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Mangrove outwelling: a review

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Abstract

The export of detritus and faunal biomass from mangroves has long been considered as an important support for offshore biological production and has been widely used as an argument for mangrove conservation. This functional role of the mangroves, like many other paradigms in mangrove ecology, has seldom been put to rigorous test since the hypothesis was postulated about 25 years ago. Past studies on which the hypothesis was based were mostly carried out in mangrove or other wetland environments, little is known about the fate and effects of outwelled detritus on oceanic, offshore, communities. Mass balance studies carried out in the last 15 years tend to suggest that export is common from tidal mangroves, the direction of flow depends, however, on the identity of the chemical species in question. Pore water and groundwater flow can affect tidal material exchange but are poorly studied. Generally, tracer methods using stable isotope ratios or other signatures have suggested that outwelling may be much less significant than expected. Further, most past studies have focussed on particulate matter while it is increasingly apparent that dissolved organics may play a more important role in matter exchange between offshore and mangrove communities. There is also evidence that benthic biomass and richness may not bear any positive or significant relationship with detritus availability.

Introduction

The export of plant detritus and faunal biomass to support offshore consumers has been considered an important functional role of mangroves as well as a strong argument for their conservation (e.g. Snedaker, 1978; Macintosh, 1981). This "outwelling" characteristic of coastal wetlands was first postulated by E. P. Odum (1968) about 25 years ago (Nixon (1980) attributed the idea to Teal (1962)), originally based upon observations on salt marsh ecosystems. Golley *et al.* (1962) made the first study of tidal exchange of materials between a mangrove and the offshore community. Despite the fact that only a small data set was used to substantiate their argument, their work nevertheless was seminal in the study of mangrove outwelling. Whereas export of plant litter is probably more conceivable in mangrove systems than in salt marshes where many producers retain their senescent leaves (Fallon *et al.*, 1985; Newell *et al.*, 1985), the outwelling behaviour of mangroves has seldom been put to test. Similar to many other paradigms of mangrove ecology, extrapolation or analogies are commonly made from findings from the temperate salt marshes.

There are, however, a few past studies which specifically addressed the outwelling problem, e.g. Nixon (1980) discussed salt marsh outwelling in detail and Ong (1984) focussed mainly on the relationship between mangrove occurrence and offshore fisheries production. Odum (1984) himself also briefly reviewed the status his hypothesis but concluded that outwelling from estuarine wetlands, while generally exists, greatly depends on the physical characteristics of the wetland. Direct evidence of mangrove outwelling is scarce and few studies comparable to the flux measurements performed on salt marshes are available. Recently, Robertson *et al.* (1992) reviewed carbon fluxes and food chain relationships in tropical mangrove ecosystems and it seems that more data are becoming available to allow a better assessment of the role played by mangroves in supporting tropical offshore consumers.

Table 1. Factors which may affect the "outwelling behaviour" of mangroves and salt marshes differently.

	Mangroves	Salt marshes
Fate of senescent plant biomass	abscissed, higher chance of export	retained, decomposed *in situ*
Turnover of component which can be exported	high, higher export possible	lower, lower degree of export
Tidal regime	usually stronger tidal energy, higher export	mostly with weak tidal energy, lower export
Litter quality	high levels of secondary compounds, low utilization by detritivores	lower level of secondary compounds, easier utilization by detritivores

Useful tools (e.g. stable isotope tracers) and novel methods (e.g., flume techniques) have become available for the study of the outwelling problem in the last 25 years. This paper examines the recent developments of the Outwelling Hypothesis with special reference to the mangroves in the light of recent data collected from such techniques and suggests research future areas to test the applicability of the hypothesis to Asia-Pacific mangroves.

