Chapter 4: BIODIVERSITY AND THE ECOSYSTEM

A main focus of the present study was to describe the biota and its organization as an ecosystem. This has been a broad scale study involving researchers, students and staff from Possum Point. Since it was not possible to study everything in the river, some components were necessarily left out of the description. For example, microbes could not be included for several logistic and practical reasons, even though they are clearly important to the functioning of the river ecosystem (Hawksworth 1996, Allsopp et al. 1993). Also, a few habitats were not included in the study, such as the hyporheic zones of the river at the interface between the groundwater and the benthos (Dahm and Valett 1996). Given these limitations however, a major effort has been made to describe the overall ecosystem of the Sittee River. The image that has emerged from these studies over a nearly 20 year period is of a diverse, relatively undisturbed tropical ecosystem with great value to the local residents and foreign visitors who interact with the river in various ways. Data and discussion of the community structure and trophic relations of the river species are presented below, starting from the base of the food web and proceeding upwards to the top predators. Throughout the chapter emphasis is given to connections between the river and the riparian forest, which highlights the need to consider both as a unit for conservation purposes.

Ecosystem Metabolism

The metabolism of an ecosystem is the sum of the metabolisms of the individual organisms within the system. Thus, as would be the case with an individual organism, measurement of ecosystem metabolism provides an index to the performance of the overall system, in terms of energy flow. The principal components of ecosystem metabolism are the production of organic matter by plants (primary production) and the consumption of organic matter by all organisms (community respiration). Ecosystem metabolism is a function of the energy sources and limiting factors that characterize the system. Energy sources, such as sunlight, tend to increase metabolism and limiting factors, such as nutrients, can restrict metabolism if the concentrations are in short supply relative to demand.

As an aside, although ecosystem metabolism is a measure of performance, it is not related to system health in any direct way. Ecosystem health is a subjective index popular among some environmental scientists that relates to the condition of the system relative to a reference ecosystem that is judged to have been undisturbed by human impact. In this sense, a healthy system would be similar to the reference system and would exhibit few signs of environmental impact. An unhealthy system would differ significantly from the reference condition and would have reduced or impaired characteristics caused by pollution or other human impact. It is difficult to apply the ecosystem health concept in a quantitative way to a river such as the Sittee because we have relatively little scientific knowledge of tropical river ecology and reference ecosystem conditions have not been established. However, the Sittee River seems to have relatively healthy ecological conditions as will be discussed throughout this book.

In a general way the trophic basis of an ecosystem is defined by the ratio of production (P) and respiration (R). On one hand, a P/R ratio of less than one indicates that the ecosystem is heterotrophic or driven by organic matter produced outside of the ecosystem boundaries. In this case for a river, the primary energy source is leaf litterfall from the floodplain and adjacent riparian forest. On the other hand, a P/R of greater than one indicates that the ecosystem is autotrophic and driven by organic matter produced within the ecosystem boundaries. In this case for a river, the primary energy source is aquatic plant production with the channel. For river ecosystems this conception of trophic basis was established by Odum (1956) and extended by Cummins (1974) and others. Although there have been challenges to the concept of trophic basis, it still stands as the generally accepted view of ecological energetics for river ecosystems.

Ecosystem metabolism is often measured by changes in concentrations of gases, such as oxygen and carbon dioxide, that occur due to metabolic processes (Hall and Moll 1975). The diurnal oxygen curve technique (Odum and Hoskin 1958, Odum and Wilson 1962) was used to measure ecosystem metabolism in the Sittee River. In this technique changes in oxygen throughout the entire water column are analyzed to provide an integrated measure of both planktonic and benthic metabolism. Dissolved oxygen concentration in the water is measured periodically over a 24-hour cycle. The concentration data is then converted into the rate-or-change of oxygen concentration by subtracting the concentration at one point in time (t+1) from the concentration at the previous point in time (t) and dividing by the length of time between the two measurements. Once suitably corrected for diffusion with the atmosphere, this data is plotted over the 24-hour cycle and graphically integrated to calculate metabolism. Thus, positive rates-of-change in oxygen concentration during the daylight represent primary production and negative rates-of-change in oxygen concentration at anytime during the day or night represent community respiration. This technique worked well in the freshwater zone at the sand bank station where oxygen was mixed throughout the water column. At this site diurnal curves had the typical pattern caused by ecosystem metabolism with daytime increase and nighttime decrease in oxygen concentration (Figure 3-). Production was low relative to respiration at the sand bank site and the P/R ratio was always less than one (Table 4-1). These results from the Sittee River are comparable to diurnal curve data from other tropical and subtropical stream ecosystems (Brinson 1973, Dudgeon 1983, Edwards and Meyer 1987, Knight 1983, Meyer and Edwards 1990, Odum 1957).

The diurnal curve technique could not be used however in the lower portions of the river where the water column was stratified, because of the complex exchanges of oxygen between the two strata of water and the atmosphere. Plankton metabolism was measured in the lower portion of the river with the light-dark bottle technique to at least establish the trophic basis for the planktonic subsystem suspended in the water column. In this technique water from the river is filled into a clear glass bottle (the light bottle) and into a similar glass bottle that has been covered with tape to exclude light penetration (the dark bottle). The initial dissolved oxygen concentration is measured and the bottles are incubated in the river during the day. After a period of time the bottles are retrieved and the oxygen concentration is measured in each one. Increases in oxygen in the light bottle

Table 4-1. Ecosystem metabolism for the Sand Bank site based on diurnal oxygen curve analysis. Gross production (P gross) = Net production (P net) + daytime respiration (R day). R night = nighttime respiration. All data are in units of g oxygen/m2/day except for the P/R ratio which is dimensionless.

Date	P net	R day	R night	P gross/R night
6/23/91-6/24/91	0.24	3.06	5.62	0.59
7/5/91-7/6/91	0.00	1.43	3.39	0.42
8/1/91-8/2/91	0.76	0.75	2.54	0.60
8/8/91-8/9/91	0.83	1.79	3.05	0.86
11/27/91-11/28/91	0.41	1.53	3.47	0.56
3/10/92-3/11/92	0.63	1.22	2.70	0.68
7/6/92-7/7/92	0.27	1.67	3.02	0.64
8/8/92-8/9/92	0.47	0.29	1.58	0.48

relative to the initial measurement are due to net photosynthesis (Pnet) and decreases in oxygen in the dark bottle are due to respiration (R). Light-dark bottle measurements were made in the lower Sittee River near Possum Point using 400 ml bottles and incubation times ranging from 4 to 6 hours. Metabolism was always low indicating that plankton is poorly developed in the Sittee River (Table 4-2). This result is not unusual since the flow rate of water causes the plankton organisms to be flushed down river before they can reproduce. Also, the low nutrient concentrations in the water, mentioned earlier, do not support much phytoplankton growth. Net production occurred on only three of the 12 sample dates and respiration was the dominant metabolic process.

In conclusion, the results of both the diurnal curve measurements at the freshwater site and the light-dark bottle measurements at the estuarine site indicate that the trophic basis of the Sittee River is heterotrophic, with higher rates of respiration than can be accounted for by primary production. This condition is typical of many types of estuaries and riverine systems, where organic detritus from the adjacent forests provide the main energy source for the aquatic food web (Sibert and Naiman 1980, Odum and Heald 1975, Darnell 1961). The overview model shown in Figure 1-1 depicts the flow of detritus from the forest as an important energy input to the river. Finally, the conclusion that the ecosystem is heterotrophic is also supported by the general scarcity of aquatic plants in the Sittee River. Algae are limited to some filamentous attached species (primarily Rhizoclonium sp.) on rock and wood substrates and to thin cyanobacterial mats (primarily Oscillatoria sp.) which cover shallow mud substrates in some locations. Aquatic macrophytes are limited to one patch of emergent plants (Typha sp.) near Sittee River village, to some submerged species found in the freshwater riffles and to a few floating leaved species scattered along the river.

The Riparian Forest

The riparian forest is connected to the river ecosystem, according to the analysis of trophic basis described above, as a source of organic detritus that supports aquatic metabolism. In fact, the riparian forest is also linked to the river in providing bank stabilization and habitat and the two systems are integrated by floods and tides and by movements of animals, such as birds, throughout the length of the river corridor. General discussions of linkages between rivers and riparian forests are given by Cummins (1980), Gregory et al. (1991), Ward (1989) and Lugo et al. (1990) and de la Rosa (1995) provides a review for Central America. Before continuing it may be useful to distinguish between the terms, riparian forest and floodplain. The word "riparian" means stream-side and it is an adjective usually used in reference to a characteristic vegetation type. Floodplain is a geomorphic term for the landscape formed by riverine processes. In general, the riparian forest occupies the floodplain so the two terms are used together in this book.

Riparian forests differ from upland forests in terms of structure and function because of the actions of floods. Although relatively infrequent, floods are high energy events which dominate the ecosystem. Flood subsidies and stressors occur at short (ecological) time scales but when projected over long (evolutionary) time scales, they act as forms of natural selection. Those species that are successful in the floodplain have adaptations to

Table 4-2. Light-dark bottle metabolism of plankton in the lower Sittee River. All light-dark bottle metabolism data were taken during normal flow conditions.

Date	net photosynthesis (mg/l/hr)	respiration (mg/l/hr)
8/9/91	-0.12	0.17
8/13/91	-0.10	0.19
8/20/91	0	0
8/23/01	0	0.01
11/24/91	0	0.03
11/30/91	-0.04	0.05
3/9/92	0.01	0.01
3/12/92	0.01	0
7/14/92	0	0.01
8/1/92	-0.02	0.02
1/4/93	-0.02	0.02
1/11/93	0.01	0.02

take advantage of the energy subsidies and/or to endure the energy stressors of the flood better than competing species that lack special adaptations (Bloom and Voesenek 1996, Kozlowski 1984). Figure 4-1 and 4-2 illustrate some of these subsidies and stressors, respectively. On one hand, as described in the flood-pulse concept, floods bring in materials (such as sediments, nutrients and seeds) which stimulate forest growth and they remove other materials (such as leaf litter and seeds) which stimulate downstream reaches of the river-floodplain ecosystem (Figure 4-1). The ability to have seeds that float in water is an example of an adaptation for taking advantage of this energy subsidy. On the other hand, floods act to reduce the oxygenation of the soil, thereby stressing root function (Figure 4-2). This occurs because the diffusion rate of oxygen is much slower in water (eg., during a flood) than in air (eg., during non-flood conditions). Many floodplain tree species have physiological (such as forms of cellular metabolism that do not accumulate toxic chemical byproducts) or morphological (such as pneumatophores, or breathing roots, that physically bring oxygen into the soil) adaptations for dealing with this stressor.

Along the Sittee River the riparian forest is largely intact, though some clearing has taken place for housing and agriculture. The forest is essentially divided into two types with mangroves found in the lower portions of the river and mixed tropical hardwood species found upstream from the mangrove zone. Mangroves are a taxonomically diverse set of tree species that have adaptations to salinity that allow them to live in seawater. Worldwide, they are a fascinating group of tropical species with unusual morphologies and physiologies that only grow in the coastal zone (Tomlinson 1986). The distribution of mangroves along the Sittee River may provide a kind of complex bioassay of the salinity distribution in the river. Mangroves form dense swamps in the delta and for several kilometers upstream from the rivermouth. Gradually, the mangrove zone narrows upstream and begins to break up into single trees along the river edge. The last mangrove growing on the river is between Possum Point and the village, approximately 8 km (5 miles) from the rivermouth. The salinity of the surface water is typically about 3 o/oo here but the saltwedge extends much beyond this point on the river. The factor or factors causing the upstream limit of mangroves are unknown but probably the metabolic costs of their salinity adaptations out weigh the benefits at some point along the salinity gradient and other tree species are able to out-complete them.

The structure of the riparian forest was studied in several places along the Sittee River and in some related sites for comparison. Measures of forest structure are one way to evaluate the development or maturity of a forest ecosystem. The standard measures are density of trees (number of individuals per unit area of land sampled), basal area (combined area of the cross-sections of tree trunks per unit area of land sampled) and tree height (usually some estimate of the maximum height for the area of land sampled). These kinds of measures are used by foresters to help estimate the amount of wood that a forest can yield upon harvest, but they are also used by ecologists to evaluate the dimensions of the forest as an ecosystem.

The mangrove forest at the mouth of the Sittee River was sampled by undergraduate students in the University of Maryland tropical ecology course during visits to the site in

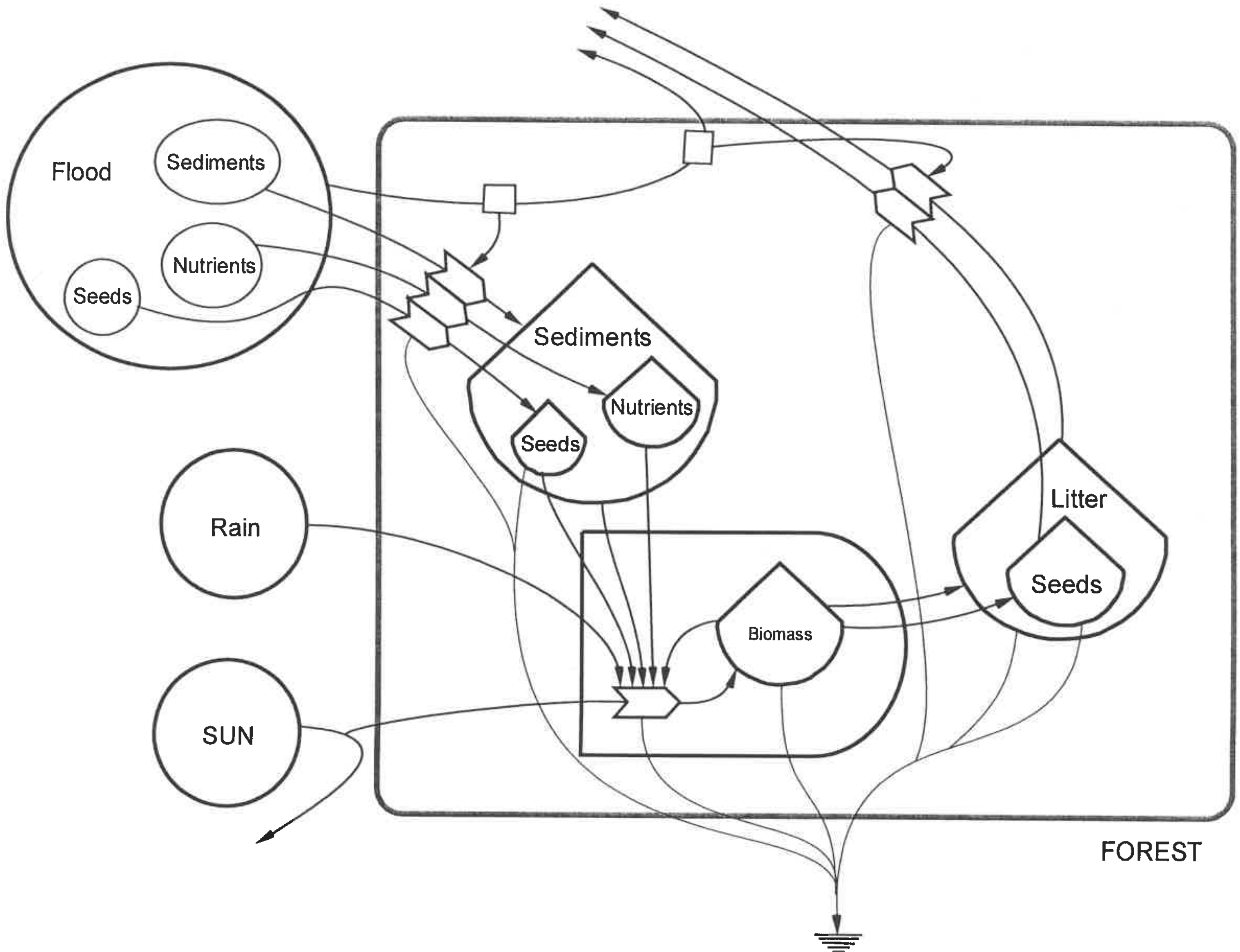

Figure 4-1. Energy circuit diagram of the energy subsidies of a flood to the riparian forest.

