# MANGROVES - A CARBON SOURCE AND SINK

# Ong Jin Eong

# Centre for Marine and Coastal Studies, Universiti Sains Malaysia 11800 Penang, Malaysia.

## ABSTRACT

The mangrove ecosystem in many wet tropical areas represents one of the most, if not the most productive of natural ecosystems. The question that has occupied the minds of many mangrove scientists is "What is the fate of this high productivity"? More recently this question has gained added relevance as a result of the increase in global carbon dioxide concentration. Are mangroves sinks of atmospheric carbon?

We try to answer these questions using 15 years of data from the Matang Mangrove Forest Reserve and the Sungai Merbok Forest Reserve, in Peninsular Malaysia.

We take a quick look at the palaeo-geological evidence on sea level changes in the Straits of Malacca during the recent past (Holocene) to give us a better perspective of the Matang and Merbok mangroves and emphasise the dynamics and ephemeral characteristics of the mangrove ecosystem.

The pristine forest of Matang has a mean nett annual above-ground productivity of 18 t dry organic matter ha<sup>-1</sup> yr<sup>-1</sup> whereas the same forest managed on a sustained yield basis is a good 20% more productive. If harvested timber is used as fuel wood then much of what is fixed is released back into the atmosphere. On the other hand, if harvested timber is used as pilings then significant amounts of mangrove carbon are locked away.

We estimate that for the mangroves of Matang some 1.5 tC ha<sup>-1</sup> yr<sup>-1</sup> is buried each year over the past 8,000 years or so. The impact of man (since the beginning of this century) has resulted in an initial increased release  $\sigma$  carbon into the atmosphere (in the first half of this century) as a result of the use of mangrove timber as fuel-wood but sustained yield management has ensured a carbon balance between what is fixed as timber and what is burned. The present management system (which produces significant amounts of slash and stumps) may result in increased amounts of burial (i.e. more than the 1.5 tC ha<sup>-1</sup> yr<sup>-1</sup>).

To demonstrate that the terms "source" and "sink" are relative terms, we show that mangroves may (at the same time as being a sink for atmospheric carbon) also be a source of carbon in that they may out-well significant amounts of carbon to adjacent coastal ecosystems and thus play a vital role in coastal fisheries production.

Conversion of mangrove to aquaculture ponds could result in the release (from about 1,000 years accumulated mangrove sediments) of some 75 t C ha<sup>-1</sup> yr<sup>-1</sup> to the atmosphere over a 10-year period. This is 50 times the sequestering rate.

#### INTRODUCTION

The mangrove ecosystem is a very dynamic system in more than one sense. As an inter-tidal ecosystem it literally moves depending on the tidal level as well as through erosion and accretion. It can be ephemeral, even on a sub-geological time scale. The mangrove ecosystem in many wet tropical areas represents one of the most, if not the most productive of natural ecosystems. We have little doubt about this when we consider nett primary productivity (although this may also be the case for gross productivity). The question that has occupied the minds of most mangrove productivity scientists is "What is the fate of this high nett productivity"? Our original interest in that question was to determine the link between mangrove primary productivity and fisheries in the mangrove and adjacent coastal ecosystems. If mangroves out-well carbon into the adjacent coastal areas then mangroves are a source of carbon. Are they? More recently this question has gained added relevance as a result of the increase in global carbon dioxide concentration. Mangroves are obviously very good at fixing carbon. What happens to this fixed carbon? Are mangroves sinks of atmospheric carbon?

We will try to answer these questions using data (representing a good 15 years of active primary research by the Universiti Sains Malaysia's Mangrove Ecosystem Research Group) we and other workers have accumulated from work on the Matang Mangrove Forest Reserve  $(4^{0}50'N, 100^{0}35'E)$  and the Sungai Merbok Forest Reserve  $(5^{0}40'N, 100^{0}25'E)$ , in Peninsular Malaysia. We like to caution that what we have to say is based on our "Matang and Merbok" experience and may not necessarily apply to all other mangroves.

We take a quick look at the palaeo-geological evidence on sea level changes in the Straits of Malacca during the recent past (Holocene) to give us a better perspective of the Matang and Merbok mangroves and emphasise the dynamics and ephemeral characteristics of the mangrove ecosystem.

