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Trophic relationships in a tropical estuary

by

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ABSTRACT: This is an investigation of trophic interrelationship in the Tortuguero estuary on the Caribbean coast of Costa Rica. Basic physical and chemical features of the estuary are described, and a preliminary carbon budget is calculated for the estuarine ecosystem. Seasonal cycles in the estuarine watershed follow the rainfall pattern with two wet and two dry seasons per year. Planktonic primary production was found to be higher during dry seasons. However, the input of allochthonous materials by river flow is greater during wet seasons. The preliminary carbon budget indicates that estuarine respiration accounts for more organic material than is produced in the estuary during either the wet or dry seasons. During wet seasons there is an increase in the number of typically freshwater fish species, and an increase in the number of typically marine forms during dry seasons. The most striking seasonal difference in the estuarine community is in the presence, during dry seasons, of dense aggregations of *tismiche* composed principally of larval shrimp and larval fishes.

For as long as man has been a seafarer, estuarine systems have been subjected to the merciless degradative stresses of human technological development because they are generally the safest type of harbor for oceangoing vessels. They have been altered by dredging and filling and have served as repositories for unneeded ballast, for the bilges of ships being cleansed in port and for the miscellaneous sewages and wastes that are discharged into their tributary rivers. This is unfortunate, because in their pristine state such systems serve as nurseries and feeding grounds for a host of organisms, many of which are of great economic importance. This incompatibility of human utilization with that of the native organisms has reduced or eliminated many plant and animal species from major estuarine systems. Some forms that have persisted have been rendered unfit for human consumption by pollutants.

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Relatively undisturbed estuarine systems—where basic community interactions can be studied—even small ones located in the less developed areas of the world, are rapidly being reduced in numbers. The Tortuguero estuary on the Caribbean Coast of Provincia de Limón, Costa Rica, was chosen as the site for such a study because it appeared at the time of choice to be a relatively unaltered estuarine system. Also some background information was available on the estuarine flora and fauna (CALDWELL, OGREN and GIOVANNOLI, 3; KING, 11) and on the climate (HIRTH, 8) because the Caribbean Conservation Corporation Field Research Station was located here. The estuarine community study was begun in 1963 by KELSO and completed as a M. S. thesis project in 1965 (10). A portion of this work was published by GILBERT and KELSO, (7). The present study includes a continuation of the work through the summers of 1970, 1971, and 1972.

Few published reports of studies of trophic relations in estuarine communities exist and descriptions of tropical or subtropical estuaries are especially rare. Some of the important works of this sort are those of DARNELL (4, 5), on Lake Ponchartrain, Louisiana, and of ODUM and HEALD (16) on the North River estuary of Florida. These studies have emphasized the importance of detritus in the estuarine economy. However, neither included quantitative considerations of energy flow in the systems involved. Other recent works, in which such quantitations have been stressed are those of BIGGS and FLEMER (1) who evaluated the particulate carbon budget of northern Chesapeake Bay, Maryland; QUASIM and SANKARANARAYANAN (18), who evaluated the role of organic detritus in the Cochin Backwater (India), and BRINSON (2), who evaluated the carbon and energy budgets of Lake Izabal, Guatemala (a freshwater lake at the upper end of an estuarine system).

The purposes of the present study were as follows:

A. To investigate certain physical and chemical features of the estuarine environment, including basin morphometry, tidal influences and salinities, insolation, water temperatures and oxygen levels, turbidity—those features most likely to be involved in determining character and activities of the estuarine biota.

B. To determine the trophic interactions of the estuarine biota and to provide a list of the forms present, giving data on their distribution in time and space and on their food habits.

C. To make a preliminary evaluation of the carbon budget of the estuarine community.

METHODS

Fluctuations in water level in the estuary produced by tides were read on a series of three-scaled plastic pipes (½ inch intervals) that were driven into the bottom. One of these was located at the Boca, a second at the Green Turtle Station and a third on the mud flat across from Tortuguero Village.

Readings were made at hourly intervals. Salinities were determined with a Beckman induction salinometer. Water temperatures were measured with either the thermister in the salinometer or that associated with the YSI oxygen meter, The latter was used both for *in situ* O_2 determinations and for measuring oxygen levels in the light and dark bottles. Measurements of solar energy income were made with a YSI pyranometer. Turbidities were recorded with a standard Secchi disk. Water current measurements were made with a Beckman Enviroflow current meter.

Plankton sampling was done with a No. 12 silk plankton net, and the *tismiche* also were sampled in this manner. Benthic sampling was done with a 0.25 ft^2 Ekman dredge. Sediment grabs were sifted through a No. 30 sieve. Motile benthic invertebrates were taken in seines along with fishes. Fishes were also taken in gill nets (made up of a graded series of 5 mesh sizes) and with baited trot lines. The light-and-dark-bottle oxygen technique was used for evaluating primary productivity of the plankton community. The bottle pairs were filled with water from a series of depths through the euphotic zone and then suspended and incubated at the depths from which the water was taken. Incubation times were 24 hours. Community respiration estimates were calculated from light and dark bottle data from the mixed layers, and from changes in oxygen concentrations in the lower portion of the water column. Oxygen measurements were made at regular intervals through the tide cycle at a station near the Boca, and at irregular intervals at other stations.

Feeding habits of the major members of the estuarine community were evaluated by qualitative examination of the contents of the alimentary canals of specimens collected with the various types of sampling devices used. Data from the literature were used for comparison, and to provide information on organisms not extensively studied here. Bathymetric tracings were made with a Sonar recording fathometer.

GEOGRAPHY

The Tortuguero estuary is located on the Caribbean coast of Costa Rica (latitude 10°37'N, longitude 83°33'W). The estuarine system is formed by the junction of two major river channels: the Laguna del Tortuguero which extends northward and joins Laguna Penitencia at a point where the latter bends and reverses its southward course, parallel to the coast, and assumes a northward source. A third river, the smaller Río Tortuguero, also discharges into the common channel at this point. Beyond the point of confluence, known as Cuatro Esquinas, the common channel extends for a distance of ca. 6.5 km (4 miles) to its present point of discharge into the Caribbean (the Boca). It is this common channel that will be referred to as the estuary.

