



HAL
open science

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

Pi-Jen Liu, Kwang-Tsao Shao, Rong-Quen Jan, Tung-Yung Fan, Saou-Lien Wong, Jiang-Shiou Hwang, Jen-Ping Chen, Chung-Chi Chen, Hsing-Juh Lin

► **To cite this version:**

Pi-Jen Liu, Kwang-Tsao Shao, Rong-Quen Jan, Tung-Yung Fan, Saou-Lien Wong, et al.. A trophic model of fringing coral reefs in Nanwan Bay, southern Taiwan suggests overfishing. *Marine Environmental Research*, 2009, 68 (3), pp.106. 10.1016/j.marenvres.2009.04.009 . hal-00563078

HAL Id: hal-00563078

<https://hal.science/hal-00563078>

Submitted on 4 Feb 2011

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Accepted Manuscript

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

Pi-Jen Liu, Kwang-Tsao Shao, Rong-Quen Jan, Tung-Yung Fan, Saou-Lien Wong, Jiang-Shiou Hwang, Jen-Ping Chen, Chung-Chi Chen, Hsing-Juh Lin

PII: S0141-1136(09)00043-9
DOI: [10.1016/j.marenvres.2009.04.009](https://doi.org/10.1016/j.marenvres.2009.04.009)
Reference: MERE 3336

To appear in: *Marine Environmental Research*

Received Date: 28 June 2008
Revised Date: 16 April 2009
Accepted Date: 25 April 2009

Please cite this article as: Liu, P.-J., Shao, K.-T., Jan, R.-Q., Fan, T.-Y., Wong, S.-L., Hwang, J.-S., Chen, J.-P., Chen, C.-C., Lin, H.-J., A trophic model of fringing coral reefs in Nanwan Bay, southern Taiwan suggests overfishing, *Marine Environmental Research* (2009), doi: [10.1016/j.marenvres.2009.04.009](https://doi.org/10.1016/j.marenvres.2009.04.009)

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.



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

3
4
5
6
7
8 Pi-Jen Liu¹, Kwang-Tsao Shao², Rong-Quen Jan², Tung-Yung Fan³, Saou-Lien Wong⁴, Jiang-
9
10 Shiou Hwang⁵, Jen-Ping Chen⁴, Chung-Chi Chen⁶ and Hsing-Juh Lin^{1,7*}
11
12

13
14
15 ¹ Department of Life Sciences, National Chung Hsing University, Taichung 402, Taiwan
16

17 ² Research Center for Biodiversity, Academia Sinica, Taipei 115, Taiwan
18

19 ³ National Museum of Marine Biology and Aquarium, Pingtung 944, Taiwan
20

21 ⁴ Department of Aquaculture, National Pingtung University of Science and Technology,
22
23 Pingtung 912, Taiwan
24

25 ⁵ Institute of Marine Biology, National Taiwan Ocean University, Keelung 202, Taiwan
26

27 ⁶ Department of Life Sciences, National Taiwan Normal University, Taipei 106, Taiwan
28

29 ⁷ Institute of Marine Environmental Chemistry and Ecology, National Taiwan Ocean
30
31 University, Keelung 202, Taiwan
32
33

34
35
36
37
38
39 * Corresponding author. Tel.: +886 4 22840416; Fax: +886 4 22874740. E-mail:

40
41
42 hmlin@dragon.nchu.edu.tw (Hsing-Juh Lin)
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

19 **Abstract**

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

30 **Key words:** Ecopath, Network analysis, Food web, Phase shift, Macroalgae

31 1. Introduction

1
2 32 In the past few decades, increased human activities have caused serious damage to coral
3
4 33 reefs (Nystrom et al., 2000), many of which have lost their resilience and are in serious
5
6
7 34 decline worldwide (Bellwood et al., 2004). Fishing is the most widespread exploitative human
8
9
10 35 impact affecting coral reefs in tropical and subtropical waters (Jackson et al., 2001). The
11
12 36 direct effects of fishing are declines in organism abundance, and changes in population
13
14 37 structures and distributions of certain species. Additionally, indirect effects of fishing
15
16
17 38 activities may strongly affect biological interactions among reef organisms (Hughes, 1994).
18
19 39 Fishing may also lead to a decline in the mean trophic level of the catch as well as changing
20
21
22 40 marine food webs (Pauly et al., 1998).

23
24 41 Anthropogenic nutrient enrichment may stimulate the prolific growth of macroalgae in
25
26 42 coral reefs. This enrichment has been considered the major cause of the shift to macroalgae
27
28
29 43 (Grigg, 1995; Lapointe, 1997). However, McCook et al. (2001) argued that the widespread
30
31 44 replacement of corals by macroalgae might have resulted from coral mortality due to external
32
33
34 45 disturbances, for example, major bleaching or typhoons, rather than competitive overgrowth.
35
36 46 The combined effects of overfishing and nutrient enrichment have also been blamed for the
37
38
39 47 decline in coral reefs worldwide (Jackson et al., 2001). Overfishing, nutrient enrichment, and
40
41 48 other human activities may reduce the resilience of coral reefs and their capacity to recover
42
43
44 49 from short-term disturbances, such as typhoons and bleaching.

45
46 50 Most previously discussed studies focused on target species or communities, not on how
47
48
49 51 these activities affect biological interactions among reef communities or degradation of coral
50
51 52 reefs. A comprehensive study of trophic interactions among reef organisms based on
52
53
54 53 quantitative descriptions of organic matter flows of the food web can provide insights into an
55
56 54 ecosystem. The Ecopath model can demonstrate trophic food web structures, component
57
58 55 functioning, and interactions in aquatic ecosystems (Christensen et al., 2004). Comparative
59
60
61
62
63
64
65

1 56 studies of trophic flows have been used to provide significant insights into the structure and
2 57 functioning of estuaries (Baird and Ulanowicz, 1993) and tropical lagoons (Lin et al., 2006).
3
4 58 Some Ecopath models have been constructed for coral reefs, including the French Frigate
5
6 59 Shoals of Hawaii (Polovina, 1984); Bolinao in the Philippines (Aliño et al., 1993); Puerto
7
8 60 Rico and the Virgin Islands in the Caribbean (Opitz, 1996); Moorea in French Polynesia
9
10 61 (Arias-González et al., 1997); the Mexican Caribbean (Arias-González, 1998); the far
11
12 62 northern Great Barrier Reef (Gribble, 2003); Uvea of New Caledonia (Bozec et al., 2004); and
13
14 63 Floreana Island of the Galapagos (Okey, 2004). However, few comparisons between coral
15
16 64 reefs are possible due to problems of data availability and quality, aggregation methods,
17
18 65 compartmental numbers, and other limitations. Despite this, Arias-González et al. (1997)
19
20 66 compared the fringing and barrier reefs in Moorea, French Polynesia, and Arias-González
21
22 67 (1998) and Arias-González et al. (2004) compared different habitats between protected and
23
24 68 unprotected reefs in the Mexican Caribbean.

25
26 69 The coral reefs of Nanwan Bay (Fig. 1) were once well known for their abundant and
27
28 70 diverse communities (Dai, 1991). However, these reefs have also been threatened by human
29
30 71 disturbances. In the past two decades, blasting, poisoning, free-diving, and three-layer gill
31
32 72 nets were employed to catch fish. Other pressures come from coastline development,
33
34 73 sedimentation, tourism, and sewage discharges. Decreases in species numbers, colony
35
36 74 numbers, reef coverage, and species diversity of corals were observed at Tiaoshih from 1987
37
38 75 to 1997 (Dai et al., 1998). There were many branching *Acropora* patches at reefs of Tiaoshih
39
40 76 and the inlet of the Third Nuclear Power Plant which were replaced by an outbreak of sea
41
42 77 anemones *Condylactis nanwannensis* and *Mesactinia genesis* after 1996 (Chen and Dai, 2004).
43
44 78 The coverage of sea anemones had increased to 46.2% at Tiaoshih by 2004 (Tkachenko et al.,
45
46 79 2007). Some coral reefs in Nanwan Bay have undergone rapid increases in macroalgae. High
47
48 80 proportions (10%~55%) of the reef area were found to be occupied by macroalgae in 1992
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

81 (Dai, 1993). The green alga *Codium edule* was often reported to rapidly spread on the reefs
82 and forms dense meadows every year (Chiang and Wang, 1987; Dai, 1997). Other macroalgal
83 blooms were composed of opportunistic algae in the genera *Enteromorpha*, *Ulva*, *Gracilaria*,
84 *Laurencia*, and *Sargassum*. The objectives of this study were to characterize the trophic
85 structure and functioning of the coral reefs of Nanwan Bay as a whole and to reveal possible
86 causes for the phase shifts by constructing a trophic model of Nanwan Bay and then
87 comparing it to those of other fringing reefs around the world.

89 2. Materials and Methods

90 2.1. Study area

91 Nanwan Bay, in the central part of Kenting National Park, is located at the southern tip of
92 Taiwan (Fig. 1; 21°57'N, 120°44'E). It is a semi-enclosed embayment bounded by two capes,
93 with well-developed fringing reefs distributed along the shoreline. In this area, 230 species of
94 scleractinian corals, 9 species of non-scleractinian reef-building corals, and 40 species of
95 alcyonacean corals have been recorded (Dai, 1991). The study area of the Nanwan Bay model
96 consisted of fringing reefs which are shallower than 15 m in depth along the coast of the bay.
97 This area has a tropical climate, with distinct dry and wet seasons. The maximum average air
98 temperature of 31.7 °C occurs in July, and the minimum average of 17.8 °C occurs in January
99 (Central Weather Bureau, 1971-2000; <http://www.cwb.gov.tw/V5/index.htm>). In the wet
100 season from May to October, average monthly rainfall is 142~475 mm, when the
101 southwesterly monsoon winds and typhoons bring considerable quantities of rain. During the
102 dry season from November to April, when the northeasterly monsoon winds prevail, average
103 monthly rainfall normally does not exceed 45 mm.