Development of the outwelling hypothesis

Nixon (1980) suggested that the concept of offshore consumer communities being supported by exported organic matter from productive coastal ecosystems such as salt marshes was first hinted, albeit lightly, in John Teal's (Teal, 1962) analysis of a Georgia salt marsh. It was, however, E. P. Odum who first put it as a formal scientific proposal a few years later. Odum (1968) tried to relate the apparent high productivity of waters adjacent to highly productive systems such as coral reefs, seagrass beds and salt marshes to the export, i.e. outwelling, of nutrients and organic detritus by these systems. It is worth pointing out, however, that little direct evidence was available to support his idea at that time. His paper also initiated numerous studies on the productivity of the coastal salt marshes, eventually leading to the formulation of many of the paradigms in wetland ecology. The concept was, however, extensively applied to the mangrove ecosystem only much later. As a result, the number of studies of materials exchange between mangroves and their surrounding water bodies is much less than that on salt marshes. A search for reports specifically discussing export of organic matter from mangroves published in the last 15 years yielded only 34 records out of a total of 1659 papers. This is another example of mangrove ecology borrowing ideas from the salt marshes. The two systems are fundamentally different in several important aspects (Thom, 1982), e.g. the fate of senescent litter, geographical influence on tidal regimes and detritus quality, most of which affecting the exchange of materials with offshore waters (Table 1). There is therefore a need to establish an outwelling picture for mangroves based on data collected from themselves.

The mass balance approach

Similar to most hypotheses in ecology, formulation of the Outwelling Hypothesis seems to have been an intuitive proposal based on the close observations of a talented ecologist on a system. Both J. M. Teal and E. P. Odum based their outwelling idea on the speculation that the high productivity of the salt marshes could probably support consumers offshore. At their time, there were few studies to give support to this relationship, but gradients in offshore production have been demonstrated by a few studies, e.g. Thomas (1966) and have been used as arguments for the hypothesis. A rapid rise in productivity studies followed the postulation of the hypothesis, which allowed Nixon (1980) to review the role of salt marshes and mangroves in exporting nutrients and organic matter in support of offshore communities. His review was mainly based on the results of mass balance studies.

Nixon (1980) concluded from 12 mass balance studies carried out in salt marshes that there seemed to be no agreement regarding whether salt marshes are net exporters or importers of organic matter, a conclusion reiterated by the later review by Hopkinson (1988) on the same topic. Rather, the actual relationship will depend strongly upon the inundation regime, the geomorphology and the form of organic matter (dissolved versus particulate) or nutrient (carbon versus nitrogen

Table 2. Reports on outwelling from mangroves published during the period 1971–92.

I. Transport of detritus and nutrients System studied	Physical characteristics	Materials	Export/import	Rate	Reference
Australia	tidal forest	detritus	Export	no rate determined conclusion based on hydrodynamics predictions	Wolanski *et al.* (1980)
Northeastern Australia	tidal forest	POC	Export	$10 kgC ha^{-1} day^{-1}$	Boto & Bunt (1981)
Everglades, USA	*Avicennia germinans* Basin forest	POC/DOC	Export	$63.7 gC m^{-2} y^{-1}$ 75% as DOC	Twilley (1983)
Westernport Bay Australia	*Avicennia marina* tidal forest	POC	Export	40% of all litter crabs can consume 50% of unbagged litter	van der Valk & Attiwill (1984)
India			Export	$261 tC y^{-1}$ to estuarine waters	Subramanian *et al.* (1984)
Malaysia		N species	Export/Import	actual direction of flow varied with tides and freshwater influx	Wong (1984)
Andamen Sea Thailand		POC	Export	only estimated for a 2-month period limited data	Chansang & Poovachiranon (1985)
Eastern Australia		OC, ON, IN	Export	inferred export based on concentrations on OC, ON & IN in soil and water	Clark (1985)
Tuff Crater New Zealand	forest with restricted tidal flow	POC, TSS, ISS, OSS	weak export	<2% of detritus produced $< 3 kgC ha^{-1} day^{-1}$ exported	Woodruffe (1985a, b)
Northeastern Australia	tidal *Rhizophora* forest	POC	Export	significant in situ consumption by crabs (30–80%), tidal export much less than expected	Robertson (1986)
Matang mangrove	estuarine influence	suspended solids, POC,PON,POP, IN,IP	mangrove as sink	not calculated	Nixon *et al.* (1980)
El Verde Lagoon Mexico	lagoon with ephemeral opening	POC	Export/storage	90% of accumulated litter exported during opening of inlet	Flores-Verdugo *et al.* (1987)
Northeastern Australia	tidal forest	OC, NO_x, P	?	No significant net flux recorded for DOC, NO_x & soluble reactive PO_4	Boto & Wellington (1988)