The estuarine system under considerations is separated from the Caribbean on the east by a longshore strip of land varying in width from 100 to 300 m, and on the west a similar strip separates the estuary from Laguna Penitencia.

brief geographic descriptions of the are found in HIRTH (8), and GILBERT and KELSO (7). The watershed that drains, at least in part, through the estuary originates on the eastern slope of the Cordillera Central, 40 km inland, and extends a similar distance along the northwest-southeast coastal axis. Headwaters of tributary streams flow through the cultivated foothills of the Cordillera Central, through the heavily cultivated inland areas of the Llanura de Tortuguero, and finally through relatively untouched coastal rain forest before the tributaries reach the estuary.

CLIMATE

Because of the lack of a weather station in the immediate vicinity of Tortuguero, systematic collections of weather information were not available for the region. HIRTH (8), recorded temperatures and rainfall for the area for a period of one year while he conducted a study of lizard behavior on the beach at Tortuguero. His data, along with our observations indicated that the Tortuguero climate is typical of the Caribbean coastal wet-forest and generally of wet-forests of the lowland tropics. The seasons are determined by variations in rainfall with two wet and two dry seasons per year at Tortuguero. The heaviest rainfall comes during the winter months of December and January and the summer months of July and August. Hirth found that 59.1% of the annual rainfall came during those four months, and that the driest months were September, October, March and April. Monthly rainfall ranged from a low of 50 mm in March to a high of 700 mm in December, with a total of 3882.5 mm during the year of his study.

According to Hirth's data, air temperatures at Tortuguero vary little during the year. Mean monthly maximum daytime temperatures varied between 24C and 25C and nighttime temperatures between 23.5C and 26.5C.

The only measurements of solar radiation at Tortuguero were made by us during August of 1972. Values ranged from a low of 175 to a high of 550 Langley/day, with a mean of 391 Langley/day. These measurements were made during a period of moderately frequent rainfall.

CHANNEL MORPHOMETRY

The major features of the estuary are illustrated in Fig. 1 which is an outline diagram constructed from an aerial photograph of the Tortuguero area. The letters A, B, C, D, E, and F on the map indicate the positions of bathymetric transects shown in Fig. 2. The deepest portion of the channel is found in transect C at Cuatro Esquinas on the village side of the river. The maximum depth there is just over 13 m. From this point on downstream to the Boca the channel is relatively uniform with only a few places deeper than 7.5 m. The maximum width of the channel is 400 m, at a point near Tortuguero Village; minimum width, 110 m, occurs at a point just inside the Boca. The surface area of the estuary (between points A and C) is 142 ha (350 acres).

TIDES: Several extensive series of measurements of tidal patterns in the estuary were carried out in 1964 and 1971. The tides generally produced a change in water level of ca. 0.25 m from dead low to dead high, and rarely did the variation exceed 0.5 m. However, since much of the channel is below sea level, the tidal influence is strong, even several kilometers upstream in the Laguna Penitencia.

SALINITY, TEMPERATURE AND OXYGEN DISTRIBUTION: Several series of salinity and temperature determinations were carried out during both wet and dry periods of the summer months, and for various tidal stages. Data from three sampling stations for the dry season are found in Figs. 3 (A and B) and 4. Station A was located at the Boca, Station B off the airstrip, and Station C at Cuatro Esquinas. It is obvious from the figures that the salinity profiles are quite similar throughout the estuary. This is not surprising, since the gradient in elevation is negligible between the Boca and Cuatro Esquinas. The depth at Station A was 6 m. The salinities here at high tide ranged from 0.2‰ at the surface during the wet season to near 2.0‰ during the dry season. Salinities, at depths of 4-5 m and greater, ranged from 25‰ to 30‰ during both seasons. Dry season salinities at low tide of Station B ranged from 1.2‰ at the surface, to 5.6‰ at 3.5 m and ot 25‰ at 6 m; at high tide the range was from 1.8‰ at the surface to 29.5‰ at 6 m. Wet season surface salinities were somewhat lower, with both high and low tide values of 0.2 to 0.3‰. Bottom values, again, were roughly equivalent between seasons. The maximum depth at Station C was 12 m, or roughly twice that of the other stations. The surface salinities here were roughly equal to those of Station B but the deeper waters were somewhat less saline at 26.4‰.

A typical water temperature profile for the estuary at high tide shows the highest temperature at the surface in the low salinity water. The temperature at a depth of 1 m (still at relatively low salinity) is generally 1 to 2 degrees C lower than at the surface. However, the temperature is higher in the deep saline water. This profile obviously results from incomplete mixing between the cool river discharge and the warmer tidal wedge. At high tide the movement of surface water is slowed and it is warmed by insolation.

Oxygen determinations made during both wet and dry seasons and at low and high tidal stages showed the mixed surface waters to be saturated or slightly subsaturated, while oxygen concentrations in the deeper unmixed tidal-wedge fluctuated. Changes in O_2 concentration over time were used in calculating community respiration. Photosynthesis was found to be limited to the upper meter or two of the water column. Since there was little mixing between the freshwater layer and the deeper waters of higher salinity there was no photosynthetic replacement of the oxygen used for respiration in the tidal wedge.

Secchi disk readings made at midday ranged during the period of study from lows of ca. 0.3 m to high values of 1.5 m. The low values were associated with heavy loads of suspended clayey materials brought in by the rivers when rainfall was heavy in the upper portions of the watershed.

ESTUARINE BIOTA

VEGETATION: The flora of the Tortuguero estuary consists of benthic and planktonic algae, rooted macrophytes and several transient macrophytes (hyacinth mats form a semi-permanent fringe in several places) that raft through the estuary. The algal flora consists of a combination of freshwater forms that are introduced by the tributary streams, and marine forms that are brought in by the tides. The principal freshwater genera encountered were *Anabaena, Dinobryon, Eudorina, Oscillatoria* and *Volvox*. These were taken in the freshwater stratum of the water column. Marine algae taken were diatoms of the genera *Bacteriastrum, Ceratium, Chaetocerus, Rhizosolenia, Skeletonema,* and *Stephanodiscus*. Rooted macrophyte growth in the estuary is mostly limited to a mudflat across from the Village, where the predominant forms are a single species each of *Najas, Potomogeton* and *Utricularia*. The most abundant macrophytes in the estuary are those that raft in from the tributary rivers. *Eichornia crassipes, Cyperus* sp., *Hydrocotyle* sp., *Panicum* sp., and *Salvinia* sp. are the principal plants involved. KING (11) described three associations among the rafts—one type of *Hydrocotyle*, a second exclusively of hyacinths, and a third combining hyacinths and grass. Hyacinth mats are by far the most abundant type.

