

Hsing-Juh Lin · Jia-Jang Hung · Kwang-Tsao Shao
Fancy Kuo

Trophic functioning and nutrient flux in a highly productive tropical lagoon

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Abstract Chiku Lagoon is a highly productive tropical lagoon with high fishery yields. Trophic networks and stoichiometrically linked water-salt-nutrient budgets were constructed to relate the functioning of the food web to nonconservative behavior of nutrients in the lagoon. Network analysis showed that the lagoon is more dependent on phytoplankton than detritus and periphyton to generate food sources for consumers. Nevertheless, detritivory is more important than herbivory in the food web. Transfer efficiency is high at low trophic levels, but declines at higher levels due to the high fishery pressure. Thus, only a small fraction of organic matter (15%) is recycled, and this all through detrital pathways, most of which involve only two compartments. Summation of individual rate measurements for primary production and respiration yielded an estimate of $+249 \text{ g C m}^{-2} \text{ year}^{-1}$, suggesting an autotrophic ecosystem. An alternative biogeochemical approach demonstrated that the lagoon is a large sink for total dissolved nitrogen and phosphorus, and the net system metabolism was calculated to be $+144 \text{ g C m}^{-2} \text{ year}^{-1}$, thus providing a biogeochemical explanation for the high productivity of Chiku Lagoon. Our results suggest that the high fishery yield in Chiku Lagoon can be attributed to high planktonic productivity induced by the high rate of nutrient loading, and the straight-through pathways of the food web.

Keywords Stoichiometrically linked water-salt-nutrient budgets · Network analysis · Net system metabolism · Autotrophic system · Chiku Lagoon

H.-J. Lin (✉)
Department of Botany, National Chung Hsing University,
Taichung, Taiwan 402, ROC
e-mail: hjlin@dragon.nchu.edu.tw
Tel.: +886-4-22840416, Fax: +886-4-22874740

J.-J. Hung · F. Kuo
Institute of Marine Geology and Chemistry,
National Sun Yat-Sen University, Kaohsiung, Taiwan 804, ROC

K.-T. Shao
Institute of Zoology, Academia Sinica, Taipei, Taiwan 115, ROC

Introduction

Fishery yields in coastal lagoons are often among the highest in aquatic systems. In a comparison of a variety of marine systems, Nixon (1982) found that the yield of lagoon fisheries per unit area ($4\text{--}1000 \text{ g wet weight m}^{-2} \text{ year}^{-1}$) is commonly as high or higher than that from the most productive coastal and offshore fisheries. Joyeux and Ward (1998) compiled data on 274 lagoons around the world and reported a range of $0.4\text{--}224 \text{ g wet weight m}^{-2} \text{ year}^{-1}$ with a mean value of $5.3 \text{ g wet weight m}^{-2} \text{ year}^{-1}$, but few data are available for tropical lagoons. Nevertheless, the reported ranges for lagoon fisheries are much higher than those from coral reefs and other tropical freshwater and marine waters (Blaber 1997).

The mechanism underlying the high fishery yield in coastal lagoons is still not clear. The accessibility and protection offered by lagoons compared with other coastal and offshore waters have been argued to account for their intensive use and high fishery yield. However, Joyeux and Ward (1998) identified nitrogen in the water as one of the important factors determining the extent of fishery yield in the coastal lagoons examined. The high yield of lagoon fisheries has also been attributed to the relatively high rates of nutrient loading compared with other marine systems (Nixon 1982). While eutrophication has been recognized as an increasing pollution problem in coastal waters worldwide (Nixon 1995), there is particular interest in understanding how nutrient loading regulates metabolism and fishery production in coastal waters (Smith and Hollibaugh 1993; Kemp et al. 1997). This transfer from imported nutrients to fishery production is a function of coastal lagoons involving the complex interactions of physical, biogeochemical, and biological processes. Less attention has been given to broader approaches examining functional linkages between fishery production and causal parameters.

Chiku Lagoon ($23^{\circ}16' \text{ N}$, $120^{\circ}08' \text{ E}$) is a sandy barrier lagoon in tropical Taiwan. It is a highly productive coastal ecosystem, with exceptionally high rates of pri-

mary production and fishery yield (Lin et al. 1999). The land surrounding the lagoon varies from mangrove swamps and salinas to aquaculture ponds producing fish, shrimp, and shellfish. Lin et al. (1999) speculated that the high primary production and fishery yield were promoted by the enriched river discharges draining the mangroves and surrounding aquaculture ponds. Coupling the measurements of nutrient behaviors in the system and interconnected flows of organic matter in the food web in which matter is assimilated, transferred, and dissipated would provide significant insight into the fate of imported nutrients and the functioning structure of Chiku Lagoon.

The availability of primary production for fishery yield can be measured by net system metabolism, which is the balance between primary production and respiration of organic matter. A system is 'autotrophic' if it produces more organic matter than it respire, and 'heterotrophic' if respiration exceeds primary production. Smith and Hollibaugh (1993) estimated the small area of the coastal zone to account for about 30% of net oceanic oxidation in the world. They postulated that coastal metabolism is likely to be altered by human activities on surrounding land. Direct mesocosm experiments (Oviatt et al. 1986) and biogeochemical budgets (Kemp et al. 1997) have demonstrated that increased inputs of inorganic nutrients tend to increase net system metabolism for estuarine systems, implying increased potential for fishery yields. Little is known about the responses of a highly productive tropical lagoon.

Two common approaches have been used for estimating net coastal ecosystem metabolism. One constructs stoichiometrically linked water-salt-nutrient budgets for biogeochemical metabolism and the fate of nutrients and carbon in the system (Gordon et al. 1995). An alternative approach involves analysis and summation of individual rate measurements for primary production and respiration of consumers. The purposes of this study were (1) to use network analysis (Field et al. 1989) to characterize the interconnected flows of organic matter in the food web from primary producers to top predators, which are commercial fishery species, (2) to present stoichiometrically linked water-salt-nutrient budgets for estimating nutrient fluxes across the boundaries and nonconservative behaviors in the lagoon, and (3) to quantify the net system metabolism in Chiku Lagoon using the two different approaches. From such analyses the functioning of the food web can be related to causal environmental features. Here we tested the hypothesis that net system metabolism in the highly productive Chiku Lagoon is autotrophic, by comparing calculations of net system metabolism generated by two different approaches.

Materials and methods

Study area

The lagoon covers about 9.6 km² of surface area and is continuously open to the sea through two narrow tidal inlets in the sandbar (Fig. 1). The average depth at low tide is 1 m, and the tidal

range is about 1 m. Climatic data derived from the local weather station of the Central Weather Bureau of Taiwan during the past decade show distinct dry and wet seasons. During the dry season of October–April, mean monthly rainfall normally does not exceed 50 mm, and in May–September, average monthly rainfall frequently exceeds 100 mm. The freshwater discharge is 265–563×10³ m³ day⁻¹ in the wet season, compared to 85–240×10³ m³ day⁻¹ in the dry season. The small volume of the lagoon makes salinity responsive to changes from freshwater inputs and evaporative losses. Consequently, salinities are lower in summer (about 21 PSU) and higher in winter (about 34 PSU). Solar insolation is lower during November–April (100–115 h month⁻¹) and higher during the rest of the year (123–180 h month⁻¹). Water temperatures range from about 33°C in summer to about 18°C in winter. Northeast winds are extremely strong from October to March, with wind speeds during this period greater (5.1–6.7 m s⁻¹) than during the rest of the year (3.2–3.9 m s⁻¹). These winds cause vertical mixing of the water column in the lagoon. A horizontal mixing of the water in the lagoon is generated by semi-diurnal tidal currents running through the southern and northern inlets (S. Jan, unpublished data).

