



Trophic structure and functioning in a eutrophic and poorly flushed lagoon in southwestern Taiwan

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Abstract

Tapong Bay, a eutrophic and poorly flushed tropical lagoon, supports intensive oyster culture. Using the Ecopath approach and network analysis, a mass-balanced trophic model was constructed to analyze the structure and matter flows within the food web. The lagoon model is comprised of 18 compartments with the highest trophic level of 3.2 for piscivorous fish. The high pedigree index (0.82) reveals the model to be of high quality. The most-prominent living compartment in terms of matter flow and biomass in the lagoon is cultured oysters and bivalves, respectively. The mixed trophic impacts indicate that phytoplankton and periphyton are the most-influential living compartments in the lagoon. Comparative analyses with the eutrophic and well-flushed Chiku Lagoon and non-eutrophic tropical lagoons show that high nutrient loadings might stimulate the growth and accumulation of phytoplankton and periphyton and therefore support high fishery yields. However, net primary production, total biomass, fishery yields per unit area, and mean transfer efficiency of Tapong Bay were remarkably lower than those of Chiku

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Lagoon. The lower transfer efficiency likely results from the low mortality of cultured oysters and invasive bivalves from predation or the lower density of benthic feeders constrained by the hypoxic bottom water as a result of poor flushing. This might therefore result in a great proportion of flows to detritus. However, the hypoxic bottom water might further reduce the recycling of the entering detritus back into the food web. In contrast to many estuaries and tropical lagoons, poor flushing of this eutrophic tropical lagoon might induce a shift from detritivory to herbivory in the food web.

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1. Introduction

Coastal zones play important roles in global carbon and nutrient cycling. The small coverage (8%) of coastal zones accounts for about 14% of ocean production in the world (Pernetta and Milliman, 1995). However, coastal metabolism is likely altered by human activities on the surrounding land (Smith and Hallibaugh, 1993). While eutrophication is recognized as a problem causing increasing pollution in coastal waters worldwide (Nixon, 1995), there is particular interest in understanding how nutrient loadings regulate metabolism in coastal zones. In the tropics, the impacts of eutrophication are expected to be greater than those at higher latitudes (Downing et al., 1999). Among the most-threatened systems are shallow tropical lagoons, many of which have relatively low volume-to-surface ratios and very restricted connections with the sea.

Tapong Bay (22°27'N, 120°26'E) is a tropical lagoon in southwestern Taiwan, with only 1 tidal inlet (1 km long, 138 m wide, 2 m deep) connecting it to the sea (Fig. 1). It is an important site for oyster culture in Taiwan. The culturing of oysters may result in increased nutrient concentrations in the water column via recycling from excretion (Sou-chu et al., 2001) and remineralization of feces and pseudofeces (Reusch and Willams, 1998). Because oysters are direct competitors with other filter feeders, it was suggested that oyster culture may modify benthic–pelagic coupling in a mudflat food web (Leguerrier et al., 2004). In addition, Tapong Bay is surrounded by a variety of aquaculture ponds producing fish and shrimps and receives waste discharges from 2 mangrove-lined creeks which drain the surrounding aquaculture ponds; these creeks provide nutrient-rich water to the lagoon. Loading rates of N and P in the lagoon reach 1.87 and 0.51 mol m⁻² yr⁻¹, respectively, and the water residence time is often >10 d (Hung and Hung, 2003). Consequently, the bottom water in the inner region becomes hypoxic (2 mg l⁻¹) in summer when the water is stratified.

The importance of flushing in estuaries is due to its regulation of responses of primary producers to eutrophication (Balls et al., 1995; Valiela et al., 1997). In Tapong Bay, the abundance and productivity of phytoplankton were greater in a poorly flushed region (Su et al., 2004). However, the abundance and species richness of macroalgal periphyton on oyster-culture pens were greater in the well-flushed region near the tidal inlet (Lin and Hung, 2004). Lin et al. (2005) further found that there might be a shift of algal biomass from phytoplankton-dominance to periphyton-dominance in the well-flushed region. While the responses of the structure and functioning of estuaries to eutrophication have been demonstrated (Oviatt et al., 1986; Kemp et al., 1997; Lin et al., 2001), little is known

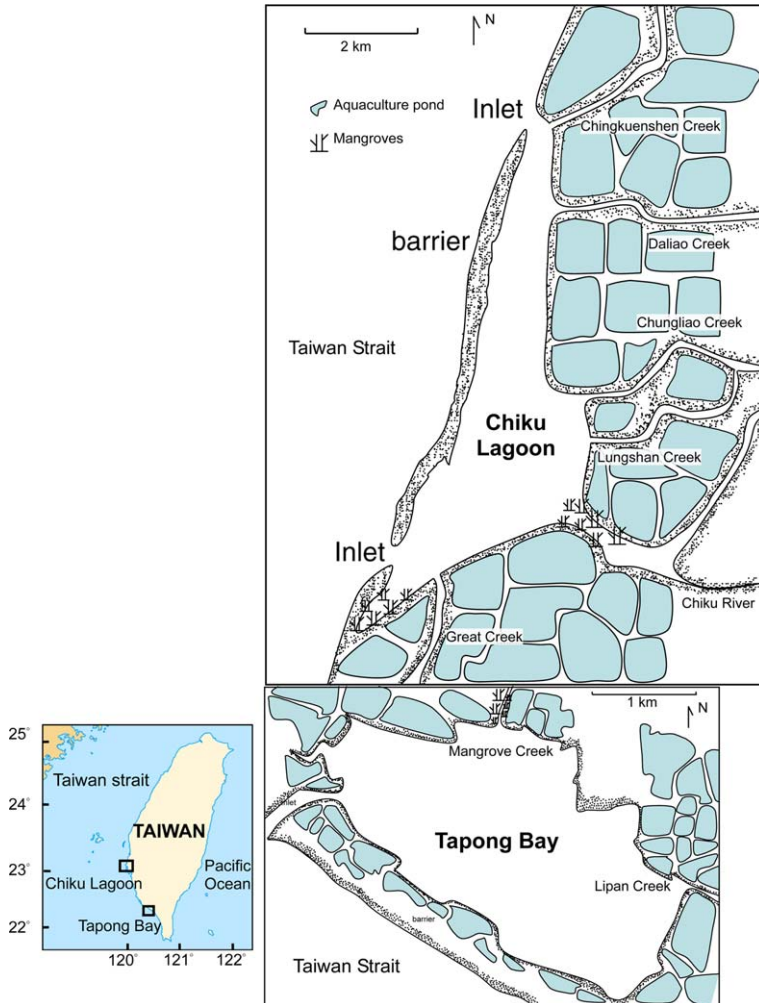


Fig. 1. Tapong Bay, Chiku Lagoon and their surrounding land uses.

of the significance of flushing on eutrophic coastal lagoons as a whole through cascading effects.

Comparative studies of trophic flows have been used to provide significant insights into the structure and functioning of estuaries (Baird and Ulanowicz, 1993). In order to better understand the significance of flushing on the trophic structure and functioning of a eutrophic lagoon, we constructed a mass-balanced model of Tapong Bay and compared with the trophic model of Chiku Lagoon (Lin et al., 2001), a eutrophic and well-flushed lagoon supporting intensive oyster culture located approximately 85 km northwest of Tapong Bay. The two eutrophic lagoon models were also compared with the trophic models of 4 non-eutrophic tropical lagoons in Mexico (Manickchand-Heileman et al., 1998; Rosado-Solórzano and Guzmán del Prío, 1998; Vega-Cendejas and Arreguín-Sánchez, 2001; Zetina-Rejón et al., 2003) to characterize the effects of eutrophication on tropical lagoons.

