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Carbon dynamics of Deep Bay, eastern Pearl River Estuary, China. I: A mass balance budget and implications for shorebird conservation

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ABSTRACT: Deep Bay is a shallow embayment (112 km^2) in the eastern Pearl River Estuary, China, and comprises 4 major wetland components: (1) a shallow brackish water body of 2.9 m average depth, (2) 2700 ha of intertidal mudflat, (3) 200 ha of tidal mangroves and (4) 300 ha of traditional tidal aquaculture ponds excavated in the mid-to-high intertidal region. A carbon budget is proposed for Deep Bay based on published information on the 4 major landscape components. Despite the usual emphasis placed on the role of mangroves as net carbon exporters in support of consumer (such as shorebird) populations, the carbon budget suggests that about 50% of all carbon available in Deep Bay originates from anthropogenic input from rapidly urbanising, as well as agricultural, areas in the local catchments. Mangrove production only contributes about 1.8% of the total carbon available in Deep Bay. Calculations based on the basal metabolic demands of the bird assemblage in winter suggest that the Deep Bay mudflats are close to carrying capacity. The annual carbon requirements of the shorebirds and availability (as demonstrated by the supply/demand ratio for the curlew) are lowest in the winter months, when bird numbers are large but production low. Considering the shorebird assemblage foraging on the mudflat, the total carbon consumption in January 1994 amounted to 16.9 t, while the carbon production during the same period was 27.8 t. These figures suggest that Deep Bay is near carrying capacity unless >50% of the invertebrate resources are made available to the birds. The results of this study also argue that organic enrichment in Deep Bay, which has usually been regarded as a 'pollutant', forms the basis of the major beneficial use of carbon (shorebird conservation), although further enrichment may result in negative impacts. This study highlights the importance of incorporating human influences into the study of the structure and function of ecosystems in urban settings.

KEY WORDS: Benthos · Hong Kong · Mangroves · Mudflat · Organic pollution · Carbon budget · Tidal ponds · Bird conservation

INTRODUCTION

Classic studies on mangrove-based food chains in Florida (e.g. Heald 1971, Odum 1971, Odum & Heald 1972, 1975, Odum et al. 1982) suggested that most mangrove litter was flushed from fringing and riverine forests by tidal action. Initial processing of litter

occurred in subtidal regions where leaf material was rapidly fragmented through the grazing action of crabs and amphipods (Heald 1971), followed by decomposition through fungal and bacterial activities (Heald 1971, Fell et al. 1975, Cundell et al. 1979). These detrital particles were then utilised by a variety of detritivores (Odum & Heald 1972, 1975). Tidal flushing was identified as the major agent determining the extent of export of mangrove organic matter (Twilley 1985, Twilley et al. 1986). The geomorphologic characteristics of a site have strong influences over the degree of export (Odum et al. 1979).

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The Florida model has been challenged by new findings from Indo-Pacific systems in the last decade. Robertson (1986) first demonstrated that leaf-consuming crabs *Sesarma* spp. played a significant role in litter turnover of mangrove ecosystems in the Indo-West Pacific, a phenomenon later supported by other studies. For example, Lee (1989b) reported that Sesarminae crabs were capable of consuming >57% of the daily leaf litter during their active season in a high intertidal *Kandelia candel* mangrove stand, and Emmerson & McGwynne (1992) estimated 44% consumption in a South African forest. Such *in situ* consumption by crabs reduces tidal export and may also initiate further processing of mangrove-derived organic carbon by way of coprophagous food chains based on crab faeces (Lee 1997).

Estimates of organic carbon export from intertidal wetlands range from 45% (Teal 1962, Axelrad et al. 1976, Twilley 1985) to less than 1% (Heinle & Flemer 1976) of their net production, while some intertidal wetlands may even import organic carbon (e.g. Woodwell et al. 1977, Lee 1990a, Asjes & Dankers 1994). Some authors consider exported mangrove particulate matter to be highly refractory and to have little influence on coastal food chains (Robertson et al. 1992). Recent application of carbon isotope techniques in subtropical and tropical mangrove systems (e.g. Rodelli et al. 1984, Rezende et al. 1990, Hemminga et al. 1994) has indicated that the number of consumers in tropical coastal regions adjacent to mangrove forests that are dependent on mangrove carbon is smaller than that suggested by the classic paradigm. The influence, if significant, is often of limited spatial extent (e.g. Moran et al. 1991). These findings have highlighted the need for a reassessment of the role of mangroves in nearshore trophodynamics, and the need to incorporate local as well as biogeographic variations in ecosystem function. Mangrove outwelling has recently been reviewed by Lee (1995a). After examining 26 post-1975 reports on mangrove material exchange with nearshore systems, this author concluded that, while most mangroves tend to export, the magnitude and direction of exchange depend on the chemical species and that export is usually smaller than previously assumed in most systems.

Another recent development that has largely been ignored in mangrove ecosystem studies is the influence of anthropogenic changes on ecosystem function. Mangroves are globally under threat from urban development and consumptive utilisation (e.g. intensive prawn culture), resulting in the loss of about 1% of world mangrove areas every year (Hatcher et al. 1989). While human disturbance undoubtedly causes large-scale mangrove destruction, the impact of human activities and interference on the trophodynamics of mangrove-dominated coastal areas is yet to be documented. While classic arguments (e.g. that mangroves provide the dominant carbon source to tropical offshore fisheries and inshore consumers) are still being used to support mangrove conservation, the actual value of mangroves in human-impacted coastal food chains requires some reassessment.

Mangroves and their associated habitats, e.g. intertidal mudflats, often provide roosting and breeding areas for shorebirds, which are usually the top consumers of the system. In the eastern Pearl River Estuary in southern China, over 320 species of birds have been recorded from the mangrove-dominated Deep Bay wetlands, of which 22 are recognised as rare and endangered (Young 1995). Only around 16% of the total bird species found here are residents, with most other species being migrants or winter visitors (Young & Melville 1993). Deep Bay lies between China and Hong Kong and comprises the Futian (110 ha) and Mai Po (380 ha) wetlands, respectively, in the 2 political entities. Areas around Deep Bay are amongst the most rapidly urbanising areas in the Pearl River estuary. In the last 10 yr, the Mai Po-Futian wetlands of Deep Bay have been the topic of extensive scientific research both in Hong Kong and China, mainly because this wetland complex supports an increasingly large number of birds. The Hong Kong Bird Watching Society has been conducting mid-winter bird counts in Deep Bay each year since 1979 (except 1980). Data from the counts are published in the *Hong Kong Bird Report* annually, the latest number being a total of >68 000 birds being counted in various parts of Deep Bay in 1996. Lee (1989a, b, 1990a, b, c, 1991, 1992) and Anderson (1994) have studied the various aspects of the production ecology of mangroves of Mai Po. Li (1993, 1997) investigated mangrove ecology on the Futian side of Deep Bay. A number of studies (Chan 1989, Yang 1996, McChesney 1997) reported on various aspects of benthic invertebrate production and consumption by birds on the mudflats in Deep Bay.

This paper, a synthesis based on the above and other works, aims at profiling the carbon dynamics from information collected from the various habitats in the bay. The carbon budgets of the main landscape components are briefly discussed below. The contribution from these components to the carbon available on the mudflats in Deep Bay will then be calculated based on known or estimated rates of exchange between these components and Deep Bay. The relative importance of anthropogenic versus natural sources of food supplies available to the shorebird populations supported by the Deep Bay wetlands is assessed, with a discussion of the implications of these findings for shorebird conservation on the mudflats.

