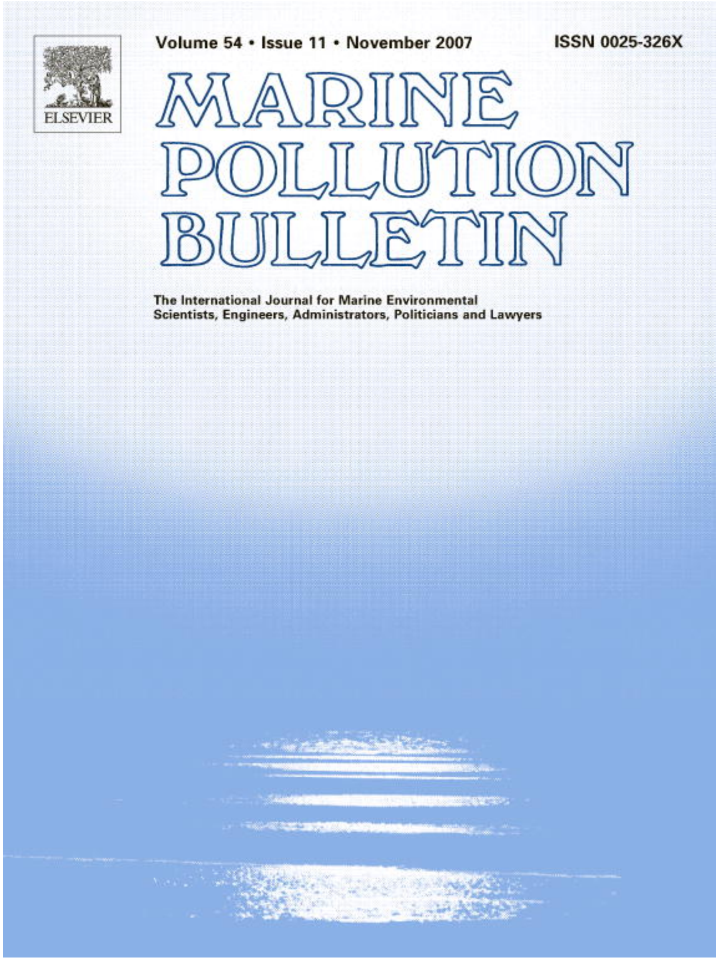
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# A trophic model for the Danshuei River Estuary, a hypoxic estuary in northern Taiwan

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**Abstract**

The estuary of the Danshuei River, a hypoxic subtropical estuary, receives a high rate of untreated sewage effluent. The Ecopath with Ecosim software system was used to construct a mass-balanced trophic model for the estuary, and network analysis was used to characterize the structure and matter flow in the food web. The estuary model was comprised of 16 compartments, and the trophic levels varied from 1.0 for primary producers and detritus to 3.0 for carnivorous and piscivorous fishes. The large organic nutrient loading from the upper reaches has resulted in detritivory being more important than herbivory in the food web. The food-chain length of the estuary was relatively short when compared with other tropical/subtropical coastal systems. The shortness of food-chain length in the estuary could be attributed to the low biomass of the top predators. Consequently, the trophic efficiencies declined sharply for higher trophic levels due to low fractions of flows to the top predators and then high fractions to detritus. The low biomass of the top predators in the estuary was likely subject to over-exploitation and/or hypoxic water. Summation of individual rate measurements for primary production and respiration yielded an estimate of $-1791$ g WW m$^{-2}$ year$^{-1}$, or $-95$ g C m$^{-2}$ year$^{-1}$, suggesting a heterotrophic ecosystem, which implies that more organic matter was consumed than was produced in the estuary.


*Keywords:* Food-chain length; Sewage effluent; Over-exploitation; System metabolism; Ecopath; Network analysis

## 1. Introduction

Estuaries have been widely recognized to be highly productive per unit area since the study of Georgia estuaries by Schelske and Odum (1962). Reasons for high estuarine productivity and understanding of the functioning of estuaries have been the inspiration and focus of estuarine ecology for the past 30 years (e.g. Nixon et al., 1986). However, the paradigm of high estuarine productivity has been based for the most part on the results from temperate estuaries. Studies on subtropical and tropical estuaries have lagged behind research on temperate estuaries (e.g. Baird and 'Ulanowicz, 1993), and the functioning of subtropical and tropical estuaries is therefore still poorly understood. Although fishery yields from tropical estuaries are much higher than those from other tropical waters (Blaber, 1997), ecosystem research has concentrated more on coral reefs than on other tropical coastal systems (Opitz, 1996; Johnson et al., 1995; Arias-Gonzalez et al., 1997; Niquil et al., 1999). There is a significant lack of detailed ecosystem studies on the functioning of tropical and subtropical estuaries.

The Danshuei River (25°10′N; 121°10′E), the largest river in northern Taiwan, is 159 km long and covers about 2726 km$^2$ of watershed area (Fig. 1). The estuary of Danshuei River is vegetated by the rare and endangered mangrove, *Kandelia obovata* Sheue, Liu and Yong (Rhizophoraceae). The fish assemblage caught in the mangrove