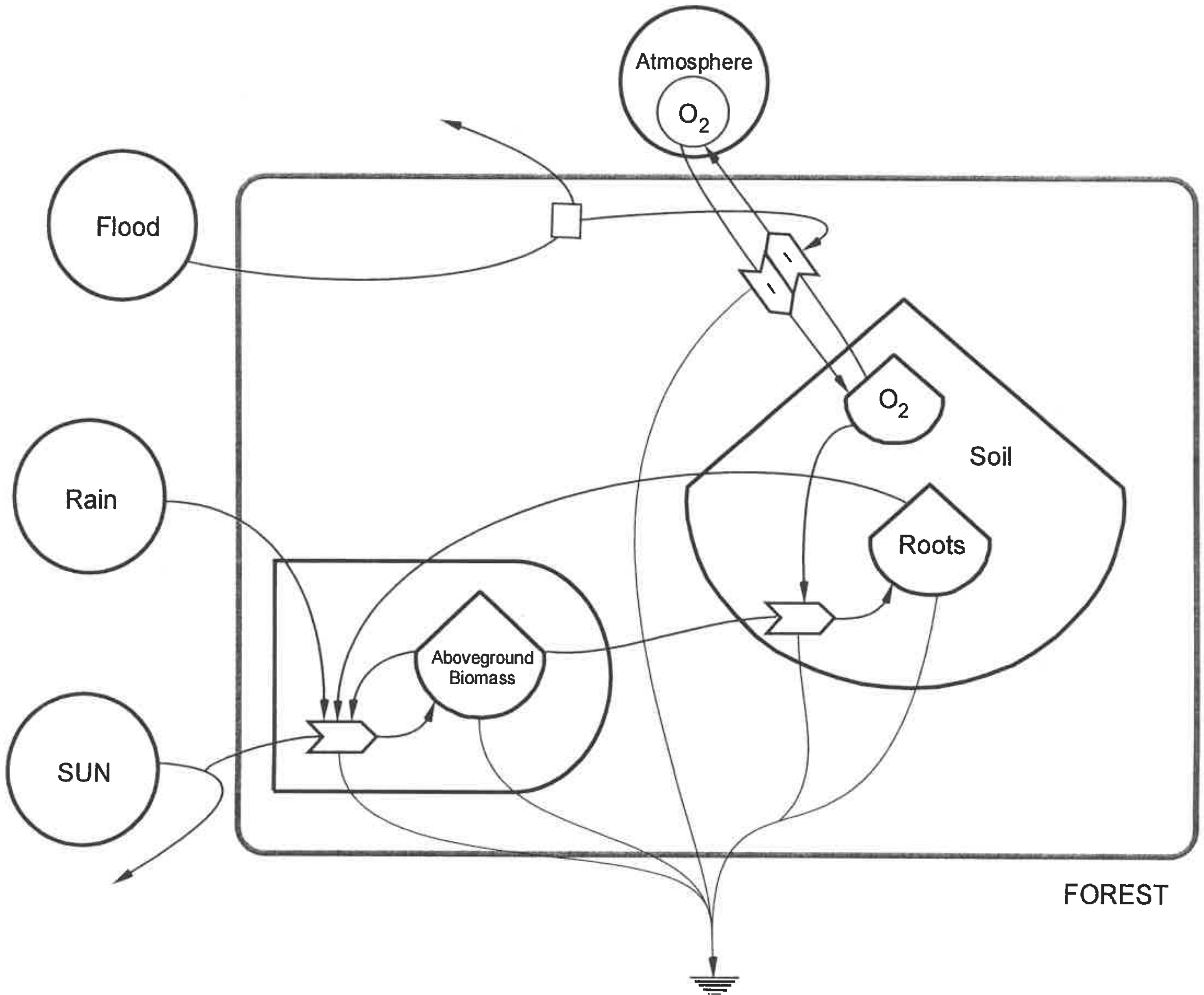

Figure 4-2. Energy circuit diagram of the impact of flooding on the diffusion rate of oxygen into the soil of the riparian forest.

March 1998 and in March 2002, using standard methods (Cintron and Novelli 1984). Measurements were made in transects of five 10 meter by 10 meter square quadrat plots, starting at random locations within the forest near the river mouth. One transect on the north side and one transect on the south side of the river were studied in both 1998 and 2002. Thus, the total sampled area was 0.1 hectare on each side of the river mouth. In each quadrat plot all trees greater than or equal to 1 centimeter in diameter at breast height were identified and their diameters at breast height (DBH) were measured. Basal area of each tree was calculated with the formula for a circle (area = 3.1416 x r^2, were r is the radius or one half of the DBH). Height of the tallest tree in each quadrat plot was measured with a Haga altimeter during sampling in 1998.

The forest at the mouth of the Sittee River is composed of three mangrove species: red mangrove (Rhizophora mangle), white mangrove (Laguncularia racemosa) and black mangrove (Avicennia germinans). Data from the sample plots are summarized in Table 4-3 with an index of the relative importance of each tree species in relation to the total forest community (Importance Value = I. V.). This index combines contributions of density and basal area for each species and it ranges between 1 and 100 with higher values indicating greater relative importance. The forest structure is dominated by red mangroves with an I. V. of 43.5, followed closely by white mangroves with an I. V. of 38.5. Red mangroves had the highest density at 55% of the total community, while white mangroves had the highest basal area at 45% of the total community. Black mangroves were subordinate with an I. V. of 18.0 because they had the smallest relative contributions of both density and basal area.

While the species composition of a mix of red, white and black mangroves shown in Table 4-3 is typical of a mangrove forest anywhere in the Caribbean region, the overall structure of the forest at the mouth of the Sittee River is substantial and, in some regards, among the highest ever reported in the scientific literature. Comparisons are made between data from the Sittee River forest and other similar mangrove forests in Table 4-4. Because mangrove species can form fundamentally different kinds of forests depending on environmental conditions such as tidal fluxes, geomorphic position and salinity levels, only the riverine-type of forests are compared in Table 4-4. The riverine forest type is characterized by optimal growth conditions (Lugo and Snedaker 1974, Cintron et al. 1985), so the data in Table 4-4 represent the maximum levels of mangrove forest structural development. For simplicity of comparison only averages from the scientific literature are compared with the Sittee River forest in the table, but these averages represent more than 20 different studies of riverine mangrove forests in the Neotropics. The Sittee River forest has a lower density but a higher basal area than the average riverine mangrove forest. This suggests that the Sittee River forest is composed of fewer but larger trees per unit of land area in comparison with similar forests. The most significant comparison is for maximum tree height, shown in the final column of Table 4-4. The Sittee River forest is characterized by much taller trees than the average riverine forest. For example, Gilmore and Snedaker (1993) report a forest height for Florida riverine mangroves of 12.6 meters and the maximum height given by Pool et al. (1977) is 17.0 meters. Several taller forests are listed by Brinson (1990) from the west coast of Panama but these forests are dominated by species adapted to freshwater (such as

Table 4-3. Relative contributions of different mangrove species to the overall forest structure at the mouth of the Sittee River. Numbers in parentheses are percentages of the total.

Species	Basal Area (m2/ha)	Density (numbers/ha)	Importance Value*
R. mangle (red mangrove)	20.8 (32)	775 (55)	43.5
L. racemosa (white mangrove)	28.7 (45)	450 (32)	38.5
A. germinans (black mangrove)	14.7 (23)	190 (13)	18.0
TOTAL	64.2	1415	

* Importance Value = average of the basal area percentage and the density percentage

Table 4-4. Forest structure data for riverine mangroves from the Neotropics. Measures of variation (standard error or range) for the data from the literature are listed as given in the original references.

Reference	Basal Area (m2/ha)	Density numbers/ha)	Tree Height (m)
Flores-Verdugo et al. 1992	mean = 41.3 standard error = 350	mean = 1730 standard error = 350	mean = 17.7 standard error = 3.7
Brinson 1990	mean = 33.2 range = 11.5-96.4	mean = 2131 range = 400-4670	mean = 14.0 range = 7.5-21.8
Sittee River	64.2	1415	26.6

Pterocarpus officinalis) rather than the typical mangrove species characteristic of higher salinities found at riverine sites such as at the mouth of the Sittee River. The finding of very tall trees at the mouth of the Sittee River is consistent with other structural characteristics described above. Comparisons of density and basal area indicated that these trees are larger in diameter relative to other riverine sites. Thus, it seems reasonable to expect that trees that are larger in diameter would also be taller than average.

The most significant conclusion from this analysis of forest structure is that the mangroves at the mouth of the Sittee River are among the tallest ever reported for the Caribbean region! Tree height is an important measure of forest structural development since it is used by foresters as a direct indication of the quality of conditions for tree growth at a site. The conclusion is that the mouth of the Sittee River represents the optimal conditions for mangrove development and the forest found there has a very high level of structural development. The causal basis for the excellent site conditions are the combination of freshwater flows and sediments carried by the river itself, draining from the Maya Mountains, along with tidal flushing from the Caribbean Sea. The soil profile of the forest supports the causal hypothesis for the fertility of the site. The generalized profile shown in Figure 4-3 was derived from three pits dug in the forest (one on the north side of the rivermouth and two on the south side). Three horizons are found in the profile with the upper layer (top 30 cm) dominated by a dense root mat. The surface root mat is characteristic of forested wetlands due to the anaerobic conditions in the soil. Mangroves have adaptations for aerating the soils but the majority of the roots are still confined to the surface layer of the soil where oxygen concentrations are higher. The most significant feature of the profile is the lack of peat, which would indicate stagnant conditions. Instead, the lower horizons are dominated by a mineral soil with silt and sand-sized particles. These sediments are likely to have been deposited by floods. Thus, the composition of the soil profile reflects the high degree of flushing by tides and river flows that bring in nutrients and contribute to the fertility of the site.

In conclusion, the forest at Sittee Point has some of the "old-growth" characteristics (Lugo 1997) that suggest that it has been free from human disturbance. The pristine conditions of the forest are probably due to its isolation from cities and towns. However, human development is beginning to increase around the forest, especially from the direction of Hopkins to the north. Impacts from this development will surely degrade the forest over time, as has happened along every other tropical coastline in the world (Valiela et al. 2001). The opportunity still exists for the people of Belize to preserve the forest at the mouth of the Sittee River as an example of the highest level of natural development of mangrove forest structure in the Caribbean region.

The data described above are for the riverine-type forest but other mangrove forest types are found nearby which have very different kinds of forest structure. Table 4-5 compares the riverine mangroves with dwarf mangroves from All Pines, which is located on the coast about 5 km south of the rivermouth, and with overwash mangroves on Wee Wee Caye. The dwarf mangrove site is a fully mature "forest" of meter tall red mangrove trees. This type of forest is found worldwide in sites where stressors limit tree height

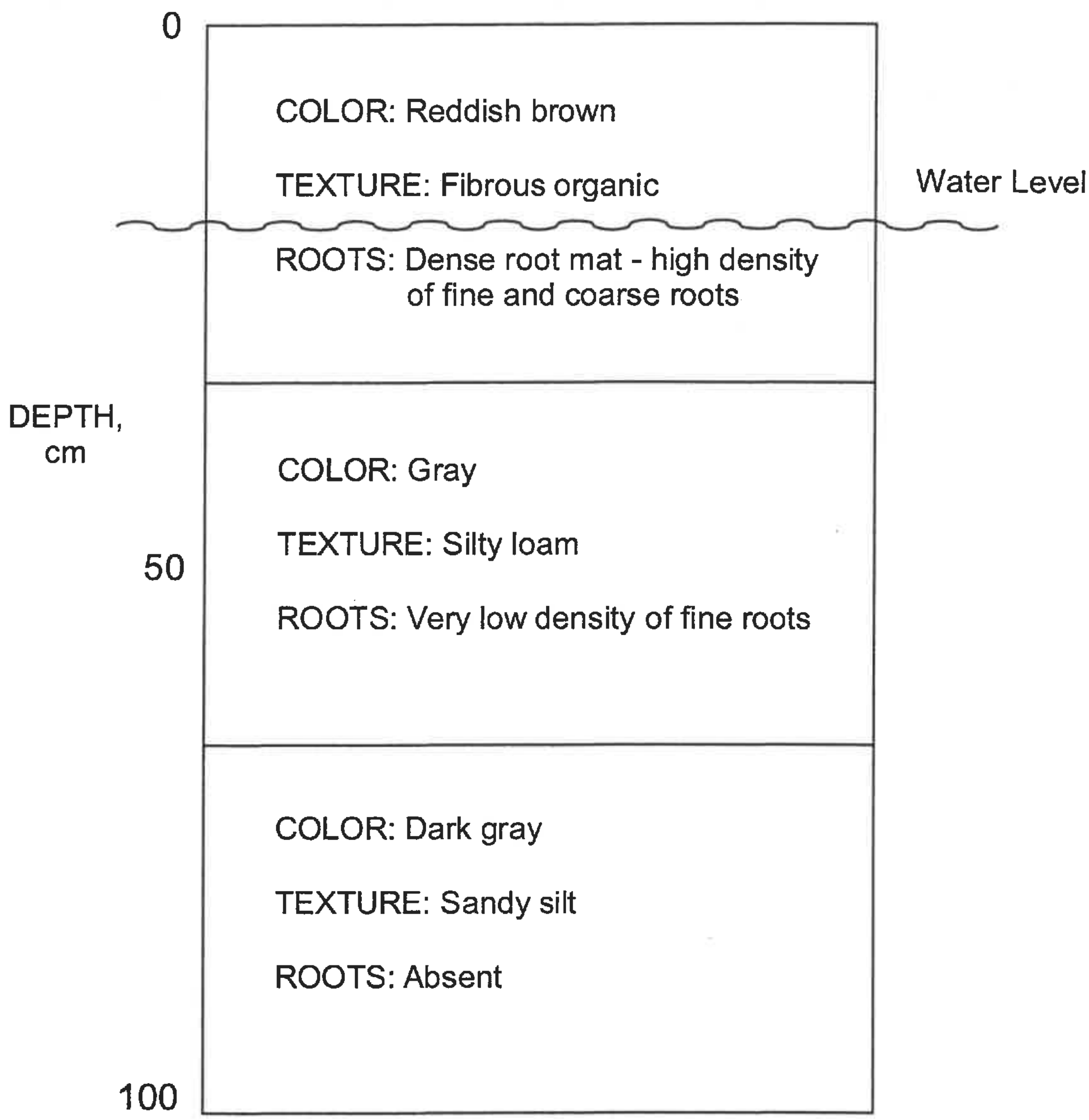

Figure 4-3. Soil profile description in the mangrove forest at Sittee Point.

Table 4-5. Comparison of forest structure measures for different kinds of mangroves. Forest types are shown in parentheses under the site names.

Site	Basal Area, m2/ha	Density, trees/ha	Tree Height, meters	Number of Species
Sittee Point (riverine)	64.2	1415	26.6	3
All Pines (dwarf)	_____*	9550	1.1	1
Wee Wee Caye (overwash)	19.9	1533	10.4	2

* Dwarf trees were all less than 1 cm DBH.

growth. The causes of dwarfing at the All Pines site are not known but may involve low fertility or hypersalinity in the soil. The site is located in a hydrologically isolated lagoon and high evaporation rates may lead to high concentrations of salts in the soil and the overlying shallow waters. The close proximity of the short mangroves at All Pines and the tall mangroves at Sittee Point is remarkable and dramatically illustrates the roles of energy sources and limiting factors in controlling ecosystem structure. The overwash forest at Wee Wee Caye has structural properties that are intermediate between the dwarf forest and the riverine mangroves. The location of this site on a small island on the barrier reef means that the forest is frequently exposed to storm surges and high winds and it is cut off from external nutrient sources. These factors limit tree growth and result in reduced structural development of the forest. In general, mangroves are very interesting trees and they form very interesting forests. At least in the Neotropics, they differ from other types of tropical forests by being composed of a low diversity of species. However, they compensate for this low species diversity with a high phenotypic plasticity which allows them to form a number of different types of forests, as reflected in the forest structure data illustrated above.

Upstream from the mangrove zone the riparian forest is composed of a diversity of tropical tree species, with adaptation for surviving seasonal flooded conditions. In many places the forest appears to match the popular image of a tropical jungle with dense foliage from the forest floor to the top of the canopy. This view is most obvious looking into the forest from a boat on the river. Here the lush plant growth is caused by the maximum intensity of sunlight across the exposed cross-section of the forest. However, inside the forest the vegetation is often quite open. The cross-sectional view of the forest drawn by Luisa Robles using the Holdridge style profile diagram (Holdridge 1967, 1970) illustrates the diversity of species and structural appearance of the riparian forest along the lower Sittee River (Figure 4-4).

Kim (1991) recorded the tree species composition of the riparian forest on the south side of the river down stream from Possum Point and on the north side of the river at Bocatura Bank. Tree identification in Kim's study and in later work was done with the help of the Possum Point staff and with the aid of a species list prepared by Paul Godfrey on a site visit in 1987. Most individual trees were identified to the genus or species level but a relatively small number could not be identified and they are listed as unknowns in the data tables. Kim found 17 species of trees in the riparian forest and only about 2% of the individuals could not be identified (Table 4-6). Coconut palm (Cocos nucifera) was the dominant species in the forest, comprising nearly two thirds of the stem density. This important tree has a Pantropical distribution and is most often found along sea coasts. The distribution of the species, both globally and locally along the Sittee River, has been influenced by humans who have planted it at some time in the past for the various useful products that can be derived from it (Cook 1910, Vandermeer 1983, Harries 2001). The coconut palms along the Sittee River were a self-reproducing "wild" population but their origin probably was due to human domestication, perhaps dating to the pre-Hispanic Maya. However, their dominance in the plant community in the early 1990s was due to their competitive superiority involving aspects of dispersal, germination and fast-growth adaptations within the riparian forest. The record of dominance by coconuts from the

Figure 4-4. Cross-section of the riparian forest in the vicinity of Possum Point.