Trophic flow model

A trophic model of Chiku Lagoon was constructed using the ECOPATH routine in the ECOPATH with ECOSIM software system of Christensen et al. (2000) to describe all the flows in the food web (Fig. 2). For each compartment, a mass-balanced budget can be expressed as: (production by *i*)-(all predation on *i*)-(nonpredation losses of *i*)-(export of *i*)-(accumulation of *i*)=0, or

$$P_i - B_i M2_i - P_i(1 - EE_i) - EX_i - AC_i = 0 \quad (1)$$

where: P_i = the production of *i*; B_i = the biomass of *i*; $M2_i$ = the predation mortality of *i*; EE_i = the ecotrophic efficiency of *i*, i.e., the part of production that is either passed up the trophic level or exported; $1 - EE_i$ = 'other mortality'; EX_i = the export of *i*; and AC_i = the accumulation of *i* during the study period.

A predator group is connected to its prey groups by its consumption (QB_j). Thus, Eq. 1) can be re-expressed as:

$$B_i \times PB_i \times EE_i - \sum_j B_j \times QB_j \times DC_{ji} - EX_i - AC_i = 0 \quad (2)$$

where PB_i is the production/biomass ratio, QB_j is the consumption/biomass ratio of predator *j*, and DC_{ji} is the fraction of prey *i* in the average diet of predator *j*. The food matrix was assumed to remain stable during the study period.

Major species of similar sizes and diets in Chiku Lagoon were grouped within the same compartment. A 13-compartment model for the lagoon was developed (Fig. 2) consisting of the following groups: (1) phytoplankton, (2) periphyton, (3) oysters, (4) herbivorous zooplankton, (5) carnivorous zooplankton, (6) shrimp, (7) crabs, (8) polychaetes, (9) herbivorous fish, (10) zooplanktivorous fish, (11) benthic-feeding fish, (12) piscivorous fish, and (13) detritus. Bacterial processes are hard to estimate reliably, and the flows may totally overshadow other flows in the system (Christensen et al. 2000). We assumed that bacteria were associated with the detritus, and that they are linked to the present model only through detrital import and export by bacterial production and respiration as recommended by Christensen et al. (2000). All parameters used to construct the model were assembled as much as possible from our own field data, and were recorded as wet weights per square meter of area per year. Data were collected at low and high tides, respectively, on each of four sampling occasions in spring, summer, autumn, and winter 1997 to take account of tidal and seasonal changes. All parameters used to construct the trophic model were averaged spatially and temporally. A few pieces of questionable data were not entered since ECOPATH links the production of each group with the consumption of all other groups, and uses the linkages to estimate the missing parameters (Christensen and Pauly 1992). DCs and EXs were always entered,