STUDY SITE

Deep Bay (or Shenzhen Bay, as it is called in China; 22.41 to 22.53° N, 113.88 to 114.00° E) is situated to the northwest of Hong Kong, lying between Hong Kong and south China. It is approximately 17.5 km long and between 4.2 and 10 km wide (Liu et al. 1988), covering an area of 112 km², and opens directly to the Pearl River Estuary to the southwest (Fig. 1). The 2 main local rivers discharging into Deep Bay are the Shenzhen River, forming the border, and the Shan Pui River, draining the largest agricultural area of Hong Kong. The head of Deep Bay *receives effluent from the Shenzhen* River, which flows through the Shenzhen Special Economic Zone in China, a metropolitan area with extremely rapid economic growth in the past 10 yr. Both sides of the Shenzhen River mouth are fringed with mangroves extending from east to west. The northern component is an 11 km long continuous mangrove belt (20 to 200 m wide) which was designated as the Futian Mangrove-Bird Nature Reserve by China in 1984. On the southern shores of Deep Bay lies the Mai Po Marshes Nature Reserve, designated in 1976 by the then Hong Kong government as an SSSI (Site of Special Scientific Interest) and declared as a Ramsar site in 1995. Both the Shenzhen and Shan Pui Rivers are heavily enriched with high organic loadings of domestic wastewater, especially from livestock wastes in the Shan Pui River catchment. The average water depth of the bay is only 2.9 m and, consequently, a large expanse of intertidal mudflats (2700 ha) is exposed during low tide. An irregular semidiurnal tide dominates this bay with a maximum tidal range of about 2.8 m. The annual average temperature (in 1995) is 22.8°C, with an average maximum of 31.2°C (June) and an average minimum of 13.5°C (February). The annual precipitation totals 2754.4 mm, with the rainy season lasting from April to September (Royal Observatory, Hong Kong 1995).

The ecological significance of the Deep Bay wetlands primarily lies in its capacity to support large populations of wintering and migrant birds. The total number of birds recorded in the most recent survey in January 1996 amounted to >68 000 individuals. In view of the immense conservation significance of the Deep
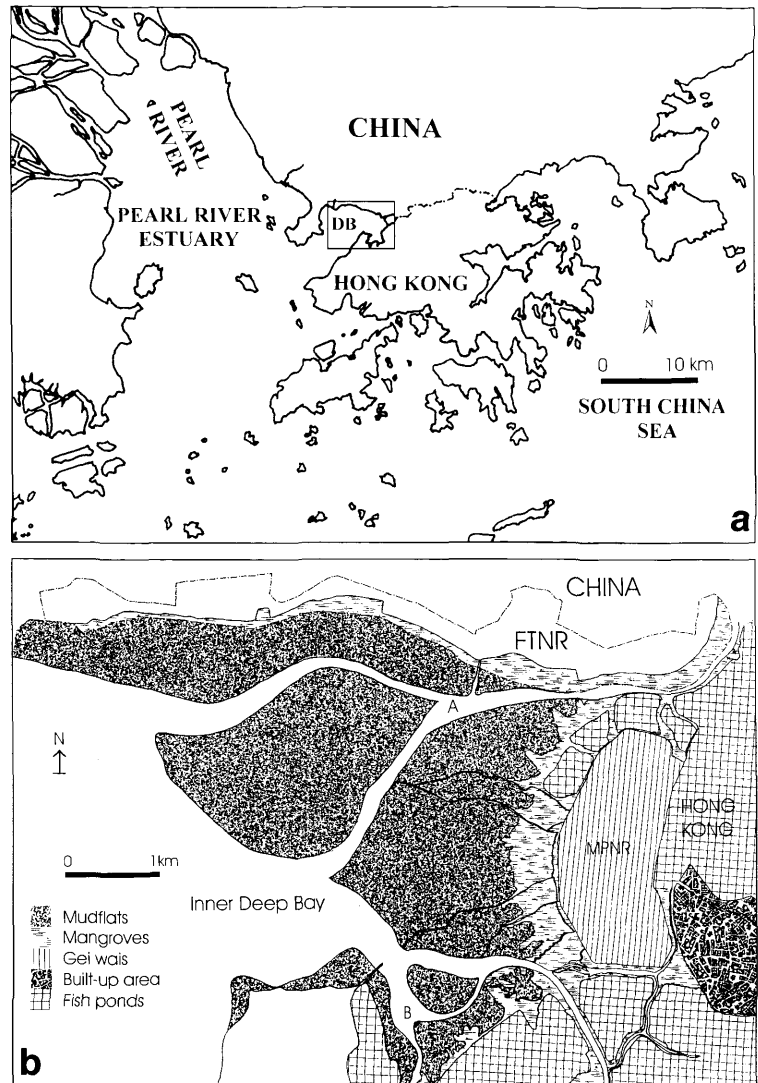

Fig. 1. (a) Geographic position of Deep Bay (DB) in the Pearl River estuary; box encloses the area of study. (b) Deep Bay study area. FTNR: Futian Mangrove-Bird Nature Reserve; MPNR: Mai Po Marshes Nature Reserve; A: Shenzhen River; B: Shan Pui River

Bay wetlands, the Hong Kong Government declared the southern half of the Deep Bay wetlands as Hong Kong's first and only Ramsar site in September 1995. The site comprises an area of 1500 ha of intertidal mudflat, mangrove forest, tidal aquaculture ponds and freshwater fish ponds in the northwestern extreme of Hong Kong (Fig. 1).

The Deep Bay wetlands comprise 4 different major habitat components: (1) large tidal aquaculture ponds (gei wai) in Mai Po, (2) tidal mangroves in Mai Po and Futian, (3) the intertidal mudflats, and (4) the water body. The characteristics and data available on the carbon dynamics of the 4 habitat types are briefly described below.

Mai Po gei wais

Gei wais (traditional tidal prawn farming ponds) in Mai Po were originally excavated from the mangrove in the 1940s (Irving & Morton 1988). Each pond is a rectangular impoundment with drainage channels and remnant mangrove stands dominated by *Kandelia candel*. There are now 270 ha of gei wais in operation, each with an average area of 9 to 10 ha. Each gei wai has a sluice gate (1.8 × 1.3 m) situated in a channel leading through the tidal mangroves and communicating with Deep Bay. The sluice gate allows water level management of the gei wai to be controlled. With decline in use and maintenance, the gei wais have been, of late, invaded by a more typically freshwater wetland species, *Phragmites communis* (Lee 1990b).

Tidal mangroves

Some 90 ha of tidal mangroves occur at Mai Po, measuring 3 km long and 200 to 500 m wide. The dominant species are *Kandelia candel*, *Aegiceras corniculatum* and *Avicennia marina*. Mangrove trees are, on average, 5 m tall but can be as high as 8 m. Unlike Mai Po, the Futian mangroves are narrower in width (20 to 200 m) and denser. The mangrove area at Futian approximates 111 ha. Here *A. corniculatum* forms relatively pure stands. The average height of this mangrove is 4.5 m, with no obvious vertical stratification. No gei wais exist but some unvegetated fish ponds occur in the back of the mangroves. Together with the forest at Mai Po, the Deep Bay mangroves represent the sixth most extensive mangrove forest along the south China coast (Li & Lee 1997). Entry to both mangroves is restricted because of their location in frontier areas.

