A trophic model of fringing coral reefs in Nanwan Bay, southern Taiwan suggests overfishing

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ARTICLE INFO

ABSTRACT

Several coral reefs of Nanwan Bay, Taiwan have recently undergone shifts to macroalgal or sea anemone dominance. Thus, a mass-balance trophic model was constructed to analyze the structure and functioning of the food web. The fringing reef model was comprised of 18 compartments, with the highest trophic level of 3.45 for piscivorous fish. Comparative analyses with other reef models demonstrated that Nanwan Bay was similar to reefs with high fishery catches. While coral biomass was not lower, fish biomass was lower than those of reefs with high catches. Consequently, the sums of consumption and respiratory flows and total system throughput were also decreased. The Nanwan Bay model potentially suggests an overfished status in which the mean trophic level of the catch, matter cycling, and trophic transfer efficiency are extremely reduced.

1. Introduction

In the past few decades, increased human activities have caused serious damage to coral reefs (Nystrom et al., 2000), many of which have lost their resilience and are in serious decline worldwide (Bellwood et al., 2004). Fishing is the most widespread exploitative human impact affecting coral reefs in tropical and subtropical waters (Jackson et al., 2001). The direct effects of fishing are declines in organism abundance, and changes in population structures and distributions of certain species. Additionally, indirect effects of fishing activities may strongly affect biological interactions among reef organisms (Hughes, 1994). Fishing may also lead to a decline in the mean trophic level of the catch as well as changing marine food webs (Pauly et al., 1998).

Anthropogenic nutrient enrichment may stimulate the prolific growth of macroalgae in coral reefs. This enrichment has been considered the major cause of the shift to macroalgae (Grigg, 1995; Lapointe, 1997). However, McCook et al. (2001) argued that the widespread replacement of corals by macroalgae might have resulted from coral mortality due to external disturbances, for example, major bleaching or typhoons, rather than competitive overgrowth. The combined effects of overfishing and nutrient enrichment have also been blamed for the decline in coral reefs worldwide (Jackson et al., 2001). Overfishing, nutrient enrichment, and other human activities may reduce the resilience of coral reefs and their capacity to recover from short-term disturbances, such as typhoons and bleaching.

Most previously discussed studies focused on target species or communities, not on how these activities affect biological interactions among reef communities or degradation of coral reefs. A comprehensive study of trophic interactions among reef organisms based on quantitative descriptions of organic matter flows of the food web can provide insights into an ecosystem. The Ecopath model can demonstrate trophic food web structures, component functioning, and interactions in aquatic ecosystems (Christensen et al., 2004). Comparative studies of trophic flows have been used to provide significant insights into the structure and functioning of estuaries (Baird and Ulanowicz, 1993) and tropical lagoons (Lin et al., 2006). Some Ecopath models have been constructed for coral reefs, including the French Frigate Shoals of Hawaii (Polovina,

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1984); Bolinao in the Philippines (Aliño et al., 1993); Puerto Rico and the Virgin Islands in the Caribbean (Opitz, 1996); Moorea in French Polynesia (Arias-González et al., 1997); the Mexican Caribbean (Arias-Gonzálezm, 1998); the far northern Great Barrier Reef (Gribble, 2003); Uvea of New Caledonia (Bozec et al., 2004); and Floreana Island of the Galapagos (Okey, 2004). However, few comparisons between coral reefs are possible due to problems of data availability and quality, aggregation methods, compartmental numbers, and other limitations. Despite this, Arias-González et al. (1997) compared the fringing and barrier reefs in Moorea, French Polynesia, and Arias-Gonzálezm (1998) and Arias-González et al. (2004) compared different habitats between protected and unprotected reefs in the Mexican Caribbean.

The coral reefs of Nanwan Bay (Fig. 1) were once well known for their abundant and diverse communities (Dai, 1991). However, these reefs have also been threatened by human disturbances. In the past two decades, blasting, poisoning, free-diving, and three-layer gill nets were employed to catch fish. Other pressures come from coastline development, sedimentation, tourism, and sewage discharges. Decreases in species numbers, colony numbers, reef coverage, and species diversity of corals were observed at Tiaoshih from 1987 to 1997 (Dai et al., 1998). There were many branching *Acropora* patches at reefs of Tiaoshih and the inlet of the Third Nuclear Power Plant which were replaced by an outbreak of sea anemones *Condylactis nanwannensis* and *Mesactinia genesis* after 1996 (Chen and Dai, 2004). The coverage of sea anemones had increased to 46.2% at Tiaoshih by 2004 (Tkachenko et al., 2007). Some coral reefs in Nanwan Bay have undergone rapid increases in macroalgae. High proportions (10–55%) of the reef area were found to be occupied by macroalgae in 1992 (Dai, 1993). The green alga *Codium edule* was often reported to rapidly spread on the reefs and forms dense meadows every year (Chiang and Wang, 1987; Dai, 1997). Other macroalgal blooms were composed of opportunistic algae in the genera *Enteromorpha*, *Ulva*, *Gracilaria*, *Laurencia*, and *Sargassum*. The objectives of this study were to characterize the trophic structure and functioning of the coral reefs of Nanwan Bay as a whole and to reveal possible causes for the phase shifts by constructing a trophic model of Nanwan Bay and then comparing it to those of other fringing reefs around the world.

2. Materials and methods

2.1. Study area

Nanwan Bay, in the central part of Kenting National Park, is located at the southern tip of Taiwan (Fig. 1; 21°57′N, 120°44′E). It is a semi-enclosed embayment bounded by two capes, with well-developed fringing reefs distributed along the shoreline. In this area, 230 species of scleractinian corals, nine species of non-scleractinian reef-building corals, and 40 species of alcyonacean corals have been recorded (Dai, 1991). The study area of the Nanwan Bay model consisted of fringing reefs which are shallower than 15 m in depth along the coast of the bay. This area has a tropical climate, with distinct dry and wet seasons. The maximum average air temperature of 31.7 °C occurs in July, and the minimum average of 17.8 °C occurs in January (Central Weather Bureau, 1971–2000; http://www.cwb.gov.tw/V5/index.htm). In the wet season from May to October, average monthly rainfall is 142–475 mm, when the southwesterly monsoon winds and typhoons bring considerable quantities of rain. During the dry season from November to April, when the northeasterly monsoon winds prevail, average monthly rainfall normally does not exceed 45 mm.

Since no large river flows into the coastal waters, salinity in the water column remains within a range of 32.6–34.7 (Lin and Shao, 1998). Chlorophyll *a* concentrations and the light extinction coefficient (k) in the water column also remain low, ranging 0.14–0.29 mg m^{-3} and 0.59–1.26 m^{-1}, respectively. Circulation along the coast is dominated by mixed diurnal and semidiurnal tides, which are modulated by a pronounced spring-neap cycle (Lee et al., 1999). In the western half of Nanwan Bay, there is daily periodic upwelling as the tidal currents ebb as a result of cyclonic eddy pumping, induced by the combined effects of tidal flow and topography (Lee et al., 1999). This tidally induced upwelling is strong during spring tides and causes sudden daily temperature drops often exceeding 10 °C. There is a nuclear power plant (the Third Nuclear Power Plant) on the coast of Nanwan Bay, on which construction began in 1979 and operation started in 1984 before the establishment of Kenting National Park. Four coral reefs were selected as representative coral reefs in Nanwan Bay for collecting data: Leidashih, a soft coral-dominated reef; the inlet of the Nucle-
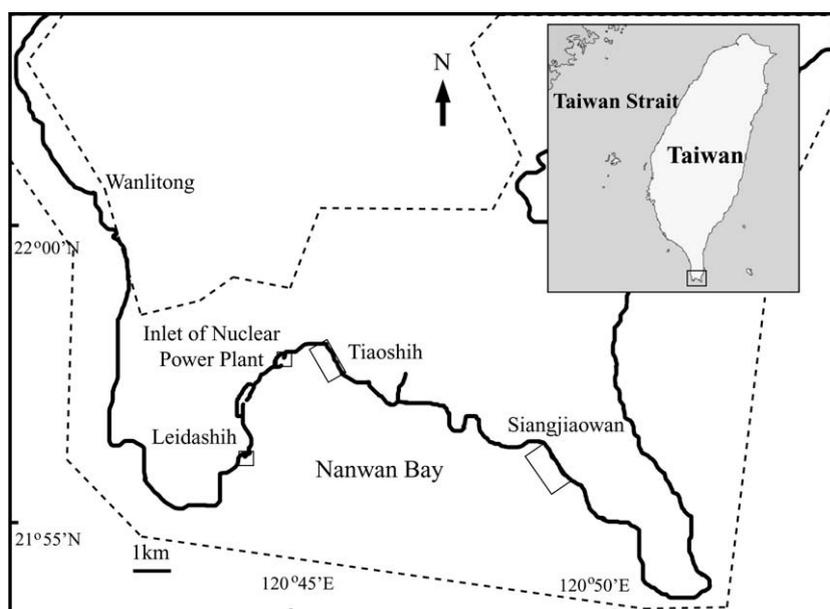