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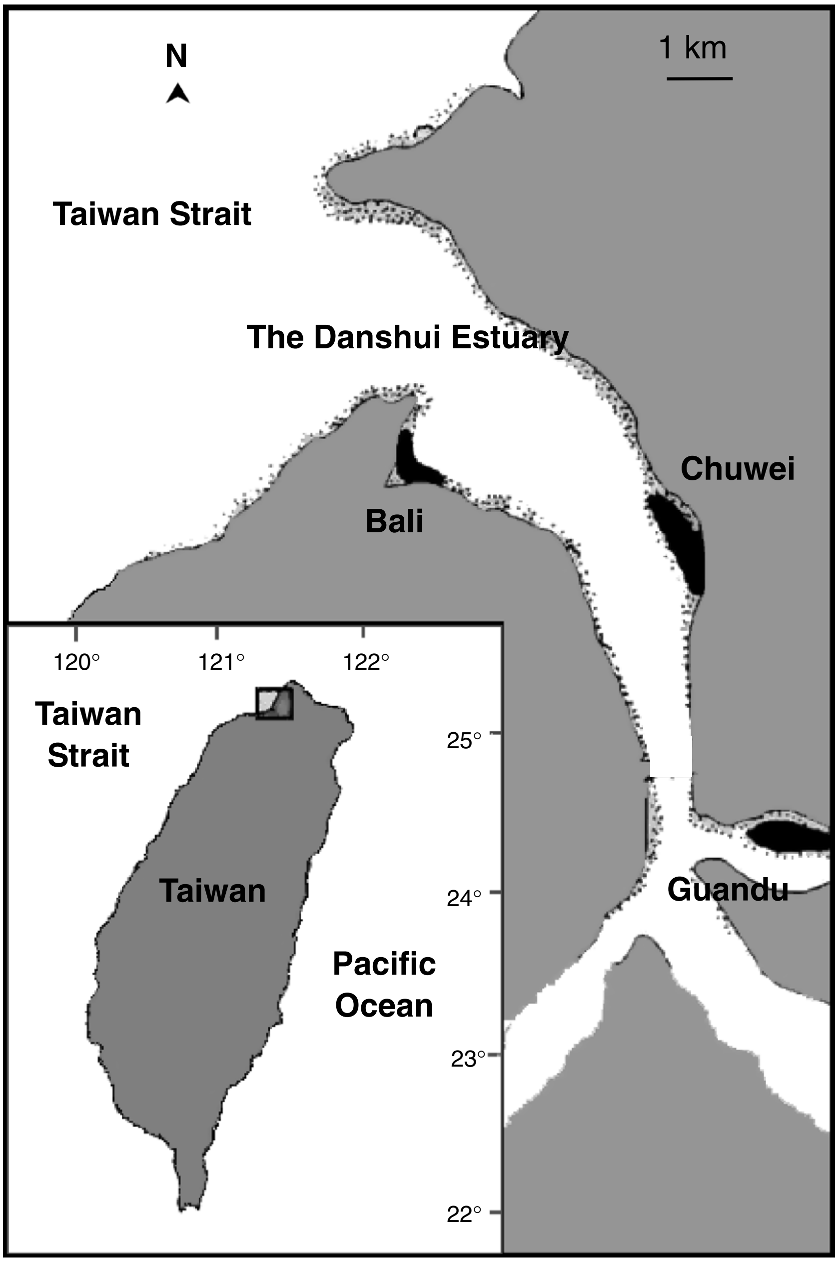


Fig. 1. Study area of the Danshuei Estuary and locations of mangroves along the estuary.

swamp is dominated by small-sized and commercially important species (Lin et al., 1999). The Danshuei Estuary has been a commercial fishing ground important for the harvesting of juvenile engraulids and clupeids for seafood, as well as anguillid elvers for aquaculture (Tzeng and Wang, 1992). However, the Danshuei River flows through the metropolitan area of Taipei (6 million people) and receives both treated and untreated domestic sewage effluents. The river pollution index (RPI) of the 1999 annual report of water quality of the Danshuei River by the Environmental Protection Agency showed that more than 90% of the area of the estuary is moderately or heavily polluted. As a result, dissolved oxygen contents in the bottom waters decline temporarily to near-zero levels (Jiann et al., 2005; Liu et al., 2005). Denitrifier microbes were detected in the sediments at 1 cm deep (Fan et al., 2006). Scarcity of integrated information for understanding its functioning has hindered the much-needed assessment of the Danshuei Estuary to determine an appropriate strategy for its ecosystem management.

Quantitative descriptions of matter flow have been used to provide significant insights into the structure and functioning of a variety of temperate aquatic ecosystems (e.g. Baird and Ulanowicz, 1993; Christensen and Pauly, 1993; Wolff, 1994), coral reefs (Opitz, 1996; Arias-Gonzalez et al., 1997), and tropical lagoons (Lin et al., 1999, 2006). Very little is known about these mechanisms in tropical/subtropical estuaries. In order to better understand the key trophic pathways in the Danshuei River estuary and the effects of heavy pollution on these trophic pathways, we constructed a mass-balanced model of the Danshuei Estuary and attempted to characterize its functioning.

The availability of algal production for consumption can be indexed 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 respires, and 'heterotrophic' if respiration exceeds primary production. Smith and Hallibaugh (1993) estimated that the small area of the coastal zone accounts for about 30% of net oceanic oxidation in the world. They postulated that coastal metabolism is likely altered by human activities on the surrounding land. However, little is known about the responses of a hypoxic estuary. Our purposes were: (1) to present a trophic model for a heavily polluted subtropical estuary; (2) to characterize the interconnected flows of organic matter in the food web; (3) to describe quantitatively the characteristics of the estuary as a whole and its components relevant to ecosystem functioning; and (4) to quantify the net system metabolism.

## 2. Materials and methods

### 2.1. Study area

The Danshuei River estuary (Fig. 1) is 9.2 km long and 8.5 m deep on average at low tide. The surface width is 1000 m and the bottom width is 85 m. It makes up a surface area of 9.2 $km^2$ and a volume of 42.4 $km^3$. Climatic data derived from a local weather station of the Central Weather Bureau of Taiwan from 1971 to 2000 show that the mean air temperature ranged from 15.1 °C in January to 28.8 °C in July. The mean annual and monthly precipitation values were 2120 and 177 mm, respectively. There were no distinct dry and wet seasons.

The estuary is subjected to semidiurnal tides with a mean tidal range of 2.17 m. The mean river discharge rate is 233 $m^3 s^{-1}$ and is often stratified. Data on water temperature, salinity, turbidity, and other environmental variables were derived from the 1999 annual report of water quality of the Danshuei Estuary by the Environmental Protection Agency. Water temperature ranged from 15 °C in February to 30 °C in July. Salinity exhibited a gradient from 30 psu of the tidal inlet to 15 psu of the upper reach at Guandu. Suspended solids were high and averaged 21 mg $L^{-1}$. As a result, the water in the estuary remained turbid, ranging from 10 to 23 NTU. $NO_3^-$ was generally lower than 0.09 mg $L^{-1}$, but $NH_4^+$ was high in the estuary, ranging from 1.1 to 6.8 mg $L^{-1}$ with a mean value of 3.2 mg $L^{-1}$. $PO_4^{-3}$ ranged 0.28–0.67 mg $L^{-1}$. Biochemical oxygen demand (BOD) ranged 19.5–46.5 mg $L^{-1}$. Tidal flushing exerts the greatest influence to the flushing of the estuary. Consequently, the residence time is short with the order of 1–2 days (Wang et al., 2004).

### 2.2. Modeling approach

A trophic model of the Danshuei River estuary was constructed using the Ecopath routine in Ecopath with Ecosim software system of Christensen et al. (2005) to describe all the 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 $P_i$ = 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 the production that is either passed up the trophic level, used for biomass accumulation or exported); $1 - EE_i$ = "other mortality"; $EX_i$ = the export of $i$ to other systems through sedimentation or fishery activities; and $AC_i$ = the accumulation of $i$ during the study period.