Intertidal mudflat and overlying water

About 2700 ha of mudflats are exposed in inner Deep Bay during low tide. These mudflats host numerous benthic animals, which form the trophic basis for a large number of shorebirds every winter. More birds concentrate on the lower reach of the mudflat than on the upper reach. The mean water volume in Deep Bay is estimated at $3.3 \times 10^8 \, m^3$ (Han et al. 1988) with high turbidity (suspended solids averaged at 31.1 mg l^{-1}; Environmental Protection Department [EPD] 1994). Salinity falls to between 5 and 15 ‰ in the wet season but increases to 28–32 ‰ in the dry season, according to the degree of freshwater influx from both the local catchment and the Pearl River, which has a peak discharge of $1800 \times 10^6 \, m^3 \, d^{-1}$ (Broom & Ng 1996).

MATERIALS AND METHODS

A carbon budget requires information on the standing stock of the main ecosystem constituents, rates of net primary production, rates of production and consumption by the main heterotrophs, storage and export. The basic information required for the calculation of these parameters is derived from various sources of published data on Mai Po and Futian (Table 1). Important fluxes and storage values are identified and quantified, as much as possible, for each of the habitat components in the bay. It should be noted, however, that this study aims to provide an overview of the pattern of carbon dynamics rather than details of the individual processes driving the pattern. Readers are referred to the respective studies for a more in-depth treatment of the component processes. The assumptions and limitations of the calculations reported upon are discussed where appropriate.

Mangroves. Some structural differences exist between mangroves in Mai Po and Futian. The mangroves in Futian are much denser than in Mai Po (11 043 vs 5650 stems ha^{-1}) and have a higher proportion of *Aegiceras corniculatum* (62.6 vs 41.7%) and *Kandelia candel* (31.1 vs 24.3%) but a much lower *Avicennia marina* (6.3 vs 34.1%) abundance. The biomass, NAPP (net aboveground primary production), and litter production of pure *K. candel/A. marina* forests in Mai Po and a pure *A. corniculatum* stand in Futian have been reported respectively by Anderson (1994) and Li (1993). Consumption by crabs and storage and export of the litter of pure *K. candel* and *A. marina* stands, as well as herbivory on *K. candel* and *A. marina* leaves have been documented (Lee 1989a, Anderson 1994, Kwok 1995), but are not available for *A. corniculatum*. Since the C/N ratio of *A. corniculatum* leaves is close to that of *K. candel* (Li 1993), the rates of herbivory, consumption, storage and export for *K. candel* have been used to allow a rough estimate for *A. corniculatum*. Li (1993) and Li et al. (in press) have measured the carbon contents of different tissues including litter components, for the 3 species. To calculate the carbon budget of the whole mangroves (generally the mixed forest), the extensive mangrove survey data for Mai Po (Peking University 1995) and in Futian (Chen et al. 1996) were used to convert the above values obtained from pure stands into the equivalents for the actual forests. These forest values were obtained by dividing the density of *K. candel/A. corniculatum* and *A. marina* in the Mai Po and Futian forests by their respective density values in the pure stands (Table 2). The net amount of organic carbon exported from these forests was then estimated based on the areal extent of the trees and the production and export rates documented in Li (1993) and Anderson (1994).

Table 1. Data sources for information used in this study. NAPP = net aboveground primary production; TOC = total organic carbon; POC = particulate organic carbon; BOD_5 = biochemical oxygen demand

Habitat	Parameter	Source
Mangroves (Mai Po and Futian)	Tree density	Peking University (1995), Anderson (1994), Chen et al. (1996), Li (1993)
	NAPP, litter fall rate	Anderson (1994), Li (1993), Li et al. (in press)
	Storage, consumption, export	Anderson (1994)
	Herbivory	Anderson (1994), Anderson & Lee (1995)
	TOC content	Li (1993), Lee (1990a, 1993)
	Benthic algal biomass	Anderson (1994)
Gei wais	NAPP of *Kandelia candel* and *Phragmites communis*	Lee (1990a, b)
	Benthic algal biomass and phytoplanktonic productivity	Lee (1990a)
	Herbivory	Lee (1990c)
	Litter fall rate and turnover	Lee (1989a, b)
	Sedimentation	Lee (1990a)
	Harvest of prawns and fish	Cha et al. (1996)
Mudflats	Benthic algal biomass	Anderson (1994), Yang (1996)
	Biomass and production of benthic invertebrates	McChesney (1996)
	Mudskipper biomass and catch	Chan (1989), Young & Melville (1993)
	Bird count	Hong Kong Bird Watching Society (1995)
	Curlew's dietary demand	Melville et al. (1995)
Water body	Phytoplanktonic productivity	Huang et al. (1996)
	POC content and equation	Chen et al. (1990), Environmental Protection Department (EPD) (1995)
	Volume and turnover rate	Han et al. (1988)
Allochthonous input	BOD_5 to TOC equation	Xie (1989)
	Water quality data	EPD (1995), Peking University (1995)

Table 2. The density-based conversion factors used to convert the data from pure mangrove stands to the actual mangrove forests in Mai Po and Futian

Species	Density in pure stands (stems ha^{-1})	Density in actual mangroves		Conversion factors	
		Mai Po	Futian	Mai Po	Futian
		(stems ha^{-1})			
Kandelia candel	11170	1370	3429	0.1226	0.3070
Avicennia marina	5450	1926	700	0.3534	0.1284
Aegiceras corniculatum	15657	2354	6914	0.1503	0.4416
Total		5650	11043		

Gei wais. The 24 prawn ponds (gei wai) in Mai Po support extensive stands of mangroves (17.5 ha) and reed (46 ha) in the central islands (Cha et al. 1996). The major primary producers in the ponds are *Kandelia candel*, *Phragmites communis*, macroalgae and phytoplankton, and consumers in the stands are mainly sesarmine crabs. All ponds are operated in the traditional manner, i.e. with no fertilisation or artificial stocking of the cultured species. The total carbon production, consumption and exchange with Deep Bay were calculated with the values collected from one of the ponds (Lee 1990a) multiplied by the respective areas of each compartment. Overall rates of herbivory loss, detritus export and consumption by crabs could then be estimated collectively for the gei wais. Harvest from the gei wais (mainly for the penaeid *Metapenaeus ensis* and fish *Sparus latus* and *Mugil cephalus*) was estimated from the mean values of the 7 ponds managed by World Wide Fund for Nature Hong Kong (Cha et al. 1996). Carbon content was not determined for prawns and fish and a TOC (total organic carbon) value of 15% of the wet weight was assumed.

Mudflats. Benthic microalgae are the main primary producers on the mudflat. Yang (1996) studied the dynamics of the microalgal community on the intertidal mudflat over 18 mo and recorded consistently higher (1 to 3.5×) phaeopigment concentrations over those of chlorophyll *a*. This pattern probably suggests a high turnover rate of the microalgal assemblage. Assuming that annual production is 3 times as large as the peak benthic algal biomass, the carbon production can be estimated with an average organic carbon content of 35% (Lee 1990a). Carbon:chlorophyll *a* ratios of 62 and 42% (Valiela 1995) were used, respectively, for the conversion to biomass values for the phytoplankton and sediment microalgae from chlorophyll *a* values (Liu et al. 1988, Chiu 1992). Invertebrate production on the mudflat was obtained from McChesney (1997), who estimated production following the method of Crisp (1984).