104 Since no large river flows into the coastal waters, salinity in the water column remains
105 within a range of 32.6~34.7 (Lin and Shao, 1998). Chlorophyll *a* concentrations and the light

106 extinction coefficient (k) in the water column also remain low, ranging 0.14~0.29 mg m^{-3} and
 107 0.59~1.26 m^{-1} , respectively. Circulation along the coast is dominated by mixed diurnal and
 108 semidiurnal tides, which are modulated by a pronounced spring-neap cycle (Lee et al., 1999).
 109 In the western half of Nanwan Bay, there is daily periodic upwelling as the tidal currents ebb
 110 as a result of cyclonic eddy pumping, induced by the combined effects of tidal flow and
 111 topography (Lee et al., 1999). This tidally induced upwelling is strong during spring tides and
 112 causes sudden daily temperature drops often exceeding 10 °C. There is a nuclear power plant
 113 (the Third Nuclear Power Plant) on the coast of Nanwan Bay, on which construction began in
 114 1979 and operation started in 1984 before the establishment of Kenting National Park. Four
 115 coral reefs were selected as representative coral reefs in Nanwan Bay for collecting data:
 116 Leidashih, a soft coral-dominated reef; the inlet of the Nuclear Power Plant and Tiaoshih,
 117 which are sea anemone-dominated reefs; and Siangjiaowan, which is a hard coral-dominated
 118 reef.

119 2.2. Modeling approach

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

$$124 \quad P_i - B_i \cdot M2_i - P_i \cdot (1 - EE_i) - EX_i - AC_i = 0; \quad \text{Eq. 1}$$

125 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
 126 the ecotrophic efficiency of i (i.e., the part of the production that is passed up the trophic level,
 127 used for biomass accumulation or export), $1 - EE_i$ is "other mortality", EX_i is the portion of i
 128 exported to other systems through sedimentation or fishery activities, and AC_i is the
 129 accumulation of i during the study period.

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

$$132 \quad B_i \cdot (P_i/B_i) \cdot EE_i - \sum_j B_j \cdot (Q_j/B_j) \cdot DC_{ji} - EX_i - AC_i = 0; \quad \text{Eq. 2}$$

133 where P_i/B_i is the production: biomass ratio of i , Q_j/B_j is the consumption: biomass ratio of
 134 predator j , and DC_{ji} is the fraction of prey i in the average diet of predator j . It was assumed
 135 that the diet composition remained stable and no biomass accumulated during the study
 136 period from 2001 to 2003.

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

$$139 \quad \sum_j B_j \times (Q_j/B_j) = P_j + R_j + UN_j; \quad \text{Eq. 3}$$

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

142 Some of the parameters used to construct the model do not have to be entered since
 143 Ecopath links the production of each compartment with the consumption of all of the other
 144 compartments, and uses the linkages to estimate missing parameters. DC and EX must always
 145 be entered, while entry of one of any of the other four parameters (B, P/B, Q/B, and EE) is
 146 optional. For further details and algorithms of the Ecopath model see Christensen et al. (2004).

147 2.3. Model compartments and sampling

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

152 Phytoplankton biomass in terms of chlorophyll a concentration was determined
 153 spectrophotometrically by immediately filtering triplicate water samples through Whatman
 154 GF/F filters in the field and then extracting the filters in 90% acetone for 24 h at 4 °C in the

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

159 Macrophyte biomass, including macroalgae and the dominant seagrass, *Thalassia*
 160 *hemprichii*, was determined in the intertidal and subtidal zones at five study sites on the reef
 161 flats of Nanwan Bay. At each site, two to three replicate parallel transects separated by
 162 100~150 m and perpendicular to the shoreline were surveyed. The transect lengths extended
 163 to the outer limits of the reefs where macroalgae and *T. hemprichii* disappeared. All
 164 macroalgae and *T. hemprichii* in a 50 × 50-cm quadrat at 20-m intervals along each transect
 165 were collected for identification and biomass determination in terms of wet weight (WW).
 166 The primary production of macroalgae was determined by changes in dissolved oxygen
 167 concentrations in microcosm incubations of dominant species which were collected from each
 168 site. The leaf growth rate of *T. hemprichii* was studied in three random plots (10 × 10 cm each)
 169 at each site using a leaf marking method described by Lin and Shao (1998). Using these
 170 increments, production was expressed as leaf production per unit area of ground and unit time
 171 ($\text{g m}^{-2} \text{day}^{-1}$).

172 Zooplankton samples were collected by towing two NorPac nets (45 cm in diameter with
 173 100- and 330- μm mesh sizes, respectively) just below the sea surface. In the laboratory,
 174 samples were identified, and the density (individuals m^{-3}) was calculated. The dry biomass of
 175 zooplankton was estimated by the length-weight relationship of dominant species using the
 176 empirical equation of Chang and Lei (1993):

$$177 \quad \ln(\text{DW}) = 1.292 \times \ln(\text{TL}) - 3.504; \quad \text{Eq. 4}$$

178 where DW is the dry weight and TL is the total length (about 200 μm in this study). The dry
 179 weight was translated to wet weight by 1 g DW = 4.5 g WW (Opitz, 1996). The P/B and Q/B

180 of zooplankton were derived from values in the South China Sea model (Pauly and
181 Christensen, 1993).

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

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

205 The P/B value of hard corals was taken from the value for corals in the Caribbean coral
1 reef model (Opitz, 1996). However, the Q/B value of hard corals of the Caribbean model was
2 206 too high. Here, we estimated the Q/B value by assuming that 20% of the total production of
3 207 hard corals was derived from feeding on zooplankton and detritus, and the P/Q value of hard
4 208 corals was 0.20. The P/B value of soft corals was taken from the value for the living bottom
5 209 structure (LBS, including sponges, gorgonians, soft corals, sea pens, sea squirts, and sea
6 210 anemones) from a Hong Kong coral reef model (Pitcher et al., 2002). The Q/B value of soft
7 211 corals was taken from the value for the LBS in a Java Sea model (Buchary, 1999). The P/B
8 212 and Q/B values of sea anemones were taken from values of sea anemones in a Floreana Island
9 213 model (Okey, 2004).
10 214

24 215 Mollusca and crustacea in the intertidal and subtidal zones were the dominant benthic
25 216 macrofauna in Nanwan Bay. Two permanent 5×10 -m quadrats were selected bimonthly at
26 217 four stations on the reef flats of the bay. All samples were collected and carried to the
27 218 laboratory for identification and biomass determination in terms of $g\ WW\ m^{-2}$. However, the
28 219 biomass of other small benthic invertebrates was difficult to reliably quantify. Therefore,
29 220 benthic macrofauna were classified into four functional groups according to the 20-
30 221 compartment model of Opitz (1996), including benthic herbivorous invertebrates, sessile
31 222 detritivorous invertebrates, semi-sessile detritivorous invertebrates, and benthic omnivorous
32 223 invertebrates. Here, these biomass values were treated as unknowns and calculated by
33 224 Ecopath. The EE value of the benthic macrofauna was assumed to be 0.95, i.e., natural
34 225 predation consumed a large proportion of benthic macrofauna production (Ricker, 1969;
35 226 Polovina, 1984). No study was conducted to determine the P/B and Q/B values of benthic
36 227 macrofauna in Nanwan Bay, so values were taken from those for Puerto Rican and the Virgin
37 228 Islands coral reefs (Opitz, 1996).
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

229 Fish were surveyed during the daytime bimonthly at four stations in Nanwan Bay by
 1
 2 230 scuba diving (English et al., 1997). A visual census is one of the most common quantitative
 3
 4 231 and qualitative methods used in coral reef surveys and was developed by the Great Barrier
 5
 6
 7 232 Reef Marine Park Authority (1979). It is a rapid, non-destructive, and inexpensive method.
 8
 9 233 Two permanent 7 × 7-m quadrats were assessed at each station. Fish species, individual
 10
 11
 12 234 number, and total length estimations were recorded. In total, 309 fish species were identified
 13
 14 235 by the underwater visual census. Seven fish functional groups were classified according to the
 15
 16 236 diet and feeding habitat (Mitsuhiko et al. 1984; The Fish Database of Taiwan,
 17
 18
 19 237 <http://fishdb.sinica.edu.tw/>), including herbivorous fish (40 species), polyp-feeding fish (15
 20
 21 238 species), omnivorous fish (57 species), zooplanktivorous fish (41 species), sessile benthic-
 22
 23
 24 239 feeding fish (11 species), mobile benthic-feeding fish (131 species), and piscivorous fish (14
 25
 26 240 species). Fish biomass in terms of WW was calculated by the assumptions and empirical
 27
 28
 29 241 equation of Opitz (1996) as:

$$W_{\text{mean}} = W_{\infty} \times 0.3 \times 0.86; \quad \text{Eq. 5}$$

31 242
 32
 33
 34 243 where W_{mean} is the mean individual weight and W_{∞} is the asymptotic weight, which can be
 35
 36 244 found for each species in Fishbase (Froese and Pauly, 2006).
 37

38
 39 245 The P/B value for each fish species was estimated using the empirical equations of Pauly
 40
 41 246 (1980) as:

$$Z = M+F = P/B \quad \text{and} \quad \text{Eq. 6}$$

$$M = K^{0.65} \times L_{\infty}^{-0.279} \times T_c^{0.463}; \quad \text{Eq. 7}$$

42
 43
 44 247
 45
 46 248 where Z is total mortality, M is natural mortality, F is fishing mortality, K is the curvature
 47
 48 249 parameter of the von Bertalanffy growth function (VBGF), L_{∞} is the asymptotic length, and
 49
 50
 51 250 T_c is the mean water temperature (°C). K and L_{∞} can be found in Fishbase (Froese and Pauly,
 52
 53 251 2006).
 54
 55 252
 56
 57
 58
 59
 60
 61
 62
 63
 64
 65

253 The Q/B value of each fish species was estimated using the empirical equation of

254 Palomares and Pauly (1989, 1998):

$$255 \log(Q/B) = 5.847 + 0.280 \log(Z) - 0.152 \log(W_{\infty}) - 1.360 T' + 0.062 A + 0.510 h + 0.390 d;$$

256 Eq. 8

257 where W_{∞} is the asymptotic weight, T' is the water temperature (expressed as $1000/(T +$
 258 $273.15)$), A is the aspect ratio of the caudal fin, h is a dummy variable expressing food type (1
 259 for herbivores and 0 for detritivores and carnivores), and d is a dummy variable also
 260 expressing food type (1 for detritivores and 0 for herbivores and carnivores). In Nanwan Bay,
 261 a mean water temperature (T) of 28.5°C was used in these calculations. Biomass, P/B , and
 262 Q/B values of each fish functional group in Nanwan Bay were determined by the weighted
 263 average of the relative abundance of each species.

