The effects of system-scale removal of oyster-culture racks from Tapong Bay, southwestern Taiwan: model exploration and comparison with field observations

Hsing-Juh Lin, Kwang-Tsao Shao, Hwey-Lian Hsieh, Wen-Tseng Lo, and Xiao-Xun Dai

Using Ecopath with Ecosim, a mass-balance trophic model was manipulated to predict temporal responses of community biomasses to the system-scale removal of oyster-culture racks from Tapong Bay, a eutrophic and poorly flushed lagoon in tropical Taiwan. The model predictions were further compared with separate field observations over a period of 2.5 years. The removal of the oysters was predicted to result in increases in most community biomasses. The model predictions approximately matched the trends of the field observations for phytoplankton, zooplankton, detritivorous fish, and detritus after the removal, so providing a trophic explanation for the responses of these communities in the lagoon. The observed biomasses of benthic communities declined, however, probably as a result of a reduction in biodeposition from the oysters. The biomasses of pelagic fish and soft-bottom fish increased, but that of reef fish decreased after the removal. The field observations demonstrated that plankton communities were controlled, but the biomasses of the benthic and fish communities were enhanced by a high density of suspended oyster culture in a eutrophic lagoon.

H-J. Lin and X-X. Dai: Department of Life Sciences, National Chung Hsing University, Taichung 402, Taiwan. H-J. Lin: Institute of Marine Environmental Chemistry and Ecology, National Taiwan Ocean University, Keelung 202, Taiwan. K-T. Shao and H-L. Hsieh: Biodiversity Research Center, Academia Sinica, Taipei 115, Taiwan. W-T. Lo: Department of Marine Resources, National Sun Yat-sen University, Kaohsiung 804, Taiwan. Correspondence to H-J. Lin: tel: +886 4 22840416; fax: +886 4 22874740; e-mail: hjlin@dragon.nchu.edu.tw.

Introduction

Aquaculture is a rapidly expanding industry in coastal waters worldwide. Oyster production ranks second in the world among the top ten aquaculture species (FAO, 2004). There is uncertainty about the ecological impacts vs. benefits of oyster culture in coastal waters. The introduction of oyster-culture racks may modify the local oceanography (Nugues *et al.*, 1996), and it may enhance system production by providing additional artificial substrata for periphyton colonization (Lin *et al.*, 2005). Cultured oysters may improve the water quality by removing a large quantity of particulate carbon, and their biodeposits may provide a food source for benthic organisms (Newell, 1988). They may transform planktonic production into nutrients which are then available to plants via recycling from excretion and the remineralization of faeces and pseudofaeces (Dame *et al.*, 1989; Reusch and Williams, 1998; Mazouni *et al.*, 2001; Peterson and Heck, 2001; Pietros and Rice, 2003). Nevertheless, cultured oysters and biofouling communities on culture racks may cause food depletion of other filter-feeders through top-down control of phytoplankton abundance (Officer *et al.*, 1982; Souchu *et al.*, 2001; Huang *et al.*, 2008), and may shift the species composition (Baker *et al.*, 1998; Dupuy *et al.*, 2000; Souchu *et al.*, 2001; Pietros and Rice, 2003; Huang *et al.*, 2008). Oyster restoration has therefore been proposed as an ecological tool for top-down control of phytoplankton blooms and for reversing cultural eutrophication in estuaries and coastal waters (Coen *et al.*, 2007). However, this ecosystem service is currently controversial (Pomeroy *et al.*, 2006; Fulford *et al.*, 2007), suggesting that the ecosystem effects of oyster culture in coastal waters have been poorly quantified.

Sustainable management of coastal ecosystems for oyster culture requires ecosystem-scale, rather than population- or community-scale, knowledge of the feedback interactions between oysters and biological and abiotic factors (Prins *et al.*, 1997). Ecosystem modelling is a useful tool for integrating these complex interactions and evaluating management strategies (Kremer and Nixon, 1978). By modelling nitrogen cycling in Thau Lagoon, France, Chapelle *et al.* (2000) found that cultured oysters affect nutrient recycling and oxygen consumption through biodeposition on sediments. Leguerrier *et al.* (2004) manipulated three scenarios of a trophic model of Marennes-Oléron Bay, France, including no oysters, the existing oyster culture, and double the amount of the current oyster culture. They concluded that primary production was enhanced and a shift from pelagic to benthic consumers was induced by cultured oysters. Cerco and Noel (2007) employed a predictive eutrophication model and found that oyster restoration in Chesapeake Bay, USA, would reduce surface chlorophyll, increase deep-water dissolved oxygen (DO) and the biomass of submerged aquatic

vegetation, and remove nitrogen through denitrification in summer. However, those studies were primarily parameterized by making spatial comparisons between oyster-introduced and native systems or between an oyster-culture area and an area with no culture. Few temporal data are available on coastal ecosystems before and after they have become culture areas, to prove that the effects are really due to the introduction of the oyster culture, rather than to spatial differences among communities in the ecosystem.

Tapong Bay (22°27′N 120°26′E) is a shallow tropical lagoon in southwestern Taiwan; it has only one tidal inlet (1 km long, 138 m wide, 2 m deep) connecting it to the sea (Figure 1). Until recently, it was an important site for culturing the oyster, *Crassostrea gigas*, in Taiwan. Almost all its area was devoted to suspended oyster culture, and the density reached as high as 2932 racks km^{-2} (Lin *et al.*, 2006). In 1997, the lagoon was designated a National Scenic Area and oyster culture was prohibited. Despite possible feedback mechanisms between cultured oysters and ecosystem processes (see Prins *et al.*, 1997) and efforts to model ecosystem-level impacts of oyster culture (Chapelle *et al.*, 2000; Leguerrier *et al.*, 2004) or oyster restoration (Cerco and Noel, 2007), there is no ecosystem model that can be used to predict the temporal response of an entire coastal ecosystem to the complete removal of oyster culture. Understanding the responses of natural systems to removal, modifications, and perturbations may become increasingly important for effective environmental management and the successful restoration of impacted ecosystems. All the oyster-culture racks were removed from Tapong Bay at the same time in June 2002. This provided an opportunity similar to an ecosystem-scale, manipulation experiment to examine the responses of an entire lagoon to the complete removal of oyster culture. Comparing model predictions with separate field observations after the rack removal may provide significant insights into the mechanisms underlying the community changes.

As Tapong Bay is a eutrophic and poorly flushed lagoon (Hung and Hung, 2003), the positive feedback from cultured oysters through the regeneration of available nutrients in the water column for plants was minor (Huang *et al.*, 2008). Therefore, cultured oysters were hypothesized to cause food depletion of other filter-feeders through top-down control of the phytoplankton biomass in the lagoon. We undertook this case study of the complete removal of oyster culture to test the hypothesis that the biomasses of phytoplankton and consumers, which directly or indirectly feed on phytoplankton, would increase after the complete removal of oyster culture from this eutrophic lagoon. Using the Ecopath approach and field measurements from October 1999 to October 2001, a mass-balance trophic model was constructed to demonstrate the trophic structure and functioning of Tapong Bay when it supported a high density of suspended oyster culture (Lin *et al.*, 2006). One of the most desirable features of a mechanistic ecological model is that it allows detailed analysis not only of the emergent biomasses of the system, but also of the many internal aspects of the dynamic processes (Kremer and Nixon, 1978). Therefore, our purposes were (i) to quantify the responses of community biomasses to the complete removal of oyster-culture racks by manipulating a trophic model of Tapong Bay; (ii) to evaluate the trophic model predictions by comparing them with concurrent field observations; and (iii) to explore the mechanisms underlying the community changes after the complete removal of oyster-culture racks from the lagoon.

Material and methods

Study area

Tapong Bay has a surface area of 4.44 km^2 and a mean depth of 2.2 m at low tide (Figure 1). It is surrounded by a variety of aquaculture ponds producing fish and shrimp and receives
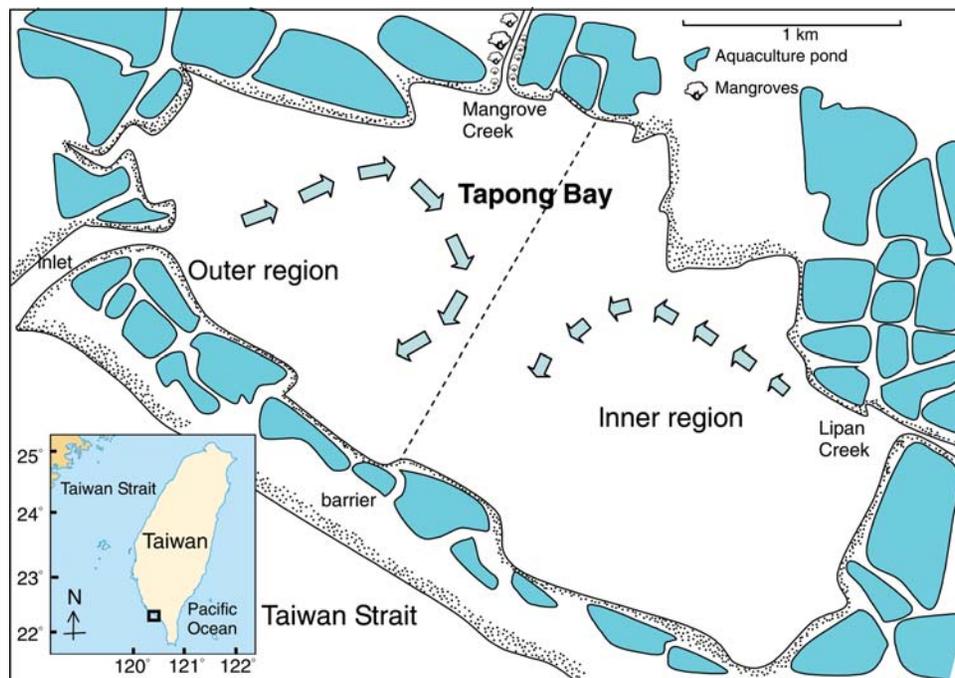

Figure 1. Outer and inner regions of Tapong Bay. The arrows show the development of two circulation eddies that meet towards the middle of the lagoon.

nutrient-rich, waste discharges averaging 172×10^3 m^3 d^{-1} from two mangrove-lined creeks that drain the surrounding aquaculture ponds (Hung and Hung, 2003). Loading rates of N and P in the lagoon reach 1.87 and 0.51 mol m^{-2} year^{-1}, respectively. Mean concentrations of dissolved inorganic (DIN) and organic (DON) nitrogen reach 16.4 and 24.4 µM. Concentrations of dissolved inorganic (DIP) and organic (DOP) phosphorus average 4.0 and 2.4 µM, respectively. Consequently, although DO concentrations in the surface water are >5.4 mg l^{-1}, the bottom water in the inner region became hypoxic (2 mg l^{-1}) in summer, when the water was partially stratified. There are normally no rooted macrophytes in the lagoon.