or phosphorus) concerned and may also be highly variable temporally even for the same wetland (e.g., Heinle & Flemer, 1976; Childers *et al.*, 1993). Such factors were also addressed by W. E. Odum's earlier paper on the same topic (Odum *et al.*, 1979) although with less supporting data. Wolanski (1992) examined the hydrodynamics of a mangrove-nearshore environment and concluded that stable coastal boundary layer water can be formed in shorelines fringed by straight mangroves sheltered by headlands. This coastal boundary layer will effectively reduce the extent of outwelling from mangroves to the offshore areas. Under such conditions, outwelling effects will only be present over restricted distances.

Twilley (1988) in his review of mangrove mass balance studies, stated that probably net export of organic matter is a common feature of most mangroves, because stronger tidal exchange, regular rainstorms and floating and non-retained litter (cf. standing dead litter in the salt-marsh) are all conducive to this difference from the saltmarsh wetlands (e.g., Chalmers *et al.*, 1985; Jordan *et al.*, 1986). The huge amounts of nutrients and carbon associated with well developed mangrove forests have also been increasingly appreciated, e.g. Gong & Ong (1990) and Twilley *et al.* (1992), making the mangroves a highly potential exporter for these materials. A survey of the literature for papers published between 1971–92 discussing exchange of materials between mangroves and offshore areas sug-

Table 2 cont..

Great Barrier Reef Australia	mangrove & coral reef	OC	Export	mangroves estimated to export $12523tCy^{-1}$	Robertson (1988)
Northeastern Australia	tidal forest	POC	Export	in situ crab consumption of litter affects exported	Robertson & Daniel (1989)
Hong Kong	high-zoned *Kandelia candel* in ponds	POC	Storage Import	low export, high accumulation and in situ processing, <1% exported	Lee (1990)
Klong Ngoa Estuary Thailand		N	Export	Expect outwelling based on hydrodynamics model (NO_2, NO_3)	Wattayakorn *et al.* (1990)
Crab Cay Bahamas	mangrove-offshore *Rhisophora mangle*	OM	Export	mangrove DOM makes up 10% of all DOM at 1km from forest	Moran *et al.* (1991)
II. Export of animal biomass from mangroves to offshore areas in the literature.					
System	physical characteristics	Group studied	Export/import	Rate	Reference
Mexico	tidal forest	*Aratus pisonii*	Export	assumed export of larvae but no measurement	Beever *et al.* (1979)
Northeastern Australia	mangrove estuary	fish		No significant nursery function for most commercially important species	Robertson & Duke (1990)
Malaysia	tidal forest and mudflat	prawns and fish		Mangrove as nursery site for prawns but not fish	Chong *et al.* (1990)
Costa Rica	tidal forest	crab zoea		No significant trend for all taxa studied	Dittel & Epifanio (1991)
Costa Rica	tidal forest	crab zoea	net export	net export of zoea of some groups	Dittel *et al.* (1991)

gests that export is a feature of most tidally inundated mangroves (Table 2). The total number of such papers is small, only in 34 of the 1659 papers published in the period (2.05%) was export or outwelling from mangrove discussed or measured. A survey of the 34 reports on mangrove materials exchange seems to support Twilley's view of mangrove generally acting as exporters of organic matter and nutrients (Table 2). There are, however, reports documenting mangroves acting as net importers of organic carbon and retain large proportions of the litter production for in situ consumption, mainly as a result of a restricted inundation regime (e.g., Twilley *et al.*, 1986; Flores-Verdugo *et al.*, 1987; Lee, 1990). Again, factors such as geomorphology and the strength and frequency of tidal inundation will affect the behaviour of the mangrove in relation to their potential in exporting the production.