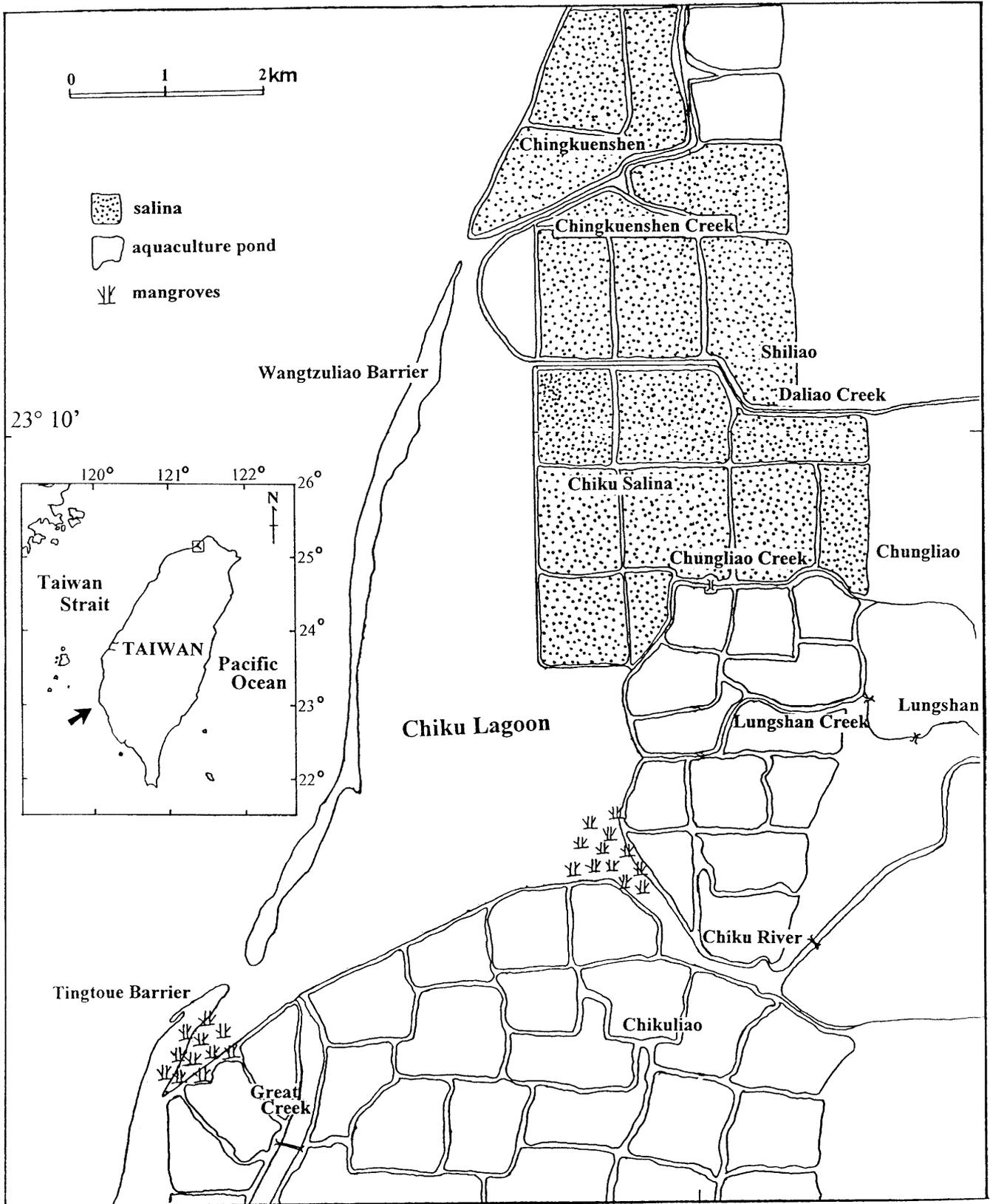


Fig. 1 Chiku Lagoon and surrounding land use within the area

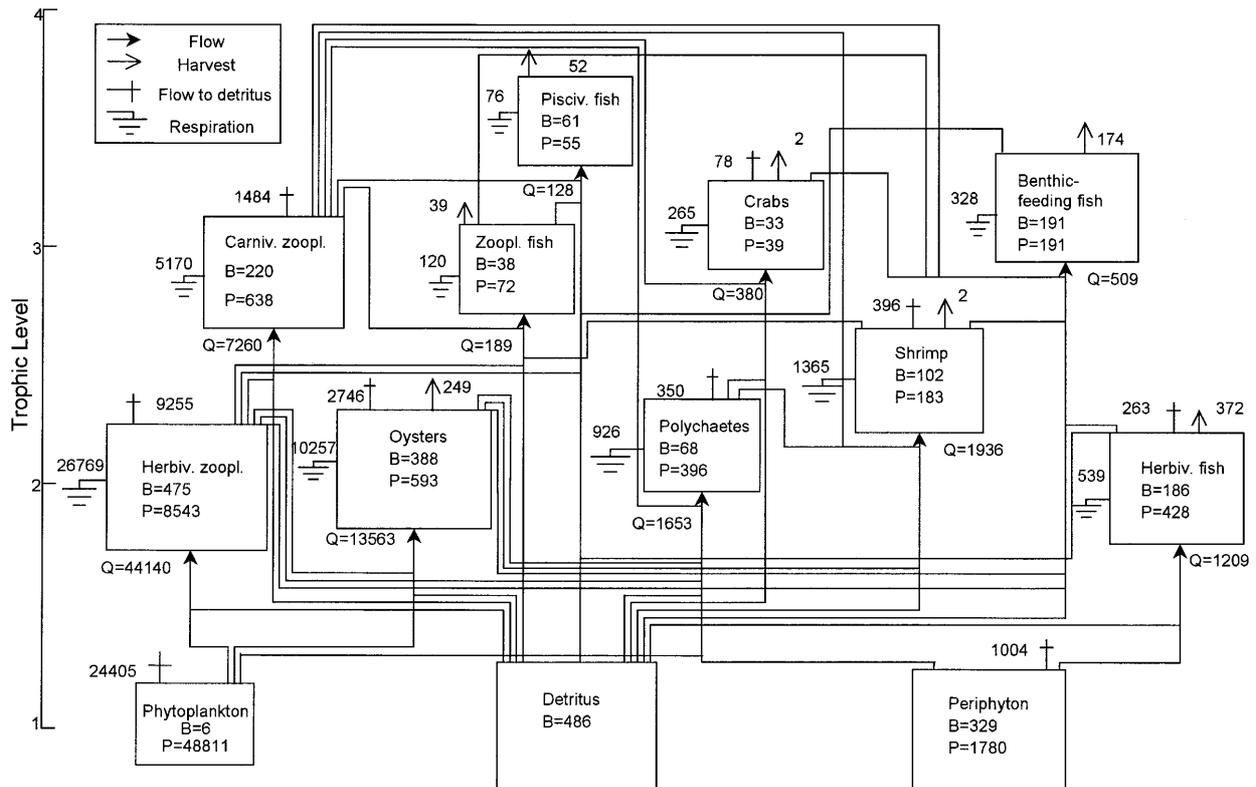


Fig. 2 Flow network of organic matter in Chiku Lagoon. *Box size* is proportional to the square root of the compartment biomass ($\text{g wet weight m}^{-2}$). Production and other flows are in $\text{g wet weight m}^{-2} \text{ year}^{-1}$

but all EEs were left for the program to estimate. The following factors were used to transform the currency to wet weight: 25 g chlorophyll $a=1$ g carbon (Parsons et al. 1977); 1 g carbon=3.3 g dry weight (Opitz 1996); 1 g dry weight=5.71 g wet weight (Opitz 1996). Methodologies of sampling, and construction, balancing, and validation of the ECOPATH model are considered elsewhere (Lin et al. 1999).

Network analysis

The network of the food web of Chiku Lagoon was analyzed using the NETWRK 4.2 software systems (Ulanowicz 1998). The required inputs of net primary production, biomass, fishery export, and flow of all matter between donor and recipient compartments for each compartment were assembled from field research data (Lin et al. 1999). The required respiratory flow for each compartment was obtained from the outputs of the ECOPATH model, which was calculated as the difference between the assimilated part of the consumption and the part of production that is not attributable to primary production (Christensen and Pauly 1992).

Input-output analysis

Input-output analysis (Kay et al. 1989) allows one to look in detail at the effects any particular flow or transformation might have on any other species. The total contribution coefficients were used to characterize the destinations of organic matter that leaves each compartment through all direct and indirect pathways. The total dependency coefficients were used to characterize the origins of matter arriving at each compartment; these coefficients can also be interpreted as combined information of the diet consumed and where it comes from.

Trophic analysis

Many consumers in the lagoon are allocated to several discrete trophic positions, because they feed on several compartments. The Lindeman trophic analysis (Kay et al. 1989) summarizes the complicated food web in terms of a single linear food chain based on the algorithms of the Lindeman trophic aggregation. The efficiency of the transfer from one aggregated trophic level to the next can be calculated as the fraction of the total matter input to a given level that is transmitted to the next higher level. The contributions of each aggregated trophic level to respiration, exports, and flows to detritus were also evaluated.

Cycle analysis

The cycling of matter and energy is considered an important process in the functioning of natural ecosystems, as they can facilitate homeostatic control over the magnitude of the flows (Odum 1969). Cycle analysis (Kay et al. 1989) characterizes the total number of cycles, their size, and the compartments that are most often involved in an ecosystem. Two indices were used to measure the retention of the lagoon system. The first is the relative importance of cycling to total flow as determined by the Finn cycling index (FCI). The other measure is the average path length (APL), which is the average number of transfers matter will experience on its trip through the food web.

Water and salt budgets

Because of complete mixing, the box model (Fig. 3) was applied to establish water and salt budgets for calculating water flows across the boundaries of Chiku Lagoon according to the guidelines recommended by Gordon et al. (1995). Assuming that the water volume in Chiku Lagoon remains constant, the exchange of water between the lagoon and adjacent coastal waters by advection (or residual flow) was estimated by the difference between freshwater inflows to the lagoon (riverine discharge and precipitation) and evaporative outflow. Precipitation and evaporation data were de-

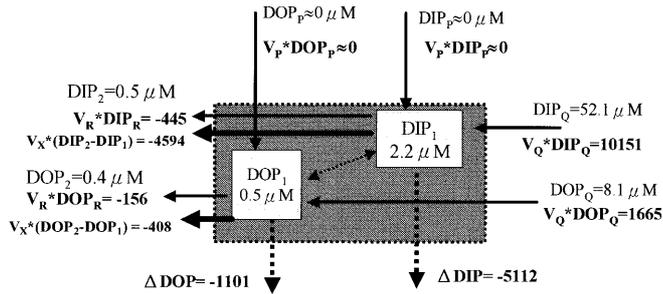


Fig. 3 Dissolved phosphorus budget for Chiku Lagoon in May 1998 (*DIP* dissolved inorganic phosphorus, *DOP* dissolved organic phosphorus, *DIP*₁ and *DOP*₁ dissolved inorganic and organic phosphorus in Chiku Lagoon, *DIP*₂ and *DOP*₂ dissolved inorganic and organic phosphorus in seawater, *V*_p precipitation, *DIP*_p and *DOP*_p dissolved inorganic and organic phosphorus of precipitation, *V*_Q riverine discharge, *DIP*_Q and *DOP*_Q dissolved inorganic and organic phosphorus of riverine discharge, *V*_R residual flow, *V*_X seawater exchange, *DIP*_R and *DOP*_R dissolved inorganic and organic phosphorus of residual flow)

rived from a local weather station, and the riverine discharges were determined from the flow velocity and the cross-sectional area of the river. Assuming that salt is conservative in the lagoon, the exchange of water between the lagoon and adjacent systems by mixing associated with tides, winds, density, and large-scale circulation patterns was estimated by salinity differences. Water and salt budgets were constructed for each of the bimonthly samples and then averaged to obtain annual budgets.