Water body. Deep Bay is the only narrow-mouth inlet in the Pearl River Estuary, which is the outlet of the largest river in south China, the Pearl River. Tidal exchange between Deep Bay and the Pearl River estuary is effected through tidal currents twice a day. The semi-residence time of Deep Bay water was documented to be nearly 4 d (Han et al. 1988); hence, the daily water exchange between Deep Bay and the estuary was about 4.125×10^7 m^3. Chen et al. (1990) reported that the POC (particulate organic carbon) concentration in this estuarine water body had an average of 292.7 µg l^{-1} (average of 22 measurement points) and this was determined by the salinity and pH of the water. Since this relation is rarely adopted for predicting POC concentrations, an alternative method of estimation was used. The POC content of inner and outer Deep Bay was calculated using the annual average suspended solids level reported in EPD (1995), and with an assumed organic carbon content of the suspended solids at 1.5%. An organic content value lower than those recorded from Shan Pui River and Shenzhen River is adopted in view of the predominantly inorganic nature of the suspended matter load in the Pearl River. The average POC value of Deep Bay was used to calculate the daily carbon flux to the estuary carried by tidal water. Carbon production by phytoplankton in the water column was calculated based on values measured by Huang et al. (1996) in the Pearl River estuary.

Anthropogenic input. The equation TOC = $1.6(BOD_5) + 21.8$ (r = 0.97, n = 18) (Xie 1989), where BOD_5 is the biological oxygen demand, was employed to estimate the anthropogenic carbon input into Deep Bay through the heavily polluted Shenzhen and Shan Pui Rivers. BOD_5 values of the 2 rivers were from EPD (1995) and Peking University (1995). Due to the expected lower levels of diffused input and the general lack of detailed information, other potential carbon sources, such as rainwater runoff from the hinterlands were excluded in this investigation. TOC from the 2 river sources was computed from the BOD_5 values over the course of a year and all TOC was assumed to be exported from the rivers into Deep Bay. This is probably an overestimation but there is to date no actual measurement of the percentage of the TOC retained by the 2 rivers.

Bird utilisation of the carbon source. At all times, only a fraction of the benthos is available to the birds. The extent of utilisation of the benthos by birds depends on both accessibility of the benthos and energetic profitability for the birds. Animals that burrow deeper than the birds can reach or exhibit active avoidance behaviour in the presence of predators are frequently inaccessible. Those with too large a size to be ingested or that are too small to be energetically profitable are usually not chosen by the birds. Of the birds regularly using the Deep Bay mudflat, only curlew have bills long enough to be capable of harvesting benthos to a depth of 12 cm (Melville & Morton 1983, McChesney 1996), and they are observed to forage mostly on the mudflats. The case of the curlew was therefore used to demonstrate the level of resources available to birds in Deep Bay. The number of curlew for each of the months of 1994 was obtained from Hong Kong Bird Watching Society (1995). The carbon requirement of the curlew population was then estimated following equations relating basal metabolic rate and body biomass (Miere et al. 1994) and with a knowledge of the number of individuals on the mudflat. We are aware of the differences between field and basal metabolic rate (Pienkowski et al. 1984, Bryant & Tatner 1991, Koteja 1991) but, as field rates are generally unavailable for the local species, the calculation here is based on basal metabolic rates estimated from body mass. The capacity of the mudflats to support the curlew population was then evaluated by calculating a supply to demand ratio (S/R) for the various months based on the total carbon requirement of the population and the biomass available on the mudflat at various times.

A second approach was adopted for estimating the capacity of Deep Bay to support wintering shorebird populations. The numbers of individuals of the major species of birds recorded in the mid-winter count conducted by the Hong Kong Bird Watching Society in January 1994 were used to calculate the carbon requirements of the bird assemblage in a peak winter migration period. The total carbon requirements of the birds were estimated following the same approach as in the curlew calculation, i.e. based on published data of bird body weight and basal metabolic rate. The requirement was then compared with the amount of

carbon available to the birds during the same period as an indication of the carrying capacity of the Deep Bay wetlands.

RESULTS

Mangrove forests

Generally, the production figures in Futian are higher than those in Mai Po, owing to its larger area (111 vs 90 ha) and higher tree density (11 043 vs 5650 stems ha^{-1}) (Table 3). *Aegiceras corniculatum* contributed most to the net aboveground primary productivity (NAPP), while *Avicennia marina* ranked last in both mangrove areas. The litter/production ratio was close to 1 for *A. marina*, but much lower for *A. corniculatum* and *Kandelia candel*, indicating that these 2 species were accumulating carbon in the community. Most litter types (leaves, twigs and small branches) probably decompose and recycle within 1 yr (Lee 1989a, b, Gong & Ong 1990). Lee (1989a) and Kwok (1995) showed that the sesarmine crabs (mainly *Perisesarma* spp. and *Parasesarma* spp.) which are abundant in the mangroves played an important role in mangrove litter turnover. Calculations based on the density figures and the consumption rate of the crabs suggest that crabs consume 34.2 and 23.5% of the litter production in the Mai Po and Futian mangroves, respectively.

Herbivory is another pathway of energy transfer apart from detritivory. Herbivory rate (7.8% of NAPP) of *Avicennia marina* is higher than that of *Kandelia candel* (4.0% of NAPP), probably due to the lower C/N ratio but higher toughness of the latter species. A recent phenomenon is that *A. marina* in the Deep Bay mangrove experiences intense herbivory almost every summer such that within 3 mo most trees are defoliated by a lepidopteran larva (Anderson & Lee 1995), but this is excluded from the present carbon budget calculation because of its transient nature. Grazing loss on benthic algae was not determined in these mangrove areas but is expected to be high. Benthic algal production was 2.5 and 3.6 t C yr^{-1}, respectively, in Mai Po and Futian, accounting for only 0.9 and 0.5% of the total NPP (net primary production) in the mangroves. *A. marina* usually has a more open canopy than the other 2 species in this forest; higher abundance of *A. marina* in the Mai Po mangrove allows more light penetration to the stand, thus leading to a relatively higher algal production than in Futian. Lee (1990a) found that production predictions based on benthic algal biomass underestimated net production by 12%; the above values may, therefore, be lower than the real production. Assuming that all benthic algal production was exported from mangroves, the carbon export was estimated to be 150.5 (50.4% of NAPP) and 440.3 t yr^{-1} (56.6% of NAPP) for Mai Po and Futian mangroves. The total export from mangroves amounted to 590.7 t C yr^{-1}, which may be an important food source for the secondary producers in Deep Bay.