Climate data derived from a local weather station at Donggang (Taiwan Central Weather Bureau, 1999–2003) show that in winter and spring (November–April), the dry season, the mean monthly rainfall normally does not exceed 40 mm, and that in summer and autumn (May–October), the wet season, the average monthly rainfall frequently exceeds 200 mm. As no large river flows into the lagoon, its small volume makes salinity responsive to changes in rainfall inputs and evaporative losses. Consequently, salinities are lower in summer ($\sim$25.4 psu) and higher in winter ($\sim$33.9 psu), with a mean value of 31.8 psu. Water temperatures range from $\sim$32°C in summer to $\sim$22°C in winter.

Tapong Bay primarily experiences semi-diurnal tides with a tidal range of $\sim$1 m. Tidal pumping is the mixing agent between the open sea and the lagoon (Chen, 2002). There are two circulation eddies, one cyclonic and the other anticyclonic, that meet in the middle of the lagoon (Figure 1). Mean water-exchange times range from 8.71 ± 1.62 d in the outer region, which is subject to fast flushing, to 11.6 ± 2.17 d in the inner region, which has poorer flushing (Hung and Hung, 2003). Hence, tidal flushing is the most important factor for spatially separating abundances and species compositions of phytoplankton (Su *et al.*, 2004), periphyton (Lin and Hung, 2004), zooplankton (Lo *et al.*, 2004), and fish (Chen *et al.*, 2003) between the inner and outer regions of the lagoon. After the complete removal of oyster-culture racks, the seawater exchange rate increased in both regions, but the circulation pattern remained (Huang *et al.*, 2008). Mean water-exchange times of the two regions of the lagoon were, respectively, reduced to 6.13 ± 0.73 and 8.18 ± 0.98 d (Huang *et al.*, 2008). Mean DIN and DON concentrations remained high and were 11.4 and 39.8 µM, respectively, but DIP and DOP concentrations decreased slightly to 1.5 and 1.2 µM, respectively (Huang *et al.*, 2008). The main communities of the lagoon, including phytoplankton, periphyton, zooplankton, oysters, macrobenthos, and fish, and detritus were, respectively, sampled at 2–30 study sites distributed from the tidal inlet to the inner region along 1–3 transects across the lagoon, to account for spatial variations of the two regions, depending on the characteristics of each community.

Ecopath model

The trophic model of Tapong Bay was constructed using the Ecopath routine in Ecopath with Ecosim (Christensen *et al.*, 2005) to quantify all matter flows in the foodweb. For each compartment (i), a mass-balance budget can be expressed as

$$P_i - B_i M2_i - P_i(1 - \mathrm{EE}_i) - \mathrm{EX}_i - \mathrm{AC}_i = 0, \quad (1)$$

where P_i is the production of i, B_i the biomass of i, $M2_i$ the predation mortality of i, EE_i the ecotrophic efficiency of i (i.e. the part of the production that is either passed up the trophic level or

exported), $1 - \mathrm{EE}_i$ is "other mortality", EX_i the portion of i exported to other systems through sedimentation or fishery activities, and AC_i the accumulation of i during the study period.

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

$$B_i \times \frac{P_i}{B_i} \times \mathrm{EE}_i - \Sigma_j B_j \times \frac{Q_j}{B_j} \times \mathrm{DC}_{ji} - \mathrm{EX}_i - \mathrm{AC}_i = 0, \quad (2)$$

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

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

$$\Sigma_j B_j \times \frac{Q_j}{B_j} = P_j + R_j + \mathrm{UN}_j, \quad (3)$$

where P_j is the production of j, R_j the respiration of j, and UN_j the unused consumption of j, which was assumed to be 20%.

Major species of similar sizes and diets in Tapong Bay were functionally grouped within the same compartment. An 18-compartment trophic model for the lagoon was developed (Figure 2), comprising the following groups: (1) phytoplankton (dominated by the diatoms *Skeletonema costatum*, *Chaetoceros* sp., *Cylindrotheca closterium*, and *Nitzschia* sp., the cyanobacterium *Oscillatoria* sp., and the dinoflagellate *Protoperidinium* sp.); (2) periphyton (dominated by the chlorophytes *Ulva fasciata*, *Ulva lactuca*, and *Enteromorpha intestinalis*, and the cyanobacterium *Lyngbya majuscule*); (3) herbivorous zooplankton (dominated by *Oithona oculata*, *Parvocalanus crassirostris*, *Acartia sinjiensis*, *Bestiolina amoyensis*, and copepod nauplii); (4) carnivorous zooplankton (mainly, the ephyrae *Aurelia aurita*); (5) oysters (*C. gigas*); (6) polychaetes (mainly, *Capitella* sp.); (7) gastropods (*Thiara riqueti*); (8) bivalves (*Mytilopsis sallei*); (9) barnacles; (10) amphipods; (11) crabs (dominated by *Thalamita crenata*, *Thalamita spinimana*, and *Varuna litterata*); (12) shrimp (dominated by *Penaeus semisulcatus*, *Metapenaeus ensis*, and *Penaeus monodon*); (13) herbivorous fish (dominated by *Pomacentrus taeniometopon*, *Acanthurus xanthopterus*, and *Scarus ghobban*); (14) zooplanktivorous fish (dominated by *Hypoatherina lacunosus*, *Ambassis buruensis*, *Ambassis urotaenia*, and *Monodactylus argenteus*); (15) benthic-feeding fish (dominated by *Acanthopagrus berda*, *Apogon lateralis*, and *Lutjanus argentimaculatus*); (16) detritivorous fish (dominated by *Liza macrolepis*, *Valamugil cunnesius*, and *Nematalosa come*); (17) piscivorous fish (*Pterois volitans*); and (18) detritus. Bacterial processes are difficult to estimate reliably, and the flows may totally overshadow other flows in the system (Christensen *et al.*, 2005). It was assumed that bacteria were associated with the detritus, so they are linked to the present model only through detrital import and export by bacterial production and respiration. The export of fish and invertebrates by birds was assumed to be small when compared with those by fisheries, so was not included in the model.

All the parameters used to construct the Ecopath model were assembled from our own studies, where possible covering the two years from October 1999 to October 2001, before the complete removal of oyster-culture racks. Because Ecopath uses linkages of production of one compartment with consumption of other

Figure 2. Trophic model of Tapong Bay. Biomass (*B*) is in gramme wet weight per square metre, and production (*P*) and all other flows are in gramme wet weight per square metre per year.

compartments to calculate one missing parameter for each group, the most questionable parameter of each compartment can be treated as unknown and calculated by Ecopath. In this study, the biomass and EX of each compartment, and primary productivity were considered the most reliable data. The EE was treated as unknown and left for Ecopath to estimate, to verify the realism of the model. Some P/B, Q/B, and DC values of invertebrates were assembled from the literature and were considered to be less reliable in the lagoon model. Therefore, they were gradually modified during the balancing exercise. However, most of the changes were rather small and remained within 15% of the input value.

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 are estimated or taken from other models in the literature. Balancing, validation, and characterization of the Tapong Bay model are considered elsewhere (Lin *et al.*, 2006).

Ecosim simulation

The Ecopath model was used to predict the effects of the complete removal of oyster-culture racks on communities in the lagoon by manipulating the scenario using the Ecosim routine (Walters *et al.*, 1997) in Ecopath with Ecosim. Ecosim is a time-dynamic, simulation model that uses the linear equations [Equation (1)] of the Ecopath model, isolating the biomass-accumulation term and setting up a series of differential equations as

$$\frac{dB_i}{dt} = g_i \times \Sigma_j Q_{ji} - \Sigma_j Q_{ij} + I_i - (M_i + F_i + e_i) \times B_i, \quad (4)$$

where dB_i/dt is the biomass-change rate during the time interval, dt, of group i, g_i the net growth efficiency (production/consumption ratio) of i, Q_{ji} the consumption rate of i, Q_{ij} the predation of all predators (j) on i, I_i the immigration rate of i, M_i the non-predation, natural mortality rate of i, F_i the fishing mortality rate of i, and e_i the emigration rate of i.

Ecosim uses a vulnerability setting for all predator–prey interactions controlling the rates (v_{ij}) with which prey groups move between a vulnerable state and one where they are not susceptible to predation by a given predator. This simulates when control is top-down (i.e. Lotka–Volterra), bottom-up (i.e. donor-driven), or of an intermediate type as mediated by temporal or spatial refugia in a system or by the strengths of physical organizing forces relative to trophic forces. The vulnerability parameter is in general not subject to direct measurement (Christensen *et al.*, 2005). For the present simulations, vulnerability values were changed in the range from 1 (bottom-up) to 5 (top-down control), to search for one best overall vulnerability that gives best fits of the Ecosim model to the time-series observations. The default setting of 2 emulating a mixed top-down and bottom-up control showed the best fit overall and was used for all functional groups.

Small fish and macrobenthos were less vulnerable to predators when they associated with oyster-culture racks, in which they were found in greater abundances (Chen *et al.*, 2003; Tew *et al.*, 2008). Ecosim uses a trophic, mediation-function setting (Christensen *et al.*, 2005) to specify such protective mediation, so that small fish and macrobenthos become more vulnerable to predators when their protective oyster-culture racks are removed. This was achieved by modifying the vulnerabilities of small fish and macrobenthos to their predators by sketching a negative sigmoid function that decreases with an increasing biomass of the mediating oysters.