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

276 There are few published data on the diet of invertebrates and fish in Nanwan Bay.

277 Stomach contents of some fish and zooplankton in Nanwan Bay have been reported and were

278 used to construct the trophic model (Chen, 2007). The diet items of other compartments were
1
2 279 determined from Fishbase (Froese and Pauly, 2006) and for similar functional groups in the
3
4 280 literature from other coral reefs (Optiz, 1996; Arias-Gonzalez et al., 1997; Bozec et al., 2004).
5
6
7 281 The diet compositions were estimated based on the relative abundance of each prey item in
8
9 282 the coral reefs of Nanwan Bay (Table 2).
10

11
12 283 The unused consumption of herbivorous fish, benthic invertebrates, and zooplankton was
13
14 284 higher than that of other animals (Bozec et al., 2004). Therefore, unused consumption was
15
16 285 assumed to be 0.40 for herbivorous fish, benthic herbivorous invertebrates, and zooplankton,
17
18
19 286 0.30 for semi-sessile and sessile detritivorous invertebrates, and 0.25 for benthic omnivorous
20
21 287 invertebrates.
22
23

24 288 Factors used for conversion between chlorophyll *a*, carbon, displacement volume, dry
25
26 289 weight, and wet weight are summarized by Opitz (1996). Biomass data were recorded as g
27
28
29 290 WW m⁻², and flow data were recorded as g WW m⁻² yr⁻¹.
30

31 291 *2.4. Model balancing and verification*

32
33

34 292 Because Ecopath uses linkages of production of one compartment with consumption of
35
36 293 other compartments to calculate one missing parameter for each group, the most-questionable
37
38 294 parameter of each compartment can be treated as an unknown and calculated by Ecopath. In
39
40
41 295 this study, the biomass of each compartment and primary productivity were generally the
42
43 296 most-reliable data. The EE was treated as an unknown and calculated by Ecopath with the
44
45
46 297 exception of those of benthic macrofauna. Some P/B, Q/B, and DC values of small
47
48 298 invertebrates were assembled from the relevant literature (Table 1) and were considered to be
49
50
51 299 less reliable in the model. Therefore, they were gradually modified during the balancing
52
53 300 exercise. Most of the changes were small and remained within 20% of the input value.
54
55

56 301 The first step in verifying the realism of the Nanwan Bay model was to check whether the
57
58 302 EE was < 1.0 for all living compartments, since it was assumed that any living compartment
59
60
61
62
63
64
65

303 cannot be consumed in excess of its production. The second step was to check if the GE (the
 1
 2 304 gross food conversion efficiency, i.e., the ratio between production and consumption) was in
 3
 4 305 the range of 0.1~0.3, as the production of most groups is about 10%~30% of the consumption
 5
 6
 7 306 with the exception of corals and sea anemones with symbiotic algae, for which production
 8
 9 307 might exceed consumption (Christensen et al., 2004). In addition, the P/Q ratio cannot be
 10
 11
 12 308 higher than the net efficiency (the ratio between production and assimilated food). The final
 13
 14 309 step was to compare output values to relevant data from the literature on other coral reefs.

16
 17 310 The pedigree routine (Funtowicz and Ravetz, 1990) was used to determine an overall
 18
 19 311 index of model ‘quality’, based on the origin and quality of each input datum of the model.
 20
 21 312 The pedigree index varies from 1.0 for a high-quality model whose inputs are based on locally,
 22
 23
 24 313 well-sampled high-precision data to 0.0 for inputs that were estimated or taken from other
 25
 26 314 models in the literature.

29 315 The sensitivity routine (Majkowski, 1982) was used to check the effect each input
 30
 31 316 parameter had on all of the “estimated” parameters for each compartment in the Nanwan Bay
 32
 33 317 model by varying all basic input parameters in steps from -50% to +50%. The output is given
 34
 35
 36 318 as:

$$(39 \text{ 319 } \text{ (Estimated parameter - original parameter) / original parameter. } \quad \text{Eq. 9}$$

41 320 The mixed trophic impact (MTI), developed by Ulanowicz and Puccia (1990), was used
 42
 43 321 to assess the effects that changes in the biomass of a compartment would have on the biomass
 44
 45 322 of other compartments in Nanwan Bay. The MTI can be regarded as a form of sensitivity
 46
 47 323 analysis for the input parameters of the model. The MTI for living groups is calculated by
 48
 49
 50 324 constructing an $n \times n$ matrix, where the i,j^{th} element representing the interaction between the
 51
 52
 53 325 impacting group i and the impacted group j is

$$(56 \text{ 326 } \text{ MTI}_{i,j} = \text{DC}_{i,j} - \text{FC}_{j,i}, \quad \text{Eq. 10}$$

327 where $DC_{i,j}$ is the diet composition term expressing how much j contributes to the diet of i ,
328 and $FC_{j,i}$ is a host composition term giving the proportion of the predation on j that is due to i
329 as a predator.

330 2.5. Fishing indicator

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

339 2.6. Comparison with other coral reefs

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

352 model structure is useful for intersystem comparisons when species groups are given an
1
2 353 equivalent status. Fish biomass of other reefs was thus aggregated into eight functional groups
3
4
5 354 as was the Nanwan Bay model.
6

7 355 The total system throughput (TST) represents the size of an ecosystem in terms of flows
8
9 356 (Ulanowicz, 1986). It is the sum of consumption, exports, respiratory flows, and flows into
10
11
12 357 detritus and is indexed in terms of how much matter the system processes. The total biomass:
13
14 358 TST ratio (B: TST) represents the amount of biomass necessary to maintain one unit of flow.
15
16
17 359 It is expected to increase along with ecosystem maturity (Odum, 1969). The net primary
18
19 360 production: respiration ratio (P: R) and the net primary production: total biomass ratio (P: B)
20
21
22 361 were used to describe how mature Nanwan Bay is. The cycling of matter is considered to be
23
24 362 an important process in the functioning of natural ecosystems, as it can facilitate homeostatic
25
26
27 363 control over the magnitude of the flows (Odum, 1969). The Finn cycling index (FCI) of the
28
29 364 cycle analysis (Kay et al., 1989), the relative importance of cycling to the TST, was used to
30
31
32 365 measure how retentive Nanwan Bay is. The Lindeman trophic analysis (Kay et al., 1989)
33
34 366 summarizes complicated food webs in terms of a single linear food chain. The trophic transfer
35
36 367 efficiency from one aggregate trophic level to the next can be calculated as the fraction of the
37
38
39 368 input of organic matter to a given level that is transferred to the next higher level. The
40
41 369 detritivory: herbivory ratio (D: H) is a measure of the relative importance of detritivory flows
42
43
44 370 in a coral reef. A nonparametric Mann-Whitney *U*- test was then used to test differences in
45
46 371 network indices and ecosystem attributes between reefs with low and high fishery catches
47
48 372 using the SAS system (vers. 9.1.3).
49

50
51 373

52 53 374 **3. Results**

54
55
56
57
58
59
60
61
62
63
64
65

375 3.1. Model balancing and sensitivity analysis

1
2 376 The EE values of soft corals, zooplankton, and polyp-feeding, zooplanktivorous, sessile,
3
4
5 377 and mobile benthic-feeding fish all exceeded 1. The diets of their predator groups were then
6
7 378 adjusted to reduce predation pressure on the six groups. However, the zooplankton biomass
8
9 379 appeared insufficient for predation, so we assumed an external import of zooplankton from
10
11 380 offshore into the coral reefs during flood tides (Table 2). Imported food accounted for only
12
13 381 2% of the total consumption by cnidarians, sessile detritivorous and semi-sessile detritivorous
14
15 382 invertebrates, and zooplanktivorous fish. The P/Q values of herbivorous, zooplanktivorous,
16
17 383 mobile benthic-feeding, and piscivorous fish were too low (< 0.1), so the values were
18
19 384 increased by 10%~20% to balance the model. However, because the P/Q value of herbivorous
20
21 385 fish was still too low, we increased the P/B ratio by 50% and decreased the Q/B ratio by 50%
22
23 386 to balance the model, so that the P/Q ratio was in the range of 0.1~0.3. After modifying the
24
25 387 P/B and Q/B ratios of these groups, the diet matrix was also iteratively adjusted ($< 20\%$) in
26
27 388 order to maintain the EE of each group to < 1.0 during the balancing exercise.
28
29
30
31
32

33
34 389 Sensitivity analysis was performed on the input parameters of the Nanwan Bay model.
35
36 390 An increase of 30% in the biomass or P/B of a group would result in a decrease of about 23%
37
38 391 in its own estimated EE value, and an increase of about 14% in the EE values of its prey
39
40 392 groups. A 30% increase in Q/B would result in about a 14% increase in the estimated EE
41
42 393 values of its prey groups. Mobile benthic-feeding fish, piscivorous fish, and benthic
43
44 394 omnivorous invertebrates were the most influential groups in the model because the 30%
45
46 395 increase in Q/B often resulted in $> 20\%$ increases in the estimated EE values of their prey
47
48
49 396 groups.
50
51
52

53 3.2. Biomasses and trophic flows

54
55 398 The total living biomass of the Nanwan Bay model was $2030 \text{ g WW m}^{-2} \text{ yr}^{-1}$ (Table 3).
56
57
58 399 Macrophytes were the most dominant group and comprised 47% of the total biomass (Fig. 3).
59
60
61
62
63
64
65

400 Benthic invertebrates, cnidarians, fish, and plankton comprised the other 30%, 19%, 4%, and
401 0.2%, respectively. Benthic invertebrates were dominated by sessile detritivores, and
402 cnidarians were dominated by hard corals. Fish were co-dominated by herbivorous,
403 zooplanktivorous, and mobile benthic-feeding fish (Fig. 4). Production of macrophytes and
404 phytoplankton contributed 86% and 6% to total production, respectively. Fish contributed
405 only 0.4% to total production. Benthic invertebrates contributed 78% to total consumption
406 and 76% to total respiration. Fish consumed only 9% of the available energy. Nevertheless, a
407 large proportion of the macrophyte production was not used, and subsequently flowed into the
408 detrital pool (Table 1).