We then present productivity data for the Matang mangroves. In order to determine whether mangroves are sources or sinks, it is vital to measure not just standing biomass but also rates. We can do this for the Matang data because we are able to determine the age of mangrove stands using forestry records. We also discuss the fate of the different biomass components, in particular the amount of mangrove biomass that becomes locked away through burial. In other words we discuss how much of a sink mangroves are.

We then briefly discuss carbon fixation by mangrove molluscs and the role of this group of mangrove fauna as a carbon sink.

Finally, we look at carbon fluxes across the mouth of a mangrove estuary and the critical question (in terms of the quantitative link between mangroves and fisheries) of mangrove out-welling. Are mangroves a source of carbon to their adjacent coastal ecosystems?

# A PERSPECTIVE OF SEA LEVEL CHANGE DURING THE HOLOCENE

To give us a temporal perspective, we step back some 15,000 years in time to the beginning of the Holocene period. Sea levels world-wide were then some 120 - 150 metres or so below the present level. It is generally agreed that there was a relatively rapid rise in sea level from the early Holocene. In most cases sea level rise did not exceed where it is today (e.g. Schnack & Pirazzoli, 1990, cited in Kamaludin, in press). For the situation in the Straits of Malacca, Geyh et al., (1979) reported rapid sea level rise from -53m to +5m at about 10,000 to 5 - 4,000 BP respectively.

Around 15,000 years ago much of the Sunda Shelf was above sea level. Peninsular Malaysia and Sumatra formed a continuous land mass and the Straits of Malacca was at best a river. Matang and Merbok were certainly not covered in mangroves then. Sea level rise was rapid (about 2 cm per year over about 5,000 years) for the next 8,000 years when the present level was reached about 7,000 BP. Matang and Merbok were possibly closest to their present form then. Sea level rose (to our present inter-glacial peak?) another 5 metres or so above the present level about 4,500 BP so that mangroves on the seaward side of Matang and Merbok, as we know today, were likely drowned. Sea level then slowly dropped (about 1 mm per year) to its present level. The trend appears to be for a fall in sea level as we head for the next glacial (i.e. barring human perturbations). Bosch (1988) reported that the Merbok drainage system has been intact since 5,000 BP. There is also evidence (Kamaludin, in press) that mangroves were located many kilometres inland 4 - 5,000 years ago when the sea level was some 5 metres above the present level. It thus appears that the Matang and Merbok mangroves as we know them today have been around for no more than about 7,000 years. This is very, very young compared to the inland rain-forests! There are also archaeological sites inland of the Merbok (the Bujang Valley) showing the existence of a sizable human settlement some 2,000 BP of a now extinct civilisation.

## MANGROVE PRODUCTIVITY AND BURIAL, OR MANGROVE AS A SINK

The Matang Mangrove Forest Reserve, comprising some 40,000 hectares of mainly Rhizophora apiculata mangroves, have been managed since the beginning of this century and is one of the rare examples of a very successful sustained yield management of a tropical rainforest. The present system involves a 30-years rotation period (e.g. see Haron, 1981 or Ong, 1982). Patches of a few hectares are harvested (clear-felled) at 30 years and cut into billets for charcoal production. The stumps and slash are left to decompose naturally (this takes 2 to 3 years). Two years after clear-felling, the area is surveyed for natural regeneration. If natural regeneration is not adequate, the area is planted (some 50% of the area in Matang needs artificial planting) manually. Fifteen years after clear-felling the first thinning is carried out during which some 35 to 50% of the trees is removed. Both this and the subsequent thinning are more economical (harvest of poles for piling and building scaffolds) than silvicultural because natural thinnings occur a few years earlier (Gong et al., 1984a). After 20 years a second thinning is carried out and again 35 - 50% of stems is harvested. Finally, clear-felling takes place at 30 years.