Ecosim also has a seasonal forcing-function setting (Christensen *et al.*, 2005) to allow environmental parameters to influence trophic interactions. The Ecopath model demonstrates that the lagoon is more dependent on herbivory than detritivory to generate food sources for consumers (Lin *et al.*, 2006). It was therefore assumed to be driven essentially by the primary producers of phytoplankton and periphyton. For the present simulations, there are two forcing-function settings for the seasonality of phytoplankton and periphyton, which can be used to modify the Q/B ratio of the consumer groups in the lagoon.

The results from the mass-balance Ecopath model before the complete removal of oyster-culture racks were used for initial parameters in the Ecosim model. The time-dynamic simulation was run for 10 years from 1997 to 2006. For the first 5.5 years (from January 1997 to June 2002), it was run without a change in the oyster culture and other fisheries, to assure initial stable conditions of the seasonal patterns (see Kremer and Nixon, 1978), after which runs continued for an additional 4.5-year period (from July 2002 to December 2006) under a scenario of the complete removal of oyster-culture racks. The relative fishing mortality of oysters was increased to simulate removing all the racks. Rates of fishing mortality of the associated periphyton, bivalves, barnacles, amphipods, and polychaetes growing on the culture racks were also proportionally increased, to simulate the decrease in their substrata in the lagoon. Consequently, 21.8, 75.8, 26.4, 16.9, and 43.3% of periphyton, polychaetes, bivalves, barnacles, and amphipods were, respectively, lost as a result of the removal of the culture racks. Biomass changes predicted by the Ecosim simulation were compared with the 2.5-year period of field observations after the complete removal in June 2002.

Field sampling

Biomass and productivity of phytoplankton and periphyton were determined every 2–3 months from June 2000 to June 2004 for four years, spanning the time of the complete removal. On each occasion, water samples for phytoplankton biomass were collected at a depth of 30 cm at low tide at six study sites along two transects across Tapong Bay (Su *et al.*, 2004). Phytoplankton biomass in terms of chlorophyll *a* was determined in a spectrophotometer by immediately filtering triplicate water samples through Whatman GF/F filters in the field, then extracting them in 90% acetone in the dark for 24 h at 4°C (Parsons *et al.*, 1984). Periphyton biomass in terms of wet weight was determined at four study sites along a transect across the lagoon by gently scraping periphyton off the submerged part of rocks and oyster-culture pens, measuring 10×60 cm^2 (Lin and Hung, 2004).

Net production rates of periphyton and phytoplankton were determined concurrently at four study sites along a transect across the lagoon as changes in DO concentrations in microcosm incubations (10-cm wide × 25-cm long × 15-cm deep); measurements were made for the water column only and for periphyton plus water column in outdoor tanks with flow-through seawater placed next to Tapong Bay (Lin *et al.*, 2005). Periphyton added to the periphyton plus water column microcosm was obtained by submerging plates of bamboo in the water column at each

site on each occasion for periphyton colonization, because bamboo was the material used for the oyster-culture pens. A row of 20 plates of bamboo, each measuring $10 \times 20 \times 1$ cm, was vertically attached to an oyster-culture pen at a depth of 30 cm, 3 weeks before the productivity determinations. After submersion for 3 weeks, all space on the plates was covered by the representative periphyton species at the natural field density at that time (Lin and Hung, 2004). The water-column microcosm was used both to determine phytoplankton productivity and to correct the DO measurements in the periphyton plus water-column microcosm. The incubations were conducted around noon when the irradiance is saturated, and each tank was exposed to different irradiances in terms of 0, 30, 50, 70, and 100% shading by interposing screens with different mesh sizes ($n = 6$ for each treatment per site). Annual production rates of periphyton and phytoplankton, respectively, were calculated via integration of the interpolated production rates under various irradiances, by referring to the relation between production rates and irradiances (the $P–I$ curve) and surface-light data at that time. DO concentrations were monitored using a spectrophotometric method with the Winkler technique modified by Pai et al. (1993). Rates of oxygen production were converted to carbon-fixation rates using a photosynthetic quotient of 1.2 (Meyercordt and Meyer-Reil, 1999).

Zooplankton samples were collected by two independent tows (2 NorPac nets, 45 cm in diameter with 100- and 330-μm mesh sizes) just below the sea surface for 5 min at 1.0 m s^{-1} at three study sites along a transect across Tapong Bay (Lo et al., 2004), monthly from January 2000 to June 2002, before the complete removal of the oyster-culture racks, and bimonthly from July 2002 to December 2004, after the complete removal. Zooplankton biomass was estimated by the displacement volume according to Ahlstrom and Thrailkill (1960). An estimate of Q/B for herbivorous zooplankton was determined in the field with the gut-fluorescence method described by Morales et al. (1993), but the P/B was obtained from the literature on a tropical coastal system (Vega-Cendejas et al., 1993).

Oyster biomass was determined monthly from June 2000 to January 2001 before the complete removal of oyster-culture racks at two study sites in the two respective regions of Tapong Bay, by randomly weighing 40–70 organisms on each sampling occasion at each site (Hsieh et al., 2003). Oyster production was estimated according to the methods of Crisp (1971), tracking the growth of 200 organisms at each site during the study period. Oyster consumption was estimated by the difference in density of organic particles between inflow and outflow water of oyster beds ($n = 15$ at each site) in September and October 2000, respectively.

No clear seasonal pattern was observed for communities of benthic invertebrates (Hsieh, 2000; Tew et al., 2008) or fish (Chen et al., 2003) in Tapong Bay. PVC corers with an inner diameter of 10 cm were pushed $\sim$20-cm deep into the sediment for lagoon-wide collection of small benthic invertebrates at 30 study sites along three transects across Tapong Bay ($n = 3$ at each site), once in August 1999 before the complete removal, and in October 2002, and January and November 2004 after the complete removal. The three replicates after the complete removal were examined to determine whether there was a time component to recovery. The contained sediment was sieved through a 0.5-mm screen. In the laboratory, specimens were sorted, counted, weighed, and identified. Few studies have been carried out on P/B and Q/B for small benthic invertebrates in Taiwan, and

their values in the lagoon were obtained by searching for the same groups in the literature from tropical coastal waters (Schwinghamer et al., 1986; Riddle et al., 1990; Vega-Cendejas et al., 1993; Opitz, 1996).

Samples of shrimp, crabs, and fish were collected using fykenets at nine study sites along three transects across Tapong Bay ($n = 4$ at each site) from July to September (the wet season) and from November to March (the dry season), 2001–2004, spanning the time of the complete removal of oyster-culture racks in June 2002. The fykenet is a passive sampler designed to use tidal dynamics to collect nekton, and is used widely by local fishers. It is composed of fence nets (15-m long, 1.5-m high, mesh size 20 mm) and a hoopnet (15 mm). The nets were set early in the morning and lifted 24 h later. Samples were then brought back to the laboratory where they were sorted, counted, weighed, and identified. Estimates of Q/B for shrimp and crabs were made in the field by the dominant species through the food-consumption model (Pauly, 1986). Estimates of Q/B for fish were computed using an empirical model developed by Palomares and Pauly (1989) for the dominant species of each group. Catches of oysters, shrimp, crabs, and fish were obtained from the local fishery bureau.

Detritus samples were collected at 10 study sites along three transects across Tapong Bay bimonthly from August 1999 to December 2001, before the complete removal of oyster-culture racks, and from February 2003 to September 2004, after their complete removal. Detritus consists of the organic material in the water column and on sediments. Water from the lagoon was filtered through acid-cleaned, dried, and preweighed Nucleopore membrane filters to determine the detrital mass in the water column. Phytoplankton biomass was subtracted from the detrital mass by calculating the sum of chlorophyll *a* plus pheophytin in the water column assuming a carbon:pigment ratio of 35:1 (Sobczak et al., 2002). Sediments were collected with an Eckman Birge Grab (15×15 cm) and dried in an oven at 60°C. The dried sediments were then ground to a powder for analyses of the organic materials. The detritus mass on sediments was limited to the top 5 cm of sediments, which is the detrital pool generally available for uptake by epifauna and fish.

Diet compositions of zooplankton, shrimp, crabs, and fish were determined by stomach-content analyses of the dominant species, and were recorded as the percentage volume of the major prey groups (for fish, see Lin et al., 2007). This is roughly equivalent to the relative weight and hence approximates the relative amount of energy extracted by consumers from various prey groups (MacDonald and Green, 1983). Stable carbon and nitrogen isotopes were used in combination with stomach-content analyses to trace the food sources of detritivorous fish, shrimp, crabs, and polychaetes in the lagoon (Lin et al., 2006). Potential food sources, including sestonic particulate organic matter, benthic microalgae (mainly diatoms, pers. obs.), macroalgal periphyton, marsh plants, and mangrove leaves were collected from January to March 2001 for stable-isotope analyses. δ^{13}C values were used to determine carbon sources. δ^{15}N values were analysed as a secondary tracer to indicate the trophic position. Because the ^{13}C content of lipids may be depleted and this can affect ecological interpretations (Kling et al., 1992), samples were washed in a 2:1:0.8 methanol:chloroform:water solution for 2 h (Bligh and Dyer, 1959), then treated with 1-N HCl to, respectively, remove lipids and carbonates (Boutton, 1991). Muscle tissues were finally freeze-dried and ground for isotope analyses. The δ^{13}C and δ^{15}N values of

samples were determined with a continuous-flow, isotope-ratio mass spectrometer (Finnigan Delta S), coupled with an elemental analyser (NA 1500, Fison). Because lipid extraction and acidification alters tissue $\delta^{15}N$ (Pinnegar and Polunin, 1999; Sweeting *et al.*, 2006), chemically treated and untreated samples were run for $\delta^{13}C$ and $\delta^{15}N$, respectively. There are few published data on the diet of other small benthic invertebrates in Taiwan, so this information was obtained by searching for the same groups in the literature from tropical waters (Opitz, 1996).

Factors used to convert between chlorophyll *a*, carbon, displacement volume, dry weight, and wet weight were based on a table summarized by Opitz (1996). Biomass data were then recorded as gramme wet weight (WW) per square metre, and flow data were recorded as gramme wet weight per square metre per year.

