerning the food selectivity of *Sphoeroides testudineus* the most interesting finding was that *Aratus pisonii* and *Uca maracoani* play probably no distinct role in the nutrition of the fish species in the Canal de Sta. Cruz mangal. A low appearance of *U. maracoani* was expected because of the temporal separation of habitat utilization of the prey and predator species. The missing of *A. pisonii* however was surprising although the absence of *Aratus* fragments during the initial macroscopic analyses of the stomach contents of *S. testudineus* (Plate 2.8) had already indicated this situation. The monthly analyses of the carbon isotopes also led to the exclusion of the food source "sediment surface layer" from the food range of the gastropod

Littorina scabra angulifera. The two most important food sources of the species were benthic and epiphytic phaeophytes and rhodophytes and mangrove leaves.

The trophic grouping (Fig. 34, 35) of the trophic key species based on the determination of the average $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$-values of all animal and plant target species, as well as of the additional food sources tested, provided valuable additional information on the trophic distances within the food web (Table 12, 13). Two distinct groups of small trophic distances ($\delta^{15}N$-values) were formed by *Callinectes danae* and *Goniopsis cruentata* as well as by *Uca maracoani*, *U. thayeri*, *Ucides cordatus*, and *Cardisoma guanhumi* (Fig. 34). *Aratus pisonii* and the gastropod *Littorina scabra angulifera* did not belong to any trophic group. The very close distance of *G. cruentata* and *C. danae* is surprising with respect to the mixed diet of the former species in contrast to the strictly carnivorous feeding of the latter. The much higher trophic level of the fish *Sphoeroides testudineus* is typical. However, here, the trophic distance to *C. danae* sees to be too large when compared to the distance between the fish and the other crab species. The relatively large trophic distance between *A. pisonii* and *L.s.angulifera* was not expected with respect to the identification of strict herbivory for both species based on the other experiment types. The author concludes that the identification of different trophic levels between species from different animal orders may not be workable due to general biochemical differences during the assimilation of body tissue from food nutrients.

Littorina scabra angulifera represented the by far lowest trophic level of all animal species. The gastropod species showed $\delta^{15}N$-values that were even lower than those of the plant food sources. An explanation for this may be the existence of food sources of *L.s.angulifera* that were lower $\delta^{15}N$-values, but were not tested during the present study. The average $\delta^{15}N$-value of the stomach content of the species was 2.6 ‰ ATMN (Table 12) supporting this hypothesis. The almost identical $\delta^{13}C$-values of *L.s.angulifera* and *Aratus pisonii* indicate very similar food sources. The close trophic grouping of the detrivorous *Ucides cordatus*, *Cardisoma guanhumi* and the mangrove tree crab, *A. pisonii*, is surprising. Although their food sources are quite different ($\delta^{13}C$-values), their trophic levels within the benthic food web of the mangal segment of the Canal de Sta. Cruz ($\delta^{15}N$-values) are not.

The analysis of the $\delta^{15}N$-values of the plant food sources did not add to the information already obtained through the analyses of the $\delta^{13}C$-values during the other experiment types. As expected, the $\delta^{15}N$-values were very close together within a range between 6.1 ‰ ATMN (surface sediment of the *U. maracoani*-zone) and 4.4 ‰ ATMN (yellow mangrove leaves). Here, the analysis of the stable sulfur isotopes proved to be very effective to enhance the methodical resolution and thus to allow the identification of primary food sources. While almost no differences of the $\delta^{34}S$-values were observed for the trophic key animal species, valuable information was obtained concerning the chemical identification of the primary sources within gastro-intestinal contents. The observed range of $\delta^{34}S$-values was extremely wide (33.4 ‰) between 17.3 ‰ CDT for the seagrass *Halodule wrightii* and -16.1 ‰ CDT for the surface sediment at the muddy plains. The identification of $\delta^{34}S$-values allowed the definite separation of the mangrove litter from the benthic or epiphytic phaeophyte and rhodophyte algae. A separation of the mangrove leaves from surface sediment influences was less significant. The possibility of a reliable separation of fresh mangrove leaves deriving from different mangrove tree species was highly advantageous.

It is concluded that the combined application of the stable isotope method of carbon, nitrogen and sulfur is workable in the course of analyses of benthic mangrove food webs and leads to reasonable budget results. Nevertheless, additional information has to be obtained from other

experimental approaches. In the present study, the separate isotopes have shown specific trophic ranges within food chains where they have highest capacities to provide information. The δ^{34}S-values are most applicable between the level of the crude primary source and the gastro-intestinal contents of separate consumer species. The δ^{13}C-values may be used for the same purpose, too, but have higher capacities in the identification of food sources from body tissue samples of separate species at one trophic level. The δ^{15}N-values are most valuable for the identification of different trophic levels but do not serve information on the specific type of primary food source is needed.

5.2.5 Monodietary Experiments

The monodietary experiments showed a strong short term influence of the specific ^{13}C-values of separate food sources on the carbon isotope ratio of the muscle tissue of all consumers tested (Fig. 36, 37). With respect to the oscillations of muscle tissue ^{13}C-values during the monthly field sampling for carbon isotope ratios (Fig. 24-33), the observed range of isotope shift during the monodietary experiments of up to 2.5 ‰ was expected for all species except for *Goniopsis cruentata* and *Aratus pisonii*. These two species had shown a delay of the correlation between the ^{13}C-values of their muscle tissue and their food sources of one and three months, respectively. During the monodietary experiments, the assimilation response of *G. cruentata* and *A. pisonii* was however not more delayed than for all other species tested. It is hypothesized that the selective fractionation of isotopes during the biochemical assimilation processes of body tissue from ingested food is dependent on a mixed diet. A conclusive determination of those mechanisms was not found in literature and remains to be examined in the future. For fish larvae of the species *Fundulus heteroclitus* the fractionation of carbon isotopes during dietary assimilation was correlated to temperature (Frith et *al.* 1985). Estep & Vigg (1985) described the influence of changing diet compositions on the isotope fractionation of scales and muscle of different fish species. A physiological explanation was however not presented.

It has to be kept in mind that none of the trophic key species except *Uca maracoani* and *U. thayeri* can be considered monodietary. In the course of the monodietary experiments, the exclusive feeding on single food sources over a period of 20 days may have caused bias effects on the consumers' metabolisms. Probably another source of bias, the specific amount of material ingested per time was not analyzed during the experiments. Only the general acceptance of all potential food sources from the initial experiments was checked by direct observation of the feeding activity of the consumers. The results should therefore be regarded to be qualitative and not quantitative and should only be discussed in combination with the results from all other experiment types in the course of the study. Nonetheless, some isolated results from the monodietary experiments and their association to particular findings during other experiment types may receive a short individual discussion already at this point.