2. Materials and methods

2.1. Study area

Tapong Bay has a 4.44-km² surface area with a mean depth of 2.2 m at low tide. It is primarily subjected to semidiurnal tides with a tidal range of about 1.0 m. Tidal pumping is the dominant cause for the mixing between seawater and lagoon water (Hung and Hung, 2003). Water residence times range from 4 to 12 d (8–25% d⁻¹) in the tidal inlet subject to good flushing to 8 to 24 d (4–12% d⁻¹) in the inner region subject to poor flushing with a mean value of 11.1 ± 0.6 d (Table 1). Climatic data derived from the local weather station during 1999–2001 (Climatological Data Annual Report, Taiwan Central Weather Bureau), show that in winter (the dry season) of October ~ April, the mean monthly rainfall normally does not exceed 40 mm, and that in summer (the wet season) from May to September, the average monthly rainfall frequently exceeds 200 mm. No large river flows into the lagoon. However, the small volume of the lagoon makes the salinity responsive to changes in rainfall inputs and evaporative losses. Consequently, salinities are lower in summer (about 25.4 psu) and higher in winter (about 33.9 psu). Water temperatures range from about 32 °C in summer to about 22 °C in winter.

Tapong Bay and Chiku Lagoon, both of southwestern Taiwan, have several features in common (Table 1). They are both shallow and microtidal tropical lagoons, with distinct dry and wet seasons. Both lagoons support intensive oyster culture, are surrounded by a variety of aquaculture ponds producing fish and shrimps, and receive waste discharges from mangrove-lined creeks which drain the surrounding aquaculture ponds. Loadings of dissolved inorganic nitrogen (DIN) and phosphorus (DIP) in both lagoons are high when compared with those recorded in most estuaries and tropical lagoons (Boynton et al., 1982; Smith et al., 1997). No rooted macrophytes are normally observed in either lagoon. Periphyton on rocks and/or oyster-culture pens and phytoplankton dominate both

Table 1
Comparisons of environmental variables between Tapong Bay and Chiku Lagoon

	Tapong Bay (Hung and Hung, 2003)	Chiku Lagoon (Hung and Kuo, 2002)
Location	22°27'N, 120°26'E	2316'N, 120°08'E
Area (km ²)	4.44	9.60
Mean depth at low tide (m)	2.2	1.5
Mean tidal range (m)	1.0	1.3
Inlet number	1	2
Temperature (°C)	22–32	16–32
Salinity (psu)	25.4–33.9	20.6–33.8
Residence time (d)	11.1 ± 0.6 (<i>n</i> = 7)	5.0 ± 0.7 (<i>n</i> = 10)
Nutrient loading (mol m ⁻² yr ⁻¹)	N: 1.87 P: 0.51	N: 5.31 P: 0.48
Nutrient concentration (μM)	DIN: 13.4 ± 2.2 DIP: 4.3 ± 0.7 DON: 24.2 ± 2.9 DOP: 2.6 ± 0.6 (<i>n</i> = 70)	DIN: 15.4 ± 5.0 DIP: 3.0 ± 0.4 DON: 17.4 ± 1.5 DOP: 0.7 ± 0.1 (<i>n</i> = 70)

DIN, dissolved inorganic nitrogen, NO₂ + NO₃ + NH₄; DIP, dissolved inorganic phosphorus, PO₄; DON, dissolved organic nitrogen; DOP, dissolved organic phosphorus.

lagoons. They differ, however, in the number of inlets. Tapong Bay is subject to poor flushing due to only 1 tidal inlet located at one end (compared to 2 inlets in Chiku Lagoon), which results in about 2-fold longer water residence time than that of Chiku Lagoon.

The 4 Mexican lagoons, including Terminos Lagoon (Manickchand-Heileman et al., 1998), Tampamachoco Lagoon (Rosado-Solórzano and Guzmán del Prío, 1998), Celestun Lagoon (Vega-Cendejas and Arreguín-Sánchez, 2001), and Huizache-Caimanero lagoons (Zetina-Rejón et al., 2003), are shallow non-eutrophic tropical lagoons, where macrophytes or seagrasses generally contribute most of the system's biomass and primary production. The trophic models were constructed with the Ecopath approach (Christensen et al., 2004). The models consist of 19–26 functional groups including detritus and primary producers and trophic levels of 3.3–3.8 for piscivorous fish. For comparisons, dry weights in the Terminos Lagoon model (Manickchand-Heileman et al., 1998) were converted to wet weights using a factor of 5.71 (Opitz, 1996). The topology, flow structure, degree of aggregation among the living compartments, and thus the currency of the trophic models are similar for comparisons with those of Tapong Bay and Chiku Lagoon as suggested by Baird and Ulanowicz (1993).

2.2. Modeling approach

A trophic model of Tapong Bay was constructed using the Ecopath routine in the Ecopath with Ecosim software system of Christensen et al. (2004) to quantify all matter flows in the food web. For each compartment (i), a mass-balanced budget can be expressed as

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

where P_i is the production of i , B_i is the biomass of i , $M2_i$ is the predation mortality of i , EE_i is the ecotrophic efficiency of i (i.e., the part of the production that is passed up the trophic level, used for biomass accumulation or exported), $1 - EE_i$ is "other mortality", EX_i is the portion of i exported to other systems through sedimentation or fishery activities, and AC_i is the accumulation of i during the study period.

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

$$B_i \cdot P/B_i \cdot EE_i - \sum_j B_j \cdot Q/B_j \cdot DC_{ji} - EX_i - AC_i = 0, \quad (2)$$

where P/B_i is the production/biomass ratio, Q/B_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 . It was assumed that the diet composition remains stable during the study period.

Consumption of a predator group (j) is then connected to its production, which can be re-expressed as

$$\sum_j B_j \times Q/B_j = P_j + R_j + UN_j, \quad (3)$$

where P_j is the production of j , R_j is the respiration of j , and UN_j is the unused consumption of j , which was assumed to be 20% (Christensen et al., 2004).

Some of the parameters used to construct the model do not have to be entered since Ecopath links the production of each compartment with the consumption of all other compartments, and uses the linkages to estimate missing parameters. DC and EX must always be entered, while entry is optional for one of any of the other 4 parameters (B ,

P/B , Q/B , and EE). For further details and algorithms of the Ecopath model see Christensen et al. (2004).

2.3. Model compartments

Major species of similar sizes and diets in Tapong Bay were functionally grouped within the same compartment. Bacterial biomass was included in the compartment of organic detritus as recommended by Christensen et al. (2004), because bacterial flow may totally overshadow other flows in the system. An 18-compartment model for the lagoon was developed (Table 2) consisting of the following groups: (1) phytoplankton, (2) periphyton, (3) herbivorous zooplankton, (4) carnivorous zooplankton, (5) oysters, (6) polychaetes, (7) gastropods, (8) bivalves, (9) barnacles, (10) amphipods, (11) crabs, (12) shrimps, (13) herbivorous fish, (14) zooplanktivorous fish, (15) benthic-feeding fish, (16) detritivorous fish, (17) piscivorous fish, and (18) detritus. The exports of fish and invertebrates by birds were assumed to be small when compared to those by fisheries and therefore were not included in the model (McLusky and Elliott, 2004).