Data analyses

Three sustainability performance indicators for cultured oysters (Gibbs, 2007) were calculated to assess the level of interactions between suspended oyster culture and the growing water environments before the complete removal of oyster-culture racks. In Tapong Bay where water temperatures range from 22 to 32°C, the mean clearance rate of oysters was assumed to be $0.5 \, m^3 \, g \, C^{-1} \, d^{-1}$ (Fulford *et al.*, 2007). The clearance efficiency was used to measure how effectively the cultured oysters can process water daily compared with the flushing time per day. Filtration pressure was used as a measure of the requirement of the cultured oysters compared with the total phytoplankton production within the lagoon. Finally, the regulation ratio was used as a measure of how much control cultured oysters had on phytoplankton within the lagoon.

As our primary aim was to detect differences before and after the complete removal of the oyster-culture racks in June 2002, Student's *t*-test was used to determine whether predicted and observed community-biomass levels differed in the 2.5 years before and after the complete removal. Before the analyses, power transformations (Clarke and Warwick, 1994) were applied for data transformation to fit the data to assumptions of normality and variance homogeneity.

Results

Trophic structure before rack removal

The pedigree index was 0.82 for the Tapong Bay model, indicating the high quality of the model, given that most inputs came from local, well-sampled, high-precision data. The Tapong Bay model revealed the structure of the foodweb to contain about four integral trophic levels (Figure 2). Trophic levels estimated by Ecopath from the weighted average of prey trophic levels varied from 1.00 for primary producers and detritus to 3.20 for piscivorous fish. Detritus was the largest compartment in terms of mass in the foodweb. The most-prominent living compartments in terms of matter flows and biomass in the lagoon were cultured oysters and other bivalves, respectively. Oysters constituted 35% of the system's total living biomass and consumed ~44% of the available production of phytoplankton. The fishery yield from the lagoon was ~119 g WW m^{-2} year^{-1}. Cultured oysters accounted for ~86% of the total yield and were the most important fishery component in the lagoon. Fish and crabs accounted for some 12 and 2% of the total yield, respectively.

The mixed trophic impacts of the Tapong Bay model indicate direct and indirect interactions among compartments in the

system and can therefore be regarded as a form of sensitivity analysis (Lin *et al.*, 2006). Phytoplankton and periphyton were the most-influential living compartments in the model. An increase in phytoplankton biomass would have a very positive effect on filter-feeders and the cultured-oyster yield. An increase in the periphyton biomass would have a positive effect on most fish biomass. A decrease in the biomass of cultured oysters would have a direct positive impact on herbivorous zooplankton and indirectly on carnivorous zooplankton and zooplanktivorous fish, through cascading effects.

The clearance efficiency of cultured oysters reached 40, indicating that lagoon water was flushing much more slowly (2.5%) than the water processed through the cultured oysters. The filtration pressure was 0.43, suggesting that ~43% of the phytoplankton production in the lagoon went towards supporting oyster culture. Similarly, the regulation ratio was 0.49, suggesting that oyster culture in the lagoon was accounting for ~49% of the turnover of phytoplankton. These sustainability performance indicators suggest that cultured oysters in Tapong Bay appeared to regulate phytoplankton biomass and redirect resources away from competitor filter-feeders of the lagoon (Gibbs, 2007).

Ecosim simulation

Before the complete removal of oyster-culture racks from Tapong Bay in June 2002, the Ecosim simulation demonstrated a clear seasonal pattern of phytoplankton biomass, with peaks in summer and autumn (Figure 3). In general, a cycle of 2−3 years was found for periphyton, zooplankton, benthic invertebrates, and detritus, but the timing of the peaks differed. No clear temporal pattern was observed for communities at higher trophic levels, such as benthic-feeding or piscivorous fish.

Under the scenario of the complete removal of oyster-culture racks from the lagoon, the biomass of oysters was manipulated by harvesting so as to be almost completely removed (Figure 3). The periphyton biomass was predicted to decline by 28% as a result of the decrease in available substrata of the oyster-culture racks for colonization and feeding by grazers in the lagoon. The phytoplankton biomass and seasonal variation were predicted to increase in response to no longer being subjected to filter-feeding by cultured oysters. The biomasses of zooplankton and benthic invertebrates in the lagoon were predicted to increase rapidly and to peak in the first year or at the beginning of the second year after the complete removal in June 2002, then to decrease to a stable plateau over the following few years. The magnitude of the biomass increase was greater for carnivorous zooplankton and shrimp, reaching 20 and 30 times the previous biomass levels, respectively (Table 1, Figure 3). The timing of the peak for crabs at higher trophic levels was slower and delayed to the third year after the complete removal. Detritus was predicted to increase by 10 times the present mass in the first year after the complete removal.

Responses of the fish communities to the complete removal of oyster-culture racks from Tapong Bay were more complex than for the other communities (Figure 3). The biomasses of all fish communities were predicted to increase rapidly after the complete removal, as were those of benthic invertebrates. The biomasses of herbivorous and benthic-feeding fish later declined to the level before the complete removal, or lower. Consequently, the mean biomass of herbivorous fish remained stable after the complete removal, but that of benthic-feeding fish was predicted to decrease slightly (Table 1). However, the biomasses of
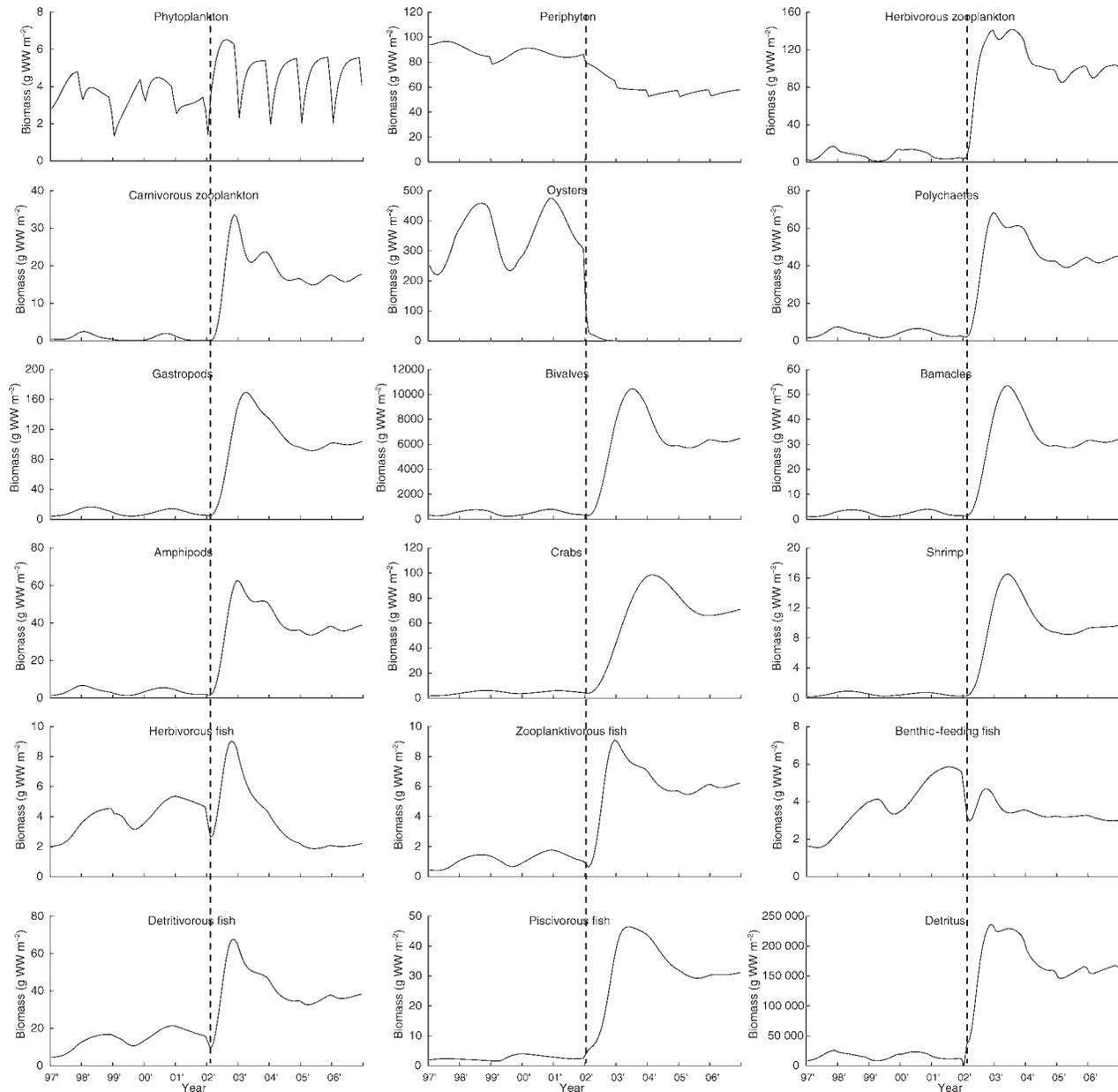
Figure 3. Predicted changes in community biomass of the Tapong Bay model before and after June 2002; the time when all the oyster-culture racks were removed (dashed line).

zooplanktivorous, detritivorous, and piscivorous fish were all predicted to greatly increase in response to the removal of cultured oysters and associated bivalves growing on the oyster-culture racks.

### Field observations after rack removal

Changes in community biomasses before and after the complete removal of oyster-culture racks from Tapong Bay were distinct. The mean phytoplankton biomass increased in a similar way to the predictions and peaked in winter and the following autumn at levels higher than those recorded before the removal (Figure 4). The mean biomass increased by 180% after complete removal (Table 2). Although the maximum biomasses of the herbivorous and carnivorous zooplankton communities were

comparable with the previous maximum values, mean values were significantly greater after the complete removal (Table 2). The magnitude of the increase in the biomass of carnivorous zooplankton was more pronounced than that of herbivorous zooplankton (Figure 5). The mean biomasses of the herbivorous and carnivorous zooplankton communities, respectively, increased by 127 and 292% after the complete removal of the oyster-culture racks. Detrital mass also increased significantly.

Contrary to the observed increases in biomasses of phytoplankton and zooplankton, most of the mean biomasses of benthic invertebrates and fish communities decreased by 39–100% after the change (Figures 6 and 7). Barnacles and amphipods were rarely observed in the lagoon, although there were notable biomasses of polychaetes and detritivorous fish. The mean biomasses

Table 1. Predicted monthly changes in community biomasses (g WW m^{-2}) of the Tapong Bay model averaged, respectively, 2.5 years before and after June 2002, the time when all the oyster-culture racks were removed.