Both biochemically very dissimilar food sources, [*Aratus pisonii*] and [brown mangrove leaves] caused no significant carbon isotope shift of the muscle tissue of *Goniopsis cruentata* after 20 days (Fig. 36), although the average ^{13}C-values of the materials was very different at -22.9 and -29.0 ‰ PDB, respectively. Additionally, the monthly field sampling had not revealed a correlation between the isotope values of the consumer and the two food sources (Fig. 25). This contradictory situation is a good example for a necessary rejection of the isolated conclusion of a preference of the two food sources based on the monodietary experiment alone. At the same time however, the almost similar effect of both food sources on

the consumer's ^{13}C-values indicates a strong influence of dissimilar grades of biochemical selectivity of heavy and light carbon isotopes depending on the type of diet.

Aratus pisonii, *Callinectes danae*, the fish *Sphoeroides testudineus* and the gastropod *Littorina scabra angulifera* displayed the widest ranges of the shift of their muscle tissue ^{13}C compared to all other trophic key species (Fig. 36, 37). This is not surprising because a relatively narrow natural food range should cause a strong isotope shift when being expanded by the ingestion of a marginal food source artificially provided in excess quantity. *Littorina irrorata* incorporated *Spartina alterniflora*-derived nitrogen into tissues at rates equal to 10 to 20 % of total snail nitrogen · 30 d^{-1} in summer and fall, and 2-5 % · 30 d^{-1} in winter at Sapelo Island, USA (Kemp et *al.* 1990). A surprising finding of the present study was the induction of almost exclusive negative isotope shifts during the experiments on *L.s.angulifera*, *Cardisoma guanhumi* and *Ucides cordatus*. All other trophic key species showed carbon isotope shifts balanced in both directions. These results allowed the selection and rejection of food causing the largest shifts on the consumers muscle tissue.

5.3 Total Biomass and Biomass Production

The average biomass of all macro-zoobenthic (1> mm) trophic key species in the Canal de Sta. Cruz mangal ecosystem (20.486 gFW · m^{-2} or 567.5 tonnesFW; Table 14) has only limited literature data to be compared to. A biomass determination of the macro-zoobenthic biomass and the of trophic key species in particular has so far not been conducted in mangrove ecosystems. The available information on this major aspect of mangrove ecology has to be considered as very inadequate with respect to the worldwide biological and commercial importance of this ecosystem type. The diversity of the mangrove fauna however has received a certain scientific interest. At the Ceara River Estuary, northeastern Brazil, the zoobenthic communities associated to roots of the red mangrove *Rhizophora mangle* are composed of cnidarians, mollusks, polychaetes, crustaceans (cirripeds, decapods, isopods and amphipods) and insect larvae (Castro Miranda et *al.* 1988). Unfortunately, no biomass data were determined by the authors. Inclan-Rivadeneira (1989) counted 27 species of sessile fauna on *R. mangle* roots. A hydroid diversity of 22 species was censored at Twin Cays, Belize (Calder 1991). Perry (1988) reported a general positive influence of associated fauna on growth of *R. mangle*. For the purpose of a principal comparison, the average macro-zoobenthic biomass including the biomass of the trophic key species on the mangrove floor that is covered by a single mangrove root was calculated as 77.3 gDW · $root^{-1}$ in the Canal de Sta. Cruz mangal zone. In spite of the constant epifaunal exchange between neighboring substrate types, the author did however not analyze the complete benthic community including the mangrove floor. The average area covered by one *R. mangle* root during the present study was 4.3 m^2 · $tree^{-1}$. The weighted average conversion factor from dry to fresh weight of all trophic key species was f = 1.41. Lalana (1986) conducted one of the few studies on the benthic faunal biomass and evaluated a total of 877 ind · $root^{-1}$ of the entire associated fauna on roots of *R. mangle* at Cuba. The average biomass was 52 gDW · $root^{-1}$.

The ichthyological (Lasserre & Toffart 1977; Thollot 1992) as well as the epifaunal and infaunal meiobenthic community on mangrove roots (Lalana & Gosselck 1986; Vanhove et *al.* 1992; Nicholas et *al.* 1991; Da Cunha-Lana & Guiss 1992) have received some more scientific interest than the macro-zoobenthos. Both communities were however not analyzed during the present study. On mangrove roots at Cuba, Lalana & Gosselck (1986) determined a

biomass of the most common meiobenthic taxa Nematoda, Copepoda, Tanaidacea, Oligochaeta, Polychaeta, Ostracoda and Amphipoda of 25-30 gDW · m^{-2}.

The distribution of the crustacean biomass in the mangal segment of the Canal de Sta. Cruz mangrove ecosystem shows daily fluctuations and a permanent exchange with the neighboring Canal de Sta. Cruz channel. Based on the feeding experiments, a migration process is concluded for the blue crab *Callinectes danae* and the pufferfish *Sphoeroides testudineus*. An internal vertical motility of biomass originates from the daily migration of *Aratus pisonii* and *Goniopsis cruentata* up and down the mangrove canopy. A conclusive evaluation of the macro-zoobenthic biomass in the mangal zone has to take these migration processes into account. On the annual scale, no significant biomass differences were observed between the dry and the rainy season because the outweighing part of the biomass is sessile. The reproduction activity of the trophic key species is continuous and recruitment to the local stocks is probably more or less constant over the year. Both aspects are important to the mangrove fishery management in the area and should receive more scientific interest in the future. *Aratus pisonii* is the only brachyuran among the trophic key species that has been studied for reproduction aspects. Conde & Díaz (1989b) concluded that the intensity of the annual reproduction rate of *A. pisonii* is dependent on the type of habitat the animals live at and that the number of eggs per female as well as the percentage of egg carrying females may differ. Emmerson (1992) described a correlation of the time and duration of the annual peak reproductive period of *Uca vocans hesperiae* and *U. urvillei* to the vertical position of the animals within the tidal range (Emmerson 1992). This correlation may also exist for *U. maracoani* and *U. thayeri* but was not tested during the present study.

The immense differences observed between the average and the maximum species-specific biomass per area (Table 14) are typical for structured complex ecosystems such as mangrove areas at Brazil (Schaeffer Novelli et *al.* 1986; Schaeffer Novelli 1989). Comparable differences were reported for coral reefs (Sournia 1977; Birkeland & Grossenbaugh 1984; Russ & Choat 1988; Sale 1988; Hughes 1989; Mundy 1989) and rocky shore littoral ecosystems (Paine 1974; Underwood & Denley 1984). During the present study, all trophic key species showed specific morphological as well as syn- and autecological behavioral adaptations to their ecological niches within the system. The high density of single species in certain segments of the mangal system and their specific behavioral adaptations are not only interesting from the ecologist's standpoint but are also very advantageous to the local fishery. Fishing or gathering of the commercially valuable brachiuran species *Callinectes danae*, *Cardisoma guanhumi*, *Ucides cordatus*, and to a lower extent of *Goniopsis cruentata*, is less workable and far more effective if the fishermen do not have to sweep the whole area for the desired animals.