All parameters used to construct the model were assembled as much as possible from our own studies covering 2 years from October 1999 to October 2001 (Table 2). Three to 6 study sites from the tidal inlet to the inner region along a transect across Tapong

Table 2
Compartments and input parameters for the Tapong Bay model

Group name	Biomass (g WW m ⁻²)	P/B (yr ⁻¹)	Q/B (yr ⁻¹)	Fishery catch (g WW m ⁻² yr ⁻¹)
1. Phytoplankton	5.7	2674	–	–
2. Periphyton	101	1.7	–	–
3. Herbivorous zooplankton	5.5	18 ^a	95	–
4. Carnivorous zooplankton	0.5	5.5 ^b	30 ^c	–
5. Oysters	270	1.5	35	102
6. Polychaetes	1.7	5.8 ^c	24 ^c	–
7. Gastropods	4.4	2.8 ^d	14 ^d	–
8. Bivalves	373	2.2 ^d	15 ^d	–
9. Barnacles	1.3	2.3 ^d	20 ^d	–
10. Amphipods	1.5	5.0 ^b	33 ^c	–
11. Crabs	1.8	1.6 ^e	14	2.1
12. Shrimps	0.2	2.8 ^f	27	0.1
13. Herbivorous fish	2.2	2.1 ^g	6.5	3.7
14. Zooplanktivorous fish	0.4	1.9 ^g	5.0	0.6
15. Benthic-feeding fish	1.7	1.0 ^g	2.7	0.9
16. Detritivorous fish	4.5	2.2 ^g	6.5	8.3
17. Piscivorous fish	2.0	0.9 ^g	2.1	1.0
18. Detritus	5538	–	–	–

P/B , production/biomass ratio; Q/B , consumption/biomass ratio.

^a Vega-Cendejas et al. (1993).

^b Schwinghamer et al. (1986).

^c Riddle et al. (1990).

^d Opitz (1996).

^e Erhardt and Restrepo (1989).

^f Garcia (1985).

^g Froese and Pauly (2004).

Bay representing a gradient in flushing were sampled at low and high tides every 2–3 months to take account of spatial, seasonal, and tidal changes.

Phytoplankton biomass in terms of chlorophyll *a* was determined spectrophotometrically by immediately filtering triplicate water samples through Whatman GF/F filters in the field and then extracting the filters in 90% acetone for 24 h at 4 °C in the dark (Su et al., 2004). Periphyton biomass in terms of wet weight was estimated by gently scraping periphyton off rocks and oyster-culture pens with a scraper (Lin and Hung, 2004). Net productivities of periphyton and phytoplankton were determined concurrently from changes in dissolved oxygen concentrations in microcosm incubations using a water column only and periphyton + a water column ($n = 3$ for each treatment per site) in outdoor flowing seawater tanks placed adjacent to Tapong Bay (Lin et al., 2005). Periphyton added to the periphyton + water column microcosm was obtained by submerging plates of bamboo in the water column at each site on each occasion for periphyton colonization because bamboo is the material used for oyster-culture pens. A row of 20 plates of bamboo, each measuring 10×20 cm and 1 cm thick, was vertically attached to an oyster-culture pen at a depth of 20 cm 3 weeks before productivity determinations. After submersion for 3 weeks, all the space on the plates was covered by the representative periphyton species at the natural field density at that time (Lin and Hung, 2004). The water column microcosm was used both to determine phytoplankton productivity and to correct the dissolved oxygen measurements in the periphyton + water column microcosm. The incubations were conducted around noon when the irradiance is saturated, and each tank was exposed to different irradiances in terms of 0%, 30%, 50%, 70%, and 100% shading by interposing screens with different mesh sizes. Annual production rates of periphyton and phytoplankton were, respectively, calculated by integrating the interpolated production rates under various irradiances by referring to the relationships between production rates and irradiances (the $P-I$ curve) and surface light data at that time. Dissolved oxygen concentrations were monitored using a spectrophotometric method with the Winkler technique modified by Pai et al. (1993). Oxygen production rates were converted to carbon fixation rates using a photosynthetic quotient of 1.2 (Meyercordt and Meyer-Reil, 1999).

Oyster biomass was determined by randomly weighing 40 organisms in Tapong Bay on each sampling occasion at each site. Oyster production was estimated according to the methods of Crisp (1971). Consumption of oysters was estimated by the difference in density of organic particles between inflow and outflow water of oyster beds. Zooplankton samples were collected by towing 2 NorPac nets (45 cm in diameter with 100- and 330- μm mesh sizes) just below the sea surface for 5 min at 1.0 m s^{-1} (Lo et al., 2004). Zooplankton biomass was estimated by the displacement volume according to Ahlstrom and Thraikill (1960). An estimate of Q/B for herbivorous zooplankton was determined in the field with the gut fluorescence method described by Morales et al. (1993), but the P/B was obtained from the literature in a tropical coastal system (Vega-Cendejas et al., 1993). Few studies have been carried out on invertebrates in southern Taiwan, and values of P/B and Q/B for other small invertebrates in the lagoon were obtained by searching the same groups in the literature from tropical coastal waters (Schwinghamer et al., 1986; Riddle et al., 1990; Vega-Cendejas et al., 1993; Opitz, 1996). Shrimps, crabs, and fish in the lagoon were collected using fyke nets. This fishing gear is a passive sampler designed to use tidal dynamics to collect nekton, and is widely used by local fishermen. Estimates of Q/B for shrimps and crabs were made in the field by the dominant species through the

food consumption model (Pauly, 1986). Estimates of Q/B for fish were computed using an empirical model developed by Palomares and Pauly (1989) for the dominant species of each group. Published data on P/B values of shrimps, crabs, and fish in Taiwan are lacking, so they were obtained by searching the same groups in the literature from tropical coastal waters (Garcia, 1985; Erhardt and Restrepo, 1989) and Fishbase (Froese and Pauly, 2004). The catches of oysters, shrimps, crabs, and fish were obtained from the local fishery bureau.

Detritus comprises the organic materials in the water column and on sediments. Water from the lagoon was filtered through acid-cleaned, dried, and pre-weighed nucleopore membrane filters to determine the detrital mass in the water column. Phytoplankton biomass was subtracted from the detritus mass by calculating the sum of chlorophyll a + phaeophytin in the water column assuming carbon: pigment of 35:1 (Sobczak et al., 2002). Sediments were collected with an Eckman Birge Grab (15 cm \times 15 cm) and dried in an oven at 60 °C. The dried sediments were then ground to powder for analyses of organic materials. Detritus mass on sediments was limited to the top 5 cm of sediments, which is the detrital pool generally available for uptake by epifauna and fish.

Diet compositions of zooplankton, shrimps, crabs, and fish were determined by stomach content analyses of the dominant species, and were recorded in the percent of volume of the major prey groups (Table 3). This is roughly equivalent to the relative weight and thus approximates the relative amount of energy extracted by consumers from various prey groups (Macdonald and Green, 1983). There are scanty published data on the diet of other small invertebrates in Taiwan, so this information was obtained by searching the same groups in the literature from tropical waters (Opitz, 1996).