One finding arising from recent mass balance studies is the overwhelming importance of dissolved forms of organic matter in the materials exchanged between the wetland and offshore communities. Twilley (1985) estimated that up to 75% of all carbon exchanged between *Avicennia* forests and a Florida estuary was in the dissolved form. Robertson (1987) also stressed that the role played by dissolved materials represents one aspect overlooked by most past studies in mangrove environments. Recent reports have suggested rapid utilisation of dissolved organic carbon or nitrogen by estuarine macrofauna and microfauna, e.g., Benner *et al.* (1986); Camilleri & Gibi (1986) and such utilisation may dominate carbon metabolism in aquatic systems (Wetzel, 1984). The behaviour of mangroves may differ with different elements important to ecosystem metabolism, e.g. carbon versus nitrogen export. Recent studies incorporating the dissolved organic matter fraction in salt marshes have indicated that DOC may not be always be significantly exported from the wetland but DON is consistently exported (Whiting *et al.*, 1987; Dame *et al.*, 1991). The same variability has also been documented for mangroves (e.g., Wong, 1984).

There are also other "missing links" in most past mass balance studies. In most earlier studies of mangrove export, it was assumed that in situ consumption of litter in tidal mangroves was insignificant. Thus Boto & Bunt (1981) have estimated that about 70% of all litter produced between high tides are exported from an Australian mangrove forest and many other studies also acknowledge a large proportion of the litter is exported offshore. Recent reports have, however, suggested that some macrodetritivores such as grapsid crabs could process significant portions of freshly fallen litter, either by direct consumption or storage, before it is exported by the next incoming tide (40% – van der Valk & Attiwill, 1984; 30–80% – Robertson, 1986; Robertson and Daniel, 1989). Other reports have also demonstrated the importance of fresh mangrove litter to these crabs (e.g. Malley, 1978; Lee, 1989).

Retention of nutrients and organic matter by porewater and transportation through groundwater flow have largely been overlooked in most of the mass balance studies. These storage compartments and transportation pathways can sometimes contribute significantly to the outwelling behaviour of mangrove swamps, e.g. Ovalle *et al.* (1990) reported upon the influence of porewater as a trap for nutrients to result in reduced net tidal outwelling from the mangrove; and Mazda *et al.* (1990) stressed the role played by groundwater movements in overall nutrient export during the tidal cycle. In other cases, in situ processing of some nutrients may confuse the apparent mass balance picture. Boto & Robertson (1990), for example, measured nitrogen fixation rate in a tropical Australian mangrove and found that nitrogen fixation (acetylene reduction) from the sediment, algal mats, decomposing logs and algal-covered prop roots closely matches previously documented nitrogen export rates. The exact role and contribution of these compartments and links in the mangrove mass balance picture require more data to refine.

Another important missing link in mangrove mass balance studies is the movement of animal biomass. Again, mangroves have been widely cited for their ability to provide refuge to adult as well as larval stages of fish and crustaceans, many of which are commercially important (Teas, 1981; Macintosh, 1981). Those species which spend their larval stages in the mangrove environment but migrate offshore as adults, e.g. most penaeid shrimps, may represent one important form of outwelled carbon originated from mangrove primary production. Rozas *et al.* (1988) investigated use of salt marsh microhabitats and found high abundance and biomass of fish associated with tidal creeks and rivulets. The relative importance of this form of outwelling has, however, rarely been acknowledged, addressed or evaluated. Lindall *et al.* (1973) demonstrated a higher abundance of juvenile crustaceans and fish in areas adjacent to mangroves and Robertson & Duke (1987) also concluded from their study in Australia that while many mangroves do provide nursery site to crustacean and fish species, the nursery value may vary considerably between particular sites. Beever *et al.* (1979) discussed the export of larval stages of the tree crab *Aratus pisonii* as one form of outwelling from mangroves but did not measure the actual value. Dittel *et al.* (1991) and Dittel & Epifanio (1991) measured movement of crab zoeae in Costa Rican mangroves and concluded that whereas significant tidal movement of zoeae were found, there was no unequivocal evidence to suggest uni-directional movement of the larvae through the mangrove (Table 2, II). The flux of assimilated mangrove-derived carbon in the form of animal biomass is still largely unknown.