409 *3.3. Trophic structure*

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

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

424 3.4. Mixed trophic impacts (MTIs)

1
2 425 The MTI analysis (Fig. 6) showed that a hypothetical increase in the macrophyte biomass
3
4
5 426 would have a great positive effect on biomass values of fish and other benthic invertebrates,
6
7 427 but would have negative effects on the biomass values of corals, which indicates that
8
9 428 macrophytes are food sources for fish and other benthic invertebrates and that they
10
11 429 competitively interact with corals. An increase in detritus would also have positive effects on
12
13 430 many compartments, but negative effects on macrophytes and zooplankton. This is because
14
15 431 detritus often accompanies macrophytes and zooplankton in the diets of many consumers. An
16
17 432 increase in detritus would therefore stimulate these consumers to feed more on macrophytes
18
19 433 and zooplankton. However, the large biomasses of macrophytes and detritus appeared to be
20
21 434 little affected by changes in other compartments. An increase in the biomass of piscivorous
22
23 435 fish and benthic omnivorous invertebrates would have negative effects on many other fish and
24
25 436 benthic invertebrates, indicating that they were the most influential groups in the coral reefs.
26
27 437 While gill netting and line fishing would have a moderate negative impact on piscivorous fish,
28
29 438 free-diving for fish would have a negative impact on sessile benthic-feeding fish.
30
31
32
33
34
35

36 439 3.5. Fishing indicators

37
38 440 The total catch of Nanwan Bay was $7.3 \text{ g WW m}^{-2} \text{ yr}^{-1}$, and the mean trophic level of the
39
40 441 catch was 2.4 (Table 4). The exploitation rates of sessile benthic-feeding, omnivorous, and
41
42 442 herbivorous fish (0.30, 0.14, and 0.10, respectively) were higher than those of other
43
44 443 consumers, but did not exceed 0.50 which indicates overexploitation. The fishing mortalities
45
46 444 were also higher in omnivorous, sessile benthic-feeding, and herbivorous fish (0.25, 0.24, and
47
48 445 0.15, respectively) than those of other consumers. The fishery catch accounted only for 1.2%
49
50 446 of the primary production in the system (PPR%).
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

447 3.6. Comparisons with other coral reefs

1
2 448 Macrophytes were the most dominant groups in reefs with high fishery catches, but might
3
4
5 449 not be in reefs with low fishery catches (Fig. 3). The total living biomass in Nanwan Bay was
6
7 450 ranked as moderate compared to other fringing reefs (Table 3). Nanwan Bay had a greater
8
9 451 biomass and a higher fraction of corals than did other reefs. However, the total fish biomass
10
11 452 was lower than those of other fringing reefs with the exception of the Bolinao and Mahahual
12
13 453 reefs with high fishery catches. Total fish biomass values in reefs with high fishery catches
14
15 454 were significantly lower than those in reefs with low fishery catches (Mann-Whitney U -test, P
16
17 455 < 0.04). The fraction of fish in Nanwan Bay was also low compared to those of other fringing
18
19 456 reefs (Fig. 3). The fraction of herbivorous fish in the fish community of Nanwan Bay was
20
21 457 lower than those of other reefs with the exception of the Bolinao reef (Fig. 4). However, the
22
23 458 fraction of zooplanktivorous fish was higher than those of other reefs with the exception of
24
25 459 Floreana Island.

26
27 460 Total catches in reefs with high fishery catches were significantly greater than those in
28
29 461 reefs with low fishery catches (Table 4, Mann-Whitney U -test, $P < 0.04$). Consequently, sums
30
31 462 of all consumption and respiratory flows and TST in the reefs with high fishery catches were
32
33 463 marginally lower than those in reefs with low fishery catches (Mann-Whitney U -test, $0.05 < P$
34
35 464 < 0.10). However, P: R ratios were marginally higher in reefs with high fishery catches than
36
37 465 in reefs with low fishery catches (Mann-Whitney U -test, $P = 0.10$). The mean trophic level of
38
39 466 the catch in Nanwan Bay was lower than those of most other fringing reefs, although it was
40
41 467 not significantly lower in reefs with high fishery catches due to the small replicate number.
42
43
44 468 The FCI and geometric mean of the trophic transfer efficiency from trophic levels II to IV in
45
46 469 Nanwan Bay were extremely low compared to those of other fringing reefs.

47
48
49
50
51 470

52 471 4. Discussion

472 The pedigree index of the Nanwan Bay model was 0.586, indicating a generally good
1
2 473 quality of the input data for the model, given that > 50% of inputs came from local, well-
3
4 474 sampled high-precision data (Table 1). However, some input biomasses of small benthic
5
6
7 475 invertebrates and cryptic coral reef organisms are difficult to directly measure in the field.
8
9
10 476 They were estimated by Ecopath using the input values of P/B, Q/B, and EE. The P/B and
11
12 477 Q/B values were derived from other coral reef models, and the EE value was assumed to be
13
14 478 0.95. Moreover, there are no published data on the diets of small benthic invertebrates in
15
16
17 479 Nanwan Bay. The diet compositions were only roughly estimated and were derived from
18
19 480 relevant literature sources and other coral reef models (Table 2). Sensitivity analysis revealed
20
21
22 481 that a 30% reduction in the P/B or EE value of benthic invertebrates would increase their
23
24 482 estimated biomass by 56%, and a 30% increase in the P/B or EE value would decrease their
25
26 483 estimated biomass by 20%. Therefore, the estimated biomass of small benthic invertebrates
27
28
29 484 may have been overestimated by the lower P/B and EE values, or have been underestimated
30
31 485 by the higher P/B and EE values. Despite this, the calculated biomasses of small benthic
32
33
34 486 invertebrates in Nanwan Bay by Ecopath were comparable to values reported from other
35
36 487 fringing reefs (Table 3). If the uncertainty caused by the input values of P/B and EE are
37
38
39 488 considered, the calculated biomasses of small benthic invertebrates in Nanwan Bay were still
40
41 489 within the range reported for other fringing reefs. The mixed trophic impacts also revealed
42
43
44 490 that changes in biomass of small benthic invertebrates would, in most cases, have minor
45
46 491 impacts on other compartments in Nanwan Bay (Fig. 6). The results of this model should be
47
48
49 492 viewed as an approximation of the interactions occurring within the fringing reefs of Nanwan
50
51 493 Bay. Nevertheless, we feel that the major pathways of the system are accurately depicted in
52
53 494 the model and that an integrated picture of the fringing reef ecosystem was obtained
54
55
56 495 compared to other fringing reef models. Further work is required to solve methodological
57
58
59
60
61
62
63
64
65

496 problems of quantifying small benthic invertebrates and cryptic organisms and their diet
1
2 497 compositions in coral reefs.
3

4
5 498 In this study, the fish survey was conducted mainly during the daytime, which may have
6
7 499 underestimated some fish species which are active during the night time. Nevertheless, most
8
9 500 fish in Nanwan Bay can be found during the daytime (Jan et al., 2001). This suggests that the
10
11 501 underestimation of fish species and abundances caused by the visual census may have been
12
13 502 small. Another problem may have been that there were no actual size measurements in the
14
15 503 visual survey. Fish length was only roughly estimated. Therefore, the average biomass was
16
17 504 primarily derived from Fishbase (Froese and Pauly, 2006). Although this method may have
18
19 505 overestimated biomass values, the fish biomass in the Nanwan Bay model was still lower than
20
21 506 those of other fringing reefs.
22
23

24
25
26 507 Comparisons with other coral reefs potentially suggest that coral reefs of Nanwan Bay are
27
28 508 overfished. It was estimated that more than 72 tons of fish per year are caught for local
29
30 509 seafood restaurants in the reefs for millions of tourists (Meng et al., 2004). Notably, the total
31
32 510 catch in Nanwan Bay was comparable to those of reefs with high fishery catches (Table 4).
33
34 511 The fish caught by free-diving and gill netting in the reefs are mostly herbivorous, benthic-
35
36 512 feeding, and zooplanktivorous fish, such as parrotfish, surgeonfish, grunts, siganids, snapper,
37
38 513 and butterfish (Cheng and Chen, 2004; Meng et al., 2004). The fish caught by line fishing are
39
40 514 mostly piscivorous and benthic-feeding fish, such as scombrids, jack, and snapper (Meng et
41
42 515 al., 2004). Consequently, the exploitation rates and fishing mortalities of sessile benthic-
43
44 516 feeding, omnivorous, and herbivorous fish were higher than other compartments in the reefs.
45
46
47
48
49 517 The total fish biomass in Nanwan Bay was also significantly lower than those in reefs with
50
51 518 low fishery catches. Only small-sized (< 25 cm) and low-economically valued fish such as
52
53 519 gobiids and damselfish are frequently observed on the fringing reefs (Shao and Jan, 2002).
54
55
56
57
58
59
60
61
62
63
64
65

520 The dominance of relatively small-sized fish is often described as stage III (McManus et al.,
1
2 521 2000) or Malthusian overfishing (Pauly, 1990).
3

4 522 The potentially overfished status of Nanwan Bay was also suggested by the lower fishery
5
6
7 523 mean trophic level compared to those of most other fringing reefs, which is an example of
8
9 524 “fishing down food webs” (Pauly et al., 1998). As a matter of fact, fishing activities have
10
11 525 already largely been reduced in Nanwan Bay. Cheng and Chen (2004) reported that only a
12
13 526 few less than 5 gross tons of fishing rafts were still engaging in gill netting in Nanwan Bay.
14
15 527 These authors also indicated that the monthly operation time for a raft averaged only 4 days.
16
17 528 Cheng and Chen (2004) found that the catch per unit effort (CPUE, the mass of fish caught in
18
19 529 kilograms per fish per hour of fishing) and incomes per unit effort (IPUE, the equivalent
20
21 530 amount of fish caught in United States dollars by each fisherman over an hour of fishing) in
22
23 531 Nanwan Bay were only about 40 kg and US\$110, respectively from 1996 to 2003. Low
24
25 532 CPUE and IPUE values are often associated with Malthusian over-fishing (McManus et al.,
26
27 533 2000; Pauly, 1990). This may explain why exploitation rates of sessile benthic-feeding,
28
29 534 omnivorous, and herbivorous fish were still less than 0.50 of overexploitation level. Likewise
30
31 535 the fact that the fishery catch accounted for only 1.2% of the primary production in the system
32
33 536 may simply be due to the lack of fish. This suggests that the exploitation rate and PPR%
34
35 537 might not clearly indicate a potentially overfished status in marine ecosystems.
36
37
38
39
40
41
42