ZOOPLANKTON: The estuarine zooplankton was found to be a composite of freshwater and marine forms, as was true of the phytoplankton. Rotifers of the genera *Asplanchna, Filinia, Hexarthra, Keratella* and *Polyarthra;* cladocerans, including *Bosminopsis, Ceriodaphnia, Diaphanosoma, Macrothrix* and *Moina;* and several hydracarina are all clearly freshwater forms. The copepod fauna consisted of several calanoid and cyclopoid species, including some freshwater and some marine forms. Other zooplankters included amphipods, a diverse group of larvae (barnacle, crab, shrimp), chaetognaths, larval fishes, isopods (*Eurydice*), small jellyfish, mysids, ostracods and protozoa (Globigerina).

BENTHOS: A striking aspect of the estuarine biota at Tortuguero is the scarcity of sessile and burrowing benthic organisms. No live bivalve molluscs were collected in any of the bottom samples taken in May of 1964 or September of 1970. Snails also were absent, though a few *Neritina reclivata* were found on pilings along the estuary. Only a few very small polychaete worms were taken. Various crustaceans constitute the bulk of benthic fauna. These include amphipods, mysids, crabs (*Callinectes boucourti* and *C. sapidus*), shrimps (*Palaemon pandaliformis, Macrobrachium acanthurus, M. jelskii, M. carcinus* and occasional specimens of *M. olfersi*). Other crustaceans that were taken in plankton collections and also in benthic sampling were shrimp of the family Atyidae including the genera *Jonga, Potimirim* and *Micratya*. In addition to these, several burrowing fishes found at Tortuguero can be considered to belong to the benthic community. These included the speckled worm eel, *Myrophis punctatus, Synbranchus marmoratus* and the wormfish *Microdesmus carri.*

FISH FAUNA: The Tortuguero fish fauna has been studied by CALDWELL, OGREN and GIOVANNOLI (3) and by GILBERT and KELSO (7). From the standpoint of trophic relationships the seasonal occurrence of the more abundant fish species is of interest. Lists of the common fishes of the estuary are found in Table 1.

TISMICHE: The most unique faunal aggregation in the Tortuguero estuary is the multispecific aggregation of larval forms known as the *tismiche.* According to GILBERT and KELSO (7) this aggregation may include juvenile shrimps of the genera *Jonga, Macrobrachium, Micratya* and *Potimirim,* crab megalops larvae, and post-larval fishes including *Awaous taiasica, Eleotris* sp., *Gobionellus fasciatus, Microdesmus carri,* and *Oostethus lineatus.* However, the diversity is usually much less, often being a monospecific group of shrimp larvae. Night collections made in mid-September of 1970, with a No. 12 plankton net hauled vertically under the light of a gasoline lantern, included post-larval shrimps, isopods of the genus *Eurydice,* ostracods and mysids, but no fish larvae. Whether or not all of these organisms can rightly be considered tismiche is debatable, since the light may have drawn some of them together.

HIGHER VERTEBRATES: The total known impact of tetrapod vertebrates on the estuarine economy is relatively small. Three species of large amphibians are found along the banks: *Bufo marinus, Leptodactylus pentadactylus* and *Rana warschewitschii.* While there are several species of freshwater turtles present in the rivers above Cuatro Esquinas and several marine forms in the sea, few turtles of any kind are found in the estuary. The occasional individuals of *Pseudemys scripta ornata, Rhinoclemys annulatus,* and *Kinosternon* spp. that occur have likely rafted downstream along with mats of vegetation. Caimans and crocodiles are now only rarely found in the estuarine community, both having been virtually eliminated by hunters within the last quarter of a century. A number of species of fish-eating birds—kingfishers, herons and shorebirds are sporadically common.

Manatees, though greatly reduced in numbers, still regularly feed in the rivers above the estuary but only rarely forage on the scant emergent flora of the estuary. A conspicuous mammalian predator of the community is the fish-eating bat (*Noctilio leporinus*) that eats not only fishes but also tismiche.

TROPHIC GROUPINGS IN THE TORTUGUERO ESTUARY

PRIMARY PRODUCERS: Plankton algae are introduced into the estuary by stream discharge and by the tides. These, and the plants that raft through the estuary (principally *Eichornia crassipes*) are transients in the community. The only permanent plants are the rooted macrophytes, a narrow and desultory fringe of water hyacinths, and benthic algae, all of which are limited in distribution and abundance by currents and turbidity.

ALLOCHTHONOUS CARBON SOURCES: Major sources of organic materials for the estuary are the plant materials carried in by tributary streams and tides, and washed in from the surrounding wet forest. Certainly the vegetation mats also fit this category, although they reach the estuary alive and may add significantly to the primary production while they remain in the estuary. Mats are caught in slack water along the shore and may remain there for weeks or months before being swept to sea by the river or tidal flow.

PRIMARY CONSUMERS: The primary consumers can be arranged into three groups: organisms that feed directly on the rooted macrophytes; organisms that feed on planktonic algae and bacteria; and organisms that feed on plant detritus.

None of the larger inhabitants of the estuarine community feed exclusively on rooted macrophytes, and only a few forms were found to utilize the rooted vascular plants to any significant extent. *Macrobrachium acanthourus and* two species of cichlids—*Cichlasoma citrinellum* and *Cichlasoma maculicauda*—were found to have eaten large quantities of vascular plant material, while *Bagre marinus,* and *Hyporhamphus roberti* had eaten small quantities. DARNELL (4) found *Callinectes sapidus, Macrobrachium ohione,* and *Strongylura marina* from Lake Ponchartrain to have fed on some vascular plant material. MCLANE (14) reported that *Dormitator maculatus* from the St. Johns River fed largely on vascular plant material. The few Tortuguero specimens of this species that have been examined were found to be carnivorous. In the estuary this species is almost restricted to the hyacinth roots, and the invertebrates and small fishes in this habitat, no doubt, provide a ready and adequate food supply.

Planktonic algae and bacteria are the food supply for a diverse group of herbivores that occupy the water column. Food analyses were carried out only in the case of the larval shrimp. Feeding relationships of other species were determined from the literature. Rotifers (except for such predaceous forms as *Asplanchna*), calanoid copepods and some of the cyclopoids, cladocera, and some of the crustacean larvae that make up the tismiche also consume algae, along with bacteria and organic detritus (PENNAK, 17; EDMONDSON, 6; ODUM and HEALD, 16). Several ciliates, polychaetes, ostracods, and mysids also depend on algae, fungi and bacteria as part of their food (16).