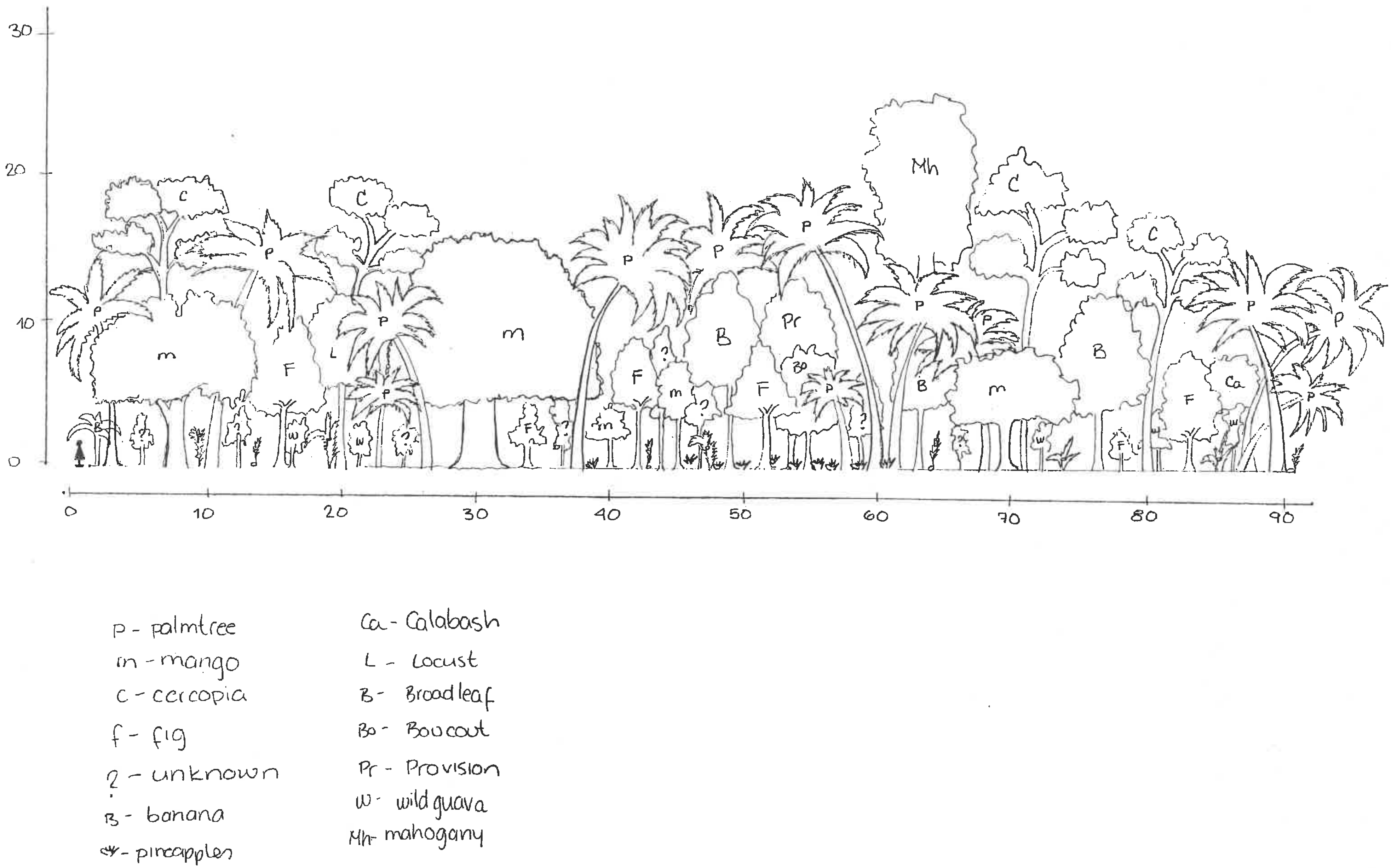

Table 4-6. Tree community composition of the riparian forest (Kim 1991). Total sample area was 0.7745ha.

Species	number of trees	relative abundance (%)
Cocos nucifera, Coconut palm	377	63.6
Cecropia peltata, Trumpet	55	9.3
Miconia punctata, Red broad leaf	39	6.6
Mangifera indica, Mango	29	4.9
Stemmadenia donell-smithii, Cojoton	18	3.0
Ficus sp., Fig	15	2.5
Guazuma ulmifolia, Bay cedar	15	2.5
Spondias mombia, Hog plum	7	1.2
Artocarpus altilis, Breadfruit	7	1.2
Eugenia malaecensis, Molly apple	5	0.8
Acosmium nitida, Billy webb	4	0.7
Hymenaea courbaril , Locust	2	0.3
Miconia argentea, White broad leaf	2	0.3
Miconia argentea, White maya	2	0.3
Cassia grandis, Bocut	1	0.2
Pinus caribaea, Pine	1	0.2
Inga rodrigueziana, Tumatuma	1	0.2
Unknowns	13	2.2
Total	593	100

early 1990s is especially noteworthy given that the species experienced high mortality due to disease in the late 1990s as will be discussed later.

Patches of specialized forest types also are scattered along the length of the river, that add to both the habitat and the species diversity of the overall riparian forest. One example is the kaway swamp, which is one of the sample locations in the salinity transect (Table 3-). The forest at this site is a depressional forested wetland. Flood waters are retained in the depression in the floodplain during the rainy season which causes anaerobic soil conditions. The tree community is highly dominated by kaway (Pterocarpus officinalis) which is a common swamp tree throughout the Caribbean region (Alvarez-Lopez 1990). Kaway has the special adaptation of highly buttressed trunks which presumably lend stability and perhaps aeration to the tree. The kaway swamp also is characterized by a thick litter layer in comparison with typical, better drained sites (Table 4-7). The thick litter layer is probably the result of reduced decomposition rates, caused by the anaerobic soil conditions. This site is thought by the Possum Point staff to support a relatively high density of the deadly fer-de-lance (Bothrops asper) in the dry season. The high density of snakes may in fact be correlated with the thick litter which provides cover for the predators. As an aside, all field work along the Sittee River is done with an awareness of the possible presence of the fer-de-lance (the local name is the yellow-jawed tommygoff). This common snake, which can grow to greater than 2 meters in length (greater than 6 feet), is in the family Crotalidae, along with rattlesnakes and other pit vipers. Juvenile fer-de-lance feed on lizards and frogs while adults feed primarily on small mammals. The species is well camouflaged in coloration to match with leaf litter and it is aggressive and highly poisonous, making for a dangerous combination of adaptations (Colwell 1985). One of the Possum Point staff (Clifford Robinson) was bitten by a fer-de-lance and nearly died from a reaction to the poison. Rabinowitz (1986) describes several encounters with this species in the nearby Cockscomb Mountains, including one bite that resulted in a trip to Sittee River for treatment of one of his field assistants by the local "snake doctor".

Early in the study it was assumed that the riparian forest was relatively undisturbed and that it represented more-or-less natural conditions. Gradually however it became clear that portions of the riparian forest, extending from the end of the mangrove zone upriver nearly to the village, were not natural assemblages of tree species but rather a mix of domesticated species, mostly fruit trees, along with wildland species. This section of the river had been sparsely settled by people dating back at least to the 1800s. However, the houses were destroyed by Hurricane Hattie in 1961 and the people moved upriver, concentrating in the location of the present day Sittee River village. Invasion of wildland species began immediately after the hurricane as natural succession engulfed the abandoned home sites. Some of the domesticated tree species that were planted around the houses, in home gardens, survived the hurricane and mixed in with the invading wildland species. Thus, the riparian forest along the Sittee River is a new forest type that has emerged as a combination of domesticated species and wildland species.

To describe this new forest type, the tree community was studied in small plots around 10 abandoned home sites (Ungar 1998). Tree communities were composed of 9

Table 4-7. Tree community structure at the Kaway swamp. Data is from a 300 m2 sample of the swamp community.

Species	number of individuals	average diameter, cm (maximum diameter)
Kaway	42	18.4 (79.0)
Fig	33	4.2 (14.8)
Provision	3	12.6 (20.5)
Poisonwood	7	8.8 (11.1)
Unknown	7	3.9 (13.6)
Wild guava	3	1.4 (1.7)
Total	95	

domesticated, fruit-bearing species from the old home gardens and 22 wildland species along with a few unknowns (Table 4-8). The old home garden species made significant contributions to the basal area of the forest plots (53.6%) but they were much less significant in terms of density (19.1%). These results indicate that the majority of the old home garden species survive as a few, large individuals among the wildland invaders. The most important fruit-bearing tree species at the abandoned home garden sites were mango (Mangifera indica), coconut (Cocos nucifera), molly apple (Eugenia malaecensis) and craboo (Byrsonima crassifolia) (Table 4-9). Wildland species found at the home sites are listed in Table 4-10. To gain further perspective on the new forest organization, existing home gardens in Sittee River village were examined. These home or dooryard gardens are a well known feature of the tropical landscape (Landauer and Brazil 1990). They consist of diverse assemblage of intentionally planted species around homes that provide useful products to the human occupants. The conservation value of home gardens has been described because they represent semi-natural islands of forest habitat analogs in otherwise deforested settings (Steinberg 1998). Five home gardens around currently occupied houses were measured for forest structure statistics (Table 4-11). The active sites were located upriver from the abandoned houses in Sittee River village. A total of 24 fruit-bearing tree species was found at these sites, including some of the species that have survived in the forests at the old abandoned home sites (Tables 4-12). The new forests at abandoned home sites have emerged through natural selection. One view is that they are an ordered assemblage derived by self-organization of available species from the old home gardens on one hand and from the surrounding forest on the other hand. From the species pool of the original home gardens (represented by the 24 species from currently active gardens) certain species survived as the wildland species invaded (represented by the 9 species from the abandoned gardens). However, many of these species are "living dead" (Janzen 1986) which are species that are still alive but can't reproduce because their habitats have changed. They will ultimately be selected out of the forest once the large, old individuals die off, leaving only those species from the original set of 24 that are preadapted to survive in the new forest. Along the Sittee River four of the domesticated fruit-bearing trees are reproducing at the abandoned home sites (mango, craboo, coconut and molly apple) and in the long run these species may survive and share the forest with the wildland species. The forests that are emerging at the abandoned home sites are models for the economic forests that conservation biologists are trying to construct throughout the Tropics. They provide the normal ecosystem services characteristic of forests (such as buffering water quality impacts in riparian forests) while producing useful, economic products that can generate income for local people (such as fruits that can be consumed or sold in a market). These forests can thus be the basis for the non-timber forest harvest paradigm from tropical conservation biology.

A final note concerning the riparian forest is an update on the species composition and forest structure data reported above. Starting in about 2000 a disease epidemic that has been sweeping across the Caribbean reached Sittee River and killed many of the coconut trees along the river. The disease is called lethal yellowing because of the effect it has on the color of the leaves (McCoy 1988). It is caused by a virus-like microbe (a phytoplasma) which is spread by a herbivorous plant-sucking insect (a plant hopper). In

Table 4-8. Forest structure of abandoned home garden sites along the Sittee River. Numbers in parentheses are the fruit tree percentage of the totals. Average sample plot size per home garden was 0.04 ha.

Site number	basal area (m2/ha)	density (number/ha)	number of species (exclusive of unknowns)
1	77.7 (28)	2571 (9)	7 (43)
2	37.7 (58)	1567 (11)	8 (38)
3	39.8 (94)	750 (42)	8 (38)
4	25.0 (82)	1658 (35)	7 (43)
5	72.4 (76)	3647 (17)	12 (42)
6	43.5 (52)	3175 (9)	11 (36)
7	27.8 (74)	4162 (3)	14 (21)
8	50.8 (21)	3560 (47)	15 (27)
9	71.0 (7)	786 (12)	8 (38)
10	20.2 (44)	2262 (6)	6 (33)
average	46.6 (53.6)	2414 (19.1)	9.6 (35.9)

Table 4-9. Structure of the fruit tree subcommunity in abandoned home gardens (n=10). Importance value is the average of relative basal area and relative density.

Species	Importance Value	Frequency
Mango	36.6	8/10
Coconut	33.6	9/10
Molly apple	14.7	2/10
Craboo	7.6	5/10
Breadfruit	3.6	2/10
Boucout	1.4	2/10
Supa palm	1.1	1/10
Orange	1.0	2/10
Calabash	0.4	1/10

Table 4-10. Wildland species of trees found at the abandoned home garden sites.

Scientific name	local common name
Ficus sp.	fig
Ficus sp.	strangler fig
Tabebuia rosea	mayflower
Alibertia edulis	wild guava
Miconia sp.	broadleaf
Swietenia macrophylla	mahogany
Spondias mombin	hogplum
Cecropia peltata	trumpet tree
Alchornea latifolia	fiddlewood
Xylopia frutescens	polewood
Pachira aquatica	provision
Calophyllum brasiliense	santa maria
Pterocarpus officinalis	kaway
Hymenaea courbaril	locust
Zanthoxylum sp.	prickly yellow
Coccoloba belizensis	wild grape
Trichilia minutiflora	wild lime
Euterpe macrospadix	cabbage palm
Inga rodrigueziana	tomatoma
Pinus caribaea	Caribbean pine
Alsophila mysuroides	tree fern
Byrsonima crassifolia?	blackberry

Table 4-11. Forest structure statistics for fruit trees in existing home gardens. Average sample plot size per home garden was 0.15 ha.

Site	basal area (m2/ha)	density (number/ha)	number of species
Terry's	12.1	257	10
Joan's	11.3	200	19
Myrna's	3.8	113	10
Clifford's father	13.8	269	11
Clifford's	10.2	126	8
Average	10.2	193	11.6

Table 4-12. Structure of the fruit tree community in existing home gardens (n=5). Importance value is the average of relative basal area and relative density.

Species	Importance Value	frequency
Mango	38.2	4/5
Orange	10.0	4/5
Coconut	7.6	4/5
Cashew	7.0	3/5
Guava	5.0	4/5
Molly apple	4.2	4/5
Sour sap	4.1	5/5
Craboo	3.9	5/5
Grapefruit	2.7	3/5
Rose apple	2.4	3/5
Chocolate	2.2	2/5
Calabash	1.6	1/5
Papaya	1.5	2/5
Boucout	1.5	1/5
Pysic nut	1.4	2/5
Jack fruit	1.2	2/5
Sweet lime	1.1	2/5
Golden plum	1.1	1/5
Cherry	0.7	2/5
Breadfruit	0.7	1/5
Mammy apple	0.6	1/5
Pisaboo	0.5	1/5
Sweet lemon	0.4	1/5
Avocado	0.4	1/5

some ways this has been a tragic event because some of the local people depended on the coconuts as a source of cooking oil that was sold to generate income. This economy has basically disappeared from the village and the impact of its loss will be discussed later. The mass mortality caused by the disease was an amazing event that demonstrates the power of disease to transform ecosystems. A few individual coconut trees that have resistance to the disease survive along the river but they are unable to set seed and reproduce. Ecologically, the riparian forest continues to function without much contribution from this once dominant species and other tree species are growing into the gaps left in the forest by the dead coconuts.

Benthic Macroinvertebrates

Benthic macroinvertebrates occupy lower levels in the river food web and they are the first macroscopic animals to interface with the litterfall from the riparian forest. Because of their relatively small size (about 0.1 – 10 cm in length) benthic macroinvertebrates are characterized by a nexus of evolutionary constraints (Figure 4-5). Their small size limits their ability to swim in strong currents and forces them either to remain in slow moving waters or to develop special adaptations to withstand higher current velocities. Limited mobility also forces macroinvertebrate taxa to adapt to particular types of substrates, often for attachment, for refuge from predators or for feeding. Within the limits of these constraints however, a taxonomically wide, variety of animals can be found among the benthic microhabitats of the Sittee River channel.

Populations of macroinvertebrates were sampled qualitatively at three sites along the salinity gradient: at the rivermouth in the marine zone, at Bocatura Bank and Possum Point in the brackish zone and at the sand bank in the freshwater zone. Intensive sampling occurred in the early 1990s with a resurvey in 2005. Invertebrates were picked off hard substrates (wood and rocks) or sorted with a strainer and picked from soft substrates (plant detritus and fine sediments). After identification relative abundances were assigned to each taxa by using four categories: rare, uncommon, common and abundant. This sample approach was biased towards shallow water habitats. The benthos of some deeper portions of the river were examined by snorkeling. Burrows were seen in the fine sediments of the river bottom indicating the presence of invertebrates. A ponar dredge was used in an effort to sample these deep water habitats but no animals were collected.

The highest number of taxa of benthic macroinvertebrates were found in the freshwater zone at the sand bank station (Table 4-13), more than twice the number found at the brackish water zone. Several kinds of microhabitats were found at this site including rock covered riffles, pools with fine sediments and leaf packs and vegetated banks. Aquatic insects dominated the taxonomic richness of the site, contributing 28 of the 34 total taxa found here. The numerically dominant taxa were mayflies (Ephemeroptera), caddisflies (Trichoptera) and freshwater shrimp (Decapoda), but many other taxa were rare which is commonly found in a diverse community. Lower numbers of taxa were found in the marine (Table 4-14) and brackish (Table 4-15) zones, with 21 taxa collected at the rivermouth and 15 taxa at Bocatura Bank/Possum Point. Only a few microhabitats

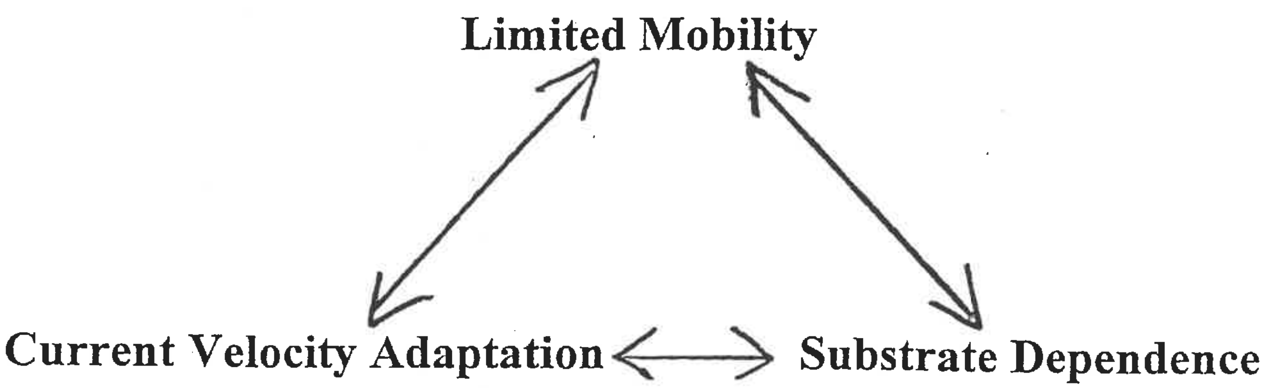

Figure 4-5. The nexus of evolutionary factors that constrain benthic macroinvertebrates.