43 538 Although macroalgal or sea anemone dominance occurred in fringing reefs of Nanwan
44
45 539 Bay, the trophic model shows that the macroalgal or sea anemone biomass was not
46
47 540 necessarily greater than those of other coral reefs. This suggests that the phase shift from coral
48
49 541 to macroalgal or sea anemone dominance in Nanwan Bay did not occur by widespread
50
51 542 replacement, but was a regional effect. Anthropogenic nutrient enrichment can stimulate the
52
53 543 prolific growth of macroalgae in coral reefs (Lapointe, 1997) and has been considered among
54
55 544 the most-serious threats due to, for example, sewage in Hawaii (Grigg, 1995). However, using
56
57
58
59
60
61
62
63
64
65

545 $\delta^{15}\text{N}$ values of macroalgae on the coast of Nanwan Bay, Lin et al. (2007) found that the high
1
2 546 rate of sewage effluents flowing into the bay underwent quick tidal mixing due to the daily
3
4
5 547 cyclonic circulation, and there was little evidence that it ever reached coral reefs in the
6
7 548 subtidal zone. This implies that anthropogenic N loading might not, in itself, be sufficient to
8
9
10 549 have stimulated the transition from coral dominance to macroalgal or sea anemone dominance
11
12 550 in Nanwan Bay. Other factors such as a lower herbivore density may also be a concern.
13
14 551 Bellwood et al. (2004) identified three functional groups, including bioeroders, scrapers, and
15
16
17 552 grazers, which are critical for resisting phase shifts from coral dominance to degraded systems
18
19 553 in the face of disturbance. A mesocosm experiment simulating sewage input in Nanwan Bay
20
21
22 554 coral reefs under a lower herbivorous condition also found that macroalgae and sea anemones
23
24 555 had strong negative impacts on *Acropora* coral (Liu et al., 2009).

26 556 The relatively low fish biomass, especially herbivorous fish, in Nanwan Bay was found to
27
28
29 557 affect not only the trophic structure (Fig. 3) but also the organic matter flows of the food web.
30
31
32 558 The sums of all consumption and respiratory flows in Nanwan Bay were low, but the P: R
33
34 559 ratio was high compared to those of other reefs (Table 4). Consequently, a large proportion of
35
36 560 the macrophyte production was not used, and subsequently flowed into the detrital pool
37
38
39 561 (Table 1). The estimated EE of detritus (0.20) further indicated that more energy was entering
40
41 562 the detrital pool than was leaving. This may be the reason why the D:H ratio (1.4) of Nanwan
42
43
44 563 Bay was > 1.0 , suggesting that the food web is more dependent on detritivory than on primary
45
46 564 production. The high flow to detritus from macrophytes produced the extremely low cycling
47
48
49 565 of organic matter (FCI) of Nanwan Bay compared to those of other fringing reefs. The FCI in
50
51 566 Nanwan Bay was also low compared to those of Takapoto Atoll Lagoon (18, Niquil et al.
52
53 567 1999), Great Barrier Reef (26, Johnson et al., 1995) and other coastal systems around the
54
55
56 568 world (7~44, Lin et al., 2001). The MTI analysis also showed that the large biomasses of
57
58 569 macrophytes and detritus were little affected by changes in other compartments (Fig. 6). As a
59
60
61
62
63
64
65

570 result, the low fraction of flows utilized by the fish community has resulted in an extremely
1
2 571 low trophic efficiency (7.8%) in Nanwan Bay.

3
4
5 572

6 7 573 **5. Conclusions**

8
9 574 The Nanwan Bay model was similar to the Bolinao and Mahahual reefs with high fishery
10
11 575 catches, showing low flows of total consumption, respiration, and TST, extremely low cycling
12
13 576 matter and trophic transfer efficiency, but a high P:R ratio. The low fish biomass in the
14
15 577 Nanwan Bay model suggests that reduced levels of herbivory, which would make the effects
16
17 578 of low-level enrichment more severe, might be more important. Our findings suggest that the
18
19 579 Kenting National Park Authority should prohibit fishing in the coral reefs of Nanwan Bay or
20
21 580 create more marine protection areas to help restore the fish community.
22
23
24
25

26 581

27 28 29 582 **Acknowledgments**

30
31 583 This study was financially supported by the National Science Council of Taiwan and
32
33 584 Kenting National Park. We gratefully acknowledge Dr. Villy Christensen of the Fisheries
34
35 585 Centre, University of British Columbia, Canada, for fruitful discussions. Comments by two
36
37 586 anonymous reviewers were helpful in revising the manuscript.
38
39
40

41 587

42 43 588 **References**

44
45 589 Aliño P.M., McManus L.T., McManus J.W., Nañola C.L. Jr, Fortes M.D., Trono G.C. Jr,
46
47 590 Jacinto G.S., 1993. Initial parameter estimations of a coral reef flat ecosystem in Bolinao,
48
49 591 Pangasinan, northwestern Philippines, in: Christensen V., Pauly D. (Eds.), Trophic models
50
51 592 in aquatic ecosystems. ICLARM Conference Proceedings 26, 252-258.
52
53 593 Arias-González J.E., 1998. Trophic models of semi-protected and unprotected coral reef
54
55 594 ecosystems in the South of the Mexican Caribbean. Journal of Fish Biology 53, 236-255.
56
57
58
59
60
61
62
63
64
65

- 595 Arias-González J.E., Delesalle B., Salvat B., Galzin R., 1997. Trophic functioning of the
1 Tiahura reef sector, Moorea Island, French Polynesia. *Coral Reefs* 16, 231-246.
- 2 596
- 3
- 4 597 Arias-González J.E., Nuñez-Lara E., González-Salas C., Galzin R., 2004. Trophic models for
5 investigation of fishing effect on coral reef ecosystems. *Ecological Modelling* 172, 197-
6 212.
- 7 598
- 8
- 9 599
- 10
- 11 600 Baird D., Ulanowicz R.E., 1993. Comparative study on the trophic structure, cycling and
12 ecosystem properties of four tidal estuaries. *Marine Ecology Progress Series* 99, 221-237.
- 13 601
- 14 602 Bellwood D.R., Hughes T.P., Folke C., Nyström M., 2004. Confronting the coral reef crisis.
15 *Nature* 429, 827-833.
- 16 603
- 17 604 Bozec Y.M., Gascuel D., Kulbicki M., 2004. Trophic model of lagoonal communities in a
18 large open atoll (Uvea, Loyalty islands, New Caledonia). *Aquatic Living Resources* 17,
19 151-162.
- 20 605
- 21 606
- 22 607 Buchary E.A., 1999. Evaluating the effects of the 1980 trawl ban in the Java Sea, Indonesia:
23 an ecosystem-based approach. M.Sc. thesis, Department of Resource Management and
24 Environment Studies, University of British Columbia.
- 25 608
- 26 609
- 27 610 Chang W.B., Lei C.H., 1993. The development and energy content of a brackish-water
28 copepod, *Apocyclops royi* (Lindberg), reared in the laboratory. *Bulletin of the Institute of*
29 *Zoology Academia Sinica (Taipei)* 32, 62-81.
- 30 611
- 31 612
- 32 613 Chen C.A., Dai C.F., 2004. Local phase shift from *Acropora*-dominant to *Condylactis*-
33 dominant community in the Tiao-Shi Reef, Kenting National Park, southern Taiwan. *Coral*
34 *Reefs* 23, 508.
- 35 614
- 36 615
- 37 616 Chen Y.T., 2007. Feeding ecology and mouthpart morphology of three copepods, *Temora*
38 *turbinata*, *Farranula gibbula* and *Cosmocalanus darwinii*. Unpublished M.Sc. thesis,
39 Institute of Marine Biology, National Taiwan Ocean University (in Chinese).
- 40 617
- 41 618
- 42
- 43
- 44
- 45
- 46
- 47
- 48
- 49
- 50
- 51
- 52
- 53
- 54
- 55
- 56
- 57
- 58
- 59
- 60
- 61
- 62
- 63
- 64
- 65

- 619 Cheng L.Z., Chen C.T.A., 2004. Feature of the fishing ground near the third nuclear power
1
2 620 plant in Taiwan. *Journal of Marine Science Technology* 12, 453-456.
3
- 4 621 Chen C.C., Shiah F.K., Lee H.J., Li K.Y., Meng P.J., Kao S.J., Tseng Y.F., Chung C.L., 2005.
5
6 622 Phytoplankton and bacterioplankton biomass, production and turnover in a semi-enclosed
7
8 623 embayment with spring tide induced upwelling. *Marine Ecology Progress Series* 304, 91-
9
10 624 100.
11
- 12 625 Chiang Y.M., Wang W.L., 1987. Distribution of seaweeds of Hengchun Peninsula, Taiwan, in:
13
14 626 Chang K.H. (Ed.), *Marine Science. National Science Council Symposium Series*, 10,
15
16 627 National Sun Yat-sen University, Kaohsiung, pp. 71-87 (in Chinese).
17
18
- 19 628 Christensen V., Walters C.J., Pauly D., 2004. *Ecopath with Ecosim: a user's guide*. University
20
21 629 of British Columbia, Fisheries Centre, Vancouver.
22
23
- 24 630 Christian R.R., Baird D., Luczkovich J., Johnson J.C., Scharler U.M., Ulanowicz R.E., 2005.
25
26 631 Role of network analysis in comparative ecosystem ecology of estuaries, in: Belgrano A.,
27
28 632 Scharler U.M., Dunne J., Ulanowicz R.E. (Eds.), *Aquatic food webs*. Oxford University
29
30 633 Press, Oxford, pp. 25-40.
31
32
- 33 634 Dai C.F., 1991. Reef environment and coral fauna of southern Taiwan. *Atoll Research*
34
35 635 *Bulletin* 354, 1-28.
36
- 37 636 Dai C.F., 1993. Pattern of coral distribution and benthic space partitioning on the fringing
38
39 637 reefs of southern Taiwan. *Marine Ecology* 42, 185-204.
40
- 41 638 Dai C.F., 1997. Assessment of the present health of coral reefs in Taiwan, in: Grigg R.W.,
42
43 639 Birkeland C. (Eds.), *Status of Coral Reefs in the Pacific*. Sea Grant Program, University of
44
45 640 Hawaii, pp. 123-131.
46
- 47 641 Dai C.F., Kao K.M., Chen Y.T., Chaun S.T., 1998. Changes of coral communities in the Nan-
48
49 642 wan Bay, Kenting National Park from 1987 to 1997. *Journal of National Park* 8, 79-99 (in
50
51 643 Chinese).
52
53
54
55
56
57
58
59
60
61
62
63
64
65