The mangrove flora of the Canal de Sta. Cruz is dominated by *Rhizophora mangle* (49 % coverage) and *Avicennia marina* (36 % coverage). The relative plant biomass of the two species of 53 % and 31 % reflect the coverage rates (Fig. 15). Corresponding relations were described between *R. mangle* and *A. germinans* at other estuaries at northeastern Brazil (Hertz 1991), the Gulf of Mexico (Putz et *al.* 1984; Everitt & Judd 1989; Imbert & Rollet 1989), at Kenya (Gang & Agatsiva 1992) and at northern Queensland (Mackey 1993). Like *Conocarpus erecta* (1% coverage), *L. racemosa* (5 % coverage) is found only in the upper littoral zone of the Canal de Sta. Cruz ecosystem which is typical for both species (Imbert & Rollet 1989; Molina-Lara & Esquivel 1993; Rey 1994). *Laguncularia racemosa* has a relatively high biomass in the area (10 %) compared to other Central and South American (CSA) mangrove ecosystems (Jiménez 1988; Imbert & Rollet 1989; Rey 1994). The maximum mangrove canopy height in the area (7 m) is lower as at other CSA

and Brazilian mangrove systems (6-11 m) having comparable species compositions (Jiménez 1987; Conde & Díaz 1992b; Lacerda et *al.* 1993). However, the average canopy height has no influence on the standing biomass and annual biomass production of mangrove systems. A lower canopy height is compensated by a higher density of the trees (Briggs 1977; Lin et *al.* 1992). The only consistent growth effects of neighboring *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa* trees were found to be positive (Rey 1994). This result may be attributed to the climatic conditions created and shared between neighboring trees.

The biomass of epiphytes (mainly lichens) within the mangrove canopy is very low ($0.03 \cdot 10^3$ gDW$\cdot$m^{-2}) and of negligible importance for the total biomass production rate of the system (Fig. 38; Table 15-17). Stevens (1979) counted 105 lichen species and calculated a much higher biomass of $0.47 \cdot 10^3$ gDW$\cdot$m^{-2} at tropical eastern Australia. Only few mosses or liverworts, typical for temperate mangrove systems (TeStrake et *al.* 1986) were found during the present study. The average epiphytic and epibenthic macroalgal biomass of chlorophytes ($0.37 \cdot 10^3$ gDW$\cdot$m^{-2}) in the Canal de Sta. Cruz mangal zone is higher than the biomass of the phaeo- and rhodophytes ($0.28 \cdot 10^3$ gDW$\cdot$m^{-2}) in the area. This difference is probably a result of the reduced light intensity on the mangrove floor and mangrove tree roots which is more limiting to the growth of the latter algal community (Davey & Woelkerling 1980; Silva et *al.* 1987; Steinke & Naidoo 1990). The algal community associated with roots of *Rhizophora mangle* at Laguna Joyuda estuary, in Puerto Rico, consists of eight macroalgal species (Rodriguez & Stoner 1990). The total algal biomass for the lagoon of $7.42 \cdot 10^4$ kg dry weight (DW) is similar to the total annual leaf litterfall from the *R. mangle* fringe ($9.31 \cdot 10^4$ kg DW), indicating the importance of the algal food web.

The annual litterfall in the mangal segment of the Canal de Sta. Cruz mangrove system of 1 724 gDW $\cdot$ m^2 $\cdot$ y^{-1} or 942 gC $\cdot$ m^2 $\cdot$ y^{-1} is higher than all literature data reported worldwide. One of the more or less corresponding results of 1 417 gDW $\cdot$ m^2 $\cdot$ y^{-1} was described for the Tecapan-Agua Brava Estuary, Mexico (Flores Verdugo et *al.* 1990). At Pagbilao Bay, the Philippines, Pinto (1992) estimated 934 gDW $\cdot$ m^2 $\cdot$ y^{-1} of which 79 % were mangrove leaves. However, biomass determinations even in the same area differ greatly. At Transkei, South Africa, the annual litterfall at a mangrove dominated by *Avicennia marina* was 451 gDW $\cdot$ m^2 $\cdot$ y^{-1} (Steinke & Ward 1990) or 653 gDW $\cdot$ m^2 $\cdot$ y^{-1} (Emmerson & McGwynne 1992). At New South Wales, Australia, it was 310 gDW $\cdot$ m^2 $\cdot$ y^{-1} (Clarke 1994). At Sundabans, India however, Gosh et *al.* (1990) reported an intense litterfall of 1 603 gDW $\cdot$ m^2 $\cdot$ y^{-1} for the species *A. marina* alone.

Mangrove litterfall is the most frequently described source of biomass primary production in mangrove ecosystems worldwide. Except for the phytoplankton in mangrove areas ($\neq$ mangal), all other primary sources have not received adequate scientific interest, although, already two decades ago, Bunt et *al.* (1979) comprehensively concluded that the analysis of the mangrove litterfall is by far not sufficient for the approximation of primary production of mangrove ecosystems. In estuarine mangrove systems, a continuous mixing process of different carbon sources occurs. The mean mangrove contribution to the particulate organic carbon POC at of Sepetiba Bay, Rio de Janeiro, Brazil varies between 16 % and 100 % (Rezende et *al.* 1990) and predominantly depends on tidal amplitudes. The primary production of the phytoplankton within a mangrove ecosystem at Thailand was 468 g C $\cdot$ m^{-2} $\cdot$ y^{-1} (Wium-Andersen 1979). The largest fraction was composed of the nanoplankton contributing 34-91 % to the production. No significant seasonality was detected. The neighboring coastal upwelling zone was considered to have a strong effect on the planktonic production rates. At the Sinai Peninsula, a region of low phytoplankton densities, the primary production of the phytobenthos within a

mangrove ecosystem was 100-fold higher than the primary production in the planktonic section of the system (Dor et *al.* 1977). There exists a very interesting parallel between mangrove ecosystems and coral reef ecosystems. Both systems have significantly more plant biomass on substrates than is living in the planktonic sections of the systems (Sournnia 1977).

Only a small portion of the annual total biomass production of 117 478 tonnesDW plant material or 49 232 tonnes of organic carbon in the Canal de Sta. Cruz mangal area is internally processed via decomposition, through consecutive plant growth, and by interlinked animal food chains (Fig. 48, 49; Table 15-17). The largest part leaves the system via tidal or riverine water drift or via animal migration to neighboring ecosystems. This aspect is very important for the assessment of the mangrove systems with respect to coastal resource management and to its importance in atmospheric carbon fixation. There always exists a net-export of organic material out of the mangrove ecosystems into the ocean which is driven by tidal currents (Wolanski et *al.* 1980, 1992; Rezende et *al.* 1990).

One outstanding result of the present study is that the benthic and epiphytic algae in the mangal segment of the Canal de Sta. Cruz mangrove ecosystem contribute 59.4 % dry weight or 47.0 % organic carbon to the annual benthic plant biomass production although they only represent 2.4 % of the benthic total standing plant biomass in the area (Fig. 48, 49; Table 15-17). For both plant groups and for old mangrove systems, the annual growth of persistent plant material can be assumed to be balanced by mortality rates and export via drift (Bunt et *al.* 1979; Goulter & Allaway 1979; Jiménez & Lugo 1985; Gosh et *al.* 1990). The relative annual organic carbon primary production (litterfall) of the mangrove trees representing 53.0 % of the total primary production in the mangal zone is low compared to the enormous production rate of the epiphytes in relation to their biomass. The hypothesis that the mangrove trees themselves are probably the most important primary producers in mangrove ecosystems published by Branch & Grindley (1979) has proven right by a very small margin.