Table 4-13. Benthic macroinvertebrate abundances in the freshwater zone of the Sittee River at the Sand Bank.

Taxa	Abundance Class	Feeding Category*
INSECTA		
Coleoptera - Psephenidae	rare	SC
- Elmidae	uncommon	GC
- Noteridae	rare	PR
- Gyrinidae	rare	PR
Anisoptera - Macromiidae	common	PR
- Libellulidae	rare	PR
Zygoptera - Coenagrionidae	uncommon	PR
- Calopterigidae	rare	PR
Hemiptera - Nepidae	rare	PR
- Notonectidae	rare	PR
- Naucoridae	rare	PR
- Gerridae	rare	PR
- Belostomatidae	rare	PR
Ephemeroptera - Leptophlebiidae	abundant	GC
- Baetidae	abundant	GC
- Heptageniidae	uncommon	SC
- Oligoneuridae	rare	FC
- Trichorythidae	rare	GC

Table 4-13. Sand bar invertebrates continued.

Taxa	Abundance Class	Feeding Category*
Trichoptera - Philopotamidae	abundant	FC
- Hydropsychidae	abundant	FC
- Polycentropodidae	rare	PR
- Helicopsychidae	uncommon	SC
Diptera - Chironomidae	rare	GC
- Simuliidae	common	FC
- Sciomyzidae	rare	PR
Megaloptera - Corydalidae	rare	PR
Plecoptera - Perlidae	rare	PR
Lepidoptera - Pyralidae	rare	SH
CRUSTACEA		
Decapoda - Palaemonidae	common	GC
- Atyidae	common	GC
- Portunidae	rare	GC
HYDRACARINA	rare	PR
OLIGOCHAETA	rare	GC
GASTROPODA - Pleuroceridae	common	SC

*PR=predator, FC=filtering collector, GC=gathering collector, SC=scraper, SH=shredder were found at these sites, including vegetated banks and fine sediments. In general, insects lack adaptations for living in saline waters so their taxonomic diversity was much reduced at the marine and brackish sites. Several insect taxa found at these sites either live on the surface film of the water (Gerridae) or have special adaptations for breathing air from the surface (Belostomatidae and Notonectidae). Crustacea and Mollusca were represented by greater numbers of taxa at the marine and brackish sites than at the freshwater sites and the numerically dominant taxa were amphipods and decapods. Shrimp (Atyidae and Palaemonidae) were important taxa at both the freshwater and brackish sites. These types of animals are known to have several direct and indirect effects in tropical streams (Crowl et al. 2001, Pringle 1996, Pringle et al. 1993). They were also important food items in fish diets within the Sittee River (Table 4-). Common benthic macroinvertebrate taxa are shown in Figure 4-6.

An overview of the taxonomic diversity of benthic macroinvertebrates sampled in this study is shown in Table 4-16. The freshwater site had the highest fidelity of taxa with 79% of the total. Lower levels of fidelity were found at the brackish and marine sites. Taxonomic diversity is especially depressed at the brackish site with only 7% of the total site taxa being found only at this site. The brackish site shares 10 taxa (67%) with the marine site and 7 taxa (47%) with the freshwater site. Only three taxa, the midge fly family Chironomidae and two decapod families (Palaemonidae and Portunidae) were found at all three sites.

From a trophic perspective, benthic macroinvertebrates are the primary consumers in the river food web. All of the main feeding types for macroinvertebrates are represented in the Sittee River taxa. These feeding types include Cummins' (1973) classification for freshwater animals: 1) scrapers (SC) that eat algal periphyton and settled particulate organic matter (POM), 2) collector-gathers (GC) that eat bacteria, fungi, and POM, 3) collector-filters (FC) that eat suspended POM, 4) shredders (SH) that eat leaf litter itself and 5) predators (PR) that eat other macroinvertebrates. Also, the classification of Day et al. (1989) for estuarine animals includes 1) suspension feeders and filter feeders that trap or filter particles from the water column, 2) deposit feeders that feed by ingesting sediment along with 3) predators and parasites. Primary consumption by invertebrates begins food chains that are classified as grazing (based on live plants) or detrital (based on dead plants or animals). As discussed in the ecosystem metabolism section, most of the energy flow in the Sittee River is through detrital pathways. The processing of detrital energy sources in aquatic ecosystems is fairly well understood for the temperate zone (Boling et al. 1975, Maltby 1992, Anderson and Sedell 1979) and this type of energy flow presumably functions in a similar way in the Tropics. Except for shredders that obtain energy directly from fallen leaf litter, most detritivores obtain more energy from the microbes that colonize the leaf litter once it becomes submerged, than from the leaf litter itself. Because the microbial biomass has a higher nutritive value than the dead plant biomass, in terms of the carbon to nitrogen ratio, the detritus becomes enriched over time in a colonization process termed conditioning. Cummins (1974) described the detritus particles that result from microbial conditioning with the metaphor of a peanut butter cracker. Thus, from the detritivores' point of view, the microbes are like the nutritious peanut butter, while the detritus particle is like the nutritionally poor cracker.

Table 4-14. Benthic macroinvertebrate abundances in the marine zone at the Rivermouth station.

Taxa	Abundance Class	Feeding Category*
INSECTA		
Diptera - Chironomidae	rare	GC
CRUSTACEA		
Decapoda - Hippidae	uncommon	GC
- Grapsidae	common	SH
- Xanthidae	common	SH
- Paguridae	rare	GC
-Majidae	rare	GC
- Portunidae	rare	GC
- Palaemonidae	uncommon	GC
- Alpheidae	rare	PR
Amphipoda - Gammaridae	abundant	GC
Isopoda - Sphaeromidae	uncommon	GC
- Ligididae	rare	GC

Table 4-14. Rivermouth invertebrates continued.

Taxa	Abundance Class	Feeding Category*
MOLLUSCA		
Gastropoda - Neritidae	common	GC
- Littorinidae	common	SC
- Modulidae	rare	SC
Bivalvia - Pholadidae	common	FC
- Teredinidae	common	FC
- Mytilidae	uncommon	FC
- Isognomonidae	rare	FC
ECHINODERMATA - Ophiuroidea	rare	GC
POLYCHAETA	uncommon	GC

*PR=predator, FC=filtering collector, GC=gathering collector, SC=scraper, SH=shredder

Table 4-15. Benthic macroinvertebrate abundances in the brackish zone at Bocatura Bank/Possum Point.

Taxa	Abundance Class	Feeding Category*
INSECTA		
Hemiptera - Notonectidae	uncommon	PR
- Nepidae	rare	PR
- Gerridae	uncommon	PR
Diptera - Chironomidae	rare	GC
- Tabanidae	rare	PR
CRUSTACEA		
Decapoda - Palaemonidae	abundant	GC
- Atyidae	common	GC
- Portunidae	rare	GC
- Grapsidae	common	SH
- Xanthidae	rare	SH
Amphipoda - Gammaridae	uncommon	GC
Isopoda - Sphaeronidae	rare	GC
MOLLUSCA		
Bivalvia - Mytilidae	rare	FC
- Teredinidae	uncommon	FC
POLYCHAETA	uncommon	GC

*PR=predator, FC=filtering collector, GC=gathering collector, SH=shredder

Table 4-16. Macroinvertebrate community comparisons.

Zone	total taxa	taxa only found in this zone	ratio of the two columns
Marine	21	11	52%
Brackish	15	1	7%
Freshwater	34	27	79%

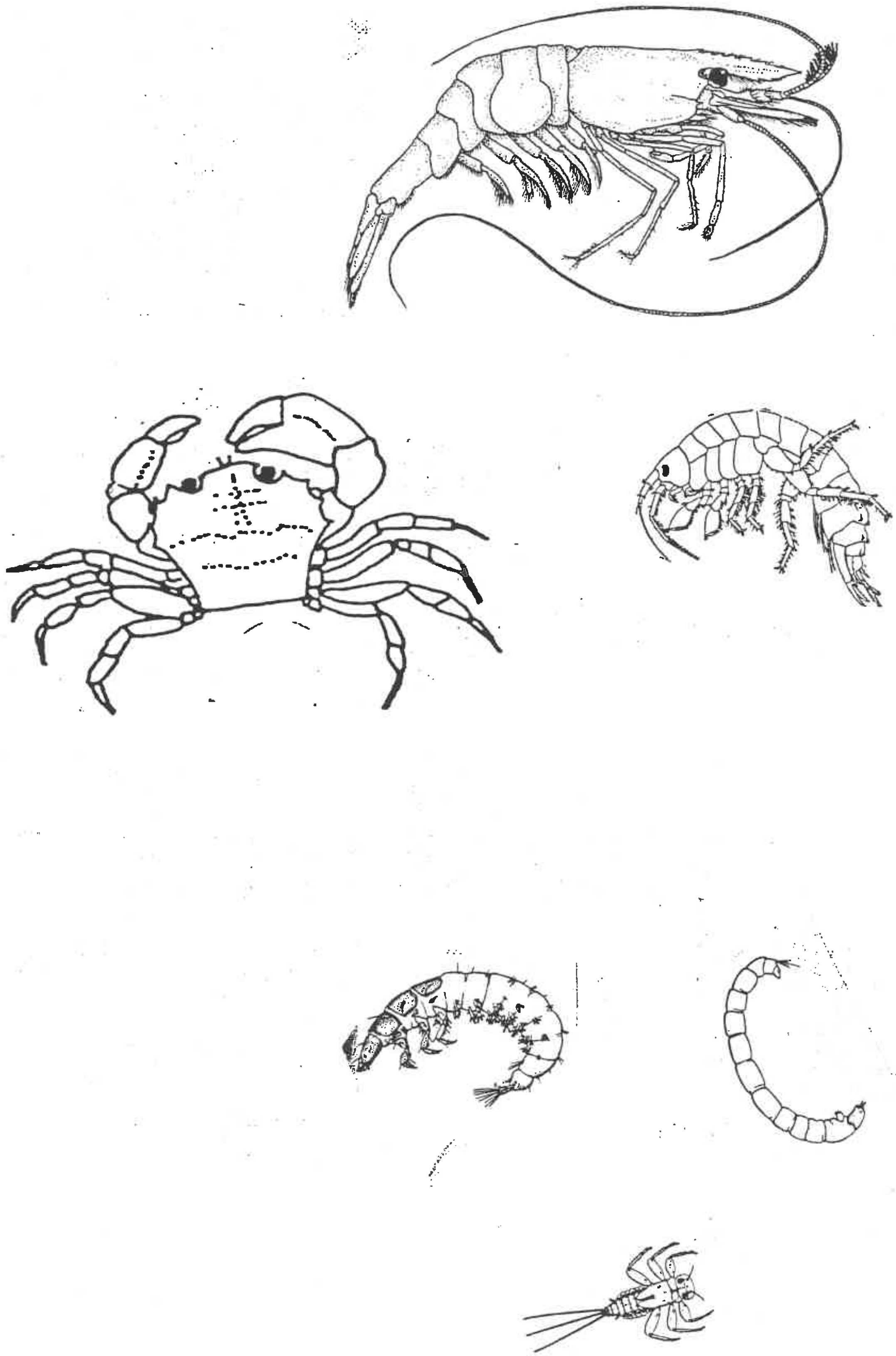

Figure 4-6. Common benthic macroinvertebrates from Sittee River.

Functional feeding categories for the individual macroinvertebrate taxa are listed in Tables 4-13 – 4-15. These determinations are primarily from Barbour et al. (1999) with input from Dudgeon (1999) and Covich and McDowell (1996). Total community data are synthesized in Figure 4-7. These pie charts were constructed by 1) first, converting the qualitative, relative abundance classes into quantitative, relative scores: abundant=10, common=7, uncommon=3, rare=1; 2) second, summing up all quantitative relative scores within the functional feeding groups; and 3) third, plotting the sums as percentages of the total for each site. Gathering collectors and filtering collectors dominate all of the macroinvertebrate communities but there are other differences between the sites. Macroinvertebrate predators are especially important at the freshwater site (with 16 taxa and 22% of the total functional feeding categories) but they are practically absent from the marine site (with only 1 taxa and 1% of the total functional feeding categories). Apparently vertebrate predators (fishes and birds) take the place of macroinvertebrate predators at the marine site. Proportions of scrapers and shredders also differ between sites. Overall, there are many differences in the longitudinal pattern of functional feeding categories in the Sittee River as compared with the classic river continuum pattern (Vannote et al. 1980). These differences are not unexpected since in the river continuum pattern changes in functional feeding categories relate to changes in energy sources (detritus vs. sunlight) as a function of stream order, while within the study area of the Sittee River all of the sites are within the same stream order and have the same energy source (detritus). The pattern of longitudinal change in Sittee River is probably due to the shifts in taxa due to the salinity gradient.

The functional feeding classifications described above emphasize how animals eat rather than explicitly what they eat. Many benthic macroinvertebrates are opportunistic omnivores that will eat algae, detritus, microfauna and carrion. This kind of trophic niche especially characterizes the more mobile decapods and amphipods that dominate the benthos in the lower portions of the Sittee River. Taken as a whole, detritus may be the least preferred food source for invertebrates but, because of its abundant supply, detrital food chains dominate the ecosystem.

One particularly interesting macroinvertebrate taxa found at the marine and brackish sites (Tables 4-14 and 4-15) is the shipworm ( ). This animal is actually not a worm but a small bivalve mollusk that burrows through dead wood that falls or washes into the river. The biology of wood boring shipworms is well known because of the need by humans to understand and control their destructive effects on wooden wharf pilings and ships (Morton 1978, Turner 1984). In the river however, the shipworms have a positive effect on the ecosystem. Figure 4-8 shows the unusual niche of this macroinvertebrate. The adult shipworm is only found within tunnels that it forms by feeding on the wood (the lower workgate symbol bringing energy into the shipworm storage). These tunnels provide protection from predators (shown as the negative drag workgate symbol on the flow of energy from shipworms to predators) and they provide habitat for filter feeding on suspended detritus in the water column which is another form of nutrition for the animal (the upper workgate symbol bringing energy into the shipworm storage). An important indirect effect of this life style is enhanced decomposition of the dead wood

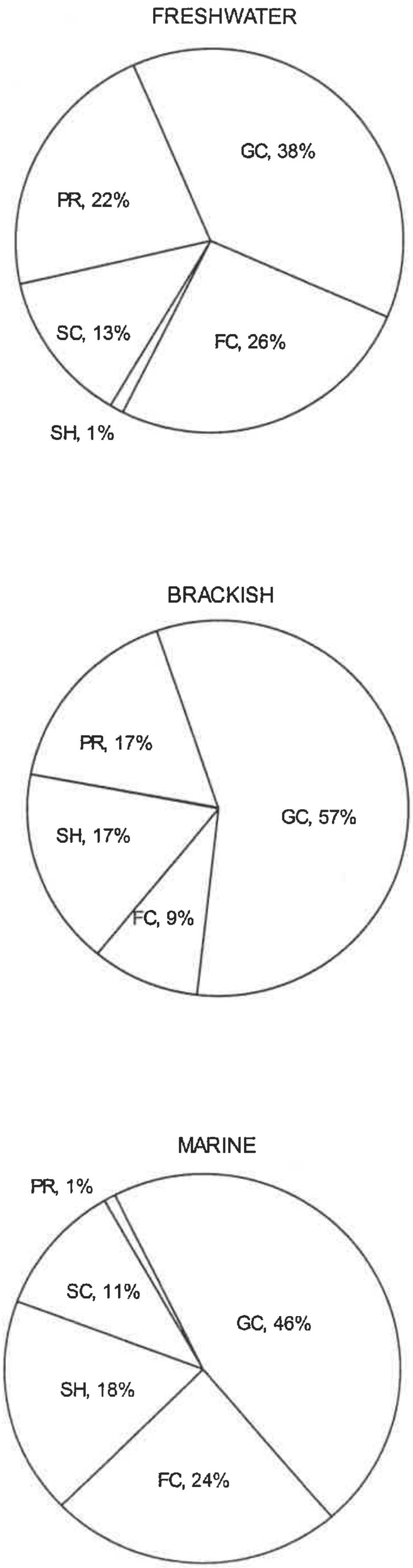

Figure 4-7. Comparisons of the distributions of functional feeding categories of macroinvertebrates at diffent locations.