Group	Before (*n* = 30)	After (*n* = 30)	*t*-test	Change
1. Phytoplankton	3.38 ± 0.80	4.85 ± 1.26	−5.92***	+43%
2. Periphyton	86.0 ± 4.78	62.0 ± 8.19	16.0***	−28%
3. Herbivorous zooplankton	7.01 ± 4.61	107 ± 37.2	−16.1***	+1 440%
4. Carnivorous zooplankton	0.58 ± 0.74	18.8 ± 8.79	−12.5***	+3 156%
5. Oysters	353 ± 82.7	5.78 ± 16.0	26.6***	−98%
6. Polychaetes	3.73 ± 1.78	46.7 ± 19.5	13.2***	+1 151%
7. Gastropods	8.50 ± 3.96	107 ± 50.9	−11.6***	+1 161%
8. Bivalves	483 ± 184	6 415 ± 3262	−10.9***	+1 229%
9. Barnacles	2.29 ± 1.02	32.4 ± 16.3	−11.0***	+1 316%
10. Amphipods	3.10 ± 1.62	40.5 ± 17.3	−12.9***	+1 206%
11. Crabs	4.90 ± 1.26	61.8 ± 35.4	−9.63***	+1 164%
12. Shrimp	0.46 ± 0.22	9.96 ± 5.16	−11.3***	+2 049%
13. Herbivorous fish	4.42 ± 0.98	4.88 ± 2.16	−1.21	+10%
14. Zooplanktivorous fish	1.23 ± 0.40	6.12 ± 2.36	−12.2***	+396%
15. Benthic-feeding fish	4.63 ± 1.38	3.63 ± 0.50	5.67***	−21%
16. Detritivorous fish	16.5 ± 4.69	43.3 ± 15.1	−10.4***	+162%
17. Piscivorous fish	2.90 ± 0.70	32.6 ± 14.3	−12.4***	+1 024%
18. Detritus	15 375 ± 5 132	177 126 ± 61 097	−15.8***	+1 052%

***$p < 0.001$.
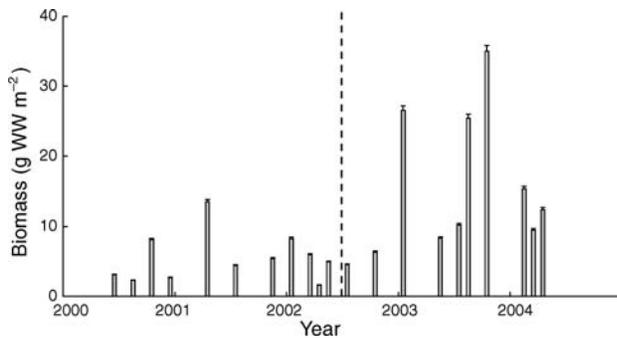
Figure 4. Observed changes in phytoplankton biomass in Tapong Bay before and after June 2002 (dashed line).

of polychaetes and detritivorous fish increased by 330 and 156%, respectively, after the complete removal, although the increase in polychaetes could not shown to be statistically significant because of the small number of samples (Table 2).

Discussion

The timing of the summer phytoplankton bloom in Tapong Bay, recorded by Su *et al.* (2004), was well represented in the Ecosim simulation. Despite there being a summer phytoplankton bloom, no clear seasonal pattern of herbivorous zooplankton, which feed primarily on phytoplankton, was shown by the Ecosim simulation. The lack of a clear seasonal pattern of zooplankton in the lagoon was also consistent with the results of a field study by Lo *et al.* (2004). This implies that temporal variations in zooplankton are not simply driven by phytoplankton, but might involve environmental factors or the top-down control by predators at higher levels. In this study, both the Ecosim simulation and the field observations demonstrated that variations in biomasses of herbivorous zooplankton appeared to follow a two-year cycle (Figures 3 and 5). This suggests that a

longer term study of >2 years is required to reveal temporal variations in zooplankton communities in this tropical lagoon.

The trends in biomass of phytoplankton, zooplankton, and detritivorous fish after the removal of the racks matched those predicted by Ecosim. Both the Ecosim predictions and the field observations showed that the biomass of these communities increased notably. Ecosim also predicted an immediate increase in detrital mass in the lagoon, consistent with the results of a separate survey (Hung, 2004) showing greater detritus accumulations of largely planktonic remains after June 2002. The increased detritus was attributable to the unused consumption of phytoplankton production by the now absent cultured oysters. It is clear, therefore, that changes in the biomass of phytoplankton, zooplankton, detritivorous fish, and detritus in the lagoon after the complete removal can be explained by their trophic relationships and the matter flows in the foodweb.

Both the Ecosim predictions and the field observations showed that the increase in the biomass of carnivorous zooplankton was more pronounced than that of herbivorous zooplankton. It is likely that other filter-feeders, including polychaetes and especially a large number of other bivalves, also competed with herbivorous zooplankton for the increased phytoplankton biomass (Figure 2). This is unlike the case of the carnivorous zooplankton because there are no other secondary consumers in sufficiently large numbers to compete for herbivorous zooplankton in the lagoon. Another contributing factor might be the disappearance of the jellyfish *A. aurita*, an important top-down controller of copepods (Lo *et al.*, 2008).

The magnitudes of the biomass increases in herbivorous and carnivorous zooplankton and detritus after the removal of the oyster-culture racks appear to have been overestimated by the Ecosim model compared with field observations. The reason for this is not clear. Kremer and Nixon (1978) indicated that the process of physical circulation in estuaries makes it difficult to investigate the dynamics of an ecological system without a hydrodynamic model that simulates at least the major tidal features. In

Table 2. Observed changes in community biomasses (g WW m^{-2}) in Tapong Bay averaged, respectively, 2.5 years before and after June 2002.

	Before		After			
Group	n	Mean ± s.d.	n	Mean ± s.d.	t-test	Change
1. Phytoplankton	11	5.48 ± 3.47	10	15.4 ± 0.66	−3.04**	+180%
3. Herbivorous zooplankton	30	5.30 ± 6.95	17	12.0 ± 8.45	−2.85**	+127%
4. Carnivorous zooplankton	30	0.45 ± 1.37	17	1.75 ± 2.39	−2.36*	+292%
6. Polychaetes	1	0.36	3	1.55 ± 0.52	−1.99	+330%
7. Gastropods	1	4.40	3	0.06 ± 0.12	37.4***	−98%
8. Bivalves	1	274	3	8.56 ± 10.2	22.6**	−97%
9. Barnacles	1	1.3	3	0.00 ± 0.00	−	−100%
10. Amphipods	1	0.51	3	0.01 ± 0.01	109***	−98%
11. Crabs	1	1.59	3	0.93 ± 1.62	0.35	−42%
12. Shrimp	1	0.12	3	0.06 ± 0.02	3.10*	−50%
13. Herbivorous fish	3	2.32 ± 0.64	4	1.34 ± 0.71	1.85	−42%
14. Zooplanktivorous fish	3	0.41 ± 0.19	4	0.13 ± 0.13	2.25*	−68%
15. Benthic-feeding fish	3	1.70 ± 0.30	4	1.04 ± 0.26	3.10*	−39%
16. Detritivorous fish	3	4.65 ± 3.20	4	11.91 ± 2.26	−3.56*	+156%
17. Piscivorous fish	3	2.06 ± 3.02	4	0.85 ± 1.70	0.68	−59%
18. Detritus	9	5 538 ± 1 773	6	7 336 ± 3 564	−1.93*	+32%
Total fish communities	3	11.14 ± 6.32	4	15.27 ± 3.47	−1.11	+37%
Pelagic fish	3	0.19 ± 0.23	4	0.70 ± 1.01	−0.57	+268%
Reef fish	3	3.33 ± 0.86	4	2.55 ± 1.04	0.48	−23%
Soft-bottom fish	3	7.62 ± 3.27	4	12.02 ± 2.15	−2.04*	+58%