Budgets of nonconservative materials

Dissolved nutrients (carbon, nitrogen, and phosphorus) in Chiku Lagoon may not behave conservatively with respect to salinity, because they may be transformed between measured (dissolved) and unmeasured (particulate or gaseous) phases. Deviations of nutrient concentrations from predictions based on water exchange defined by the water and salt budgets can be quantitatively attributed to net nonconservative reactions of nutrients in the lagoon. Because there is no gas phase for phosphorus flux, the nonconservative flux of dissolved inorganic phosphorus (*DIP*) was assumed to be an approximation of net metabolism in Chiku Lagoon. Most conversion between dissolved and particulate phosphorus in open seawater involves organic material. Thus, the nonconservative flux of *DIP* (Δ *DIP*), multiplied by the ratio of C:P (the Redfield ratio, 106:1) in the particulate material, becomes a measure of net primary production (*p*) minus respiration (*r*), or net ecosystem metabolism. A system with Δ *DIP* > 0 is interpreted to be producing dissolved inorganic carbon (*DIC*) via net respiration ($p-r < 0$), while a system with Δ *DIP* < 0 is interpreted to be consuming *DIC* via net organic production ($p-r > 0$) (Gordon et al. 1995).

Analysis of water samples

Surface water samples were taken bimonthly from seven stations evenly distributed in Chiku Lagoon using an Alpha water sampler between November 1996 and October 1998. Four liters of each sample was stored in a polyethylene bottle and immediately brought back to the laboratory. Salinity, pH, and dissolved oxygen were measured in situ with a salinometer (Hydro-Bios), a pH meter (Orion Research) and a DO-meter (YSI model 58), with a reproducibility exceeding 5, 2, and 7%, respectively. Salinity was again determined via an Autosol salinometer (Guildline 8400B) in the laboratory to obtain more precise salinity values.

In the laboratory, a part of each water sample was filtered through an acid-cleaned, dried, preweighed Nucleopore membrane

filter to determine the concentration of total suspended matter. Part of each water sample was filtered through precombusted (at 450°C for 4 h) GF/F filters to determine dissolved inorganic nutrients and total dissolved nutrients. Dissolved inorganic nitrogen (*DIN*: $\text{NO}_3 + \text{NO}_2 + \text{NH}_4$) and phosphate (*DIP*: PO_4) were determined colorimetrically (Strickland and Parsons 1972) with a flow injection analysis method (Pai et al. 1990). Total dissolved nitrogen (*DN*) was measured with high-temperature oxidation and chemiluminescent detection (Antek N/S analyzer). Total dissolved phosphorus (*DP*) was measured with the UV-persulfate oxidation and colorimetric method (Ridal and Moore 1990). Dissolved organic phosphorus (*DOP*) and dissolved organic nitrogen (*DON*) were then determined from the differences between *DP* and *DIP*, and *DN* and *DIN*, respectively.

Results

Network analysis

Input-output analysis

Total primary production in Chiku Lagoon is high, reaching about 51 kg wet weight $\text{m}^{-2} \text{year}^{-1}$, or 2,660 g C $\text{m}^{-2} \text{year}^{-1}$. The most prominent compartment in terms of consumption of primary production in the lagoon is herbivorous zooplankton, consuming about 58% of the total primary production. Total contribution coefficients (Table 1) showed that 76% and 40% of the production of phytoplankton and periphyton eventually enter herbivorous zooplankton, respectively. More than 50% of organic matter leaving detritus enters herbivorous zooplankton. About 21–32% of primary production and the matter leaving detritus eventually enters cultured oysters in the lagoon. Less than 1% of primary production or the matter leaving detritus enters top predators. Only 21% of the matter leaving detritus eventually re-enters detritus forming a biogeochemical cycle, suggesting that most of the detritus is effectively consumed in the pathway.

Food sources of organisms in Chiku Lagoon come primarily from phytoplankton and secondarily from detritus. Total dependency coefficients (Table 2) showed that most diets of organisms in the lagoon come from phytoplankton. About 50–80% of diets depend upon detritus. Periphyton does not appear to be the main food source for consumers in the lagoon.

Trophic analysis

The effective trophic level of each compartment was estimated by the weighted average of prey trophic levels and varied from 1.0 for primary producers and detritus to 3.6 for piscivorous fish (Table 3). The trophic analysis aggregates compartmental throughput of the 13 groups in a simple Lindeman food chain with five integer trophic levels. Primary producers (trophic level I) comprise the phytoplankton, periphyton, and detritus. A large proportion (>80%) of matter flowing on trophic level II occurs through oysters, herbivorous zooplankton, polychaetes, and herbivorous fish. While 90% of the flow of

Table 1 Total contribution coefficients in Chiku Lagoon. Each value corresponds to the percentage of matter directly and indirectly leaving the vertical compartment and entering the horizontal compartment. The diagonal elements give the amount by which each compartment is dependent upon itself in cyclic pathways

(*PHY* phytoplankton, *PER* periphyton, *OYS* oysters, *HZO* herbivorous zooplankton, *CZO* carnivorous zooplankton, *SHR* shrimp, *CRA* crabs, *POL* polychaetes, *HFI* herbivorous fish, *ZFI* zooplanktivorous fish, *BFI* benthic-feeding fish, *PFI* piscivorous fish, *DET* detritus)

	PHY	PER	OYS	HZO	CZO	SHR	CRA	POL	HFI	ZFI	BFI	PFI	DET
PHY	0	0	25	76	14	4	1	2	2	<1	<1	<1	62
PER	0	0	21	40	8	6	3	25	22	<1	2	<1	67
OYS	0	0	7	12	3	3	<1	1	1	<1	<1	<1	21
HZO	0	0	11	15	18	2	<1	1	1	<1	<1	<1	25
CZO	0	0	7	13	3	4	2	1	1	<1	2	1	22
SHR	0	0	6	12	3	1	<1	1	1	<1	9	<1	21
CRA	0	0	7	12	3	1	<1	1	1	<1	10	<1	21
POL	0	0	8	15	3	14	10	1	1	<1	2	<1	26
HFI	0	0	7	13	3	1	<1	1	1	<1	2	2	22
ZFI	0	0	0	0	0	0	0	0	0	0	5	10	0
BFI	0	0	0	0	0	0	0	0	0	0	0	2	0
PFI	0	0	0	0	0	0	0	0	0	0	0	0	0
DET	0	0	32	60	12	5	1	3	3	<1	1	<1	21

Table 2 Total dependency coefficients in Chiku Lagoon. Each value corresponds to the percentage of matter directly and indirectly entering the horizontal compartment from the vertical com-

partment. The diagonal elements give the amount by which each compartment is dependent upon itself in cyclic pathways (see legend to Table 1 for key to abbreviations)