Organisms for which plant detritus is a principal component of the diet include amphipods (16), larval shrimp, larval and adult *Macrobrachium, Sphoeroides testudineus, Hyporhamphus roberti, Poecilia mexicana* (MCLANE, 14, considered the closely related *P. latipinna* to be phytophagous), and *Mugil curema.* Many of these forms also ingest algae, fungi and bacteria.

Carnivorous planktivores in the estuary include cyclopoid copepods; the rotifer, *Asplanchna* (EDMONDSON, 6); jellyfish; and the fishes *Anchoa lamprotaenia* and *Anchoviella elongata.* No Tortuguero data on the latter two species are available, but REID (19), and DARNELL (4), showed that *Anchoa mitchelli* fed largely on small crustaceans and larval fishes.

Forms that prey on macroscopic benthic animals include: *Callinectes sapidus, C. boucourti, Citharichthys spilopterus, Myrophis punctatus, Arius mela-*

nopus, Bagre filamentosus, Dipterus rhombeus, Eucinostomus pseudogula, Pomadasys crocro, Bairdiella ronchus, and *Micropogon furnieri.* Both species of *Callinectes* were found to be opportunistic feeders, operating as scavengers as well as predators.

The top carnivores of the Tortuguero community were found to include: *Carcharhinus leucas, Centropomus pectinatus, C. parallelus, C. undecimalis, Strongylura marina, Lutjanus jocu, Caranx hippos, Cichlasoma friedrichsthalii, Elops saurus* and *Megalops atlantica.* Most of these combine fish and shrimp, or fish, shrimp, and crabs in their diets. The bull shark (*Carcharhinus*) certainly represents the ultimate carnivore in the estuary, but also was found to scavenge. Feeding relationships within the estuarine community are summarized in Fig. 5.

SEASONAL VARIATIONS IN TROPHIC RELATIONSHIPS

The most obviously observed seasonal changes in the consumer levels of the estuarine food pyramid were associated with the greater abundance of the tismiche and the increased feeding activity during the dry season at both the herbivore and the carnivore levels in the planktonic region. Systematic collections were not made in all months of the year but tismiche was recorded in the estuary in the months of May, July, August, September and October. Some tismiche may appear in the wet months, but the dense aggregations have been found to occur only when there is little fresh water flow. Heaviest concentrations were taken in the month of August. Tismiche was taken in all parts of the estuary, but greatest concentrations occurred just upstream from the Boca. Numerous sight records of organisms gorging themselves on the tismiche suggest that these swarms provide a sort of manna for both regular and transient estuarine inhabitants. The fish-eating bat, *Noctilio,* was found to aggregate in exploiting this easily taken prey.

Table 1, mentioned previously, lists the common year-round fishes of the estuary, tre wet-season species, and those of the dry season. Those lists were composed from the data of Kelso (10) and Gilbert and Kelso (7), from spot collections made in 1970 and 1971, and from extensive collections in wet months of the summer of 1972. A total of 28 species appeared to be common permanent residents of the estuarine comunity. An additional 10 species were restricted to or were more abundant during wet seasons, and 7 species seemed associated with dry seasons. The total number of common species present in dry seasons is roughly equal to the number present in wet seasons. The lists are not exhaustive as they exclude forms taken in token numbers. Gilbert and Kelso (7) reported a total of 67 species in the estuary during the wet seasons. The lists of common forms presented here total 45 species, including year-round, wet season and dry season forms. However, if one includes in the list of dry season invaders, those forms known only from the Boca and forms from the surrounding shallow oceanic waters which may enter the Boca in dry seasons, that list is more than doubled. Additionally, one is impressed in dry seasons by the numbers present of certain conspicuous species such as tarpon and snook and the schooling anchovies and sprats. It is suspected that further carbon budget quantitation will reveal a much greater impact of consumers during dry seasons as compared with wet seasons than is suggested by comparisons of numbers of species. It can be seen from these data that most of the species taken in the estuary may occur there at all seasons, although their numbers and size classes change markedly. All of the wet season invaders, with the exception of *Anchoviella*, are forms that retreat upstream during dry seasons. *Anchoviella* is probably not typically a wet season invader but happened to be captured in numbers in such a time. Extensive gill-netting and trot-line fishing during an exceptionally wet period in early August, 1972, yielded a total of only 13 species of fishes from the open waters of the estuary This aggregation perhaps typifies the fauna of the channel during the wet seasons. The species taken were: *Carcharhinus leucas, Bagre filamentosus, Arius melanopus, Strongylura marina, Hyporhamphus roberti, Centropomus pectinatus, Diapterus rhombeus, Pomadasys crocro, Bairdiella ronchus, Micropogon furnieri, Citharichthys spilopterus,* and *Achirus lineatus.* Only the catfishes, bigbone snook, and croaker were taken in abundance. Other larger species of fishes observed in the estuary, but not taken in the nets or on set lines at this time, were *Megalops atlantica* and *Centropomus parallelus* and/or *undecimalis* (snook caught on hook and line at the Boca were not identified to species). *Cichlasoma citrinellum, C. friedrichsthalii, C. maculicauda,* and *Sphoeroides testudineus* were abundant in the shallows at the time. While the total number of species reported from the estuary during wet months is roughly equal to the number recorded for dry periods, the number of species that occur regularly in abundance in wet seasons is relatively small. Dry season invaders included such marine-pelagic forms as *Elops saurus, Scomberomorus maculatus, Sphyraena guachancho,* and the anchovy, *Anchoa lamprotaenia.* Two species of jacks (*Caranx*) and the snook *Centropomus undecimalis* entered the estuary in numbers during dry periods, either directly or indirectly attracted by the hordes of tismiche. However, most of the species involved regularly enter estuaries, and are even found in fresh water lakes (MILLER, 15), where a seasonal food supply analogous to the tismiche is lacking. Such immigrations are more common during dry seasons, although high salinities are obviously not required by all of the species involved. Whatever the factors involved, the estuary becomes more of an extension of the freshwater river system during the wet seasons, while in the dry seasons it may become essentially an inland extension of the sea.

PRELIMINARY CARBON BUDGET FOR THE ESTUARY

In temperate zone communities one expects to find seasonal cycles of productivity that reflect cyclic variations in solar input, and thus in temperatures and related phenomena. In the tropics, while seasonal variations in solar input are minimal, a pronounced seasonality based on rainfall cycles occurs. This alters the community, not only in terms of the species present but also in the rate of organic production and in the import of allochthonous organic materials.