Stable carbon and nitrogen isotopes were used in combination with stomach content analyses to trace the food sources of detritivorous fishes and invertebrates in the lagoon. Potential food sources, including sestonic particulate organic matter (SPOM), benthic microalgae (mainly diatoms, authors' pers. obs.), macroalgal periphyton, marsh plants, and mangrove leaves were collected in January–March 2001 for stable isotope analyses. Dominant species of detritivorous fish, shrimps, crabs and polychaetes were also collected as close in time as possible for stable isotope analyses. Because the ^{13}C content of lipids may be depleted and this can affect ecological interpretations (Kling et al., 1992), samples were washed in a 2:1:0.8 methanol:chloroform:water solution for 2 h (Bligh and Dyer, 1959) and then treated with 1 N HCl to, respectively, remove lipids and carbonates (Boutton, 1991). Muscle tissues were finally freeze-dried and ground for isotope analyses. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of samples were determined with a continuous-flow isotope ratio mass spectrometer (Finnigan delta S) coupled with an elemental analyzer (Carlo Erba NA 1500 NCS). The precision of the measurements was $\pm 0.1\text{‰}$ for both the stable carbon and nitrogen isotope analyses. Stable isotope data were reported as the relative difference between ratios of a sample and standards in standard notation as: $\delta X(\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ is the per-mil (‰) deviation of that sample from the recognized isotope standard, i.e., PeeDee Belemnite (PDB) limestone for $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$ (Gearing, 1991).

Factors used for conversion between chlorophyll a , carbon, displacement volume, dry weight, and wet weight were based on a table summarized by Opitz (1996). Biomass data were then recorded as wet weight (WW) m^{-2} , and flow data were recorded as $\text{WW m}^{-2} \text{yr}^{-1}$.

Table 3
Diet composition for the Tapong Bay model

Prey/predator	3	4	5 ^a	6 ^a	7 ^a	8 ^a	9 ^a	10 ^a	11	12	13	14	15	16	17
1. Phytoplankton	0.70		0.70	0.145		0.70	0.55								0.05
2. Periphyton				0.25	0.45			0.49			0.69		0.368	0.286	0.078
3. Herbivorous Zooplankton		0.90	0.005			0.005	0.05	0.01			0.01	0.51			
4. Carnivorous zooplankton				0.005					0.05	0.02	0.001	0.13			
5. Oysters				0.02	0.02					0.02	0.005		0.022		
6. Polychaetes					0.08				0.10	0.11	0.065			0.006	0.02
7. Gastropods				0.02					0.34		0.001		0.001	0.025	0.001
8. Bivalves				0.02	0.03				0.067	0.06	0.006		0.027		
9. Barnacles											0.005				
10. Amphipods				0.02	0.02				0.12	0.09	0.019	0.05	0.20	0.019	0.008
11. Crabs													0.089		
12. Shrimps								0.003					0.053		0.003
13. Herbivorous fish										0.02					0.172
14. Zooplanktivorous fish															0.034
15. Benthic-feeding fish										0.02					0.131
16. Detritivorous fish										0.04					0.357
17. Piscivorous fish															0.154
18. Detritus	0.30	0.10	0.295	0.52	0.40	0.295	0.40	0.50	0.29	0.59	0.198	0.31	0.24	0.614	0.042

^a Opitz (1996).

The pedigree routine (Funtowicz and Ravetz, 1990) was used to determine an overall index of model ‘quality’, based on the origin and quality of each input datum of the model. The pedigree index varies from 1.0 for a high-quality model whose inputs are based on locally, well-sampled high-precision data to 0.0 for inputs that were guessed, or taken from other models in the literature.

2.4. Model balancing

The first step in verifying the realism of the model was to check whether the EE was less than 1.0 for all living compartments, since it was assumed that any living compartment would not be consumed in excess of its production. The second step was to check if the GE (the gross food conversion efficiency, i.e., the ratio between production and consumption) was in the range of 0.1–0.3, as the production of most groups is about 10–30% of the consumption. In addition, the GE cannot be higher than the net efficiency (the ratio between production and assimilated food). The final step was to compare the output values to relevant data from the literature on other tropical coastal waters.

Because Ecopath uses linkages of production of one compartment with consumption of other compartments to calculate one missing parameter for each group, the most-questionable parameter of each compartment can be treated as an unknown and calculated by Ecopath. In this study, the biomass of each compartment and primary productivity were the most-reliable data. The EE was treated as an unknown and calculated by Ecopath. Some P/B , Q/B , and DC values of small invertebrates were assembled from the relevant literature (Table 1) and were considered to be less reliable in the lagoon model. Therefore, they were gradually modified during the balancing exercise. But most of the changes were rather small and remained within 15% of the input value.

2.5. Network analysis

Details of the transfer of organic matter from primary producers and detritus to top predators in the food web of Tapong Bay can be revealed by network analysis (Field et al., 1989). The mixed trophic impacts (Ulanowicz and Puccia, 1990) were calculated to assess the direct and indirect impacts of a change in the biomass of each compartment and fishery activities on the other compartments. Many consumers in the lagoon were 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. The trophic efficiency of the transfer from one aggregated trophic level to the next can be calculated as the fraction of the input of organic matter to a given level that is transferred to the next higher level.

The throughput of a compartment is the total amount of matter flowing through that compartment, which is a measure of its activity. The sum of these throughputs is called the total system throughput (TST). The activity of a lagoon system or the TST (the sum of consumption, exports, respiratory flows, and flows into detritus) is indexed in terms of how much matter the system processes. The cycling of matter is considered to be an important process in the functioning of natural ecosystems, as it can facilitate homeostatic control over the magnitude of the flows (Odum, 1969). The Finn cycling index (FCI) of the

cycle analysis (Kay et al., 1989), the relative importance of cycling to the total flow, was used to measure how retentive the lagoon is.

3. Results

3.1. Trophic structure

In Tapong Bay, the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of macroalgal periphyton were -10.6‰ to -12.7‰ and 10.4‰ to 11.4‰ , respectively. For dominant species of detritivorous fish, shrimps, crabs and polychaetes, the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were -13.0‰ to -17.3‰ and 10.0‰ to 16.2‰ , respectively. Assuming little fractionation of $\delta^{13}\text{C}$ ($<1\text{‰}$ per trophic

Table 4

Summary of $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) of potential food sources and dominant species of detritivorous fish (total length), shrimps, crabs and polychaetes collected in Tapong Bay