- 644 English S., Wilkinson C., Baker V., 1997. Survey manual for tropical marine resources. 2nd
1
2 645 edition. Australian Institute of Marine Science, Townsville, Australia.
3
4
5 646 Field J.G., Wulff F., Mann K.H., 1989. The need to analyze ecological networks, in: Wulff F.,
6
7 647 Field J.G., Mann K.H. (Eds.), Network analysis in marine ecology: methods and
8
9 648 applications. Springer-Verlag, New York, pp. 3-12.
10
11
12 649 Froese R., Pauly D. (Eds.), 2006. Fishbase. World Wide Web electronic publication.
13
14 650 (<http://www.fishbase.org>).
15
16
17 651 Funtowicz S.O., Ravetz J.R., 1990. Uncertainty and Quality in Science for Policy. Kluwer,
18
19 652 Dordrecht.
20
21
22 653 Great Barrier Reef Marine Park Authority, 1979. Workshop on coral trout assessment
23
24 654 techniques. GBRMPA workshop series 3, Great Barrier Reef Marine Park Authority,
25
26 655 Townsville Australia.
27
28
29 656 Gribble N.A., 2003. GBR-prawn: modelling ecosystem impacts of changes in fisheries
30
31 657 management of the commercial prawn trawl fishery in the far northern Great Barrier Reef.
32
33
34 658 Fisheries Research 65, 493-506.
35
36 659 Grigg R.W., 1995. Coral reefs in an urban embayment in Hawaii: a complex case history
37
38 660 controlled by natural and anthropogenic stress. Coral Reefs 14, 253-266.
39
40
41 661 Hughes T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean
42
43 662 coral reef. Science 265, 1547-1551.
44
45
46 663 Jackson B.C., Kirby M.X., Berger W.H., Bjorndal K.A., Botsford L.W., Bourque B.J.,
47
48 664 Bradbury R.H., Cooke R., Erlandson J., Estes J.A., Hughes T.P., Kidwell S., Lange C.B.,
49
50
51 665 Lenihan H.S., Pandolfi J.M., Peterson C.H., Steneck R.S., Tegner M.J., Warner R.R.,
52
53 666 2001. Historical overfishing and the recent collapse of coastal ecosystem. Science 293,
54
55 667 629-638.
56
57
58 668 Jan R.Q., Chen J.P., Lin C.Y., Shao K.T., 2001. Long-term monitoring of the coral reef fish
59
60
61
62
63
64
65

- 669 communities around a nuclear power plant. *Aquatic Ecology* 35, 233-243.
- 670 Johnson C., Klumpp D., Field J., Bradbury R., 1995. Carbon flux on coral reefs: effects of
671 large shifts in community structure. *Marine Ecology Progress Series* 126, 123-143.
- 672 Kay J.J., Graham L.A., Ulanowicz R.E., 1989. A detailed guide to network analysis, in: Wulff
673 F., Field J.G., Mann K.H. (Eds.), *Network analysis in marine ecology: methods and
674 applications*. Springer-Verlag, New York, pp. 15-61.
- 675 Lapointe B.E., 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral
676 reefs in Jamaica and southeast Florida. *Limnology and Oceanography* 42, 1119-1131.
- 677 Lee H.J., Chao S.Y., Fan K.L., 1999. Flood-ebb disparity of tidally induced recirculation
678 eddies in a semi-enclosed basin: Nan Wan Bay. *Continental Shelf Research* 19, 871-890.
- 679 Lin H.J., Shao K.T., 1998. Temporal changes in the abundance and growth of intertidal
680 *Thalassia hemprichii* seagrass beds in southern Taiwan. *Botanical Bulletin of Academia
681 Sinica* 39, 191-198.
- 682 Lin H.J., Hung J.J., Shao K.T., Kou F., 2001. Trophic functioning and nutrient flux in a
683 highly productive tropical lagoon. *Oecologia* 129, 395-406.
- 684 Lin H.J., Dai X.X., Shao K.T., Su H.M., Lo W.T., Hsieh H.L., Fang L.S., Hung J.J., 2006.
685 Trophic structure and functioning in a eutrophic and poorly flushed lagoon in southwestern
686 Taiwan. *Marine Environmental Research* 62, 61-82.
- 687 Lin H.J., Wu C.Y., Kao S.J., Kao W.Y., Meng P.J., 2007. Mapping anthropogenic nitrogen
688 through point sources in coral reefs using $\delta^{15}\text{N}$ in macroalgae. *Marine Ecology Progress
689 Series* 335, 95-109.
- 690 Liu P.J., Lin S.M., Fan T.Y., Meng P.J., Shao K.T., Lin H.J., 2009. Rates of overgrowth by
691 macroalgae and attack by sea anemones are greater for live coral than dead coral under
692 conditions of nutrient enrichment. *Limnology and Oceanography*, in press.

- 693 Majkowski J., 1982. Usefulness and applicability of sensitivity analysis in a multispecies
1
2 694 approach to fisheries management, in: Pauly D., Murphy G.I. (Eds.), Theory and
3
4 695 management of tropical fisheries. ICLARM Conference Proceedings 9, 149-165.
5
6
7 696 McCook L.J., Jompa J., Diaz-Pulido G., 2001. Competition between corals and algae on coral
8
9 697 reefs: a review of evidence and mechanisms. *Coral Reefs* 19, 400-417.
10
11
12 698 McManus J.W., Meñez L.A.B., Reyes K.N.K., Vergara S.G., Ablan M.C., 2000. Coral reef
13
14 699 fishing and coral-algal phase shifts: implications for global reef status. *ICES Journal of*
15
16 700 *Marine Science* 57, 572-578.
17
18
19 701 Meng P.J., Chen J.P., Chung K.N., Liu M.C., Fan T.Y., Chang C.M., Tian W.M., Chang Y.C.,
20
21 702 Lin H.J., Fang L.S., Shao K.T., 2004. Long-term ecological studies in Kenting National
22
23 703 Park neighboring marine areas, on monitoring the impact factors from anthropogenic
24
25 704 activities to the marine ecosystem and a preliminary database of its marine ecosystem.
26
27 705 *Journal of National Park* 14:43-69 (in Chinese).
28
29
30
31 706 Mitsuhiro S., Makoto S., Yukio N., 1984. Food habits of teleostean reef fishes in Okinawa
32
33 707 Island, southern Japan. The University Museum, University of Tokyo, Bulletin 25.
34
35
36 708 Moloney C., Jarre A., Arancibia H., Bozec Y.M., Neira, S., Roux J.P., Shannon, L.J., 2005.
37
38 709 Comparing the Benguela and Humboldt marine upwelling ecosystems with indicators
39
40 710 derived from inter-calibrated models. *ICES Journal of Marine Science* 62, 493-502.
41
42
43 711 Niquil N., Arias-Gonzalez J.E., Delesalle B., Ulanowicz R.E., 1999. Characterization of the
44
45 712 planktonic food web of Takapoto Atoll lagoon, using network analysis. *Oecologia*
46
47 713 118:232-24.
48
49
50
51 714 Nystrom M., Folke C., Moberg F., 2000. Coral reef disturbance and resilience in a human-
52
53 715 dominated environment. *Trends in Ecology and Evolution* 15, 413-417.
54
55
56 716 Odum E.P., 1969. The strategy of ecosystem development. *Science* 104, 262-270.
57
58
59
60
61
62
63
64
65

- 717 Okey T.A., 2004. Shifted community states in four marine ecosystems: some potential
1
2 718 mechanisms. Ph.D. thesis, University of British Columbia.
3
- 4 719 Opitz S., 1996. Trophic interactions in Caribbean coral reefs. ICLARM Technical Report 43.
5
6
- 7 720 Palomares M.L.D., Pauly D., 1989. A multiple regression model for predicting the food
8
9 721 consumption of marine fish populations. Australian Journal of Marine and Freshwater
10
11 722 Research 40, 259-273.
12
13
- 14 723 Palomares M.L.D., Pauly D., 1998. Predicting food consumption of fish populations as
15
16 724 functions of mortality, food type, morphometrics, temperature and salinity. Marine and
17
18 725 Freshwater Research 49, 447-453.
19
20
- 21 726 Pauly D., 1980. On the interrelationships between natural mortality, growth parameters, and
22
23 727 mean environmental temperature in 175 fish stocks. Journal du Conseil permanent
24
25 728 International pour l' Exploration de la Mer 39, 175-192.
26
27
28
- 29 729 Pauly D., 1990. On Malthusian overfishing. Naga, ICLARM Quarterly 13, 3-4.
30
- 31 730 Pauly D., Christensen V., 1993. Stratified models of large marine ecosystems: a general
32
33 731 approach and an application to the South China Sea, in: Sherman K., Alexander L.M.,
34
35 732 Gold B.D. (Eds.), Large marine ecosystems: stress, mitigation and sustainability. AAAS
36
37 733 Press, Washington, DC, pp. 148-174.
38
39
40
- 41 734 Pauly D., Christensen V., Dalsgaard J., Froese R., Torres, F., 1998. Fishing down marine food
42
43 735 webs. Science 279, 860-863.
44
45
- 46 736 Pitcher T.J., Buchary E.A., Trujillo P. (Eds.), 2002. Spatial simulation of Hong Kong's
47
48 737 marine ecosystem: ecological and economic forecasting of marine protected areas with
49
50 738 human-made reefs. Fisheries Centre Research Reports 10(3).
51
52
- 53 739 Polovina J.J., 1984. Model of a coral reef ecosystems I. The ECOPATH model and its
54
55 740 application to French Frigate Shoals. Coral Reefs 3, 1-11.
56
57
58
59
60
61
62
63
64
65