Our measurements of nett productivity are based on allometric techniques (e.g. see Ong et al., 1984, Gong et al., 1984b). Basically plots are established in different age stands and the GBH (girth at breast height i.e. 1.3m) of trees measured. The biomass of different plant components are then estimated using the various allometric regression equations. This gives estimates of standing biomass in different age stands. From this it is possible to estimate mean annual standing biomass increment. We also estimate leaf production by measuring litter fall using 1m X 1m nets strung out below the trees with monthly collections over at least a year. We add this to annual biomass increment to get estimates of nett primary productivity. This would, if anything give us a conservative estimate as we assume zero herbivory and do not take into account fine root turnover (which some authors claim may be as much as leaf litter turnover). Our nett productivity estimates are presented in Table 1. Most of these and other data have been published (e.g. Gong & Ong, 1990). As can be seen, nett productivity is extremely high for young trees but slows down as the trees age. Putz & Chan (1986) estimated above-ground productivity in an almost pristine stand of much older (over 80 years) trees in Matang to be about 9t C (18 t organic matter) ha<sup>-1</sup> yr<sup>-</sup> <sup>1</sup> and above-ground standing biomass to be about 200 t C (400 t organic matter) ha<sup>-1</sup>. This compares with the mean annual above-ground productivity over the 30 years rotation period of about 12 t C ha<sup>-1</sup> yr<sup>-1</sup> and above-ground standing biomass of about 150 t C ha<sup>-1</sup>. Thus under sustained yield management the forest is at least 20% more efficient as a nett producer. This confirms the fact that old pristine stands are not very efficient carbon sinks. Indeed, if the rotation period is reduced then the difference would be even more dramatic (about 40% more efficient than old forests).

Age (years)	Biomass (tC ha <sup>-1</sup> )	MAI (tC ha <sup>-1</sup> )	Litter (tC ha <sup>-1</sup> yr <sup>-1</sup> ) (tC	NPPa.g. ha <sup>-1</sup> yr <sup>-1</sup> )	TPP# (t C ha <sup>-1</sup> yr <sup>-1</sup> )
5	8	1.6	3.5	5.0	7.0
10	90	9.0	5.0	14.0	17.5
15	100*	6.5	5.0	11.5	18.0
25	150**	6.0	5.5	11.5	16.0

Table 1. Standing biomass, mean annual increment (MAI), litter, above-ground net primary productivity (NPPa.g.) and estimated total primary productivity (TPP) in stands of different ages of <u>Rhizophora apiculata</u> in the Matang Mangrove Forest Reserve, Malaysia.

# Based on below ground biomass increment being 10 % of above-ground MAI +root turnover based on 50% litter production. For 15 and 25 year-old stands, also takes into account thinnings I & II.

\* Does not take into account Thinning I.

\*\* Does not take into account Thinning II.

A high proportion of the carbon assimilated is eventually released from the system through litter fall (2-6 t C ha<sup>-1</sup> yr<sup>-1</sup>). In some areas all the litter is eaten by "sesarmid" crabs as soon as it falls, in others only a small proportion is eaten. Where the litter is not directly eaten, the soluble fraction is leached by inundating tides or rain. Some 20 to 25% (by dry weight) can be lost in a matter of days. Parts of what remains on the forest floor are microbiologically degraded (by fungi, bacteria and protozoa). This microbial process is relatively slow and takes up to about six months. In areas of high sedimentation, burial of litter may be a significant process and here indeed is a carbon sink. The whole process is extremely variable and highly site specific (e.g. see Japar, 1989), making precise estimates for the whole forest extremely difficult.

Slash, stumps and standing dead trees, in general, take 2 to 3 years to decompose. The fate of these is possibly not as variable as for leaf litter but we do not have data as to how much is buried or exported. Sink or source?

We know very little about fine root turnover. In some stands we encounter mats of fine roots while in other stands root mats are entirely absent. There are extremely few macroscopic animals living in the soil apart from the crabs in their burrows. We encountered some small <u>Thalassina anomala</u> (mud lobsters), a few sipunculid peanut worms, (<u>Phascolosoma lurco</u>) and the occasional polychaetes in our diggings. So, if microbial decomposition of fine roots is low, much carbon from mangrove roots may be tied up this way. Another possible significant sink?

First let us look at the gross/nett primary productivity story. Rates of nett carbon dioxide assimilation (as measured with infrared carbon dioxide analyser based photosynthesis measuring instruments) range from about 0 - 20 umol CO<sub>2</sub> m<sup>-2</sup> (of leaf) s<sup>-1</sup> for Rhizophora apiculata. Our rough estimate of gross primary productivity is about 10 umol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>. Based on a leaf area index of 5 (i.e. 50,000 m<sup>2</sup>) of leaf per hectare) we get an estimate of about 100 t C ha<sup>-1</sup> vr<sup>-1</sup>. Total (above- and below-ground) nett primary productivity was an estimated 18 t C ha<sup>-1</sup> yr<sup>-1</sup>. This figure is in the top part of the range given by Twilley (1988) for Florida and Puerto Rico mangroves. This would mean that mangroves utilise a rather high percentage (80%-90%) of total assimilated carbon for respiration and other metabolic needs. This is not surprising since they live in a harsh environment. The gross primary productivity figure is extremely high. How do mangroves achieve this? That is another story and not within the scope of this paper.