The distribution and the ecological structure of the biomass of the benthic animal species in the Canal de Sta. Cruz mangal ecosystem are a result of two influences, the particular adaptations to specific environmental niches and the local fishery. Prominent seasonal changes of abundances or of the diversity of the trophic key species in the mangal area were not observed. Souza et *al.* (1994) described an obvious seasonal change (monthly diversity of 2-29 species) of the composition of the brachyuran community in the Canal de Sta. Cruz open channel region. The non-existent reflection of these changes in the neighboring mangal area is surprising and remain unexplained. Migrations of the semi-terrestrial brachyurans out of the mangal zone are probably of only minor importance for the changes at the open channel.

A fishery-induced frequency reduction of length classes above certain (commercial) body weights is particularly evident for *Goniopsis cruentata*, *Callinectes danae* and *Ucides cordatus*, and less evident for *Cardisoma guanhumi*. The remaining non-commercial species *Aratus pisonii*, *Uca maracoani*, *U. thayeri*, *Littorina scabra angulifera* and *Sphoeroides testudineus* do not show any fishery impact on their normal distributed weight frequencies in the study area. The commercial size of *G. cruentata* (standing biomass = 235.8 tonnesFW) as read from the relative weight frequency data (Fig. 39) was 35 gFW which corresponds to the preferred minimum fresh weight of the specimens named during interviews with the local fishermen. The relatively sharp drop of the relative weight frequencies above 35 gFW is however surprising because the species is of only minor commercial value and rarely found on local fish markets at all. The fishermen explained this discrepancy by telling that they prefer *G. cruentata* for subsidence fishery and for their own diet just because of its low market value. The other commercial crab species are too valuable for private consumption. The

comparatively intensive gathering of *G. cruentata* has been underestimated in scientific literature so far. This finding is of particular importance with respect to the highest biomass and the central position of the species within the mangal segment of the Canal de Sta. Cruz mangrove food web.

The distribution of the relative body weight frequency of *Callinectes danae* (biomass = 162.2 tonnesFW) reflects both the strong fishery pressure on and the migratory behavior of the species. The biomass within the mangal zone is second highest of all benthic trophic key species during the present study and it is dominated by small animals up to 50 gFW (Fig. 39). These weight classes are probably not equally represented in a migratory exchange with the Canal de Sta. Cruz channel because of a higher predation pressure in the open waters (Roman-Contreras 1986; Del-Castillo et *al.* 1992). This aspect was however not quantified during the present study and should receive further scientific interest. Above a body fresh weight of 90 g, the relative frequencies of the weight classes decline. Although this body weight corresponds to the commercially accepted minimum weight at the local market, the additional migration behavior of the larger specimens should be kept in mind. Another important aspect for the interpretation of the structure of the standing stock of *C. danae* is that smaller specimens are also accepted as a welcome by-catch by the local fishermen. Animals down to a body fresh weight of 20 g were retained from the fishermen's hauls. These undersized animals are used for private consumption by the fishermen instead of offering them on the market. Like all along the Brazilian coast, the fishermen in the Itamaracá region are almost exclusively paid the undersized portion of the daily catch before being handed larger animals of any kind. The cash profit at the local fish market is almost exclusively kept by the owner of the fishing boat. Fishermen on own boats are rarely seen. Consequently, gathering benthic animals by hand or using a line while walking the mangrove areas is a typical form of fishery in the area.

The reduction of the relative frequencies of *Ucides cordatus* (biomass = 10.1 tonnesFW) above 130 gFW has to be exclusively accounted to fishery pressure (Fig. 40). The local fishermen respect this minimum body weight because they know that the market price of animals above this weight is by far higher than the price of undersized individuals. Additionally, even the undersized individuals of this high-priced species are rarely consumed privately. Concerning *Cardisoma guanhumi* (biomass = 11.4 tonnesFW), the same fishing strategy is followed above a body fresh weight of 90 g (Fig. 40), as told by the fishermen at Itapiçuma Village. Fortunately, the fishermen are able to assess the probable size of specimens by the diameter, general appearance and location of the animals' burrows before they place their tin traps.

With only a few exceptions, all weight classes of the brachyuran crab species were represented during the biomass censoring in the study area. This indicates a stationary behavior of the animals over their entire life-span. A scarcity of very small juveniles was observed for *Aratus pisonii*, *Uca maracoani*, *Cardisoma guanhumi* and *Ucides cordatus*. A possible methodical explanation for the inadequacy of juvenile *U. maracoani* may be the distribution of its small size classes in the very low littoral zone (Brunenmeister 1980) where a representative sampling was difficult without sieving the upper substrate layers. An explanation for the scarcity of the other species was not found. The patchy distribution of the adult crabs is contradictory to their planktonic larval phase (Beever et *al.* 1979). *U. maracoani*, *U. thayeri*, *U. cordatus* and *C. guanhumi* showed significantly different average body fresh weights between sexes. Concerning the fiddler crabs, this is a result of the very dissimilar morphology of their chelae (Plate 1.8, 2.1). Concerning the latter two species it is a result of a faster growth of the males' extremities at equal carapace width compared to the female crabs (Plate 2.3, 2.4).

A very peculiar distribution was found for the relative size frequencies of *Aratus pisonii* (biomass = 23.5 tonnesFW). The grapsid crab showed different size distributions depending on the height above ground the animals were censored at (Fig. 39). The average carapace width of the animals decreases with distance to the mangrove floor. This distribution pattern was already described by Conde & Diaz (1989a, 1989b) and may be a result of an autecological competition for locations of higher nutrient concentrations and of the predation pressure by *Goniopsis cruentata*. The classification into separate reproductive groups seems to be feasible because of the significantly different average size at maturation. The log-normal weight distribution for all animals in the area supports the existence of separate populations. It should be interesting to analyze the mechanism of recruitment of *A. pisonii*.