- 741 Ricker W.E., 1969. Food from the sea, in: Resources and man. Reports of the committee on
1
2 742 Resources and Man. US National Academy of Science, San Francisco, California, pp. 87-
3
4 743 108.
5
6
7 744 Shiah F.K., Chung S.Y., Kao S.J., Gong G.C., Liu K.K., 2000. Biological and hydrographical
8
9 745 responses to tropical cyclones (typhoons) in the continental shelf of the Taiwan Strait.
10
11 746 Continental Shelf Research 20, 1-16.
12
13
14 747 Sobczak W.V., Cloern J.E., Jassby A.D., Müller-Solger A.B., 2002. Bioavailability of organic
15
16 748 matter in a highly distributed estuary: The role of detrital and algal resources. Proceedings
17
18 749 of the National Academy of Science of the United States of America 99, 8101-8105.
19
20
21 750 Sorokin Y.I., 1981. Aspects of the biomass, feeding and metabolism of common corals of the
22
23 751 Great Barrier Reef, Australia. Proceedings of the Fourth International Coral Reef
24
25 752 Symposium 2, 27-32.
26
27
28 753 Strickland J.D.H., Parsons T.R., 1972. A practical handbook of seawater analysis. Fisheries
29
30 754 Research Board of Canada, Ottawa.
31
32
33 755 Tkachenko K.S., Wu B.J., Fang L.S., Fan T.Y., 2007. Dynamics of a coral reef community
34
35 756 after mass mortality of branching *Acropora* corals and an outbreak of anemones. Marine
36
37 757 Biology 151, 185-194.
38
39
40 758 Ulanowicz R.E., 1986. Growth and Development: Ecosystem Phenomenology. Springer
41
42 759 Verlag, New York.
43
44
45 760 Ulanowicz R.E., Puccia C.J., 1990. Mixed trophic impacts in ecosystems. Coenoses 5, 7-16.
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1 761 **Figure captions**

2
3
4 762 **Fig. 1.** Nanwan Bay of Kenting National Park, southern Taiwan. The boundaries of the park
5
6 763 are indicated by the dotted line.

7
8
9 764 **Fig. 2.** Locations of seven fringing reefs analyzed by Ecopath for comparison with the
10
11 765 Nanwan Bay model. 1. Nanwan Bay, 2. Puerto Rico and the Virgin Islands (PRVI), 3.
12
13
14 766 Tiahura, 4. the Bolinao, 5. Mahahual, 6. Boca Paila, 7. Tampalam, 8. Floreana Island.

15
16 767 **Fig. 3.** Biomass fractions (%) of communities in the seven fringing reefs for comparison with
17
18
19 768 the Nanwan Bay model.

20
21 769 **Fig. 4.** Biomass fractions (%) of the fish community in the seven fringing reefs for
22
23
24 770 comparison with the Nanwan Bay model.

25
26 771 **Fig. 5.** Flow network of organic matter and trophic efficiencies (%) in Nanwan Bay. The flow
27
28 772 (g wet weight (WW) m⁻² yr⁻¹) web is aggregated into a concatenated chain of transfers
29
30
31 773 through five integral trophic levels. Flows from primary producers (P), from detritus
32
33 774 (D), and out of the tops of boxes represent export, while flows out of the bottoms
34
35
36 775 represent respiration.

37
38 776 **Fig. 6.** Direct and indirect impacts that an increase in the biomass of the compartments on the
39
40
41 777 left of the histograms would have on compartments positioned above them. Bars
42
43 778 pointing upwards indicate positive impacts while those pointing downwards indicate
44
45 779 negative impacts. Impacts are relative, not absolute, but are comparable between
46
47
48 780 histograms. f, fish; ben, benthic; inv, invertebrates; det, detritivorous.

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	1170.9	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. Semisessile 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).

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 Semisessile 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.

Table 3 Comparisons of living biomass (g wet weight m⁻² yr⁻¹) of Nanwan Bay with other fringing coral reefs. ** $p < 0.05$, * $0.05 < p < 0.10$.

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	1,624	229	1,300	4,015	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	2,030	1,896	332	3,048	4,554	1,019	1,015	2,620

^a Aliño et al. (1993); ^b Arias-González et al. (2004); ^c Opitz (1996); ^d Arias-González et al. (1997); ^e Okey (2004).

Table 4 Comparisons of ecosystem attributes of Nanwan Bay with other fringing coral reefs. ** $p < 0.05$, * $p < 0.10$.

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*	8,373		5,433			20,496	18,347	51,600
Sum of all exports	16,200		920			3,783	3,376	-5,412
Sum of all respiratory flows*	4,629	18,965	3,313	32,523		12,360	11,226	27,638
Sum of all flows into detritus	20,115	18,405	3,503	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		4,152	20,025	11,350	15,889	14,293	13,250
Sum of all production	21,553	1,938	5,267	51,282		20,180	18,053	17,337
Net system production	15,570		838			3,529	3,067	-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.

^a Aliño et al. (1993); ^b Arias-González et al. (2004); ^c Opitz (1996); ^d Arias-González et al. (1997); ^e Okey (2004).