Now let us look to see how much carbon is tied up in the mangrove ecosystem. Say each hectare of sediment is about 10 metres thick (e.g. see Kamaludin, 1989 & Kamaludin, in press) so we have 100,000 m<sup>3</sup> per hectare of mangrove sediments. Take the density of this sediment to be 0.7. This is approximately 70,000 tonnes dry weight per hectare. Take a carbon content of 15% dry weight. This would give us a total of 10,500 t C ha<sup>-1</sup>. Take the age to be 7,000 years and we have a sink that sequesters about 1.5 t C ha<sup>-1</sup> yr<sup>-1</sup>. How reasonable is this estimate? We know that carbon from litter, slash, stumps and dead trees is in the region of 15 t C ha<sup>-1</sup> yr<sup>-1</sup>. Fine root turnover could account for another 2-4 t C ha<sup>-1</sup> yr<sup>-1</sup>. So we get about 10% of production being buried. This appears to be a very reasonable estimate. Modellers, I am certain, would be able to use it (even without their various fudging factors) but is this good enough ?

#### MANGROVE MOLLUSCS AS CARBON SINKS

There is a tendency to regard only plants as fixers of carbon but some animals (corals in particular) play significant roles. Next to the Crustacea (dominated by crabs), Molluscs form a very visible and significant part of the mangrove benthic fauna. In the mangrove mudflats the blood cockle <u>Anadara granosa</u> occurs in extremely high densities. The shells of these molluscs would probably form a very significant sink for carbon dioxide. Choy (1991) reported that 3,002 hectares of mangrove mud flats in Matang were used for cockle culture, producing 11,385 tonnes in 1990. This works out to 3.8 t ha<sup>-1</sup> yr<sup>-1</sup>. At least half of this weight is dry shell weight. So this is equivalent to about 0.25 tonne C fixed per hectare of cockle bed per year. From the point of reduction of greenhouse gases alone, there is thus much merit in encouraging mollusc (in particular cockles and oysters) culture in mangrove mud-flats and waterways.

# MANGROVE OUT-WELLING OR MANGROVE AS A CARBON SOURCE

One method to determine if mangroves are sources or sinks of carbon is to determine the flux of carbon from the mangrove estuary. To do this one can use a hydrodynamics approach. A number of stations are established at the mouth of the mangrove estuary and current, salinity and water samples (for analysis of carbon concentrations) collected at tidal hourly or 2-hourly intervals over a number of tidal cycles. From such data sets it is possible (in theory, if not in practice) to compute the flux of salt (salt is usually measured because it is a conservative component and gives a good indication of the reliability of flux estimates) and carbon (e.g. Kjerfve, 1979). This approach may be simpler to apply for mangrove estuaries that have a single opening into the sea like the Sungai Merbok (Ong et al., 1991).

We have tried this approach for the Merbok (in the process we have acquired one of the most comprehensive time-series data set of its kind available - 4 stations over 31 continuous tidal cycles), but the estimates we have appear to be about an order of magnitude too high (as compared to alternate considerations and the fact that we are unable to obtain a salt balance). Even if we take the order of magnitude lower estimate, there is still an export, so the Merbok Mangroves are a source of carbon to its adjacent coastal ecosystem (i.e. there is out-welling of carbon from the Merbok). To be able to quantify this output more precisely is vital for the management of the mangrove ecosystem with respect to mangrove and coastal fisheries. We are presently working on this, with the help from a few non blue-water physical oceanographers as well as ecological and mathematical modellers.