Biomass levels of benthic invertebrates (i.e. groups 6–12) growing on the oyster-culture racks were excluded from the analyses.
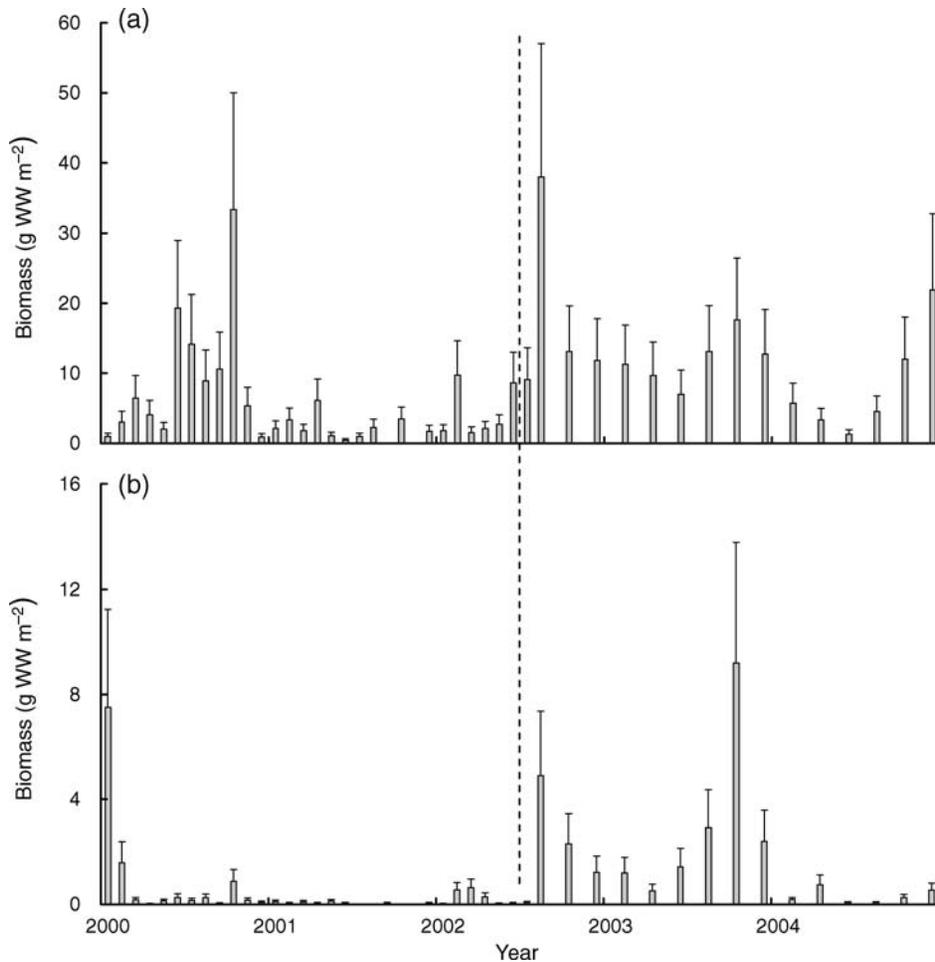*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Figure 5. Observed changes in biomass of (a) herbivorous zooplankton, and (b) carnivorous zooplankton in Tapong Bay before and after June 2002 (dashed line).
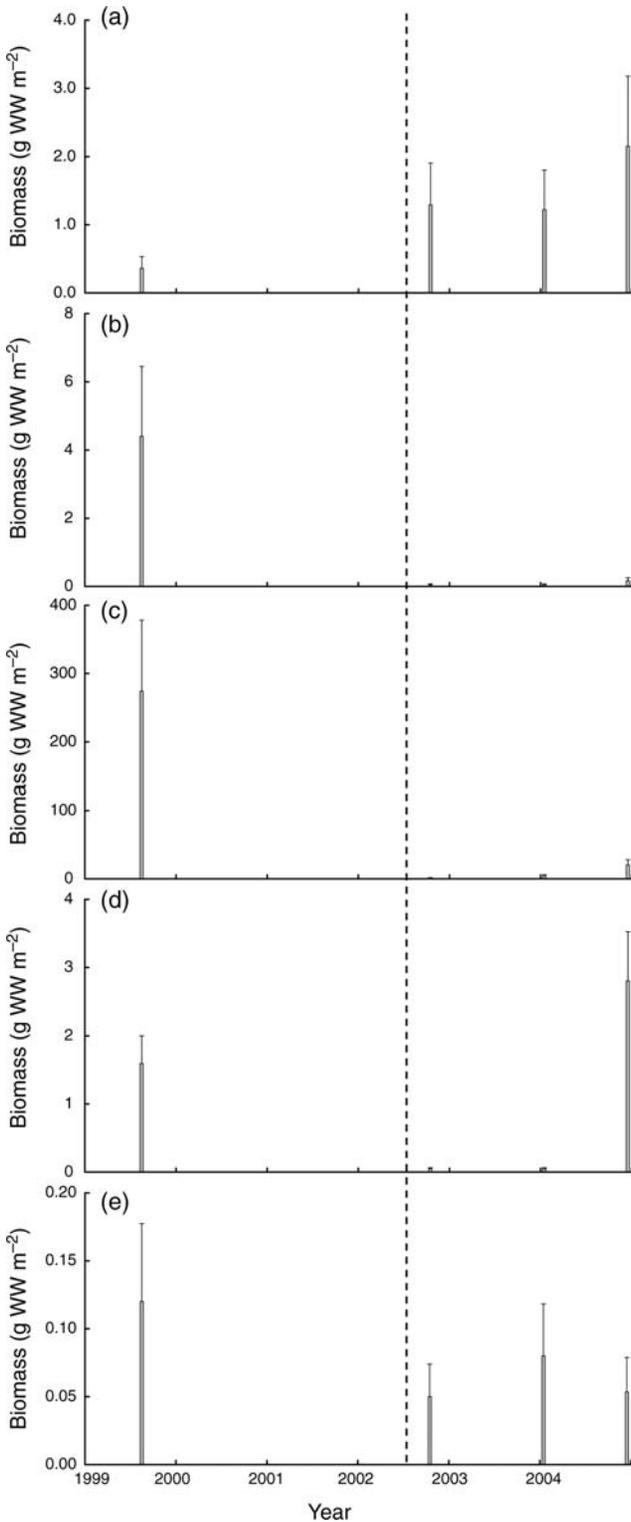
Figure 6. Observed changes in biomass of (a) polychaetes, (b) gastropods, (c) bivalves, (d) crabs, and (e) shrimp in Tapong Bay before and after June 2002 (dashed line).

Figure 7. Observed changes in biomass of (a) herbivorous fish, (b) zooplanktivorous fish, (c) benthic-feeding fish, (d) detritivorous fish, and (e) piscivorous fish collected by electric fishing in Tapong Bay before and after June 2002 (dashed line).

this study, the Tapong Bay model was constructed to represent our current understanding of the foodweb but, as indicated by Nugues *et al.* (1996), it cannot predict the compartmental changes that may result from changes in the hydrodynamic circulation resulting
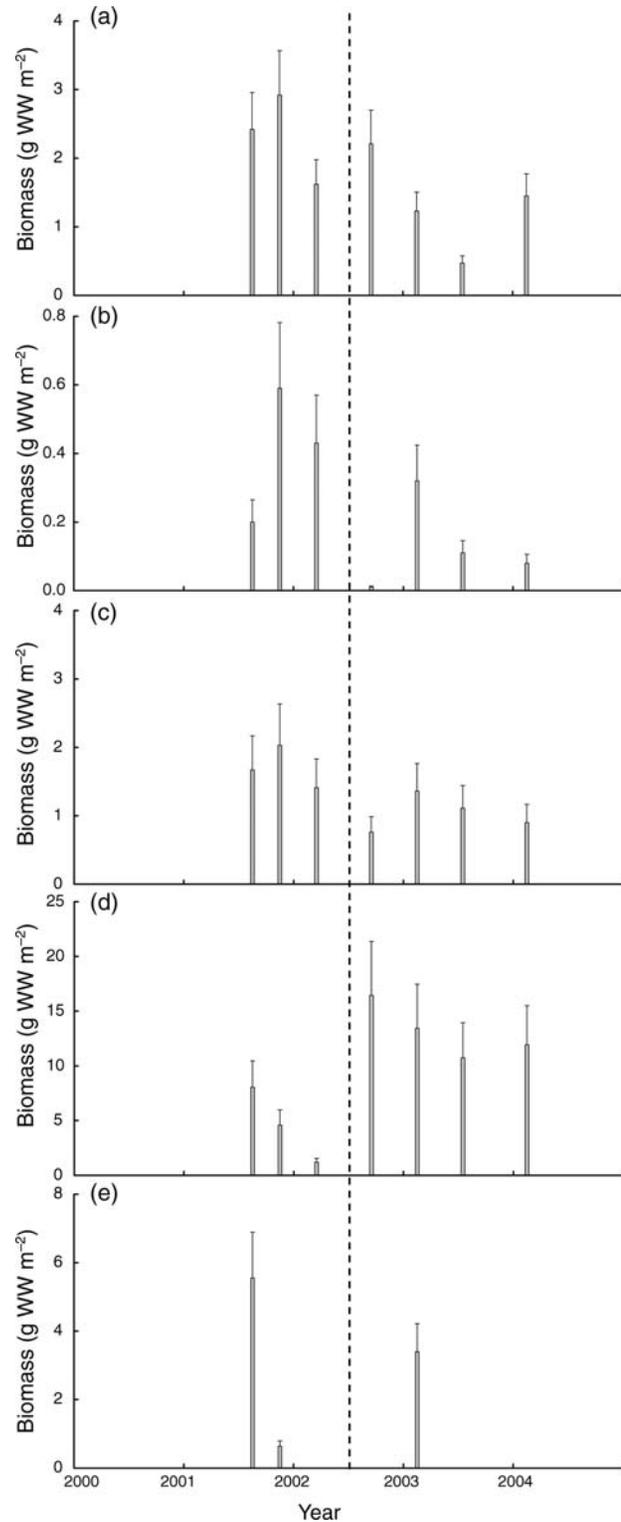
from the complete removal of oyster-culture racks. The change increased the water motion and reduced the mean residence time from 11.1 ± 0.6 to 6.1 ± 1.9 d (Hung, 2004), which might

have resulted in the flushing out of more zooplankton populations and detritus.

Another possibility is the occurrence of shifts in the phytoplankton composition after being released from the filtering pressure caused by the cultured oysters (Baker *et al.*, 1998; Pietros and Rice, 2003). The dominant species of the phytoplankton community shifted from the sole dominance of diatoms (Su *et al.*, 2004) to a co-dominance of diatoms, dinoflagellates, and cyanobacteria after the removal (Huang *et al.*, 2008). Langdon and Newell (1990) suggested that oyster particle retention was a function of cell size, with efficiency declining sharply for particles <2 μm. Similarly, Dupuy *et al.* (2000) found that the oyster *C. gigas* cannot retain picoparticles <5 μm, and suggested that microphytoplankton, particularly diatoms, were the main food resource for oysters. In Tapong Bay, the cell numbers of diatoms did increase remarkably, but their relative dominance decreased once the oyster-culture racks had gone (Huang *et al.*, 2008). Alternatively, the relative dominance levels by dinoflagellates and cyanobacteria increased. They might not have been preferentially grazed by herbivorous zooplankton, so the production rate of herbivorous zooplankton in the lagoon dropped after the complete removal. Further experiments and formulation of the relative roles of these factors should improve Ecosim modelling.