	PHY	PER	OYS	HZO	CZO	SHR	CRA	POL	HFI	ZFI	BFI	PFI	DET
PHY	0	0	97	98	98	94	86	73	67	97	94	93	96
PER	0	0	3	2	2	6	13	27	33	3	6	7	4
OYS	0	0	7	4	5	18	7	9	6	7	16	6	8
HZO	0	0	32	15	93	37	49	28	21	66	50	69	30
CZO	0	0	4	2	3	15	35	5	3	36	32	58	5
SHR	0	0	1	1	1	1	1	1	1	6	33	4	1
CRA	0	0	<1	<1	<1	<1	<1	<1	<1	<1	7	1	<1
POL	0	0	1	1	1	12	43	1	1	2	8	1	1
HFI	0	0	1	<1	<1	1	1	<1	1	1	4	16	1
ZFI	0	0	0	0	0	0	0	0	0	0	2	15	0
BFI	0	0	0	0	0	0	0	0	0	0	0	6	0
PFI	0	0	0	0	0	0	0	0	0	0	0	0	0
DET	0	0	79	50	55	88	68	58	70	74	80	66	21

Table 3 Effective trophic level of each compartment and the percentage of repartition of consumers into each trophic level of the Lindeman trophic aggregation in Chiku Lagoon

Compartment	Trophic level	Level II	Level III	Level IV	Level V
Phytoplankton	1.0				
Periphyton	1.0				
Oysters	2.1	90	10		
Herbivorous zooplankton	2.0	100			
Carnivorous zooplankton	2.9	10	90		
Shrimp	2.5	7	20	13	
Crabs	3.1	25	39	35	1
Polychaetes	2.2	84	14	2	
Herbivorous fish	2.0	100			
Zooplanktivorous fish	2.9	40	29	30	1
Benthic-feeding fish	3.2	25	38	30	7
Piscivorous fish	3.6	11	31	52	6

carnivorous zooplankton occurs on trophic level III, more than half the flows of piscivorous fish occur on trophic level IV. On trophic level V, flows are ascribed only to benthic-feeding and piscivorous fish.

Although the total dependency coefficients showed that Chiku Lagoon is greatly dependent on phytoplankton to generate food sources for consumers, the detrit-

ivory to herbivory ratio (D:H) of 1.4 indicates that detritivory flow is more important than herbivory flow in the lagoon (Fig. 4). Trophic level II achieved the highest trophic transfer efficiency of 15% for the combined flows from primary production and detritus. Transfer efficiencies decline to about 8% for trophic levels III and IV, and to 3% for trophic level V. The low trophic effi-

Table 4 Total system attributes derived from network analysis in Chiku Lagoon

Parameter	Unit	Value
Net primary production	g weight wet m ⁻² year ⁻¹	50,600
Sum of respiratory flow	g weight wet m ⁻² year ⁻¹	45,864
Sum of export	g weight wet m ⁻² year ⁻¹	890
Total biomass (excluding detritus)	g weight wet m ⁻²	2,096
Net system production	g weight wet m ⁻² year ⁻¹	4736
Primary production/respiration		1.1
Total system throughput (TST)	g weight wet m ⁻² year ⁻¹	208,270
Average residence time (ART)	days	16
Average path length (APL)		3.1
Finn cycling index (FCI)	%	15
Detritivory:herbivory ratio		1.4
Trophic transfer efficiency (geometric mean)	%	12

Fig. 4 Flow network of organic matter and trophic efficiencies (%) of Chiku Lagoon. The flow (g wet weight m⁻² year⁻¹) web is aggregated into a concatenated chain of transfers through five integer trophic levels. Flows from producers (P) and from detritus (D) and flows out of the tops of boxes represent export, and flows out of the bottoms represent respiration

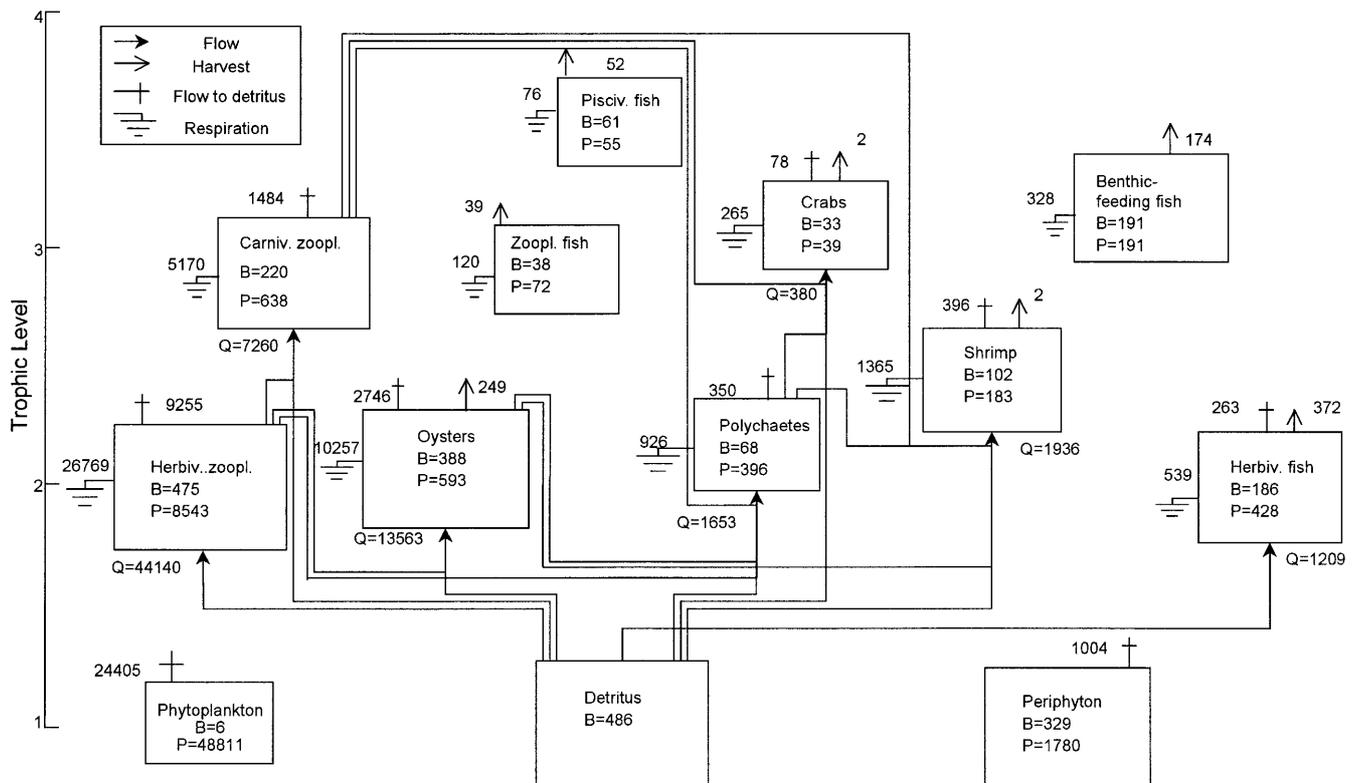
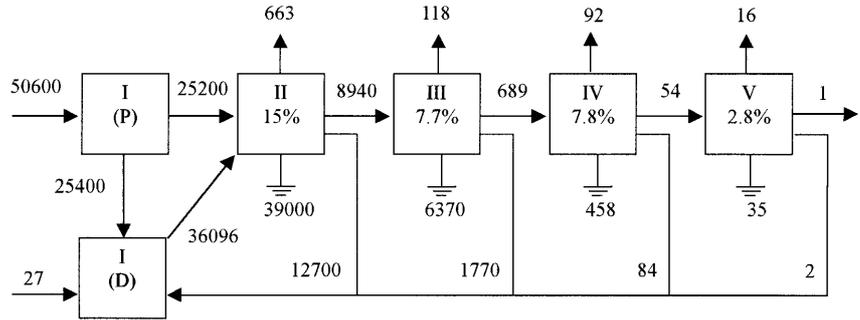


Fig. 5 Composite cycling of organic matter in Chiku Lagoon. Box size is proportional to the square root of the compartment biomass (g wet weight m⁻²). Production and other flows are in wet weight m⁻² year⁻¹

ciencies at higher levels are attributable to the high fishery catch. About 15% of the throughput for trophic level V is exported as fishery catch, compared to less than 1% for trophic level II. The geometric mean of transfer efficiencies for the aggregated food chain was calculated as 12%.