### DISCUSSION

From what is said above, mangroves act as a source (carbon out-welling) as well as a sink (burial of mangrove assimilated carbon in sediments) - an apparent contradiction! The fact of the matter is that the terms source and sink are relative terms:

- 1. The Matang mangroves acts as a sink for atmospheric carbon, fixing an estimated 75-150 t C ha<sup>-1</sup> yr<sup>-1</sup> (as gross primary productivity). Of this 80% - 90% is returned to the atmosphere as respired carbon dioxide, leaving an estimated 7-18 t C ha<sup>-1</sup> yr<sup>-1</sup> as net productivity. Some 5 t C ha<sup>-1</sup> yr<sup>-1</sup> of this net productivity is shed as litter. In a mature stand (30 year-old) there is a standing biomass of about 150 t C ha<sup>-1</sup>. An estimated 1.5 t C ha<sup>-1</sup> yr<sup>-1</sup> is sequestered in the sediments. It is estimated that under sustained yield management the system is about 20% more efficient at sequestering carbon than if left undisturbed.
- 2. Carbon that is not buried in the sediments either remains as standing biomass or is exported from the ecosystem. In this way mangroves are a source of carbon to its adjacent coastal system. The quantity of export has not been determined but there is an ongoing project to determine this.

One question that is relevant to the recent increase in atmospheric carbon dioxide levels is the role played by man. In the Matang and Merbok situation man probably did not play a very significant role until the early part of this century (although there was an ancient civilisation located in the Merbok area - the Bujang Valley about 2,000 BP). For Matang at least, exploitation of mangrove timbers started at the beginning of the century for poles, charcoal and firewood. It took about 50 years to complete the first rotation (initially there was a smaller annual coupe than the present 1,000 hectares per year). Return from the first rotation is estimated to be 200 t C ha<sup>-1</sup>. Over the first half of this century an average of 160,000 t C yr<sup>-1</sup> would have been removed. The rate of removal in the second half of this century is estimated as  $150,000 \text{ t C yr}^{-1}$  (which is also the replacement rate - hence sustained yield management). There was thus an excess of 10,000 t C yr  $^{-1}$  over replacement by growth in the first half of this century. If we assume that more mangrove timber was used for piling during the first half of this century, then there would be hardly any difference in terms of loading carbon in the atmosphere.

So with a sustained yield system where harvested timber is used mainly as fuel, there will be an initial (duration of the first rotation) increased input of carbon into the atmosphere after which there will be a balance, as we now see in Matang.

If however the timber that is harvested is used for piling (as is the case with much of the timber removed during thinnings) then this would be buried in the soil and locked away. Sustained yield management contributes very significantly to reducing carbon input into the atmosphere but a change in the final use (e.g. from use as fuel to use as piles) of the harvested timber is just as critical in determining the carbon balance. Sustained yield managed forests are almost certainly no less carbon sinks than pristine forests; certainly better if the timber is used as piles or products that last longer than the time taken to produce the timber.

Still, irrespective of how the mangrove timber is used, the Matang mangroves acts as a carbon sink in the accumulation of carbon (some 1.5 t C ha<sup>-1</sup> yr<sup>-1</sup>) in its sediment. The amount of organic carbon sequestered in non-wetland forests is comparatively insignificant. It is only when mangroves are converted to aquaculture ponds that there will be a release of carbon back to the atmosphere not only from the removal of the forest (loss of 150 t C ha<sup>-1</sup> of standing biomass) but even more so from the the perturbation (and oxidation) of about 2 metres of mangrove soil during pond construction. This will return to the atmosphere what has been accumulating in the mangrove sediments for about a thousand years (about  $750 \text{ t C ha}^{-1}$ , even if only about half the carbon in the mangrove sediment is oxidised; even if this process takes 10 years we are looking at a very significant 75 t C ha<sup>-1</sup> yr<sup>-1</sup>). This is a hidden cost of pond aquaculture in mangrove forests and yet another good reason why pond aquaculture in mangroves should be discouraged. Thus, if the increasing concentration of atmospheric carbon dioxide is of concern, then the mangrove ecosystem is an important one to carefully manage or conserve.

#### ACKNOWLEDGMENTS

Data used in this paper was collected through a number of years through projects funded by a number of local and foreign funding agencies. First we thank the Universiti Sains Malaysia for giving us a seed grant, the time and providing vital infrastructural support. We also thank BIOTROP (SEAMEO), IDRC (of Canada), AIDAB (of Australia), the Malaysian National Science Development Council, and the Malaysian Government (for funding through its Integrated Research in Priority Areas R.& D. programme under the 5th. & 6th. Malaysian Development Plans). I particularly like to thank Dr. Gong Wooi Khoon for her constructive suggestions and critical reading of this manuscript.