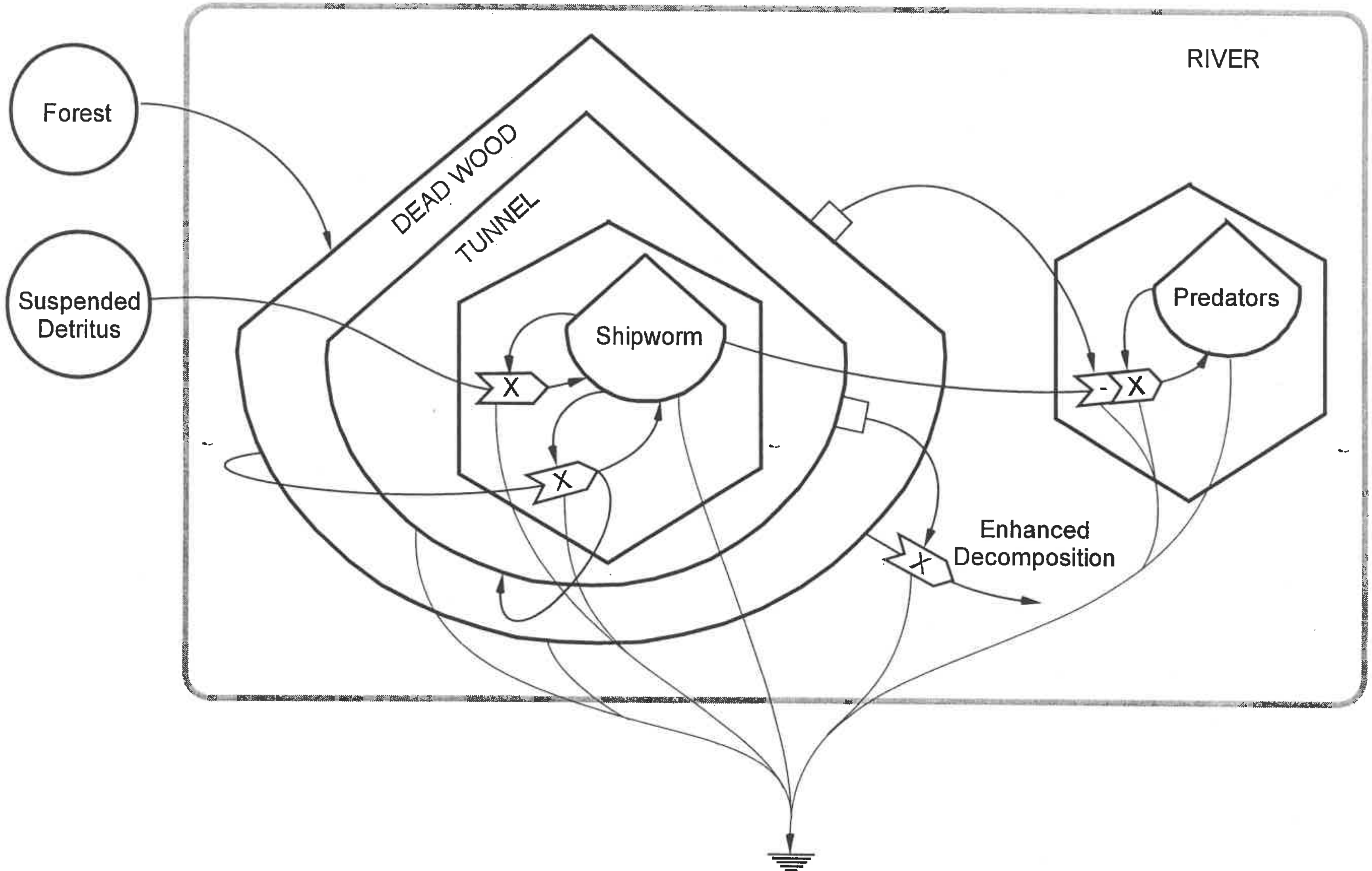

Figure 4-8. Energy circuit diagram for ecological interactions of the shipworm in the lower Sittee River.

(see the workgate on the lower right-hand side of the diagram). This occurs through fragmentation because the tunnels eventually reduce the structural integrity of the wood and lead to breakage. In this way the shipworm acts like the termites in the terrestrial forest by increasing the rate of recycling of dead wood. Several taxa of crustaceans found in the brackish and marine sites also feed on wood though they live on the surface rather than in tunnels and therefore they probably have a smaller impact on decomposition in comparison with shipworms.

The land crab (Cardisoma guanhumi) is an important macroinvertebrate species that does not live in the river but rather it inhabits burrows in the riparian forest soil located adjacent to the river. This amphibious species stays in the burrow, which extends below the water table, during the day and comes out on to the forest floor at night to forage primarily on freshly fallen leaf litter, which is taken down into the burrow for feeding. Figure 4-9 illustrates some of the main aspects of the land crab niche. The burrows are dug in the floodplain soils and they provide protection from predators (as indicated by the negative drag workgate on the energy flow pathway from crabs to predators). Several student research papers have involved studying patterns of land crab burrows both vertically and horizontally (Wanger 1991, Bustamante 1992, Samosky 1991). The burrows probably affect hydrology and aeration of the soil and are known to provide habitat for mosquito larvae. The main role of the land crabs within the ecosystem relates to leaf litter processing, which has been studied for similar species in other forest systems (Robertson 1986, Sherman 2003, Kellman and Delfosse 1993). The crabs can remove a significant mass of leaves into their burrows where it is eaten or stored. Leaf decomposition may be accelerated for stored leaves and the leaves also undergo conditioning and conversion into dissolved organic carbon while in the burrows. Floods periodically flush out the burrows causing advection of both dissolved and particulate organic matter into the river system. Because of the potential importance of land crabs to the river-forest system, some studies of their relationships with leaf litter have been undertaken. Litter mass has consistently shown an inverse relationship with the density of crab holes (Figure 4-10), suggesting a regulatory role for the crabs. Crabs seem to be absent from some of the forest types with the highest litter masses, such as the kaway swamp and the bamboo patch (see Appendix Table 4-1), perhaps because of anaerobic soil conditions (in the swamp) or poor nutritive quality of the leaf litter. Baiting experiments have also been used to study preferences by the crabs (Table 4-17). In these experiments a small number of leaves of known species are placed around the entrance of active crab holes in the evening (usually 3-5 leaves per hole). Monitoring of the leaves on the following morning reveals which leaves were removed and therefore preferred by the crabs. Data indicate a range of preferences though most species were accepted at least 70% of the time. Only a few species seem to be avoided, curiously including wild guava (________________) which is one of the most common understory trees in the riparian forest. Perhaps this species produces defensive chemicals in the leaves in order to deter herbivores and the chemicals also make the leaves less desirable to the crabs once they have fallen on the forest floor. These leaf litter-crab studies will continue in an effort to develop an understanding of the trophic role of the land crab in the riparian forest.

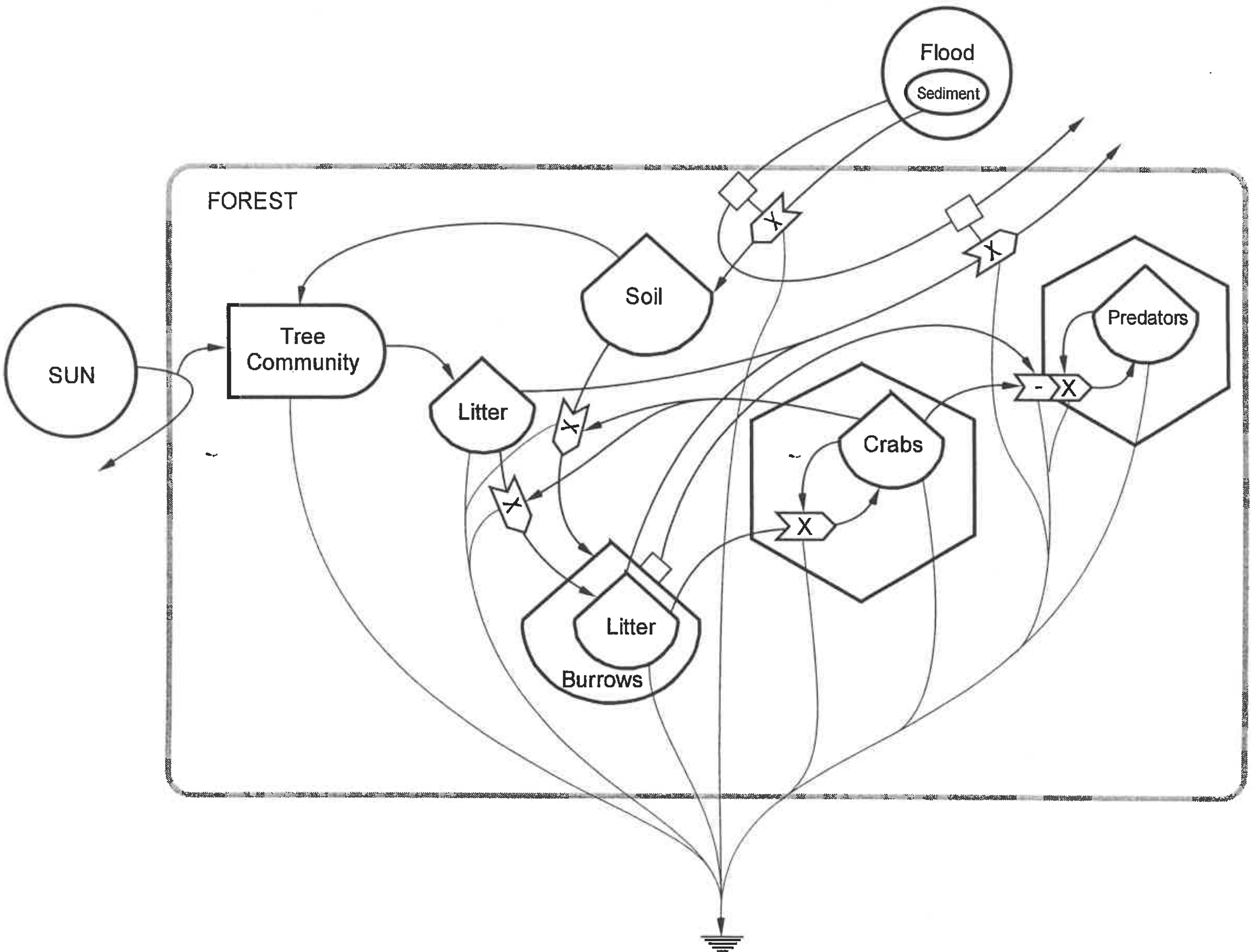

Figure 4-9. Energy circuit diagram for ecological interactions of the land crab in the riparian forest along the Sittee River.

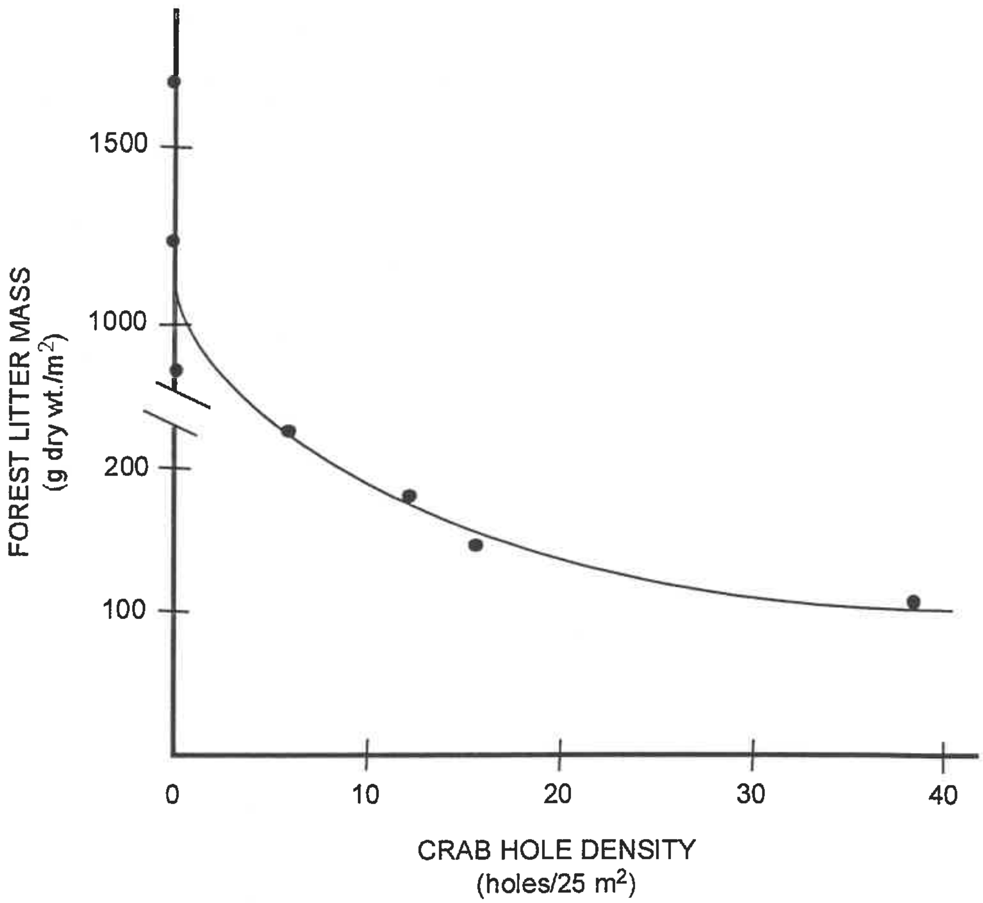

Figure 4-10. Relationship between the density of crab holes and the mass of leaf litter on the floor of the riparian forest.

Table 4-17. Results of land crab baiting trials with leaves from different tree and other plant species.

Tree species	# leaves removed/# leaves offered (percentages)
Mammy apple	0/5 (0)
Wild guava	13/35 (37)
Mahogany	8/15 (53)
Palmetto	3/5 (60)
Cashew	10/15 (67)
Bocout	17/25 (68)
Red Mangrove	21/30 (70)
Coconut Palm	28/35 (80)
Mango	12/15 (80)
Bri Bri	20/25 (80)
White Broad Leaf	19/22 (86)
Fig	26/30 (87)
Bamboo	23/25 (92)
Breadfruit	9/9 (100)
Kaway	5/5 (100)
Starvation Fruit	5/5 (100)

Fishes

Fishes are important animals within the river ecosystem, both from an ecological perspective and from a human perspective, Fish species occupy many ecological niches and they directly regulate detrital processing through predation on benthic macroinvertebrates. Recreational fishing and, to a much lesser degree, fishing for subsistence also cause humans to focus on the many fish species in the river. In general, the ecology of fishes has been studied to a much greater degree than any other component of tropical aquatic ecosystems, because of their economic importance (Lowe-McConnell 1975, 1987).

Fishes were sampled with seines and a large gill net that was stretched across the river. Extensive sampling with these net methods was done throughout the 1990s in order to characterize the fish community. Some limited sampling with hook and line from the shore has also been conducted. Use of these different techniques has allowed more species and size classes of fish to be sampled. Seining was often inefficient, because a steep drop off at the river edge made water too deep to pull the net and because soft sediments made movement of the net too slow to catch fish. Seining was done during daylight hours while the gill net was set in the river over a 24-hour cycle. Fishes caught in seining were identified and released except for those kept for a reference collection. The gill net was owned and employed by local fishermen and the fish caught by this method and by hook and line were usually eaten by the fishermen after data on standard length and weight were recorded. Fish weight was measured on a Homs portable scale. Some larger fishes were kept for stomach analysis. In this analysis stomachs and digestive tracts of fishes were removed and examined for presence of food types. Field dissecting microscopes with flashlights for light sources were used to examine stomach contents early in the study but contents have more often been described by unaided visual inspection. Fishes were initially identified with help from the Possum Point staff of local people who could name many species by using a folk taxonomy. Final identifications were confirmed with the taxonomic key by Greenfield and Thomerson (1997).

Seine sampling for fishes matched the macroinvertebrate sampling pattern with samples taken in the marine zone at the rivermouth, in the brackish zone at Bocatura Bank and Possum Point and in the freshwater zone at the Sand Bank. Gill net samples were also taken at Bocatura Bank/Possum Point and at the Sand Bank. However, the gill net could not be used at the rivermouth because of the possible risk of the net fouling the propeller of a passing boat. Gill net samples were taken at the mouth of Boom Creek in order to collect fishes that were either moving into or out from the creek.

A total of 37 species from 25 families were collected from the Sittee River. Most of these species have been classified as peripheral species or marine invaders (Appendix Table 4-2) that occur only sporadically in freshwater (Miller 1966). Many of these are marine species collected only at the rivermouth or from the salt wedge strata of the river profile. Nine species are classified as secondary species, which can tolerate some degree of salinity, and only two species are classified as primary species that occur only in freshwater (Appendix Table 4-3). The dominance of peripheral and secondary species in the collections probably occurred because the majority of the study area is located in the estuarine end of the river gradient. However, biogeographers have also noted a general poverty of primary freshwater fish species throughout Central America due to its relatively recent geologic age (Bussing 1976, Myers 1966, Miller 1966).

Seine sample data are given in Tables 4-18 to 4-20. The most abundant species at the Sand Bank in the freshwater zone was a Characid (Astyana fasciatus), which is one of the two primary fish species collected in this study. At the brackish water stations (Bocatura Bank and Possum Point) Gambusia sp. was the most abundant taxa. This taxa (also the second most abundant in the freshwater station) is probably quite important in the river food web, based on studies of similar species (Bence 1988, Hurlbert et al. 1972, Kneib 1986). Greenfield et al. (1983) studied Gambusia in Belize and found that species in the genus feed on nearly 50 different taxa of aquatic organisms. The highest number of fish species in the seine samples was found at the rivermouth in the marine zone. Many species were represented by only a few individuals at this site. Anchoviella sp. was the most abundant species sampled primarily because it occurs in dense schools of small fry that move along the shore and, therefore, it was easy to catch. Common fish species are shown in Figure 4-11.

A summary of the seine collections is given in Table 4-21. Diversity and abundance was depressed at the brackish water site, to an even greater degree that was found for the benthic macroinverterates. In fact, there was 0% site fidelity of species at the brackish site. This result means that no fish species were limited to the brackish zone and the fish communities were able to span broad ranges of the salinity gradient. This breadth of distributions contrasts with that of the macroinvertebrates (Table 4-16) but it is not unexpected since even the small sized fishes caught in the seines are more mobile than the benthic macroinvertebrates. Inaddition to the mobility factor, the broad distributions suggest that, as a group, fishes may have greater behavioral and/or physiological adaptation to salinity variation than the macroinvertebrates.

A total of 351 individuals from 17 species were collected with the gill net (Table 4-22). Included in these samples were the three main sport fish of the Caribbean sea: snook (Centropomus ensiferus), tarpon (Megalops atlanticus) and bonefish (Albula vulpes) (Figure 4-12). The mackaka, Brycon guatemalensis, was the most abundant species collected at the Sand Bank site, making up 87% of the total individuals. This Characid is one of the two primary species collected in the lower Sittee River during the study. Snook and tarpon dominated the Boom Creek site. This finding suggests these species were relying on the blackwater habitat of this tributary, probably either for feeding or breeding. Bonefish were the most abundant species in the open water, mid-channel habitat at the Bocatura Bank/Possum Point site. This species was only collected from the lowest portions of the gill net that extended into the saltwedge, indicating that they were limited to the highest salinity waters.