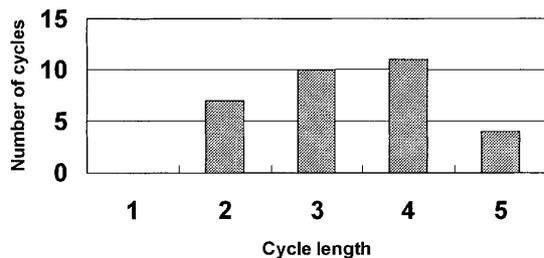


Fig. 6 Number of cycles for various cycle lengths (the number of compartments constituting the cycle)

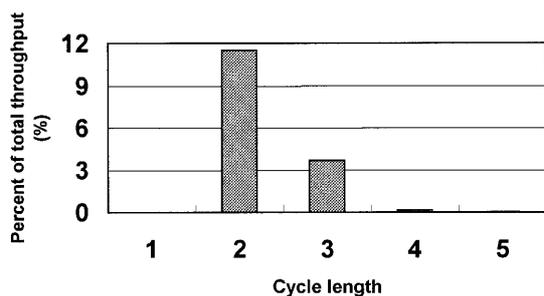


Fig. 7 Cycled flow for various cycle lengths as percent of total system throughput

Cycle analysis

The sum of consumption, export, respiratory flows, and flows into detritus in a food web is called the total system throughput (TST). It is a measure of how much matter a system processes. TST in the food web was calculated to be 208 kg wet weight $m^{-2} year^{-1}$. About 15% of the TST is involved in cycling among compartments (FCI), and all cycled flows are associated with detritus (Fig. 5). APL was estimated to be 3.1 (Table 4), suggesting that on average the cycles involved 3.1 compartments.

A total number of 32 cycles in the food web were identified. Most of the cycles comprise fewer than five compartments (Fig. 6). About one-third of the cycles comprise three compartments, and the other third are comprised of four compartments. Only 12% of the cycles consist of five compartments. Although a cycle length of two was not dominant in the cycles, the flow of matter with cycle length of two reached 77% of the cycled throughput (Fig. 7), or 12% of the TST, indicating short pathways in the cycling flow.

Net system metabolism

The difference between primary production and all respiratory flows (i.e., net system production) was calculated to be 4,736 g wet weight $m^{-2} year^{-1}$, or 249 g C $m^{-2} year^{-1}$ (Table 4). The primary production to total respiratory ratio of 1.1 indicates that Chiku Lagoon is autotrophic, implying that more organic matter is produced than is consumed in the lagoon. The average residence time (ART) of organ-

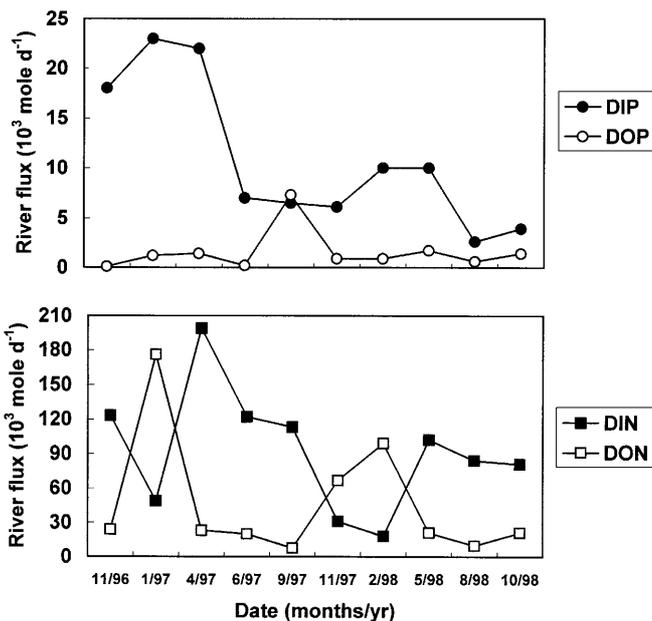


Fig. 8 Temporal variations of riverine nutrient fluxes during the study period in Chiku Lagoon (DIP dissolved inorganic phosphorus, DOP dissolved organic phosphorus, DIN dissolved inorganic nitrogen, DON dissolved organic nitrogen)

ic matter in the system is the ratio between the total biomass, excluding detritus, and the sum of all outputs (respiration and exports). The ART of organic matter in the food web is about 16 days.

Stoichiometrically linked water-salt-nutrient budgets

Water and salt budgets

The water budget in Chiku Lagoon estimated that the residual outflow, or the net input of freshwater, was $163 \times 10^3 \text{ m}^3 \text{ day}^{-1}$. According to the difference in salinity between Chiku Lagoon and adjacent seawater in the salt budget, the seawater exchange rate was therefore estimated to be $3,080 \times 10^3 \text{ m}^3 \text{ day}^{-1}$. The residence time of lagoon water was thus about 6 days.

Nonconservative nutrient budget

Large quantities of dissolved nutrients were observed to enter from the Chiku River and Daliao Creek which drains mangrove swamps and surrounding aquaculture ponds (Fig. 8). The fluxes of dissolved nutrients were attributable to temporal variations in river discharge, which are greatly influenced by the frequency of summer typhoons. In 1997, the high frequency of summer typhoons tended to result in higher fluxes of dissolved nutrients. To obtain representative annual fluxes of nutrients, nutrient flux data were collected for over 2 years and averaged temporally to take account of interannual