The responses of the fish communities to the changes made were, to some extent, unexpected. Both the Ecosim predictions and the field observations showed an increase in the biomass of detritivorous fish, as determined by the increased detrital mass that serves as their main food source in the lagoon. However, in contrast to the predicted increase in the biomasses of zooplanktivorous fish and piscivorous fish, field observations showed that the biomass of those fish decreased massively after the complete removal. This is surprising because the biomass of zooplanktivorous and piscivorous fish did not increase with the increasing biomass of their prey in the same period. When we reclassified the fish communities in Tapong Bay by habitat type, we found that the biomass levels of pelagic fish, dominated by *Sphyraena putnamae*, *Sphyraena jello*, *H. lacunosus*, and *A. buruensis*, and soft-bottom fish, dominated by *Liza macrolepis*, *A. berda*, *V. cunnesius*, and *N. come*, increased, but that of reef fish, dominated by *A. lateralis*, *L. argentimaculatus*, *Pelates quadrilineatus*, and *Apogon cookie*, tended to decrease after the racks had gone (Table 2). It is likely that their removal provided more space and hence supported colonization of the area by pelagic and soft-bottom fish. However, Posey (1988) found that the introduction of seagrasses may change the physical habitat as well as the richness and communities of resident fauna. In Tapong Bay, joint analyses of stomach contents and stable isotopes showed that periphyton on the oyster-culture racks was the most important assimilated food for the dominant fish species (Lin *et al.*, 2007). Powers *et al.* (2007) also found that macroalgal growth on the bottom mesh of hard clam *Mercenaria mercenaria* aquaculture leases supported elevated densities of mobile invertebrates and juvenile fish. The oyster-culture racks might have attracted reef fish by reducing predation or enhancing grazing on cultured oysters and the associated biofouling communities on the racks (Einbinder *et al.*, 2006). Although the protective mediation function of the oyster-culture racks was considered in the Ecosim simulations, our results suggest that their function as artificial habitats for reef fish was more significant than we originally had expected.

The Ecosim predictions were less satisfactory in determining the responses of benthic invertebrates to the changed environment. In contrast to the predicted increases in response to increased detrital mass, the field observations showed that the biomass of many benthic invertebrates remarkably decreased in response to the removal. Tew *et al.* (2008) suggested the protective function of the oyster-culture racks for shrimp and crabs in Tapong Bay. Another possibility is that the Ecosim simulations might fall short in representing biodeposition loading from the cultured oysters. Pietros and Rice (2003) found increased biodeposition rates in mesocosms with oysters. Mitchell (2006) estimated that mean daily biodeposition rates reached 39.6–180.5 g DW m^{-2} in Pipe Clay Lagoon, Australia, with a comparable cultured density of *C. gigas* as in Tapong Bay. Biodeposits from cultured oysters might provide a food source for benthic organisms (Newell, 1988). By modelling the impacts of oyster farming in Thau Lagoon, France, Chapelle *et al.* (2000) showed that nitrogen cycling and oxygen reduction in the water column were driven by biodeposition. Although Nugues *et al.* (1996) found that the mean numbers of individual and species of benthos were significantly lower in samples collected from beneath oyster-cultured zones than in adjacent, uncultured zones, they attributed the community changes to an increase in the organic and silt compositions and a reduction in the depth of the oxygenated layer of the culture zones. In Tapong Bay, DO in the bottom water improved and remained at >4.1 mg l^{-1} after the complete removal (Hung, 2004). In addition, much of the detritus at that time was largely planktonic remains (Hung, 2004). It is likely that the decreased biomass of benthic invertebrates resulted from a reduction of biodeposition from cultured ousters.

Although the impacts of oyster culture on coastal ecosystems are of great concern (Prins *et al.*, 1997; Kaiser, 2001), the complete removal of oyster-culture racks from Tapong Bay provided an opportunity to examine the impacts on an entire lagoon ecosystem. In Thau Lagoon, France, Chapelle *et al.* (2000) halved the oyster biomass in the model and found greater abundances of phytoplankton and zooplankton. In Marennes-Oléron Bay, France, however, Leguerrier *et al.* (2004) manipulated the density of cultured oysters in the model and found that primary and secondary production were enhanced by the presence of cultured oysters. They concluded that oyster culture had a small impact on the stability of their system, in which only 16% of the area was devoted to it. Our field observations support the suggestion of sustainability performance indicators, and clearly demonstrated that a high density of suspended oyster culture exerted a negative feedback on the plankton communities, but a positive feedback on benthic and fish communities in the lagoon.

Our field observations also provided an opportunity to evaluate the effectiveness of system-wide oyster restoration as an ecological tool for top-down control of phytoplankton blooms and to reverse cultural eutrophication in coastal lagoons. It has been argued that oysters are unlikely to be able to control phytoplankton blooms because of spatial and temporal mismatches between oyster and phytoplankton biomasses in coastal waters (Pomeroy *et al.*, 2006; Fulford *et al.*, 2007). Similarly, in a predictive model, Cerco and Noel (2007) showed that the effect of surface chlorophyll reduction by increased oyster biomass would be limited in deep waters. In Tapong Bay, temporal mismatches are unlikely because the oyster clearance rate would remain high year-round given the water temperature range of 22–32°C (Fulford *et al.*, 2007). Fluxes of N and P into Tapong Bay were higher than those of most Mexican tropical lagoons (Smith *et al.*, 1997).

Before the complete removal of oyster-culture racks in June 2002, however, the phytoplankton chlorophyll *a* concentrations were low to moderate when compared with those recorded in non-eutrophic Mexican lagoons (Lin *et al.*, 2006). After the oyster racks had gone, the rapid and dramatic increase in phytoplankton chlorophyll *a* was much greater than values reported in most estuaries and coastal lagoons (Boynton *et al.*, 1982). This suggests that a high density of suspended oyster culture might be a means for oysters to have access to all lagoon water and to control phytoplankton blooms, despite the summer stratification of lagoon water in the inner region. Additional ecological benefits of suspended oyster culture may be the increase in biodiversity by attracting reef fish and enhancing the biomass of benthic invertebrates. However, unlike the prediction of Cerco and Noel (2007) that oyster restoration is projected to increase deep-water DO, hypoxia in the bottom waters of Tapong Bay was not observed after the racks had gone. Conversely, the DO in bottom waters improved notably (Hung, 2004), which might be more related to the increased water motion and reduced flushing times.

Acknowledgements

References

Ahlstrom, E. H., and Thrailkill, J. R. 1960. Plankton volume loss with time of preservation. CalCOFI Report, 9: 57–73.

Baker, S. M., Levinton, J. S., Durdziel, J. P., and Shumway, S. E. 1998. Selective feeding and biodeposition by zebra mussels and their relation to changes in phytoplankton composition and seston load. Journal of Shellfish Research, 17: 1207–1213.

Bligh, E. G., and Dyer, W. J. 1959. A rapid method of total lipid extraction and purification. Canadian Journal of Biochemistry and Physiology, 37: 911–917.

Boutton, T. W. 1991. Stable carbon isotope ratios of natural material. 1. Sample preparation and mass spectrometric analysis. *In* Carbon Isotope Techniques, pp. 155–171. Ed. by D. C. Coleman, and B. Fry. Academic Press, NY. 260 pp.

Boynton, W. R., Kemp, W. M., and Keefe, C. W. 1982. A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. *In* Estuarine Comparisons, pp. 69–90. Ed. by V. S. Kennedy. Academic Press, NY. 704 pp.

Cerco, C. F., and Noel, M. R. 2007. Can oyster restoration reverse cultural eutrophication in Chesapeake Bay? Estuaries and Coast, 30: 1–13.

Chapelle, A., Ménesguen, A., Deslous-Paoli, J. M., Souchu, P., Mazouni, N., Vaquer, A., and Millet, B. 2000. Modelling nitrogen, primary production and oxygen in a Mediterranean lagoon. Impacts of oysters farming and inputs from the watershed. Ecological Modelling, 127: 161–181.

Chen, C. Y., Chen, J. P., and Shao, K. T. 2003. Spatial and temporal variations of the fish assemblage in the Tapon-Bay lagoon in the southern Taiwan. Journal of the Environmental Protection Society, ROC, 26: 71–95.

Chen, J. N. 2002. Numerical modeling of primary productivity in Tapong Bay. MSc thesis, National Sun Yat-sen University, Taiwan. 169 pp.

Christensen, V., Walters, C. J., and Pauly, D. 2005. Ecopath with Ecosim: a User's Guide. Fisheries Centre, University of British Columbia, Vancouver. November 2005 edn, 154 pp.

Clarke, K. R., and Warwick, R. M. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, UK. 144 pp.

Coen, L. D., Brumbaugh, R. D., Bushek, D., Grizzle, R., Luckenbach, M. W., Posey, M. H., Powers, S. P., *et al.* 2007. Ecosystem services related to oyster restoration. Marine Ecology Progress Series, 341: 303–307.

Crisp, D. J. 1971. Energy flow measurements. *In* Methods for the Study of Marine Benthos, pp. 197–279. Ed. by N. A. Holme, and A. D. McIntyre. IBP Handbook 16. Blackwell Scientific, Oxford. 334 pp.

Dame, R. F., Spurrier, J. D., and Wolaver, T. G. 1989. Carbon, nitrogen and phosphorus processing by an oyster reef. Marine Ecology Progress Series, 54: 249–256.

Dupuy, C., Vaquer, A., Lam-Höai, T., Rougier, C., Mazouni, N., Lautier, J., Collos, Y., *et al.* 2000. Feeding rate of the oyster *Crassostrea gigas* in a natural planktonic community of the Mediterranean Thau lagoon. Marine Ecology Progress Series, 205: 171–184.

Einbinder, S., Perelberg, A., Ben-Shaprut, O., Foucart, M. H., and Shashar, N. 2006. Effects of artificial reefs on fish grazing in their vicinity: evidence form algae presentation experiments. Marine Environmental Research, 61: 110–119.

FAO. 2004. The State of World Fisheries and Aquaculture. FAO, Rome. 153 pp.

Fulford, R. S., Breitburg, D. L., Newell, R. I. E., Kemp, W. M., and Luckenbach, M. 2007. Effects of oyster population restoration strategies on phytoplankton biomass in Chesapeake Bay: a flexible modeling approach. Marine Ecology Progress Series, 336: 43–61.

Funtowicz, S. O., and Ravetz, J. R. 1990. Uncertainty and Quality in Science for Policy. Kluwer, Dordrecht. 254 pp.

Gibbs, M. T. 2007. Sustainability performance indicators for suspended bivalve aquaculture activities. Ecological Indicators, 7: 94–107.

Hsieh, H. L. 2000. The detrital food webs on the Kaoping coast. 1. Detrital origin and distribution. Annual Report to National Science Council, Taiwan. 18 pp.