TABLE 1

Fishes recorded in the Estuary at Tortuguero, Costa Rica

Species taken throughout the year

Megalops atlantica (tarpon)
Carcharhinus leucas (Bull shark)
Myrophis punctatus (speckled worm eel)
Hyphessobrycon tortuguerae (characin)
Arius melanopus (catfish)
Bagre filamentosus (gaftopsail catfish)
Poecilia mexicana (marbled molly)
Strongylura marina (Atlantic needlefish)
Strongylura timucu (needlefish)
Hyporhamphus roberti (halfbeak)
Citharichthys spilopterus (bay whiff)
Achirus lineatus (lined sole)
Oostethus lineatus (opposum pipefish)
Melaniris chagresi
Mugil curema (white mullet)
Centropomus parallelus (fat snook)
Centropomus pectinatus (tarpon snook)
Lutjanus jocu (dog snapper)
Pomadasys crocro (burro grunt)
Diapterus rhombeus (mojarra)
Eucinostomus pseudogula (slender mojarra)
Bairdiella ronchus (pis-pis)
Micropogon furnieri
Cichlasoma citrinellum (mountain tuba)
Cichlasoma friedrichsthalii (viejita)
Cichlasoma maculicauda (tuba)
Dormitator maculatus (fat sleeper)
Awaous taiasica (river goby)
Sphoeroides testudineus (checkered puffer)

Species taken only during the wet season

Anchoviella elongata (anchovy)
Astyanax fasciatus (characin)
Cichlasoma centrarchus
Eleotris amblyopsis
Gobiomorus dormitor (bigmouth sleeper)
Bathygobius soporator (frillfin goby)
Evorthodus lyricus (lyre goby)
Gobionellus boleosoma (darter goby)
Gobionellus fasciatus
Gobionellus spes

Species taken only during the dry season

Elops saurus (ladyfish)
Anchoa lamprotaenia (longnose anchovy)
Sphyraena guachancho (barracuda)
Scomberomorus maculatus (Spanish mackerel)
Caranx hippos (crevalle jack)
Caranx latus (horse-eye jack)
Centropomus undecimalis (snook)

TABLE 2

Planktonic primary productivity for wet and dry seasons

Dry season		Wet season	
1971	$gC/m^2/day$	1972	$gC/m^2/day$
Sept. 7	0.19	Aug. 9	0.04
8	0.42	10	0.08
9	0.62	11	0.07
$\bar{x}$	0.41	$\bar{x}$	0.06

PRIMARY PRODUCTIVITY: Determinations of planktonic primary productivity were carried out in the estuary on three days during the summer dry season of 1971, and on three days of the summer wet season of 1972. Results are shown in Table 2. Productivity was much higher during the dry period, with a mean level of 0.41 $gC/m^2/day$ as opposed to a wet season mean of 0.06 $gC/m^2/day$.

IMPORT OF ALLOCHTHONOUS ORGANIC MATERIALS: The contribution of allochthonous organic matter to the estuarine economy has not been directly assessed but estimates of the importance of this source of fixed carbon were made from several sources of information. Rates of import of hyacinth mats were based on the data of KING (11) who made rough determinations of the area of the vegetation mats that passed a point along the estuary per unit time in wet summer months of 1960. His estimates ranged from low values of 0.05 m^2/min upward to 95 m^2/min. Calculations based upon these data suggest a mean rate of import of rafts (principally hyacinths) to the estuary of 7885 m^2/day. Assuming a dry weight of 1.5 kg/m^2 (unpublished data of KANE, 9) this approaches a maximum of 12 metric tons/day. Distributed over the surface of the estuary (142 ha) this amounts to ca. 8.5 g organic material/m^2/day, or 4.25 $gC/m^2/day$ (assuming organic material to be 50% carbon). Much of this organic material is flushed out to the Caribbean. Just how much remains to be determined. Since some of the rafts remain in the estuary for considerable periods of time, production during these periods must be included in the final budget calculations.

The rate of import of suspended organic materials from the freshwater tributaries was also estimated. Flow measurements were made on two days during the wet season in 1972. However, since no organic-load data were obtained for Tortuguero, data for the organic-load in the Río Polochic, a tributary of Lake Izabal, Guatemala (BRINSON, 2), were used in this calculation. The drainage pattern there is similar to that for the Tortuguero estuary. The quantity of organic material thus estimated to enter the estuary with stream flow is 0.2 gC/m²/day for the wet season. This quantity is roughly ½ the daily planktonic primary production of the dry season but ca. 3.5× that of the wet season. Thus the two processes would seem to complement one another in stabilizing the base for respiration.

COMMUNITY RESPIRATION: Daily respiration values were calculated from changes in ambient oxygen concentrations for a single station at the lower end of the estuary near the end of the summer rainy season. The values obtained were 1.15 gC/m²/day and 1.80 gC/m²/day, yielding a mean of 1.48 gC/m²/day. These values greatly exceed the primary production values for either season and exceed the sum of primary production plus estimated allochthonous carbon input from freshwater tributaries. If our estimates are correct, the rafts of vegetation and organic materials contained in the tide wedge play important roles in the metabolism of this estuary. Whatever the case, it seems almost certain that this estuarine community is similar to those of higher latitudes (DARNELL, 5; ODUM and HEALD, 16) in producing only a small fraction of the fixed carbon consumed by the system.

DISCUSSION

The organization of the Tortuguero estuarine ecosystem can be conceptualized by considering the interactions among 6 environmental compartments: the estuarine waters; the atmosphere and space; the sea (Caribbean); the tributary stream system; estuarine sediments; and the surrounding lowlands (involving several plant associations). Interactions with the space and atmosphere compartment come about through solar energy input and the various related meteorological phenomena, including air temperature, rainfall, cloud cover, and wind, and through the cycles of gaseous elements involved in the nutrient budgets of the estuary. This compartment shows a bimodality corresponding to the wet and dry cycles. The tidal influence has two daily pulses. The tides vary little during the lunar cycle, so one can generally ignore this rhythm.