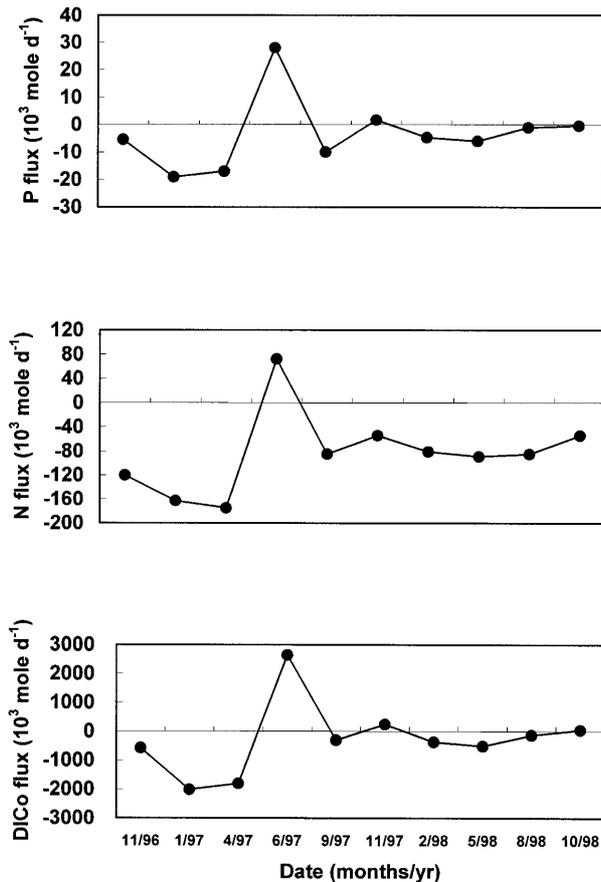


Fig. 9 Nonconservative nutrient fluxes and stoichiometric calculation of net system metabolism during the study period in Chiku Lagoon (*DICO* dissolved inorganic carbon due to organic metabolism)

changes. Despite the interannual variability, there was a clear seasonal pattern with nutrient fluxes in summer greater than in winter. Annual inputs of DN and DP by the river discharge were estimated to be 51×10^3 and 4.6×10^3 mol $year^{-1}$, respectively. According to the water

and salt budgets, nonconservative fluxes of DN and DP in the lagoon were generally negative on all sampling dates (Fig. 9). The annual mean values of ΔDN and ΔDP were -3.0 and -0.1 mol $m^{-2} year^{-1}$, respectively, suggesting that Chiku Lagoon is a large sink for total dissolved nitrogen and phosphorus. Despite the rapid water exchange, the concentrations of DIN and DON in the lagoon were 15 and 17 μM , and DIP and DOP were 3.0 and 0.7 μM , respectively.

The annual net ecosystem metabolism was estimated from ΔDIP and the C:P ratio in particulate organic matter, assuming that the internal reaction flux of DIP was proportional to production and consumption of particulate organic matter (Gordon et al. 1995). The particulate C:P ratio was assumed to be 106 because planktonic metabolism dominates the net ecosystem metabolism in Chiku Lagoon (Lin et al. 1999). Generally, calculations of net ecosystem metabolism were negative on all sampling dates (Fig. 9), and the mean value was estimated to be 12 mol C $m^{-2} year^{-1}$, which is equivalent to 144 g C $m^{-2} year^{-1}$, suggesting that Chiku Lagoon is an autotrophic system.

Discussion

Details of the transfer of organic matter from primary production to top predators (commercially important species) in a food web can be revealed by network analysis. A comparative approach with other coastal ecosystems using the results from network analysis is helpful to characterize the flow of matter in Chiku Lagoon and to decide which features are common to tropical lagoons (Table 5). Net primary production of Chiku Lagoon is high compared with other coastal systems, but falls within their reported range. The value for Chiku Lagoon ($2,660$ g C $m^{-2} year^{-1}$) is comparable to the mean value of salt marshes ($2,741$ g C $m^{-2} year^{-1}$; Smith and Hollibaugh 1993). The highest value occurs at the Great

Table 5 Comparisons of net primary production (*NPP*; g wet weight $m^{-2} year^{-1}$), trophic transfer efficiency for each level and the geometric mean (*II-V*), detritivory to herbivory ratio (*D:H*),

average path length (*APL*), and Finn cycling index (*FCI*) among coastal ecosystems (*NA* data not available)

Study site	Climate	NPP	II (%)	III (%)	IV (%)	V (%)	Mea (%)	D:H	APL	FCI (%)
Chiku Lagoon (this study)	Tropical	50,600	15	7.7	7.8	2.8	12	1.4	3.1	15
Terminos Lagoon (Manickchand-Heileman et al. 1998)	Tropical	11,754	6.7	6.9	7.4	6.8	7	4.6	10	7
Takapoto Atoll lagoon (Niquil et al. 1999)	Tropical	4,254	23	12	16	NA	17	0.6	NA	18
Great Barrier Reef (Johnson et al. 1995)	Tropical	97,163	5.7	17	18	0.5	5.4	1.0	3.5	26
Tiahura Reef ^a (Arias-Gonzalez et al. 1997)	Tropical	17,650	8.7	9.2	9.0	4.8	7.7	NA	NA	NA
Tongoy Bay (Wolff 1994)	Subtropical	7,125	14	11	14	14	14	0.8	4.9	10
Sundays Beach (Heymans and McLachlan 1996)	Temperate	10,556	24	10	7	11	12	12	2.3	13
Ythan Estuary (Baird and Ulanowicz 1993)	Temperate	12,000	6.4	2.4	3.2	5.6	3.7	10	2.9	25
Swartkops Estuary (Baird and Ulanowicz 1993)	Temperate	12,652	3.5	8.3	0.8	1.1	2.8	1.5	3.9	44
Kromme Estuary (Baird and Ulanowicz 1993)	Temperate	16,046	1.7	7.1	3.2	7.1	3.4	6.7	2.4	26
Ems Estuary (Baird and Ulanowicz 1993)	Temperate	1,409	17	7.0	3.3	NA	7.4	0.5	3.4	30
Chesapeake Bay (Wulff and Ulanowicz 1989)	Temperate	17,436	18	7.2	7.0	1.2	5.7	5.0	3.6	30
Baltic Sea (Wulff and Ulanowicz 1989)	Temperate	8,594	19	20	5.9	14	13	1.5	3.3	23

^a Mean for the fringing reef and the barrier reef

Barrier Reef (Johnson et al. 1995), which is about two-fold that of Chiku Lagoon. However, the great variation in net primary production and the limited data mask differences between tropical lagoons and coral reefs and between tropical and temperate coastal systems.

The geometric mean of trophic efficiencies of Chiku Lagoon is also high when compared with those of the other coastal systems (Table 5), but the trophic efficiencies of tropical lagoons are not necessarily higher than those of coral reefs. No distinct latitudinal trend can be seen in trophic efficiency. Almost all trophic efficiencies are lower than the value of 15% proposed by Ryther (1969) for coastal waters with the exception of Takapoto Atoll lagoon. Many trophic efficiencies are even lower than the range (10–20%) commonly reported in the literature (Odum 1971).

Despite the high mean trophic efficiency of Chiku Lagoon, efficiencies are lower at higher trophic levels when compared with other coastal systems. The low efficiencies can be attributed to high exports as fishery yields (Fig. 4). Exports from trophic levels IV and V are higher than flows to detritus and predation loss on these levels. This indicates that the fishing pressure on piscivorous and benthic-feeding fish is high. Fishing is thus very likely a major feature structuring the communities of higher trophic levels in the lagoon. This is reflected in the high gross efficiency of the lagoon (Lin et al. 1999). Little has been reported on gross efficiency in other tropical lagoons. However, the gross efficiency (the catch to net primary production ratio) for the fisheries of Chiku Lagoon (1.8%) is higher than values reported from Tongoy Bay (0.89%; Wolff 1994), the Peruvian upwelling system (0.90%; Jarre et al. 1991), and the Tiahura coral reefs (0.006%; Arias-Gonzalez et al. 1997).