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

$$B_i \cdot P_i/B_i \cdot EE_i - \Sigma_j B_j \cdot Q_j/B_j \cdot DC_{ji} - EX_i - AC_i = 0, \quad (2)$$

where $P_i/B_i$ is the production/biomass ratio, $Q_j/B_j$ is the consumption/biomass ratio of the predator $j$, and $DC_{ji}$ is the fraction of the prey $i$ in the average diet of predator $j$. It was assumed that the food matrix remains stable during the study period.

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

$$\Sigma_j B_j x Q_j/B_j = P_j + R_j + UN_j, \quad (3)$$

where $P_j$ = the production of $j$; $R_j$ = the respiration of $j$, and $UN_j$ = the unused consumption of $j$, which was assumed to be 20% (Christensen et al., 2005).

Not all parameters used to construct the model do have to be entered since Ecopath links the production of each group with the consumption of all other groups, and uses the linkages to estimate missing parameters (Christensen and Pauly, 1992). DC and EX must always be entered, while entry is optional for one of any of the other four parameters (B, P/B, Q/B, and EE). To balance the model, the software may change the value of EE. For further details and algorithms of the Ecopath model structure, see Christensen et al. (2005).

### 2.3. Model compartments

Major species of similar sizes and diets in the Danshuei Estuary were grouped within the same compartment. Bacterial biomass was included in the compartment of detritus as recommended by Christensen and Pauly (1992), because bacterial flow may totally overshadow other flows in the system. A 17-compartment model for the estuary was developed (Table 1), consisting of the following groups: (1) phytoplankton, (2) periphyton, (3) trochophores (polychaete

Table 1
The compartments and input parameters for the construction of the Danshuei Estuary model (P/B, production/biomass ratio; Q/B, consumption/biomass ratio)

| Compartment | Biomass (g WW $m^{-2}$) | P/B ($year^{-1}$) | Q/B ($year^{-1}$) | Import (g WW $m^{-2}$ $year^{-1}$) | Fishery catch (g WW $m^{-2}$ $year^{-1}$) |
|---|---|---|---|---|---|
| 1. Phytoplankton | 7.92 | 250 | – | – | – |
| 2. Periphyton | 11.9 | 1.45 | – | – | – |
| 3. Trochophores | 0.25 | 68[a] | 200[a] | – | – |
| 4. Copepods | 0.92 | 65[a] | 277[a] | – | – |
| 5. Nauplii | 0.25 | 65[a] | 310[a] | – | – |
| 6. Amphipods | 0.75 | 33[b] | 112[d] | – | – |
| 7. Molluscs | 1.50 | 3.80[b] | 13[e] | – | 1.95 |
| 8. Polychaetes | 19.7 | 8.10[b] | 57[d] | – | – |
| 9. Shrimps | 110 | 2.70[b] | 26 | – | 0.16 |
| 10. Crabs | 45 | 1.40[b] | 14 | – | 4.05 |
| 11. Fish larvae | 2.81 | 50[c] | 150[f] | – | 3.62 |
| 12. Herbivorous fish | 5.77 | 3.66[c] | 13.4[f] | – | 2.23 |
| 13. Omnivorous fish | 4.93 | 1.07[c] | 4.81[f] | – | 0.93 |
| 14. Carnivorous fish | 0.98 | 1.30[c] | 5.60[f] | – | 0.80 |
| 15. Piscivorous fish | 0.25 | 3.30[c] | 9.45[f] | – | 0.73 |
| 16. Detritus | 33,219 | – | – | 89,923 | – |

[a] Empirical relationships developed by Chang (1992).
[b] Empirical relationships developed by Brey (1999).
[c] Natural mortality was computed using an empirical relationship developed by Pauly (1980).
[d] Riddle et al. (1990).
[e] Opitz (1996).
[f] An empirical model developed by Palomares and Pauly (1989).

larva), (4) copepods, (5) nauplii, (6) amphipods, (7) molluscs, (8) polychaetes, (9) shrimps, (10) crabs, (11) fish larvae, (12) herbivorous fish, (13) omnivorous fish, (14) carnivorous fish, (15) piscivorous fish, and (16) 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 research data (Table 1). The research data were collected at low and high tides, respectively, on each of four sampling occasions in spring, summer, autumn, and winter 1999 to take account of tidal and seasonal variations. They were collected at Bali, Chuwei, and Guandu, respectively, to take account of spatial variations of the estuary (Fig. 1). Biomass of phytoplankton and periphyton on sediments in terms of chlorophyll *a* was measured using a Turner fluorometer according to standard procedures (Parsons et al., 1984). Daily production rate of phytoplankton or periphyton was calculated by plotting the oxygen evolution as a function of irradiance and temperature according to Lin et al. (2005). Oxygen evolution of phytoplankton and periphyton on sediments was determined concurrently in acrylic tube incubations using water column only and periphyton + water column ($n = 3$ for each treatment), receiving various levels of irradiance in a water bath system for 2–4 h centered on noon when the irradiance was stable. The water column tubes were used both to determine production rates of phytoplankton and to correct the dissolved oxygen measurements in the periphyton + water column tubes. Changes in oxygen concentration in the tubes were monitored by an electrode DO meter (Model 52, YSI) corrected by a modified Winkler technique (Pai et al., 1993).

Samples of trochophores, copepods and nauplii were collected by towing 2 NorPac nets (45 cm diameter, 330 μm mesh size) just below the sea surface for 10 min at 1.0 m $s^{-1}$. The zooplankton biomass was estimated by displacement volume according to Ahlstrom and Thrailkill (1960). Estimates of P/B and Q/B for the zooplankton were computed using empirical relationships developed by Chang (1992) for a dominant species of herbivorous zooplankton in the estuary. PVC cores with an inner diameter of 10 cm were pushed about 20 cm deep into the sediment for collection of amphipods, mollusks and polychaetes. Shrimps, crabs, and fish in the estuary were collected using fyke nets. This fishing gear is a passive sampler designed to use tidal dynamics to collect nekton. P/B ratios for invertebrates were computed based on empirical relationships derived by Brey (1999). Production rate for fish is the sum of natural mortality and catch mortality (Christensen et al., 2005). The catches of shrimps, crabs, molluscs, fish larvae, and fish were obtained directly from the local fishery bureau. Estimates of natural mortality for fish were computed using an empirical relationship developed by Pauly (1980) for the dominant species of each group. Q/B ratios for small invertebrates in the estuary were obtained by searching the same groups in the literature from tropical coastal waters (Riddle et al., 1990; Opitz, 1996). 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.