Primary production oscillates between the superficial algae-bearing stratum of freshwater during wet seasons, and the tide-pulsed salt water wedge during dry seasons. Because of the lack of mixing between the lighter freshwater stratum and the tide wedge it was assumed that the flora of the upper layer obtained its nutrients from the river discharge (runoff from areas higher in the watershed as well as local runoff) enriched by the rainfall. Gaseous elements diffuse into the turbulent surface layer. However, nutrients available to algae in the tide water must either be carried in from the Caribbean with the water or diffuse into the water from the somewhat sparse estuarine sediments. Gaseous exchanges between the tide wedge and the atmosphere are not possible beyond the Boca, at least during the wet seasons. Nutrient inputs to the estuary from the terrestrial, atmospheric and freshwater compartments are likely greatest during the wet season when the photosynthetic assimilatory capacity of the planktonic region is least, although photosynthesis in the rafts may offset this limitation. Discharge from the estuary during the rainy season may be of direct or indirect benefit to the activities of the near-shore marine community (RYTHER, MENZEL and CORWIN, 20).

Considering the overall economy of the estuarine ecosystem, it would appear to be in a steady state, being regularly replenished with both inorganic and organic materials as well as with organisms from the associated compartments. There is little deposition of organic sediments in the estuary, suggesting that what is not immediately utilized is exported to the sea. This is also true of the floating mats of vegetation. There is some export to the terrestrial compartment via human harvest of fish, crabs and a few turtles, but this must constitute a relatively small fraction of the total yield of the system. The impacts of exploitation by other terrestrial vertebrates was not extensively explored, but seemed to be quite limited.

The evaluation of trophic relationships among consumers in the estuary suggests opportunistic feeding at all trophic levels, with the exception of a few specialized herbivores. The preliminary carbon budget calculations showed the food chains to be dominated by allochthonous materials through all seasons. It seems an established principle that trophic bases of estuarine communities differ from those of typical freshwater lakes and ponds and the open oceans in that respiration is largely dependent on the input of allochthonous materials. This was shown by DARNELL (5) and by ODUM and HEALD (16), and is borne out in this study. The estuarine food webs also seem to be rendered somewhat loose by the opportunistic feeding behavior of most of the larger inhabitants. While there are several definable food webs, they are based principally on the habitat localizations of the smaller organisms, rather than on feeding specializations, and these webs merge at higher trophic levels because of the greater motility of larger organisms. Organisms that feed on benthic algae, bacteria, fungi and detritus during the day may feed on similar materials in the planktonic region at night when they move away from the bottom. This appears true of amphipods, isopods, mysids, post-larval shrimp, etc. The organisms that feed in the root masses of the floating mats are also only partially isolated.

The evaluation of trophic relationships among consumers in the estuary sugclearly the arrival of the tismiche. Most of the species of consumers known from the estuary were recorded during both wet and dry seasons, though several species of fishes are resident only during the wet seasons, and others only during the dry seasons. Several of the large predaceous fishes either are dry season immigrants or increase in numbers in the estuary during the dry seasons. These changes are clearly demonstrated in the catches of sport anglers. During wet periods of the year intensive angling is generally unrewarded unless one concentrates on the ubiquitous pan-fishes of the estuary. However, after a few relatively rain-free days tarpon and snook can be caught in the vecinity of the Boca, sometimes in great numbers. During extended dry periods jack and ladyfish appear, and during the height of the dry season such pelagic forms as Spanish mackerel and barracuda are taken in the estuary.

When one ponders what the future holds for this and other relatively pristine estuarine communities, several possibilities come to mind. In the case of the Tortuguero estuary, a likely encroachment of man will be the clearing of the land surrounding the estuary and of the watershed just upstream. Much of the land in the headwater areas has already been cleared and put into cultivation. Long-time inhabitants of Tortuguero say that the results of this have been an increased siltiness of the river. Any marked increase in the silt load would further reduce the already very limited rate of planktonic photosynthesis in the estuary. The watershed immediately above the estuary is floodplain forest and as such is not suitable for agriculture, but extensive timbering there would produce an increased rate of runoff and certainly alter the pattern of delivery of detrital materials. Plant detritus which seems to provide much of the food for estuarine primary consumers may itself pose a threat to the integrity of the ecosystem if the detritus is derived in part from cultivated areas. Such organic detritus may contain "hard" pesticide residues that are toxic either directly to primary consumer organisms (MAHOOD, MCKENZIE, BOLLER and DAVIS, 13; LEEFLER, 12) or through biological magnifications to organisms at higher trophic levels (WOODWELL, WURSTER and ISAACSON, 21). Any one or combinations of these influences could greatly reduce the estuarine species diversity and productivity.

RESUMEN

Este es un estudio de las interrelaciones tróficas del estuario Tortuguero, situado en la costa Caribe de Costa Rica. Se describen sus características básicas, tanto físicas como químicas, y se ha calculado un conteo preliminar del carbón para el ecosistema estuarino. Los ciclos estacionales en la cuenca estuarina siguen el patrón de la precipitación, registrándose dos estaciones húmedas y dos secas por año. Las investigaciones demuestran que la producción planctónica primaria es mayor durante las estaciones secas. Sin embargo, el insumo de materias extrínsecas por medio del flujo del río es mayor durante las estaciones húmedas. El conteo preliminar de carbón indica que la respiración del estuario origina más material orgánico que el producido en el estuario durante ambas estaciones. Durante las estaciones húmedas se registra un aumento en el número de especies de peces típicamente de agua dulce y asimismo un aumento en el número de formas típicamente marinas durante las estaciones secas. La diferencia estacional más extraordinaria en la comunidad estuarina radica en la presencia durante las estaciones secas de numerosos grupos de *tismiche,* agregaciones densas de camarones y peces larvales.

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Fig. 1. Outline diagram illustrating the major features of the Tortuguero estuarine system. Transects labeled A-F indicate positions of bathymetric profiles similarly labeled in Figure 2. Transect A is at the Boca, B at the airstrip (which is located just inland from the Caribbean), and C is at Cuatro Esquinas. Tortuguero Village is at 1, 2 indicates Lagunas del Tortuguero and 3 Laguna Penitencia.