Based on the body size data, *Uca maracoani* (biomass = 81.2 tonnesFW) is the only crustacean species in the mangal segment of the Canal de Sta. Cruz mangrove ecosystem having two clearly distinguishable cohorts (Fig. 39). A very surprising finding is the almost balanced sex ratio of *U. maracoani* and *U. thayeri* of 1 : 1.11 and 1 : 1.03, respectively. Various publications report of highly unbalanced sex ratios (1 : 2-3) of the genus *Uca* at other geographical areas (Hyatt & Salmon 1978; Frith & Brunenmeister 1980; Spivak et *al.* 1991; Chakraborty & Choudhurry 1992). The discrepancy may be a consequence of a more representative sampling of the standing stock (sweep-sampling) and the integration of the entire intertidal zone and all habitat types during the present study. The research conducted so far exclusively concentrated on the open muddy plains in mangrove areas. During the present study, the sex ratio of both fiddler crab species shifted in favor of the male crabs in the landward direction. However, it never reached figures as high as reported by other authors. The small fiddler crab *U. thayeri* (biomass = 3.8 tonnesFW) showed a normal weight distribution of a different shape compared to *U. maracoani* (Fig. 39). The higher relative frequency of individuals below a body fresh weight of 4 g may be an effect of a relatively stronger recruitment or a higher local concentration compared to the latter species. The increase of the average body size with distance from the shoreline as observed by Frith & Brunenmeister (1980) was confirmed for both species, but was not quantified in detail during the present study.

The standing stock of the gastropod *Littorina scabra angulifera* (biomass = 8.9 tonnesFW) can be divided into at least two separate cohorts. Higher densities of the animals at vegetation boundaries like channels or mud plains as reported by Murty & Rao (1977) were confirmed. The seize-weight relation of the species showed obvious undulations around a shell width of 13 mm and 17 mm (Fig. 40), respectively. A reason for this unevenness may be a shift of growth activity going to the shell and to the animal itself which has been already reported for other marine gastropods (Yamaguchi 1977; Cubit et *al.* 1984; Hughes & Jones 1985). The animals display either enhanced body or shell growth at a time. The checkered puffer *Sphoeroides testudineus* (biomass = 30.5 tonnesFW) is normal distributed (Fig. 40) concerning body fresh weight and several age classes can be suspected of which two were identified by statistical means. The very unbalanced sex ratio of the fish species (1 : 0.15, ♀/♂) may be explained by a sex-specific migration behavior of *S. testudineus* between the mangrove ecosystem and the channel region.

5.4 Conclusions: Trophic Structures / Combined Discussion of Field and Tank Experiments

The annual total food requirement of all benthic trophic key species during the present study was 7 827 tonnes dry weight or 10 819 tonnes fresh weight (Table 14-17; Fig. 48) excluding *Cardisoma guanhumi* and *Ucides cordatus*, which had not been tested for their daily ratios. Dry weight was converted to fresh weight using the species-specific conversion factors for the individual gastro-intestinal contents (Table 9). *Goniopsis cruentata* was identified as the only omnivorous species during the experiments having an annual food requirement of 3 188 tonnesFW of mixed diet. In consideration of this variable food selectivity of *G. cruentata* it was possible to subdivide the total food requirement of the trophic key species into a plant biomass of 4 080-7 268 tonnesFW and a required animal biomass of 3 551-6 739 tonnesFW per year.

Table 18: Quantitative food requirements of selected benthic species in the mangal segment (27.7 km^2) of the Canal Sta. Cruz mangrove ecosystem, Itamaracá Island, Pernambuco State, northeastern Brazil, from February 1995 until March 1996. (1) brachyurans; (2) gastropod; (3) fish; $\mathbf{DR_{DW}}$ = daily dry-weight food ratio; $\mathbf{AR_{DW}}$ = annual dry-weight food ratio; $\mathbf{AReq_{FW}}$ = annual fresh-weight food requirement (Table 1); $\mathbf{f_{DF}}$ = conversion factor from dry to fresh weight of the gastro intestinal content; **DW** = dry weight; **FW** = fresh weight; $\mathbf{f_{AR}}$ = annual fresh-weight food requirement ($f_{AR} = DR_{DW} \cdot 365\ d \cdot f_{DF} \cdot 100^{-1}$); BFW = body fresh weight.

species	biomass [10^3 kg]	DR_{DW} [% BFW]	AR_{DW} [% BFW]	f_{DF} []	$AReq_{FW}$ [10^3 kg · y^{-1}]	f_{AR} []
(1) *G. cruentata*	235.8	2.6	959	1.41	3 188	13.4
A. pisonii	23.5	3.6	1 311	1.49	459	19.6
C. danae	162.2	3.4	1 230	1.51	3 012	18.7
U. maracoani	81.2	8.8	3 216	1.22	3 168	39.2
U. thayeri	3.8	21.4	7 827	1.18	350	92.2
C. guanhumi	11.4	not evaluated				
U. cordatus	10.1	not evaluated				
(2) *L. s. angulifera*[a]	8.9	2.4	868	1.34	103	11.7
(3) *S. testudineus*	30.5	3.3	1 210	1.46	539	17.6
Σ^*	545.9				10 819	19.8

*: excluding *C. guanhumi* and *U. cordatus*; [a]: including shell

Excluding *Cardisoma guanhumi* and *Ucides cordatus*, the combined annual fresh-weight food requirement of all trophic key species was 19.8 fold their standing biomass (Table 9). The provision of a sufficient plant biomass was managed without great exertion by the mangrove ecosystem. The annual plant biomass production of 117 478 tonnesDW exceeded the food requirements of the strictly herbivorous trophic key species *Aratus pisonii* (459 tonnesFW; Table 14) and *Littorina scabra angulifera* (103 tonnesFW) by 209 fold. The food requirements of *Uca maracoani* (3 168 tonnesFW, sediment) and *U. thayeri* (350 tonnesFW, sediment) had to be balanced by benthic diatom biomass production which was not quantified during the project. As a simplification, the latter two species are here included in the

herbivorous group, although correctly to be classified as detrivorous animals. It has to be kept in mind that the digestible fraction of the surface sediment material ingested by the *Uca* species was considerable small compared to the diets of the other benthic species (Dye & Lasiak 1986; Wolfrath 1992, 1993).