It is interesting to compare the species compositions of fishes caught with the two techniques. Only seven of the 37 total species were caught in both the seines and the gill net: snook, tuba, snapper, catfish, hog choker, mullet and shad (Table 4-23). For these

Table 4-18. Abundance of fishes caught in seine samples at the sand bar (freshwater) site on seven dates. Frequency is the percentage of the dates that a taxa was caught.

Taxa	Number of Individuals	Frequency
Astyana fasciatus	189	57
Gambusia sp.	94	86
Xiphophorus sp.	74	43
Cichlisoma sp.	62	100
Unknown Poeciliidae	9	14
Belonesox belizanus	4	43
Agonostomus monticola	4	29
Oostetus lineatus	3	14
Gerres cinereus	2	29
Gobionellus sp.	2	29
Centropomus ensiferus	2	14
Achirus maculates	2	14
Heterandria bimaculata	1	14
Eleotris amblyopsis	1	14
Dormitator maculatus	1	14
Anchoviella sp.	1	14
Total	451	

Table 4-19. Abundances of fishes caught in seine samples at the Bocatura Bank (brackish water) site on eight dates. Frequency is the percentage of the dates that a taxa was caught.

Taxa	Number of Individuals	Frequency
Gambusia sp.	128	75
Cichlisoma sp.	68	88
Gerres cinereus	50	36
Sphoeroides sp.	14	25
Gobionellus sp.	12	36
Unknown Poeciliidae	6	36
Oostetus lineatus	5	50
Eleotris amblyopsis	3	25
Achirus maculates	2	25
Centropomus ensiferus	1	13
Lutjanus griseus	1	13
Belonesox belizanus	1	13
TOTAL	291	

Table 4-20. Abundance of fishes caught in seine samples at the rivermouth (marine) site on seven sample dates. Frequency is the percentage of the dates that a taxa was caught.

Taxa	Number of Individuals	Frequency
Anchoviella sp.	717	100
Eucinostomus melanopterus	57	29
Bairdiella sp.	11	43
Unknown Sciaenidae	8	29
Polydactylus sp.	5	14
Unknown Serranidae	4	29
Unknown Ariidae	4	14
Trachurus lathami	3	43
Gerres cinereus	3	29
Centropristis ocyurus	3	14
Strongylura marina	2	14
Caranx latus	2	14
Sphoeroides sp.	1	14
Belonesox belizanus	1	14
Lupinoblennius dispar	1	14
Lutjanus griseus	1	14
Lobotes surinamenis	1	14
Centropomus ensiferus	1	14
Unknown Synodontidae	1	14
TOTAL	826	

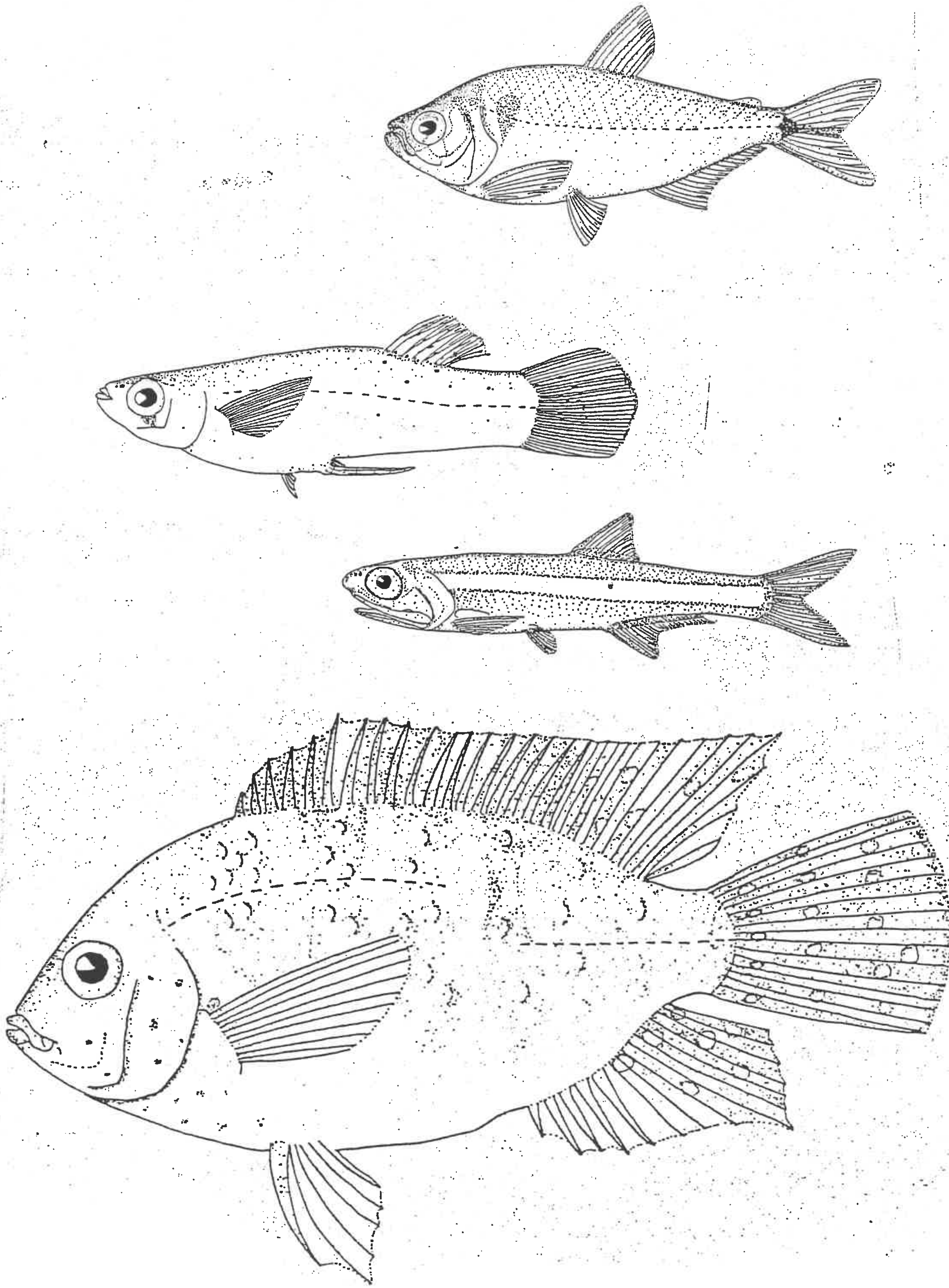

Figure 4-11. Common fish species caught with seines.

Table 4-21. Small fish community comparisons.

Zone	total taxa	taxa only found in this zone	ratio of the two columns
Marine	19	13	68%
Brackish	12	0	0%
Freshwater	16	5	31%

Table 4-22. Abundances of fishes caught in gill net samples.

Taxa	sand bar	Boom Creek	Bocatura Bank
Brycon guatemalensis	61	0	1
Cichlasoma sp.	2	7	4
Unknown Sciaenidae (drummer)	1	9	2
Megalops atlanticus	1	23	2
Lutjanus griseus	1	8	4
Centropomus ensiferus	1	59	23
Sphyraena barracuda	0	2	2
Unknown Ariidae (catfish)	1	3	1
Caranx latus	0	7	5
Unknown Gerreidae (stone bass)	0	6	6
Achirus maculates	0	2	0
Unknown Gerreidae (shad)	0	1	28
Petenia splendida	1	1	0
Agonostomus monticola	1	1	5
Albula vulpes	0	0	67
Oligoplites saurus	0	0	1
Pomadasys crocro	0	0	1
TOTAL	70	129	152
Number of sample dates	8	34	25

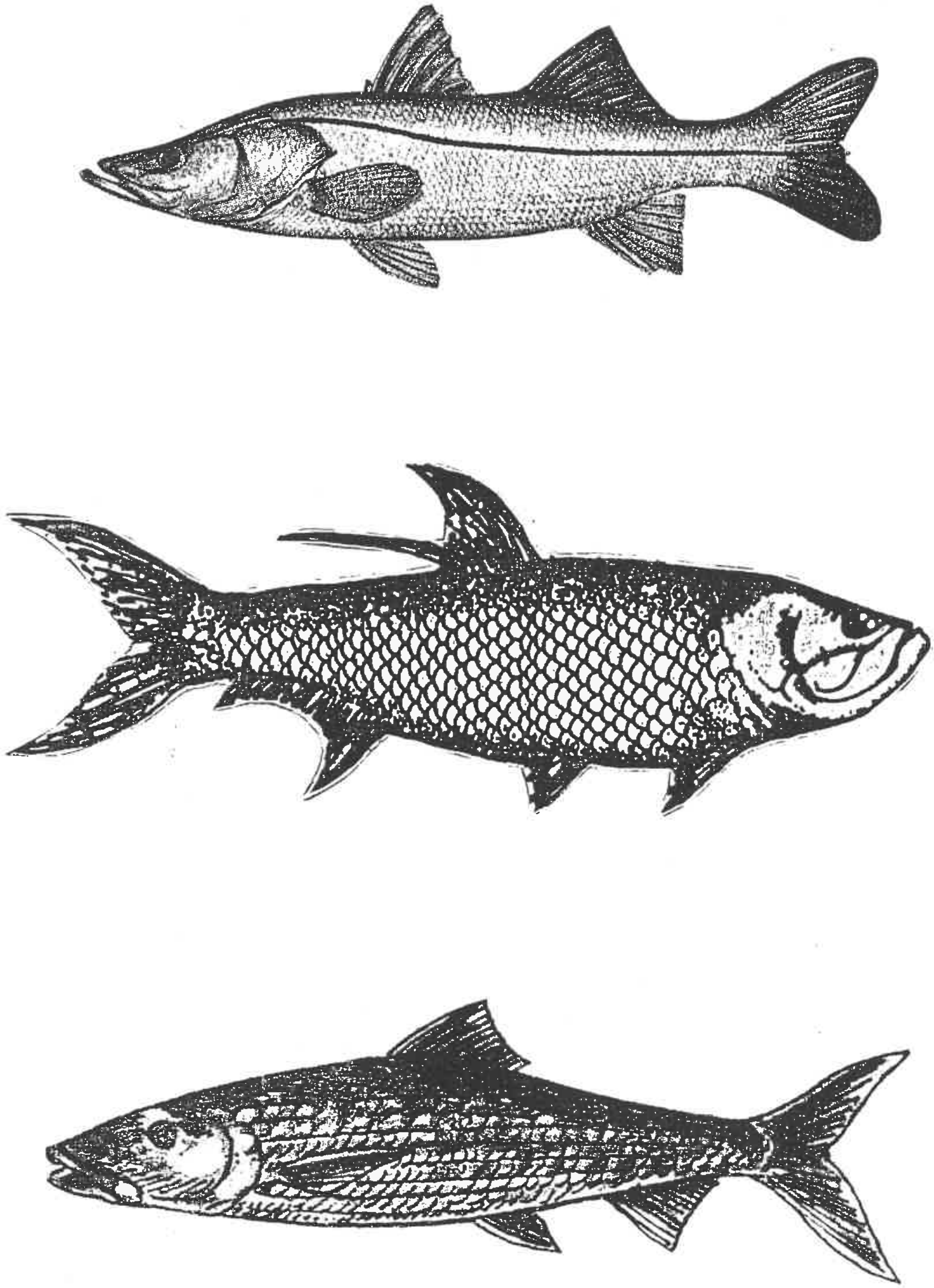

Figure 4-12. Game fishes from the Sittee River.

Table 4-23. Taxa found in both seine and gill net samples.

Scientific Name	Common Name
Centropomus ensiferus	snook
Cichlasoma sp.	tuba
Lutjanus griseus	snapper
Unknown Ariidae	hog choker
Agonostomus monticola	mountain mullet
Gerres cinereus (?)	shad (?)

species the populations recorded in the river included both small and large individuals. Since most of these species are marine invaders, this finding suggests that the river is serving as both a nursery zone and an adult habitat. The use of the river as a nursery for snook is particularly noteworthy. Because of the economic importance of this species to the local people and to the tourist sportfishing industry, a conservation plan for the river may be justified.

In conclusion, the fish caught during the study period listed above are only a sample of the total diversity in the Sittee River. Some species might be over-represented, as mentioned earlier with Anchoviella sp., while other species that were caught, are under-represented in the collections. For example, the needlefish (Strongylura marina) was rarely collected but commonly seen swimming along the shore. Additional species, known to be found in the river, that have either been caught by local fishermen or observed while snorkeling, were completely missing from the collections. A more complete inventory of the fish diversity would require greater and more focused effort, but the data reported here probably reflect the essence of the fish community structure in the Sittee River.

From a trophic perspective fishes feed on all available aquatic energy sources from detritus to other fish (Figure 4-13). They are important consumers in all salinity zones and in all microhabitats from the shallow riffles to the deepest parts of the open channel. Predation by fishes causes a kind of "top down" control over food chains (Power 1990, Northcote 1988) and changes in fish populations can cause cascading effects in aquatic systems (Carpenter and Kitchell 1993). Trophic niches of many of the fish species from the Sittee River have been described in studies of other tropical streams and estuaries (Bussing 1994, Yanez-arancibia et al. 1980, Angermeier and Karr 1984). Here some original data (including data from Gwaltney et al. 1991, Hew and Cada 1994, Moody, 1992, Semmens and Zepp 1991) are reported for food habits of large fish by stomach content analyses (Appendix Table 4-4). Stomachs were examined for a total of 282 fish from 18 taxa and 74% of the fish studied had food items in their stomachs at the time of capture. The most commonly utilized food items were decapod crustaceans (crabs and shrimps) and plant material. Fourteen of the 18 taxa studied had fed on these items. Utilization of decapods, which are generally considered to be detritivores, and plant material indicate the importance of detritus as a base for the food web leading to the fish community. One half of the taxa studied had feed on fish, indicating the importance of carnivory at the ends of river food chains.

Diets of common large fishes are given in Table 4-24. This table shows data for the nine species which had at least four full stomachs out of the total sample (from Appendix Table 4-4). Only two species are completely carnivorous, in eating only animals, with barracuda (Sphyraena barracuda) feeding solely on fish (a pure piscivore) and bonefish specializing on decapods. Most species are omnivorous in feeding on several food items, with no particular prey providing more than about 50% of the diet. The extreme is the tarpon which fed on six out of the 10 food items found in the study. Two species are herbivorous with machaka specializing on higher plant materials and tuba feeding nearly

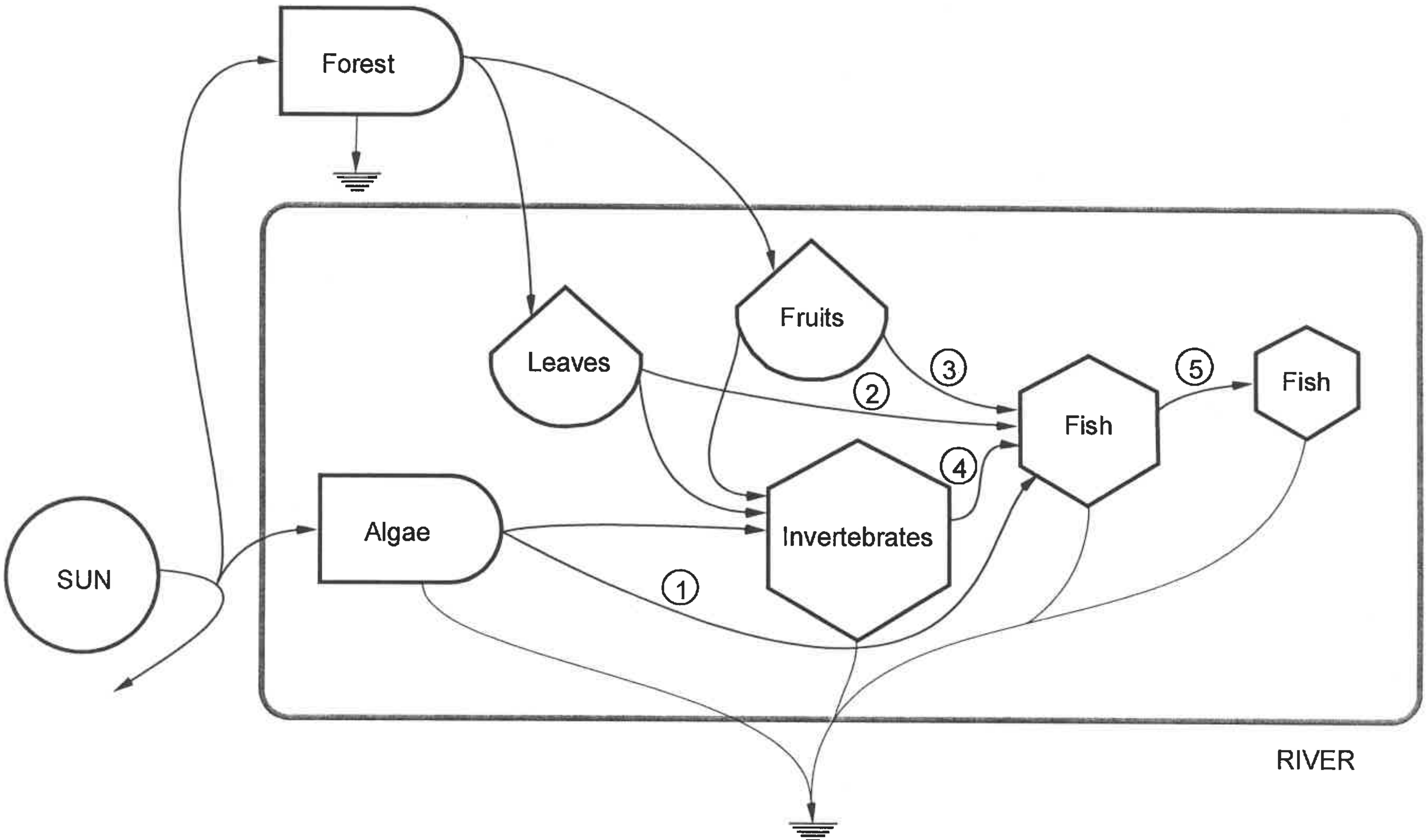

Figure 4-13. Energy circuit diagram showing the different feeding pathways of fishes in the Sittee River. See the text for a description of the different pathways.