Fig. 1. Nanwan Bay of Kenting National Park, southern Taiwan. The boundaries of the park are indicated by the dotted line.

ar Power Plant and Tiaoshih, which are sea anemone-dominated reefs; and Siangjiaowan, which is a hard coral-dominated reef.

2.2. Modeling approach

The trophic model of coral reefs in Nanwan Bay was constructed using the Ecopath with Ecosim (EwE) software system of Christensen et al. (2004) to quantify organic matter flows within the food web. The Ecopath model is a mass-balance model. For each compartment (i), a mass-balance budget can be expressed as

$$P_i - B_i \cdot M2_i - P_i \cdot (1 - EE_i) - EX_i - AC_i = 0 \tag{1}$$

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 export), $1 - EE_i$ 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 (Q_j/B_j). Thus, Eq. (1) can be re-expressed as

$$B_i \cdot (Pi/Bi) \cdot EE_i - \Sigma_j B_j \cdot (Q_j/B_j) \cdot DC_{ji} - EX_i - AC_i = 0 \tag{2}$$

where P_i/B_i is the production: biomass ratio of i, Q_j/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 remained stable and no biomass accumulated during the study period from 2001 to 2003.

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

$$\Sigma_j B_j \times (Q_j/B_j) = P_j + R_j + UN_j \tag{3}$$

where P_j is the production of j, R_j is the respiration of j, and UN_j is the unused consumption of j.

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 of the other compartments, and uses the linkages to estimate missing parameters. DC and EX must always be entered, while entry of one of any of the other four parameters (B, P/B, Q/B, and EE) is optional. For further details and algorithms of the Ecopath model see Christensen et al. (2004).

2.3. Model compartments and sampling

Most of the data for the Nanwan Bay model were assembled from an integrative study, the Long-Term Ecological Research in Kenting (Kenting-LTER) from 2001 to 2003 (Table 1). Major species of similar sizes, habitats, and diets in the coral reefs of Nanwan Bay were functionally grouped within the same compartment, resulting in an 18-compartment model.

Phytoplankton biomass in terms of chlorophyll *a* concentration 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 (*sensu* Strickland and Parsons, 1972). The survey was conducted on the *RV Ocean Researcher I*. The cruise collected water samples at various depths at 11 stations which were evenly distributed in the bay (Chen et al., 2005). Primary production of phytoplankton was determined by an *in situ* ^{14}C assimilation method.

Macrophyte biomass, including macroalgae and the dominant seagrass, *Thalassia hemprichii*, was determined in the intertidal and subtidal zones at five study sites on the reef flats of Nanwan Bay. At each site, two to three replicate parallel transects separated by 100–150 m and perpendicular to the shoreline were surveyed. The transect lengths extended to the outer limits of the reefs where macroalgae and *T. hemprichii* disappeared. All macroalgae and *T. hemprichii* in a 50 × 50-cm quadrat at 20-m intervals along each transect were collected for identification and biomass determination in terms of wet weight (WW). The primary production of mac-

Table 1
Compartments, input parameters and calculated outputs for the Nanwan Bay model.

Group name		Input parameters				Calculated outputs									
		B	P/B	Q/B	Catch	EE	GE	TL	NE	Omnivory index	Resp	Fishing mort	Predat mort	Other mort	Flow to detritus
1.	Phytoplankton	1.08	1185.88	–		0.40	–	1.00	–	0.00	–	0.00	478.07	707.80	760.9
2.	Macrophytes	944.48	19.70	–		0.11	–	1.00	–	0.00	–	0.00	2.23	17.47	16498.9
3.	Hard corals	273.30	1.09[b]	1.09		0.31	1.00	1.10	1.25	0.27	226.4	0.00	0.34	0.75	264.3
4.	Soft corals	69.50	0.25[c]	0.50[d]		0.75	0.50	1.22	0.63	0.08	29.9	0.00	0.19	0.06	11.3
5.	Sea anemones	52.87	2.00[e]	4.00[e]		0.17	0.50	1.44	0.63	0.11	152.3	0.00	0.34	1.66	130.1
6.	Ben herbivorous inv	68.03[a]	1.53[b]	14.01[b]	0.03	0.95	0.11	2.11	0.18	0.10	467.8	0.00	1.45	0.08	386.5
7.	Sessile det inv	333.02[a]	1.51[b]	7.18[b]		0.95	0.21	2.00	0.30	0.01	1170.1	0.00	1.44	0.08	742.5
8.	Zooplankton	2.62	32.00[f]	192.00[f]		0.91	0.17	2.00	0.28	0.001	217.9	0.00	29.25	2.75	208.4
9.	Herbivorous fish	21.04	1.49[g]	12.76[g]	3.20	0.63	0.12	2.03	0.20	0.03	129.8	0.15	0.79	0.55	119.0
10.	Semi-sessile det inv	138.45[a]	1.62[b]	7.20[b]	0.03	0.95	0.23	2.01	0.32	0.01	473.5	0.00	1.54	0.08	310.3
11.	Polyp–feeding fish	0.41	3.40[g]	18.32[g]		0.84	0.19	2.16	0.23	0.02	4.6	0.00	2.86	0.54	1.7
12.	Ben omnivorous inv	65.14[a]	3.79[b]	33.68[b]	0.43	0.95	0.11	2.35	0.15	0.25	1398.5	0.01	3.59	0.19	560.8
13.	Omnivorous fish	4.05	1.78[g]	13.05[g]	1.01	0.76	0.14	2.58	0.17	0.26	35.1	0.25	1.11	0.42	12.3
14.	Zooplanktivorous fish	22.82	0.89[g]	8.60[g]	1.11	0.76	0.10	2.34	0.13	0.35	136.7	0.05	0.63	0.21	44.1
15.	Sessile ben-feeding fish	2.34	0.80[g]	7.37[g]	0.56	0.74	0.11	2.93	0.14	0.25	11.9	0.24	0.35	0.21	3.9
16.	Mobile ben-feeding fish	21.25	0.98[g]	9.45[g]	0.56	0.72	0.10	3.10	0.13	0.17	139.9	0.03	0.68	0.27	46.0
17.	Piscivorous fish	9.98	0.51[g]	4.84[g]	0.35	0.09	0.11	3.45	0.13	0.17	33.5	0.04	0.01	0.47	14.3
18.	Detritus	118.07	–	–		0.20	–	1.00	–	0.15	–	–	–	–	–

B, biomass (g wet weight (WW) m^{-2}); P/B, production/biomass ratio (yr^{-1}); Q/B, consumption/biomass ratio (yr^{-1}); EE, ecotrophic efficiency; GE, gross efficiency; TL, trophic level; NE, net efficiency; Resp, respiration; mort, mortality; Predat, predator; ben, benthic; inv, invertebrates; det, detritivorous; Catch, Resp, and Flow to detritus are in g WW m^{-2} yr^{-1}.