Gei wais

Gei wais in Mai Po comprise a raised zone of mangrove stands surrounded by a shallow canal (usually <1 m). These mangroves are rarely inundated (<10%

Table 3. Carbon budget of mangroves in Mai Po and Futian. All values are in t C yr^{-1}. NAPP = net above-ground primary production; NPP = net primary production

Mangrove	NAPP(NPP)	Herbivory	Litter fall	Storage decomposition	*In situ* consumption	Crab litter consumption	Export
Mai Po							
Kandelia candel	90.0	3.6	76.8	5.7	0.6	13.7	56.9
Aegiceras corniculatum	126.9	4.2	69.9	6.9	0.8	16.7	69.4
Avicennia marina	79.2	6.2	71.8	5.3	0.6	44.4	21.7
Benthic algae	2.5						2.5
Sub-total	298.6	14.0	218.5	17.9	2.0	74.8	150.5
Futian							
Kandelia candel	279.7	11.1	237.6	17.5	2.0	42.3	175.7
Aegiceras corniculatum	459.5	15.2	252.6	25.1	2.8	60.5	251.3
Avicennia marina	35.5	2.8	32.3	2.4	0.3	19.9	9.7
Benthic algae	3.6				3.6		
Sub-total	778.3	29.1	522.4	45.0	5.1	122.7	440.3
Total	1077.0	43.1	740.9	62.8	7.1	197.5	590.7

carbon available to the birds during the same period as an indication of the carrying capacity of the Deep Bay wetlands.

RESULTS

Mangrove forests

Generally, the production figures in Futian are higher than those in Mai Po, owing to its larger area (111 vs 90 ha) and higher tree density (11043 vs 5650 stems ha^{-1}) (Table 3). *Aegiceras corniculatum* contributed most to the net aboveground primary productivity (NAPP), while *Avicennia marina* ranked last in both mangrove areas. The litter/production ratio was close to 1 for *A. marina*, but much lower for *A. corniculatum* and *Kandelia candel*, indicating that these 2 species were accumulating carbon in the community. Most litter types (leaves, twigs and small branches) probably decompose and recycle within 1 yr (Lee 1989a, b, Gong & Ong 1990). Lee (1989a) and Kwok (1995) showed that the sesarmine crabs (mainly *Perisesarma* spp. and *Parasesarma* spp.) which are abundant in the mangroves played an important role in mangrove litter turnover. Calculations based on the density figures and the consumption rate of the crabs suggest that crabs consume 34.2 and 23.5% of the litter production in the Mai Po and Futian mangroves, respectively.

Herbivory is another pathway of energy transfer apart from detritivory. Herbivory rate (7.8% of NAPP) of *Avicennia marina* is higher than that of *Kandelia candel* (4.0% of NAPP), probably due to the lower C/N ratio but higher toughness of the latter species. A recent phenomenon is that *A. marina* in the Deep Bay mangrove experiences intense herbivory almost every summer such that within 3 mo most trees are defoliated by a lepidopteran larva (Anderson & Lee 1995), but this is excluded from the present carbon budget calculation because of its transient nature. Grazing loss on benthic algae was not determined in these mangrove areas but is expected to be high. Benthic algal production was 2.5 and 3.6 t C yr^{-1}, respectively, in Mai Po and Futian, accounting for only 0.9 and 0.5% of the total NPP (net primary production) in the mangroves. *A. marina* usually has a more open canopy than the other 2 species in this forest; higher abundance of *A. marina* in the Mai Po mangrove allows more light penetration to the stand, thus leading to a relatively higher algal production than in Futian. Lee (1990a) found that production predictions based on benthic algal biomass underestimated net production by 12%; the above values may, therefore, be lower than the real production. Assuming that all benthic algal production was exported from mangroves, the carbon export was estimated to be 150.5 (50.4% of NAPP) and 440.3 t yr^{-1} (56.6% of NAPP) for Mai Po and Futian mangroves. The total export from mangroves amounted to 590.7 t C yr^{-1}, which may be an important food source for the secondary producers in Deep Bay.

Gei wais

Gei wais in Mai Po comprise a raised zone of mangrove stands surrounded by a shallow canal (usually <1 m). These mangroves are rarely inundated (<10%

Table 3. Carbon budget of mangroves in Mai Po and Futian. All values are in t C yr^{-1}. NAPP = net above-ground primary production; NPP = net primary production

Mangrove	NAPP(NPP)	Herbivory	Litter fall	Storage de- composition	*In situ* con- sumption	Crab litter consumption	Export
Mai Po							
Kandelia candel	90.0	3.6	76.8	5.7	0.6	13.7	56.9
Aegiceras corniculatum	126.9	4.2	69.9	6.9	0.8	16.7	69.4
Avicennia marina	79.2	6.2	71.8	5.3	0.6	44.4	21.7
Benthic algae	2.5						2.5
Sub-total	298.6	14.0	218.5	17.9	2.0	74.8	150.5
Futian							
Kandelia candel	279.7	11.1	237.6	17.5	2.0	42.3	175.7
Aegiceras corniculatum	459.5	15.2	252.6	25.1	2.8	60.5	251.3
Avicennia marina	35.5	2.8	32.3	2.4	0.3	19.9	9.7
Benthic algae	3.6				3.6		
Sub-total	778.3	29.1	522.4	45.0	5.1	122.7	440.3
Total	1077.0	43.1	740.9	62.8	7.1	197.5	590.7

time) by tidal water (Lee 1990a). Impoundment and reduced tidal influence have resulted in a gradual transition to a more freshwater-wetland habitat, as is reflected by the spread of the reed *Phragmites communis*. The main producers, *Kandelia candel* and *P. communis*, contributed more than 95 % of the total production in gei wais (Table 4). The macroalgae community was dominated by the chlorophyte *Enteromorpha crinata* and peak biomass was reached in late April (Lee 1990a), with an annual carbon production of 17.9 t. Phytoplankton production (6.3 t C yr^{-1}) was negligible because of the high turbidity in the tidal water and frequent cropping through tidal water exchange. Unlike in tidal mangroves, in gei weis almost all vascular plant litter was decomposed or consumed *in situ*, resulting in little export to and out of the ponds (Table 4). The total carbon export to the ponds was 24.6 t yr^{-1}, of which 98 % was from non-vascular plants. Mangroves (or reeds) are unlikely to provide significant amounts of food for the cultured species in the ponds as expected. The water-column consumers (prawns and fish) have to derive their carbon from allochthonous sources. The tidal water from Deep Bay compensated for the carbon deficit in the ponds by carrying in 988.4 t each year and this becomes the major carbon source in the water column. Lee (1990a) reported an extremely high sedimentation rate of 1.7 cm yr^{-1} inside the ponds and this land-building process through accretion and litter accumulation seems to pose a problem to the prawn farming practice. Annual prawn and fish production in Mai Po gei wais were estimated to be 5.0 and 8.1 t, equivalent to 0.8 and 1.2 t C, respectively. The average prawn harvest from gei wais has declined significantly in the last 6 yr, and this decline may be attributed to the abundance of predatory fish in the gei wais and dwindling larval abundance due to increasing water pollution in Deep Bay (Cha et al. 1996). This reduction, together with commercial harvest, decreases the food available for birds when the intertidal mudflats are inaccessible as feeding grounds during high tides.