Stable isotope and other techniques

Whereas new data have become available to evaluate the fate of mangrove production within the mangrove forests, little new light is available to explain the value of such organic matter on offshore communities. Challenging the assumption that the excess primary production from wetlands is always exported, Haines (1977, 1979) employed the stable isotope technique to trace the origin of organic matter in a Georgia estuary. There was no direct evidence from the stable isotope studies to support a consumer community based upon organic matter exported from coastal salt-marshes. Moran *et al.* (1991) directly measured the extent of the export of mangrove-derived organic matter and concluded that dissolved organic matter from mangroves may support, despite only for up to ca. 1km, offshore bacterioplankton growth. Similar findings have been reported by Rodelli *et al.* (1984) using stable carbon isotopes to study outwelling effects of mangroves in Malaysia. Drawing evidences from various studies making use of stable isotopes as tracers, Gearing (1988) concluded that in most cases terrestrial organic matter is exported no more than a few kilometers offshore.

Few stable isotope analyses have been performed to understand trophic relationships between mangroves and offshore consumers. Fleming *et al.* (1990) documented some export of mangrove detritus from Florida mangroves to support nearshore consumers but, similar to the findings of Moran *et al.* (1991), the geographical extent of export is small. As pointed out by Fry & Sherr (1984), Twilley (1988) and Gearing (1988, 1991), the use of stable isotopes in trophic analyses is still problematic and cannot be used as unambiguous evidence in support of outwelling, especially when more than two potential sources of similar isotopic ratios are present. This latter situation is likely to be the norm rather than the exception, as one feature often

Table 3. Documented effects of "outwelled" mangrove detritus on consumer communities.

System	physical characteristics	Group studied	Enrichment effects	Reference
Florida, USA	mangrove estuary	all macrofauna	90% of all species had significant amounts of mangrove detritus in gut, suspected trophic dependence	Odum & Heald (1975)
Northeastern Australia	laboratory tests + field sampling	meiofauna	mangrove-derived tannins negatively affected meiofaunal density	Alongi (1987)
Australia	soft mud in estuary	bacteria	bacterial respiration increased with detritus exported but no significant net DOC flux across sediment despite high DOC level	Alongi *et al.* (1989)
Australia	soft mud	bacteria	concentration of OC and TN (but not P) proportional to mangrove litter abundance bacterial production increased with proximity to mangrove	Alongi (1990a)
Australia	soft mud	ciliates	exported detritus increased densities by changing edaphic characteristics, e.g. C/N ratio	Alongi (1990b)
Northeastern Australia	creek-bottoms in tidal mangrove, estuary & open embayments	epibenthos	positive effect on epibenthos but may be due to the provision of refuge	Daniel & Robertson (1990)
Great Barrier Reef Lagoon Australia	shallow sand, silt bottom	infauna (macro & meio)	densities negatively correlated with detritus and tannin levels, so were diversity and evenness	Alongi & Christoffersen (1992)

quoted of mangroves is their diverse array of primary producers (Odum *et al.*, 1982). Fry and Sherr (1989) suggested that ^{13}C fractionation increases across trophic levels steadily in offshore food chains, making it difficult to use this method to trace feeding relationships. In some studies utilising the stable isotope approach, e.g. Rezende *et al.* (1990), mangrove carbon was suggested to contribute to highly variable proportions of the total POC available and oceanic carbon may make up significant portions of the carbon pool.

More glamourous arguments for mangrove outwelling has, however, been cited based on the positive correlation relationship between mangrove areal extent and offshore shrimp catch in southeast Asia (Martosubroto & Naamin, 1977) and the salt marshes in the Gulf of Mexico (Turner, 1977).

Fate of detritus and impact on consumer communities

Another assumption of the Outwelling Hypothesis is the benign and beneficial nature of mangrove detritus to consumer communities. Whereas this may be true from an intuitively appealing, there is few evidence to suggest that mangrove detritus, when exported offshore, will enhance secondary productivity. Alongi (1987) and Alongi *et al.* (1989) investigated the effects of exported detritus on a bacterial community adjacent to a mangrove and concluded that high concentrations of tannins associated with mangrove detritus may deter meiofaunal and macrofaunal colonisation and bacterial production. It is likely that positive associations between detritus and macrofaunal standing crop result from the provision of extra spatial heterogeneity rather than a nutritional source by the mangrove detritus (Daniel & Robertson, 1990). Recent studies of the effect of outwelled mangrove detritus on the benthic community is summarized in Table 3. As a matter of fact, most past reports on decomposition and enrichment effects of mangrove litter to detritivores are based on findings of studies carried out in the mangrove environment, not in the recipient communities, i.e., more oceanic communities.