[a] Estimated by Ecopath.
[b] Opitz (1996).
[c] Pitcher et al. (2002).
[d] Buchary (1999).
[e] Okey (2004).
[f] Pauly and Christensen (1993).
[g] Determined by empirical equations compiled in Fishbase (Froese and Pauly 2006).

roalgae was determined by changes in dissolved oxygen concentrations in microcosm incubations of dominant species which were collected from each site. The leaf growth rate of *T. hemprichii* was studied in three random plots (10 × 10 cm each) at each site using a leaf marking method described by Lin and Shao (1998). Using these increments, production was expressed as leaf production per unit area of ground and unit time (g m^{-2} day^{-1}).

Zooplankton samples were collected by towing two NorPac nets (45 cm in diameter with 100- and 330-μm mesh sizes, respectively) just below the sea surface. In the laboratory, samples were identified, and the density (individuals m^{-3}) was calculated. The dry biomass of zooplankton was estimated by the length–weight relationship of dominant species using the empirical equation of Chang and Lei (1993):

$$\ln(\text{DW}) = 1.292 \times \ln(\text{TL}) - 3.504 \tag{4}$$

where DW is the dry weight and TL is the total length (about 200 μm in this study). The dry weight was translated to wet weight by 1 g DW = 4.5 g WW (Opitz, 1996). The P/B and Q/B of zooplankton were derived from values in the South China Sea model (Pauly and Christensen, 1993).

Cnidarian coverage was assessed with underwater photographs by scuba diving along three 30-m isobathic transects at depths from 5 to 15 m at four fixed stations in Nanwan Bay. Photographs of a 20 × 20-m quadrat were continuously taken along each transect. Species and growth forms were identified, and their coverage was estimated by random point counts using ImagePro Plus software. Cnidarians were classified into three major groups of hard corals, soft corals, and sea anemones. Three growth forms of hard corals (massive/encrusting, plate, and branching) were sampled in a 5 × 5-cm area to determine the biomass in g WW m^{-2} by measuring the coverage area and then extracting the tissues. Three dominant genera of soft corals (*Sinularia*, *Sacrophyton*, and *Lobophytum*) in a 5 × 5-cm area were also sampled to determine the biomass in g WW m^{-2} by measuring the coverage area. Three dominant species of sea anemones (*Megalactis* sp., *Entacmaea quadricolor*, and *Mesactinia ganesis*) were also collected to determine the biomass in g WW m^{-2} of each polyp. Total biomasses of hard and soft corals and sea anemones in Nanwan Bay were determined by the weighted average of coverage of the growth forms or dominant species.

In general, corals and sea anemones are both primary producers and consumers. In the Ecopath model, one can specify a degree of heterotrophy for such facultative consumers (Christensen et al., 2004). Sorokin (1981) suggested that 70% of the energy requirement of corals is provided by zooxanthellae, 20% from feeding on zooplankton, and 10% from feeding on detritus. However, both hard and soft corals have higher energy requirements provided by zooxanthellae than do sea anemones (authors' observations). For the present model, it was assumed that 80% of the energy of hard and soft corals was from zooxanthellae and 20% from zooplankton and detritus. For sea anemones, 60% of the energy was provided by zooxanthellae and 40% by zooplankton and detritus.

The P/B value of hard corals was taken from the value for corals in the Caribbean coral reef model (Opitz, 1996). However, the Q/B value of hard corals of the Caribbean model was too high. Here, we estimated the Q/B value by assuming that 20% of the total production of hard corals was derived from feeding on zooplankton and detritus, and the P/Q value of hard corals was 0.20. The P/B value of soft corals was taken from the value for the living bottom structure (LBS, including sponges, gorgonians, soft corals, sea pens, sea squirts, and sea anemones) from a Hong Kong coral reef model (Pitcher et al., 2002). The Q/B value of soft corals was taken from the value for the LBS in a Java Sea model (Buchary, 1999). The P/B and Q/B values of sea anemones were taken from values of sea anemones in a Floreana Island model (Okey, 2004).

Mollusca and crustracea in the intertidal and subtidal zones were the dominant benthic macrofauna in Nanwan Bay. Two permanent 5 × 10-m quadrats were selected bimonthly at four stations on the reef flats of the bay. All samples were collected and carried to the laboratory for identification and biomass determination in terms of g WW m^{-2}. However, the biomass of other small benthic invertebrates was difficult to reliably quantify. Therefore, benthic macrofauna were classified into four functional groups according to the 20-compartment model of Opitz (1996), including benthic herbivorous invertebrates, sessile detritivorous invertebrates, semi-sessile detritivorous invertebrates, and benthic omnivorous invertebrates. Here, these biomass values were treated as unknowns and calculated by Ecopath. The EE value of the benthic macrofauna was assumed to be 0.95, i.e., natural predation consumed a large proportion of benthic macrofauna production (Ricker, 1969; Polovina, 1984). No study was conducted to determine the P/B and Q/B values of benthic macrofauna in Nanwan Bay, so values were taken from those for Puerto Rican and the Virgin Islands coral reefs (Opitz, 1996).

Fish were surveyed during the daytime bimonthly at four stations in Nanwan Bay by scuba diving (English et al., 1997). A visual census is one of the most common quantitative and qualitative methods used in coral reef surveys and was developed by the Great Barrier Reef Marine Park Authority (1979). It is a rapid, non-destructive, and inexpensive method. Two permanent 7 × 7-m quadrats were assessed at each station. Fish species, individual number, and total length estimations were recorded. In total, 309 fish species were identified by the underwater visual census. Seven fish functional groups were classified according to the diet and feeding habitat (Mitsuhiko et al., 1984; The Fish Database of Taiwan, http://fishdb.sinica.edu.tw/), including herbivorous fish (40 species), polyp-feeding fish (15 species), omnivorous fish (57 species), zooplanktivorous fish (41 species), sessile benthic-feeding fish (11 species), mobile benthic-feeding fish (131 species), and piscivorous fish (14 species). Fish biomass in terms of WW was calculated by the assumptions and empirical equation of Opitz (1996) as

$$W_{\text{mean}} = W_{\infty} \times 0.3 \times 0.86 \tag{5}$$

where W_{mean} is the mean individual weight and W_{∞} is the asymptotic weight, which can be found for each species in Fishbase (Froese and Pauly, 2006).

The P/B value for each fish species was estimated using the empirical equations of Pauly (1980) as

$$Z = M + F = P/B \quad \text{and} \tag{6}$$
$$M = K^{0.65} \times L_{\infty}^{-0.279} \times T_c^{0.463} \tag{7}$$

where Z is total mortality, M is natural mortality, F is fishing mortality, K is the curvature parameter of the von Bertalanffy growth function (VBGF), L_{∞} is the asymptotic length, and T_c is the mean water temperature (°C). K and L_{∞} can be found in Fishbase (Froese and Pauly, 2006).

The Q/B value of each fish species was estimated using the empirical equation of Palomares and Pauly (1989, 1998):

$$\log(Q/B) = 5.847 + 0.280 \log(Z) - 0.152 \log(W_{\infty}) - 1.360T'$$
$$+ 0.062A + 0.510h + 0.390d \tag{8}$$

where W_{∞} is the asymptotic weight, T is the water temperature (expressed as $1000/(T + 273.15)$), A is the aspect ratio of the caudal fin, h is a dummy variable expressing food type (1 for herbivores and 0 for detritivores and carnivores), and d is a dummy variable also expressing food type (1 for detritivores and 0 for herbivores and carnivores). In Nanwan Bay, a mean water temperature (T) of 28.5 °C was used in these calculations. Biomass, P/B, and Q/B values

of each fish functional group in Nanwan Bay were determined by the weighted average of the relative abundance of each species.