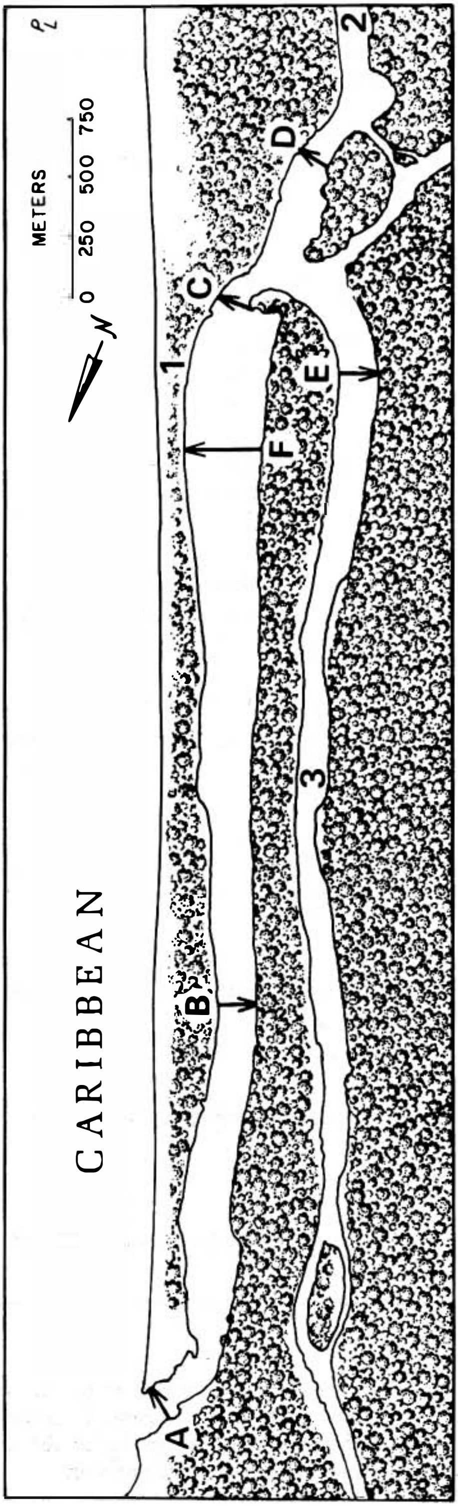

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Fig. 2 Bathymetric profiles for stations A-F in the Tortuguero estuarine system. Arrows on Figure 1 indicate the direction of travel followed in producing the profile. Scales on diagrams indicate 10 ft intervals.