Mudflats

The primary production of microalgae (dominated by the diatom *Nitzchia palea*) on the mudflat was estimated to be 1462.2 t C yr^{-1} (Table 5). Although this may be an underestimate, it is more than 5 times higher than figures in the mangrove stands. Secondary production on the mudflat was assessed separately for 3 groups of organisms: crabs (mainly *Macropthalmus* spp.), other invertebrates (including gastropods, bivalves, polychaetes and oligochaetes) and mudskippers. Crabs on the mudflat are less abundant than in the mangroves (dominated by sesarmines), and the upper mudflats (dominated by *Uca* spp.) adjoining mangroves usually have more crab burrows than the lower mudflats (McChesney 1997). Crab production based on the density values was estimated to be 40.7 t C yr^{-1} for the whole mudflat. Other invertebrates' production amounted to 657.8 t C yr^{-1} (Table 5). Benthic invertebrate production varied from month to month, and the production to average biomass ratio (P/B) for the Mai Po mudflat was approximately 3 (McChesney 1997). Three species of mudskippers, i.e. *Periophthalmus cantonensis*, *Boleophthalmus pectinirostris*, and *Scartelaos viridis*, were found on the Mai Po mudflat. The average density was 3.9 ind. m^{-2} (Chan 1989) and the mean wet weight was assumed to be 8 g (Young & Melville 1993). These implied an annual production of 2540.2 t, equivalent to 381.0 t C on the mudflat using the P/B ratio of 3. The total secondary production on the mudflat therefore amounted to 1079.5 t C yr^{-1} (crabs + other invertebrates + mudskippers). These mudflat benthos are the base of the food supply for the resident and migrant birds foraging in Deep Bay.

Traditionally, the mudflats in Deep Bay have supported a local fishery harvest of mudskippers and other mangrove-associated fauna, e.g. the mangrove crab *Scylla serrata* and the large goboid fish *Bostrichthys sinensis*, but this harvest has declined recently. No detailed work has been done on the amount of mudskippers collected by the fishermen, but Young &

Table 4. Carbon dynamics in Mai Po gei wais. Carbon exchange in dissolved form is excluded from the calculation. All values are in t C yr^{-1}. NAPP = net aboveground primary production; NPP = net primary production

Source	NAPP(NPP)	Herbivory rate	Litter	Storage in stands	Export to the ponds	Harvest from the ponds
Kandelia candel	152.1	4.9	87.5	87.2	0.3	
Phragmites communis	353.9	0	81.3	81.3	0.1	
Phytoplankton	6.3				6.3	
Algae	17.9				17.9	
Sedimentation					988.4	
Prawns						0.8
Fish						1.2

Table 5. Total carbon production on the mudflat and in the water column of Deep Bay, and the allochthonous carbon input into Deep Bay from Shenzhen River, Shan Pui River and the Pearl River estuary. Productivity/availability rates are calculated based on areas of 2700 ha and 11 200 ha for the mudflat and the water body, respectively

Source	Total production (t C yr^{-1})	Productivity/availability rate (t C ha^{-1} yr^{-1})
Autochthonous sources		
Autotrophic production		
Phytoplankton	12631.9	1.13
Benthic algae	1462.2	0.54
Heterotrophic production		
Crabs	40.7	0.015
Other invertebrates	657.8	0.24
Mudskippers	381.0	0.14
Sub-total	15173.6	
Allochthonous sources		
Shenzhen River	9076.7	0.81
Shan Pui River	12715.7	1.14
Pearl River estuary	−2065.9	−0.18
Sub-total	19726.5	
Total	34900.1	

Melville (1993) have made a crude estimate. Assuming that mudskipper collection takes place over the months of April to June (90 d) and there are on average 50 collectors each catching 2.5 kg d^{-1}, the annual harvest by fishermen is equal to 11.3 t (1.7 t C), representing only 0.4% of the production.

Water body

Phytoplankton is the main producer in the water column. In the Pearl River Estuary, Huang et al. (1996) reported the annual means of chlorophyll *a* and primary productivity to be 4.0 µg l^{-1} and 309 mg C m^{-2} d^{-1}, respectively. Assuming that the same values are found in Deep Bay, the annual carbon production in the water column will be 12631.9 t yr^{-1} (Table 5). It is worth pointing out that the phytoplanktonic biomass in Deep Bay water recorded by some reports (2.14 µg chl *a* l^{-1}, EPD 1995; 1.40 µg chl *a* l^{-1}, Zhang et al. 1987) was lower, and, because the higher turbidity may prohibit phytoplankton production, the above value is likely an overestimate. Apart from the autochthonous carbon sources, Deep Bay receives anthropogenic carbon input from Shenzhen River and Shan Pui River and exchanges POC with the estuary through tidal flushing. Both Shenzhen River and Shan Pui River are heavily polluted, with high BOD$_5$ loading. Using the BOD$_5$ data from Peking University (1995) and EPD (1995), the annual TOC discharge was estimated to be 9076.7 and 12715.7 t, respectively, for the Shenzhen River and Shan Pui River (Table 6). A pollution trend and changes in the benthic fauna at different distances

away from the river mouth have been documented for both Shenzhen River (McChesney 1997) and Shan Pui River (Chiu 1992, Lee 1995b). Chen et al. (1990) found that the main POC sources in the estuarine water are not from phytoplanktonic production, but from sediment input from the Pearl River, which probably also applies to Deep Bay. The average POC concentration in Deep Bay water was 429.9 µg l^{-1}, much higher than that in the estuarine water. This is calculated to be 5.7 t POC d^{-1} (or 2065.9 t POC yr^{-1}) of net export to the estuary via tidal flushing.

Bird utilisation of carbon source

Based on the curlew's theoretical energy demands for benthic biomass (Melville et al. 1995), a comparison between the required and the available carbon from Deep Bay during a year is presented in Table 7. During the winter season when the curlew population is relatively large (same as most other species), the S/R ratio is much lower than 1, reflecting that there is a serious shortage of food from December to February, and that there would be even if all the benthic standing crop biomass were harvestable by the curlew. The potential carbon on the mudflat only contributed on average 47% of the requirements by curlew. Under the actual conditions, probably only 50% of the benthic biomass is available. The curlew cannot, therefore, obtain enough food on the mudflats during most of the year (from August to March) and will have to forage elsewhere (Table 7).

According to the published count data for January 1994, 41888 individuals of 74 bird species were

Table 6. Summary of the carbon sources and sinks in Deep Bay. Total production and import/export values are in t C yr^{-1}. Productivity/availability rates and import/export rates are in t C ha^{-1} yr^{-1} and are calculated based on areas 270 ha, 2700 ha, 200 (110 at Futien and 90 at Mai Po) ha and 11200 ha for the gei wais, the mudflats, the tidal mangroves and the water body, respectively. About 88% of the production within Deep Bay is available to consumers within the system. +: import into Deep Bay; −: export from Deep Bay

Habitat	Total production	Import/export	Productivity/availability	Import/export rate
Gei Wais	530.2	−965.8	1.96	−3.58
Mangroves	1077.0	+590.8	5.39	2.95
Mai Po	298.6	+150.5	3.32	1.67
Futian	778.3	+440.3	7.08	4.00
Mudflats	2541.7	+2540.0	0.94	0.94
Primary	1462.2	+1462.2	0.54	0.54
Secondary	1079.5	+1077.8	0.40	0.40
Water column	12631.9	+12631.9	1.13	1.13
Shenzhen river	9076.7	+9076.7	0.81	0.81
Shan Pui River	12715.7	+12715.7	1.14	1.14
Tidal exchange		−2065.9		−0.18
Total	38573.2	+34523.9		