Detritus comprises the organic material in the water column and on sediments. Water from the coral reefs was filtered through acid-cleaned, dried, and pre-weighed Nucleopore membrane filters to determine the detrital mass in the water column (Shiah et al., 2000). Phytoplankton biomass was subtracted from the detrital mass by calculating the sum of chlorophyll *a* and pheophytin in the water column assuming a carbon:pigment ratio of 35:1 (Sobczak et al., 2002). Sediments were collected using a 3.75-cm-diameter tube core by scuba diving, and samples were dried in an oven at 60 °C. The dried sediments were then ground to a powder for analyses of organic materials. The detrital mass of sediments was limited to the top 5 cm of sediments, which is the detritus pool generally available for uptake by epifauna and fish. Bacterial biomass was included in the compartment of organic detritus as recommended by Christensen et al. (2004), because bacterial flows may overshadow other flows in the system.

There are few published data on the diet of invertebrates and fish in Nanwan Bay. Stomach contents of some fish and zooplankton in Nanwan Bay have been reported and were used to construct the trophic model (Chen, 2007). The diet items of other compartments were determined from Fishbase (Froese and Pauly, 2006) and for similar functional groups in the literature from other coral reefs (Optiz, 1996; Arias-González et al., 1997; Bozec et al., 2004). The diet compositions were estimated based on the relative abundance of each prey item in the coral reefs of Nanwan Bay (Table 2).

The unused consumption of herbivorous fish, benthic invertebrates, and zooplankton was higher than that of other animals (Bozec et al., 2004). Therefore, unused consumption was assumed to be 0.40 for herbivorous fish, benthic herbivorous invertebrates, and zooplankton, 0.30 for semi-sessile and sessile detritivorous invertebrates, and 0.25 for benthic omnivorous invertebrates.

Factors used for conversion between chlorophyll *a*, carbon, displacement volume, dry weight, and wet weight are summarized by Opitz (1996). Biomass data were recorded as g WW m^{-2}, and flow data were recorded as g WW m^{-2} yr^{-1}.

2.4. Model balancing and verification

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 generally the most-reliable data. The EE was treated as an unknown and calculated by Ecopath with the exception of those of benthic macrofauna. 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 model. Therefore, they were gradually modified during the balancing exercise. Most of the changes were small and remained within 20% of the input value.

The first step in verifying the realism of the Nanwan Bay model was to check whether the EE was <1.0 for all living compartments, since it was assumed that any living compartment cannot 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 with the exception of corals and sea anemones with symbiotic algae, for which production might exceed consumption (Christensen et al., 2004). In addition, the *P/Q* ratio cannot be higher than the net efficiency (the ratio between production and assimilated food). The final step was to compare output values to relevant data from the literature on other coral reefs.

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 estimated or taken from other models in the literature.

The sensitivity routine (Majkowski, 1982) was used to check the effect each input parameter had on all of the "estimated" parameters for each compartment in the Nanwan Bay model by varying all basic input parameters in steps from −50% to +50%. The output is given as

$$(\text{Estimated parameter} - \text{original parameter}) / \text{original parameter} \quad (9)$$

The mixed trophic impact (MTI), developed by Ulanowicz and Puccia (1990), was used to assess the effects that changes in the biomass of a compartment would have on the biomass of other compartments in Nanwan Bay. The MTI can be regarded as a form of sensitivity analysis for the input parameters of the model. The

Table 2
Diet composition of the Nanwan Bay model.

Prey/predator		3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1.	Phytoplankton		0.100	0.050		0.020	0.899									
2.	Macrophytes			0.010	0.758			0.875	0.310		0.361	0.372	0.100	0.137	0.035	
3.	Hard corals			0.001	0.010			0.002	0.001	0.670	0.030	0.001		0.001	0.055	
4.	Soft corals			0.001	0.002			0.001	0.001	0.160	0.002	0.001		0.001	0.020	
5.	Sea anemones				0.005					0.140	0.002	0.146				
6.	Ben herbivorous inv			0.002	0.005			0.001			0.031	0.245		0.214	0.030	0.056
7.	Sessile det inv			0.002	0.080			0.001			0.160	0.120		0.304	0.190	
8.	Zooplankton		0.080	0.090	0.080		0.002	0.001		0.007		0.002	0.007	0.080			
9.	Herbivorous fish												0.005	0.001	0.028	0.012	0.273
10.	Semi-sessile det inv				0.001	0.006			0.010			0.084	0.040		0.090	0.082	
11.	Polyp-feeding fish															0.001	0.020
12.	Ben omnivorous inv				0.021	0.008			0.010			0.045	0.040	0.020	0.120	0.548	0.050
13.	Omnivorous fish												0.005			0.003	0.075
14.	Zooplanktivorous fish												0.006	0.001	0.010	0.002	0.274
15.	Sessile ben-feeding fish														0.020		0.010
16.	Mobile ben-feeding fish														0.025	0.012	0.240
17.	Piscivorous fish																0.002
18.	Detritus		0.333	0.800	0.812	0.126	0.880	0.100	0.100	0.678	0.030	0.283	0.012	0.112	0.050	0.010	
	Importation		0.587	0.010	0.020		0.098		0.003					0.686			

ben, benthic; inv, invertebrates; det, detritivorous.

MTI for living groups is calculated by constructing an $n \times n$ matrix, where the i,jth element representing the interaction between the impacting group i and the impacted group j is

$$\mathrm{MTI}_{i,j} = \mathrm{DC}_{i,j} - \mathrm{FC}_{j,i} \tag{10}$$

where $\mathrm{DC}_{i,j}$ is the diet composition term expressing how much j contributes to the diet of i, and $\mathrm{FC}_{j,i}$ is a host composition term giving the proportion of the predation on j that is due to i as a predator.

2.5. Fishing indicator

Fishing activities in the coral reefs of Nanwan Bay primarily include free-diving for fish, line fishing, and gill netting. The estimated catch of fish and invertebrates was derived from monthly surveys of local fishermen. Fish species and WW were recorded. Because there are few seabirds observed in Nanwan Bay, the exports of fish and invertebrates by birds were assumed to be very small compared to those by fisheries and therefore were not included in the model. The fishing impact was assessed by the mean trophic level of the catch, the exploitation rate, fishing mortality, and the percentage of primary production required to sustain the fishery (PPR%).

2.6. Comparison with other coral reefs

A network analysis developed by Ulanowicz (1986) was used to characterize the interconnected flows of organic matter in the food web (Field et al., 1989). It is a tool for comparative analyses of ecosystems (Christian et al., 2005) that may be helpful in characterizing the trophic structure and functioning of the fringing reefs of Nanwan Bay. Indices of network flows and ecosystem attributes from the seven Ecopath models of other fringing reefs (Fig. 2), including the Bolinao (Aliño et al., 1993), Puerto Rico and the Virgin Islands (PRVI, Opitz, 1996), Tiahura (Arias-González et al., 1997), three Mexican Caribbean sites (Arias-González et al., 2004), and Floreana Island (Okey, 2004), were selected for comparison with the Nanwan Bay model. The eight models were separated into two categories based on fishery catch: low-catch reefs <5 g wet weight m^{-2} yr^{-1} (PRVI, Tiahura, Boca Paila, Tampalam,

and Floreana Island) and high-catch reefs >5 g wet weight m^{-2} yr^{-1} (Nanwan Bay, Bolinao, and Mahahual). Moloney et al. (2005) indicated that a common model structure is useful for intersystem comparisons when species groups are given an equivalent status. Fish biomass of other reefs was thus aggregated into eight functional groups as was the Nanwan Bay model.