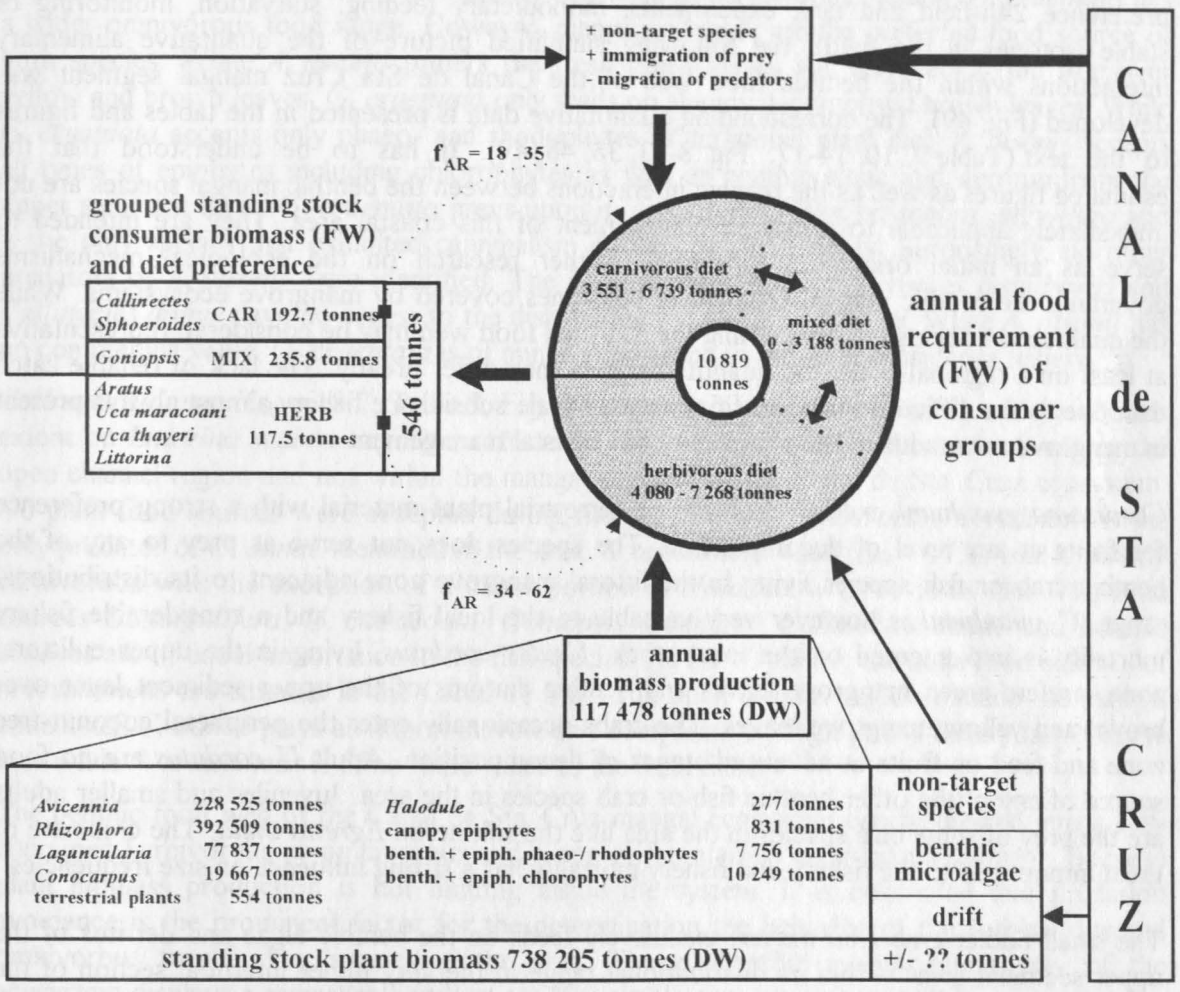

Fig. 48: Flow-chart on estimated annual food requirements of all trophic key species in the benthic mangal segment (27.7 km^2) of the Canal de Sta. Cruz ecosystem, northeastern Brazil. The total requirement was calculated from the specific average daily requirements analyzed through multiple 24h-experiments on each consumer. The type of food (**CAR**nivorous, **MIX**ed, **HERB**ivorous) preferred by a particular consumer was identified via observations of feeding behavior and analyzes of the stable isotope ratios $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ of food sources, gastro-intestinal contents, and consumer tissue. The standing biomass was evaluated during three transect sweep-sampling events. All experiments were conducted between February 1995 and March 1996. **DW** = dry weight, **FW** = fresh weight, f_{AR} = factor of annual fresh-weight food requirement $\mathbf{AReq}_{FW}$ (= f_{AR} · biomass).

The combined annual food requirements of the carnivorous trophic key species *Callinectes danae* and *Sphoeroides testudineus* of 3 551 tonnesFW can not be produced by the benthic mangal analyzed during the present study. Thus, it is not surprising that those two species are the only migratory ones analyzed. *C. danae* as well as *S. testudineus* are dependent on food sources outside the mangal segment of the Canal de Sta. Cruz ecosystem. Additional balancing

effects may be the (temporary) immigration of food sources other than those tested or the greater importance of food sources not evaluated during determination of the standing biomass through transect sampling. *Penaeus schmitti* and *P. brasiliensis* or holopelagic fish species may be of particular importance (Robertson 1988; Vance et *al.* 1990; Börner 1994)

Combining the results from all series of experiments conducted during the project (e.g. food preference, 24h-field and tank experiments, monodietary feeding, starvation, monitoring of stable isotopes in the field), the following simplified picture of the qualitative alimentary interactions within the benthic food web of the Canal de Sta. Cruz mangal segment was developed (Fig. 49). The corresponding quantitative data is presented in the tables and figures to the text (Table 9, 10, 14-17; Fig. 8-23, 38, 48, 49). It has to be understood that the estimated figures as well as the trophic interactions between the benthic mangal species are not immediately applicable to a desired management of this coastal area. They are intended to serve as an initial orientation preceding further research on the ecological mechanisms governing the benthic mangal segment of coastlines covered by mangrove ecosystems. While the qualitative conclusions concerning the analyzed food web may be considered representative at least on a regional scale, the quantitative data may differ greatly. The lack of reliable catch data due to the difficulties to quantify the small scale subsidence fishery almost always present in mangrove areas adds to the complexity of a coastal management.

Cardisoma guanhumi exclusively feeds on terrestrial plant material with a strong preference for fruits at any level of decomposition. The species does not serve as prey to any of the benthic crab or fish species living in the littoral mangrove zone adjacent to its distributional range. *C. guanhumi* is however very valuable to the local fishery and a considerable fishery mortality is implemented on the local stock. *Ucides cordatus*, living in the upper eulittoral zone, prefers green mangrove leaves and benthic diatoms of the upper sediment layer over brown and yellow mangrove leaves. The crabs occasionally enter the peripheral coconut-tree zone and feed on fruits at advanced stages of decomposition. Adult *U. cordatus* are no food source of any of the other benthic fish or crab species in the area. Juveniles and smaller adults are the prey of some bird species in the area like the silk heron *Egretta thula*. The crabs are of great importance to the fishery and fishery mortality has a strong influence on size frequencies.

The small fiddler crab *Uca thayeri* exclusively feeds on the benthic algae and detritus of the upper sediment layer within its distributional range in the very upper intertidal section of the mangal zone. The annual fresh-weight food requirement factor $f_{AR} = 92.2$ (Table 9; Fig. 49) exceeds the requirements of all other benthic mangrove species by far and is even more than 2-fold higher than the factor of the taxonomically closely related *U. maracoani* ($f_{AR} = 39.2$). This divergence is a result of the relatively low nutrient content of the sediments ingested by *U. thayeri*. *Egretta thula*, the striped green heron, *Butroides striatus*, and other birds are the only considerable predators on *U. thayeri*. None of the other benthic carnivorous or omnivorous crab species enters the distribution zone of the small fiddler crab during low tide. During high tides, the crabs are protected within their burrows. Having a distribution range stretching into the mangal zone, the fiddler crab *U. maracoani* also feeds exclusively on the algae and detritus of the upper sediment layer. The fiddler crab serves as prey to the local heron populations and plays a considerable role within the diet of *Sphoeroides testudineus*. A corresponding situation was found at Chesapeake Bay, USA, where fiddler crabs represented 94 % of the prey of the yellow-crowned night heron, *Nycticorax violaceus* (Watts 1988). *Littorina scabra angulifera* feeds on epiphytic algae without a clear preference for chlorophytes, phaeophytes or rhodophytes. However, all algal types have to be present. The annual fresh-weight food requirement factor of the gastropod is $f_{AR} = 11.7$ times its standing biomass (Table 9; Fig. 49). Benthic diatoms and detritus from the upper sediment layers are a

secondary food source. Plant material including mangrove leaves at any level of decomposition is not accepted. *Sphoeroides testudineus*, *Goniopsis cruentata* and *Callinectes danae* prey upon *L.s.angulifera*. The species has no commercial importance.