Group	<i>n</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
C_3 marsh plants			
<i>Clerodendrum inerme</i>	1	-23.7	9.9
<i>Excoecaria agallocha</i>	1	-25.5	10.1
<i>Derris laxiflora</i>	1	-27.6	1.4
Mangrove <i>Avicennia marina</i>	1	-26.3	5.6
Macroalgal periphyton			
<i>Ceramium cimbriicum</i>	3	-10.6 ± 0.1	10.9 ± 0.1
<i>Chaetomorpha crassa</i>	5	-11.4 ± 0.7	10.4 ± 0.1
<i>Enteromorpha intestinalis</i>	30	-11.7 ± 0.6	11.1 ± 0.1
<i>Ulva fasciata</i>	9	-11.3 ± 0.7	11.4 ± 0.8
<i>Ulva lactuca</i>	22	-11.2 ± 0.3	11.0 ± 0.2
<i>Lyngbya majuscula</i>	24	-12.7 ± 0.6	10.5 ± 0.2
Benthic microalgae	3	-22.9 ± 0.1	11.6 ± 0.1
SPOM at ebb tide	1	-19.0	7.0
Detritivorous fish			
<i>Liza macrolepis</i> (134.7 ± 3.5 mm)	10	-15.3 ± 0.6	16.2 ± 0.1
<i>Pomacentrus taeniometopon</i> (91.7 ± 1.8 mm)	3	-15.2 ± 0.1	13.3 ± 0.2
<i>Scarus ghobban</i> (179.0 ± 26.0 mm)	2	-16.0 ± 0.1	12.5 ± 0.2
<i>Scatophagus argus</i> (110.0 ± 10.0 mm)	2	-16.9 ± 1.1	12.6 ± 0.5
<i>Siganus guttatus</i> (119.3 ± 2.6 mm)	3	-13.0 ± 1.6	14.6 ± 0.9
<i>Valamugil cunnesius</i> (184.3 ± 6.4 mm)	3	-13.8 ± 1.2	14.1 ± 0.6
Shrimps			
<i>Penaeus monodon</i>	2	-17.1 ± 2.0	11.5 ± 0.9
<i>Penaeus penicillatus</i>	2	-17.3 ± 0.2	14.0 ± 0.5
Crabs			
<i>Thalamita danae</i>	2	-15.6 ± 0.4	11.9 ± 0.5
<i>Charybdis hellerii</i>	1	-16.2	12.9
Polychaetes			
<i>Amphitrite</i> sp.	2	-16.4 ± 0.6	10.0 ± 0.4

Means (\pm SE) and replicate numbers (*n*) are shown below.

SPOM, sestonic particulate organic matter.

level) and the usual trophic enrichment of $\delta^{15}\text{N}$ (+2‰ to +4‰ per trophic level) between consumers and their presumed food, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values indicated that the macroalgal periphyton on oyster-culture pens are the most probable food sources for these

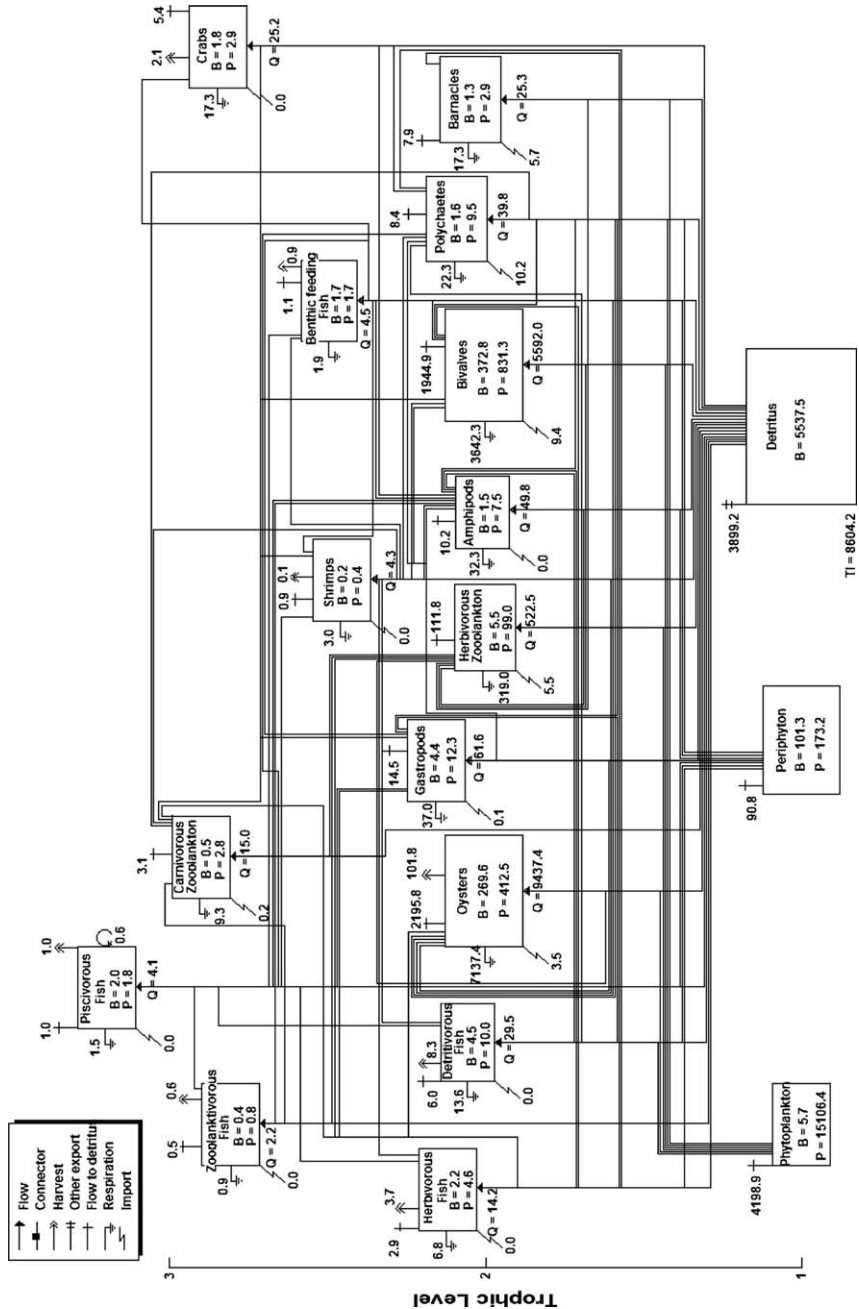


Fig. 2. Trophic model of Tapong Bay. Biomass is in g WW m^{-2} . Production and other flows are in $\text{g WW m}^{-2} \text{ yr}^{-1}$.

groups in Tapong Bay (Table 4). Contributions from marsh plants, mangroves and benthic microalgae appeared to be minor.

Trophic levels estimated by Ecopath from the weighted average of prey trophic levels varied from 1.00 for primary producers and detritus to 3.20 for piscivorous fishes (Fig. 2). The Tapong Bay model shows that the structure of the food web comprised 4 integer trophic levels. The most-prominent living compartments in terms of matter flow and biomass in the lagoon were cultured oysters and bivalves, respectively. Oysters comprised 35% of the system's total living biomass and consumed about 44% of the available production of phytoplankton. About 75% of the consumption of oysters was respired and was not used in the system (Table 5). The other 23% was not immediately used and entered the detrital pool. The remaining 2% was predated upon and exported. The EE of oysters was therefore low. The trophic level of oysters was 2.01. An omnivory index of almost zero indicates that oysters feed on a single trophic level of 1.0. About 30% of the diet depended upon detritus.

Detritus was the largest compartment in Tapong Bay. The EE of detritus is defined as the ratio between what flows out of and what flows into the detrital pool. The estimated EE of detritus was only 0.55 (Table 5), which indicates that more was entering the pool than was leaving. The difference most likely ended up as accumulated detritus, being buried as sediment, decomposed by microheterotrophs, or exported to the adjacent Taiwan Strait (Hung and Hung, 2003).