The total system throughput (TST) represents the size of an ecosystem in terms of flows (Ulanowicz, 1986). It is the sum of consumption, exports, respiratory flows, and flows into detritus and is indexed in terms of how much matter the system processes. The total biomass:TST ratio (B:TST) represents the amount of biomass necessary to maintain one unit of flow. It is expected to increase along with ecosystem maturity (Odum, 1969). The net primary production:respiration ratio (P:R) and the net primary production:total biomass ratio (P:B) were used to describe how mature Nanwan Bay is. 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 TST, was used to measure how retentive Nanwan Bay is. The Lindeman trophic analysis (Kay et al., 1989) summarizes complicated food webs in terms of a single linear food chain. The trophic transfer efficiency from one aggregate 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 detritivory:herbivory ratio (D:H) is a measure of the relative importance of detritivory flows in a coral reef. A nonparametric Mann–Whitney U-test was then used to test differences in network indices and ecosystem attributes between reefs with low and high fishery catches using the SAS system (vers. 9.1.3).

3. Results

3.1. Model balancing and sensitivity analysis

The EE values of soft corals, zooplankton, and polyp-feeding, zooplankivorous, sessile, and mobile benthic-feeding fish all ex-
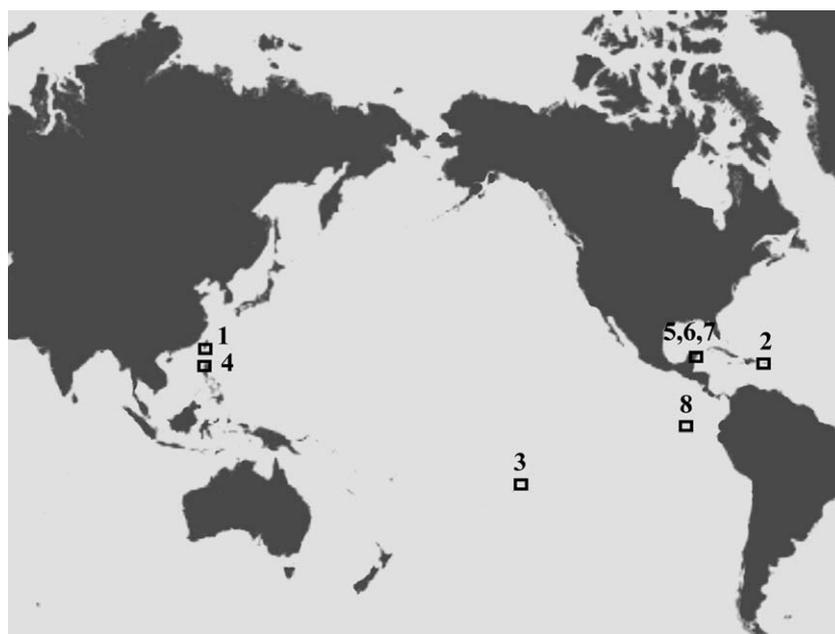

Fig. 2. Locations of seven fringing reefs analyzed by Ecopath for comparison with the Nanwan Bay model. 1. Nanwan Bay, 2. Puerto Rico and the Virgin Islands (PRVI), 3. Tiahura, 4. The Bolinao, 5. Mahahual, 6. Boca Paila, 7. Tampalam, 8. Floreana Island.

ceeded 1. The diets of their predator groups were then adjusted to reduce predation pressure on the six groups. However, the zooplankton biomass appeared insufficient for predation, so we assumed an external import of zooplankton from offshore into the coral reefs during flood tides (Table 2). Imported food accounted for only 2% of the total consumption by cnidarians, sessile detritivorous and semi-sessile detritivorous invertebrates, and zooplanktivorous fish. The P/Q values of herbivorous, zooplankivorous, mobile benthic-feeding, and piscivorous fish were too low (<0.1), so the values were increased by 10–20% to balance the model. However, because the P/Q value of herbivorous fish was still too low, we increased the P/B ratio by 50% and decreased the Q/B ratio by 50% to balance the model, so that the P/Q ratio was in the range of 0.1–0.3. After modifying the P/B and Q/B ratios of these groups, the diet matrix was also iteratively adjusted (<20%) in order to maintain the EE of each group to <1.0 during the balancing exercise.

Sensitivity analysis was performed on the input parameters of the Nanwan Bay model. An increase of 30% in the biomass or P/B of a group would result in a decrease of about 23% in its own estimated EE value, and an increase of about 14% in the EE values of its prey groups. A 30% increase in Q/B would result in about a 14% increase in the estimated EE values of its prey groups. Mobile benthic-feeding fish, piscivorous fish, and benthic omnivorous invertebrates were the most influential groups in the model because the 30% increase in Q/B often resulted in >20% increases in the estimated EE values of their prey groups.

3.2. Biomasses and trophic flows

The total living biomass of the Nanwan Bay model was 2030 g WW m^{-2} yr^{-1} (Table 3). Macrophytes were the most dominant group and comprised 47% of the total biomass (Fig. 3). Benthic invertebrates, cnidarians, fish, and plankton comprised the other 30%, 19%, 4%, and 0.2%, respectively. Benthic invertebrates were dominated by sessile detritivores, and cnidarians were dominated by hard corals. Fish were co-dominated by herbivorous, zooplanktivorous, and mobile benthic-feeding fish (Fig. 4). Production of macrophytes and phytoplankton contributed 86% and 6% to total production, respectively. Fish contributed only 0.4% to total production. Benthic invertebrates contributed 78% to total consumption and 76% to total respiration. Fish consumed only 9% of the available energy. Nevertheless, a large proportion of the macrophyte production was not used, and subsequently flowed into the detrital pool (Table 1).

3.3. Trophic structure

Trophic levels estimated by Ecopath from the weighted average of prey trophic levels varied from 1.00 for primary producers and detritus to 3.45 for piscivorous fish (Table 1). Net efficiencies of corals exceeded 1.0 because they are facultative consumers, capturing a part and photosynthesizing the other part of their food. The estimated EE of detritus was 0.20, indicating that more energy was entering the detrital pool than was leaving.

The Lindeman trophic analysis aggregated compartmental throughputs of the 18 compartments in a simple food chain with five integrated trophic levels (Fig. 5). The trophic transfer efficiency was 13.9% at trophic level II. The efficiency decreased at higher levels and was only 2% for trophic level V. The geometric mean of the trophic transfer efficiencies for the food chain from levels II to IV was 7.8%. The $D{:}H$ ratio was 1.4, which indicates that more energy was derived from detritus than from primary producers (Table 4). The cycle analysis showed that all cycled flows accounted for only 3.5% of the TST (FCI). The net primary production:respiration ratio ($P{:}R$) was 4.4, indicating that the fringing reefs of Nanwan Bay are autotrophic.

3.4. Mixed trophic impacts (MTIs)

The MTI analysis (Fig. 6) showed that a hypothetical increase in the macrophyte biomass would have a great positive effect on biomass values of fish and other benthic invertebrates, but would have negative effects on the biomass values of corals, which indicates that macrophytes are food sources for fish and other benthic invertebrates and that they competitively interact with corals. An increase in detritus would also have positive effects on many compartments, but negative effects on macrophytes and zooplankton. This is because detritus often accompanies macrophytes and zooplankton in the diets of many consumers. An increase in detritus would therefore stimulate these consumers to feed more on macrophytes and zooplankton. However, the large biomasses of macrophytes and detritus appeared to be little affected by changes in other compartments. An increase in the biomass of piscivorous fish and benthic omnivorous invertebrates would have negative effects on many other fish and benthic invertebrates, indicating that they were the most influential groups in the coral reefs. While gill netting and line fishing would have a moderate negative impact on piscivorous fish, free-diving for fish would have a negative impact on sessile benthic-feeding fish.

Table 3
Comparisons of living biomass (g wet weight m^{-2} yr^{-1}) of Nanwan Bay with other fringing coral reefs.