Aratus pisonii (f_{AR} = 19.6, Table 9; Fig. 49), together with *Goniopsis cruentata* (f_{AR} = 13.4), plays a central role within the benthic mangrove ecosystem in general and in the mangal zone in particular. While *A. pisonii* is completely restricted to herbivorous feeding, *G. cruentata* has a wider omnivorous food range. However, mangrove leaves are the preferred food source of both species. While *A. pisonii* prefers the fresh green leaves still attached to the tree over yellow and brown leaves, *G. cruentata* only feeds on already decomposed brown leaves. While *G. cruentata* accepts only phaeo- and rhodophytes as additional plant diet, *A. pisonii* accepts all types of epiphytes including chlorophytes as well as benthic algae and detritus from the upper sediment layer. *G. cruentata* preys upon *A. pisonii* and *Littorina scabra angulifera* and is the only species that exhibited cannibalism during the experiments. Surprisingly, no other predators of *A. pisonii* were identified. The potential predators *Sphoeroides testudineus* and *Callinectes danae* have no access to the distributional range of *A. pisonii*. While *A. pisonii* has no commercial value, *G. cruentata* is of minor importance to the local subsidence fishery.

Callinectes danae (f_{AR} = 18.7, Table 9; Fig. 49) feeds on *Goniopsis cruentata* and to a lower extent on *Littorina scabra angulifera*. Its main food source however has to be found in the open channel region and not within the mangal segment of the Canal de Sta. Cruz ecosystem. No plant food sources were accepted during the experiments. *Sphoeroides testudineus* is the only predator of *C. danae* identified in the area. *S. testudineus* itself (f_{AR} = 17.6) is also strictly carnivorous with the exception of a minor portion of *Halodule wrightii* in its diet. The food sources *L.s.angulifera*, *U. maracoani*, *Goniopsis cruentata*, *Callinectes danae* and benthic bivalves are of equal importance to the fish species. As for *C. danae*, the main food sources of *S. testudineus* are situated in the Canal de Sta. Cruz open channel region outside the mangal zone itself. *C. danae* plays an important role as a comparatively high priced fishery target in the area while *S. testudineus* is of no importance to the local fishery.

The benthic food web of the Canal de Sta. Cruz mangal ecosystem can be divided into a self-contained herbivorous or omnivorous and a non-self-contained carnivorous segment. Because plant biomass production is not limiting inside the system, it is concluded that predation avoidance is the prominent factor for the determination the behavior of the herbivorous and omnivorous trophic key species in the area. The zoobenthic mangal community of the ecosystem displays a remarkable utilization of available space both horizontally and vertically. From the very tips of the mangrove canopy to a substrate depth of up to 1.5 m various specialists have made use of a high number of ecological niches. Predation avoidance is managed in different ways either by complete or partial separation of the specific distributional ranges or by temporal separation of the active utilization of particular habitats within the system. *Aratus pisonii* retreats to the upper canopy regions. In addition to the morphological protection by its shell, the gastropod *Littorina scabra angulifera* never enters the water. *Uca maracoani* keeps a minimum distance to hard substrates during low tides and retreats into burrows when threatened. *Uca thayeri* inhabits a zone offering minimum protection against avian predation to potential invaders. The small size of the animals makes them more difficult to be spotted and their more social behavior compared to *U. maracoani* enhances a faster escape response. The small diameter of the burrows does exclude all potential predators in the area. The most evolved distributional separation is displayed by *Cardisoma guanhumi* and *Ucides cordatus* who have extended their habitat into the terrestrial zone. Their large size, their physical strength and the protection by their solid carapaces are certainly a result of energy constraints of the extreme habitat type with respect to brachyuran physiology, but are also highly effective concerning the protection against potential large terrestrial predators.