Detritus comprises the organic materials in the water column and on sediments. Water from the estuary was filtered through an acid-cleaned, dried, and pre-weighed Nucleopore membrane filter to determine the detrital mass in the water column. Sediments were collected by Eckman Birge Grab (15 cm × 15 cm) and dried in an oven at 60 °C. The dried sediments were then ground to powder for analyses of organic materials. Detritus on sediments was limited to the top 5 cm of sediments, which is generally available for uptake by epifauna and fish. Input of detritus comprises the organic materials from mangroves and the upper reaches of the Danshuei River.

Diet compositions of zooplankton, shrimps, crabs, and fish were estimated by stomach content analyses of the dominant species, and were recorded in percent of volume of major prey groups (Table 2). This is roughly equivalent to relative weight and thus approximates the relative amount of energy extracted by consumers from various prey groups (Macdonald and Green, 1983). The diet of fish larvae and other small invertebrates were obtained by searching directly in the literature, respectively (Chern and Tzeng, 1993; Opitz, 1996).

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

### 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 groups, since it was assumed for any group not to 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 consumption of most groups is about 3–10 times higher than their production. In addition, the GE cannot be higher than the net efficiency (the ratio between production and assimilated food).

Because Ecopath uses linkages of production of one group with consumption of other groups to calculate one missing parameter for each group, the most questionable parameter of each group can be treated as an unknown and calculated by Ecopath. In this study, some Q/B and DC values of small invertebrates were obtained directly from the literature (Table 1) and were considered to be less reliable in the estuary model. Therefore, they were gradually modified during the balancing exercise. But, the changes were rather small (±10%).

### 2.5. Network analysis

Details of the transfer of organic matter from primary production to top predators in the food web of the Danshuei Estuary can be revealed by network analysis (Field et al., 1989). The required inputs of net primary production, biomass, fishery export, and each matter flow between donor and recipient compartments for each compartment were assembled from the research data. 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).

Many consumers in the estuary 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

Table 2
Diet composition in percentage of volume of prey groups for the construction of the Danshuei Estuary model

| Prey/predator | 3[a] | 4[a] | 5[a] | 6[a] | 7[a] | 8[a] | 9 | 10 | 11[b] | 12 | 13 | 14 | 15 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. Phytoplankton | 0.50 | 0.80 | 1.0 | | 0.44 | 0.50 | | | 0.95 | 0.208 | 0.300 | | |
| 2. Periphyton | | | | 0.01 | 0.02 | 0.01 | | | | 0.120 | | 0.020 | 0.063 |
| 3. Trochophores | | | | 0.02 | 0.01 | | 0.004 | | | | | | |
| 4. Copepods | | | | 0.15 | | | | | 0.05 | 0.020 | 0.120 | 0.080 | 0.180 |
| 5. Nauplii | | | | 0.04 | | | 0.003 | | | | | | |
| 6. Amphipods | | | | | | | 0.006 | 0.008 | | 0.002 | 0.013 | 0.181 | 0.030 |
| 7. Molluscs | | | | | | | 0.001 | | | | 0.001 | | 0.004 |
| 8. Polychaetes | | | | | | | 0.010 | 0.050 | | | 0.142 | 0.189 | 0.112 |
| 9. Shrimps | | | | | | | | 0.060 | | | 0.004 | 0.265 | 0.200 |
| 10. Crabs | | | | | | | | | | | 0.006 | 0.182 | 0.120 |
| 11. Fish larvae | | | | | | | 0.045 | | | | | 0.002 | 0.054 |
| 12. Herbivorous fish | | | | | | | | | | | 0.002 | 0.014 | 0.082 |
| 13. Omnivorous fish | | | | | | | | | | | 0.002 | 0.012 | 0.070 |
| 14. Carnivorous fish | | | | | | | | | | | <0.001 | <0.001 | 0.016 |
| 15. Piscivorous fish | | | | | | | | | | | <0.001 | <0.001 | 0.004 |
| 16. Detritus | 0.50 | 0.20 | | 0.78 | 0.53 | 0.49 | 0.931 | 0.882 | | 0.668 | 0.410 | 0.054 | 0.065 |

[a] Opitz (1996).
[b] Chern and Tzeng (1993).

to a given level that is transmitted 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 the estuary system or the TST was indexed in terms of how much matter the system processes. The cycling of matter and energy is considered 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 estuary was.

## 3. Results

### 3.1. Model validation

The estimated EE values (Table 3) for all consumers were less than 1.0 and were consistent with values suggested by Christensen and Pauly (1992). The EE of detritus is defined as the ratio between what flows out of and what flows into the detritus. The estimated EE value of detritus was much less than 1, which indicates that more was entering the detritus group than was leaving. The difference most likely ended up as accumulated detritus, being buried as sediment, decomposed by microheterotrophs (Nixon et al., 1986), or exported to other systems. GE values were physiologically realistic as suggested by Christensen et al. (2005), and were in the range of 0.1–0.3 for most consumers and generally higher for small organisms (i.e. trochophores, amphipods, and fish larvae). They were lower than the net efficiency.

### 3.2. Trophic structure

Trophic levels estimated by Ecopath from the weighted average of prey trophic levels varied from 1.0 for primary producers and detritus to 3.0 for carnivorous and piscivorous fishes (Fig. 2). The Danshuei Estuary model showed that the structure of food web comprised three integer trophic levels. Detritus was the largest compartment in the model. The most prominent living group in terms of both biomass and matter flow in the estuary was shrimps. It comprised 51% of the system's total living biomass (excluding detritus) and 25% of the total throughput of living compartments (Table 3). Most of the activity in terms of flow occurred in the lower part of the trophic web where there was intensive use of detritus as a food source. Consequently, of the 13 consumer groups, 9 fell within trophic levels <2.2.

Fishery yield from the Danshuei Estuary was about 14.5 g WW $m^{-2}$ $year^{-1}$. Crabs and fish larvae accounted for more than 50% of the total yield and were the most important fishery compartment in the estuary (Table 1).