Community	High fishery catch			Low fishery catch				
	Nanwan Bay	Bolinao[a]	Mahahual[b]	PRVI[c]	Tiahura[d]	Boca Paila[b]	Tampalam[b]	Floreana Island[e]
Fish[**]	81.9	6.8	43.2	104.4	144.5	149.2	108.5	778.8
Phytoplankton	1.1	0.3	7.9	40.0	0.2	35.4	28.0	12.0
Macrophytes	945	1624	229	1300	4015	666	700	650
Zooplankton	2.6	2.9	6.0	32.0	1.5	38.4	19.7	6.8
Corals	396			121	15			170
Other invertebrates	605	261	45	1,449	358	125	155	985
Other consumers[*]		0.7	1.1	2.0	19.2	4.3	4.2	17.5
Total living biomass	2030	1896	332	3048	4554	1019	1015	2620

[*] 0.05 < P < 0.10.
[**] P < 0.05.
[a] Aliño et al. (1993).
[b] Arias-González et al. (2004).
[c] Opitz (1996).
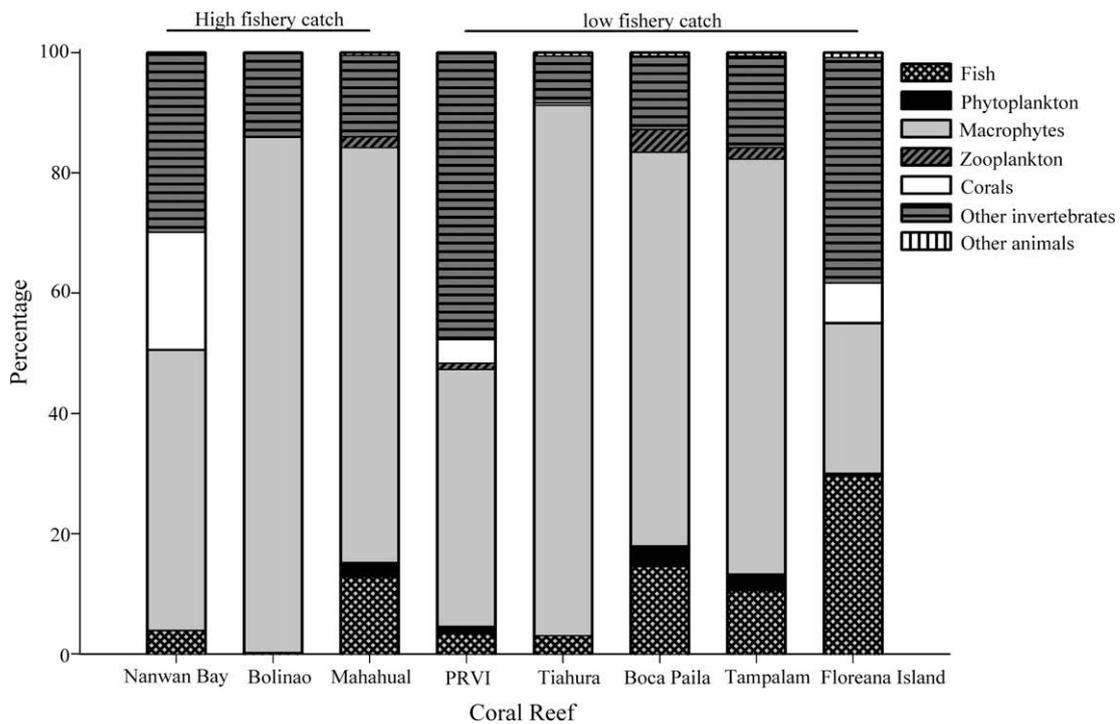[d] Arias-González et al. (1997).
[e] Okey (2004).

Fig. 3. Biomass fractions (%) of communities in the seven fringing reefs for comparison with the Nanwan Bay model.
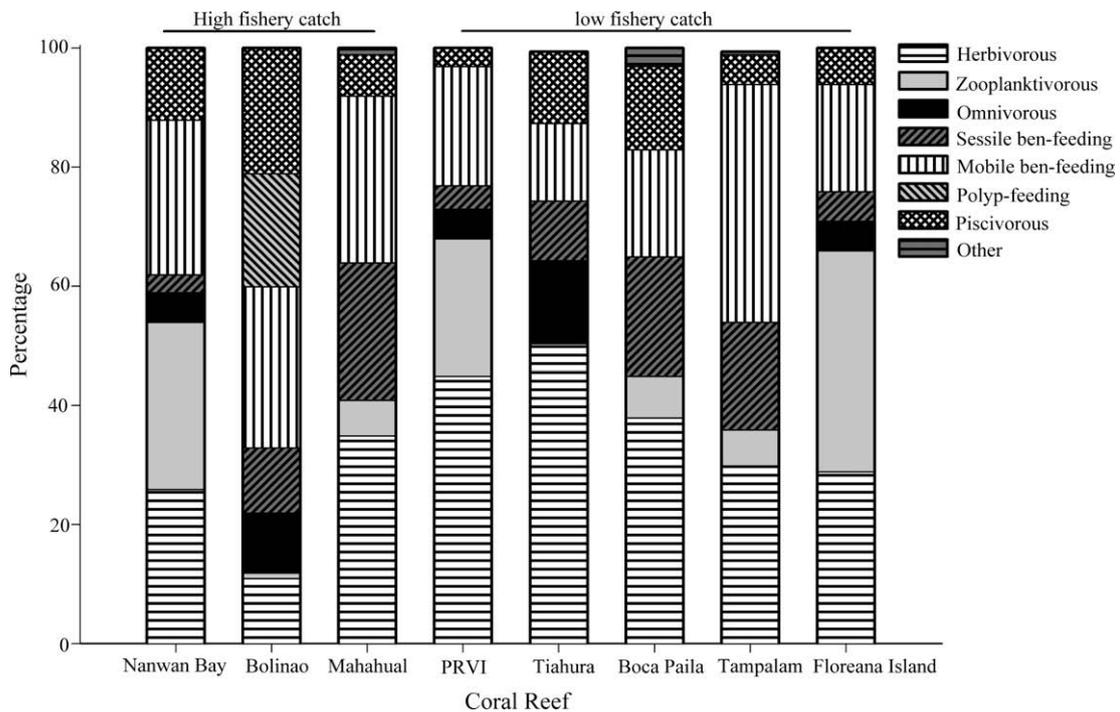

Fig. 4. Biomass fractions (%) of the fish community in the seven fringing reefs for comparison with the Nanwan Bay model.

3.5. Fishing indicators

The total catch of Nanwan Bay was 7.3 g WW m^{-2} yr^{-1}, and the mean trophic level of the catch was 2.4 (Table 4). The exploitation rates of sessile benthic-feeding, omnivorous, and herbivorous fish (0.30, 0.14, and 0.10, respectively) were higher than those of other consumers, but did not exceed 0.50 which indicates overexploitation. The fishing mortalities were also higher in omnivorous, sessile benthic-feeding, and herbivorous fish (0.25, 0.24, and 0.15,

respectively) than those of other consumers. The fishery catch accounted only for 1.2% of the primary production in the system (PPR%).

3.6. Comparisons with other coral reefs

Macrophytes were the most dominant groups in reefs with high fishery catches, but might not be in reefs with low fishery catches (Fig. 3). The total living biomass in Nanwan Bay was ranked as

Table 4
Comparisons of ecosystem attributes of Nanwan Bay with other fringing coral reefs.