Table 7. Carbon requirements of a typical wader, the curlew, and carbon supplied by the benthos of the mudflats in Deep Bay. Bird number: count data compiled by G. Carey (unpubl.) from various sources. Carbon required: theoretical required values derived from energy requirements for birds reported in Meire et al. (1994) and Melville et al. (1995). Potential carbon: supposing that the food resources were evenly allocated to all birds, the percentage for curlew was calculated using the curlew's numbers divided by the total bird numbers for the 5 mo reported by the Hong Kong Bird Watching Society (1995); invertebrate biomass carbon was derived from McChesney (1997); since no value for October was available, the mean of the September and November values was used here. S/R = supply to requirement ratio

Month:	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Avg
Bird number	450	650	100	10	10	20	20	30	50	75	100	300	151.3
Carbon required (kg C)	863.2	1246.8	191.8	19.2	19.2	38.4	38.4	57.6	95.9	143.9	191.8	575.5	290.1
Potential carbon (kg C)	188.7	130.0	161.8	145.6	178.5	155.8	82.4	77.1	124.0	151.2	178.4	93.5	137.8
S/R	0.22	0.10	0.84	7.59	9.31	4.06	2.15	1.34	1.29	1.05	0.93	0.16	0.47
S/R (50% available)	0.11	0.05	0.42	3.80	4.65	2.03	1.07	0.67	0.65	0.53	0.46	0.08	0.24

recorded in the portion of Deep Bay under Hong Kong jurisdiction. Of these birds, 23 species had a population size greater than 100, representing >99% of the total number of bird individuals in Deep Bay at that time. The total carbon required by these birds amounted to 40.7 t, with *Anas clypeata* and *Larus ridibundus* accounting for about half of the consumption. During January, the carbon production in the mudflat was only 27.8 t (data derived from McChesney 1997); competition for food was probable unless alternative carbon sources were available. Since only a part of the benthic production (equal to the benthic biomass in January 1994) was expected to be harvestable by birds, the maximum carbon supply met only 68.3% of the birds' needs. This indicates that the Deep Bay mudflats are probably at carrying capacity for wintering shorebirds (Table 8). By supposing that the birds' consumption is just equal to the carbon production on the mudflat and this state represents the sustainable

utilisation of food resources, the monthly bird biomass which the mudflat can support, in this ideal case, can be estimated at 11574.6 kg.

DISCUSSION

Relative importance of natural and anthropogenic carbon sources

The annual carbon production of Deep Bay totalled 36966 t, of which autochthonous autotrophic and heterotrophic sources contributed 14726 (39.8%) and 1080 t (2.9%), respectively (Table 5). Of the autotrophic carbon, vascular plants contributed only 1577 t (10.7%) with the remainder (89.3%) coming from phytoplankton and benthic algae. Anthropogenic carbon input accounted for 58.0% of the total, suggesting that the trophodynamics were heavily interfered with

Table 8. Carbon requirements of bird species foraging on the Deep Bay mudflat in January 1994. A total of 74 species was recorded in this count, but only 23 species with greater than 100 individuals were included in the calculation. They represent over 99% of the total number of individuals on the mudflat. Species count data from the Hong Kong Bird Watching Society (1995). Bird weights are mostly from Guangdong Entomology Institute & Zhongshan University (1983) and South China Institute of Endangered Animals (1991). These figures are calculated based on the theoretical energy requirement per gram fresh body weight of non-passerines (Aschoff & Pohl 1970), assuming that bird biomass of all species is the same in the way they consume energy. BMR: Basal metabolic rate. Carbon required: energy equivalence assumed to be 1 g C = 50.28 kJ (Heymans & Baird 1995)

Species	Number	Average weight (g)	BMR (kcal d^{-1})	3.5×BMR (kcal d^{-1})	Total for population	Carbon required (kg C mo^{-1})
Numenius arquata	1005	800	77.34	270.7	272043	702.1
Egretta garzetta	452	400	46.66	163.3	73816	190.7
E. alba	207	875	82.56	289.0	59815	154.4
Ardea cinerea	410	1020	92.32	323.1	132479	341.9
Tadorna tadorna	1400	1100	97.55	341.4	478002	1233.8
Anas penelope	1282	750	73.78	258.2	331051	854.7
A. crecca	1316	320	39.65	138.8	182634	471.5
A. poecilorhyncha	148	890	83.59	292.6	43300	111.9
A. acuta	1563	850	80.83	282.9	434550	1121.6
A. clypeata	6700	650	66.47	232.7	1558755	4023.8
Ducks	2190	500[a]	54.90	192.2	420809	1086.2
Recurvirostra avosetta	770	275	35.51	124.3	95703	247.1
Charadrius alexandrinus	3180	42	9.02	31.6	100393	259.2
C. mongolus	106	58	11.42	40.0	4237	10.9
Pluvialis fulva	220	165	24.47	85.7	18843	48.7
P. squatarola	538	220	30.18	105.6	56829	146.6
Calidris alpina	2820	50	10.25	35.9	101182	261.3
Tringa erythropus	819	140	21.71	76.0	62236	160.6
T. stagnatilis	668	63	12.13	42.5	28363	73.2
T. nebularia	386	150	22.83	79.9	30845	79.7
Larus saundersi	102	500[a]	54.9	192.2	19599	50.5
L. ridibundus	15000	290	36.9	129.2	1937850	5002.2
L. heuglini	290	1050	94.29	330.0	95706	247.1
Total	41888				6538994	16879.5

[a]Assumed values since the actual values are not available

by human activities. Carbon loss through harvest (of prawn, fish and mudskippers) from the Deep Bay system was negligible. The net carbon input into Deep Bay was 34523.4 t yr^{-1}, most of which was from phytoplankton and the 2 polluted rivers. Mangrove-derived carbon only contributed <2% and seems unlikely to be the main food source for the birds utilising Deep Bay or nearshore consumers.

The hypothesis that coastal wetlands serve as the major supplier of carbon for supporting nearshore secondary consumers (the Outwelling Hypothesis; Odum 1980) is still controversial (Dame 1994, Lee 1995a). The magnitude and direction of net material flux are determined by a combination of physical parameters, such as geomorphology, tidal inundation regime and topography, and biotic factors such as the species and growth form of vegetation, seasonal growth patterns and rates of primary production, and the development stages of the marsh-estuarine system (Odum 1969, Dame & Lefeuvre 1994). It is interesting that in Deep Bay, the outer mangrove is a net exporter of organic carbon while the landward gei wai, a semi-enclosed

tidal pond, acts as a net importer. This difference may be caused mainly by the tidal inundation regime. The mangroves are inundated twice a day, but only spring high tides can reach the mangrove stands in the gei wais. The ponds act as sediment traps and accelerate accretion, leading to a progressive increase in elevation of the stands. Less inundated sites allow more litter accumulation to be processed by crabs (Perisesarma spp. and Parasesarma plicata) in the stands, thus leading to little export. This shift from a net exporter to a net importer of organic carbon is probably characteristic of the transition into nutrient-conservative terrestrial systems, a process catalysed by the increased sedimentation rate typical of such impoundments (Lee 1990a).

Capacity for supporting wintering shorebird populations

Prediction of the actual energy expenditure of birds requires a lot of dedicated effort to clarify the response

of the species' metabolism to factors such as microhabitat type, temperature regime, wind speed and flocking pattern (e.g. Wiersma & Piersma 1994) and data on feeding pattern (Pienkowski et al. 1984). Predatory behaviour of shorebirds may also be influenced by many complex processes (Piersma 1987). The calculations on bird utilisation of the Mai Po mudflat carbon resources presented in this paper are, therefore, meant to be only a rough picture. The exact scenario will require clarification of important links, such as the response of the energy demand of various species to changes in environmental conditions.