Table 3
Output parameters for the Danshuei Estuary model

| Group name | EE | GE | Respiration (g WW $m^{-2}$ $year^{-1}$) | Flow to detritus (g WW $m^{-2}$ $year^{-1}$) | Predation mortality (g WW $m^{-2}$ $year^{-1}$) | Net efficiency | Trophic level | Omnivory index |
|---|---|---|---|---|---|---|---|---|
| 1. Phytoplankton | 0.66 | – | – | 684 | 164 | – | 1.0 | – |
| 2. Periphyton | 0.98 | – | – | 0.31 | 1.43 | – | 1.0 | – |
| 3. Trochophores | 0.79 | 0.34 | 23.0 | 13.6 | 53.4 | 0.43 | 2.0 | 0.00 |
| 4. Copepods | 0.63 | 0.24 | 144 | 73.2 | 40.8 | 0.29 | 2.0 | 0.00 |
| 5. Nauplii | 0.74 | 0.21 | 45.8 | 19.8 | 47.9 | 0.26 | 2.0 | 0.00 |
| 6. Amphipods | 0.95 | 0.30 | 42.2 | 18.0 | 31.7 | 0.37 | 2.2 | 0.17 |
| 7. Molluscs | 0.85 | 0.29 | 9.90 | 4.75 | 1.94 | 0.37 | 2.0 | 0.01 |
| 8. Polychaetes | 0.41 | 0.14 | 737 | 318 | 3.31 | 0.18 | 2.0 | 0.00 |
| 9. Shrimps | 0.14 | 0.10 | 2000 | 831 | 0.36 | 0.13 | 2.1 | 0.07 |
| 10. Crabs | 0.09 | 0.10 | 441 | 184 | 0.03 | 0.13 | 2.1 | 0.12 |
| 11. Fish larvae | 0.95 | 0.33 | 289 | 0.00 | 46.0 | 0.42 | 2.1 | 0.05 |
| 12. Herbivorous fish | 0.12 | 0.27 | 40.7 | 34.0 | 0.06 | 0.34 | 2.0 | 0.01 |
| 13. Omnivorous fish | 0.23 | 0.22 | 13.7 | 8.82 | 0.06 | 0.28 | 2.3 | 0.21 |
| 14. Carnivorous fish | 0.66 | 0.23 | 3.12 | 1.53 | 0.04 | 0.29 | 3.0 | 0.09 |
| 15. Piscivorous fish | 0.88 | 0.35 | 1.08 | 0.58 | 0.04 | 0.44 | 3.0 | 0.16 |
| 16. Detritus | 0.04 | – | – | 0.00 | – | – | 1.0 | 0.07 |

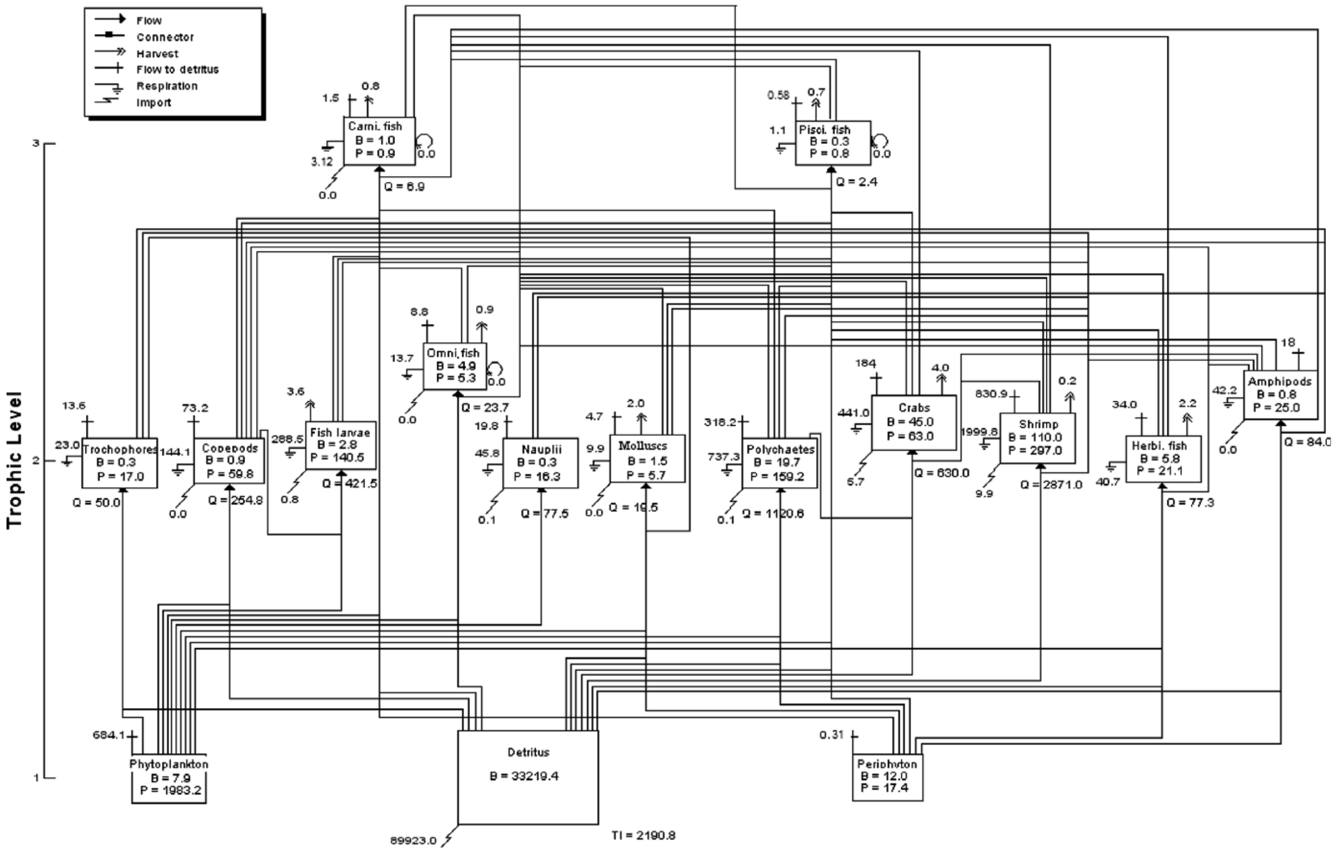


Fig. 2. Trophic model of the Danshuei Estuary. The box size is proportional to the square root of the compartment biomass in terms of g WW $m^{-2}$. Production and other flows are in g WW $m^{-2}$ $year^{-1}$.

Herbivorous fish comprised 15% of the total yield, and molluscs (mainly clams) comprised another 13%.