## REFERENCES

Bosch, J. H. A., 1988. The Quaternary deposits of the coastal plains of Peninsular Malaysia. Geological Survey of Malaysia. Quaternary Geology Section, Report No. QG/1 of 1988.

Choy, S. K., 1991. The commercial and artisanal fisheries of the Larut and Matang District of Perak. Paper presented at the ASEAN-Australia Marine Science Project on Living Coastal Resources' "Workshop on Mangrove Fisheries and Connections", 26-30 August, 1991, Ipoh, Perak, Malaysia. 7 pp +x Figs. & Tables.

Geyh, M. S., Kudrass, H. R. and Streif, H., 1979. Sea-level changes during the late Pleistocene and Holocene in the Straits of Malacca. Nature 278: 441-443.

Gong, W. K., Ong, J. E. & Wong, C. H., 1984a. Demographic studies on <u>Rhizophora apiculata</u> Bl. in the Matang Mangrove Forest, Malaysia. In Ecological Effects of Increasing Human Activities on Tropical and Subtropical Forest Ecosystems. Technical Report of the Malaysian National MAB Committee. pp. 64-67.

Gong, W. K., Ong, J. E., Wong, C. H. & Dhanarajan, G., 1984b. Productivity of mangrove trees and its significance in a managed mangrove ecosystem in Malaysia. In Proceedings of the UNESCO Asian Symposium on "Mangrove Environment: Research and Management" (Soepadmo, E., Rao, A. N. & Macintosh, D. J., eds). Universiti Malaya, Malaysia. pp. 216-225.

Gong, W. K. and Ong, J. E., 1990. Plant biomass and nutrient flux in a managed mangrove forest. Estuarine, Coastal and Shelf Science 31: 519-530.

Haron, Hj. A. Hassan, 1981. A working plan for the second 30-year rotation of the Matang mangrove forest reserve Perak. State Forestry Department, Perak. Rajan & Co. (Printers) Sdn. Bhd., Ipoh, Perak. 109 pp.

Japar, S. Bujang, 1989. Studies on leaf litter decomposition of the mangrove, <u>Rhizophora apiculata</u> Bl. Ph.D. Thesis, School of Biological Sciences, Universiti Sains Malaysia, Penang, Malaysia. 322 pp. Kamaludin bin Hassan, 1989. Palynology of the lowland Seberang Prai and Kuala Kurau areas North-West Peninsular Malaysia. Geol. Soc. Malaysia, Bull. 23: 199-215.

Kamaludin bin Hassan (in press). The changing mangrove shorelines in Kuala Kurau, Peninsular Malaysia. Paper submitted to Sedimentary Geology.

Kjerfve, B., 1979. Measurement and analysis of water current, temperature, salinity, and density. pp. 186-226. In: Estuarine Hydrography and Sedimentation. K. R. Dyer (ed.). Cambridge University Press, Cambridge.

Ong, J. E., 1982. Mangroves and aquaculture in Malaysia. Ambio 11, 252-257.

Ong, J. E., Gong, W. K., Wong, C. H. and Dhanarajan, G., 1984.

Contribution of aquatic productivity in a managed mangrove ecosystem in Malaysia. In Proceedings of the UNESCO Asian Symposium on

"Mangrove Environment: Research and Management" (Soepadmo, E., Rao, A. N. & Macintosh, D. J., eds). Universiti Malaya, Malaysia. pp. 209-215.

Ong, J. E., Gong, W. K., Wong, C. H., Zubir Hj. Din & Kjerfve, B., 1991. Characterisation of a Malaysian mangrove estuary. Estuaries 14: 38-48.

Putz, F. E. and Chan, H. T., 1986. Tree growth, dynamics, and productivity in a mature mangrove forest in Malaysia. For. Ecol. Manage. 17: 211-230.

Schnack, E. and Pirazzoli, P., 1990. Quaternary sea-level changes. Palaeogeography, Palaeoclimatology, Palaeoecology (Global and Planetary Change Section) 82: 65-68.

Twilley, R. R., 1988. Coupling of mangroves to the productivity of estuarine and coastal waters. pp.155 - 180. In: B. O. Jansson (Ed.) Coastal-Offshore Ecosystem Interactions. Lecture Notes on Coastal and Estuarine Studies, Vol. 22. Springer Verlag, Berlin.