Table 4-24. Diets of common, large fishes in the lower Sittee River. Data shown are relative contributions (percentages) of food items given in Appendix Table 4-4.

Species	Fish	Decapod	Isopod	Amphipod	Annelid	Mollusc	Insect Larvae	Plant Material	Seed	Algae
Jack	57	14	0	0	0	0	0	29	0	0
Snook	40	38	0	0	0	0	3	16	0	3
Tarpon	43	22	0	7	0	7	0	14	0	7
Shad	0	19	0	0	0	0	0	25	0	56
Bonefish	2	82	0	8	2	6	0	0	0	0
Muchaka	0	0	0	0	0	0	1	69	30	0
Snapper	22	56	11	0	0	0	0	11	0	0
Barracuda	100	0	0	0	0	0	0	0	0	0
Tuba	0	0	0	0	0	0	0	41	5	54

equally on higher plant materials and algae. Studies on herbivory by fishes in the Sittee River have been carried out by Evans (1991) and Winnaker (1991).

Seeds were found in nearly half of the stomaches of the machaka (Brycon guatemalensis). Such frugivory was first found for fish in the Amazon (Goulding 1980). Certain fish feed on fruit in the Amazon when floodwaters submerge the canopies of trees. However, in Belize fruits from riparian trees fall into the river and are fed upon by aquatic organisms. This feeding niche has also been described by Bussing (1994) for Costa Rica. Local fishermen also use fruit as bait along the Sittee River. Fruits of several tree species from the riparian community of the river are fed upon by fish (Table 4-25) and studies of this feeding niche in the Sittee River have been carried out by. In the Amazon fish actually disperse some of the seeds and this unique dispersal pathway may also operate in Belize.

Aquatic Birds

Aquatic birds are top predators of the Sittee River ecosystem, feeding on benthic macroinvertebrates and fishes. Because of their high trophic position, aquatic birds have often been used as indicators of the ecosystem they feed in (Steinmetz et al. 2003, Weller 1995, Erwin and Custer 2000, Frederick and Ogden). Although the ecology and natural history of most of the aquatic birds is well known (see for examples, Remsen 1991, Poole 1989, Kushlan et al. 1985), their role in the overall ecosystem has received less attention. To some extent the aquatic birds integrate the river and the riparian forest (Figure 4-14). The birds utilize the trees for perches while feeding and for roosts while resting or sleeping. Through their excretion they move nutrients from the river to the forest which stimulates tree growth. Individually birds move only small amounts of nutrients but this recycle pathway is especially effective for colonial species, which concentrate the inputs of many birds in a small space. This nutrient cycling role for aquatic birds has been reported for systems similar to Sittee River (Burton et al. 1979, Onuf et al. 1977, Oliver and Schoenberg 1989, Bildstein et al. 1992) and it was described for a rookery island on the Belizean barrier reef by Kricher (1989).

Aquatic birds were surveyed in this study by making counts during boat trips on the river. This approach has yielded a large amount of data over the years because boats are the main mode of transportation at the Possum Point Biological Station. Thus, birds could always be counted whenever trips were made along the river for any purpose. Bird counts were initiated by Martin (1992) and Seder (1992) and have continued throughout the study period. A total of 1647 bird sightings have been recorded along the river (Table 4-26). The bird community was nearly equally divided between diving bird species and wading bird species across the entire length of the study area. The little blue heron and the American egret were the birds most commonly observed and they were found in all of the three salinity zones of the river, as were many of the other species. However, marine diving birds were observed only at the rivermouth. Data on linear density, or birds observed per kilometer of boat travel on the river, are given in Table 4-27. No seasonal differences have been found during the study. Excluding the marine species found only at the rivermouth, the linear density of aquatic birds was 2.66 individuals/km (1.65

Table 4-25. List of tree species whose fruits are eaten by fishes in the Sittee River. The sources of the list are local fishmen.

Scientific Name	Common Name
Musaceae	
Musa sp.	fragoon
Mimosaceae	
Inga rodrigueziana	tamatama
Inga edulis	bribri
Moraceae	
Ficus sp.	fig
Artocarpus altilis	breadfruit
Cecropia peltata	trumpet tree
Palmae	
Cocos nucifera	coconut
Malpighiaceae	
Byrsonima crassifolia	craboo
Anacardiaceae	
Mangifera indica	mango
Myrtaceae	
Pisidium guajava	guava
Polygonaceae	
Cocoloba coronata	wild grape

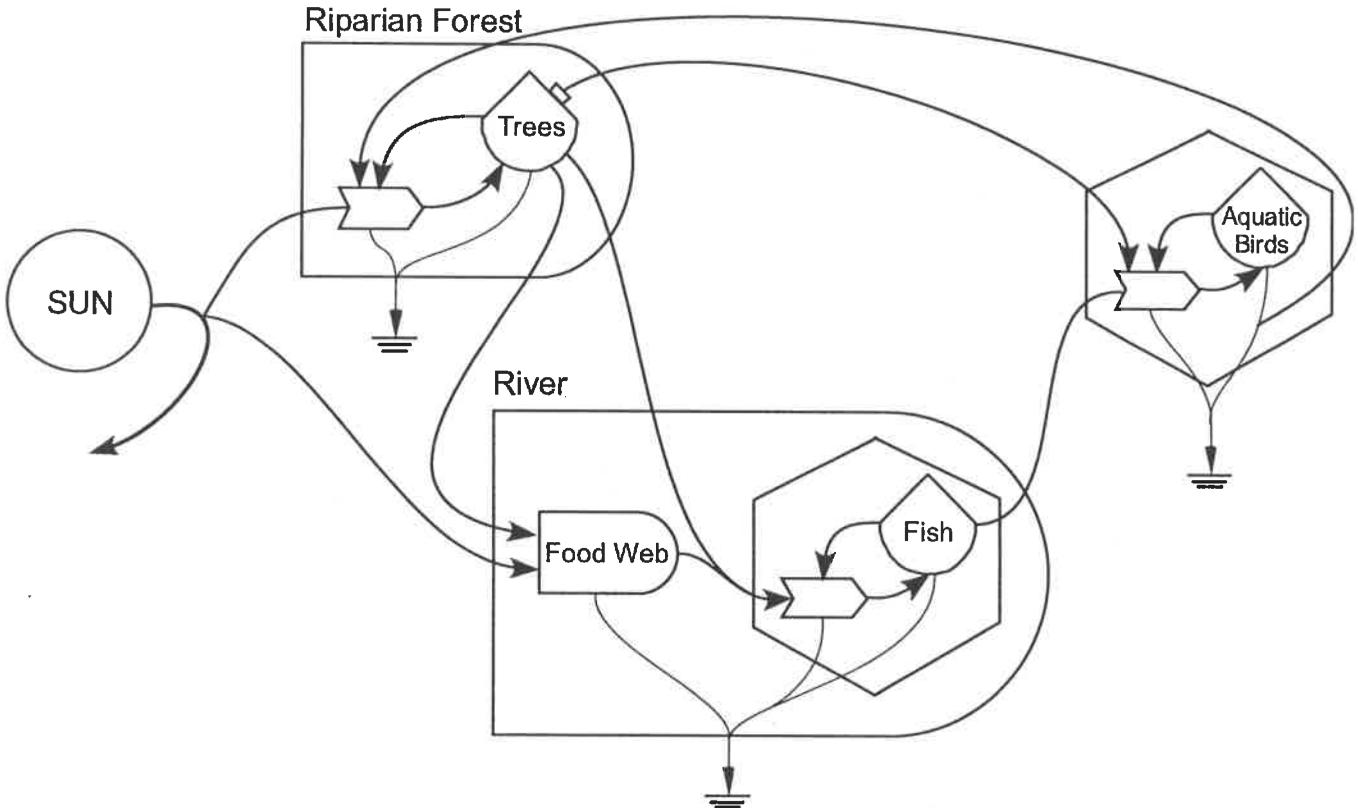

Figure 4-14. Energy circuit diagram of interactions between aquatic birds and ecosystem.

Table 4-26. Comparison of aquatic bird communities along the Sittee River, 1991-2005.

Taxa	Numbers seen		Numbers seen
FRESHWATER Wading Bird Species		Diving Bird Species	
little blue heron (Florida caerulea)	351	kingfisher species (Alcedinidae)	100
egret (Casmerodius albus)	328	anhinga (Anhinga anhinga)	25
ibis (Eudocimus albus)	66	osprey (Pandion haliaetus)	17
great blue heron (Ardea herodias)	59	black bellied tree duck (Dendrocygna autumnalis)	14
night heron (Nyctanassa violacea)	44	sun grebe (Podiceps sp.)	8
tiger heron (Nycticorax sp.)	43	gallinule (Gallinula chloropus)	1
green heron (Butorides virescens)	10	coot (Fulica Americana)	1
bittern (Botaurus lentiginosus)	4	Total	166
snowy egret (Leucophoyx thula)	3		
limpkin (Aramus guarauna)	1		
Total	909		
MARINE Diving Bird Species			
frigate bird (Fregata magnificens)	204		
pelican (Pelecanus occidentalis)	185		
tern species (Sterna sp.)	139		
cormorant (Phalacrocorax sp.)	44		
Total	572		

Table 4-27. Comparison of linear densities of aquatic birds along the Sittee River. n is the number of boat trips over which means and standard errors are calculated.

Time period	mean (birds/km)	standard error	sample size
Total Year	3.2	0.3	127
Dry Season	3.3	0.4	65
Rest of the Year	3.1	0.5	62

individuals/mile) of river distance. This value seems somewhat low and probably is a reflection of the oligotrophic nature of the river water quality. Also, the habitat is not ideal for wading birds since the shorelines were often steep, making the water too deep for foraging. A major exception to this general rule occurs at the rivermouth where the bar across the mouth creates an extensive shallow zone for feeding. Prey may be more available to the predatory birds at the rivermouth because of the clarity of the water, which may explain the high concentration of marine birds found there. Finally, the counts reported in Table 4-26 are certainly underestimates since not all birds could be seen during boat trips. Some may have been frightened away by the sound of the boat motors before sighting was possible and others may have been hidden in the tree foliage and not directly visible from the boats. Furthermore, boat trips usually took place between 9:00AM and 4:00PM, thus excluding birds that use the river at other times of the day. Despite these limitations, the data presented above provide a baseline of aquatic birds that can be used for comparison with other rivers and for monitoring changes due to development along the Sittee River in the future.

Other Aquatic Vertebrates

In addition to fishes and birds a number of other aquatic vertebrates were observed on the Sittee River. Although these species were not formally studied, they may play important roles in the river ecosystem. Amphibians are rarely seen in the river but aggregations of tadpoles have been observed in the shallow edges of the freshwater riffles.

The green iguana (Iguana iguana) is a common large (up to 2 meters in length) reptile seen in the riparian forest along the Sittee River. The species is herbivorous, eating tree leaves, and largely arboreal. Although not an aquatic organism, the green iguana will dive into the river from an overhanging tree branch as a predator escape response if disturbed.

Aquatic reptiles are not abundant but are regularly seen during boat trips. Especially in the brackish zone, approximately from the Canal to Red Bank, the linear density of large reptiles rivals that of aquatic birds, making the reptiles important consumers in the river food web. Aquatic reptiles include turtles and crocodiles. Turtles were often seen sunning on logs in the river and, in fact, the campsite at Bocatura Bank was named after the local river turtle. Three species of turtles were found along the river: Chrysemys scripta (bokatura), Staurotypus tripopcatus (loggerhead) and Kinosternon acutum (mud turtle) but they were seldom caught. Turtle density is difficult to quantify but they have been found to be important in river ecosystems (Moll and Moll 2004).

Crocodiles are no longer common in Belize due to harvesting for their hides in the past (Charnock-Wilson 1970, Frost 1977, Abercrombie et al. 1980). Morelet's crocodile (Crocodylus moreletii) is found along the Sittee River. A wide range of size classes of individuals from ½ meter to greater than 3 meters in length can be seen in shallow waters. The presence of small individuals is important because it indicates that the species is reproducing in the river and thus recovering from its endangered status. Crocodiles are obviously top predators in the river and they may locally influence nutrient cycling and primary production through their excretion (Fittkau 1970, 1973).

The most important aquatic mammal in the Sittee River is the manatee. This species has been fairly common in Belize (Charnock-Wilson 1968, Bengston and Magor 1979) but, as with most other wildlife species, it is threatened by exploitation (Frost 1977). Manatees are usually sighted by their wakes from swimming animals seen from the shore or from boats. River otters (the local name is water dog) have also been occasionally sighted along the river but local residents report more frequent sightings of this species.

The River Food Web

Although little direct data on linkages in the river food web was gathered in this study, because the general food habits of many of the species in the river are known, some impressions can be given. Based on the distributions of biodiversity found in this study, there are actually several food webs along the river in the different salinity zones (Figures 4-15 - 4-17). Food web diagrams are only caricatures of the actual networks, which are composed of tens or hundreds of species. They are useful however in showing dominant species and a sense of the structure of the network. The main energy flow in all of these webs is through detritus processing but the species composition changes depending on the location along the salinity gradient. In general, benthic macroinvertebrates are strongly tied to particular salinity zones due to their limited mobility. Fishes have more mobility but they are still at least weakly restricted to particular salinity zones. Aquatic birds move easily between the salinity zones and integrate the whole system through their predation. There seems to be a kind of sliding organization to the river food webs with food chains anchored to particular salinity zones through the primary consumers. Top predators are linked to these anchors but they move fluidly back and forth along the salinity gradient providing top-down control over prey populations.

Another feature of the food web is that it seems to be made up of pockets of strong interactions that are connected to the rest of the web through weaker interactions. Examples of these pockets are the deep water marine invader fishes, such as the bonefish, feeding on decapods and the multitude of diving and wading birds feeding in the shallow waters on pupsies and tubas. Broad cascading effects may be possible to occur across the whole food web but, because no major changes have taken place in the river during the study period, the impression one gets of the entire food web is that it is a system with small subsets or pockets of a few strong interactions embedded in a large, diverse network of more loosely, or perhaps fluidly, connected interactions.

Connections occur both vertically in the food web from detritus to top predators but horizontal connections also occur with movements of animals between salinity zones. Simenstad et al. (2000) called these kind of movements "trophic relays" when the movements extend across several zones of the estuarine gradient. Species moving horizontally, either upstream or downstream, face a gauntlet of predators and competitors but the forces causing the movements may be strong in terms of rich food sources or seasonal reproductive periods. There is clearly a depression in biodiversity in the

FRESHWATER FOOD WEB

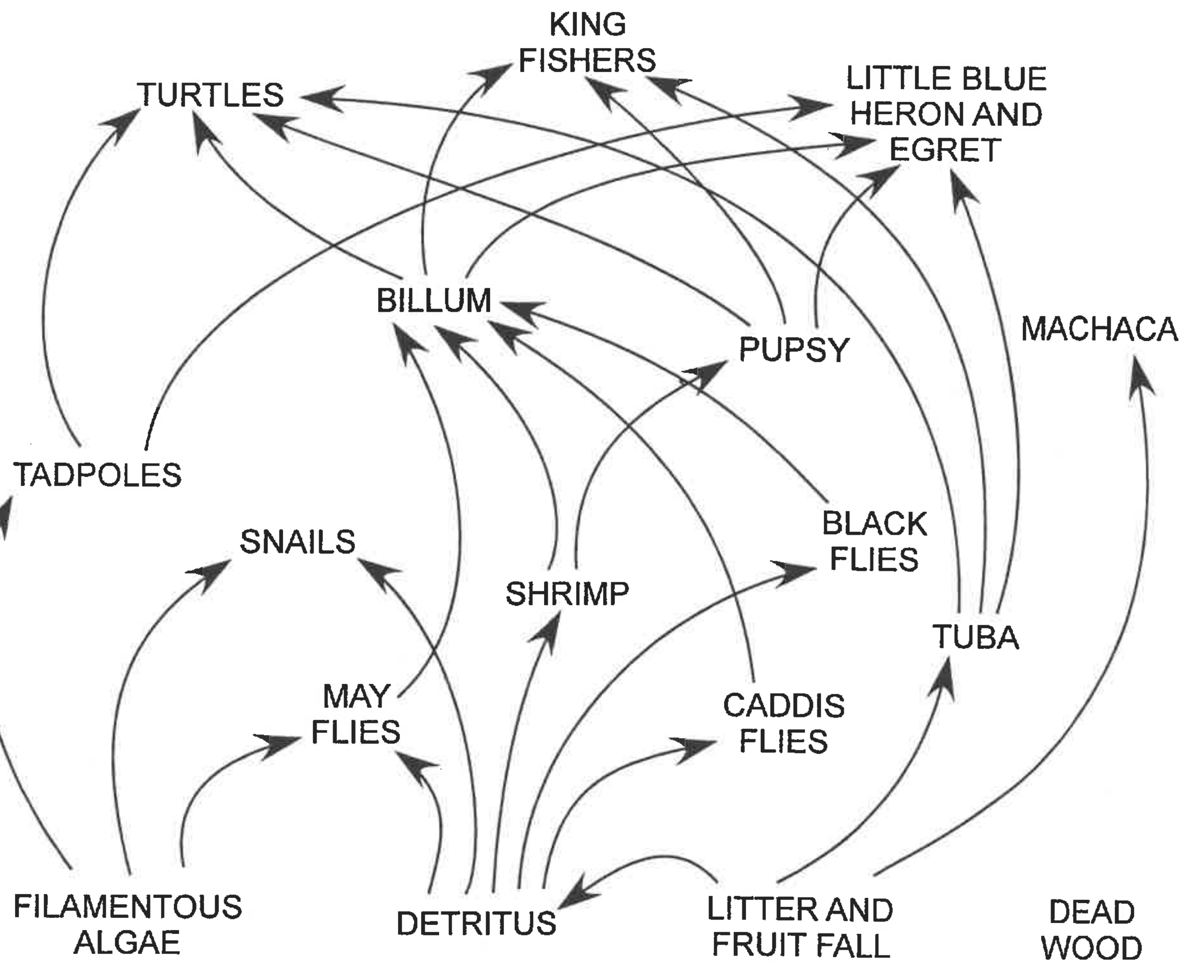

Figure 4-15. Food web diagram for the freshwater zone of the Sittee River.