### 3.3. Mixed trophic impacts

Using the mixed trophic impact routine in Ecopath with Ecosim, direct and indirect interactions among compartments and impacts of fishery activities in the Danshuei Estuary can be assessed (Ulanowicz and Puccia, 1990). This routine indicates the effect that a change in the biomass of one group will have on the biomass of other groups in a system and can thus be regarded as a form of sensitivity analysis (Fig. 3). An increase in phytoplankton biomass, for example, has a great positive effect on nauplii and fish larvae, which feed largely on phytoplankton. Consequently, the catch of fish larvae would increase. The increase in phytoplankton biomass has no effect on detritus due to the large organic nutrient loading from the upper reaches of the Danshuei River. An increase in detritus would also have a large positive effect on many biomasses and fishery catches with an exception of fish larvae. However, an increase in periphyton biomass would have only a slight effect on herbivorous fish, suggesting the minor importance for the food source in the estuary.

The mixed trophic impact routine shows that the most influential biological compartments in the estuary were shrimps and crabs. The routine demonstrated that increasing the biomass of shrimps would have a large negative impact on many biomasses because of their large biomass, general diet and competition for detritus. This is consistent with our identification of shrimps as the most prominent group in terms of both biomass and compartmental throughput in the estuary. However, an increase of the biomass of crabs would have a positive impact on some biomasses since crabs had a negative impact on shrimps. The routine also showed that crab-catch and long line were the most influential fishery activities in the estuary, but their impacts were different. Increasing the activity of long line would have a largely negative impact on fish groups.

### 3.4. Ecosystem attributes

The trophic analysis aggregated compartmental throughputs of the 16 groups in a simple Lindeman food chain with four integer trophic levels (Fig. 4). Primary producers (trophic level I) comprised phytoplankton, periphyton, and detritus. Flows of most of the compartments including trochophores, copepods, nauplii, amphipods, molluscs, polychaetes, shrimps, crabs, fish larvae, herbivorous fish, and omnivorous fish occurred on trophic level II. On trophic level III and IV, flows were generally ascribed to carnivorous and piscivorous fish. The detritivory to

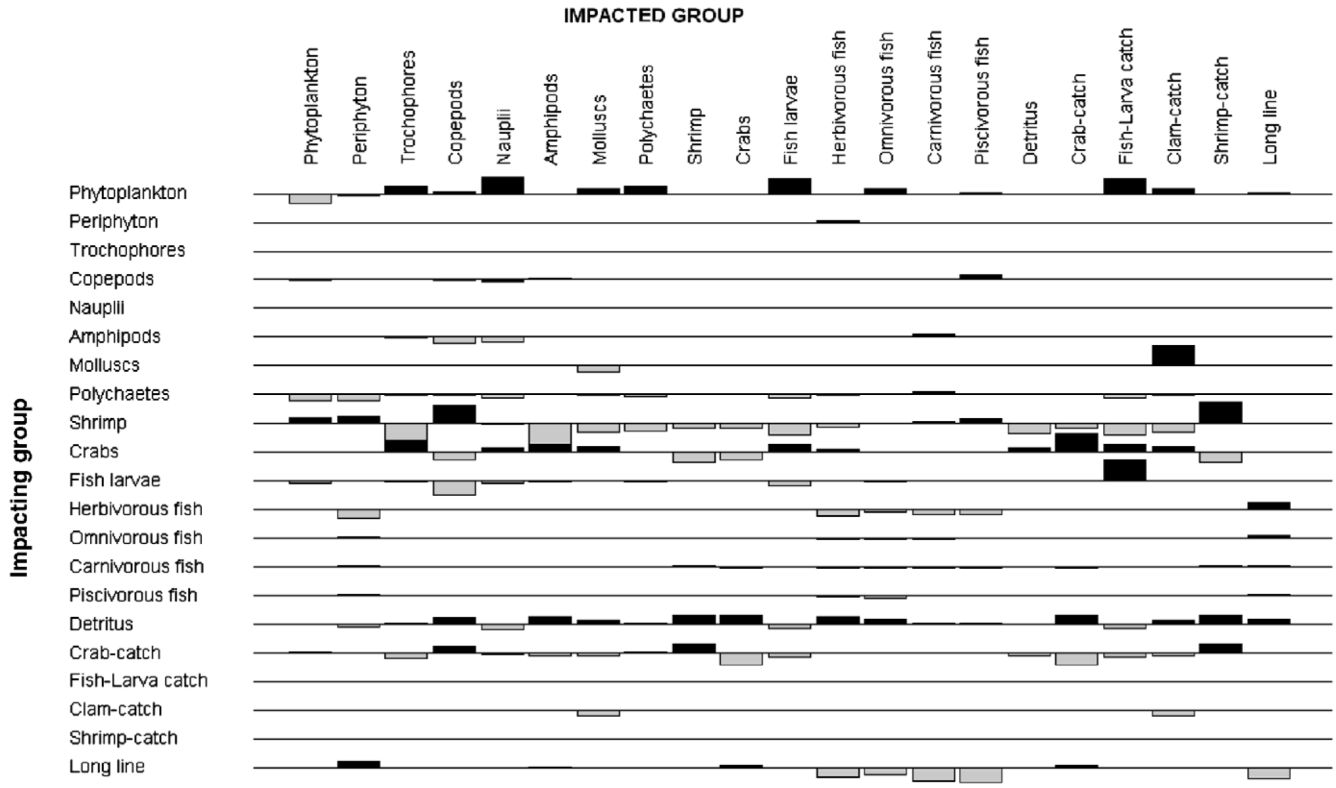


Fig. 3. Mixed trophic impacts of the Danshuei Estuary model. Direct and indirect impacts an increase in the biomass of groups to the left of the histograms would have on the groups positioned above them. The bars pointing upwards show positive impacts, while those pointing downwards show negative impacts.

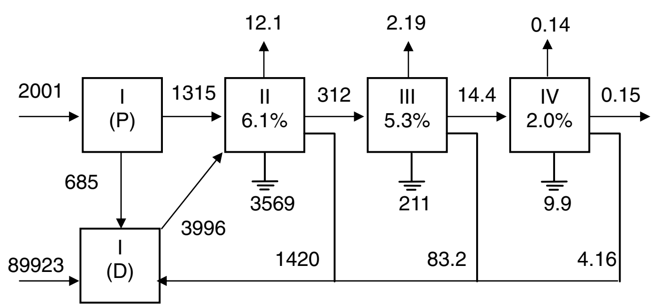


Fig. 4. Flow network of organic matter and trophic efficiencies (%) of the Danshuei Estuary model. The flow (g WW $m^{-2}$ $year^{-1}$) web was aggregated into a concatenated chain of transfers through four integer levels. The flows were from primary producers (P) and detritus (D). Flows out of the tops of boxes represent export, and flows out of the bottoms represent respiration.

herbivory ratio (D:H ratio) of 3.0 indicated that detritivory flow was more important than herbivory flow in the estuary. Trophic level II achieved a trophic efficiency of 6.1% for the combined flows from primary production and detritus. Trophic efficiencies declined for higher trophic levels, dropping to only 2.0% for trophic levels IV. The geometric mean of trophic efficiencies for the aggregated food chain from levels II to IV was calculated as 4.0%.