The fishery yield was about $119 \text{ g WW m}^{-2} \text{ yr}^{-1}$. Cultured oysters accounted for about 86% of the total yield and were the most-important fishery component in the lagoon (Table 2). Fishes and crabs accounted for only about 12% and 2% of the total yield, respectively.

3.2. Mixed trophic impacts

The mixed trophic impacts indicate direct and indirect interactions among compartments in a system and can thus be regarded as a form of sensitivity analysis (Fig. 3). Phytoplankton and periphyton were the most-influential living compartments in the model. An increase in phytoplankton biomass would have a great positive effect on filter feeders and the cultured oyster catch. An increase in periphyton biomass would have a positive effect on most fish biomass values, implying the significance of periphyton as a food source for fish groups. Nevertheless, increases in the biomasses of phytoplankton and periphyton would have no effect on detritus due to the large detrital pool in the lagoon. An increase in detritus would also have a large positive effect on many biomass values and fishery catches.

The mixed trophic impacts demonstrate that increasing the biomass of cultured oysters would directly have a negative impact on herbivorous zooplankton and indirectly on carnivorous zooplankton and zooplanktivorous fish through cascading effects since cultured oysters compete with herbivorous zooplankton for phytoplankton. An increase in the activity of set nets and gill nets would have a negative impact on crabs and almost all fish groups.

3.3. Trophic flows

The TST (the sum of consumption, exports, respiratory flows, and flows into detritus) of Tapong Bay was estimated to be $35,812 \text{ g WW m}^{-2} \text{ yr}^{-1}$. The Lindeman trophic analysis aggregated compartmental throughputs of the 18 compartments in a simple food chain with 4 integer trophic levels (Fig. 4). The detritivory:herbivory ratio (D:H ratio) of 0.4 indicated that herbivory flow exceeds detritivory flow in the lagoon. Although

Table 5
Output parameters for the Tapong Bay model

Group name	EE	GE	Respiration (g WW m ⁻² yr ⁻¹)	Flow to detritus (g WW m ⁻² yr ⁻¹)	Predation mortality (g WW m ⁻² yr ⁻¹)	Net efficiency	Trophic level	Omnivory index
1. Phytoplankton	0.72	–	–	4199	1930.53	–	1.00	0.000
2. Periphyton	0.48	–	–	90.9	0.81	–	1.00	0.000
3. Herbivorous zooplankton	0.93	0.19	319	111	16.67	0.237	2.00	0.000
4. Carnivorous zooplankton	0.95	0.18	9.25	3.15	5.21	0.229	2.90	0.090
5. Oysters	0.25	0.04	7137	2196	0.01	0.055	2.01	0.005
6. Polychaetes	0.95	0.24	22.3	8.41	5.53	0.300	2.09	0.097
7. Gastropods	0.82	0.20	37.0	14.5	2.30	0.250	2.16	0.142
8. Bivalves	0.01	0.15	3642	1945	0.01	0.186	2.01	0.005
9. Barnacles	0.02	0.12	17.3	7.89	0.06	0.144	2.05	0.048
10. Amphipods	0.97	0.15	32.3	10.2	4.86	0.189	2.01	0.010
11. Crabs	0.87	0.11	17.3	5.42	0.22	0.143	2.85	0.342
12. Shrimps	0.96	0.10	2.99	0.88	2.05	0.130	2.45	0.314
13. Herbivorous fish	0.98	0.32	6.79	2.94	0.36	0.404	2.12	0.114
14. Zooplanktivorous fish	0.91	0.38	0.93	0.52	0.32	0.475	2.81	0.378
15. Benthic-feeding fish	0.91	0.37	1.95	1.06	0.37	0.463	2.49	0.427
16. Detritivorous fish	0.99	0.34	13.6	5.98	0.36	0.423	2.05	0.057
17. Piscivorous fish	0.93	0.43	1.53	0.95	0.32	0.536	3.20	0.360
18. Detritus	0.55	–	–	0.00	–	–	1.00	0.255

EE, ecotrophic efficiency; GE, gross efficiency.

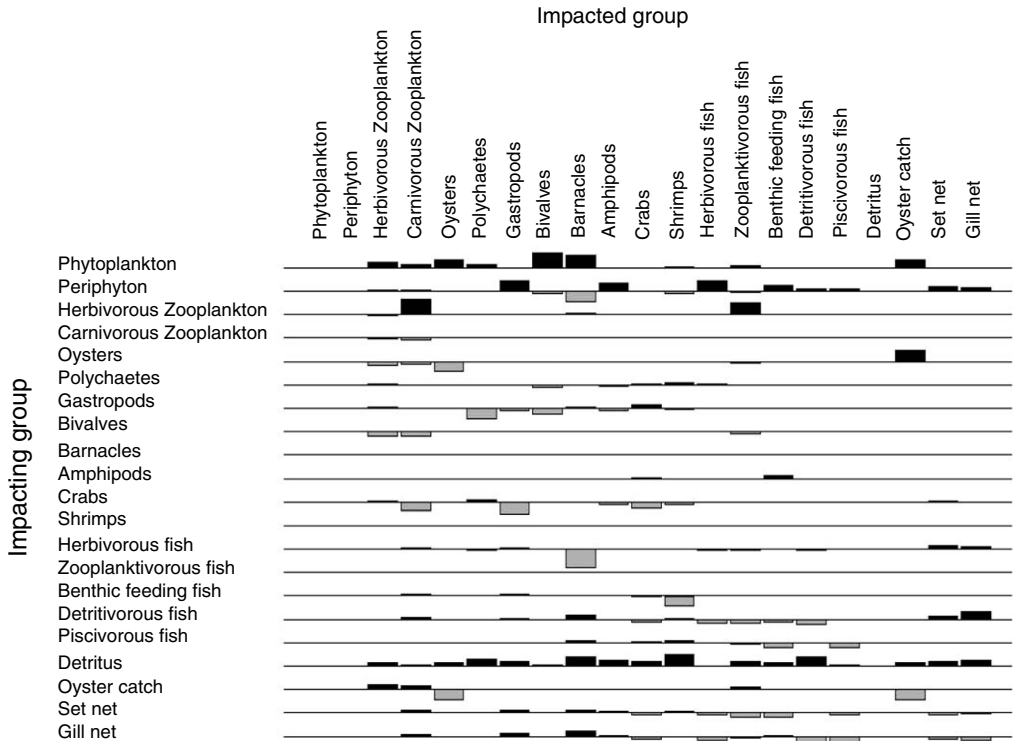


Fig. 3. Direct and indirect impacts that an increase in the biomass of the compartments on the left of the histograms would have on compartments positioned above them. Bars pointing upwards indicate positive impacts while those pointing downwards indicate negative impacts. Impacts are relative, not absolute, but are comparable between histograms.