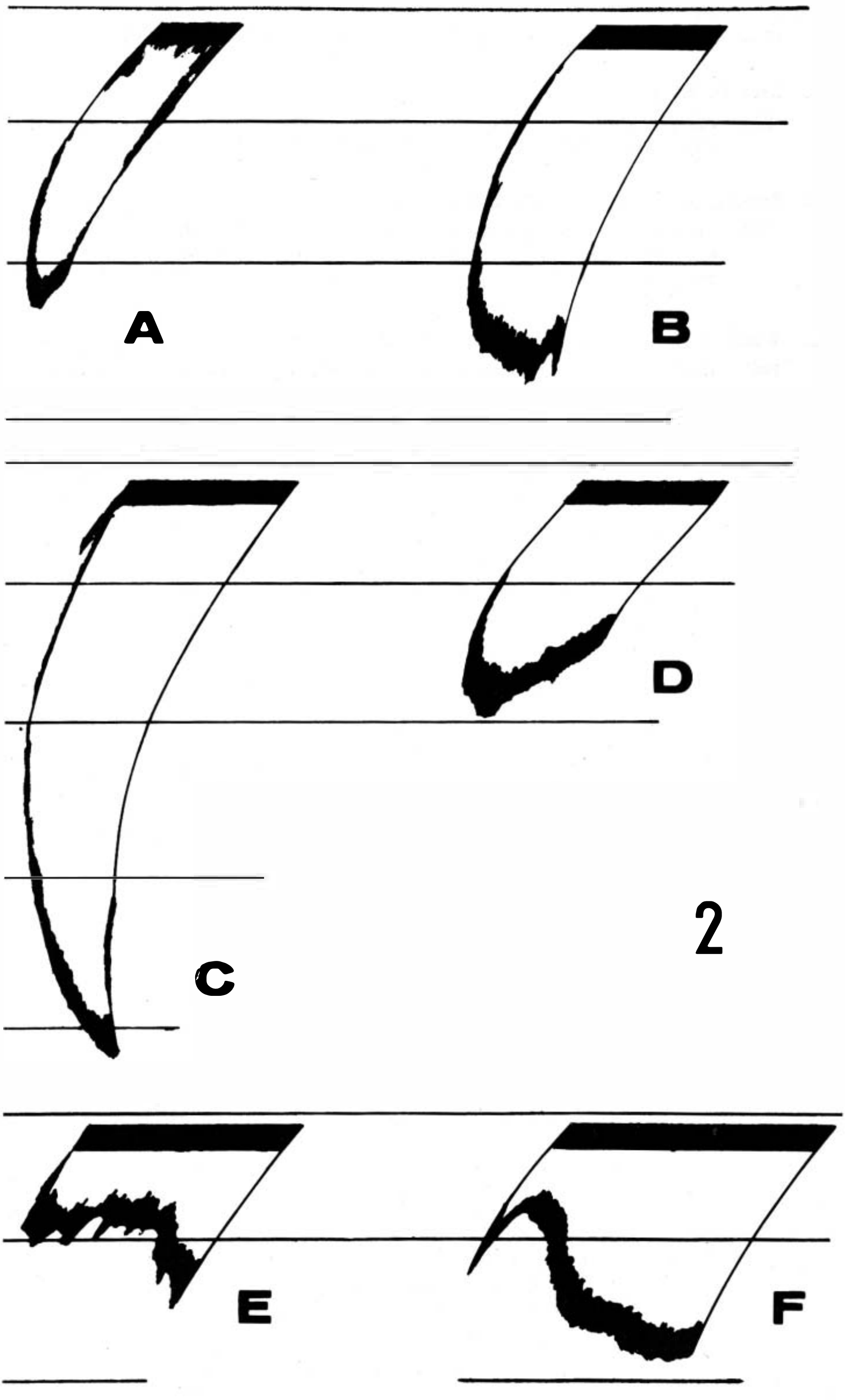

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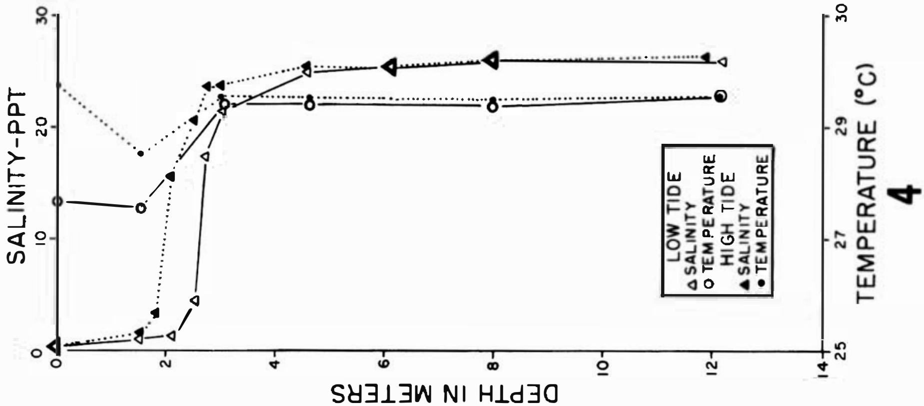
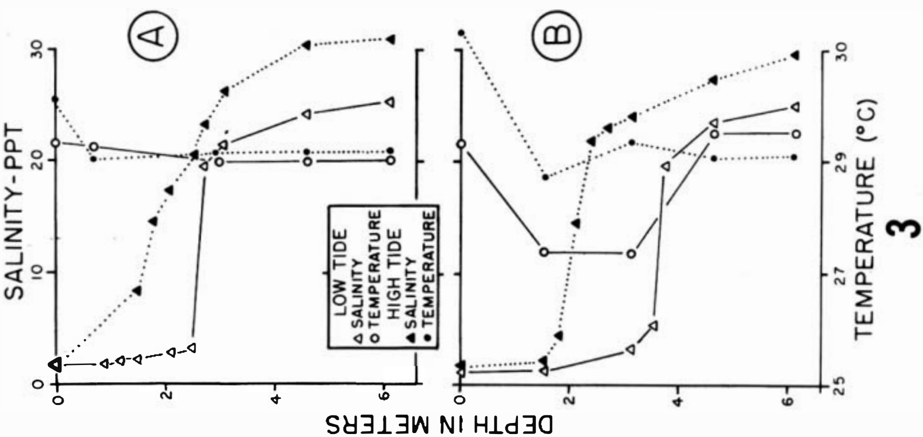
Fig. 3. Temperature and salinity profiles at high and low tides at stations A and B (Fig. 1).

Fig. 4. Temperature and salinity profiles at high and low tides at station C (Fig. 1).

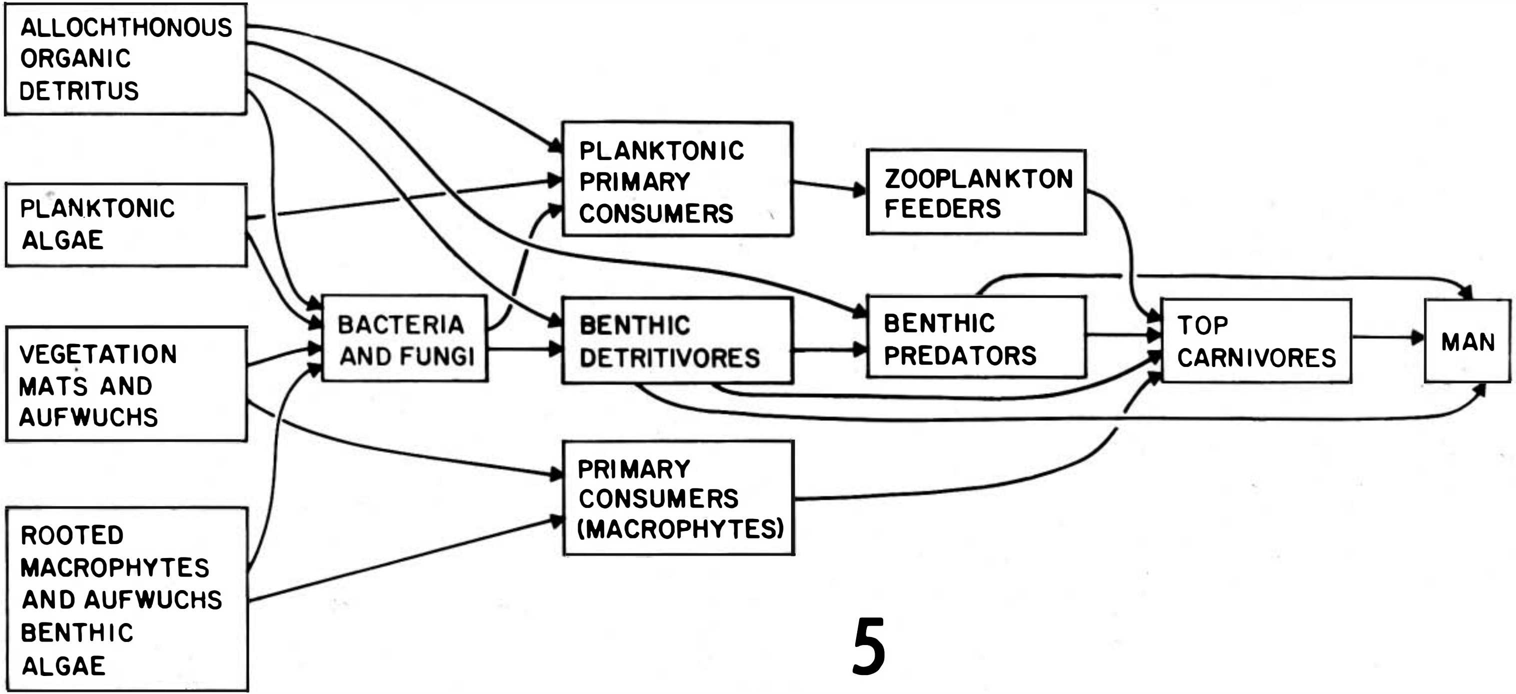

SALINITY-PPT
DEPTH IN METERS
TEMPERATURE (°C)
LOW TIDE
SALINITY
TEMPERATURE
HIGH TIDE
SALINITY
TEMPERATURE

4


A
B
SALINITY-PPT
DEPTH IN METERS
TEMPERATURE (°C)
LOW TIDE
SALINITY
TEMPERATURE
HIGH TIDE
SALINITY
TEMPERATURE

3

Fig. 5. Diagrammatic summary of trophic relationships of the Tortuguero estuarine community.


ALLOCHTHONOUS ORGANIC DETRITUS
PLANKTONIC ALGAE
VEGETATION MATS AND AUFWUCHS
ROOTED MACROPHYTES AND AUFWUCHS BENTHIC ALGAE
BACTERIA AND FUNGI
PLANKTONIC PRIMARY CONSUMERS
BENTHIC DETRITIVORES
PRIMARY CONSUMERS (MACROPHYTES)
ZOOPLANKTON FEEDERS
BENTHIC PREDATORS
TOP CARNIVORES
MAN

5