Odum & Heald (1975) first provided evidence that most estuarine consumers ingest significant amounts of mangrove detritus and suggested that this formed the trophic basis of the community. Subsequent studies on the nutritional value of detritus to consumers have indicated, however, that mangrove or marsh plant detritus usually has poor nitrogen content and may only be assimilated at low efficiencies by estuarine consumers, e.g., Kreeger *et al.*, (1990); Langdon & Newell, (1990). Assimilation efficiency was greatly enhanced by the colonisation of the detritus by bacteria, increasing from 3% to 10% in *Crassostrea virginica* (Langdon & Newell, 1990). Such microbial enrichment action is probably required in order that most macro-detritivores can beneficially utilise mangrove detritus. Such microbial enrichment has been shown to be important for detritivores to derive nutrition from vascular plant detritus (Bärlocher, 1985; Bärlocher *et al.*, 1989; Graça *et al.*, 1993). Most detritivores probably cannot effectively utilise unconditioned mangrove detritus containing high levels of refractory compounds, e.g. lignin. One counter example is the active consumption of fresh mangrove detritus by mangrove grapsids, which are apparently unaffected by the lack of microbial enrichment (Malley, 1978; Robertson, 1986; Lee, 1989). The exact digestive mechanism of these intertidal macro-detritivores still needs to be examined.

What is still unknown ?

Most past studies on mangrove outwelling were conducted in macro-tidal, "typical" mangrove communities. Whereas it seems likely from the literature that most tidal mangroves do serve as net exporters of organic carbon and nutrients, future studies should encompass the whole range of tidal regimes experienced by natural mangroves before a complete picture may be known.

Material exchange studies conducted in mangroves mostly also lack the resolution attained by studies with similar aims conducted in salt marshes. The role of the mangrove is often ascribed based upon only a crude mass balance calculation involving mostly only the particulate forms, and with little information on the extent of spatial and temporal integration and variability in the exchange pattern. This general low resolution of the mangrove studies may have been a result of 1) a more complex hydrodynamic environment in the mangroves, leading to flux calculations using the "flume" type design difficult; 2) a much shorter history of investigations on mangrove outwelling as compared with those on the salt marshes; and 3) a tendency to overstress the importance of the much more apparent particulate fraction and neglecting "invisible" exchanges taking place through water flow. This last point is of particular interest, as field biologist are often inclined to studying subjects which are "apparent". In the salt marsh where the bulk of the senescent materials are retained in the marsh and undergo in situ decomposition, this apparency problem is less important and might have facilitated the transfer of attention to the soluble fraction.

The mechanism of utilisation of mangrove detritus by offshore as well as mangrove consumers represents another gap of our knowledge. It has been shown that whereas most detritivores will prefer detritus enriched by micro-organisms, some consumers are adapted to utilising fresh detritus in particular environments such as the intertidal region, where they compete with the tide for organic matter.This competition between export and in situ consumers for organic matter in the tidal mangrove deserves more attention. Several questions are of interest: 1) how is adequate nutrition achieved by the detritivore if no prior microbial enrichment is present? 2) How important generally is in situ consumption and storage compared with tidal export? Since sesarmid crabs (agents reportedly consume significant amounts of litter) are a common and abundant feature of the Asia-Pacific mangroves (Jones, 1984), the effects on export should be assessed for more mangrove systems in the region.

The fate of outwelled detritus in offshore environments should also be scrutinized. Most past speculative studies on the beneficial effects of outwelling extrapolate from nutrient release data based on works carried out in the mangrove environment itself. By definition, however, outwelled detritus have their transformation and subsequent utilization in the oceanic or estuarine environment with a different suite of physical and chemical characteristics as well as different communities of microbial organisms. This extrapolation is inappropriate and the value of outwelled detritus to non-mangrove consumers can only be inferred from studies carried out in the receiving environments.

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