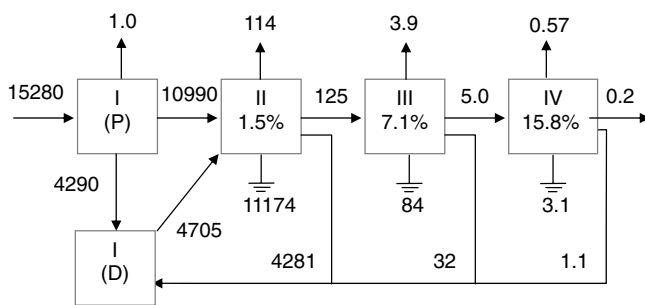


Fig. 4. Flow network of organic matter and trophic efficiencies (%) in Tapong Bay. The flow ($\text{g WW m}^{-2} \text{ yr}^{-1}$) web is aggregated into a concatenated chain of transfers through 4 integer trophic levels. Flows from primary producers (P) and from detritus (D) and flows out of the tops of boxes represent export, while flows out of the bottoms represent respiration.

the biomass per unit area of phytoplankton was lower than that of periphyton, the higher turnover rate (production) of phytoplankton makes it the major source of food and detritus in the lagoon (Fig. 2). The contribution of primary production to the lagoon by

phytoplankton was about $15,106 \text{ g WW m}^{-2} \text{ yr}^{-1}$ or $801 \text{ g C m}^{-2} \text{ yr}^{-1}$ compared to $173 \text{ g WW m}^{-2} \text{ yr}^{-1}$ or $9.2 \text{ g C m}^{-2} \text{ yr}^{-1}$ by periphyton.

The difference between net primary production (NPP) and all respiration (i.e., net system production) in Tapong Bay was calculated to be $4018 \text{ g WW m}^{-2} \text{ yr}^{-1}$ or $213 \text{ g C m}^{-2} \text{ yr}^{-1}$. The NPP:total respiration ratio (P:R ratio) of 1.36 indicates that the lagoon is autotrophic, which implies that more organic matter is produced than is being consumed in the lagoon.

The trophic efficiency was only 2.3% for the combined flows from primary production and detritus for trophic level II (Fig. 4). The efficiencies increased for higher levels and reached 15.8% for trophic level IV. The geometric mean of trophic efficiencies for the aggregated food chain from levels II to IV was calculated to be 5.5%. The cycle analysis shows that all cycled flows accounted for only 10% of the TST (i.e., FCI).

3.4. Ecosystem comparisons

TSTs of Tapong Bay and Chiku Lagoon were high in terms of flow per unit area when compared to non-eutrophic tropical lagoons (Table 6) due to the high consumption and respiration of cultured oysters in both lagoons. This indicates that Tapong Bay and Chiku Lagoon are active lagoons in terms of matter flows despite the small lagoon area. Harvest pressures are high in both lagoons, which are reflected in the high fishery catches and gross efficiencies when compared with the reported values from other tropical lagoons.

However, Tapong Bay differed remarkably from Chiku Lagoon in some ecosystem attributes (Table 6). NPP, total biomass, and mean transfer efficiency of Tapong Bay were comparable to the reported values of non-eutrophic tropical lagoons, but were lower than those of Chiku Lagoon. Accumulated detritus in Tapong Bay was over 10-fold greater than that in Chiku Lagoon (Lin et al., 2001). Nevertheless, the lower FCI value indicates that a lower proportion of matter is recycled through detrital pathways in Tapong Bay than in Chiku Lagoon. Consequently, the D:H ratio of Tapong Bay was extremely low when compared with Chiku Lagoon and other tropical lagoons, suggesting that the lagoon is more dependent on herbivory than on detritivory for generating TST. The geometric mean of trophic efficiencies of Tapong Bay was also low when compared with those of Chiku Lagoon and other tropical lagoons.

The mean trophic level of 2.05 for the Tapong Bay fishery was lower than the level of 3.40 for the Chiku Lagoon fishery (Table 6), because the Tapong Bay fishery focuses almost exclusively on cultured oysters. Although the oyster harvest in Chiku Lagoon is higher ($249 \text{ g WW m}^{-2} \text{ yr}^{-1}$) than that in Tapong Bay, the Chiku Lagoon fishery concentrates not only on oysters, but also on a variety of species of higher trophic levels including piscivorous fish, benthic-feeding fish, crabs, and shrimps (Lin et al., 1999).

4. Discussion

In the Tapong Bay model, some input values of P/B and Q/B of small invertebrates, including polychaetes, gastropods, bivalves, barnacles, and amphipods, were difficult to measure directly in the field. We used rough estimates assembled from relevant literature sources (Tables 1 and 2). Despite this, an error in these parameters would not, in most cases, have significantly altered the system's biomass budget. The mixed trophic impacts revealed that changes in biomass of small invertebrates would have minor impacts on

Table 6
Comparisons of ecosystem attributes among Tapong Bay and other tropical lagoons

	Tapong Bay	Chiku Lagoon ^a	Terminos Lagoon ^b	Tampamachoco Lagoon ^c	Celestun Lagoon ^d	Huizache-Caimanero lagoons ^e
Sum of all consumption	15,828	70,966	3607	715	1931	2052
Sum of all exports	119	4775	6.48	1526	0.26	7.40
Sum of all respiration	11,262	45,815	2096	427	1040	1138
Sum of all flow into detritus	8604	39,983	15,471	1873	1609	3471
Total system throughput (TST)	35,812	157,653	21,181	4541	4581	6669
Total net primary production (NPP)	15,280	50,600	14,912	1953	15,550	3816
NPP: total respiration ratio (P:R)	1.36	1.10	7.11	4.57	15.9	3.35
Net system production	4018	4736	12,816	1524	14,510	2678
Total biomass (excluding detritus)	777	2096	1505	95	259	486
FCI (%)	10	15	7.0	NA	13	9.9
Fishery's mean trophic level	2.05	3.40	3.60	3.08	3.57	2.50
Total catches	119	890	6.48	16.9	0.26	7.40
Gross efficiency (catch/NPP) (%)	0.8	1.8	0.04	0.9	0.002	0.2
Geometric mean of trophic transfer efficiency (II–IV) (%)	5.5	12	7.0	13	9.6	8.3
Detritivory: herbivory ratio (D:H)	0.4	1.4	4.6	1.0	1.9	1.0

Biomasses are in g WW m⁻² and flows are in g WW m⁻² yr⁻¹.

NA: data not available.

^a Lin et al. (2001).

^b Manickchand-Heileman et al. (1998).

^c Rosado-Solórzano and Guzmán del Próo (1998).

^d Vega-Cendejas and Arreguín-Sánchez (2001).

^e Zetina-Rejón et al. (2003).

other compartments in Tapong Bay (Fig. 3). Nevertheless, greater impacts would occur in the cases of phytoplankton and periphyton since they were shown to be the most-influential compartments in the lagoon. All input values of biomass and productivity of phytoplankton and periphyton were directly determined in the field during the 2-year study period (Lin and Hung, 2004; Su et al., 2004; Lin et al., 2005). The pedigree index was 0.82 for the Tapong Bay model, indicating a high quality of the model, given that most inputs came from local, well-sampled, high-precision data. We feel that the major pathways of Tapong Bay were accurately depicted in the model (Fig. 2) and that an integrated picture of the lagoon system was obtained.