Koteja (1991) reported the lack of correlation between mass-independent basal and field metabolic rates in birds. A review of the data on intraspecific variations in energy expenditure in small birds also revealed equivocal interspecific patterns for the effect of factors such as body mass, age, temperature and food availability (Bryant & Tatner 1991). We are also aware that the field to basal metabolic rate ratio may not be constant with body mass (Degen & Kam 1995). The actual energetic demand of the birds on the Mai Po mudflat is therefore difficult to assess without the availability of field metabolic rates but we believe that the calculation based on basal metabolic rate should still give a reasonable estimate of how well the basic energetic demands of the birds are met by the wetlands. As it is expected that the field metabolic rate of most species is higher than the basal rate, e.g. Pienkowski et al. (1984) and Bryant & Tatner (1991) suggested, respectively, field rates 2–4 and 3+ times higher, the present calculation based on 3.5×BMR should represent a realistic estimate of the actual energetic demands of the birds.

The consumption pattern of carbon sources, as demonstrated by the calculation based on the curlew population, generally agrees with the conclusion of McChesney (1997). A predator exclusion experiment conducted by McChesney (1997) on the Mai Po mudflats showed that birds can remove a significant portion (48 to 55%) of the large bivalves (*Macoma* sp., *Theora* sp., *Sinonovacula* sp.) on the mudflat. Bird predators on the Oosterschelde, SW Netherlands, consumed 30 to 37% of autumn standing crop biomass (Meire et al. 1994) when the Oosterschelde was thought to be at carrying capacity (Schekkerman et al. 1994). Predation impact (the percentage of invertebrate production taken by birds) on the Mai Po benthic assemblage is much higher than at sites on the East Atlantic Flyway (see Moreira 1997). The picture obtained based on the curlew probably exaggerates the energetic demand of the overall bird assemblage, as the curlew is one of the larger species and Table 7 is constructed assuming equal allocation of resources to bird species by numbers.

Energy requirements of the overall bird assemblage based on 3.5×BMR suggest that the Mai Po mudflats are near carrying capacity, i.e. further increases in bird numbers will probably result in significant food competition, decline in body condition, or displacement of the populations to alternative feeding grounds. The requirement amounted to 16.9 t C for January 1994, compared to the production figure of 27.8 t C for the same month. Bearing in mind that not all of the invertebrates were available to the birds, the Deep Bay mudflats were likely to be near their carrying capacity. One characteristic of this system is that there is considerable storage of production in terms of crab and mudskipper biomass in summer but much larger food demands in winter. The crabs and mudskippers grow actively and are available in summer when bird numbers are low. In contrast, these potential food items are generally not available during the winter migratory season. A parallel study on the trophodynamics of Deep Bay using stable isotopes of carbon and nitrogen suggests that the predominant carbon source for benthic consumers (crabs, prawns and fish) is probably of either anthropogenic or estuarine plankton origin (Lee unpubl.).

Drained-down freshwater fish ponds and gei wais present alternative feeding habitats for the birds in winter. Fish harvesting from these ponds occurs in winter (December to February), when the ponds are drained successively for periods of up to 2–3 wk. Large numbers of birds congregate at the ponds and feed on the high concentration of high-energy food (fish) during this time. This alternative food supply has not been factored into the above calculations (because of the high variability in food availability and it is a resource outside of the mudflat system) but probably represents an important subsidy to the apparent tight budget for the Deep Bay mudflats.

Many parameters can affect the bird carrying capacity of the Deep Bay mudflat, among which anthropogenic input is a major factor. More than 20000 t pollutant carbon enter Deep Bay per year through wastewater discharge from the 2 main rivers and this has become a major source of carbon budget from the system. Water quality deterioration from the central Mai Po marshes to the Shan Pui River mouth has been recorded (Chiu 1992), and poor quality water has adversely affected the stocking of prawn larvae in the gei wais (Cha et al. 1996). According to the model proposed by Pearson & Rosenberg (1978), with mild organic pollution, species diversity may increase because of increased food and nutrient availability. With increasing pollution, fundamental changes in community structure occur: (1) a shift from dominance by large, long-lived species to small, opportunistic species and (2) an overall decrease in biomass, species

diversity and richness. These phenomena have been documented for Shan Pui River (Lee 1995b), Shenzhen River and the mudflats (McChesney 1997). McChesney (1997) recorded the dominance of *Capitella* spp. in areas around the discharge points of the rivers and the largest common non-air-breathing macrofauna as being the polychaete *Dendroneries pinnicirratus* (<15 cm long). Lee (1995b) argued that species that are air-breathing deposit feeders that are active during low tide, e.g. fiddler crabs, can probably benefit from even gross organic pollution (such as along the Shan Pui River) by avoiding the problems of anaerobiosis and benefiting from the enrichment. Although a livestock waste control ordinance has been enforced since 1991 in Hong Kong, no significant improvement of water quality in Shan Pui River is to date apparent in terms of BOD_5 input. As for the Shenzhen River, a joint Shenzhen River Regulation Project has been in progress to improve river quality (Peking University 1995). Nevertheless, it is expected that a collapse of benthic biomass will occur on the mudflat, followed by an exacerbated shortage of food for bird populations, if the present pollution trend is not curtailed. The present situation, however, still seems to be reflective of a biostimulation effect associated with organic enrichment, but future discharges should be closely monitored. What appears to be a major pollution problem from the viewpoint of water quality management is actually a blessing, at least for now, to the conservation value of this mangrove-fringed embayment.

Mudflat habitat loss will reduce the food for birds. This may arise from both mangrove expansion and urban development in the Deep Bay area. The mangrove encroachment rate at Mai Po was estimated to be 3.5 m yr^{-1} (Peking University 1995). Based on aerial photographs, Duke & Khan (in press) obtained an overall encroachment rate of 7.6 m yr^{-1}. A mudflat loss of 4.9 (0.2%) or 10.6 (0.4%) ha yr^{-1} has resulted for the mangroves in Deep Bay. Furthermore, the artificial transplanting of *Kandelia candel* saplings, currently conducted at the Futian Mangrove-Bird Nature Reserve (authors' pers. obs.) to enhance mangrove conservation, may not benefit birds. The infaunal biomass in mangrove stands was lower than on the mudflat (5–15 vs 10–65 g dry wt m^{-2}) (McChesney 1997); thus the food resources available will be proportionally reduced for shorebirds. Twenty-eight major development projects around Deep Bay area (Young & Melville 1993) were identified, 2 of which were the Shenzhen River Regulation Project and the Binhai Causeway in Shenzhen. Habitat loss through the Shenzhen river widening and infilling of ponds will be relatively small and be compensated for by the creation of new wetland habitat at a ratio of 1:1 (Peking University 1995). In contrast, the Binhai Causeway has

been designed to cross the north of inner Deep Bay and is likely to involve infilling to the north, resulting in loss of about 20% of the intertidal area of Deep Bay (McChesney 1997). This will substantialy impact the quantity and the distribution pattern of shorebirds on the mudflat, which may warrant further detailed studies.

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