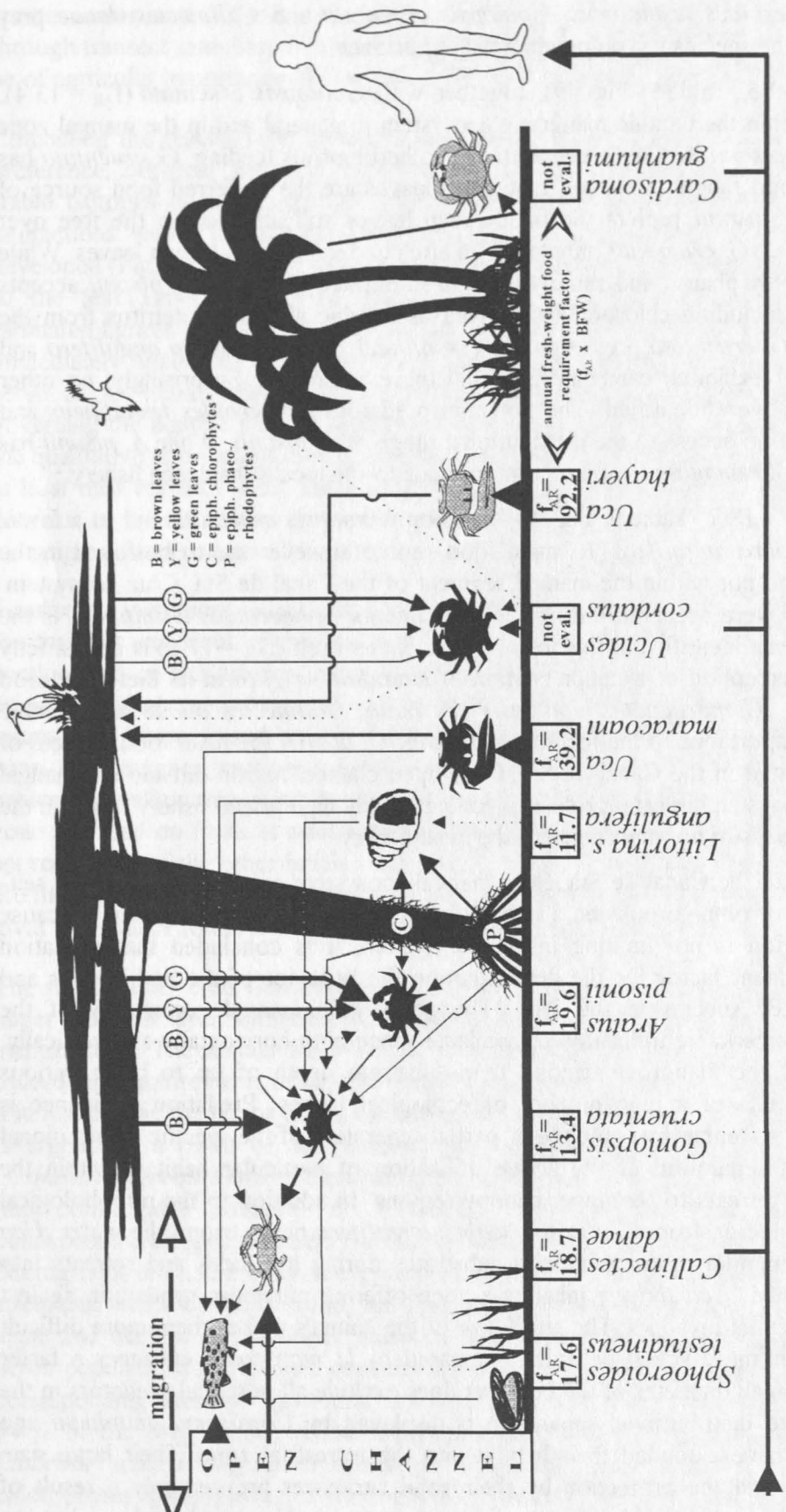

Fig. 49. Trophic structure of the benthic mangal compartment of the Canal de Sta. Cruz mangrove ecosystem, NE Brazil. Arrows indicate primary alimentary relationships. Arrow thickness corresponds to the graduation of the importance of a particular food source. The location of species symbols is not intended to be zoogeographical. The chart is based on results from field observations, 24h-field and tank experiments, monodietary experiments, starvation experiments, and experiments on the stable isotope ratios of carbon, nitrogen and sulfur. All experiments were conducted between February 1995 and March 1996. BFW = body fresh weight, * = here artificially separated for presentation purpose.

Predation avoidance through temporal separation of activity periods is most advanced by *Uca maracoani*. The potential intertidal predators of the animals are not able to reach the prey both during low and during high tides as well. However, this behavioral pattern has three major disadvantages. First, the animals are restricted to a habitat of comparatively low nutrient density and a requirement of a highly specialized feeding mode. Second and moreover, the burrowing behavior requires a high energy input. Third, the animals are confronted to an intense avian predation during low tides (Pennycuick & de-Santo 1989; Palmer 1990; Thibault & McNeil 1994). The swarm effect does not provide additional protection from avian predation (Enns et *al.* 1993).

Goniopsis cruentata plays the most central role in the benthic mangal food web due to its high behavioral flexibility and its physical and morphological capacity to enter almost all zones of the ecosystem. At the same time, the species displays an extremely omnivorous feeding behavior not being dependent on any single type of diet alone. Of all trophic key species during the present study, the only predators of the species are the blue crab *Callinectes danae* and the tetraodontid *Sphoeroides testudineus*. The animal groups have contact only during high tides and consequently *G. cruentata* is predominantly found on the roots, stems and in the lower canopy region during this period.

From the nutritional standpoint, the benthic mangal ecosystem strongly supports herbivorous and omnivorous over carnivorous species because the animal biomass production in the area is not sufficient to any predatory species. Thus, in contrast to all other benthic trophic key species, the predatory *Callinectes danae* and *Sphoeroides testudineus* are not restricted to the mangal zone during their adult life stage. Both species are migratory between the open channel region and the mangrove tree zone of the Canal de Sta. Cruz. Aside the utilization as a nursing area, the mangal zone only serves as an additional feeding area to the two predators. All other trophic key species spend only their juvenile life stages in the neighboring ecosystems of the continental shelf region, the estuarine and open channel region of the Canal, where they play an important role within the plankton community (Robertson et *al.*; 1988; Morgan 1990; Robertson & Blaber 1992; Schwamborn 1997).

Fishery for the commercial trophic key species *Callinectes danae*, *Cardisoma guanhumi* and *Ucides cordatus* in the Canal de Sta. Cruz mangal area is intense because of its subsidence character to the local fishing communities. With the exception of *C. danae*, it is however selective for specimens above the age of maturation. It has to be noted that all commercial species are either migratory or inhabit the outer mangal zone. Thus, the ecological effect on the central mangal macro-zoobenthic community in general and the effect on its food web in particular is even smaller. It can be concluded that the immediate effects of fishery in the area are rather unimportant to the mangal segment of the mangrove ecosystem compared to the effects caused by land claiming (Lahmann et *al.* 1987; Aksornkoae et *al.* 1993; Kjerfve & Lacerda 1993; Mastaller 1996) and pollution (Linden & Jernelov 1980; Lugo 1980; Jackson et *al.* 1989; Klekowski et *al.* 1994). Effects on the entire mangrove ecosystem may however be considered different. A highly comprehensive review of the literature on various aspects of mangrove biology was presented by Schwamborn & Saint-Paul (1996).

Costa & Macedo (1989) conducted a chemical and physical study in the Timbo River Estuary at Itamaracá, near the Santa Cruz channel, in order to make an hydrological survey of the area and to detect signs of industrial pollution. The estuarine area showed high levels in some of the parameters monitored (alkalinity: 174.9 mg $\cdot$ l^{-1}, material in suspension: 174.9 mg $\cdot$ l^{-1},

silicate: 101.8 $\mu g \cdot l^{-1}$), but they concluded that the area doesn't yet reveal biologically critical conditions, because dissolved oxygen saturation was still above of 50 %. It is questionable, whether this one factor can be employed to state this hypothesis. The fact that mangrove tree species are able to tolerate high levels of heavy metals has often been abused to justify relatively high levels of these elements in mangrove areas compared to other coastal ecosystems. Under pollution pressure *Rhizophora mangle* is capable to bind Cd, Cr, Cu, Ni, Pb and Zn within the epidermis of its roots (Montgomery & Price 1979). An immediate pathological effect could not be seen, but unfortunately, the authors did neither analyze the rest of the plants nor the animal community in the area.

Aside the enormous primary production and plant biomass output and its indisputable character as a nursing area, feeding ground and refuge to a variety of organisms (Robertson & Duke 1987), the benthic mangal section of the mangrove ecosystem of the Canal de Sta. Cruz is a self-contained rim system of only minor alimentary importance concerning its animal biomass output to other systems. In fact, it is questionable whether there exists any export of benthic animal biomass at all. This situation was already postulated by Robertson (1991). Only in combination with the open channel region and the estuarine region as a whole, the ecological significance of the specific ecological structure of the animal community of the Canal de Sta. Cruz mangal can be understood. The present study has shown that it is likewise not always conclusive to combine all habitats in mangrove ecosystems to one large unit without reflecting on smaller-scale ecological aspects. Sometimes instead of, -for understandable scientific reasons-, expanding the mangrove ecosystem, it seems to be advised to focus on the central habitat, the habitat that gave the system its name, the mangrove tree zone or the mangal.

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