TST was about 101 kg WW $m^{-2}$ $year^{-1}$ (Table 4). Because of the large detrital input and export, the cycle analysis shows that all cycled flows accounted for only 1.9% of TST (i.e., FCI). The difference between net primary production (NPP) and all respiratory flows (i.e., net system production) in the Danshuei Estuary was calculated to be −1790 g WW $m^{-2}$ $year^{-1}$, or −95 g C $m^{-2}$ $year^{-1}$ (Table 4). The NPP to total respiratory ratio (P:R ratio) of 0.53 indicates that the estuary is heterotrophic, which implies that more organic matter is consumed than is produced in the system.

## 4. Discussion

A comparative approach with other coastal ecosystems is helpful to characterize the structure and matter flow in the Danshuei Estuary. However, there are very limited quantitative descriptions of food webs for the tropical/subtropical coastal systems. The food-chain length of the Danshuei Estuary was relatively short when compared with other tropical/subtropical coastal systems. The maximum trophic position in the estuary was only 3.0, which was lower than 3.6–4.0 of the top predator recorded in Tongoy Bay (Wolff, 1994), Chiku Lagoon (Lin et al., 1999), Kuosheng Bay (Lin et al., 2004), and Tapong Bay (Lin et al., 2006). In addition, energy often passes through about four or five species in a food chain (Morin and Lawler, 1995). There were only three trophic levels of the food-web structure in the estuary (Fig. 2), which were lower than the four trophic levels for the other tropical/subtropical coastal

Table 4
Comparisons of ecosystem attributes of the Danshuei Estuary model with other tropical/subtropical coastal models

| | Danshuei Estuary (this study) | Kuosheng Bay (Lin et al., 2004) | Tongoy Bay (Wolff, 1994) | Chiku Lagoon (Lin et al., 1999) | Tapong Bay (Lin et al., 2006) | Units |
|---|---|---|---|---|---|---|
| Sum of all consumption | 5638 | 14,701 | 7669 | 70,966 | 15,828 | g WW $m^{-2}$ $year^{-1}$ |
| Sum of all export | 14.5 | 381 | 3103 | 890 | 119 | g WW $m^{-2}$ $year^{-1}$ |
| Sum of all respiratory flow | 3790 | 6328 | 4021 | 45,815 | 11,262 | g WW $m^{-2}$ $year^{-1}$ |
| Sum of all flow into detritus | 92,115 | 8281 | 6040 | 39,983 | 8604 | g WW $m^{-2}$ $year^{-1}$ |
| Total system throughput (TST) | 101,558 | 29,692 | 20,835 | 157,653 | 35,812 | g WW $m^{-2}$ $year^{-1}$ |
| Fishery's mean trophic level | 2.17 | 3.32 | 3.63 | 3.40 | 2.05 | |
| Total catches | 14.5 | 1.23 | 63 | 890 | 119 | g WW $m^{-2}$ $year^{-1}$ |
| Gross efficiency (catch/NPP)(%) | 0.007 | 0.02 | 1.80 | 1.80 | 0.80 | |
| Total net primary production (NPP) | 2001 | 6710 | 7125 | 50,600 | 15,280 | g WW $m^{-2}$ $year^{-1}$ |
| NPP: total respiration ratio (P:R ratio) | 0.53 | 1.06 | 1.77 | 1.10 | 1.36 | |
| Net system production | −1790 | 381 | 3103 | 4775 | 4018 | g WW $m^{-2}$ $year^{-1}$ |
| NPP/total biomass | 9.4 | 40 | 30 | 24 | 20 | |
| Total biomass/TST | 0.002 | 0.006 | 0.011 | 0.013 | 0.022 | |
| Total biomass (excluding detritus) | 213 | 167 | 263 | 2096 | 777 | g WW $m^{-2}$ |
| Finn's cycling index (FCI) | 1.9 | 32 | 10 | 15 | 10 | |

food webs (Tongoy Bay, Wolff, 1994; Chiku Lagoon, Lin et al., 1999; Kuosheng Bay, Lin et al., 2004; Tapong Bay, Lin et al., 2006). Consequently, only a small amount of matter flow was left for system utilization after trophic level III in the estuary (Fig. 4).

Energetic and dynamic constraints have been widely proposed as important factors in determining food-web structure (Morin and Lawler, 1995). Food-chain length might be controlled either by the amount of energy entering the food web (energetic constraints) or by time span between consecutive disturbances relative to time needed to build up a population (dynamic constraints). The energetic hypothesis or the productive space hypothesis (Schoener, 1989) predicts that food-chain length should increase as total availability of primary production or detrital input increases. The dynamic constraints hypothesis predicts that longer food chains are less stable than short food chains (Pimm and Lawton, 1977). However, there is very limited theoretical and empirical support for the dynamic stability hypothesis (Post, 2002).

The shortness of food chains in the Danshuei Estuary was inconsistent with the prediction by the productive space hypothesis (Schoener, 1989). NPP of the Danshuei Estuary was low when compared with other tropical/subtropical and temperate coastal systems (Table 5). Despite the low NPP of the Danshuei Estuary, its TST was higher than those of most other coastal ecosystems (Table 4). As a matter of fact, a high fraction of TST of the Danshuei Estuary was attributable to the large organic nutrient loading from the upper reaches, because the sum of all consumption, export, respiration, and production were not higher than the other two subtropical coastal systems. As a result, the D:H ratio of the Danshuei Estuary was higher than most of the ratios of coral reefs and tropical/subtropical coastal systems (Table 5), suggesting that the estuary was more dependent on detritus than on primary producers. The high rate of untreated sewage effluent has led to the very low FCI value of the Danshuei Estuary when compared with those of other coastal systems (Table 5). The lower conservation of organic matter in the Danshuei Estuary was probably subsidized by the high rate of organic nutrient loading as the high-energy Sundays Beach (Heymans and McLachlan, 1996) and the upwelling of Tongoy Bay (Wolff, 1994). Therefore, resource was unlikely limited in the Danshuei Estuary. Our results did not support the productive space hypothesis (Schoener, 1989) for the shortness of food-chain length. Post (2002) indicated that resource availability limits food-chain length only in systems with very low resource availability.