Ecosystem attribute	High fishery catch			Low fishery catch				
	Nanwan Bay	Bolinao[a]	Mahahual[b]	PRVI[c]	Tiahura[d]	Boca Paila[b]	Tampalam[b]	Floreana Island[e]
Sum of all consumption*	8373		5433			20,496	18,347	51,600
Sum of all exports	16,200		920			3783	3376	−5412
Sum of all respiratory flows*	4629	18,965	3313	32,523		12,360	11,226	27,638
Sum of all flows into detritus	20,115	18,405	3503	23,193		11,397	12,253	21,024
Total system throughput (TST)*	49,317	39,307	13,169	107,473		48,037	45,202	94,850
Total net primary production (NPP)	20,199		4152	20,025	11,350	15,889	14,293	13,250
Sum of all production	21,553	1938	5267	51,282		20,180	18,053	17,337
Net system production	15,570		838			3529	3067	−14,388
Biomass:TST ratio (B:TST)	0.041	0.048	0.025	0.028		0.021	0.022	0.028
NPP:total respiration ratio (P:R)*	4.4		1.3	0.6	1.1	1.3	1.3	0.5
NPP:total biomass ratio (P:B)	9.9		12.5	6.6		15.6	14.1	5.1
Mean trophic level of the catch	2.4		3.3			3.5	3.5	2.3
Total catch**	7.3	13.1	10.0	0	0.68	1.3	2.5	4.2
FCI (% of TST)	3.5				18.3	58.0		
Detritivory:herbivory ratio (D:H)	1.4				10.4			0.7
Geometric mean of trophic transfer efficiency (II–IV)	7.8	10.4	15.4	12.9	8.8	13.4	13.5	

Biomasses are in g wet weight (WW) m^{-2} and flows are in g WW m^{-2} yr^{-1}.
* $P < 0.10$.
** $P < 0.05$.
[a] Aliño et al. (1993).
[b] Arias-González et al. (2004).
[c] Opitz (1996).
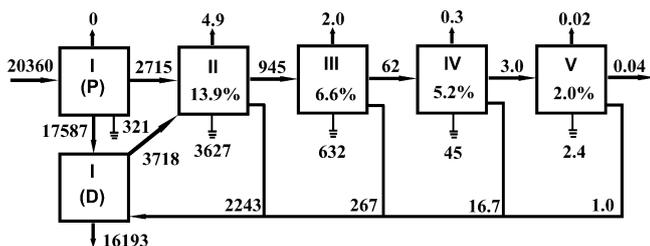[d] Arias-González et al. (1997).
[e] Okey (2004).

Fig. 5. Flow network of organic matter and trophic efficiencies (%) in Nanwan Bay. The flow (g wet weight (WW) m^{-2} yr^{-1}) web is aggregated into a concatenated chain of transfers through five integral trophic levels. Flows from primary producers (P), from detritus (D), and out of the tops of boxes represent export, while flows out of the bottoms represent respiration.

moderate compared to other fringing reefs (Table 3). Nanwan Bay had a greater biomass and a higher fraction of corals than did other reefs. However, the total fish biomass was lower than those of other fringing reefs with the exception of the Bolinao and Mahahual reefs with high fishery catches. Total fish biomass values in reefs with high fishery catches were significantly lower than those in reefs with low fishery catches (Mann–Whitney U-test, $P < 0.04$). The fraction of fish in Nanwan Bay was also low compared to those of other fringing reefs (Fig. 3). The fraction of herbivorous fish in the fish community of Nanwan Bay was lower than those of other reefs with the exception of the Bolinao reef (Fig. 4). However, the fraction of zooplanktivorous fish was higher than those of other reefs with the exception of Floreana Island.

Total catches in reefs with high fishery catches were significantly greater than those in reefs with low fishery catches (Table 4, Mann–Whitney U-test, $P < 0.04$). Consequently, sums of all consumption and respiratory flows and TST in the reefs with high fishery catches were marginally lower than those in reefs with low fishery catches (Mann–Whitney U-test, $0.05 < P < 0.10$). However, P:R ratios were marginally higher in reefs with high fishery catches than in reefs with low fishery catches (Mann–Whitney U-test, $P = 0.10$). The mean trophic level of the catch in Nanwan Bay was

lower than those of most other fringing reefs, although it was not significantly lower in reefs with high fishery catches due to the small replicate number. The FCI and geometric mean of the trophic transfer efficiency from trophic levels II–IV in Nanwan Bay were extremely low compared to those of other fringing reefs.

4. Discussion

The pedigree index of the Nanwan Bay model was 0.586, indicating a generally good quality of the input data for the model, given that >50% of inputs came from local, well-sampled high-precision data (Table 1). However, some input biomasses of small benthic invertebrates and cryptic coral reef organisms are difficult to directly measure in the field. They were estimated by Ecopath using the input values of P/B, Q/B, and EE. The P/B and Q/B values were derived from other coral reef models, and the EE value was assumed to be 0.95. Moreover, there are no published data on the diets of small benthic invertebrates in Nanwan Bay. The diet compositions were only roughly estimated and were derived from relevant literature sources and other coral reef models (Table 2). Sensitivity analysis revealed that a 30% reduction in the P/B or EE value of benthic invertebrates would increase their estimated biomass by 56%, and a 30% increase in the P/B or EE value would decrease their estimated biomass by 20%. Therefore, the estimated biomass of small benthic invertebrates may have been overestimated by the lower P/B and EE values, or have been underestimated by the higher P/B and EE values. Despite this, the calculated biomasses of small benthic invertebrates in Nanwan Bay by Ecopath were comparable to values reported from other fringing reefs (Table 3). If the uncertainty caused by the input values of P/B and EE are considered, the calculated biomasses of small benthic invertebrates in Nanwan Bay were still within the range reported for other fringing reefs. The mixed trophic impacts also revealed that changes in biomass of small benthic invertebrates would, in most cases, have minor impacts on other compartments in Nanwan Bay (Fig. 6). The results of this model should be viewed as an approximation of the interactions occurring within the fringing reefs of Nanwan Bay. Nevertheless, we feel that the major path-
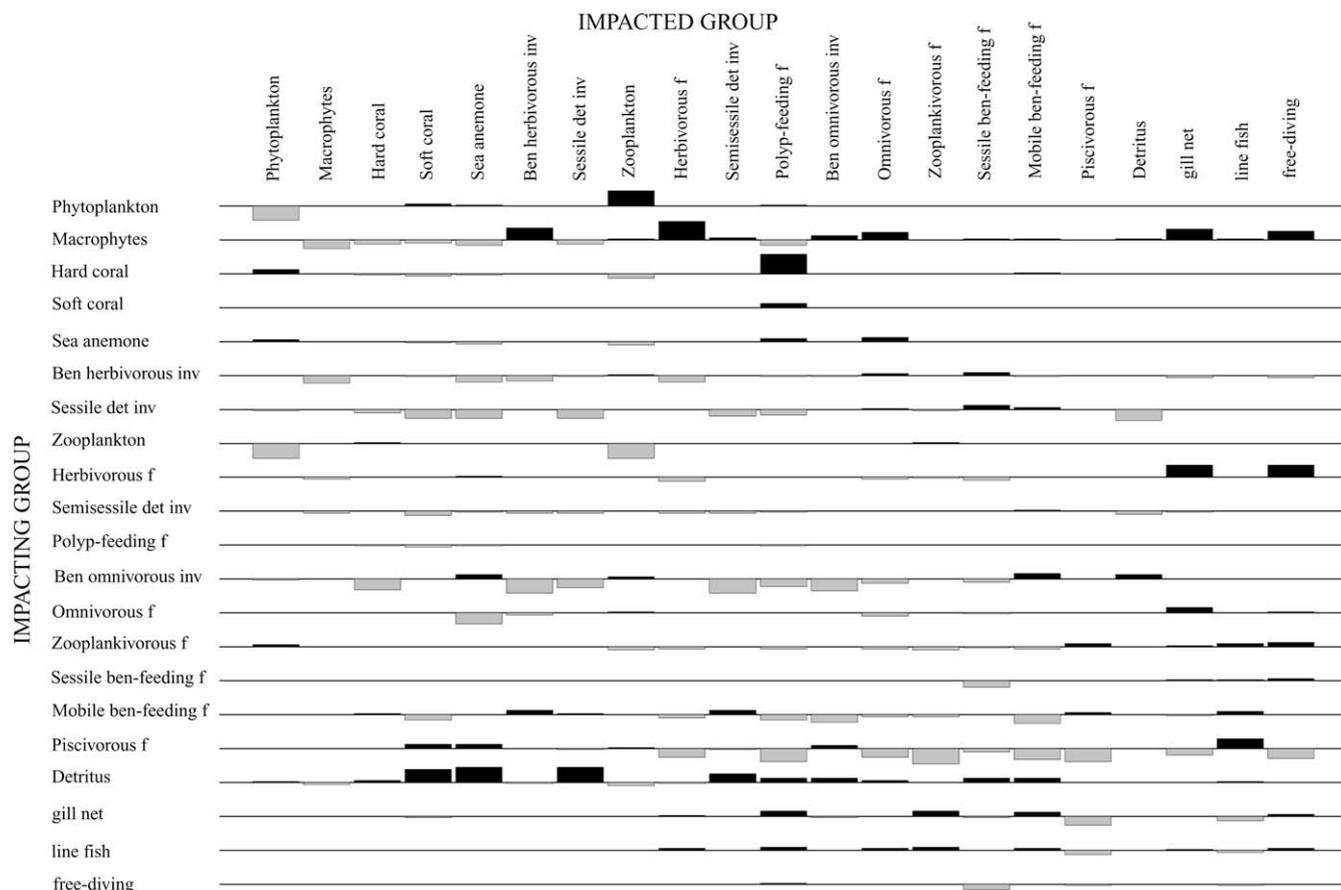
Fig. 6. Direct and indirect impacts that an increase in the biomass of the compartments on the left of the histograms would have on compartments positioned above them. Bars pointing upwards indicate positive impacts while those pointing downwards indicate negative impacts. Impacts are relative, not absolute, but are comparable between histograms. f, fish; ben, benthic; inv, invertebrates; det, detritivorous.