Like the eutrophic Chiku Lagoon (Lin et al., 2001), the high nutrient loadings in Tapong Bay also stimulated the growth and accumulation of algae and therefore fishery yields. The mean phytoplankton chlorophyll *a* concentrations and production rates were higher than those recorded in most estuaries and coastal lagoons (Su et al., 2004). The mean biomass (Lin and Hung, 2004) and production rates (Lin et al., 2005) of periphyton on oyster-culture pens were also within the same order of magnitude of periphyton collected from eutrophic estuaries and coastal lagoons. In non-eutrophic tropical lagoons, macrophytes or seagrasses generally contribute most of the system's biomass and primary production (e.g., Manickchand-Heileman et al., 1998; Rosado-Solórzano and Guzmán del Prío, 1998; Vega-Cendejas and Arreguín-Sánchez, 2001; Zetina-Rejón et al., 2003). However, Tapong Bay and Chiku Lagoon are mainly driven by planktonic primary production, which is likely promoted by enriched waste discharges from the surrounding aquaculture ponds. The high phytoplankton production rates of both lagoons place them among the most-productive coastal fishery ecosystems (cf. Nixon, 1982; Joyeux and Ward, 1998). The dominance of planktonic primary production also occurs in the shallow subtropical Tongoy Bay, Chile, which is governed by periodic intrusions of upwelling water (Wolff, 1994). In an enriched mesocosm experiment by Oviatt et al. (1986), increased loadings of inorganic nutrients to temperate estuarine systems also stimulated planktonic primary production.

The availability of net primary production (NPP) for fishery yields can be measured by net system metabolism, which is the balance between primary production and respiration of organic matter. NPP and fishery yields per unit area in Tapong Bay subjected to poor flushing were remarkably lower than those of Chiku Lagoon subjected to better flushing, although their nutrient loadings were very similar. An alternative biogeochemical approach of stoichiometrically linked water–salt–nutrient budgets also showed that net system production was lower in Tapong Bay (Hung and Hung, 2003) than in Chiku Lagoon (Hung and Kuo, 2002). Su et al. (2004) found that phytoplankton *P/B* was lower in the poorly flushed region of Tapong Bay, which might have resulted from the reduction in flow velocity or turbulence thickening of the boundary layer around a phytoplankton cell. Few data of water residence times are available for comparisons among tropical lagoons. The residence times of Tapong Bay and Chiku Lagoon were within the range of 2.6–32.8 d reported for Mexican tropical lagoons (Smith et al., 1997). The residence time of Chiku Lagoon was shorter than that of most Mexican lagoons. On the other hand, the mean residence time of Tapong Bay was ranked in the middle compared to those Mexican lagoons. The residence times of the outer and inner portions of Tapong Bay (Hung and Hung, 2003) were comparable to the 10 d of Terminos Lagoon (Nipper et al., 2005) and the 25 d of Celestun Lagoon (Rivera-Monroy et al., 2004), respectively. As a result, the NPP of the eutrophic lagoon Tapong Bay was reduced to the same level of

the non-eutrophic Terminos Lagoon and Celestun Lagoon, where macrophyte biomass and production dominate (Table 6).

The mean transfer efficiency in Tapong Bay was also low when compared with Chiku Lagoon and other tropical lagoons (Table 6). As a matter of fact, the transfer efficiencies for trophic levels III (7.1%) and IV (15.8%) of Tapong Bay were comparable to those of Chiku Lagoon (Lin et al., 2001) and other tropical lagoons (Manickchand-Heileman et al., 1998; Vega-Cendejas and Arreguín-Sánchez, 2001; Zetina-Rejón et al., 2003). However, the efficiency declined sharply for trophic level II (1.5%), where most of the herbivorous flows occurred. The low efficiencies might have resulted from the respiration of cultured oysters and bivalves. They are the most-prominent living compartments in terms of matter flows and biomass in the lagoon. Both lagoons support intensive oyster culture, but a high population density of bivalves occurs only in Tapong Bay. In total, cultured oysters and bivalves consumed about 70% of the available production of phytoplankton, but about 71% of the consumption was respired and was not used in the lagoon (Table 5).

However, in our view, the more-likely cause for the lower transfer efficiency of Tapong Bay than of Chiku Lagoon is the small predation mortality of cultured oysters and bivalves by predators on higher trophic levels (Table 5), so that less than 1% of the throughput of trophic level II is passed up the food web. In Tapong Bay, the total biomass per unit area of predators on higher trophic levels was only about 38% of that of Chiku Lagoon (Lin et al., 1999). Most of the flows on higher trophic levels occurred with benthic feeders, including crabs, shrimps, benthic-feeding fish, and piscivorous fish (Table 5). The lower density could therefore be ascribed to the hypoxic bottom water (2 mg l^{-1} , Hung and Hung, 2003) as a result of poor flushing. On the other hand, the black striped mussel *Mytilopsis sallei* is the dominant bivalve species, which is native to Central and South America and is a well-known invasive pest in Tapong Bay (Chang, 1985). It often forms dense monocultures on oyster-culture pens and on the hard shell surfaces of oysters and other bivalves that smother and exclude most other species, leading to a substantial reduction in biodiversity in introduced waters. The rapid growth rate and early reproductive age of the black striped mussel allows it to reach high densities very quickly (Morton, 1989). In Tapong Bay, this mussel is not known to be the main diet of any predator (Table 3). This might therefore result in a great proportion of flows not being transferred to higher trophic levels but moving to detritus instead. The flow to detritus contributed 27% of the throughput for trophic level II (Fig. 4), which was high compared to 20% in Chiku Lagoon (Lin et al., 2001).

In Chiku Lagoon, most of the detritus is directly consumed and passed up the food web (Lin et al., 1999), which results in high recycling of organic matter in the food web when compared with other tropical lagoons (Table 6). Like many tropical lagoons and estuaries (see Lin et al., 2001), the D:H ratio of Chiku Lagoon is >1.0 , suggesting that the food web is more dependent on detritivory. However, the importance of detritus in an atoll lagoon would decrease by augmenting primary productivity by 10% (Niquil et al., 1999). The Swartkops estuary, South Africa mildly polluted by agriculture and industry (Baird and Ulanowicz, 1993) and the eutrophic Baltic Sea (Wulff and Ulanowicz, 1989) also showed lower D:H ratios than values for other estuaries. A D:H ratio of <1.0 even occurred 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, the Netherlands also created a D:H ratio of <1.0 (Baird and Ulanowicz, 1993). In Tapong Bay, despite the higher proportion of flow to detritus

on trophic level II, the hypoxic bottom water might further reduce the recycling of entering detritus back into the food web (Fig. 4). Detritus might therefore accumulate and become the largest compartment in the lagoon. Consequently, Hsieh (2000) found organic content of the sediments was generally >2% in Tapong Bay when compared to <0.5% in Chiku Lagoon. In contrast to many tropical lagoons (Table 6), a D:H ratio of <1.0 suggests that the food web is more dependent on herbivory, rather than on the accumulation of detritus in the sediment, despite the shallow water. This was supported by joint analyses of stable isotopes and stomach contents of detritivorous fishes and invertebrates whose food sources are primarily the macroalgal periphyton on the oyster-culture pens in Tapong Bay (Table 4). While oyster culture was suggested to induce a shift from pelagic to benthic consumers of a food web (Leguerrier et al., 2004), our results show that poor flushing in this eutrophic tropical lagoon supporting intensive oyster culture not only reduces the NPP, predator biomass, the transfer efficiency, and the recycling of organic matter, but also induces a shift from detritivory to herbivory in the food web.

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