In our view, the most likely explanation for the shortness of food-chain length in the Danshuei Estuary is the low biomass of top predators. The total biomass excluding detritus of the Danshuei Estuary was not lower than those of the subtropical coastal systems (Table 4). However, the fraction of biomass of top predators in the food web was lower than that of the other tropical/subtropical coastal systems. This was supported by the finding that the fish assemblage caught in the estuary was dominated by small-sized species (Lin and Shao, 1999). The geometric mean of trophic efficiencies in the estuary was low when compared with those of other coastal systems, regardless of whether they were in temperate or tropical/subtropical waters (Table 5). In the Danshuei Estuary, the trophic efficiencies for trophic level II (6.1%) and III (5.3%) were comparable to those of other estuaries. However, the trophic efficiencies declined sharply for trophic level IV (2.0%). The low efficiencies could be attributed to the low fractions of flows utilized by the top predators, so that high fractions of flows to detritus.

The low biomass of top predators in the Danshuei Estuary was likely subject to frequent and extreme disturbance by human activities. Human activities have been found to strongly influence food-chain length directly through the over-exploitation of top predators (Pauly et al., 1998).

Table 5
Comparisons of net primary production (NPP: g WW $m^{-2}$ $year^{-1}$), geometric mean of trophic transfer efficiency (II-IV), detritivory:herbivory ratio (D:H ratio), average path length (APL), and Finn cycling index (FCI) of the Danshuei Estuary model with other models

| Study site | Climate | NPP | Mean transfer efficiency (%) | D:H ratio | FCI (%) |
|---|---|---|---|---|---|
| Chiku Lagoon (Lin et al., 2001) | Tropical | 50,600 | 12 | 1.4 | 15 |
| Tapong Bay (Lin et al., 2006) | Tropical | 15,280 | 5.5 | 0.4 | 10 |
| Terminos Lagoon (Manickchand-Heileman et al., 1998) | Tropical | 11,754 | 7.0 | 4.6 | 7.0 |
| Takapoto Atoll lagoon (Niquil et al., 1999) | Tropical | 4254 | 17 | 0.6 | 18 |
| Great Barrier Reef (Johnson et al., 1995) | Tropical | 97,163 | 5.4 | 1.0 | 26 |
| Tampamachoco lagoon (Rosado-Solórzano and Guzmán del Próo, 1998) | Tropical | 342 | 7.9 | 1.0 | NA |
| Caeté Mangrove Estuary (Wolff et al., 2000) | Tropical | 3134 | 9.4 | 1.1 | 18 |
| Yucaton Paninsula (Vega-Cendejas and Arreguín-Sánchez, 2001) | Tropical | 15,550 | 12 | 1.9 | 13 |
| Huizache-Caimanero lagoon (Zetina-Rejón et al., 2003) | Tropical | 3816 | 8.3 | 0.9 | 9.9 |
| Gulf of Paria (Manickchand-Heileman et al., 2004) | Tropical | 1389 | 12 | 1.7 | 7.3 |
| Seine Estuary (Rybarczyk and Elkaïm, 2003) | Tropical | 853 | 2.7 | 2.5 | 16 |
| Tiahura Reef[a] (Arias-Gonzalez et al., 1997) | Tropical | 17,650 | 7.7 | NA | NA |
| Tongoy Bay (Wolff, 1994) | Subtropical | 7125 | 14 | 0.8 | 10 |
| Kuosheng Bay (Lin et al., 2004) | Subtropical | 6710 | 6.5 | 2.4 | 30 |
| Danshuei Estuary (this study) | Subtropical | 2001 | 4.0 | 3.0 | 1.9 |
| Sundays Beach (Heymans and McLachlan, 1996) | Temperate | 10,556 | 12 | 12 | 13 |
| Ythan Estuary (Baird and Ulanowicz, 1993) | Temperate | 12,000 | 3.7 | 10 | 25 |
| Swartkops Estuary (Baird and Ulanowicz, 1993) | Temperate | 12,652 | 2.8 | 1.5 | 44 |
| Kromme Estuary (Baird and Ulanowicz, 1993) | Temperate | 16,046 | 3.4 | 6.7 | 26 |
| Ems Estuary (Baird and Ulanowicz, 1993) | Temperate | 1409 | 7.4 | 0.5 | 30 |
| Chesapeake Bay (Wulff and Ulanowicz, 1989) | Temperate | 17,436 | 5.7 | 5.0 | 30 |
| Baltic Sea (Wulff and Ulanowicz, 1989) | Temperate | 8594 | 13 | 1.5 | 23 |

[a] Mean for the fringing reef and the barrier reef. NA: data not available.

The Danshuei Estuary traditionally has been a commercial fishing ground. The mixed trophic impact shows that an increase of long-line activities in the estuary would have a great negative impact on carnivorous and piscivorous fishes (Fig. 3). The long-term over-exploitation of top predators has resulted in low total catches and gross efficiency, and then lowered food-chain length (Pauly et al., 1998). Nevertheless, the Danshuei Estuary was moderately or heavily polluted, receiving large organic nutrient loading from sewage, and industrial and agricultural effluents. As a result, the near-zero levels of dissolved oxygen contents in the waters might also constrain the biomass of top predators in the estuary. Our results support the dynamic stability hypothesis as a more likely explanation of the shortness of food chain in the estuary.

The availability of algal production in the Danshuei Estuary was assessed quantitatively in terms of net system metabolism using integrated rates of primary production and respiration in the system (Table 4). Consistent with the findings of Smith and Hallibaugh (1993) that most temperate estuaries are heterotrophic, our results suggest that an heterotrophic condition existed in this subtropical estuary, where total respiration exceeds NPP within the estuary. The net system production of $-1791$ g WW $m^{-2}$ $year^{-1}$, or $-95$ g C $m^{-2}$ $year^{-1}$ in the Danshuei Estuary was comparable to values for other estuaries (Smith and Hallibaugh, 1993). 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. As the loading of organic matter increases, so do suspended solids and turbidity or imbalance of nutrient supply (Wu and Chou, 2003), which may lower algal productivity in the estuary. Therefore, the heterotrophy of the Danshuei Estuary can be attributed to the high rate of organic nutrient loading and to low primary productivity.

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