ways of the system are accurately depicted in the model and that an integrated picture of the fringing reef ecosystem was obtained compared to other fringing reef models. Further work is required to solve methodological problems of quantifying small benthic invertebrates and cryptic organisms and their diet compositions in coral reefs.

In this study, the fish survey was conducted mainly during the daytime, which may have underestimated some fish species which are active during the night time. Nevertheless, most fish in Nanwan Bay can be found during the daytime (Jan et al., 2001). This suggests that the underestimation of fish species and abundances caused by the visual census may have been small. Another problem may have been that there were no actual size measurements in the visual survey. Fish length was only roughly estimated. Therefore, the average biomass was primarily derived from Fishbase (Froese and Pauly, 2006). Although this method may have overestimated biomass values, the fish biomass in the Nanwan Bay model was still lower than those of other fringing reefs.

Comparisons with other coral reefs potentially suggest that coral reefs of Nanwan Bay are overfished. It was estimated that more than 72 tons of fish per year are caught for local seafood restaurants in the reefs for millions of tourists (Meng et al., 2004). Notably, the total catch in Nanwan Bay was comparable to those of reefs with high fishery catches (Table 4). The fish caught by free-diving and gill netting in the reefs are mostly herbivorous, benthic-feeding, and zooplanktivorous fish, such as parrotfish, surgeonfish, grunts, siganids, snapper, and butterfish (Cheng and Chen, 2004; Meng et al., 2004). The fish caught by line fishing are mostly piscivorous and benthic-feeding fish, such as scombrids, jack, and snap-

per (Meng et al., 2004). Consequently, the exploitation rates and fishing mortalities of sessile benthic-feeding, omnivorous, and herbivorous fish were higher than other compartments in the reefs. The total fish biomass in Nanwan Bay was also significantly lower than those in reefs with low fishery catches. Only small-sized (<25 cm) and low-economically valued fish such as gobbiids and damselfish are frequently observed on the fringing reefs (Shao and Jan, 2002). The dominance of relatively small-sized fish is often described as stage III (McManus et al., 2000) or Malthusian overfishing (Pauly, 1990).

The potentially overfished status of Nanwan Bay was also suggested by the lower fishery mean trophic level compared to those of most other fringing reefs, which is an example of "fishing down food webs" (Pauly et al., 1998). As a matter of fact, fishing activities have already largely been reduced in Nanwan Bay. Cheng and Chen (2004) reported that only a few less than 5 gross tons of fishing rafts were still engaging in gill netting in Nanwan Bay. These authors also indicated that the monthly operation time for a raft averaged only 4 days. Cheng and Chen (2004) found that the catch per unit effort (CPUE, the mass of fish caught in kilograms per fish per hour of fishing) and incomes per unit effort (IPUE, the equivalent amount of fish caught in United States dollars by each fisherman over an hour of fishing) in Nanwan Bay were only about 40 kg and US$110, respectively, from 1996 to 2003. Low CPUE and IPUE values are often associated with Malthusian over-fishing (McManus et al., 2000; Pauly, 1990). This may explain why exploitation rates of sessile benthic-feeding, omnivorous, and herbivorous fish were still less than 0.50 of overexploitation level. Likewise the fact that the fishery catch accounted for only 1.2% of the primary pro-

duction in the system may simply be due to the lack of fish. This suggests that the exploitation rate and PPR% might not clearly indicate a potentially overfished status in marine ecosystems.

Although macroalgal or sea anemone dominance occurred in fringing reefs of Nanwan Bay, the trophic model shows that the macroalgal or sea anemone biomass was not necessarily greater than those of other coral reefs. This suggests that the phase shift from coral to macroalgal or sea anemone dominance in Nanwan Bay did not occur by widespread replacement, but was a regional effect. Anthropogenic nutrient enrichment can stimulate the prolific growth of macroalgae in coral reefs (Lapointe, 1997) and has been considered among the most-serious threats due to, for example, sewage in Hawaii (Grigg, 1995). However, using δ^{15}N values of macroalgae on the coast of Nanwan Bay, Lin et al. (2007) found that the high rate of sewage effluents flowing into the bay underwent quick tidal mixing due to the daily cyclonic circulation, and there was little evidence that it ever reached coral reefs in the subtidal zone. This implies that anthropogenic N loading might not, in itself, be sufficient to have stimulated the transition from coral dominance to macroalgal or sea anemone dominance in Nanwan Bay. Other factors such as a lower herbivore density may also be a concern. Bellwood et al. (2004) identified three functional groups, including bioeroders, scrapers, and grazers, which are critical for resisting phase shifts from coral dominance to degraded systems in the face of disturbance. A mesocosm experiment simulating sewage input in Nanwan Bay coral reefs under a lower herbivorous condition also found that macroalgae and sea anemones had strong negative impacts on *Acropora* coral (Liu et al., 2009).

The relatively low fish biomass, especially herbivorous fish, in Nanwan Bay was found to affect not only the trophic structure (Fig. 3) but also the organic matter flows of the food web. The sums of all consumption and respiratory flows in Nanwan Bay were low, but the *P:R* ratio was high compared to those of other reefs (Table 4). Consequently, a large proportion of the macrophyte production was not used, and subsequently flowed into the detrital pool (Table 1). The estimated EE of detritus (0.20) further indicated that more energy was entering the detrital pool than was leaving. This may be the reason why the *D:H* ratio (1.4) of Nanwan Bay was >1.0, suggesting that the food web is more dependent on detritivory than on primary production. The high flow to detritus from macrophytes produced the extremely low cycling of organic matter (FCI) of Nanwan Bay compared to those of other fringing reefs. The FCI in Nanwan Bay was also low compared to those of Takapoto Atoll Lagoon (18, Niquil et al. 1999), Great Barrier Reef (26, Johnson et al., 1995) and other coastal systems around the world (7–44, Lin et al., 2001). The MTI analysis also showed that the large biomasses of macrophytes and detritus were little affected by changes in other compartments (Fig. 6). As a result, the low fraction of flows utilized by the fish community has resulted in an extremely low trophic efficiency (7.8%) in Nanwan Bay.

5. Conclusions

The Nanwan Bay model was similar to the Bolinao and Mahahual reefs with high fishery catches, showing low flows of total consumption, respiration, and TST, extremely low cycling matter and trophic transfer efficiency, but a high *P:R* ratio. The low fish biomass in the Nanwan Bay model suggests that reduced levels of herbivory, which would make the effects of low-level enrichment more severe, might be more important. Our findings suggest that the Kenting National Park Authority should prohibit fishing in the coral reefs of Nanwan Bay or create more marine protection areas to help restore the fish community.

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