Hsieh, H. L., Chen, T. A., and Lin, H. J. 2003. Effects of eutrophication on the production of the oysters (*Crassostrea giga*) in Tapeng Lagoon. Journal of the Environmental Protection Society, ROC, 26: 135–151.

Huang, C. H., Lin, H. J., Huang, T. C., Su, H. M., and Hung, J. J. 2008. Responses of phytoplankton and periphyton to system-scale removal of oyster-culture racks from a eutrophic tropical lagoon. Marine Ecology Progress Series, 358: 1–12.

Hung, J. J. 2004. Biogeochemical process and fluxes of carbon, nutrients and trace elements in the Kaoping coastal zone. 3. Annual Report to National Science Council, Taiwan. 65 pp.

Hung, J. J., and Hung, P. Y. 2003. Carbon and nutrient dynamics in a hypertrophic lagoon in southwestern Taiwan. Journal of Marine Systems, 42: 97–114.

Kaiser, M. J. 2001. Ecological effects of shellfish cultivation. *In* Environmental Impacts of Aquaculture, pp. 51–75. Ed. by K. D. Black. Sheffield Academic Press, Sheffield, UK. 320 pp.

Kling, G. W., Fry, B., and O'Brien, W. J. 1992. Stable isotopes and planktonic trophic structure in Arctic lakes. Ecology, 73: 561–566.

Kremer, J. N., and Nixon, S. W. 1978. A Coastal Marine Ecosystem: Simulation and Analysis. Springer, New York. 217 pp.

Langdon, C. J., and Newell, R. I. E. 1990. Utilization of detritus and bacteria as food sources by two bivalve suspension-feeders, the oyster *Crassostrea virginica* and the mussel *Geukensia demissa*. Marine Ecology Progress Series, 58: 299–310.

Leguerrier, D., Niquil, N., Petiau, A., and Bodoy, A. 2004. Modeling the impact of oyster culture on a mudflat food web in Marennes-Oléron Bay (France). Marine Ecology Progress Series, 273: 147–162.

Lin, H-J., Dai, X-X., Shao, K-T., Su, H-M., Lo, W-T., Hsieh, H-L., Fang, L-S., *et al.* 2006. Trophic structure and functioning in a eutrophic and poorly flushed lagoon in southwestern Taiwan. Marine Environmental Research, 62: 61–82.

Lin, H-J., and Hung, J. 2004. Factors affecting macroalgal distribution in a eutrophic tropical lagoon in Taiwan. Marine Biology, 144: 653–664.

Lin, H-J., Kao, W-Y., and Wang, T. 2007. Analyses of stomach contents and stable isotopes reveal food sources of estuarine detritivorous fish in tropical/subtropical Taiwan. Estuarine Coastal and Shelf Science, 73: 527–537.

Lin, H-J., Wang, T-C., Su, H-M., and Hung, J. 2005. Relative importance of phytoplankton and periphyton on oyster-culture pens in a eutrophic tropical lagoon. Aquaculture, 243: 279–290.

Lo, W. T., Chung, C. L., and Shih, C. T. 2004. Seasonal distribution of copepods in Tapong Bay, southwestern Taiwan. Zoological Studies, 43: 464–474.

Lo, W-T., Purcell, J. E., Hung, J-J., Su, H-M., and Hsu, K. 2008. Enhancement of jellyfish (*Aurelia aurita*) populations by extensive aquaculture rafts in a coastal lagoon in Taiwan. ICES Journal of Marine Science, 65: 453–461.

MacDonald, J. S., and Green, R. H. 1983. Redundancy of variables used to describe importance of prey species in fish diets. Canadian Journal of Fisheries and Aquatic Sciences, 40: 635–637.

Mazouni, N., Gaertner, J. C., and Deslous-Paoli, J. M. 2001. Composition of biofouling communities on suspended oyster cultures: an *in situ* study of their interactions with the water column. Marine Ecology Progress Series, 214: 93–102.

Meyercordt, J., and Meyer-Reil, L. A. 1999. Primary production of benthic microalgae in two shallow coastal lagoons of different trophic status in the southern Baltic Sea. Marine Ecology Progress Series, 178: 179–191.

Mitchell, I. M. 2006. *In situ* biodeposition rates of Pacific oysters (*Crassostrea gigas*) on a marine farm in southern Tasmania (Australia). Aquaculture, 257: 194–203.

Morales, C. E., Harris, R. P., Head, R. N., and Tranter, P. R. G. 1993. Copepod grazing in the oceanic northeast Atlantic during a 6 week drifting station: the contribution of size classes and vertical migrants. Journal of Plankton Research, 15: 185–211.

Newell, R. I. E. 1988. Ecological change in Chesapeake Bay: are they the result of overharvesting the American oyster, *Crassostrea virginica*? *In* Understanding the Estuary: Advances in Chesapeake Bay Research, pp. 536–546. Ed. by M. P. Lynch, and E. C. Krome. Chesapeake Research Consortium, Edgewater, MD. 638 pp.

Nugues, M. M., Kaiser, M. J., Spencer, B. E., and Edwards, D. B. 1996. Benthic community changes associated with intertidal oyster cultivation. Aquaculture Research, 27: 913–924.

Officer, C. B., Smayda, T. J., and Mann, R. 1982. Benthic filter feeding: a natural eutrophication control. Marine Ecology Progress Series, 9: 203–210.

Opitz, S. 1996. Trophic interactions in Caribbean coral reefs. ICLARM Technical Report, 43. 341 pp.

Pai, S. C., Gong, G. C., and Liu, K. K. 1993. Determination of dissolved oxygen in seawater by direct spectrophotometry of total iodine. Marine Chemistry, 41: 343–351.

Palomares, M. L. D., and Pauly, D. 1989. A multiple regression model for predicting the food consumption of marine fish populations. Australian Journal of Marine and Freshwater Research, 40: 259–273.

Parsons, T. R., Maita, Y., and Lalli, C. M. 1984. A Manual of Chemical and Biological Methods for Seawater Analysis. Pergamon Press, Oxford. 184 pp.

Pauly, D. 1986. A simple method for estimating the food consumption of fish populations from growth data and food conversion experiments. Fishery Bulletin US, 84: 827–840.

Peterson, B. J., and Heck, K. L. 2001. An experimental test of the mechanism by which suspension feeding bivalves elevate seagrass productivity. Marine Ecology Progress Series, 218: 115–125.

Pietros, J. M., and Rice, M. A. 2003. The impacts of aquacultured oysters, *Crassostrea virginica* (Gmelin, 1791) on water column nitrogen and sedimentation: results of a mesocosm study. Aquaculture, 220: 407–422.

Pinnegar, J. K., and Polunin, N. V. C. 1999. Differential fractionation of $\delta^{13}C$ and $\delta^{15}N$ among fish tissues: implications for the study of trophic interactions. Functional Ecology, 13: 225–231.

Pomeroy, L. R., D'Elia, C. F., and Schaffner, L. C. 2006. Limits to top-down control of phytoplankton by oysters in Chesapeake Bay. Marine Ecology Progress Series, 325: 301–309.

Posey, M. H. 1988. Community changes associated with the spread of an introduced seagrass, *Zostera japonica*. Ecology, 69: 974–983.

Powers, M. J., Peterson, C. H., Summerson, H. C., and Powers, S. P. 2007. Macroalgal growth on bivalve aquaculture netting enhances nursery habitat for mobile invertebrates and juvenile fishes. Marine Ecology Progress Series, 339: 109–122.

Prins, T. C., Smaal, A. C., and Dame, R. F. 1997. A review of the feedbacks between bivalve grazing and ecosystem processes. Aquatic Ecology, 31: 349–359.

Reusch, T. B. H., and Willams, S. L. 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. Oecologia, 113: 428–441.

Riddle, M. J., Alongi, D. M., Dayton, P. K., Hansen, J. A., and Klumpp, D. W. 1990. Detrital pathways in a coral reef lagoon. Marine Biology, 104: 109–118.

Schwinghamer, P., Hargrave, B., Peer, D., and Hawkins, C. M. 1986. Partitioning of production and respiration among size groups of organisms in an intertidal benthic community. Marine Ecology Progress Series, 31: 131–142.

Smith, S. V., Ibarra-Obando, S., Boudreau, P. R., and Camacho-Ibar, V. F. 1997. Comparison of carbon, nitrogen and phosphorus fluxes in Mexican coastal lagoons. LOICZ Reports and Studies, 10. LOICZ, Texel, The Netherlands. 84 pp.

Sobczak, W. V., Cloern, J. E., Jassby, A. D., and Müller-Solger, A. B. 2002. Bioavailability of organic matter in a highly distributed estuary: the role of detrital and algal resources. Proceedings of the National Academy of Sciences of the United States of America, 99: 8101–8105.

Souchu, P., Vaquer, A., Collos, Y., Landrein, S., Deslous-Paoli, J. M., and Bibent, B. 2001. Influence of shellfish farming activities on the biogeochemical composition of the water column in Thau Lagoon. Marine Ecology Progress Series, 218: 141–152.

Su, H. M., Lin, H. J., and Hung, J. J. 2004. Effects of tidal flushing on phytoplankton in a eutrophic tropical lagoon in Taiwan. Estuarine Coastal and Shelf Science, 61: 739–750.

Sweeting, C. J., Polunin, N. V. C., and Jennings, S. 2006. Effects of chemical lipid extraction and arithmetic lipid correction on stable isotope ratios of fish tissues. Rapid Communications in Mass Spectrometry, 20: 595–601.

Taiwan Central Weather Bureau. 1999–2003. Climatological Data Annual Report. 1 Surface Data (Taiwan area). Taiwan CWB, Taipei. 173 pp.

Tew, K. S., Chou, W-R., Chuang, S-F., He, C-C., Liao, J-H., and Fang, S. 2008. Comparison of the decapod communities in an anthropogenic impacted lagoon and its adjacent coastal waters. Hydrobiologia, 607: 1–10.

Vega-Cendejas, M. E., Arreguin-Sanchez, F., and Herandez, M. 1993. Trophic fluxes on the Campeche Bank, Mexico. *In* Trophic Models of Aquatic Ecosystems, pp. 206–213. Ed. by V. Christensen, and D. Pauly. ICLARM Conference Proceedings, 26. 390 pp.

Walters, C., Christensen, V., and Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries, 7: 139–172.