RIVERMOUTH FOOD WEB

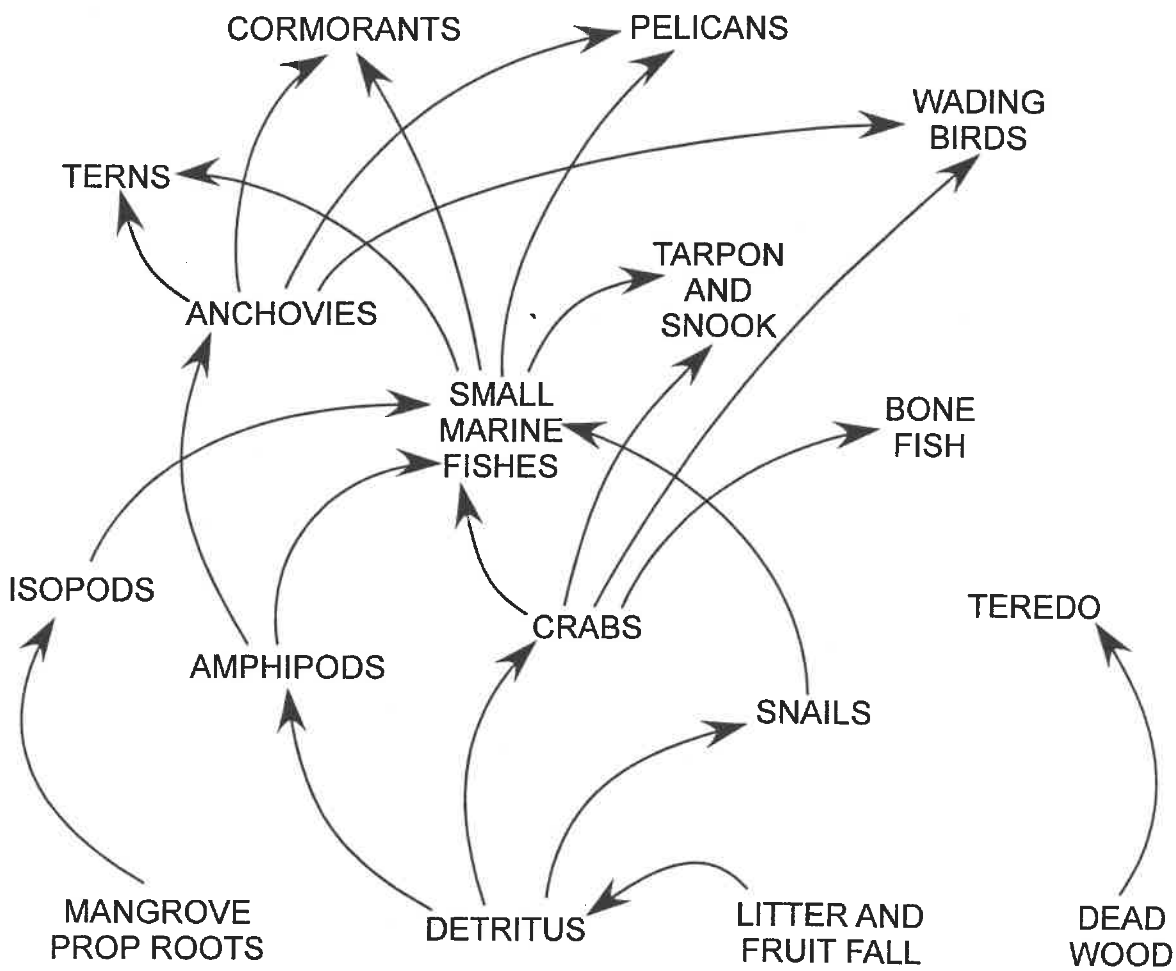

Figure 4-16. Food web diagram for the marine zone of the Sittee River as represented at the rivermouth.

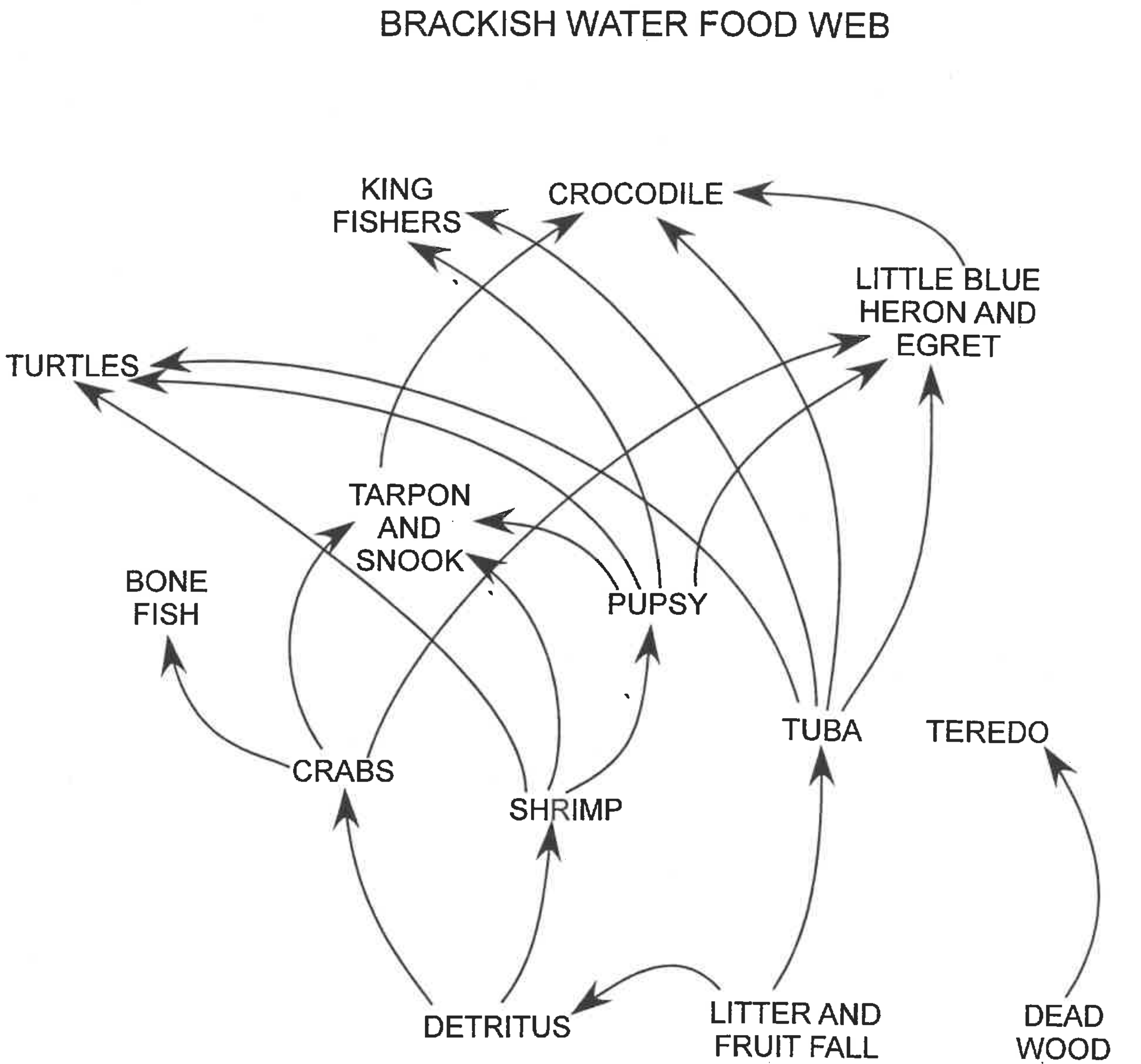

Figure 4-17. Food web diagram for the brackish zone of the Sittee River.

brackish zone, due to the difficulty that animals face in adapting to low but variable salinity, but movements do occur through this zone.

A whole field of network ecology has emerged to quantitatively examine the properties of food webs and other interactive networks (Higashi and Burns 1991, Pimm 1982, Ulanowicz 1986, Pascual and Dunne 2006). This is an important abstract perspective for understanding food webs that compliments the natural history descriptions given above. To illustrate the network perspective for Sittee River, a detailed food web was constructed for the brackish water section of the river (Appendix Table 4-5). More information on biodiversity is available for this section of the river, partly because it has received the greatest amount of sampling effort and partly because it has the fewest species due to the changing salinity stress. A food web of 21 taxa was constructed including four macroinvertebrates, three small-sized fishes, six large-sized fishes, six aquatic birds and two reptiles. This total number of taxa does not include all of the diversity of species found in the brackish water zone of the river but it focuses on the most abundant and most frequent encountered organisms. This food web includes significantly greater detail than the simple diagram given in Figure 4-17 and it provides the basis for considering the trophic network as a whole entity. Appendix Table 4-5 is termed an adjacency matrix and it includes the presence (designated by a 1) or absence (designated by a 0) of a trophic link between each pair of taxa. The matrix was constructed with informed speculation based on natural history knowledge and the food habit information for large fishes described earlier in this chapter. Table 4-28 lists some basic indices of the trophic network: the first four relate to the structure of the food web as a network and the last four relate to the many food chains that comprise the food web. 82 total feeding links are included in the network, yielding an average number of links per taxa of 3.9. This index means that on average a taxa in the river feeds on about four different prey items and, in turn, is fed upon by about four different predators. The index of connectance describes the actual number of linkages relative to the total number possible for the given number of taxa included in the network. The value of 0.20 essentially is a percentage and it means that the brackish water food web has 20% of the feeding linkages that are possible to occur with 21 taxa. A total of 149 food webs are imbedded in the detailed food web. These are chains of trophic linkages that extend from a food source (detritus, fruit, algae, dead wood) to a top predators. The great number of food chains is a demonstration of the complexity of the food web. However, much of this complexity is in the form of redundancy, since there are many parallel pathways included in the network. The average length of a food chain is about four taxa. An example of a four link food chain would be detritus-crabs-snook-crocodile. The maximum food chain length is five and there were 42 of these imbedded in the food web. The feeding of crocodiles on the aquatic birds, which is possible, was left out of the network but had this linkage been included, the maxium length of a food chain would have been six instead of five and the average length of a food chain would have increased. The minimum food chain length is two and there was only a single food chain of this length: dead wood to Teredo (see Figure 4-17).

A final note about the food web in the Sittee River concerns the top predator. These organisms can be important in structuring the whole ecosystem through their feeding

Table 4-28. Summary of network indices for the detailed brackish water food web given in Appendix Table 4-5.

Index	Value
Number of taxa (S)	21
Number of trophic links between taxa (L)	82
Linkage Density (L/S)	3.9
Connectance (L/[S(S-1)])	0.20
Number of food chains	149
Average food chain length	4.04
Maximum food chain length	5
Minimum food chain length	2

actions which regulate prey populations in a cascading fashion down the food web (Ray et al. 2005). Throughout much of the study area, especially in the brackish zone of the river, the top predator role is shared between reptiles (crocodiles and turtles) and aquatic birds (such as the little blue heron, etc.). In fact, in the analysis of the food web described above, out of the total number of food chains, 72 ended in reptiles and 72 ended in aquatic birds! While the presence of all of these fairly large carnivores is an indicator of the ecological integrity of the ecosystem, the question remains, "Who is the top predator in the Sittee River"? To at least address the question, calculations were made on the theoretically possible metabolisms of the two top predator groups (Appendix Table 4-6). Standard allometric equations were used along with assumptions about linear densities and body masses in order to calculate which group has the highest metabolism and therefore consumes the most food within Sittee River. Of course, the calculations are quite crude due to the number of assumptions that had to be made, but they do illustrate one approach to deciding the identity of the top predator. The results showed that even though the reptiles have a higher biomass in the river, aquatic birds consume more energy per unit time (52.0 watts vs. 13.7 watts), because of their higher metabolic rate. Thus, aquatic birds are the more dominant top predator because of the greater energy flow they command.

A dominant aspect of the river food web is the connection with the riparian forest. Various energy flows connect the river to the forest and to some extent integrate these two systems into a single functional unit. Impacts to the riparian forest are likely to affect the river ecosystem in negative ways. Loss of the riparian forest would directly reduce the energy input of detritus to the river and perhaps change the food web structure. Although the riparian forest is mostly intact along the Sittee River, deforestation is occurring as the forest is converted to citrus plantations and cleared for houses. Preservation of the riparian forest would consist of maintenance of existing forest and restoration of forest in impacted areas. Only a corridor of forest along the river may be needed. Development need not be eliminated entirely from the area but could be controlled within the riparian forest zone. Either the biosphere reserve model (Batisse 1986) or the community sanctuary model (Horwich 1990) may be appropriate for the Sittee River. Both of these approaches provide for human use of the system but with control over development pressure and management of natural resources for the benefit of both humans and nature.

Tributary Habitats

All of the data and discussion about biodiversity and the ecosystem in this chapter have referred to the habitats of the main channel. However, the two tributaries of the main channel that are found within the study area have different habitat conditions and therefore they have different mixes of biodiversity. The two tributaries connect with the main channel within the brackish zone of the river: Boom Creek near Possum Point and Fanny Young near Red Bank (Figure 2-). Some basic morphological characteristics of the tributaries are listed in Table 3- . Fanny Young is short, only about 100 meters long, and it arises from a series of small springs within the floodplain. Historically, this tributary was a source of freshwater for local people during the dry season and it is named after a woman who lived along the stream in the past. Boom Creek is much longer, extending through the pine savanna to the edge of the Maya Mountains. It is named after the heavy iron chain that was stretched across streams and rivers to catch mahogany logs that were floated downstream from the site of cutting to a central collection and processing location during the 1800s and early 1900s. An example of one of these kinds of chains can be seen on display in a roadside park in the town of Burrel Boom, northwest of Belize City. Both of the tributaries are narrow and shallow with sluggish currents during normal flows, relative to the main channel of the Sittee River. One special geomorphic feature of Boom Creek is that it passes through a deep mangrove-lined lagoon (4-5 meters deep) about a kilometer upstream from its connections with the Sittee River.

In addition to the differences in basic morphology, the tributaries have different background chemistries relative to the main channel. Table 4-29 compares the tributaries to the nearest water quality stations on the river. Both tributaries have lower surface salinities, surface dissolved oxygen concentrations and pH values in comparison with the river. Additionally, Boom Creek is a blackwater stream (Meyer 1990) with dark, stained waters due to high humic acid concentrations. The origin of the blackwater is runoff of dissolved organic matter from the forested riparian zone, especially the deep mangrove lagoon that the stream passes through. Evidence of the staining of the water is apparent from Secchi disk readings, which measure transparency of the water (see Pages _____). The average Secchi depth in Boom Creek was 94 cm while in the river at Possum Point the average Secchi depth was 245 cm. Thus, the high concentration of humic acids reduces transparency in Boom Creek.

The biodiversity is general similar between the tributaries and the river in terms of macroinvertebrates (Appendix Tables 4-7 and 4-8) and small-sized fishes (Appendix Tables 4-9 and 4-10). However, because of their lower salinities, the tributaries have more freshwater taxa than is found in the adjacent brackish water main channel into which the tributaries drain. For examples, insect taxa make up a higher proportion of the total communities for macroinvertebrates and primary fish taxa from the Characidae (especially the billum, Astyana faciatus) are represented in both tributaries. Fanny Young in particular is an isolated refuge for freshwater taxa that only appear in the main channel above the salt wedge at the sand bar sampling station. In general, the low pH (e. g., the high acidity) of the tributaries seems to reduce both abundance and diversity of macroinvertebrates and fishes, though mud turtles are rather common in these habitats.

Table 4-29. Comparison of chemical parameters for Sittee River tributaries and corresponding sample stations in the main channel. Data are for normal flow conditions (Boom Creek with Possum Point and Fanny Young with Red Bank).

Chemical parameter	Boom Creek	Possum Point	Fanny Young	Red bank
Surface salinity, o/oo	0.9	1.9	0	0.7
Bottom* salinity, o/oo	5.4	33.3	0.1	21.8
Surface dissolved oxygen, mg/l	2.4	6.5	4.0	6.7
Bottom* dissolved oxygen, mg/l	1.6	1.6	4.4	2.1
Median pH	6.0	6.8	4.9	6.7

* Bottom depths in the tributaries equate with the 2 meter mark for sample stations on the main river channel.