The higher D:H ratios of tropical lagoons when compared with coral reefs (Table 5) suggest that they are more dependent on detritus than on primary producers to generate TST. However, Chiku Lagoon differs from Terminos Lagoon in the extent that detritivory dominates over herbivory, i.e., primary production in Chiku Lagoon is exploited more by consumers than it is in Terminos Lagoon. Niquil et al. (1999) found that the D:H ratio in Takapoto Atoll lagoon would decrease by augmenting primary productivity by 10%. In temperate systems, the Swartkops estuary mildly polluted by agriculture and industry (Baird and Ulanowicz 1993) and the eutrophic Baltic Sea (Wulff and Ulanowicz 1989) showed much lower D:H ratios than values for other estuaries. The high planktonic primary production of Chiku Lagoon places it among the most productive coastal ecosystems (Lin et al. 1999). Therefore, the greater dependence on herbivory in Chiku Lagoon is likely to be induced by the high rate of nutrient loading.

In addition to trophic status (i.e., degree of eutrophication), there appears to be some correlation between growth form of the dominant producer and the D:H ratio in coastal systems. For coral reefs, the Takapoto planktonic system differs from the benthic systems of the

Great Barrier Reef (Johnson et al. 1995) and the Tiahura reef (Arias-Gonzalez et al. 1997). In Takapoto, consumers in the water mainly exploit planktonic primary production directly, whereas on the Great Barrier Reef and at Tiahura, macroalgae and zooxanthellae are mainly indirectly consumed by benthic feeders via detritus. Furthermore, Johnson et al. (1995) demonstrated that the D:H ratio of coral reefs would increase with a shift in community structure from a coral-dominated to algal-dominated state, regardless of whether algal production goes to detritus or is grazed. A lower D:H ratio also occurs in Tongoy Bay, where the dominance of planktonic production is governed by periodic intrusions of upwelling water (Wolff 1994). The higher ratio of pelagic production to benthic production in the Ems estuary also decreases the D:H ratio (Baird and Ulanowicz 1993). In this case, the extremely rapid turnover rate of phytoplankton fosters continuous transfer to detritus in Chiku Lagoon. Thus the food web of the lagoon is mainly based on detritus.

The FCIs of Chiku Lagoon and Terminos Lagoon are low when compared with those of other coastal systems (Table 5). Like the Tiahura reef (Arias-González et al. 1997), coral reefs have a greater fraction of recycled matter than do tropical lagoons. The FCIs of tropical lagoons are also lower than those of temperate estuaries and coastal waters with the exception of the high-energy Sundays Beach and the upwelling of Tongoy Bay, where frequent subsidizations occur by wave energy and upwelling water, respectively. High net primary production or physical subsidy in coastal systems appears to result in lower conservation of organic matter. This can be demonstrated further by the difference in APL between the two tropical lagoons (Table 5). The APL of 3.1 for Chiku Lagoon is lower than that of Terminos Lagoon. The different profile in organic matter cycling can be ascribed to the relatively high nutrient loading in Chiku Lagoon. The lower conservation of organic matter in the lagoon is subsidized by the high net primary production and transfer efficiency.

The lower conservation of organic matter in Chiku Lagoon can also be ascribed to the feeding by cultured oysters in the water column. The cultured oyster has become the most important fishery species in terms of biomass per unit area in the lagoon (Lin et al. 1999). By using stable carbon isotopes ($^{12}\text{C}/^{13}\text{C}$), Hsieh et al. (2000) found that oysters in the lagoon feed primarily in the water-column rather than on sedimentary particulate organic matter despite the shallow water. They also found that the $\delta^{13}\text{C}$ of particulate organic matter is similar to that of estuarine phytoplankton. Most of the particulate organic matter derived from phytoplankton is evidently consumed immediately and exported as fishery yields rather than being recycled in the benthic detrital pool.

Nutrient fluxes in the lagoon are high when compared with those in other tropical lagoons or other marine systems. The fluxes of DIP ($0.10 \text{ mol m}^{-2} \text{ year}^{-1}$) and DIN ($2.2 \text{ mol m}^{-2} \text{ year}^{-1}$) in Chiku Lagoon are higher than those of most Mexican tropical lagoons (Smith et al.

1997). The flux of DIN in particular is about tenfold those in Mexican lagoons. Kaneohe Bay, on the north-east coast of Oahu in the Hawaiian Islands, consists of broad lagoon areas. The total nitrogen loading in Chiku Lagoon ($3.0 \text{ mol m}^{-2} \text{ year}^{-1}$) is also higher than that in Kaneohe Bay ($0.21 \text{ mol m}^{-2} \text{ year}^{-1}$), and remained so even before 1978 ($0.48 \text{ mol m}^{-2} \text{ year}^{-1}$) when the loading of Kaneohe Bay was reduced sharply by sewage diversion (Nixon et al. 1986). The nitrogen loading in Chiku Lagoon is of the same order as the loading to highly enriched temperate lagoons such as Moriches Bay ($2.4 \text{ mol m}^{-2} \text{ year}^{-1}$; Ryther 1989).

The nonconservative nutrient budgets showed that Chiku Lagoon is a sink for DIP and DIN. This finding supports the latitudinal trend hypothesized by Smith et al. (1997) of DIP uptake in tropical lagoons and DIP release in warmer temperate or subtropical lagoons. The geographic position of Chiku Lagoon ($23^{\circ}16' \text{ N}$) is comparable to that of the tropical lagoon Bahía de Altata-Ensenada del Pabellón ($24^{\circ}25' \text{ N}$) or Teacapan-Agua Brava-Marisma Nacionales in Mexico ($22^{\circ}08' \text{ N}$). However, about tenfold more nitrogen is taken up in Chiku Lagoon than in the other two tropical lagoons. On a latitudinal scale, biogeochemical processes within lagoons may be affected primarily by climate. But the large sink of nitrogen in Chiku Lagoon compared with the other two Mexican lagoons indicates that other factors such as human activities on the surrounding land are important at a local scale.

Contrary to the overall trend found by Smith and Hollibaugh (1993) that estuaries are heterotrophic, our result suggests that an autotrophic condition exists in Chiku Lagoon, where total net primary production exceeds total respiration within the system. Kemp et al. (1997) indicated that the net system metabolism of an estuary depends largely on the ratio of inorganic to organic nutrient inputs, with high ratios favoring autotrophy and low ratios favoring heterotrophy. This has been demonstrated clearly in an enriched mesocosm experiment by Oviatt et al. (1986), in which increased inputs of inorganic nutrients to temperate estuarine systems tended to stimulate both gross primary production and system metabolism.

The autotrophy of Chiku Lagoon was assessed quantitatively in terms of net system metabolism by a biological approach using integrated rates of primary production and respiration in the system. Both biogeochemical and biological approaches showed that there is positive system metabolism in Chiku Lagoon and that both estimates of net system metabolism yielded comparable results. It implies that about 60% of net system metabolism can be explained by nutrient loading in the lagoon. The other fraction of net system metabolism may be attributed to the remineralization of inorganic nutrients by oysters, zooplankton, and the benthic system (Nixon et al. 1986). Y.-C. Chen and Y.-W. Tsai (unpublished data) estimated that about 20% of the DIN and DIP in the water column of Chiku Lagoon is supplied by benthic fluxes. The coupling of the two independent approaches thus

provides a biogeochemical explanation for the high productivity of Chiku Lagoon. As nutrient loading increases, so does the net primary production, which represents increased availability of food to support fishery harvests from the system. Therefore, the high fishery yield in Chiku Lagoon can be attributed to the enriched river discharge and high planktonic production.

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