Figure 1

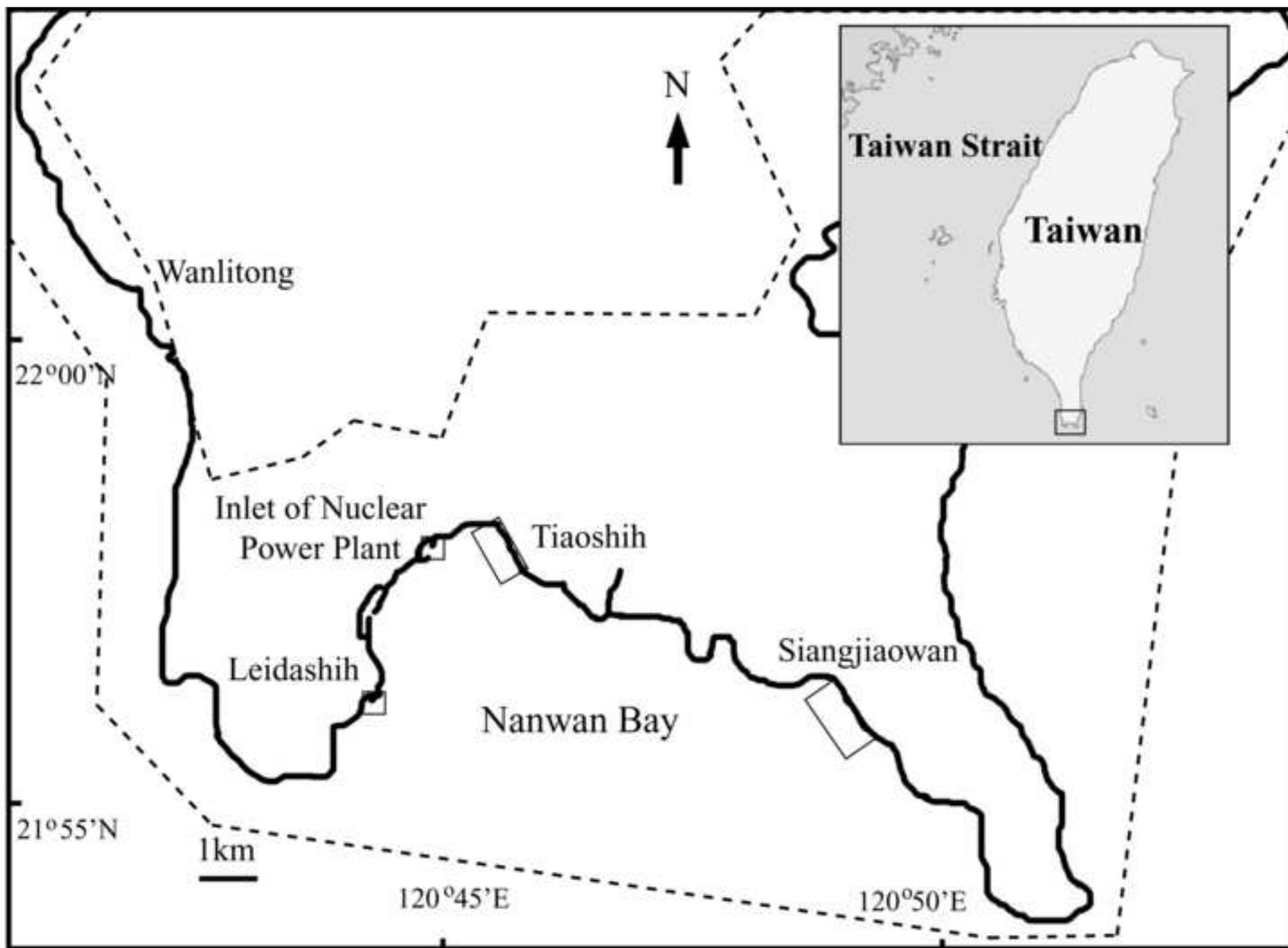


Figure 2



Figure 3

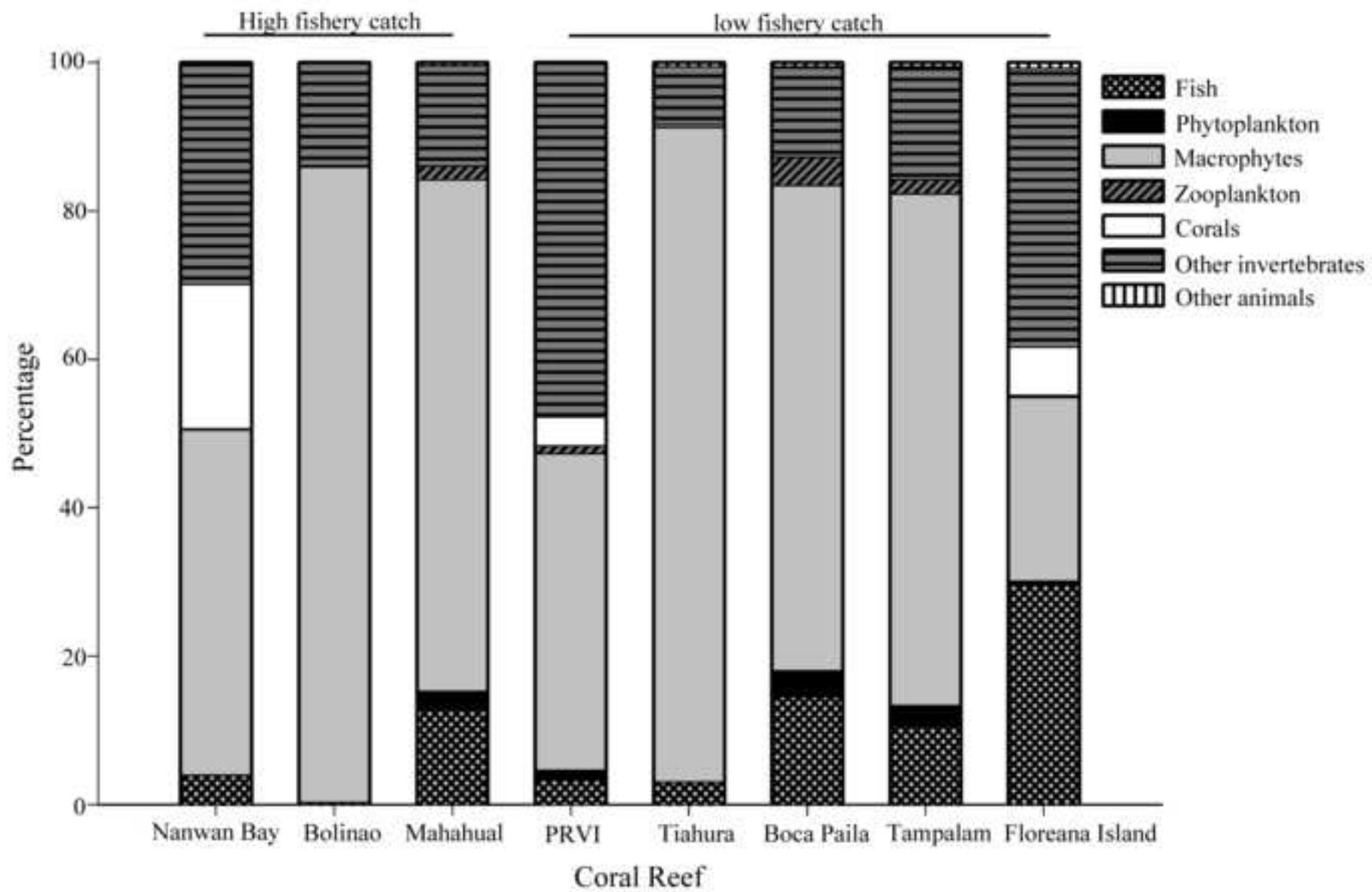


Figure 4

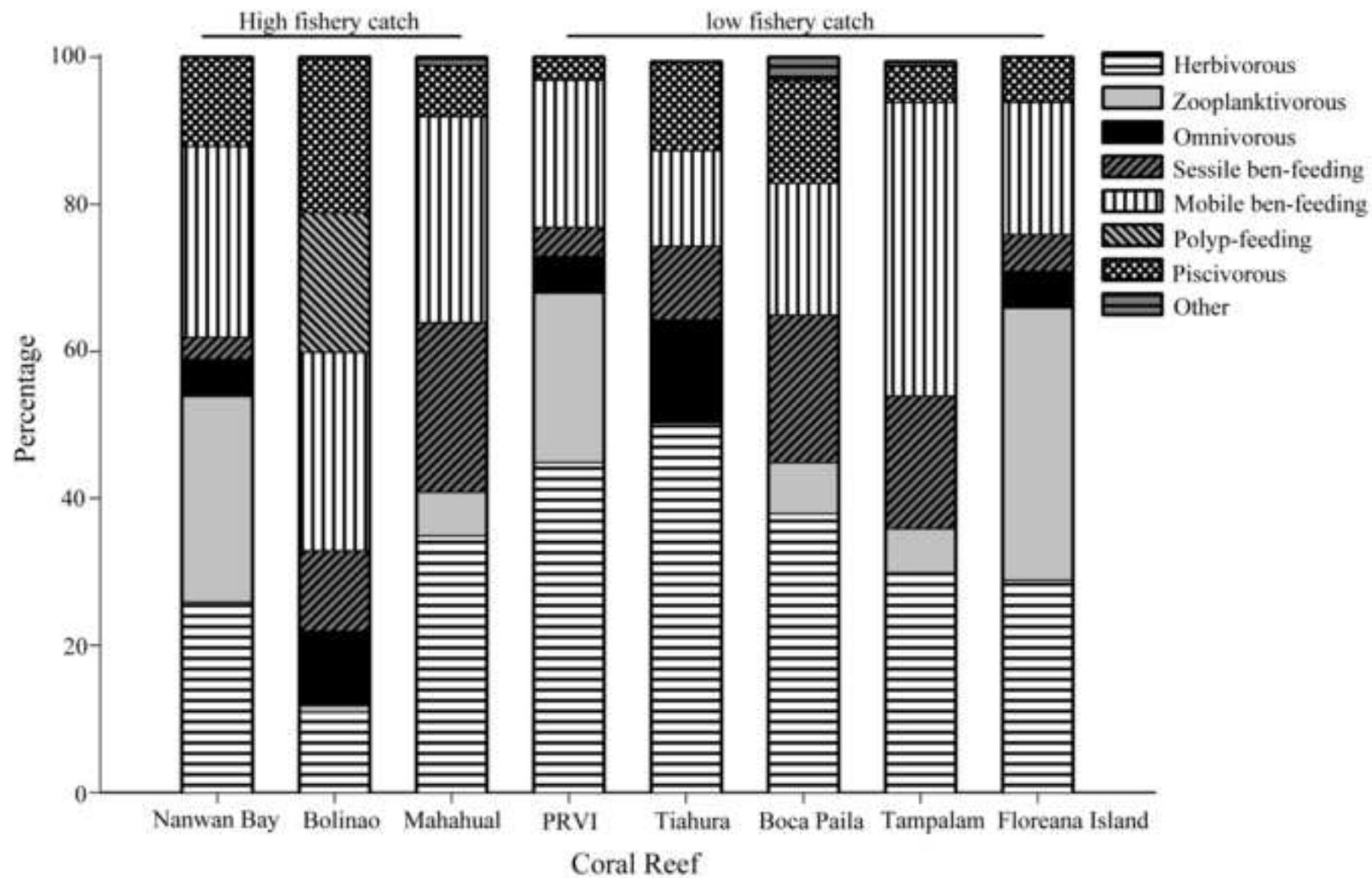
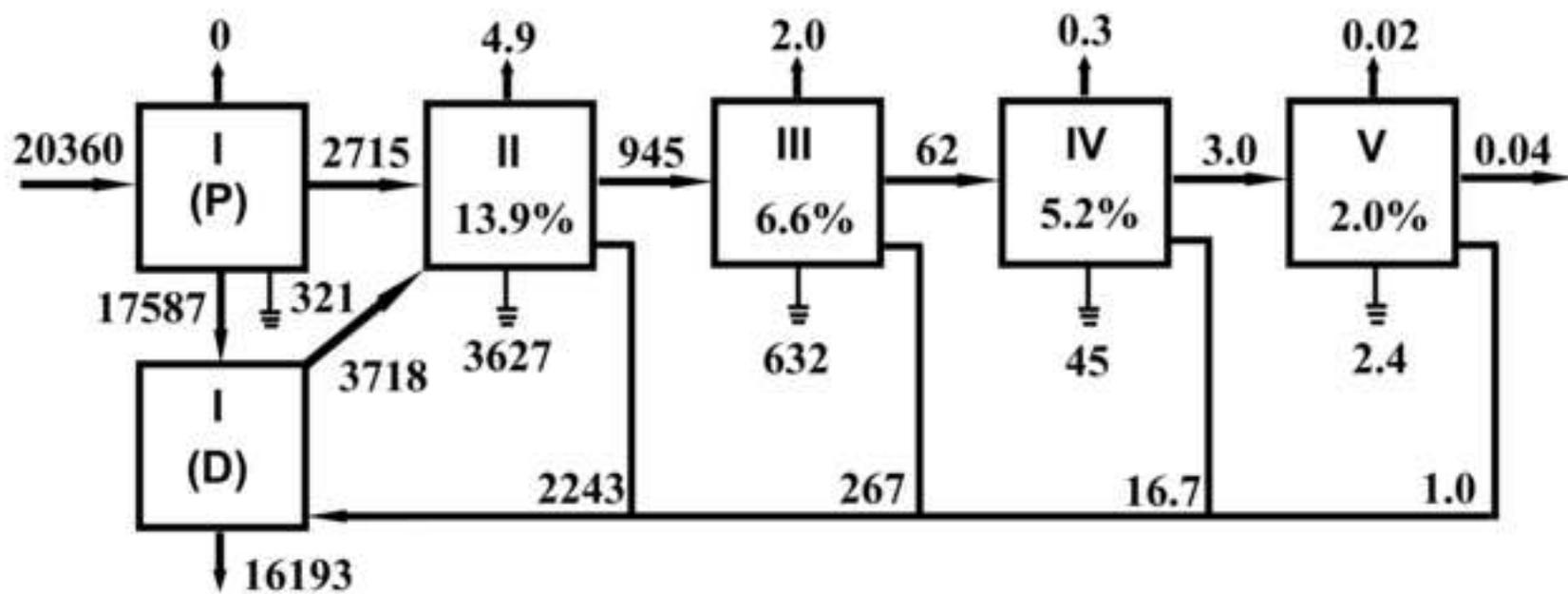


Figure 5



ACCE

RIPT

